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5 **Habitat characteristics and species interference influence space use and nest-site occupancy:**
6 **implications for social variation in two sister species**

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26 **Abstract**

27 Nest-site selection is an important component of species socio-ecology, being a crucial factor in
28 establishment of group living. Consequently, nest-site characteristics together with space-use proxies may
29 reveal the social organization of species, which is critical when direct observation of social interactions is
30 hindered in nature. Importantly, nest-site choice is expected to be under strong selective pressures and the
31 object of intra- and interspecific competition. Although the bulk of research on sociality focuses on its
32 ecological drivers, our study introduces interspecific competition as a potential factor that could influence
33 social evolution. We investigated the influence of habitat and interspecific competition on the social
34 organization of two sister species of the African four striped mouse (*Rhabdomys dilectus dilectus* and
35 *Rhabdomys bechuanae*) in a similar macroenvironment. These species diverged in allopatry and occupy
36 distinct environmental niches. We radiotracked 140 adults to identify their nest-sites, determine nest
37 characteristics and record groups that shared nest-sites. Group cohesion was estimated from nest-site
38 fidelity, group association strength, and home range overlap within versus between group members. We
39 compared the two species in sympatry versus parapatry to determine the impact of species interference on
40 sociality. In parapatry, the two species selected distinct nest-site types, interpreted as different anti-
41 predator strategies: *R. bechuanae* selected fewer, spaced, less concealed nest-sites whereas *R. d. dilectus*
42 selected clumped and less visible nest-sites. *Rhabdomys bechuanae* also showed more cohesive and stable
43 social groups than *R. d. dilectus*. In sympatry, compared to *R. bechuanae*, *R. d. dilectus* occupied similar
44 nest-sites, however slightly more exposed and clumped, and displayed similar nest-site fidelity and group
45 association strength. We conclude that although habitat selection may be an important driver of social
46 divergence in *Rhabdomys*, species interference, by limiting *R. d. dilectus* movements and forcing nest-site
47 sharing may induce new ecological pressures that could influence its social evolution.

48 Key words: habitat selection, home range overlap, interspecific competition, nest-site sharing,
49 radiotracking, *Rhabdomys*, secondary contact, social groups

50 **Introduction**

51 Nest-sites are important components of the habitat requirements of species, and generally of
52 their socio-ecology (Santos and Lacey 2011, Webber and Vander Wal 2018). Being critical
53 environmental features for survival and reproduction (Edelman et al. 2009, Auclair et al. 2014), nest-
54 site choice is expected to be under strong selection pressure (Forstmeier and Weiss. 2004, Mainwaring
55 et al. 2017), and the object of both intra- and interspecific competition (Schradin 2005, Duckworth et
56 al. 2015).

57 Nest-sites are crucial resources for the establishment and maintenance of group-living in many
58 species (e.g. rodents, Lacey & Sherman 2007; Ebensperger *et al.* 2008; Santos & Lacey 2011; birds,
59 Banda and Blanco 2009; Duckworth et al. 2015; and, insects, Rangel, Griffin & Seeley 2010).
60 Moreover, group members establish bonds and sometimes breed communally (Hayes 2000, Schradin
61 2013, Auclair et al. 2014) in nest-sites that they defend and compete for against other groups (e.g.
62 *Peromyscus sp.*, Dooley and Dueser 1996; *Pseudophryne bibronii.*, Heap and Byrne 2013; *Rhabdomys*
63 *pumilio*, Schradin et al. 2006). When social interactions are difficult to observe directly in nature,
64 proxies such as nest-site occupancy could be particularly helpful in revealing the social organization
65 (i.e. the size, sexual composition and spatiotemporal cohesion of a group; Kappeler and Schaik van
66 2002) of cryptic species (Radespiel et al. 2003, Schradin 2013). For example, multiple occupancy of a
67 nest-site could indicate group living. Further, nest-site switching is expected to be less costly for
68 solitary species, because it involves a single individual's decision, compared to social groups where
69 individuals are expected to show higher nest-site fidelity and group association strength (Hayes 2000).
70 Finally, combining space use and nest-site occupancy studies could help to further elucidate group
71 membership in cryptic species: e.g. home range overlaps are expected to be greater for members
72 within than between groups (Mappes et al. 1995, Atwood and Weeks 2003, Stow and Sunnucks 2004,
73 Schradin and Pillay 2005).

74 By coupling space use proxies with nest-site characteristics and occupancy, our study aims to
75 elucidate how local habitat characteristics and species interference influence spatial group
76 establishment and therefore its social organization. Competition between sister species is known to
77 impact resource use (Dufour et al. 2017), reproduction (Pfennig and Pfennig 2009) and agonistic

78 interactions (Latour and Ganem 2017), enhancing species divergence or convergence in sympatry
79 (Grant 1972, Grether et al. 2009) or resulting in the exclusion of one of the species (Violle et al. 2011).
80 Species interference has been largely neglected in the study of sociality. It is crucial to recognize
81 however, that interspecific competition may directly alter social behavior, because it may drive shifts
82 in resource use (such as nest-site selection), as shown in colonies of native and invasive fire ants
83 (*Solenopsis sp.*) in the USA (Holway and Suarez 1999). This competitive pressure may be particularly
84 important when the two competing species are closely related since they are expected to exploit
85 similar resources (Violle et al. 2011) and display similar behaviors (Lichtenstein et al. 2017).
86 Moreover, although environmental impact on social variation within and between species has been the
87 focus of much research (reviewed in Lacey & Sherman 2007; Silk 2007; Gardner *et al.* 2015), few
88 have addressed the impact of microhabitat variations on sociality, particularly in cryptic species.

