

Variation in survival rates for the alpine marmot (*Marmota marmota*): effects of sex, age, year, and climatic factors

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Abstract: We examined variation in annual survival rates in a population of alpine marmots (*Marmota marmota*) according to intrinsic (sex and age) and extrinsic (year and climate) factors. We tested predictions concerning (i) a sex effect in a monogamous non-dimorphic species, (ii) age structure of survival rates in a mesomammal, and (iii) the annual variability effect and the contribution of stochastic climatic factors, especially snow cover, frost, and rainfall. We used a 8-year dataset of 367 marmots that were livetrapped and marked in La Sassièrè Nature Reserve in the French Alps between 1990 and 1997. Survival and recapture rates were modelled using recent developments in capture–recapture models. Sex had no effect on survival rates, which agrees with the predictions of sexual selection. Survival rates for young of the year (YOY, from weaning to first birthday) were, on average, lower than in the older age class. In the older age class, annual variation occurred that was strongly related to the intensity of autumn frost. By determining the soil temperature at the beginning of hibernation, this factor, though short-lived, could have determined the energetic cost of hibernation. Neither annual variation nor an environmental effect was detected in YOY despite a large sample size. Social thermoregulation could contribute to the stability of YOY survival rates. As infanticide was common after the immigration of a new dominant male, survival of YOY seemed to depend more on social events than on stochastic climatic ones.

Résumé : Nous avons étudié les variations des taux annuels de survie dans une population de marmottes alpines (*Marmota marmota*). Les taux de survie ont été étudiés en fonction de facteurs intrinsèques (sexe et âge) et extrinsèques (années et climat). Nous avons testé des prédictions sur (i) l'effet du sexe chez une espèce monogame non dimorphique, (ii) la structuration en âge de ce mésomammifère et (iii) l'effet de la variabilité annuelle et la contribution de facteurs climatiques, en particulier le couvert neigeux, le gel et les précipitations. Nous avons utilisé un jeu de données de 8 ans portant sur 367 marmottes qui ont été capturées et marquées dans la réserve de la Sassièrè (Alpes françaises, à 2350 m d'altitude) entre 1990 et 1997. Les taux de survie et de recapture ont été modélisés à partir des modèles récents de capture–recapture. Le sexe n'avait pas d'effet sur la survie, ce qui est en accord avec la prédiction de la sélection sexuelle. La survie des jeunes de l'année (du sevrage au premier anniversaire) était plus faible que celle des animaux plus âgés. Dans cette dernière classe, les variations annuelles de survie étaient liées à l'intensité du gel automnal. Parce qu'elle était responsable de la température du sol au début de l'hibernation, cette courte période pouvait sans doute déterminer le coût de l'hibernation. La survie des jeunes de l'année ne dépendait ni de l'année ni d'effets environnementaux, bien que la taille de l'échantillon se soit avérée importante. La thermorégulation sociale pourrait contribuer à stabiliser la survie des jeunes de l'année. L'infanticide est commun après le changement de mâle dominant; la survie des jeunes de l'année pourrait donc dépendre d'événements sociaux plutôt que des conditions climatiques.

Introduction

Variation in survival rates has different effects on population size, depending on sex and age (Caswell 1989; Charlesworth 1994). The estimation of survival rates and understanding survival patterns are thus major issues in population biology (Lebreton et al. 1993). In mammal species, the major extrinsic causes of variation in mortality rates are stochastic weather variations, diseases, and variations in size of predator populations, while sex and age are the main intrinsic factors

(Sinclair 1989; Jorgenson et al. 1997; Van Horne et al. 1997; Gaillard et al. 1998). The general pattern of variation in mortality with age described by Caughley (1966) shows an increase and then a decrease in survival with age. Also, a difference in mortality rates between the sexes occurs within polygynous species (Clutton-Brock et al. 1982; Boer 1988; Jorgenson et al. 1997), and this difference is positively correlated with sexual dimorphism (Promislow 1992).

Little is known about survival rates among marmot species, and all our present knowledge is based either on observed proportions of individuals seen alive in 2 consecutive years (Arnold 1990a; Lenti Boero 1994, 1999) or on life-table analysis (Armitage and Downhower 1974; Bryant 1996; Schwartz et al. 1998). Estimations based on life tables depend critically on basic assumptions, i.e., stationary age distribution and equal sampling probability (Caughley 1977), that are unlikely to be met in wild mammal populations (Menkens and Boyce 1993). New developments in capture–recapture models have led to a single comprehensive statisti-

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cal framework of capture–recapture analysis (Burnham et al. 1987; Lebreton et al. 1992), which nowadays provides a powerful and flexible tool for studying survival rates when recaptures are not perfect.

