# SEXUAL ACTIVITY AND REPRODUCTION IN THREE FERAL SUBPOPULATIONS OF THE FAT DORMOUSE (*MYOXUS GLIS*)

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Bieber, C.: **Sexual activity and reproduction in three feral subpopulations of the fat dormouse** (*Myoxus glis*), Nat. Croat., Vol. 6, No 2., 205–216, 1997, Zagreb

Population ecology and reproduction in three subpopulations of the fat dormouse (*Myoxus glis* Linn, 1776) were studied in central Germany in the years 1992 and 1993. Animals were captured in wooden livetraps twice a month, during trapping periods lasting three days, and marked individually by tattooing. Surprisingly, after a year with good reproductive success (1992), a total lack of reproduction was observed in all three areas in 1993. Reproductive failure coincided with a lack of food resources in fall 1993. Presumably, bad weather conditions or predictive environmental signals, such as missing flower buds in the dry spring of 1993, prevented gonadal development in males.

**Key words:** body-weight, food, *Myoxus glis* / *Glis glis*, population ecology, seasonality

Bieber, C.: **Spolna aktivnost i razmnožavanje u tri divlje subpopulacije sivog puha** (*Myouxus glis*), Nat. Croat., Vol. 6, No 2., 205–216, 1997, Zagreb

Proučavana je ekologija populacije i razmnožavanje u tri divlje subpopulacije sivog puha (*Myouxus glis* Linn, 1776) u centralnoj Njemačkoj 1992. i 1993. godine. Životinje su hvatali u drvene živolovke dvaput mjesečno, tijekom trodnevnih lovnih perioda, a markirane su tetoviranjem. Nakon godine s uspješnom reprodukcijom (1992), najednom je zabilježen potpuni izostanak reprodukcije na sva tri područja 1993. godine. Izostanak reprodukcije poklopio se s manjkavim izvorima hrane ujesen 1993. Pretpostavlja se da su loši vremenski uvjeti ili predvidljivi uzroci iz okoliša, npr. izostanak cvjetanja bukve u suho proljeće, spriječili razvoj gonada kod mužjaka.

**Ključne riječi:** tjelesna težina, hrana, *Myoxus glis* / *Glis glis*, populacijska ekologija, sezonalnost

## INTRODUCTION

The arboreal and nocturnal fat dormouse (*Myoxus glis* Linné, 1766, formerly *Glis glis*, WILSON & REEDER 1993) is an inhabitant of deciduous forests in central Europe (STORCH 1978). Although the fat dormouse is, by its name, a commonly known ani-

mal, we know almost nothing about its ecology and especially its reproductive biology. Several authors have described extremely low reproduction success (v.VIETINGHOFF-RI-ESCH 1960; LÖHRL 1955; HÖNEL 1991; KULZER et al. 1993) or even a total reproduction failure (BIEBER 1995; SCHLUND 1996) in fat dormouse populations in certain years.

New long-term studies on population dynamics in dormouse populations have shown a correlation between population peaks (reproduction success) and food availability in fall (KULZER et al. 1993, SCHLUND 1996). The abundance of dormice is high in years with beech and oak mast, a main energy source for this hibernating rodent. These results may indicate that reproduction success is influenced by food resources, as known in connection with other species (e.g., DOBSON 1995). However, so far we have failed to understand the actual environmental factors and physiological mechanisms involved in the regulation of reproduction in this species.

The aim of this paper is to present more details on the reproduction failure in three subpopulations of the fat dormouse observed in 1993. What differences in population-structure, sexual activity, body mass and environmental conditions are there in years with successful reproduction or reproduction failure? What factors are responsible for this reproduction failure?

## MATERIAL AND METHODS

The present study was carried out in central Germany (near Marburg 50°48'N, 8°48'E). The average annual temperature in this area is 8.5 °C and the average precipitation is 650 mm per year.

