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Individual differences in the behavior of juvenile yellow-bellied marmots

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Summary. Yellow-bellied marmots express considerable individuality as measured by behavior in a maze, mirror-image stimulation (MIS), and social behavior in the field. Maze behavior discriminated between residents and dispersers; residents explored the maze more widely than did dispersers. Males could not be distinguished from females nor survivors from non-survivors by their maze behavior. A group of six yearling females was established to examine the relationship between individual behavioral phenotypes (as determined by MIS) and social behavior in the field. This experiment provided a situation in which social behavior was not influenced by age, sex, or reproduction (female yearlings are non-reproductive). The number of social interactions per individual ranged from 25 to 69. The number of observed interactions per individual differed significantly from the expected for greeting, allogrooming, total amicable, play, and total social interactions. Rankings of greeting, total amicable, and total interactions were directly correlated with rankings on the “avoidance” axis; play was inversely correlated with the “approach” axis. These results suggest that marmots have individual behavioral phenotypes that are expressed in their social interactions with their conspecifics.

Introduction

Variability among individuals has generally been considered a problem that forced biologists to adopt statistical methods for describing behavioral patterns. Experimental procedures incorporated inbred lines and standard rearing conditions in attempts to reduce variability. These solutions tend to produce consistency at the expense of generalizability (Altmann 1974). However, individual dif-

ferences may be important in their own right, especially where the environment is unpredictable and behavioral choices can only be probabilistic (Slater 1981).

Most progress in assessing individual differences has come from the application of game theory to the analysis of behavior which demonstrated that individual differences in behavior could exist in stable equilibria (Maynard Smith 1982). Game-theoretic models emphasize alternative acts or strategies that may be conditional on environment (do different acts in different places), or on phenotype (defend a territory, if large; become satellite, if small) or may represent a frequency-dependent equilibrium (the better strategy depends on what other members of the population are doing) (Davies 1982). In general, these models treat variation that is readily classified into two or a few types; the models do not deal with continuous variation.

Individual behavioral characteristics affect foraging patterns (Frase and Armitage 1984), social behavior (Svendsen and Armitage 1973, Armitage 1977), social grouping (Svendsen and Armitage 1973) and reproductive success (Svendsen 1974) of yellow-bellied marmots (*Marmota flaviventris*). Individual differences are implicated in the timing of dispersal of yearlings (Downhower and Armitage 1981). Although virtually all male yearlings disperse, about half of the female yearlings remain in their natal population (Armitage 1984). The importance of individual differences among yearlings in determining who disperses is confounded by two factors. First, all adults are dominant to all yearlings (Armitage 1962; Downhower and Armitage 1981). Thus, yearlings typically behave submissively in encounters with adults even if the yearling's behavioral phenotype is aggressive. Second, behavior between adults and yearlings is kin-related (Ar-

mitage and Johns 1982). A yearling's behavioral response to an adult or another yearling is some combination of its behavioral phenotype and its relatedness to its protagonist. Therefore, an independent measure of individual behavioral phenotypes is necessary in order to dissect individuality from the background of age, sex, and kinship.

This paper reports on measures of individuality in juvenile yellow-bellied marmots and relates these measures to behavior.

Methods

Maze behavior

Thirty-one young or yearling marmots produced 59 cases (16 animals were run two or more times) of maze behavior. The maze consisted of an entrance pen 0.8 m on each side. The maze was divided into two mirror-image halves connected by a passageway at the top of the maze. Entrance from the pen into the maze proper occurred through two parallel 0.25 m wide passages extending from each corner on the upper side of the pen. Movement into the passages was blocked at each entrance by a removable partition. The passages were laid out so that an animal had to make a left or right turn every 1.0 m of distance traveled. On the right-hand maze, a consistent preference for right turns eventually led an animal into one of four blind ends. However, an animal could retrace its steps or by making left turns reach the left-handed maze and eventually return to the entrance pen. The passages were 0.25 m on all sides which allowed adequate space for normal movement and turning. The sides and bottom were wooden and the top was wire mesh. A photocell was placed at each strategic turning place. When the light from the photocell was broken by a moving marmot, a mark for that photocell was recorded on an Esterline-Angus 20 channel event recorder (Downhower 1968). The room in which the maze was housed was lit by four 100-watt lightbulbs that provided uniform lighting over the maze. Although the room was draped off from the rest of the building, a low level of background noise occurred from other workers in the building.

