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YELLOW-BELLIED MARMOTS (*MARMOTA FLAVIVENTRIS*) HIBERNATE SOCIALLY

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Of 14 species of marmots (genus *Marmota*, Family Sciuridae), only 2, the woodchuck (*M. monax*) and yellow-bellied marmot (*M. flaviventris*), have not been reported to be obligate social hibernators. There is one published report of yellow-bellied marmot juveniles hibernating together at a subalpine site, and social hibernation was reported at a single high-alpine site. Solitary hibernation is expected in woodchucks because they do not share burrows during summer, but is unexpected in yellow-bellied marmots, a harem-polygynous species where females may share burrows and have extensive home-range overlap with female kin during summer. We documented emergence patterns in 13 matrilines to determine whether adult marmots hibernate socially. We found that adult males hibernated with 1 or more adult females, and mothers hibernated with their offspring. Therefore, we conclude that yellow-bellied marmots hibernate socially. There is, however, no evidence that suggests that yellow-bellied marmots receive social thermoregulatory benefits from social hibernation. Documenting social hibernation required us to quantify patterns of emergence from hibernation. Throughout our subalpine site, emergence appears to be getting earlier; a result consistent with a previous report based on 1 colony site and which suggests the effects of global climate change are affecting hibernation patterns.

Key words: climate change, evolution of sociality, *Marmota flaviventris*, social hibernation, yellow-bellied marmots

In particularly harsh winter conditions, some species require thermoregulatory benefits from conspecifics to survive winter (Arnold 1988; Madison 1984). The benefits from social thermoregulation during hibernation are considered to be important in the evolution of sociality among sciurid rodents (Arnold 1993). Specifically, complex sociality in sciurid rodents is characterized by several characteristics: delayed maturation; delayed dispersal; and social groups consisting of overlapping generations (Blumstein and Armitage 1999). Large-bodied species living in environments with short growing seasons are unable to gain sufficient body mass in their first year of life and thus hibernate in their natal social group (Armitage and Blumstein 2002). In alpine marmots (*Marmota marmota*—Arnold 1988, 1990, 1993, 1999), thermoregulatory help from parents and older siblings has been demonstrated to be essential for juvenile overwinter survival. But social hibernation and thermoregulation are not ubiquitous in the genus *Marmota*.

The behavior and ecology of yellow-bellied marmots (*Marmota flaviventris*) living in the East River Valley around the Rocky Mountain Biological Laboratory, Gothic, Gunnison County, Colorado, has been continuously studied since 1962, making these marmots some of the best studied groups of mammals in the world (Armitage 1991; Schwartz and Armitage 2003). A considerable amount of effort has been spent studying marmots during the summer active season (Armitage 1991), and some studies have focused on overwinter hibernation physiology and behavior in the laboratory (Armitage et al. 2003; Armitage and Woods, in press; Woods et al. 2002). With the exceptions of one study at a lower elevation colony in Wyoming (Armitage 1965) and another in California (Nee 1969), less effort has been focused on documenting patterns of emergence of yellow-bellied marmots from hibernation in the field. Information on patterns of emergence is essential because theories of sciurid sociality depend on the opportunity for social thermoregulatory benefits that are possible only through social hibernation (Armitage 1999; Arnold 1993; Blumstein and Armitage 1999). We quantified emergence to infer social hibernation and the opportunity for social thermoregulation. However, social hibernation may also be a reproductive strategy by males in which they associate with females with which they intend to mate following emergence (see Armitage 1998).

In most of the 14 species of marmots, both adults and young are reported to hibernate socially (Bibikow 1996), and members of social groups have overlapping home ranges

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throughout the summer active season (Armitage and Blumstein 2002; Blumstein and Armitage 1999). Exceptions to this pattern of social hibernation include woodchucks (*Marmota monax*), which typically hibernate alone (Ferron 1996; Hamilton 1934), and yellow-bellied marmots, where only young have been reported to hibernate socially (Lenihan and Van Vuren 1996) at our subalpine study site. Marmots at a higher elevation site in Gunnison County, Colorado (North Pole Basin), were reported to hibernate in groups of 2–11 individuals, but no specific details were provided about emergence behavior (Johns and Armitage 1979). Yellow-bellied marmot social behavior qualitatively differs from that of woodchucks in that woodchuck young typically disperse as juveniles before their first hibernation (Meier 1992; but see an important notable exception in Ferron 1996), whereas yellow-bellied marmot females form matrilines (female kin groups) by recruiting yearling daughters to join their social group (Armitage 1991). Lack of social hibernation in subalpine yellow-bellied marmots has been attributed to their hibernation efficiency, which is greater than other studied species (Armitage et al. 2003). Lack of social hibernation may also reflect a milder winter environment than higher elevation and latitude populations and species (Arnold 1993; Johns and Armitage 1979).

