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Individual differences and reproductive success in yellow-bellied marmots

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Mirror-image stimulation (MIS) was used to determine the individual behavioral phenotypes of 90 adult, 132 yearling, and 135 young yellow-bellied marmots (*Marmota flaviventris*). Linear typal analysis (LTA) was used to group individuals based on similarities in their MIS scores. Principal component analysis (PCA) was used to evaluate the patterns of variation in behaviors and discriminant function analysis (DFA) was used to determine if there were consistent differences in marmot behavior. LTA produced two interpretable groups that were significantly and negatively correlated. Marmots in each group formed a shy-bold continuum. Bold animals were those that approached the mirror early and made nose contact with the image whereas shy animals approached the mirror late in the run, spent time in the back half of the arena, and frequently chirped at the image. Behaviors shifted with age; young were predominantly bold and adults were predominantly shy. This shift appears to be developmental and not genetically determined. Reliability and predictability analyses indicated that there is a 75% probability that a MIS run correctly identifies an individual's behavioral phenotype. The probability increases to 90% for those individuals with high loading scores. Play, agonistic, and amicable behaviors of female yearlings recorded in the field were significantly correlated with their MIS behavioral phenotypes whereas only play of male yearlings was so correlated. Correlations among eight life-history traits of adult females were independent of behavioral phenotypes. Shy females were more likely to be associated with female non-kin, produced more daughters, and were more likely to be immigrants. Among female yearlings, shy phenotypes were likely to become recruits and bold phenotypes were more likely to disperse. Bold adult females recruited yearlings regardless of their behavioral phenotype whereas shy adult females recruited primarily shy yearlings and the majority of bold yearlings dispersed. Among adult males, shy phenotypes were more likely to be territorial-colonial and to produce more young. Lifetime reproductive success (LRS) of females was strongly related to the number of years of residency, which was strongly correlated with the frequency of reproduction and the production and recruitment of offspring. The demographic patterns were independent of behavioral phenotype. Behavioral phenotype impacts demographic trends mainly by increasing the recruitment of daughters by bold females. LRS of males depends on the length of residency. Shy males have a higher LRS because they are territorial-colonial for a longer time and produce more young. Bold individuals appear to be those that are sub-

ordinate and attempt to affiliate with other marmots whereas shy individuals appear to be dominant and less likely to be affiliative. By being more aggressive, the shy marmot is more likely to achieve residency as a yearling or adult whereas the more affiliative adult is more likely to recruit offspring, but affiliative yearlings are less likely to become recruits, especially when the adults are the dominant, "shy" individuals.

KEY WORDS: *Marmota flaviventris*, individuality, mirror-image stimulation, reproductive success, behavioral phenotypes, life-history traits, shy-bold continuum.

INTRODUCTION

The presence of individual differences in animal behavior is a well-established but incompletely understood phenomenon (CLARK & EHLINGER 1987). Individual variation was reported in behaviors associated with breeding by northern fulmars, *Fulmaris glacialis* (HATCH 1990), in the playback responses of female cowbirds, *Molothrus ater* (KING & WEST 1990), in the feeding behavior of adult male zebra finches, *Taeniopygia guttata* (SLATER 1981), in the ecological characters of carabid beetles (VAN DIJK 1982), in the anti-predator responses of 3-spined sticklebacks, *Gasterosteus aculeatus* (HUNTINGFORD & GILES 1987), in behavior after recognition of snakes in the anti-snake behavior of California ground squirrels, *Spermophilus beecheyi* (COSS & BIARDI 1997), and in the responses of yellow-bellied marmots (*Marmota flaviventris*) to mirror-image stimulation (SVENDSEN & ARMITAGE 1973).

The widespread occurrence of individual differences suggests that the differences are adaptive and that phenotypic plasticity is a diversifying factor in evolution (CLARK & EHLINGER 1987, WEST-EBERHARD 1989). In general, the behavioral

variability is postulated to enable individuals to adjust to changing or unpredictable environments (e.g., SLATER 1981). Two major advantages of being different were suggested by CLARK & EHLINGER (1987): (1) animals can be behaviorally fine-tuned to local situations and (2) a behavioral phenotype may provide a "fit" with the phenotypes of kin or other cooperators so that the benefits of cooperation are increased.

For many animals, the behavioral phenotypes form a shy-bold continuum; shy individuals retreat or become quiet and vigilant and bold individuals act normally or become actively exploratory (WILSON et al. 1994). Differences in behavior of pumpkinseed sunfishes (*Lepomis gibbosus*) are relatively stable in nature but apparently disappear when fish are held in social and ecological isolation in the laboratory (WILSON et al. 1993). The individual differences in shyness and boldness in these fish are context-specific (COLEMAN & WILSON 1998).

The pumpkinseed sunfish results point to a major question about individuality: to what degree are behavioral phenotypes stable over an individual's lifetime (HAYES & JENKINS 1997)? In this paper we investigate the following characteristics of individuality in yellow-bellied marmots: (1) the identity and stability of behavioral phenotypes, (2) the inheritance of behavioral phenotypes, (3) the relationship between social behavior and behavioral phenotypes, and (4) the relationship of behavioral phenotypes to fitness (measured as reproductive success).

METHODS

Marmot biology

Yellow-bellied marmots are large, diurnal, ground-dwelling sciurids that occur primarily in montane and alpine environments in the mountains of the western United States (FRASE & HOFFMANN 1980). Marmots typically inhabit rocky outcrops or talus slopes with adjoining grass and forb meadows on moderate, south to southeastern facing slopes (ARMITAGE 2000). In our study area in the Upper East River Valley, Colorado (elevation 2900 m), marmots emerge from hibernation in early May and immerge in late August or early September. Mating occurs soon after emergence and young are weaned in late June or early July (ARMITAGE 1998). Young hibernate in their natal home range. Yearlings, animals 1 year old, do not breed and are the major dispersers. Virtually all male yearlings and about 50% of the female yearlings disperse (ARMITAGE 1991). Females live in social groups ranging from one to five in number (ARMITAGE & SCHWARTZ 2000); an adult male becomes resident with one or more female social groups (ARMITAGE 1998).

Female associations consist of mother:daughter or sister:sister groups that persist through time as matrilines (ARMITAGE 1984). Survivorship and per capita reproduction increase with an increase in matriline size, then decrease in the largest matrilines (ARMITAGE & SCHWARTZ 2000). Populations are relatively stable through time; population increase occurs primarily when mothers recruit daughters and population decrease occurs primarily from predation and mortality during hibernation (ARMITAGE 1991, SCHWARTZ et al. 1998).

Trapping and measurements of individuality

Every year since 1962 all resident marmots in six major study sites were trapped and individually marked with numbered tags affixed to each ear. Marmots at an additional 10 sites were trapped in most years. Because young were trapped upon emergence, we could

assign young to a specific adult female. Because males are territorial, we could identify the father (SCHWARTZ & ARMITAGE 1980, 1981). Thus, relatedness of all individuals was known (ARMITAGE 1989, 1996a). Marmots used in this study came from 15 sites. For each site, the total number of residents, number of transient adult males, number of kin and non-kin, number of reproductive females, number of male and of female yearlings, and number of young of each sex were known.

Behavioral phenotypes were determined by mirror-image stimulation (MIS) (SVENDSEN & ARMITAGE 1973). Marmots were trapped in the morning and taken to the MIS arena located in a neutral area. The entrance to the 92 × 92 × 31 cm arena was at the back; opposite the entrance was a 42 × 30 cm glass mirror covered with an opaque partition. Fresh food, mainly cow parsnip (*Heracleum*) or dandelion (*Taraxacum*), was placed in the center of the arena. The marmot was released into the arena and the observer climbed into a blind atop a 1.5 m tower. After a 2 to 5 min acclimation period, the cover over the mirror was removed by remote control and 19 behaviors were recorded for 10 min, termed a "run". Each behavior that occurred in each minute was recorded and summed over the 10 min. Thus, the score for any behavior could range from 0 (did not occur) to 10 (occurred at least once in each minute). Marmots were returned to their burrow site by early afternoon.

