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Annual and seasonal variation of survival rates in the garden dormouse (*Eliomys quercinus*)

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Abstract

Annual local survival of the garden dormouse *Elyomis quercinus*, a small, hibernating rodent, was studied by Cormack–Jolly–Seber models. The survival rates differed significantly between the 4 years of the study; the average rate was 0.38 (95% confidence interval: 0.25–0.52). Survival rates were not significantly different between sexes. Because all garden dormice were captured after weaning, pre-weaning survival could not be estimated. After weaning, the annual survival rates did not differ between age cohorts. In order to find out which phases within the annual cycle were more prone to mortality, survival was studied on a bimonthly scale as well. Survival during hibernation was estimated to be close to unity, while survival during the active phase of life in summer was considerably lower. The winter temperatures of the study years were similar to the long-year average; thus garden dormice were well adapted to these average conditions. Although hibernation is energetically challenging, it is not necessarily accompanied by increased mortality, as found in other studies focusing on survival during hibernation.

Key words: capture–recapture, *Elyomis quercinus*, garden dormouse, hibernation, survival

INTRODUCTION

Survival and reproduction are both crucial elements in the life history of organisms (Stearns, 1992) and they are the most important components of individual fitness. While the number of offspring can be counted, survival rates cannot be observed directly in the field and therefore are more difficult to study. For many species, mean and variation of survival rates are unknown, or based on unrealistic assumptions.

Mortality, the complement of survival, is an instantaneous process. At any point of time an animal may die. For describing this process, a time period is defined and the proportion of animals dying within that period is used as an estimate of the average mortality over that time period. Choosing different lengths of time periods allows mortality to be studied on different time scales and thus different questions can be addressed. The interest is often in having an average estimate of mortality involving the whole annual cycle. Finer scales relate mortality to different phases of the annual life cycle, for example which phases in an annual life cycle are more prone to mortality.

We studied survival of the garden dormouse *Eliomys quercinus*, a small, omnivorous, hibernating and nocturnal rodent (Gliridae) at different time scales. First we investigated the variation of survival rates within the annual cycle, focusing on the comparison of survival during the active phase in summer compared to survival during hibernation. Secondly, variation of annual survival rates was studied, focusing on differences between age cohorts and sexes.

Hibernating animals often suffer high mortality during this inactive period (e.g. Armitage & Downhower, 1974; Arnold, 1990; Blumstein & Arnold, 1998). Survival during winter is critical, since the energy demands of hibernation may not be predicted exactly by the animals when they enter hibernation. The main reasons for variable energy demands during hibernation are weather factors. If the winter is unusually cold or warm, if its onset is earlier than usual or its end delayed, the animal might die because of a lack of energy stores (Lyman *et al.*, 1982). In order to avoid running short of energy, an animal should accumulate as much energy as possible before hibernation so there is a safety margin of resources for unusual weather situations. However, the accumulation of energy stores before hibernation might be risky as well. Predation risk might be increased because the animals have to move more in search of food, or because heavy animals are probably less able to

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escape predators. An optimal adjustment of energy storage before hibernation which maximizes survival is therefore expected. High winter mortality is especially obvious for animals living in severe climatic conditions and with large variations in winter harshness (e.g. Arnold, 1990; Blumstein & Arnold, 1998). The selective pressures for minimizing winter mortality can be so strong that alpine marmots *Marmota marmota* are forced to hibernate in groups, which is thought to be an important factor for the evolution of the social system in this species (Arnold, 1990).

Physiological aspects of hibernation in garden dormice are well studied (e.g. Ambid, Berlan & Agid, 1971; Daan, 1973; Pajunen, 1974; Vogel, 1997), but to our knowledge, survival rates during hibernation have never been estimated in the field. Garden dormice hibernate in holes either in the ground or in trees (Storch, 1978). The onset and the termination of hibernation are usually slightly shifted between sexes, males enter and finish hibernation earlier than females (Vaterlaus-Schlegel, 1998). Survival might therefore differ between sexes.

Average annual survival rates of garden dormice and possible causes of variation are also unknown, but capture–recapture studies have shown that garden dormice rarely reach the age of 3 years in the wild (Baudoin, 1979), and the highest reported age is about 6 years (Storch, 1978). In many species annual survival has been shown to depend on age and sex. If survival is dependent on age, it typically increases with age close to maturity and decreases slightly thereafter (e.g. Gaillard *et al.*, 1993; Owen-Smith, 1993; Newton, Rothery & Wyllie, 1997). Reasons for a higher juvenile mortality might be a greater predation risk because young animals are often less experienced and less able to escape, or they may be more sensitive to diseases or parasite infections. The decrease in survival probability with age (senescence) might arise from increased tooth wear (Gaillard *et al.*, 1993), from cumulative effects of reproductive activities (Sydeman *et al.*, 1991) or from deleterious mutations that have their effects later in life (Rose, 1991). Survival rates are typically different for the sexes if males have different life cycles than females. For example, survival rates of males not participating in brood rearing, but trying to mate as often as possible, are reduced (Owen-Smith, 1993; Jorgenson *et al.*, 1997), probably because their life is more risky or because they might additionally suffer from intraspecific fights. Male garden dormice do not assist in offspring rearing, but try to mate again, and we would therefore expect that their annual survival rates are lower than those of females.

