

# Male-biased litter sex ratio in the southernmost Iberian population of edible dormouse: a strategy against isolation?

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## Abstract

Litter sex ratio is a key component of parental fitness due to its impact on lifetime reproductive success. Multiple causes may lay at the origin of sex ratio variation among species and populations, such as maternal condition, local resource competition, presence of helpers, habitat quality or inbreeding levels. Whereas variation in sex allocation between species is relatively well understood, it is still unclear how and why litter sex allocation differs within species. Here, we present an analysis of litter sex ratio variation in two populations of edible dormice (*Glis glis*) over nine years of study. Populations are situated in the Montnegre and Montseny massifs in Catalonia (NE Iberian Peninsula). The Montnegre population is nowadays an isolated population located at the southernmost range edge of the species in the Iberian Peninsula. Litter sex ratio was male-biased in Montnegre but balanced in Montseny, whereas both populations showed a balanced adult sex ratio. We suggest that this differential sex allocation investment in Montnegre, may be a strategy to overcome isolation effects in this massif, as males are the dispersing sex in this and other rodent species.

## Keywords

Adaptive sex ratio variation; dispersal; dispersion; fat dormouse; *Glis glis*; sex allocation; sex ratio

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## Introduction

Fisher's principle argues that natural selection should produce balanced sex ratios if the cost of production of both sexes is the same (Fisher, 1930). This principle has been corroborated in many species, but a large amount of studies have also found evidence of a biased sex ratio at birth (Clutton-Brock, 1986; Clutton-Brock & Iason, 1986; Cockburn et al., 2002; Komdeur, 2012).

There is now substantial empirical and theoretical evidence that multiple causes may lay at the origin of this bias, especially in taxa with complex life histories and social systems such as birds or mammals (Cockburn et al., 2002). First, females in better condition (i.e., status, territory quality or body characteristics) should produce a higher proportion of males (Trivers and Willard hypothesis, Trivers & Willard, 1973). The underlying explanation is that by producing sons they may achieve a greater fitness return for an equal investment (Trivers & Willard, 1973). Second, in species with sex biased competition, sex allocation should be biased towards the dispersing sex. Under intensified competition, the dispersing sex should be overproduced to promote a reduction in competition by increasing the number of potential dispersers in the population (local resource competition hypothesis, Clark, 1978; Silk, 1983). Third, when offspring of one sex cooperate with each other or with their parents, the helping sex should be overproduced (local resource enhancement hypothesis, Emlen et al., 1986; Komdeur et al., 1997). Fourth, given that environment varies spatially, reproductive performance should also vary according to the quality of the reproductive habitat (Julliard, 2000). Thus, if dispersal behavior is biased, it would be adaptive to overproduce the dispersing sex in low-quality habitats since this sex is more likely to disperse to another habitat with better quality. On the contrary (in high-quality habitats), it would be adaptive to overproduce the philopatric sex. Finally, in inbred populations an overproduction of the dispersing sex is expected to increase the fitness return for females. Indeed, given that a negative relationship between inbreeding and fitness is often observed (see Kempnaers, 2007 for a review) and relatives tend to be clustered around the natal site (Greenwood, 1980), the dispersing sex would achieve major fitness by mating with unrelated individuals.

Despite decades of interest, sex allocation studies still give unexpected results, especially in higher vertebrates (West et al., 2002). Furthermore, most studies on variation in sex allocation have been based on among-species comparisons, despite the fact that proposed mechanisms should also apply within species. In fact, recent work has shown within-species variation in sex allocation (Stauss et al., 2005; Michler et al., 2012). The aim of this study was to investigate litter sex ratio variation in the two southernmost wild populations of edible dormice (*Glis glis*) of the Iberian Peninsula, situated in Catalonia (the Montseny and Montnegre massifs). Although the two studied massifs are only separated by 10 km, the population of edible dormouse of Montnegre (located further south) is virtually isolated from the nearest population (Montseny). Additionally, the Montnegre population has suffered from a recent retreat of its deciduous forest, suffers from drier conditions than

the Montseny population and, therefore, has an uncertain future in terms of survival (Ribas et al., 2009). Because there are important differences in habitat quality between these two sites, we predicted that sex allocation and, as a consequence, litter sex ratio differs among Montseny and Montnegre edible dormice populations.