One possible source of error in the measurements was heat. Yellow-bellied marmots that were obviously heat-stressed generally lay stretched-out at one side of the arena and would lie in any available shade. The animal could see the mirror but otherwise did not react. Runs for animals obviously heat-stressed were discarded; however, some animals may have been heat-stressed, but the stress was not obvious to the observer and the run was included. Heat-stressed animals behaved like "avoiders" (SVENDSEN & ARMITAGE 1973), which resulted in a low score on Axis I or a high score on Axis II (Table 1) and may account for some of the shifts in scores when runs were repeated in the same year.

Table 1.

Mean scores of major behaviors for pure type profiles of adults (n = 169) for LTA analyses set to produce two or three groups, expressed as axes. Scores that are underlined are those that had major effects for determining that axis. Major effects were determined from the order of entry into the DFA analysis (see Table 2).

	Two Axes		Three Axes		
Behavior	Axis I	Axis II	Axis I	Axis II	Axis III
Self-groom	0.2	0.1	0.1	0.2	0.1
Chirping	1.1	0.1	1.3	0.2	0.8
Lying	1.8	1.5	1.1	1.3	4.3
Eating	1.2	4.4	1.1	3.9	0.7
Investigation	0.6	5.0	0.3	4.6	0.2
Approach	7.3	1.3	9.4	1.5	4.0
Conflict	0.2	0.1	0.2	0.1	0.2
Nose contact	1.0	5.4	0.4	4.9	1.7
Retreat	0.6	0.4	0.5	0.6	0.5
Pawing/muzzling	0.2	1.9	0.1	1.7	1.0
Front half	3.7	8.4	2.0	7.7	7.9
Back half	6.5	5.2	8.2	5.5	1.7
Lie flat	0.5	0.2	0.1	0.2	1.7
Under 30 cm	1.0	3.2	0.4	3.1	1.5
Change	1.1	4.8	0.6	4.6	0.7
Tail-wag	0.3	2.5	0.1	2.2	0.2
Tooth chatter	0.4	0	0.4	0	0.5
Orient toward	7.9	8.7	7.4	8.6	9.4
Orient away	4.5	7.6	4.6	7.4	2.7

MIS was measured on 169 adults (90 individuals, 79 repeat runs), 132 yearlings (111 individuals, 21 repeats), and 139 young (135 individuals, 4 repeats). Fifty-six young (31 males, 25 females) were rerun as yearlings and 22 yearlings (6 males, 16 females) were rerun as adults. The sample size in this study is about 11 times greater than that used in earlier studies (Svendsen & Armitage 1973, Svendsen 1974) and permits testing of several concerns (e.g., number of groups, reliability) about the nature of individuality and its relationship to life-history traits.

Analysis of MIS scores

Linear typal analysis (LTA) was used to group individuals based on similarities in their MIS scores (Overall & Klett 1972). LTA was run using a computer program provided in Overall & Klett. LTA uses all the behavioral information to form the number of groups as determined by the investigator. LTA assumes that there is a pure type or a small number of pure types underlying any collection of heterogenous individuals. The procedure discovers the pure types and then determines the similarity of each individual to the hypothetical pure types (Overall & Klett 1972). By contrast, the factor analysis that we previously used (Svendsen & Armitage 1973) had two major drawbacks; it was not designed as a grouping system and it did not use all the available information. Furthermore, factor analysis partitions the variance into multiple, independent variables, some of which are not biologically interpretable. Cluster analysis also assigns individuals to initially undefined classes so that individuals within a class are more similar to each other than to individuals in other classes. There are a number of clustering procedures. We did not use cluster analysis as cluster analysis and LTA provide similar grouping of MIS data (Balfour 1979).

Repeated runs were used to estimate reliability and predictability for adults. There were too few replicate runs for young and yearlings to do a similar analysis. Reliability is a measure of how well a given run agrees with all other runs for that individual. Because repeat runs within a year could affect an animal's response in the arena because of familiarity, the analysis was redone using only the first run each year for each animal. For each animal the modal LTA group was scored as the most common group assignment among the replicates. Reliability was calculated as the number of runs classified in the modal group divided by the total number of runs.

Predictability is the comparison of the first run for each animal with all other runs of the animal. This measure is important because most animals undergo only one run. Because one sex may be less predictable than the other, male and female adults were analyzed separately. Predictability was calculated by determining the modal LTA group as shown by all the animal's runs and comparing the group assigned by the first run with the modal group.

Principal component analysis (PCA) was used to evaluate the patterns of variation in behaviors. PCA was run using BMDP4M and the axes were rotated for interpretation. Because some of the MIS behaviors seem correlated, e.g., "front" and "back", we expected that considerable correlation would occur among the 19 variables, which would collapse into a much smaller set of uncorrelated variables.

Discriminant function analysis (DFA) was used to determine if there are consistent age-related differences in marmot behavior. MIS runs of all animals, classified according to age, were analyzed with BMDP7M. Criteria for entering the model were set at $F = 3.0$. A second DFA was run only on adults ($n = 169$) to establish the order of entry of behaviors into the model in order to determine which behaviors were most important for interpreting LTA groups.

Heritability was estimated for mother and offspring (25 litters) and for father and offspring (24 litters) (Faulkner 1989) and the slopes of the mother and father regressions were compared for possible maternal effects.

To test whether adult female behavioral phenotypes classified by LTA were associated with social groups, social groups were classified into three "coloniality" categories. Solitary individuals were those who were the only females living in their habitat patch. Mini-colonial

individuals were those typically associated with one additional adult female on the same habitat patch, and colonial individuals were those that occupied a habitat typically with two or more additional adult females. Female residency was classified as immigrant or recruit (resident in natal colony).

To compare MIS results with social behavior observed in the field, social behavior was recorded for 27 male yearlings and 17 female yearlings. Behaviors were classified as amicable, agonistic, or play (ARMITAGE 1974, 1986b). Rates of behavior were calculated as number per hour per individual (yearling or adult) with whom the marmot could interact. The number of animals available for social interactions varied from one to five adults and from none to 10 yearlings.

RESULTS AND DISCUSSION

Number of groups

LTA was set to produce two or three groups expressed as axes (Table 1). For two groups, axis I was characterized by chirping, which is the characteristic alarm call, delay in approaching the mirror, and spending time in the back half of the arena. Nose contact occurred infrequently. Axis II was characterized by animals that ate, investigated the arena, made nose contact with the mirror image, pawed and muzzled the image, and spent time in the front half of the arena (Table 1). Several behaviors, self-groom, conflict, retreat, and orient toward, had little or no effect in determining axis membership.

For three groups, axes I and II were similar to axes I and II, respectively, for two groups. Axis III was characterized by lying, mainly in the front half, lying flat, approaching the mirror with moderate latency, and maintaining orientation toward the image (Table 1). Axis III animals scored mainly on axis I in the analysis of two groups and generally were located in the middle range of that axis. Thus their scores were low for axis I (three-axis analysis), and some animals scored slightly higher on axis II than on axis I. The biological interpretation of animals scoring high on axis III is not clear other than they were less interactive with the image than axis II marmots, but are distinguished from axis I marmots primarily by spending more time lying in the front of the arena. Lying and lying flat is similar to behavior observed in agonistic encounters in the field (ARMITAGE 1962, 1974). Both animals may assume the lying position and oriented toward the other marmot. Either may suddenly flee or attack the other or each may slowly turn and walk away. In the field, the decision to flee or attack probably is conditioned on the behavior of the other animal. In MIS, the image presents the same signal that the animal presents and probably leads to a longer time before a decision is reached. Furthermore, one behavior, approach, differed significantly ($P < 0.001$) between the sexes. Females did not approach the image whereas males approached the image early in the run and spent considerable time within 30 cm of the image. Because no additional biological interpretation resulted from establishing three groups, we chose two groups for further analyses.

Discriminant function analysis

DFA was used to identify behaviors that were most important in the separation of adults into two groups (Table 2). The first eight behaviors that entered the

Table 2.

Order of entry of behaviors in discriminant function analysis for two axes. Behaviors marked with an asterisk differed significantly between groups (one-way ANOVA for each behavior).