Survival rates can be studied reliably by analysing capture–recapture data with Cormack–Jolly–Seber models (Lebreton, Burnham *et al.*, 1992; Lebreton, Pradel & Clobert, 1993) and we applied these methods to our investigations. These models provide separate estimates of the survival and the recapture rates and allow similar facilities of modelling as general linear models. For example, it can be tested whether survival rates vary over time or whether different groups of animals have different survival rates.

Table 1. Weather data from the Meteorological Institute Basel-Binningen (Switzerland, situated 10 km south of the study area). Winter was defined as the average of November, December, January and February values. Values of the individual winters are deviations from the long-term means 1961–90 (average temperature, 2.43 °C; average minimum temperature, −7.63 °C; number of days with frost, 58.5)

Winter	Average temperature	Average minimum temperature	Number of days with frost
1993–94	+1.43	+1.15	−12.5
1994–95	+3.13	+3.78	−26.5
1995–96	−0.43	+1.15	+22.5
1996–97	+0.05	−1.18	+ 5.5

MATERIAL AND METHODS

Study area and data collection

The study was conducted in the Petite Camargue Alsacienne (France; 47°37′ N, 7°32′ E, 240 m a.s.l.) situated 7 km north of Basel (Switzerland) between March 1993 and December 1997. This nature reserve is part of a former alluvial forest and is now dominated by oaks *Quercus* sp., alders (*Alnus glutinosa*, *A. incana*), ash *Fraxinus excelsior* and locust tree *Robinia pseudoacacia*. Part of the area is covered by reed *Phragmites australis*; in the centre there are some houses.

Garden dormice were captured with 140 live-traps (LUNA-mouse trap, size 280 × 62 × 75mm Deutsche Fallenfabrik), positioned either on the ground or on low branches of trees that were set in a grid system in the forest, covering an area of about 19.4 ha. The traps were baited with peanut butter, rolled oats and raisins. Trapping was performed during 2 consecutive nights every 2 weeks from March 1993 until November 1993 and from March 1995 until December 1997. All captured garden dormice were sexed, aged, weighed and marked individually by ear tattooing. Recaptures were recorded. All captured animals were released immediately after handling.

Weather data from the meteorological institute of Basel-Binningen (Switzerland, situated 10 km south of the study area) were used for estimating the severity of the winters during the study. Regarding different measurements of temperatures, the first 2 winters (1993–94 and 1994–95) were milder than the long-term average (1961–90; Table 1). Winter 1995–96 was slightly colder and 1996–97 was very similar to the long-term average. Winter 1993–94 started early, with temperatures already low in October and in November, average temperatures being 1.4 °C and 2.5 °C, respectively, lower than the long-term average.

General statistical analysis

The capture–recapture data were analysed using Cormack–Jolly–Seber models (Cormack, 1964; Jolly, 1965; Seber, 1965), which allows separate estimates of the local survival (ϕ) and the recapture (p) probabilities. The local survival probability is the probability that an animal which is in the population at time t is still alive and in the population at time $t+1$, hence true mortality and emigration are confounded. The recapture probability is defined as the probability of trapping an animal which is alive and in the population at time t. The local survival and recapture probabilities may vary over time, can differ by cohort and depend on individual covariates. The estimation of these parameters requires several assumptions which can be tested by goodness-of-fit tests (Burnham *et al.*, 1987). Once a global model has been found to adequately fit the data, it may be simplified, e.g. in an analogous way as backwards elimination of non-significant variables in analyses of variance, until the most parsimonious model has been found (Lebreton, Burnham *et al.*, 1992).

A parametric bootstrap implemented in program mark (White & Burnham, 1999) was used for testing the goodness-of-fit and for estimating the degree of overdispersion. Overdispersion caused by extra-multinomial variation in the data has to be taken into account for model selection (see below) and for calculating the confidence intervals of the parameter estimates (Burnham & Anderson, 1998). For identifying overdispersion we calculated $\hat{c}$, as the quotient of the observed value of $\hat{c}_o$ from the original data and the mean of the simulated values of $\hat{c}_s$ from the bootstraps. In each model (either original or bootstrap), $\hat{c}_o$ or $\hat{c}_s$ is the model deviance divided by the deviance degrees of freedom. If the data are not overdispersed, then $\hat{c}$ is equal to 1. Different models were fitted to the data with program SURGE (Reboulet *et al.*, 1999). SURGE gives for each model a relative deviance, dev = $-2\ \ln(L)$ (where L is the maximum likelihood), as a measure of relative quality of fit. The most parsimonious model was then selected using a modified Akaike's information criterion (QAIC*c*), which accounted for overdispersion and sample size. It is calculated as:

$$\mathrm{QAICc} = \frac{dev}{\hat{c}} + \frac{2K(K+1)}{n-K-1} + 2K \qquad (1)$$

where K is the number of estimated parameters and n is the sample size. QAIC*c* has been found to be a reliable and objective tool for selecting the best model(s) out of the ones fitted (Burnham & Anderson, 1998); better models have lower QAIC*c* values than poorer. The model notations followed Lebreton, Burnham *et al.* (1992), and the significance of all models is summarized in Table 2. The estimation of survival within the year was performed on a bimonthly scale, that of the annual survival on an annual scale. This required 2 different arrangements of the data.

