# LONG LIVING AND REPRODUCTION SKIPPING IN THE FAT DORMOUSE

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*Abstract.* We studied the reproductive strategy of a population of fat dormice (*Myoxus glis*) breeding in nest boxes in a beech forest on the southern Alps, Italy. In eight years of data collection (1991–1998), we observed births only in 1991, 1992, and 1995. We did not observe young during the autumn dispersal in the remaining five years. Reproduction was not correlated with high rainfall, low temperature in summer, or with population density. Reproduction was only observed in years of beech mast seeding. Body condition of adults when they emerged from hibernation did not differ between years with and without reproduction, suggesting that the adults may avoid breeding when the young have a low probability of surviving their first winter. A capture–recapture analysis on individually marked adult fat dormice identified a very high yearly survival rate (0.86–0.92), close to that of large herbivorous mammals and much higher than that typical of other rodent species with similar body size. No influence of sex on survival or recapture probability was detected. The long life span expectancy of an adult dormouse (averaging nine years) is the prerequisite for the infrequent breeding strategy adopted by this rodent species to cope with an unpredictable food source. A high survival rate despite the small body size may have been possible because of the long hibernation time (>6 months). Long life span and intermittent breeding make the life history of fat dormice unique among rodents.

*Key words: beech mast seeding; capture–recapture models; fat dormouse; hibernation; intermittent breeding; Italian southern Alps; life-history trade-off; Myoxus glis; reproductive strategy; rodent; survival; unpredictable food source.*

## INTRODUCTION

A commonly accepted trade-off in animal life histories is the one between the cost of current reproduction (i.e., investment in offspring) and a parent's future survival and reproductive opportunities (Williams 1966). In long-living species, even a small change in adult survival rate can greatly affect the number of future breeding attempts and the lifetime reproductive success (Stearns 1992). In stochastic environments, the conditions in which parents give birth and rear their offspring are variable and unpredictable. As a consequence, costs of reproduction may vary greatly among years. In years when environmental conditions make it difficult to produce offspring, it might be expected that some breeders would safeguard their own survival probability by ceasing to breed at any stage. Indeed, reproductive failure in female ungulates has been associated with high population density and difficulty in regaining body mass after lactation (Clutton-Brock and Albon 1989, Sæther 1997, Coulson et al. 2001). A trade-off between a parent's survival and its future reproductive success may not be the only reason for reproductive failure: food shortage before birth or during lactation can permanently impair the growth and future breeding success of offspring (Clutton-Brock et al.

1983, Green and Rothstein 1993). In short-lived species, such as most small mammals and rodents, most individuals are only able to breed in one or two consecutive years. In such cases, the effect of skipping reproduction on the survival of a parent must be very strong to compensate for the loss of a reproductive opportunity, which may be the only one available during its lifetime. Consequently, in these species the strategy adopted to cope with a variable environment is to adjust litter size to suit environmental conditions, rather than to skip a breeding opportunity (Gandelman and Simon 1977, Fuchs 1982, Elwood 1992, Wolff 1992). Perhaps not surprisingly, skipping of reproduction has been reported rarely for small mammals.

One exception is represented by the fat dormouse (*Myoxus glis*), a rat-sized nocturnal, arboreal rodent with a prolonged hibernation period (up to seven months), which is frequent in mixed forests of central and southern Europe (Niethammer and Krapp 1978). Several authors have reported that entire populations of fat dormouse exceptionally fail to breed in particular years (Niethammer and Krapp 1978, Marin and Pilastro 1994, Bieber 1998). This behavior has been hypothesized to occur in summers characterized by low temperatures and high rainfall (Niethammer and Krapp 1978) or low beech (*Fagus sylvatica*) seed production (Pilastro et al. 1996, Bieber 1998).

Here we present the results of a long-term study of a fat dormouse population breeding in nest boxes in the southern Alps, Italy. We show that (1) individuals

bred only when beech mast occurred, i.e., in three out of eight years; (2) body condition of adult females did not differ between years with and without reproduction; and (3) yearly survival rate in our population was exceptionally high compared to that observed in other rodent species of similar body size. Prolonged life span, low fecundity, and intermittent breeding strategy make the fat dormouse's life history unique among rodents and allow this rodent species to rely on an unpredictable food source for reproduction.

