# Do evolved, ecological, or social constraints affect hoary marmot reproduction? An analysis of a presumed biennial breeder

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**Abstract**

Biennial breeding is a rare life-history strategy observed in several long-lived bird and mammal species found in harsh, unproductive environments. This behavior is thought to occur in 10 of 14 species in the genus Marmota, making marmots useful model organisms for studying its ecological and evolutionary implications. Biennial breeding in marmots is frequently described as an obligate behavior which evolved as a mechanism to mitigate the energetic costs of reproduction (The Evolved Constraint hypothesis). However, recent anecdotal evidence suggests that it is a facultative behavior controlled by annual variation in climate and food availability (The Environmental Constraint hypothesis). Finally, in social animals like marmots, biennial breeding could result from reproductive competition between females within social groups (The Social Constraint hypothesis). We evaluated these three hypotheses using mark-recapture data from an 8-year study of hoary marmot (*Marmota caligata*) population dynamics in the Yukon. Annual variation in breeding probability was modeled using multi-state mark-recapture models, while other reproductive life-history traits were modeled with generalized linear mixed models. Hoary marmots were neither obligate or facultative biennial breeders, and breeding effort was insensitive to evolved, environmental, or social factors. However, newly mature females were significantly less likely to breed than older individuals. Annual breeding did not result in increased mortality. Average fecundity and female survival were correlated with winter climate, as indexed by the Pacific Decadal Oscillation. Hoary marmots are less conservative breeders than previously believed, and the evidence for biennial breeding throughout Marmota, and in other alpine animals, should be re-examined. Prediction of future population dynamics requires an accurate understanding of life history strategies, and of how life history traits allow animals to cope with changes in weather and other demographic influences.

**Introduction**

Biennial breeding, or reproductive skipping, is an uncommon vertebrate life history strategy that is characteristic of a few groups of long-lived birds and mammals (Heezik et al. 1994, Chastel 1995, Blumstein and Armitage 1999, Dane 2002). Most biennial-breeding species live in harsh, unproductive environments such as arctic and alpine habitat, and this behavior is generally explained as a consequence of environmental constraints on reproduction. (Wasser and Barash 1983, Chastel 1995, Jouventin and Dobson 2002, Griffin et al. 2007). However, harsh environments can also be highly stochastic (Wingfield and Kitaysky 2002, Schwartz and Armitage 2004, Martin and Wiebe 2004). In such situations, a conservative life history strategy involving biennial breeding may be maladaptive, because animals that skip one reproductive opportunity may not live long enough to reproduce in the future (Benton et al. 1995).

Most research on biennial breeding has involved long-lived seabird species with small clutch sizes (Heezik et al. 1994, Chastel 1995, Jouventin and Dobson 2002). For example, most albatross species can live for 40 years or more and lay only one egg at a time (Jouventin and Dobson 2002). Reproductive skipping may be beneficial for these species because their life histories prioritize parental investment in a limited number of young. Biennial breeding has not been well-studied in mammals, or in animals with less extreme K-selected life histories. Among mammals, it is most common in the genus *Marmota*. Of the fourteen extant marmot species, ten have been reported to skip one or more years when breeding (Blumstein and Armitage 1999). Although marmots are capable of living 10-15 years in the wild, adult survival rates can vary widely from one year to the next (Patil et al. in review, Bryant and Page 2005, Schwartz and Armitage 2004, Griffin 2008; Farand et al. 2002) Litter sizes are typically around 3-4, but can be as large as 7 in some species (Schwartz et al. 1998, Allaine et al. 2000). Three alternative but not mutually exclusive hypotheses could explain biennial breeding in marmots: the Evolved Constraint hypothesis, the Ecological Constraint hypothesis, and the Social Constraint hypothesis.

The Evolved Constraint hypothesis, which is similar to the explanation proposed for albatrosses, predicts that biennial breeding in marmots is a highly canalized evolved strategy for minimizing the costs of reproduction in a harsh environment. This hypothesis is difficult to test directly. However, it implies that biennial breeding is an essentially obligate behavior, leading to the prediction that annual breeding should be extremely rare, and that females who breed twice in a row should incur a heavy fitness cost (Weimerskirch et al. 1987). There is apparently a physiological cost to reproduction for at least two marmot species: breeding female hoary and Olympic marmots spend more time foraging, stay active later in the fall, and weigh less at immergence than non-breeders (Barash 1980). However, the impact of this energetic loss on survival and lifetime fitness has not been determined.

Both Olympic and hoary marmots are supposedly biennial breeders, but annual breeding has been anecdotally observed in both species (Kyle et al. 2007, Griffin et al. 2007). It is unclear how common such events are, but frequent annual breeding would imply that the reproductive strategies of marmots are more flexible than previously believed. This leads to the Ecological Constraint hypothesis, which predicts that biennial breeding in marmots may only occur when the environment is too unproductive or the animal’s condition is too poor to support more frequent reproduction. Animals that live in harsh environments often have plastic life histories that allow them to mitigate the costs of bad years while taking advantage of good years (Wingfield and Kitaysky 2002). Such plasticity would make sense for alpine-dwelling marmot species, because their habitats can be extremely variable (Schwartz and Armitage 2004). Based on this hypothesis, both annual and biennial breeding may occur, but previous breeding state should be correlated with current breeding probability (due to the physiological costs described in Barash 1980).. The Ecological Constraint Hypothesis also leads to the prediction that the probability of breeding for all females should be a function of environmental conditions. However, the effects of climate and breeding history could be additive or interactive. Finally, under this hypothesis there could still be a survival cost to reproduction, but it should either be attenuated or compensated for by change in another demographic variable during unusually ‘good’ years.

