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Local environmental factors affect reproductive investment in female edible dormice

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Edible dormice (*Glis glis*) are exposed temporally and spatially to a tremendous variation in food resources. This variation strongly influences reproduction; in edible dormice reproduction is tightly linked to the availability of energy-rich seeds. Although most dormice reproduce in full mast years of beech or oak, entire populations skip reproduction in years without seed production; however, nearly 50% of all years are intermediate mast years, during which only part of the dormouse population reproduces. We investigated how the beech mast pattern, local habitat characteristics, and individual traits (body mass and age class) influence whether individual female edible dormice invest in reproduction in intermediate mast years. Our field study, conducted during 2006–2009 in the Vienna Woods, revealed that in intermediate mast years the probability of females reproducing increased with the age of trees but not with the proportion of beech trees within their home ranges. Mean litter size was larger in years with higher seed availability and also increased with the mean age of trees within the home range of the dormice. More adult than yearling females reproduced, but this effect was modulated by yearly and local variation in food availability. Whether a female edible dormouse reproduces in an intermediate mast year depends mainly on the local food availability and age of the individual.

Key words: delayed maturity, environmental factors, food availability, *Glis glis*, pulsed resources, reproduction

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In small mammals energy demands for reproduction are extremely high, and during peak lactation the level of energy turnover in females exceeds maintenance levels severalfold (e.g., Speakman et al. 2004). Food availability is one of the most important factors affecting reproduction (Hubbs and Boonstra 1997; Karels et al. 2000; Koskela et al. 1998, 2004). Food resources are typically not distributed uniformly, but vary on a spatial and temporal scale. Pulsed resources—occasional, short periods of resource superabundance followed by a decrease over time—represent a naturally occurring, extreme type of erratic food availability (Ostfeld and Keesing 2000; Yang et al. 2008). A prime example of pulsed resources are tree seeds (e.g., of beech [*Fagus* spp.] or oak [*Quercus* spp.]), which can be completely absent in some years but overabundant in mast years. Mast years of beech occur, on average, every 7 years and have been found to be fairly synchronized over large areas (Hilton and Packham 2003). Typical consumers of these seeds, such as a variety of rodents and wild boar (*Sus scrofa*), increase reproduction after a mast event, which often leads to a period of population growth (Bieber and Ruf 2005; Murúa and Briones 2005; Selås et al. 2002).

An interesting species in which to study responses to pulsed resources is the edible dormouse (*Glis glis*). This small mammal is a specialized seed predator that must cope with high annual variability in tree seed production. Edible dormice are born very late in the summer season, from July to August. Thus, the energetically expensive lactation period coincides with phases of high food availability. A supply of energy-rich food during autumn is essential for juveniles after weaning, because they need to gain sufficient body fat reserves within a very short time period to survive their 1st hibernation season (Bieber and Ruf 2004). Therefore, although adults can live on a variety of alternative food sources (including leaves, fruits, and insects), entire populations of edible dormice in deciduous forests of northern Europe typically reproduce in full mast

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years and skip reproduction in years with no seed production (Bieber 1998; Pilastro et al. 2003; Schlund et al. 2002). However, approximately 50% of all years are intermediate mast years (Hilton and Packham 2003). Variation in mean seed production across a particular area among years is primarily caused by the high variation among individual trees (Herrera 1998). Intermediate mast years therefore arise when only a part of the tree population produces seeds, rather than from all trees producing seeds at an intermediate level. In those intermediate mast years varying fractions of edible dormice reproduce (Kager and Fietz 2009; Ruf et al. 2006). Theoretically, the presence of a single, large, seeding beech tree in the home range of an edible dormouse should be sufficient to provide ample food resources to support the high energy requirements of reproduction.

