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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 be 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 somewhat 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*) along 9 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; dispersion; fat dormouse; *Glis glis*; sex allocation

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). The Fisher's 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 be 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 underling explanation is that by producing sons they may achieve greater fitness return for an equal investment (Trivers & Willard, 1973). Second, in species with sex biased competition, sex allocation should be biased towards the dispersal sex. Under intensified competition the dispersing sex should be overproduced to promote a reduction of 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 dispersing 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 inbreed populations an overproduction of the dispersing sex is expected to increase fitness return for females. Indeed, given that a negative relationship between inbreeding and fitness is often observed (see Kempenaers, 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 gave unexpected results, especially in higher vertebrates (West et al., 2002). Further, most studies on variation in sex allocation have been based on among-species comparisons, in spite of 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 points a worrying future (Ribas et al., 2009). Because there are important differences in habitat quality between these two sites, sex allocation and, as a consequence, litter sex ratio may differ among Montseny and Montnegre edible dormice populations.

Material and Methods

Studied species

The edible dormouse is an arboreal, nocturnal and a hibernating small mammal with a global distribution across Europe (Amori et al., 2008). From mid-June to mid-August, they mate (Bieber & Ruf, 2004; Özkan, 2006). They give birth to one litter per year (sometimes two) (Santini, 1978; Pilastro, 1992) in Southern Europe. 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 from 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 1,078-1,143 m.a.s.l., 41º47'59"N, 2º25'14"E), with a mean temperature of 9.5ºC and a precipitation of 975 mm per year (Figure 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 ~~a~~ Mediterranean forest. It is situated in the northern slopes at the top of the Montnegre massif (range 700-764 m.a.s.l., 41º39'37"N, 2º34'44"E), with an mean precipitation of 840 mm per year (Figure 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 likely to strongly hinder the dispersion of animals from one population to the other.

For data collection, nest boxes (30 cm x 15 cm x 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 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 according to the color of their fur for pups (pink pups; grey and eyes close pups; grey and eyes open pups) and according to their body size and tibia length for juveniles (≥ 30 days of life), yearlings (after their first hibernation, already sexually mature) and adults (after their second hibernation) (Schlund, 1997; National dormouse monitoring programme, 2015). Juveniles, yearlings and adults were marked using a transponder (AVID Musicc, 8 × 2,1mm) 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 (authors unpub.). 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 individuals sex ratio in the studied populations, two-tailed Wilcoxon paired tests were used to compare yearly sex ratio of mature individuals at 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 (± SD) litter size of 5.21 ± 1.62) and in Montnegre, for 26 litters (154 pups from 22 different mothers and a mean (± SD) litter size of 5.92 ± 1.65). More than the 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) (Figure 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 (Figure 2). According to our prediction, litter sex ratio was found to significantly depend on the studied population (Table 3, Figure 2). No significant relationship between litter sex ratio and year was observed (Table 3).

The Montseny population was bigger despite an equal sampling effort in both sites (mean ± SE number of mature females in Montseny: 15.75 ± 10.96; mean ± SE number of mature females in Montnegre: 4.75 ± 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).

Discussion

Litter sex ration was male-biased in an 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 in the German study (Koppmann-Rumpf et 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 former population would be responsible of 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 that 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 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 to be effective in Montnegre given the few 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 and conducting GPS surveys.

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 adult 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 young 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 (ie, 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 are leading females to produce 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, 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 southern most populations of the Iberian Peninsula, threatened by oak forest decline due to climate change and land uses (Ninyerola et al., 2007).

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Figure 1. Location of our two sampling locations (Montseny and Montnegre)

