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Behavior of Juvenile Yellow-bellied Marmots: Play and Social Integration

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With 7 figures

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Abstract

This study is a quantitative examination of the behavior of juvenile yellow-bellied marmots (*Marmota flaviventris*), especially play, and an attempt to relate play to the social and population biology of marmots. An hypothesis of adaptive fine-tuning (social integration) of individual behavioral traits through play is advanced. While the data do not directly support social integration as a function of play, the results are a sine qua non of this hypothesis.

Introduction

Play behavior has long been conjectured to be critical to social development (Beach 1945; Bekoff 1972; Poirier and Smith 1974). Many studies, especially those concerning primates, attempted to relate early play experiences to the social growth of an individual (e.g. Harlow and Harlow 1966; Baldwin and Baldwin 1974). However, the essentially qualitative nature of these studies prevents one from drawing any clear conclusions. Field studies are especially lacking in this respect (but see Owens 1975 a) and little work has been done on non-primates.

The yellow-bellied marmot (*Marmota flaviventris*) demonstrates complex social behavior. Marmots exhibit a polygynous mating system that is characterized by differing patterns of social interaction depending upon the age, sex, and rank of the participants (Armitage 1962, 1974, 1975; Downhower and Armitage 1971). Marmot social structure varies in a number of respects: size of harem, degree of tolerance among and between ♂♂ and ♀♀, and male fidelity to ♀♀. Barash (1973, 1974) has suggested that climatic stress, created by altitudinal differences, is the major cause of this variability. However, Armitage (1977) successfully demonstrated that a multitude of additional factors, many evoking microhabitat differences, are also involved.

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This paper quantitatively describes the behavior of juvenile marmots, especially their play behavior, and attempts to ascertain whether a functional relationship may exist between play and the development of the yellow-bellied marmot's social system. Emphasis is placed on sex differences and individual variability. The yellow-bellied marmot is an excellent subject for this research for two reasons. First, much of the sociobiology of the species is known and some is understood in great detail (Armitage 1962, 1973, 1974, 1975, 1977; Svendsen 1974). Second, marmots are easily trapped and marked, allowing individual identification in the field. The same individuals may be tested in the lab for subtle "personality" differences (Svendsen and Armitage 1973).

Study Areas and Methods

The marmot populations studied were located near the Rocky Mountain Biological Laboratory, Gothic, Colorado (elevation 2,900 m), situated in the East River Valley of the Gunnison National Forest. Of three study sites, two (Localities 4 and 5) were completely described by Armitage (1974).

Two ♀♀, both with litters, occupied Locality 4 in 1976. No social interactions (with a single notably aggressive exception) occurred between the groups and data were taken for each litter separately. The Locality 4A litter consisted of four ♀♀, while the Locality 4B litter consisted of two ♂♂ and three ♀♀.

In 1976 two ♀♀ at Locality 5 brought litters to term. These ♀♀ were sisters and highly sociable. The young of both litters freely intermixed and even shared common burrows. It was impossible to assign correct maternity and they were treated as a single (though complex) family group.

The third site, Horse Mound (HM), was a satellite site (Svendsen 1974) in 1976. It is the smallest site and encompasses a rocky outcropping on a grassy slope above a river bank. About 0.2 ha, it is bound on three sides by willow thickets and on the fourth by a short slope leading to the road. A single ♀ and her litter (two ♂♂) occupied this site.

Yellow-bellied marmots are divided into three age classes: juveniles, defined as animals born that year; yearlings, born the previous year (that is, in their second summer of life); and adults. Juveniles are usually trapped within a few days after they appear above ground. Trapping, handling, and marking procedures are presented in detail elsewhere (Armitage 1974).

All juveniles were MIS (Mirror Image Stimulation) tested about one month after their initial appearance above ground. Svendsen and Armitage (1973) provide a complete description of MIS procedure and analysis.

At Localities 4 and 5, observations were made from a distance of at least 200 m using 7×35 binoculars and a 30× telescope. A parked jeep was used as an effective blind (Armitage 1974). HM was observed from a bank across the river, about 40 m away, using only binoculars and natural cover as a partial blind.

All notes were recorded on tape and later transcribed. Interactions proceeded at a sufficiently moderate pace to allow the observer to monitor the continuous behavior of all individuals at a site. The continuous activities of each individual were recorded with special attention given to social interactions ("Focal group sampling", Altmann 1974). Rate analysis followed the format of Altmann and Altmann (1977), although the specific manipulations were independently derived (see especially "Case 6: Interactions with Hypothetical Class-Specific Rates", Altmann and Altmann 1977, p. 371).

Most observations were made between 06.00—09.00 and 15.00—18.00 h MST when marmots are most active (Armitage 1962). Observations at Locality 5 were reduced halfway through the study because high vegetation obscured many of the activities of the young. The study continued from 6 July, when the young first began to appear above ground, until 20 August 1976. A total of 117 focal group observation hours were accumulated.

Results

Operational Definition of Play

The lack of a satisfactory definition of play is due in part to the subjective criteria by which each investigator delineates the behavior. Even with the most precise film analysis and measurement techniques, the observer is left with the decision of the extent to which a behavior must be "exaggerated", "repeated", "out of context", and so on, to be considered playful. BEKOFF (1972) partially overcomes this problem by basing his definition more on universals than on structural specifics. Even his definition, though, describes more what play is not, instead of what it is: "Social play is that behavior which is performed during social interactions in which there is a decrease in social distance between the interactants, and no evidence of social investigation or of agonistic (offensive or defensive) or passive-submissive behaviors on the part of the members of the dyad (triad, etc.) although these actions may occur as derived acts during play" (BEKOFF 1972, p. 417).

Although this definition does not easily accommodate transition stages between play and non-play, no such behaviors are exhibited by juvenile yellow-bellied marmots and BEKOFF's (1972) definition was used to operationally define play. A general description of the behaviors of young marmots, including play patterns, will be useful as a reference to this effect.

Sociogram — Behavioral Patterns of Juveniles

While the social interactions of marmots are extensively described elsewhere (ARMITAGE 1962, 1965, 1973, 1974), there is no systematic review of juvenile behavior. This section presents a compendium of behaviors commonly seen in juvenile marmots (Table 1); three categories of play and other incompletely described behaviors are emphasized. The division of play into three major categories (Table 1) does not imply a necessary functional division

Table 1: Behavior patterns of juvenile marmots. Expl. in text

Category	Behavior Patterns
A. Play-fighting	1 mouth-spar 2 grapple 3 nose-push 4 slap 5 wrestle
B. Chasing play	1 chase 2 flee
C. Sexual play	1 mount 2 grasp-mount 3 head-over-shoulder
D. Other social behaviors	1 approach 2 withdraw 3 allogroom 4 greet 5 social investigation 6 bite
E. Non-social investigation	1 explore 2 chase (NS) 3 dig
F. Comfort movements	1 self-groom 2 stretch 3 yawn 4 scratch
G. Other behaviors	1 forage 2 sit 3 alert 4 enter burrow

or that patterns from different categories cannot occur in the same play sequence. The divisions are made solely on the basis of unifying structural characteristics.

A. Play-fighting. This is "rough-and-tumble" play, delineated by physical contact and energetic struggling between the interactants. The term, first defined for marmots by ARMITAGE (1962), was then generally described and used as a category for social analysis (ARMITAGE 1974). Although ARMITAGE did not further subdivide the term, the individual patterns which he lumped together as "play-fighting" are essentially the same as those outlined here.

1) mouth-spar. ARMITAGE (1974) used this in reference to "jabbing of the head at the head, shoulders, or chest of the other animal while the other animal does likewise". The animals face each other quadrupedally, although occasionally one forepaw is raised to touch the opponent. The mouths are always open during this behavior, but biting motions occur infrequently. As with all play-fighting patterns, the action is sustained for only several seconds in most cases.

2) grapple. "Two protagonists rear up on their hindlegs and push at one another with the forepaws" (ARMITAGE 1974). BARASH (1973) felt the immediate goal of this behavior was to push the opponent over backwards. It frequently ends with one animal losing its balance and falling, but one or both animals can also turn away to end the grapple. Again, the mouth is open at all times, possibly with more biting motion than is seen in mouth-sparring. BARASH (1973) incorrectly stated that grappling did not occur in medium elevation yellow-bellied marmots (2,650 m). The pattern was observed in all populations observed so far (2,700 m, 2,900 m, 3,300 m, 3,400 m).

3) nose.push. Less frequently observed, this behavior involves one animal quickly pushing its partner away by extending its head, neck, and shoulders forward, either in a quadrupedal or standing position. The mouth is open, but the action is clearly an attempt to push the partner away and not to bite it.

4) slap. This position is also rare. While standing or in a quadrupedal position, the animal bats at its opponent sharply with a forepaw. The slap seems to be a response to a partner who is being too rough, but does not necessarily terminate a play bout.

5) wrestle. ARMITAGE (1974) described this as struggling in the prone position with "much flailing of legs in the air". The mouth is always open while wrestling and the animals often orient mouth to mouth. Head jabs are directed at all parts of the opponent's body. ARMITAGE's subjective impression was that the animals rolled about, often flipping from the top to the bottom position. Such role flexibility is often cited as a characteristic of play. However, very few "flips" occurred during wrestling (to be discussed in detail below).