## Material and methods

### *Studied species*

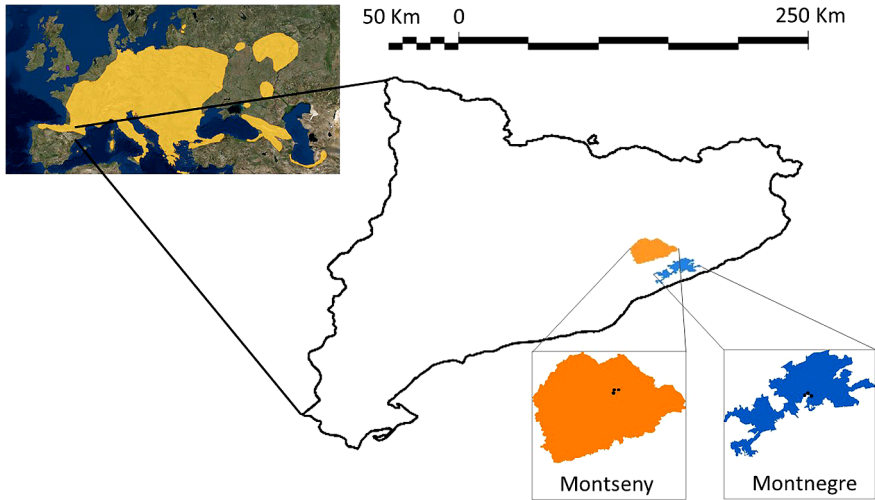
The edible dormouse is an arboreal, nocturnal and hibernating small mammal with a general distribution across Europe (Amori et al., 2008). From mid-June to mid-August, they mate (Bieber & Ruf, 2004; Özkan, 2006) and give birth to one litter per year in Southern Europe (occasionally two; Santini, 1978; Pilastro, 1992). On the contrary, in central and northern Europe edible dormice are characterized by low or no reproduction in years with low food availability (i.e., low beech or oak crops; Pilastro et al., 2003). A litter is composed of 1 to 11 pups, with an average of 4.75 to 6.80 pups depending on the geographical location (Kryštufek, 2010). Pups are born hairless, develop their fur at 16 days, open their eyes after 3 weeks and leave the nest at 30 days (Kryštufek, 2010).

### *Study sites and sample collection*

The data used for this study were obtained from a capture-mark-recapture study monitoring the two southernmost populations of the edible dormouse on the Iberian Peninsula: Montseny and Montnegre. The sampled area in Montseny is a 5-ha deciduous forest (*Quercus petraea*, *Fagus sylvatica*, *Corylus avellana* and *Acer opalus*) mixed with *Q. ilex* and *Ilex aquifolium*, surrounded by beech-dominated deciduous forest. It is situated in the center of the Montseny Biosphere Reserve (range 1078-1143 m a.s.l., 41°47'59"N, 2°25'14"E), with a mean temperature of 9.5°C and a precipitation of 975 mm per year (fig. 1).

The sampled area in Montnegre is a 5-ha deciduous forest (*Q. canariensis*, *Q. petraea*, *C. avellana*, *Castanea sativa* and *Prunus avium*) mixed with *Q. ilex* and *I. aquifolium*, surrounded by Mediterranean forest. It is situated in the northern slopes at the top of the Montnegre massif (range 700-764 m a.s.l., 41°39'37"N, 2°34'44"E), with a mean precipitation of 840 mm per year (fig. 1). The southernmost population of Montnegre is virtually isolated from the nearest population (Montseny). Indeed, despite the short distance (10 km) among populations they are separated by open unsuitable habitat and a freeway that is likely to strongly hinder the dispersion of animals from one population to the other.

For data collection, nest boxes (30 cm × 15 cm × 15 cm, with a 5 cm entry hole) were attached to trees at a height of approximately 3 m aboveground (Freixas et al., 2011). Nest boxes are frequently used by dormice during the active period. Data collection differed from 2007 to 2011 and from 2012 to 2015 regarding the sampling design and the frequency of sampling (table 1). While from 2007 to 2011



**Figure 1.** Location of our two sampling areas (Montseny and Montnegre). The light area over Europe in the left map represents the distribution range of the edible dormouse. This figure is published in colour in the online version.

sampling was designed to obtain data during the reproductive period, 2012-2015 sampling was designed to increase data quantity and quality by increasing monitoring effort in order to encompass the overall active period of the species (table 1).

