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Population Biology of the Woodland Dormouse *Graphiurus murinus* in a Riverine Combretum Forest, South Africa

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(Article begins on next page)

1 **Original Research; Full-length paper**

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4 **Population biology of the woodland dormouse, *Graphiurus***
5 ***murinus* in the Thicket Biome of South Africa**

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7

8 **Zimkitha JK Madikiza^{1*}, Sandro Bertolino², and Emmanuel Do Linh San³**

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10

11 **Addresses**

12 ¹ *School of Animal, Plant and Environmental Sciences, University of the*
13 *Witwatersrand, Wits, South Africa*

14 ² *DIVAPRA, Entomology & Zoology, Grugliasco (Torino), Italy*

15 ³ *Department of Zoology and Entomology, University of Fort Hare, Alice, South Africa*

16 * Corresponding author, email: kim.madikiza@gmail.com

17

18 The population biology of the woodland dormouse, *Graphiurus murinus* was
19 investigated between February 2006 and June 2007 in a riverine *Combretum*
20 forest at the Great Fish River Reserve, South Africa. Data were collected by
21 means of a monthly live-trapping and nest-box monitoring programme. The
22 dormouse population showed a steady increase from winter to spring, and a
23 peak of 16 individuals/ha in summer as a result of the influx of juveniles. Winter
24 mortality and/or spring dispersal accounted for the disappearance of 55% of
25 subadults. The annual adult:juvenile ratio was 1.08, whereas the overall sex
26 ratio was 1.94 females per one male. In females, reproductive activity was
27 observed from September to end January (spring–summer). The pattern
28 observed in males was similar, as dormice with descended testes were
29 exclusively found from October to end January. Parturition occurred from the
30 second half of October to the beginning of December, but an anecdotal
31 observation made in 2011 indicated that births can take place as late as mid-
32 February. Litters ($n = 15$) recorded between 2006 and 2017 at the study site
33 consisted of an average (\pm SD) of 3.88 ± 0.81 young. We provide evidence that
34 some females can give birth to two litters during the same breeding period,
35 with a 5- to 6-week interval. This indicates the occurrence of post-partum
36 mating in woodland dormice. Multi-year data from different habitat types are
37 needed in order to confirm or perfect our knowledge on this species'
38 population biology and dynamics.

39
40 **The range in population density estimates varied between 1.2 and 16 dormice**
41 **per ha, with the lower value likely an underestimate due to low winter activity**
42 **and preferential use of natural cavities vs. nest boxes.**

43
44
45 **Keywords:** age structure, breeding period, capture–mark–recapture, Gliridae, litter
46 size, live trapping, MNA, nest box, population dynamics

Commentato [EDLS1]: Put aside for now. Reviewers indicated that it should be removed from the abstract. Could be added to Discussion in case it's worth highlighting that there. Otherwise to be deleted.

47 **Introduction**

48 The family Gliridae (dormice) represents a group of largely arboreal rodents
49 distributed in the Palearctic and Ethiopian faunal regions. Holden (2005) evaluated
50 that it comprises of 28 extant species divided into three subfamilies and nine genera,
51 but recent reviews propose the existence of two additional species in Africa (Holden
52 2013; Monadjem et al. 2015), while at the same time highlighting the need for a
53 comprehensive taxonomic revision. Whereas several studies have been conducted
54 on European dormouse species (e.g. garden dormouse, *Eliomys quercinus*: Bertolino
55 et al. 2001; Bertolino 2007; Bertolino and Cordero di Montezemolo 2007; Viñals et al.
56 2017; edible dormouse, *Glis glis*: Kryštufek et al. 2003; Ivashkina 2006; Jurczyszyn
57 and Zgrabczyńska 2007; Ściński and Borowski 2007; forest dormouse, *Dryomys*
58 *nitedula*: Nowakowski 2001; Ściński and Borowski 2006; common dormouse,
59 *Muscardinus avellanarius*: Sorace et al. 1998, 1999; Bright et al. 2006; Juškaitis
60 2014), very little is known of the population biology and ecology of African dormice.

61 The woodland dormouse, *Graphiurus murinus* is one of the possibly 17 glirid
62 species – 15 belonging to the genus *Graphiurus* – occurring on the African continent
63 (Holden 2013; Monadjem et al. 2015). Its distribution is very broad and stretches
64 from north-eastern (Ethiopia) to southern Africa (Monadjem et al. 2015). In the
65 southern African subregion, *G. murinus* has been recorded in countries including
66 Mozambique, Zimbabwe, Swaziland, Lesotho and South Africa (Madikiza et al.
67 2016). Throughout its distributional range, *G. murinus* is usually associated with
68 forests and woodlands, where it was notably found to use tree holes in old gnarled
69 *Acacia* trees (Smithers and Wilson 1979) and *Combretum* trees as nest sites
70 (Lamani 2011; Madikiza 2017). Its conservation status has been recently categorised
71 as Least Concern in South Africa, Swaziland and Lesotho, as this species has a wide
72 distribution and its population is not suspected to be declining as there are no major
73 threats (Madikiza et al. 2016).

