Social organization, reproductive success and population dynamics in a high-elevation Yellow-bellied Marmot colony

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Abstract. High elevation marmots have a short growing season caused primarily by prolonged snow cover. The short growing season may affect sociality and/or reproductive success. This proposal was tested by examining the social organization and reproductive success of a yellow-bellied marmot population at 3400m. The organization of females in mother: daughter: sister matrilines did not differ from that of marmot populations at about 500m lower elevation. Rates of recruitment and immigration in the high elevation population were similar to those of the lower elevation population. The major differences between the two populations was the much lower frequency of weaning and much higher frequency of failed reproduction (reproduction initiated, but no young weaned) in the high (alpine) elevation population than in the lower (montane) elevation population. During the seven-year study, only one female weaned litters in successive years. High frequencies of reproductive success were associated with years of early snowmelt and high frequencies of failed reproduction occurred in years of heavy snowpack and late snowmelt. A winter of low snow precipitation was associated with high mortality. The short growing season (late snowmelt) primarily affected reproductive success but did not affect sociality. Therefore, the proposal that the short growing season is associated with change in social structure of yellow-bellied marmots is rejected.

Key words: matriline organization, failed reproduction, snowmelt, immigration, recruitment

Introduction

Yellow-bellied marmots (*Marmota flaviventris*) in western North America occur over elevations ranging from 800m (Webb 1980) to 4000m (Armstrong 1972). It is generally accepted that with increasing elevation, the growing season decreases (Andersen *et al.* 1976, Barash 1974, Webb 1980). The shorter growing season is associated with delayed dispersal; i.e., low-elevation yellow-bellied marmots disperse as young (Webb 1980) whereas high-elevation marmots disperse as yearlings (Armitage *et al.* 2011). Large body size coupled with a short active season resulted in the retention of offspring through at least their first hibernation and the formation of social groups (Armitage 1981). Barash (1973a) suggested that high-elevation colonies were more social, but this interpretation is contradicted by the variability in social behavior associated with population density, the age-sex structure of the population, degree of familiarity among the residents, individual behavioral phenotypes, and the way space is shared (Armitage 1977). Another way to explore whether the shorter growing season at high elevation affects sociality is to determine whether the basic social structure is the same at high-elevation (>3300m) and low-elevation (<3000m) sites. At low elevation sites yellow-bellied marmots colonizing a habitat form matrilines by recruiting daughters (Armitage 1973); matrilineal structure characterizes colony organization in the Upper East River Valley, Colorado (Armitage 1991). Therefore, this paper examines social structure in North Pole Basin, a high-elevation alpine area.

Higher elevation sites are considered to be a harsher environment than lower elevation sites because of longer snow cover. Longer snow cover may restrict access to vegetation in the early period following emergence from hibernation, thus requiring marmots to utilize body fat, which may decrease the likelihood of weaning a litter (Andersen *et al.* 1976). Marmot species occupying harsh mountain environments where the early post-hibernation season may be cold and/or stormy frequently fail to reproduce (Armitage 2000). A dramatic effect of late snow cover at North Pole Basin occurred in 2008 when snow cover lasted until mid July and no young were weaned and no young of the previous year were recaptured as yearlings (Woods *et al.* 2009). Climate change is expected to mitigate the harsh environment and result in more reproduction and higher survivorship (Ozgul *et al.* 2010). Thus, this paper explores the frequency of reproduction and provides a benchmark for determining the effects of climate change on high-elevation marmot populations.

Previous studies at North Pole Basin (NPB) indicate that individual adult females reproduce less frequently than those in the Upper East River Valley (ERV) and the number of offspring a female weaned was closely associated with her food resources. Females deposited fat at a single rate regardless of reproductive history (Andersen *et al.* 1976,

Johns and Armitage 1979). In this paper I explore the issues of reproductive frequency and success over a 7-year period to provide a more comprehensive account of yellow-bellied marmot life at a high elevation site.