Each animal was placed in the entrance pen for one minute. Then the partitions were removed, the event recorder was turned on, and the animals were permitted to wander freely for 30 min. At the completion of the run, the animal was removed, any feces or urine was cleaned out, and the trace from the event recorder was marked with the animal's number, date, and time of day. The following data were derived from the chart recordings: time to trigger first photocell, time to last photocell triggered, length of time of activity, length of time between triggering first and last photocells, number of different photocells triggered, total number of times photocells were triggered. Survivorship over the first hibernation period and whether an animal dispersed were subsequently determined for each individual.

Individuality and social behavior

Individual behavioral phenotypes were determined by mirror-image stimulation (MIS) for a group of six female yearlings that occupied a common home burrow. Only female yearlings were used in order to remove the effects of sex and age on the expression of behavior in free-ranging animals. Four of the yearlings were at least half-sibs; the others were unrelated

to each other or to the half-sibs. In June of the yearling year MIS was determined for each animal as part of a larger study of individuality. The entire data set of 59 animals was analyzed by factor analysis (Svendsen and Armitage 1973; Svendsen 1974). Factor scores for the six yearlings were extracted from the larger data set and used to determine the rank order of the yearlings on the MIS axes.

Each animal was identified by placing a numbered tag in each ear and by dyeing the fur with individual patterns of stripes or blots. The animals occupied the main burrow system of Marmot Meadow (Frase and Armitage 1984). The animals were observed for 55 h spaced from May 16 to August 13 inclusive. Observations were concentrated in the morning and evening hours when marmots are most active (Armitage 1962). All social interactions were recorded and every 10 min the location of each animal was recorded on a map of the locality. The locations were later converted to grid coordinates and space-use was plotted as a perspective block diagram (Sampson 1975). An index of similarity that preserved the three-dimensionality of the census data was used to calculate overlap in space-use (Frase and Armitage 1984). Space-use overlap with each of the other five colony residents was calculated for each yearling. The mean of the five values for each animal was calculated as an overall index of overlap.

Social interactions were classified as amicable, agonistic, or play (Nowicki and Armitage 1979). Amicable behaviors consisted of greeting and allo-grooming; agonistic behavior consisted of chase, flight, and avoidance (Armitage 1962, 1973, 1974). Four of the animals returned as two-year-olds; their social interactions were again compared with their previously-measured MIS behavior.

Results

Maze behavior

Discriminant function analysis was employed to determine if the maze behavior of dispersers could be distinguished from that of recruits. When all 59 cases were included, classification was poor. Twelve cases representing nine animals were deleted from the analysis. Each case consisted of a young who was completely inactive; i.e., did not leave the entrance pen. Most of these cases occurred when the animals were run late in the afternoon or when we suspected the animals were disturbed by trapping and handling. Our experience indicates such disturbance is common. Eight of these young were placed in the maze at other times and produced normal runs. Therefore, only one animal was omitted from the analysis. Residents differed significantly from dispersers ($F_{2,44} = 8.3$; $P < 0.001$). Two variables entered the model: total number of photocells triggered and number of different photocells triggered; total number was by far the more important variable. Residents triggered more photocells ($\bar{x} = 117$ vs 50) and more different photocells ($\bar{x} = 15$ vs 13.2). The model correctly classified 91.1% of the cases; four dispersers were incorrectly classified as residents.

Among the four animals mis-classified, one was moved from its birth site into another colony and failed to become a resident. This dispersal by an animal introduced into a strange population characterizes marmot behavior (Armitage 1974, 1975). A second animal was a member of a group of four yearlings living in a small habitat area and who were treated agonistically by the resident adult females. All the yearlings dispersed. Survivors could not be distinguished from non-survivors nor males from females by their maze behavior.

