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1 **Male-biased litter sex ratio in the southernmost Iberian population of edible**
2 **dormouse: A strategy against isolation?**

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13 **Abstract**

14 Litter sex ratio is a key component of parental fitness due to its impact on lifetime reproductive
15 success. Multiple causes may be at the origin of sex ratio variation among species and populations,
16 such as maternal condition, local resource competition, presence of helpers, habitat quality or
17 inbreeding levels. Whereas variation in sex allocation between species is somewhat well
18 understood, it is still unclear how and why litter sex allocation differs within species. Here, we
19 present an analysis of litter sex ratio variation in two populations of edible dormice (*Glis glis*) along
20 9 years of study. Populations are situated in the Montnegre and Montseny massifs in Catalonia (NE
21 Iberian Peninsula). The Montnegre population is nowadays an isolated population located at the
22 southernmost range edge of the species in the Iberian Peninsula. Litter sex ratio was male-biased in
23 Montnegre but balanced in Montseny, whereas both populations showed a balanced adult sex ratio.
24 We suggest that this differential sex allocation investment in Montnegre, may be a strategy to
25 overcome isolation effects in this massif, as males are the dispersing sex in this and other rodent
26 species.

27

28 Keywords: adaptive sex ratio variation; dispersion; fat dormouse; *Glis glis*; sex allocation

29 **Introduction**

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

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

54 major fitness by mating with unrelated individuals.

55 Despite decades of interest, sex allocation studies still gave unexpected results, especially
56 in higher vertebrates (West et al., 2002). Further, most studies on variation in sex allocation have
57 been based on among-species comparisons, in spite of the fact that proposed mechanisms should
58 also apply within species. In fact, recent work has shown within-species variation in sex allocation
59 (Stauss et al., 2005; Michler et al., 2012). The aim of this study was to investigate litter sex ratio
60 variation in the two southernmost wild populations of edible dormice (*Glis glis*) of the Iberian
61 Peninsula, situated in Catalonia (the Montseny and Montnegre massifs). Although the two studied
62 massifs are only separated by 10 km, the population of edible dormouse of Montnegre (located
63 further south) is virtually isolated from the nearest population (Montseny). Additionally, the
64 Montnegre population has suffered from a recent retreat of its deciduous forest, suffers from drier
65 conditions than the Montseny population and points a worrying future (Ribas et al., 2009). Because
66 there are important differences in habitat quality between these two sites, sex allocation and, as a
67 consequence, litter sex ratio may differ among Montseny and Montnegre edible dormice
68 populations.

69

70 **Material and Methods**

71 *Studied species*

72 The edible dormouse is an arboreal, nocturnal and a hibernating small mammal with a global
73 distribution across Europe (Amori et al., 2008). From mid-June to mid-August, they mate (Bieber &
74 Ruf, 2004; Özkan, 2006). They give birth to one litter per year (sometimes two) (Santini, 1978;
75 Pilastro, 1992) in Southern Europe. On the contrary, in central and northern Europe edible dormice
76 are characterized by low or no reproduction in years with low food availability (*i.e.* low beech or
77 oak crops; Pilastro et al., 2003). A litter is composed from 1 to 11 pups, with an average of 4.75 to
78 6.80 pups depending on the geographical location (Kryštufek, 2010). Pups are born hairless,

79 develop their fur at 16 days, open their eyes after 3 weeks and leave the nest at 30 days (Kryštufek,
80 2010).

81

82 *Study sites and sample collection*

83 The data used for this study were obtained from a capture-mark-recapture study monitoring the two
84 southernmost populations of the edible dormouse on the Iberian Peninsula: Montseny and
85 Montnegre. The sampled area in Montseny is a 5-ha deciduous forest (*Quercus petraea*, *Fagus*
86 *sylvatica*, *Corylus avellana* and *Acer opalus*) mixed with *Q. ilex* and *Ilex aquifolium* surrounded by
87 beech-dominated deciduous forest. It is situated in the center of the Montseny Biosphere Reserve
88 (range 1,078-1,143 m.a.s.l., 41°47'59"N, 2°25'14"E), with a mean temperature of 9.5°C and a
89 precipitation of 975 mm per year (Figure 1).

90 The sampled area in Montnegre is a 5-ha deciduous forest (*Q. canariensis*, *Q. petraea*, *C.*
91 *avellana*, *Castanea sativa* and *Prunus avium*) mixed with *Q. ilex* and *I. aquifolium* surrounded by a
92 Mediterranean forest. It is situated in the northern slopes at the top of the Montnegre massif (range
93 700-764 m.a.s.l., 41°39'37"N, 2°34'44"E), with an mean precipitation of 840 mm per year (Figure
94 1). The southernmost population of Montnegre is virtually isolated from the nearest population
95 (Montseny). Indeed, despite the short distance (10 km) among populations they are separated by
96 open unsuitable habitat and a freeway likely to strongly hinder the dispersion of animals from one
97 population to the other.