We hypothesized that in years of intermediate tree seeding, investment in reproduction in edible dormice will be affected by local food availability, in particular by the proportion of beech trees in an individual's home range or by the age of trees, because older trees produce more seeds (Genet et al. 2009; Isagi et al. 1997; Yamauchi 1996). To test this hypothesis we collected data on the occurrence or absence of reproduction over a 4-year period of intermediate tree seeding in edible dormice inhabiting nest boxes in a deciduous forest in the Vienna Woods in Austria. We then used detailed forest inventory data to analyze if the proportion and average age of beech trees in an individual dormouse's home range influences whether a female invests in reproduction. Previous studies found no effect of body mass on reproductive investment in edible dormice, but these studies focused mainly on full mast and mast failure years (Bieber 1998; Fietz et al. 2005; Pilastro et al. 2003). Hence, we considered it possible that body mass affects reproduction in years of intermediate mast seeding. We also expected that food availability could affect different age classes differentially. Yearling edible dormice, which are not fully grown, might be less likely to reproduce under suboptimal local conditions and delay the onset of reproduction for another year. In other rodents low territory quality or high population density can lead to a delayed 1st reproduction (*Tamiasciurus hudsonicus* [Descamps et al. 2006] and *Xerus inauris* [Waterman 2002]). Consequently, we included both body mass and age class in our analysis.

Materials and Methods

Study species.—Edible dormice are small (~80–130 g—Bieber 1998; Lebl et al. 2010), nocturnal rodents living in mixed and deciduous forests in central and southern Europe (Vietinghoff-Riesch 1960). Dormice are hibernators and can spend up to 8 months in hibernation (Vietinghoff-Riesch 1960; Wyss 1932). Although dormice are arboreal during their summer active period, they hibernate in underground burrows (Vietinghoff-Riesch 1960). Edible dormice are principally solitary animals (Vietinghoff-Riesch 1960), but cases of communal breeding of females are recorded (Pilastro 1992), and males use huddling behavior (mainly in spring) as a mechanism for social thermoregulation (Fietz et al. 2010). Both yearlings and adults show extremely high site fidelity, suggesting that dormice disperse as juveniles (Bieber and Ruf 2009; Ruf et al. 2006; Vietinghoff-Riesch 1960). Reports of home-range size vary from ~0.5 to 7 ha, with males having larger home ranges than females (Hönel 1991; Jurczyszyn 2006; Morris and Hoodless 1992; Scinski and Borowski 2008). Although yearling dormice are not fully grown, they are already sexually mature (Bieber 1998). Mating takes place from mid-June to mid-July; the gestation period lasts 30–32 days, and juvenile dormice are weaned at approximately 6 weeks of age (König 1960; Vietinghoff-Riesch 1960). Edible dormice have only 1 litter per year, with a mean litter size of ~5.5 young (Kager and Fietz 2009; Lebl et al. 2010; Pilastro et al. 2003). The mean life expectancy of edible dormice varies among investigated populations, ranging for females from 2.4 years in a population in Germany to 5.6 years in northern Italy (Lebl et al. 2011).

