

**Determinants of Annual and Lifetime Reproductive Success in Female  
Yellow-bellied Marmots: a Cross-Generational Study**

By

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Submitted to the Department of Ecology and Evolutionary Biology  
and the Graduate Faculty of the University of Kansas  
in partial fulfillment of the requirements for the degree of Doctor of Philosophy

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## **Abstract**

**Kathleen R. Nuckolls**

Despite the importance and broad understanding of fitness as a concept in evolutionary biology, there remains wide disagreement about the ways in which fitness is described and measured in the field. In particular, fitness is generally taken to refer to the contribution of genes to future generations relative to the contribution of others. However, field biologists generally measure individuals, not genes. Moreover, there is a problem of scale and what exactly is meant by “future generations.” Should the appropriate measure of fitness be the number of offspring, the number of reproductive offspring, or the reproductive success of those offspring? It is generally assumed that measuring the number of offspring and the number of grand-offspring will give essentially equivalent answers, but this is not necessarily the case. These questions are complicated by the time-limited nature of most field studies. Only truly long-term data sets can be used to measure the effects of covariates on the production of offspring and grand-offspring, but this type of study is difficult to complete. It would, therefore, be useful to know to what extent long term patterns can be predicted from a single year’s data. This study examines the determinants of annual and lifetime reproductive success in female yellow-bellied marmots (*Marmota flaviventris*) measured at three different time points: the number of offspring produced, the number of reproductively competent two-year-old daughters produced, and the number of grand-offspring produced. Using a 40-year data set, I examine the social and environmental variables present during the year of the mother’s reproduction to predict these measures of reproductive success. Thus, although I am using a very long-term data set, I am testing the feasibility of making accurate predictions using only one year’s data.

For the Doctors Dahl, who set my feet on this path  
For Scott, who walked beside me, “even if”  
And for Anna and Molly, who improve my life and my fitness in so many ways...

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# Introduction

## Background

From the time that Darwin proposed the idea of fitness, researchers have been trying to perfect ways to measure this elusive concept. Reproductive success is a relatively straightforward measure and has been particularly popular with field biologists (Stearns 1992). Studies of reproductive success have the potential to shed light on selection, and to generate new hypotheses concerning the adaptive significance of behaviors and morphology. Such studies can also help determine to what extent variation in reproductive success is due to environmental stochasticity rather than phenotypic variation (Clutton-Brock 1988).

Although reproductive success can be measured using comparisons among individuals for single reproductive episodes, inferences are best made using long-term data on individuals. In particular, longitudinal data are necessary to examine the relationship between age and reproductive success; because reproductive success and longevity may be positively or negatively correlated, the use of cross-sectional data can produce or conceal a relationship between age and reproductive success (Clutton-Brock 1988). Longitudinal studies also have the benefit of being able to compare the total fitness of different categories of individuals, and of being buffered from the influences of short-term environmental fluctuations.

Because of the benefits of longitudinal data sets, there has been a recent trend towards collecting these types of life history data. Several authors have attempted to relate reproductive success of females to environmental conditions, demographic variables, social or behavioral variables, or characteristics of the reproductive female (e.g., Loison et al. 1999, Altmann and Alberts 2003, Fedigan et al. 2008). These studies have contributed greatly to our understanding

of the life history of their respective study organisms, as well as the workings of natural selection.

Although these studies benefit from longitudinal data on known individuals, they suffer from a statistical difficulty that has not been adequately addressed; repeated observations of the same individual violate the common assumption of independence of observations. Some authors ignore this, treat the data as independent, and run regressions or linear models anyway. However, it is likely that with life history data, the number of offspring produced in one breeding attempt will be correlated (positively or negatively) with the next attempt. A positive autocorrelation will lead to a higher probability of rejecting the null hypothesis, while a negative autocorrelation will decrease the probability of rejecting the null. In many cases it is difficult to even assess the severity of the autocorrelation problem because most standard autocorrelation analyses require “runs” that are longer than the available data.

Until recently, there were few options if autocorrelation is suspected in the data. Some researchers turned to repeated measures design, but this method has strict requirements that are difficult to meet. For example, a repeated measures design initially assumes equality of variances, although there are procedures available if this assumption is not met. A more difficult restriction for most field projects is that data must be balanced, and that there are no missing values. Repeated measures designs assume that each individual is observed the same number of times. The standard advice given to those wishing to use this approach is to discard all data beyond the median reproductive event. This procedure risks losing the data on the most successful phenotypes, and obscuring some potentially interesting patterns.

In addition, those wishing to characterize the total lifetime reproductive success are faced with a difficult conundrum; many of the variables that are known or suspected to affect

reproductive success change on a yearly basis. Should the variables be averaged over the course of the individual's lifespan? Obviously, much of the variability in the predictor variables will be lost this way and over- or under estimation of the relationship between variables will result (Bryk and Raudenbush 1992).

Fortunately, there is now a statistical approach available to solve these problems. Hierarchical Linear models, also known as Linear Mixed Models, Multilevel Analysis, or Latent Growth Curves, were developed primarily in the fields of sociology, education research, and economics. They are designed for data that are inherently nested, such as students who are nested within schools, or consumers who are nested within counties or states. Similarly, observations that are repeatedly gathered on the same individual are nested within that individual. Individuals, may in turn, be nested within sites or colonies. At the lowest level, the analysis is similar to that of ordinary least squares regression, where a dependent variable is predicted as a function of a linear combination of one or more "level one" variables, plus an intercept (Bryk and Raudenbush 1992). On subsequent levels, the level one slope and intercept become additional dependent variables being predicted from level two variables.

The advantages of linear mixed effects modeling is that it explicitly accounts for the nested structure of the data, allows for several different variance structures, including autocorrelation, and does not assume equality of variances. It allows examination of unbalanced data, data with missing values, and does not require a normal distribution. It has been used extensively in the social and economic sciences to examine the importance of individual variables and interactions of variables. One of the most interesting applications for life history is that it can be used to fit non-linear functions as well. Thus, we can model the reproductive success of individuals over the course of the reproductive span. Linear mixed effects models

provide an important tool for examining proposed adaptations and for elucidating relationships between various components of reproductive success.

### **Description of subjects**

This study uses hierarchical linear modeling to examine a long-term data set on yellow-bellied marmots (*Marmota flaviventris*). Detailed long-term data are reasonably easy to collect on relatively large, diurnal mammals such as marmots. Marmots are a semi-fossorial hibernating species, widely distributed in the mountainous regions of the western United States. They are long-lived, with females living up to 14 years (although survival after age 11 is rare). Marmots produce one litter per year immediately after hibernation. Young are confined to the natal burrow until weaning and can usually be captured and assigned maternity (and paternity) immediately upon emergence. Litter size ranges from three to eight pups, with a mean of 4.32 at emergence.

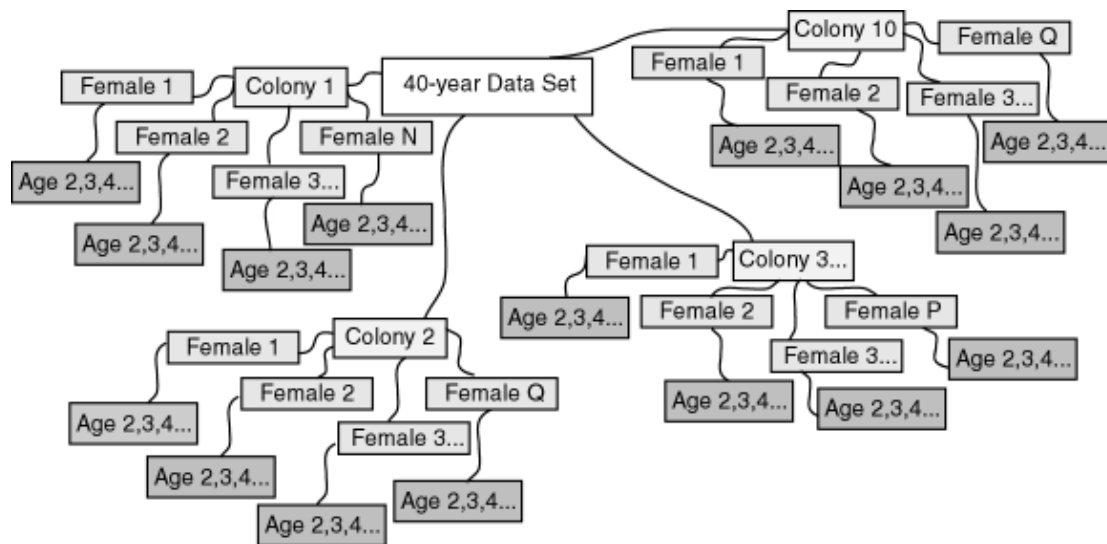
Marmots live in social groups called “matrilines” made up of closely-related females (e.g., mother, daughter or sister, sister pairs). Marmots prefer vegetated talus slopes with rocky outcrops for burrow construction (Svendsen 1976). Depending on the size of the habitat patch, one or more matrilines may share a habitat patch. Collectively, these groups of matrilines are known as colonies. Matriline size is variable and may range from one to five adult females, with their young of the year and yearlings. One adult male may be associated with one or more matrilines, but more than one male seldom associates with a matriline. Individuals may be marked with fur dye for identification from a distance, and with ear tags for permanent identification.

## **The data**

This study will make use of existing data collected between 1963 and 2004 in the East River Valley, near Rocky Mountain Biological Laboratory, in Gunnison County, Colorado. This data set is not merely longitudinal, it is truly *long-term* in nature; many of the same variables have been tracked on individually marked marmots for over 40 years. These data allow a truly rare opportunity for examination of reproductive success. A number of authors have questioned at what point reproductive success should be measured. Three commonly proposed measures are the number of offspring, the number of offspring who reach reproductive age, and the number of offspring who actually reproduce (alternatively the number of those grand-descendants). Our unique long-term data set allows an examination of reproductive success at all three stages.

Thus, the first response variable in the hierarchical linear model will be the number of female offspring produced by a female. These data will be modeled as a level one variable “nested” by individual. Individuals are in turn “nested” into colonies (Figure 1). Predictor variables are grouped into three general categories – characteristics of the female, social variables, and environmental variables (Table 1). Most of the variables will affect the lowest level; they are predicted to change from year to year and to affect reproduction differently each time the female has the opportunity to reproduce. At the next level up, that of the individual marmot, the variables “resident,” lifespan, and the age at first reproduction are the only important predictors.





**Figure 1. Structure of the marmot data. Level one variables are in the darkest gray, lower in the figure. Different females are at "level two," and colonies represent "level three" variables in this nested hierarchy.**

**Table 1. Covariates used in the analysis of reproductive success.**

	Variable	Description of Data
Intrinsic to Female	Age	Age of the marmot in years
	Resident	Whether marmot was born in a colony or immigrated into it
	Reproduced last	Whether or not the female reproduced the previous year
	Lifespan	Lifespan of female in years (age at last observation)
	Alpha	Age at first reproduction
	Environmental	First snowfall
Last snowfall		Julian day of last snowfall >2.54 cm in spring prior to weaning (year of reproduction for analysis of recruits)
First snow cover		Julian day of first snow cover >2.54 cm – fall prior to reproduction (year of reproduction for analysis of recruits)
Last snow cover		Julian day of last snow cover >2.54 cm in spring prior to weaning
Precip: Sept–May		Precipitation during hibernation prior to reproduction, cm (year of reproduction for analysis of recruits)
Precip: June		cm of precipitation in June in the year prior to reproduction (year of reproduction for analysis of recruits)
Precip: July		cm of precipitation in July in the year prior to reproduction (year of reproduction for analysis of recruits)
Precip: Aug		cm of precipitation in August in the year prior to reproduction (year of reproduction for analysis of recruits)
Temp: Sept–Nov		Mean temp. Sept. – Nov., fall prior to reproduction (year of reproduction for analysis of recruits)
Precip: Deviation Active		Deviation from normal active season precipitation, summer prior to reproduction (year of reproduction for analysis of recruits)
Precip: Deviation Hibernation		Deviation from normal hibernation precipitation prior to reproduction (year of reproduction for analysis of recruits)
Precip: Mean Active		Mean precipitation during active season in the year prior to reproduction (year of reproduction for analysis of recruits)
Precip: Mean Hibernation		Mean precipitation during hibernation, prior to reproduction (year of reproduction for analysis of recruits)
Precip: Variance Active		Variance in precipitation during active season in the summer prior to reproduction (year of reproduction for analysis of recruits)

	Precip: Variance Hibernation	Variance in precipitation during hibernation, prior to reproduction (year of reproduction for analysis of recruits)
	Temp: Deviation Active	Deviation from normal active season temperature in the summer prior to reproduction (year of reproduction for analysis of recruits)
	Temp: Deviation Hibernation	Deviation from normal hibernation temperature, prior to reproduction (year of reproduction for analysis of recruits)
	Temp: Mean Active	Mean temperature during active season in the summer prior to reproduction (year of reproduction for analysis of recruits)
	Temp: Mean Hibernation	Mean temperature during hibernation, prior to reproduction (year of reproduction for analysis of recruits)
	Temp: Variance Active	Variance in temperature during active season in the summer prior to reproduction (year of reproduction for analysis of recruits)
	Temp: Variance Hibernation	Variance in temperature during hibernation, prior to reproduction (year of reproduction for analysis of recruits)
	Colony	Identity of colony or satellite
Demographic	Male yearlings	Number of male yearlings present from previous year's litter
	Female yearlings	Number of female yearlings present from previous year's litter
	Matriline	Density of related females present (number present/average)
	Other females	Density of non-matriline females present in the colony
	New Male	Whether the male observed was new to the site
	Younger adult	Number of younger adult matriline females present
	Offspring of younger	Number of pups produced by younger matriline adults
	Older adult	Number of older adult matriline females present
	Offspring of older	Number of pups produced by older matriline adults
	Same-age adult	Number of matriline females the same age as the subject
	Offspring of same-age adults	Number of pups produced by matriline females of the same age

The second response variable is the number of two-year-recruits – defined as the number of female young from a particular litter that settle in their natal territory. This stage represents the earliest age that a female might begin reproducing. About half of females disperse, a tactic that potentially frees them from reproductive suppression from their mother, but also exposes them to higher predation risk (Armitage 1991). Undoubtedly, some females survive to reproduce outside the natal colony, but this number is difficult to estimate. Because the number of female recruits is dependent on the number of offspring that were produced in the original litter, the number of young produced is used as an “offset” variable in the analysis of the number of recruits (Zuur et al. 2009). Similarly, the number of two-year-recruits is used as an offset in the third and final analysis, number of grand-pups.

### *Statistical analysis*

The best approach for these data is a General linear mixed effects model. The response variables are all count data, and thus the data are best modeled using either a Poisson or negative binomial distribution. Because data are not overly dispersed, the Poisson distribution is the best match for these data. Reproductive failure is relatively common; there are 550 observations of zero offspring, and 418 observations of one or more offspring. These zeros add an additional complication to the analysis. However, it is vital to assess the covariates that affect whether an individual reproduces or fails to reproduce in a given year. Selection for the abandonment of reproduction is likely to be an important process in the overall evolution of life histories; in some situations individuals may leave more offspring over the course of their lifespan if they occasionally forgo reproduction under unfavorable conditions (Wasser and Barash 1983). This type of data can be approached with either a zero-inflated or a zero-adjusted model. The zeros in the data set can be thought of as occurring from a number of different processes. “True” zeros are those that are generated by the same process as the one that generated the count data. “False” zeros would be those in which no count could reasonably be expected, such as counting the number of offspring produced by juveniles. It is best to remove these zeros from the data before analyzing them. For example, the years in which no male was observed in a colony were removed in this analysis. However, in some data sets, it is difficult to determine which zeros are “true” and which are “false.” In this data set, female-years during which a colony included a new male are such a case. If the male arrived sufficiently early in the season, a lack of reproduction is likely due to other factors, such as social or environmental variables. These zeros would be “true” zeros, while data from colonies where the male arrived after the reproductive season would be “false” zeros. In these cases where true and false zeros are mixed, the best model is a

Zero Inflated model. Zero Altered models can be used when only “true” zeros are included in the data (Zuur et al. 2010b). Thus, annual reproduction was modeled using a Zero Inflated Poisson model, while Lifetime reproductive success was modeled with Zero adjusted models, because no female had a new male for her entire reproductive span.

A Zero Inflated Poisson model consists of two parts. The first part attempts to explain the binary process that produces the presence or absence of reproduction. The second part of the model attempts to explain the count data using a Poisson distribution; it models how many offspring are produced, given that reproduction has occurred. These models take the following form:

$$Y_{ijk} \sim ZIP(\pi_{ijk}, \mu_{ijk})$$

$$E(Y_{ijk}) = \mu_{ijk} \times (1 - \pi_{ijk}) \text{ and } \text{var}(Y_{ijk}) = (1 - \pi_{ijk}) \times (\mu_{ijk} + \pi_{ijk} \times \mu_{ijk}^2)$$

The parameters are  $\pi_{ijk}$ , the probability of observing reproduction and  $\mu_{ijk}$ , the expected value for the count process. Observations for different years (for the same animal) are represented by  $k$ , different animals are represented by  $j$ , and colonies are represented by  $i$ .

These parameters are modeled as a function of the covariates:

$$\text{logit}(\pi_{ijk}) = \alpha + \gamma_1 + X_{1ijk} + \dots + \gamma_n \times X_{nijk} + d_i + d_{ij} \text{ (this models the zeros)}$$

$$\log(\mu_{ijk}) = \alpha + \beta_1 + X_{1ijk} + \dots + \beta_n \times X_{nijk} + b_i + b_{ij} \text{ (this models the counts)}$$

The random error terms,  $d_i$ ,  $d_{ij}$ ,  $b_i$ , and  $b_{ij}$ , are assumed to be independent of each other.

I used a Markov Chain Monte Carlo (MCMC) technique to fit a two-way nested ZIP model in R 2.7.2 (R Development Core Team 2009). MCMC is a Bayesian statistical method that uses an iterative process to estimate model parameters. Unlike more familiar frequentist statistical methods, Bayesian statistics use information about the prior distribution of parameters, combined with information contained in the sample data themselves, to estimate the “posterior” distribution. The posterior distribution is a density function, which estimates the parameter of interest, and can be interpreted as the “degree of belief” in the parameter value. The MCMC technique is iterative; it makes repeated estimations of the parameters of interest, using the previous iteration for the prior distribution. In this study, we lacked information about the initial prior distribution. Thus, we used “uninformative priors” and discarded the first 2000 iterations from further consideration. These “burn in” iterations give the model a chance to converge on the true parameter distribution. The next 6000 iterations are saved, and the mean of the parameter estimates is used as the parameter estimate in the resulting model.

For each “round” of the forward selection process, the R MCMC runs 8000 iterations to estimate the parameters of the null model (no variables, or the variables pre-selected by the user). It then adds each covariate to the model in turn, for comparison. The code generates a list of models and DIC (Deviance Information Criterion) values which are a measure of how well each model fits the data. Smaller DIC values are considered better, but differences in DIC of less than five units are not considered to be meaningful. The MCMC code draws samples from the posterior distribution of the regression parameters and reports the mean (and SD) of the sampled parameters. These parameters are also associated with 95% credible intervals, which are used to assess whether the estimated regression parameter is “significant.” If the credible interval overlaps zero it is assumed that zero is a feasible value for the parameter.

At each step in the forward selection process, I selected the next covariate to go into the model based on the lowest DIC that included “significant” covariates. In some cases, the model with the lowest DIC included a covariate whose credible interval overlapped zero, in these cases, I would examine the next best model, based on the DIC. If the next best model was within 10 DIC units and contained significant covariates based on the credible interval, I would select that covariate and proceed. If the next best model with significant covariates was not within 10 DIC units, I halted model selection.

The R code produces models and parameter estimates for both the Binary and Poisson portions of the overall model. Users can elect to place the covariates into the Binary, the Poisson, or both. When selecting covariates, I considered both the Binary and Poisson parts for each round. I kept variables within their respective portions of the model; that is, if round one selected a covariate in the binary portion, all subsequent rounds had that covariate in the binary portion for all models (but not the Poisson).

Although the data used in this study have many features that make them problematic for traditional statistical analysis and are at the limits of what can currently be analyzed using general linear mixed models (Alain Zuur, pers. comm.), they offer the opportunity for significant insights into the evolution of life histories. When analyzed with the appropriate statistical methods, these data provide insight into the factors that affect reproductive failure and that influence the differences in reproductive output among individuals. Moreover, because of the long-term nature of the study, these data offer unprecedented opportunities to compare these effects at different points in the lifespan and with different measures of reproductive success.

## **Chapter 1: Determinants of annual and lifetime reproductive success in female yellow-bellied marmots: I. production of offspring.**

### **Abstract**

Understanding the determinants of reproductive success is centrally important to address the adaptive significance and ecological consequences of traits. Until recently, attempts to determine the predictors of reproductive success were hampered by statistical and data constraints. This study uses a linear mixed effects model to assess the social and environmental predictors of annual and lifetime reproductive success in female yellow-bellied marmots (*Marmota flaviventris*). Age, lifespan, residency status, presence of a new male, previous reproductive status, number of same-aged females, number of yearlings present, number of offspring produced by same-aged females, number of offspring produced by older females and matriline density were associated with the probability of reproductive failure. The number of offspring produced by older females, matriline density, and fall temperatures were associated with litter sex ratio. Lifespan, number of female yearlings present, time spent with an established male, and the date of last snow fall affected the total number of offspring produced by reproductive females. There were some similarities, but different factors affected the annual production and the lifetime production of young. Both the social environment and the ability to gain and retain sufficient mass for reproduction appear to affect female marmot reproduction.

**Key Words:** *Marmota*, annual reproductive success, lifetime reproductive success, fitness, senescence.

## **Introduction**

An individual's contribution to the next generation has clear evolutionary and ecological importance. The number of offspring left by individuals determines their relative contributions to population growth and to the gene pool (Shaw et al. 2008). Individuals should be expected to maximize the total number of offspring that they produce. However, because individual resources are limited, maximizing the number of offspring at one age may reduce survival or the number offspring produced at other life stages (Williams 1957, Kirkwood and Holliday 1979, Partridge and Barton 1996). Similarly, when conditions for successful reproduction become poor, individuals may have a higher lifetime reproductive output if they abandon reproduction altogether in difficult years (Wasser and Barash 1983). An understanding of the factors that affect reproductive success across the lifespan is central to attempts to understand the adaptive significance of traits, selective pressures, and their demographic consequences (Caughley 1977, Arnold 1983, Endler 1986).

