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Kin-based spatial structure in a solitary small mammal as indicated by GPS dataloggers

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Lindelani Makuya^{a*}, Neville Pillay^a, Carsten Schradin^{a,b}

^a School of Animal, Plant & Environmental Sciences, University of the Witwatersrand, Johannesburg, South Africa

^b IPHC, UNISTRA, CNRS, Strasbourg, France

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*Corresponding author.

E-mail address: lindelanimakuya@gmail.com (L. Makuya).

LM: <https://orcid.org/0000-0002-2986-1627>

NP: <https://orcid.org/0000-0002-0778-726X>

CS: <https://orcid.org/0000-0002-2706-2960>

Kin selection is important for understanding the evolution of social behaviour in group-living species. Yet, the role of kinship in solitary species has received little attention. We studied how kinship influences intraspecific variation in social organization and spatial structure in a predominantly solitary species, the bush Karoo rat, *Otomys unisulcatus*, from the Succulent Karoo semidesert of South Africa. We predicted that if social groups occur, they should consist of close kin. We further predicted that the spatial structure is not random, but that close kin live closer to each other. Over 5 years we performed trapping and focal animal observations and fitted mini-GPS dataloggers simultaneously on 125 neighbouring female bush Karoo rats to investigate how their spatial structure was influenced by kinship. Females were mainly solitary, although small social groups also occurred, all consisting of close kin, typically females, such as a mother and her adult daughter or sisters. Although females did have more nonkin than kin neighbours, kin lived closer to each other than nonkin. Daily ranges were larger in the breeding than in the nonbreeding season and overlapped more between kin than nonkin females. We conclude that kinship should be considered when studying solitary species as it might influence variation in social organization and spatial structure.

38

39 **Keywords:** intraspecific variation in social organization; kinship; kin selection; social
40 organization; social structure; social system; solitary; spatial structure

41

42

43 Kin selection (Hamilton, 1964a) has been used to explain why species live in groups (Lacey &
44 Wiczorek, 2004) but has rarely been considered of importance for solitary species. Kin
45 groups often form when individuals delay dispersal and remain philopatric (Williams &
46 Rabenold, 2005), but dispersal can also influence spatial kin structure in solitary species
47 (Cutrera, Lacey, & Busch, 2005).

48

49 A species' spatial structure forms the basis on which their social system (i.e. social
50 organization, social structure, care and mating systems) develops and evolves (He,
51 Maldonado-Chaparro, & Farine, 2019; Kappeler, 2019; Webber et al., 2023; Webber & Vander
52 Wal, 2018). The spatial structure of a species is influenced by different factors such as food
53 availability, the presence of conspecifics, geographical barriers and dispersal (Schlichting et
54 al., 2022). Of these factors, dispersal is one of the most important (Cooper & Randall, 2007;
55 Cutrera et al., 2005; He et al., 2019; Webber et al., 2023). In mammals, females are often
56 philopatric while males disperse (Li & Kokko, 2019; Williams & Rabenold, 2005). If females
57 disperse, then it is often for shorter distances from their natal territory, whereas males
58 disperse over larger distances (Lawson Handley & Perrin, 2007). In the solitary giant kangaroo
59 rat, *Dipodomys ingens*, the spatial structure is characterized by female kin living close
60 together, especially at high population densities (Meshriy, Randall, & Parra, 2011). While
61 philopatry is considered a promotor of group living, dispersal in its broad sense (i.e. remaining
62 in the natal area) can also be important to understand the social systems of solitary species
63 (Cooper & Randall, 2007).

64

65 In mammals, solitary species are characterized by males and females only meeting for
66 courtship and mating, and offspring leaving their mother in the period between weaning and
67 the end of puberty (Makuya & Schradin, 2024a). Examples of solitary species are some shrews
68 (Valomy, Hayes, & Schradin, 2015), and large predators, such as black bears, *Ursus*
69 *americanus* (Kovach & Powell, 2003) and leopards, *Panthera pardus* (Rafiq et al., 2020).
70 Solitary living is often assumed to be an adaptation to sparsely distributed food that cannot
71 be shared (Dalerum, 2007; Makuya & Schradin, 2024a; Nowak & Wilson, 1999). While
72 individuals of solitary species do not share the same home range and sleeping sites, they do
73 interact with conspecifics (Makuya & Schradin, 2024a). For example, the solitary puma, *Puma*
74 *concolor*, has complex social networks with individualized relationships (Elbroch & Wittmer,
75 2012). Many solitary species do not have a random distribution but display a kin-based spatial
76 structure, although this has rarely been studied.