Behavioral phenotypes and social behavior

The six female yearlings engaged in 161 social interactions. Three were agonistic; 61 were play bouts (Nowicki and Armitage 1979) and 97 were amicable. The number of social interactions per individual ranged from 25 to 69. Because the animals lived in the same burrow system, I assumed that each had equal probability of engaging in social behavior. The distribution of observed social interactions was compared with the expected (Altmann and Altmann 1977). For all categories of behavior, the number of observed interactions differed significantly from the expected ($df=5$ in all cases): greeting, $\chi^2=13.7$, $P<0.025$; allogrooming, $\chi^2=10.9$, $P<0.06$; total amicable (greeting plus allogrooming), $\chi^2=16.0$, $P<0.01$; play, $\chi^2=38.4$, $P<0.001$; total social interactions (amicable plus play), $\chi^2=32.8$, $P<0.001$). I also assumed that each marmot had equal probability of initiating a social interaction. The number of social interactions initiated differed significantly from the expected: greeting, $\chi^2=12.0$, $P<0.05$; total amicable, $\chi^2=26.3$, $P<0.001$; play, $\chi^2=33.9$, $P<0.001$; total social interactions, $\chi^2=46.2$, $P<0.001$.

The factor analysis of the MIS data from 59 adult and yearling marmots produced three axes that explained 85% of the variance. Animals scoring high on axis I spent most of their time in the front on the arena, sitting or lying near the mirror, and oriented toward the image. This factor was designated "approach" (Svendsen 1974). Animals scoring high on axis II spent most of their time in the rear of the arena and often oriented away from the image. This factor was designated "avoidance". Axis III was designated "sociability" because marmots nosed and pawed at the image, wagged their tails, moved freely between the front and rear of the arena, and engaged in other activities such as feeding and investigation of the arena.

The rank order of each yearling was determined for each MIS axis and for each of the social

Table 1. Kendall rank and partial rank correlations between number of social interactions and factor score on MIS axes for 6 female yearling yellow-bellied marmots. Only significant relationships are included. Axis I="approach"; axis II=avoidance

Social behavior	MIS Axis	Γ	P	Partial Γ
Greeting	II	0.6	0.068	0.63
Total amicable	II	0.73	0.028	0.78
Play	I	-0.73	0.028	-0.64
	II	0.6	0.068	0.43
Total interactions	II	0.73	0.028	0.78

behaviors. All rankings were from high to low values. Similarity among the ranks was determined by the Kendall coefficient of concordance (Siegel 1956:229). There was no similarity among the ranks on the MIS axes ($W=0.34$ NS). By contrast, rankings for social behaviors ($W=0.7$, $P=0.01$) and for the initiation of social behaviors ($W=0.8$, $P=0.01$) were similar. Therefore, the relative number of amicable or play interactions of an individual is independent of the kind of interaction. Furthermore, the rankings for total social interactions and initiation of social interactions were identical ($r_s=1.0$, $P<0.01$). Thus, an animal initiates social contacts in proportion to its total social behavior. These relationships suggest that an individual's social behavior as measured in the field may be a consequence of its behavioral phenotype; i.e., its individuality.

The relationship between individuality and social behavior was tested by comparing rankings on the MIS axes with rankings for social behaviors. Greeting, total amicable, and total interactions were correlated with axis II, "avoidance" (Table 1). Animals that had the highest levels of avoidance of their image in the MIS arena had the highest numbers of social interactions in the field. These same animals also initiated more amicable interactions (axis II: total amicable initiated, $r_s=0.91$, $P<0.05$). Rankings for play were inversely related with rankings on axis I and directly related with rankings on axis II. The partial rank correlation suggests that the association between play and axis II is not significant (Table 1). Animals that scored high on "approach" played less than those who scored low. It was not possible to separate behavior related to kinship from MIS rankings in this analysis.

The social behavior and MIS behavioral phenotypes were determined for these animals the previous year when they were young. Because social behavior may undergo ontogenetic change result-