Because marmots are social animals, reproductive skipping may also be caused by competition between females (the Social Constraint Hypothesis). Dominant females suppress reproduction by subordinates in both alpine and yellow-bellied marmot social groups (Armitage and Schwartz 2000, Hackländer et al. 2003). In alpine marmots, this behavior leads to higher survival among the dominant female’s offspring, which benefit from the presence of non-breeding subordinate adults during hibernation (Arnold 1990). There is speculation in the literature that most or all marmot species that supposedly breed biennially practice reproductive suppression, but suppression has been difficult to document in wild populations (Wasser and Barash 1983, Griffin et al. 2007). If this hypothesis is true, the average probability of breeding should decrease as the number of mature females per group increases (Blumstein and Armitage 1998). Reproductive suppression may also result in decreased breeding probability for younger females, especially in larger groups (Armitage and Schwartz 2000).

We studied the breeding patterns of hoary marmots in the Yukon, Canada using multi-state mark-recapture models. This study was the first formal analysis of variation in breeding probability in a marmot species classified as a biennial breeder. Our main objectives were to determine the probability of annual and biennial breeding, and to evaluate the relative support for the three hypotheses described above. To help address our hypotheses, we also quantified the survival cost associated with reproduction, and compared this cost with the physiological costs (slower mass accumulation in summer, lower body mass at immergence) described by Barash (1980), and with the influence of winter climate on survival. Finally, we examined sources of variation in litter size and average social group fecundity to determine whether the processes that governed breeding probability also influenced other reproductive life history traits.

**Methods**

Study species

Hoary Marmots are highly social arctic and alpine herbivores that live near patches of exposed talus scattered throughout the mountains of western Canada (Barash 1989). Unlike other alpine marmot species, hoary marmot family groups may exhibit both monogamous and polygonous mating strategies (Kyle et al. 2007). Although dominant females may suppress reproduction by subordinates or practice infanticide, multiple litters per family group, from multiple females, are common. Typically, family groups contain only one dominant male, who fathers all offspring. In our study site, extra-pair paternity was infrequent, and the timing of juvenile emergence suggests that most reproduction occurs prior to emergence from hibernacula in the spring (Kyle et al. 2007).

Study Site

This study was conducted on Hoary Marmots inhabiting a single 4 km2 valley in the Southwest Yukon (61º12’N, 138º16’W; 1700-2100m). The valley is entirely above treeline, and is characterized by a mix of wet and dry tundra interspersed with talus. Dominant plant species include *Dryas octopetala, Cassiope tetragona, Carex spp.*, and a variety of dwarf willow species (*Salix spp*.) Hoary Marmots, Collared Pikas (*Ochotona collaris*), and Arctic Ground Squirrels (*Urocitellus parryii*) are the dominant herbivores, although Caribou and Dall Sheep are also present.

### Capture methods

From May to August, 1999 to 2004, we live-captured, marked and released most marmots in the population, Live-traps of various sizes (Tomahawk Live Trap Company, Tomahawk, WI) were baited with human urine (Taulman 1989) and live vegetation from the adjacent alpine meadows (Hansen 1975; Holmes 1984b). Juveniles were captured upon emergence from the natal burrow in early- to mid-July. At first capture, all marmots were marked in each ear using No. 3 monel tags (National Band and Tag, Newport, Kentucky) and a small piece of colored wire. A unique alphanumeric combination was dyed (Clairol Hydrience, #52 Black Pearl, Clairol Canada, Montreal, Quebec or Nyanzol-D American Colour and Chemical Corp., Charlotte, NC) into the fur above the tail to allow for individual identification atup to 200 m with binoculars. Colored wires were replaced annually, and faded dyed markings were reapplied as necessary at subsequent recaptures. Marmots were also resighted opportunistically by all field personnel throughout the summer, and their locations recorded according to a north-oriented grid marked at 50m intervals with wooden stakes.

### Social group assignment

Most individuals were assigned to a social group based on observations of spring emergence from a common hibernaculum. If animals were not observed at emergence, we assigned social groups based on observation of social interactions and home-range overlap (Kyle et al. 2007). Individual home ranges were estimated using location data for resighted and radio-tagged marmots, which were analyzed in program Ranges V (Kenward and Hodder 1996). In a subset of marmots with known social group affiliations, group members had >75% overlap in the 95% kernel estimate of home range (Worton 1989). We therefore used 75% as a cutoff for statistical social group assignments. These assignments were then verified based on social interactions between individuals. Juveniles were assigned to the social group of their putative mother, which was subsequently verified using genetic markers (Kyle et al. 2007). Only marmots that could be confidently assigned to a social group in our study area (i.e. non-transients) were included in our analyses.

