

## Notes and Discussion

### Female Olympic Marmots (*Marmota olympus*) Reproduce in Consecutive Years

**ABSTRACT.**—Olympic marmots (*Marmota olympus*) are reported to skip at least one year between reproductive efforts. We observed several female marmots weaning infants in consecutive years. There was no evidence that reproductive skipping was more common than annual reproduction. High spring food availability resulting from climate change may allow females to wean consecutive litters regularly.

#### INTRODUCTION

Life-history traits such as age of first reproduction, litter size, frequency of reproduction and survival often vary across and within species as a function of environmental conditions or local density (Reznick and Endler, 1982; Dobson and Murie, 1987; Oli *et al.*, 2001; Arendt and Reznick, 2005). Changes in life-history parameters can have significant impacts on population growth rate (Mills and Lindberg, 2002; Oli and Dobson, 2003), so the degree of plasticity in these parameters may dictate whether a species can successfully survive environmental change or other stressors or respond favorably to habitat enhancement by management.

Olympic marmots (*Marmota olympus*) are large ground-dwelling squirrels endemic to the mountains of the Olympic Peninsula, WA, USA. Like other high-elevation marmots, they hibernate for 7–8 mo a year, with snow cover preventing foraging from Sept. through May or Jun. This leaves a narrow window available for growth, reproduction and accumulation of fat necessary for hibernation. Olympic marmots, and the closely related hoary (*M. caligata*) and Vancouver Island marmots (*M. vancouverensis*), delay any dispersal until after the second hibernation, first reproduce at age three or four and breed infrequently thereafter (Barash, 1973; Barash, 1974; Bryant, 2005). Female hoary and Olympic marmots are reported to not wean litters in consecutive years (Barash, 1973; Wasser and Barash, 1983; Holmes, 1984); Vancouver Island marmots seldom breed in consecutive years in the wild (Bryant, 2005). Females should be under selective pressure to produce as many successful offspring as possible so there must be a compelling reason for them to forego annual reproduction.

The proximate causes of reproductive skipping in female alpine-dwelling marmots are not fully resolved. The immediate costs of reproduction appear to be particularly high in these species. Reproductive females typically do not begin mass gain until after lactation ends in late-Jul., and so, in just 6–8 wk must accumulate enough fat to survive hibernation. Reproductive females forage more at dawn and dusk (Barash, 1980) and remain active later in the fall than their non-reproductive counterparts (Barash, 1976), possibly exposing themselves to an increased risk of predation (S. C. Griffin, pers. obs.). Despite the additional time spent foraging, reproductive females enter hibernation at a lower body mass (Barash, 1989) and may risk over-winter mortality (Armitage *et al.*, 1976). There is evidence that reproductive success in other *Marmota* species is dependent on spring body condition (Hackländer and Arnold, 1999) and duration of snow cover (Van Vuren and Armitage, 1991; Schwartz and Armitage, 2005), suggesting that regularly lost reproductive opportunities are a cost of living in a harsh environment (Armitage and Blumstein, 2002).

Alternatively, there is some evidence that social pressures limit reproductive effort in marmots when dominant females suppress reproduction by subdominants or delay the age of first reproduction of young animals (Blumstein and Armitage, 1999; Hackländer *et al.*, 2003). In the alpine marmot (*Marmota marmota*), aggressive behavior of the dominant female induces stress related hormonal changes in subdominants that prevent subdominants from successfully reproducing (Hackländer *et al.*, 2003). When older females are present, the age of first reproduction is delayed in yellow-bellied marmots (Armitage, 2007). It has been proposed that in Olympic, hoary and Vancouver Island marmots, suppression leads to reproductive skipping (Wasser and Barash, 1983).

In 2002 we began demographic studies of Olympic marmots. In this note we report on observations of annual reproduction (*i.e.*, successful weaning of litters in two consecutive years) by several Olympic marmots during the first four years of our study and consider the evidence these data provide for environmental harshness and reproductive suppression as driving mechanisms of reproductive skipping.