B. Chasing play. As the name implies, an animal may either (1) chase its partner or (2) flee from its partner. The chase-flee interaction may occur simultaneously or not. An animal may flee from another without being chased, or an animal may "chase" into another without that animal fleeing. Few play chases extend further than 5 m and probably none over 10 m. In contrast, adult agonistic chases usually extend well over 10 m. The tail sometimes jerks up during a play chase, but no behavior resembling adult aggressive tail-flagging (ARMITAGE 1974) occurs in juvenile play.

C. Sexual play. This category includes mounting and mounting-related behaviors which occur in a playful context. One outstanding characteristic is their incomplete and inaccurate appearance as compared to adult sexual patterns. This contrasts with the complete appearance of other play patterns.

1) mount. Any action whereby one animal places its paws on the back of, and raises itself above, its partner. A mount can be oriented from any direction.

2) grasp-mount. This was scored if the mounting animal extended its forepaws at least partially around the mounted animal, similar to the sexual mount (ARMITAGE 1965). Orientation is more uniformly to the rear.

3) head-over-shoulder. The mounted animal performs this action by turning its head over its shoulder towards the mounting animal. This action is similar to that of an unresponsive adult female marmot when mounted (ARMITAGE 1965). Head-over-shoulder occurred rarely and grasp-mounts were also infrequent. Therefore, all mounting behavior was combined for analysis.

D. Other social behaviors.

1) approach. A direct movement towards another animal who is less than 2 m away.

2) withdraw. This is a slow avoidance motion, directed away from another animal.

3) Allogrooming. This behavior was well described and discussed elsewhere (ARMITAGE 1962, 1974). There seems to be no qualitative difference between juvenile and adult allogrooming.

4) greet. This term was first used by ARMITAGE (1962) to describe the common naso-nasal contact of marmots. The behavior occurs throughout the Sciurid rodents and its importance has been the subject of much discussion (ARMITAGE 1962, 1974, 1975, 1977; BARASH 1973, 1974; KING 1955). Its function in young marmots will be discussed below.

5) social investigation. The sniffing of one animal by another (like a one-sided greeting) was scored as social investigation. Actual contact did not necessarily occur. Sniffing was directed at any body part, although the neck and anogenital regions were preferred.

6) bite. Biting was observed only 5 times. These were low intensity actions and never occurred in play sequences.

E. Non-social investigation.

1) exploration. Exploratory movements involved sniffing and manipulating objects and substrates in the environment.

2) chase NS (non-social). Non-conspecifics were often chased.

3) dig. This behavior was never observed to substantially alter existing burrows or create new ones, but the possibility cannot be ruled out.

F. Comfort movements. This category includes 1) self-grooming, 2) stretching, 3) yawning, and 4) scratching.

G. Other behaviors.

1) forage. Any food-searching or feeding behaviors of the animal.

2) sit. The sitting position, occurring most often on a conspicuous rock or ledge, is as important to surveillance as it is to resting and sunning (ARMITAGE 1962).

3) alert. This behavior was scored when an animal raised its head in response to a possible disturbance and craned its neck to survey its surroundings. The animal may stand on its hind paws to afford a better view. Alarm calls may be given while alert, but these occurred less frequently in young than adults.

4) enter burrow. This category was scored each time an animal entered a burrow for a period exceeding 5 s.

General Structure of Juvenile Behavior

On the first day animals emerge from the maternal burrow, wobbly and no clearly directed play occurs. Only one or two days later the animals are reasonably coordinated and play patterns appear in normal form. Play initially occurs in groups, but a rapid increase in directedness of play causes it to become exclusively dyadic. Rare triadic interactions are unstable and transitory. Juvenile play decreases towards the end of the summer, corresponding to a general lower rate of interactions for marmots at this time (ARMITAGE 1962).

A. Rate analysis. Foraging and sitting, both solitary behaviors, comprise the bulk of the young marmot's activities (Table 2 A). Of the social behaviors, greeting predominates, followed by play-fighting. However, the estimate of the relative frequency of play from this table is misleading. A play "bout" typically consists of a sequence of events, while all other categories involve

Table 2: Observed rates of behaviors. Rates are in terms of interactions/marmot-h and are based on 276.5 marmot-h of observation. (Certain categories were combined or dropped — see "Sociogram" and Table 1 for expl.)

A. All Behaviors	
Non-social investigation	0.48
Forage	2.15
Enter burrow	1.55
Approach	0.47
Withdraw	0.43
Play-fight (& chases)	0.89
Sexual play	0.29
Allogroom	0.65
Greet	1.06
Social investigation	0.68
Sit	3.20
Alert	1.07
Comfort movements	0.99
Total	13.91

B. Play Behaviors	
Chase	0.19
Flee	0.30
Mouth-spar	0.35
Grapple	0.69
Wrestle	0.69
All mounts	0.31
Total	2.53

only single events. A play sequence averages 3.4 events, with a maximum observed length of 30 consecutive events. If play is divided into more discrete components (Table 2B), play interactions comprise nearly 20% of the behavior observed and over 40% of all social interactions.

B. Sequential analysis. A diagrammatic representation of the sequential relationships between all behaviors (Fig. 1) was generated by calculating transition probabilities from a matrix of observed percentage frequencies of following events. It is unclear in Fig. 1, however, whether the transitions occur at random or whether they represent some Markovian relationship. For example, transitions to and from sitting behavior are very common (Fig. 1). However, sitting occurs with the highest rate of any behavior (Table 2). Therefore, many transitions involving sitting should occur, simply due to its ubiquity.

The behavior "withdraw" presents a similar problem. No behavior leads to withdraw with an observed probability greater than 0.10. Withdraw is a relatively rare behavior (Table 2) and so cannot be expected to occur frequently in transitions. Its rareness does not imply insignificance; indeed, its rarity may indicate that it only occurs under special circumstances.

The statistical significances of the transitional linkages (Fig. 2) clarify these problems. Expected probabilities were calculated for each cell of the transition matrix and from these the normal variate (Z) values were derived by the binomial test (SIEGEL 1956; POOLE and FISH 1975). The general flow is still apparent, but without the many non-significant linkages.

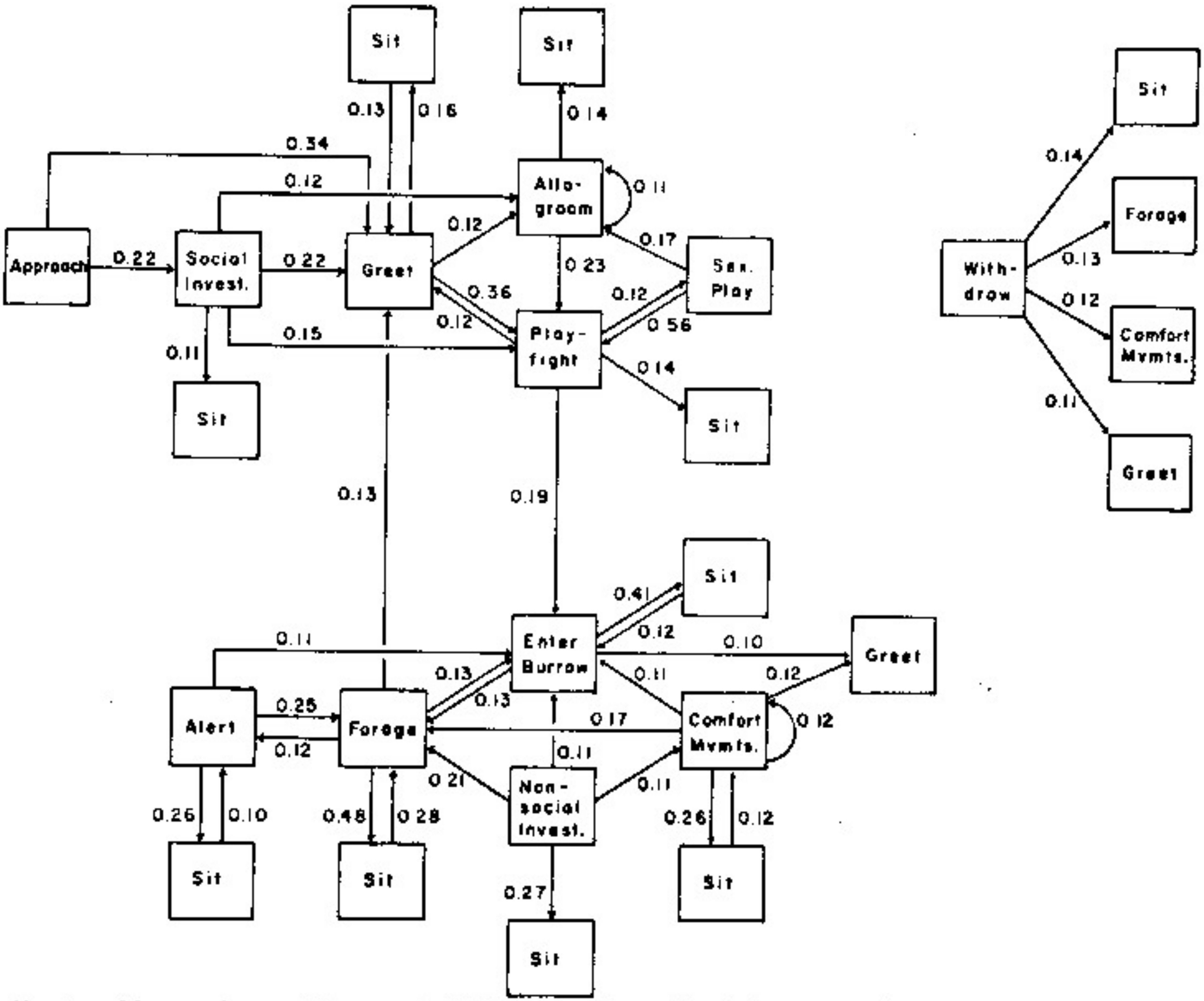

Fig. 1: Observed transition probabilities for juvenile behavior. Values represent observed probabilities of transition, with only probabilities greater than 0.10 shown. "Sit", "greet", "forage", and "comfort movements" are entered more than once for clarity. Arrows turning back on a box indicate the pattern is followed by itself. Data are based on 4448 transitions

