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CORRELATIONS BETWEEN WEATHER FACTORS AND LIFE-HISTORY TRAITS OF YELLOW-BELLIED MARMOTS
КОРРЕЛЯЦИЯ МЕЖДУ ФАКТОРАМИ ПОГОДЫ И ОСОБЕННОСТЯМИ ЖИЗНЕННОГО ЦИКЛА ЖЕЛТОБРЮХИХ СУРКОВ
CORRELATIONS ENTRE FACTEURS CLIMATIQUES ET TRAITS D'HISTOIRE DE VIE CHEZ LES MARMOTTES A VENTRE JAUNE

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Abstract

*Sixteen measures of variation in survival and reproduction of yellow-bellied marmots (*Marmota flaviventris*) were correlated with 15 measures of weather. Colony size, survival, and litter size were the life-history traits most affected by weather factors. Precipitation, length of the growing season, and length of winter are the major weather factors affecting reproduction and survival. No measure of temperature was significantly correlated with life-history variables. Generation length, degree of iteroparity, percentage maternal survival, percentage young survival, and percentage yearling survival were not significantly correlated with any weather factor. We suggest that weather factors that affect the general body condition of marmots are especially important.*

Key-words: *Weather, survival, reproduction, precipitation, length of winter, length of growing season.*

Резюме

*Шестнадцать особенностей биологии и размножения желтобрюхих сурков (*Marmota flaviventris*) коррелируют с 15 показателями погоды. Размер колонии, выживаемость и размер выводка испытывают на себе наиболее сильное влияние погодных факторов. Осадки, длительность сезона вегетации и продолжительность зимнего периода являются главными факторами погоды, влияющими на размножение и выживаемость. Температура достоверно не коррелирует с особенностями жизненного цикла. Число генераций, повторность родов, процент материнской выживаемости, процент детской выживаемости и процент выживаемости годовиков достоверно не связаны ни с одним из фокторов погоды. Мы установили, что погодные условия особенно сильно влияют на общее состояние тела сурков.*

Ключевые слова: *погода, выживаемость, репродуктивность, осадки, длительность зимнего периода, длительность вегетационного периода.*

Résumé

*Les corrélations entre seize mesures de la variation de la survie et de la reproduction chez les marmottes à ventre jaune (*Marmota flaviventris*) et quinze mesures climatiques ont été calculées. La taille de la colonie, la survie et la taille des portées sont les traits d'histoire de vie les plus affectés par les facteurs climatiques. Les précipitations, la durée de la période de croissance et la durée de l'hiver sont les principaux facteurs climatiques affectant la reproduction et la survie. Aucune mesure de température ne présente une corrélation significative avec les variables d'histoire de vie. Aucune corrélation significative n'a été mise en évidence entre la durée des générations, le degré d'itéroparité, le pourcentage de survie maternel, le pourcentage de survie des jeunes et le pourcentage de survie des animaux d'un an et les différents facteurs climatiques. Nous suggérons que les facteurs climatiques affectant la condition corporelle générale des marmottes sont particulièrement importants.*

Mots-clés : *Climat, survie, reproduction, précipitation, durée de l'hiver, durée de la saison de croissance*

Introduction

From 1962-1986, numbers of yellow-bellied marmots (*Marmota flaviventris*) in our study area ranged from 44 to 133; regulation of marmot populations is primarily density-dependent and extrinsic (Schwartz et al. 1998). Marmots hibernate to avoid a prolonged season of food shortage or unavailability. During their active season they not only must reproduce but also accumulate energy in the form of body fat for use during hibernation and the following spring before food becomes available. The length of time available for body fat gain or utilization varies with the length of winter and the associated snow cover (Armitage & Downhower 1974, Bibikow 1996, Armitage & Blumstein 1997). Precipitation also is important. In summers of drought, marmots may hibernate in poor condition and die overwinter (Armitage 1994, Bibikov 1996). Thus, available evidence suggests that weather can affect survival and reproduction in marmots.

We examine the relationship between weather factors and life-history traits of yellow-bellied marmots living in the Upper East River Valley, Gunnison County, Colorado, USA.

Methods

Eight weather factors were used. For temperature, precipitation, growing season, and length of winter, two or more measures were used, which resulted in 15 measures of weather (Table 1). Weather data were obtained for Crested Butte, Colorado, about 10 km from our study area (U.S. Weather Bureau, 1962-1986). We used weather data from the current year; i.e., the effects of weather in one year on life-history traits in that same year, and weather data from the previous year; i.e., the effects of weather in one year on life-history traits in the following year, in order to test for lag effects (Fig. 1). All measures of weather were arranged from low (or early) to high (or late).