Analyses

From an initial dataset of 217 marmots trapped between 1999 and 2004, we created a second, more limited dataset consisting only of female marmots two years old or older (76 individuals, 203 marmot-years). We excluded yearlings from this dataset because hoary marmots are not reproductively mature until age two, and generally do not reproduce until age three. In each year, we classified marmots as breeders or non-breeders based on two criteria: genetic parentage assignment and evidence of lactation during capture. Finally, we generated an encounter history for each animal in which the individual was considered present if sighted or captured at least once that year.

In 2007-2009, a subset of four social groups was trapped, representing approximately half the population of the valley. All measurements and marking techniques were identical to those used in the earlier census. We could not definitively assign all litters to parents or determine the breeding status of all females in 2007-2009, so these data were excluded from our CMR analyses. However, the number of litters, and the number of juveniles per litter (within a week of emergence), were counted for all four social groups trapped in 2007-2009. Hoary marmot females produce one litter per year (Barash 1975), so we used the number of litters as an estimate of the number of breeding females in those years. Data from 2007-2009 were used to evaluate the ability of our CMR models to predict the number of breeding females in a given year, and were incorporated into models of fecundity and litter size.

### Multi-state CMR analysis framework

We analyzed the adult female mark-recapture dataset using multi-state models (Lebreton et al. 1992, Nichols et al. 1994). This involved constructing a set of candidate models to explain variation in three parameters: Survival (S), detection probability (p), and a ‘movement’ parameter describing the probability of moving between a ‘Non-breeder’ state and a ‘Breeder’ state (Ψ). Before analyzing the data, we conducted a goodness-of-fit (GOF) test using program U-CARE (Choquet et al. 2009). Because we did not detect significant lack of fit in a fully time- and group-dependent global model, we were able to use Akaike’s Information Criterion corrected for sample size (AICC) to compare models (Burnham and Anderson 2002). Based on previous analyses (Patil et al. in review), p was modeled as a constant. The mean detection probability was 0.96 *±* 0.02 (SE).

Candidate model set

Probability of breeding

We selected the models in our candidate model set to represent all alternative hypotheses about the effects of age, social structure, climate, and previous breeding state on the probability of an individual choosing to breed. Age effects were included because we expected that older, more experienced marmots would be more likely to attempt reproduction than those which had recently matured. Previous breeding state was constrained to affect only older (> three year) marmots, because two-year-olds generally do not breed. Only 2 two-year-olds reproduced during the course of the study, and these individuals were excluded to simplify analyses.

We used the mean value of the Pacific Decadal Oscillation index (PDO) from November and May to model annual winter weather (<http://www.esrl.noaa.gov/psd/data/climateindices>). PDO is a 20-30 year cyclic pattern of climate variation in the North Pacific Ocean that correlates well with temperature and precipitation throughout northwestern North America (Mantua and Hare 2002; Mantuaet al. 1997). Within its multidecadal cycle, PDO also fluctuates annually. These annual fluctuations were negatively correlated with the date of spring snowmelt in an earlier study at our site (Morrison and Hik 2007), annual snow accumulation on nearby Mt. Logan (~100 km; Moore et al. 2002), and snow depth at weather stations across the Yukon (Hegel et al. 2009). There was also a positive relationship between PDO and air temperature in the Yukon (Hegel et al. 2009).

The social environment was measured as i) the total number of non-juvenile marmots within the social group that were resighted or captured after July 1 during the previous summer (Group), and ii) the number of reproductively mature females in the group (Ad. fem). Both covariates would be negatively related to breeding probability if reproductive suppression were common in the population. A complete list of covariates used, as well as their abbreviations, is given in Table 3-1.

Survival

Survival models included only three covariates: winter PDO, winter PDO lagged by one year, and current breeding state. Previous survival analyses suggested that winter climate was by far the dominant influence on survival; however, those analyses did not include breeding state. We therefore chose this simplified model set in order to test the cost-of-reproduction hypothesis while accounting for the large known influence of climate on survival.

CMR analyses / evaluation of fit

We constructed all mark-recapture analyses using program MARK and the RMark package in R (Laake and Rexstad 2007, R Development Core Team 2009). We ranked models using AICC (Akaike et al. 1973), and evaluated the relative importance of covariates by summing their AICC weights across the entire model set (Burnham and Anderson 2002). We also model-averaged Ψ and S across the entire model set (Burnham and Anderson 2002, Anderson 2008). Finally, we used the averaged Ψ values to predict the number of breeding females in 2007-2009. These predictions were compared with the estimated number of breeders from those years to test the generality of our results.

Fecundity models

We used generalized linear mixed models (GLMM’s) to examine the effects of winter PDO, lagged winter PDO, group size, and group\*climate interactions on three measures of hoary marmot fecundity. Models were fit using the lme4 package in R (Bates and Maechler 2010). The three response variables were juveniles per social group (n = 78), average fecundity (juveniles per adult female w/in group; n=66), and litter size using a dataset of all fully enumerated litters with known mothers (n = 41). Error distributions were chosen after testing for conformity to a Poisson distribution (Scrucca 2004). Random effects were included based on likelihood ratio tests using the most parameterized fixed-effects model in each model set (Bolker et al. 2009). Results of overdispersion tests, the error distributions and the random effects used for each response variable are shown in Table 3-2 . In all cases, we ranked models and calculated the relative support for individual variables using AICC. Beta-coefficients were model-averaged, and unconditional standard errors for those coefficients were estimated by bootstrapping with 10,000 replications. The covariates used in all models are listed in Table 3-1.