Order	Behavior	Description
1	*Nose contact	Makes nose contact with the mirror-image
2	*Investigation	Explores the arena
3	*Change	Moves from front half to back half or reverse
4	*Approach	The time at which the animal contacts the mirror
5	*Eating	Feeding on the food placed in the arena
6	*Pawing/muzzling	Rubs cheeks and/or fore paws on the mirror-image
7	*Front half	Time spent in the front half of the arena
8	*Tail-wag	Waving the tail from side-to-side
9	*Orient away	Marmot faces away from the mirror
10	*Under 30 cm	Sits or lies within 30 cm of the mirror-image
11	*Chirping	Animal emits alarm calls
12	*Tooth chatter	Rapid striking together of incisors while facing image
13	*Back half	Time spent in the back half of the arena
14	Orient toward	Animal facing image
15	Retreat	Animal backs away from the image
16	Conflict	Animal moves toward then away from the image
17	Lie flat	Animal lies with head flat to the ground, oriented to image
18	Lying	In prone position, head up, orientation toward or away
19	Self-groom	Marmot chews or scratches trunk or limbs

DFA model describe the activity of axis II animals. These marmots approached the mirror early in the run, made nose contact with the image, frequently pawed/muzzled the image, and then spent most of the remaining time eating, investigating the arena, and moving frequently between the front and back halves of the arena (Table 2). These animals were characterized as bold and axis II was designated the bold axis. By contrast, axis I animals were characterized by approaching the mirror late in the run, spending time in the back half of the arena, frequently chirping at the image, and sometimes tooth-chattering at the image. These animals may be characterized as having little or no contact with the image. We designated these animals as shy and axis I was designated the shy axis. Thus the formation of two axes provided two biologically interpretable groups, bold and shy (Wilson et al. 1994), albeit there is additional phenotypic complexity embedded in these groups, especially in axis I.

For subsequent analyses, we divided the animals into two groups based on their group loadings. Those marmots whose loading scores were > 0.5 on axis I were placed in group 1; those whose scores were < 0.5 were placed in group 2. Similarly, marmots whose scores were high on axis II were members of group 2 and those with low scores on axis II were in group 1. Thus group 1 contains the marmots categorized as shy and group 2 consists of the marmots designated as bold. Because there were fewer bold phenotypes among adults (Table 6), we divided the axes into two halves to provide equal numbers in the two groups for statistical comparisons. Animals in the upper half of axis I were categorized as “more-shy” and those in the lower half of the axis, as “more-bold”.

Principal components analysis

Of a possible 171 correlations among the 19 behaviors used to classify adults, only 19 had an $r > 0.5$ (Table 3). Ten of the correlations were among nose contact, investigation, tail-wag, paw/muzzle, and change, which had high positive factor loadings on PCA1 (Table 4) and three behaviors in this group were negatively related to approach, which had moderately high negative factor loadings on PCA 1. These correlations suggest that a marmot that approaches the mirror early in the run is also likely to make nose contact, paw the image, and move between the front and back halves of the arena while investigating it. This pattern is very similar to axis II of the LTA groupings and indicates that these behaviors characterize the bold animals. PCA 2 is characterized by animals spending time in the back half of the arena, delaying or avoiding nose contact with the image, and approaching the image late in the run. These characteristics are also prominent in animals scoring high on axis I of LTA and indicate that these behaviors characterize the shy animals. Thus, animals that avoid contact with their image are likely to spend most of their time in the back half of the arena.

The behaviors loading on PCA 1 and PCA 2 are generally similar among the three age groups (Table 4). We suggest that the first two axes represent fundamental behavior common to all age groups. Essentially, a marmot responds to an image either by being bold or shy. The bold response is associated with "confidence"; thus the bold marmot feeds, investigates, and moves around the arena. On the other hand, the shy marmot appears to lack "confidence" and does not engage in these activities and remains distant from the image.

PCA axes 3 to 5 are much more diverse and there is little similarity among age groups. For example, on PCA 3, yearlings have high scores for lunge and conflict, young have high orientation toward the image associated with eating, and adults have high orientation toward the image associated with lie flat (Table 4). We interpret these axes to represent age-related differences in behavior. These axes are also largely non-interpretable and do not add much to the variance explained.

Comparing Tables 4 and 5 demonstrates the interpretative value of choosing two groups in the LTA analysis. Note that in PCA 3, yearlings are characterized by conflict and lunging at the image and on PCA 4, yearlings face the image and chirp. Both these axes represent shy behavior, which may be aggressive with some

Table 3.

Correlations among adult behaviors that exceed 0.50.

	Investigation	Tail-wag	Paw/muzzle	Front half	Change	Approach	< 30 cm	Back half	Orient toward
Nose contact	0.72	0.56	0.71	0.52	0.70	– 0.71	0.51		
Investigation		0.61	0.60		0.81	– 0.52			
Tail-wag			0.57		0.58				
Paw/muzzle					0.62				
Front half					0.52			– 0.57	
Change						– 0.54			
Eat					0.56				
Orient away									– 0.57

Table 4.

Summary of factor loadings for the first five PCA factors extracted from young (YG), yearling (YR), and adult (AD) yellow-bellied marmots. Based on V_{max} rotation.

	PCA Axes														
	1			2			3			4			5		
	YG	YR	AD	YG	YR	AD	YG	YR	AD	YG	YR	AD	YG	YR	AD
Behaviors															
Investigation	0.8	0.9	0.8							– 0.4					0.3
Nose	0.7	0.8	0.8	– 0.5	– 0.3					– 0.3		0.4			0.3
Pawing	0.8	0.8	0.8												
Tail-wag	0.8	0.7	0.8												
Change	0.9	0.9	0.9							– 0.3					0.4
Front	0.5	0.5	0.4	– 0.6	– 0.8	– 0.8									0.3
Back				0.9	0.9	0.9						– 0.4			
<30 cm	0.4	0.3		– 0.6								0.9	– 0.3		
Approach	– 0.4	– 0.7	– 0.5	0.6	0.5	0.3									– 0.5
Eat	0.5		0.3				0.3			– 0.3					0.8
Orient toward							0.9		0.9		0.9				
Orient away	0.5	0.6	0.3				– 0.7		– 0.8	– 0.4	– 0.5				
Chirp		– 0.3								0.8	0.6			– 0.4	
Lying														0.8	
Lye flat					– 0.4				0.3					0.6	– 0.3
Lunge								0.9							
Conflict								0.8					0.8		
Retreat													0.7		
Chatter															
Groom															
Eigenvalue	4.2	4.7	4.1	2.4	2.0	1.7	1.5	1.6	1.7	1.5	1.5	1.5	1.4	1.3	1.4
% Variance	21	24	21	12	10	8	8	8	8	8	8	8	7	7	7
Cummulative %	21	24	21	33	34	29	41	42	37	49	50	45	56	57	52

Table 5.

Scores of major behaviors for pure type profiles for LTA analyses set to produce two axes for young and yearlings. Scores that are underlined are those that had major effects for determining that axis.

	Young		Yearlings	
	I	II	I	II
Nose contact	4.3	0.1	0.7	5.3
Paw/muzzle	1.5	0	< 0.1	2.3
Eat	3.4	1.9	1.6	3.5
Investigation	3.6	0.4	0.4	4.9
Front half	5.7	1.2	3.7	8.8
Back half	5.9	9.4	6.8	5.4
Change	3.2	0.6	1.0	4.6
Orient toward	8.7	8.5	8.9	8.7
Orient away	7.0	4.2	2.9	7.6
Chirp	0.9	3.1	3.5	0.2
Approach	3.1	9.6	8.3	1.3

submissive elements (e.g., conflict) and are incorporated into axis I of the LTA (Table 5).

Age related changes in behavior

The DFA discriminated among young, yearlings, and adults. Six behaviors entered the model in the following order: lying, under 30 cm, chirping, back half, conflict, and self-groom. Only the group centroids differed; young and yearlings were most similar and adults and young were least similar. Correct classification of individuals was very poor and averaged less than 50%. Poor classification is not unexpected given the similarity in behaviors on PCA axes I and II (Table 4). Additional evidence supports that behavior shifts with age.

If we assume that there is equal probability that the high loading score of a young can occur on either LTA axis I or axis II, we can test the null hypothesis that there is no difference in the number of bold and shy young. The hypothesis is rejected (males: $\chi^2 = 9.3$, $P < 0.005$; females: $\chi^2 = 7.9$, $P < 0.005$); there are more-bold phenotypes than expected (Table 6). There is no difference between the sexes ($G = 0.05$, $P > 0.5$) in the distribution of behavioral phenotypes (Table 6). There were four repeat runs on young; three did not change group designation and one changed from shy to bold.