Table 2. Models used to describe either survival or recapture pattern. The table shows the model notations (following Lebreton, Burnham *et al.*, 1992) and its biological significance. *s*, sex; *t*, time; *a2*, 2 age classes; *y*, year. Note that the notation is similar to that of general linear models, thus a model denoted as *a*b* contains the two main effects *a* and *b* and the interaction between *a* and *b*

Model notation	Biological significance
*a2*t*s*	Rate is dependent on age, time and sex
*a2*t+s*	Rate is dependent on age and time with an additive sex effect
*a2*t*	Rate is dependent on age and time
a2+t	Rate is dependent on age with an additive time effect
t	Rate is dependent on time
.	Rate is constant
Summer: *t*y*; winter.	Rate in summer is dependent on time and year, rate in winter is constant
Summer: *t+y*; winter.	Rate in summer is dependent on time with an additive year effect, rate in winter is constant
Summer: *t*; winter.	Rate in summer is dependent on time, rate in winter is constant
Summer: *y*; winter.	Rate in summer is constant but different between years, rate in winter is constant
Summer.; winter.	Rate in summer is constant, rate in winter is constant

Bimonthly survival

Trapping was undertaken every second week from March 1995 until December 1997, and this period was taken for the estimation of the bimonthly survival rates. All captures within 2 months were pooled, resulting in a data set with 17 capture occasions. All animals that were trapped only before March 1995 were excluded. In total, this data set contained 131 males and 85 females. Testing for age dependence on a certain scale requires that the animals can be aged on this scale. Since we could not determine the age of juvenile garden dormice with an accuracy of 2 months, we did not test for age dependence. Instead we focused only on sex-differences and on the variation of survival within the annual cycle. The most complex model had time- and sex-dependent survival and recapture parameters (ϕ_{t*s}, p_{t*s}), and was used for testing the goodness-of-fit. The recapture part of this model was simplified first, and then the survival part. November, December, January and February were defined as winter, because during this time most garden dormice hibernate (Vaterlaus-Schlegel, 1997), and the remaining months were defined as summer.

Annual survival

Because the first young garden dormice were usually captured from July onwards, annual survival was estimated from July–August of 1 year to July–August of the next year to ensure a proper estimate of juvenile survival. Only captures in July and August of each year were considered. All captures in these months of each year (1993–97) were pooled resulting in individual capture histories that contained 5 capture occasions. Although we did not capture garden dormice in 1994, we included this year in the data file. This had the advantage that the captures of 1993 could be used in the analysis and the survival rate from July–August 1993 to July–August 1995 could be estimated (see also below). While modelling, the capture probability of 1994 was then always fixed to 0. Two age classes were defined: young animals born in the same calendar year; adults born in a preceding year. This data set consisted of 187 animals (captured as young, 58 males and 35 females; captured as adults, 47 males and 47 females). We suspected that survival rates might depend on age and sex classes of the animals, that they vary between years and that recapture probabilities also vary between years. We further suspected that the factors interact with each other, thus the most complex model was (ϕ_{a2*t*s}, p_t). This model was used also for testing the goodness-of-fit. Simpler models with fewer parameters were fitted next until the most parsimonious model was found. First, we simplified the model structure of the recapture probability, then the best structure was kept and survival was modelled.

RESULTS

Bimonthly survival

Of the 216 garden dormice marked, we recaptured 53 once, 29 twice, 22 three times, 9 four times, 3 five times, 3 six times, 4 seven times 1 eight times and 1 eleven times. The goodness-of-fit test of the most global model (ϕ_{t*s}, p_{t*s}) was not significant ($P = 0.140$, 1000 runs in the bootstrap) and the data were only slightly over-dispersed ($\hat{c} = 1.205$), and thus fitted the data adequately.

The recapture rates did not differ between sexes but depended on time (model ϕ_{t*s}, p_t had the lowest QAICc of all p-models; Table 3). The best structure for describing the survival rate had only a time effect (ϕ_t, p_t). The model with an additional sex effect (ϕ_{t+s}, p_t) estimated female survival rate to be up to 15% higher than male survival rate, but had a poorer fit.