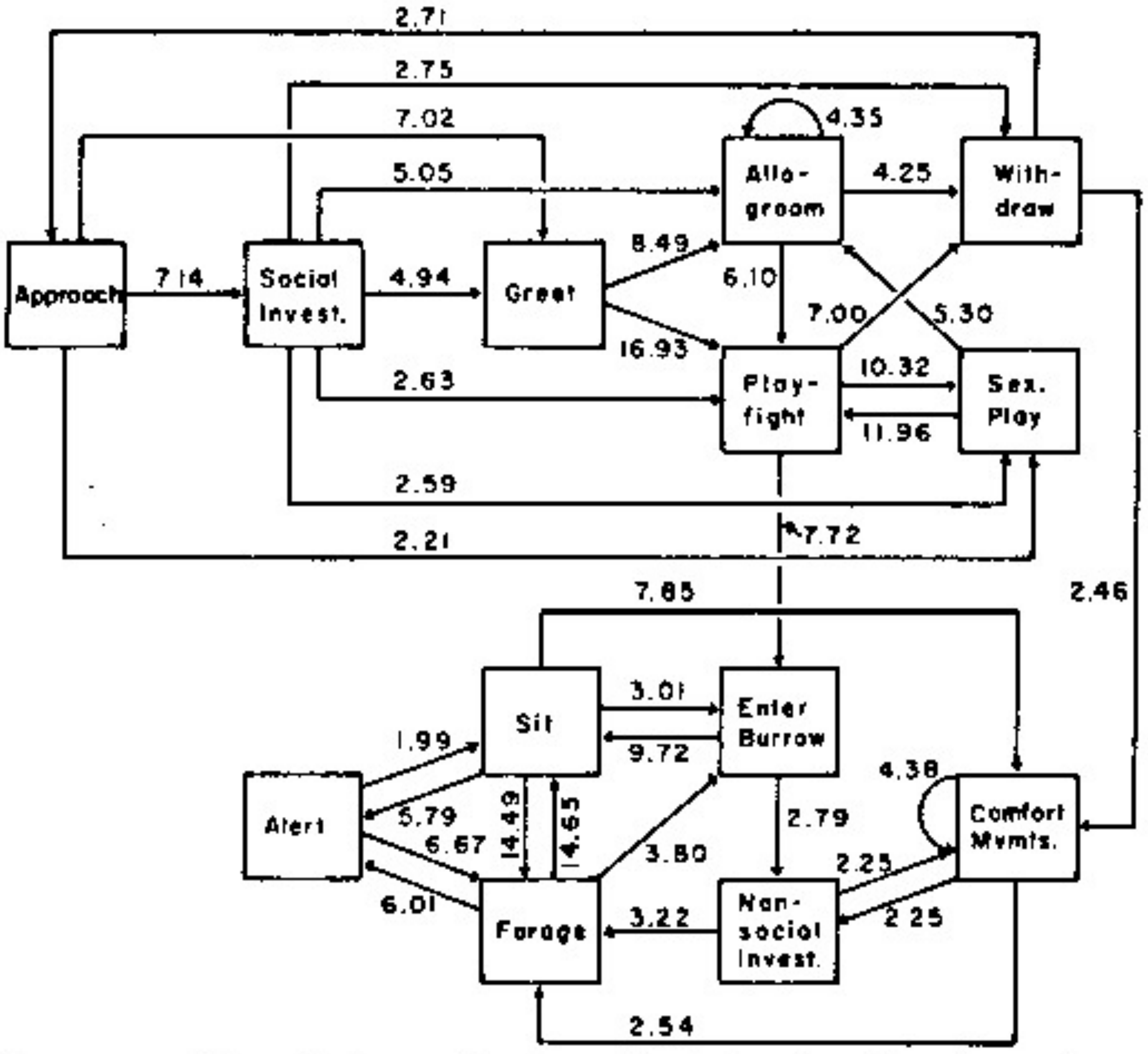

Fig. 2: Significant transition linkages for juvenile behavior. Based on data from Fig. 1. Expecteds were calculated as in Poole and Fish (1975). Values represent estimates of Z from the binomial test. If $Z \geq 1.96$, $p < 0.05$. If $Z \geq 2.58$, $p < 0.01$ (two-tailed test)

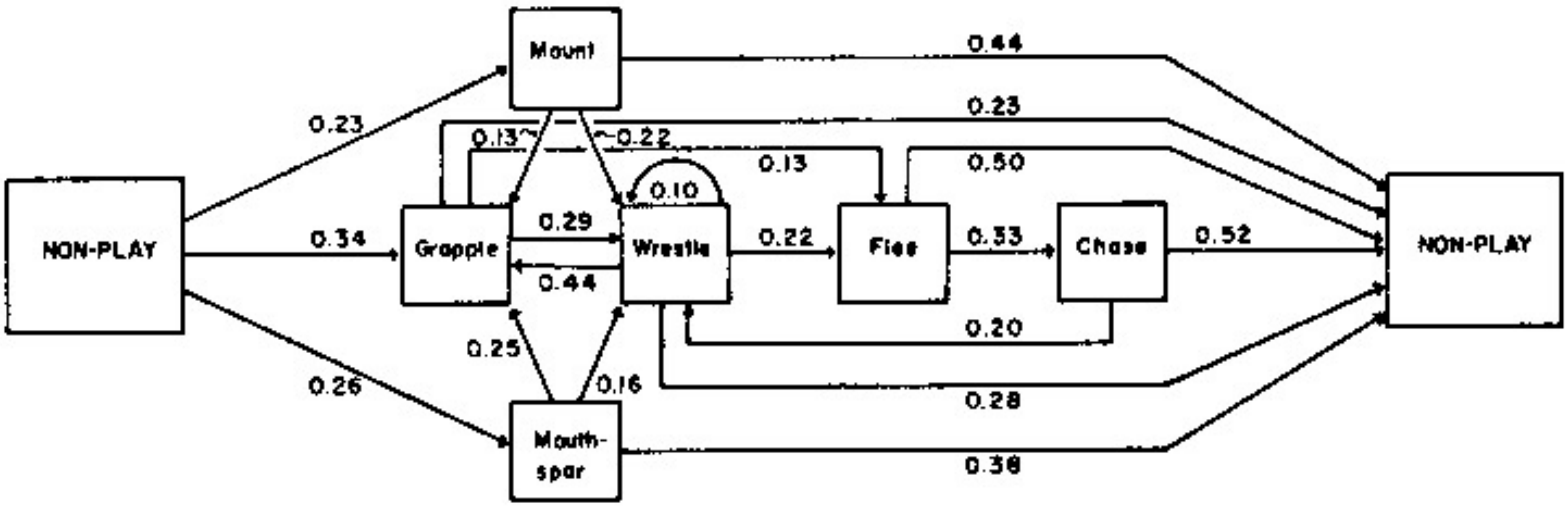

Fig. 3: Observed transition probabilities for juvenile play. Same conventions as Fig. 1. Data are based on 917 transitions (237 complete play sequences)

