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Social enhancement of fitness in yellow-bellied marmots

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The yellow-bellied marmot (*Marmota flaviventris*) is a social, ground-dwelling squirrel that lives either individually or in kin groups of from two to five adult females. Philopatry and daughter recruitment lead to the formation and persistence of matrilineal sites. By using 37 years of demographic data for 12 habitat sites, we could determine long-term trends in the effects of group size on two measures of fitness, survivorship and net reproductive rate, which otherwise are obscured by annual fluctuations in these measures. Both size and number of matrilineal sites varied among sites and survivorship and net reproductive rate varied among sites and among matrilineal sites. The role of social organization was explored further by examining the effect of matriline size, averaged over all years and sites, on fitness. For both survivorship and net reproductive rate the relationship with matriline size was curvilinear. Fitness increased with the increase in matriline size and then decreased in the largest groups. Decreased fitness in matrilineal sites of four or five was associated with agonistic behavior, a large number of 2-year-old females in the social group, and reproductive suppression. There is no evidence that females acted to increase their fitness by increasing indirect fitness; i.e., by assisting relatives, but attempted to increase direct fitness. Direct fitness increased when mortality and fission of large matrilineal sites reduced group size and the surviving females increased reproduction.

Because sociality in mammals is potentially costly due to intraspecific competition, parasite transmission, or suppressed reproduction (1), sociality must enhance inclusive fitness directly through the production of offspring and possibly indirectly through the production of nondescendant relatives when compared with nonsocial conspecifics. However, in many societies, sociality is associated with reproductive skew; a few individuals do all or most of the breeding (2). Reproductive skew may be associated with a trade-off between reproduction and survival. For example, highly social species of marmots, such as *Marmota olympus* and *M. vancouverensis*, which do not reproduce before age 3, have higher survival at ages 1–4 than the less social *M. flaviventris*, which reproduces at age 2 (3–5). Increased group size is widely associated with reduced per capita reproductive success; e.g., increased social complexity among species of ground-dwelling sciurids is associated with decreased litter size and a smaller proportion of females breeding (6). Among cooperatively breeding species reproduction may be limited to a single female in a group (3, 7), and per capita reproductive success is lower in large colonies than in small colonies of black-tailed prairie dogs (8). In contrast, by using 37 years of field observations, we report that net reproductive rate (R_0), a direct measure of fitness (9), initially increases with increased group size in the yellow-bellied marmot (*Marmota flaviventris*), then decreases in the largest groups. Furthermore, our data indicate that females in large groups act to increase their direct fitness rather than increasing indirect fitness by assisting relatives.

Methods

Marmot Biology. Yellow-bellied marmots typically inhabit montane meadows in the mountainous regions of western North

America (10). Annual mortality of young and yearlings is approximately 50% and adult mortality by age class ranges from 20 to 40% (11). About 25% of yearling females live to age 4 and 10% of 4-year-old females live to age 9 (11). Mortality results from unsuccessful hibernation and predation (11, 12). Social factors affecting fitness include competition between matrilineal sites and cooperative and competitive behavior within matrilineal sites. Between matrilineal sites competition may be expressed by infanticide (13), agonistic behavior (14), and reproductive suppression (4, 15); competitive behavior within matrilineal sites includes agonistic behavior directed toward close kin (15, 16) and reproductive suppression of daughters by their mothers (4). Cooperative behavior is expressed as amicable social interactions; i.e., allogrooming and greeting (16), and by defense of home range against conspecific intruders (4).

Yellow-bellied marmots form social groups on habitat patches that range in size from 0.15 to 7.2 ha (17). Social groups occur when yearling daughters are recruited into the natal group to form mother:daughter:sister matrilineal sites that may persist for several generations (4, 18). About 50% of female yearlings are philopatric, whereas nearly all males disperse from their breeding units and dominant males establish and defend a territory that includes one or more matrilineal sites on the same or different resource patches (4, 19, 20).