89 Here, we studied two species of the African four striped mouse, *Rhabdomys dilectus dilectus*
90 and *Rhabdomys bechuanae*, which have distinct environmental niches in southern Africa, where they
91 diverged in allopatry (Meynard et al. 2012, du Toit et al. 2012, Dufour et al. 2015a). The distributions
92 of the two species overlap partially in the central part of South Africa (Fig. 1 here; Dufour et al.
93 2015a), forming patches of parapatric (i.e. biogeographically abutting monospecific populations) and
94 sympatric (i.e. mixed-species) populations within the same macroenvironment (Ganem et al. 2012,
95 Dufour et al. 2015a). In allopatry (i.e. monospecific populations distant from contact areas), *R. d.*
96 *dilectus* occurs predominantly in mesic areas and occupies habitats of continuous vegetative cover,
97 while *R. bechuanae* occurs in arid to semi-arid areas with more patchily distributed cover. In
98 parapatry, *R. d. dilectus* is mostly found in riverine vegetation with dense cover, whereas *R.*
99 *bechuanae* uses patchy open shrubland vegetation (Dufour et al. 2015a). In sympatry, *R. d. dilectus*
100 still appears to select microhabitats with more cover than *R. bechuanae* (Dufour et al. 2015a).
101 Importantly, in sympatry, home range overlaps between the two species are more restricted than
102 expected, suggesting avoidance due to interspecific competition (Dufour et al. 2015a). Having been
103 recognized only recently (du Toit et al. 2012), our knowledge of the specific biology of these two
104 species is largely unknown (Dufour et al. 2015a, Table A1). Nonetheless, all *Rhabdomys* species are

105 diurnal and previous studies also suggested that *R. bechuanae* (sleeping and breeding in shrub nests)
106 would be more social than *R. d. dilectus* (sleeping and breeding in covered grass nests) in allopatry
107 (Table A1). Moreover, *R. bechuanae* has larger home ranges (Dufour et al. 2015a) and is considered to
108 be bolder (because it exploits open habitats more exposed to predation) than *R. d. dilectus* which avoids
109 open habitats even when supplemented with food (Abu Baker and Brown 2010).

110 The conditions in the areas where the two species distributions abut allow for comparisons of
111 their social organization in similar climatic, latitudinal and altitudinal conditions, as well as in the
112 presence or absence of interspecific competition. Few systems offer such natural experimental
113 settings, as in our study system, to test the role of local habitat characteristics and species interference
114 on species social divergence.

115 We used a population-level approach, testing 11 parapatric and three sympatric populations of
116 the two species, and adopted an indirect method to assess sociality using spatial and nest-site
117 occupancy proxies. Nest-sites were considered as a critical resource, particularly in the context of
118 intra- and interspecific competition. We radiotracked adult striped mice during the breeding season
119 (when intraspecific reproductive competition is expected to peak; Schoepf and Schradin 2012) to
120 locate their nest-sites. Since the characteristics of nest-sites and their accessibility to predators (e.g.
121 safe cover versus risky open sites) can influence survival (Kotler et al. 1991, Schooley et al. 1996,
122 Ebensperger et al. 2008), we assessed the distribution and external features of occupied nest-sites and
123 also determined nest-site fidelity and group association strength. Moreover, we ascertained group
124 membership and cohesion by assessing home range overlaps, which were expected to be the highest
125 between group members (Mappes et al. 1995, Atwood and Weeks 2003, Schradin and Pillay 2004).

126 We tested two hypotheses. 1) Patchily distributed nest-sites are expected to induce spatial
127 grouping of individuals with high group association strength and nest-site fidelity (Atwood and Weeks
128 2003, Schradin and Pillay 2004). Since *R. bechuanae* occurs in open-shrubland type habitats and *R. d.*
129 *dilectus* occurs in habitats with more continuous cover in allopatry and parapatry (Table A1; Dufour et
130 al. 2015a), different constraints on their nest-site characteristics and distribution could influence their
131 social organization: *R. bechuanae* is expected to show more cohesive groups than *R. d. dilectus* in

132 parapatry. In addition, we also expect the two species to have similar social organization in sympatry,
133 where they both occupy open-shrubland habitats (Dufour et al. 2015a). 2) Species interference could
134 induce further pressure on space use, microhabitat selection (Dufour et al. 2015a, 2017) and nest-site
135 occupancy (Dooley and Dueser 1996, Duckworth et al. 2015). In our study system, interspecific
136 interference was suggested by the low home range overlaps between the species in sympatry (Dufour
137 et al. 2015a). *Rhabdomys bechuanae* occupies similar microhabitats in the two biogeographical
138 contexts, and hence any shift in its social organization in sympatry, as compared to parapatry, might
139 be ascribed to interference with *R. d. dilectus*. Since *R. d. dilectus* occupies different microhabitats in
140 parapatry and sympatry, both microhabitats and species interference could interact to shape its social
141 organization. Yet, if species interference influenced *R. d. dilectus* social organization we would expect
142 changes in space use (e.g. more clumped or less clumped nest-sites compared to *R. bechuanae*) or the
143 quality of selected nest-sites (e.g. worse or better than *R. bechuanae*). In Table 1, we summarized the
144 hypotheses, predictions and results.

145 **Material and methods**

146 **Ethical note**

147 This study followed the ABS/ASAB guidelines for ethical treatment of animals, and care was taken to
148 ensure the well-being of the mice throughout the duration of the study. Permits to trap, handle and fit
149 striped mice with radio collars were obtained from the French ethics authorities (C34–265) and Animal
150 Ethics Screening Committee of Witwatersrand University (ethics number AESC 2012/13/2A), and from
151 the ethics authorities of the Free State (n° 01/15700) and North-West provinces (n° 01/11262), South
152 Africa.

153 **Study area**

154 This study took place in four South African nature reserves within the savanna and grassland biomes:
155 Sandveld (SA; S27° 43' E25° 45'), Soetdoring (SO; S28° 50' E26° 03') and Tussen die Riviere (TDR;
156 S30° 28' E26° 09') in the Free State Province, and Bloemhof Dam (BLH; S27° 38' E25° 40') in the
157 North-West Province (Fig. 1). The study was conducted during the austral spring (October–November

158 2011, 2012 and 2013), which coincided with the breeding season of *R. bechuanae* and *R. d. dilectus* in
159 these areas. In total, 14 populations (several populations per reserve, Table 2, Fig. 1) were sampled in
160 14 sites (hereafter study sites), separated by a minimum of 1 km from each other (details provided in
161 Dufour et al. 2015a).

162 **Trapping procedures**

163 Mice were captured using Sherman and PVC live-traps. Traps were set along lines, with a distance of
164 approximately 10m between traps (10 to 30 traps/line). The number of trap lines varied with the
165 study site size (for more details on the procedure and general handling see Dufour et al. 2015a).
166 Individuals were marked with ear tags (7mm, 0.17g; National Band and Tag Co., Newport, KY, USA),
167 sexed and measured (body length to the nearest mm). Males were considered as adult when their body
168 length was ≥ 7.8 cm (on the basis of the size of the smallest scrotal male), and females when their body
169 length was ≥ 7.5 cm (i.e. size of the smallest pregnant female). Because the two species could not be
170 distinguished visually, a tail sample (< 1 cm) was collected from each mouse and subsequently used for
171 post-hoc species identification, using Cytochrome Oxidase I genotyping (as described in Ganem et al.
172 2012). The trap lines were maintained for the duration of the radiotracking period. When trapped, a
173 radiotracked mouse was immediately released and no radiotracked mouse spent the night in a trap.

