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Influence of mortality and dispersal on sex ratio of the edible dormouse (*Glis glis*)

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Abstract. While most mammal populations show equalized sex ratios in their offspring, some species reveal deviations as a reaction to environmental circumstances. The recent study focuses on mortality, dispersal and biased sex ratio in the offspring of the edible dormouse (*Glis glis*) and their influence on next year's subadult population. Between 2002 and 2008 a male biased sex ratio in the offspring but an almost equal sex ratio of next year's subadult population has been found. Our results reveal that this deviation from the 1:1 sex ratio compensates a higher mortality rate of young males. The data used for this study were obtained from a mark and recapture project of monitoring the population biology of the edible dormouse performed north-east of Frankfurt/Main, Germany.

Key words: individual marking, daily nest box checks, young dormice, biased sex ratio, sex allocation

Introduction

While most mammal populations show equalized sex ratios according to the “Fisher's principle” (Fisher 1930), adaptive adjustment of sex ratio has been found among many animals including e.g. primates (Silk & Brown 2008), red deer (Clutton-Brock et al. 1984) or birds (Komdeur et al. 1997, Sheldon et al. 1999). For most of these species biased sex ratio is a reaction to environmental circumstances like e.g. temperature, availability of food or population density that may affect competition, mortality or dispersal rates in either males or females. For example, the sex of the offspring of some turtles and crocodile species is determined by temperature and day length (Bull 1980, Ferguson & Joanen 1982). Hamilton (1967) hypothesized that biased sex ratios can also result when mothers benefited from the presence of other relatives. Evidence for biased sex ratios in favour of helpers has been found in a number of animals, including African wild dogs (McNutt & Silk 2008) and various primates (Silk & Brown 2008). The competition for local resources like e.g. food, nesting places or mates has been recognized by Hamilton (1967) to be the reason selection may favour population sex ratios with unequal investment in males and females under some conditions. Appleby et al. (1997) observed that parents of tawny owls

(*Strix aluco*) adjust the sex ratio of their offspring based on the availability of food, with a female sex bias in areas of high prey density and a male sex bias in areas of low prey density. Clark (1978) described a male biased sex ratio in the offspring of the African bushbaby (*Otolemur crassicaudatus*) due to the fact that daughters remain longer in the mother's territory and compete with their mothers for resources. The exact mechanisms of such allocations are unknown, but several studies indicate that hormonal, preovulatory control may be responsible (Komdeur et al. 2002, Pike & Petrie 2006). However, biased sex ratio in the offspring can be a possibility to improve the aggregate productivity of a trait group by balancing competition, mortality or dispersal. The recent study focuses on biased sex ratio in the offspring of the edible dormouse (*Glis glis*).

Material and Methods

The data used for this study were obtained from a mark- and recapture project monitoring the population biology of the edible dormouse near the town of Steinau an der Straße (50°20' N, 9°30' E), 65 km north-east of Frankfurt am Main, Germany. The sample area which – due to intensive forestry use – shows nearly no natural holes comprises 94 nestboxes installed on a 25 × 25 m grid of 5.6 ha. The study area

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contains mixed deciduous woodland of approx. 120 years with oak *Quercus robur*, common beech *Fagus sylvatica* as well as hornbeam *Carpinus betulus* and a well developed shrub layer. From April to late autumn 2002 to 2008 once a week all nestboxes were opened and all dormice found were captured and marked with passive transponders (ID 162/MC968 in cannula). Additionally all nestboxes were scanned daily with a transponder reading device without opening them to keep disturbance at a minimum. Both transponders and reading device are products of AEG ID GmbH. We distinguished between juveniles that were

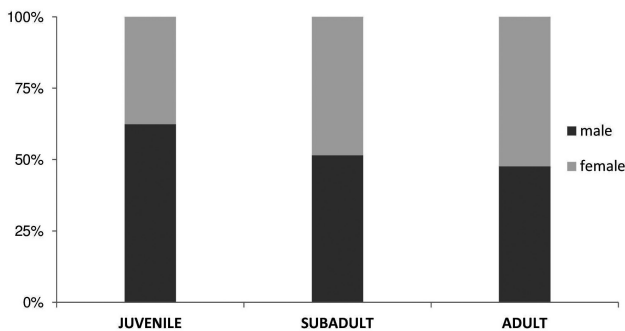


Fig. 1. Percentage of males and females in different age classes from 2002-2008.

