Journal of Mammalogy, 90(5):1184–1187, 2009

SOCIAL EFFECTS ON EMERGENCE FROM HIBERNATION IN YELLOW-BELLIED MARMOTS

DANIEL T. BLUMSTEIN*

Department of Ecology and Evolutionary Biology, University of California, 621 Young Drive South, Los Angeles, CA 90095-1606, USA (DTB)

The date that yellow-bellied marmots (*Marmota flaviventris*) emerge at a site in Colorado has been used as evidence that climate is affecting hibernating species. Over 6 springs, and at 16 marmot groups, the date of 1st emergence of males, females, and the group as a whole was recorded. Emergence date of males was a function of the number of males in a group (a metric of reproductive competition) and the date that 50% of the ground was snow free in the marmot group (a metric of climatic variation). The number of adult males explained no variation in the date that the 1st adult female was detected, or the date by which one-half of the group emerged, but the 1st female was sighted earlier in groups with more females. Thus, to understand climatic effects on the phenology of social species, researchers must consider the potential for reproductive competition as well as climatic factors such as the timing of snow melt.

Key words: climate change, hibernation emergence, marmot, phenology, reproductive competition

Phenology is often quantified by the 1st date that an individual of a species is seen or otherwise detected (Miller-Rushing et al. 2008). Several biases in this date of 1st emergence have been identified that become important when one wishes to understand phenological trends. For instance, population abundance, population trajectory, and sampling effort will influence the date of 1st sighting (e.g., Miller-Rushing et al. 2008; Sparks 1999; Tryjanowski et al. 2005; van Strien et al. 2008). Long-term data sets will be systematically biased because the date of the vernal equinox gets earlier throughout a century (Sagarin 2001). However, potential biases uniquely associated with sociality have remained unstudied.

Sociality is characterized by reproductive competition (Blumstein and Armitage 1998). Males may compete for breeding opportunities and may have to begin their breeding season earlier than females (as seen in most socially monogamous, migratory, territorial birds—Morbey and Ydenberg 2001). Individuals of species that live in social groups may engage in other forms of reproductive competition; males may compete for access to females within a social group, as seen in elephant seals (*Mirounga*—Ling and Bryden 1992; Stewart and Huber 1993), and females may compete for breeding opportunities, as seen in wolves (*Canis lupus*—Mech 1974).

* *Correspondent: marmots@ucla.edu*

Hibernation or seasonal torpor is a widespread adaptation to inhospitable climates (Geiser and Ruf 1995), and the 1st emergence following the termination of hibernation is widely used as a metric of the start of the season (e.g., Inouye et al. 2000). Although individuals of many species hibernate alone, social species may hibernate socially and may (Arnold 1993) or may not benefit from social thermoregulation (Blumstein and Arnold 1998). Regardless of benefits obtained while hibernating, social species may engage in reproductive competition following the termination of hibernation (Preston et al. 2003; Waterman 2007). In many species of hibernating sciurid rodents (and other taxa—e.g., Körtner and Geiser 1998), males emerge 1st to initiate spermatogenesis (Christian et al. 1972), and once females emerge, receptivity may be limited (Waterman 2007). If reproductive competition influences the date by which individuals emerge following the termination of hibernation, then it should explain some variation in the date animals (which are likely to be males) are 1st sighted.

Yellow-bellied marmots (*Marmota flaviventris*) are facultatively social, hibernating sciurid rodents (Armitage 2003a). They are a somewhat iconographic species because of a long-term study that tracks the emergence date at 1 colony site at the Rocky Mountain Biological Laboratory in Gothic, Colorado (Inouye et al. 2000). Since 1975, the date that the 1st marmot has been sighted at this colony site is getting earlier. Emergence dates are correlated with measures of spring air temperature and suggest that the marmots are using air temperature as a cue to terminate hibernation (Inouye et al. 2000); the mechanism by which they do so remains to be studied given that their hibernacula are beneath a blanket of snow.