77

78 The spatial structure of solitary species can change by season (Johansson et al., 2018). In
79 particular, males of solitary species increase their home ranges more than females during the

80 breeding season to overlap with many females to increase their reproductive success (Dillon
81 & Kelly, 2008). Females might change their home ranges seasonally as a response to changes
82 in resource availability (Potts & Lewis, 2014). For example, home range sizes of female striped
83 mice (*Rhabdomys* spp.) vary with the seasonal availability of food (Schradin et al., 2010b). The
84 impact of season and sex on home range size is well understood in group-living species
85 (Schradin et al., 2010b; Stamps, 1994) but not much is known about solitary species. Studying
86 variation in home range size of solitary species will provide an indication of their intraspecific
87 variation in social organization (IVSO), particularly among the females.

88

89 In some species social organization is not fixed (Schradin, 2013). Factors that influence IVSO
90 include population density and reproductive competition (Schradin, Hayes, Pillay, &
91 Bertelsmeier, 2018). The African striped mouse, *Rhabdomys pumilio*, shows IVSO, being able
92 to switch from solitary living at low population density to group living when both population
93 density increases and reproductive competition decreases (Schoepf & Schradin, 2012;
94 Schradin, König, & Pillay, 2010a). Generally, population density and competition are the main
95 drivers of IVSO at the species level (Schradin, 2013). IVSO may be adaptive in harsh
96 environments (Makuya, Pillay, Rimbach, & Schradin, 2023) and also occurs in species that are
97 typically regarded as solitary (Valomy et al., 2015). It is not known, however, whether
98 population density and reproductive competition might lead to IVSO in predominantly
99 solitary species, leading to some of them forming groups when population density is very
100 high.

101

102 Solitary mammals are often either small, nocturnal and live in dense habitats (shrews,
103 rodents), or large and nocturnal, occupying large areas (large predators), making them
104 challenging to study (Kovach & Powell, 2003; Waser & Jones, 1983). The solitary bush Karoo
105 rat, *Otomys unisulcatus*, from the Succulent Karoo semidesert is a good model to study
106 solitary living since it is a small diurnal mammal that occupies an open habitat characterized
107 by low-growing annuals and dispersed shrubs, has small home ranges and is easily habituated
108 to the presence of observers (Schradin, 2005; Vermeulen & Nel, 1988; Wolhuter, Thomson,
109 Schradin, & Pillay, 2022).

110

111 We studied how kinship influences the social organization, especially deviation from its
112 primarily solitary living, and spatial distribution of the bush Karoo rat. We focused on females,
113 which are the more philopatric sex. We ascertained the social organization of the bush Karoo
114 rat from trapping data and behavioural observations and made five predictions. (1) Bush
115 Karoo rats are mainly solitary, but when groups occur, these will be mainly female kin groups,
116 occurring after the breeding season and when population density is high. (2) Females have
117 more female kin than nonkin neighbours. (3) The geographical distance between female kin
118 neighbours is shorter than between nonkin neighbours. We used mini-GPS dataloggers to
119 provide a better assessment of the spatial structure and ascertain the daily range sizes and
120 overlap of daily ranges, and how these are influenced by kinship and season. We predicted
121 (4) that the daily ranges of females vary seasonally, being larger in the food-restricted dry
122 season, and (5) the daily ranges of kin neighbours overlap more than those of nonkin.

123

124 <H1>Methods

125 <H2>Study Species

126 The 100 g bush Karoo rat is endemic to semiarid and arid regions of South Africa, particularly
127 the Karoo and the Succulent Karoo, one of the world's most important biodiversity hotspots
128 (Cowling, Esler, & Rundel, 1999; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000).
129 The bush Karoo rat builds stick-lodges inside shrubs, which provide a favourable microclimate
130 with high humidity and mild temperatures for protection against the external environment
131 (Brown & Willan, 1991; du Plessis & Kerley, 1991; du Plessis, Kerley, & Winter, 1992). It is a
132 central-place forager, foraging within a short distance (less than 25m) from its lodge and then
133 returning to the lodge (Schradin, 2005).