**Results**

Breeding probability

Models with previous breeding state as a predictor of Ψ were weakly supported (Table 3-3), and the model-averaged effect size (difference in Ψ between breeders and non-breeders) was < 0.01. Model selection did not support PDO as a predictor of Ψ, the probability of moving into the ‘Breeder’ state (Table 3-3; Table 3-4). Social group size and the number of reproductively mature females per group were both moderately supported (Table 3-3; Table 3-4). However, model-averaged Ψ estimates varied by less than 1 SE from year to year in both age-classes (Fig. 3-1). Age-class had the strongest support of any model covariates, and had the largest effect size (Table 3-4; Fig. 3-1). Annual variation in Ψ was more pronounced for females in their first year of reproductive maturity, but the uncertainty in parameter estimates was also greater for this age-class (Fig. 3-1). On average, the breeding probability of females four years old or older was 0.33 greater than that of three-year-old individuals (Fig. 3-1).

When model-averaged estimates of breeding probabilities were used to predict the number of breeding females in a subset of the population during 2007-2009, the results were within 1-2 litters of the observed values in each year (Fig. 3-2). Year-to-year variation in the number of breeding females was also predicted accurately (Fig. 3-2).

Survival / cost of reproduction

Although there was moderate support for breeding state as a predictor of survival, its effect size was negligible (Table 3-3; Table 3-4; Fig. 3-3). Winter climate was a much stronger predictor of survival (Table 3-3; Table 3-4). PDO and lagged PDO were negatively correlated with survival, which declined over the course of the study by ~0.35 (Fig. 3-3).

The body condition index (log mass/zygomatic arch) of non-breeding females increased faster over the course of the season than that of breeders (Fig. 3-4). The difference in slopes was highly significant (Δ = 0.0021, p < 0.001, adjusted R2 = 0.60). On average, non-breeders had a greater body condition at the end of August than non-breeders (Fig. 3-4).

Group fecundity

The juveniles per group dataset contained significant Poisson overdispersion, so negative binomial models were used (Table 3-2). Likelihood-ratio tests did not support either slope or intercept random effects (Table 3-2). Model selection strongly favored social group size as a positive predictor of the number of juveniles produced per group (Table 3-5). Each additional group member corresponded to ~1 additional juvenile (e 0.06 = 1.06; Table 3-6). There was also strong support for a negative relationship between group fecundity and winter PDO (Table 3-6). The bootstrap 95 % confidence interval for the beta coefficient corresponding to PDO’s effect was large and overlapping with 0, but this overlap was very small (Table 3-6). Support for PDOlag and climate\*group size effects was weak (Table 3-6).

Juveniles per female (average fecundity)

AIC weights strongly supported a negative relationship between average fecundity and winter PDO, and moderately supported a positive relationship with PDOlag (Table 3-6). However, the 95 % confidence interval for the model-averaged PDO and PDOlag beta coefficients overlapped with zero. Social Group effects were moderately supported, but did not show a consistent negative or positive relationship with fecundity (Table 3-6). Interactions between climate and social effects were not as well supported, and the confidence intervals for their beta coefficients all included positive and negative values. Likelihood ratio tests indicated significant random effects of social group (intercept effect) on average fecundity, but no random slope effects were supported (see table 3-2).

Litter size

The null model had the smallest AICC value in the litter size model set, which means that litter size was not well predicted by group size, winter climate, or a combination of the two. The probability of a type II error was low. For example, for a model with litter size as a function of PDO alone, power associated with an effect size (Cohen’s f2) of 0.33, which corresponds to an R2 of 0.25 , was 0.95. Litter size ranged from one to six individuals, although these extreme values were rare. The mean litter size was three (Table 3-6). Average litter size did not vary significantly between social groups (F9,41 = 0.606, p = 0.78; Fig. 3-5).

**Discussion**

Hoary marmots are not obligate biennial breeders. Although a mature female marmot’s probability of breeding was close to 50% on average, none of the three hypotheses we examined (Evolved Constraints, Ecological Constraints, and Social Constraints) could adequately explain variation in breeding probability.

Evolved Constraints

Contrary to the predictions of the Evolved Constraint Hypothesis, breeding in the previous year had almost no effect on the probability that an individual would breed in the current year. These findings contrast with the only other study of hoary marmot breeding patterns (Barash 1974) in which biennial breeding was first suggested. However, the former study was based on a sample of only 9 adult females, and took place during a single summer. In fact, the hypothesis of biennial breeding was derived primarily from Barash’s (1974) observation of behavioral associations between adult female marmots, yearlings, and juveniles, and from the observation that approximately half of all females successfully weaned young in a given year.