We divided the time scale into winter and summer in order to better understand the time variation of survival (Table 4). Because survival during winter was estimated to be 1 in the full time-dependent model (ϕ_t, p_t), the next simpler model ($\phi_{\text{summer: } t*y;\ \text{winter.}}$, p_t), where winter survival was constrained to be equal at all time intervals during winter, had the same deviance, but the number of estimated parameters was lower, hence revealed more parsimony. Next, we modelled the summer survival to vary each year in the same way but having an additional year effect ($\phi_{\text{summer: } t+y;\ \text{winter.}}$, p_t). This model fitted the data well. A simpler model, in which summer survival was different due to years only ($\phi_{\text{summer: } y;\ \text{winter.}}$, p_t), had almost the same QAICc as the previous model ($\phi_{\text{summer: } t+y;\ \text{winter.}}$, p_t). Since fewer parameters were used for the simpler model, it is regarded as the more parsimonious one. Models without year effect ($\phi_{\text{summer: } t;\ \text{winter.}}$, p_t and $\phi_{\text{summer: .; winter.}}$, p_t) did not fit well.

Table 3. Model selection of recapture and survival rates from 1995 to 1997 over bimonthly intervals. Dev, relative deviance given by surge; K, number of estimated parameters; (QAICc_i, difference in the quasi-likelihood and small sample size corrected Akaike's information criterions, computed as $\Delta\mathrm{QAIC}c_i = \mathrm{QAIC}c_i - \mathrm{QAIC}c_{\min}$. The most parsimonious model is in bold

Model	Dev	K	ΔQAICc
Modelling recapture rates			
1: ϕ_{t*s}, p_{t*s}	1169.5	62	42.5
2: ϕ_{t*s}, p_{t+s}	1179.3	49	3.1
3: ϕ_{t*s}, p_t	1179.6	48	0.0
4: ϕ_{t*s}, $p.$	1376.3	33	117.4
Modelling survival rates			
3: ϕ_{t*s}, p_t	1179.6	48	39.6
5: ϕ_{t+s}, p_t	1189.6	33	2.0
6: ϕ_t, p_t	**1193.8**	**31**	**0.0**
7: $\phi.$ p_t	1240.4	17	3.0

Table 4. Model selection of survival rates from 1995 to 1997 over bimonthly intervals with respect to differences in summer and winter survival. Dev, relative deviance given by surge; K, number of estimated parameters; ΔQAICc_i, difference in the quasi-likelihood and small sample size corrected Akaike's information criterions, computed as $\Delta\mathrm{QAIC}c_i = \mathrm{QAIC}c_i - \mathrm{QAIC}c_{\min}$. The most parsimonious model is in bold. Note that the model 1 given here is the same as model 6 in Table 3. It could be also denoted as $\phi_{\text{summer: } t*y;\ \text{winter: } t*y}$, p_t

Model	Dev	K	ΔQAICc
1: ϕ_t, p_t	1193.8	31	15.4
2: $\phi_{\text{summer: } t*y;\ \text{winter.}}$, p_t	1193.8	28	7.3
3: $\phi_{\text{summer: } t+y;\ \text{winter.}}$, p_t	1200.7	23	0.1
4: $\phi_{\text{summer: } t;\ \text{winter.}}$, p_t	1215.1	21	7.0
5: $\phi_{\text{summer: } y;\ \text{winter.}}$, p_t	**1209.6**	**20**	**0.0**
6: $\phi_{\text{summer.; winter.}}$, p_t	1227.1	18	9.7

From the two best models ($\phi_{\text{summer: } y;\ \text{winter.}}$, p_t and $\phi_{\text{summer: } t+y;\ \text{winter.}}$, p_t), survival during winter was estimated to be 1 (95% confidence interval: 0.90–1.00) and lower during the summer months. In the most parsimonious model ($\phi_{\text{summer: } y;\ \text{winter.}}$, p_t), the bimonthly survival rate during the summer of 1995 was 0.72 (0.64–0.79), 0.88 (0.80–0.93) in 1996 and 0.96 (0.22–0.99) in 1997. The recapture rates of this model had an annual cycle, being high in the summer and almost zero during winter (Fig. 1). Because animals were trapped only when they move around, recapture can be regarded as a rough indication of the activity pattern of the garden dormice. The activity steadily increased following hibernation; it peaked in July–August and decreased thereafter. The lowest activity was observed from November to February when garden dormice hibernate. Seventeen captures of 13 different animals during these

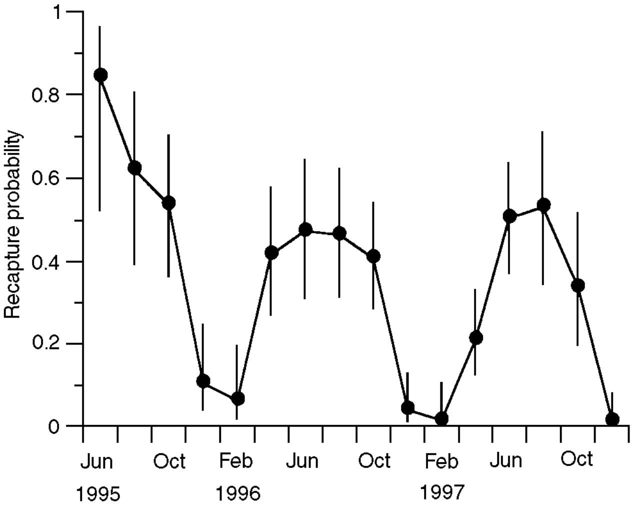

Fig. 1. Mean recapture probabilities and 95% confidence intervals over 2 months of *Eliomys quercinus* in the Petite Camargue Alsacienne, based on the most parsimonious model ($\phi_{\text{summer: } y\text{; winter.}}$, p_t). Note that the recapture probability of the first capture period (March–April 1995) cannot be estimated.

months demonstrate that hibernation was sometimes interrupted.