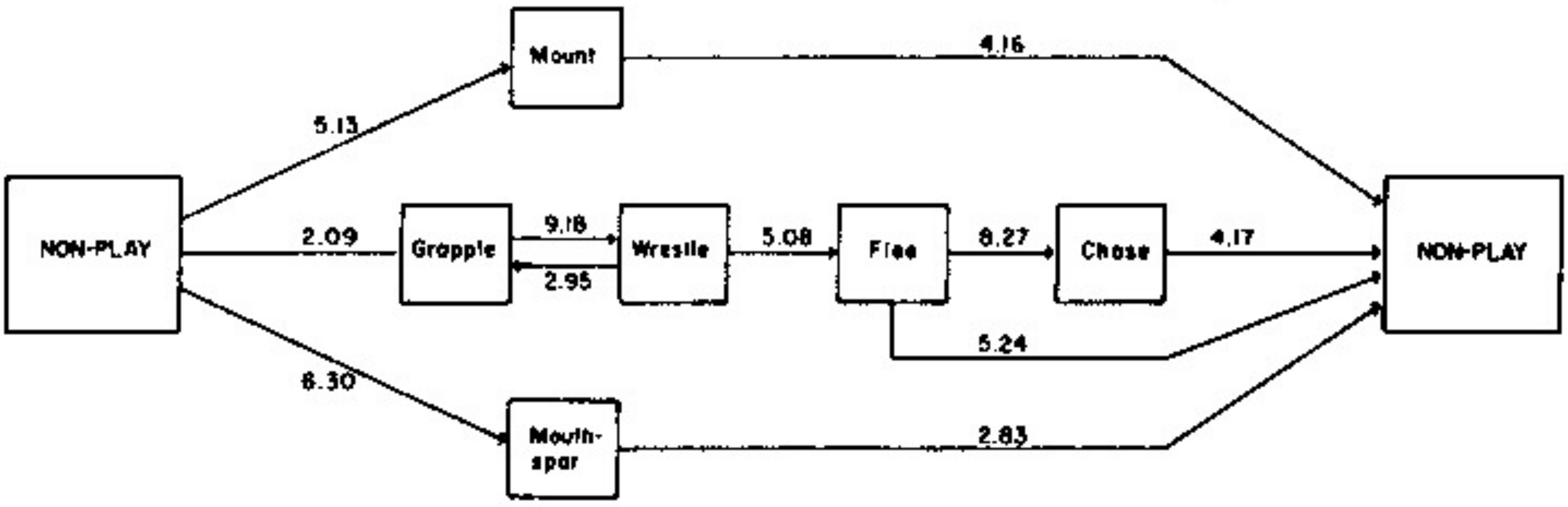

Fig. 4: Significant transition linkages for juvenile play. Same conventions as Fig. 2. Data are from Fig. 3

Similar data manipulations were performed on play behaviors alone. Many transitions to non-playful activities occur which are compatible with chance expectancy (Fig. 3). Comparing Fig. 1 with Fig. 3, play elements seem more structured than the entire behavioral repertoire considered together. However, the average Z value (5.77) for all behavior (Fig. 2) is slightly higher than that (5.02) of play behavior alone (Fig. 4); many individual values range much higher.

C. Spatial analysis. Due to the complexity and variability of microhabitats, a rigorous spatial analysis of behaviors could not be performed on the field data. The observer could, however, record whether a behavior occurred at or within 2 ± 0.5 m of the main burrow system, or at some distance further away. Thus, frequency data were pooled by "at" and "away from" the burrow and statistically tested for differences. All behaviors examined occurred highly significantly more often within 2 m of the main burrow system (Table 3). The only exception, as expected, was foraging, which occurred significantly more often away from the burrow. This burrow-centric spatial distribution of behaviors becomes more striking when one considers that the young typically range 20 m from the burrow and often much further.

Table 3: Rates of selected behaviors pooled by "at" and "away from" burrow. Rates are total rates (not just initiation rates). "At" signifies within a 2 m radius of the burrow site (see text). P values are from the Walsh test (one-tailed, SIEGEL 1956)

	"at" burrow	"away from" burrow	p value
explore	0.25	0.04	< 0.005 **
forage	0.34	1.81	< 0.005 **
approach	0.43	0.04	< 0.005 **
withdraw	0.40	0.03	< 0.005 **
play-fight	1.72	0.08	< 0.005 **
chase	0.17	0.02	< 0.005 **
flee	0.28	0.03	< 0.005 **
sexual play	0.57	0.02	< 0.005 **
allogroom	1.06	0.01	< 0.005 **
greet	1.75	0.24	< 0.005 **
social invest.	1.07	0.09	< 0.005 **
sit	2.45	0.76	< 0.005 **
alert	0.72	0.35	< 0.005 **
comfort movements	0.67	0.05	< 0.005 **

** — highly significant.

Male-Female Behavioral Dimorphism

A. Summary of adult behavior. Frequency analysis reveals strong sexual differences in the social behavior of adult marmots. Although individual variability is high, a number of tendencies are apparent when data from several groups are pooled by sex. In a generalized scheme, based on 50 colony-years (ARMITAGE 1974, 1975), the most striking feature is the strong aggressive component between ♂♂ (A) (Fig. 5). Of all ♂-♂ encounters (n = 36), 97 % are classed agonistic. Only one amicable interaction between adult ♂♂ was observed in 50 colony years; this component was considered negligible. Interactions between ♀♀ (n = 132) are likely to be agonistic (62 % — component B), but there is also a strong amicable component (38 % — C).

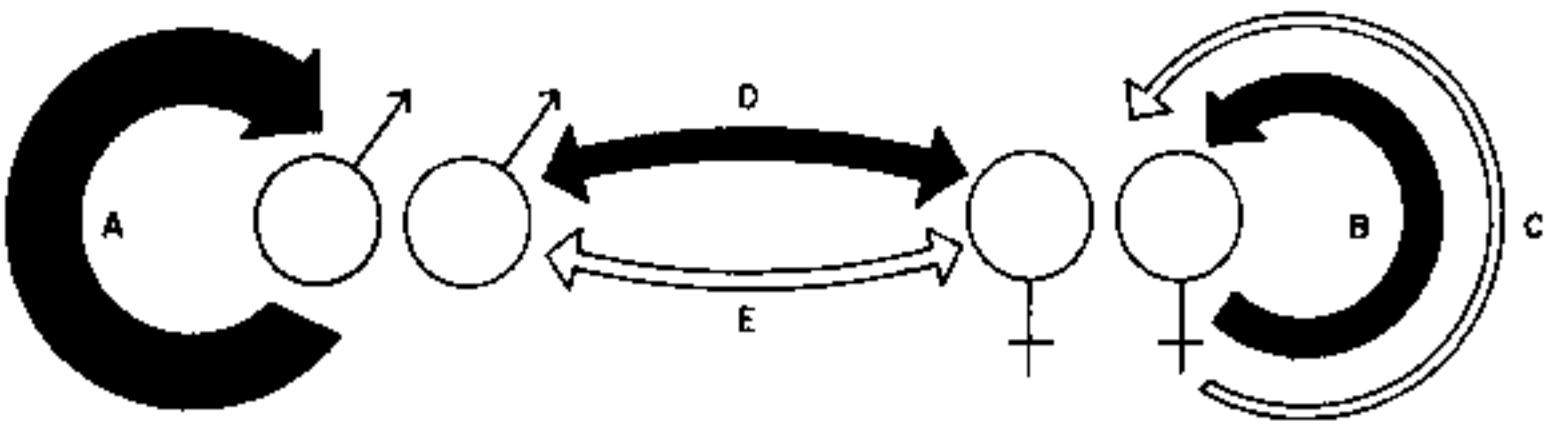

Fig. 5: Generalized adult social interactions. "Vectors" are based on data from ARMITAGE (1974, 1975). Dark arrows represent agonistic interactions, while light arrows are amicable. Line thickness is a relative estimate of percentage (A>B>D; E>C). See text for details

51 % of ♂-♀ interactions (n=204) are agonistic, while 49 % are amicable. Most of the agonistic interactions occur when a ♀ flees from or aggressively rebuffs the ♂'s sexual aggression. Most amicable interactions occur when the ♂ approaches and greets the ♀. More precise determination of initiation of these encounters is impossible from ARMITAGE's (1974, 1975) data. It should be stressed that amicable encounters between ♀♀ represent the most variable component of this scheme. Variability in tolerance between ♀♀ may be the single most important proximate factor in determining group size (ARMITAGE 1975, 1977).

B. Play dimorphism. ♂-♀ differences also occur in juvenile play (Table 4). Only 11 individuals (3 litters) are included because of the difficulty in obtaining complete data at Locality 5 (7 individuals, 2 litters) due to poor visibility.

Table 4: Individual rates for selected behaviors. The rates (interactions/marmot-h) include only data for initiation of a given behavior and are based on 276.5 marmot-h of observation. P values are from the Mann-Whitney U test (one-tailed, SIEGEL 1956) really

	Animals														
	HM		Locality 4B					Locality 4A				♂	♀	♂+♀	p
	♂898	♂894	♂991	♂913	♀971	♀955	♀915	♀909	♀911	♀918	♀957	ave.	ave.	ave.	value
explore	0.45	0.60	0.21	0.26	0.32	0.14	0.42	0.25	0.15	0.15	0.22	0.38	0.24	0.29	0.082
forage	2.83	3.25	1.65	1.83	1.74	1.33	1.55	2.47	2.07	2.40	2.51	2.39	2.01	2.15	0.206
enter burrow	2.72	2.75	1.11	0.99	1.11	1.06	1.51	1.49	1.64	1.13	1.53	1.89	1.35	1.55	0.394
approach	0.57	0.68	0.21	0.33	0.11	0.37	0.28	0.65	0.47	0.65	0.87	0.45	0.49	0.47	0.464
withdraw	0.53	0.49	0.45	0.48	0.37	0.51	0.38	0.44	0.44	0.25	0.44	0.49	0.40	0.43	0.021 *
play-fight	1.09	1.25	0.95	1.25	0.84	0.87	1.08	0.76	0.22	0.51	1.02	1.13	0.76	0.89	0.012 *
chase	0.38	0.42	0.12	0.18	0.05	0.18	0.19	0.11	0.07	0.18	0.22	0.28	0.14	0.19	0.115
flee	0.42	0.49	0.12	0.18	0.42	0.18	0.61	0.40	0.11	0.22	0.15	0.30	0.30	0.30	0.464
mouth-spar	0.83	0.53	0.45	0.59	0.21	0.32	0.33	0.29	0.00	0.11	0.15	0.60	0.20	0.35	0.003 **
grapple	1.43	1.02	0.82	1.03	0.42	0.51	0.42	0.58	0.29	0.33	0.73	1.08	0.47	0.69	0.003 **
wrestle	1.17	1.06	0.66	0.84	0.68	0.60	0.80	0.44	0.18	0.36	0.76	0.93	0.55	0.69	0.021 *
sexual play	0.34	0.64	0.29	0.33	0.16	0.18	0.38	0.22	0.18	0.11	0.40	0.40	0.23	0.29	0.082
allogroom	0.83	1.40	0.66	0.59	0.63	0.41	0.61	0.65	0.33	0.51	0.62	0.87	0.52	0.65	0.036 *
greet	1.43	1.40	0.82	1.17	1.16	0.74	1.27	1.09	0.36	0.80	1.45	1.21	0.98	1.06	0.158
social invest.	0.91	1.66	0.67	0.55	0.26	0.32	0.33	0.76	0.69	0.62	0.80	0.94	0.54	0.68	0.115
sit	5.55	5.13	2.02	2.39	1.47	1.56	2.31	4.15	3.16	3.78	2.71	3.77	2.88	3.20	0.206

* — significant, ** — highly significant.