## MATERIALS AND METHODS

### Study area and data collection

The study area was located in the southern Alps, at ~1000 m a.s.l., in the national forest Riserva Naturale del Pian Cansiglio (Treviso, Italy). We set up 100 wooden nest boxes in ~60 ha of a large mixed forest with beech as the dominant species (~80% of coverage), the rest being mostly spruce (*Picea excelsa*) and fir (*Abies alba*). The nest boxes were checked for the presence of dormice twice a month, on average, from late May through November, 1991–1998. During the breeding season (mid-July to mid-September), boxes were checked more often. All of the adults found in the nest boxes were weighed to the nearest 1 g, aged into two age classes (first year and older), sexed, and individually marked using toe clipping (1991–1992) or ear tagging (1992–1998). Pups found in the nest were aged according to von Vietinghoff-Riesch (1960), with the date of birth being determined on the basis of the degree of toe separation, the presence of visible teeth, and whether ears and eyes were open or still closed (for more details on the methods, see also Marin and Pilastro [1994], Pilastro et al. [1994, 1996]). Within one week after parturition, the mother was weighed to the nearest 1 g and litter size (number of pups in the nest) was determined. At the age of ~25 days, pups were sexed, weighed to the nearest 1 g, and individually marked using ear tags.

### Environmental and demographic correlates of reproduction

In order to determine whether the occurrence of synchronous skipping of reproduction was associated with environmental condition, four factors were selected that have been reported to influence the reproductive strategy of dormice or, more generally, small rodents. These included summer temperature (average of daily temperature of June, July, and August), total monthly rainfall (from July to August), population density, and beech seed production (Niethammer and Krapp 1978, Wolff 1997, Bieber 1998). Weather variables were taken from a station of the Meteorological Service of the Regione Veneto (Teolo, Italy), located 1 km from the study site. As a measure of population density, we considered the number of adult dormice observed in the nest boxes during each year, from June through September. Beech seed is the main food item of the fat dormouse in forests similar to that of our study (Niethammer and Krapp 1978, Spitzenberger 1983). Seed production is extremely variable in beech, and years with very high seed production (seed mast) are normally followed by at least one year with virtually no seeds (Jenni 1987; this study). The resulting yearly variation of seed production is among the highest observed in mast-seeding trees (Silvertown 1980). On average, seed production occurs every three years, but without any obvious temporal regularity (Jenni 1987, Hilton and Packham 1997). For example, records collected in southern Sweden, Denmark, and Germany evidenced abundant fructification in 26 out of 83 years (Jenni 1987). An estimate of the quantity of beech seed available for the study population during the eight years of this research was obtained by averaging the quantity of beech seed gathered yearly by forest workers for forest plantations in 14 localities within 10 km of our study area. The data (kilograms of seed collected) were provided by the Stabilimento di produzione sementi forestali di Peri (VR, Italy). The association between the number of breeding females and the environmental variables was tested using Spearman rank correlation.

The body condition of adults may vary among years and could also influence reproductive strategy. Body mass of adult dormice in years with and without reproduction (hereafter, RY and NRY, respectively) was compared using body mass variation of individuals that were weighed in both situations. In particular, body mass of adults found in RYs and NRYs (dependent variable) were compared using repeated-measures ANOVA, where the month of observation was the factor (Norušis 1993). Analyses were performed using SPSS 9.0 (SPSS 1998). Where not otherwise stated, mean ± 1 SD is given.

### Survival estimate

Local survival of dormice from spring to spring was estimated using the maximum likelihood procedure from capture–recapture histories of adults (only those >1 year old were selected) with software MARK 1.9 (White and Burnham 1999). Only captures made between May, when animals emerge from hibernation, and July, when births first occur, were selected. In order to reduce heterogeneity among individuals, data collected in August when breeding females actively exclude nonbreeding females and males from the nest were not used in the analyses (Pilastro 1992, Pilastro et al. 1996). Model selection procedure started by assessing the goodness of fit of the general model [$\phi_{t*s}$; $p_{t*s}$], which assumed both recapture and survival probabilities dependent on time (denoted $t$) and sex ($s$). The presence of the interaction between the effects is noted by "*" whereas a "+" denotes an additive relationship. We started model selection by assigning the fit of this general model using program U-CARE (Choquet et al. 2002). The general goodness-of-fit $\chi^2$ test can be

divided into two components named TEST2 and TEST3 for further investigations (Burnham et al. 1987, Pollock et al. 1990). TEST2 determines whether parameters are the same for release at different occasions $i, i + 1, i + 2 \ldots$ and is a general test to compare the future of animals belonging to different cohorts. TEST3 compares the proportion of later recaptures between new and previously marked individuals, i.e., the future of animals of different subcohorts inside a cohort (see also Lebreton et al. 1992). A significant test might result from structural problems (important effects have not been considered) or from the incorrect assumption that animals behave independently (overdispersion; Nichols and Conley 1982, Pollock et al. 1990, Lebreton et al. 1992, Pradel 1993). Program U-CARE provides directional $Z$ tests built on the result of TEST2 and TEST3 contingency tables to help distinguish between these two hypotheses and further investigate the presence of heterogeneity among individuals (Choquet et al. 2002). In particular, the significance of $Z$ test 2 would indicate a trap-dependence effect, i.e., animals are more or less likely to be recaptured after $i$ if they have experienced capture at $i$ (see also Pradel 1993). On the other hand, a significant $Z$ test 3 might suggest the presence of transients, i.e., an excess of animals never seen again (see also PrevotJulliard et al. 1998). If none of these two tests is significant, we assume that lack of fit was due to a general overdispersion of data. In this case, a variance inflation factor, $c$, equal to the ratio of the $\chi^2$ value to its degrees of freedom, must be computed to correct model deviance (Lebreton et al. 1992).