Here we present a capture–recapture analysis of survival rates for the alpine marmot (*Marmota marmota* L.). The alpine marmot is a large ground-dwelling squirrel (Rodentia, Sciuridae) that is highly social (Arnold 1990a; Perrin et al. 1993) and primarily socially monogamous (Goossens et al. 1998). The social unit is a family group, which is usually composed of a dominant pair, juveniles (young of the year (YOY) and yearlings), and subordinate adults (2, 3, and sometime 4 years old). Alpine marmots reproduce once a year, and YOY emerge from burrows at weaning in June and July. Alpine marmots hibernate socially, and social thermoregulation occurs, which could limit the energetic cost of hibernation for YOY (Arnold 1988, 1990b). Sexual maturity is reached at 2 years of age, and dispersal occurs equally in both sexes and is delayed until 2–4 years of age or more.

We tested three predictions: (1) Survival rates are independent of sex. Indeed, in the alpine marmot, monogamy is associated with very limited sexual dimorphism in size or behaviour (Allainé et al. 1998). Therefore, the intensity of sexual selection is assumed to be low, and no difference between male and female survival rates is expected. (2) Survival rates fit the general pattern for mammals, increasing from birth to the post-juvenile stage, then decreasing in old adults (Caughley 1966). (3) Survival rates vary among years. Alpine marmots at La Sassiére Nature Reserve are exposed to a typical alpine climate, with a growing season that is short and highly variable from year to year. Significant year-to-year variability in vital rates in relation to weather variations is therefore expected. The weather factors tested were presumed to be critical ones: snow cover in spring, summer rainfall, summer temperature, and autumn frost. Indeed, long winters were found to be associated with higher mortality in *Marmota flaviventris* (Armitage and Downhower 1974) because snow cover during spring could limit food resources by delaying vegetation growth (Van Vuren and Armitage 1991). Summer rainfall and summer temperature more specifically affect the postweaning growth of YOY. Low rainfall in summer was correlated with high mortality of juvenile *Spermophilus townsendii* (Van Horne et al. 1997) and *M. flaviventris* (Lenihan and Van Vuren 1996). Drought limited food resources, which limited increase in mass before hibernation and lowered over-winter survival of YOY. High summer temperature could either increase the energetic cost of foraging for the YOY or limit activity of marmots (Türk and Arnold 1988). Finally, autumn frost could affect the temperature of hibernacula during hibernation. A decrease in survival rates was therefore predicted when autumn-frost intensity and spring snow cover increased and summer rainfall decreased.

Methods

Study area

The study site is in La Sassiére Nature Reserve (45°29'N, 6°59'E, elevation 2280–3747 m) in the eastern part of Vanoise National Park (Savoie, French Alps). The climate is typical of high mountains, very harsh and highly variable, with con-

siderable snowfall. The average daytime temperature is 9.9° in July and –5.8° in January and the snow depth in winter was 140 ± 43 cm (mean $\pm$ SE) between 1990 and 1997. The study population consisted of 17 contiguous family-group territories (average elevation 2350 m) with different exposures (north-facing slopes, valley, and south-facing slopes) situated in various kinds of rocky alpine grassland (Allainé et al. 1994). From 1990 to 1997, marmots were live-trapped each year with two-door traps ($n = 18$) baited with salt and food. Catch effort increased through the years: captures began in late May from 1990 to 1992; in early May in 1993 and 1994; and in early April, as soon as marmots emerged from winter hibernation, from 1995 to 1997. Indeed, average dates of emergence ranged from 12 to 23 April on south- and north-facing slopes, respectively (Allainé et al. 1998). On this basis we defined three levels of catch effort: low (1991 and 1992), medium (1993 and 1994), and high (1995–1997). Every year, trapping ceased in midsummer. From 1990 to 1997, 433 marmots were captured a total of 1061 times. Each animal was individually marked, permanently with numbered ear tags and by injection of TROVAN™ transponders and, for visual identification, with coloured ear tags and fur dye. Sex was determined by means of anogenital morphology (Zelenka 1965). Biometric measurements were used to age animals at first capture and allowed us to distinguish three classes: YOY, yearling, and 2 years of age or older.