Although reproductive success has been an important and productive area of research (Clutton-Brock 1988), detecting the overall pattern of reproductive effort has remained difficult in natural populations. High mortality rates lead to low sample sizes in the oldest age classes, making inferences about reproductive scheduling difficult. The short term nature of many empirical studies exacerbates these difficulties; reproductive success may be positively or negatively correlated with longevity, so cross-sectional data may obscure the relationship between age and reproductive success (Clutton-Brock 1988). Similarly, the effects of environmental and social covariates on reproductive success across the lifespan are best examined using longitudinal data. Thus, longitudinal studies of wild populations are the most powerful way to detect relationships between reproductive success and age, social or



environmental variables, and to compare the relative success of different phenotypes (Clutton-Brock 1988, Nussey et al. 2008).

Unfortunately, there are few longitudinal studies of wild populations, and until recently, the analysis of longitudinal data has been complicated by statistical problems. By their nature, longitudinal data involve repeated observations of individuals, and these individuals are often grouped into subpopulations. Such data are hierarchical in nature and do not meet the assumption of independence required by most tests. Ignoring this fundamental data structure can obscure the relationships of interest and increase the probability of making a type I error (Osborne 2000, Raudenbush and Bryk 2002).

A linear mixed effects model is the best tool to control for between-individual heterogeneity and ensure that the variance in reproductive success is evaluated at the appropriate level (Pinheiro and Bates 2000, Nussey et al. 2008). These models have been used extensively in economic and sociology studies, but have only recently made their way into ecological studies (Osborne 2000, Parn et al. 2009). Although linear mixed effects models allow for more accurate evaluations of variables across the lifespan, the nature of reproductive success adds an additional complication to these analyses. Because observations of reproductive success usually involve counts of weaned offspring, the data are not normally distributed, but rather follow a Poisson or negative binomial distribution, depending on the dispersion of the data. Moreover, complete reproductive failure is very common in natural populations (Wasser and Barash 1983), which leads to a very large number of zeros in these data. Often, studies ignore the zeros, choosing instead to focus on the variables that affect litter size and interbirth interval, given that at least one reproductive event has occurred (e.g., Bercovitch and Berry 2009, Sharp and Clutton-Brock 2009). However, the variables that cause an individual to abandon reproduction altogether are at

least as important as those that affect litter size. Thus, data on reproductive success are usually best modeled using a zero-inflated or zero altered Poisson or Negative Binomial distribution (ZIP, ZAP, ZINB or ZANB; for a discussion of these models, see Zuur et al. 2010b. Few statistical packages are equipped to handle zero-inflated, two-way nested data (Zuur et al. 2010a).

Because of these difficulties, long-term studies of wild populations that adequately address the statistical distribution and hierarchical data structure are exceedingly rare. Herein, we analyze reproductive success using 40 years of data on yellow-bellied marmots (*Marmota flaviventris*) using a linear mixed effects model that accounted for the zero-inflated Poisson distribution. This method represents a powerful approach to examine the determinants of reproductive success in a wild population.

## **Methods**

### *Subjects and study site*

Marmots, the largest sciurid (squirrel), are diurnal and semi-fossorial, which facilitates long-term monitoring of marked individuals. A population of yellow-bellied marmots (*Marmota flaviventris*) was observed from 1962 to 2004 at 18 sites in the Upper East River Valley in Gunnison County, Colorado. Nearly all the marmots at these sites were trapped and individually marked annually. A few sites were added during the course of the study, and not all sites were occupied each year (Armitage and Schwartz 2000).

Yellow-bellied marmots, hereafter “marmots.” are widely distributed across the mountain areas of western North America (Frase and Hoffmann 1980). Marmots usually occupy sites above 2000 m; elevations at our site range from 2867 m to 2992 m (Schwartz and Armitage

2005). These alpine and sub-alpine environments are characterized by large daily and yearly temperature changes. Marmots are subject to intense solar radiation in the summer, followed by low temperatures and several months of snow cover in the winter (Armitage 1991). To cope with these extremes, marmots enter hibernation in August and September, and do not emerge until April or May. Thus, marmots must reproduce and gain enough mass to survive hibernation during a relatively short summer active season. Reproduction is limited to a single annual event immediately after emergence. Gestation is about 30 days, and young are weaned at the age of three to four weeks. Yearlings may disperse or stay in their natal colony. Nearly all males and about half the females disperse as yearlings (Armitage 1991). Females can reproduce at the age of two years, but the average age of first reproduction is 3.02 years (Schwartz et al. 1998).

Marmots are clumped on patches of talus or rocky outcrops and meadows that range in size from 0.15 to 7.2 ha (Armitage and Schwartz 2000), and prefer relatively open sites, free of trees and shrubs. Burrows are constructed under rock outcrops or boulders to provide protection from predators (Svendsen 1976). These meadows are characterized by grasses and showy perennial forbs. Although marmots often emerge from hibernation through the snow, forage is available during gestation. Forage becomes abundant during lactation and reaches its peak biomass after weaning. Vegetation usually senesces by early September (Kilgore and Armitage 1978, Frase and Armitage 1989, Armitage 2003a). Vegetation in the East River Valley forms a mosaic of suitable meadow habitat and unsuitable forest habitat (Svendsen 1974).

The fundamental social unit of yellow-bellied marmots is the matriline, composed of one to five closely-related adult females, usually sisters or mothers and daughters. The number of females resident on a habitat patch varies from site to site, and generally is related to patch size. The smallest patches (also known as satellites) usually support only one female, her young, and

possibly a male (Armitage 1991). Males are territorial, and defend one or more matriline in colonies or may defend females on more than one small patch (Armitage 2004a).

### *Variables*

We measured several aspects of marmot social and physical environments, as well as some characteristics of the potentially reproductive female (Table 2). Aspects of the social environment included the number of individuals present in the matriline: male and female yearlings, younger adult females, older adult females, and same-aged adult females. We also recorded the total number of adults in the matriline, the number of offspring produced by matrilineal adults of different ages, and whether the male was established or had immigrated into the colony during the year of reproduction. Because the number of adult females present on a habitat patch is correlated with patch size (Armitage 1991), we calculated a density index in a matriline and for number of other female residents on the site as the number of females present in a given year at a given site, divided by the average number present at that site. We excluded data from all years when a male was not present in the colony. Female characteristics included female age, whether or not she had reproduced the previous year, and whether the female was a recruit or an immigrant.

**Table 2: Covariates used in the analysis of offspring production.**

	Variable	Description of Data
Intrinsic to Female	Age	Age of the marmot in years
	Resident	Whether marmot was born in a colony or immigrated into it
	Reproduced last	Whether or not the female reproduced the previous year
	Lifespan	Lifespan of female in years (age at last observation)
	Alpha	Age at first reproduction
Environmental	First snowfall	Julian day of first snowfall >2.54 cm in fall prior to reproduction
	Last snowfall	Julian day of last snowfall >2.54 cm in spring prior to weaning
	First snow cover	Julian day of first snow cover >2.54 cm – fall prior to reproduction
	Last snow cover	Julian day of last snow cover >2.54 cm in spring prior to weaning
	Precip: Sept–May	Precipitation during hibernation prior to reproduction, cm
	Precip: June	cm of precipitation in June in the year prior to reproduction
	Precip: July	cm of precipitation in July in the year prior to reproduction
	Precip: Aug	cm of precipitation in August in the year prior to reproduction
	Temp: Sept–Nov	Mean temp. Sept. – Nov., fall prior to reproduction
	Precip: Deviation Active	Deviation from normal active season precipitation
	Precip: Deviation Hibernation	Deviation from normal hibernation precipitation
	Precip: Mean Active	Mean precipitation during active season
	Precip: Mean Hibernation	Mean precipitation during hibernation
	Precip: Variance Active	Variance in precipitation during active season
	Precip: Variance Hibernation	Variance in precipitation during hibernation
	Temp: Deviation Active	Deviation from normal active season temperature
	Temp: Deviation Hibernation	Deviation from normal hibernation temperature
	Temp: Mean Active	Mean temperature during active season
	Temp: Mean Hibernation	Mean temperature during hibernation
	Temp: Variance Active	Variance in temperature during active season
Temp: Variance Hibernation	Variance in temperature during hibernation	
Colony	Identity of colony or satellite	
Demographic	Male yearlings	Number of male yearlings present from previous year's litter
	Female yearlings	Number of female yearlings present from previous year's litter
	Matriline	Density of related females present (number present/average)
	Other females	Density of non-matriline females present in the colony
	New Male	Whether the male observed was new to the site
	Younger adult	Number of younger adult matriline females present
	Offspring of younger	Number of pups produced by younger matriline adults
	Older adult	Number of older adult matriline females present
	Offspring of older	Number of pups produced by older matriline adults
	Same-age adult	Number of matriline females the same age as the subject
Offspring of same-age adults	Number of pups produced by matriline females of the same age	

Because temperature and precipitation affect marmot demography (Schwartz and Armitage 2005), we used several of these variables to assess their effect on recruitment. Weather

data were obtained from the National Weather Service for Crested Butte, Colorado, (NOAA 1962–2004) which is about 10 km from the study site. These data included the date of first and last snowfall, the date of first and last snow cover (greater than 2.54 cm), the amount of precipitation in each month of the active season, the amount of precipitation during hibernation, mean temperature during the active season, and mean temperature during the fall. In addition, we used data on the variance of temperature and precipitation during hibernation and during the active season. Finally, we calculated the average deviation from normal temperature and precipitation for the active season and the hibernation period. Deviation from normal is a monthly variable available from NOAA, and uses a 30-year average for comparison. The comparison mean is updated once a decade during years ending in 2 (NOAA 1962–2004). All environmental variables were calculated for periods preceding reproduction. Thus, “active season” variables were for the active season in which the marmot was gaining mass prior to hibernation, and leading up to her attempt at reproduction.

A number of other characteristics, such as elevation and size of the foraging area, differ among colonies. We controlled for these differences by using colony identity as a factor in all our two-way nested models.

### *Statistical methods*

We analyzed the effects of social and environmental variables using a linear mixed effects model, because the data included repeated observations of the same individual and these individuals were grouped into a smaller number of colonies. Mixed effects models explicitly allow this type of hierarchical data structure.

When evaluating annual reproductive success, we assessed the number of offspring that each female produced each year. The data are counts of weaned offspring, but more than half of the female-years resulted in no reproduction. Thus, the data followed a Zero-Inflated Poisson (ZIP) distribution with two-way nesting. We used an algorithm in R 2.7.2 (R Development Core Team 2009) to fit such a model using a Markov Chain Monte Carlo (MCMC) technique. For more details about the algorithm and nested ZIP models see (Zuur et al. 2010a, Zuur et al. 2010b). Our algorithm allows estimation of the effects of covariates on reproductive failure and on the number of offspring produced, given that reproduction occurred.

Our algorithm fit a model with the following form:

$$Y_{ijk} \sim ZIP(\pi_{ijk}, \mu_{ijk})$$

$$E(Y_{ijk}) = \mu_{ijk} \times (1 - \pi_{ijk}) \text{ and } \text{var}(Y_{ijk}) = (1 - \pi_{ijk}) \times (\mu_{ijk} + \pi_{ijk} \times \mu_{ijk}^2)$$

where  $\pi_{ijk}$  is the probability of observing reproduction and  $\mu_{ijk}$  is the expected value for the count process. Observations for different years (for the same animal) are represented by  $k$ , different animals are represented by  $j$ , and colonies are represented by  $i$ .

These are modeled as a function of the covariates:

$$\text{logit}(\pi_{ijk}) = \alpha + \gamma_1 \times X_{1ijk} + \dots + \gamma_n \times X_{nijk} + d_i + d_{ij}$$

$$\log(\mu_{ijk}) = \alpha + \beta_1 \times X_{1ijk} + \dots + \beta_n \times X_{nijk} + b_i + b_{ij}$$

The random error terms,  $d_i$ ,  $d_{ij}$ ,  $b_i$ , and  $b_{ij}$ , are assumed to be independent of one another.

We ran the MCMC algorithm with uninformative prior probabilities and a 2000 run burn in to allow for model convergence. After this burn-in, we averaged every 10th of the next 6000

model runs to get estimates for the model parameters. We used a stepwise procedure to decide which covariates to include in our final model. For each round of parameter estimation, our algorithm included each covariate one at a time; for each covariate the algorithm produced estimates of the parameters  $\pi_{ijk}$  and  $\mu_{ijk}$ , and a Deviance Information Criterion (DIC) value (Spiegelhalter et al. 2002). We selected the next variable for inclusion in the model based on the lowest DIC value for a covariate that was significant. We considered a covariate to be significant if the credible interval for the parameter estimate did not overlap zero. In some cases, the model with the lowest DIC value included a covariate that was not significant as judged by the credible interval. In these cases, we selected the covariate with the next lowest DIC value and significant parameter estimates. We included this “next best” covariate in the model if the DIC values were not separated by more than 5; differences in DIC of less than 5 are generally not considered to be important differences (Spiegelhalter et al. 2003). Each covariate was added to either the Binary (logit) or the count (log) portion of the model, depending on which portion of the model included the significant parameter estimate ( $\pi_{ijk}$  or  $\mu_{ijk}$ ). We continued adding covariates in a stepwise fashion until there were no covariates that met both the DIC and significant parameter criteria. Because inclusion of additional covariates will sometimes change the estimation of parameters for covariates already in the model, we also performed a backwards procedure on the model that was selected in the forward selection process; each covariate was dropped one at a time to examine the effects on the overall model. The only covariates included in the final model were those whose inclusion improved the overall model DIC and had parameter estimates whose credible interval did not overlap zero. In cases where no Poisson parameters were selected, the models were re-analyzed using a standard logistic regression procedure in Minitab (Minitab 2007) so that the relative importance of each parameter could be estimated.



Because younger female marmots are known to experience reproductive suppression (Armitage 2003b) and the ZIP procedure models reproductive output across the entire lifespan, there is the possibility that reproductive suppression occurring in the youngest age class would be obscured by the successful reproduction at later ages. For this reason, we also examined the production of offspring by two-year-olds, in a separate Zero Altered Poisson (ZAP) analysis.

For our assessment of lifetime reproductive success, we averaged most predictor variables for each female during the years she was trapped. All weather variables were averaged, as well as all social variables that did not concern the colony male. For the logical variable, male presence, we calculated the percentage of female years when a male was present in the colony. The variable “new male” was also calculated as a percent. Residency status was considered to be a fixed characteristic of the female and remained unchanged. In addition, we calculated the age at first reproduction and the length of the reproductive span. These data were used in a Zero Altered Negative Binomial (ZANB) model to predict the total number of young that each female produced during her lifespan.

Finally, because the partial coefficients generated by multiple regression can conceal the gross associations between the predictor and response variables, we conducted univariate regressions with all the variables that were chosen in our models. In addition, we ran univariate regression for the variables that have been suggested previously to affect reproductive success: the number of same-aged females, the number of younger females, the number of older females, and the matriline density (Armitage 2003b).

## Results

### *Multivariate Analysis of Annual Reproductive success*

The final model included five variables that were the most influential in affecting whether a female marmot successfully produced offspring. Given that a female produced at least one litter, there no variables that significantly predicted litter size. The final model had the following form:

$$\text{Logit } \pi_{ijk} = -1.9569 + (0.6877 \times \text{Age}) - (0.0484 \times (\text{Age})^2) - (0.6098 \times (\text{NewMale})) + (0.4124 \times (\text{Reproduced previous year})) - (0.2274 \times (\text{Number of Same-aged Females})) + (0.1925 \times (\text{Number of Offspring of Same-aged Females}))$$

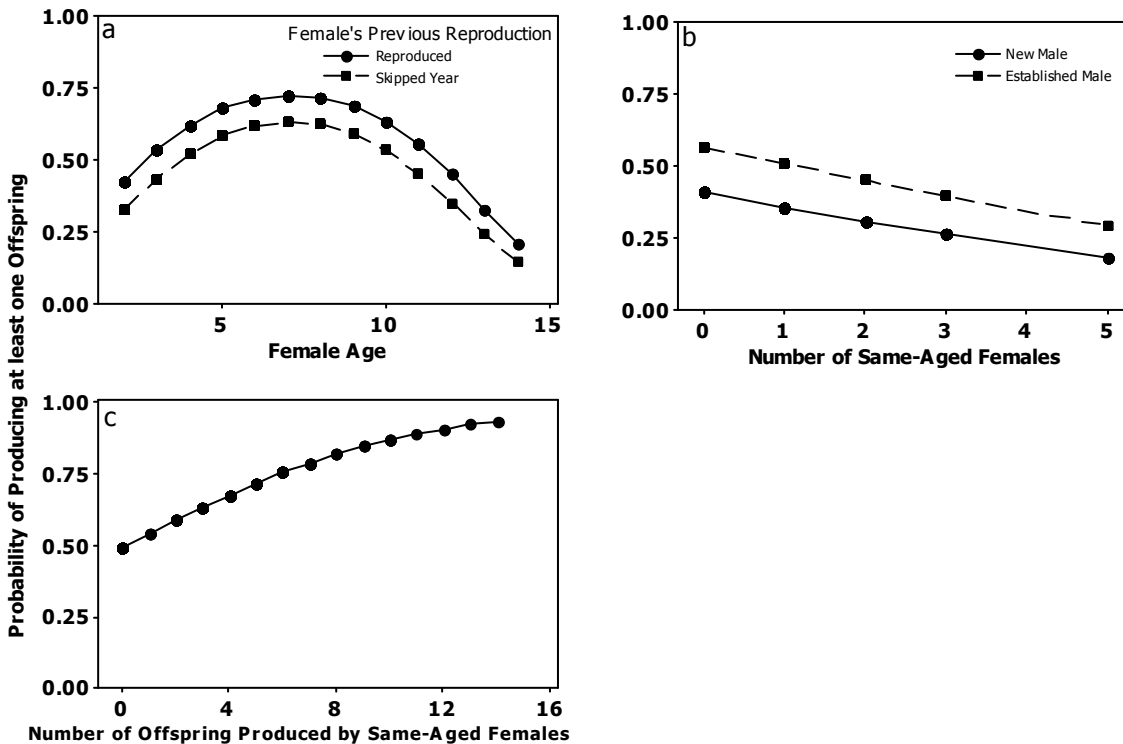
Two measures of matriline composition were significantly associated with the probability of producing at least one offspring. The probability of reproducing during a given year was negatively associated with the number of same-aged females present (Figure 2b, Table 3) and positively associated with the number of offspring produced by those same-aged females (Figure 2c, Table 3).

Two characteristics of the female were good predictors of her probability of reproducing. Female age and whether she had reproduced the previous year each significantly increased the likelihood of reproduction (Table 3). Females who reproduced the previous year had 51% higher odds of reproducing (Table 3). In addition, for each additional year of age, females were almost twice as likely to reproduce as they were at the previous age (Table 3). Probability of reproduction does not continue to increase throughout the lifespan however, and appears to decrease after about seven years of age (Figure 2a). These age effects are partial effects, in that they are found when the other significant effects have been incorporated into the estimation; after

adjusting for the effects of prior reproduction and the social environment, the odds of reproduction improve with age in a curvilinear function (Figure 2a, Table 3).

**Table 3. Predictors of the annual probability of reproducing. Positive coefficients indicate a higher probability of reproduction, while negative coefficients indicate lower probability. The amount that the odds ratio differs from one indicates the percent increase or decrease in the probability of producing offspring for each unit change in the predictor.**

Predictor	Coefficient	Odds Ratio	Z	P
Intercept	-1.9569		-5.56	<0.001
Age	0.6877	1.99	4.88	<0.001
(Age) <sup>2</sup>	-0.0484	0.95	-4.19	<0.001
Presence of New Male	-0.6098	0.64	-3.96	<0.001
Reproduced previous year	0.4124	1.51	2.38	0.017
Number of Same-Aged Females	-0.2274	0.80	-1.98	0.048
Number of Offspring of Same-Aged Females	0.1925	1.21	4.43	<0.001
Test that all slopes are zero: $G = 115.956$ , $DF = 6$ , $P\text{-Value} = <0.001$				



**Figure 2. Partial effects of covariates on the annual probability of producing one or more offspring. For each covariate, the line represents the effect of the variable when all other significant covariates are set to their mean.**

Because partial effects can be difficult to interpret, it can be informative to examine the univariate relationships to see if the same patterns are found as that found in the multivariate model. When considering only the effects of age, young females are much less likely to reproduce than older females and there is no reduction in overall reproduction at older ages (Figure 3a), (Schwartz et al. 1998, Oli and Armitage 2003). Similarly, the univariate relationship between the number of offspring produced by same-aged females and the probability of producing at least one young has a different shape (Figure 3b); although the relationship is still positive, the univariate relationship indicates that the probability of reproduction is much higher if same-aged matriline females produce at least one offspring, whereas the partial effect from the multivariate model indicates that the increase in probability is more gradual (Figure 2c, Figure 3b). Similar to the multivariate partial effects, the univariate relationships with the probability of reproduction indicated that the probability of reproduction was higher for females who had reproduced the previous year (Figure 3c), were sharing a colony with an established male (Figure 3d), or who lived with fewer same-aged females (Figure 3e).

Two other covariates were significantly associated with the probability of reproduction in univariate logistic regression. The probability of reproduction was negatively associated with the number of older females in the matriline (Figure 3f) and positively associated with the number of younger females in the matriline (Figure 3g). Many of these matriline variables are correlated (Table 4); once the variables related to the number of same-aged females and the number of young produced by same-aged females were entered into the multivariate model, neither the number of older nor the number of younger females had significant partial coefficients (Table 3). In particular, the number of same-aged females is positively associated with both the number of older adults and the number of offspring produced by older adults; the number of same-aged

females was also negatively associated with the number of younger females (Table 4). Thus, it is possible that the number of same-aged females acts as a proxy for one of these other variables.