Calculations of Survivorship and R_0 . Nearly all yellow-bellied marmots at study sites in the East River Valley, Gunnison County, CO, were live-trapped, permanently marked, and observed yearly from 1962 to 1998. Not all sites were trapped every year, as some sites were added during the study period and some sites were unoccupied by marmots for one or more years. For the 12 sites where matrilineal sites were observed, we determined annual survivorship (l_x) and maternity (m_x) for marmots living individually and in matrilineal sites by group size (here all called matrilineal site size), and used the product to calculate net reproductive rate (R_0) for each matrilineal site at each site for each year. In a second analysis, we calculated R_0 across all sites for each year for all matrilineal sites of the same size combined. These calculations produced R_0 values for 36 years, as we could not know if the animals in the 37th year (1998) survived to 1999. We obtained yearly means to avoid variation introduced by differences among years.

Second-order polynomials were calculated for each site using the weighted average of annual survivorship and net reproductive rate as dependent variables and mean matrilineal site size as the independent variable over 36 years for each habitat patch (= site). In subsequent analyses, survivorship and net reproductive rate (R_0) were determined for each year for each matrilineal site

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Abbreviation: GRR, gross reproductive rate.

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Table 1. Mean matriline size for each site (= colony)

Site	<i>n</i>	Mean size	SE	95% C.I.
Copper Creek	48	1.17	0.054	±0.109
Beaver	22	1.27	0.097	±0.201
North Picnic	89	1.34	0.064	±0.127
Bend	27	1.52	0.098	±0.201
Marmot Meadow	66	1.65	0.098	±0.196
Upper Picnic	98	1.82	0.111	±0.220
Cliff	40	1.90	0.147	±0.297
Gothic Townsite	65	1.98	0.100	±0.199
Lower Picnic	106	2.05	0.088	±0.175
Boulder	59	2.08	0.178	±0.356
River	174	2.24	0.100	±0.197

n = number of females.

(1–5) over all habitat sites and the average per year determined, and second-order polynomials were calculated. We also calculated gross reproductive rate (GRR, m_x) over all years and sites for each matriline size.

Because large (≥ 4) matriline sizes are short-lived, we predicted that per capita reproduction should increase when the matriline sizes became smaller and that the increase should be greater among those females that lived in those matriline sizes with low R_0 . Therefore, we divided the matriline sizes into two groups, more productive and less productive. Initially there were 15 matriline sizes; however, one matriline had no resident male the following year and was removed from the analysis, which left 14 large matriline sizes that were divided into two groups of seven each. The more productive matriline sizes were those in which 50% or more of the females weaned litters in the first year, and the less productive group consisted of matriline sizes in which 25% or fewer of the females weaned litters the first year. We compared the same females in the two sequential years.

Results

The number of matriline sizes used in the analysis varied among sites and mean matriline size among sites varied from 1.17 to 2.24 (Table 1). The total number of matriline sizes was 544 (Table 2). Fitness as measured by survivorship and net reproductive rate varied among sites (Fig. 1). Survivorship and net reproductive rates increased and then declined with mean matriline size. Apparently site quality affected mean matriline size and the level of a resident's fitness. Although we could not directly index site quality, factors known to affect it are length of snow cover (21), number of burrows, area, angle of vision, and mean distance to trees (22). Because area could be a surrogate for quality, e.g., larger areas could have more resources such as food and burrow sites, we tested for the effect of area by Spearman rank correlation. R_0 was not significantly related to area ($r_s = 0.035$, $P > 0.5$) but survivorship was nearly so ($r_s = 0.45$, $0.1 > P > 0.05$). Because the number of females on a habitat patch is positively correlated with area ($r_s = 0.54$, $0.05 > P > 0.02$), the greater number of females on a patch may provide increased detection

Table 2. The relationship between matriline size and gross reproductive rate (GRR)

Matriline size	<i>n</i>	Mean GRR	95% C.I.
1	395	0.82	±0.125
2	109	1.01	±0.168
3	26	1.32	±0.428
4	12	1.25	±0.473
5	2	0.20	±0.861