Study area and data collection.—The study was conducted within the Vienna Woods near St. Corona, Austria (48°05′N, 15°54′E; elevation 500–850 m). The study area comprised approximately 1,860 ha of deciduous forest dominated by beech (*Fagus sylvatica*; 65%), the other species being mainly spruce (*Picea abies*; 14%), larch (*Larix decidua*; 8%), and fir (*Abies alba*; 5%). In 1984 wooden nest boxes were installed at a height of 2–3 m, and since then the total number of dormice inhabiting the 184 boxes has been recorded once per year in fall (Bieber and Ruf 2004). Nest-box distribution was irregular (along trails) and not ordered in a grid pattern; mean distance ($\pm$ *SD*) to the nearest neighbor nest box was 123.1 $\pm$ 7.1 m. Dormice use the nest boxes during their active season to rest during the daytime and to rear their young. From 2006 to 2009, every 2 weeks from mid-April to the end of October, nest boxes were checked for the occurrence of edible dormice, and all individuals found in nest boxes were captured. In 2007 data from only two-thirds of the study area were analyzed, because a supplemental feeding experiment was conducted in the remaining one-third. Females did not move between the supplemental feeding area and remaining study area that year (Lebl et al. 2010). Newly captured dormice were marked individually with subcutaneously injected passive integrated transponder chips (PIT tags, 13.8 $\times$ 2.1 mm; Virbac, BackHome BioTec, Bad Oldesloe, Germany). The puncture wound was closed with a tissue adhesive to minimize tag-loss rate (years 2007–2009—Lebl and Ruf 2010). Dormice were weighed to the nearest 1 g using a 300-g spring balance (precision = 2 g), and sex and age class were recorded. Dormice can be classified reliably as juveniles (before 1st hibernation), yearlings (after 1st hibernation, already sexually mature), and adults (after 2nd hibernation) from their size, tibia length, and fur color (Bieber 1998; Schlund 1997). Females were classified as reproductive if they were found in the same nest box with juveniles $<$ 4 weeks old or if they were captured with visible, enlarged mammae. If a female was captured at least twice within the time of young-rearing (end

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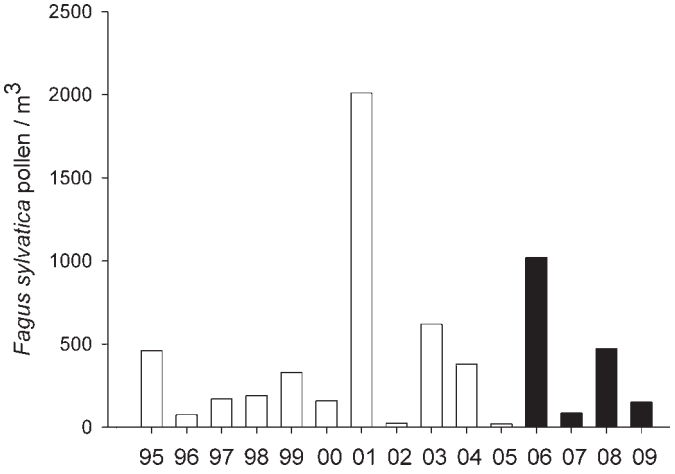


Fig. 1.—Number of vernal beech pollen grains/m^3 air over 15 years (1995–2009) in the Vienna Woods near St. Corona, Austria. Only 2001 was a full mast year, and 2002 and 2005 were mast failure years. During our study period (black bars) all years were intermediate mast years; 2006 and 2008 were high intermediate mast years, and 2007 and 2009 were low intermediate mast years.

of July to end of September) without young or visible mammae, it was classified as nonreproductive. Because 2 captures encompass a minimum of 4 weeks, lactation lasts ~6 weeks, and enlarged mammae are visible for approximately another week, it is unlikely that reproduction could have been missed by using this classification. In 2009, 5 females appeared to have killed or abandoned their young. We found these females without juveniles within 2 weeks of encountering them with young that were only a few days old. Infanticide is the most likely explanation for these observations because the small size of nest-box entrances precluded the intrusion of predators, such as martens. Because the main costs for reproduction arise for females during late lactation, these 5 cases were excluded because their investments in reproduction represented an intermediate state between reproductive and nonreproductive females. After the measurements, all captured dormice were immediately returned to their nest boxes. To avoid major disturbances to mothers with small young (<15 days) we recorded only the mother's identity and litter size and did not make any additional measurements. This study was approved by the University of Veterinary Medicine of Vienna ethics committee and complies with guidelines of the American Society of Mammalogists for use of mammals in research (Gannon et al. 2007) and the current laws of Austria.