Model selection procedure followed the parsimony principle using the $QAIC_c$ criterion, based on model deviance, the number of parameters in the model, and effective sample size (Burnham and Anderson 1998). The significance of specific effects could be tested using a log-likelihood ratio test (LRT) between nested models only. When extramultinomial variance is significant, a $F$ distribution test should be used instead (Lebreton et al. 1992). Models with a similar value of $QAIC_c$ (within the arbitrary threshold of four points) can be considered as equivalent. A way to account for such incertitude would be to consider the relative importance of each model when estimating parameter values and standard errors (model averaging based on model $QAIC_c$ weight; for more details see Burnham and Anderson [1998], Anderson and Burnham [1999]). However when parameters are close to the boundary limits of 0 or 1, the use of model averaging is no longer recommended because the standard error for boundary estimates may be skewed in such models. Alternatively we selected the model with the highest $QAIC_c$ weight. When survival estimates were 0 or 1, upper and lower confidence interval limits, respectively, were investigated using the profile likelihood method (i.e., successively fixing the parameter at different values until deviance changed significantly).

## RESULTS

In the study population, reproduction was observed only in 1991, 1992, and 1995, when 52, 90, and 42 females, respectively, were found with pups at the nest. In the other five years, no pregnant females, no females with young, and no young of the year during autumn dispersal were observed. In 1994 and 1998, however, females began to collect leaves in the nests, but no subsequent litters were observed. Breeding females represented 91.2% ($n = 57$), 54.2% ($n = 166$), and 19.8% ($n = 212$) of adult females observed during 1991, 1992, and 1995, respectively. For the 119 (1991, $n = 29$; 1992, $n = 54$; 1995 $n = 36$) breeding attempts whose fate was known (i.e., females did not leave the nest box with their pups before weaning), mean litter size was $5.34 \pm 1.84$ pups. Mean body mass of breeding females was $140.2 \pm 17.0$ g (range 102–195 g, $n = 119$). Mean litter size and mean body mass of the mothers did not differ among years (litter size, $F_{2, 116} = 2.10$, $P = 0.13$; maternal body mass, $F_{2, 107} = 1.20$, $P = 0.31$; Fig. 1a, b). Mean body mass of pups at 25 days was $31.3 \pm 6.40$ g ($n = 119$) and differed significantly among years ($F_{2, 116} = 3.95$, $P = 0.022$), being significantly larger in 1992 than in 1991 (Scheffé post hoc comparison, $P < 0.05$; Fig. 1c). Births were concentrated in August (mean date $225.3 \pm 7.75$, range 30 July–11 September, with 1 January being day 1). The mean date of parturition was significantly earlier in 1991 than in 1992 and 1995 ($F_{2, 116} = 28.35$, $P < 0.00001$; Scheffé post hoc comparison, $P < 0.05$; Fig. 1d). Summarizing these results, females reproduced earlier in 1991 and produced heavier pups in 1992.