Methods

The study site

The research was conducted from 1973 through 1979 at North Pole Basin (NPB). NPB is located at 3400m elevation in the ELK Mountains of Gunnison County, in west-central Colorado, and is about 10km from the Upper East River site. The glacially scoured basin is a 3.2 x 1.6km hanging valley; the slope and floor of the basin support a single expanse of open meadow of forbs, sedges, and grasses. Willow thickets are common in the wet meadows along an ephemeral stream that flows through the area. Rock outcrops provide burrow sites (Johns and Armitage 1979). A few clumps of woody vegetation occur, but do not restrict marmot movements. Essentially the entire basin is open to marmot settlement. For this study, a 270 x 270m site located on the floor and lower slope was chosen for concentrated study (Fig. 1).

Trapping and reproductive status

NPB was trapped each year from 1972 through 1981. Only in years 1973 through 1979 was trapping extensive and only for those years were data analyzed. Trapping occurred throughout the summer in 1974 through 1976; in the other years trapping was concentrated in a 3-week period in late July and early August when young had emerged. In most years, some trapping occurred in late June and early July and also in early September. The area trapped extended beyond the limits of the study site in order to detect whether marmots moved into or out of the site between years.

At the time of first capture, the marmot received a uniquely numbered tag in each year, was weighed, and age, sex, and reproductive condition were determined. The age of young (animals in their first summer), yearlings (animals in their second summer), and two-year-old adults (animals in their third summer) was readily determined by body mass (Armitage *et al.* 1976). Adults that could not be aged by body mass were assigned the age of 3+ (at least three-years-old, possibly older) in the year of first capture; age was increased for each year of recapture.

Reproductive condition of adult females was determined primarily by nipple development
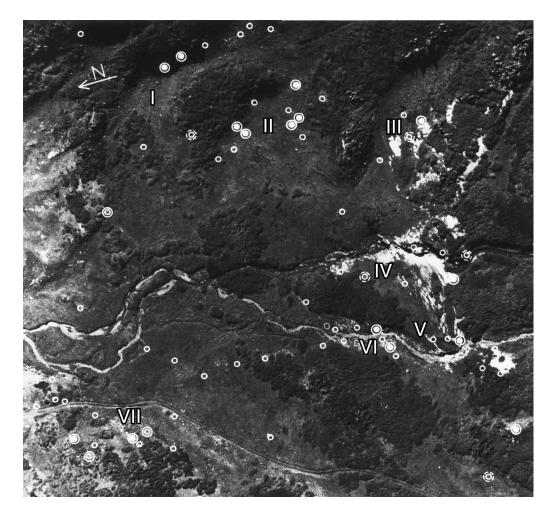

Fig. 1. An aerial view of the North Pole Basin (NPB) study site. The numbered areas within the site coincide with the numbered matriline areas in figures 6 to 8. The white areas are rock outcrops; the dark areas are primarily willow thickets. Note the two branches of an ephemeral stream that join below area I. Not all burrows were used in a given year. Photograph courtesy of Alan Hegeman, Crested Butte, Colorado.

(Armitage and Wynne-Edwards 2002). Females with essentially no nipple development were recorded as non-reproductive (NR). Females that were lactating and successfully weaned a litter were recorded as reproductive (WL). Females who were recorded as lactating but failed to wean a litter were recorded as failed reproduction (FR). These patterns of reproduction were reflected in changes in body mass. All marmots lost mass initially after emergence from hibernation; non-reproductive females soon began to gain mass (by day 180) whereas reproductive females did not begin to gain mass until about day 220. Failed-reproduction females initially had a period of no mass gain (or some mass loss) followed by a period of mass gain that began before day 200 and no young was weaned (Fig. 2).

Matriline groups

Young were assigned to the female with whom they shared a burrow and became a member of that female's matriline if they survived to two-years-old as a resident. Initially, matrilines were determined by association. Females that shared burrows, hibernated together, and foraged in the same meadow were assumed to be highly related and were grouped in the same matriline. This assumption of relatedness and matriline membership is supported by the long-term study in the East River Valley. Only closely-related females shared burrows and had high space-overlap in foraging areas; no unrelated females ever formed a matriline and no immigrant ever successfully joined an existing matriline (Armitage 1964, 1986, 2012). Behavioral observations supported the assignment of females to matrilines; amicable behaviors occurred between members of the same matriline and agonistic behavior occurred between females of different matrilines. This pattern characterizes social behavior among female yellow-bellied marmots (Armitage 1987, 1989).