Annual survival

Of the 187 garden dormice captured in the 5 years under study, 152 were captured in 1 year only, 29 in 2 years and six in 2 years. The most complex model (ϕ_{a2*t*s}, p_t) fitted the data well ($P = 0.526$; from a bootstrap with 1000 runs), and the data were slightly underdispersed ($\hat{c} = 0.948$). We fixed $\hat{c} = 1$ for this analysis to ensure a conservative model selection.

First, we modelled the recapture parameters. The recapture rates did not differ between study years (model ϕ_{a2*t*s}, p_t had a higher QAIC*c* value than model ϕ_{a2*t*s}, $p.$, Table 5). The survival rates were not significantly different between sexes (models ϕ_{a2*t*s}, $p.$ and ϕ_{a2*t+s}, $p.$ had a higher QAIC*c* value than model ϕ_{a2*t}, $p.$, Table 5). Furthermore, survival rates of young and of adult garden dormice were not significantly different from each other (models ϕ_{a2*t}, $p.$ and ϕ_{a2+t}, $p.$ had a higher QAIC*c* value than model ϕ_t, $p.$, Table 5). The annual survival rates differed significantly between the 4 study years (model ϕ_t, $p.$ had a lower QAIC*c* value than model $\phi.$, $p.$, Table 5).

Table 5. Model selection of annual recapture and survival rates from July 1993 to July 1997. Dev, relative deviance given by SURGE; *K*, number of estimated parameters; ΔQAICc_i, difference in the quasi-likelihood and small sample size corrected Akaike's information criterions, computed as ΔQAICc_i = QAICc_i − QAICc_{min}. The most parsimonious model is in bold. Note that the recapture rate of the year 1994 was fixed to zero in all models. Therefore recapture rates of models with a time-independent structure ($p.$) were modelled to be equal in 1995, 1996 and 1997 and zero in 1994

Model	Dev	*K*	ΔQAIC*c*
Modelling recapture rates			
1: ϕ_{a2*t*s}, p_t	161.4	16	6.3
2: ϕ_{a2*t*s}, $p.$	162.5	13	0.0
Modelling survival rates			
3: ϕ_{a2*t*s}, $p.$	162.5	13	12.6
4: ϕ_{a2*t+s}, $p.$	163.4	10	6.6
5: ϕ_{a2*t}, $p.$	164.9	8	3.5
6: ϕ_{a2+t}, $p.$	168.5	6	2.8
7: $\boldsymbol{\phi_t}$, $\boldsymbol{p.}$	**170.1**	**4**	**0.0**
8: $\phi.$, $p.$	179.8	2	5.6

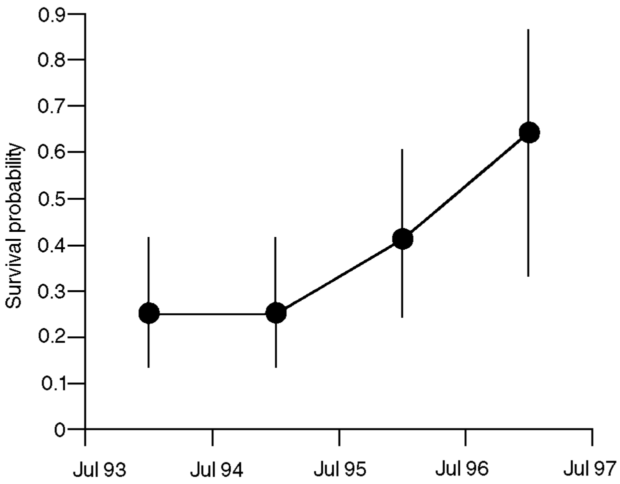

Fig. 2. Annual survival rates and 95% confidence intervals of *Eliomys quercinus* in the Petite Camargue Alsacienne, based on the most parsimonious model (ϕ_t, $p.$). Note that we assumed the survival rates in the first 2 years to be the equal (see text for further discussion).

From the most parsimonious model (ϕ_t, $p.$), the recapture probability was estimated to be 0.67 (95% confidence intervals 0.37–0.88). Because there were no captures in July and August 1994, we can only estimate the survival rates over the first 2 years, which equals 0.06 (95% confidence intervals 0.02–0.18). This value is the product of the annual survival rates of each year. Therefore the minimal possible annual survival rate in 1 year was 0.06 provided that the rate in the other year was 1. However, it is more likely that the rates were somewhere in between these limits. Assuming the rates are equal in both years, gives an annual survival rate of 0.25 (see Fig. 2). Given this assumption, the annual survival rates of the following 2 years were higher (Fig. 2). The average annual survival rate was 0.38 (95% confidence interval: 0.25–0.52). This estimate is not affected by the non-monitoring of the population in 1994.