**Table 4. Correlations among the number of members in different age classes of the matriline. For each cell, the top number is the Pearson correlation coefficient, while the bottom number gives the p-value. Significant correlations are given in bold.**

	Number of Same-Aged Females	Number of Offspring Produced by Same-Aged Females	Number of Older Adults	Number of Offspring Produced by Older Adults	Number of Younger Adults
Number of Offspring Produced by Same-Aged Females	<b>0.515</b> <b>&lt;0.001</b>				
Number of Older Adults	<b>0.325</b> <b>&lt;0.001</b>	<b>0.094</b> <b>0.004</b>			
Number of Offspring Produced by Older Adults	<b>0.220</b> <b>&lt;0.001</b>	<b>0.130</b> <b>&lt;0.001</b>	<b>0.800</b> <b>&lt;0.001</b>		
Number of Younger Adults	<b>-0.109</b> <b>0.001</b>	-0.033 0.304	-0.038 0.241	0.005 0.868	
Number of Offspring Produced by Younger Adults	-0.088 <0.006	-0.004 0.890	-0.033 0.298	0.014 0.671	<b>0.612</b> <b>&lt;0.001</b>

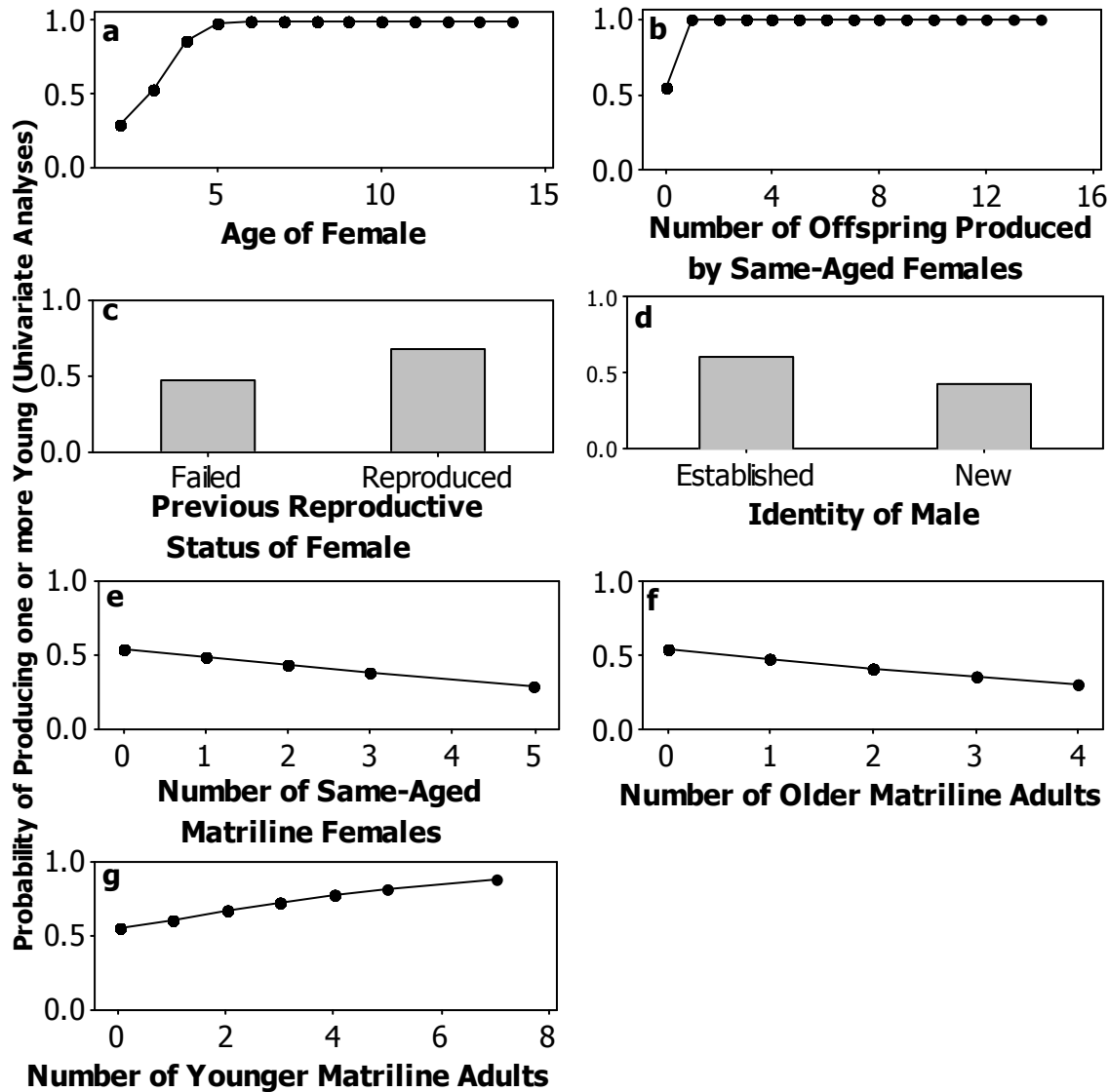


Figure 3. Univariate relationship between selected variables and the probability of producing at least one offspring.

The identity of the colony male was a significant predictor of female success in the univariate and multivariate models. The odds of reproduction were about 40% higher when the colony contained a male who had over-wintered at the same site as the female (Figure 2b, Table 3).

Although we did not identify any variables that predicted litter size, we were interested in the possibility that females did not produce the same number of male and female offspring. The

population sex ratio was approximately 1:1; but when we examined the sex ratio of individual litters, a large number of litters were either all male or all female (Figure 4). Therefore, we examined whether any of our measured variables could predict sex ratio within litters. One environmental and one social variable were significantly associated with litter sex ratio (Table 5). The odds of producing male-biased litters increased by 5% for each additional offspring produced by older adults (Table 5, Figure 5a). In addition, females who experienced cooler average fall temperatures prior to the spring of reproduction had 8% higher odds of producing males (Table 5, Figure 5b). Both of the partial effects that were associated with litter sex ratio were very similar to the effects found in univariate models (Table 6, Figure 6), which suggests that the two significant variables were little affected by other variables in the model.

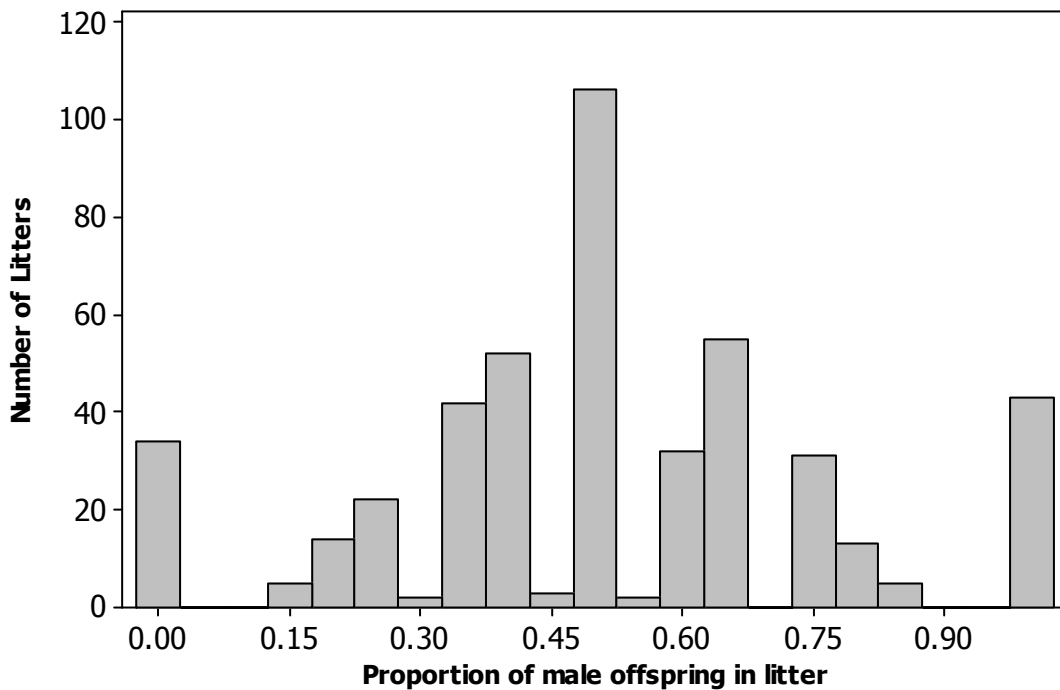


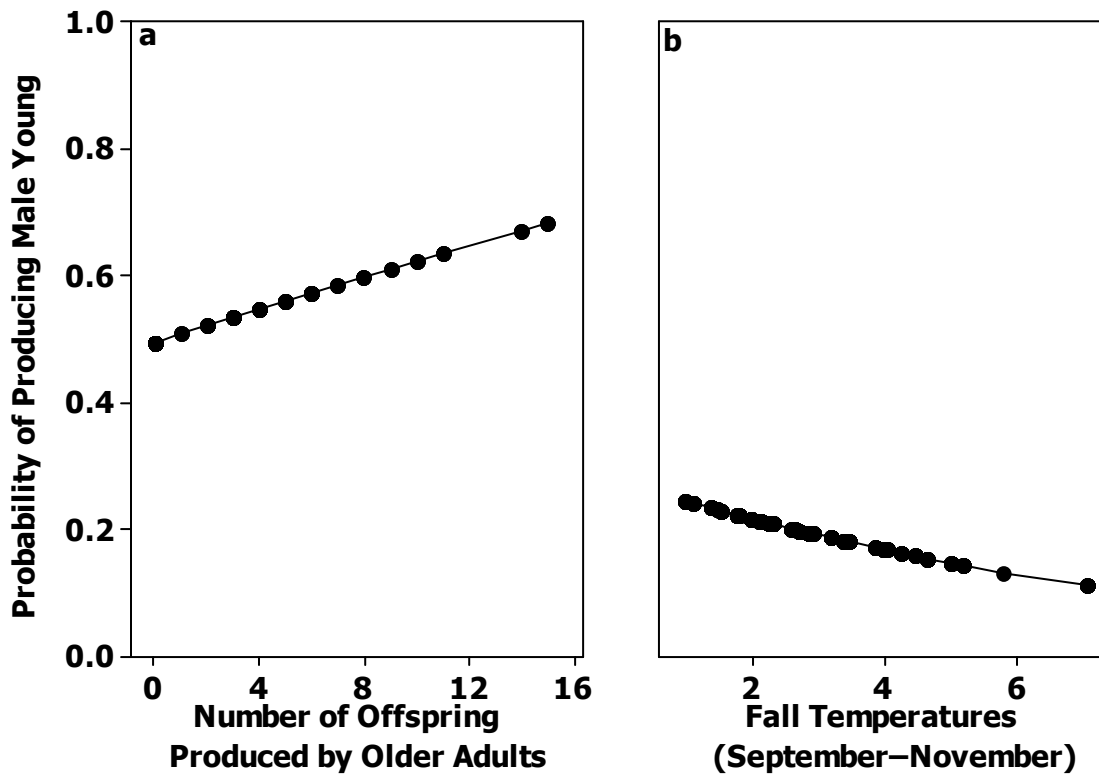
Figure 4. Observed sex ratio of litters.

**Table 5. Predictors of the sex ratio of litters. A positive coefficient indicates a higher probability of producing male young. The amount that the odds ratio differs from one indicates the percent increase or decrease in the probability of producing a male for each unit change in the predictor.**

Predictor	Coefficient	Odds Ratio	Z	P
Constant	0.1291		1.67	0.096
Number of Offspring Produced by Older Adults	0.0524	1.05	2.59	0.010
Fall Temperatures (September–November)	-0.0441	0.92	-1.97	0.049
Test that all slopes are zero: $G = 10.952$ , $DF = 2$ , $P\text{-Value} = 0.004$				

**Table 6. Univariate analyses of factors associated with litter sex ratio.**

Predictor	Coefficient	Odds Ratio	Z	P
Number of Offspring Produced by Older Adults	0.0529	1.05	2.61	0.009
Fall Temperatures (September–November)	- 0.0881	0.95	-2.00	0.045



**Figure 5. Partial effects of covariates on the probability of producing male young in individual litters. For each covariate, the line represents the effect of the variable when all other significant covariates are set to their mean. Temperatures are given in degrees Celsius.**



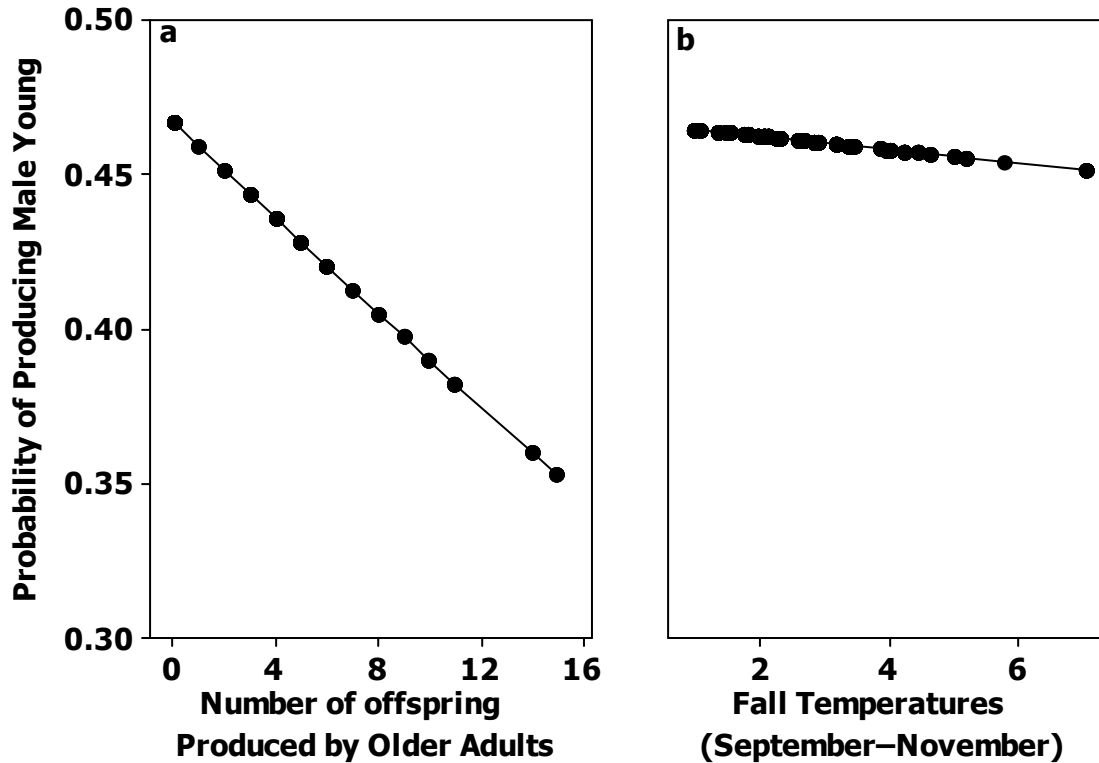


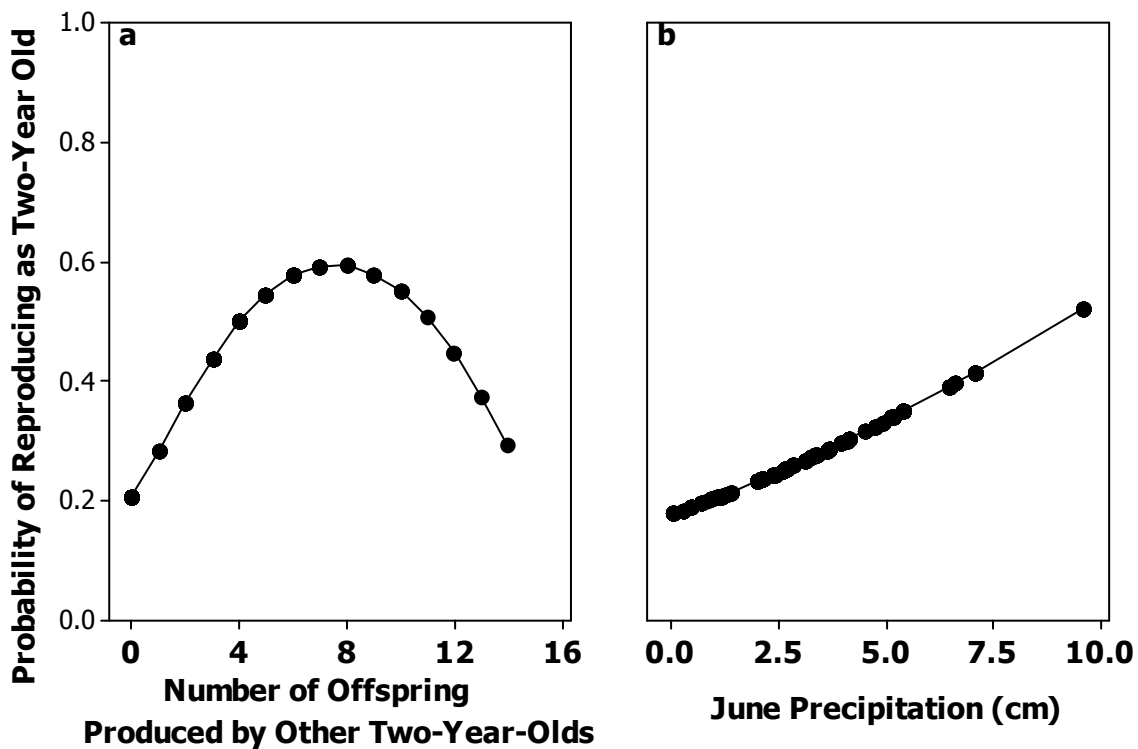
Figure 6. Univariate relationships between selected variables and the probability of producing a male-biased litter.

*Reproduction by two-year-olds*

The probability of reproduction by two-year-olds is always low and was influenced by both social and environmental variables (Table 7, Figure 7). Like females of other ages, two-year-olds were more likely to reproduce when another two-year-old was also able to reproduce (Table 7, Figure 7a). However, this effect was reversed when more than one other two-year-old reproduced; two-year-olds who lived in a matriline where more than seven offspring were produced by same-aged females were less likely to reproduce (Figure 7a). In addition, two-year-olds were affected by summer precipitation the year before they attempted reproduction. Females who experienced a wet June as yearlings were 18% more likely to reproduce as a two-year-old, than those experiencing a drier June (Table 7, Figure 7b).

**Table 7. Predictors of the probability of producing one or more young as a two-year-old. Positive coefficients indicate a higher probability of reproducing. The amount that the odds ratio differs from one indicates the percent increase or decrease in the probability of producing offspring for each unit change in the predictor.**

Predictor	Coefficient	Odds Ratio	Z	P
Constant	-1.8848		-6.01	<0.001
Offspring produced by Other Two-Year-Olds	0.4581	1.58	3.30	0.001
(Offspring produced by Other Two-Year-Olds) <sup>2</sup>	-0.0303	0.97	-1.98	0.047
June Precipitation (cm of water)	0.1675	1.18	2.30	0.022
Test that all slopes are zero: $G = 23.975$ , $DF = 4$ , $P\text{-Value} < 0.001$				



**Figure 7. Partial effects of covariates on the probability of producing one or more offspring as a two-year-old. For each covariate, the line represents the effect of the variable when all other significant covariates are set to their mean. Matriline density was calculated as the number of matriline females present, divided by the average number of females found at a given site.**

The univariate relationship between the probability of reproducing and the number of offspring produced by other two-year-olds was similar to the partial effect found in the multivariate model. (Table 8, Figure 8a). However, after accounting for the effects of the amount of precipitation received during the previous June, the relationship between the number of offspring produced by two-year-olds and the number of offspring produced by same-aged females is initially positive, and turns negative if more than one other two-year-old reproduces (Table 7, Figure 7a). The univariate relationship between June precipitation and the probability of reproducing as a two-year-old was similar to the one found in the multivariate model (Table 8, Figure 7b, Figure 8b). In addition, in a univariate analysis, there was a trend for the probability of reproduction to increase with the number of offspring produced by older females. This trend was nearly significant (Table 8, Figure 8f). The univariate relationships between the probability of reproduction, matriline density and the number of same-aged females in the matriline were non-significant.

**Table 8. Univariate analyses of the probability of producing offspring as a two-year-old.**

Predictor	Coefficient	Odds Ratio	Z	P
Number of Offspring Produced by Other Two-Year-Olds	0.2192	1.25	3.81	<0.001
June Precipitation (cm)	0.1701	1.19	2.44	0.015
Number of Other Two-year-olds	0.0081	1.01	0.07	0.944
Matriline Density	-0.0464	0.95	-0.28	0.780
Number of Older Matriline Females	0.0432	1.04	0.27	0.791
Number of Offspring Produced by Older Adults	0.0745	1.08	1.92	0.055

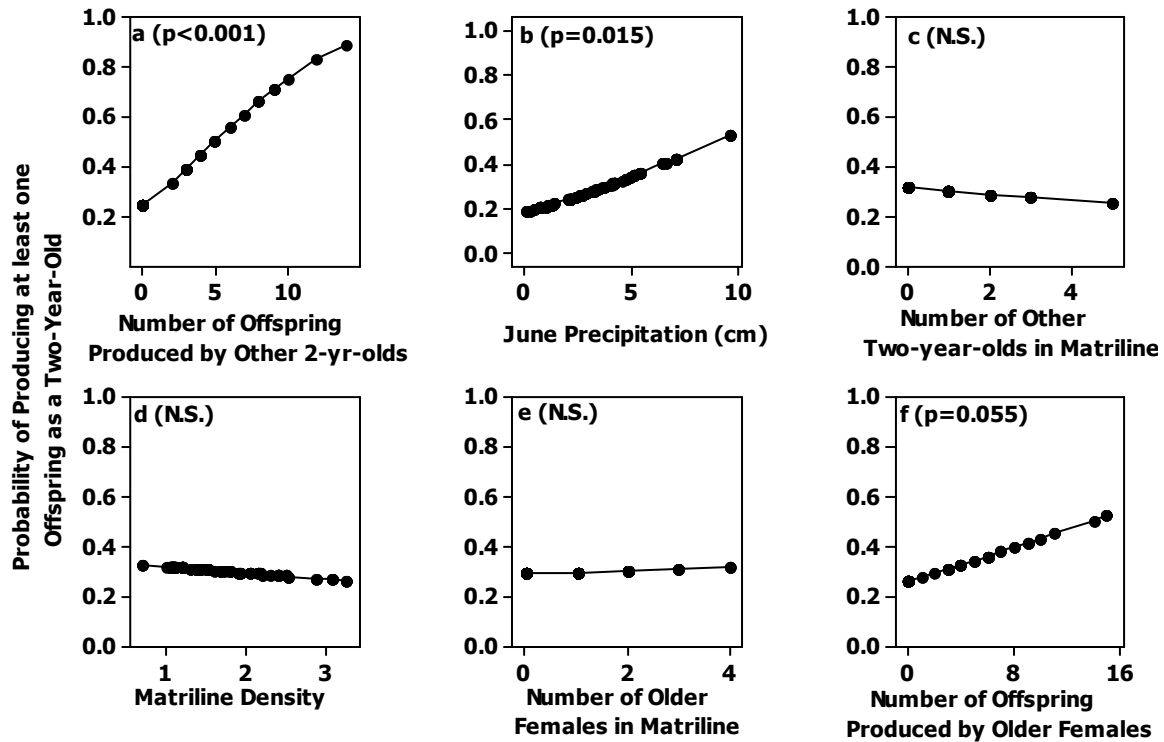


Figure 8. Univariate relationship between selected variables and the probability of producing at least one offspring as a two-year-old.

Once reproduction was initiated, the total number of offspring produced by a two-year-old was influenced by an environmental variable. Females who experienced a late date of last snowfall during gestation or lactation were more likely to produce larger litters (Wald  $\chi^2 = 6.05$ , 1df,  $p = 0.014$ ). When the last snowfall occurred in June, females had much larger litters than when the last snowfall occurred in late April or Early May (Figure 9). We did not find any evidence of sex ratio bias in the litters produced by two-year-old females.