Snow cover

The snowpack was estimated from snowfall recorded at the Rocky Mountain Biological laboratory (RMBL) in the Upper East River Valley at 2881m (Barr, pers. com.). The time when snowmelt occurred over 50% of the NPB study site was determined for three years (Johns and Armitage 1979). The timing of snowmelt in the ERV was compared with the known times in NPB and used as a basis for estimating whether snowmelt in NPB was early to late based on the early to late patterns at RMBL. These estimates were compared with snow-cover observations made by the marmot team and were used to verify early/late estimates.

Results

Number of resident adult females

The number of resident adult females, two-years-old or older, increased from 20 in 1973 to 25 in 1975 and then declined to seven in 1979. The mortality of two females during population increase was offset by the recruitment of five two-year-olds and the immigration of one three-year-old or older female. Both the 1973 cohort (p = 0.000) and the total number of resident adult females (p = 0.02) declined linearly with time (Fig. 3). There was a major decline in numbers between 1976 and 1977 which was strongly influenced by mortality in the 1973 cohort. Seven of the 12 members of this cohort died over the 1976/77 winter; five had a minimum age of 6+ and one was five years old. In addition three recruits (marmots born on the study site) and a 1976 immigrant also died (Fig. 5). Population declined slightly prior to 1977 because five recruits and two immigrants compensated for the mortality of seven members of the 1973 cohort and two immigrants from 1974.

The population continued to decline as the 1973 cohort continued to decrease and immigration and recruitment failed to maintain population numbers. During the 7-year study, 12 recruits (x=2.0/yr) and five immigrants (x=0.83/yr) became residents. Thus, the rate of recruitment was 2.4 times the rate of immigration, a pattern similar to that in the East River Valley where the rate of recruitment (average over six sites and 37 years) was 2.2 times the rate of immigration (Armitage 2003a).
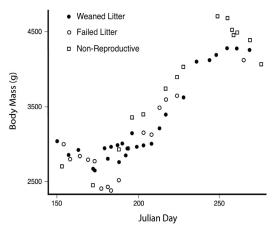

Fig. 2. Mass gain of adult females at NPB. WL= reproductive female that weaned a litter. FR= a female that initiated reproduction, but failed to wean a litter. NR= a female that did not initiate reproduction.
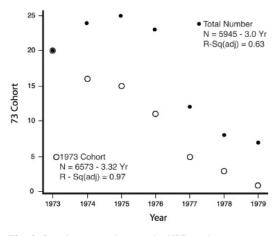

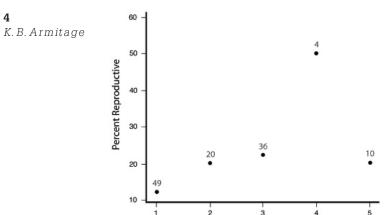**Fig. 3**. Population numbers at the NPB study site.

Fig. 4. The relationship between the percent of adult females that were reproductive (WL) and matriline size. The numbers above the points are the total number of matriline-years. A matriline-year is a matriline of a given size in one year. The number of matriline-years for each matriline size for each year were summed to determine the total number of matriline-years.

Reproductive success

On average, 19.3% of the adult females weaned a litter annually (WL) (Table 1). This value is much lower than the 52% of females that successfully reproduce annually in the East River Valley (ERV) (Armitage 1996). Annually, 21% of the NPB females initiated reproduction but failed to wean a litter (FR) (Table 1). This rate of FR is much higher than the average annual rate of 6.7% in ERV. The remaining 60.5% of the females were categorized as non-reproductive (NR); i.e., there was no evidence that reproduction was initiated.