### Condition of adults in breeding and nonbreeding years

On average, males weighed significantly more during NRY than during RY (repeated-measures ANOVA, $F_{1, 148} = 10.5$, $P = 0.001$) and differed significantly between months ($F_{2, 148} = 10.9$, $P < 0.0001$). In particular, the difference between NRY and RY was limited to July and August (interaction, $F_{2, 148} = 8.42$, $P < 0.0001$), whereas the body mass of males in June did not differ between RY and NRY (Dunnett's C post hoc test, $P > 0.05$; Fig. 2). Body mass of females was also higher in NRY than RY, but the difference was nonsignificant ($F_{1, 129} = 3.22$, $P = 0.075$; month, $F_{2, 129} = 0.12$, $P = 0.89$; interaction, $F_{2, 129} = 1.59$, $P = 0.21$). Despite the fact that males were lighter in RY, their body mass in June (i.e., at the emergence from hibernation) was higher in years following reproduction than in years after NRY ($-16.6 \pm 8.32\%$, mean $\pm$ 1 SD of the body mass after RY; $t_9 = 5.21$, $P = 0.001$, paired $t$ test). A similar analysis for females was possible only when adding data from the first half of July, because only two observations were available for June. Results showed that females are not significantly heavier after a RY ($150.1 \pm 36.4$ g) than after a NRY ($142.6 \pm 12.3$
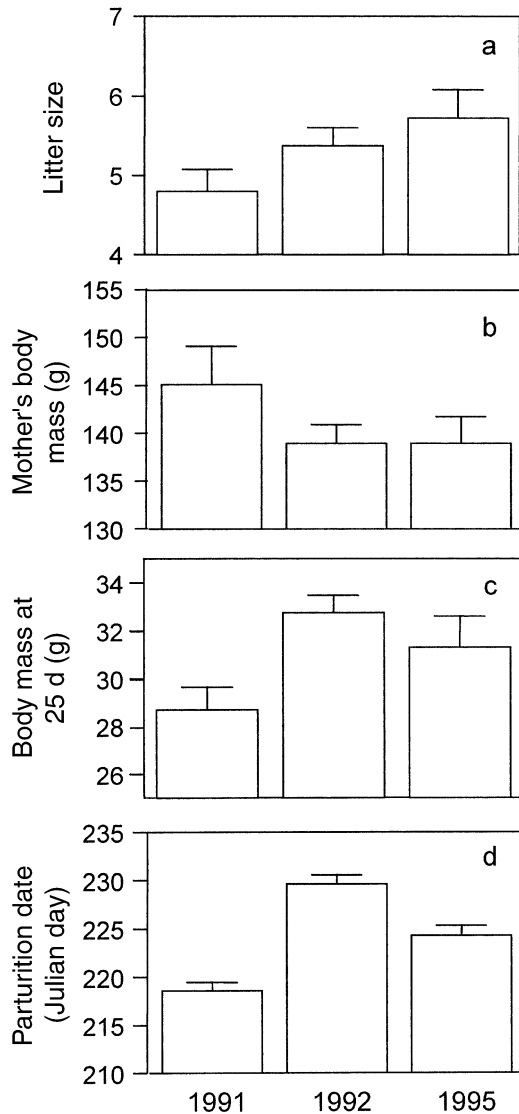
FIG. 1. Fat doormouse litter size, mother body mass within one week after parturition, body mass of pups at 25 d, and parturition date (Julian day; 1 January = 1) in the three years in which the population bred over the total study period (1991–1998). Values are mean + 1 SE.

g; paired $t_{19} = 0.96$, $P = 0.35$). When the same period is considered for males, these remained on average in better condition after a RY than after a NRY (paired $t_{28} = 2.21$, $P = 0.035$).

### Environmental conditions in breeding and nonbreeding years

Four factors were considered as likely to have an influence on reproductive decisions in our population: temperature, rainfall, population density, and seed production of the beech (Fig. 3). None of these variables was correlated with the proportion of females that reproduced in each year (all $P > 0.25$), with the exception of the production of beech seeds ($r = 0.87$, $n = 8$, $P =$

0.005, Spearman rank correlation). This correlation remains significant after correcting for multiple comparisons using Bonferroni's method ($\alpha = 0.0125$; Sokal and Rohlf 1995). The probability that reproductive failure and lack of beech seed production were associated by chance is 0.018 (Fisher's exact test).

### Survival estimate

Survival estimates were based on 807 capture histories of adult ($>1$ yr old) dormice, 398 of which were females (Table 1). The overall goodness-of-fit test of the general model [$\phi_{t*s}$; $p_{t*s}$] was significant ($\chi^2_{40} = 67.26$, $P = 0.005$). Results from additional specific tests (TEST2 and TEST3; see *Methods*) suggested that this lack of fit was due to a general overdispersion of the data rather than to structural problems. A scale parameter of 1.6815 was used to correct for the extra-multinomial variance. Model selection started by eliminating the interaction term between sex and time effect in recapture probability (Table 2). The difference between males and females on recapture was not significant ($F_{1,40} = 1.678$, $P > 0.10$), but the model assuming constant recapture probability was strongly rejected (for [$\phi_{t*s}$; $p_t$ vs. $\phi_{t*s}$; $p.$], $F_{5,40} = 84.91$, $P < 0.001$). As for recapture, sex effect was not significant on survival ($F_{1,40} = 2.092$, $P > 0.10$), but the time effect was retained ($F_{5,40} = 13.084$, $P < 0.001$). Although model [$\phi_t$; $p_t$] was retained as being the more parsimonious one, several models had a similar (within the arbitrary threshold of four points) QAIC$_c$ value (Table 3). Despite this, the model-averaging technique was not used because some parameters were estimated at the 1.00 boundary (Fig. 4), with a 0.00 standard error. Consequently, we estimated the 95% confidence interval using the profile likelihood method (see *Methods*) of estimates from the model [$\phi_t$; $p_t$] with the lowest QAIC$_c$ value that had the highest relative importance (50% of the total QAIC$_c$ weight). The mean value of survival (calculated as the geometric mean of the time-specific values) was 0.86. Note that because of the presence of boundary values and the impossibility of including model selection incertitude in survival estimates, model [$\phi.$; $p_t$] should also be considered. This model suggested a constant value of 0.918 (Fig. 4b). Thus the average survival probability of adult dormice should range between 0.86 and 0.92. Using these estimates, mean adult life expectancy is ~9 yr (range 6–12 yr). These values are surprisingly high, but in agreement with the age structure of marked animals observed in the data set (see also Table 1). Indeed, out of 36 individuals released as adults in 1991, five were recaptured in the last year of the study at a minimum age of 9 yr. These numbers allow the calculation of an underestimate of yearly survival (because recapture probability is not considered) of 0.76 (as $0.76^7 \cong 5/36$).