The distribution of behavioral phenotypes differs significantly between young and yearlings ($G = 19.9$, $P < 0.001$) and young and adults ($G = 28.7$, $P < 0.001$). There are more shy than bold yearlings (Table 6, $\chi^2 = 4.94$, $0.05 > P > 0.025$) and more shy than bold adults ($\chi^2 = 12.2$, $P < 0.001$). However, the distribution of behavioral phenotypes does not differ between yearlings and adults ($G = 1.58$, $P > 0.1$). The distribution of behavioral phenotypes of yearlings differs between the sexes ($G = 3.6$, $P = 0.06$); males are more likely to be shy and females are just as likely to be bold as shy (Table 6). Although there is a tendency for a greater propor-

Table 6.

Number of bold and shy phenotypes for the three age classes of yellow-bellied marmots derived from LTA for two groups. M = males, F = females. Group 1 is the bold group for young, but the shy group for yearlings and adults. Group 2 is the bold group for yearlings and adults.

	Young			Yearlings			Adults		
	M	F	Total	M	F	Total	M	F	Total
Bold	46	45	91	18	24	42	13	11	24
Shy	21	22	43	40	25	65	22	33	55

tion of female than of male adults to be shy, the difference between the sexes is not significant ($G = 1.35$, $P > 0.1$).

We hypothesized that the change in the distribution of behavioral phenotypes from predominantly bold in young to predominantly shy in yearlings and adults occurred because some young changed behavioral phenotypes as yearlings. We tested this hypothesis by repeating the MIS run of 56 young as yearlings. Half of the young changed their behavioral phenotypes. There was no difference between the sexes in the proportion changing behavioral phenotypes ($G = 1.8$, $P > 0.1$). Two males and two females changed from shy to bold and 11 males and 13 females changed from bold to shy; there was no difference between the sexes in the pattern of change ($G = 0.02$, $P > 0.5$). Each sex changed from bold to shy more frequently than would be expected if change of behavioral phenotype was random (males: $\chi^2 = 6.2$, $0.025 > P > 0.01$; females: $\chi^2 = 8.1$, $P < 0.005$).

Twenty-two yearlings were re-run as adults; two males and two females changed from group 2 (bold) to group 1 (shy) and one female barely changed from group 1 to group 2. Given that 50% of the young changed behavioral phenotypes, we tested whether the 22.7% of the yearlings that changed behavioral phenotype differed significantly from the expected 50% ($\chi^2 = 6.5$, $0.025 > P > 0.01$); fewer yearlings changed behavioral phenotypes than expected. Thus, most of the shift in behavioral phenotypes from bold young to shy adults occurred when the marmots were yearlings.

Reliability and predictability

There were 113 replicate runs on 35 adult marmots. A modal group assignment was established for 31 (89%) of the animals. When all runs were considered, 76.1% were correct, e.g., agreed with the modal group to which the animal was assigned. When all replicates within a year were excluded, reliability was 80.2%. If there is no biological basis to the groupings, then by chance alone reliability should be 50%. In effect, any run of an animal has about a 75% chance of placing the animal in the correct group.

The first run predicted a marmot's modal group in 29 of 31 cases for a predictability of 94%. If the four cases for which a modal group could not be determined are added to the incorrect cases, predictability decreases to 82.9%. Considering the results from the reliability and predictability analyses, we conclude conservatively that there is a 75% probability that a MIS run correctly identifies an individual's behavioral phenotype.

Of the seven changes in the group membership between years by adult females, five were minor shifts in loading scores by animals located in the mid range of the axis, where a small change in score caused a shift in the group membership. No female with a loading score > 0.751 on an axis changed group membership and only three female adults with scores > 0.6 changed groups. Therefore, one can be confident that for the 30 adult females with scores > 0.6 on LTA axis I, the probability that the behavioral phenotype is correct is 90%. Thus the extremes of the behavioral continuum were phenotypically more stable than the middle, a condition that may reflect the presence of inflexible phenotypes at the extremes and flexible phenotypes in the middle of the continuum (Wilson et al. 1994).

Because females might change LTA groups as a consequence of changes in their social environment, we looked at the relationship of age, reproductive status (weaned a litter or not), number of non-kin adult females present, increase or decrease in non-kin females, number of female kin present, and increase or decrease in female kin, with LTA group membership. Only one variable, number of non-kin adult females, entered the stepwise discriminant analysis model (P = 0.061). A group 1 (shy) female was more likely to be associated with non-kin adult females. However, classification of females into groups was poor; 21 of the 58 runs were misclassified and the overall error rate was 0.36. We repeated the analysis with one additional variable, whether the female was a new immigrant or a resident who was born there or who was a former immigrant. No variable entered the stepwise discriminant analysis model. Twenty-three of the 58 runs were misclassified and the overall error rate was 0.38. We conclude that the variables that we had available were inadequate to explain change in the group classification. Two important variables that were unavailable were degree of home range overlap and the frequency and nature of social interactions.

We looked for correlations among the seven social-environment variables in order to determine which factors might be more important or independent of behavioral phenotype. One such factor was age. Older females were more likely to be reproductive regardless of group membership (r varied from 0.368 to 0.643; P varied from 0.02 to 0.0039) and an increase or decrease in the number of female kin was more likely to occur with older females independent of group membership (Group 1, r = 0.36, P = 0.02; Group 2, r = 0.56, P = 0.03). Also there was a trend for a female to be non-reproductive as the number of non-kin females increased (r varied from – 0.21 to – 0.31, P varied from 0.055 to 0.17). This result is consistent with the suppression of reproduction in a single female when she lives next to a matriline of two or more females (Armitage 1986a, 1998) and with agonistic behavior directed to non-kin preferentially over kin (Armitage & Johns 1982).

Heritability

The regression of the offspring MIS score against the mother's score was marginally significant (F = 2.96, P = 0.09) and the amount of variation (R^2) explained by the regression was 2.7%. The regression of offspring score against the father's score did not explain any of the variation (F = 0.09, P = 0.77). The regressions were rerun using mean litter scores. There was no significant relationship between mean litter score and mother's score (F = 1.61, P = 0.22, R^2 = 2.5%) or father's score (F = 0.27, P = 0.61, R^2 = 0.0%). A two-level nested ANOVA (father, mother, offspring) gave heritability estimates of 0 for fathers, 1.55 for mothers, and 0.78 for mother +

father. These data suggest a maternal effect, which could be environmental as offspring always associate with their mother and usually not with their father.

Inheritance of behavioral phenotypes

Each individual marmot received a unique loading score based on its behaviors during MIS, which we generalized into two behavioral phenotypes, bold and shy. Here we address the question does a marmot inherit its behavioral phenotype or is its behavioral phenotype a result of experience? In one sense, the fundamental behaviors shared by all age groups are inherited. That is, those behaviors that load on PCA axes 1 and 2 (Table 4) likely have a genetic basis. However, our results suggest that the combination of behaviors that produces an individual's behavioral phenotype is strongly influenced by experience.

Three major lines of evidence support this interpretation. First, there is no relationship between MIS scores of fathers and offspring and only a weak relationship between the scores of mothers and offspring. The low R^2 further supports a minimal genetic contribution to individual behavioral phenotypes. Second, the DFA group centroids differ among the three age groups. Compared to adults, young are relatively uniform behaviorally (Nowicki & Armitage 1979). Young are bolder than either yearlings or adults. Agonistic behavior among littermates has never been observed (Armitage 1982). Young interact only amicably with their mothers and other members of the maternal matriline (Rayor & Armitage 1991). By contrast, yearlings frequently interact agonistically with adult members of a matriline (Armitage & Johns 1982, Armitage 1986a), although agonistic behavior among yearlings is rarely observed. In this study, agonistic behavior accounted for only 1.4% and 1.8% of the social behaviors among male and female yearlings, respectively. Both young and yearlings play (Nowicki & Armitage 1979, Jamieson & Armitage 1987). Play terminates about mid summer of the yearling year and virtually never occurs among adults (Armitage 1962). Play was suggested to function to socially integrate individual behavioral traits (Nowicki & Armitage 1979) and the motor patterns are similar to those observed among adults engaged in agonistic behavior (Jamieson & Armitage 1987). We suggest that play is a major environmental experience that shapes the behavioral phenotypes of developing marmots primarily by incorporating elements of agonistic behavior in a context (play) that is not harmful. Analysis of play indicated that play was more significant for males than females; in yearlings more males are shy than expected by chance whereas females are evenly distributed between the bold and shy groups (Table 6).