Table 1. Number of edible dormice in each age class from 2002 to 2008.

| Year | Juvenile | | Subadult | | Adult | |
|-------|----------|---------|----------|---------|-------|---------|
| | Males | Females | Males | Females | Males | Females |
| 2002 | 63 | 33 | | | | |
| 2003 | 11 | 5 | 27 | 31 | 35 | 32 |
| 2004 | 48 | 31 | 3 | 2 | 42 | 45 |
| 2005 | 0 | 0 | 36 | 40 | 24 | 27 |
| 2006 | 44 | 24 | 0 | 0 | 42 | 52 |
| 2007 | 58 | 42 | 22 | 14 | 31 | 35 |
| 2008 | 0 | 0 | 16 | 11 | 23 | 26 |
| Total | 224 | 135 | 104 | 98 | 197 | 217 |

Table 2. Number of disappeared young males and females after each reproduction year.

| Year of birth | Males | Females |
|---------------|-------|---------|
| 2002 | 46 | 17 |
| 2003 | 10 | 4 |
| 2004 | 29 | 18 |
| 2005 | - | - |
| 2006 | 33 | 20 |
| 2007 | 48 | 33 |
| 2008 | - | - |
| Total | 166 | 92 |

Table 3. Number of recaptured and immigrated subadult males and females each year from 2003 to 2008.

| Year | Males | | Females | |
|-------|------------|------------|------------|------------|
| | Recaptured | Immigrated | Recaptured | Immigrated |
| 2003 | 17 | 10 | 16 | 15 |
| 2004 | 1 | 2 | 1 | 1 |
| 2005 | 19 | 17 | 13 | 27 |
| 2006 | 0 | 0 | 0 | 0 |
| 2007 | 11 | 11 | 4 | 10 |
| 2008 | 10 | 6 | 9 | 2 |
| Total | 58 | 46 | 43 | 55 |

born in the respective year, subadult animals that had overwintered only once and adults, that had overwintered at least twice. The age of the animals was determined by their body size and the colour of their fur according to Schlund (1997).

We statistically tested data according to the Gaussian distribution curve (number of males/females born, number of animals that disappeared during first hibernation) with paired t-test. The data describing immigration and recapture were tested with paired t-test as well as the non-parametric Wilcoxon Matched Pairs Test.

Results

The number of juveniles born in the nestboxes varied between the years. In 2003 only few litters were born and only few subadult animals could be found in the following year. There was no reproduction in 2005 and 2008 and no subadult animals in the following year.

As Table 1 shows, we registered a significantly male biased sex ratio in the offspring of edible dormice ($p = 0.0237$, $df = 6$) throughout all years in which reproduction took place. This deviation from the 50:50 sex ratios could neither be found in the subadult nor in the adult populations of the following years (Fig. 1). Still, male subadult and female adult animals outweighed during the study period but these variances from an equal sex ratio were not significant. Less than 30% ($n = 101$) of all juveniles born ($n = 359$) in our study area could be recaptured. Significantly more males than females disappeared before the following activity period ($p = 0.0322$, $df = 6$) (see Table 2).

Daily checks with a scanner allowed recording each marked edible dormouse using nestboxes at least for one day. In spite of the high number of young males born, there is no significant difference in the number

of male and female subadult animals in the following year ($p = 0.696$, $df = 6$, $n = 202$). Additional to the recaptures each year following a reproduction year new edible dormice would immigrate as Table 3 shows: the number of recaptured and immigrated animals would change from year to year. In total approximately half of the subadult population consists of immigrated animals. There is no significant difference between males and females ($p = 0.4859$, $t = 0.7521$, $df = 5$) but a trend towards a higher immigration rate of female subadult edible dormice.