Only a few of the many ♂-♀ differences in the means are significant. Play-fighting (in general) and the specific elements of play-fighting occur significantly more often in ♂♂. The male averages for chasing and sexual play are about twice that of ♀♀ and, while not statistically significant, the low p values indicate there may be biological significance. The approach rate of ♀♀ is slightly higher than that of ♂♂, but ♂♂ withdraw significantly more often. ♂♂ also allogroom significantly more.

Even if not significant, one must still account for the apparent sexual variability in rates of other behaviors. The sites were partially assorted by sex (not intentionally). Thus it is possible that differences in the sex-pooled data may be due in part to microhabitat differences. Therefore, the data were grouped by site (Table 5).

Table 5: Rates of selected behaviors pooled by site. Rates (interactions/marmot-h) are total rates (not just initiation rates). P values are form the Kruskal-Wallis one-way ANOVA by ranks test (SIEGEL 1956)

	Locality			P value
	HM	4 B	4 A	
explore	0.53	0.27	0.19	= 0.052*
approach	0.63	0.26	0.66	< 0.009**
withdraw	0.51	0.44	0.39	> 0.101
play-fight	2.32	2.03	1.23	> 0.101
chase	0.40	0.14	0.15	> 0.101
flee	0.46	0.30	0.22	> 0.101
sexual play	0.92	0.56	0.45	= 0.050*
allogroom	1.91	0.83	0.96	= 0.098
greet	2.47	1.99	1.74	> 0.101
social invest.	2.02	0.75	1.23	< 0.009**

* — significant, ** — highly significant.

As expected, exploration is significantly site-dependent (note that HM was subjectively considered to be the most variable habitat). Other conclusions are not as clear. One might expect sexual play to be most common at a site where young of both sexes are present (Locality 4 B). Instead, the rate is significantly higher at the site with only ♂♂ (HM). This result supports the idea of a motivational link between juvenile mounting and male sexual-aggression. The sample size (n = 3 sites) is too small to be conclusive, however. Play-fighting, chasing, greeting, and allogrooming are not significantly biased by site differences.

Weight differences are a potential source of bias in the data. However, in this study, no same-day capture weight differences were greater than 10 % of the total body weight, with most differences being much less. There are too few data to analyze these differences statistically, but they are probably negligible.

A generalized diagram of juvenile play interactions appears in Fig. 6. While components A and D combined are larger than B and E combined, the data in Table 4 do not reveal the sex towards which any behavior was directed. To examine these trends, data from both Localities 4 A and HM were discarded. Obviously, young at these sites had no choice in the sex of a play partner. The reduced sample size (n = 5, 1 litter) precludes statistical treatment. Nonetheless, after correcting for the skewed sex ratio (and therefore the relative number of each sex available as a partner), trends in the data become clear.

♂♂ initiated play towards ♀♀ over 30 % more often than ♀♀ towards ♂♂, indicating that D is greater than E (Fig. 6). This difference was true both of play-fighting in general and specific play patterns such as mouth-spar and grapple. Only in wrestling, where ♀♀ preferred ♀♀, did ♀♀ express a sexual preference for play partners. One can conclude that B is approximately equal to E (meaning D is also greater than B). There were insufficient data to directly compare A and D (Fig. 6) so indirect measures were employed.

C. Additional measures of behavioral dimorphism. The primary non-playful social behaviors of juveniles (allogrooming, greeting, social investiga-

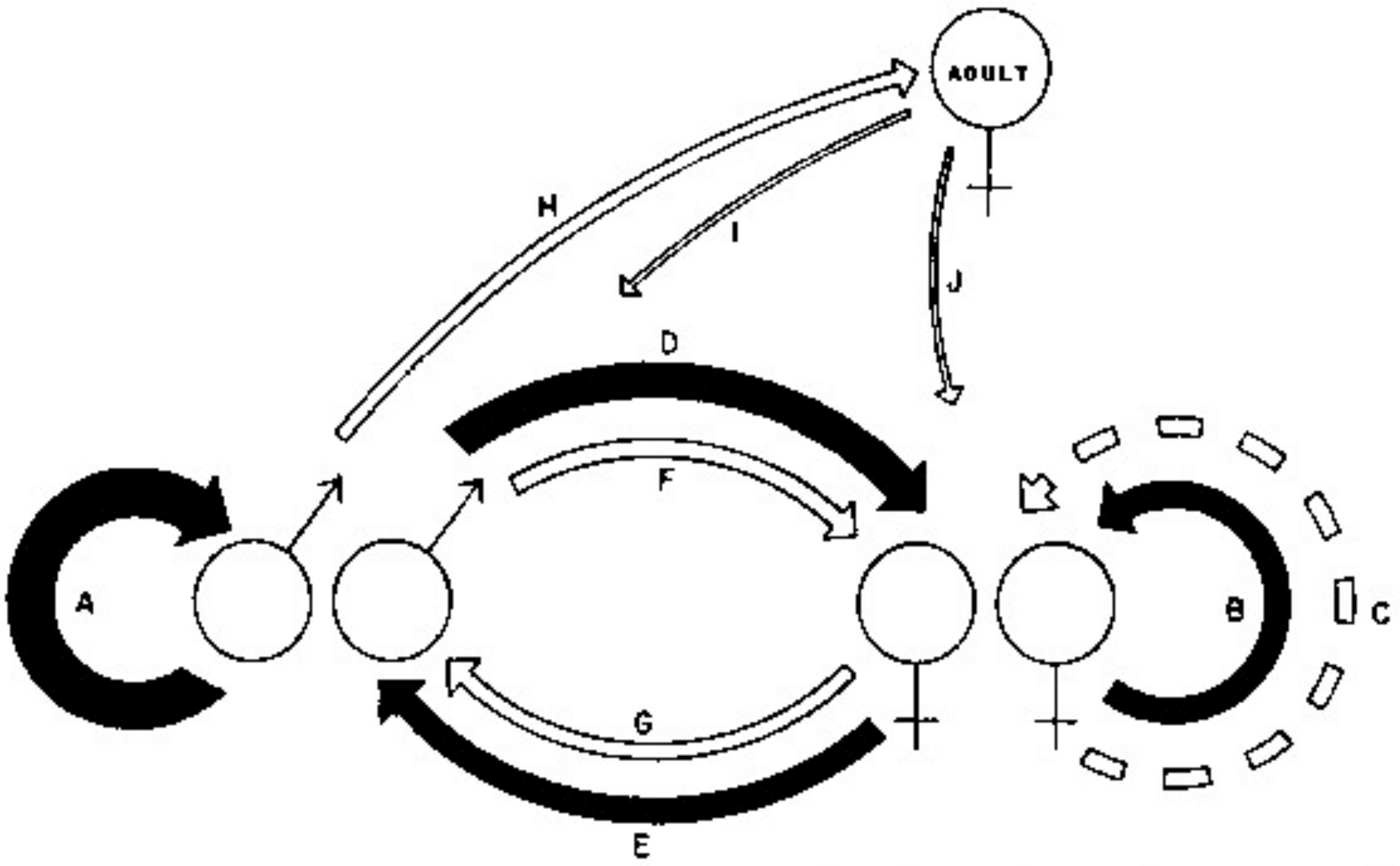

Fig. 6: Generalized juvenile interactions. See text for derivation of vectors ($A+D>B+E$; $D>E$; $B\cong E$; $A>D>B\cong E$; C highly variable; $F\cong G$ [?]; $H>I=J$). Line thickness is a relative estimate of percentage

tion) are all considered to be "amicable" (ARMITAGE 1974). All play elements are either aggressive or sexual analogs. Inferences about the amicable components (Fig. 6) were drawn from non-play behaviors. Only the means of allogrooming differed significantly between ♂♂ and ♀♀ (Table 4). Adjusted data from Locality 4 B show no sexual partner preferences except for allogrooming; ♂♂ are 70 % more likely to groom other ♂♂. If allogrooming is not included (see below), F and G (Fig. 6) may be considered equal.