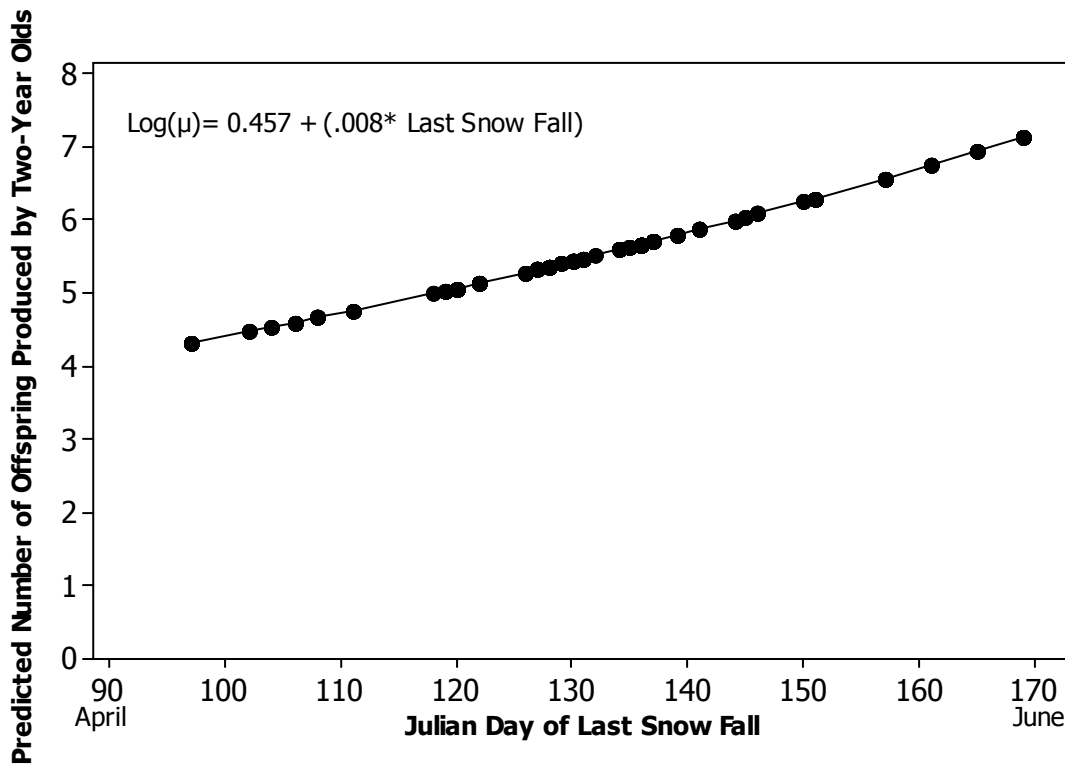


Figure 9. Relationship between date of last snowfall and the predicted total number of offspring produced by two-year-olds.

*Lifetime reproductive success*

Variables that affect the annual probability of reproducing may or may not predict total lifetime reproduction. Therefore, we also examined the variables that were associated with the lifetime reproductive output of females. The average number of female yearlings present in a colony was significantly related to whether a female ever produced offspring during her life (Table 9). Females who never lived in matriline containing female yearlings were unlikely to have reproduced during their lifespan (Figure 10b).

**Table 9. Predictors of the probability of producing one or more young during the lifespan. Positive coefficients indicate a higher probability of reproducing. The amount that the odds ratio differs from one indicates the percent increase or decrease in the probability of producing one or more young for each unit change in the predictor.**

Predictor	Coefficient	Odds Ratio	Z	P
Constant	-6.63703		-4.35	<0.001
Lifespan	0.6013	1.82	4.79	<0.001
Resident of Natal Colony	1.2934	3.65	3.53	<0.001
Percent of Years Spent Resident with Established Male	3.6736	39.39	2.80	0.005
Average Number of Female Yearlings	7.8552	2579.18	3.13	0.002
Test that all slopes are zero: $G = 163.60$ , $DF = 4$ , $P\text{-Value} < 0.001$				

In addition, the probability of reproducing was significantly related to lifespan, male residency, and philopatry (Table 9). As expected, females who lived longer were more likely to leave offspring (Figure 10a). In addition, females who lived more of their lifespan in a colony with an established male were more likely to have reproduced than those who were often resident with new males (Table 9, Figure 10c). Finally, females who lived in their natal colony were more likely to reproduce than females who were immigrants (Table 9, Figure 10a). All of the univariate analyses had similar results to the multivariate partial effects (Table 10, Figure 11a–d). In addition, there was a significant positive univariate relationship between the probability of reproducing at least once during the lifespan and the average number of younger females in the matriline during a female’s lifespan (Table 10, Figure 11f). Finally, there was a significant negative univariate relationship between the average number of older adults present and the lifetime probability of reproduction (Table 10, Figure 11g).

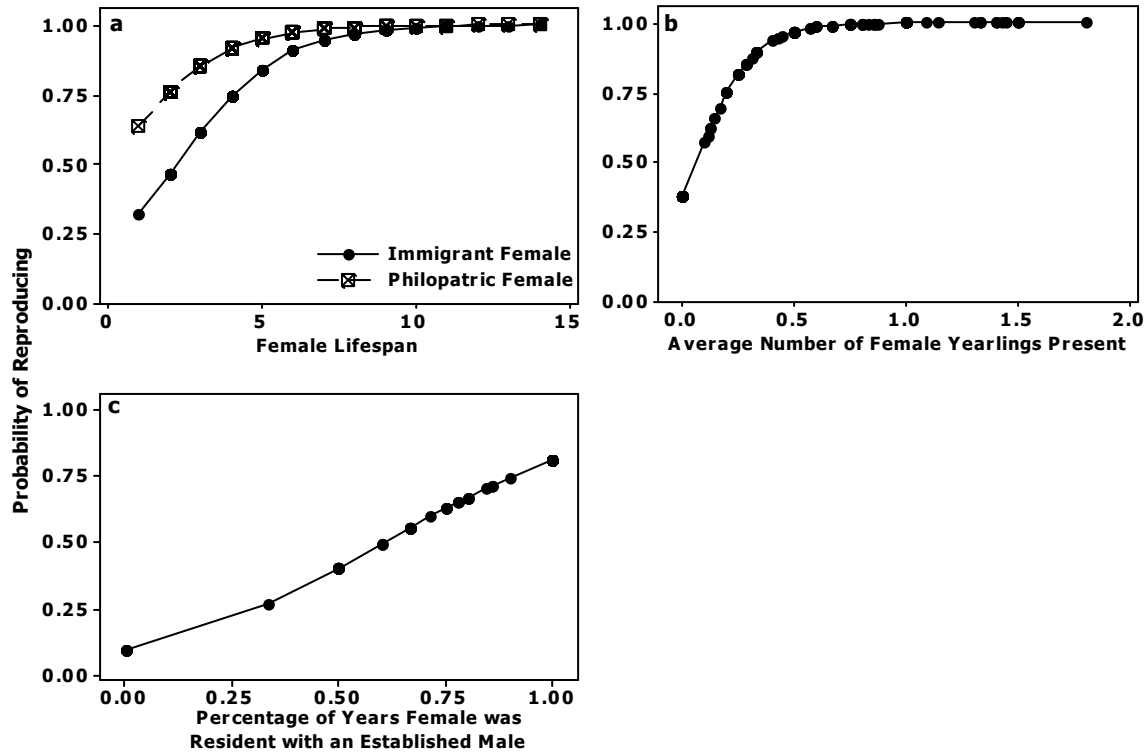


Figure 10. Partial effects of covariates on the lifetime probability of producing one or more offspring. For each covariate, the lines represents the effect of the variable when all other significant covariates are set to their mean.

Table 10. Univariate analyses of the probability of reproducing at least once during the lifespan.

Predictor	Coefficient	Odds Ratio	Z	P
Female Lifespan	0.8303	2.29	6.80	<0.001
Residency Status of Female	0.7259	0.013	2.49	0.013
Established Male	1.8545	6.39	2.59	0.01
Number of Male Yearlings Present	11.4384	21.32	3.84	<0.001
Number of Female Yearlings Present	11.7231	123384.72	3.90	<0.001
Number of Same-Aged Matriline Females	-0.2970	-2.31	-2.31	0.21
Number of Younger Matriline Females	3.5851	36.06	3.71	<0.001
Number of Older Matriline Females	-0.3859	0.68	-2.15	0.031

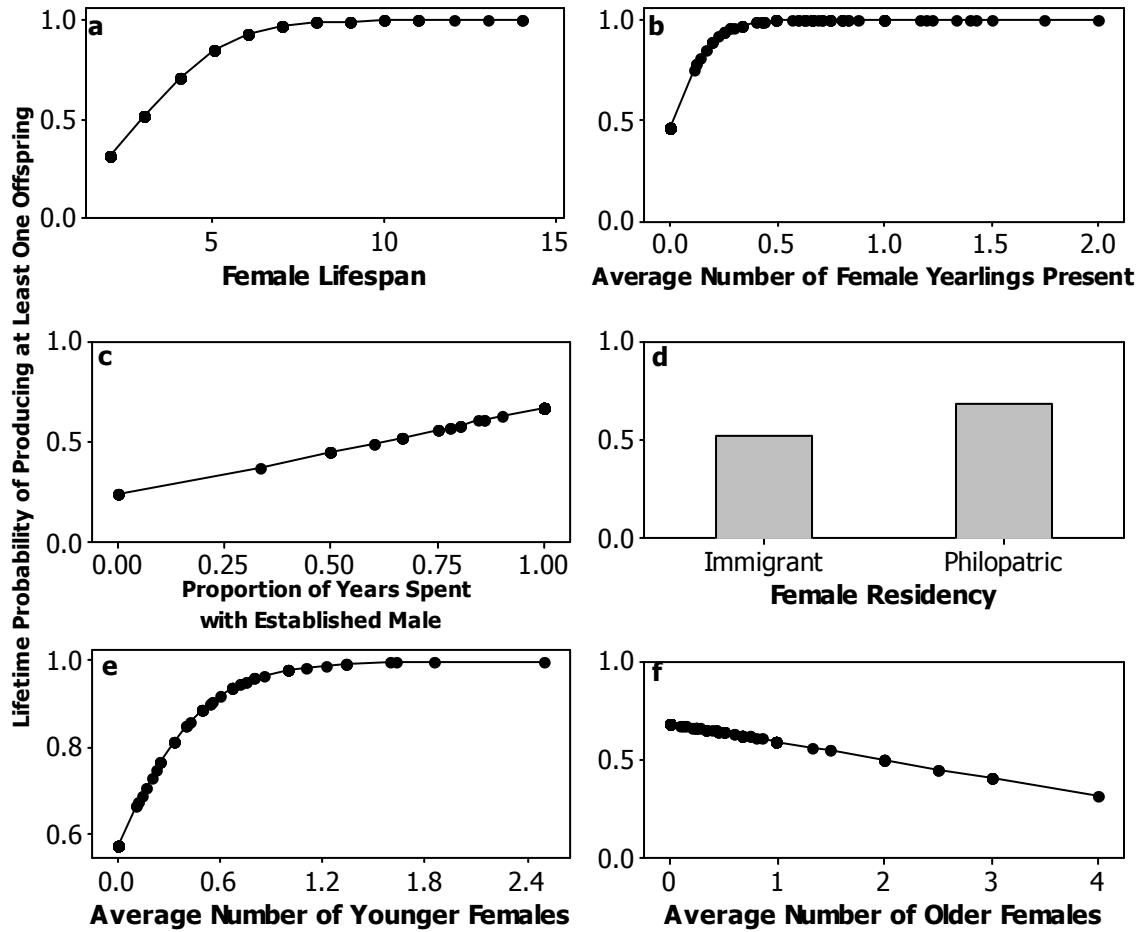


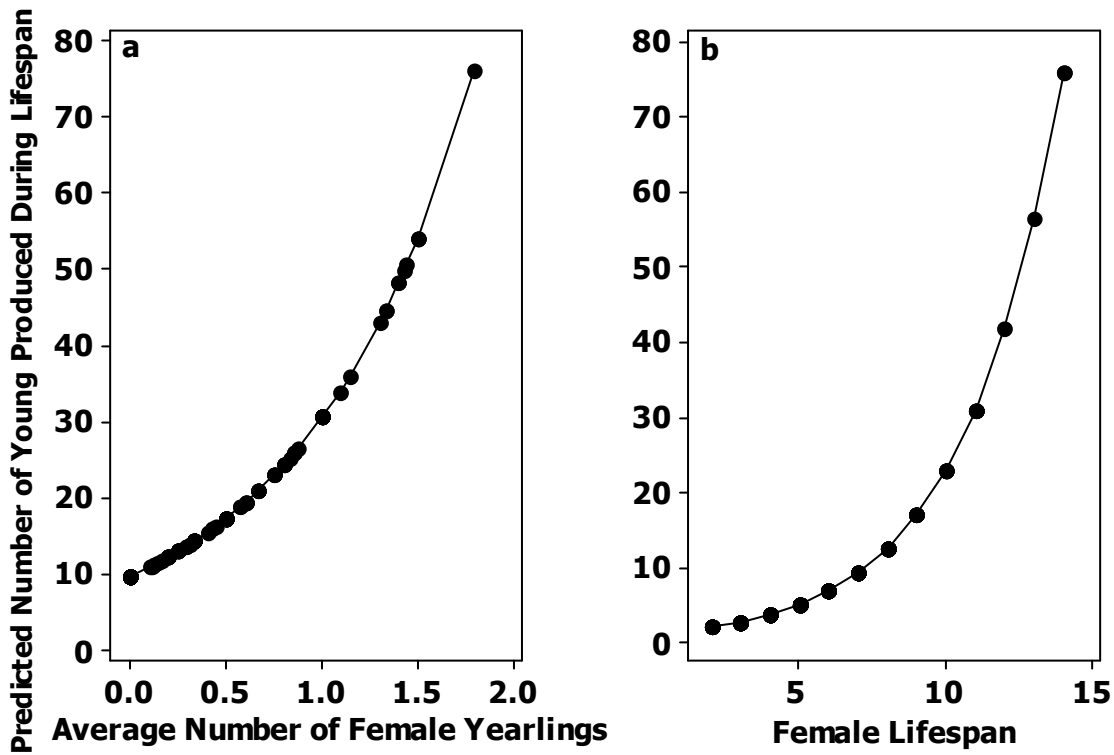
Figure 11. Univariate relationship between selected variables and lifetime probability of producing offspring.

The females who successfully reproduced at least once in their lifespan left very different numbers of offspring. In this sample, females who reproduced at least once produced an average of 9.47 offspring during their reproductive lives, but one produced at least 52. There were only two variables that were significantly associated with the number of offspring left by a female (Table 11). Females who reproduced in matrilineal groups that, on average, contained female yearlings were likely to produce a larger number of offspring during their reproductive life (Table 11, Figure 12a). Similarly, females who had a longer reproductive lifespan left more offspring (Table 11, Figure 12b).



**Table 11. Predictors of the total lifetime reproductive success of females. Positive coefficients indicate greater number of offspring produced.**

Predictor	Coefficient	Wald $\chi^2$	df	P
Constant	0.205	1.662	1	0.197
Number of Female Yearlings	1.138	29.616	1	<0.001
Female Lifespan	0.299	74.164	1	<0.001



**Figure 12. Relationship between partial effects of covariates and the total lifetime production of offspring. For each covariate, the line represents the number of offspring predicted by the variable when all other significant covariates are set to their mean.**

The univariate relationships between the total lifetime production of young and the number of female yearlings and female lifespan were very similar to those found in the multivariate analyses (Table 12, Figure 13 a,c). Once female yearlings and female lifespan were included in the multivariate model, no other covariates had significant partial effects. However, several additional covariates were significant in univariate analyses. The average number of male

yearlings present and the average number of younger adults present were each positively associated with the total number of offspring produced during the lifespan (Table 12, Figure 13b, e). The average number of older adults, the average number of same-aged females present and the relative matriline density were each negatively associated with the number of offspring produced during the lifespan (Table 12, Figure 13d, f, g).

**Table 12. Univariate analyses of the total lifetime reproductive success of females. Positive coefficients indicate greater total number of offspring produced.**

Predictor	Coefficient	Wald $\chi^2$	df	P
Average Number of Female Yearlings Present	2.084	102.952	1	<0.001
Average Number of Male Yearlings Present	2.195	112.188	1	<0.001
Female Lifespan	0.396	154.100	1	<0.001
Average Number of Older Females Present	-0.498	26.219	1	<0.001
Average Number of Younger Females Present	1.429	30.726	1	<0.001
Average Number of Same-Age Females Present	-0.368	16.805	1	<0.001
Average Number of Females in the Matriline	-0.310	9.542	1	0.002

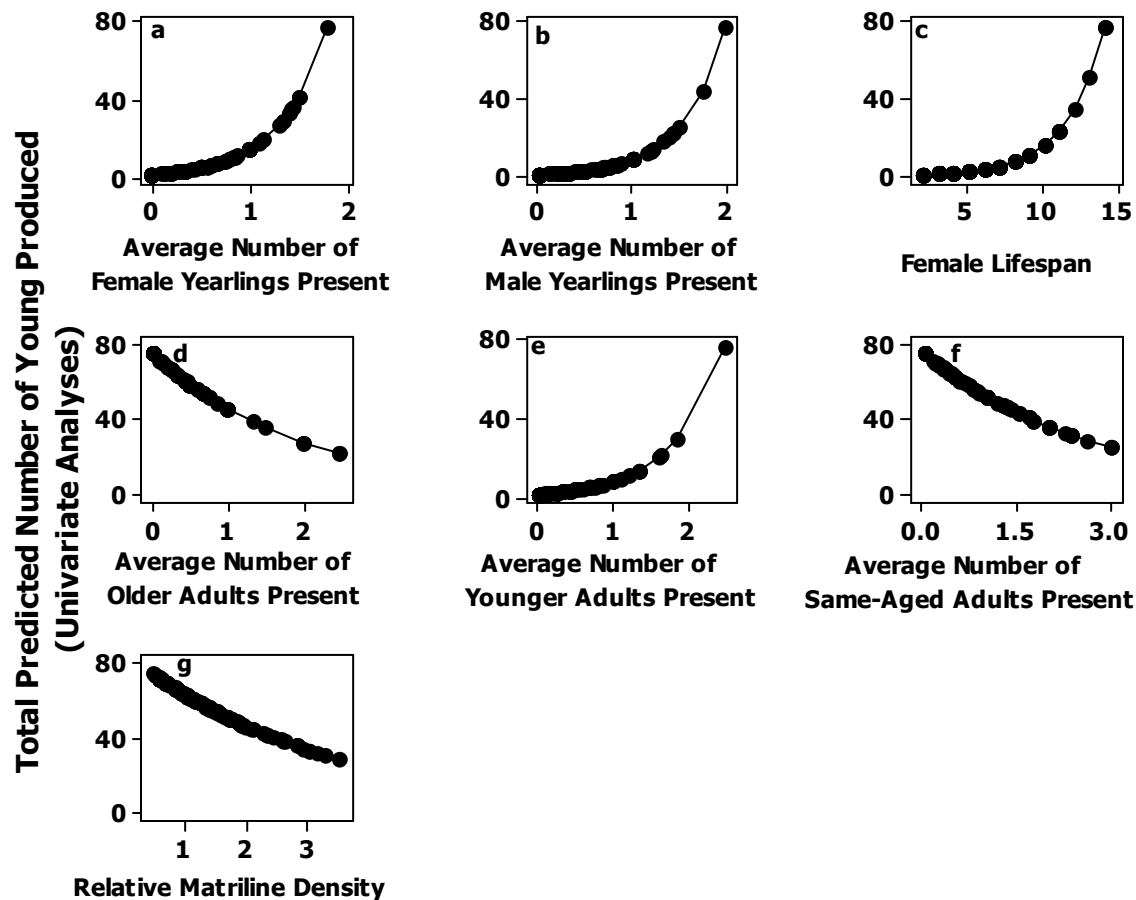


Figure 13. Univariate relationships between partial effects of covariates and the total lifetime production of offspring. For each covariate, the line represents the number of offspring predicted by the variable when all other significant covariates are set to their mean.

## Discussion

### *Annual reproductive success*

We identified the following factors that predicted whether females of all ages would reproduce successfully in a given year: female age, reproduction by the female the previous year, and reproductive success of same-aged females increased the likelihood of reproduction; the presence of a new male, and the presence of same aged females in the matriline decreased the probability of reproduction. No variables predicted the litter size of these successful females. These results are not entirely surprising given the options available to individual marmots. There

are likely to be a large number of endocrine events that would cause temporary infertility, and these events could be influenced by reproductive suppression or the presence of unfavorable environmental conditions.

Social variables had a large impact on whether a female reproduced in a particular year. We anticipated that the number of older females in the matriline or the total number of females in the matriline would be significant predictors of annual reproductive success, particularly for two-year-olds. Reproductive suppression is common in mammals (Wasser and Barash 1983) and occurs in many scuirids, including prairie dogs and all 14 marmots (Rayor 1985, Armitage 1986, Hoogland 1995, Blumstein and Armitage 1999, Blumstem and Armitage 1999, Armitage 2003b, Hacklander et al. 2003). Two-year-olds are particularly vulnerable to suppression; they are significantly less likely to reproduce when living in matriline with older females, including their mothers (Armitage 2007). Surprisingly, in this study, neither the number of older females nor the total number of females in the matriline were significant predictors of annual reproductive success. However, when the data are divided into the categories of presence or absence of older females, females were significantly more likely to reproduce when older females were completely absent ( $\chi^2 = 385.8$ ,  $n = 997$ , 3df,  $p < 0.0001$ ). Similarly, two-year-olds were more likely to reproduce when older females were absent, than when they were present ( $\chi^2 = 49.1$ ,  $n = 240$ , 3df,  $p < 0.0001$ ). Thus the presence of any older adults suppresses reproduction, but the total number of females has no significant effect.

Interestingly, the number of offspring produced by same-aged matriline females was the best predictor of the probability of reproductive success for two-year-olds. For each additional pup produced by another two-year old, females were almost 60% more likely to reproduce (Table 7). However, two-year-olds living with more than one other reproductive two-year-old

were likely to fail to reproduce (Table 7, Figure 7a). The number of offspring produced by other two-year-olds was positively related to the probability of reproduction in univariate analysis (Table 8). These results suggest that, overall, if the probability of reproduction is good for one two-year-old, it will be good for other two-year-olds. However, if the other social conditions in the matriline lead to reproductive suppression, it is particularly difficult for more than one female to escape suppression.