74 Until now, most studies dealing with woodland dormice focussed on physiological
75 and dietary aspects, as well as on their spatial ecology. Indeed, the thermoregulatory
76 capabilities of this species have been well investigated, especially under laboratory
77 conditions (e.g. Lachiver and Petter 1969; Webb and Skinner 1996; Whittington-
78 Jones and Brown 1999). Ellison and Skinner (1991) found that cold-acclimatised
79 woodland dormice entered hibernation, characterised by a fall in body temperature
80 and in body weight. Similar results have now been observed in the field, with

81 woodland dormice undergoing multiple-day torpor bouts of up to 96 h during winter
82 and their body temperature reaching a minimum of 2.5°C (Mzilikazi et al. 2012). As
83 regards the diet, *G. murinus* is reported as essentially frugivorous and herbivorous
84 (Delany and Happold 1979), although some authors consider the species to be
85 omnivorous with a preference for vegetable matter (Pienaar et al. 1980; De Graaff
86 1981; Happold 1987). In the Great Fish River Reserve, Lamani (2014) found it to be
87 largely dependent on millipedes and beetles. Fruit consumption only took place in
88 late summer and early winter and supplemented the invertebrate-dominated diet. In
89 the same study area, using live-trapping and nest-box monitoring data, Madikiza *et*
90 *al.* (2011) recorded extensive intra- and intersexual home range overlaps, with males
91 exploiting areas twice larger than females.

92 So far, however, basic aspects such as the reproductive biology and population
93 dynamics of this species have not been thoroughly examined, with limited data
94 collected during a short-term, unpublished project (Qwede 2003). The purpose of this
95 study was therefore to determine, estimate or record the following parameters of the
96 biology of the woodland dormouse over a full yearly cycle: (a) the population density
97 at the study site; (b) the age structure and sex ratio of the population; (c) population
98 dynamics; (d) the start and the end of the breeding period; (e) litter size and the
99 percentage of breeding females; and (f) winter survival and dispersal of juvenile
100 dormice.

101

102 **Materials and methods**

103

104 *Study site*

105 The study was carried out in the Great Fish River Reserve (GFRR; 33°11'S, 26°38'E)
106 which is situated about 30 km north of Grahamstown, in the Eastern Cape Province,
107 South Africa (Figure 1). The conservation area was designated in 1973 and enlarged
108 in 1983 and 1987, respectively (Birch 2000), and the total combined size is
109 approximately 445 km². The reserve complex was created from cattle farms with
110 heavily transformed natural vegetation. It is currently made up of three entities
111 (Figure 1). Our study site was located in the western part, namely the Andries Vosloo
112 Kudu Nature Reserve. The region is characterised by an undulating terrain, with the
113 elevation ranging from 170 m at the river up to 800 m on the ridges (Palmer and
114 Tanser 1999). The area is relatively arid and summer temperatures are often >40°C.

115 The annual rainfall varies between 400–500 mm, and peaks are recorded in
116 October–November and February–March (Madikiza 2010).

117 The area falls within the Albany Thicket Biome with the Great Fish Thicket being
118 the dominant vegetation category throughout the GFRR complex (Hoare et al. 2006).
119 This type of vegetation is characterized by dense thickets and clumps of thorny and
120 succulent shrubs. Our study was conducted in a stretch of Riverine *Combretum*
121 Forest (altitude: 310 m) dominated by stands of Cape bushwillows (*Combretum*
122 *caffrum*). This tree is prone to rotting from the inside, resulting in numerous holes and
123 hollows used as resting sites by woodland dormice (Lamani 2011). The riverine
124 forest is composed of several other tree species, namely *Acacia karoo*, *Acalypha*
125 *glabrata*, *Olea europaea* ssp. *africana*, *Ziziphus mucronata* and *Schotia afra*. The
126 often dense understory comprises of *Azima tetracantha*, *Ehretia regida*, *Scutia*
127 *myrtina*, *Maytenus heterophylla* and *Carrisa bispinosa* ssp. *bispinosa*.