174 **Nest-sites localization and assessment of nest-site sharing**

175 In order to investigate nest-site occupancy, 140 adult striped mice (73 males and 67 females) were
176 radiotracked (an average of 49% of the total adult population trapped was radiotracked, with about
177 62% in eight study sites, and 95% in four study sites). They were equipped with VHF collars (MD_2C
178 Holohil, Carp, Ontario, Canada). Since the striped mouse is diurnal, geo-localization data were
179 collected at sunset (confirmed at sunrise) to locate and confirm nest-sites. A group was identified on
180 the basis of nest-site sharing. In total, 334 nest-sites were identified in 78 sampling nights. Once nest-
181 sites were identified, we placed additional traps (at sunset and checked them at sunrise) at the entrance
182 of a subsample of 36 nest-sites to detect the presence of additional adults, which were not radiotracked

183 during our study, in traps very close to these nest-sites. We found a strong positive correlation
184 (Pearson test: $t = 6.5973$, d.f. = 34, $P < 0.001$, $R^2 = 0.75$) between group size obtained by trapping with
185 that obtained by radiotracking, confirming the reliability of our estimation of minimum size of adult
186 groups based on radiotracked individuals. Pairs of two radiotracked adults, sometimes composed of a
187 male and a female, were considered as a group, because we were limited by the number of mice we
188 could radiotrack and hence our index might have under-estimated the actual group size (radiotracked
189 mice that appeared to nest solitarily might have shared their nest with non radiotracked mice). Social
190 groups in the sister species *R. pumilio* were comprised of an adult male and one or more adult females
191 and their progeny of different ages (Schradin and Pillay 2005).

192 **Nest-site characterization**

193 Because nest-sites are important determinants of group living, we assessed the characteristics of nest-
194 sites used by the radiotracked mice from two photographs: one depicting the external features (i.e.
195 entire vegetation constituting the nest-site); and the other focusing on the most visible entrance of the
196 nest-site, when visible (Fig. 2). From these photographs, we recorded external features and the state of
197 the vegetation (if any), as well as an index of visibility of the nest-site entrance, assessing whether a
198 snake, mammal carnivore or bird of prey could access the nest entrance (i.e. a measure of protection
199 from predation; Table 3).

200 **Nest-site distribution**

201 The surface area of each of the 14 study sites was small enough (2-19 ha) for an individual striped
202 mouse to traverse entirely during the study period; the longest distance between re-captures of an adult
203 individual was 900m in our study, and Schradin (2006) showed that both male and female striped mice
204 travel a maximum distance of about 900m per day. Hence, we hypothesized that all nest-sites
205 identified within a study site could be exploited by any striped mouse, unless constrained by exposure
206 to predators and/or territoriality (intra- and interspecific). To test our hypothesis, we calculated the
207 distance between 1) all nest-sites used by a focal mouse (nest-site network) over a period of at least

208 five days (when the home range size stabilized and reached asymptotic values; Dufour et al. 2015a),
209 and 2) all nest-sites identified within each study site during a radiotracking session. Because of
210 statistical constraints, only study sites in which at least five mice were radiotracked for a period of at
211 least five days were considered here. Hence, a total of 105 radiotracked mice (mean \pm SD distance
212 between nest-sites used by a mouse: 26.1 ± 24.3 m) geo-localized in 312 nest-sites (mean \pm SD
213 distance between nest-sites in a given study site: 124.0 ± 91.5 m) in 9 study sites, were considered in
214 this analysis.

215 **Nest-site fidelity**

216 Nest-site fidelity is assumed to characterize group living, and may also be an indication of nest-site
217 attraction. Nest-site fidelity was calculated as the number of different nest-sites occupied by a given
218 individual divided by the number of nights he was radiotracked (at least five nights - see above). This
219 analysis involved 117 mice. In order to validate the appropriateness of this ratio, nest-site fidelity of
220 lactating ($n = 14$) and non-lactating ($n = 47$) females were compared. Striped mice female produce
221 offspring in a nest where pups stay during the lactating period (10-16 days, Pillay 2000). Since pup
222 survival requires suckling, and transport of new-born between relatively distant nest-sites may not
223 occur (Pillay 2000), we expected that lactating females would not risk leaving their progeny alone
224 over-night and hence would show the highest nest-site fidelity. While the distance between utilized
225 nest-sites did not differ between lactating (19.9 ± 12.8 m) and non-lactating females (20.8 ± 16.3 m;
226 Mann-Whitney U test, $W = 313$, $P = 0.790$), lactating females showed greater nest-site fidelity ($0.4 \pm$
227 0.1 ; a score of 1 indicating use of a different nest-site each night) than non-lactating females ($0.6 \pm$
228 0.2 ; $W = 557.5$, $P = 0.005$), validating the use of our index.

229 **Group association strength based on frequency of nest-site sharing**

230 In order to assess cohesion between adult mice sharing the same nest-site, we calculated an association
231 strength index (AS; see details below) derived from VanderWaal et al. (2013). We hypothesized that
232 individuals which shared a nest-site for at least one night during the radiotracking period were part of

233 a group. The association strength index of any group was calculated as the number of different nest-
234 sites shared by these individuals divided by the number of nest-sites they did not share. For example,
235 if a group was composed of three individuals *i, j and k*, occupying *Y=number of nest-sites*, the
236 following formula was applied:

$$AS(i,j,k) = \frac{Y \text{ shared by } ijk + Y \text{ shared by } ij + Y \text{ shared by } ik + Y \text{ shared by } jk}{Y_i \text{ without } jk + Y_j \text{ without } ik + Y_k \text{ without } ij}$$

237 Of the 117 individuals involved in the nest-site fidelity analysis, 102 mice shared at least one
238 nest-site and were included in the group association strength analysis.