### DISCUSSION

The temporal reproductive pattern in this population of fat dormice is unusual for a small mammal. We are
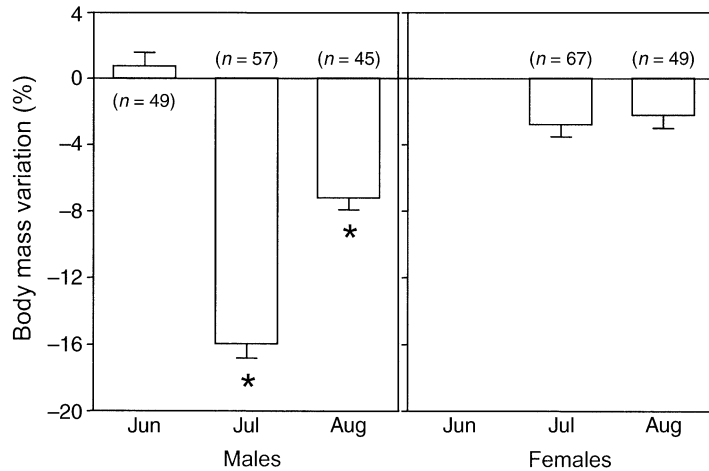
FIG. 2. Body mass variation between non-reproductive years (NRY) and reproductive years (RY) in adult male and female fat dormice. Body mass variation is expressed as (RY body mass − NRY body mass)/(RY body mass) × 100. Only two individual females were observed in June of both RY and NRY, and these were omitted from the analysis. Asterisks (*) indicate significance at $P < 0.05$.

confident that reproductive failure occurred not only in our study area, but also in neighboring populations, because in autumns following reproductive failure, no young of the year were observed. In contrast, in years when reproduction took place, many unmarked young dormice immigrated from the surrounding woods during the autumn (Pilastro et al. 1994; A. Pilastro, *unpublished observations*). General reproductive failure previously had been reported to occur occasionally in the fat dormouse, during cold and rainy summers (Löhrl 1955, von Vietinghoff-Riesch 1960). More recently, on the basis of a two-year study, Bieber (1998) suggested that general reproductive failure could instead be associated with years of poor beech seed production. Results from the present eight-year study confirmed that
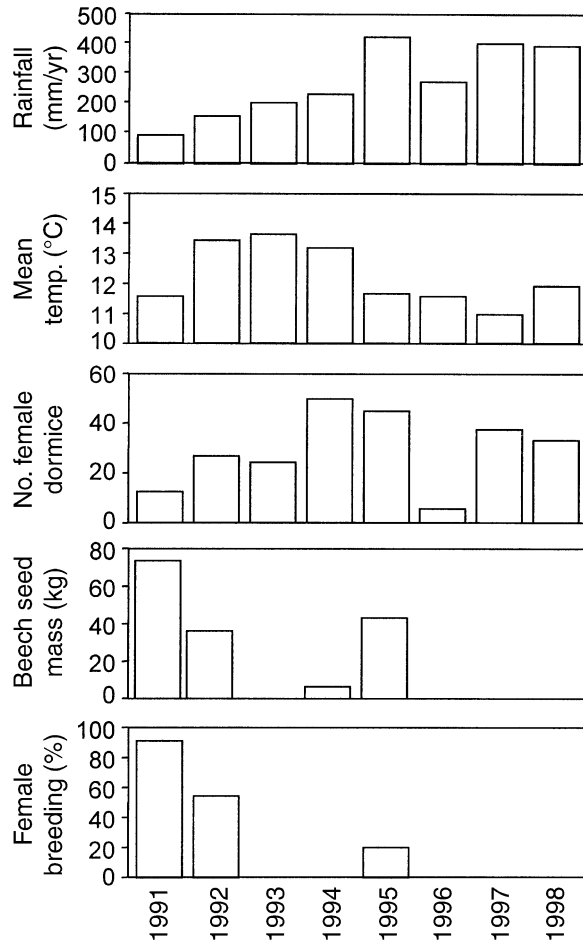


FIG. 3. Environmental conditions (rainfall, mean temperature, population density, and beech seed production) and percentage of female fat dormice breeding over the total density (number of adult female dormice per 100 nest boxes) observed each year in 1991–1998. For more details, see *Methods*.