Although yellow-bellied marmots are efficient hibernators, there have been no previous studies at the subalpine Rocky Mountain Biological Laboratory study site that focused specifically on hibernation emergence behavior. The date of first marmot emergence has been documented in 1 location (the Rocky Mountain Biological Laboratory town site has contained 1–6 matrilines over the past 26 years; K. Armitage, in litt.) annually beginning in 1976 (Inouye et al. 2000). Inouye et al. (2000) noted that the date of first sighting is becoming earlier; the predicted date has shifted 23 days between 1976 and 1999. They also reported marmots emerging as early as 1 April (in 1992). However, there have been no studies on marmot emergence of the other routinely studied matrilines, and no researchers have looked for signs of emergence earlier than 2 May; a time by which many groups had already emerged (D. Van Vuren, in litt.).

We report results of a study on the emergence behavior of Rocky Mountain Biological Laboratory marmots begun in early April 2003. In particular, we looked for evidence of social hibernation, which (following Bibikow 1996; Blumstein and Arnold 1998) we inferred from more than a single individual emerging from a burrow. We focused on 14 matrilines in the East River Valley at 9 different colony sites that, in August 2002, were inhabited by approximately 137 individuals.

Materials and Methods

We began regular visits of matriline sites at Rocky Mountain Biological Laboratory (38°57′N, 106°59′W on 11 April, when there was >2 m of snow on the ground at all sites (because of avalanche conditions, snow depth was not routinely recorded at all sites), and continued until all snow had melted (1 June). We noted percentage snow cover at each of the sites and attempted to identify any animals seen above ground. Marmots emerged from burrows of 13 matrilines; there was no evidence of emergence by the 14th matriline and we concluded they had died during the winter.

Marmot colonies in our study area occupy suitable habitat patches along an elevational gradient characterized by significantly different climatic patterns and growing seasons. Four matrilines were classified as lower elevation sites (mean elevation = 2,874 m ± 9.2 *SD*; matrilines were named for trapping sites—River-South, River-Spruce, Bench, Gothic); the remaining 10 were classified as higher elevation sites (mean elevation = 2,981 m ± 36.2 *SD*—Cliff, Marmot Meadow-Aspen, Marmot Meadow-Spruce, Lower Picnic, Middle Picnic, Upper Picnic, Boulder, North Picnic, Stonefield-main mound, Stonefield-south mound). Snow melts 12 days earlier, on average, at lower elevation sites, leading to an earlier start of the vegetation growing season (the end of the growing season is primarily a function of the first killing frosts, which affect both high- and low-elevation populations around the same date—Van Vuren and Armitage 1991). Marmots wean young 12 days earlier at lower elevation sites than at higher elevation sites (K. Armitage, pers. comm.).

We routinely trapped marmots at Rocky Mountain Biological Laboratory, permanently marked them with numbered ear tags, and marked them until the next molt with nontoxic fur dye (details in Armitage 1982). Thus, marmots were often individually identifiable upon emergence. In April and May, yearlings have, on average, 48% of the body mass of adults ($n = 149$ yearlings, $n = 38$ adults), which make them easily identifiable from afar. Adult females are, on average, 77% the size of adult males (masses recorded from 26 females and 12 males) and males have distinctively wider heads. Moreover, some behavioral differences are sex specific; for instance, dominant adult males flag their tails substantially more than other age–sex classes (Armitage 1965). Thus, even without marks, it was generally possible to distinguish between age and sex classes. Our identifications, based on these observations, were then validated by live trapping animals as soon as conditions became safe for trapping.

We used unpaired t-tests to compare mean emergence dates and to study snowmelt patterns. We report P-values <0.05 as significant. Values are presented as mean ± *SD*.