239 **Home range overlaps: a validation of group membership**

240 We expected group members to show greater home range overlap than non-group members (Mappes
241 et al. 1995, Atwood and Weeks 2003, Schradin and Pillay 2004). To test this prediction, individual
242 geo-locations (radiotracked points during the day at 7am, 9am, 11am, 2pm, 4pm and sunset at 7pm)
243 were used to calculate the individual home range size. Home ranges were defined as the areas
244 encompassed within the 0.95 cumulative isopleth of the Utilization Distributions (UDs), estimated
245 using the fixed kernel method with the reference smoothing parameter in R software (Worton 1989).
246 Only mice with at least 27 geo-locations over at least five days (n=111 mice with stable home ranges)
247 were included in this analysis (see Dufour et al. 2015a for details). The presence of baited traps during
248 the radiotracking period may have caused an underestimation of home range size, similarly for both
249 species and contexts.

250 Based on UD estimates, the home range overlaps between individuals of the same species were
251 determined as the Volume of Intersection (VI; Seidel 1992) of UD's for all pairs in a given study site
252 (overlap computations were performed with a home-made *Pascal* program following the method
253 described in Dufour et al. 2015a). The VI corresponds to the overlap area under the lower UD of the
254 two individuals. Because UD's were truncated at the 0.95 cumulative isopleth (to exclude poorly
255 estimated UD tails), overlap values were normalized between 0 and 1 by dividing VI by 0.95 (see

256 Benhamou et al. 2014 for details). The VI for each pair of individuals was calculated and averaged
257 between members of a group (within-group VI values) and then compared to averaged overlaps
258 between members of different groups (between-group VI values).

259 **Statistics**

260 All statistical analyses were conducted using R-v3 software (R Development Core Team 2012).
261 Significance levels were set at $\alpha = 0.05$, and adjusted for multiple testing with the sequential (top
262 down) Bonferroni correction when necessary. Normality and heteroscedasticity of distributions were
263 checked by plotting the model residuals; data were transformed when necessary.

264 To test the similarity of nest-site characteristics between the species and contexts (i.e.
265 parapatry and sympatry), we performed χ^2 contingency table analyses with likelihood ratios. We
266 assessed whether nest-sites used by a given mouse were randomly distributed by comparing within
267 study site versus within individual nest-site distances using Wilcoxon tests (11 tests). A Spearman test
268 was performed to assess the correlation between study site surface area and distance between occupied
269 nest-sites.

270 Linear mixed-effect models were used to primarily test the influence of species and context on
271 i) log-transformed values of distance between used nest-sites, ii) nest-site fidelity, iii) group
272 association strength, and iv) home range overlap. To account for pseudo-replication, all linear mixed-
273 effect models included the study site identity (i.e. population) as a random factor (random intercepts),
274 while sex differences were accounted for by adding sex as a fixed factor for individual-centered tested
275 variables. To control for the potential influence of sex effect on analyses involving group
276 characteristics (association strength and home range overlap), we calculated the sex-ratio of each
277 group as the number of radiotracked adult males divided by the total number of radiotracked adults.
278 We did not detect any significant variation of the sex-ratio between species, context and their
279 interaction (Table 5, Table A3), and hence sex-ratio was not included in the analyses involving group
280 characteristics.

281 The full models considered all the variables and interactions according to the species and the
282 context (for all traits), the sex (for nest-site distance and fidelity), the group size (for AS), and the
283 group state (intragroup versus intergroup for VI, Table A3). The best-fitted model for each tested trait
284 (and with random effect) was selected based on the Akaike weight (relative likelihood of a model to
285 be the best among the set of models tested) and $\Delta AICc$ (see Table A3 for details about the models).
286 Tukey HSD tests were used for pairwise post-hoc comparisons for significant fixed factors.

287 **Results**

288 **Nest-site characteristics**

289 In parapatry, nest-site characteristics differed significantly between the two species (all comparisons P
290 < 0.001 , Table 4; Fig. 3). Nest-sites of *R. bechuanae* were predominantly located inside bushes that
291 were either alive or composed of a mixture of alive and dead vegetation, while the nest-sites of *R. d.*
292 *dilectus* were exclusively in grass type vegetation (mostly alive). Moreover, nest-sites occupied by *R.*
293 *d. dilectus* appeared to be more protected from predation than those occupied by *R. bechuanae*, the
294 latter showing low to intermediate protection from predation (Fig. 2 & 3).

295 In sympatry, the nest-sites of the two species also differed significantly in their external
296 features, confirming selection for more woody type vegetation by *R. bechuanae* and more grass type
297 vegetation by *R. d. dilectus* (Table 4, Fig. 3). However, nest-sites of *R. d. dilectus* also occurred in bare
298 soil and woody microhabitat and tended to show lower protection from predation compared to the
299 nest-sites of *R. bechuanae* (Table 4, Fig 3).

300 Nest-site characteristics of *R. bechuanae* did not vary significantly between parapatric and
301 sympatric populations (Table 4), whereas those of *R. d. dilectus* were more diverse in their external
302 features, offered significantly less predation protection and were composed of more mixed dead and
303 alive vegetation in sympatry than in parapatry (Table 4, Fig. 3).

304 These results suggest selection of nest-sites with distinct characteristics by the two species
305 when in parapatry, while some convergence occurred in sympatry due to *R. d. dilectus* occupying nest-
306 sites more similar to those of *R. bechuanae* than to their parapatric counterparts.

307 **Nest-site distribution**

308 The distances between nest-sites used by a focal individual were not related to the study site surface
309 area (Spearman correlation test $Rho = 0.22$, $P = 0.50$). Both in parapatry and in sympatry, the average
310 distance between nest-sites used by a mouse was significantly lower than expected by random use of
311 all nest-sites identified in a given site (Fig. 4, Table A2, all $P < 0.001$). The distance between nest-sites
312 occupied by a mouse was significantly greater for the males than for the females and for *R. bechuanae*
313 females (10/35 being lactating) compared to *R. d. dilectus* ones (5/31 being lactating) in both contexts
314 (Table 5A & B, Fig. 4). While the spatial distribution of nest-sites occupied was constrained for both
315 species, *R. bechuanae* used more distantly-spaced nest-sites than *R. d. dilectus*.