Third, developmental/experiential changes are indicated by the large number of young that have different phenotypes as yearlings and the smaller number of yearlings that change behavioral phenotypes as adults. Presumably these changes are a consequence of play and other social experiences. The fewer changes of behavioral phenotypes by yearlings to adults than by young to yearlings could be expected as animals become mature. Yearlings become mature and can reproduce as 2-year-olds following their second hibernation (Schwartz et al. 1998). Thus the distribution of individuals in the two behavioral phenotypes did not differ between yearlings and adults (Table 6). However, there is a trend for increasing numbers of shy phenotypes among females from young (32.8%) to yearlings (51.0%) to adults (75%). The difference between young and adults ($G = 19.6$, $P < 0.001$) and between yearlings and adults ($G = 5.78$, $0.005 > P > 0.001$) is highly significant.

To summarize, differences in the DFA centroids of the three age groups, the very low to no heritability of MIS scores, and the shifting from predominantly bold to predominantly shy phenotypes with age support a strong environmental component in the formation of behavioral phenotypes. Similarly, an ontogenetic component was proposed as a major contributor to the expression of behavioral variability in *M. marmota* (PERRIN et al. 1993).

Behavioral phenotypes and social behavior

The previous section suggests that social experiences have a prominent role in determining behavioral phenotypes. Therefore, we examined the relationships between behavioral phenotype and rates of social behavior in yearlings. Initially we ranked the 44 yearlings based on their loading scores on LTA axis I (shy) from high to low. We than tested whether males and females were distributed equally throughout the rankings and determined that the sexes were unequally distributed ($G = 4.8$, $0.05 > P > 0.025$); more males occurred in the upper than in the lower half and more females occurred in the lower than in the upper half of the axis. Because characteristics of play differ between males and females (JAMIESON & ARMITAGE 1987), we tested whether the frequency of play differed between the sexes. Males had significantly higher rates of play (number/h/animal) than females (0.21 vs 0.06, $t = 3.8$, $df = 25$, $P < 0.001$). Because these two differences between the sexes could bias the analysis of the relationship between social behavior and behavioral phenotypes, we analyzed each sex separately.

Each yearling was ranked from high values to low values by its score on LTA axis I (shy) and its rates of amicable, agonistic, and play behavior. For the 17 female yearlings, all rankings were significant (play: $r_s = 0.78$, $P < 0.01$; agonistic behavior: $r_s = 0.47$, $P = 0.05$; amicable behavior: $r_s = 0.48$, $P = 0.05$). The higher a female ranked on axis I (i.e., the more "shy" she was), the higher her rate of social interactions. For the 27 male yearlings, only play was significant (play: $r_s = 0.33$, $P = 0.05$; agonistic behavior: $r_s = 0.11$, $P > 0.05$; amicable behavior: $r_s = 0.15$, $P > 0.05$). Play behavior was more frequent the higher the male ranked on the "shy" axis. Thus, play is the behavior most strongly related to behavioral phenotype in both sexes. The relationship is correlational and does not indicate cause and effect. However, the relationship is consistent with the suggestion that play is a major experience that shapes behavioral phenotypes.

Why male and female yearlings differ in their relationships between social behaviors and behavioral phenotypes is unclear. Male yearlings encounter considerable agonistic behavior from adult males (ARMITAGE & JOHNS 1982) and frequently spend much of their time in areas of their habitat that are distant from the resident adult male (ARMITAGE 1974), which probably changes the nature of social contacts with adults such that when such contacts occur, all male behavioral phenotypes respond similarly. In general, mean male yearling space-use overlap with adults is 17.9 ± 2.8%.

By contrast, space-use overlap of female yearlings with adults (mean = 32.1 ± 2.9%) is significantly greater than that of male yearlings ($t = 3.1$, $0.01 > P > 0.001$), which increases the likelihood for social interactions whose rates would more likely be correlated with the behavioral phenotype. Female yearlings have significantly higher rates of amicable behavior with adults than do male yearlings (0.07 vs 0.03, $t = 2.06$, $P = 0.05$) and these rates are correlated with behavioral phenotype in

female yearlings (r_s = 0.38, P = 0.1) but not in male yearlings (r_s = 0.20, P > 0.3). The difference in rates reflects proximity to adults, not a greater propensity to interact socially as male yearlings have higher overall rates of social behavior than female yearlings (0.29 vs 0.14, t = 2.47, 0.02 > P > 0.01).

Behavioral phenotypes and life-history traits of females

The rankings of individual adult females on axes I and II are negatively correlated (r_s = – 0.961, P < 0.001). Because rankings vary, both axes were analyzed, but results will be presented only for axis I as no new relationships were revealed by the analysis of axis II. Two DFA analyses were performed. One looked for characters that distinguished group 1 (shy) animals from group 2 (bold) individuals and the other looked for characters that distinguished animals on the upper half (more-shy) from those on the lower half (more-bold) of axis I. These analyses produced three classes of females: group 1 (shy), group 2 (bold), and the upper half of axis I (more-shy). A correlation matrix revealed correlations among the eight life-history variables (Table 7).

Table 7.

Correlation matrix for eight life-history variables for adult females (n = 44) scored as members of group 1 (shy group) or that ranked in the upper half of axis I (more-shy phenotypes). Only statistically significant correlations are presented. Those relationships that were also significant for group 2 females (bold phenotypes) are marked with an *. Values for the upper half of axis I are underlined. Bold = r values, italics = P. Kin, non-kin, and recruits refer to females only.

	Number					
	Young weaned	Daughters	2-yr-old recruits	Kin	Non-kin	Residency status
Age	**0.551***	**0.511***	**0.361**	**– 0.280**		
	0.0001	*0.0001*	*0.005*	*0.03*		
	0.553	**0.491**		**– 0.346**		**– 0.342**
	0.0001	*0.001*		*0.02*		*0.03*
Number of young weaned		**0.810***	**0.525***			
		0.0001	*0.0001*			
		0.813	**0.420**			
		0.0001	*0.006*			
Number of daughters			**0.520***			
			0.0001			
			0.422			
			0.005			
Number of kin						**0.509***
						0.0001
						0.499
						0.0008
Coloniality					**– 0.263**	
					0.05	
					– 0.363	
					0.02	

Nine significant relationships occurred among the life history variables for shy females; six of these were related to reproductive success (Table 7). Older females weaned more young, more daughters, and more 2-year-old recruits; the more young that were weaned resulted in more daughters and more 2-year-old recruits. The same pattern prevailed for bold females except that age was not related to the number of 2-year-old recruits. When the analysis was restricted to females that ranked in the upper half of axis I, age was unrelated to the number of 2-year-old recruits, but was related to the other reproductive success variables.

Given that sex ratio at weaning averages 1:1 (ARMITAGE 1987a), the weaning of more young would naturally lead to weaning more daughters and the more daughters that are produced, the more likely the recruitment of 2-year-old daughters will occur (ARMITAGE 1984, 1987a). The correlation between age and litter size reported here differs from that reported by SCHWARTZ et al. (1998) who reported a non-significant ($P = 0.15$) trend. We suggest that the relationship between age and litter size may be biologically significant and this suggestion is supported by our results (Table 7). A female that was a recruit was associated with a greater number of female kin in all three classes of females. This association is not surprising. By definition, a recruit is an individual that becomes resident in her natal habitat patch and recruitment rarely occurs unless kin are present (ARMITAGE 1986b, 1996b). These correlations that occurred among all classes of females represent basic marmot biology and may be considered to be independent of individual behavioral phenotypes.

The remaining correlations are specific to one or two of the phenotypic classes. For group 1 (= shy) females and females ranked in the upper half of axis I, the degree of coloniality was negatively correlated with the number of female non-kin, which suggests that the more likely a female is associated with other females, the less likely she is associated with non-kin. This relationship is consistent with the organization of marmot social groups being based on closely-related females (ARMITAGE 1991) and that an increase in the number of females on a habitat patch occurs primarily by mothers recruiting their daughters into the local population (ARMITAGE 1996a). Only for shy females was age positively correlated with the number of 2-year-old recruits. In part, this relationship reflects the correlation between age and number of daughters weaned (Table 7), but there is no obvious explanation why the correlation with age and 2-year-old recruits occurred only for group 1 females. This difference may be a function of sample size; 2-year-old recruitment occurred 11 times in the shy group and only three times in the bold group; thus there was a much larger sample for relating recruitment to age in group 1, the shy group.