Reproductive success varied over the seven years (Table 1). The higher rate of WL and lower rate of FR occurred in 1974, a year characterized by early snowmelt. The lowest rate of WL occurred in 1973, the year of heaviest snowfall and late snowmelt. Late snowmelt also occurred in 1975, a year of relatively low WL. Low WL also occurred in 1976 when FR was highest. The year was characterized by light snowfall and relatively late snowmelt, but earlier than 1975. The low WL in 1976 may have been influenced
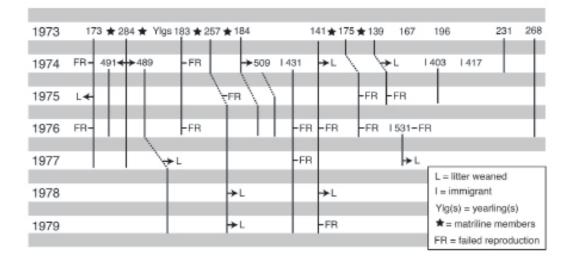

Fig. 5. The composition of the matrilines at NPB. The identification number for each female is recorded in the first year when she was trapped. The vertical lines indicate the years a female was present when she was present for two or more years. A horizontal line that connects with vertical lines indicates that litters were intermingled and precise parentage could not be determined. An arrow connects a recruit with her mother in the year the recruit was born. When no young was recruited, a dash points to L, which indicates that a litter was weaned.

Year	Weaned Litter		Failed Reproduction		Non-reproductive		Total
	No.	%	No.	%	No.	%	Number
1973	2	10.0	0	0.0	18	90.0	20
1974	9	37.5	2	8.3	13	54.2	24
1975	4	16.0	5	20.0	16	64.0	25
1976	2	8.7	10	43.5	11	47.8	23
1977	3	25.0	3	25.0	6	50.0	12
1978	2	25.0	2	25.0	4	50.0	8
1979	1	14.3	3	42.9	3	42.9	7
Total	**23**	**19.3**	**25**	**21.0**	**71**	**59.7**	**119**

Table 1. The number (No.) of females that weaned a litter (WL), that initiated reproduction, but failed to wean (FR), and that were non-reproductive (NR) for each year of the study. N= 36 individual females.

by reproductive history; four FR females had either weaned a litter or failed to do so the previous year (Fig. 5). Four other FR females never weaned a litter during their residency, which suggests that female quality affects reproductive success.

Matriline size may have affected reproductive frequency. The percentage of females reproducing increased as matriline size increased, then decreased at the largest size (Fig. 4). Although this pattern is similar to that of ERV females (Armitage and Schwartz 2000), the ERV study included a much larger sample size and measured net reproductive rate rather than frequency of reproduction. Mean matriline size in NPB was 2.2, about 59% larger than the ERV mean of 1.38. This difference probably reflects local habitat not elevational differences because several ERV sites had mean matriline sizes >2.0 (Armitage and Schwartz 2000). In general, this relationship between matriline size and reproductive success suggests that there is no fundamental difference in social organization between the ERV and NPB study areas.

Reproductive success varied with age (Table 2). Two-year-olds had the lowest frequency of WL and the highest frequency of NR. This pattern is typical of two-year-old females in ERV where they are unlikely to reproduce when an older female is present (Armitage 2003b, 2007). Eight of the NR two-year-olds were associated with one or more older females. The frequency of NR known-aged females declined with age, but WL did not increase with age because the frequency of FR also increased with age (Table 2). The same general trend occurred in the females of uncertain age. Numbers of females at the older ages are too few to quantify any age-trend. A greater percentage of older females attempted reproduction; 57.6% of females six-years-old or older initiated reproduction when only 37.5% of females three-to five-years-old did so. This pattern is similar to that of ERV females where older females have an overall higher rate of reproduction (Nuckolls 2010). The major difference between the ERV and NPB populations is the high rate of FR at NPB.