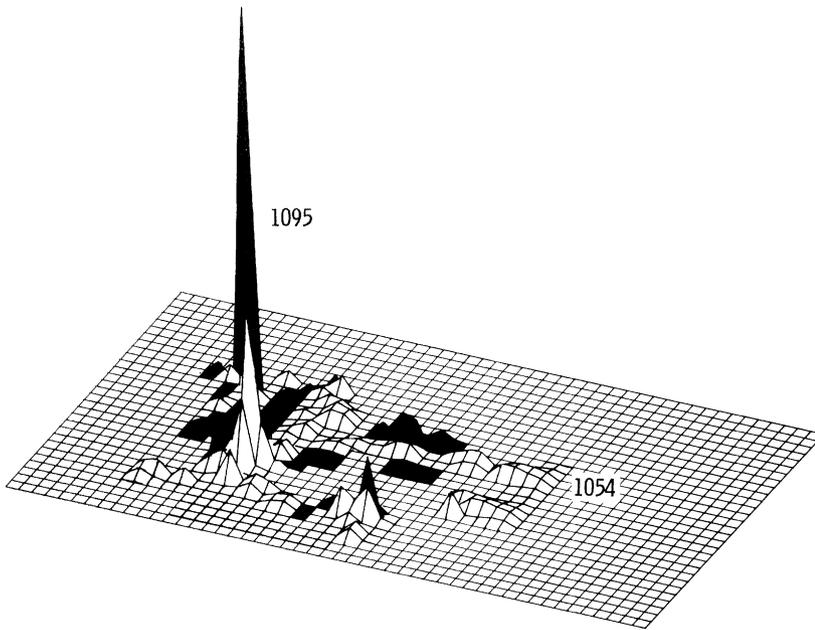


Fig. 1. Patterns of space-use by two female yearling yellow-bellied marmots. These two animals were chosen to represent extremes in space-use patterns. Space-use overlap for the two females was 41.3%

ing from social experiences, rankings for total social interactions and rankings on the three MIS axes were compared between the two years.

The rank orders for total social interactions were not correlated ($r_s=0.03$). With such a small sample size, a change in rank of one animal can markedly affect the results and interpretation of the analysis. For example, the difference between the two years was mainly attributable to one animal that ranked first as a young but last as a yearling. If that animal is eliminated from the analysis, $r_s=0.87$, which is nearly significant ($n=5$, $r_{s0.05}=0.9$). This manipulation of the analyses does not change the result that rank orders for total social interactions were not related between young and yearlings, but does suggest that most animals behaved similarly relative to each other in the two years.

The variation in MIS rankings is consistent with the variation in social behavior. Only five of the animals were exposed to MIS in both years. The rank orders on the MIS axes were not correlated (axis I, $r_s=-0.7$; axis II, $r_s=0.3$; axis III, $r_s=0.3$). For axis I, the bottom and top ranking animals switched positions between years. On axes II and III, a major shift by one animal accounted for the lack of significant correlation.

Factor scores on MIS axes may change because of minor quantitative differences in one or more behaviors during MIS. These changes may affect rankings on axes but may not reflect changes in major groupings of behavioral phenotypes (Svendsen and Armitage 1973). Therefore, animals were

placed in one of three groups corresponding to the three major axes (Svendsen 1974). Three of the animals were in the same group each year and two animals changed groups. One shifted from "sociability" and one from "approach" to "avoidance". The score of a third animal shifted markedly from "sociability" toward "avoidance".

An adult male joined the population during the summer. There were no differences in the rank orders for any of the social behaviors when social interactions with the male were included compared to social interactions among the females only.

Space-use was similar among the six yearling females (Fig. 1). All animals used the burrow system at the main talus (see Frase and Armitage 1984 for a photograph of this area) and foraged in the surrounding meadow. The index of space-use overlap varied from 39.4% to 55.5%; however, only one animal had a mean index less than 53.0%. The mean indexes of space-use overlap were ranked from high to low. The index of space-use overlap was significantly correlated with total social interactions ($r_s=0.94$, $P=0.01$). The index of space-use overlap was correlated with the "avoidance" MIS axis ($r_s=0.77$, $P\approx 0.05$) and negatively correlated with the "approach axis" ($r_s=-0.83$, $P=0.05$).

Four females returned as two-year-olds. The two females that did not return ranked 1 and 3 on axis III and 5 and 1 on axis II, respectively. The sample size is almost too small for analysis, but there was a tendency for rank order of total amicable behavior to be inversely correlated with

the rank order on MIS axis I ($r = -0.67$, $P = 0.167$). Interestingly, the female that produced a litter of young as a two-year-old had the fewest social interactions as a two-year-old and as a yearling. She ranked number one on axis I, "approach" and at the bottom of axis II, "avoidance". However, the only female to survive as a three-year-old and who established a matriline (Armitage 1984), ranked fifth on axes I and III ("sociability") and third on axis II. Again, the sample is small, but there is no obvious relationship between behavior, survival, and reproduction. Probably many factors affecting survival are independent of social behavior. The lack of any obvious relationship between behavior and survival is consistent with the lack of a relationship between survival and maze behavior.

Discussion

Yellow-bellied marmots express considerable individuality whether that individuality is measured in the field or in the laboratory in such disparate measures as maze behavior and MIS performance. All measures revealed a pattern of continuous variation, but the continuous variation could be grouped into two or more types by statistical procedures.