Data analysis and capture–recapture models

The original dataset has been reduced to avoid major bias due to unequal catchability (Carothers 1979; Anderson et al. 1994; Pradel et al. 1997). In particular, all individuals known to be transients were discarded from the original dataset. An individual was considered to be a transient if it had never been captured before in the study population and was not observed subsequently. Daily observations often confirmed the wandering habit of these individuals. Regardless of whether the individuals were visually identified, only physical recaptures were taken into account in the capture–recapture analysis because resightings were not homogeneous among studied groups. Finally, the 8-year dataset was reduced to 367 individuals (210 males and 157 females). Of these, 272 were juveniles of known age at first capture (YOY or yearling) and 95 were adults of unknown age at first capture, i.e., at least 2 years old.

Data analysis followed four main steps (Lebreton et al. 1992). In the first step we tested whether a global model compatible with our biological knowledge fitted our data with regard to the “3i hypothesis” (Burnham et al. 1987). We used goodness-of-fit tests that were computed using the RELEASE software. The second step was to select a more parsimonious model. To limit formal tests, Akaike’s Information Criterion (Akaike 1973) corrected for small sample size (AICc) was used to estimate model parsimony (Lebreton et al. 1992; Burnham and Anderson 1998). The lower the AICc value, the more parsimonious the model. The third step was to test the biological questions of interest by comparing the most parsimonious model with neighbouring ones using the likelihood ratio test (LRT) (Lebreton et al. 1992). Finally, the fourth step was to compute maximum-likelihood estimates of model parameters. Deviance and estimates of

Table 1. Key steps in the modelling of recapture rates.

Biological meaning of the comparison	Recapture-rate model*	No. of parameters [†]	AICc
Recapture depends on 2-age-class catch effort	$3a \times t \times s$	78	1033.2
	$3a \times e \times s$	54	988.6
Catch-effort effect important	$3a \times e \times s$	54	988.6
	$3a \times s$	48	994.6
Sex effect concerns only adults (3 years old or more)	$3a \times e \times s$	54	988.6
	$3a \times e \times s_{>2}$	50	984.9
Catch-effort effect limited to 2-year-olds and adults	$3a \times e \times s_{>2}$	50	984.9
Adult females (adf)	$3a \times e_{2,adf} \times s_{>2}$	48	978.6
Variation in recapture rates important	$3a \times e_{2,adf} \times s_{>2}$	48	978.6
	Constant	43	1009.7

Note: For all the models the survival rate is the same and corresponds to the global-model recapture rate (see the text). For each step presented, the more parsimonious model (i.e., with lower AICc) is shown in boldface type. The final model is shown in boldface type and underlined.

[†]3a, 3 age classes (1 year old, 2 years old, and 3 years old or more); t, time (year effect); e, catch effort in 2 classes (weak: 91 and 92; medium or high: 93–97); s, sex.

*Number of parameters used in the current model.

all capture–recapture models were computed with the logit link function, using the MARK software (White and Burnham 1999).

Climatic data

Daily data were used to describe autumn frost, spring snow cover, summer rainfall, and summer temperature. Data were from Météofrance weather stations at Tignes and Val d'Isère, 7 and 5 km from the site, respectively, and 500 m lower in elevation, and from the Centre d'Étude de la Neige in Grenoble, France, a section of the Centre National de Recherches Météorologiques. Temperatures were corrected for the difference in elevation by considering that the temperature decreases 0.55°C for an increase of 100 m in elevation (Ozenda 1985). Snow cover was corrected with mathematical models (taking into account the altitude, slope, and exposure to the sun) developed by the Centre d'Étude de la Neige. The autumn deep-frost variable (AUF), the minimal daily air temperature in October and November when snow cover had no insulating effect, i.e., snow depth was less than 10 cm ($-9.1 \pm 3.6^\circ\text{C}$; mean $\pm$ SD), provided information about the intensity of soil freezing at the beginning of hibernation. Unfortunately, we do not have precise information concerning the date when winter ended (i.e., when the soil was free of snow; Armitage and Downhower 1974; Arnold 1990b; Van Vuren and Armitage 1991), especially for the first years of the study. The average spring snow cover (SPS) was therefore assumed to be inversely correlated with the end of winter (i.e., with the earliest date when food became accessible). Because significant snowfall regularly occurred in March, April, and even May, SPS was the average snow depth in April and May (170 ± 45 cm; mean $\pm$ SD). The average summer temperature (SUT) was the mean of minimum and maximum daily temperature in July and August ($10.0 \pm 1.1^\circ\text{C}$). The cumulative summer rainfall (SUR) was the sum of all precipitation (rain or snow) in July and August (157 ± 77 mm).