128 The 2.5 ha (breadth × length: 100 × 250 m) study area is bordered on both sides
129 by large expanses of Bushclump Karroid Thicket, a semi-open habitat composed of
130 *Rhus* spp. and *Scutia myrtina* bushclumps and a karroid herbaceous layer. The size
131 of the study area provided above includes a small proportion (estimated to about
132 10%) of bordering Bushclump Karroid Thicket habitat.

133

134 *Live trapping*

135 Population biology data for resident woodland dormice were obtained through a live-
136 trapping and nest-box monitoring programme (see below). We adopted two live-
137 trapping protocols during the study period. The first one (test phase) was
138 implemented between February and July 2006. Thirty-three Sherman aluminium
139 traps (23 × 8 × 9 cm) were placed above ground in trees, bushes and on logs along
140 an irregular trail. In order to sample dormice that would potentially venture on the
141 ground both inside and outside the forest, a 7 × 4 grid of ground PVC traps (Willan
142 1979) was set during the same period, with 12 stations in the riverine forest, 12
143 stations in the Bushclump Karroid Thicket and four stations set along the ecotone.
144 The stations were spaced 10 m apart, with two traps per station ($n_{\text{total}} = 56$ traps).
145 PVC traps were preferred to aluminium traps for ground trapping, because they are
146 more resistant to trampling by large ungulates and less susceptible to overheating.
147 Both types of traps were baited with a mixture of rolled oats and sunflower seed oil
148 (Wirminghaus and Perrin 1993). Traps were set out for two to three consecutive

149 nights in February, April, May and July. They were checked twice daily, early morning
150 and late afternoon. During the winter season, small cloths were inserted inside traps
151 to prevent captured dormice from dying of cold. At the end of July 2006, trapping on
152 the ground was stopped, as we did not trap any woodland dormouse on the ground
153 either inside or outside the riverine forest (for more details, see Madikiza et al.
154 2010a). Therefore, a decision was made to rather increase the number of traps on
155 tree trunks and branches in the forest. The second protocol was initiated in
156 September 2006 and lasted until March 2007. Sixty Sherman traps were randomly
157 placed on tree branches and logs and were set for two to three consecutive nights
158 every month, with the exception of November – during the core of the mating season
159 (see below) – when two trapping sessions of three days each were organised. The
160 position of traps was slightly changed (± 15 m) from one monthly trapping session to
161 another in order to cover the study site as much as possible.

162

163 *Nest-box monitoring*

164 Seventy wooden nest boxes with an entrance hole diameter of 3 cm and removable
165 lid were erected at the study site (Madikiza et al. 2010b). Nest boxes were spaced
166 irregularly along a curvilinear path across the forest, at variable heights, from 1.10 m
167 to 2.35 m above the ground (on average 1.65 ± 0.26 m). Nest boxes were made of
168 wood (2 cm thick) with internal dimensions of 11.5 × 13.0 × 12 cm (breadth × length
169 × height). They were suspended on nails by a wire sling, with the entrance hole
170 facing the tree trunk spaced by two 2.5-cm thick transverse bars, so as to be more
171 accessible to small mammals climbing the tree or branch. This design would also
172 deter birds from entering by obstructing their direct line of flight to the entrance hole
173 (Morris et al. 1990).

174

175 *Manipulation and marking of dormice*

176 At the first capture, dormice were transferred into a pre-weighed Ziploc® plastic bag
177 and weighed to the nearest gram with a spring balance (Pesola, Baar, Switzerland).
178 Dormice were then lightly anaesthetized using diethyl ether, aged and sexed. The
179 apparent age of individuals was determined based on body size, body mass, fur
180 characteristics and trapping month (as related to the breeding cycle). Juveniles
181 generally weighed <25 g and were considered as subadults during their first winter
182 onward. Adults (>1-year old) weighed between 25 g and 38 g, except in late

183 autumn/early spring when body mass could drop to 21–22 g in some individuals.
184 Based on the position of testes, adult males were classified as reproductive (scrotal
185 testes) or non-reproductive (abdominal testes). The reproductive status of females
186 was determined through visual inspection of the external genitalia (vaginal orifice
187 perforate or not), palpation of the abdomen (pregnancy) and presence/absence of
188 swollen nipples. Dormice were individually tattooed on one or two ears with a unique
189 code using single-digit spiked tattoo numbers (Hauptner Herberholz, Solingen,
190 Germany) attached to forceps. Tattoo-ink was then rubbed into the perforations.

191

192 *Data analysis*

193 Population density was calculated as the minimum number of dormice known to be
194 alive (MNA), divided by the surface of the study area. MNA was calculated on a
195 monthly basis from February 2006 to June 2007. Hence, MNA includes all dormice
196 caught in a particular month, plus all those marked previously which were recaptured
197 at a later date (Bronner and Meester 1987; Krebs 1999). Dormice that were not
198 retrapped between a month M and the end of the study (June 2007) were assumed
199 to have emigrated or died.