Males and females may hibernate in the same or different hibernacula (Blumstein et al. 2004), and social groups may contain multiple active hibernacula. Marmots mate immediately following emergence and mating opportunities for males are typically restricted to females in the immediate area (Armitage 1991; Blumstein et al. 2004). Marmots are social and about 50% of the social groups studied between 2003 and 2008 had more than a single male present during the short mating season. Thus, there is the opportunity for males to compete for access to females.

I tested the hypothesis that the number of adult males in a yellow-bellied marmot social group, a metric of male reproductive competition, explains variation in the date that marmots were 1st sighted, as it would if males in multimale groups emerged earliest. I fitted general linear models with the following independent variables: the number of adult males, the number of adult females, and the date that 50% of the snow cover in a marmot group territory had melted, a climatic metric (Blumstein et al. 2004; Van Vuren and Armitage 1991). I also fitted similar models to explain the date that the 1st identifiable male and female were sighted, as well as a metric of group emergence (the date that 50% of the members of the group had been seen).

Materials and Methods

In the springs of 2003 through 2008, in and around the Rocky Mountain Biological Laboratory (38°57′N, 106°69′W), at 16 different marmot groups along a 5-km elevational gradient, assistants and I noted the date that we 1st saw marmots and, when possible, identified the individuals. Marmots are matrilineal and groups contained 1 or more females and their offspring that hibernated in 1 or more hibernacula (Blumstein et al. 2004). We searched for emergences in areas where we had seen marmots during the previous summer. During the previous summers, animals were livetrapped, and age and sex were determined. Methods followed guidelines approved by the American Society of Mammalogists (Gannon et al. 2007). We permanently marked each individual with unique ear tags, and unique marks were dyed into their dorsal pelage. These fur marks permitted identification from afar and were typically present at emergence.

We visited sites as often as weather permitted (we aimed to visit at least every other day) and either skied through them, looking for signs of emergence in the snow, or scanned them with binoculars and spotting scopes. Although some sites were inaccessible due to avalanche hazards, on those steep slopes burrowing activity in the snow was obvious from afar and marmots were easily spotted. If we detected signs of marmot activity, we waited for the marmots to emerge and identified animals. In most years we began searching for emergences on 17 April; in 2003, we began on 11 April (excluding this year did not change the nature of our results), and in 2008 (a year with an exceptionally deep snowpack) we began on 19 April. When a site was visited, we also estimated the percentage snow cover. Snow cover was estimated with reference to the anticipated home-range size that was based on the previous summer's home range. Observers visually estimated snow cover. Observers were trained until their estimates were within 5% of a trained ''reference'' observer. We continued these censuses until all animals in a group had been accounted for. In 2007, the snow pack melted unseasonably early, and a marmot was detected (and photographed) by the Laboratory's winter caretaker on 24 March at the Rocky Mountain Biological Laboratory town site. I included this emergence date in the final data set (setting it to 17 April did not change the nature of the results).

We classified sighted animals as yearlings or adults, and then tabulated the date the 1st marmot was seen, the date the 1st identified adult male was seen, the date the 1st identified adult female was seen, and the dates that 50% of the group (this metric included yearlings) and 50% of the adult females had emerged. In the cases where individuals were killed by predators or starved before the entire group had emerged, we counted those individuals in the cumulative total. In some cases, we detected marmots but could not identify them. Thus, sample sizes between the categories (1st in group, 50% of group, 1st adult male, and 1st adult female) vary. If we could assign an animal to an age class (adult or yearling), but not precisely identify it (i.e., we could not read its mark), I scored it in the appropriate category.

I treat the group-year as statistically independent observations and justify this because social composition, and social relationships, changed annually through births, deaths, immigration, and dispersal. Thus, emergence groups varied annually.