Age-class definitions

Age classes were defined in relation to marmot natural history. For recapture modelling, three age classes were used:

yearling, 2 years old, and 3 years of age and older. Based on our field experience, these classes represent increasing trap avoidance. To assess whether the change in survival rate with age fitted Caughley's (1966) pattern, we compared three classes of models. First, a 2-age-class model distinguished only a YOY stage (survival from 0 to 1 year) and an older stage (OLD, individuals 1 year of age and older). According to this model, the survival rate was lower in juveniles than in the other age classes whose survival rate was then constant. Second, a 3-age-class model was composed of a YOY stage (survival from 0 to 1 year), a yearling stage (from 1 to 2 year), and an adult stage (individuals older than 2 years). This second model tested the hypothesis that the yearling survival rate was intermediate between those of juveniles and adults. These two models tested for lower survival rates in young age classes but did not consider senescence in old age classes. Finally we tested for the occurrence of senescence, for which an alternative survival model was defined, with age as an external variable (Loison et al. 1999), and the possibility of senescence was tested using a quadratic logistic regression.

Results

Preliminary analyses

The global model, $P(3a \times t \times s) \phi(3a \times t \times s)$ (see Table 1 for details), defined the recapture rate, P , and the survival rate, ϕ , as a function of the 3 factors studied (sex (s), 3 age classes (a), and time (t)) and their interactions. Because of the limited sample size, the goodness-of-fit test had to be performed on a simpler model that did not take age classes into account. As $P(t \times s) \phi(t \times s)$ this model defines P and ϕ as functions of time (t) and sex (s) and their interactions. The goodness-of-fit test revealed no bias in the data: adjustment of the dataset to the model $P(t \times s) \phi(t \times s)$ under the 3i hypothesis was far from being rejected ($\chi^2_{[22]} = 17.41$, $p = 0.74$), and we can reasonably suppose that this was so for the global model, since it was more complex than the tested one.

The initial model of recapture rate, $P(3a \times t \times s)$ (AICc = 1033.2; 78 parameters), was reduced to a simpler one. The

Table 2. Summary of the modelling of survival rates.

Biological meaning of the comparison	Survival-rate model*	No. of parameters [†]	AICc
Two age classes better than 3 age classes	$3a \times t \times s$	48	978.6
	$2a \times t \times s$	34	953.8
Additive effect of sex	$2a \times t \times s$	34	953.8
	$(2a \times t) + s$	21	942.3
No sex effect on survival rates	$(2a \times t) + s$	21	942.3
	$2a \times t$	20	940.1
Additive effect of age on variation with time	$2a \times t$	20	940.1
	$2a + t$	14	937.9
Survival rates vary according to time in YOY age class only	$2a + t_{\text{YOY}}$	14	947.1
Survival rates vary with time in older age class only	$2a + t$	14	937.9
	$2a + t_{\text{OLD}}$	14	931.8
No time variation in survival rate	$2a + t_{\text{OLD}}$	14	931.8
	$2a$	8	939.4
No age-class variation in survival rate	$2a + t_{\text{OLD}}$	14	931.8
	t	13	937.6
No variation in survival rate	$2a + t_{\text{OLD}}$	14	931.8
	Constant	7	938.9

Note: For all models the recapture-rate model is the same and corresponds to the most parsimonious model of recapture rates: $P(3a \times e_{2,\text{adf}} \times s_{>2})$. For each step presented, the more parsimonious model (i.e., with lower AICc) is shown in boldface type. The final model is shown in boldface type and underlined.

*3a, 3 age classes (0–1 year old; 1–2 years old; older); 2a, 2 age classes (0–1 year old; older); t, time (year effect); s, sex.