The study site (altitude: 300–320 m a.s.l.) was divided into three different trapping-areas, each approximately 50 m apart from the other, separated by agricultural land (for more details see BIEBER 1994, 1995). Area one (1 ha, »Forest«) was part of a deciduous beech forest (*Fagus sylvatica*; 111–124 years old). A partial undergrowth was present, consisting of *Sambucus racemosa* and *Sambucus nigra*. The edge of the forest was well defined and included some specimens of *Carpinus betulus, Salix* sp. and *Prunus spinosa*. Area two (1 ha, »Shrub«) comprised 1ha of an isolated bushy woodland (35–40 years old, total size 2.2 ha) characterised by highly diverse vegetation (e. g., *Fagus sylvatica, Pinus sylvestris, Picea abies, Quercus petraea, Q. robur, Tilia cordata, Salix spp., Juglans regia, Robinia pseudoacacia, Prunus domestica, Malus domestica, Pyrus communis* and *Prunus avium*). The third trapping-area (0.5 ha/»Hedge«) was an isolated hedge (35–40 years old, total size 0.5 ha). The vegetation of the hedge was similar to that of »Shrub« but with lower diversity. The dominant plants were *Prunus domestica, P. spinosa, Malus domestica* and *Corylus avellana*.

The study lasted from March 1992 to October 1993 in the areas Forest and Shrub, and from August 1992 to October 1993 in the area Hedge. Consequently, the area »Hedge« could not be taken into account for some evaluations. Dormice were captured in wooden live-traps (30 cm length; 6.5 cm width, 8 cm height). The trap-density was 100 traps/ha. Fifty traps were installed in trees and bushes 1–2 m above the ground, and 50 on the ground. Since traps had to be mounted on suitable

branches of trees 1–2 m above the ground, trap distribution was irregular and not ordered in a grid pattern. Apples, oats and sunflower-seeds were used as bait. Animals were trapped regularly twice a month in each area (I = first capture season per month; II = second capture season per month; comp. Fig. 1, 2 and 3).

Each trapping period lasted three nights (3 times 12 hours). A total of 20,700 trap-nights were evaluated. All dormice captured were registered (e. g., age, weight, trap-no.) and tattooed (ear-tattooing, tattoo-pliers/5 mm) before being released at the capture point. Age was classified according to POPOW (in VIETINGHOFF-RIESCH 1960: juvenile = 2–3 months old, before first hibernation; subadult = 11–14 months old, after first hibernation; adult = fully grown animals, beyond second hibernation) as determined by fur-colour. Sexual activity was determined in males by by testes in the scrotum or tangible in the abdomen. The oestrus cycle in females was determined by a visible, perforated vulva. Sexually competent females could be further determined indirectly by visible mammae.