Two-year-old females were also affected by the amount of precipitation received during the summer prior to attempting reproduction. For each additional centimeter of rain received during the June of her yearling summer, a female was 18% more likely to reproduce as a two-year-old (Table 7, Figure 7b). This summer precipitation would increase the availability of high-quality forage, and improve a female's chances of gaining sufficient mass to overwinter and reproduce the following spring.

Environmental conditions in the spring were also important; the date of the last spring snowfall was a significant predictor of the total number of offspring produced by two-year-olds (Figure 9). Two-year-olds produced more offspring in years when there was a late snowfall than in years when snow stopped falling in April or May. Late snowfall was also reported to increase offspring survival and net reproductive rate (Schwartz and Armitage 2005). Late snowfall effectively combines both precipitation and temperature. A late snowfall may provide more moisture for the growth of forage plants, and it implies that at least some of the days in June were characterized by cooler temperatures. Marmots are intolerant of high temperatures. They are selected for heat and water conservation and are unable to mobilize water for evaporative cooling. The thermoneutral zone extends approximately from 10° to 15° C for adults and yearlings (Armitage 2004b), and marmots reduce the length of foraging bouts when temperatures

are too high (Melcher et al. 1990). Adult marmots balance the demands of foraging and thermoregulation by allowing transient increases in body temperature and by cooling themselves on rocks, where the increased wind speed assists with convective cooling (Melcher et al. 1990). Thus, an increased number of cool days would allow marmots to forage longer and these marmots would have more energy available for investment in lactation. Similarly, moisture availability during the active season affects survivorship and reproduction, with higher mortality and lower reproduction in years with low precipitation (Armitage 1994, Lenihan and Van Vuren 1996, Schwartz and Armitage 2005). Thus, while a late snow cover might be expected to reduce reproduction (Van Vuren and Armitage 1991), late snowfall may indicate that adequate moisture is available.

Similar to two-year-olds, the reproduction of older females was significantly related to the number and reproductive success of same-aged adults in the matriline. When females lived in matriline that contained other females of the same age the probability of reproduction decreased; however the odds of reproduction were 21% higher when some of those same-aged females also reproduced (Table 3) and increased as the number of offspring increased (Figure 2c). Interestingly, the odds of reproduction were about 20% greater for females if there were fewer females their age (Figure 2b, Table 3).

Thus, females are more likely to reproduce if there are no same-aged females present, but in the presence of full or half-sisters, females reproduce more often if those same-aged females are successful as well. Possibly these females benefit from associating with reproductive littermates by hearing anti-predator calls; females with emergent young are the most likely to give anti-predator calls (Blumstein et al. 1997, Armitage and Schwartz 2000). Alternatively,

females may not directly benefit from the reproduction of other females, but rather these results simply demonstrate the overall suitability of conditions for reproduction.

Immigration of a new male was also a significant predictor of annual reproductive success. The odds of producing any young were 36% less if a female lived in a colony with a new male (Figure 2b, Table 3); the median number of young produced in the presence of a new male was zero. These newly immigrated males did not over-winter with the females, but arrived sometime after emergence from hibernation. Some of these males arrived soon after females emerged, and had an opportunity to father young. However, some of these males arrived after all the females completed estrous. Females in these colonies effectively have no male available for reproduction until the following year. The frequency of this condition may explain why there is no evidence for mate selection by female yellow-bellied marmots (Armitage, pers. comm.).

#### *Lifetime reproductive success*

A newly immigrated male reduces the probability that a female will reproduce during the year of immigration. Similarly, the odds of a female successfully reproducing during her life were almost 40 times lower if she regularly shared a colony with newly immigrated males (Table 9). The immigration status of females was significantly associated with her reproductive output. Females who reproduced in their natal colony were more than three times more likely to produce at least one pup during their lifespan, than those who were immigrants (Figure 10a, Table 9).

Although the reproductive success of same-aged was a significant predictor of annual reproductive success, the presence of yearlings was a significant predictor of lifetime reproductive success. Lifetime reproductive success was positively associated with the presence of female yearlings (Figure 10b, Figure 12a, Table 9, Table 11). Females whose matriline, on

average, contained more female yearlings were likely to have high lifetime reproductive success. These females were more likely to have reproduced at least once (Figure 10b), and were more likely to have produced a larger number of pups (Figure 12a). Moreover, although we selected a final model which included the number of female yearlings, the number of male yearlings was a nearly equivalent predictor. This finding is not unexpected—females who produce many offspring are likely to have many of their own yearling sons and daughters in their matriline.

### *Sex ratio of litters*

Sex ratio was influenced by the composition of the matriline. Females produced more female pups when older females produced relatively few young (Figure 5a, Table 5). Because of decreased competition, these females may be more likely to recruit their daughters into the local population. Thus, their best strategy is to produce female-biased litters when older females are either not present or not reproductively active, and the probability of recruiting daughters is high (see also Armitage 1987).

The sex ratio of litters was also influenced by an environmental variable. Females who experienced a relatively warm fall were more likely to produce female-biased litters the following spring (Figure 5b). Although this effect was significant, it was not large; an increase in average temperature of one degree increased the probability of producing female young by 8% (Table 5). Possibly, the cooler fall temperatures affected the energy budget of marmots in early hibernation. Cooler temperatures during the fall would increase the probability of a consistent snow cover, which would assure a more constant and favorable burrow temperature. However, the variation in burrow temperature is much smaller than the variation in air temperatures, and fall burrow temperatures generally vary by only about three degrees Celsius (Kilgore and



Armitage 1978). The mechanism by which fall temperatures influence sex ratio the following spring requires further investigation.

### *Effects of female age and lifespan*

The final predictors of reproductive success relate to female age and lifespan. Marmots in this population appear to have reduced reproductive capacity at advanced ages. After adjusting for the effects of the social environment, females were most fecund at mid-life (from about age four until age seven or eight). The youngest females are always less likely to reproduce (Schwartz et al. 1998, Oli and Armitage 2003) because of reproductive suppression (Armitage 2003b). In addition, although the overall probability of reproduction by older females is high, these females appear to be less fecund, once the effects of same-aged females, male identity, and prior reproductive status are taken into account. Older females are more likely to have reproduced the previous year ( $r = 0.386$ ,  $p < 0.001$ ), and are less likely to live in a matriline containing same-aged females ( $r = -0.285$ ,  $p < 0.001$ ). Because reproducing the previous year and living with few same-aged females are associated with higher rates of reproduction, these older females have a higher overall rate of reproduction. However, once the effects of same-aged females and previous reproduction are taken into account, females are less likely to reproduce at these older ages (Table 3, Figure 2a).

As would be expected, females who had a longer reproductive lifespan were more likely to reproduce at least once during their lives and produced more offspring during their lifespan. For each additional year that a female lived, the odds of completing at least one reproductive event almost doubled (Table 9). Similarly, longer-lived females were much more likely to produce more young during their lives (Figure 12b). Male marmots are similarly influenced by

mating opportunities; the number of years spent resident with females and the number of females are significantly related to the number of young fathered by males. Interestingly, once covariation is accounted for, the number of females is the only significant predictor of male lifetime reproductive success (Armitage 2004a). Similarly, the number of years spent with an established male was an even stronger predictor of whether a female would reproduce at least once; an increase of 1% of the lifespan spent resident with an established male increased the odds of a female successfully reproducing almost forty times (Table 9). However, for females who successfully reproduced at least once, lifespan was a much better predictor of the total number of offspring produced (Table 11).

This study found both social factors and those intrinsic to the female to be most important in determining annual and lifetime reproductive success. There were few environmental factors that explained variation in reproductive success. Moreover, the factors that explained the production of more than zero offspring differed from those that explained the number of offspring produced. Similarly, total lifetime reproductive success (number of offspring) could not be predicted by the same factors that influenced annual reproductive success. In addition, the univariate relationship between a given variable and reproductive success was often different from the effect found when other variables were accounted for in a multivariate model. These differences underscore the need for a comprehensive approach to studies of reproductive success. A complete picture can only be formed when both annual and lifetime reproductive output, along with the determinants of complete reproductive failure, are considered.

## **Chapter 2: Determinants of annual and lifetime reproductive success in female yellow-bellied marmots: II. recruitment**

### **Abstract**

Despite numerous studies on reproductive success in mammals, questions remain about when reproductive success is best measured. Many studies use the number of offspring as the best measure of reproductive success, but it is not always clear how well this measure correlates with later measures such as the number of offspring who reach reproductive age. This study examines the determinants of recruitment of females in yellow-bellied marmots. We assessed to what degree recruitment could be predicted from litter size and other variables measured during the pups' first year. No significant predictors of cohort success could be found after the effects of litter size were taken into account. However, the number of younger females present in the matriline, as well as temperatures and winter snowfall were significant additional predictors of female lifetime production of recruits. These results imply that significant predictions are possible from data gathered during a relatively short field season.

**Key Words: reproductive success, marmots, recruitment, fitness**

### **Introduction**

Although fitness is a well-understood concept in evolutionary biology, it remains difficult to assess in the field. One problem with measuring fitness is that it is not entirely clear what units should be used. Many studies equate the production of offspring with fitness, but this is not always the best measure. Because fitness implies genetic contribution to future generations, it may be more reasonable to measure the number of offspring who are successfully reared to reproductive age rather than the number originally produced.

There are numerous studies that measure fledging success or the production of reproductively capable offspring (e.g., Charpentier et al. 2008, Kontiainen et al. 2009), but the use of the total number of offspring born or hatched remains prevalent (e.g., Setchell et al. 2004, Hodge et al. 2008, Kekkonen et al. 2008). One reason for this involves the difficulty of measuring the number of reproductively competent individuals. Marked populations must be followed for a long period of time to measure the number of offspring that survive to reproductive age. Moreover, longitudinal data provide the best opportunity to assess which environmental or social variables are the most important influences on the number of young reared to reproductive age (Clutton-Brock 1988, Nussey et al. 2008). The time-limited nature of most field studies precludes longitudinal assessment of these variables. It remains unclear to what extent the measurement of fitness on an annual basis reflects long-term fitness trends.

We analyzed annual and lifetime production of reproductively competent offspring in a population of yellow-bellied marmots (*Marmota flaviventris*). We evaluated the determinants of reproductive success at these different time scales and compared them with the factors that determine the production of offspring. These analyses provide an evaluation of the potential usefulness of single year data that are most readily sampled in the field.

## **Methods**

### *Subjects and study site*

Marmots, the largest sciurid (squirrel), are diurnal and semi-fossorial, which facilitates long-term monitoring of marked individuals. A population of yellow-bellied marmots (*Marmota flaviventris*) was observed from 1962 to 2004 at 18 sites in the Upper East River Valley in Gunnison County, Colorado. Nearly all the marmots at these sites were trapped and individually

marked annually. A few sites were added during the course of the study, and not all sites were occupied each year (Armitage and Schwartz 2000).

Yellow-bellied marmots (*Marmota flaviventris*, hereafter “marmots”) are widely distributed across the mountain areas of western North America (Frase and Hoffmann 1980). The species usually occupies sites above 2000 m; elevations at our site range from 2867 m to 2992 m (Schwartz and Armitage 2005). This alpine and sub-alpine environment is characterized by large daily and yearly temperature changes. Marmots are subject to intense solar radiation in the summer, followed by low temperatures and several months of snow cover in the winter (Armitage 1991). To cope with these extremes, marmots enter hibernation in August and September, and do not emerge until April or May. Thus, marmots must reproduce and gain enough mass to survive hibernation during a relatively short summer active season.

Reproduction is limited to a single annual event immediately after emergence. Gestation is about 30 days, and young are weaned at the age of three to four weeks. Nearly all males and about half of the females disperse as yearlings (Armitage 1991). Females are capable of reproduction at the age of two years, but the average age of first reproduction is three years (Schwartz et al. 1998).

Marmots prefer relatively open meadows, free of trees and shrubs. Burrows are constructed under rock outcrops or boulders for protection from predators (Svendsen 1976). Although marmots often emerge from hibernation through the snow, forage is available during gestation and lactation. Vegetation usually senesces by early September (Kilgore and Armitage 1978, Frase and Armitage 1989, Armitage 2003a). Vegetation in the East River Valley forms a mosaic of suitable meadow habitat and unsuitable forest habitat (Svendsen 1974), and marmots are clumped on these patches, which range in size from 0.15 to 7.2 ha (Armitage and Schwartz 2000).

The fundamental social unit of yellow-bellied marmots is the matriline, composed of one to five closely-related adult females, consisting of sisters or mothers and daughters. The number of females resident on a habitat patch varies from site to site, and generally is related to patch size. The smallest patches (also known as satellites) usually only support one female, her young, and possibly a male (Armitage 1991). Males may be monogamous or polygamous and may defend more than one matriline (Armitage 2004a).

### *Variables*

We measured several aspects of marmot social and physical environments, as well as some characteristics of the potentially reproductive female (Table 13). Characteristics of the female included residency status, previous reproduction, age at first reproduction, age, and lifespan. Aspects of the social environment included the number of individuals present in the matriline: male and female yearlings, younger adult females, older adult females, and same-aged adult females, and the territorial male. We also recorded the total number of adults in the matriline, the number of offspring produced by matrilineal adults of different ages, and whether the male was established or had immigrated into the colony during the year of reproduction. Because the number of adult females present on a habitat patch is correlated with patch size (Armitage 1991), we calculated a density index for the matriline and the number of other females resident on the site—the number of females present in a given year at a given site, divided by the average number present at that site. We excluded data from all years when a male was not present in the colony. Female characteristics included female age, whether or not she had reproduced the previous year, and whether the female was a recruit or an immigrant.

**Table 13: Covariates used in the analysis of recruitment.**

	Variable	Description of Data
Intrinsic to Female	Age	Age of the marmot in years
	Resident	Whether marmot was born in a colony or immigrated into it
	Reproduced last	Whether or not the female reproduced the previous year
	Lifespan	Lifespan of female in years (age at last observation)
	Alpha	Age at first reproduction
Environmental	First snowfall	Julian day of first snowfall >2.54 cm in fall of the young's first year
	Last snowfall	Julian day of last snowfall >2.54 cm in spring of the young's first year
	First snow cover	Julian day of first snow cover >2.54 cm – fall of the young's first year
	Last snow cover	Julian day of last snow cover >2.54 cm in spring of the young's first year
	Precip: Sept–May	Precipitation during hibernation of the young's first year, cm
	Precip: June	cm of precipitation in June of the young's first year
	Precip: July	cm of precipitation in July of the young's first year
	Precip: Aug	cm of precipitation in August of the young's first year
	Temp: Sept–Nov	Mean temp. Sept. – Nov., fall of the young's first year
	Precip: Deviation Active	Deviation from normal active season precipitation of the young's first year
	Precip: Deviation Hibernation	Deviation from normal hibernation precipitation of the young's first year
	Precip: Mean Active	Mean precipitation during active season of the young's first year
	Precip: Mean Hibernation	Mean precipitation during hibernation of the young's first year
	Precip: Variance Active	Variance in precipitation during active season of the young's first year
	Precip: Variance Hibernation	Variance in precipitation during hibernation of the young's first year
	Temp: Deviation Active	Deviation from normal active season temperature of the young's first year
	Temp: Deviation Hibernation	Deviation from normal hibernation temperature of the young's first year
	Temp: Mean Active	Mean temperature during active season of the young's first year
	Temp: Mean Hibernation	Mean temperature during hibernation of the young's first year
	Temp: Variance Active	Variance in temperature during active season of the young's first year
Temp: Variance Hibernation	Variance in temperature during hibernation of the young's first year	
Colony	Identity of colony or satellite	
Demographic	Male yearlings	Number of male yearlings present from previous year's litter
	Female yearlings	Number of female yearlings present from previous year's litter
	Matriline	Density of related females present (number present/average)
	Other females	Density of non-matriline females present in the colony
	New Male	Whether the male observed was new to the site
	Younger adult	Number of younger adult matriline females present
	Offspring of younger	Number of pups produced by younger matriline adults
	Older adult	Number of older adult matriline females present
	Offspring of older	Number of pups produced by older matriline adults
	Same-age adult	Number of matriline females the same age as the subject
Offspring of same-age adults	Number of pups produced by matriline females of the same age	

Because temperature and precipitation affect marmot demography (Schwartz and Armitage 2005), we used several of these variables to assess their effect on recruitment. Weather

data were obtained from the National Weather Service for Crested Butte, Colorado (NOAA 1962–2004) which is about 10 km from the study site. These variables included the date of first and last snowfall, the date of first and last snow cover (greater than 2.54 cm), the amount of precipitation in each month of the active season, the amount of precipitation during hibernation, mean temperature during the active season, and mean temperature during the fall. In addition, we used data on the variance of temperature and precipitation during hibernation and during the active season. Finally, we calculated the average deviation from normal temperature and precipitation for the active season and the hibernation period. Deviation from normal is a monthly variable available from NOAA, and uses a 30-year average for comparison. The comparison mean is updated once a decade during years ending in 2 (NOAA 1962–2004). All environmental variables were calculated for the pups' first year. Thus, “active season” variables were for the active season in which the pups were gaining mass prior to their first hibernation and winter variables refer to the pups' first winter. A number of other characteristics, such as elevation and size of the foraging area, differ among colonies (Armitage 2009). We controlled for these differences by using colony identity as a factor in all our two-way nested models.

### *Statistical methods*

We analyzed the effects of social and environmental variables using a linear mixed effects model, because the data included repeated observations of the same individual and these individuals were grouped into a smaller number of colonies. Mixed effects models explicitly allow this type of hierarchical data structure.

When evaluating annual reproductive success, we assessed the number of two-year recruits that each female produced by following a single year's cohort (a single year's litter



produced by the female). Only females who produced at least one litter were included. We assessed the number of young recruited from a cohort of young that were predicted by the variables that were present during the year of birth for that cohort. Thus, for each female-year, we recorded the number of young females that remained in the natal territory two years later. This created an additional statistical problem, however, because more than half of the female-years resulted in no female recruits. Thus, the data followed a Zero-Inflated Poisson (ZIP) distribution with two-way nesting. We used an algorithm in R 2.7.2 (R Development Core Team 2009) to fit such a model using a Markov Chain Monte Carlo (MCMC) technique. For more details about the algorithm and nested ZIP models see Zuur et al. (2010a, 2010b). Our algorithm allows estimation of the effects of covariates on reproductive failure and on the number of recruits produced, given that reproduction occurred. We also incorporated an “offset” variable, which accounted for the number of offspring in the original cohort that were available to become recruits (Zuur et al. 2009). Details about the algorithm, model form and model selection are provided elsewhere (see Chapter 1, Zuur et al. 2010a)

## **Results**

The best model predicting recruitment from a cohort of young included only the amount of precipitation during August of the cohort’s first year (Figure 14). Pups who experienced a wet August were much more likely to be found in the colony as two-year-olds. Once this variable was in the model, no additional covariates improved the model. We did not find any significant covariates predicting the number of recruits produced from a cohort of young.

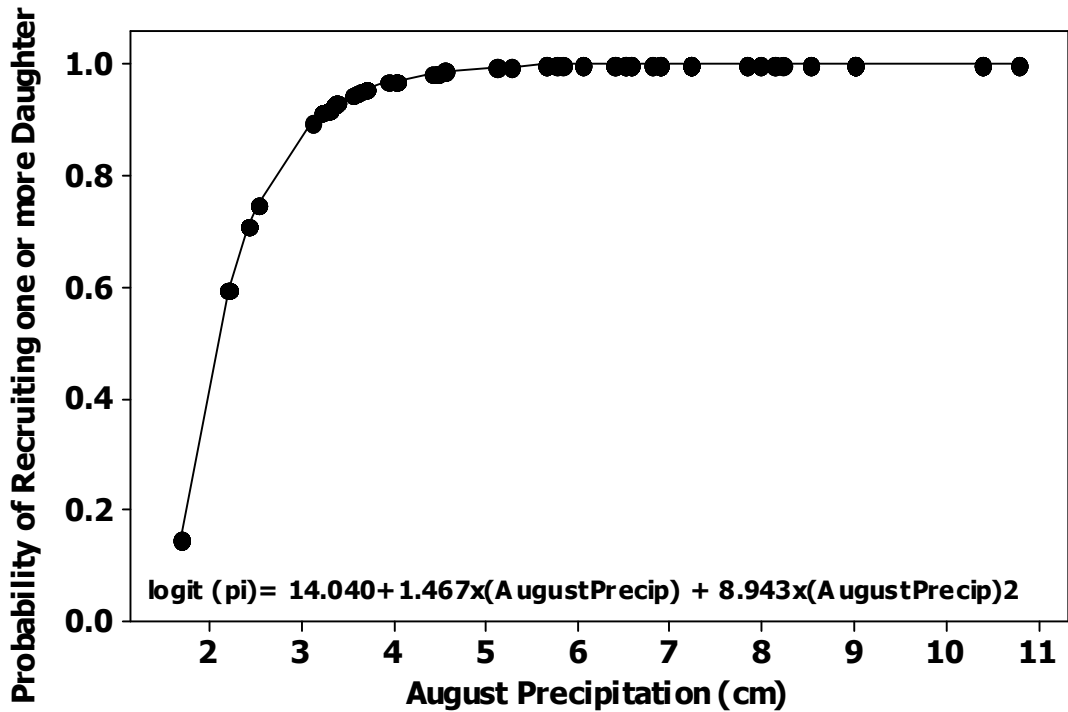


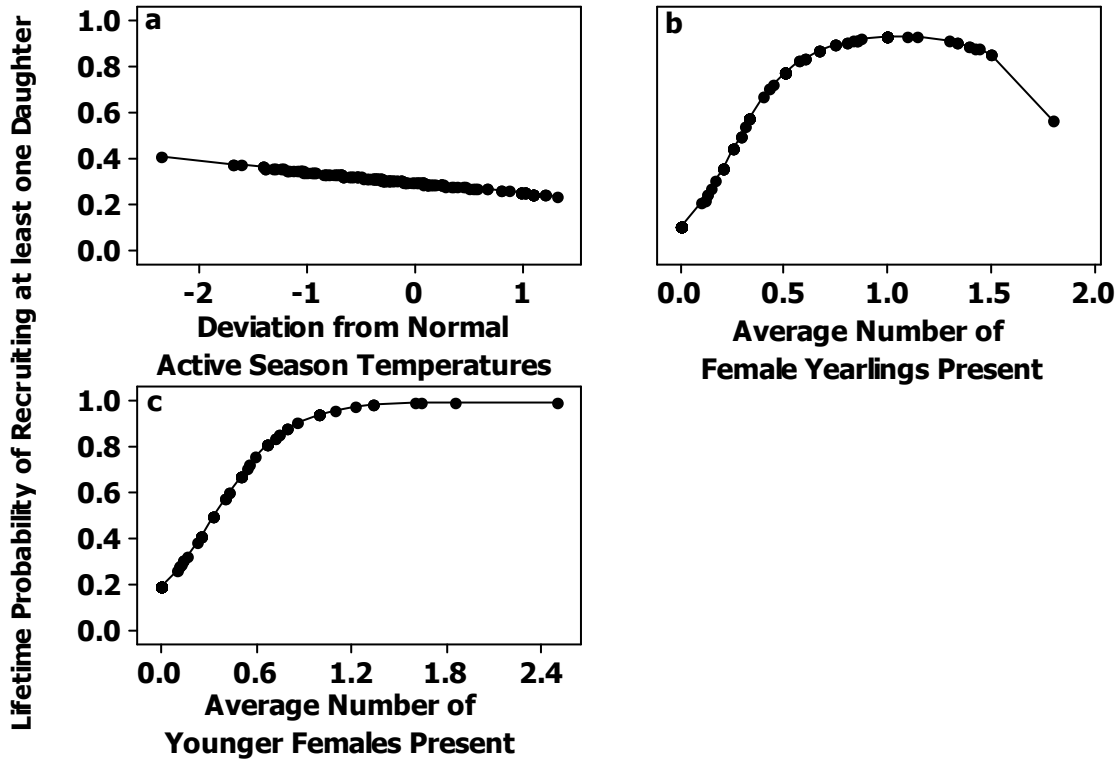
Figure 14. Effect of August precipitation on the probability of recruiting at least one daughter from a litter of young. Rainfall was measured during the year that the young's first year.