Estimates of intersexual amicability in juveniles may also be made indirectly from play data. Greeting is important as a play initiator (Fig. 2). If sequential data are pooled by sex, however, significant differences are found. 62 % of male-initiated play was preceded by greeting while only 47 % of female-initiated play began with greeting ($p < 0.05$, chi^2 test). Conversely, 55 % of all female-initiated greetings led to behaviors other than play, compared to 45 % for ♂♂ ($p < 0.001$, chi^2 test). Thus, the meaning of greeting as a play-initiator may be different for ♂♂ and ♀♀.

Sexual variation occurs in the percentages of play wrestling sequences in which the animals "flipped" by varying amounts (Table 6). A flip was scored when the animals exchanged top and bottom positions in wrestling at any time within a given play sequence. Few flips occurred in sequences involving ♀♀; most cases involved no flipping. The situation is quite different if two ♂♂ wrestle; more sequences involving flips than not. If a flip is an indication of the jockeying for a preferred position (on top), then the conspicuous lack of flips involving ♀♀ could indicate a lower degree of aggressive competition.

Table 6: Percentage frequency of "flips" in play sequences with wrestling. The data are subdivided by the sex of the play partners. Numbers outside parentheses represent percentages; numbers inside parentheses are observed frequencies

	Number of "flips" in a sequence				
	0	1	2	3	4+
♂ : ♂	43 (10)	30 (7)	13 (3)	9 (2)	4 (1)
♂ : ♀	78 (21)	15 (4)	7 (2)	0 (0)	0 (0)
♀ : ♀	74 (31)	21 (9)	0 (0)	0 (0)	5 (2)

D. Mother-young interactions. Adult yellow-bellied marmots do not play, so no play interactions were recorded between mother and young. (Yearling-young and father-young interactions are extremely rare and not treated here.) Occasionally a juvenile initiated a play pattern towards its mother, but this was either ignored or gently repulsed. No serious mother-young aggression was observed.

Table 7: Rates of interactions initiated by the mother towards her young. Rates are based on a variable number of marmot-h, depending on the site. P values are from the Mann-Whitney U test (Siegel 1956)

	♂ ave.	♀ ave.	♂ + ♀ ave.	p value
allogroom	0.12	0.09	0.10	0.464
greet	0.11	0.09	0.10	0.464
social invest.	0.05	0.06	0.06	0.464
total amicable	0.28	0.25	0.26	0.324

Table 8: Rates of interaction initiated by young towards the mother. Rates are based on a variable number of marmot-h, depending on the site. P values are from the Mann-Whitney U test (Siegel 1956)

	♂ ave.	♀ ave.	♂ + ♀ ave.	p value
allogroom	0.42	0.32	0.35	0.324
greet	0.23	0.12	0.16	0.036*
social invest.	0.37	0.17	0.24	0.158
total amicable	1.02	0.64	0.78	0.036*

* — significant.

The mother shows little active interest in the young after they emerge from the maternal burrow, as demonstrated by low rates of social interactions (Table 7). Both sexes are treated alike. However, the young seek contact with the mother to a much higher degree (compare Tables 7 and 8). ♂♂ are significantly more active in directing amicable behavior towards the mother (Table 8). This difference results primarily from the significantly higher rate of greetings initiated by ♂♂ towards their mothers.

Individual variability

All juveniles were MIS tested approximately one month after their first emergence from the maternal burrow. Experimental procedures and factor analysis techniques used were the same as those reported by Svendsen and Armitage (1973) with two exceptions. Animals were scored on 23 instead of 22 events and the matrix used to extract eigenvalues was a correlation of scoring categories (23×23), not test animals. Both approaches lead to the same end. Data from the young were analyzed with all other 1976 adult scores (the majority of the data) to insure that the factor scores of the young were generated on a scale relative to adult variance.

A. MIS factors. The first five factors extracted from the data (Table 9) accounted for 56.7% of the total variance. By examining the factor matrix (Table 9), the first two factors may be biologically interpreted. Factor I, "social, confident", an admixture between the "approach" and "sociable" factors of Svendsen and Armitage (1973), characterizes marmots which are both social and socially aggressive in a dominant manner. Factor II is an "avoidance" factor characterizing marmots which non-aggressively avoid contact. Animal scores of Factors I and II are negatively correlated ($r_s = -0.664$, $p < 0.05$, Spearman rank correlation, Siegel 1956). Factors III and IV are positively correlated ($r_s = 0.673$, $p < 0.05$) and may be interpreted as "aggressive, asocial". No unambiguous interpretation could be given to Factor V.

B. MIS variability of juveniles. When factor scores of Factors I and II are plotted on a scale of adult variance (Fig. 7), the comparative behavioral uniformity of the young becomes apparent. Juvenile scores are clustered in the upper half of the south-east quadrant, while the representative adult scores are distributed throughout all four quadrants.

C. Factor correlations with juvenile behavior. The factor scores of each individual may be considered its behavioral profile or an index of its personality. Variability in the juveniles' scores (when analyzed with adults) was insufficient to assign animals to behavioral "classes" (see Svendsen and Armitage 1973; Svendsen 1974). However, the young could be ranked relative to each other. These rankings for the first two factors were then correlated with the animal's relative rankings on the rates of several categories of behavior (Table 10).

Table 9: Sorted rotated factor matrix. Behaviors have been sorted (listed) by relative factor contributions. Factors have been rotated by Kaiser's normal varimax method (Rummel 1970; Svendsen and Armitage 1973). Only correlations greater than ±0.250 are shown. Events are described more fully in Svendsen and Armitage (1973)

Event	Factor I	Factor II	Factor III	Factor IV	Factor V
nose	0.917				
change	0.905				
pawing	0.827				
invest.	0.808	0.286			
30 cm	0.778				
tailwag	0.724				
front	0.657	-0.581			
away	0.546	0.627			
back		0.819			
towards		-0.665			
conflict			0.717		
leaning				0.701	
lie			-0.327	0.659	
retreat		0.353	0.352	0.578	
approach					0.803
groom		0.266			0.545
stretch		-0.352	0.465	0.458	
eat	0.405				0.301
chatter			-0.286		-0.303
lunge		-0.373	0.371		0.471
chirp	0.346	-0.425			
lying			-0.345		
tailup	0.490		0.464		
% variance explained	25.0	11.1	7.7	7.0	5.9

There is no significant correlation between either of the factors and any form of playful behavior. In fact many play categories are striking in their lack of any trend in correlation. This lack of correlation indicates that at the stage at which these MIS profiles were taken, one can make no predictive connections between an animal's play and its behavioral profile (or vice-versa).

However, correlations exist for certain non-play behaviors, showing some relationship exists between individual rates of behaviors and the independently derived measure of individual variability from MIS.