[†]Number of parameters used in the current model.

key steps of the model-selection process are summarized in Table 1. The final and more parsimonious recapture-rate model, $P(3a \times e_{2,\text{adf}} \times s_{>2})$ (AICc = 978.6), uses only 6 different parameters to describe recapture rate variations. It relies on the 3 age classes defined for recapture (yearling, 2 years old, and 3 years old or more), on catch effort (low versus medium or high), and on sex in the older age class. The probability of recapture is constant for yearlings, and increases with catch effort for 2-year-old marmots. For older marmots, the probability of recapture was constant for males and increased with catch effort for adult females (adf). Estimates were computed from the most parsimonious model, $P(3a \times e_{2,\text{adf}} \times s_{\text{adult}}) \phi(2a + t_{\text{OLD}})$ (see the next section for survival modelling). The yearling recapture rate, P , was high: 0.92 (95% confidence interval (CI) = 0.82; 0.97 (CIs were asymmetrical because of logit link)). Recapture rates for 2-year-olds increased with catch effort: 1991 and 1992: $P = 0.68$, CI = 0.39; 0.88; 1993–1997: $P = 0.96$, CI = 0.80; 0.99. For adult males, $P = 0.61$ (CI = 0.49; 0.71), while the recapture rate for adult females increased with catch effort: 1991 and 1992: $P = 0.37$, CI = 0.14; 0.68; 1993–1997: $P = 0.88$, CI = 0.73; 0.95.

Test of the predictions

The process of selecting models of survival rates is summarized in Table 2. The initial model of survival rates, $\phi(3a \times t \times s)$ (AICc = 978.6) was reduced to a parsimonious model, $\phi(2a + t_{\text{OLD}})$ (AICc = 931.8). This final model revealed only age and year effects on survival rates.

Prediction 1: sex effect

The most parsimonious model did not reveal any sex effect on survival rates. The absence of a sex effect was con-

firmed with LRTs for the 2 age classes ($p = 0.223$) and for each one separately (YOY: $p = 0.534$; OLD: $p = 0.176$; Table 3). The bias in the sex ratio (SR; proportion of males) observed in the data (SR = 0.572 ± 0.05 , $n = 367$) was observed in all age classes and was significant only among juveniles (adults: SR = 0.579 ± 0.099 , $n = 95$; yearlings: SR = 0.571 ± 0.13 , $n = 49$; juveniles: SR = 0.57 ± 0.064 , $n = 223$). Thus, the male bias in our dataset was not the consequence of differences in mortality rates between the sexes but resulted from overproduction of males by mothers (Allainé et al. 2000; see also Lenti Boero 1999). Thus, prediction 1 is confirmed.

Prediction 2: age effect

The most parsimonious model corresponds to the 2-age-class model. Then, an effect of age on survival was revealed, which distinguished only survival of YOY from that of older individuals (OLD). LRTs confirmed that survival rates of yearlings were not significantly different from those of older animals ($p = 0.633$; Table 3). In the YOY age class, the annual survival rate, ϕ , was 0.62 (CI = 0.54; 0.70). In the OLD age class, the annual survival rate was higher, on average, than that for younger animals: $\phi = 0.71 \pm 0.14$ (mean $\pm$ SD; range = 0.51–0.92). The occurrence of senescence was tested using age as an external variable. In this model, the survival rate is a quadratic function of age. Because the exact age of individuals was needed in this analysis, it was necessary to distinguish between animals of known and unknown age (Table 4). Survival rates for unknown-age marmots were then defined as varying according to year. Survival rates for known-age marmots were defined as varying according to year and age (external variable). No quadratic effect of age was revealed ($p > 0.465$), indicating the absence of senes-

that yearlings avoided the cost of dispersal because they did not usually disperse, while dispersal occurred in all older age classes (Magnolon 1999; for studies in other populations see also Arnold 1990a; Lenti Boero 1999). Another possibility is that adult survival is underestimated. Indeed, many individuals were not recaptured after dispersal, so the actual survival rates for adults should be higher than the apparent ones. In our study we did not consider the effect of social status, and further investigations should include such an effect. In particular, the adult age class was composed of dominant and subordinate individuals (Arnold 1990a; Perrin et al. 1993), and we would reasonably expect survival rates to differ between these two social categories for a given age.