200 Population dynamics was calculated based on the monthly variation of MNA. Both
201 the variation in the total number of dormice and the number of specific age- and sex-
202 classes (adult males, adult females, juveniles) were determined. Natal dispersal and
203 winter mortality were estimated based on the percentage of juvenile dormice marked
204 in February–July 2006 that were not retrapped or found in nest boxes from
205 September 2006 onwards (i.e. after their first winter). These two biological events
206 could not be differentiated as death is virtually impossible to prove unless animals
207 are radio-tagged and their remains recovered; and as no trapping was conducted in
208 the stretches of forest northwest and southeast of the study plot, dispersal could not
209 be confirmed.

210 Population structure was calculated monthly as the proportion of adults and
211 juveniles. We also estimated the sex ratio in adults, juveniles and in the dormice
212 population as a whole.

213 The onset and the end of the mating season were evaluated based on the monthly
214 changes in the reproductive condition of male and female dormice. The birth period
215 was determined by monitoring the presence of litters in nest boxes and evaluating
216 the age of “newborns” (up to two months old). Age determination was based on body

217 size, fur density and appearance, and level of mobility of young dormice. The
218 percentage of breeding females and the average litter size were also calculated.
219 Additional data on litter size collected haphazardly from 2008 to 2017 (when carrying
220 out other field projects at the study site) were included in the calculations in order to
221 increase sample size.

222 The following seasons were considered: spring (September–November), summer
223 (December–February), autumn (March–May) and winter (June–August). Potential
224 departure of sex ratio from parity were investigated with a χ^2 test with Yates'
225 correction (Fowler et al. 1998). Values are reported as the mean \pm SD.

226

227 **Results**

228

229 *Population density, structure and dynamics*

230 Between February 2006 and June 2007, 75 dormice were caught: these were 39
231 adults (13 males, 21 females, 5 undetermined) and 36 juveniles (5 males, 14
232 females, 17 undetermined). As the age of dormice changed during the study period,
233 the number of adults mentioned here above is as from 1 September 2006.

234 The population showed a steady increase from June 2006 to November 2006 and
235 a peak in December 2006 and January 2007 as a result of the influx of juveniles
236 (Figures 2 and 3). The minimum number of dormice known to be alive (MNA) varied
237 between a high of 40 in December 2006 and January 2007 (summer), and a low of
238 three in June 2007 (winter; Figure 2). The range of population density estimates was
239 therefore between 1.2 and 16 individuals/ha.

240 The overall adult:juvenile ratio was 1.08, a value very similar to that (0.95 ± 0.54)
241 obtained by averaging the ratios for the months ($n = 11$) during which both categories
242 of age structures were present. However, this ratio changed dramatically in the
243 course of the study period, obviously in association with the life-history traits
244 (reproductive cycle, body growth) of the woodland dormouse, but also based on the
245 chosen criteria of age categorization. Hence, the dormouse population only consisted
246 of (sub)adults during winter, whereas up to three juveniles for one adult were
247 recorded in April 2007 (MNA = 23).

248 Sex ratio (females/males) was 1.62 in adults ($n = 34$), 2.8 in juveniles ($n = 19$) and
249 1.94 overall ($n = 53$). Only the overall sex ratio was significantly different from parity

250 (χ^2 test with Yates' correction, $\chi^2 = 4.83$, $df = 1$, $p = 0.028$; $p > 0.066$ otherwise). The
251 sex ratio obtained by averaging monthly MNA values ($n = 15$) was also largely female
252 biased (2.3 ± 0.84 females for 1 male).

253 A few adult males ($n = 2$), adult females ($n = 6$) and one unsexed adult were only
254 caught between February and April 2006 and probably died before the start of the
255 nest-box monitoring sessions. Of 11 juvenile dormice (two males, nine females)
256 marked in early 2006, six individuals (one male, five females) were never retrapped
257 or found in nest boxes after September 2006. Therefore, winter mortality and/or
258 spring dispersal accounted for the disappearance of 55% of subadults. The
259 remaining dormice were regularly retrapped as (sub)adults up to January–April 2007.

260

261 *Reproduction*

262 In females, reproductive activity was observed during a single period, from
263 September 2006 to end January 2007 (Figure 3). The pattern observed in males was
264 similar, as reproductive individuals were exclusively found from October to end
265 January, when all males caught were scrotal (four in October, five in November, four
266 in December, and two in January).