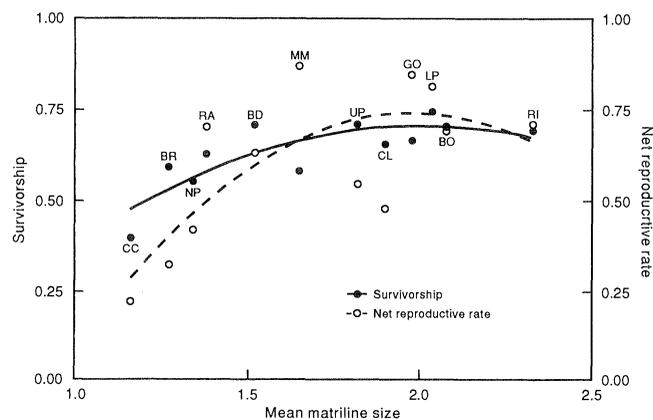


Fig. 1. The relationship between survivorship, net reproductive rate, and matriline size by site. The relationships are described by significant second order polynomials. For survivorship, $Y = -0.553 + 1.248X - 0.311X^2$; $P = 0.006$, $R^2 = 0.67$; for R_0 , $Y = -2.388 + 3.281X - 0.865X^2$; $P = 0.018$, $R^2 = 0.59$. The names of the 12 sites where matriline sizes were observed are abbreviated on the figure: CC, Copper Creek; BR, Beaver Talus; NP, North Picnic; RA, River Annex; BD, Bend; MM, Marmot Meadow; UP, Upper Picnic; CL, Cliff; GO, Gothic Townsite; LP, Lower Picnic; BO, Boulder; RI, River.

of predators. The lack of significant area effects suggests that differences among sites in fitness are a consequence of differences in habitat quality unrelated to area.

Although area and the number of resident adult females are correlated, area is not correlated with either the mean number ($r_s = 0.39$, $0.2 > P > 0.1$) or the mean size ($r_s = 0.36$, $0.2 > P > 0.1$) of matriline sizes. However, the mean number of resident females is significantly correlated with the mean number ($r_s = 0.797$, $0.005 > P > 0.0005$) and the mean size ($r_s = 0.601$, $0.025 > P > 0.01$) of matriline sizes. However, mean size and mean number of matriline sizes are not correlated ($r_s = 0.084$, $P > 0.5$). Two different processes affect matrilineal number and size: matrilineal size increases when daughters are retained in their natal group and number of matriline sizes increases because of immigration and the fission of large matriline sizes (14, 15, 17, 18). Fission of large matriline sizes is much more important than immigration in those habitat patches that typically support more than one matriline (16). The rank order of sites for survivorship is not significantly correlated ($r_s = 0.426$, $0.1 > P > 0.05$) with the rank order of sites for R_0 , which suggests that resources and social organization act somewhat differently on these two measures of fitness.

The role of social organization was further explored by examining the effects of matriline size on fitness. First, we looked at the relationship between matriline size and GRR. The relationship between GRR and matriline size (Table 2) was similar to that for the relationship between R_0 and matriline size (Fig. 2). The relationship between mean GRR and matriline size was not statistically significant (1-way ANOVA, $F_{4,539} = 1.96$, $P = 0.099$), but the relationship was described by a significant polynomial equation ($y = 0.393 + 0.494X - 0.078X^2$, $P = 0.044$). GRR increased with increasing matriline size and then decreased. The relationship was also curvilinear for both survivorship and R_0 (Fig. 2). Survivorship was less affected by matriline size, whereas R_0 was strongly affected. Of particular interest is the effect of small and large matriline sizes on R_0 . Matriline sizes of one had reduced R_0 for two major reasons. First, immigrants form matriline sizes of one; of 77 immigrant adult females, only 20 (26%) reproduced in their year of immigration. Immigration was highest at North Picnic and Copper Creek colonies with low mean group size and low R_0 (Fig. 1). Second,