Results

Marmots emerged when their summer home ranges were 95–100% covered with snow, and through what appeared to be >1 m of dense, spring snow. One matriline (Upper Picnic) completely failed to emerge from hibernation, leaving us with 13 remaining matrilines. The average date that we detected the first individual was 22 April (±11.5 days; range 12 April—13 May 2003).

While the earliest observed emergences were at higher elevation sites, overall, there was no significant difference between the average date of first sighting at higher and lower elevation sites ($P = 0.545$). However, adults emerged before yearlings and, using the date of yearling emergence as an indication of when the entire group had emerged, we found that entire groups at the lower elevation sites emerged 14 days earlier ($P = 0.011$). Additionally, if we use the date by which 50% of the individuals emerged as an indication of group emergence, lower elevation sites emerged significantly earlier (25 April) than higher elevation sites (Fig. 1; 7 May; $P = 0.048$). The first date that the home range was 50% snow free (a metric of the beginning of the growing season—Van Vuren and Armitage 1991) was significantly earlier at the lower elevation sites ($P < 0.0001$; $\bar{X}_{\text{low}}$ = 4 May; $\bar{X}_{\text{high}}$ = 21 May).

Adults emerged an average of 9 days before yearlings, and yearlings of both sexes from a litter emerged synchronously. However, some adults and yearlings also emerged simultaneously from the same burrow 8 of 10 applicable times (3 of the surviving matrilines had no young in 2002 and were excluded from this analysis). Adults were observed emerging from the same burrow with other adults 9 of 10 times (3 matrilines had only a single adult and were excluded from this analysis). Adult males were observed emerging from the same burrow as adult females 9 of 12 times (1 matriline had no obvious male associated with it and was excluded from this analysis).

Assuming a 32-day gestation period and a 28-day lactation period (e.g., Frase and Hoffmann 1980; K. Armitage, pers. comm.), the median date of estimated fertilization (9 May) was 10 days following female emergence (range 0–26 days; $n = 12$ litters) and 5 days following the date at which 50% of the group emerged (range 5–25 days; $n = 15$ litters).

Discussion

Contrary to our previous understanding of marmot behavior, our 1-year study demonstrates that subalpine yellow-bellied marmots hibernate socially. Because not much is known about the complexity and connectivity of hibernacula, it remains to be demonstrated whether in fact marmots seen emerging from the same burrow opening actually hibernated together. Observations of marmots hibernating in captivity (e.g., Armitage et al. 2003; Armitage and Woods, in press) demonstrate that, when housed socially in the same cage, individual yellow-bellied marmots are in physical contact with their cage mates. Remote telemetry (e.g., Arnold 1995) will be required to determine whether they exhibit the coordinated bouts of hibernation seen in alpine marmots, the only species for which data are available (Arnold 1993). Laboratory data on juvenile yellow-bellied marmots that were housed alone, or in groups of 3, over winter, demonstrate that bouts of torpor were not synchronized (Armitage and Woods, in press). Thus, group-housed marmots had a higher daily mass loss, spent more time engaged in costly euthermy, and took a longer time to reach deep torpor following arousal (Armitage and Woods, in press). Moreover, there was no evidence of differential survival of juveniles hibernating in the field in 256 natural litters ranging in size from 1 to 8 individuals (Armitage and Woods, in press). Clearly, benefits of social thermoregulation do not necessarily follow social hibernation.

Currently available evidence suggests that only the woodchuck typically hibernates alone and that yellow-bellied marmots, at the well-studied Rocky Mountain Biological Laboratory site, hibernate socially. Unlike the obligately social alpine marmot (Arnold 1993), the most-common yellow-bellied marmot matriline at Rocky Mountain Biological Laboratory contains a single female (Armitage and Schwartz 2000). Nevertheless, these solitary females hibernated with their young of the year and/or the group's adult male.

Even without benefits from social thermoregulation, there are other reasons why animals may hibernate together. Removing the plug from the hibernaculum and tunneling through several meters of snow involves energetic cost. By