Environmental factors.—We used the number of beech pollen grains/m^3 air in spring as an indicator for the yearly beech reproduction (Fig. 1). The number of beech pollen grains was provided by the Austrian Federal Forest Office and represents a reliable indicator for the mast pattern of beech in late summer (Litschauer 2001). Although the measurement station was located at a distance of ~25 km from our study area, we were able to use these data because the mast pattern of beech is synchronized over very large areas (Hilton and Packham 2003). In the last 15 years only 1 full beech mast year (2001) and 2 mast failure years (2002 and 2005) occurred in our study area (Fig. 1). All other years, including the years of our study period (2006–2009), represent intermediate beech mast years. The mean number of beech pollen grains/m^3 air in spring in those intermediate years was 342.5 pollen grains/m^3 air. We defined intermediate years with pollen density below this mean as low intermediate mast years and years above this mean as high intermediate mast years. Therefore, 2 low intermediate mast years (2007 and 2009) and 2 high intermediate mast years (2006 and 2008) comprised our study period (Fig. 1).

ArcGIS (version 9.1; ESRI Inc., Redlands, California) with extensions from Beyer (2006) were used to process habitat information on the proportion of beech trees and tree age. The Austrian Federal Forests provided a digitized polygon shape file of the study area and forest inventory data containing the proportion of tree species and tree age for each polygon. The position of each nest box was recorded via global positioning system (eTrek Summit; GARMIN International, Inc., Olathe, Kansas) to an accuracy of 6 m. Based on reports of home-range requirements in edible dormice (Hönel 1991; Jurczyszyn 2006; Morris and Hoodless 1992), we created a buffer layer with a 100-m-radius circle around each nest box, resulting in areas of approximately 3 ha. For our further analysis we used habitat information from within these buffers only, which we hereafter call the surrounding area of a nest box.

Statistical analysis.—Reproductive activity of females was analyzed using generalized mixed-effect models, with having reproduced or not in a certain year as the binominal response variable and the animal's identity as the random effect to adjust for repeated measurements. We tested for effects of age class, prereproductive body mass, year, age of the surrounding trees, and proportion of beech in the surrounding trees. Further, we tested whether litter size (using linear mixed-effect models) was affected by the same factors. Because the prereproductive phase covered only a time period of 6 weeks (end of May to beginning of July; therefore only 3 capture occasions), we were able to obtain the prereproductive body mass for only a small proportion of females. The body mass of females during the prereproductive time period was available in only 37 of 210 cases and for the analysis of factors affecting litter size in 25 of 94 cases.

To test if the prereproductive body mass differed between the age classes, years, and reproductive states we also used linear mixed-effect models. To verify that differences in yearly food availability even show a measurable effect on body mass, and to test whether the costs of reproduction in terms of body mass loss were still observable at the end of the season, we conducted the same analysis for the prehibernation (mid-September) body mass. Mean body mass during the respective time period was entered as the response variable and the animal's identity as the random effect. Starting from the null model we used a combined approach of forward and backward model selection to identify the model with the lowest Akaike information criterion (AIC) score (Akaike 1973). We included or excluded single terms in a stepwise procedure, used likelihood-ratio tests (χ^2) to compare models,

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Table 1.—Analysis of deviance (Hastie and Pregibon 1992) table of factors affecting reproductive state in female dormice ($n = 210$). A) Final model. B) Effect of nonsignificant factors prior to their removal. * $P < 0.05$, ** $P < 0.01$.

	χ^2	*d.f.*	*P*
A)			
Year	9.896	3	0.019*
Age class	1.523	1	0.217
Tree age	3.861	1	0.049*
Proportion beech	0.005	1	0.943
Year × age	8.214	3	0.042*
Year × tree age	13.847	3	0.003**
Age × tree age	4.528	1	0.033*
Year × proportion beech	11.838	3	0.008**
B)			
Prereproductive body mass	0.024	1	0.876