DISCUSSION

For the interpretation of the results, two important points have to be kept in mind. First, the type of

Cormack–Jolly–Seber model selected cannot separate between mortality and emigration, so it can only estimate the local survival rates; the true survival rates are higher. One juvenile and six adult garden dormice were followed by radio-transmitters during 1–3.5 months and none of them left the study area permanently (Vaterlaus-Schlegel, 1998). Despite the low sample size and the rather short period of the individual tracking, either dispersal is not very strong in this population or the area covered by traps was large enough to have access to most of the dispersed animals, so that the local survival rates were likely to be close to true survival. Secondly, the survival rates are estimated for the time following the marking of the animals. Hence, the estimated survival rates in our study refer to the time after the young garden dormice have left the nest, which is at the age of about 40 days.

The estimated average annual survival rates show that the garden dormouse is a short-lived species. Its survival rate is slightly lower than that of brown hares *Lepus europaeus* (Marboutin & Hansen, 1998), but is higher than that of small mice (e.g. *Zapus* sp.; Nichols & Conley, 1982; *Peromys* sp., Millar & Innes, 1983; *Microtus* sp., Paradis, Guedon & Pradel, 1993; Lambin & Yoccoz, 1998). Surprisingly, annual adult survival rates of closely related species were much higher than that of garden dormice in this study: fat dormouse *Glis glis* have an annual survival rate of > 0.8 (A. Pilastro & G. Tavecchia, pers. comm.), in hazel dormice *Muscardinus avellanarius* it was found to vary between 0.56 and 0.74 (Berg & Berg, 1999). The between-years variation in the survival rates of garden dormice was considerable (Fig. 2) and perhaps included a year (1993 or 1994) with an unusually low survival rate. The winters of these 2 years were milder than average winters, and one had an early onset. This might have lowered the survival probability during one or both winters resulting in a lower annual survival rate. In this study the winter survival rates could not be studied for these winters and we could not check this presumption. The average annual survival rate of 1996 and 1997 was higher and approached closer to that of the hazel dormouse (Berg & Berg, 1999). Only long-term studies would help to understand the between-year variation of garden dormice survival rates and to estimate average annual survival with more confidence. Based on the average annual survival rates (0.38), the expected life span (Seber, 1982) of garden dormice was 1.03 years (95% confidence intervals 0.72–1.55). In the Petite Camargue Alsacienne garden dormouse females have one to two litters per year; hence a female surviving to independence can expect to reproduce at least once.

On both scales, local survival rates were not different between sexes, which is not in accordance with our expectation of a lower survival rate in males. Although garden dormice sexes differ in their life cycle (males do not assist in offspring rearing, but try to mate gain) their survival rates were similar. It can furthermore be concluded that emigration out of the study area, if occurring, was similar between the sexes. However, when the estimates of the survival rates from the models with sex-dependent rates were considered, the survival rates of males were always considerably lower than that of females, but the confidence intervals were widely overlapping. Further studies on survival rates and dispersal including more animals or lasting longer would be necessary to answer with more certainty whether there are sex differences in survival and/or dispersal and how large these effects are.

No significant indication of age-dependent survival in the garden dormouse was found. This untypical finding might result from a too small a sample size. The juvenile survival rates estimated with model $\phi_{a2+t}, p.$ were lower than those of adults, but the estimates were not precise enough to treat them as significantly different. A larger sample might have increased precision of the estimates and might have rendered the difference significant. Another possible explanation for the apparent lack of age-dependence in the survival rates is that differences in survival due to age might have lasted too short a time for detection with our study design. Because the first young animals were marked and monitored after they had left the nest at the age of about 40 days, mortality in early life before marking can only be estimated by an extrapolation. If we assume that the population size remains constant, that immigration and emigration are equal, that the mean litter size is six (Storch, 1978; Vaterlaus-Schlegel, 1998), that half of the females make a second mating with equal litter size (Vaterlaus-Schlegel, 1998) and that the sex ratio at birth is even, we can estimate roughly the survival during the first 40 days. The average annual survival rate of females was about 0.4, hence every female should produce 1.5 female offspring each year that survive until maturity to maintain the population. Most garden dormice reproduce for the first time at the age of 1 year, only few reproduced in the year of birth (Vaterlaus-Schlegel, 1998). Each female bears 4.5 females on average, of which 1.8 will still be alive after 1 year if all survive the first 40 days. Only 1.5 females would be necessary for maintaining the population, hence survival during the first 40 days for females should be 0.83. Calculated on an annual basis this gives a survival rate of about 0.19. This value would be higher if the population increased or if the mean litter size was smaller. Nevertheless, it is likely that survival in the first days after birth is lower than later on. Once an animal has survived to an age of about 40 days, its survival rate was not different from that of adult garden dormice. This pattern of higher juvenile mortality in the first days of life and constant, age-independent mortality thereafter was confirmed in other small mammals as well (e.g. mountain deer mouse *Peromyscus maniculatus*, Millar & Innes, 1983; *Microtus duodecimcostatus*, Paradis *et al.*, 1993; common shrew *Sorex araneus*, Churchfield, Hollier & Brown, 1995; Townsend's vole *Microtus townsendii*, Lambin & Yoccoz, 1998) and might be common for small short-living mammals.