TABLE 1.—Frequency of annual breeding in Olympic marmots (*Marmota olympus*; n represents the number of females available to wean second litters) and corresponding May 1 snowpack at Cox Valley, Olympic National Park, Washington, USA as a percent of the 1968–2005 average. The Cox Valley snow course is located on a north-facing slope of Hurricane Ridge at 4750 m

Year	Snowpack May 1 <sup>1</sup>	Females weaning second litter
1968	98%	0% (n = 5) <sup>2</sup>
1969	147%	0% (n = 3)
2003	86%	0% (n = 3)
2004	68%	57% (n = 7)
2005	14%	43% (n = 7)

<sup>1</sup> Snowpack data are from the USDA Natural Resource Conservation Service, National Water and Climate Center and can be accessed online at <http://www.wcc.nrcs.usda.gov/snowcourse/sc-data.html>

<sup>2</sup> 1968 and 1969 reproductive data from BARASH, D. P. 1973. The social biology of the Olympic marmot. *Anim. Behav. Monogr.*, 6:171–249

#### OBSERVATIONS

As part of an ongoing study, Olympic marmots from 14 colonies located on Hurricane Ridge, Obstruction Point and in Royal Basin (elevation 1500–1800 m) in Olympic National Park have been monitored since 2002 or 2003. All marmots were marked with uniquely numbered ear-tags and a subset implanted with radio-transmitters. Adult female marmots and their primary burrows were observed multiple times each week mid-Jul. through Aug. to determine which females successfully weaned litters. When we found a litter, we attempted to trap and mark the infants within a week of discovery to facilitate counting them. Alternatively, we observed the infants on several occasions during the first 10 d following emergence to determine litter size. Infants remain close to their natal burrow and so are easily located and counted during this period. We began observations at most colonies in 2002. Therefore, 2003 was the first year in which it was possible to observe annual reproduction. We began studying marmots at two sites in 2003, and so could not have observed annual reproduction at these sites until 2004. We refer to the first of the two litters weaned by the same female in consecutive years as the “first” litter and the second of these litters as the “second” litter.

Reproduction in consecutive years by Olympic marmot females was relatively common during our study (Table 1). Several females produced second litters in 2004 and 2005 and one female weaned three successive litters. Of 17 females that produced litters in one year and survived to the following Jul., seven (41%) successfully weaned a second litter. Of 29 marmots that skipped the previous year despite being of breeding age, 13 (45%) produced litters. Of the remaining population of 37 3-y-olds and animals whose success in the previous year was unknown 14 (37%) produced litters. The proportions of reproducing females in these three groups are not statistically different ( $\chi^2_2 = 0.44$ ,  $P = 0.8$ ). During this time, 14 adult females were present for  $\geq 3$  y. Only three of these (21%) demonstrated the stereotypical “reproductive skipping” by producing two litters with a single year between, while five (36%) failed to reproduce in  $\geq 2$  consecutive years.

Breeding in consecutive years did not result in lower reproductive output in the second year, as might be expected if females were energetically stressed (Table 2). The number of infants in the seven second litters ( $3.29 \pm 0.95$ ; mean  $\pm$  sd) was the same as in the first litters produced by the same females ( $3.29 \pm 1.11$ ; [for the female that produced three consecutive litters, the 2004 litter was included twice: once as a second litter paired with the 2003 litter and once as a first litter paired with the 2005 litter]). In all cases, related yearlings and infants appeared to mix freely.

Females produced second litters under conditions of intermediate densities and in a range of social situations (Table 2). No female at Royal Basin, the largest, most densely populated site ( $>5$  marmots  $\text{ha}^{-1}$ ; S. C. Griffin, pers. obs), produced litters in consecutive years. Although 7–10 adult females were present each year at Royal Basin, reproduction was generally low – only three females successfully weaned a litter and then survived to the following summer. Likewise, no female bred in consecutive years at any site where densities of marmots were extremely low ( $<1$  marmot  $\text{ha}^{-1}$ ).