Interestingly, the latter finding is consistent with the results of our breeding probability estimates for mature (>3 years) females (Fig. 3-1). Hoary marmot breeding patterns were also consistent between the two periods of our study (1999-2004 and 2007-2009). We were able to accurately predict the number of litters produced in 2007-2009 using models that were parameterized with data from 1999-2004 (Fig. 3-2). Hoary marmots do not produce multiple litters per year (Kyle et al. 2007), so the number of litters is a reasonable surrogate for the number of breeding females. This temporal consistency in breeding probability suggests that there is an intrinsic constraint on reproduction in hoary marmots, although the mechanism behind such a constraint is still unknown.

Ecological Constraints

Breeding probability was insensitive to the depth and duration of snowpack the previous winter. Winter conditions may have consistently been harsh enough that their influence overwhelmed the effects of female body condition and breeding history. Alternatively, a constant breeding probability could have evolved as a response to environmental variability and the resulting uncertainty in the probability that an individual marmot will survive from one breeding opportunity to the next. Finally, a constant breeding effort may come at the expense of fecundity, which was inversely related to winter PDO (highest in years with deep snowpack during hibernation.

Social Constraints

Our results did not support the Social Constraint Hypothesis. Complete reproductive suppression can be said to occur when only one female per social group is allowed to breed (Blumstein and Armitage 1999). Genetic parentage analyses have already shown that hoary marmot social groups are facultatively polygynous, meaning that complete suppression is not universal (Kyle et al. 2007). We add to that result by showing that the number of adult females per social group had almost no influence on breeding probability, meaning that partial reproductive suppression (a reduction in subordinate fecundity due to harassment by dominant animals; Blumstein and Armitage 1999) was also unimportant. Similarly, social group size had no influence on average fecundity, and was positively related to the number of juveniles born per group in a given year. When social structure was modeled using the number of adult females as a covariate instead of total group size, the results were essentially the same.

Age can influence breeding success in most mammal species (Harvey and Zammuto 1985), so it is not surprising that age-class was an important variable in our models of breeding probability. However, the biological significance of this result is ambiguous. A positive relationship between age and breeding success could be the result of partial reproductive suppression if older, more experienced females were more likely to be dominant, as is the case in alpine marmots (Hackländer et al. 2003). On the other hand, social mechanisms are not required to explain a link between age and reproduction: younger females could simply be less effective at caring for their young, or less likely to reach parturition successfully. Because mating, birth, and weaning took place primarily underground at our site (Kyle et al. 2007), we cannot conclusively determine which explanation is correct.

Cost of reproduction

The seasonal activity patterns of breeding adult females in our study were consistent with those described by Barash (1980), which means they probably incurred similar energetic costs. In addition, breeders were at an energetic disadvantage by the end of the season (Fig. 3-4). Nevertheless, unlike alpine marmots (Hackländer and Arnold 2003), breeders from the previous year were no more likely to forgo future reproductive opportunities than other females.

Given the harsh enviornment in which they live, and the importance of adequate energy reserves during hibernation, Barash (1980), suggested that maximizing survival at the expense of frequent breeding was an adaptive strategy for hoary marmots. However, the energetic costs associated with breeding and weaning young had no measurable impact on survival in our study. This result was consistent with the absence of biennial breeding, because without a high fitness cost of annual reproduction, there is no selective pressure for reproductive skipping . Non-breeders and breeders had similar survival probabilities throughout the study period, despite a decline in average annual adult female survival from 0.88 to 0.55 (Fig. 3-3). This decline was strongly related to PDO and PDOlag, meaning that adult female survival probabilities were sensitive to winter climate and the timing of spring snowmelt (cite patil et al., Morrison and hik).

Comparisons with other marmot species

Despite its potential importance, variation in breeding probability has received much less attention than fecundity or survival in demographic studies of mammals (Ozgul et al. 2007). At a coarse scale, average breeding probability is remarkably similar across the genus *Marmota* (Bryant 2005). This consistency provides additional support for the notion of an intrinsic constraint on reproductive success that is unrelated to social pressures or environment. However, breeding success is influenced by winter weather in yellow-bellied marmots, and potentially in Olympic marmots as well (Schwartz and Armitage 2004, Griffin et al. 2007). In addition, the marmot species with the lowest reported rate of breeding success, the golden marmot (*Marmota caudata*), lives in an environment that, while no colder than our study site, is more arid and less productive (Blumstein and Arnold 1998). For alpine marmots, winter weather does not affect breeding success, but body condition at the end of hibernation is important (Hackländer and Arnold 1999). Taken together, these studies support the Ecological Constraint hypothesis as a potential influence on breeding probability for the genus *Marmota as a whole*.

It is not clear why hoary marmot breeding patterns were less sensitive to climate than those of other marmot species. Spatial variation in habitat quality can affect reproduction (Ozgul et al. 2007), so differences between social group territories could have obscured some underlying climate-related pattern. However, the amount of food naturally available to hoary marmots in our study area was not a constraint on growth, body condition, or survival (cite). Adult marmots that were fed rabbit chow *ad libidum* over the course of a growing season did not show significant differences in mass accumulation rates or fall body mass compared to control animals, and had equivalent overwinter survival rates (T.J. Karels et al. unpublished data). Given this lack of a relationship between food availability and growth or survival, it is conceivable that hoary marmots have also evolved breeding patterns that are insensitive to body condition, and therefore to the timing and abundance of food availability.