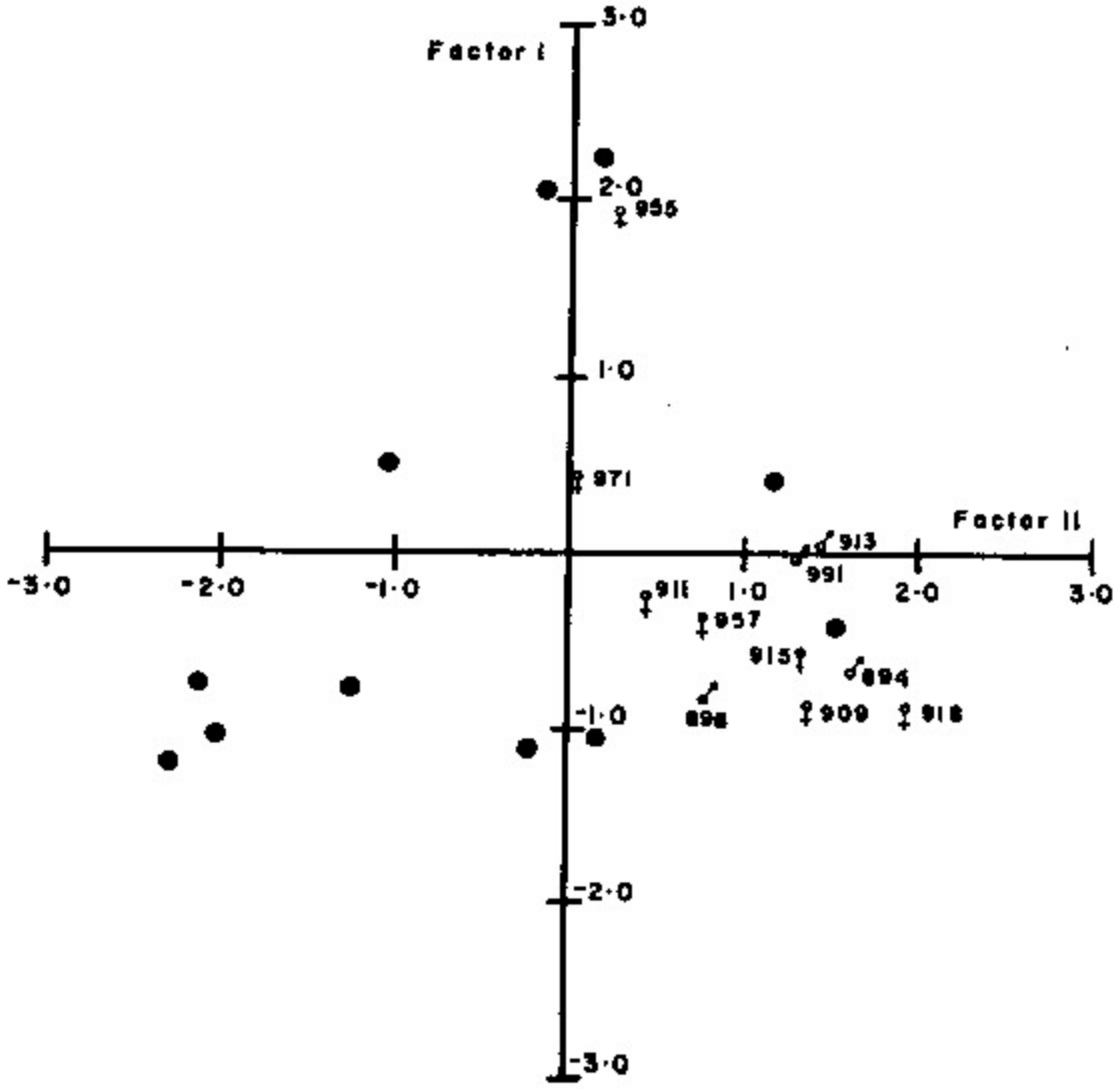

Fig. 7: Plot of MIS scores. Open circles with numbers identify individual young. Sex is also indicated. Closed circles are 11 adults chosen haphazardly from the sample for comparison. Range of the plot is based on adult variance. See text for further explanation

Table 10: Behavior-MIS factor correlations. Rates are for initiation data only. Values shown are r_S (Spearman rank correlation coefficient, SIEGEL 1956)

Behavior	Factor I	Factor II
explore	−0.189	0.257
enter burrow	−0.573*	0.218
approach	−0.630*	0.389
withdraw	0.209	0.064
play-fight	0.091	0.282
chase	−0.436	0.409
flee	−0.318	0.227
mouth-spar	0.045	0.264
grapple	−0.045	0.264
wrestle	−0.009	0.155
sexual play	−0.182	0.245
allogroom	−0.318	0.218
greet	−0.245	0.155
social invest.	−0.673*	0.391
sit	−0.836**	0.556*

* — significant ($p < 0.05$), ** — highly significant ($p < 0.01$).

Discussion

On the Definition of Play

What conclusions can be drawn from yellow-bellied marmot behavior which may help clarify the concept of play? The traditional approach to this question involves a search for unifying characteristics indicative of "playfulness". Loizos (1966) summarizes commonly accepted characteristics of this sort, of which "repetition" and "exaggeration" of motor patterns are the most widely used in descriptive play studies.

Compared to the analogous behavior patterns of adult marmots, juvenile mouth-sparring, grappling, and wrestling are highly exaggerated and repetitious. However, comparison to adult behavior may not be valid. The motor patterns used by adults occur with such high intensity that repetition and exaggeration have little chance to appear. "Lower intensity" or "typical intensity" (Morris 1957) could be a better criterion for play if the degree of repetition or exaggeration is a secondary consequence of this quality. But intensity is itself a subtle, graded phenomenon which does not contribute to an unambiguous definition.

Another common notion of play is that behaviors occur in "reordered sequences" (Loizos 1966) or that increased randomness of sequences identifies behavior as play (Bekoff 1974, 1975). Evidence now indicates that, statistically, play behaviors may be highly ordered (Poole and Fish 1975: laboratory *Mus* and *Rattus*, LeResche 1976: zoo-kept *Hamadryas* baboons, this study: Fig. 4). This orderliness does not discount Bekoff's point, however, inasmuch as he suggests relative differences. A comparison of Z values indicates that play is less ordered than non-play (Figs. 2 and 4). Unfortunately, this comparison is not a statistically valid approach to the question. Bekoff's (1975) information-theoretical approach is far more rigorous, but may not be practical due to the requirement of symmetry between play and non-play patterns.

why

"Reordered", not necessarily implying randomness, may be useful on its own account. However, the average order of sequences for marmots is as one might expect to find in "functional" adult contexts (Fig. 4). Less logical sequences do occur (Fig. 3), but these are averaged out statistically, returning the problem to one of relative randomness. As with intensity, randomness may be a valid play criterion, but its graded nature and difficulties in evaluation limit its application.

Aldis (1975) suggests that mouthing of the partner is a common aspect of all play. This suggestion is surprisingly consistent with observations on marmots, where no play was observed to occur without the mouth being partly open. While not a consistent element of rodent play in general, the open mouth has been shown to be important to play in both carnivores and primates (Poole 1978).

open

Considering the intraspecific vagaries as well as interspecific inconsistencies found in the relatively uncomplicated play of marmots, it seems unlikely that the concept can be made precise on the basis of unifying characteristics. Possibly, as Hill and Bekoff (1977) suggest, a careful study of behavioral morphology would clarify many of these problems. However, we predict that, outside of specific play signals, one is unlikely to find truly discrete (and thus unambiguous) characteristics of play. These characteristics are likely to grade smoothly from play to non-play, leaving the observer in the same bind as before.

Rather than attempting to divide behaviors into "play" and "non-play", perhaps it would be more constructive to realize, as GENTRY (1974) suggests, that the underlying motivation of any pattern may vary along a continuum. Where along the play-aggression continuum should a given pattern be assigned? Obviously context, as well as subtle variations in form, becomes a key source of information. Instead of superimposing the "grammar" from unrelated functions, one can logically analyze the frequency, form, sequential order, and so forth, of motor patterns with no a priori assumptions and make more precise statements about both the structure and function of "play".

Communication in Play

Are there specific elements of communication which can be used, at least by the marmots, to differentiate between motor patterns used playfully and otherwise? Such cues could be in the form of metacommunication (BATESON 1955; ALTMANN 1967; BEKOFF 1972) or specific play signals (BEKOFF 1974). The nature of metacommunication makes it difficult to evaluate. This study did not involve the close-up analysis required to empirically test for the presence of subtle auditory or postural cues. We can only suggest that the open mouth is a likely possibility for a metacommunicative trait.

Play signals may involve metacommunication, but differ by being specific motor patterns, not simply modifications of other patterns. In marmots, greeting is a likely play signal. It is the single element found in play sequences that one would not expect to find in adult aggression. Secondly, the significance of the transitional linkage between greet and play-fight represents the strongest linkage of any transition considered in this study (Fig. 2). While it commonly precedes play, greeting also occurs within play sequences, although these transitions are not significant (Fig. 1).

In adults, the functional significance of greeting probably involves recognition and the formation of subtle social relationships (ARMITAGE 1962, 1977; BARASH 1973). Greeting must function similarly for juveniles, but with a shifted emphasis. One would expect that, if juvenile greeting served mainly for recognition or social bond maintenance, its rate would increase sharply with the reappearance of an absent individual. ♀915 (Locality 4 B) was missing (for unknown reasons) for three days in early August. After her reappearance there was no increase in the general rate of greeting or in greetings directed specifically towards her, suggesting that greeting may function primarily as a play signal in juveniles.

Play and Aggression

Some link between play and aggression is often assumed, but not supported outside of the similarities of motor patterns involved. In marmots, sequential analysis (Fig. 2) shows that play-fighting has a strong tendency to end a social encounter, such as an aggressive act would. Juvenile play does not grade into aggression in this species, so one cannot assume that contact is terminated because play becomes "too rough". Therefore, "true" play can act by itself, like aggression, as a limiting factor in social contact.

An important difference between play and aggression is assumed to be the ability of interactants to switch roles freely and the "self-handicapping" of stronger individuals (see OWENS 1975 b). STEINER (1971) subjectively states that role-reversal in wrestling is important in the play of Columbian ground squirrels. The same has been stated for yellow-bellied marmots (ARMITAGE

1974). However, the opposite is true (Table 6). Significant flipping occurred only in a minority of interactions between ♂♂. Interactions between ♀♀ rarely demonstrated role exchange.

Two other male-female differences should be considered. First, ♂♂ prefer ♀♀ as play partners more than ♀♀ prefer ♂♂. This preference is especially evident in wrestling which involves the most physical contact of all motor patterns in play. Second is the differential use of greeting by the sexes. Greeting clearly acts as a play initiator for juveniles (see above), but is less important in this respect for ♀♀. That is, ♀♀ initiated play without a greeting significantly more often than ♂♂.

One might conclude that ♀♀ are more "serious" in play (or less likely to handicap themselves) because they do not reverse roles. But role reversal can be considered in two ways. The upper animal may limit its own effort to stay on top, and allow itself to be flipped. Alternatively, the lower animal could *increase* its effort to get to the top, independent of the upper animal's action. For marmots, the latter seems more plausible. ♂♂ are more serious in that they struggle more to "get on top". This seriousness explains the increased dependence on greeting by ♂♂ for play initiation. The importance of a play signal is to unambiguously state that what follows is not aggression in an otherwise aggressive species (Loizos 1966; Bekoff 1974). In marmots, the signal is more important in the more aggressive sex.