and retained the model with the lower AIC for the next step until we gained a model where the AIC could not be further improved. If the likelihood ratio test showed that models did not significantly differ, the model with fewer terms was selected. In the process of model selection for the response variables reproductive activity and litter size the random effect of the individual was nonsignificant (likelihood ratio tests [Pinheiro and Bates 2000]; reproductive activity: $\chi^2_1 < 0.0001$, $P > 0.99$; litter size: $\chi^2_1 < 0.0001$, $P = 0.99$). We therefore reduced the model for reproductive activity to a generalized linear model and the model for litter size to a linear model. We used plots of residual versus fitted values and quantile–quantile plots to verify that the model assumptions were met. We computed analyses of variance for linear model fits to estimate whether the factors included in the final models contributed significantly to the explanation of the observed variance in response variable. For generalized linear model fits we used an analysis of deviance based on the chi-square (χ^2) statistic (Hastie and Pregibon 1992). If not mentioned otherwise, we give results of actual proportions or the marginal means (i.e., group means adjusted for the other effects in the model—Fox 2003), calculated from the final model, with 95% confident intervals (95% *CI*s). All statistical analyses were carried out with the statistical software R (version 2.10.1; R Development Core Team, Vienna, Austria).

Results

We found a proportion of 0.84 females reproducing in 2006, 0.60 in 2007, 0.78 in 2008, and 0.27 in 2009. The final statistical model correctly predicted the reproductive activity in 84.8% of all cases (for factors retained in this model see Table 1). As expected, the proportion of reproductive females differed among the years, but reproductive activity also was affected significantly by age class (Table 1). In 2006 a higher proportion of yearling females reproduced than in the subsequent years (Fig. 2a). The proportion of females reproducing was always lower in yearlings compared to adults (Table 1; Fig. 2a). Further, the age of the surrounding trees affected the 2 age classes differently (Table 1; Fig. 2b). In adult females, the probability to reproduce increased with increasing tree age until the mean age of surrounding trees was about 60 years. Beyond this tree age nearly all females reproduced. For yearling females the relationship was roughly linear; the probability to reproduce steadily increased with increasing tree age. The age of trees had a higher impact on reproduction in the years 2007 and 2009 compared with 2006 and 2008 (Table 1; Fig. 2c).

The influence of the proportion of beech in the surrounding trees on female reproductive activity differed among the years. We observed no effect of the proportion of beech on the proportion of reproductive females from 2006 to 2008 but a strong negative effect in 2009 (Fig. 2d). These differences were reflected by a strong interaction between year and proportion of beech in the statistical analysis (Table 1).

Mean litter size varied among the years, and was approximately 1 juvenile less in 2009 than in the other years (Table 2; Fig. 3a). Further, litter size was affected positively by the age of surrounding trees (Table 2; Fig. 3b).

Body mass during the prereproductive period was influenced only by the individual's age ($F_{1,35} = 53.50$, $P < 0.001$). Adult females had a mean body mass of 97.3 g (95% *CI* = 92.1–102.4 g, $n = 26$), and mean body mass of yearling females was 63.1 g (95% *CI* = 55.1–71.0 g, $n = 11$). Prereproductive body mass did not differ between subsequently reproductive (87.1 g, 95% *CI* = 82.9 – 91.9, $n = 31$) and nonreproductive females (87.4 g, 95% *CI* = 76.2–98.5 g, $n = 6$; $F_{1,34} = 0.001$, $P = 0.974$). Neither reproductive activity ($\chi^2_1 = 0.024$, $P = 0.875$) nor litter size ($F_{1,19} = 0.002$, $P = 0.962$) were significantly affected by prereproductive body mass. These factors were not included in the final statistical models (Tables 1 and 2).

Body mass before the onset of hibernation differed among years ($F_{3,37} = 10.85$, $P < 0.001$) and between the age classes ($F_{1,37} = 7.88$, $P = 0.008$). During this period females had a body mass of 137.3 g (95% *CI* = 124.8–149.8 g, $n = 12$) in 2006, 122.1 g (95% *CI* = 110.6–133.6 g, $n = 14$) in 2007, 117.0 g (95% *CI* = 85.9–148.0 g, $n = 2$) in 2008, and 91.3 g (95% *CI* = 79.9–102.8 g, $n = 14$) in 2009. Before the onset of hibernation yearling females still had a lower body mass (106.8 g, 95% *CI* = 97.5–116.1 g, $n = 22$) than adult females (126.0 g, 95% *CI* = 116.2–135.8 g, $n = 20$).