134

135 <H2>Study Site and Study Period

136 We conducted our study on a 3.5 ha site next to the Succulent Karoo Research Station in the
137 Goegap Nature Reserve, Northern Cape, South Africa. The Succulent Karoo is characterized
138 by cold winters (mean temperatures of 16.8 °C in June 2019 at our field site with a minimum
139 of -2.6 °C on one night) and hot summers (mean temperature in January 2019 was 27.3 °C,
140 maximum was 46.7 °C). The study site occurs in a winter rainfall area with average rainfall of
141 160 mm per year at our field site (Schradin, 2005). In our study area, the breeding season of
142 bush Karoo rats is from June to November (austral winter and spring), and the nonbreeding
143 season is from December to May (austral summer and autumn). We used trapping and
144 observation data collected from bush Karoo rats from September 2017 to March 2020 (when
145 the field site closed due to the COVID-19 pandemic) and January 2021 to July 2023.

146

147 <H2>Sampling Regime

148 <H3>Trapping and marking of bush Karoo rats

149 Trapping was conducted at lodges that showed signs of being occupied (fresh faeces, active
150 runways, rats observed). The field site was divided into four to six areas, with one to two areas
151 trapped at the same time by two teams (Fig. 1). All lodges within one area were trapped for
152 three consecutive days before moving on to the next area. Traps were set in the morning
153 before sunrise, checked after 45 and 90 min and then left closed during the hottest times of
154 the day. In the afternoon, traps were set 45 min before sundown, checked after sundown and
155 then left closed during the night. We used a combination of foldable Sherman traps
156 (<https://shermantraps.com/>) and locally produced heavy metal traps of the Sherman style.
157 Traps were baited with a combination of bran flakes, salt and sunflower oil and rebaited each
158 morning and afternoon. They were arranged around the entrances of the lodges and along
159 runways. No injuries due to trapping were recorded. The details of trapped rats were
160 recorded, including their weight to the nearest 0.1 g, reproductive status and lodge number.
161 Bush Karoo rats were removed from the traps in a plastic bag and weighed with the bag,
162 before being taken out for inspection and then released at their lodge. Then the weight of the
163 plastic bag was subtracted from the total weight. We marked individuals with metal band ear
164 tags with a unique reference number for later identification (National Band and Tag Co.,

165 Newport, KY, U.S.A.; Schoepf & Schradin, 2012). To aid in visual identification during
166 observations, individuals were marked with nontoxic hair dye (Inecto Rapido, Pinetown,
167 South Africa), in combinations (females: head and chest/sides/back; males: hindquarters and
168 chest/sides/back). Age was estimated from body mass at first capture, using a species-specific
169 growth curve validated by our field data (Pillay, 2001). The bush Karoo rats were classified
170 according to their age, with pups being up to 2 weeks old and weighing less than 30 g (weaning
171 is at 14 days; Pillay, 2001), juveniles being 2 - 6 weeks old and weighing between 30 and 70 g,
172 and adults being older than 6 weeks and weighing more than 70 g, when both sexes can start
173 reproduction (Pillay, 2001).

174

175 <H3>*Determination of kinship*

176 Relatedness between individuals was assessed from trapping records and observations. Pups
177 and juveniles that were trapped at a lodge with an adult female were considered as the
178 offspring of that female. Pups and juveniles were always trapped at only one lodge, such that
179 our combination of trapping and observations allowed us to reliably estimate female kinship
180 for them, although we have no information on paternal kinship. Following dispersal, juveniles
181 either lived alone or with a sibling. This was confirmed through focal animal observations
182 which we conducted at the lodges where pups and juveniles were located. Females from one
183 matriline were regarded to be closely related kin: mother and her offspring, maternal
184 siblings, females that had the same grandmother as well as maternal cousins, i.e. females
185 whose mothers were sisters. All other individuals were considered nonkin.