Age	Weaned Litter		Failed Reproduction		Non-reproductive		Total
	No.	%	No.	%	No.	%	Number
2	1	7.7	1	7.7	11	84.6	13
3	1	10.0	2	20.0	7	70.0	10
4	1	11.1	4	44.4	4	44.4	9
5			1	33.3	2	66.7	3
6	1	100.0					1
7	1	100.0					1
3+	3	14.3	1	4.8	17	81.0	21
4+	9	45.0	1	5.0	10	50.0	20
5+	3	71.6	5	29.4	9	52.9	17
6+	1	8.3	6	50.0	5	41.7	12
7+	1	16.7	1	16.7	4	66.7	6
8+	1	25.0	2	50.0	1	25.0	4
9+			1	50.0	1	50.0	2
Total	**23**	**19.3**	**25**	**21.0**	**71**	**59.7**	**119**

Table 2. Age and reproductive success of female yellow-bellied marmots at North Pole basin (NPB). Age followed by a + indicates a female of uncertain age; the age assigned is the youngest possible age. N=36 individual females.

Matrilineal organization

Seventeen matrilines were identified; two of these divided to form three separate matrilines, making a total of 20 (Fig. 5). Nine matrilines were non-reproductive and one was FR only; all were matrilines of one adult female. Of the 11 matrilines that produced litters, only three recruited residents. Failure to reproduce or to recruit daughters from weaned litters commonly occurs in yellow-bellied marmot matrilines (Armitage 1991, 2002).

Matrilines developed in seven major areas (Fig. 6). In 1973, all the major areas had matrilines and four single-female matrilines were adjacent to the major areas (e.q. 116, 157, 231, 268). None of the burrow areas occupied by these females consistently had residents.

Females frequently changed burrow residency; most changes occurred within the area occupied by the matrilines. The marmots commonly moved from a hibernaculum to a summer residence burrow. Half of the translocations occurred between mid June and mid July (Johns and Armitage 1979). In some instances females were moving to snow-free areas where foraging was possible (Andersen *et al.* 1976). The matriline in area VII was unstable; 175 shifted to area VI where she was joined by 139 in 1974 as they formed a matriline independent of 141.

Several shifts in residency occurred by 1976 (Fig. 7). Female 42 moved from area II to area III

as the other matriline in area II in 1973 increased in size by recruiting six daughters, expanding over the entire area, and dividing into two matrilines, one on the north, and one on the south side of area II. The composition of the matriline in area IV changed as 35 died and two recruits were added.

The population decline after 1976 was associated with a major reorganization. Area I was settled by 489, who moved from area II to form an independent matriline (Fig. 8) and 597, born in area IV and who wandered as a two-year-old, settled in area II. Female 141 moved from area VII (Fig. 6) to area VI and immigrant 431 now resided in area VII. Female 595, daughter of 42 (Fig. 5), first settled in area VI, but shifted to area IV coincident with 141 moving to area VI. Presumably, the decrease in population allowed females to occupy more favorable sites. However, only 257 reproduced; she also reproduced at the same site in 1978. She was the only female that reproduced in consecutive years during the seven-year study. Area II apparently offered a better environment than other areas; the matriline persisted throughout the study period and litters were weaned in five of the seven years (Fig. 5). Successful weaning occurred in no more than two years at the other sites. However, these translocations did not result in higher reproductive success (Table 1); the winter of 1978/1979 had a heavy snowfall and late snowmelt characterized 1979.
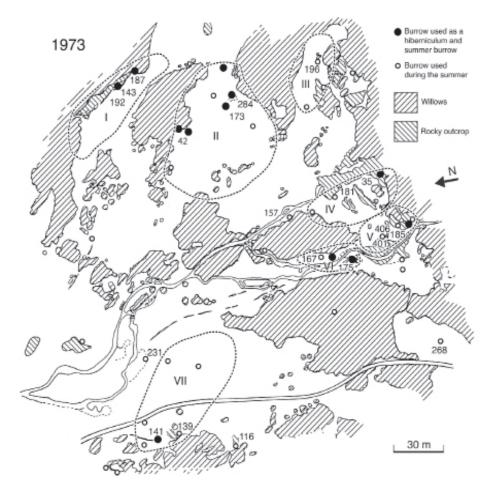