*Lifetime recruitment success*

There were both social and environmental variables that predicted the recruitment of daughters over the course of a female's lifespan. The probability of recruiting one or more daughters was influenced by the temperature in the active season. Females who regularly experienced cooler than normal temperatures during the active season had 52% higher odds of recruiting at least one daughter (Table 14, Figure 15a). The total number of daughters recruited during a female's lifespan was influenced by winter conditions; females whose pups experienced cool winters recruited more daughters than those who experienced warmer winters (Figure 16b, Table 15).

**Table 14. Predictors of the probability of recruiting one or more daughters during the lifespan. Positive coefficients indicate a higher probability of reproducing. The amount that the odds ratio differs from one indicates the percent increase or decrease in the probability of producing one or more recruit for each unit change in the predictor.**

Predictor	Coefficient	Odds Ratio	Z	P
Constant	-2.8331		-9.28	<0.001
Deviation in Temperature During the Active Season (Celsius)	-0.8906	0.48	-2.89	0.004
Number of Female Yearlings in Matriline	8.2244	3730.88	6.20	<0.001
(Number of Female Yearlings in Matriline) <sup>2</sup>	-3.8906	0.02	-3.81	
Number of Younger Adult Females in Matriline	3.1603	23.58	4.00	<0.001
Test that all slopes are zero: G = 165.982, DF = 3, P-Value = 0.000				



**Figure 15. Partial effects of covariates on the lifetime probability of producing one or more two-year-olds. For each covariate, the line represents the effect of the variable when all other significant covariates are set to their mean. Temperature was measured during the pup's first year, two years before recruitment occurred.**

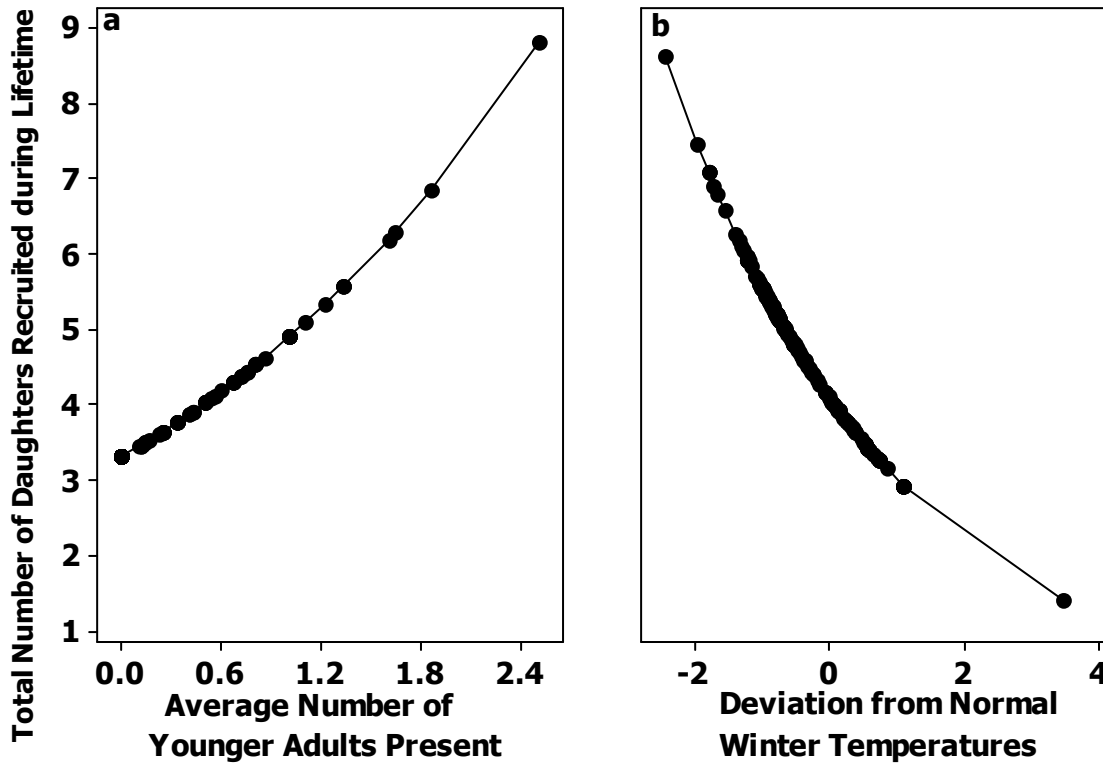


Figure 16. Partial effects of covariates on the total number of daughters recruited during a female's lifespan. Temperatures are in degrees Celsius.

Table 15. Partial effects of covariates on total lifetime recruitment.

Predictor	Coefficient	Wald $\chi^2$	df	P
Constant	-2.613	358.450	1	<0.001
Number of Younger Matriline Females	0.392	9.457	1	0.002
Deviation from Normal Hibernation Temperatures	-0.306	5.863	1	0.015

The average number of female yearlings present was positively associated with the probability of recruiting at least one daughter (Figure 15b, Table 14). Similarly, the average number of younger adult females in the matriline was positively associated with both the probability of recruiting at least one daughter (Table 14, Figure 15c) and the total number of

daughters recruited during a female’s lifetime (Table 15, Figure 16a,). However the relationship between the number female yearlings and the probability of recruitment was lower at the highest number of female yearlings (Figure 15b).

All the univariate relationships between lifetime recruitment and the covariates were similar to the partial effects found in the multivariate models (compare figures 15 with 17 and 16 with 18), but only the number of younger females was significant when analyzed univariately (Tables 16 and 17).

**Table 16. Univariate analyses of the probability of recruiting at least one daughter during a female's lifespan.**

Predictor	Coefficient	Odds Ratio	Z	P
Deviation from normal temperatures, active season	-0.0697	0.93	-0.49	0.624
Average number of female yearlings in matriline	0.0681	1.07	-.58	0.561
Average number of younger adult females in matriline	0.2301	1.26	1.73	0.083

**Table 17. Univariate analyses of the total lifetime number of recruits.**

Predictor	Coefficient	Wald $\chi^2$	df	P
Number of Younger Matriline Females	0.321	6.541	1	.011
Deviation from Normal Hibernation Temperatures	-0.181	1.921	1	.166

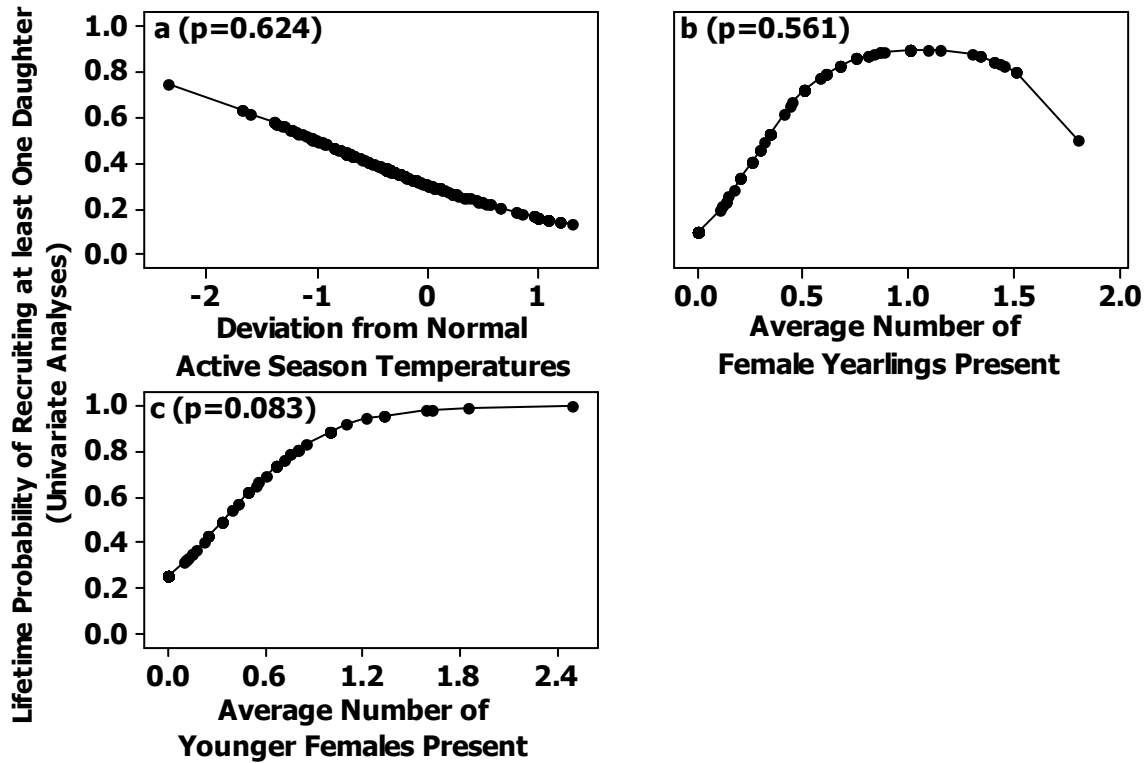


Figure 17. Univariate relationships between selected variables and the probability of recruiting at least one daughter during the lifespan.

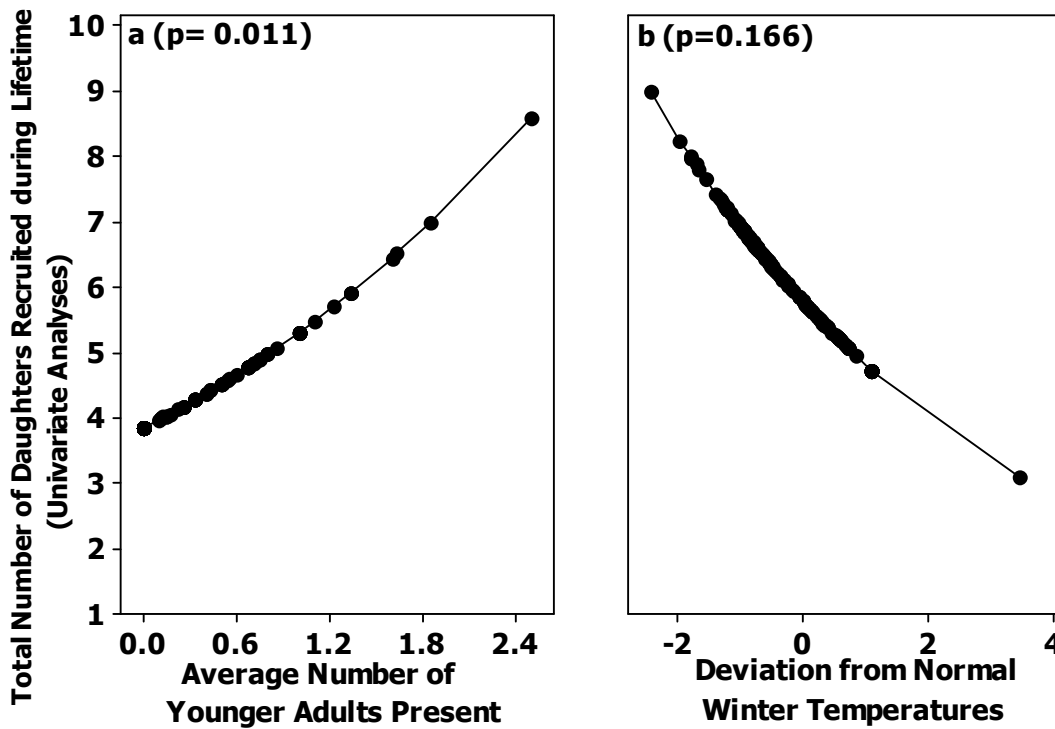


Figure 18. Univariate analyses of total lifetime recruitment. Temperatures are in degrees Celsius.

## Discussion

Although a number of social variables are important for predicting the number of offspring produced (Armitage and Schwartz 2000, Chapter 1, Oli and Armitage 2003), we found relatively few social variables that explained the number of two-year-old recruits, after the effects of initial cohort size were taken into account. The numbers of yearlings and younger adult females living in a matriline were positively associated with the probability of recruiting one or more daughters during the lifespan and with the total number of daughters recruited (Table 14, Table 15, Figure 15c, Figure 16a). This result is not altogether surprising, and it does not necessarily imply that the presence of these younger females enhances recruitment; females who recruit a larger than average number of daughters will inevitably live in matriline with younger females and yearlings, many of whom will be their daughters. Thus, there is likely to be an amicable environment that increases the likelihood of recruitment (Armitage 1986b, Armitage et al. 2010). Moreover, females who successfully rear female yearlings are more likely to recruit two-year-olds, and the number of surviving yearlings is a better predictor of recruitment than the number of offspring produced (Armitage 1984, Chapter 1).

There were significant effects of temperature and precipitation on both the probability of recruitment and the total number of daughters recruited. Females who reproduced during a year following high August precipitation were less likely to recruit a daughter from that litter (Figure 14). Similarly, females who regularly reproduced during years that included cooler than average active season temperatures were more likely to recruit at least one daughter (Table 14, Figure 15a). Previous studies also reported that summer drought and high active season temperatures were negatively associated with offspring survival (Schwartz and Armitage 2005). Thus, it is likely that the failure to recruit daughters from litters produced during warm, dry years is due to

higher pup mortality during those years. During the summer, marmots are subject to heat stress and cease foraging during mid-day when temperatures are highest (Melcher et al. 1990). Thus, young that experience unusually high summer temperatures may have increased thermoregulatory costs and/or decreased foraging time. In addition, growth is slower during hot, dry weather (Armitage 1994). These constraints may not allow daughters to gain sufficient mass to survive their first hibernation.

Similarly, temperature during this first winter affect the number of two-year-olds recruited. Recruitment of two-year-olds was most likely when the first winter was characterized by cooler than average temperatures (Table 15, Figure 16b). The amount of snow cover is important for maintaining burrow temperatures. Snow cover acts as insulation and keeps burrow temperatures within a relatively narrow range. During the peak of the winter, adequate snow cover is critical to keep the ground from freezing and maintain the burrow above the lower critical temperature (Svendsen 1976). Cool temperatures would maintain this essential snowpack at a more consistent depth between snowfall events. In addition, increased snowfall would provide more moisture for spring plant growth, which would favor mass gain after hibernation and increase growth and survival of yearlings.

It is interesting that these environmental effects on lifetime recruitment were only significant in the multivariate analysis. In univariate analyses only one variable, the number of younger matriline females, was a significant predictor of recruitment. It was only after this variable was entered into the model that the significant partial effects of temperature became apparent. Moreover, the p-values were higher and the odds ratios were lower for the environmental variables in the multivariate model. Thus, it appears that recruitment is related to the social system, but it is also impacted by environmental variables that affect survival.



It is also significant that only one cohort predictor was found after the effects of initial cohort size were taken into account. This result implies that the traditional measure of reproductive success, number of offspring produced, is a good predictor of the number of two-year-old recruits. Predictions based on the number of weaned offspring can be strengthened by a relatively few environmental variables, such as winter precipitation and temperature during winter and the active season, measured during the pups' first year. This finding is particularly important for practical applications; although long-term research is still the ideal for elucidating the determinants of reproductive success, considerable information can be gathered in the more limited time frames available for most field studies.

## **Chapter 3: Determinants of annual and lifetime reproductive success in female yellow-bellied marmots: III. multi-generational effects.**

### **Abstract**

Although fitness is a well-understood concept in evolutionary biology, its measurement remains problematic. Lifetime reproductive success, measured as the total production of offspring, is a logical choice for measuring fitness, but the number of grand-offspring could be used as well. It is often assumed that the factors that affect the production of offspring will be the same as those that predict the number of grand-offspring, but this assumption has seldom been tested empirically. One of the barriers to testing the cross-generational predictors of reproductive success has been the time-limited nature of most field studies. This study examines the factors that predict the production of grand-offspring in yellow-bellied marmots (*Marmota flaviventris*). In addition, we attempt to predict production of grand-offspring from factors occurring in the year of the daughter's birth. Thus, for each reproductive bout, we use a single year's worth of data to predict long-term population and fitness consequences. Relative matriline density decreased both the probability of producing grand-offspring and the total number of grand-offspring produced from a cohort of young. The number of offspring produced by same-aged females, the relative density of non-matriline females and fall temperatures were negatively associated with the number of grand-offspring produced from a particular cohort. The number of same-aged females was positively related to the number of grand-offspring produced. The total number of grand-offspring left by a female was positively related to the number of older adults present and negatively related to the variance in winter temperatures. Finally, the relationship between the total number of grand-offspring produced and the average number of younger adults

present was initially negative, but became positive at higher numbers of younger adults. These relationships were similar to, but not identical to those that predict the production of offspring.

**Key Words:** *Marmota*, reproductive success, fitness, trans-generational effects, epigenetics.

## **Introduction**

Darwinian fitness is a central concept of evolution, and its measurement is key to addressing questions of adaptation and selection. However, this generally well-understood concept is difficult to measure in the field. In particular, there has been widespread disagreement over the proper units for measurement. Fundamentally, fitness is the contribution of genes to future generations. As such, many authors have chosen the production of offspring or fertilized eggs as the appropriate and most easily measured approximation of fitness (Borgerhoff-Mulder 1988, Clutton-Brock et al. 1988, Howard 1988, Partridge 1988). Others have focused on the production of reproductively competent individuals (McCleery and Perrins 1988, Fitzpatrick and Woolfenden 1989, Parn et al. 2009), but the production of offspring of reproductive age does not guarantee that those offspring will actually become successful breeders (Rickard et al. 2007). Because fitness is a measure of the contribution to future generations, the production of grand-offspring might be the most appropriate measure.

Longitudinal studies of marked individuals offer the best method to investigate the contributions of grand-offspring to individual fitness. However, time constraints in the field limit the ability of researchers to use this method. Recent laboratory and epidemiological studies may offer a new way to address this problem. The conditions that affect a mother during gestation can impact not only her offspring, but her grand-offspring as well (Anway 2010, Franklin and

Mansuy 2010). These findings open the possibility that single-year studies might have the power to predict the production of offspring and grand-offspring as well.

We used longitudinal data from individually marked yellow-bellied marmots to determine which factors, present during the year in which females reproduced, are associated with the production of grand-offspring. Significant covariates from the year during which females produced litters can then be used for predictors of long-term reproductive success.

## **Methods**

### *Subjects and study site*

Marmots, the largest sciurid (squirrel), are diurnal and semi-fossorial, which facilitates long-term monitoring of marked individuals. A population of yellow-bellied marmots (*Marmota flaviventris*) was observed from 1962 to 2004 at 18 sites in the Upper East River Valley in Gunnison County, Colorado. Nearly all the marmots at these sites were trapped and individually marked annually. A few sites were added during the course of the study, and not all sites were occupied each year (Armitage and Schwartz 2000).

Yellow-bellied marmots (hereafter “marmots”) are widely distributed across the mountain areas of western North America (Frase and Hoffmann 1980). The species usually occupies sites above 2000 m; elevations at our site range from 2867 m to 2992 m (Schwartz and Armitage 2005). This alpine and sub-alpine environment is characterized by large daily and yearly temperature changes. Marmots are subject to intense solar radiation in the summer, followed by low temperatures and several months of snow cover in the winter (Armitage 1991). To cope with these extremes, marmots enter hibernation in August and September, and do not emerge until April or May. Thus, marmots must reproduce and gain enough mass to survive

hibernation during a relatively short summer active season. Reproduction is limited to a single annual event immediately after emergence. Gestation is about 30 days, and young are weaned at the age of three to four weeks. Nearly all males and about half the females disperse as yearlings (Armitage 1991). Females can reproduce at the age of two, but the average age of first reproduction is three (Schwartz et al. 1998).

Marmots are clumped on patches of talus or rocky outcrops and meadows that range in size from 0.15 to 7.2 ha (Armitage and Schwartz 2000). Marmots prefer relatively open meadows, free of trees and shrubs. Burrows are constructed under rock outcrops or boulders to protect from predators (Svendsen 1974). These meadows are characterized by grasses and showy perennial forbs. Although marmots often emerge from hibernation through the snow, forage is available during gestation. Forage becomes abundant during lactation and reaches its peak biomass after weaning. Vegetation usually senesces by early September (Kilgore and Armitage 1978, Frase and Armitage 1989, Armitage 2003a). Vegetation in the Upper East River Valley forms a mosaic of suitable meadow habitat and unsuitable forest habitat (Svendsen 1974).

The fundamental social unit for yellow-bellied marmots is the matriline, composed of one to five closely-related adult females, consisting of sisters or mothers and daughters. The number of females resident on a habitat patch varies from site to site, and generally is related to patch size. The smallest patches (also known as satellites) usually support only one female, her young, and possibly a male (Armitage 1991). Males are territorial, and defend one or more matriline in colonies or may defend females on more than one small patch (Armitage 2004a).

## Variables

We measured several aspects of marmot social and physical environments, as well as some characteristics of the potentially reproductive female (Table 18). Characteristics of the female included residency status, previous reproduction, age at first reproduction, age, and lifespan. Aspects of the social environment included the number of individuals present in the matriline: male and female yearlings, younger adult females, older adult females, and same-aged adult females. We also recorded the total number of adults in the matriline, the number of offspring produced by matrilineal adults of different ages, and whether the male was established or had immigrated into the colony during the year of reproduction. Because the number of adult females present on a habitat patch is correlated with patch size (Armitage 1991), we calculated a density index for a matriline or for all females at the site as the number of females present in a given year at a given site, divided by the average number present at that site. We excluded data from all years when a male was not present in the colony. Female characteristics included female age, whether or not she had reproduced the previous year, and whether the female was a resident or an immigrant.