Discussion

The investigated dormouse population experienced only intermediate beech mast years during the study period. Within those years 2006 and 2008 represent high intermediate years and 2007 and 2009 represent low intermediate mast years. The reproductive activity of dormice was also at an intermediate level, as we found, consistent with Bieber (1998) and Kager and Fietz (2009), neither years of complete reproductive failure nor years in which nearly all dormice reproduced. The overall proportion of females reproducing varied among the years according to the beech mast situation. It was high in the

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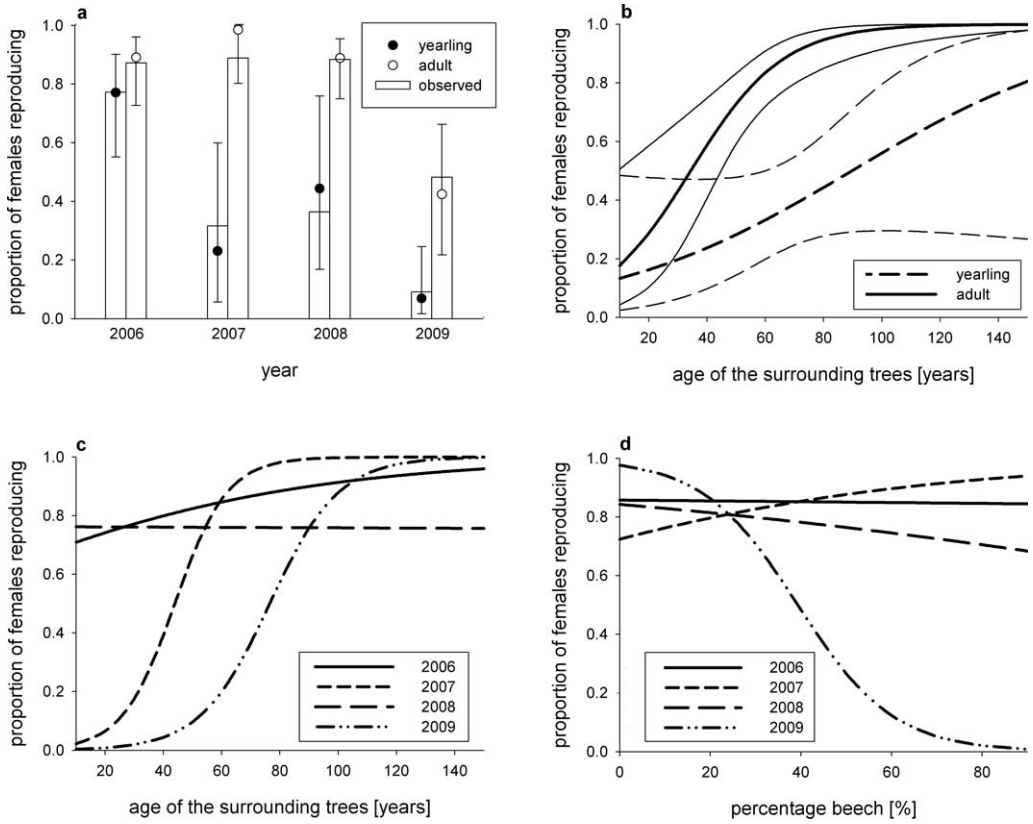


Fig. 2.—Significant factors from the final generalized linear model affecting the proportion of reproductive edible dormouse females at a study site in the Vienna Woods near St. Corona, Austria, 2006–2009. a and b) Marginal means (see ''Materials and Methods'') with 95% *CI*s are shown (part a also includes the observed proportion of reproductive females for each year and age class).