Nest boxes were inspected during the day, when dormice can be found sleeping inside the boxes, and lasted a maximum of 15 min per individual. All captured dormice were identified by a unique number, sexed and aged. Pups were aged according to the color of their fur (pink pups; grey and eyes close pups; grey and eyes open pups); juveniles were aged according to their body size and tibia length ( $\geq 30$  days of life); yearlings (after their first hibernation, already sexually mature) and

**Table 1.**

Summary of the sampling designs of the two studied periods.

|                              | 1st period (2007-2011)  | 2nd period (2012-2015)  |
|------------------------------|---|---|
| Type of sampling design      | Transects <sup>A</sup> with 6 nests/transect  | Plots <sup>B</sup> with 20 nests/plot                           |
| Number of nests in Montseny  | 24 nests  | 60 nests  |
| Number of nests in Montnegre | 48 nests  | 60 nests  |
| Monitoring effort            | Once/twice a year during the <i>reproductive</i> period (mid-August to mid-October) | Every two weeks during the <i>active</i> period (June-December) |

<sup>A</sup>20 m.

<sup>B</sup>5 × 4 nest boxes placed in a grid and separated of 30 m, occupying just over 1 ha (the plots of the same population are separated by a maximum distance of 675 m).

adults (after their second hibernation) (Schlund, 1997; National Dormouse Monitoring Programme, 2015). Juveniles, yearlings and adults were marked using a transponder (AVID Musicc,  $8 \times 2.1$  mm) injected under the skin of the neck. The implantation of the transponder has no obvious adverse effects. Also, a numbered metal ear-tag (National Band and Tag Co., USA) was placed on the ear.

We measured litter size as the number of pups with less than fifteen days (i.e., pink pups or grey eyes close pups) because there is a low rate of mortality at this stage in both studied populations (personal observations, unpublished). The analysis of sex ratio was performed only on litters with at least two pups (only one litter had a single pup) for which the sex of all pups was known. The number of captured mature individuals (yearlings and adults) each year was used to calculate sex ratio of mature individuals.

### *Statistical analysis*

A Generalized Linear Mixed Model (GLMM) was used to investigate whether the sex ratio differed between populations (Montseny and Montnegre). The GLMM was performed using the function “GLMR” of the R package “LME4” (Bates et al., 2011), with the proportion of males per litter as response variable. The GLMM was used with a logit link and a variance given by a Binomial distribution. The population and the year of sampling were included as fixed factors. To control for females having reproduced several times during their lives, maternal identity was included as a random effect.

To investigate mature individual sex ratio in the studied populations, two-tailed Wilcoxon paired tests were used to compare yearly sex ratio of mature individuals within each population. All statistical analyses were conducted using the R software version 3.3.0 (R Development Core Team, 2016).

## **Results**

Litter sex composition was determined for 74 complete litters (404 pups from 60 different mothers) (see table 2 for details on litter sex composition per year). In Montseny, sex composition was determined for 48 complete litters (250 pups from 38 different mothers and a mean ( $\pm$  SD) litter size of  $5.21 \pm 1.62$ ) and in Montnegre, for 26 litters (154 pups from 22 different mothers and a mean ( $\pm$  SD) litter size of  $5.92 \pm 1.65$ ). More than half of the marked juveniles were not recaptured (i.e., either dispersed or dead) after their first hibernation (Montseny: 91% of males and 87% of females; Montnegre: 72% of males and 54% of females).

In Montseny, the litter sex ratio (proportion of males in a litter) was 0.52 and did not significantly differ from 0.50 (95% CI = 0.46-0.58; fig. 2). On the contrary, the litter sex ratio in Montnegre was 0.61 and significantly departed from 0.50 (95% CI = 0.55-0.67) showing a male-biased litter sex ratio (fig. 2). According to our

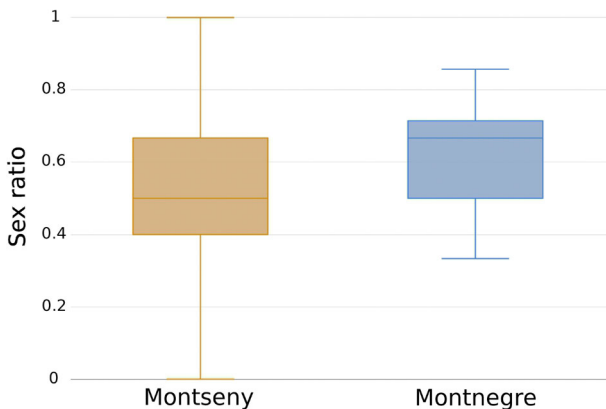
**Table 2.**

Mean litter sex ratio (proportion of males/litter) in the two studied populations (Montseny and Montnegre) each year.