Table 1.

Weather factors used in the analysis of the correlations between weather and reproduction and survivorship of yellow-bellied marmots.

Temperature, °C	The mean and variance of the average temperature and the deviation from long-term average temperature from April to October each year.
Precipitation	The mean and variance of the average monthly precipitation for 12 months (October through September) and the total precipitation for the same period (Fig. 1).
Last Snowfall	The Julian date of the last snowfall of any amount in the spring (Fig. 1).
Last Snowcover	The Julian date of the last snowcover of one inch in the spring (Fig. 1).
First Snowfall	The Julian date of the first snowfall of any amount in the autumn (Fig. 1).
First Snowcover	The Julian date on which at least 1 inch of snowcover occurred in the autumn (Fig. 1).
Growing Season	Two measures of the length of the growing season were used: (I) the number of days between the last snowfall in the spring until the first snowfall in the autumn; (II) the number of days between the last snowcover in the spring until the first snowcover in the autumn (Fig. 1).
Length of Winter	Two measures were used: (I) the number of days between the first snowfall in the autumn and the last snowfall in the spring; (II) the number of days between the first snowcover in the autumn until the last snowcover in the spring (Fig. 1).

Nine life-history traits were used to provide 16 measures of variation in survival and reproduction (Table 2). Three measures of survival, percentage of young surviving, percentage of yearlings (animals one-year-old) surviving, and the ratio of adult survival to juvenile survival, were not correlated with any weather factor and are not included in Table 2. All data were obtained from the demographic records maintained since 1962 (Armitage 1991). All life-history variables were arranged from low to high.

Univariate correlations between weather variables and life history factors were calculated using the Biomedical Data Processing program (BMDP) 1R (Dixon 1988). Stepwise multiple correlations were calculated for each life history factor as the dependent variable and all weather factors as independent variables using BMDP program 2R (Dixon 1988). In the process of stepping the best correlation is first found, than the next best and the next, until other factors no longer have statistical significance. All correlations are combined to produce a multiple R, the total correlation of all significant factors. If two independent variables are highly correlated, such as the mean and variance of precipitation ($r = 0.692$), the best correlation is selected and the other is no longer considered since they are both deemed to have the same information content.

Table 2.

Life-history traits (survivorship and reproduction) used in the correlations between weather factors and life-history traits.

Colony Size	The mean number (and variance) of animals alive of all ages and sexes in each colony trapped that year.
Total Survival	The percentage of all colony animals that reappeared the following year
Adult Survival	The percentage of those animals aged two or older that reappeared the following year.
Maternal Survival	The percentage of females that weaned litters that reappeared the following year.
Non-maternal Survival	The percentage of adult females that failed to wean a litter that reappeared the following year.
Juvenile Survival	The percentage of animals aged one or younger that reappeared the following year.
Maternity	The percentage of animals aged two or older that weaned litters.
Litter Size	The mean and variance of the number of individuals per litter for all litters that were weaned and captured.
Generation Length	Defined as $T = \Sigma x 1_x m_x / \Sigma l_x m_x$ (Zammuto and Millar 1985).
Degree of Iteroparity	$DI = \Sigma l_x m_x \log l_x m_x$ (Zammuto and Millar 1985).
Mean Age at Maturity	The average age of breeding females aged two and three in that year.

Results and discussion

Univariate correlations

For univariate correlations for the current year, mean and variance in colony size were negatively correlated with last snowcover and positively correlated with first snowcover and growing season II (Table 3). These correlations indicate that colony size is larger the earlier snowcover disappears in the spring and the later snowcover begins in the autumn. Furthermore, the longer the time period between the last snowcover in the spring and the first snowcover in the autumn; i.e., the length of the growing season, the larger is the colony size. Age at maturity was negatively correlated with first snowcover. This relationship suggests that the early onset of winter retards the development of maturity such that females first breed at an older age. This relationship is not possible as it requires the onset of winter in the fall to act back on events in the previous spring. However, first snow cover is positively correlated with growing season I. A longer growing season would permit younger females to breed as a longer growing season is associated with an earlier spring.

Table 3.

Univariate correlation coefficients, r (p), between weather factors and life-history traits for current year (values in italics) and lag (weather from previous year) year (values in bold). S^2 = variance.