316 **Nest-site fidelity**

317 Nest-site fidelity varied interactively between species and context (Table 5A). In parapatry, *R.*
318 *bechuanae* showed significantly greater nest-site fidelity than *R. d. dilectus* (Table 5B, Fig. 5), while,
319 in sympatry, nest-site fidelity did not differ between the two species (Table 5B). Sympatric
320 populations of *R. d. dilectus* showed significantly higher fidelity than their parapatric counterparts
321 (Table 5B), while *R. bechuanae* displayed similar nest-site fidelity in sympatry and parapatry (Table
322 5B, Fig. 5). However, although *R. bechuanae* individuals exhibited high nest-site fidelity, most did not
323 use exclusive nest-site, since they were observed to use at least two different nest-sites over a period of
324 five or more days (fidelity index > 0.2).

325 **Group association strength based on frequency of nest-site sharing**

326 *Rhabdomys bechuanae* displayed greater group association strength (AS) than *R. d. dilectus* in
327 parapatry (Table 5B), but not in sympatry (Table 5B) where *R. d. dilectus* group association strength
328 was as high as that of *R. bechuanae* (Fig. 6).

329 In both species, groups of more than three individuals were observed in the two contexts, and
330 groups of more than four individuals in parapatry (group size was similar between the species and
331 contexts): among the 83 groups (i.e. comprising a minimum of two radiotracked mice; 44 *R. d.*
332 *dilectus* and 39 *R. bechuanae*), 22 (13 *R. d. dilectus* and 9 *R. bechuanae*) were composed of three to
333 five adults.

334 **Home range overlaps: a validation of group membership**

335 Home range overlaps (VI) were significantly greater between members of the same group than
336 between members of different groups (Table 5A, Fig. 7). This result did not differ significantly
337 between species and was consistent across contexts (i.e. parapatry versus sympatry; Table 5A).
338 Moreover, home range overlap between group members was positively correlated with their group
339 association strength index (Spearman Rho = 0.311, P = 0.009), further validating our assessment of
340 group membership and cohesion based on nest-site occupancy. These results suggest that group
341 members share a territory and avoid those of other groups, a pattern confirmed in sympatry.

342 **Discussion**

343 Consistent with their microhabitat selection (Dufour et al. 2015a), the two *Rhabdomys* species selected
344 distinct nest-site types in parapatry and more similar ones in sympatry. Further, as revealed by our
345 approach using two indirect but complementary proxies of sociality – nest-site sharing and home-
346 range overlaps— both species displayed group living in parapatry and sympatry, although *R.*
347 *bechuanae* showed greater group cohesion than *R. d. dilectus* in parapatry. High nest-site fidelity and
348 group association strength, as displayed by *R. bechuanae* in parapatry and both species in sympatry,
349 suggest the importance of microhabitat features and predation (i.e. open habitat and relatively exposed
350 nest-sites) as facilitators of group living and cohesion. However, compared to *R. bechuanae*, slightly
351 less protective and more clumped nest-sites occupied by *R. d. dilectus* in sympatry suggest that species
352 interference may constrain *R. d. dilectus* movement and indirectly force group living and cohesion.
353 Altogether, our study shows the importance of microhabitat features in shaping *Rhabdomys* social

354 organization and points out for the first time that species interference, by constraining space use, may
355 contribute to evolution of social organization (Table 1).

356 **Microenvironment impacts social organization**

357 The patchiness of resources in general, and of nest-sites and shelters in particular, is often considered
358 as a driver of sociality. For instance, greater nest-site fidelity, greater home range overlaps between
359 relatives and larger social groups are among the observed responses to habitat fragmentation in the
360 bank vole (*Clethrionomys glareolus*; Mappes et al. 1995), coyote (*Canis latrans*; Atwood and Weeks
361 2003) and Cunningham's skink (*Egernia cunninghami*; Stow and Sunnucks 2004). Consistent with
362 these general findings, in parapatry, the nest-site fidelity and group association strength were higher in
363 *R. bechuanae* occupying habitats characterized by patchily distributed vegetation and nest-sites,
364 compared to *R. d. dilectus* found mostly in continuous habitats with important cover (Dufour et al.
365 2015a).

366 Both *R. d. dilectus* and *R. bechuanae* selected nest-sites significantly closer together than
367 expected by chance. Space use is shaped by mobility, territoriality, environmental features, foraging,
368 and predation risk (Börger et al. 2008). In terms of mobility, the sampled surface area of each site in
369 our study was small enough to be explored by both *R. bechuanae* and *R. d. dilectus* under ideal free
370 conditions. However, the patterns of home range overlap observed in both species (i.e. larger overlaps
371 within group members than between groups and positive correlation between association strength and
372 home-range overlap) suggest that territoriality between groups may limit space use and hence may
373 impact the distance between nest-sites occupied by an individual or a group. Further, the distances
374 between nest-sites used by a focal individual (both species), being smaller than expected by chance,
375 might reflect sufficient and clumped distribution of resources in our study sites, refuting the limited
376 foraging resource hypothesis as an explanation of the observed species space use (Silk et al. 2014).

377 *Rhabdomys d. dilectus* females used a more clustered network of nest-sites than *R. bechuanae*
378 females in both contexts. Clustered nesting may represent a way to reduce exposure to predators (e.g.

379 reduce mobility in open area). However, the perception of predation risk may also favor the use of
380 more distant nest-sites that could serve as refuges, particularly when the nest-sites are more exposed to
381 predation (Godsall et al. 2013), which is the case for *R. bechuanae* and both species in sympatry.
382 Radespiel et al. (2003) reported that while the social mouse lemur species – *Microcebus murinus* –
383 slept in protected and sheltered nest-sites, *M. ravelobensis* formed smaller sleeping social groups in
384 open vegetation and less protected sleeping sites with frequent nest switching. These authors attributed
385 differences in social behavior and nest-site utilization to the ecological divergence between the species
386 in allopatry, as a result of different thermoregulation and predation strategies. Our study reveals that
387 evolution under distinct ecological conditions may have also resulted in different nesting characteristics
388 in the two striped mouse species, although, unlike for the mouse lemur, greater nest fidelity and higher
389 group association strength were associated with less protected and more distant nest-sites. These
390 contrasting responses indicate that although the environment influences sociality (Lacey and Sherman
391 2007, Webber and Vander Wal 2018), its precise consequences may not be generalizable across species.

392 The natural setting of our experiments allowed for direct comparisons of the two species under
393 similar environmental conditions (grassland and shrubland microhabitats being available in all sites;
394 Dufour et al. 2015a). Therefore, the finding that they selected distinct microhabitats and nest-site types in
395 parapatry strongly suggests divergence during evolution in allopatry and possibly divergent adaptation
396 (e.g. boldness or mobility in open risky habitat type). Further, the fact that *R. d. dilectus* could thrive in
397 habitats similar to *R. bechuanae* in sympatry and adjust its social organization suggests its flexibility.