high intermediate mast years 2006 and 2008, but only a small proportion of females reproduced in the low intermediate mast year 2009. In 2007 the proportion of reproductive females was, although still relatively low, higher than the beech mast pattern would indicate; such an occasional divergence also was found in other studies (see Bieber and Ruf 2004; Kager and Fietz 2009; Ruf et al. 2006). This suggests that in 2007 local effects caused a pattern of food availability that was not reflected by the large-scale magnitude of the beech mast. The finding that females had high average body mass at the end of the active season in mid-September 2007, compared to 2009, indicates that edible dormice in 2007 had access to food resources that were not available in 2009. Further, that we had indication of infanticide solely in 2009 is another cue that this year seems to have been unfavorable for raising juveniles, most likely due to locally low food availability. We previously found some indication for infanticide in females following a sudden decline in food availability (Lebl et al. 2010).

Table 2.—Analysis of variance table of the factors affecting litter size in edible dormice ($n = 94$). A) Final model. B) Effect of nonsignificant factors prior to their removal. * $P < 0.05$, ** $P < 0.01$.

	F	*d.f.*	*P*
A)			
Year	2.937	3, 89	0.038*
Tree age	13.619	1, 89	<0.001**
B)			
Age	0.663	1, 88	0.418
Prereproductive body mass	0.005	1, 88	0.944
Proportion beech	0.332	1, 88	0.566

One important factor affecting the local availability of seeds is tree age, because older beech trees produce more seeds (Genet et al. 2009; Nilsson and Wastljung 1987), and they also produce seeds more often (Yamauchi 1996). Therefore, the age of surrounding trees should provide a suitable indicator for local food availability, and the probability of reproduction did increase with tree age. However, the local variation in beech seed availability between home ranges is more pronounced in low mast years, when only a limited fraction of trees produce seeds (Herrera 1998). Local food availability had a much stronger effect in the low intermediate mast years 2007 and 2009, and females reproduced only when the presence of older trees increased local food availability. Other vertebrate seed predators also appear to prefer feeding on larger trees, because they contain a high amount of food within a relatively small area (Nilsson and Wastljung 1987). Because competition between seed predators might lead to a swift depletion of smaller food patches, only large amounts of seeds (i.e., old trees) will guarantee a continuous supply.

We found no relationship between the proportion of beech trees within an individual's home range and the reproductive activity in most years. In 2009, however, when the fraction of females reproducing was very low, the proportion of beech

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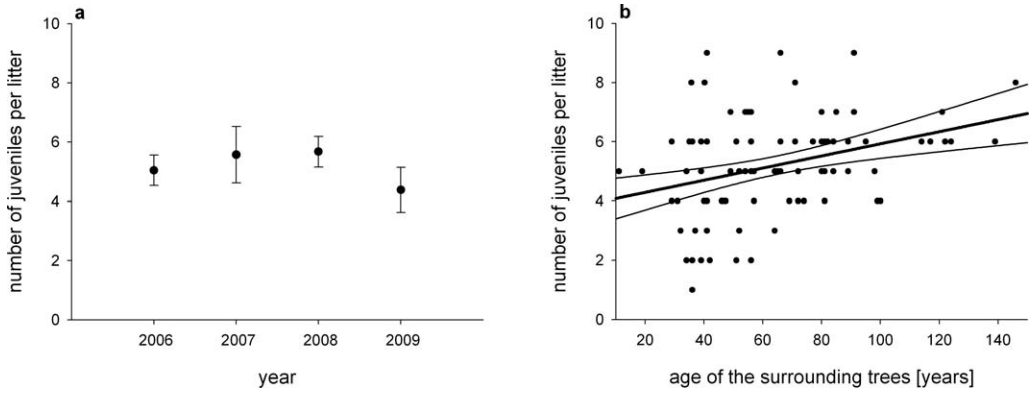