	Precipitation S^2	Last Snowcover	First Snowcover	Growing Season II
Colony Size:				
Mean	**0.43 (0.04)**	*-0.52 (0.01)*	*0.47 (0.02)*	*0.60 (0.001)*
S^2	**0.50 (0.01)**	*-0.66 (0.001)*	*0.44 (0.03)*	*0.67 (0.001)*
Total Survival			**0.52 (0.01)**	**-0.41 (0.04)**
Litter Size S^2		**-0.50 (0.01)**		**0.53 (0.01)**
Age at Maturity			*-0.44 (0.04)*	

For univariate correlations for the previous year (lag effect), colony size was positively correlated with the variance in precipitation. Because the variance in precipitation is positively correlated ($r = 0.63$) with mean precipitation, the relationship between colony size and precipitation in the previous year suggests that high precipitation enhances the general condition of animals so that they survive better and should also increase reproduction which leads to larger colony size in the next year. This interpretation is supported by the positive correlation between total survival and first snowcover and the negative correlation between total survival and growing season II (Table 3). The later the first snowcover, the better the condition of the marmots, which carries over into the next summer and enhances their survival the following winter. By contrast, a short growing season in one year reduces the condition of the animals, which means that they survive in poorer condition and have decreased survivorship the following winter. Finally, the variance in litter size is negatively correlated with last snowcover and positively correlated with growing season II (Table 3). Litter sizes are more variable the earlier the last snowcover and the longer the growing season. Earlier last snowcover and longer growing season should permit more females to reach reproductive condition the following year and condition of females should also vary. Females in poorer condition should produce smaller litters whereas females in good condition should produce larger litters, thus increasing the variance in litter size.

Some of the life-history traits were correlated (Table 4). In general, the various measures of survival were correlated, which suggests that weather factors that affect survival do not discriminate among age classes. Degree of iteroparity was negatively correlated with adult survival; when adult survival is high, fewer females repeat reproduction. Mean age of maturity was negatively correlated with colony size and maternity. Larger colony size in one year is associated with a lower age of maturity the next year and a higher proportion of females breeding one year results in a reduced mean age of maturity the following year. These relationships indicate that when conditions favor large colony size and high reproduction in one year, the good conditions result in increased maturity such that more younger animals reproduce the following year.

Multiple correlation analysis: current year's weather

Mean colony size was positively correlated with the variance in precipitation and growing season II (Table 5). The variance in colony size was also positively correlated with growing season II. Colony size is larger when precipitation is greater and the growing season is longer.

Total survival was positively related to growing season I and II and to winter length II. Total survival is greater when the growing season is longer. A longer growing season allows marmots to gain mass and to enter winter in good condition. It is not clear why a long winter should enhance survival unless the snowcover provides insulation that prevents cold temperatures from reaching the hibernaculum and increasing metabolic rate, which could cause a depletion of fat reserves and death by starvation. Juvenile survival was positively correlated with mean precipitation and first snowfall. Juvenile survival was greater the higher the precipitation and the later the first snowfall. High precipitation should enhance the quality of forage and late snowfall should provide more time for growth; therefore, time to utilize quality forage should result in animals entering hibernation in good condition.

Maternal survival was not correlated with any measure of weather, but non-maternal survival was positively correlated with first snowfall. The later snowfall occurred, the more likely a non-reproductive adult female would survive. This difference between maternal and non-maternal survival suggests that individual quality has a critical role in survival and reproduction. A high quality female can both reproduce and survive, whereas, a low quality female cannot reproduce and is less likely to survive unless she has a lengthy period for fattening.

Maternity was positively related to winter length I; more females successfully wean litters when winters are longer. This relationship could have two causes. Long winter may reduce energy use by maintaining favorable conditions for hibernation or the late snow may increase plant productivity and thus reduce energy stress after emergence.

Mean litter size was positively correlated with growing season II and the variance in litter size was negatively correlated with last snowfall. Litter sizes were larger when the growing season was longer. Growing season II was negatively correlated ($r = -0.9$) with last snowcover; thus, a longer growing season was associated with an earlier disappearance of snow, which permits early growth of vegetation that provides energy and nutrients for reproduction. When snowfall occurs later in the spring, litter size is less variable. Probably lower quality females cannot reproduce under those conditions. But when last snowfall occurs earlier, lower quality females also reproduce, but probably produce smaller litters than high quality females and hence variance in litter size increases.