To our knowledge, all studies which focused on the comparison of survival during the active phase and hibernation found that it was lower during hibernation (Armitage & Downhower, 1974; Arnold, 1990; Blumstein & Arnold, 1998; Juškaitis, 1999). In the garden dormouse we found the contrary, mortality was almost absent during hibernation but more common during the active phase. In fact, survival during hibernation was estimated to be 1, which is unlikely to be exactly true. When survival rates are close to boundary values (0 or 1) and recapture rates low, it is sometimes not possible to estimate survival rates accurately with Cormack–Jolly–Seber models. Nevertheless, the survival rates during hibernation were close to 1. Dormice prepare for hibernation by accumulating adipose tissue, which is burned thereafter (Lyman *et al.*, 1982; Vogel, 1997). Garden dormice show a steady body mass increase during summer, and during hibernation in central Europe their body mass decreases by *c.* 40% (Lachiver & Boulouard, 1965; Vaterlaus-Schlegel, 1998). Hibernation is critical: (1) if the animals are unable to accumulate enough fat before it starts (Lenihan & Van Vuren, 1996); (2) if minimum temperatures during hibernation are very low; (3) if the average temperatures during hibernation are too high (then more fat is used because metabolism is not reduced sufficiently); (4) if winter is unusually long (Armitage & Downhower, 1974; Van Horne *et al.*, 1997). None of these conditions seems to have been unfavourable during the two winters we followed the animals. Winter temperatures in 1995–96 and 1996–97 were typical for the region, 1995–96 was a bit colder than the long-term average. Garden dormice are well adapted to these conditions. However, survival might be reduced under more severe conditions than during our study.

Mortality mainly occurred during the active phases of life. We have no observations on the reasons of death. However, since mortality is highest when the animals are active, predation may be a serious cause. The garden dormouse is nocturnal and lives on the ground and in low bushes (Vaterlaus-Schlegel, 1997) and is most active during the summer (Fig. 1). Possible predators in the study area are tawny owl *Strix aluco* (see Missbach, 1956), long-eared owl *Asio otus*, beech marten *Martes foina*, stoat *Mustela erminea*, red fox *Vulpes vulpes* and domestic cats. Other small but non-hibernating mammals also survived better during winter than in summer (*Peromyscus maniculatus*, Millar & Innes, 1983; *Sorex araneus*, Churchfield *et al.*, 1995), as predation risk in summer is likely to be higher, because the predators themselves rear young at that time and therefore need more food.

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REFERENCES

Ambid, L., Berlan, M. & Agid, R. (1971). Contribution de la graisse brune à la mobilisation des lipides au cours des réveils périodiques chez un hibernant, le lérot (*Eliomys quercinus* L.). *J. Physiol. Paris* **63**: 505–522.

Armitage, K. B. & Downhower, J. F. (1974). Demography of yellow-bellied marmot populations. *Ecology* **55**: 1233–1245.

Arnold, W. (1990). The evolution of marmot sociality II. Costs and benefits of joint hibernation. *Behav. Ecol. Sociobiol.* **27**: 239–246.

Baudoin, C. (1979). Behavioural mechanisms of population regulation in a hibernating mammal *Eliomys quercinus* L. (Rodentia Gliridae). *Proc. XVI International Ethology Conference*. Vancouver: University of British Columbia.

Berg, L. & Berg, A. (1999). Abundance and survival of the hazel dormouse *Muscardinus avellanarius* in a temporary shrub habitat: a trapping study. *Ann. Zool. Fenn.* **36**: 159–165.

Blumstein, D. T. & Arnold, W. (1998). Ecology and social behavior of golden marmot (*Marmota caudata aurea*). *J. Mammal.* **79**: 873–886.

Burnham, K. P. & Anderson, D. R. (1998). *Model selection and inference: a practical information–theoretic approach*. New York: Springer-Verlag.

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H. (1987). Design and analysis methods for fish survival experiments based on release–recapture. *Am. Fish. Soc. Monogr.* **5**: 1–437.

Churchfield, S., Hollier, J. & Brown, V. K. (1995). Population dynamics and survivorship patterns in the common shrew *Sorex araneus* in southern England. *Acta Theriol.* **40**: 53–68.

Cormack, R. M. (1964). Estimates of survival from sighting of marked animals. *Biometrika* **51**: 429–438.

Daan, S. (1973). Periodicity of heterothermy in the garden dormouse, *Eliomys quercinus* (L.). *Neth. J. Zool.* **23**: 237–265.

Gaillard, J.-M., Delorme, D., Boutin, J.-M., Laere, G. V., Boisaubert, B. & Pradel, R. (1993). Roe deer survival patterns: a comparative analysis of contrasting populations. *J. Anim. Ecol.* **62**: 778–791.