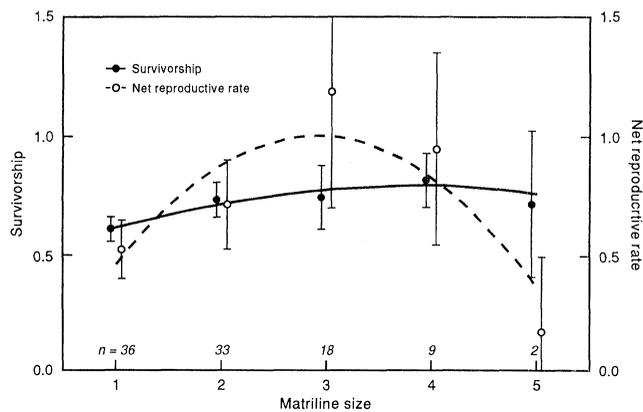


Fig. 2. The relationship between survivorship, net reproductive rate, and matriline size; n , number of years in which that matriline size occurred. Vertical bars indicate the 95% confidence intervals of the mean. For survivorship, $Y = 0.460 + 0.179X - 0.025X^2$, $P = 0.008$, $R^2 = 0.97$. Differences among means were tested by one-way ANOVA, $F_{4,93} = 2.75$, $P = 0.033$; prior/posterior tests did not identify any group size as different from another. For R_o , $Y = 0.158 + 0.751X - 0.122X^2$, $P = 0.0028$, $R^2 = 0.12$. One-way ANOVA ($F_{4,93} = 4.44$, $P = 0.0025$) was significant and a LSD test reveals that R_o was significantly lower for matriline of 5 than for matriline of 3.

matrilines of one reproduced significantly less often than expected when they were contiguous with a matriline of two or more (15). A matriline of one may persist for several years; as a consequence, reproductive output of immigrants measured as mean number of female young (0.753 ± 0.09 , $n = 216$) did not differ significantly ($t = 0.71$, $P = 0.24$) from that of philopatric females (0.849 ± 0.15 , $n = 140$) when each group formed matriline of one.

The decline of R_o in matriline of four and five suggests that females in large matriline did not benefit equally and that some females incurred a reproductive cost in matriline of four or five that was greater than such costs in smaller matriline. Only two matriline of five occurred; in one a 6-year-old female was associated with four 2-year-old daughters, in the other a 4-year-old female was associated with four 2-year-old daughters and nieces. Of these 10 females, only the 4-year-old weaned a litter. No reproduction occurred in one of 13 matriline of four. This matriline consisted of four 2-year-old sisters living next to a matriline of two. The 6-year-old reproductive female of the smaller matriline frequently chased the 2-year-old females, who were either maternal half-sisters or nieces of the 6-year-old female. Two-year-old females are less likely to reproduce when living with older females than when living alone or with other 2-year-old females (4, 11). However, GRR (0.46 ± 0.14 , $n = 51$) of 2-year-old females in matriline of one did not differ significantly ($t = 0.63$, $df = 182$, $P = 0.27$) from GRR (0.57 ± 0.91 , $n = 135$) of 2-year-old females living in matriline of two to five. Only 2 of the 15 large (≥ 4) matriline persisted as large matriline into the following year; none persisted longer than that. The number of reproductive females in these two matriline of four did not differ between the 2 years. The 13 remaining matriline were reduced in size the following year by mortality (15 animals presumably died in hibernation), dispersal (one female moved to a nearby habitat patch where she formed a matriline of 1), and matrilineal fission (4 females formed matriline of 1, and 2 littermate sisters formed a matriline of 2).