398 **Species interference and evolution of sociality**

399 In sympatry, the shift in microhabitat selection observed in *R. d. dilectus* was associated with greater
400 nest-site fidelity and higher group association strength. Dooley and Dueser (1996) attributed the
401 change of sleeping sites in *Peromyscus leucopus* in terms of the external features (from tree to ground)
402 and quality (nesting on ground is less favorable to winter survival and predator protection) to
403 competition for nest-sites with the dominant *P. maniculatus*.

404 Greater nest-site fidelity and group cohesion of *R. d. dilectus* observed in sympatry could be
405 the result of either interspecific competition (or its indirect impact on intraspecific competition),
406 predation (indirect influence of microhabitat selection), or both: fewer nest-sites available for *R. d.*
407 *dilectus* and high perceived predation risks in a relatively open habitat may limit its movements.
408 Indeed, *R. d. dilectus* individuals occurring in grassland avoided open woody patches even when they
409 were supplemented with food (Abu Baker and Brown 2010). In addition, in another study involving the
410 same populations of *R. bechuanae* and *R. d. dilectus*, home-range overlap between the species in
411 sympatry was significantly lower than expected by chance, further suggesting that interspecific
412 competition could occur (Dufour et al. 2015a). Moreover, in sympatry, *R. bechuanae* are significantly
413 heavier than similar sized *R. d. dilectus* adults (Ganem et al. unpublished) which suggest they may
414 dominate *R. d. dilectus*. Finally, although potential breeders of the two species can discriminate between
415 conspecifics and heterospecifics, they still do engage in mating attempts with the other species (Dufour
416 et al. 2015b). Thus, it appears plausible that during the breeding season and in sympatry, interspecific
417 competition for both mates and nest-sites may occur and limit the access of *R. d. dilectus* to shelters
418 (numbers and quality). Such competition could explain the slightly lower quality nest-site occupied and
419 relatively low mobility of *R. d. dilectus*, particularly of females, compared to *R. bechuanae* under the
420 same conditions. Additional studies during the non-breeding season, when competition is expected to be
421 low, would allow us to disentangle the relative role of habitat versus competition in shaping social
422 organization of *R. d. dilectus* in sympatry.

423 **Social variation within the genus *Rhabdomys***

424 The genus *Rhabdomys* radiated along a climatic gradient in southern Africa, ranging from the dry and
425 open environment of the west-northwest to mesic and grassland vegetation in the east (Meynard et al.
426 2012, du Toit et al. 2012). It has long been considered as a monospecific genus, showing population-
427 level variations in social behavior ascribed to variable environmental conditions: open, patchy and dry
428 environment favoring group-living as opposed to mesic continuous grassland hosting solitary
429 individuals (Schradin and Pillay 2005, Schoepf and Schradin 2012).

430 A literature survey (Table A1) indicates that the two semi-arid striped mouse species, *R.*
431 *bechuanae* and *R. pumilio*, are more social than their two mesic counterparts, *R. d. dilectus* and *R. d.*
432 *chakae*, confirming the general view of the impact of environmental conditions on evolution of social
433 behavior (Lacey and Sherman 2007, Silk 2007, Schradin 2013, Gardner et al. 2015). *Rhabdomys*
434 *bechuanae* has been described as socially tolerant at the core of its distribution (Kalahari; Table A1), and
435 the present study shows that this also applies at the distribution margins of the species. However, unlike
436 *R. pumilio* whose social groups occupy a single nest-site (Schradin and Pillay 2004, Schradin 2013), *R.*
437 *bechuanae* seems to display a fission- fusion group structure type (Couzin 2006), suggesting lower group
438 cohesion and sociality compared to *R. pumilio* (Schradin 2013). Differences in sociality between the two
439 species may be an indication that they experience different environmental constraints, a hypothesis that
440 could be tested in the future. In particular, the aridity food distribution hypothesis (AFDH) offers a
441 possible theoretical model to consider evolution of sociality in the genus *Rhabdomys*. In mole rat species,
442 the AFDH suggests that more complex social organization evolved under arid environments and patchy
443 distribution of food (e.g. Jarvis et al. 1994).

444 **Conclusions**

445 Habitat characteristics and their impact on nest-site quality and distribution appear to be important
446 drivers of social divergence in the genus *Rhabdomys*. Moreover, at least two *Rhabdomys* species – *R.*
447 *d. dilectus* (this study) and *R. pumilio* (Schoepf and Schradin 2012) – adjust some aspects of their
448 social behavior in response to environmental constraints. Importantly, the present study introduced the
449 idea that interspecific competition may generate novel environmental pressures, by restricting
450 individual movements and constraining nest-site sharing, which could influence the social
451 organization of species. Consequently, the role of interspecific competition on social evolution appears
452 as a promising avenue of future research.

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462 **Data accessibility**

463 The data will be deposited at the open archive HAL

464

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582

583 **Figures**

584 **Figure 1** Study area in South Africa (A) –Bloemhof (BLH), Sandveld (SA), Soetdoring (SO) and
585 Tussen die Riviere (TDR) Nature reserves— and details of the distribution of the sites sampled in
586 BLH and SA (B), TDR (C) and SO reserves (D) according to species occurrence (parapatry and
587 sympatry of *R. bechuanae* and *R. d. dilectus*). The TDR1 and SA2 sites were resampled (TDR1 in
588 2012 and 2013 where parapatric *R. bechuanae* occurred; SA2 in 2011 was sympatric and became
589 parapatric for *R. bechuanae* in 2012).

590 **Figure 2.** Photographs showing examples of nest-site characteristics and indicating social tolerance in
591 *R. bechuanae*. (A) A nest-site relatively exposed to terrestrial predators, with the bottom image
592 showing details of the nest covered with dead grass beneath a bush. (B) A nest-site that we excavated
593 out at the end of the study. Concealed entrances led to connected burrows and to a large central
594 chamber containing nesting material. This nest-site was occupied by a large group (more than five
595 individuals) of adults as well as juveniles. The central, large chamber contained a large nest made of
596 grass (second from top image in panel B) within which we found pups and unweaned juveniles. The
597 last image of the panel (bottom right corner; B) shows two independent tunnels with entrances under
598 thick bush that both led to the central chamber. (C) Social behavior captured using a camera trap: the
599 top image taken in a very early morning (5:30 am) shows three mice basking in the early sun (several
600 meters from their nest); the bottom image shows two mice approaching a trap together in the middle of
601 the afternoon.