## RESULTS

### Population structure

The number of captured dormice was significantly higher in 1992 than in 1993. In the »Forest« 129 dormice and in the »Shrub« 53 dormice were captured in 1992.
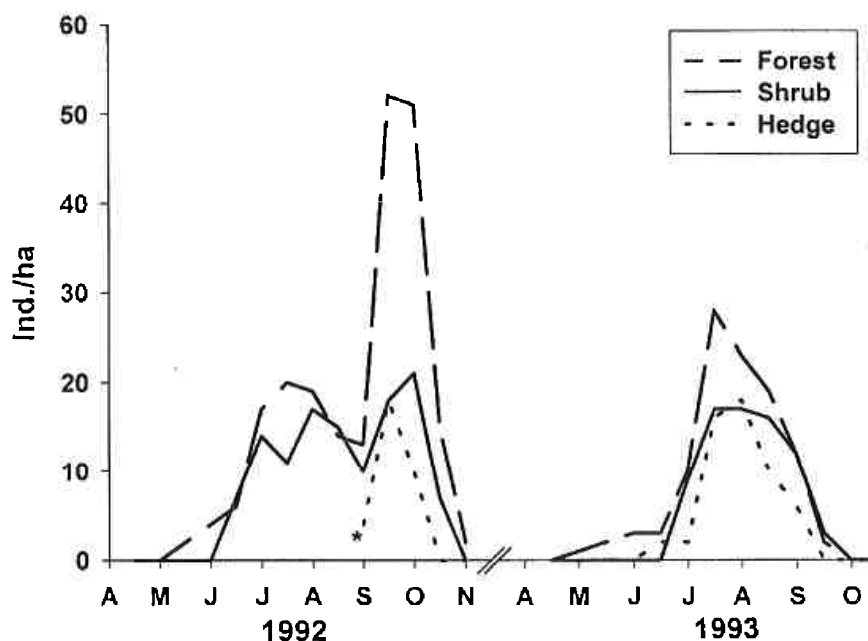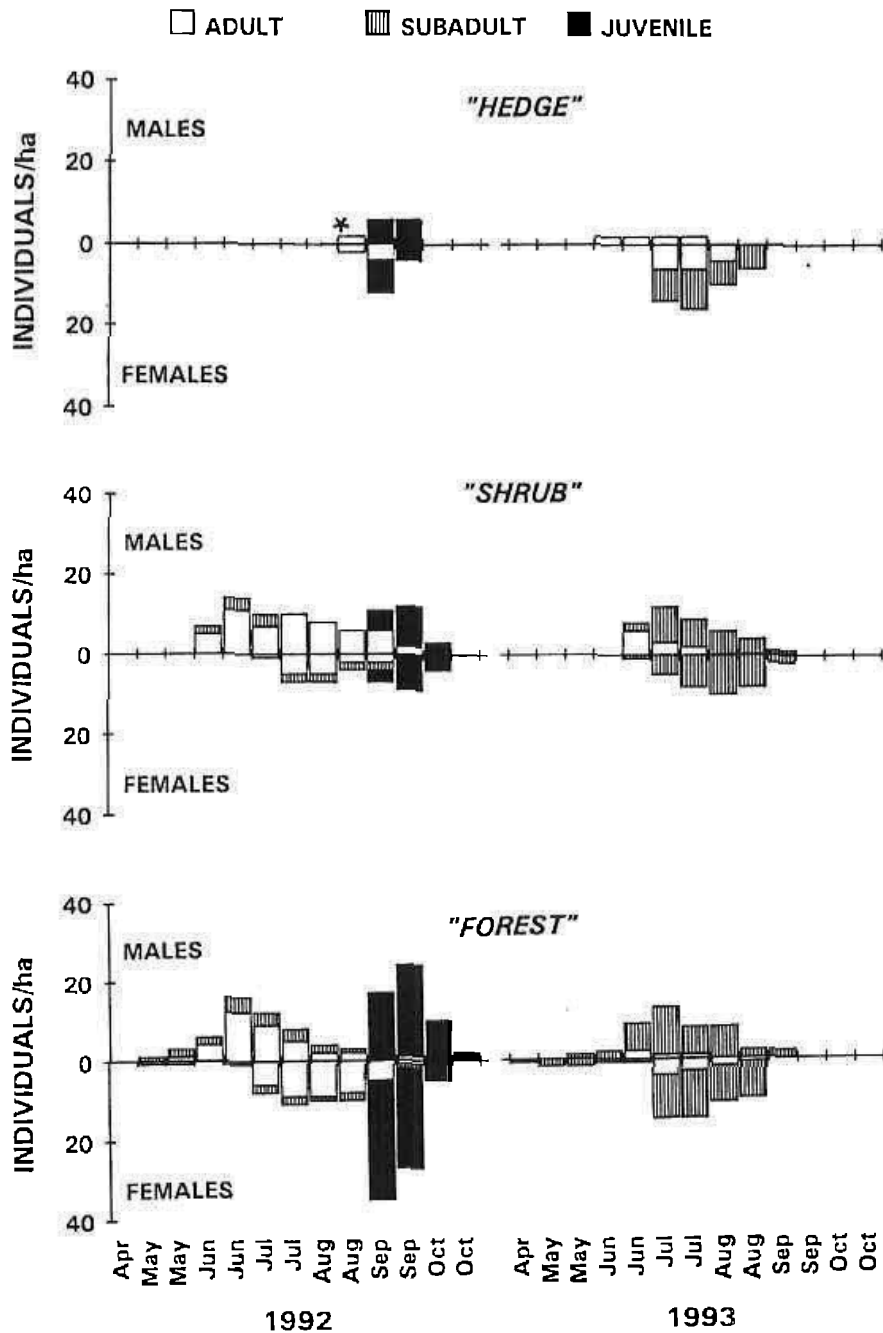


Fig. 1. Number of captured fat dormice per hectare in the courses of the years 1992 and 1993. The star indicated the start of the capture season in the area »Hedge« in 1992. For the area »Hedge« the number of animals was doubled to get individuals/ha (see material and methods).

**Fig. 2.** Number of captured fat dormice subdivided in age and sex in the years 1992 and 1993. The star indicated the start of the capture season in the area »Hedge« in 1992. For the area »Hedge« the number of animals was doubled to get individuals/ha (see material and methods).