Marmots that dispersed were less active in the maze than those that became residents. The differences in maze behavior are unlikely to be related to exploratory behavior in the sense that exploratory behavior leads to dispersal. Residents may be socially confident phenotypes; hence, these animals may be more likely to wander in a maze because they are not inhibited by the possibility of encountering conspecifics. Studies on other species support this interpretation. There were no differences in the exploratory behavior of male cotton rats (*Sigmodon hispidus*) prior to a period of social interactions. However, following social interactions, subordinate animals, but not dominants, decreased their activity (Summerlin and Wolfe 1971). Juvenile deer mice (*Peromyscus maniculatus*) were restricted to a small area of a maze when adults were also present (Sadleir 1965). By contrast, the dominant adults roamed freely throughout the maze. Introduced adult females, presumably more confident than juveniles, usually roamed freely and intermingled with the resident adults. In another experiment, resident *P. maniculatus* moved through a maze more readily than dispersers (Fairbairn 1978a).

Individual behavioral phenotypes that may be grouped into several behavioral types may occur

commonly among social ground-dwelling sciurids. Columbian ground squirrels (*Spermophilus columbianus*) exposed to MIS form three behavioral types (Balfour 1979) classified as "sociable", "avoider", and "conflict". The basic behavior of the "sociable" and "avoider" types was remarkably similar to that of the "sociable" and "avoider" marmot types. The "conflict" type included behaviors displayed by the "approach" type of marmots. "Sociable" animals were most likely to live in colonies whereas "conflict" animals were more likely to live as satellites. This pattern is similar to that reported for "sociable" and "approach" marmots (Svendsen 1974). Among adult, "sociables" had a higher proportion of amicable and agonistic behaviors and "avoiders" had a higher proportion of avoidance behaviors (Balfour 1979).

Sib interaction rates in the field for young marmots of both sexes were negatively correlated with factor scores on the "sociability" axis in satellite groups and were positively correlated with factor scores on the "avoidance" axis in colonial groups (Rains 1979). Factor scores on the "avoider" axis of mothers at satellite sites were significantly correlated with the rate of their social interactions with their young (Rains 1979).

The general pattern that marmots scoring high on the "avoidance" axis during MIS have higher rates of social interactions than animals scoring high on the other axes (Rains 1979; Armitage 1982) suggests that animals that tend to avoid a "stranger" (the mirror-image) initiate and engage in more social interactions with familiar animals. Their behavior in the MIS arena suggests "social insecurity". Among coyote pups, social rank and success in soliciting social play from another littermate were negatively correlated (Bekoff 1974). The inverse relationship between play and ranking on MIS axis I for yearling marmots (Table 1) indicates a similar relationship. All of these cases suggest that socially subordinate (=insecure) animals attempt to establish or maintain social bonds.

When the yearlings in this study were part of a group of eight young females from four different litters, rates of social interactions were correlated, not with kinship, but negatively with axis III ("sociability") (Armitage 1982). This relationship between field behavior and the behavioral phenotype persisted despite large changes in individual behavior. The rate of social interactions among the yearlings was 58.5% of the rate among the young, but the change in rate of two animals was greater than 100%. The persisting relationship between MIS performance, field behavior, and space-use overlap

indicates that MIS is measuring some underlying behavioral phenotype that is expressed in its social behavior with its conspecifics. The inter-relatedness of MIS rankings, field behavior, and space-use overlap does not specify cause and effect. It is tempting to suggest that the underlying behavioral phenotype determines all three behaviors. However, one cannot exclude the possibility that the behavioral phenotype determines space-use patterns and that social interactions follow as a consequence of proximity.

The change of behavioral phenotype from one category to another between the young and yearling years suggests that the behavioral phenotype is affected by experiences during growth and maturity. Ontogenetic experiences may affect an individual's subsequent sociability and its tendency toward dispersal (Bekoff 1977). Although dispersal may be a consequence of social pressure (Fairbairn 1978b), the lack of any obvious relationship between rates of social interactions and dispersal (Holekamp 1984) may be a consequence of individuality. Thresholds of response to social pressure from adults may differ among behavioral phenotypes; some individuals may disperse after encountering high levels of agonistic behavior whereas others may disperse following a single agonistic encounter. The analyses of the role of social interactions in animal population biology require increased emphasis on the role of individual behavioral phenotypes.

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