267 The birth period could be determined by the size and mobility of young at first
268 discovery; hence, females gave birth as early as the second half of October and as
269 late as the beginning of February (Table 1). Litters recorded between 2006 and 2017
270 ($n = 15$) consisted of an average 3.88 ± 0.81 young, with a minimum of three and a
271 maximum of six young per litter (Table 1).

272 Overall, six out of the seven adult females known to frequent the study site during
273 the reproductive season bred successfully (Table 1). Five other adult females were
274 found in August and/or September 2006, but then disappeared from the population.
275 Finally, two other adult females were found on two and three occasions, respectively,
276 in January and February 2007. These dormice were probably transient and were
277 therefore not considered as belonging to the breeding cohort.

278 Among the adult females present during the breeding season, one (B7) gave birth
279 to two successive litters in late October and early December (Table 1). Another
280 female (B13), was found pregnant on 7 October and again on 22 November 2006;
281 she was the most likely mother (deducted from spatial proximity) of at least two
282 young found dead on 18 November, and then of four young first discovered on 17
283 December. Finally, nest box monitoring sessions conducted during summer 2010–

284 2011 indicated that female B25 gave birth to two successive litters around end
285 November–early December and early January, respectively (Table 1).

286

287

288 **Discussion**

289

290 *Population density, structure and dynamics*

291 Except for our study site, there is only one quantitative report on *Graphiurus*
292 population densities in the literature. Wirminghaus and Perrin (1993) found the mean
293 density of *G. murinus* in a southern temperate forest in Natal to remain relatively
294 stable at a mean of 4.2 individuals/ha throughout the year. In the GFRR, woodland
295 dormouse population density varied between 1.2 and 16 individuals/ha. The MNA
296 method has been found to have the widest applicability (Bronner and Meester 1987)
297 and is known to represent a reliable estimate of population size, including in
298 dormouse species (Bieber 1998; Schlund et al. 2002). The maximal density of 16
299 individuals/ha was probably quite accurate, as the use of Sherman traps and nest
300 boxes was associated with high recapture rates (Madikiza et al. 2010a, 2010b), and
301 the combination of both techniques seemed to allow us to catch most of the dormice.
302 As the dormouse population was constrained by the width of the riverine forest – no
303 dormice were caught on the ground outside the forest (see also Madikiza et al.
304 2010b) nor in other non-forested habitats of the reserve (Kryštufek et al. 2007) – it is
305 unlikely that the area used by the marked dormice was larger than 2.5 ha; hence,
306 there is probably no need to reduce our population density estimates. In an earlier
307 short trapping study at the same study site, Qwede (2003) estimated the maximal
308 dormouse density to be 10 individuals/ha. The increase in density recorded between
309 2003 and 2007 would require an abundant food supply and might have been
310 facilitated by an extensive spatial overlap among individuals, as was indeed the case
311 in our population (Madikiza et al. 2011). However, a positive effect of nest boxes on
312 density could not be discarded (Morris et al. 1990). The lower estimate of 1.2
313 individuals/ha was likely an underestimate due to low winter activity (Mzilikazi et al.
314 2012) and preferential use of natural cavities in trees vs. nest boxes during that
315 season (Madikiza et al. 2010a; Lamani 2011).

316 **However, the minimal value mentioned above was probably largely underestimated,**
317 **considering that nest box utilisation and trapping success decreased during winter.**

318 As the study came to an end in June 2007, the MNA could therefore not be adjusted
319 to potential recaptures of dormice in the following spring (September–November
320 2007), as was the case for the previous year. Hence, the lower MNA value of 20 for
321 winter 2006 is probably a more realistic value corresponding to a minimal density of
322 10 individuals/ha. Similarly, the MNA values obtained for the period February–May
323 2006 are probably an underestimate since no nest box monitoring sessions were
324 conducted during that period.

Commentato [EDLS2]: Repetition and could be deleted.

325 The study population increased between June–November 2006 and peaked in
326 December 2006–January 2007 (summer) through the influx of juveniles. As a result,
327 population size and therefore population density almost doubled between winter and
328 summer. Our data suggest that winter mortality and/or spring dispersal accounted for
329 the disappearance of 55% of juveniles. However, this information is preliminary, as
330 the sample size relative to the fate of juveniles was relatively small. In addition, a
331 distinction between mortality and natal dispersal could not be established.