Annual variations in survival rates are well documented in wild populations of mammals, especially in variable environments such as mountains. The effects of climate usually vary according to interactions between several factors, and timing of events can be critical (Van Horne et al. 1997). Survival of marmot populations is doubtless related to winter severity, which changes hibernation success (Armitage and Downhower 1974; Barash 1989). To estimate winter severity, both the total number of days of snow cover and the duration of spring snow cover have been used. A negative correlation between annual survival rates and spring snow cover was established for both the yellow-bellied marmot and the alpine marmot (Armitage and Downhower 1974; Arnold 1990b; Van Vuren and Armitage 1991). In the present study there was no significant correlation between spring snow cover and annual survival rates. This was probably due to the fact that our index of snow cover in spring may not be the best measure of the end of winter. Instead, our results indicate that deep frost in the soil in autumn (AUF), a factor not yet studied in marmots, could be a key parameter after the first year of life. Although hard frosts were short climatic events (the number of days of hard frost in autumn ranged from 1 to 6), they probably affected the circumstances of hibernation, and consequently survival. Indeed, measurements of oxygen consumption in natural hibernacula showed that alpine marmots increased heat production when the ambient temperature dropped below 1.5°C (Arnold 1993). Heat production is energetically costly, particularly when young are present (Arnold 1988, 1990b), therefore the air temperature in the hibernaculum should be critical for survival during hibernation (Arnold et al. 1991). As air temperature decreases exponentially from about 12°C in autumn to 0°C in spring (Arnold et al. 1991), a deep autumn frost before winter snowfall may influence the initial temperature in the burrow.

Surprisingly, young (YOY) were not affected by frost, and their annual survival rate appeared to be constant over the years even though the sample size was large (223 young). Our results suggest a potential negative effect of high summer rainfall on survival, which differs from results from American Sciuridae (Lenihan and Van Vuren 1996; Van Horne et al. 1997). The summer climate at La Sassièrre Nature Reserve is not dry, and droughts are rare events; none occurred during our study. Rather, summers at La Sassièrre Nature Reserve are often wet, and too-wet summers were problematic for the young, which stayed in their burrows for long periods when it rained, probably because of the need to thermoregulate (field observation; see also Türk and Arnold 1988; Armitage et al. 1990). Consequently, frequent rainfall may reduce for-

aging time, and therefore summer mass gain. Although biologically meaningful, this trend remains to be confirmed. Thus, weather conditions during both winter and summer did not affect the survival of young, probably because social thermoregulation reduced their impact and lowered the mortality rate for the young (Arnold 1993; Allainé et al. 2000). Rather, most of the mortality of young might have occurred during the active period because of social events. Infanticide that resulted from the males' take-over (Coulon et al. 1995; Lenti Boero 1999) could have been the main cause of mortality at La Sassièrre Nature Reserve. Infanticide seemed to be frequent (more than 50% of juvenile mortality) and constant over the years (field observations). We suggest, therefore, that social events might have been more important than annual stochastic climatic events for annual survival of YOY. However, more work is needed to determine the relative importance of social and climatic factors in the survival of juvenile alpine marmots.

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Table 3. Likelihood-ratio test (LRT) of survival-rate (ϕ) models when the alternative models are more complex than the reference one.

Biological meaning of the null hypothesis	Model	No. of parameters	DEV	AICc	χ^2	df	p^*
Reference model	$2a + t_{\text{OLD}}$	14	255	931.8			
Alternative model							
Sex effect							
No sex effect on any age class	$2a + t_{\text{OLD}} + s$	21	245.4	937.4	9.42	7	0.223
No sex effect on OLD age class	$2a + t_{\text{OLD}} + s_{\text{OLD}}$	20	245.9	935.7	8.96	6	0.176
No sex effect on YOY age class	$2a + t_{\text{OLD}} + s_{\text{YOY}}$	15	254.4	933.5	0.40	1	0.534
Age-class effect							
No independent yearling age class	$3a + t(\text{yearling}, \geq 2)$	21	249.6	941.6	5.22	7	0.633
Time effect							
Time effect on YOY age class	$2a \times t$	20	250.3	940.1	4.54	6	0.602
Climate effect on YOY age class							
AUF does not explain time variation	$2a \times t \text{ YOY} = f(\text{AUF})$	15	254.5	933.6	0.37	1	0.541
SPS does not explain time variation	$2a \times t \text{ YOY} = f(\text{SPS})$	15	254.4	933.5	0.45	1	0.505
SUT does not explain time variation	$2a \times t \text{ YOY} = f(\text{SUT})$	15	254.8	933.9	0.05	1	0.825
SUR does not explain time variation	$2a \times t \text{ YOY} = f(\text{SUR})$	15	252.9	932.0	1.99	1	0.158

Note: The null hypothesis is that the reference model is sufficient to describe the data. ϕ is the survival rate; DEV and AICc are the deviance and Akaike Information Criterion value of the tested model, respectively. $3a$, 3 age classes (0–1 year old; 1–2 years old; older); $2a$, 2 age classes (0–1 year old; older); t , time (year effect); t_{OLD} , time variation limited to survival rates after 1 year of age; s , sex; AUF, autumn deep-frost variable; SPS, average spring snow cover; SUR, cumulative summer rainfall; SUT, average summer temperature.