Fig. 6. The distribution of matrilines in 1973. The identification number of each female is recorded in the area in which her matriline lived. Note: two matrilines occupy area II. Also note the females that occupied burrows outside the seven major areas.
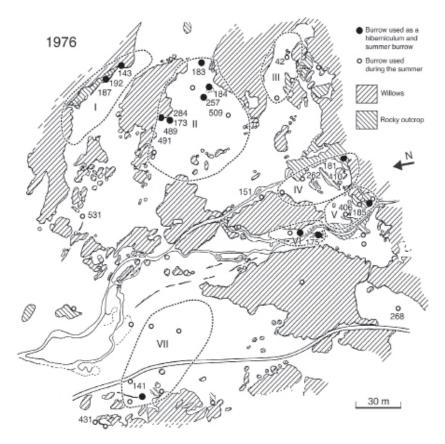
Fig. 7. The distribution of matrilines in 1976. Numbers as in Figure 6. Note: one extended matriline occupies area II, and the females live in different burrows. Some females are present at burrows outside the numbered areas, but none recruited daughters and only two weaned litters (compare figures 5 and 7).
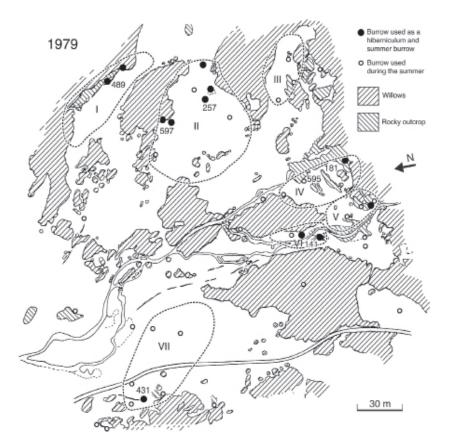

Fig. 8. The distribution of matrilines in 1979. All matrilines consist of a single female. Several females changed areas; e.g., 489 from II to I; 141 from VII to VI. Note that there are no residents outside the seven major areas.

Discussion

The recruitment/immigration patterns at NPB are similar to those in ERV and are consistent with the population organized in matrilines. Furthermore, the close association of the same females in one of the habitat areas over two or more years and the settlement of recruits in their areas of birth with their mothers demonstrate the prevalence of matrilineal organization. The distribution of matrilineal size does not differ from that of ERV. The division of a large matriline into smaller matrilines is also typical of yellow-bellied marmot matrilines at lower elevations. Translocations occur in all yellow-bellied marmot colonies (Armitage 1984, 2003a, Armitage and Schwartz 2000). Translocations enable individuals to access better resources and/or escape reproductive suppression (Armitage 2003b). For example, at NPB, both 489 and 139 weaned litters in the year in which they moved to a new location (Fig. 5).

Because the basic social organization of yellow-bellied marmots is female-based, male activity was not described. Nearly all adult males are immigrants; a successful male then defends one or more matrilines (Armitage 1998, 2004). Seven two-year-old males were recruits, but only one returned as a three-year-old. He did not settle in the same area as his mother. This lack of persistent residency by males born at a site also characterizes male behavior in ERV (Armitage 2004, Schwartz *et al.* 1998). Overall, males formed and maintained harems at NPB similar to that activity in ERV (Johns and Armitage 1979).

I conclude that the basic social organization of yellow-bellied marmots does not differ between the high elevation NPB population and the lower elevation ERV population. Thus, the short growing season at NPB does not affect the basic matrilineal organization of yellow-bellied marmots.

The striking difference between the two elevations is the much higher frequency of failed reproduction (FR) at NPB. The higher frequency of FR is related to snowfall. In 1974, a year of early snowmelt, the frequency of FR was at its lowest and the frequency of weaning (WL) was at its highest. In 1975, a year of late snowmelt, the percentages of FR and WL were at the long-term average (Table 1) when the expectation was that WL would increase and FR would decrease. However, reproductive performance in one year influences reproductive success the following year (Nuckolls 2010). Of the nine females that weaned litters in 1974, six were NR and three were FR in 1975. Thus, the potential number of females that might wean offspring was reduced. Three of the four WL females in 1975 were NR in 1974, thus they had an increased likelihood of reproducing. Eight of the 1974 NR females were NR in 1975; four of them never reproduced. If one subtracts these four and those that were WL in 1974, 12 females were probable reproducers, but only four did so. Thus, reproductive success was low as expected in a year of late snowmelt. Late snowmelt occurred in 1979; as expected, WL was low and FR was high. In 1978, snowmelt was late and two females (25%) weaned young. Neither

female had reproduced for three or more years; both were the sole survivors of their matrilines and one moved to a different area in the colony. Presumably, each was independent of any reproductive competition from other matriline members, had access to the resources in their area, and several years to accumulate sufficient fat to provide their energy until they could forage (Andersen *et al.* 1976). The females that did not wean young in 1978 were classified as FR or were classified as FR or WL the previous year, which decreased the likelihood that they had sufficient fat reserves to sustain reproduction.