This number changed to 51 and 33 dormice respectively in 1993 (»Forest«: $\chi^2 = 33.80$, $d.f. = 1$, $p < 0.001$; »Shrub«: $\chi^2 = 4.651$, $d.f. = 1$, $p < 0.05$). For this comparison, »Hedge« could not taken into account because of the late start of the capture season in 1992.
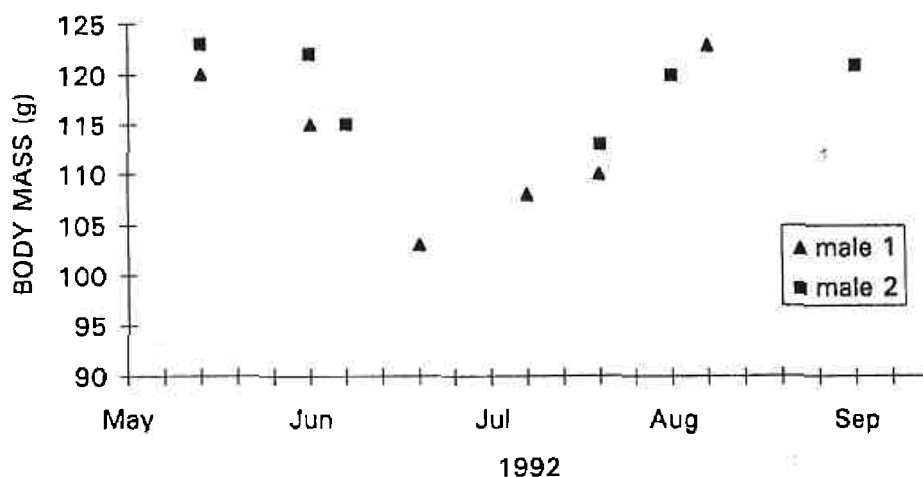
**Fig. 3.** The body mass of two adult males recaptured several times in the year 1992.

Furthermore, dormouse abundance was different in the areas »Forest« and »Shrub« in 1992 and in 1993. The most obvious difference is that in both areas the abundance peak was registered in September 1992, while only few animals could be captured in September 1993 (Fig. 1).

The abundance of subadult and adult dormice differed significantly in the areas »Forest« and »Shrub« in 1992 and in 1993. In 1992, more adult than subadult dormice were trapped, the reverse being found in 1993 (»Forest«: $\chi^2 = 35.6$, df = 1, p < 0.001; »Shrub«: $\chi^2 = 18.7$, df = 1, p < 0.001).

Subadult dormice occurred before or together with adult dormice ($\chi^2$-test, NS). Among adult animals, more males were captured in the first part of the activity season than in the second part and the reverse was found for females of this age-group (»Forest«: 1992: $\chi^2 = 24.0$, df = 1, p < 0.001; »Shrub«: 1992: $\chi^2 = 9.5$, df = 1, p < 0.01; Fig. 2). In 1993 the number of adult animals captured per trapping area was too small for separate statistical analysis. However, pooled data from the areas »Forest« and »Shrub« showed the same pattern for presence above ground for adult animals in 1993 (»Forest« + »Shrub«: $\chi^2 = 4.4$, df = 1, p < 0.05). This sex difference was not detectable among subadult dormice ($\chi^2$-test, NS). Males and females of this age-group occurred in both areas at the same time.

In 1992 the first captures of juvenile dormice were registered at the beginning of September (Fig 2). The main difference between the years 1992 and 1993 was that in 1993 no juvenile dormice were captured at all, neither in the »Forest« nor in the »Shrub« or »Hedge« (Fig. 2).

## Sexual activity

In all three trapping areas a successful reproduction in dormice in 1992 and a total lack of reproduction in 1993 could be observed. A separation of age classes into subadult and adult animals seems not very useful for describing the state of

sexual activity because it is well known (v. VIETINGHOFF-RIESCH 1960; KOENIG 1960; BIEBER 1995) that subadult males may also become sexually competent and that subadult females are able to have offspring. Therefore, sexual activity data were pooled for all three areas and for the adult and subadult age classes (Table 1).

The percentage of sexually active males in the population was zero at the beginning of the active season in 1992. It reached up to 100 percent in the second half of July. In September no sexually competent male could be captured (Table 1). The sexual activity (lactating) of females was determined indirectly by visible mammae because even in 1992, the year with high reproduction success, only one female could be captured with a perforated vulva. This indicates a short oestrus- cycle which is not detectable with the 2-week trapping-pattern used here. The percentage of lactating females reached a maximum of 93 percent in the second half of August. The first capture of lactating females minus pregnancy (30–31 days, Koenig 1960) allows the mating time to be estimated. In the present study, females mated directly after emergence, at the beginning of July (Table 1).