General linear models were fitted to explain variation in these dependent variables (1st emergence, 50% of group emergence, 1st male emergence, and 1st female emergence). The independent variables were the number of adult males at the site, the number of adult females at the site, and the date of 50% snow cover (transformed into the number of days since 1 January of that year). I used the date of 50% snow cover as the ''start of the growing season'' because 2 previous studies at this site used it this way (Blumstein et al. 2004; Van Vuren and Armitage 1991). As the snow melted, the vegetation immediately began growing. Thus, the date of 50% snow cover reflected the date by which one-half the area a group occupied had some green vegetation. Finally, this date varied between groups and among years. I also calculated *B*-values, partial η^2-values, and adjusted R^2 values. The variables met assumptions of general linear models. Data were examined for multicollinearity (independent variables were not excessively correlated: snowmelt–*n* adult females—$r = -0.001$, $P = 0.990$; snowmelt–*n* adult males—$r = 0.136$, $P = 0.208$; *n* adult males–*n* adult females—$r = 0.665$, $P < 0.001$), and residuals from the model appeared normally distributed.

Results

A total of 88 marmot group-years contributed data to these analyses (not all sites had marmots each year; in some years

TABLE 1.—General linear model results explaining variation in the date that the 1st yellow-bellied marmot (*Marmota flaviventris*) was sighted in a group, the date 50% of the group had emerged, the date that the 1st adult male was sighted, and the date that the 1st adult female was sighted. Independent variables included the number of adult males in the group and the date that 50% of the ground was clear of snow (50% snow melt) in the group.

Dependent variable	*n*	Adjusted R^2	*P*	Intercept *B*-score	50% snow-melt *B*-score	50% snow-melt *P*	50% snow-melt η^2	*n* adult males *B*-score	*n* adult males *P*	*n* adult males η^2	*n* adult females *B*-score	*n* adult females *P*	*n* adult females η^2
1st group	87	0.317	<0.001	70.602	0.374	<0.001	0.249	−2.347	<0.001	0.046	−0.586	0.151	0.025
50% group	87	0.438	<0.001	57.737	0.488	<0.001	0.445	0.367	0.711	0.002	−0.112	0.741	0.001
1st adult male	72	0.265	<0.001	67.570	0.409	<0.001	0.236	−2.730	0.117	0.036	−0.241	0.646	0.003
1st adult female	78	0.357	<0.001	74.764	0.343	<0.001	0.310	1.048	0.286	0.015	−1.009	0.004	0.105

we were not sure of locations of hibernacula, which may change annually). Group size averaged 9 marmots (*SD* = 7.6; range: 1–44), consisting of an average of 1 adult male (*SD* = 1.1; range: 0–6) and 3 adult females (*SD* = 3.1; range: 0–16) plus an average of 4 yearlings (*SD* = 4.1; range: 0–16). The maximum group size (44) was not equal to the sum of the maximum in each cohort because, in this very large group, 6 nonyearling marmots were unmarked and hence their sex was not known. First emergences averaged 26 April (*SD* = 10.5 days; range: 24 March–30 May) and the date by which 50% of the group emerged averaged 3 May (*SD* = 9.7 days; range: 16 April–31 May). The date of 50% snow cover averaged 15 May (*SD* = 13.5 days; range: 17 April–7 June).

As previously reported (Inouye et al. 2000), emergence of marmots was influenced by climatic factors. What was not known is that marmots were 1st detected earlier when the snow melted earlier as well as when there were more males in the group (Table 1). These effects were additive. For each additional male in the group, marmots emerged about 2 days earlier, and for each additional day it took for one-half of the snow to melt, marmots emerged about one-half of a day later. Although not significant (because of a smaller sample size), the effect of males on the date the 1st male was sighted was similar (Table 1). By contrast, variation in the date by which one-half of the group was seen, or the date at which the 1st adult female was seen were not explained by the number of adult males, but were consistently explained by the date of 50% snow cover. Moreover, the number of adult females in a group only explained variation in the date that the 1st adult female was detected (Table 1).

DISCUSSION

The date that marmots emerge in and around the Rocky Mountain Biological Laboratory is influenced by climatic factors. Marmots typically emerge earlier at lower elevations (Blumstein et al. 2004) and in years when it is warmer and there is less snow (Inouye et al. 2000). Inouye et al. (2000) focused on 1 marmot group, the Gothic town site. These results extend their previous findings to 5 km of the valley and to both lower and higher altitudes, and reaffirm the importance of climatic factors on duration of hibernation.