Mean age at maturity was negatively correlated with the variance in precipitation and the time of first snowcover (Table 5). Mean age at maturity is younger when the variance in precipitation is greater and when first snowcover is later. More younger animals may mature when conditions are favorable in the spring. High precipitation, which occurs when the variance is greater, and a longer growing season, which is associated with late snowcover, as late snowcover is associated with an earlier spring, provide more resources following emergence. These resources enable younger animals to reproduce, thus lowering the mean age at maturity. As described above under univariate analyses, the relationship between mean age at maturity and the time of first snowcover probably represents a relationship between time of first snowcover and length of growing season.

Table 4.

Correlation between life-history variables, r (p). Italics = current year; bold = lag year.

	Total Survival	Juvenile Survival	Degree of Iteroparity	Colony Size	Maternity
Total Survival		*0.83 (0.001)* **0.82 (0.001)**			
Adult Survival	**0.54 (0.004)**	*0.49 (0.01)* **0.044 (0.03)**	*-0.48 (0.05)*		
Mean Age at Maturity				*-0.45 (0.03)*	*-0.47 (0.02)*

Multiple correlation analysis: previous year's weather

Mean colony size was positively correlated with mean precipitation and first snowfall and negatively correlated with winter length II (Table 5). Colony size was greater the following year when precipitation was high, first snowfall was late, and winter length was short. These conditions favor the survival of animals. The variance in colony size was positively correlated with the variance in precipitation, last snowcover, first snowfall, winter length I and negatively correlated with winter length II. Variance in colony size was larger when variance in precipitation was larger, when last snowcover was later, when first snowfall was later, when winter length I was longer and when winter length II was shorter. The weather factors probably affect body condition and animals with variable body condition are more variable in their survivorship.

Table 5.

Statistically significant partial correlation coefficients (p <0.05) and multiple R for a multiple correlation analysis between weather variables and life-history traits for yellow-bellied marmots. Italics = current year, bold = previous (lag) year.

	Precipitation		Last Snow-fall	Last Snow-cover	First Snow-fall	First Snow-cover	Growing Seasons		Winter Length		Multiple R	
	Mean	S^2					I	II	I	II		
Colony Size:												
Mean	**0.54**	*0.77*			**0.57**			*0.69*		**-0.54**	*0.89*	**0.90**
S^2		**0.76**		**0.51**	**0.56**			*0.75*	**0.55**	**-0.75**	*0.75*	**0.97**
Survival												
Total							*0.6*	*0.55*		*0.64,* **0.64**	*0.86*	**0.64**
Adult	**-0.51**							**-0.50**				**0.67**
Juvenile	*0.62*				*0.56*						*0.76*	
Non-maternal					*0.81*						*0.81*	
Maternity	**0.65**								*0.48*		*0.48*	**0.65**
Litter Size												
Mean		**0.58**						*0.55*			*0.55*	**0.58**
S^2			*-0.52*	**-0.56**							*0.52*	**0.56**
Mean Age at Maturity		*-0.51* **-0.52**				*0.52*					*0.68*	**0.52**

Adult survival was negatively related to mean precipitation and growing season II. High precipitation and a long growing season the previous year were associated with a lower percentage of adult survival during the winter of the following year. The mechanism of this lag effect is not clear.

Maternity was positively correlated with mean precipitation (Table 5); high rainfall in one year was associated with a high percentage of reproductive females the following year. Precipitation is associated with good conditions for gain in mass and females in good condition are more likely to reproduce.

Mean litter size was positively correlated with the variance in precipitation. This relationship suggests that when conditions were favorable the previous summer, females could produce larger litters. The variance in litter size was inversely correlated with last snowcover the previous year. The length of the previous summer probably affects the number of females reproducing. Marginal females can reproduce which increases the variance in litter size.

The mean age at maturity was negatively correlated with the variance in precipitation the previous year (Table 5). Because the variance in precipitation is correlated with mean precipitation, high variance in precipitation is associated with a good growing season and enables more females to reach reproductive maturity. Hence, younger females reproduce the following year and mean age at maturity is lower.

Summary and Conclusions

No measure of temperature was significantly correlated with life-history variables when either the current year or the previous year was considered. Generation length, degree of iteroparity, percentage maternal survival, percentage young survival, and percentage yearling survival were not significantly correlated with any weather factor in any of the analyses. In the multiple correlation analyses, adult survival was not correlated with any weather factor when the current year was considered and juvenile survival and non-maternal survival were not correlated with any weather factor when lag effects; i.e., the previous year, were considered.