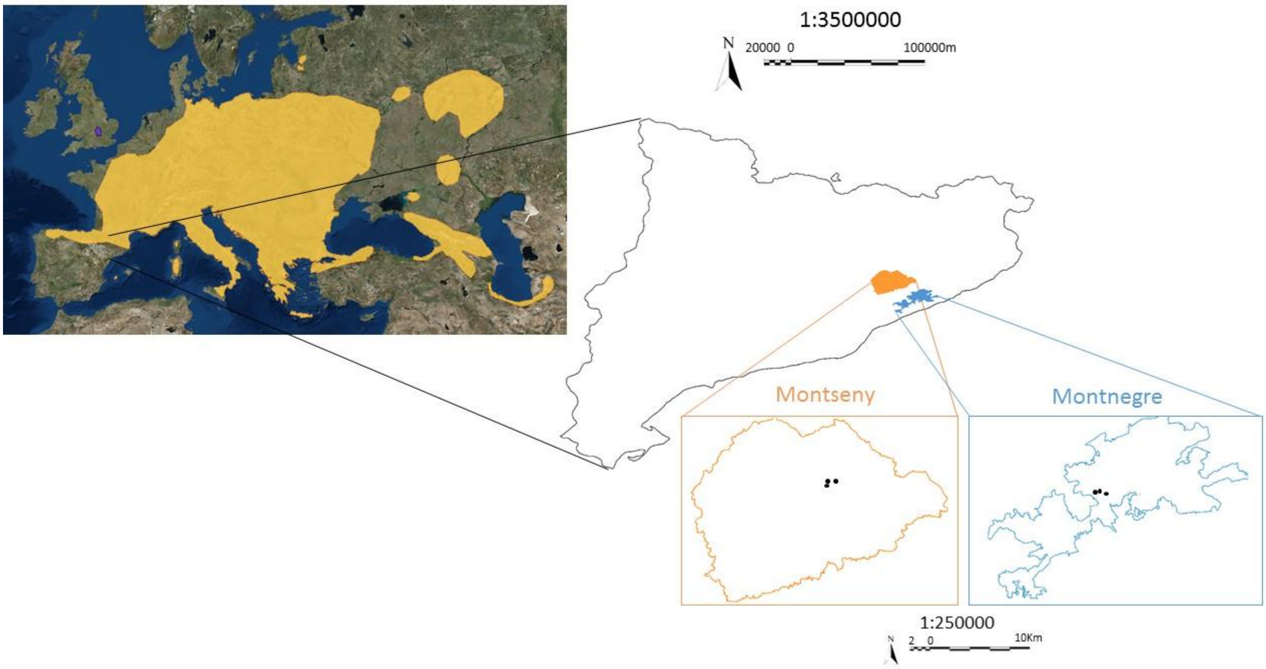

Figure 2. A boxplot representing litter sex ratio (proportion of males/litter) in the two studied populations (Montseny and Montnegre)

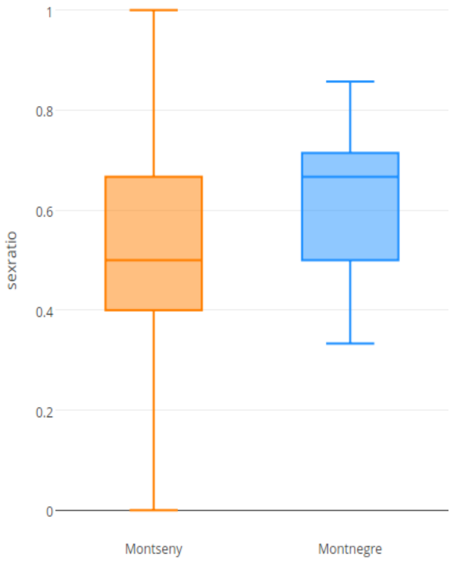

Table 1. Summary of the sampling designs of the two studied periods.

	1st period (2007-2011)	2nd period (2012-2015)
Type of sampling design	Transects^A with 6 nests/transect	Plots^B 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 reproductive period (Mid-August to Mid-October)	every two weeks during the active period (June-December)

^{A}20 m. ^{B} 5x4 nest boxes placed in a grid and separated of 30 meters, occupying just over 1-ha (the plots of the same population are separated by a maximum distance of 675m.

Table 2. Mean litter sex ratio (proportion of males/litter) in the two studied populations (Montseny and Montnegre) each year.

Year	Sex ratio Montseny	Sex ratio 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

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 (χ2) and the degrees of freedom (df).

Independent variable		estimate ± SE	p-value	Wald test		
				χ2	df	p-value
Intercept		0.99 ± 0.39	0.01	6.3	1	0.01
Population		-0.56 ± 0.23	0.02	5.6	1	0.02
Year	2008	-0.99 ± 0.51	0.05	10.7	8	0.22
	2009	-0.22 ± 0.53	0.68			
	2010	-0.87 ± 0.52	0.10			
	2011	-0.94 ± 0.53	0.08			
	2012	-0.39 ± 0.49	0.43			
	2013	-0.21 ± 0.48	0.66			
	2014	-0.03 ± 0.46	0.95			
	2015	-0.39 ± 0.49	0.42			

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.

	Montseny		Montnegre	
Year^A	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	

^{A}: 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