332 If our data reflects reality (several dormice could not be sexed), the observed sex
333 ratio in favour of females (almost 2 females for 1 male) is not readily explainable.
334 This type of ratio could predict rapid shifts in population size (Kruuk et al. 1999) and a
335 longer-term study would be needed to see whether such fluctuations would take
336 place. In comparison, Channing (1984) reported that the female to male sex ratio in
337 the spectacled dormouse (*Graphiurus ocularis*) was near to parity (1.25), but sample
338 size was relatively small ($n = 18$). Juškaitis (1994) also reported near to 1:1 birth and
339 adult sex ratios in common dormice. Although in our study more males were found
340 during the breeding season, we suspect that this was caused by males searching for
341 females having a higher likelihood to use traps or nest boxes (Madikiza et al. 2010a,
342 2010b). Our adult to juvenile ratio (1.08) was only slightly higher than values reported
343 for the garden dormouse in alpine woodland (0.72–0.92, Bertolino et al. 2001).

344

345 *Reproduction*

346 In our study, *G. murinus* exhibited a well-defined breeding season, starting in late
347 October with the first births, and ending mid-March at the latest, with the
348 independence of the last-born dormice. Hence, the breeding season was slightly
349 longer than that recorded in the Afromontane population of Hogsback (November–
350 February; Qwede 2003). This slight extension of the breeding season is possibly due
351 to the warmer, and therefore more favourable, climatic conditions found at the GFRR.

352 Qwede (2003) reported that the Hogsback forest tends to have long, cold days.
353 However, the breeding season of woodland dormice is seasonal at both sites. These
354 observations are supported by several other authors, who reported that in southern
355 Africa, birth of young occurs during the hot, wet summer, as early as October and up
356 to February (Ansell 1960; De Graaff 1981; Wirminghaus and Perrin 1993).

357 Our woodland dormice were sexually receptive from October to January. During
358 the main study period, pregnant females were found in October and November only,
359 but additional data collected haphazardly from 2008 to 2017 suggested that
360 pregnancy could be recorded up to the first half of February. Rowe-Rowe and
361 Meester (1982) mentioned that, in the Natal Drakensberg, pregnant females can
362 even be found from March to May. In GFRR, over 80% of resident adult females bred
363 successfully and one third of them produced two litters yearly. Fluctuations in litter
364 size and the presence of a second litter in dormouse species is typically influenced
365 by weather conditions and food availability (Likhachev 1966, Bright and Morris 1996,
366 Juškaitis 2014).

367 Channing (1984), from his data on *G. ocularis*, also noted that two litters may be
368 produced six to eight weeks apart by each female, with each litter containing four to
369 six young. In Germany, single cases of common dormice females with a second litter
370 in the same year were also recorded (Büchner et al. 2003). Some authors stress that
371 the proportion of two-year old and older females in the population is very important in
372 this respect, because these females can produce two litters, whereas one-year old
373 females, born in late summer of the previous year can manage only one litter
374 (Likhachev 1966; Juškaitis 1997). Storch (1978), as well as Bertolino et al. (2001)
375 deduced that second litters are possible only in the southern and warmer parts of the
376 distribution ranges of some dormouse species.

377 Male reproduction was also clearly defined. Sexually active males were
378 exclusively found in the population from October to January, with all the males
379 trapped or found in nest boxes having descended testes. These data slightly contrast
380 with Qwede's (2003) study, in which scrotal males were recorded between October
381 and April in Hogsback, and between September and April in GFRR. The author also
382 noted that in GFRR 63% of males were reproductively active in February, whereas
383 80% from Hogsback had descended testes.

384 In *G. murinus*, litters generally consist of four young with an average litter size of
385 3.9. Several authors reported that litter size in *G. murinus* is three to four (Shortridge

386 1934; Ansell 1960; De Graaff 1981), though up to six fetuses have been found
387 (Lynch 1989). In comparison Channing (1984) reported that, in the spectacled
388 dormouse, four to six young are produced per female. Whereas litters with three
389 young probably occur in *G. murinus*, at least in some cases this resulted from the
390 early death of one to three young in four- to six-young strong litters. In Germany,
391 Büchner et al. (2003) clearly showed that average litter size of similar-sized common
392 dormice dropped from 4.2 among newborn nestlings to 3.6 among 4–6 week old
393 juveniles.

394 Millar (1981) suggested that food resources are the most likely factor determining
395 breeding patterns in small mammals. Similarly, Ruf et al. (2006) highlighted that
396 reproduction in dormice is almost completely driven by the availability of food
397 resources. Our results are in agreement with this statement, as in GFRR woodland
398 dormice reproduced in the summer months, which are characterized by a higher
399 rainfall and a high abundance of insects and fruits. No reproduction took place during
400 autumn and winter. The importance of food resources for reproduction is particularly
401 marked in some European glirids like the edible dormouse that skips reproduction in
402 non-mast years (Bieber 1998; Schlund et al. 2002; Pilastro et al. 2003; Morris and
403 Morris 2010).