602 **Figure 3.** Comparisons of nest-site characteristics, determined from photographic analyses (an A4
603 white sheet is included for scale), by species and context.

604 **Figure 4.** Pairwise distance in meters between all nest-sites used by a given individual (indiv) *R. d.*
605 *dilectus* (in black) and *R. bechuanae* (in orange) or identified in each site (in grey) in both contexts
606 (parapatry and sympatry). Box-plots show the median (thick line), first and third quartiles. The vertical
607 lines indicate the lowest datum within 1.5 IQR (interquartile range) of the lower quartile, and the
608 highest datum still within 1.5 IQR of the upper quartile. Individual dots represent outliers.

609 **Figure 5.** Nest-site fidelity assessed as the ratio of number of nest-site used / number of nights when
610 *R. d. dilectus* (in black) and *R. bechuanae* (in orange) individuals were radiotracked in paraptry and
611 sympatry. A score of 1 indicates use of a different nest-site each night. Box-plots show the median
612 (thick line), first and third quartiles. The vertical lines indicate the lowest datum within 1.5 IQR
613 (interquartile range) of the lower quartile, and the highest datum still within 1.5 IQR of the upper
614 quartile. Individual dots represent outliers.

615

616 **Figure 6.** Group association strength index according to species (*R. d. dilectus* in black; *R. bechuanae*
617 in orange) and context (parapatry and sympatry). Box-plots show the median (thick line), first and
618 third quartiles. The vertical lines indicate the lowest datum within 1.5 IQR (interquartile range) of the
619 lower quartile, and the highest datum still within 1.5 IQR of the upper quartile. Individual dots
620 represent outliers.

621

622 **Figure 7.** Volume of Interaction (VI, area in m²) of home range overlaps between members of the
623 same nest-site group (intragroup, dashed lines) versus between members of different groups
624 (intergroup, solid lines) according to species (*R. d. dilectus* in black; *R. bechuanae* in orange) and
625 context (parapatry and sympatry). Box-plots show the median (thick line), first and third quartiles. The
626 vertical lines indicate the lowest datum within 1.5 IQR (interquartile range) of the lower quartile, and
627 the highest datum still within 1.5 IQR of the upper quartile. Individual dots represent outliers.

628 **Tables**

629 Table 1. A synthesis of the two hypotheses tested in the study, the traits used to test them, the predicted outcomes in parapatry and sympatry in *R. d. dilectus* and *R.*
 630 *bechuanea*, and a brief summary of the results.

HYPOTHESES	MEASURED TRAITS	PREDICTIONS				RESULTS
		<i>R. d. dilectus</i>		<i>R. bechuanea</i>		
		parapatry	sympatry	sympatry	parapatry	
1. Microhabitat and nest-site selection drive social organization in <i>Rhabdomys</i>	Nest-site characteristics	dense cover in grass with high predation protection	open shrubland with medium to low predation protection	open shrubland with medium to low predation protection	open shrubland with medium to low predation protection	YES
	Nest-site distribution	clustered	patchy	patchy	patchy	YES (in parapatry for both species) NO (in sympatry for <i>R. d. dilectus</i>)
	Nest-site fidelity	low	high	high	high	YES
	Group Association Strength	low	high	high	high	YES
	Volume of Interaction	intragroup = intergroup	intragroup > intergroup	intragroup > intergroup	intragroup > intergroup	YES (in sympatry for both species) NO (in parapatry for <i>R. d. dilectus</i>)
2. Interspecific interference induces new ecological pressures that impact the social organization of <i>Rhabdomys</i> .	Same traits as above	Same predictions as above in parapatry	Any deviation from above predictions, leading to species differences in sympatry		Same predictions as above in parapatry	YES (in sympatry: <i>R. d. dilectus</i> occupied clustered nest-sites, less protected from predation than <i>R. bechuanea</i>)

631 Table 2. Sample size of populations, individuals and nest-sites in this study, as well as radiotracking
 632 duration by context (parapatry vs sympatry) and species (*R. bechuanae* and *R. d. dilectus*).

	Parapatry <i>R. d. dilectus</i>	Sympatry	Parapatry <i>R. bechuanae</i>	Total/Average
Number of populations (= study sites)	4	3	7	14
Radiotracking duration (mean \pm SD number of days)	11.19 \pm 0.96	14.9 \pm 2.58	12.17 \pm 2.61	12.3 \pm 2.76
Number of nest-sites identified	125	84	125	334
Number of nest-sites characterized	106	58	112	276
Number of radiotracked individuals	45	22 <i>R. bechuanae</i> 14 <i>R. d. dilectus</i>	59	140
Number of mice radiotracked for at least five days	41	18 <i>R. bechuanae</i> 11 <i>R. d. dilectus</i>	47	117
Number of individuals with identified nest-sites	37	14 <i>R. bechuanae</i> 10 <i>R. d. dilectus</i>	44	105
Number of individuals sharing (with another striped mouse) at least one nest-site	41	12 <i>R. bechuanae</i> 5 <i>R. d. dilectus</i>	44	102
Number of adults obtained from traps set within a 4m zone around each of 36 nest-sites	52	18 <i>R. bechuanae</i> 6 <i>R. d. dilectus</i>	53	129

633

634

635 Table 3. Nest-site characteristics (parameters considered and variables measured) from photographic
 636 analysis.

Parameters	Categories	Description
External features	Grass	The main vegetation (> 50%) around nests was composed of grass, reeds or rushes (e.g. <i>Juncus sp</i> ; <i>Digitaria sp.</i> ; <i>Eragrostis sp.</i>)
	Bushy	The main vegetation (> 50%) was woody (e.g. <i>Asparagus sp.</i> ; <i>Acacia sp.</i> <i>Ziziphus sp.</i> ; <i>Lycium sp</i>)
	Bushy/Grass	A mixture of grass (50%) and bush (50%)
	Bare soil	No vegetation (a burrow surrounded by bare soil, or a burrow in a termite mound)
Vegetation state	Dead	The surrounding vegetation (> 50%) was dead, dry and/or uprooted
	Alive	The vegetation was alive (>50%)
	Mixed	Mixed dead (50%) and alive (50%) vegetation
	None	Only bare soil
Predation protection	Low	Birds (e.g. <i>Haliaeetus vocifer</i>), small mammals (e.g. <i>Cynictis penicillata</i>) and snakes (e.g. <i>Bitis arietans</i>) could see the nest entrance and access the nest
	Intermediate	Some of the predators might not have access (e.g. entrance visible only from the ground or the entrance was narrow)
	High	The nest-site entrance was completely (100%) hidden and/or presence of obstacles such as dense thorns.