Fig. 3.—Significant factors from the final linear model affecting litter size in edible dormice at a study site in the Vienna Woods near St. Corona, Austria, 2006–2009. Marginal means (see ''Materials and Methods'') with 95% *CI*s are shown. Dots in part b represent the actual (uncorrected) values.

trees within home ranges correlated negatively with the proportion of reproductive females. This suggests that in very low intermediate mast years a high proportion of beech trees actually means a low availability of food resources, whereas in areas with lower beech content alternative food resources (e.g., berries, fruits, and seeds of other trees—Fietz et al. 2005; Gigirey and Rey 1998) might have led to a higher proportion of females reproducing compared to areas with a relatively high content of beech trees. Bieber and Ruf (2009) found that edible dormice can reproduce in the absence of large trees providing seeds but with a much lower reproductive output compared to that in a beech forest.

Litter size increased with food availability, as indicated by mast seeding pattern and age of the surrounding trees, and therefore differed between the years and home ranges. This concurs with the results of Kager and Fietz (2009), who found that litter size in edible dormice increased with the degree of seed mast and in response to continuous supplemental feeding. For some small mammal species food supplementation results in no increase in litter size (Hubbs and Boonstra 1997; Koskela et al. 2004; O'Donoghue and Krebs 1992) or only a slightly larger litter size (Karels et al. 2000). Provided that reproduction is limited by food availability, this indicates that in these species the reproductive value of the offspring does not vary much between years, probably due to a relatively constant food supply and thus constant survival probability for the young. For edible dormice, however, food supply during lactation, and afterward for juveniles, varies considerably among years. Because survival of edible dormouse juveniles depends on sufficient food availability, the reproductive value of juveniles also varies among years. In certain other small mammals a strong variation in food availability among years also causes females to adjust their yearly reproductive investment to the current food supply (Boutin et al. 2006; Brommer et al. 2000; Dobson and Kjelgaard 1985).

We found an extremely high variation in the proportion of reproducing yearling females. Although yearling female edible dormice are able to breed, they are less likely to give birth than adults (Lebl et al. 2010; Ruf et al. 2006). Because yearling edible dormice still need to invest in somatic growth, a trade-off between growth and reproduction could render it adaptive for yearling females to show a lower investment in reproduction (Descamps et al. 2007). Further, older females are likely to invest more in their current reproduction, because it does not pay for them to save resources for a future they likely will not experience (Curio 1983; Forslund and Pärt 1995; Stearns 1992; Williams 1966). Because good mast years are rare and occur at irregular intervals, it should be beneficial for yearling dormice to reproduce in the presence of ample food resources but to skip reproduction in suboptimal years or in areas with low local seed availability, with the prospect of surviving to the next good mast year. A similar pattern of reduced investment in reproduction in suboptimal years can be found in American and European tree squirrels (Boutin et al. 2006).

Our results confirm previous data showing that in edible dormice body mass is not a crucial factor affecting reproduction in females, even in years of intermediate food supply (Bieber 1998; Fietz et al. 2005; Lebl et al. 2010; Pilastro et al. 2003). This independence of reproductive investment from stored energy reserves makes edible dormice a typical example for income breeders (e.g., Houston et al. 2007). A likely mechanism for effects of current food availability on reproduction involves metabolic fuels for oxidation (i.e., glucose and fatty acids), which can affect both gonadotropin-releasing hormone secretion and mating behavior, independent of body mass (Furman and Wade 2007; Wade and Jones 2004; Wade et al. 1996).

In conclusion, our study reveals that variation in the proportion of females reproducing among years is due mainly to differences in the proportion of yearling females reproducing. Further, we showed the importance of the age of surrounding trees on whether a female edible dormouse reproduces in an intermediate mast year. Because tree age probably reflects local food availability, these effects were most pronounced in years of low intermediate tree seeding. Therefore, our results underline the strong adaptation of dormice to fluctuating seed production of trees.

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