*The value in boldface type is the only one that indicates statistical tendency.

Table 4. Test for the occurrence of senescence in survival rates (ϕ), using LRTs.

Biological meaning	Model	χ^2	df	p
Reference model	$K(2a \times t_{\text{OLD}}), U(t)$			
Alternative model				
Interaction between age and year	$K(2a: \text{YOY} = \text{constant}, \text{OLD} = \text{quad } a \times t), U(t)$	3.90	7	0.791
No interaction between age and year	$K(2a: \text{YOY} = \text{constant}, \text{OLD} = \text{quad } a + t), U(t)$	0.53	1	0.465

Note: Age is an external variable. The null hypothesis is that the reference model is sufficient to describe the data. The reference model discriminates animals of known age (K) and unknown age (U). Animals of known age are separated into 2 age classes ($2a$), 2 age classes (0–1 years old (= YOY); OLD (= older than 1 year). t , time (year effect); quad a , quadratic function of age.

cence in survival rates. Thus, the second prediction is only partially validated.

Prediction 3: year effect

LRTs confirmed that in the YOY age class, annual variations in survival rate were not significantly different from constancy ($p = 0.602$; Table 3). None of the four environmental variables had significant effects on survival of YOY (Table 3). Of these variables, the results concerning SUR might indicate a tendency ($p = 0.158$), since the model using SUR was parsimonious (AICc = 932.0). Survival rates for YOY tended to decrease as SUR increased; this trend was in the opposite direction to that predicted.

LRTs confirmed that variations in survival rates with time (Fig. 1) were significant for the OLD age class ($p = 0.003$; Table 5). Weather conditions could structure these time variations in the OLD age class (Table 5) because the effect of AUF was not rejected ($p = 0.465$). By comparing the model $\phi[2a \times t_{\text{OLD}}(\text{AUF})]$ with a simpler one, $\phi(2a)$, we confirmed that the AUF effect was highly significant ($p < 0.001$). Furthermore, the model $\phi[2a \times t_{\text{OLD}}(\text{AUF})]$ is more parsimonious (AICc = 926.0) than the reference one (AICc = 931.8). An increase in the number of days of hard frost led to a decrease in survival rates.

Thus, our third prediction is also partially validated, since survival rates in the YOY age class were constant over time and did not depend on climatic factors.

Discussion

The recapture model selected was simple, and estimates of recapture rates were consistent with field experience. Recapture rates increased with catch effort, at least for the 2-year-old and adult female age classes. In 1991 and 1992, capture began only in late May. At this time dominant females were nursing and were rarely trapped after mid-May. Also, dispersal of subordinate adults (2, 3, and sometimes 4 years old) usually occurred in April and May (Magnolon 1999). After 1992, captures began earlier and trapping of adult females and subordinates before dispersal was easier. This catch-effort effect was therefore taken into account in the analysis of survival rates.

The survival rates of alpine marmots did not vary with sex. This absence of sex effect was consistent with sexual selection, since the alpine marmot is monogamous and sexual dimorphism is very limited. Among mammals, a strong correlation between sexual dimorphism and sex-biased mortality has been observed (Promislow 1992), and sexual dimorphism is usually correlated with polygyny. This correlation

Fig. 1. Annual survival rates of alpine marmots estimated from the parsimonious model $\phi(2a \times t_{\text{OLD}})$. Estimates are presented with their 95% confidence intervals, which are asymmetrical because of logit link in the models. YOY, young of the year (from weaning to first birthday); OLD, after first birthday.