The apparent absence of social constraints on hoary marmot reproduction was also an anomaly among marmot species. In *Marmota* and other groups of ground squirrels, social complexity and breeding probability are generally negatively correlated (Armitage and Schwartz 2000, Blumstein and Armitage 1998). This pattern is most evident in alpine marmots, the most socially complex member of the genus. In alpine marmot social groups, only one dominant female is allowed to breed (Arnold 1990, Hackländer et al. 2003). However, even the dominant female’s reproductive output is reduced in large social groups, apparently due to reproductive competition with subordinates (Hackländer et al. 2003). In yellow-bellied marmot the optimum matriline size is three, but net reproductive rate and matriline size are negativley related beyond that point as the potential for reproductive competition increases (Armitage and Schwartz 2003).

Hoary marmot reproduction may be less constrained by group size because females within a group are closely related. In alpine marmots, the dominant female is less likely to breed when subordinates are unrelated, but not when subordinates are her siblings (Hackländer et al. 2003). Although genetic relatedness has not been determined in our population, females rarely disperse from their natal group, and extra-pair copulation is almost non-existent (Kyle et al. 2007), so females within a social group are mostly offspring, grand-offspring, or siblings of each other. In addition, the number of adult females per social group is highly variable from one year to the next (Kyle et al. 2007), so the social dominance structure must also be unstable. Given these circumstances, all females in a social group may receive enough direct and indirect fitness benefits that reproductive competition is unnecessary.

Another potential explanation comes from life history theory, which predicts that life history parameters with the greatest potential influence on population dynamics should be the least variable (Ozgul et al. 2007). Hoary marmots may therefore have evolved a consistent probability of breeding because breeding probability is more important, demographically, than other aspects of their life history.

Breeding at a consistent rate every year may confer a long-term selective advantage on hoary marmots, but it may also result in maternal stress effects being passed on to juveniles (Sheriff et al. 2009). We cannot test this hypothesis directly, but juvenile hoary marmot survival is correlated with winter climate lagged by one year, which implies the operation of maternal effects (Patil et al. in review). Ultimately, it may be impossible to pinpoint exactly how hoary marmot breeding patterns evolved, because a stochastic environment can select for more than one optimum life history strategy (Orzack and Tuljapurkar 2001).

General conclusions / implications for marmot population dynamics

There has been speculation that marmots are able to compensate for the negative effects of warm winters with reduced snowpack by increasing their reproductive output during the resulting longer, more productive growing seasons (Griffin et al. 2007). We did not find evidence for this hypothesis, although climate-driven life history tradeoffs may be more important for marmots in less severe alpine environments than the Yukon (Griffin et al. 2007). In addition, our findings show that small, newly formed social groups containing younger females have lower reproductive output, and are therefore at greater risk of extinction than older groups with more experienced breeders. Demographic mechanisms of Allee effects have also been identified in yellow-bellied and alpine marmot populations (Armitage and Schwartz 2000, Stephens et al. 2002), and should be considered whenever effects of climate change on social animals are being studied.

The absence of biennial breeding means that hoary marmots are less conservative in their breeding habits than previously believed. More generally, obligate biennial breeding is probably much less common in Marmota, and in arctic/alpine fauna, than previous research suggests (see Griffin et al. 2007). Accurate characterizations of species' life histories are essential for understanding how other factors, like climate, influence population dynamics, and for predicting future population trends (Winkler and Dunn 2002, Jiguet et al. 2007). The evidence for biennial breeding and other unusual life-histories traits should therefore be re-examined.

**Figure Legends**

Figure 3-1: Model-averaged probability of breeding as a function of age, previous breeding state, and time. Results are based on 6 years of trapping data (1999-2004) for adult female hoary marmots in the Ruby Range, Yukon. Values are model-averaged annual parameter estimates ± 1 SE.

Figure 3-2: Observed and predicted number of breeding females summed across four hoary marmot social groups from the Ruby Range, Yukon, 2007-2009. Predictions were based on model-averaged breeding probability estimates derived from the same study site in 1999-2004, assuming one litter per breeding female per season. Predictions were rounded to the nearest whole number.

Figure 3-3: Overwinter survival for adult female hoary marmots in the Ruby Range, Yukon, between 1999 and 2004. Survival rates for breeding and non-breeding individuals are shown. Values are model-averaged parameter estimates ± 1 SE.

Figure 3-4: Change in log-transformed body condition index (mass / zygomatic arch width) over time for non-breeding and breeding female hoary marmots in the Ruby Range, Yukon. Data from 1999-2004 are shown pooled across years. The best fit lines for linear regressions are shown.

Figure 3-5. Mean litter size (± 1 SE) for all hoary marmot social groups in the study area in the Ruby Range, Yukon, between 1999-2009. Mean litter size did not vary significantly between groups (F41,9 = 0.606, p = 0.78).