If reproduction of some females is suppressed in large matriline, then in the following year with reduced matriline sizes, we predict improved reproductive performance. In the first year, 43.1% of the females weaned litters; there were 1.97 young per resident female. In the following year, reproduction improved:

59.1% of the females weaned litters that produced 2.43 young per resident female. The difference between years in the percentage of reproductive females was not statistically significant ($G = 2.57$, $P = 0.11$). However, we reasoned that the improvement should have occurred primarily among females that initially were in matriline of low R_o . Therefore, we compared the weaning success of females who were in the more productive group (50% or more of the females weaned litters in the first year) with those in the less productive group (25% or fewer of the females weaned litters the first year). By definition, the more productive matriline weaned litters at a much higher rate than the less productive matriline in the first year (71.4% vs. 16.7%, $G = 9.38$, $P = 0.002$). In the following year, there was no significant difference in reproductive rate (more productive matriline, 63.6%; less productive matriline, 54.5%; $G = 0.44$, $P = 0.49$). The proportion of females reproducing each year in the more productive matriline did not differ significantly ($G = 0.40$, $P = 0.45$), whereas the proportion of reproductive females significantly increased in the less productive matriline ($G = 8.36$, $P = 0.003$). The increase in weaning by females in the less productive matriline cannot be attributed to whether they reproduced the previous year. Of 24 females that reproduced the first year, 15 reproduced the second year; of 23 females that were barren the first year, 11 reproduced the second year and 12 remained barren. Thus, reproductive success in one year does not necessarily increase or decrease reproductive success the next year ($G = 1.02$, $P \gg 0.1$). Movement out of large matriline enhanced reproductive performance. Six of the seven females weaned litters in the year of movement; only two reproduced the previous year ($G = 5.0$, $P = 0.025$). All seven females survived to the year after movement; five weaned litters.

Discussion

The optimal group size is three, but matriline of three occur only 4.7% of the time, and the overall mean matriline size is 1.38. Why is the optimal group size so uncommon? The main reason seems to be habitat availability. Small sites never develop large matriline. For example, at Copper Creek and Beaver, only three matriline as large as two occurred at each site. Twenty-two of the 40 large matriline (≥ 3) occurred at Lower Picnic, River, and Marmot Meadow. These sites are among the larger in area, which is a necessary but not sufficient condition for the development of large matriline. These three sites also have numerous burrow sites (22) and large meadows with abundant forage (23, 24). Thus, resources at these sites are sufficient to support a large population of yellow-bellied marmots, which is evident in the average number of matriline and mean size of matriline at these sites in comparison to other sites (17). By contrast, the widely spaced, small resource patches at North Picnic, the largest site, result in a large number of small matriline (17).

Although matriline size significantly affected reproductive success, there was great variation (Fig. 2). Some of the variation is a consequence of habitat differences; matriline of similar size have markedly different R_o values (Figs. 1 and 2). The low R_o of matriline of five and of many matriline of four (Fig. 2) suggest that competition was more severe in large matriline. Why would a yearling female join a large matriline with the prospect of poor reproductive success? The alternative is to disperse as a yearling, but mortality of dispersing yearlings is significantly higher than that of yearling residents, and there is no future compensatory decrease in the age of first reproduction or increase in the frequency of reproduction (25). Because R_o is higher in matriline of 2, 3, and 4 than in a matriline of 1, philopatric females may gain indirect fitness. For example, they may increase survivorship of infant kin by alarm-calling when predators are present. However, 42% of the variation in alarm-calling was a function of whether the caller was a female with emergent pups. Measures of indirect

fitness were not significantly related to alarm calling (26). Nor is there any evidence for social thermoregulation in this species at these study sites (3) nor any evidence that allogrooming removes external parasites. Alternatively, philopatric females (those remaining in their natal site) may increase their direct fitness; by foregoing dispersal, they increase the probability of reaching reproductive age, and they can escape reproductive suppression either by moving away from competitors and budding off a new matriline or by waiting for mortality to reduce the size of the matriline and, hence, the number of competitors. Philopatry, movement, alarm calling, and social

interactions between and within matriline (15, 27) strongly suggest that females act to enhance direct fitness and that any indirect fitness gains are a by-product of a direct fitness strategy.

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