In 1993 the situation changed dramatically. No sexually active male and no lactating female could be captured. The most interesting fact is that none of the males ever reached a state of sexual competence (tangible testes) in 1993.

## Body mass

Due to large fluctuations in body mass in the course of the year, body mass data were compared for each trapping period. Each animal was registered at the first

Table 1. Percent of sexually active dormice in the years 1992 and 1993. Sexual activity was determined in males by visible or tangible testes, in females *indirectly* by visible mammae (=lactating, compare material and methods).

| sexual activity | males 1992 | | females 1992 | | males 1993 | | females 1993 | |
|---|---|---|---|---|---|---|---|---|
| trapping-period | % sex. active | n | % lact. | n | % sex. active | n | % lact. | n |
| April II | | | | | | | 0 | 1 |
| May I | 0 | 1 | 0 | 1 | | | 0 | 2 |
| May II | 0 | 3 | 0 | 1 | 0 | 1 | 0 | 2 |
| June I | 54 | 13 | | | 0 | 3 | 0 | 1 |
| June II | 100 | 30 | 0 | 1 | 0 | 18 | 0 | 2 |
| July I | 100 | 22 | 0 | 9 | 0 | 26 | 0 | 27 |
| July II | 89 | 18 | 0 | 18 | 0 | 18 | 0 | 31 |
| August I | 83 | 12 | 82 | 17 | 0 | 14 | 0 | 26 |
| August II | 20 | 10 | 93 | 15 | 0 | 6 | 0 | 21 |
| September I | 0 | 6 | 0 | 11 | 0 | 3 | 0 | 2 |
| September II | 0 | 3 | 0 | 2 | | | | |

capture per trapping period. Statistics were calculated for trapping periods with a number of at least 4 animals in each group. Evaluation with ANOVA showed significant effects of the factors age and year. Animals were generally heavier in 1993 than in 1992 (ANOVA, $d.f.$ = 2, p < 0.001). In particular, adult animals were also significantly heavier than subadult dormice (ANOVA, $d.f.$ = 2, p < 0.001). There was no difference in body mass between the sexes.

In adult males, a large fluctuation of body mass in the course of the year 1992 was detectable (Tab. 2). Evaluation of individual body mass changes indicated that male dormice lost weight between the end of hibernation and mating time. This effect is illustrated in fig. 3 for two males with a high recapture frequency. Male 1 lost 17 g of his weight (–14 %, from 120 g down to 103 g) and male 2 lost at least 10 g (–8,1 %, from 123 g down to 113 g). Actually, a loss of body mass occurred in all adult males recaptured during mating-time. The highest observed body mass loss in an adult male in 1992 was –31 % (from 138 g down to 94 g).

In 1993 the situation changed. There was no body mass decline among males between emergence and mating (Table 2). Furthermore, adult males could only be captured over a shorter time period (Fig. 2).

## Environmental conditions

Monthly temperatures and total monthly precipitation were slightly different in 1992 and in 1993. However, significant climatic differences occurred only during spring. Air temperature in April was significantly higher in 1993 than in 1992 (1992: +8.8 °C, 1993: +11.8 °C, paired t-test, t = –3.86, p < 0.001). Furthermore, March was significantly drier in 1993 than in 1992 (March 1992: 93 mm, March 1993: 7.1 mm, Wilcoxon-test, Z = –3.82, p < 0.0001). Thus, the spring of 1993 was unusually dry, with profound damage to the flowering of trees. Consequently, food availability was extremely different for dormice in 1992 and 1993. In 1992, all beeches and oaks had many flower buds in spring and hence considerable mast in fall. In addition, apple trees, cherry trees and plum trees had a lot of fruit in the fall. In contrast, 1993 was characterised by a total lack of mast and fruit. While these differences were not analysed statistically, they were striking, and probably biologically significant.

## DISCUSSION

All three trapping areas showed a general change in population structure in the years 1992 and 1993. The number of captured animals was lower in 1993 than in 1992. Furthermore, the age structure changed, there being a higher number of subadult and a lower number of adult animals in 1993. The area »Hedge« showed the same tendency in all of these points. However, data from this area were too small for statistical analysis. Further comparisons of the population-structure between the three trapping-areas will be published elsewhere because they are not the main focus here.