| Year | Sex ratio |           |
|------|-----------|-----------|
|      | Montseny  | Montnegre |
| 2007 | 0.61      | 0.72      |
| 2008 | 0.31      | 0.49      |
| 2009 | 0.56      | 0.68      |
| 2010 | 0.45      | 0.51      |
| 2011 | 0.36      | 0.56      |
| 2012 | 0.50      | 0.67      |
| 2013 | 0.52      | 0.72      |
| 2014 | 0.60      | 0.67      |
| 2015 | 0.51      | 0.53      |

prediction, litter sex ratio was found to significantly depend on the studied population (table 3, fig. 2). No significant relationship between litter sex ratio and year was observed (table 3).

The Montseny population of mature individuals was bigger despite an equal sampling effort in both sites (mean  $\pm$  SE number of mature females in Montseny:  $15.75 \pm 10.96$ ; mean  $\pm$  SE number of mature females in Montnegre:  $4.75 \pm 0.96$ ; table 4). In Montseny, sex ratio of mature individuals was found to be balanced (Wilcoxon paired test:  $V = 0$ ,  $P = 0.18$ ,  $N = 112$ ). Surprisingly, the male biased litter sex ratio found in Montnegre was no longer existent in mature individuals, where sex ratio was found to be balanced (Wilcoxon paired test:  $V = 3$ ,  $P = 0.58$ ,  $N = 34$ ).



**Figure 2.** A boxplot representing litter sex ratio (proportion of males/litter) in the two studied populations (Montseny and Montnegre). This figure is published in colour in the online version.

**Table 3.**

Generalized Linear Mixed Model showing the effects of terms on the proportion of males in a litter. We used Wald's test to measure the contribution of each categorical factor to the overall model and included the statistic ( $\chi^2$ ) and the degrees of freedom (df).

| Independent variable | Estimate $\pm$ SE | <i>p</i> -value | Wald test |    |                 |
|----------------------|-------------------|-----------------|-----------|----|-----------------|
|                      |                   |                 | $\chi^2$  | df | <i>p</i> -value |
| Intercept            | 0.99 $\pm$ 0.39   | 0.01            | 6.3       | 1  | 0.01            |
| Population           | -0.56 $\pm$ 0.23  | 0.02            | 5.6       | 1  | 0.02            |
| Year                 |                   |                 |           |    |                 |
| 2008                 | -0.99 $\pm$ 0.51  | 0.05            | 10.7      | 8  | 0.22            |
| 2009                 | -0.22 $\pm$ 0.53  | 0.68            |           |    |                 |
| 2010                 | -0.87 $\pm$ 0.52  | 0.10            |           |    |                 |
| 2011                 | -0.94 $\pm$ 0.53  | 0.08            |           |    |                 |
| 2012                 | -0.39 $\pm$ 0.49  | 0.43            |           |    |                 |
| 2013                 | -0.21 $\pm$ 0.48  | 0.66            |           |    |                 |
| 2014                 | -0.03 $\pm$ 0.46  | 0.95            |           |    |                 |
| 2015                 | -0.39 $\pm$ 0.49  | 0.42            |           |    |                 |

## Discussion

Litter sex ratio was found to be male-biased in one isolated southernmost population of edible dormice, but not in other close-by population. The bias towards males reported in Montnegre is consistent with observations from a German population (Koppmann-Rumpf et al., 2015). No sex ratio bias was found for mature individuals in both populations, as was also the case in the German study (Koppmann-Rumpf et

**Table 4.**

Number of mature (either reproductive or not) edible dormice captured each year in the studied populations (inter-year recaptured individuals are included as many times as they have been recaptured) and mean annual sex ratio of mature edible dormice.

| Year <sup>A</sup> | Montseny |         | Montnegre |         |
|-------------------|----------|---------|-----------|---------|
|                   | Males    | Females | Males     | Females |
| 2012              | 5        | 10      | 0         | 4       |
| 2013              | 6        | 6       | 3         | 4       |
| 2014              | 23       | 31      | 4         | 5       |
| 2015              | 15       | 16      | 8         | 6       |
| Sex ratio         | 0.44     |         | 0.36      |         |

<sup>A</sup>Data from the 1st period (2007-2011) is not detailed here since data collection is likely female-biased during this period since populations were only monitored during the reproductive period (table 1), a period in which almost no male is captured.

al., 2015). Litter sex ratio variations at Montseny (balanced) and Montnegre (male-biased) may be due to the fact that different selection pressures may be operating at close-by populations.