98 For data collection, nest boxes (30 cm x 15 cm x 15 cm, with a 5-cm entry hole) were
99 attached to trees at a height of approximately 3 m aboveground (Freixas et al., 2011). Nest boxes
100 are frequently used by dormice during the active period. Data collection differed from 2007 to 2011
101 and from 2012 to 2015 regarding the sampling design and the frequency of sampling (Table 1).
102 While from 2007 to 2011 sampling was designed to obtain data during the reproductive period,
103 2012-2015 sampling was designed to increase data quantity and quality by increasing monitoring

104 effort in order to encompass the overall active period of the species (Table 1).

105 Nest boxes were inspected during the day, when dormice can be found sleeping inside the
106 boxes and lasted a maximum of 15 min per individual. All captured dormice were identified by a
107 unique number, sexed and aged according to the color of their fur for pups (pink pups; grey and
108 eyes close pups; grey and eyes open pups) and according to their body size and tibia length for
109 juveniles (≥ 30 days of life), yearlings (after their first hibernation, already sexually mature) and
110 adults (after their second hibernation) (Schlund, 1997; National dormouse monitoring programme,
111 2015). Juveniles, yearlings and adults were marked using a transponder (AVID Musicc, $8 \times 2,1\text{mm}$)
112 injected under the skin of the neck. The implantation of the transponder has no obvious adverse
113 effects. Also, a numbered metal ear-tag (National Band and Tag Co., USA) was placed on the ear.

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

120

121 *Statistical analysis*

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

129 To investigate mature individuals sex ratio in the studied populations, two-tailed Wilcoxon
130 paired tests were used to compare yearly sex ratio of mature individuals at each population. All
131 statistical analyses were conducted using the R software version 3.3.0 (R Development Core Team,
132 2016).

133

134 **Results**

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

142 In Montseny, the litter sex ratio (proportion of males in a litter) was 0.52 and did not
143 significantly differ from 0.50 (95% CI = 0.46-0.58) (Figure 2). On the contrary, the litter sex ratio in
144 Montnegre was 0.61 and significantly departed from 0.50 (95% CI = 0.55-0.67) showing a male-
145 biased litter sex ratio (Figure 2). According to our prediction, litter sex ratio was found to
146 significantly depend on the studied population (Table 3, Figure 2). No significant relationship
147 between litter sex ratio and year was observed (Table 3).

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

154

155 **Discussion**

156 Litter sex ration was male-biased in an isolated southernmost population of edible dormice but not
157 in other close-by population. The bias towards males reported in Montnegre is consistent with
158 observations from a German population (Koppmann-Rumpf et al. 2015). No sex-ratio bias was
159 found for mature individuals in both populations, as in the German study (Koppmann-Rumpf et al.
160 2015). Litter sex ratio variations at Montseny (balanced) and Montnegre (male-biased) may be due
161 to the fact that different selection pressures may be operating at close-by populations.

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

177 Second, small and isolated populations may experience reduced genetic diversity and
178 increasing levels of inbreeding, leading to inbreeding depression (Wright, 1931; Nei et al., 1975).

179 Increasing dispersal may be effective to reduce inbreeding because dispersers are more likely to
180 mate with unrelated individuals (Motro, 1991; Gandon, 1999; Perrin & Mazalov, 1999). As
181 Montnegre is a small isolated population, we expect high inbreeding levels. Thus, given that males
182 are the main dispersing sex in edible dormouse (Bieber, 1995; Ściński & Borowski, 2008), the
183 overproduction of males found in Montnegre could be a mechanism to increase the number of
184 dispersers and ultimately to increase fitness return for females.

185 Contrary to the Montnegre population, edible dormice population of Montseny has a
186 suitable habitat connecting it with the northern populations of the Iberian Peninsula (Torre et al.
187 2010). Thus, we expect low inbreeding levels and a high quality habitat in this population. Contrary
188 to Montnegre, dispersion may not be a driver of litter sex ratio in Montseny, which may explain
189 balanced litter sex ratio in this population. Although the inability to quantify inbreeding levels as
190 well as dispersal behavior of edible dormice is a limitation of this data set, it may be solved in the
191 near future by sequencing and conducting GPS surveys.

192 There is an important difference between litter sex ratio (biased) and mature individuals
193 sex ratio (balanced) in Montnegre. One reason that may explain this difference may be a sex-biased
194 mortality rate as has been already found in birds and mammals (Promislow, 1992; Liker & Székely,
195 2005) or a sex-biased mortality due to a sex-biased dispersion (Lucas et al., 1994). We suggest that
196 biased litter sex ratio (but unbiased adult ratio) in Montnegre may be a strategy to compensate
197 biased dispersal with limited immigration and/or high male mortality. Accordingly, Koppmann-
198 Rumpf et al. (2015) proposed that juvenile sex ratio deviations were compensated by higher
199 mortality rates of young males in a German edible dormouse population. Caution is required since
200 no information is available regarding mortality rates in our study populations, although data
201 collection is ongoing. In fact, our data cannot distinguish between mortality and dispersal, since
202 individuals that are no longer detected (ie, recaptured) could be actually dead or emigrated.