For females in the upper half of axis I (more-shy), age was negatively correlated with residency status (recruit or immigrant); younger females were more likely to be recruits. This correlation also is consistent with recruitment of daughters at age two (ARMITAGE 1986b). This relationship would be expected to occur in all phenotypic classes; therefore, we looked at female yearlings to determine if bold or shy individuals were more likely to become recruits. Of 51 yearlings, 29 were classified as shy and 23 became recruits, whereas only six of the 22 bold yearlings became recruits ($G = 14.4$, $P < 0.001$). Thus, more-shy recruits would be expected in the upper half of axis I, which would provide a sample size adequate for testing the age:residency relationship and there would be too few young individuals in group 2 for analysis. In fact, there were thirteen 2-year-old females in the shy group and 6 in the bold group.

One factor, number of female non-kin ($P = 0.14$), entered the stepwise DFA of axis I. More non-kin females were present with shy females. Discrimination was poor, 30 of 84 were misclassified and the overall error rate was 0.333. Three traits

entered the DFA to distinguish females on the upper half of the axis from those on the lower half of the axis. More daughters occurred in the upper half ($P = 0.006$), the number of 2-year-old recruits was slightly greater in the upper half ($P = 0.15$), and about twice as many animals became residents as recruits rather than as immigrants in the upper half ($P = 0.004$). Discrimination was better, but poor; 20 of 84 were misclassified and the overall error rate was 0.238.

Three factors entered the DFA analysis of axis II: number of female non-kin ($P = 0.16$), number of daughters ($P = 0.14$), and residency status ($P = 0.22$). Discrimination was poor; 28 of 83 were misclassified and the overall error rate was 0.30. There were more immigrants and more female non-kin with group 1 females and group 1 females produced more daughters. A close inspection of error rates revealed that they were much lower for individuals classified on the lower half of axis I (0.119 vs 0.357) and were lower for bold females (0.21 to 0.269) than for shy females (0.39 to 0.397). This pattern of error rate indicates that females whose behavioral phenotypes are more-bold (rank in the lower half of axis I) are more consistent in their social/demographic patterns. Thus, the marmots tending toward shy are more variable in their social/demographic patterns.

Several life-history traits had consistent patterns in the DFAs. Shy females were associated with a larger number of female non-kin, produced more daughters, and were more likely to be immigrants (31 in the shy group, 16 in the bold group). Because immigrants initially are associated with unrelated females, the association of shy females with non-kin and immigrant status is consistent with settlement patterns in marmot populations (Armitage 1991). However, when axis I was divided into halves, more immigrants were brought into the lower half. Of the 17 individuals shifted from the shy group to the bottom half of axis I, 13 were immigrants. This pattern indicates that many immigrants scored in the mid range of the axis such that their contribution to the DFA depended on how the axes were divided.

Behavioral phenotypes and age of first reproduction

Reproductive suppression occurs widely among species of marmots (Armitage 1996b). In yellow-bellied marmots, young females are far less likely to reproduce when living in the same matriline with older females (Armitage 1998, 2003a). Reproductive suppression occurs as a delay in the age of first reproduction; there is no evidence that a female is suppressed subsequent to her first reproduction (Armitage 2003a). Therefore, we examined whether age of first reproduction was related to behavioral phenotype of 22 females 2-years-old or older that had not previously reproduced; only six weaned litters. Reproduction was more likely if no older female was present ($G = 6.4$, $0.025 > P > 0.01$). Reproductive success did not differ between females ranked in the upper or lower half of axis I ($G = 0.21$, $P > 0.5$). For those females that failed to reproduce when an older female was present, it made no difference whether the adult female was in the shy group or the bold group ($\chi^2 = 0.02$, $P > 0.5$). Thus, reproductive suppression is unrelated to behavioral phenotype and apparently is a function of age dominance.

Behavioral phenotypes and coloniality

We hypothesized that there would be no difference in the distribution of bold and shy females among the three categories of coloniality. The hypothesis was not

rejected (G = 3.3, $P > 0.1$). There was no association of a behavioral phenotype with a particular category of coloniality. Likewise, SVENDSEN (1974) reported that marmots from non-colonial sites were distributed among his three behavioral phenotypes.

Behavioral phenotypes and recruitment

We noted previously that female yearlings with shy phenotypes were more likely to be recruits whereas female yearlings with bold phenotypes were more likely to disperse. Recruitment is more likely when the mother is present (Table 8, G = 14.7, $P < 0.001$). Although sample sizes are small, there are clear trends in the likelihood that a yearling female will be recruited when her mother is absent. Recruitment is highly unlikely even when other kin are present (Table 8, G = 1.3, $P > 0.1$). However, when both the mother and non-kin adult females are present, the yearling female is more likely to be a recruit, but the trend is not statistically significant (Table 8, $\chi^2 = 1.1$, $P > 0.1$). Although the presence of the mother is critical to recruitment, shy yearling females are more likely than bold yearlings to become recruits when the mother is absent (Table 8, G = 3.95, $P < 0.05$). This result suggests that the behavioral phenotypes of both the mother and the yearling affect yearling recruitment. All bold adult females recruited yearlings regardless of their behavioral phenotype; nearly all shy yearlings were recruited by shy adult females, but only 1/3 of the bold yearlings were recruited (Table 9, G = 16.2, $P = 0.001$).

Table 8.

Recruitment of yearling females in relationship to the presence or absence of the mother or other kin or non-kin adult females and the behavioral phenotype of the yearlings. Group 1 = shy; Group 2 = bold.

	Mother Absent						
	Mother		Other kin		Yearlings		Mother and non-kin females present
Yearlings	Absent	Present	Present	Absent	Group 1	Group 2	
Recruit	4	26	1	1	2	0	9
Disperse	13	7	2	13	5	10	5

Table 9.

The relationship between behavioral phenotype of mother and yearling daughters and recruitment when behavioral phenotype of both groups was known.

	Mother: Shy Group Yearling		Mother: Bold Group Yearling	
	Shy	Bold	Shy	Bold
Recruit	13	4	5	2
Disperse	1	8	0	0

Behavioral phenotypes and life-history traits of males

Social status of adult males was classified in one of five categories: (1) territorial-colonial (associated with a colony of females), (2) peripheral-colonial (living adjacent to a colony of females), (3) transient (moving through a habitat patch), (4) resident-non-colonial (usually living with one female), and (5) solitary (living alone). The analysis of axis I revealed that for shy males social status was negatively correlated with the number of young produced ($r = -0.45$, $P = 0.01$); territorial-colonial males produced more young. Discriminant function analysis (DFA) identified two significant factors, number of females ($P = 0.02$) and social status ($P = 0.07$). More females were associated with shy males and there were more territorial-colonial males in the shy group. However, 15 of 49 males were misclassified and nine were borderline. The error rate for the shy group was 0.29; for the bold group, 0.33; total rate was 0.31.

In the analysis of axis II, age of bold males was negatively correlated with social status ($r = -0.432$, $P = 0.05$) and positively correlated with the number of young ($r = 0.464$, $P = 0.03$). Older males were more likely to be territorial-colonial and produced more young. The social status of shy (group 1) males was negatively correlated with the number of young ($r = -0.485$, $P = 0.009$). Territorial-colonial males produced more young. The DFA identified two major factors, age ($P = 0.14$) and number of young ($P = 0.18$); bold males were older and shy males had more young. On average, shy males produced 1.37 ± 0.44 SE young and bold males, 0.47 ± 0.33 SE young ($t = 1.64$, $P = 0.1$).

The analyses of the differences between males on the lower or upper half of axis I revealed that the number of young was negatively correlated with social status of males on the upper half of the axis ($r = -0.505$, $P = 0.01$). Colonial-territorial males produced more young. Social status of males was negatively correlated with age of males on the lower half of axis I ($r = -0.397$, $P = 0.055$). Older males were more likely to be colonial-territorial, which is consistent with the DFA analysis of axis II. This result suggests that bold males take longer to achieve colonial-territorial status than the shy males.