**Table 2.** Average body mass with standard deviation (X) of subadult and adult males in 1992 and 1993. Values in parenthesis indicate a low number of individuals (n).

| males trapping-period | subadults 1992 body mass (g) | adults 1992 body mass (g) | subadults 1993 body mass (g) | adults 1993 body mass (g) |
|---|---|---|---|---|
| April II | | | | |
| May I | (71) | | | |
| May II | (66 ± 19) | (105) | (91) | |
| June I | 64 ± 10 | 115 ± 15 | (86 ± 11) | (126) |
| June II | 62 ± 10 | 112 ± 11 | 82 ± 13 | 129 ± 12 |
| July I | 66 ± 7 | 97 ± 9 | 87 ± 7 | 131 ± 11 |
| July II | (82 ± 17) | 102 ± 11 | 93 ± 14 | 147 ± 28 |
| August I | (91 ± 1) | 106 ± 11 | 103 ± 16 | |
| August II | (110) | 109 ± 9 | 104 ± 9 | |
| September I | | 118 ± 10 | (99 ± 16) | |
| September II | | (134 ± 19) | | |

**Table 3.** Average body mass with standard deviation (X) of subadult and adult females in 1992 and 1993. Values in parenthesis indicate a low number of individuals (n).

| females trapping-period | subadults 1992 body mass (g) | adults 1992 body mass (g) | subadults 1993 body mass (g) | adults 1993 body mass (g) |
|---|---|---|---|---|
| April II | | | (73) | |
| May I | (83) | | (86 ± 11) | |
| May II | (93) | | (83 ± 5) | |
| June I | | ι | (82) | |
| June II | (87) | | (78 ± 14) | |
| July I | (99 ± 33) | 100 ± 13 | 85 ± 12 | 117 ± 13 |
| July II | 82 ± 24 | 113 ± 12 | 85 ± 10 | 127 ± 11 |
| August I | (82 ± 19) | 106 ± 11 | 92 ± 13 | 135 ± 16 |
| August II | 95 ± 18 | 112 ± 12 | 100 ± 16 | (136) |
| September I | (86 ± 2) | 111 ± 14 | (105 ± 6) | |
| September II | (99) | (96) | | |

The data presented here show clearly that in 1993 a reproduction failure occurred in all three trapping areas. Data of sexual activity indicate that in 1993 no sexually competent male and no lactating female could be captured in the whole study site. The reproduction failure in 1993 accounts for the lower number of individuals captured in 1993.

Up to now, several hypotheses explaining low success, or even a complete lack of reproduction, have been discussed. One common explanation is that female dor-

mice may reabsorb embryos under unfavourable environmental conditions (v. VI-ETINGHOFF-RIESCH 1960). Other authors observed that males were also less sexually active and had small testes in years with a low reproductive success (LÖHRL 1955; HÖNEL 1991). These results suggest that not only females, but also males, may cause a lack of reproduction. Furthermore, I could observe that males in 1992 became sexually active (comp. NIESSING 1956) well before females occurred in the study-site. This indicates that males decide early, and independently of the females, whether to invest in the effort of mating and reproduction or not. These conclusions raise questions about the costs of reproduction in particular for males. The body mass data show clearly that adult males significantly lost body weight between emergence and mating in 1992, the year with a high reproductive success. These results indicates that adult males had high energy expenditures prior to mating and thus high costs for reproduction in 1992. These costs may be caused, for example, by the defence of territories (MÜLLER 1989; HÖNEL 1991). Actually, males seem to have energetic costs of reproduction that are at least comparable to those of females (comp. KENAGY et al. 1989). The energetic requirements for males may be even higher because females showed only a slight decline in body weight prior to lactation in 1992.

In 1993, the year without reproduction, no weight loss in adult males was detectable. This observation suggests that males saved the energy required for reproductive effort in 1993. This change in male sexual activity may represent an adaptation to fluctuating food supplies, such as the observed mast of beech and oak in 1992, and a total lack of seeds in 1993. Beech and oak seeds are very important for prehibernation fattening, and body weight losses due to mating effort may well be hazardous for males in years with a low food supply prior to hibernation.