203 In conclusion, previous and present investigations of litter sex ratios in edible dormice

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

217

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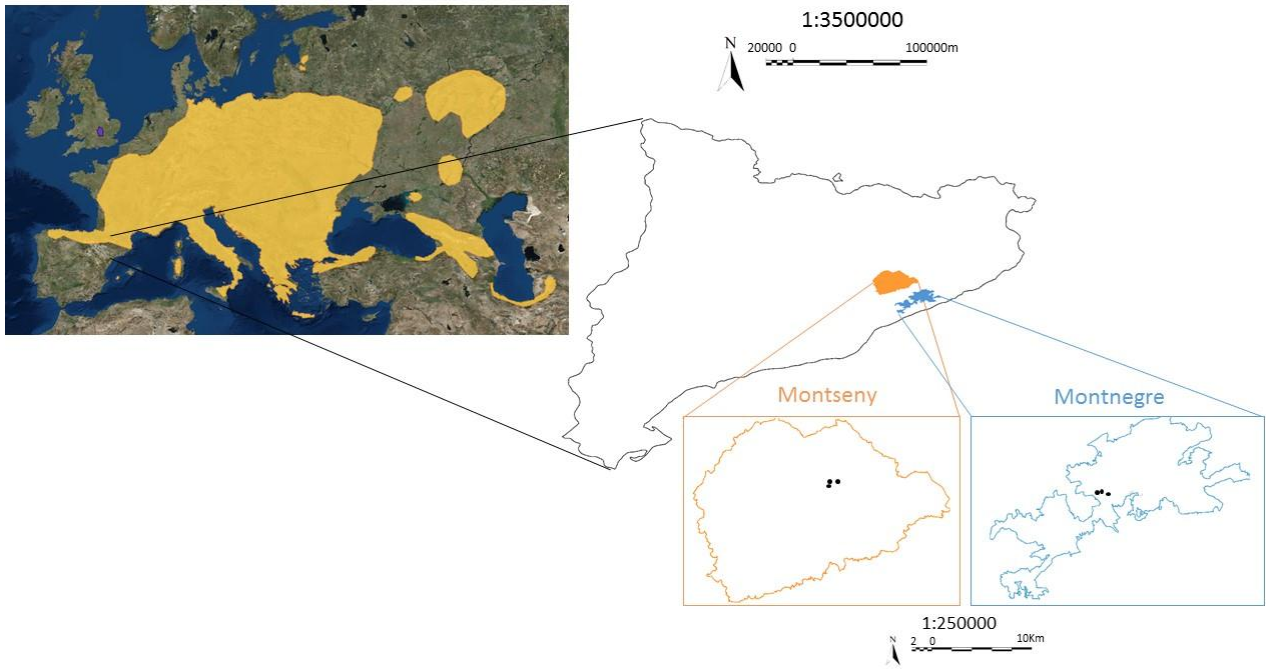
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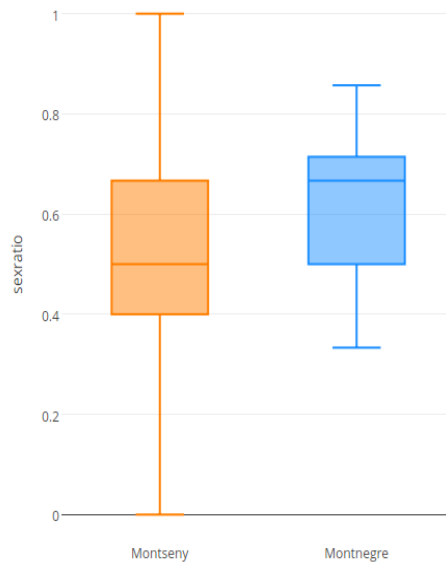
311 **Figure 1.** Location of our two sampling locations (Montseny and Montnegre)



312

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

315



316

317

318 **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 <u>reproductive</u> period (Mid-August to Mid-October)	every two weeks during the <u>active</u> period (June-December)

319 ^A20 m. ^B 5x4 nest boxes placed in a grid and separated of 30 meters, occupying just over 1-ha (the
 320 plots of the same population are separated by a maximum distance of 675m.
 321
 322
 323
 324

325 **Table 2.** Mean litter sex ratio (proportion of males/litter) in the two studied populations (Montseny
 326 and Montnegre) each year.
 327

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

328 **Table 3.** Generalized Linear Mixed Model showing the effects of terms on the proportion of males
 329 in a litter. We used Wald's test to measure the contribution of each categorical factor to the overall
 330 model and included the statistic (χ^2) and the degrees of freedom (df).
 331

Independent variable		estimate \pm SE	p-value	Wald test		
				χ^2	df	p-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			

332 **Table 4.** Number of mature (either reproductive or not) edible dormice captured each year in the
 333 studied populations (inter-year recaptured individuals are included as many times as they have been
 334 recaptured) and mean annual sex ratio of mature edible dormice.
 335
 336

Year ^A	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	

337 ^A: Data from the 1st period (2007-2011) is not detailed here since data collection is likely female-
 338 biased during this period since populations were only monitored during the reproductive period