The interpretation of the importance of snow cover is complicated because of a lack of snowmelt patterns. Snowmelt is not uniform across the study site (Johns and Armitage 1979) and probably varies from year to year. For example, aspect affects the probabilities of survival (Ozgul *et al.* 2006a) and reproduction (Ozgul *et al.* 2007). Aspect is associated with timing of snowmelt; later snowmelt reduces survival and reproduction. The importance of aspect is apparent in the location of marmot populations. For example, in a wide-ranging review of habitat distribution in the alpine marmot, Lenti Boero (2003) reported that 80% of 15 habitats had southern exposure where snowmelt occurs earlier than on other exposures.

Snowfall may affect survival and reproduction differently. The lightest snowfall occurred in the winter of 1976/77 when mortality was high. Adequate snow cover is necessary to insulate hibernacula from low air temperature that increases metabolic rates (Arnold *et al.* 1991, Armitage 2008). Higher metabolism may cause marmots to deplete their fat stores, thus die of starvation or have reduced resources for initiating reproduction. Sparse winter snow cover decreases the probability of survival in alpine marmots (Allainé *et al.* 2008) and increases mortality in Olympic marmots (Barash 1973b).

Although the light snowfall of 1976/77 was associated with high mortality, the subsequent early snowmelt was associated with a relatively high percentage of WL females; none weaned a litter in 1976. Early snowmelt favors reproduction in Olympic marmots (Griffin 2007), conversely, delayed snowmelt reduces reproduction in the black-capped (*M. camtschatica*) (Mosolov and Tokarsky 1994) and hoary (*M. caligata*) marmots (Karels and Hik 2003) and increased mortality of young and yearling alpine marmots (*M. marmota*) (Arnold 1993). Generally, harsh conditions after emergence from hibernation are associated with poor survival and reduced reproductive success (Armitage and Blumstein 2002).

In conclusion, the amount of snowfall and timing of snowmelt account for the major differences in reproduction, recruitment, and survival between the high elevation North Pole Basin (NPB) and the lower montane East River valley (ERV) yellow-bellied marmot populations. The timing of snowmelt is wide-ranging; its effects are apparent within ERV. ERV is conveniently divided into upper valley and lower valley networks (Ozgul *et al.* 2006b). Marmots in the upper valley network where snowmelt occurs later reproduce less frequently and have smaller litters than females in the lower valley

network where snowmelt may be as much as 21 days earlier (Van Vuren and Armitage 1991). Thus, with increasing elevation, the quantitative effects of delayed snowmelt increase. These effects of snow cover allow me to speculate on the potential effects of climate change, and the associated global warming, on the NPB population.

Two possibilities come to mind. If climate change significantly reduces winter snowpack, then mortality will increase. The population may persist if some hibernacula are located in areas where adequate snow cover occurs. If the winter snowpack is sufficient to provide adequate insulation and early snowmelt becomes the norm, the frequency of reproductive success will increase and the frequency of failed reproduction will decrease. Increased reproductive success should maintain aviable population unless (and until) winter snowpack no longer insulates the hibernaculum from stressful, low temperatures.

In the short run, climate change is more likely to produce extreme weather patterns. A period of years of early snowmelt will favor reproduction, survival, and population growth (Ozgul *et al.* 2010). But one or more years of heavy snow and late snowmelt will increase mortality and reduce reproduction, such has occurred in ERV (50% adult, 80% young mortality, Blumstein per. Com.) and NPB (no reproduction, 100% young mortality, Woods *et al.* 2009) in 2008.

Acknowledgements

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