404 **Multi-year data from different habitat types are needed in order to confirm or**
405 **perfect our knowledge on this species' population biology and dynamics.**

406
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408 authorization to carry out the research in the Great Fish River Reserve. The study
409 was partly financed by a Govan Mbeki Research and Development Centre grant to
410 ZJKM. This article is dedicated to the memory of Rod Baxter, who left us too soon and
411 is sorely missed.

412

Commentato [EDLS3]: Conclusion a bit short. Maybe add 2-3 sentences summarising the main findings?

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Legends of figures

Figure 1: Location of the Great Fish River Reserve complex. AVKNR: Andries Vosloo Kudu Nature Reserve, SKNR: Sam Knott Nature Reserve, DDGR: Double Drift Game Reserve. The sampling site of “Junction 9” is indicated by a grey-shaded star

Figure 2: Minimum number of woodland dormice (*Graphiurus murinus*) known to be alive (MNA, continuous line) and mean number of dormice captured per month at the “Junction 9” site (grey bars). Numbers below bars denote the number of monthly trapping sessions and/or nest box checks carried out

Figure 3: Minimum number of adult male, adult female and juvenile woodland dormice known to be alive each month at the “Junction 9”

Figure 4: Monthly changes in the reproductive condition of female woodland dormice found in nest boxes between June 2006 and June 2007 in the study area. Numbers below bars denote the total number of females found each month