TABLE 1. Matrix of capture–recapture data for fat dormouse adult individuals used in the survival analysis.

| Release occasion $i$ | $R_i$ | Recapture occasion $j$ | | | | | | | $r_i$ |
|---|---|---|---|---|---|---|---|---|---|
| | | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 | 1998 | |
| Males | | | | | | | | | |
| 1991 | 19 | 12 | 0 | 1 | 5 | 0 | 0 | 0 | 18 |
| 1992 | 62 | | 2 | 8 | 24 | 0 | 0 | 2 | 36 |
| 1993 | 24 | | | 5 | 2 | 0 | 0 | 0 | 7 |
| 1994 | 119 | | | | 33 | 3 | 3 | 4 | 43 |
| 1995 | 163 | | | | | 1 | 4 | 21 | 26 |
| 1996 | 25 | | | | | | 7 | 1 | 8 |
| 1997 | 82 | | | | | | | 20 | 20 |
| Females | | | | | | | | | |
| 1991 | 17 | 10 | 0 | 0 | 2 | 0 | 0 | 2 | 14 |
| 1992 | 68 | | 1 | 22 | 11 | 0 | 2 | 3 | 39 |
| 1993 | 13 | | | 6 | 1 | 0 | 0 | 0 | 7 |
| 1994 | 131 | | | | 36 | 4 | 6 | 6 | 52 |
| 1995 | 137 | | | | | 5 | 15 | 16 | 36 |
| 1996 | 26 | | | | | | 10 | 2 | 12 |
| 1997 | 109 | | | | | | | 15 | 15 |

*Notes:* Notation is as follows: $R_i$ is the number of marked individuals released in occasion $i$; $r_i$ is the total number of individuals recaptured to those released at occasion $i$; the cell $ij$ contains the number of individuals released at $i$ and recaptured for the first time at $j$; the total number of individuals released at $i$ and never seen again is $R_i - r_i$.

TABLE 2. Goodness of fit of the general model for survival estimate [$\phi_{s*t}$; $p_{s*t}$] in which survival and probability of recapture were assumed to vary according to sex ($s$) and time ($t$).

| Sex | TEST3 | | TEST2 | | Z | |
|---|---|---|---|---|---|---|
| | $\chi^2$ | df | $\chi^2$ | df | TEST3 | TEST2 |
| Males | 11.83 | 11 | 27.55* | 9 | 1.85 | −1.47 |
| Females | 8.89 | 11 | 19.00* | 9 | 1.11 | −1.71 |

*Notes:* Asterisks indicate $\chi^2$ and $Z$ values that are significant at $\alpha = 0.05$. When both $Z$ tests are not significant, extra-multinomial variation is due to a general overdispersion of the data, and a scale parameter must be computed to correct model deviance. For more details, see *Methods: Survival estimate*, and Choquet et al. (2002).

breeding failure was significantly associated with years of beech mast seeding, but was not influenced by temperature and rainfall during the summer months.

The percentage of years in which beech produced seeds (3/8) in this study is similar to that observed in a much longer data series (31.3% of 81 years) collected over most of the beech's geographical range (Jenni 1987). Consequently, our observations are probably typical of fat dormouse breeding in forest areas in which beech is the dominant tree species. Interestingly, during the two years in which our study temporally overlapped with Bieber's (1998) study, conducted in Austria in 1992 and 1993, general reproductive failure (and absence of beech seeds) was synchronized in the two populations. Beech is known to synchronize mast seeding over a wide geographical range (Silvertown

TABLE 3. Model selection for survival estimate, eliminating nonsignificant effects from the general model [$\phi_{t*s}$; $p_{t*s}$] that assumes time and sex effect on recapture and survival probability.

| Model | mDEV | np | QAIC$_c$ | QAIC$_c$ weight |
|---|---|---|---|---|
| Recapture probability | | | | |
| $\phi_{s*t}\, p_{s*t}$ | 1011.66 | 26 | 1065.12 | 0.001 |
| $\phi_{s*t}\, p_{s+t}$ | 1016.09 | 21 | 1059.09 | 0.024 |
| $\phi_{s*t}\, p_t$ | 1017.77 | 20 | 1058.63 | 0.031 |
| $\phi_{s*t}\, p_s$ | 1102.68 | 16 | 1135.24 | 0.000 |
| Survival probability | | | | |
| **$\phi_{s+t}\, p_t$** | **1024.57** | **15** | **1055.05** | **0.182** |
| **$\phi_t\, p_t$** | **1026.66** | **13** | **1053.03** | **0.501** |
| $\phi_s\, p_t$ | 1039.12 | 9 | 1057.30 | 0.059 |
| **$\phi_{.}\, ;\, p_t$** | **1039.74** | **8** | **1055.89** | **0.120** |
| $\phi_{s+t}\, p_{s+t}$ | 1024.10 | 16 | 1056.66 | 0.082 |