**Table 18: Covariates used in the analysis of grand-offspring production.**

	Variable	Description of Data
Intrinsic to Female	Age	Age of the marmot in years
	Resident	Whether marmot was born in a colony or immigrated into it
	Reproduced last	Whether or not the female reproduced the previous year
	Lifespan	Lifespan of female in years (age at last observation)
	Alpha	Age at first reproduction
Environmental	First snowfall	Julian day of first snowfall >2.54 cm in fall prior to reproduction
	Last snowfall	Julian day of last snowfall >2.54 cm in spring prior to weaning
	First snow cover	Julian day of first snow cover >2.54 cm in fall prior to reproduction
	Last snow cover	Julian day of last snow cover >2.54 cm in spring prior to weaning
	Precip: Sept–May	Precipitation during hibernation prior to reproduction, inches of water
	Precip: June	Inches of precipitation in June in the year prior to reproduction
	Precip: July	Inches of precipitation in July in the year prior to reproduction
	Precip: Aug	Inches of precipitation in August in the year prior to reproduction
	Temp: Sept–Nov	Mean temp. Sept. – Nov., fall prior to reproduction
	Precip: Deviation Active	Deviation from normal active season precipitation
	Precip: Deviation Hibernation	Deviation from normal hibernation precipitation

	Precip: Mean Active	Mean precipitation during active season
	Precip: Mean Hibernation	Mean precipitation during hibernation
	Precip: Variance Active	Variance in precipitation during active season
	Precip: Variance Hibernation	Variance in precipitation during hibernation
	Temp: Deviation Active	Deviation from normal active season temperature
	Temp: Deviation Hibernation	Deviation from normal hibernation temperature
	Temp: Mean Active	Mean temperature during active season
	Temp: Mean Hibernation	Mean temperature during hibernation
	Temp: Variance Active	Variance in temperature during active season
	Temp: Variance Hibernation	Variance in temperature during hibernation
	Colony	Identity of colony or satellite
Demographic	Male yearlings	Number of male yearlings present from previous year's litter
	Female yearlings	Number of female yearlings present from previous year's litter
	Matriline	Density of related females present (number present/ average for that site)
	Other females	Density of non-matriline females present in the colony
	New Male	Whether the male observed was new to the site
	Younger adult	Number of younger adult matriline females present
	Offspring of younger	Number of pups produced by younger matriline adults
	Older adult	Number of older adult matriline females present
	Offspring of older	Number of pups produced by older matriline adults
	Same-age adult	Number of matriline females the same age as the subject
	Offspring of same-age adults	Number of pups produced by matriline females of the same age

Because temperature and precipitation affect marmot demography (Schwartz and Armitage 2005), we used several of these variables to assess their effect on recruitment. Weather data were obtained from the National Weather Service for Crested Butte, Colorado (NOAA 1962–2004) which is about 10 km from the study site. These variables included the date of first and last snowfall, the date of first and last snow cover (greater than 2.54 cm), the amount of precipitation in each month of the active season, the amount of precipitation during winter, mean temperature during the active season, and mean temperature during the fall. In addition, we used data on the variance of temperature and precipitation during winter and during the active season. Finally, we calculated the average deviation from normal temperature and precipitation for the active season and the hibernation period. Deviation from normal is a monthly variable available from NOAA, and uses a 30-year average for comparison. The comparison mean is updated once a decade during years ending in 2 (NOAA 1962–2004). All environmental variables were

calculated for periods preceding reproduction. Thus, “active season” variables were for the active season in which the marmot was gaining mass prior to hibernation, and leading up to her attempt at reproduction.

A number of other characteristics, such as elevation and size of the foraging area, differ among colonies (Armitage 2009). We controlled for these differences by using colony identity as a factor in all our two-way nested models.

### *Statistical methods*

We analyzed the effects of social and environmental variables using a linear mixed effects model, because the data included repeated observations of the same individual and these individuals were grouped into a smaller number of colonies. Mixed effects models explicitly allow this type of hierarchical data structure.

When evaluating annual reproductive success, we assessed the number of grand-offspring that each female produced by following a single year’s cohort. Thus for each female-year, we recorded the number of grand-offspring that were eventually produced by the daughters of that year. The data followed a Zero-Inflated Poisson (ZIP) distribution with two-way nesting. We used an algorithm in R 2.7.2 (R Development Core Team 2009) to fit such a model using a Markov Chain Monte Carlo (MCMC) technique. For more details about the algorithm and nested ZIP models see (Zuur et al. 2010a, Zuur et al. 2010b). Our algorithm allows estimation of the effects of covariates on reproductive failure and on the number of offspring (or grand-offspring) produced, given that reproduction occurred. We also incorporated an “offset” variable which accounted for the number of offspring from the original cohort who recruited into the population as two-year-olds and were thus available to produce grand-offspring (Zuur 2009). Because the



overwhelming majority of males disperse and most leave the study area, we estimated the production of both male and female grand-offspring left by daughters only. Details about the algorithm, model form and model selection are provided elsewhere (see Chapter 1, Zuur et al. 2010a)

## **Results**

Models run without the offset variable, which accounts for the number of recruits produced, were identical to the models chosen for the production of two-year-old recruits. Thus, the most important variable predicting the production of grand-offspring is the number of daughters recruited into the local population (see Chapter 2). However, after accounting for the number of daughters recruited, there were significant social and environmental conditions that predicted the production of grand-offspring.

### *Grand-offspring produced by cohorts*

Only one social variable predicted whether female marmots left any grand-offspring from a cohort of offspring. Females who produced litters while living in larger than average matriline were less likely to leave any grand-offspring (Figure 19). Similarly, matriline density was also negatively related to the total number of grand-offspring that was eventually produced from a litter of a given size (Table 19, Figure 20a). In addition, the relative density of non-matriline females was negatively associated with the total number of grand-offspring produced from a given year's daughters (Table 19, Figure 20d). The composition of the matriline was also important for determining the total number of grand-offspring produced by daughters. Producing daughters in the presence of full or half, same-aged sisters increased the likelihood of leaving

grand-offspring (Table 19, Figure 20b). However, the number of grand-offspring decreased as the number of offspring produced by same-aged females increased (Table 19, Figure 20c). Only one environmental variable predicted the number of grand-offspring produced by a cohort of young. Females who experience relatively cool fall conditions during the year prior to reproduction were more likely to produce reproductively successful daughters in the spring.

The relationship between each variable and the production of grand-offspring was very similar in multivariate and univariate analyses (Table 20, Figure 21). However, without the partial effects of matriline density, non-matriline density and fall temperatures, the number of same-aged and the number of offspring produced by same-aged females were not significant predictors of the production of grand-offspring.

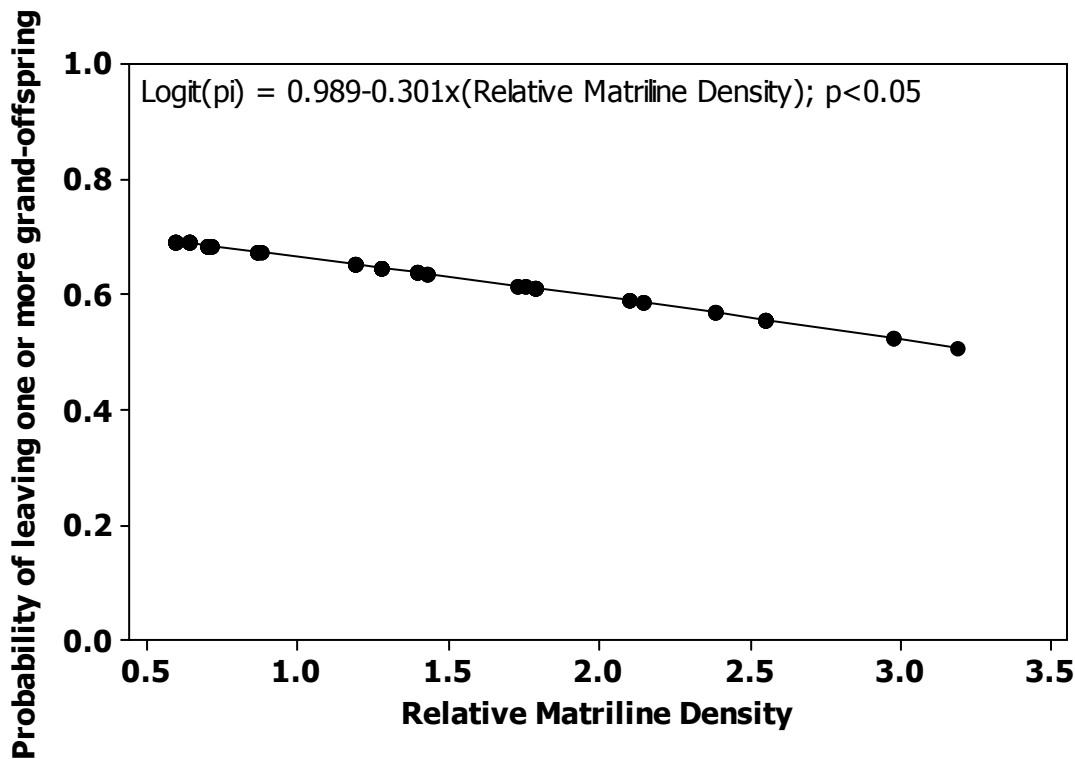


Figure 19. Effects of relative matriline density on the probability of producing one or more grand-offspring from a cohort of offspring. For each covariate, the line represents the effect of the variable when all other significant covariates are set to their mean. Covariates were measured the year the original cohort of young were born.

Table 19. Partial effects of covariates on total number of grand-offspring produced from a cohort.

Predictor	Coefficient	Wald $\chi^2$	df	P
Constant	2.622	360.261	1	<0.001
Relative Matriline Density	-0.186	13.673	1	<0.001
Number of Same-Aged Females in Matriline	0.679	23.261	1	<0.001
Number of Offspring Produced by Same-Aged Females	-0.152	10.701	1	0.001
Relative Density of Non-Matriline Females	-0.089	21.932	1	<0.001
Fall Temperatures (September–November)	-0.288	42.202	1	<0.001

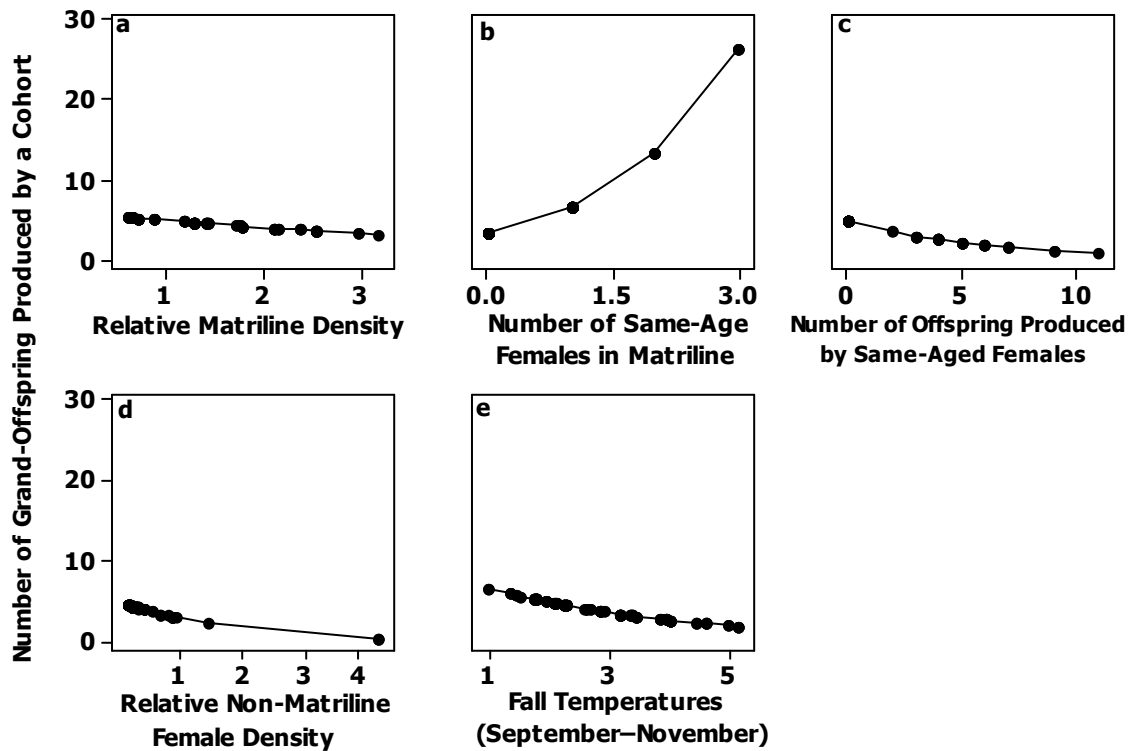


Figure 20. Relationship between partial effects of covariates and the number of grand-offspring produced from a cohort of young. For each covariate, the line represents the effect of the variable when all other significant covariates are set to their mean. Covariates were measured the year the cohort of young were produced. Temperatures are in degrees Celsius.

Table 20. Univariate analyses of the total number of grand-offspring produced from a cohort.

Predictor	Coefficient	Wald $\chi^2$	df	P
Relative Matriline Density	-0.094	4.526	1	0.033
Number of Same-Aged Females in Matriline	0.058	0.637	1	0.425
Number of Offspring Produced by Same-Aged Females	-0.008	0.125	1	0.723
Relative Density of Non-Matriline Females	-0.080	15.950	1	<0.001
Fall Temperatures (September–November)	-0.303	42.044	1	<0.001

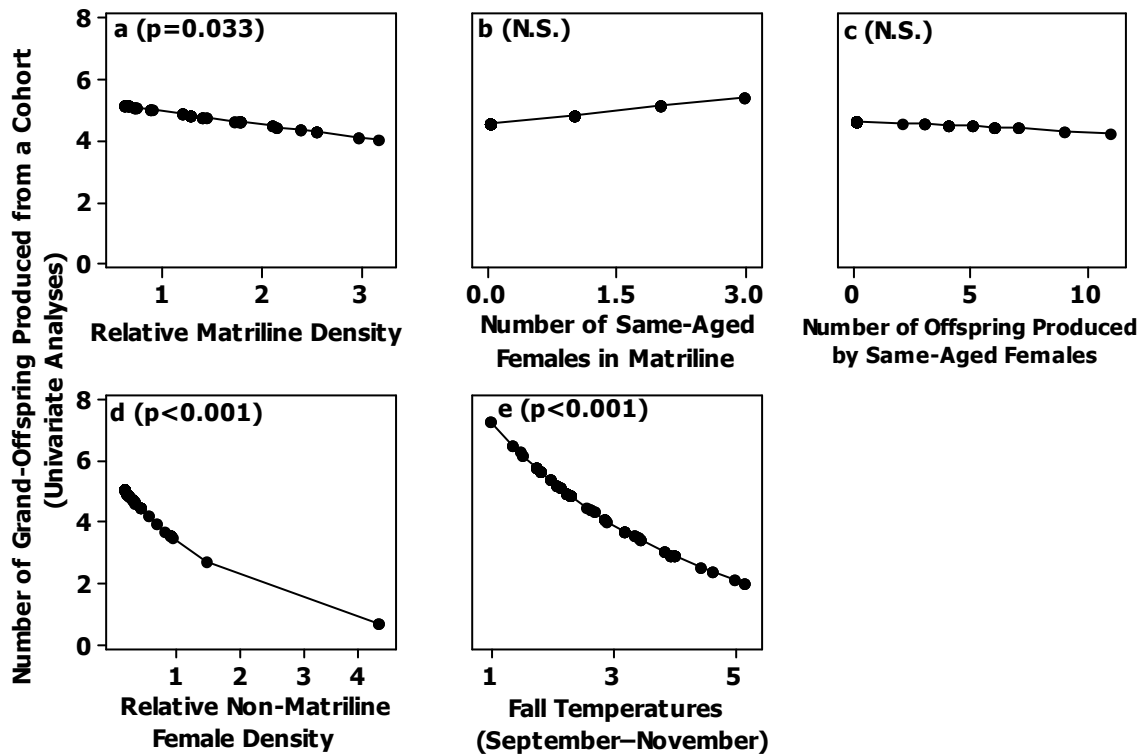


Figure 21. Univariate analyses of the number of grand-offspring produced by daughters in a cohort. Temperatures are in degrees Celsius.

### *Sex-ratio of grand-offspring*

Many substances that are known to have epigenetic effects on grand-offspring affect male and female grand-offspring differently (Nilsson et al. 2008, Franklin and Mansuy 2010, Titus-Ernstoff et al. 2010). Thus, it is possible that although females may leave grand-offspring, they may leave different numbers of male and female grand-offspring. When examining the overall sex ratio of grand offspring, an interesting pattern emerges. The overall sex ratio is nearly equal, with a slight male bias. However, there are more females than expected who leave only male grand-offspring (Figure 22). We analyzed the sex ratio of grand-offspring using a stepwise logistic regression. The Julian day of the last snow cover in the spring was significantly associated with the number of male grand-pups produced. Females who experience late snow melt produced daughters who gave birth to slightly more males than females ( $Z = 2.30$ ,  $p = 0.021$ , Figure 23). No other social or environmental variables were significantly associated with grand-offspring sex ratio.

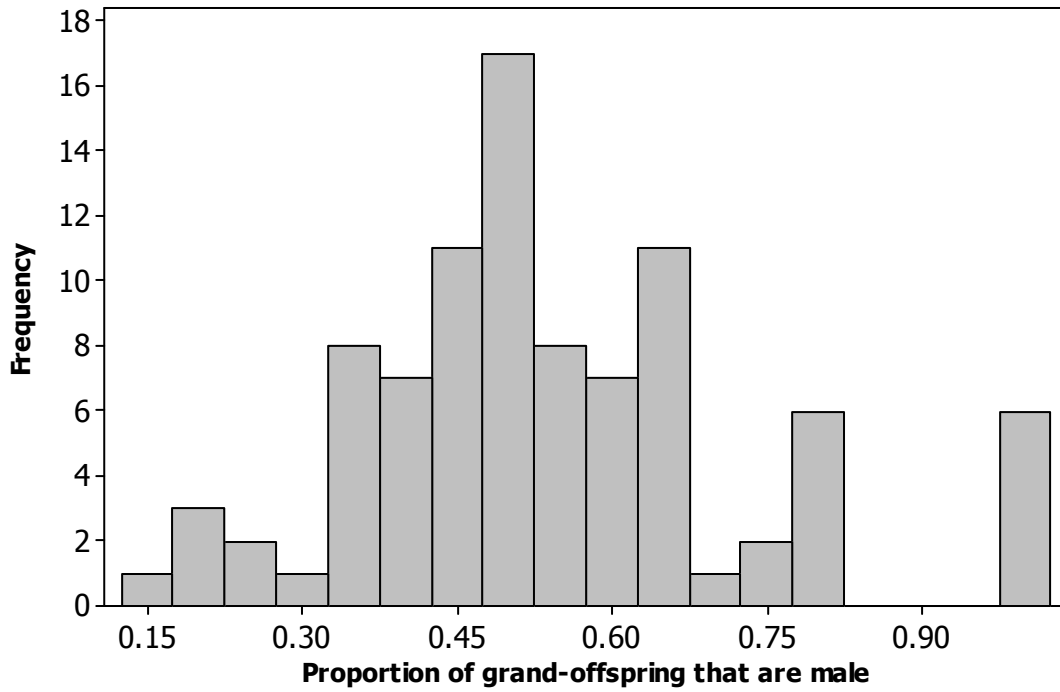


Figure 22. Observed sex ratio of grand-offspring.

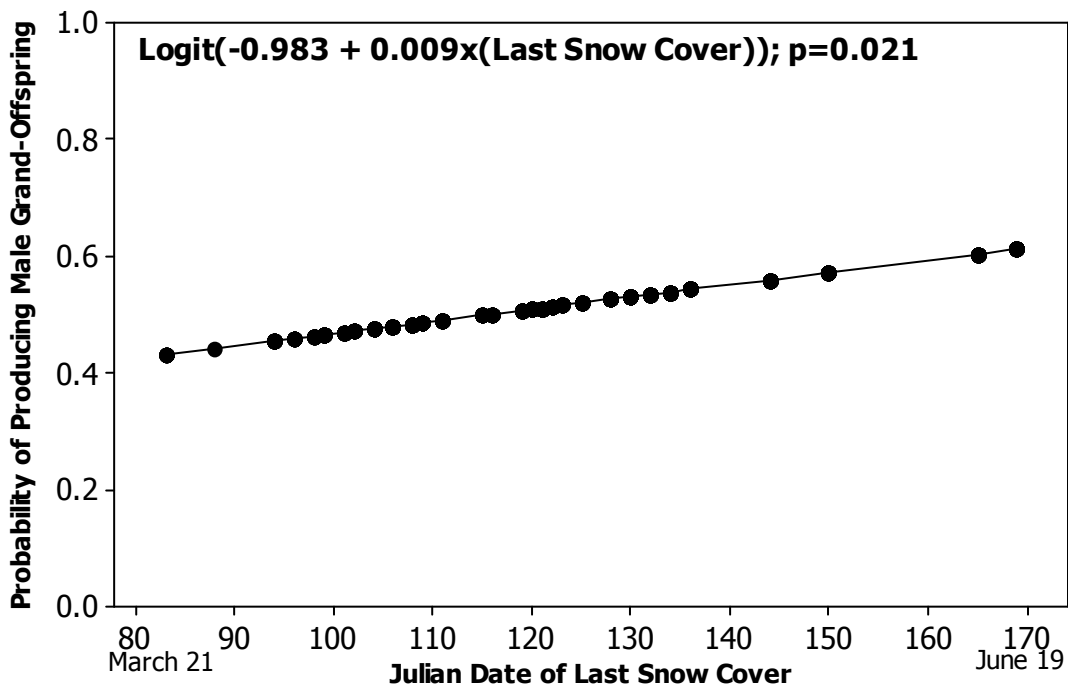


Figure 23. Effect of the date of last snow cover on the probability of producing male grand-offspring.