TABLE 2.—Summary of reproductive efforts and social environment of Olympic marmots (*Marmota olympus*) that successfully weaned litters in consecutive years. Shown are the year of the first and second litter with litter size in parentheses, and the number of females in social group in year of second litter. One female weaned litters in three consecutive years – she is represented twice in the table

Female	1st litter year (size)	2nd litter year (size)	Females in social group
Miwa	2003 (2)	2004 (3)	1 <sup>1</sup>
Beanbag	2003 (3)	2004 (3)	2 <sup>2</sup>
Nao	2004 (4)	2005 (4)	1
Graygirl	2003 (2)	2004 (2)	1 <sup>3</sup>
Matt's Marmot	2004 (5)	2005 (3)	1
Lena	2003 (3)	2004 (5)	2 <sup>4</sup>
Lena	2004 (5)	2005 (3)	1
Litter size $\pm$ SD	3.29 $\pm$ 1.11	3.29 $\pm$ 0.95	

<sup>1</sup> Home range abutted another adult female that produced litter of six infants

<sup>2</sup> Subordinate produced litter of six infants

<sup>3</sup> Home range abutted a non-reproductive adult female

<sup>4</sup> Subordinate produced litter of four infants

All second litters occurred in 2004 and 2005, years of early spring melt-out (Table 1). No second litters occurred in 2003 when snowpack was approximately normal, although the sample size was small, with only three females alive that year known to have littered in 2002.

#### DISCUSSION

During the years 2003–2005 no evidence exists that skipping was the predominant reproductive pattern in female Olympic marmots. Our data are too preliminary to conclude that annual reproduction is common in Olympic marmots but it could be under certain conditions. Our observations are consistent with the hypothesis that environmental harshness leads to reproductive skipping in high-elevation marmots (Armitage and Blumstein, 2002) and, importantly, suggest a potentially positive response to climate change for this species.

In particular, the availability of early spring forage may dictate whether high-elevation marmots can breed in consecutive years. Hoary marmots, high-elevation (3400 m) yellow-bellied marmots and (until this study) Olympic marmots have all been reported to skip one or more years between weaning litters (Barash, 1973; Johns and Armitage, 1979; Wasser and Barash, 1983; Holmes, 1984). However, Johns and Armitage (1979; Fig. 1) indicate that snow covered the majority of their study area well into Jun. in all years and Barash (1973; Wasser and Barash, 1984) studied both Olympic (Table 1) and hoary marmots during periods of generally higher spring snow packs (Mote *et al.*, 2005). All observed second litters in this study occurred in the two years of early spring melt-out (Table 1). Mid-elevation (2900 m) female yellow-bellied marmots (which often breed annually) have higher reproductive success in years with earlier snowmelt (Van Vuren and Armitage, 1991; Schwartz and Armitage, 2005). Thus, when food resources are scant in May, females of many high-elevation *Marmota* may be forced to skip a year to recoup body condition, whereas in years of abundant spring forage, they are capable of breeding in consecutive years. If this is true, consecutive year reproduction will become more common if spring snow-pack continues to decline in the Olympic Mountains.

Our observations provide less support for a release from high population densities as a cause of consecutive year reproduction. Although we did not observe annual reproduction at the most densely populated site, females did reproduce in consecutive years at several sites where marmot densities were similar to those recorded by Barash (1973). Similarly, our limited data do not directly support the reproductive suppression hypotheses, although we cannot rule out the possibility that reproductive suppression may occur in particular situations (Armitage, 2007). To effectively evaluate this would require substantial behavioral, demographic and, optimally, hormonal data to evaluate the influence of

older or dominant females on the stress levels and reproductive success of subdominant or younger animals (Hackländer *et al.*, 2003).

There has been considerable concern about the potential impacts of climate change and increased predation on high-elevation species, including marmots (Inouye *et al.*, 2000; Krajick, 2004; Bryant and Page, 2005) and both Vancouver Island marmots and Olympic marmots have declined in the last two decades (Bryant, 1998; S. C. Griffin, pers. obs). Annual reproduction potentially represents a positive response to a warming climate or reduced densities resulting from predation, but it represents only one piece of the story. Recovering and protecting these species in the face of simultaneous changes in predation pressure, climate and other yet to be identified factors will require an understanding of how marmot reproductive, survival and dispersal rates respond to changing densities and resource availability. Future studies should include a component directed at partitioning the relative importance of conspecific densities, local social structure, individual body condition, habitat and weather in determining whether an individual breeds annually or skips one or more years.

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