*Notes:* Notation is as follows: "*" denotes the presence of an interaction between two terms; "+" denotes models in which interactions between two effects are not considered; $t$ is time; $s$ is sex; np is the number of parameters in the model; a variance inflation factor ($c = 1.6815$) has been used to correct model deviance (mDEV); QAIC$_c$ weight is the relative contribution of each model and can be used to incorporate model selection uncertainty in parameter estimates (for more details, see Burnham and Anderson [1998]); model [$\phi_t$; $p_t$] had the lowest QAIC$_c$ value and the greatest QAIC$_c$ weight, but two other models (also in boldface) may be considered, given the relative importance of their QAIC$_c$ weight.
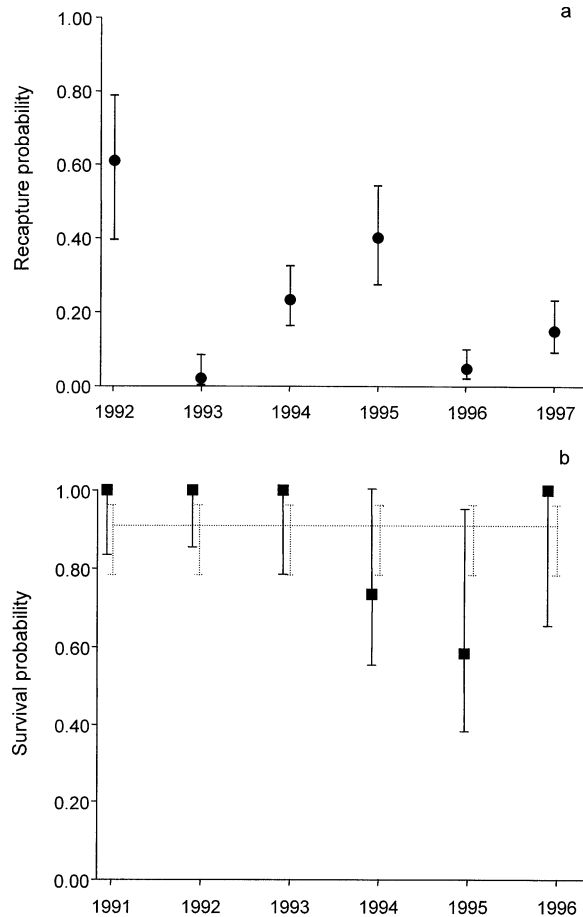


FIG. 4. Time-dependent estimates and 95% confidence intervals of (a) recapture probability and (b) survival probability. Note that recapture probability in 1998 is not estimable in model [$\phi_t$; $p_t$]. Lower survival confidence limits (vertical dotted bars) for boundary values were estimated using the profile likelihood technique (see *Methods: Survival estimate*). The dotted line indicates the constant survival value of 0.918 from the model [$\phi_{.}$; $p_t$]. Estimates from model [$\phi_{s+t}$; $p_t$] were very similar to those of [$\phi_t$; $p_t$] and are not shown.

1980, Jenni 1987, Hilton and Packham 1997). The beech–fat dormouse system may therefore be an example of predator–prey spatiotemporal synchronization (Koenig 1999). In contrast, in the southern part of the fat dormouse range, where food availability is more constant, fat dormice breed regularly every year (e.g., Santini 1978, Pilastro 1992).

Reproductive suppression in mammalian social groups usually occurs in subordinate females, as a result of behavioral dominance by older females, or as an adaptive response to the threat of infanticide (Wolff 1997). Because female fat dormice do not form large breeding groups (usually one, rarely more than two, closely related females; Marin and Pilastro [1994]), and population density was not correlated with the number of reproducing females, social mechanisms are unlikely to account for the pattern of reproduction skipping. To

our knowledge, the fat dormouse is the first case, among small mammals, of breeding suppression occurring at the population level with such high frequency. As a consequence of intermittent breeding and of the small size (5.3 pups) of the single litter produced in breeding years, the overall annual fecundity per dormouse female is about two pups, much lower than that of other similarly sized Palaearctic rodents, which usually produce two broods per year, consisting of up to 12 pups (Niethammer and Krapp 1978).

In contrast to what is observed in other mammals, in which reproductive skipping is a state-dependent decision (e.g., Sand 1996), in the fat dormouse it was not linked with the females' state: the average female body mass in July and August (when mating and birth occur) was similar in reproductive and nonreproductive years (see also Bieber 1998). Moreover, in years without reproduction, 70% of the adult females had a body mass value greater than the minimum value (102 g) observed in breeding females (A. Pilastro, *unpublished data*). The fact that body mass of adult females did not differ between mast and nonmast seeding years in June and August is not surprising, because beech seeds mature in September–October (Gellini and Grossoni 1997). This suggests that the adults' decision whether or not to breed in a given year is taken about two months before beech seeds are actually mature. Because fat dormice usually feed on floral buds in spring and summer (Santini 1992), it may be possible that such buds contain some specific compounds that trigger reproduction well before the fruits are actually available. A similar mechanism has been reported for at least one other rodent species, the montane meadow vole *Microtus montanus* (Berger et al. 1981, Sanders et al. 1981).