The DFA analysis identified the number of females ($P = 0.1$) as the main discriminator. More females were associated with males on the upper half of the axis. Discrimination was poor; 19 of 49 males were misclassified and there were 13 borderline cases. The error rate was 0.375 for both the upper and lower halves.

For all analyses, the number of females present was positively correlated with the number of males present (r varied from 0.517 to 0.595, P varied from 0.003 to 0.009). More females occur on the larger habitat patches (Svendsen 1974, Armitage & Schwartz 2000) and it is not surprising that higher numbers of females would attract more males, either as residents with independent territories, transients, or peripheral-colonial residents, who must seek out and obtain residency with females in order to achieve reproductive success (Armitage 1974, 1998). This demographic pattern partially explains the higher production of young by territorial-colonial males who often are associated with more females, which, on average, results in the production of more young. This result is consistent with an earlier report that male reproductive success increased as harem size increased (Armitage 1986a). In conclusion, shy males are more likely to be territorial-colonial and achieve high reproductive success by producing more young.

Behavioral phenotypes and LRS of females

LRS (lifetime reproductive success) was obtained for 28 female yellow-bellied marmots. Because analyses of both axes tend to produce similar results, this analysis was limited to comparing the females in the upper half (more-bold) with those in the lower half (more-shy) of axis II. In order to determine to what degree LRS is a consequence of demography or behavioral phenotype, demographic factors common to both behavioral phenotypes must be ascertained. Significant relationships among the demographic variables characterized both phenotypic groups (Table 10). The longer a female was resident, the more years she was reproductive and the more young, daughters, and recruits she produced. Not unexpectedly, the number of years reproductive was significantly related to the number of young, the number of daughters, the number of yearling recruits, and the number of 2-year-old recruits (Table 10). The more young that were produced, the more daughters, yearling recruits, and 2-year-old recruits were produced. Thus, the length of time a female is resident appears to drive reproductive success independently of behavioral phenotype. However, for 11 of the 13 correlations among the demographic variables, the correlations were higher for the more-shy females and sometimes were much higher (e.g., Table 10; number of years reproductive vs number of yearling recruits). This pattern suggests that the measures of reproductive success were strongly driven by demographic factors in the more-shy females, but were more strongly influenced by the behavioral phenotype of the more-bold females.

The very high correlation between the number of yearling female recruits and number of 2-year-old recruits for more-bold females indicates that virtually all yearling recruits were retained and that more-bold and more-shy females differed in recruitment. Although more-bold females produced fewer daughters, they

Table 10.

Correlations among demographic variables during the lifetime of adult female yellow-bellied marmots; r for upper half of axis 2 (more-bold) in bold type, *P* = italics.

	Years reproductive	Young produced	Number daughters produced	Yearling recruits	2-year-old recruits
Number of years resident	**0.86**	**0.78**	**0.67**	**0.56**	**0.54**
	0.0001	*0.0099*	*0.009*	*0.04*	*0.05*
	0.87	0.89	0.89	0.80	0.70
	0.0001	*0.0001*	*0.0001*	*0.0006*	*0.005*
Number years reproductive		**0.93**	**0.81**	**0.57**	**0.52**
		0.001	*0.004*	*0.04*	*0.06*
		0.98	0.91	0.89	0.61
		0.001	*0.0001*	*0.0002*	*0.02*
Number of young produced			**0.91**	**0.70**	**0.75**
			0.0001	*0.005*	*0.002*
			0.98	0.91	0.73
			0.0001	*0.0001*	*0.003*
Number of yearling recruits					**0.99**
					0.0001
					0.84
					0.0002

recruited more yearlings (G = 4.4, 0.05 > *P* > 0.02) and 2-year-old females (G = 6.1, 0.025 > *P* > 0.01) than did more-shy females (Table 11). The rate of recruitment of 2-year-olds/daughter weaned was 0.18 for more-shy females and 0.46 for more-bold females. This result for LRS is consistent with the earlier analysis of annual reproductive success in which bold females recruited all yearlings (Table 9). These results agree with previous reports that females designated as social, recruited more yearlings than those characterized as asocial (ARMITAGE 1984) or those categorized as "sociable" as one of 3 MIS groups produced more yearling and 2-year-old recruits than females categorized as "approach" or "avoiders" (ARMITAGE 1986b). The females categorized as "social" or "sociable" are roughly comparable to the bold females of this study and those designated as "asocial" or "approach" are comparable to the shy group. The shy group also includes some individuals that were classified as "avoiders" in the earlier study.

The DFA analysis was re-run with the reproductive variables that were highly correlated on both halves of axis II removed in order to look for relationships that were more strongly related to behavioral phenotypes. Bold females that were recruits were more likely to be associated with female kin, a pattern consistent with the formation of matrilines (ARMITAGE 1998). Recruitment was more likely when more kin were present, but immigration was more likely when fewer non-kin were present (Table 12). For both bold and shy females, the number of 2-year-old recruits was directly related to the number of years of residency; this relationship was stronger in the shy females (Table 12) and is consistent with the previous analysis that the more-bold females recruit more 2-year-old daughters (Table 11); i.e., recruitment depends less on length of residency in bold females.

For both groups of females, the total number of female kin was significantly correlated with the number of female kin present at residency (Table 12). This relationship suggests that the initial conditions at residency determined the number of kin with whom a female associated and subsequent mortality and recruitment had only minor effects on number of kin associates. The number of female kin at residency was negatively correlated with the number of non-kin females present for bold females (Table 12); non-kin were unlikely to be present when kin were present. For this group of bold females, kin were present when seven females began residency and non-kin were present when six females became residents. Only once were both kin and non-kin present when residency began. By contrast, for shy females, the number of non-kin present at the onset of residency was positively correlated with the number of non-kin present. For six females, both kin and non-kin were present when residency occurred. More kin (19) than non-kin (10) were asso-

Table 11.

Number of female recruits by lower half (more-shy) and upper half (more-bold) adult females on axis II during their lifetime. There was no significant difference in the number of years of residency between females in the two halves ($\chi^2 = 0.46$, $P = 0.5$).

	More-bold females		More-shy females	
	Yearlings	2-year-olds	Yearlings	2-year-olds
Recruited	23	21	20	12
Not recruited	23	2	46	8

ciated with the onset of residency in the bold group and more non-kin (18) than kin (7) were associated with the onset of residency in the shy group; this difference is significant (G = 7.8, P = 0.005). Apparently the more-bold females of the upper half are more likely to become residents when kin or no other females are present whereas the more-shy females of the lower group can obtain residency even in the presence of hostile non-kin (ARMITAGE & JOHNS 1982, ARMITAGE 1987b).

Longer residency of shy females was correlated with the presence of more kin, but that of bold females, with more non-kin (Table 12). These correlations probably represent both the initial conditions of residency and demographic trends as the total number of kin associated with the females is greater for bold females (56 vs 44) and the total number of non-kin is greater for shy females (37 vs 55); this difference is significant (G = 48, 0.05 > P > 0.025). We hypothesize that over time, bold females are unable to exclude non-kin from becoming resident whereas shy females can exclude non-kin immigrants while recruiting kin.

The DFA identified five traits that distinguished upper (= bold) from lower (= shy) females. The number of non-kin females at residency was greater in the shy group (P = 0.02) and a female immigrant was more likely in the bold group (P = 0.03). Female kin were more likely to be present when bold females initiated residency (P = 0.15) and more 2-year-old recruits (P = 0.19) and more female kin (P = 0.15) were present with bold females. Only one misclassification of the 28 females occurred. The error rate for the lower half was 0, for the upper half, 0.071, and overall, 0.036.

To summarize, LRS of all females was strongly related to the number of years of residency which affected the number of years of reproduction, the production of

Table 12.

Correlation matrix for seven life-history variables for adult females ranked as more-bold (upper half) or more-shy (lower half) on axis II. Only statistically significant correlations are presented. B = bold, S = shy. Bold = r values, italics = P values. Kin, non-kin, and 2-year-old marmots refer only to females.