### *Lifetime reproductive success*

All of the females who produced two-year-old recruits produced at least one grand-offspring. Thus, the probability of leaving at least one grand-offspring during the lifespan was entirely determined by the factors that influenced recruitment (See Chapter 2). The number of grand-offspring produced by a female was highly variable; some females left only one grand-offspring, while others produced as many as 64. Two social and one environmental variables affected the total lifetime number of grand-offspring produced by females. Females who lived in a matriline containing a larger than average number of older females were more likely to produce daughters who were reproductively successful, although the effect was small (Table 21, Figure 24b). The relationship between the average number of younger females in the matriline and the production of grand-offspring was curvilinear; females living with the lowest or highest average number of younger females were the most likely to leave grand-offspring, while those living with an average of 1.2–1.6 left fewer grand-offspring (Table 21, Figure 24a). The univariate effects of younger and older adult females were similar in sign, but larger than the partial effects found in the multivariate analysis (Table 22, Figure 25).

**Table 21. Predictors of the total number of grand-offspring produced by females. Positive coefficients indicate greater number of grand-offspring produced.**

Predictor	Coefficient	Wald $\chi^2$	df	P
Constant	2.380	50.913	1	<0.001
Average Number of Younger Adult Females Present	-4.845	881.507	1	<0.001
(Average Number of Younger Adult Females Present) <sup>2</sup>	1.671	245.674	1	<0.001
Number of Older Adult Females in Matriline	0.380	21.246	1	<0.001
Variance of Temperatures in Winter	-0.539	4.150	1	0.042
Site Effect	varies	446.621	9	<0.001

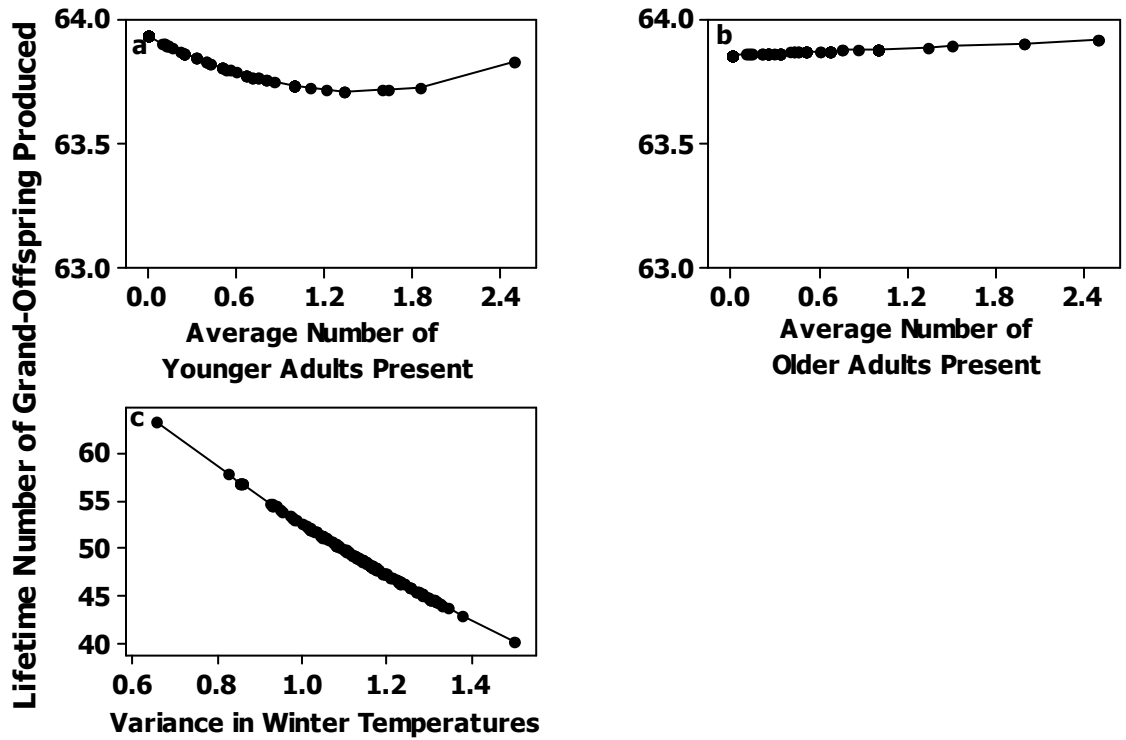


Figure 24. Relationship between partial effects of covariates and the number of grand-offspring produced from all the daughters produced during a female's lifetime. For each covariate, the line represents the number of offspring predicted by the variable when the other three significant covariates are set to their mean. Covariates were measured the prior to the production of the cohort of young. Temperatures are in degrees Celsius.

Table 22. Univariate analyses of the total lifetime number of grand-offspring produced.

Predictor	Coefficient	Wald $\chi^2$	df	P
Average Number of Younger Adult Females Present	-5.888	1528.681	1	<0.001
(Average Number of Younger Adult Females Present) <sup>2</sup>	2.102	339.890	1	<0.001
Average Number of Older Adult Females Present	1.899	1308.01	1	<0.001
Variance of Temperatures in Winter	-9.569	1391.51	1	<0.001
Site Effect		99.222	9	<0.001



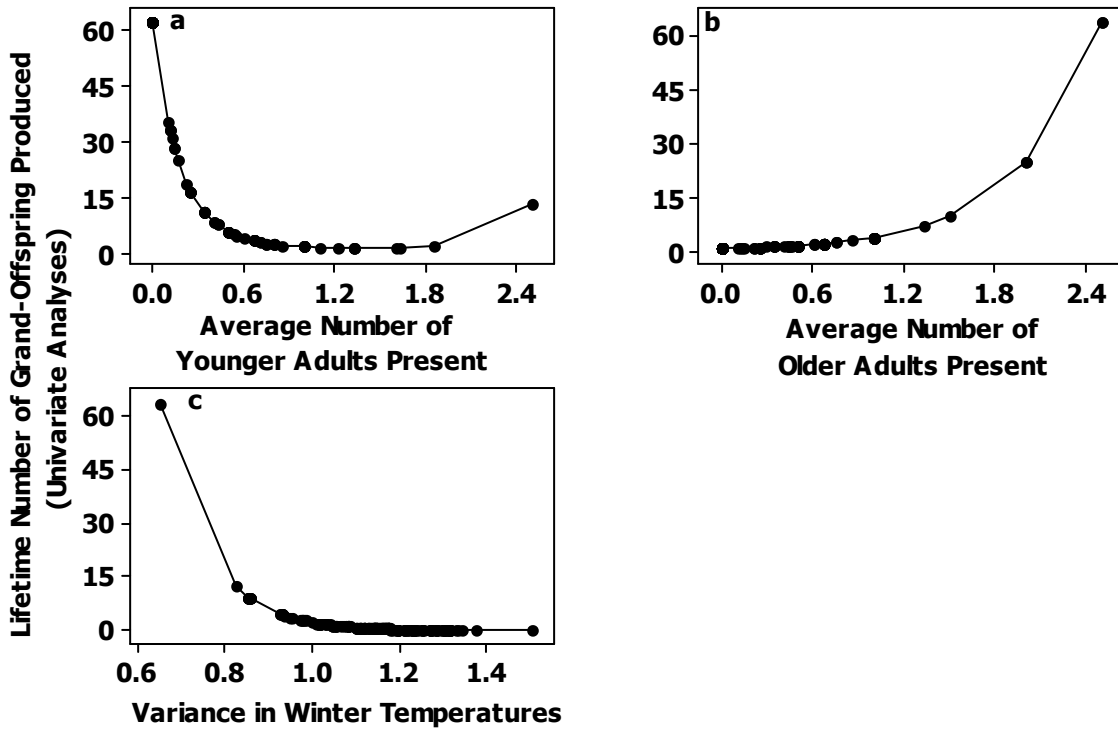


Figure 25. Univariate analyses of the total number of grand-offspring left by females during their lifespan. Temperatures are in degrees Celsius.

Winter conditions also influenced the production of grand-offspring. Daughters who were born after a winter in which temperatures were relatively constant were more reproductively successful (produced more offspring) than daughters who were born after more variable conditions. (Table 21, Figure 24c). The univariate relationship between winter temperatures and the production of grand-offspring was very similar, although the univariate relationship indicated a steeper decline as variance increased (Table 22, Figure 25c). In addition to these social and environmental factors, there was also a significant site effect on the number of grand-offspring produced. In a univariate analysis, females in the larger sites, such as Marmot Meadow, Gothic, and River/Bench, left significantly more grand-offspring during their lifespan than females living in satellites or marginal colonies such as Beaver Talus and North Picnic (Figure 26). However,

once the partial effects of variance in winter temperatures and the average number of younger and older adults were accounted for, the site effect on the production of grand-offspring was different. Once these other effects were accounted for, the largest number of grand-offspring were produced in the two largest, east-northeast facing colonies at high elevation, Boulder and Cliff (Figure 27). These two colonies face east-northeast and are above 2975 m. Females in lower elevation, southwest facing, and smaller sites had lower production of grand-offspring. This relationship is more complicated in the colonies that produced fewer grand-offspring, however. It is not entirely clear what variables explain these colony effects.

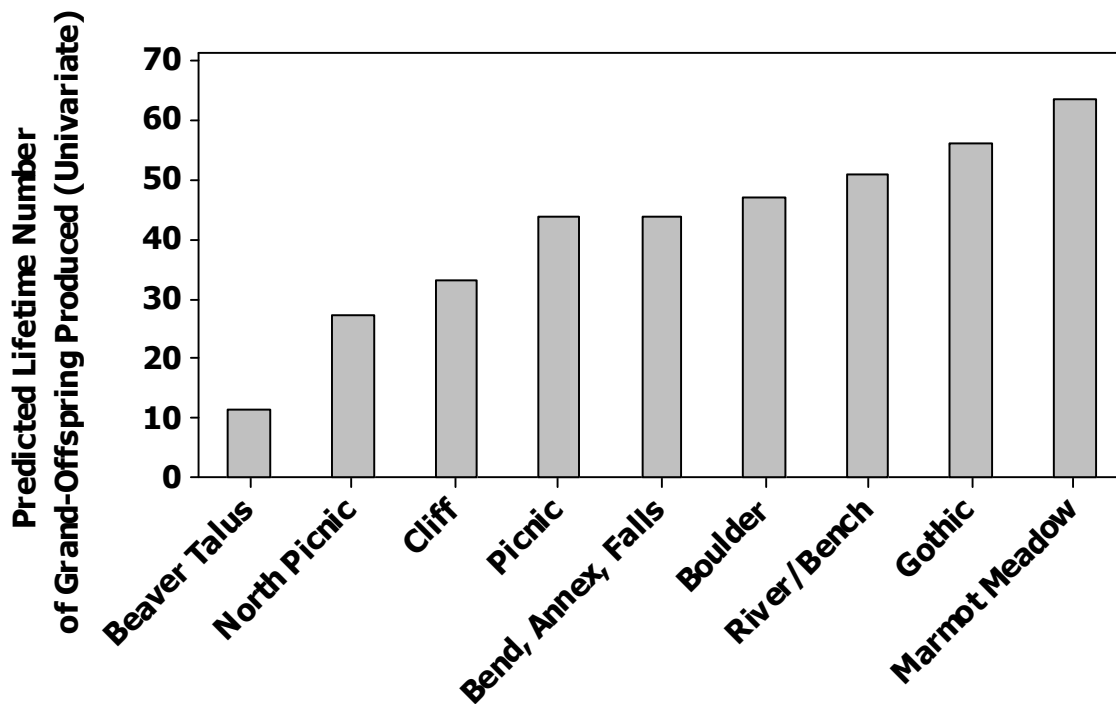


Figure 26. Univariate relationship between location and lifetime number of grand-offspring produced.

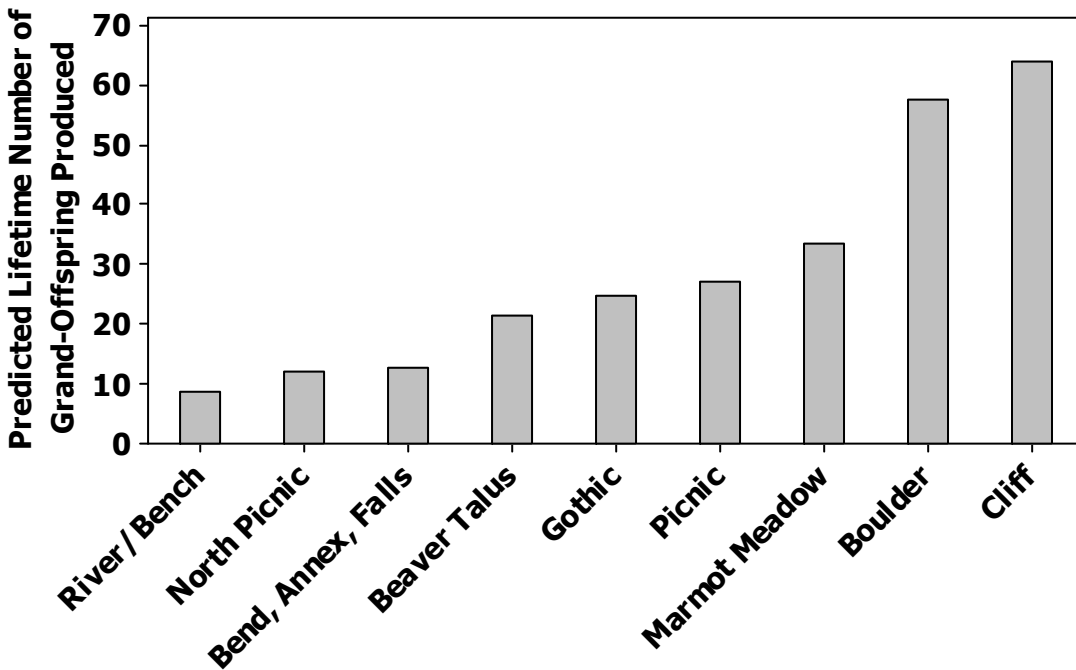


Figure 27. Relationship between location and the number of grand-offspring produced by females. Other variables in the model includes the average number of younger females present, the average number of older adult females in the matriline and the variance in winter temperatures.

## Discussion

The single most important factor predicting the production of grand-offspring was the recruitment of daughters. Models which did not account for recruitment were identical to the models predicting recruitment, indicating that the processes driving recruitment were the most important factors determining the number of grand-offspring produced. Moreover, all females who recruited at least one daughter during their lifespan produced at least one grand-offspring. Nevertheless, we were able to identify several social factors that predicted the production of grand-offspring. Relative matriline density as well as the matriline composition was an important predictor of grand-offspring production. There was also a strong site effect, and three significant, but smaller, environmental effects.

### *Social factors that affect the production of grand-offspring*

The social conditions in which females produced daughters affected the probability of reproduction by those daughters. Daughters recruited into the natal population inherit social conditions derived from the social conditions that were present at their time of birth. These social factors, in turn, can substantially influence the daughters' reproductive success.

Females who were living alone when they produced litters were more likely to recruit daughters who successfully reproduced at least once and were likely to produce more grand-offspring during their lifespan (Figure 19). These daughters recruit into matriline that include only their mother. Young females are frequently reproductively suppressed by older females, and the rate of suppression by the mother is slightly less (Armitage 1998). In addition, young females who live with no older females are much more likely to reproduce (Armitage 1998). Since reproduction does not occur for at least two years after the daughters are born, daughters living with only their mothers are more likely to obtain sole occupancy than those who live in larger matriline.

Matriline composition also influenced the production of grand-offspring. Daughters were likely to be more reproductively successful if they were born into a matriline that contained females the same age as their mothers or older (Figure 20b, Figure 24b). Daughters were less successful if they were born into matriline containing females younger than their mother (Figure 24a). Although these competing females are younger than the mother, they would represent older females for the daughter, and could cause the daughter to be reproductively suppressed. Moreover, because these females are between the age of the mother and the daughter, they would be expected to remain in the matriline longer than females who are the same age or older than the

mother. Thus, daughters living in similar sized matriline would suffer less competition with older females if the females present at their birth are older than the mother, than if the competing females are the same age or younger than the mother.

Competition with females in other matriline also had a small, but highly significant effect on the production of grand-offspring. Daughters who were born into colonies containing many non-matriline females were less likely to produce young than daughters who lived with few non-matriline females (Figure 20d). Numerically dominant matriline can reduce the reproductive performance of the smaller matriline, possibly by forcing members of the smaller matriline to forage in inferior areas (Frase and Armitage 1984, Armitage 1986a). Thus, the reproductive output of daughters is reduced when living in a colony containing a large competing matriline.

#### *Weather factors affecting the production of grand-offspring*

Several weather factors affected the production of grand-offspring. Unlike the social factors, these variables would be expected to exert their influence through the phenotype of the daughter. Conditions surrounding the daughter's birth influence her ability to produce offspring when she matures. These effects would be expected to be non-genetic factors such as the transmission of epigenetic, cytoplasmic, or somatic factors. Such effects were found for a broad range of taxonomic groups and for numerous phenotypic traits, and many affect components of fitness (Rickard et al. 2007, Nilsson et al. 2008, Bondriansky and Day 2009, Anway 2010, Franklin and Mansuy 2010).

Fall temperatures influenced the total number of grand-offspring eventually produced by daughters in a cohort. Females who experienced warmer temperatures during the fall season in

the year prior to producing a litter produced daughters who were less productive during their lifespan (Figure 20e). Cooler fall temperatures maintain more favorable burrow temperatures and reduce energy expenditure by marmots; lower temperatures increase the likelihood of consistent snow cover during early hibernation. Adequate snow cover insulates burrows and helps maintain temperatures within the thermoneutral zone (Schwartz and Armitage 2005). Thus females experiencing more consistent fall snow cover would likely expend less energy in thermal regulation and would be in better condition for reproduction. As has been found in other species, this better condition can then translate to increased reproductive success for the offspring produced in the spring (Rickard et al. 2007). Similarly, low variance in winter temperatures increased the likelihood of reproduction for daughters born in the spring (Figure 24c). High variance in winter temperatures stress females with extremely low temperatures and with warm temperatures that remove snow pack.

Weather factors were also significant predictors of the sex ratio of grand-offspring. Females who produced litters during years with long-lasting spring snow cover had a small, but significant increase in the number of male grand-offspring (Figure 23). Females who experienced a late date of last snow cover had less forage available during gestation, and their daughters produced significantly more males when they reproduced. Possibly an epigenetic effect subtly alters the daughter's reproductive performance. More research is needed to tease out the mechanism and possible implications of this finding.

### *Effects of location*

Finally, there was a significant site effect on the total number of grand-offspring produced. This effect likely combines social factors and environmental factors that vary among sites, such as

size, elevation, aspect, and vegetation characteristics. Social factors vary among colonies in that the different habitat patches affect the typical density of a site, the space use overlap among females (Frase and Armitage 1984), and patterns of residency (Armitage 2009). The univariate probability of producing grand-offspring was highest for colony sites, such as Marmot Meadow, Gothic, and River, and lowest for satellite sites, such as Beaver Talus (Figure 26). These trends match the trends in population growth rate ( $\lambda$ ), with the larger sites having the highest  $\lambda$  (Ozgul et al. 2009). However, once the effects of winter temperature and matriline composition were taken into account, a different pattern emerged. The two sites with the highest grand-offspring production combined large physical size with high elevation and east-northeast aspect (Figure 27). These sites combine the benefits of large size with the consistent winter snow cover provided by higher elevation east-northeast facing sites.

It is significant that we identified so many social and environmental variables during the year surrounding a daughter's birth that subsequently impacted her reproductive success. Normally, an examination of long-term, multigenerational effects requires a substantial research investment, spanning many years. However, most field studies are of relatively short duration. This study demonstrates that long-term population consequences can be predicted from a relatively time-limited study. Moreover, we demonstrated some subtle trans-generational effects that have, until now, been almost exclusively examined in a laboratory setting (e.g. Nilsson et al. 2008, Anway 2010). Demonstration of possible epigenetic effects in a field study, under natural conditions represents a significant advance in this area.

## Conclusions

This study identified several social and environmental variables that affected reproductive success, as measured by the production of offspring, the recruitment of daughters, and the reproduction of those daughters (Table 23). There were no variables that were influential at every stage, and some variables increased reproduction at one stage, while decreasing the production during other stages.

**Table 23. Summary of all significant predictors of reproductive success. A + indicates a positive association with reproduction, - indicates a negative association. A +- indicates that the linear term is positive, while the square term is negative. A -+ indicates that the linear term is negative, while the square term is positive.**

	Abbreviation	Annual Young binary	Annual Young produced by 2-year-olds (binary)	Total Young produced by 2-year-olds	Lifetime Young, binary	Lifetime Young, total	Sex ratio Young (Prop. Male)	Recruits From a cohort, binary	Lifetime Recruits, binary	Lifetime Recruits, total	Grand-offspring from a cohort, binary	Grand-offspring from a cohort, total	Lifetime Grand-offspring total	Sex Ratio Gpup
Intrinsic to Female	Age	+-												
	Resident				+									
	Reproduced last	+												
	Lifespan				+	+								
Environmental	Last snow cover													+
	Last snow fall			+										
	Temp: Sept-Nov.						-					-		
	June Precipitation		+											
	August Precipitation													
	Temp: Deviation Active								-					
	Temp: Deviation Winter									-			-	
	Variance in winter Temp.													
Colony													varies	
Demographic	Male yearlings													
	Female yearlings				+	+			+-					
	Matriline Density										-	-		
	New male	-			-									
	Younger adult females								+	+			-+	
	Older adult females												+	
	Offspring produced by older females						+							
	Same-age females	-										+		
	Offspring produced by same-age adults	+	+-									-		
	Density of Females in Other Matriline											-		



Matriline size and composition were important predictors of reproductive success. Larger matriline reduced the likelihood of leaving any grand-offspring and reduced the total number of grand-offspring produced. Marmots were also affected by the presence of their sisters. Marmots living in matriline containing a large number of same-aged females were more likely to fail to produce any offspring. However, when they did produce offspring in the presence of sisters or half-sisters, they and were more likely to produce grand-offspring from that year's daughters. The presence of younger adults in the matriline increased the probability of recruiting daughters. In contrast, the presence of adults younger than the mother during the year of the daughter's birth reduced the probability that the daughter would later produce offspring, most likely due to reproductive suppression.

A number of weather variables were also important predictors. The different reproductive stages were influenced by different variables and weather conditions at different times of the year, but a few trends are evident. Cool year-round temperatures improved the chances of recruiting daughters, and low fall temperatures increased the production of grand-offspring. In addition, more grand-offspring were produced if a female experience low variance in hibernation temperatures, possibly because these conditions provided consistent snow cover which maintained favorable burrow temperatures. Wet conditions were also broadly favorable for reproduction. Late snow fall in the spring and increased June rainfall improved reproduction by two-year-olds.

It is important to emphasize that these results, although considering long-term measures of reproductive output, are based on single-year observations of social and environmental conditions. Thus, I could predict the production of young, recruitment of daughters, and the eventual production of grand-offspring from the conditions that were present during the year that

the original litter was born. These far-ranging effects from a single year are surprising, and have implications for evolution, ecology, and the implementation of field studies.

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