A strategy of reproducing only in years when food is available for the young after weaning may be selected for if an individual's fertile life is long and the recruitment and fertility of young raised under conditions of poor nutrition are low (Andreassen and Ims 1990, Lindström 1999). In other words, if juvenile mortality fluctuates because of stochastic environmental variations, life histories with delayed reproduction (and therefore high adult survival) and low reproductive effort are predicted (Stearns 1977). The annual survival probability estimate of adult fat dormice is much higher than in other rodents (e.g., multimammate rat *Mastomys natalensis*, 0.57/month [Julliard et al. 1999]; red squirrel, 0.69/year [Wauters and Dhondt 1989]; garden dormouse *Eliomys quercinus*, 0.38/year [Schaub and Vaterlaus-Schlegel 2001]; pine vole *Microtus duodecimcostatus*, 0.68/month [Paradis et al. 1993]; Townsend's vole *M. townsendii*, 0.96/week [Lambin and Yoccoz 1998]; meadow jumping mouse *Zapus hudsonius*, 0.84/week [Nichols and Conley 1982]; deer mouse *Peromyscus maniculatus*, 0.87/14 days [Millar and Innes 1983]), and it is similar to that observed among large herbivores, which ranges from 0.79 to 0.98

(Gaillard et al. 1998, 2000). The fat dormouse also has highly variable recruitment rates and fairly constant adult survival (coefficient of variation of survival probability = 0.19), which is a common life history trait in large herbivorous mammals (Gaillard et al. 1998). The fat dormouse life history pattern is thus in accord with theoretical work, which predicts that when the environment is variable, long-lived, late-reproducing iteroparous life histories are advantageous (e.g., Orzack and Tuljapurkar 1989). Fecundity in the fat dormouse is lower than in most short-lived rodents, but is higher than in other long-lived mammals, such as large herbivores, which are also strongly iteroparous (Gaillard et al. 2000). In herbivores, iteroparity is associated with low adult and high juvenile interannual variance of survival rates (Gaillard et al. 2000). The mean survival rate of juveniles in this population was 0.41 (0.33–0.49; G. Tavecchia and A. Pilastro, *unpublished data*), but annual variation of local survival of juveniles was difficult to estimate because reproduction occurred only in three years. Moreover, recapture probability was very low in two of the three post–reproduction years (1993 and 1996), rendering first-year survival difficult to estimate for those two cohorts.

The long period of hibernation in subterraneous refuges may have contributed to high values of adult survival if, as found in the garden dormouse (Schaub and Vaterlaus-Schlegel 2001), mortality is virtually absent during this period. Blueweiss et al. (1978) estimated the allometric relationship between body mass and longevity expressed in number of days. Following this relationship on the base of the annual number of days of activity (from May through October), the value of annual survival should be 0.88, which is similar to the one found in this study. If hibernation is not accounted for, the predicted value is 0.78 (although these estimations should be taken with caution, because the relationship of Blueweiss et al. included a taxonomically large range of organisms). Contrasting results are obtained using a relationship between body mass and annual survival rate after maturity that does not account for hibernation (Millar and Zammuto 1983). Following this relationship, the predicted life span after maturity would be just 1.1 years. Hibernation might therefore be a life history trait selected to enhance survival probability. Additional support for this hypothesis comes from the results, at an individual level, of Lyman et al. (1981), who found that individual Turkish hamsters (*Mesocricetus brandti*) that hibernated longer had higher survival than those that hibernated for shorter periods.

In our study population of the fat dormouse, there is a large variance in the mean body mass of young at weaning and at hibernation (Pilastro et al. 1994). Body mass of young fat dormice at their first hibernation is positively correlated with body mass values observed in subsequent years, a determinant of future reproductive success of females and males. Moreover, young

with low body mass ($<100$ g) at hibernation have never locally recruited in the following years, and body mass at hibernation is significantly and positively correlated with body mass in the following year (Pilastro et al. 1996; A. Pilastro, *unpublished data*). This suggests that poor conditions due to insufficient nutrition during growth of juveniles cannot be made up for by later growth, as observed in other mammalian species (e.g., Green and Rothstein 1993).

In conclusion, the fat dormouse represents an example of extreme adaptation to an unpredictable environment. The hibernation strategy, common to other dormice with shorter longevity, is likely to be a pre-adaptation for its life history characterized by a long life span and intermittent breeding. It also represents one of the clearest examples thus far of a mammalian breeding cycle that is synchronized with a single, variable trophic source.

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