		Number				
					Present at Residency	
		Kin	Non-kin	2-year-olds	Kin	Non-kin
Immigrant or recruit	B	**0.671** *0.009*			**0.763** *0.002*	**– 0.691** *0.006*
Number of years resident	S	**0.586** *0.03*		**0.701** *0.005*		
	B		**0.529** *0.05*	**0.537** *0.05*		
Number of kin	S				**0.693** *0.006*	
	B				**0.749** *0.002*	
Number of non-kin	S					**0.809** *0.006*
Number of kin at residency	B					**– 0.555** *0.04*

young and daughters, and the recruitment of yearling and 2-year-old daughters. These demographic patterns characterize marmot populations. An earlier DFA analysis of recruitment (retention of daughters in their natal locality) indicated that the number of female yearlings produced was the most important variable characterizing successful recruiters and that recruiters were resident for a longer time and produced more young and more daughters (ARMITAGE 1984). The behavioral phenotype impacts the demographic trends mainly by increasing recruitment by the bold females. Thus, recruitment is not as strongly related to demography in the bold females as it is in the shy females. Also, bold females appear to be more strongly associated with kin than the shy females and the shy females apparently cope better with the presence of non-kin females.

Behavioral phenotypes and LRS of males

LRS was obtained for 19 adult males. The males formed two groups, 13 males with loading scores > 0.505 on axis I formed group 1, the shy group, and the remaining six formed group 2, the bold group. For both groups, the number of years territorial-colonial was negatively correlated with the number of years peripheral (shy group: $r = -0.61$, $P = 0.036$; bold group: $r = -0.82$, $P = 0.04$) and positively correlated with the number of young produced (shy group: $r = 0.65$, $P = 0.02$; bold group: $r = 0.92$, $P = 0.01$). The number of young produced was significantly correlated with number of females aged three or older for shy males ($r = 0.88$, $P = 0.0002$). DFA identified the number of years peripheral ($P = 0.06$) as the only factor that discriminated between the two groups. Only one male was misclassified and the overall error rate was 0.042. On average, shy males spent 1 year living peripherally to a colony whereas bold males spent 1.83 years. Although, on average, shy males were territorial-colonial for a longer time than bold males (2.54 year vs 1.6 year) and produced more young (9.96 vs 6.5), neither difference was statistically significant ($t = 0.87$, $P > 0.2$ and $t = 0.80$, $P > 0.4$, respectively). These trends of longer residency and higher production of young by shy males is consistent with the earlier analysis that revealed that territorial-colonial males and shy males produced more young. Variation among males is considerable and production of young is strongly affected by female behavior (ARMITAGE 1998); much larger sample sizes would be needed to clarify the relationship between behavioral phenotype of males and production of young.

When the males on axis I were divided between the lower (more-bold) and upper (more-shy) halves (which moves some shy males into the bold), the production of young was significantly correlated with the number of years a male was territorial-colonial (more-shy: $r = 0.78$, $P = 0.01$; more-bold: $r = 0.67$, $P = 0.05$) and with the number of females aged 3 years or older that were present (more-shy: $r = 0.74$, $P = 0.02$; more-bold: $r = 0.73$, $P = 0.03$). For the entire group of males ($n = 19$), the production of young was highly correlated with the number of 3-year-old or older females ($r = 0.72$, $P < 0.01$). In addition, the number of 3-year-old or older females present was significantly correlated with the number of years a male was territorial-colonial for the more-shy males ($r = 0.67$, $P = 0.05$).

To summarize, male reproductive success strongly depends on the length of residency as a territorial-colonial and the number of females with whom he is associated. The more-shy males have higher LRS because they have a longer residency, which leads to the production of more young. However, not all males of either

group become territorial-colonial. All males disperse, typically as yearlings, from their natal locality and may undergo considerable movement while seeking females (VAN VUREN 1990). Mortality is high; by age three years only about 16% of the yearling males are still alive and no male of known age has lived past age nine (SCHWARTZ et al. 1998). Thus, males that live to age three have a high probability of reproducing regardless of behavioral phenotype. Many males spend one or more years living peripherally to a colony of females (ARMITAGE 1974), but shy males spend less time peripheral than bold males. Finally, male reproductive success is strongly affected by what females do. For example, younger females may be reproductively suppressed by older females (ARMITAGE 2003a), thus decreasing a male's reproductive success regardless of his behavioral phenotype.

GENERAL DISCUSSION AND CONCLUSIONS

Variation in behavioral phenotypes characterizes yellow-bellied marmot populations. An individual marmot's behavioral phenotype seems to be primarily determined by experience. The distribution of behavioral phenotypes changes with age from highly bold in young to mainly shy in adults. Low heritability strongly indicates that behavioral phenotypes are developmental and are formed as a result of experience in which play is postulated to have a major role.

The distribution of phenotypes on the behavioral axes forms a shy-bold continuum. The bold marmots are those that approach the image and make contact. But boldness in this context may not be associated with dominance (WILSON et al. 1993). In MIS the individual being tested controls the stimulus. Thus, a marmot expressing a "sociable" or cohesive stimulus will receive that stimulus in return. An aggressive (shy) marmot presents a "threat" or agonistic stimulus and receives that stimulus from the image. The "social" stimulus may indicate acceptance and the "social" marmot thus makes contact with the image. The contact is very similar to the greeting between members of a matriline (ARMITAGE 1962, 1974, 1987b). The "threat" posture is similar to that observed in the field between two individuals in an agonistic encounter. In the field, one individual eventually turns away and flees the other or one individual attacks the other, or both turn away with no further conflict. Thus there may be a long latent period before the "agonistic" marmot chooses to approach the image. Sometimes a marmot chirps or tooth chatters at another marmot during an agonistic encounter. Interestingly, tooth chatter loaded only on axis I and chirping had a major effect for determining that axis (Table 1). The "social" marmots may be subordinates that express a "social" stimulus to indicate a nonaggressive or affiliative status and to determine if they will be accepted by the other animal. By contrast, the "shy" individual is a dominant who is less likely to be affiliative and who is prepared to be agonistic to the stranger (i.e., the image). Some marmots never approach the image, which suggests avoidance of social contact and possible submissive status. Probably there are subtle signals that are not detected by the human observer but which guide the marmot's responses and determine whether the marmot will behave as a dominant or submissive animal. While it would be interesting to know the dominance status of each individual, what is significant is that phenotypic differences occur and that they are related to fitness.

Thus, more "shy" yearlings became recruits and the more "bold" adult females recruit a greater proportion of female yearlings than "shy" adult females. Over their

lifetimes, "bold" females recruit more daughters than "shy" females, but "shy" females are more likely to become recruits. Thus, a bold phenotype would be fit as a recruiter and a shy phenotype would be fit as a recruit. The differences in fitness at different stages of life history should maintain phenotypic plasticity as a trait and act against genetic fixation of the traits. Recruitment appears to be the major life-history trait related to behavioral phenotypes as other demographic factors that relate reproductive output to residency are independent of behavioral phenotypes.

For males, there is a slight advantage to being "shy" because "shy" males spend more years as territorial-colonial and produce more young. But this advantage is offset in part by the high mortality rate of males (SCHWARTZ et al. 1998) such that nearly any male 3-years-old or older has a very high probability of reproductive success.

For both males and females, mortality appears to be independent of behavioral phenotype. Factors, such as predation (VAN VUREN 2001) and severe weather events (ARMITAGE 1994, SCHWARTZ & ARMITAGE 2002) do not discriminate between behavioral phenotypes and neither phenotype had a longer life span than the other.

Finally, recruitment is affected by kinship. Regardless of behavioral phenotype, a yearling is unlikely to obtain residency if her mother and/or other kin are absent. In effect, the behavioral phenotype interacts with kinship to determine successful recruitment and reproduction.

The evolution of marmot sociality is associated with retention of offspring in their natal group (ARMITAGE 2000). In woodchucks (*M. monax*) affiliative behavior occurs between mother and offspring, but the young disperse or are driven away by their mother and affiliative behavior does not occur among adult females (ARMITAGE 2003b). By contrast, yellow-bellied marmot young remain at home and associate with older kin as yearlings. Affiliative behaviors continue and social bonds are formed with closely-related kin (ARMITAGE 1996a, 1998). These social bonds are based on familiarity; there is no evidence that kin recognition per se occurs in yellow-bellied marmots (ARMITAGE 1987b, 1989). Thus, "shy" marmots are reluctant to affiliate with a stranger whereas "bold" marmots attempt to be affiliative in the absence of an agonistic signal. But in the presence of familiar individuals, the "shy" animals express their social confidence and are interactive whereas the "bold" marmots express their social insecurity by being less interactive.

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