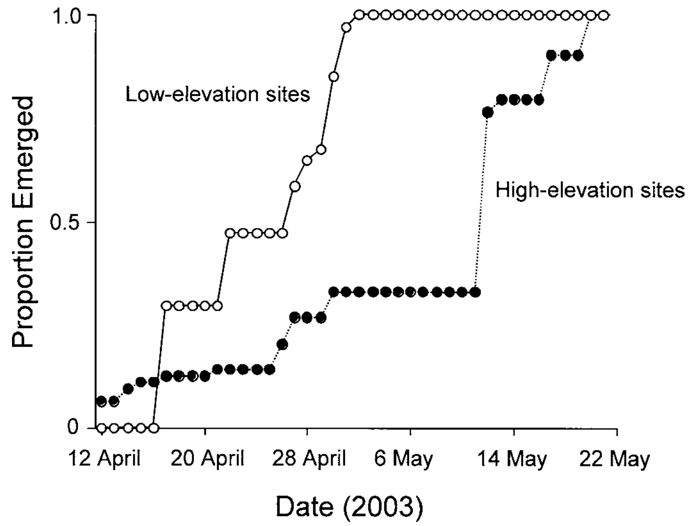

Fig. 1.—Cumulative distribution function illustrating the proportion of yellow-bellied marmots that emerged from hibernation at the 4 low-elevation (2,874 m) matrilines and 9 high-elevation matrlines (2,981 m) in the East River Valley, Gunnison County, Colorado, in 2003 ($n = 34$ marmots from low-elevation matrilines; $n = 64$ marmots from high-elevation matrilines).

hibernating socially, older animals may help unplug the burrow and save yearlings with less fat reserves energy needed to survive the postemergence period. Moreover, if adult males emerge first to begin spermatogenesis (Barnes et al. 1987; Christian et al. 1972), they may incur the cost of unplugging the burrow and digging through the snow pack, thereby allowing females to allocate more energy for reproduction.

Additionally, by sharing a hibernaculum, adult males may be better able to monopolize females upon emergence through the snow. Thus, mate choice decisions may, to some extent, be made before hibernation. Salsbury and Armitage (1994a, 1995) noted that field metabolic rates of males peaked after the mating season, a period when males wandered widely in exploratory excursions and defended their harems from intruders (Salsbury and Armitage 1994b). Such excursions allow males to gauge future reproductive opportunities. Thus, hibernating with potential mates would conceivably be important for this harem-polygynous species that emerges and breeds in a landscape covered with snow (see also Armitage 1998).

In order to study social hibernation, we documented patterns of emergence. The only published data on emergence patterns comes from a 2-year study of juvenile and yearling growth patterns (Lenihan and Van Vuren 1996). In 1991 and 1992, Lenihan and Van Vuren (1996) used radio telemetry to locate yearlings at emergence and reported some evidence of yearlings hibernating in the same burrow. In 2003, yearlings emerged on average 10 days before they had in 1991 and 16 days before they had in 1992. These results are thus consistent with the directional shift in marmot phenology reported by Inouye et al. (2000). Comparable data for adults are not available, but in 2003, adults emerged 19 days before yearlings were observed emerging in 1991 and 25 days before yearlings were observed emerging in 1992. In 2003, adults emerged an average 9 days earlier than yearlings, providing additional evidence that marmot emergences are getting earlier.

Spring temperatures around Rocky Mountain Biological Laboratory have increased by 1.4°C since 1976 (Inouye et al. 2000), with a substantial portion of this increase occurring in the past decade (D. Inouye, pers. comm.). Published (Inoyue et al. 2000) and unpublished reports (D. Inoyue and b. barr, pers. comm.) demonstrate that date of first emergence at the Gothic town site has become earlier in the past 27 years. The average date on which we observed 50% of each matriline to emerge in 2003 varied by elevation (low elevation = 25 April; high elevation = 7 May). Both averages were later than the day (21 April) marmots were first sighted above ground in 2003 at the well-studied Gothic town site (b. barr, personal communication).

Warmer temperatures in April may be the trigger for marmot emergence (Inoyue et al. 2000), but other climatic factors such as precipitation both in the winter and summer may also be important. In heavy-snow years, marmots must emerge from hibernation with more snow on the ground. In those conditions, individuals must survive in a euthermic state until food becomes available. While adults may emerge synchronously, the delay in the onset of the growing season at higher elevation sites compared with lower elevation sites appears to influence marmot reproductive phenology. This combination of early emergence and delayed onset of growing season may provide novel stresses for these higher elevation marmots. Prolonged euthermy may reduce fat reserves necessary for reproduction (Andersen et al. 1976; Bibikow 1996), thus reducing both probability of reproduction and litter size. If climatic trends continue, warmer April temperatures combined with heavier spring precipitation might adversely affect yellow-bellied marmot survival and reproduction.

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