186

187 <H3>*Determination of reproduction*

188 The reproductive condition of the females was determined from trapping data when
189 pups/juveniles were trapped at the adult female's lodge. The month of birth of the
190 pups/juveniles (estimated from their body mass at first trapping) was used as the
191 reproductive month for the adult female. The gestation period of the bush Karoo rat is 39
192 days (Pillay, 2001). It was possible to tell when females were pregnant from their weight and
193 when they gave birth due to a sudden drop in weight. We used this information to confirm
194 the calculated pup/juvenile date of birth and therefore the breeding period of the females.

195

196 <H3>*Behavioural observations in the field*

197 Focal observations were conducted five times a week at lodges with evidence of being
198 occupied by bush Karoo rats to determine occupancy of lodges (which individuals were
199 present) and to identify when pups emerged and juveniles/young adults dispersed. The
200 morning observations started 5 min before the sun started shining on the lodges and lasted
201 for 30 min; afternoon observations started 25 min before the sun stopped shining on the
202 lodges. Lodges were usually observed on 2 days a month. The lodges that contained juveniles
203 or a pregnant female were monitored more than twice in a month. The behaviours recorded
204 during the observations included activities (e.g. foraging and feeding), lodge building and
205 social behaviours including the following groups of behaviour: (1) amicable behaviours (i.e.

206 grooming, body contact); (2) social investigation (i.e. sniffing); and (3) aggression (i.e. chasing,
207 fighting). Behavioural data will be presented elsewhere.

208

209 <H2>*Determination of social organization*

210 We used a combination of trapping and behavioural observations to assess the social
211 organization (i.e. group size and composition) of each adult bush Karoo rat for every month
212 they were observed in the study site. We identified four forms of social organization (Table
213 1). Because lodges occupied by bush Karoo rats showed clear signs of use such as collected
214 plant material, active runways and fresh faeces, we were certain that we had trapped at all
215 occupied lodges on the field site (bush Karoo rats on our field site always live in a lodge). The
216 open habitat (no trees, low-growing shrubs) ensured we did not miss a lodge and we
217 continuously surveyed the field site for occupied lodges. If we did not trap a bush Karoo rat
218 at a lodge with an indication of occupancy within the normal trapping regime of 3 days, we
219 continued trapping and also observed the lodge, to ensure that trap-shy individuals were
220 trapped and marked. Our behavioural observations confirmed that bush Karoo rats trapped
221 at a lodge also inhabited that lodge, although some inhabited several neighbouring lodges.
222 Apart from roaming males, we very rarely observed any bush Karoo rats at a lodge that they
223 did not inhabit.

224 We used a linear mixed-effects model (LME) run in the lme4 R package using the “lmer”
225 function (Bates, Maechler, Bolker, & Walker, 2015) to analyse factors that influence the
226 percentage of solitary adult females. We used data collected from September 2017 to July
227 2023 (54 months), with season and population density as fixed effects and the year as a
228 random variable. The population density was calculated every month ($N = 54$) from the total
229 number of adult rats divided by the study site size. The model used was as follows:

230 percentage of solitary individuals = season + population density + (1|year).

231 <H2>*Monthly determination of neighbours and distance between neighbours*

232 We ascertained the number of adult kin and adult nonkin neighbours for each adult female
233 every month. A neighbour was defined as any adult individual that occupied a lodge not more
234 than 25 m away from the focal individual with no other individual occupying a lodge in
235 between. This distance was selected since we never observed a rat foraging more than 25 m
236 away from its focal lodge, which is confirmed by data from GPS dataloggers (Makuya &
237 Schradin, 2023). For each female, we recorded the distance from its lodge to the lodges of
238 its nearest kin and its closest nonkin neighbour in QGIS using the ‘shortest distance feature’
239 tool (QGIS, 2009; Fig. 1). We ran a generalized linear mixed-effects model (GLMM) with a
240 Poisson distribution to analyse factors influencing the number of neighbours, with the focal
241 rat’s ID number as a random effect and the relationship between neighbours (kin versus
242 nonkin) and season as fixed effects. We had a sample size of 172 focal rats over 21 months
243 (from January 2021 to July 2023) in the following model:

244 number of neighbours = relationship (kin versus nonkin) + season (breeding versus
245 nonbreeding) + (1|Focal ID) + (1|year).