We hypothesize that a lack of mature males in the population with unequal sex ratio would be responsible for the overproduction of young males to compensate for losses at the mature age. Indeed, the population of edible dormouse of Montnegre is virtually isolated and it is composed by few mature individuals. Isolated populations experience particular environmental, demographic and genetic contexts that may favor sex allocation strategies different from those in nearby non-isolated populations. First, overproducing the dispersing sex is expected to generate higher benefits in terms of fitness if dispersers are established in a better habitat than in the one they were born, because in a favorable habitat reproductive performance should be higher (Julliard, 2000). Montnegre population may be considered to thrive in a low-quality habitat (isolated and small population). In these conditions, breeding females may enhance their fitness by producing a higher number of individuals of the dispersing sex. However, since Montnegre is surrounded by Mediterranean forests, less suitable for this species, we expect that dispersing individuals will have lower chances to reach suitable territories. Thus, although plausible, an overproduction of males may not be effective in Montnegre given the limited suitable habitat and longer dispersal distance (i.e., individuals moving from Montnegre to Montseny should travel a minimal distance of 10 km of unsuitable habitat).

Second, small and isolated populations may experience reduced genetic diversity and increasing levels of inbreeding, leading to inbreeding depression (Wright, 1931; Nei et al., 1975). Increasing dispersal may be effective to reduce inbreeding because dispersers are more likely to mate with unrelated individuals (Motro, 1991; Gandon, 1999; Perrin & Mazalov, 1999). As Montnegre is a small isolated population, we expect high inbreeding levels. Thus, given that males are the main dispersing sex in edible dormouse (Bieber, 1995; Ściński & Borowski, 2008), the overproduction of males found in Montnegre could be a mechanism to increase the number of dispersers and ultimately to increase fitness return for females.

Contrary to the Montnegre population, edible dormice population of Montseny has a suitable habitat connecting it with the northern populations of the Iberian Peninsula (Torre et al., 2010). Thus, we expect low inbreeding levels and a high quality habitat in this population. Contrary to Montnegre, dispersion may not be a driver of litter sex ratio in Montseny, which may explain balanced litter sex ratio in this population. Although the inability to quantify inbreeding levels as well as dispersal behavior of edible dormice is a limitation of this data set, it may be solved in the near future by sequencing large number of single-nucleotide polymorphisms and conducting GPS surveys, respectively.

There is an important difference between litter sex ratio (biased) and mature individuals sex ratio (balanced) in Montnegre. One reason that may explain this difference may be a sex-biased mortality rate, as has been already found in birds and mammals (Promislow, 1992; Liker & Székely, 2005) or a sex-biased mortality



due to a sex-biased dispersion (Lucas et al., 1994). We suggest that biased litter sex ratio (but unbiased mature sex ratio) in Montnegre may be a strategy to compensate biased dispersal with limited immigration and/or high male mortality. Accordingly, Koppmann-Rumpf et al. (2015) proposed that juvenile sex ratio deviations were compensated by higher mortality rates of juvenile males in a German edible dormouse population. Caution is required since no information is available regarding mortality rates in our study populations, although data collection is ongoing. In fact, our data cannot distinguish between mortality and dispersal, since individuals that are no longer detected (i.e., recaptured) could be actually dead or emigrated.

In conclusion, previous and present investigations of litter sex ratios in edible dormice populations, carried out at different locations across the species' range, showed different results. These differences could reflect variation in selective pressures acting on sex ratios. In Montnegre, poor habitat quality, small population size and isolation may lead females to produce a higher number of males per litter in order to increase dispersal. Alternatively, maternal conditions, local resource competition or communal breeding (i.e., the Trivers and Willard hypothesis, 1973; the local resource competition hypothesis: Clark, 1978; Silk, 1983; and the helper repayment hypothesis: Emlen et al., 1986; Komdeur et al., 1997) could also explain litter sex ratio variations in edible dormice. Because testing such hypothesis requires additional data, preferably also comparing more than two populations, future analysis linking mother condition, seed production, dispersal or survival patterns on litter sex ratios could shed light on the relative costs or benefits of producing unbiased (Montseny) versus biased (Montnegre) litters in edible dormice. Finally, further studies of population dynamics of this species may provide some tools for conservation purposes in the southernmost populations of the Iberian Peninsula, threatened by oak forest decline due to climate change and land use (Ninyerola et al., 2007).

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