637

638 Table 4. Statistical results of contingency analyses of nest-site characteristics (external features,
639 vegetation state and predation protection) comparing species and context (p values which remained
640 significant after application of the Bonferroni α sequential adjustment for multiple tests are indicated
641 in bold).

Type of comparison	Statistic	External features	Vegetation state	Predation protection
Parapatry n=218 (<i>R. bechuanae</i> vs <i>R. d. dilectus</i>)	χ^2	181.25	79.24	39.08
	d.f.	3	2	2
	P	<0.001	<0.001	<0.001
Sympatry n=58 (<i>R. bechuanae</i> vs <i>R. d. dilectus</i>)	χ^2	14.56	8.14	7.35
	d.f.	3	2	2
	P	0.002	0.016	0.025
<i>R. bechuanae</i> n=142 (parapatry vs sympatry)	χ^2	6.34	6.89	4.33
	d.f.	3	2	2
	P	0.096	0.032	0.115
<i>R. d. dilectus</i> n=134 (parapatry vs sympatry)	χ^2	49.12	100.81	74.11
	d.f.	3	2	2
	P	<0.001	<0.001	<0.001

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643

644 Table 5. Statistical results from the best-fitted linear mixed-effect models with random effects (A) for the
645 distance (log transformed) between nest sites used by the individuals, nest-site fidelity, group association
646 strength (AS), home range overlap (VI) and variation in radiotracked group sex-ratio. The full models
647 considered all the variables and their interactions (see Table A3): species and context (for all models), sex (for
648 nest-site distance and fidelity), group size (for AS), and group state (i.e. intragroup versus intergroup for VI).
649 The site identity was set as a random effect (intercepts) in all models. The best-fitted models were then
650 selected based on the Akaike Information Criterion (Δ AICc and weight, Table A3). When an interaction was
651 significant, Tukey post-hoc tests were performed (B). Bold p-values highlight significant effects of the fixed
652 variable.

A.

Trait	Variable	Fixed/Random	n.d.f.	d.d.f.	Value	Std.Error	F	P-value
Distance (log) between nest-sites used by individuals	(Intercept)		1	409	2.27	0.18	637.56	<0.001
	species	F	1	81	0.79	0.22	6.74	0.011
	context	F	1	12	-0.11	0.28	0.14	0.713
	sex	F	1	81	0.66	0.17	8.43	0.005
	species:sex	F	1	81	-0.62	0.25	5.95	0.017
	site indiv	R			0.42 ^a	71.46 ^b	<0.001	
Nest-site fidelity*	(Intercept)		1	101	0.70	0.03	780.24	<0.001
	species	F	1	101	-0.25	0.04	28.82	<0.001
	context	F	1	12	-0.22	0.07	4.92	0.047
	species:context	F	1	101	0.20	0.08	6.14	0.015
	site	R				0.03 ^a	0.24 ^b	0.623
AS	(Intercept)		1	130	0.27	0.04	216.42	<0.001
	species	F	1	130	0.15	0.05	4.03	0.047
	context	F	1	12	0.19	0.09	0.82	0.384
	species:context	F	1	130	-0.25	0.12	4.13	0.044
	site	R				0.07 ^a	2.21 ^b	0.137
VI*	(Intercept)		1	129	8.55	2.50	337.56	<0.001
	species	F	1	129	-2.32	3.26	1.86	0.175
	context	F	1	12	9.64	6.73	0.37	0.553
	group state	F	1	129	41.15	2.72	231.67	<0.001
	species:context	F	1	129	-13.94	8.88	2.47	0.119
	site	R				2.00 ^a	0.17 ^b	0.677
SR	(Intercept)		1	131	0.37	0.05	159.59	<0.001
	species	F	1	131	0.09	0.07	1.72	0.192
	context	F	1	12	-0.02	0.09	0.03	0.862
	site	R				0.09 ^a	7.93 ^b	0.005

653 ^a Standard deviation

654 ^b Likelihood ratio

655 * The best-fitted models did not include the random effect (Table A3) but to consider pseudo-replication, we provided the
656 best models with the random factor. The models with and without the random effect generated the same general results
657 (Table A4).

B.

Trait	Tukey test (lower; upper confident interval 95%)		estimate	SE	d.f.	t.ratio	<i>P.value</i>
Distance nest-sites (log)	<i>R. d. dilectus. Female (1.79; 2.63)</i>	<i>R. bechuanae. Female (2.62; 3.39)</i>	-0.79	0.22	81	-3.64	<0.001
	<i>R. d. dilectus. Male (2.44; 3.30)</i>	<i>R. bechuanae. Male (2.61; 3.47)</i>	-0.17	0.23	81	-0.72	0.473
Nest-site fidelity	<i>R. d. dilectus. parapatry (0.63; 0,77)</i>	<i>R. bechuanae. parapatry (0.38; 0.51)</i>	0.25	0.04	101	5.77	<0.001
	<i>R. d. dilectus. Parapatry (0.63; 0,77)</i>	<i>R. d. dilectus. sympatry (0.35; 0.60)</i>	0.22	0.07	12	3.33	0.030
	<i>R. bechuanae. Parapatry (0.38; 0.51)</i>	<i>R. bechuanae. sympatry (0,32; 0,53)</i>	0.02	0.06	12	0.31	0.990
	<i>R. d. dilectus. Sympatry (0.35; 0.60)</i>	<i>R. bechuanae. Sympatry (0,32; 0,53)</i>	0.05	0.07	101	0.71	0.890
AS	<i>R. d. dilectus. parapatry (0.19; 0.36)</i>	<i>R. bechuanae. parapatry (0.34; 0.50)</i>	-0.15	0.05	130	-2.72	0.008
	<i>R. d. dilectus. sympatry (0.29; 0.64)</i>	<i>R. bechuanae. sympatry (0.19; 0.53)</i>	0.10	0.11	130	0.92	0.360

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