246 We ran an LME to test for a difference in the distance between the closest kin versus nonkin
247 neighbour. For every female, we took the mean distance to the kin neighbours and the mean

248 distance to the nonkin neighbours such that each focal rat had a maximum of two neighbour
249 values per month for the analyses. This was done to control for pseudoreplication. We
250 included relationship (kin versus nonkin) and season as fixed effects and the ID of the focal
251 rat and the year as random effects:

252 distance = relationship (kin versus nonkin) + season (breeding versus nonbreeding) + (1 | Focal
253 ID) + (1 | Month)

254

255 <H2>Mini-GPS dataloggers

256 Three to five neighbouring adult females were fitted with mini-GPS dataloggers (Gipsy 6
257 model from Technosmart, Italy <https://www.technosmart.eu/gipsy-remote-copy/>) on the
258 same day, from August 2021 to April 2023. The mini-GPS weighed 4.5 g including the
259 protective coating, and the rats weighed 96.6 + 19.3 g (range 67.5 - 131.2 g) Therefore, the
260 mini-GPS represented less than 7% and in most cases less than 5% of their body weight
261 (Murray & Fuller, 2000). GPS dataloggers were fitted like a rucksack with a neck and a belly
262 belt consisting of a wire running through a small rubber tube to avoid any skin irritation,
263 fastened with a fishing crimp. The procedure lasted 1 - 3 min and involved holding the rat in
264 one hand and fitting the unit. We fitted 227 Gipsys on a total of 125 females. Of these, useful
265 data were obtained from 156 Gipsys; the remaining units ($N = 73$) either failed (did not switch
266 on), were lost or switched off too early. Gipsy collars collected the location (longitude, latitude
267 and altitude) of an individual and the date, time and daily ranges used, including the occupied
268 lodges and foraging grounds (Makuya & Schradin, 2023). The Gipsys were programmed
269 following a successfully validated protocol (Makuya & Schradin, 2023). Data collection was
270 delayed by 2 days after fitting the collar to allow the rats to become accustomed to the Gipsys.
271 On the third day, the Gipsys collected GPS fixes every 5 min; the battery life did not allow us
272 to collect data for more than 1 day. On day 4, we started to retrap rats to remove the Gipsys.
273 Because range estimates can be skewed due to outliers and locations with low accuracy, we
274 cleaned the data from the mini-GPS loggers by first removing fixes with a horizontal accuracy
275 of > 50 m and then visualizing fixes obtained from the Gipsys in QGIS to exclude obvious
276 outliers, as validated in Makuya and Schradin (2023). To analyse the daily range sizes and
277 overlap, we used the autocorrelated kernel density estimation (AKDE) implemented in the R
278 packages “ctmm” (Calabrese, Fleming, & Gurarie, 2016) and “ctmmweb” (Dong, Fleming,
279 Noonan, & Calabrese, 2018). The overlap was calculated for every pair on the daily range data
280 from the same month. The AKDE approach allowed us to account for location error in the
281 calculations of range sizes within the ctmm workflow through two stages (Fleming et al.,
282 2021). The calculations from the autocorrelation and bandwidth were error-informed, which
283 mitigates various biases in autocorrelation and bandwidth estimates that would otherwise
284 occur had location error been ignored. Then, location estimates were fed through a Kalman
285 smoother before kernel placement, which counteracts overdispersal (Silva et al., 2022). To
286 determine the overlap between a pair of home range estimates, we used the Bhattacharyya
287 coefficient within the “ctmmweb” R package, following Winner et al. (2018). We used an LMM
288 to determine what factors influenced the daily range sizes (DRS), in which season and
289 relationship (kin versus nonkin) were used as fixed predictors and the ID of the rat was a
290 random effect. This was followed by an LMM to assess the influence of the season and
291 relationship on the overall overlap between ranges. The models we used were:

292 DRS = season + (1 | ID)

293 overlap = season + relationship+ (1 | ID)

294

295 <H2>Statistical Analysis

296 All statistical analyses were done in R (version 4.3.1; R Core Team, 2022). Model assumptions
297 were assessed by inspecting Q–Q plots and by plotting model residuals against fitted values
298 for every model used. Before running each model, we checked for multicollinearity in models
299 that contained more than one fixed factor by calculating variance inflation factors (vifs; Zuur,
300 Ieno, & Elphick, 2010) for the predictor variables using the vif function in the “car” package
301 (Fox & Weisberg, 2011). Models that contained vif values above 2 were removed to prevent
302 multicollinearity. The study focused on social organization, which by definition is the adult
303 composition of social units, with pups and juveniles not considered (Kappeler, 2019). First,
304 we describe the social organization for both sexes. Since males disperse early and then float
305 (have no permanent lodge) and are only present at the field site for a few days before
306 disappearing for weeks, the social units on the field site were characterized by females and
307 all further statistical tests therefore involved females only.