Jolly, G. M. (1965). Explicit estimates from capture–recapture data with both death and immigration – stochastic model. *Biometrika* **52**: 255–247.

Jorgenson, J. T., Festa-Bianchet, M., Gaillard J.-M. & Wishart, W. D. (1997). Effects of age, sex, disease, and density on survival of bighorn sheep. *Ecology* **78**: 1019–1032.

Juškaitis, R. (1999). Winter mortality of the common dormouse (*Muscardinus avellanarius*) in Lithuania. *Folia Zool.* **48**: 11–16.

Lachiver, F. & Boulouard, R. (1965). Evolution du poids corporel chez un hibernant lérot (*Eliomys quercinus*) dans la période hivernale et au cours de l'exposition au froid en été. *Mammalia* **29**: 343–366.

Lambin, X. & Yoccoz, N. G. (1998). The impact of population kin–structure on nestling survival in Townsend's voles, *Microtus townsendii*. *J. Anim. Ecol.* **67**: 1–16.

Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. (1992). Modelling survival and testing biological hypothesis using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**: 67–118.

Lebreton, J.-D., Pradel, R. & Clobert, J. (1993). The statistical analysis of survival in animal populations. *Trends Ecol. Evol.* **8**: 91–95.

Lenihan, C. & Van Vuren, D. (1996). Growth and survival of juvenile yellow-bellied marmots. *Can. J. Zool.* **74**: 297–302.

Lyman, C. P., Willis, J. S., Malan A. & Wang, L. C. H. (1982). *Hibernation and torpor in mammals and birds*. London: Academic Press.

Marboutin, E. & Hansen, K. (1998). Survival rates in a nonharvested brown hare population. *J. Wildl. Manage.* **62**: 772–779.

Millar, J. S. & Innes, D. G. L. (1983). Demographic and life cycle characteristics of montane deer mice. *Can. J. Zool.* **61**: 574–585.

Missbach, D. (1956). Sperber und Gartenschläfer als Waldkauzbeute. *Der Falke* **3**:70.

Newton, I., Rothery, P. & Wyllie, I. (1997). Age–related survival in female Sparrowhawks *Accipiter nisus*. *Ibis* **139**: 25–30.

Nichols, J. D. & Conley, W. (1982). Active-season dynamics of a population of *Zapus hudsonius* in Michigan. *J. Mammal.* **63**: 422–430.

Owen–Smith, N. (1993). Comparative mortality rates of male and female kudus: the costs of sexual size dimorphism. *J. Anim. Ecol*. **62**: 428–440.

Pajunen, I. (1974). Body temperature, heart rate, breathing pattern, weight loss and periodicity of hibernation in the French garden dormouse, *Eliomys quercinus* L. at 4.2 ± 0.5 °C. *Ann. Zool. Fenn.* **11**: 107–119.

Paradis, E., Guedon, G. & Pradel, R. (1993). Estimation of sex- and age-related survival rates in a microtine population. *J. Wildl. Manage.* **57**: 158–163.

Reboulet, A.-M., Viallefont, A., Pradel, R. & Lebreton, J.-D. (1999). Selection of survival and recruitment models with surge 5.0. *Bird Study (Suppl.)* **46**: 148–156.

Rose, M. R. (1991). *Evolutionary biology of ageing*. New York: Oxford University Press.

Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika* **52**: 249–259.

Seber, G. A. F. (1982). *The estimation of animal abundance and related parameters*. 2nd edn. New York: Macmillan.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.

Storch, G. (1978). Eliomys quercinus – Gartenschläfer. In *Handbuch der Säugetiere Europas*: 208–225. Niethammer, J. & Krapp, F. (Eds). Wiesbaden: Akademische Verlagsgesellschaft.

Sydeman, W. J., Huber, H. R., Emslie, S. D., Ribic, C. A. & Nur, N. (1991). Age-specific weaning success of northern elephant seals in relation to previous breeding experience. *Ecology* **72**: 2204–2217.

Van Horne, B., Olson, G. S., Schooley, R. L., Corn, J. G. & Burnham, K. P. (1997). Effects of drought and prolonged winter on Townsend's ground squirrel demography in shrubsteppe habitats. *Ecol. Monogr.* **67**: 295–315.

Vaterlaus-Schlegel, C. (1997). The garden dormouse (*Eliomys quercinus* L.) in the Petite Camargue Alsacienne (Nature Reserve, France). An ecological study by trapping and radio tracking. *Natura Croatica* **6**: 233–241.

Vaterlaus-Schlegel, C. (1998). *Der Gartenschläfer (**Eliomys quercinus** L.). Ökologie, Populationsstruktur, Populationsdynamik und die Verbreitung in der Schweiz*. PhD thesis, Universität Basel.

Vogel, P. (1997). Hibernation of recently captured *Muscardinus*, *Eliomys* and *Myoxus*: a comparative study. *Natura Croatica* **6**: 217–231.

White, G. C. & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study (Suppl.)* **46**: 120–139.