From all these conclusions one question arises: how could males in spring and early summer, at the time when testicular growth occurs in »regular« years, predict the fruit situation in fall? This problem is illustrated in Fig 4. At present, we know
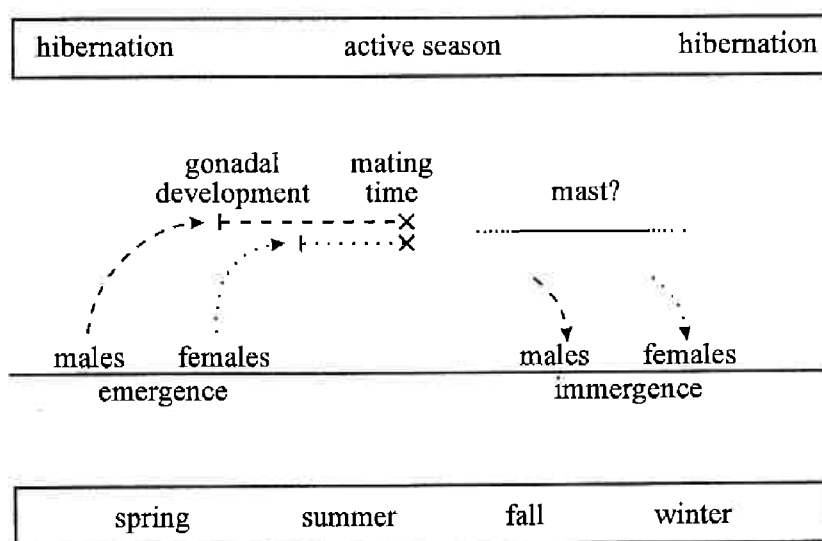


**Fig. 4.** Reproduction cycle in the fat dormouse. For details see text.

nothing about the environmental cues responsible for this prediction. A hypothesis based on the different body condition between the years and population density has so far been rejected because dormice were even heavier after hibernation in 1993 even heavier than in 1992. Two hypotheses seem plausible: Firstly, male dormice may be directly influenced by weather conditions in spring or, secondly, they may use secondary plant components (e. g. in flowers buds, comp. KORN 1988) for an early adjustment of gonadal development. However, we certainly need more information to reveal the mechanisms underlying these adjustments.

## ACKNOWLEDGEMENTS

## REFERENCES

BIEBER, C., 1994: Dispersal Behaviour of the edible dormouse (*Myoxus glis* L.) in a fragmented landscape. – Hystrix, (n.s.) 6 (1–2), 257–263 (1995).

BIEBER, C., 1995: Ökologische Untersuchungen zur Populationstruktur und -dynamik sowie zur Reproduktionsbiologie an drei Subpopulationen des Siebenschläfers. – PhD thesis, Philipps-Universität Marburg, Wissenschaft in Dissertationen Bd. **25**. Marburg, Verlag Görich & Weiershäuser GmbH.

DOBSON, F. S., 1995: Regulation of population size: evidence from columbian ground squirrels. – Oecologia. **102**, 44–51.

HÖNEL, B., 1991: Raumnutzung und Sozialsystem freilebender Siebenschläfer (*Glis glis* L.). – PhD thesis, Fakultät für Bio- und Geowissenschaften der Universität Karlsruhe.

KENAGY, G. J., SHARBAUGH, S. M., NAGY, K. A., 1989: Annual cycle of energy and time expenditure in a golden-mantled ground squirrel population. – Oecologia. **78**, 269–282.

KOENIG, L., 1960: Das Aktionssystem des Siebenschläfers (*Glis glis* L.). – Zeitschrift für Tierphysiologie. **17**, 427–505.

KORN, H., 1988: A feeding experiment with 6-methoxybenzoxazollnone and a wild population of the deer mouse (*Peromyscus maniculatus*). – Canadian Journal of Zoology. **67**, 2220–2223.

KULZER, E., LINDEINER-WILDAU, A. v. and WALTERS, I.-M., 1993: Säugetiere im Naturpark Schönbuch – Übersicht über die Biologie der Arten und Ergebnisse einer faunistisch-ökologischen Untersuchung in den Jahren 1989–1991. – Beiheft zu den Veröffentlichungen für Naturschutz und Landschaftspflege in Baden-Württemberg, pp. 78–85. Karlsruhe.