The study has identified a heretofore-ignored source of bias. Until now, phenological variation in behavior was assumed to reflect environmental variation, and biases were considered to be sampling artifacts. This study demonstrates that, for social animals, the start of a key event (emergence from hibernation) may be influenced by social factors as well as climatic ones. Male marmots emerge and must find mates. The 1st date that an individual in a group was sighted was influenced by the number of males in a group, but not the number of females. Although not significant (because of a smaller sample size), a similar effect was identified for the date that the 1st male was detected. By contrast, the number of females in a group did not explain variation in the date that a marmot was 1st sighted, 50% group emergence, or the date a male was 1st detected. However, females were 1st sighted earlier in groups with more females and this finding is consistent with observed patterns of reproductive competition among female marmots (Armitage 2003b). As Armitage (2003b) noted, 2-year-old and 3-year-old females in groups with older breeding females in them are less likely to wean young than when found in groups without older breeding females. Perhaps in these larger groups, there is competition for younger females to emerge earlier and mate and thus avoid competition with other females for access to males. Future work could explore the relationship between age and emergence date in more detail.

Together, these results reveal a pattern that reflects reproductive competition rather than a statistical sampling artifact. For instance, one might assume that observers would detect animals in larger groups simply because there are more animals to detect. If so, we would expect that the number of adult females should explain substantial variation in the date of 1st emergence because marmot social groups are mostly composed of adult females. Rather, it was specifically the number of adult males that explained variation in the date that individuals were 1st detected. Additionally, only snow cover, not males or females, explained the date that 50% of the group had emerged. These observations are consistent with the hypothesis that male reproductive competition creates a potential bias in the ability to study phenology when annual cycles are quantified by dates of 1st sighting.

Males may or may not hibernate socially (Blumstein et al. 2004). If they do not hibernate in the same burrow, how might they assess reproductive competition? I speculate that before hibernation, males assess the number of potential competitors and then base their emergence decision on the results of this assessment. This is likely because field metabolic rates of male marmots increase after the brief mating season throughout their active season (Salsbury and Armitage 1994a). This finding is consistent with males' ongoing competition with other males. Additionally, after the mating season, resident males may leave their home range and explore surrounding areas (Salsbury and Armitage 1994b). Together, these findings and observations suggest that males assess future reproductive opportunities before hibernation and likely base their emergence date on perceived competition.

Future studies of hibernation phenology for social animals aiming to document emergence date should account for variation explained by social factors. Alternatively, as proposed for other studies, phenological studies of social animals may focus on estimates less influenced by biases introduced by behavior (e.g., Miller-Rushing et al. 2008). For yellow-bellied marmots, the date by which one-half of the group emerged is unaffected by the number of males in a group and could serve as a better indicator of behavioral responses to climate change than the day of 1st sighting.

Acknowledgments

I thank K. Armitage, B. Barr, P. Bednekoff, D. Inouye, A. Miller-Rushing, L. Olson, P. Jones, D. Van Vuren, T. Wey, and 2 anonymous reviewers for comments, discussions, and assistance. Research was conducted under permits from University of California Los Angeles, The Colorado Division of Wildlife, and the Rocky Mountain Biological Laboratory, and was partially supported by University of California Los Angeles, The Unisense Foundation, the National Geographic Society (8140-06), and the National Science Foundation (IDBR-0754247 to DTB and DBI-0242960 to the Rocky Mountain Biological Laboratory).

Literature Cited

Armitage, K. B. 1991. Social and population dynamics of yellow-bellied marmots: results from long-term research. Annual Review of Ecology and Systematics 22:379–407.

Armitage, K. B. 2003a. Marmots (*Marmota monax*) and allies. Pp. 188–210 in Wild mammals of North America: biology, management, and conservation (G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds.). 2nd ed. Johns Hopkins University Press, Baltimore, Maryland.

Armitage, K. B. 2003b. Reproductive competition in female yellow-bellied marmots. Pp. 133–142 in Adaptive strategies and diversity in marmots (R. Ramousse, D. Allainé, and M. Le Berre, eds.). International Marmot Network, Lyon, France.