Figure 1

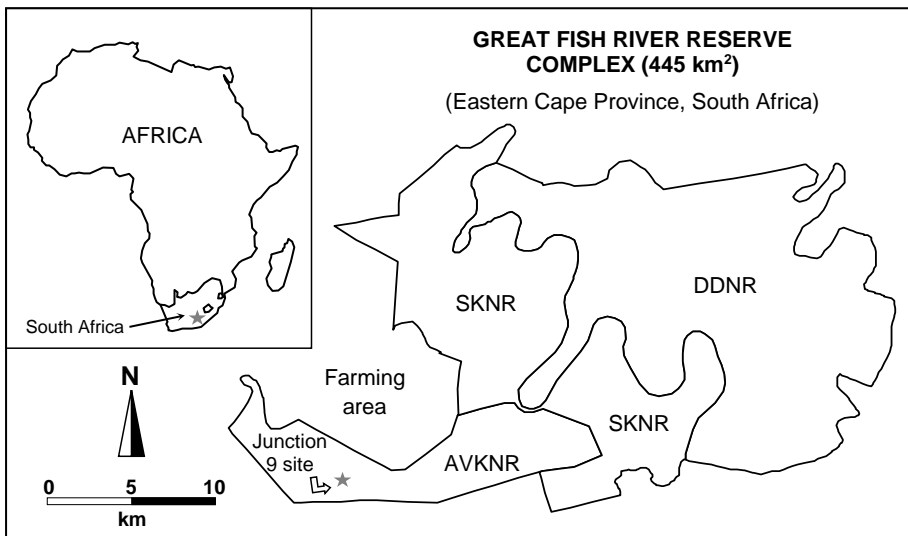


Figure 2

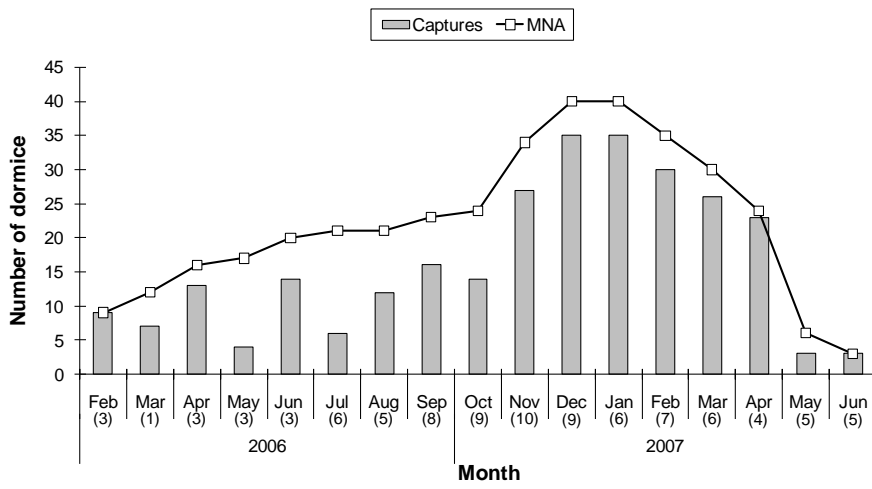


Figure 3

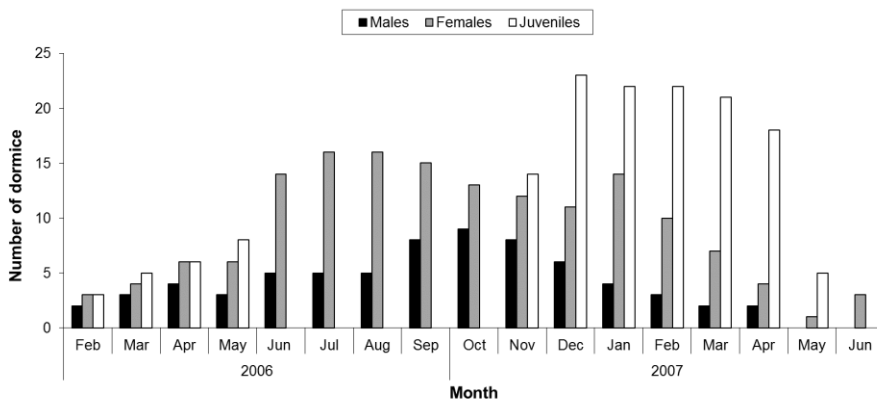


Figure 4

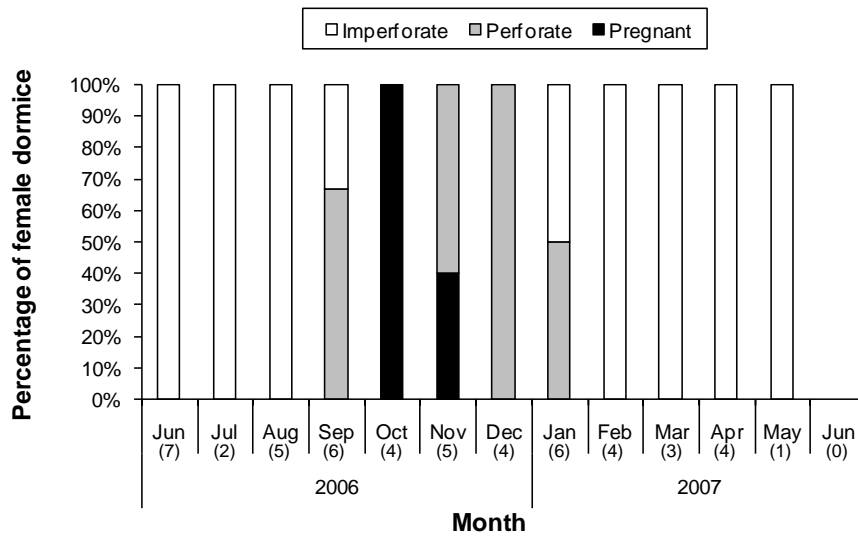


Table 1: Litter size and estimated birth date of woodland dormice at the study site

Female code	Date of first observation	Nestbox No	Litter size	Estimated age of young	Estimated birth date
B7	03.11.2006	3	4 ^a	2 weeks old	20–25 October 2006
B12	05.11.2006	8	4 ^b	2 weeks old	20–25 October 2006
B17	06.11.2006	46	4	2 weeks old	20–25 October 2006
B13	17.12.2006	3	4	3 weeks old	25–30 November 2006
B7	19.12.2006	2	3 ^c	2–3 weeks old	01–05 December 2006
B20	18.11.2006	4	4	2–3 weeks old	01–05 November 2006
B7	06.01.2008	2	4	2–3 weeks old	18–23 December 2007
B7	17.02.2009	2	4	2 months old	20–30 December 2008
Unmarked	17.02.2009	25	4	2 weeks old	01–05 February 2009
Unmarked	18.02.2009	29	3	2 weeks old	01–05 February 2009
B7	06.12.2009	2	3	4–5 weeks old	02–09 November 2009
B25	06.12.2010	39B ^d	5	5–7 days old	29 Nov.–01 Dec. 2010
B25	15.01.2001	25	4	1 week old	06–08 January 2011
B22	22.02.2011	73 ^e	3	3–4 weeks old	27–31 January 2011
N/A	12/13.04.2011	– ^f	3	2 months old	05–15 February 2011
N/A	12.12.2017	– ^g	6	1 day old	12 December 2017

^a One young disappeared (probable death) a few days later

^b Only three young were detected on 5 November, but four were present the following day

^c The nestbox contained two litters (consisting of 3 young each) of different size

^d In 2010, nestbox 39 was moved to another location; hence the code change

^e In 2010, twelve new nestboxes (Nos 71–82) were added in the study site

^f These animals were trapped at the same location and were assumed to belong to the same litter

^g The female was captured in the forest and gave birth during the night in the trap