Table 3-1. Abbreviations and descriptions of covariates used in analyses of female hoary marmot reproductive parameters.

|  |  |
| --- | --- |
| **Abbreviation** | **Definition and Description** |
| PDO | Mean Pacific Decadal Oscillation from November to May in the winter during the most recent winter |
| PDOlag | Mean Pacific Decadal Oscillation from November to May during the previous year |
| Age | Two age classes: Young (3 years old), and Old (>3 years) |
| Mother Age | Minimum mother age in years, for litter size analysis only |
| Group | Total number of non-juvenile marmots within social group |
| Ad. fems | Number of reproductively mature adult females in a social group |
| Time | Random annual variation |
| Brd. State | Factor variable. 1 = females that bred during the previous year, 0 = previous nonbreeders |
| 1 | No time variation (constant) |
| Young | Denotes a linear covariate applied only to female marmots 3 years of age. |
| Old | Covariates applied only to female marmots >3 years old. |
|  |  |

Table 3-2. Results of Poisson overdispersion tests (Scrucca 2004) for three measures of hoary marmot fecundity, based on data from 10 hoary marmot social groups in the Ruby Range, Yukon Territory, 1999-2004 and 2007-2009. The corresponding linear model types used to model those variables are also shown. Error distributions were chosen based on test results. If significant overdispersion was present, negative binomial generalized linear models were used. If Poisson underdispersion was detected, Gaussian errors were used. Random effects (Social Group affiliation, and interaction between Social Group interaction and fixed effect slopes) were included based on likelihood-ratio tests using the most parameterized fixed-effect model in each model set (Bolker et al. 2009).

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Response Variable** | **Obs./Theor.Var** | **Statistic** | **p** | **Error Distribution** | **Random Effects** |
| Juveniles/Group | 3.83 | 248.64 | 0.00 | Neg. Binomial | None |
| Juveniles/Female | 1.29 | 84.14 | 0.06 | Poisson | Social Group,  Social Group\*PDO |
| Known Litter Size | 0.57 | 23.33 | 0.99 | Gaussian | None |

75

Table 3-3. Model-selection results for multistate CMR analyses of adult female hoary marmot survival and breeding probability in the Ruby Range, Yukon Territory from 1999-2004. Parameters shown are survival probability (S), and the probability of breeding in a given year (Ψ). Detection probability (p) was modeled as a constant, and was estimated at 0.96 ± .02 (SE). Descriptions and abbreviations for all covariates are in Table 3-1. K is the number of estimated model parameters and ωis the model’s AIC weight.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Model** | **K** | **AICC** | **∆ AICc** | **ω** | **Deviance** |
| **S** PDO + PDOlag **Ψ** Age | 6 | 384.19 | 0 | 0.29 | 185.02 |
| **S** PDO + PDOlag **Ψ** Old: (Brd. State + Group),  Young: Group | 8 | 385.28 | 1.09 | 0.17 | 368.38 |
| **S** PDO + PDOlag  **Ψ** Old: Brd. State, Young: 1 | 7 | 385.73 | 1.55 | 0.14 | 184.39 |
| **S** PDO + PDOlag + Brd. State **Ψ** Age | 7 | 385.93 | 1.75 | 0.12 | 184.59 |
| **S** PDO + PDOlag + Brd. State **Ψ** Old: Brd. State + Group, Young: Group | 9 | 387.09 | 2.9 | 0.07 | 367.96 |
| **S** PDO + PDOlag + Brd. State **Ψ** Old: Brd. State, Young: 1 | 8 | 387.51 | 3.33 | 0.06 | 183.96 |
| **S** PDO + PDOlag **Ψ** Old: Ad. Fems, Young: 1 | 6 | 387.91 | 3.73 | 0.05 | 375.4 |
| **S** (PDO + PDOlag ) \* Brd. State **Ψ** Age | 9 | 388.71 | 4.53 | 0.03 | 182.93 |
| **S** PDO + PDOlag + Brd. State **Ψ** Old: Ad. Fems, Young: 1 | 7 | 389.66 | 5.47 | 0.02 | 374.96 |
| **S** PDO + PDOlag **Ψ** Old: Group, Young: 1 | 6 | 389.85 | 5.66 | 0.02 | 377.33 |
| **S** (PDO + PDOlag ) \* Brd. State **Ψ** Old: (Brd. State + Group) + Young: Group | 11 | 389.97 | 5.79 | 0.02 | 366.3 |
| **S** (PDO + PDOlag ) \* Brd. State **Ψ** Old: Brd. State, Young: 1 | 10 | 390.36 | 6.17 | 0.01 | 182.32 |
| **S** PDO + PDOlag  **Ψ** Old: Brd. State + PDO + PDOlag + Group,  Young: PDO + PDOlag + Group | 12 | 390.75 | 6.57 | 0.01 | 364.76 |

Table 3-4. Summed AIC weights (ω) for all covariates in a multi-state CMR analysis of adult female hoary marmots in the Ruby Range, Yukon, 1999-2004. Covariates of both survival (S) and breeding probability (ψ) are shown. Covariate descriptions are in Table 3-1.