Colony size, survival, and litter size were the life-history traits most affected by weather factors. This analysis indicates that precipitation, length of the growing season, and length of winter are the major weather factors affecting reproduction and survival. Interpretation of the way that weather factors affect life-history traits suggests that those that affect the condition of the animals are especially important and that weather factors that influence how long marmots must rely on their condition for survival and reproduction are also critical.

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FIGURES / *РИСУНКИ*

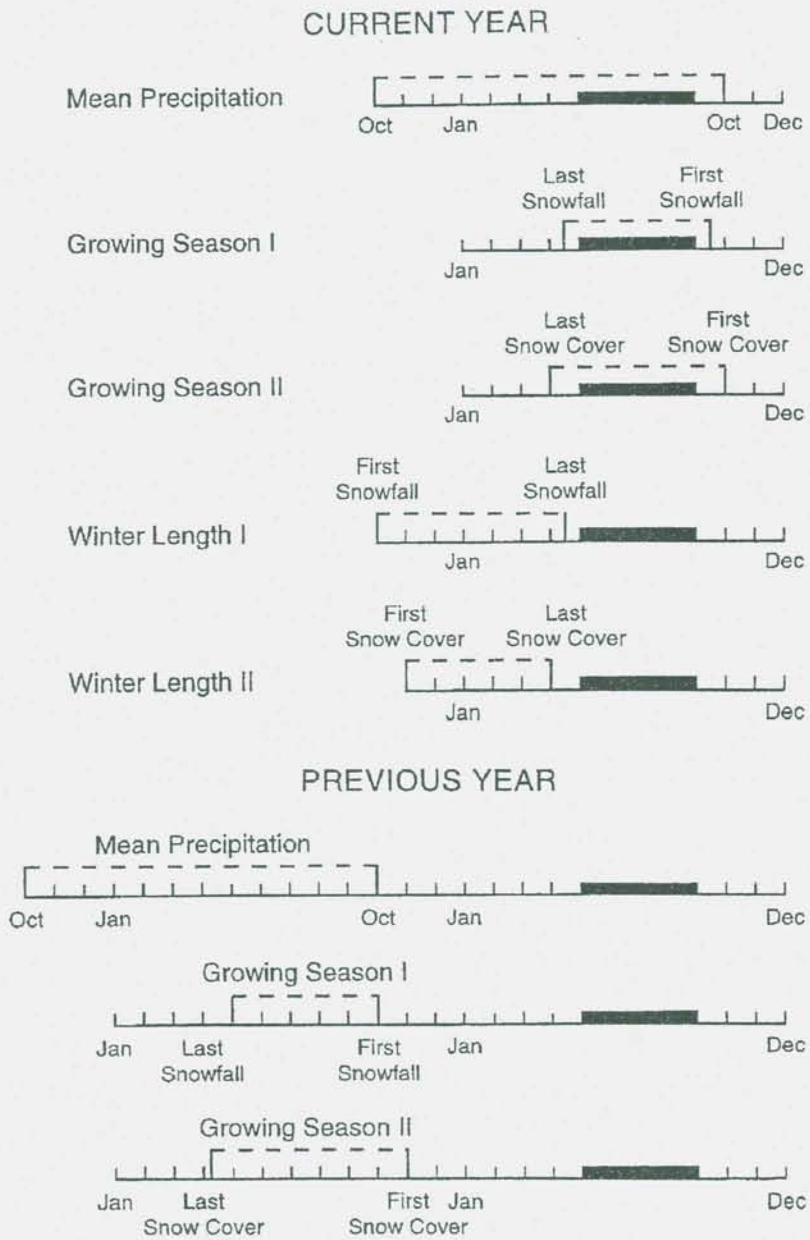

Fig. 1. Diagram of the weather factors used in the analysis of the relationship between weather variables and life-history traits of yellow-bellied marmots. Solid bar represents the active period (May through August) of marmots for which the life-history traits were measured. Dashed line represents the time period for which the weather factor was measured. First and last snowfall and first and last snowcover are represented as dates of occurrence.

Рис. 1. *Диаграмма факторов погоды, используемых в анализе взаимоотношения между погодой и особенностями жизненного цикла у желтобрюхих сурков. Закрашенная полоска представляет активный период (с мая по август) сурков, в пределах которого были получены данные о жизненном цикле. Пунктирная линия - время, за которое измерены факторы погоды. Первый и последний снегопад и первый и последний снежный покров представлены соответстевующими датами.*