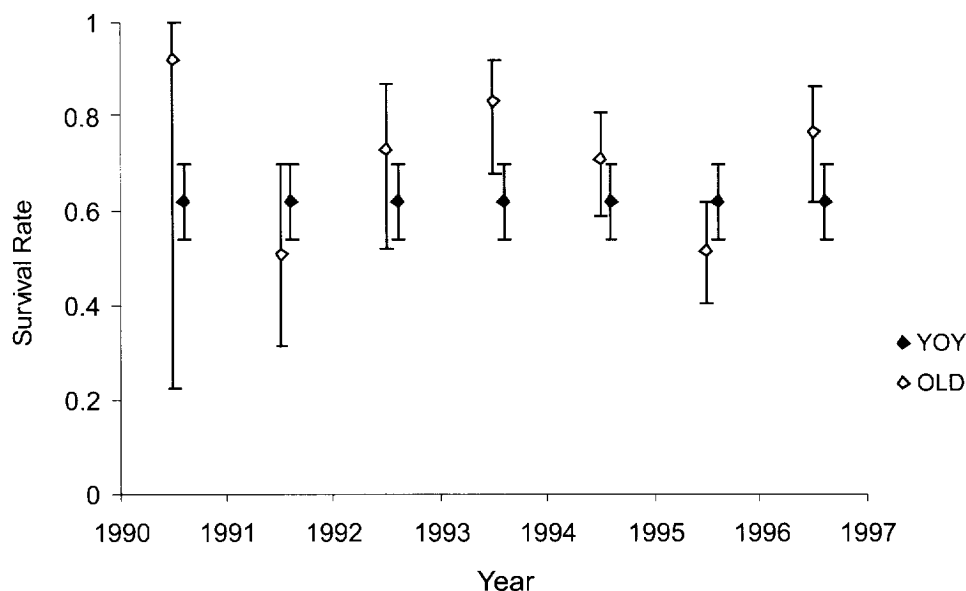


Table 5. LRT of survival-rate (ϕ) models, when the alternative models are less complex than the reference one.

Biological meaning	Model	No. of parameters	DEV	AICc	χ^2	df	p^*
Reference model	$2a + t_{\text{OLD}}$	14	254.9	931.8			
Alternative model							
Age-class and time effect							
No variation in survival rates	Constant	7	276.5	938.9	21.6	7	0.003
Time effect							
No time effect on OLD age class	$2a$	8	274.9	939.4	20.1	6	0.003
Climate effect on OLD age class							
Time effect explained by AUF	$2a + t_{\text{OLD}}(\text{AUF})$	9	259.5	926.0	4.7	5	0.465
Time effect explained by SPS	$2a + t_{\text{OLD}}(\text{SPS})$	9	266.3	932.8	11.5	5	0.043
Time effect explained by SUT	$2a + t_{\text{OLD}}(\text{SUT})$	9	274.4	940.9	19.5	5	0.002
Time effect explained by SUR	$2a + t_{\text{OLD}}(\text{SUR})$	9	269.4	935.9	14.5	5	0.013
Confirming AUF effect							
H_0 : AUF has no effect on variation in survival rates	Model 1: $2a$	8	274.9	939.4			
	Model 2: $2a + t_{\text{OLD}}(\text{AUF})$	9	259.5	926.0	15.4	1	<0.001

Note: The null hypothesis (H_0) is that the alternative model is sufficient to describe the data. The last LRT compares models 1 and 2 combined. DEV and AICc are the deviance and Akaike Information Criterion value of the tested model, respectively. $2a$, 2 age classes (0–1 year old; older); t_{OLD} , time variation limited to survival rates after 1 year of age; s , sex.

*The value in boldface type is the only one that led to a different conclusion from the reference model.

was observed in some marmot species. In the polygynous yellow-bellied marmot (*Marmota flaviventris*), the survival rate for adult females (0.685) was higher than that for adult males (0.580) (Schwartz et al. 1998). In the Vancouver Island marmot (*Marmota vancouverensis*), females lived longer (0.78) than males (0.54), but the relationship with the breeding system is not known; monogamy seemed to be the most common situation, but polygyny was observed each year (Bryant 1996).

The survival pattern according to age differed slightly from the general one described by Caughley in 1966. As predicted, survival rates of the YOY age class were, on average, lower than those for the OLD age class (marmots older than

1 year of age). The juvenile survival rate (0.62) was close to that observed for marmots in Germany (Arnold 1990a) but higher than that observed for those in Italy (Lenti Boero 1994, 1999). We were unable to reveal senescences; there are two possible reasons for this. First, the number of individuals in the oldest age classes was too small to yield precise estimates of survival in these age classes. Second, some animals that were yearlings in 1990 were still alive in 1997. So the study may have been too short to reveal senescence. Our results indicate that survival rates were constant after age 1. Surprisingly, the survival rate of yearlings was not lower than that of adults, although yearlings were far from attaining adult body size and sexual maturity. One possibility is