Discussion

The data of the recent study show a strictly male biased sex ratio in the offspring of edible dormice throughout all study years. Biased sex ratios in the offspring are a phenomenon which has been found among many animals and is supposed to increase the fitness of a trait group of a species. Trivers & Willard (1973) first proposed a verbal model for polygynous mammals in which a mother may allocate offspring to different sexes according to her condition: male biased investment when she is in good condition and female biased investment when she is in bad condition. However, edible dormice are known to be deliberate towards investing into offspring and reproduction will only occur in years with rich seed mast (Bieber 1998, Schlund et al. 2002, Pilastro et al. 2003) and therefore good conditions of females. Fisher (1930) postulated a 1:1 primary sex ratio unless parental care is involved. If parents have to put a different amount of energy into one sex a biased sex ratio towards the gender that is less costly to raise will result. In our study area, young female dormice are found more often together with adult females (Koppmann-Rumpf et al. 2012). An increased parental care for daughters would therefore lead to a male biased offspring. Martin & Pilastro (1994) found in their study area several closely related females e.g. mother and daughter sharing nestboxes. In cooperative breeders, mothers are assisted by their previous daughters in raising new offspring. In animals with these systems, females are predicted to preferentially have offspring biased towards the helping gender if there are not enough helpers. However, if there are already enough helpers, females would invest in offspring of the other sex, as this would allow them to increase their own fitness by having dispersing offspring with a greater rate of reproduction than the helpers (McNutt & Silk 2008). Although this would be an explanation for biased sex ratio in both male and female direction, communal nesting with kin relatives does not seem

to be a regular phenomenon in our study area and is therefore not suitable to explain the local male biased sex ratios.

The high disappearance rate of young males during first hibernation leads to a nearly equal sex ratio in the next year's subadult population. Obviously edible dormice do have a 1:1 sex ratio in subadult and adult populations. One reason for a biased offspring in various species can be found in dispersal. Besides the genetic consequences, competition for local resources like food, mates or nesting places is a reason for leaving natal places. Although some studies showed that dormice might disperse already before their first hibernation (e.g. Bieber 1995, Worschech 2012) we consider the principle part of animals dispersing to be subadult dormice. Our data show that the subadult population is nearly equally composed of immigrated dormice and animals marked in the study area the year before. Sex biased dispersal is a widespread pattern in vertebrate organisms and it often includes a biased sex ratio towards the dispersing gender (Gowaty 1993). In general, mammals exhibit male-biased dispersal (Prugnolle & de Meeus 2002). Following the idea of a male biased sex ratio due to a distinct male biased dispersal there should be an explicitly higher number of immigrated subadult males. From 2002 to 2008 an equal immigration rate of both male and female subadult dormice with even a trend towards females can be observed in our study area. Therefore we assume a high male mortality before or during first hibernation.

There are several studies trying to explain sex differences in survival of various species of mammals. After Moore & Wilson (2002) there is a link between sex biased parasite load, sexual dimorphism and risky male behaviour that might lead to a biased mortality. Additionally, a higher testosterone level should be responsible for a decreased immuno competence in males (e.g. Zuk & McKean 1996). However, these studies do not explain the loss of especially young males. Once young dormice survived their first winter, life expectation of males and females does not differ significantly (Lebl et al. 2011) which still reveals the question why the period between weaning and first activity period is so dangerous for young males respectively why female offspring has better chances to survive its first winter. Studies on communal nesting of edible dormice could show an increased nestbox sharing of young and subadult females with adult animals (Koppmann-Rumpf et al. 2012). Nestbox sharing can be a strategy to save energy (Fietz et al. 2010) which is supposed to be of high value for

surviving hibernation. To share sleeping places – especially during the cold season – gives young females an advantage towards males especially if this would include hibernation. Additionally Pilastro (1992) discussed communal nesting as a strategy to improve protection from predation, which is supposed to be the major factor determining the life span of small rodents (Norrdahl & Korpimäki 1995). We assume that biased sex ratio in the offspring of edible dormice is a strategy to compensate biased mortality which might be influenced by various factors such as e.g. deviating parental care, unequal demand for energy or physiological differences leading to biased vulnerability towards environmental circumstances.

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