|  |  |
| --- | --- |
| **Covariate** | **ω+** |
| **Ѱ** |  |
| Age | 1.00 |
| Group | 0.44 |
| Ad. Fems | 0.31 |
| Brd. State | 0.14 |
| Age\*Brd. State | 0.07 |
| Age\*Group | 0.07 |
| PDO | 0.00 |
| PDOlag | 0.00 |
| Age\*PDO | 0.00 |
| Age\*PDOlag | 0.00 |
| Age\*Ad. Fems | 0.00 |
|  |  |
| **S** |  |
| PDO | 1.00 |
| PDOlag | 1.00 |
| Brd. State | 0.34 |
| Brd. State\*PDO,PDOlag | 0.06 |
|  |  |

Table 3-5. Model-selection results for linear models of hoary marmot reproductive parameters. K is the number of estimated model parameters and ω is the AIC weight. Response variables were the number of juvenile produce per social group and average fecundity (juveniles per female within social group). Data were collected 1999-2004 and 2007-2009 from 10 social groups in the Ruby Range, Yukon Territory. The error distribution used and the type of model are shown in italics below the name of each response variable. GLMM’s are Generalized Linear Mixed Models, and GLM’s are Generalized Linear Models. Only models with ∆ AICC < 7 are shown.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **Model** | **K** | **AICC** | **∆ AICC** | **Ω** |
| Juveniles Per Group |  |  |  |  |
| (*Negative Binomial GLM's*) |  |  |  |  |
| Group | 3 | 315.63 | 0 | 0.22 |
| Group+PDO | 4 | 315.88 | 0.25 | 0.19 |
| Group+PDOlag | 4 | 316.12 | 0.48 | 0.17 |
| Group+PDO+PDOlag | 5 | 316.55 | 0.92 | 0.14 |
| Group\*PDO | 5 | 317.91 | 2.28 | 0.07 |
| Null | 2 | 318.33 | 2.69 | 0.06 |
| PDO | 3 | 318.35 | 2.71 | 0.06 |
| Group\*PDOlag | 5 | 318.46 | 2.82 | 0.05 |
| PDOlag | 3 | 320.45 | 4.82 | 0.02 |
| PDO+PDOlag | 4 | 320.56 | 4.93 | 0.02 |
| Group\*(PDO+PDOlag) | 7 | 320.87 | 5.24 | 0.02 |
|  |  |  |  |  |
| Juveniles Per Female |  |  |  |  |
| (*Poisson GLMM's*) |  |  |  |  |
| PDO+PDOlag | 4 | 185.04 | 0 | 0.38 |
| Group\*(PDO+PDOlag) | 7 | 186.98 | 1.94 | 0.14 |
| Group+PDO+PDOlag | 5 | 187.23 | 2.19 | 0.13 |
| Group\*PDO | 5 | 187.32 | 2.28 | 0.12 |
| PDO | 3 | 187.66 | 2.62 | 0.1 |
| Group+PDO | 4 | 188.34 | 3.3 | 0.07 |
| PDOlag | 3 | 189.87 | 4.83 | 0.03 |

Table 3-6. Model-averaged beta coefficients (β) , bootstrapped unconditional standard errors (SE), 95% confidence interval lower and upper limits (LCL and UCL), and summed AIC weights (ω) of parameters for models of group fecundity, individual fecundity (juveniles/adult female), and litter size of hoary marmots in the Ruby Range, Yukon Territory. SEs and 95% confidence limits were bootstrapped with 1000 replications. Except for litter size, analyses were based on data from 1999-2004 and 2007-2009. Due to highly significant poisson overdispersion, juveniles per group were modeled using negative binomial linear models. Juveniles per female were modeled using Poisson mixed models with social group random effects. Litter size data were approximately normally distributed, and were modeled as such.

|  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- |
| **Model** | **Model-averaged β** | **SE** | **LCL** | **UCL** | **ω+** |
| Juveniles Per Group |  |  |  |  |  |
| (*Negative Binomial GLM's*) |  |  |  |  |  |
| PDO | -0.13 | 0.36 | -1.24 | 0.03 | 0.73 |
| PDOlag | 0.09 | 0.19 | -0.17 | 0.58 | 0.41 |
| Group | 0.06 | 0.04 | 0.00 | 0.14 | 0.85 |
| Group\*PDO | 0.00 | 0.03 | -0.02 | 0.12 | 0.08 |
| Group\*PDOlag | 0.00 | 0.02 | -0.02 | 0.05 | 0.07 |
|  |  |  |  |  |  |
| Juveniles per female |  |  |  |  |  |
| (*Poisson GLM's*) |  |  |  |  |  |
| PDO | -0.26 | 0.49 | -1.69 | 0.17 | 0.99 |
| PDOlag | 0.20 | 0.37 | -0.50 | 1.03 | 0.69 |
| Group | 0.00 | 0.04 | -0.08 | 0.09 | 0.48 |
| Group\*PDO | 0.01 | 0.05 | -0.05 | 0.16 | 0.26 |
| Group\*PDOlag | 0.00 | 0.05 | -0.11 | 0.10 | 0.15 |
|  |  |  |  |  |  |
| Lithter Size |  |  |  |  |  |
| (*Gaussian GLM's*) |  |  |  |  |  |
| Intercept | 3.00 | 0.19 | 2.64 | 3.38 | 1.00 |

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