The interpretation of amicable behaviors in juvenile marmots (allogrooming, social investigation, greeting) is also not completely straight-forward. In marmots, grooming commonly occurs between all members of a group in both amicable and incipiently agonistic encounters. For example, allogrooming of the territorial ♂ by a male yearling can clearly be an appeasement gesture (Armitage 1974). A reasonable interpretation of social investigation is that it is performed by sociable or amicable animals towards any animal they happen to encounter. The reverse appears to be the case (Table 10); socially confident and sociable animals (scoring high on Factor I) tend to have significantly lower field rates of social investigation and approach.

These results and the transition linkages (Fig. 2) suggest that it is the responsibility of the less confident animal to initiate contact with other animals. In so doing it can keep track of the relationships and relative social positions of the animals around it, analogous to the subordinate member of a peck order keeping an eye out for dominants. Allogrooming may be related to appeasement in juveniles. Such a relationship would explain the much higher occurrence of allogrooming between ♂♂ and the strong tendency for greeting to lead to allogrooming as well as play-fighting.

On Variability and Social Integration

The discussion to this point largely has avoided the issue of adaptive function. Indeed, adaptiveness in play, due to its ex post facto nature, is notoriously difficult to assess. There is almost surely no single function of play and its adaptiveness must differ among varied groups of animals. In marmots, the correlations between play and adult social "vectors" (Figs. 5 and 6) and other evidence strongly suggest that play is involved in the social development of juveniles.

Play may have additional values. Some authors (e.g. Welker 1971) suggest that play may be a complex manifestation of exploratory behavior and that one of the primary functions of play is to maximize information input from the environment. Because play activity occurs predominantly at the burrow (Table 3), compared to the extensive ranging of juveniles, we suggest that such input is not a function of play in marmots. This conclusion is supported by a complete lack of sequential relatedness (Fig. 2).

Physical training can be an important benefit of play in animals (Fagen 1976; Fagen and George 1977) and there is no reason to doubt this function in marmots. However, Fagen (1976) points out that *social* play must have implications beyond simple exercise.

Behaviorists have long associated the term "socialization" with play (Beach 1945) but very imprecisely, never quite offering satisfying definitions of their terminology. Amid the confusion, four main themes emerge: social coordination, social cognizance, social perception, and social integration.

Social coordination simply involves the practice of coordinated group activities; e.g., hauling-out in the group play of seals (Wilson 1974). Improved group coordination may be adaptive to the individual through improved predator defense or more efficient group foraging or hunting.

Social cognizance (for reviews, see Baldwin and Baldwin 1974; Poirier and Smith 1974) includes the development of interindividual bonds (Owens 1975 a), dominance hierarchies, and other learned social relationships. Closely related, but more specific, is social perception which refers to the acquisition of "social skills", especially social communication (Bekoff 1972; Fedigan 1972).

Social integration is defined here as the expression of developmental plasticity in an individual's behavioral phenotype (this definition differs from Poirier and Smith 1974, who combine "social integration" with the concepts of social cognizance and social perception). Environmental factors (both social and physical) modify the development of an individual to fit it adaptively into a given social structure. The social structure, of course, may vary with the environment (Crook 1970; Emlen and Oring 1977). Social integration does not imply an optimal fit, nor does it imply that each of the behavioral alternatives available to an animal are equally advantageous.

Compared to adults, juvenile marmots are behaviorally relatively uniform (Fig. 7). Obviously the animals are not identical and, if young are analyzed separately from the adults, a range of behavioral profiles occurs even one month after weaning (Svendsen 1974). The important point is that the extent of personality differences found in adult marmots is not seen in juveniles. One could argue that the later divergence is a delayed genetic effect, but Svendsen's (1974) data indicate little relationship between the mother's social traits and those of her young.

Whether or not play acts in social integration may be impossible to prove. For example, play studies often attempt to correlate trends in play with later dominance rank (Poirier and Smith 1974). This approach is potentially circular. If a trend is found, possibly the same ultimate factor which determined rank also determined play. One should expect no correlation between play and the factors it is presumed to affect, in the same developmental time period. Instead, play should be flexible with respect to these factors. Such flexibility occurs in marmots between play rates and MIS ratings taken during the relatively brief time when yellow-bellied marmots are playful (Table 10). This negative result does not prove that a relationship exists, but it is necessary if play acts as a vehicle for social integration.

How is the ability to fine-tune behavioral types adaptive in marmots? Consider the development of sexual differences. Sexual roles may not be highly influenced by play (considering the strong similarity between adult [Fig. 5] and juvenile [Fig. 6] social vectors). However, as Downhower and

Armitage (1971) point out, there is much variability in the individual and intersexual relationships, especially for ♀♀, as each tries to maximize its reproductive output. For example, recruitment of ♀♀ often occurs in sib groups (Armitage unpubl. data). In this case, it is advantageous for a ♀ to be more amicable towards other ♀♀ than if she were recruited into a population with no close relatives. This variability, contrasted with ♂♂, may occur in play.

Armitage (1975, 1977) postulates a population-behavior model, acting independently of simple population density, to explain social dynamics in the yellow-bellied marmot. Briefly stated, population stability is maintained by a combination of physical-demographic factors and the behavioral types of the animals present in the group. The model attempts to account for the stability and success of marmots living within an extremely wide range of physical factors, densities, and social structures. Its importance is that it integrates the individual strategies of different marmots instead of considering the behavior of the population as a uniform whole.

Armitage (1975, pp. 353, 351) states: "The density that is likely to be critical to an organism is behavioral density . . . the critical factor in determining behavioral density seems to be a mix of behavioral types in a population. . . . The possibility remains that the cycle may be modified by the availability of behavioral types." In other words, at various points on the "population-behavior continuum", different behavioral profiles become more or less adaptive. As the young receive information concerning the local population-behavior conditions (from the environment, resident adults, or transients), they may fine-tune to the best adaptive type possible within whatever genetic-developmental constraints exist. Interactions (through play) within the cohort of young must facilitate the fine-tuning process. Wilson (1973) suggests social interactions during ontogeny contribute to population changes in voles. Similarly, Bekoff (1977) concludes that interactions between young can lead to variations in adult social organization.

One must heed Armitage's (1977) warning against generalizing conclusions based on limited field data. Uncontrolled variations in marmot behavior may affect the whole structure of play between seasons. Although there is as yet no conclusive evidence that play has any socializing function, it is hoped this paper has contributed to the view of play as a mechanism of behavioral phenotypic plasticity.

Summary

The polygynous social system of the yellow-bellied marmot is characterized both by differential responses between its members depending on age, sex, and social status, as well as a high degree of individual variability. In an attempt to understand mechanisms for non-genetic variability in this system, the behavior of young animals was examined, especially play behavior.

Five litters of juveniles (animals in their first summer of life) were studied in July and August of 1976. Behavioral patterns were ~~descriptively~~ categorized and then quantified. Over 40 % of all social interactions were playful.

Sequential analysis shows that play patterns are less ~~structured than~~ non-play behaviors, although not entirely unstructured. Greeting behavior was significantly important as a play initiator; significantly more so in ♂♂ than in ♀♀. Juveniles show sexual dimorphism in play, both in frequency and form of behaviors, corresponding to behavioral dimorphism seen in adults.

It is concluded that play cannot be satisfactorily examined on the level of distinguishing criteria or characteristics because of its graded nature. The relationship between play and aggression in this species is discussed. An hypothesis of adaptive fine-tuning of behavioral traits (social integration) through play is proposed. While the data do not prove a socializing function of play, the results are a sine qua non of this hypothesis.

Zusammenfassung

Das polygyne Sozialsystem von *Marmota flaviventris* zeichnet sich sowohl durch unterschiedliche alters-, geschlechts- und rangabhängige Verhaltensmuster zwischen seinen Mitgliedern als auch durch große individuelle Variabilität im Verhalten der Mitglieder aus. Als Beitrag zum Verständnis genunabhängiger Mechanismen der Variabilität in diesem System wurde das Verhalten von Jungtieren, insbesondere Spielverhalten, genauer untersucht.

Im Juli und August 1976 wurden fünf Würfe von Jungen, die im gleichen Jahr geboren waren, untersucht. Verhaltensmuster wurden beschrieben und kategorisiert und dann quantifiziert. Mehr als 40 % aller sozialer Interaktionen hatten Spielcharakter.

Die Sequenzanalyse zeigte, daß Spielmuster weniger stark das Sozialverhalten anderer Tiere beeinflussen als Verhaltensmuster, die nicht mit Spielen zusammenhängen, obwohl Spielfolgen keineswegs unstrukturiert sind. Grußverhalten war von signifikanter Bedeutung zur Spielauslösung, vor allem bei ♂♂. Die Häufigkeit und auch die Art des Spielverhaltens sind bei Jungen und Erwachsenen geschlechtsspezifisch.

Das Spiel ließ sich nicht zufriedenstellend nach starren Kriterien beschreiben. Die Beziehung zwischen Spiel und Aggression wurde für diese Art diskutiert. Es wird eine Hypothese über die adaptive Feineinstellung von Verhaltensmerkmalen (zur sozialen Integrierung) durch Spiel vorgeschlagen. Die Daten beweisen nicht, daß Spiel eine Sozialisierungsfunktion hat, bilden jedoch ein sine qua non dieser Hypothese.

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