LÖHRL, H., 1955: Vermehrungsausfall beim Siebenschläfer im Jahre 1954.-Säugetierkundliche Mitteilungen. **3**, 177.

MÜLLER, H., 1989: Untersuchungen zum Raum-Zeit-System freilebender Siebenschläfer (*Glis glis* L.). – Diploma thesis, Universität des Saarlandes, Saarbrücken 1988; Durchsicht und Verbesserung, 1989.

NIESSING, K., 1956: Cytodynamik des Hodens und Nebenhodens beim Siebenschläfer (*Myoxus glis* L., *Glis glis* L.). – Zeitschrift für Zellforschung und mikroskopische Anatomie. **43**, 566–593.

SCHLUND, W., 1996: Vergleich von Siebenschläferpopulationen (*Myoxus glis* L.) in zwei unterschiedlichen Waldgebieten – Einfluß von Habitatqualität auf Populationsstruktur, Morphologie und Reproduktion von Siebenschläfern. – PhD-Thesis, Eberhard-Karls-Universität Tübingen, Schwäbische Verlagsgesellschaft Tübingen.

STORCH, G., 1978: Gliridae. – In: Niethammer, J. & Krapp, F.: Handbuch der Säugetiere Europas, Band 1, Rodentia I. 201–280. Wiesbaden, Akademische Verlagsgesellschaft.

VIETINGHOFF-RIESCH, A. Frhr. v., 1960: Der Siebenschläfer (*Glis glis* L.). – Monographien der Wildsäugetiere, **14**, Jena, pp. 196.

WILSON, D. E. & REEDER, D. M., 1993: Mammal species of the world: A Taxonomic & Geographical Reference, 2. Edition. – Washington, Smithsonian Institution Press.

# SUMMARY

## Sexual activity and reproduction in three feral subpopulations of the fat dormouse (*Myoxus glis*)

### C. Bieber

Population-ecology and reproduction in three subpopulations of the fat dormouse (*Myoxus glis* Linné, 1766) were studied in central Germany in the years 1992 and 1993. Animals were captured in wooden livetraps twice a month, during trapping-periods lasting three days, and marked individually by tattooing.

Surprisingly, after a year with good reproductive success (1992), a total lack of reproduction was observed in all three areas in 1993. Juvenile dormice were found neither in traps nor in nest-boxes. The assessment of gonadal states indicated that all males (adult and subadult) remained in a state of testicular regression throughout the year 1993. Also, no female was found lactating. Reproductive failure coincided with a lack of food resources in fall 1993 (e. g., oak and beech-nuts).

Body mass changes indicate high energy expenditure and body mass loss prior to mating in adult males. It seems likely that in years with low food availability males do not invest energy in reproduction. Presumably, bad weather conditions or predictive environmental signals, such as missing flower buds in the dry spring of 1993, prevented gonadal development in males.

# SAŽETAK

## Spolna aktivnost i razmnožavanje u tri divlje subpopulacije sivog puha (*Myouxus glis*)

### C. Bieber

Proučavana je ekologija populacije i razmnožavanje u tri divlje subpopulacije sivog puha (*Myoxus glis* Linn, 1776) u centralnoj Njemačkoj 1992. i 1993. godine. Životinje su hvatane u drvene živolovke dvaput mjesečno, tijekom trodnevnih lovnih perioda, i markirane tetoviranjem. Nakon godine s uspješnom reprodukcijom (1992), najednom je zabilježen potpuni izostanak reprodukcije na sva tri područja u 1993. godini. Mladi puhovi nisu pronađeni ni u klopkama ni u kućicama. Pregledom stanja gonada uočeno je da su kod svih mužjaka (adultnih i subadultnih) testisi ostali u regresivnom stanju tijekom cijele 1993. godine. Također nije pronađena nijedna ženka u laktirajućem stanju. Izostanak reprodukcije poklopio se s manjkavim izvorima hrane ujesen 1993. (npr. žir i bukvica). Promjene u tjelesnoj težini ukazuju na veliki utrošak energije i gubitak težine prije parenja kod odraslih mužjaka. Čini se vjerojatnim da mužjaci u godinama sa slabo dostupnom hranom ne ulažu energiju u reprodukciju. Pretpostavlja se da su loši vremenski uvjeti ili predvidljivi uzroci iz okoliša, kao izostanak cvjetnih pupova u suho proljeće 1993. godine, spriječili razvoj gonada kod mužjaka.