Arnold, W. 1993. Social evolution in marmots and the adaptive value of joint hibernation. Verhandlungen der Deutschen Zoologischen Gesellschaft 86:79–93.

Blumstein, D. T., and K. B. Armitage. 1998. Life history consequences of social complexity: a comparative study of ground-dwelling sciurids. Behavioral Ecology 9:8–19.

Blumstein, D. T., and W. Arnold. 1998. Ecology and social behavior of golden marmots (*Marmota caudata aurea*). Journal of Mammalogy 79:873–886.

Blumstein, D. T., S. Im, A. Nicodemus, and C. Zugmeyer. 2004. Yellow-bellied marmots (*Marmota flaviventris*) hibernate socially. Journal of Mammalogy 85:25–29.

Christian, J. J., E. Steinberger, and T. D. McKinney. 1972. Annual cycle of spermatogenesis and testis morphology in woodchucks. Journal of Mammalogy 53:708–716.

Gannon, W. L., R. S. Sikes, and Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Geiser, F., and T. Ruf. 1995. Hibernation versus daily torpor in mammals and birds: physiological variables and classification of torpor patterns. Physiological Zoology 68:935–966.

Inouye, D. W., B. Barr, K. B. Armitage, and B. D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences 97:1630–1633.

Körtner, G., and F. Geiser. 1998. Ecology of natural hibernation in the marsupial mountain pygmy-possum (*Burramys parvus*). Oecologia 113:170–178.

Ling, J. K., and M. M. Bryden. 1992. *Mirounga leonina*. Mammalian Species 391:1–8.

Mech, L. D. 1974. *Canis lupus*. Mammalian Species 37:1–6.

Miller-Rushing, A. J., T. L. Lloyd-Evans, R. B. Primack, and P. Satzinger. 2008. Bird migration times, climate change, and changing population sizes. Global Change Biology 14:1959–1972.

Morbey, Y. E., and R. C. Ydenberg. 2001. Protandrous arrival timing to breeding areas: a review. Ecology Letters 4:663–673.

Preston, B. T., I. R. Stevenson, J. M. Pemberton, D. W. Coltman, and K. Wilson. 2003. Overt and covert competition in a promiscuous mammal: the importance of weaponry and testes size to male reproductive success. Proceedings of the Royal Society of London, B. Biological Sciences 270:633–640.

Sagarin, R. 2001. False estimates of the advance of spring. Nature 414:600.

Salsbury, C. M., and K. B. Armitage. 1994a. Resting and field metabolic rates of adult male yellow-bellied marmots, *Marmota flaviventris*. Comparative Biochemistry and Physiology, A. Comparative Physiology 108:579–588.

Salsbury, C. M., and K. B. Armitage. 1994b. Home-range size and exploratory excursions of adult, male yellow-bellied marmots. Journal of Mammalogy 75:648–656.

Sparks, T. H. 1999. Phenology and the changing pattern of bird migration in Britain. International Journal of Biometerology 42:134–138.

Stewart, B. S., and H. R. Huber. 1993. *Mirounga angustirostris*. Mammalian Species 449:1–10.

Tryjanowski, P., S. Kuzniak, and T. H. Sparks. 2005. What affects the magnitude of change in first arrival dates of migrant birds? Journal of Ornithology 146:200–205.

van Strien, A. J., W. F. Plantenega, L. L. Soldaat, C. A. M. van Swaay, and M. F. WallisDeVries. 2008. Bias in phenology assessments based on first data of butterflies. Oecologia 156:227–235.

Van Vuren, D., and K. B. Armitage. 1991. Duration of snow cover and its influence on life-history variation in yellow-bellied marmots. Canadian Journal of Zoology 69:1755–1758.

Waterman, J. 2007. Male mating strategies in rodents. Pp. 27–41 in Rodent societies: an ecological and evolutionary perspective (J. O. Wolff and P. W. Sherman, eds.). University of Chicago Press, Chicago, Illinois.

Submitted 7 November 2008. Accepted 23 February 2009.

Associate Editor was Fritz Geiser.