308

309 <H2>Ethical Note

310 We adhered to the ASAB/ABS Guidelines for the Use of Animals in Research (Buchanan et al.,
311 2012). Bush Karoo rats ($N = 507$ rats trapped 10 711 times over the study period) were
312 captured and handled using protocols approved by the Animal Ethics Screening Committee
313 of the University of the Witwatersrand (AESC clearance numbers 2003/34/3 and 2018-03-
314 15B). The field site was selected such that even under low population density conditions, at
315 least eight solitary females were present, and regular trapping was necessary to ensure we
316 kept track of all individuals on the field site. To reduce the stress caused to the animals after
317 fitting them with mini-GPS dataloggers, we placed the rats in cages with food in a field
318 laboratory and monitored them for 1 h before releasing them into the field. Following their
319 release, we also conducted focal animal observations on the rats that carried loggers and
320 found that they foraged as normal, and the loggers did not seem to negatively affect them.
321 We adhered to the relevant South African laws concerning the use of animals for
322 experimental purposes, including obtaining Section 20 permit.

323

324 <H1>Results

325

326 <H2>Social Organization

327 Most adult female and adult male bush Karoo rats were solitary (mean \pm SD % solitary:
328 females: $96.6 \pm 10.26\%$; males: $98.9 \pm 2.97\%$; Fig. 2). Adult groups made up a small percentage
329 of the population and consisted of adult female kin (mother and adult daughter or sisters, 6.6
330 $\pm 9.5\%$ of all social units), mother and adult son ($0.32 \pm 0.93\%$) and sibling pairs (brother and
331 sister, $0.13 \pm 0.66\%$; Fig. 2). In total, we observed 97 groups in 23 of the 51 months of study,
332 with a group size of two or three individuals (2.2 ± 0.397). Of these, 50 groups consisted of a

333 mother and one ($N = 31$ groups) or two ($N = 19$ groups) daughters and 31 of two ($N = 28$
334 groups) or three ($N = 3$ groups) sisters. We observed 12 groups consisting of a mother and her
335 adult son and four groups of a sister and brother. For the groups consisting of two or three
336 females, none of the females bred in 65 groups (end of the breeding season), one bred in
337 seven groups and both females bred in five groups. There were no significant effects of season
338 (LME; $t_{46} = 0.4$, $P = 0.69$; Table A1) or population density (LME; $t_{48} = -1.6$, $P = 0.116$; Table A1)
339 on the percentage of solitary living females.

340

341 <H2>*Spatial Structure*

342 The mean numbers of kin and nonkin neighbours were very similar (Fig. 3a), but female bush
343 Karoo rats had more nonkin than kin neighbours (GLMM; $t = 2.53$, $P = 0.01$; Table A2).
344 However, kin neighbours lived closer to each other than nonkin neighbours (LME; $t_{966} = 21.36$,
345 $P < 0.001$; Fig. 2, 3b, Table A3). Season did not influence the number of neighbours (GLMM; t
346 $= 1.01$, $P = 0.29$), or the distance to the nearest neighbour (LME; $t_{11} = -0.882$, $P = 0.40$; Tables
347 A2, A3).

348

349 <H2>*Daily range size and overlap*

350 The daily range sizes were influenced by season (LME; $t_{62} = 3.04$, $P < 0.001$; Fig. 4a), with
351 range sizes being significantly larger in the breeding season. Overlap of ranges was not
352 influenced by season (LME; $t_{104} = -0.99$, $P = 0.32$; Fig. 4b). However, it was influenced by
353 kinship (LME; $t_{97} = -4.57$, $P < 0.001$; Table A5), with females overlapping significantly more
354 with kin than with nonkin (Fig. 4b, Table A5).

355

356 <H1>**Discussion**

357 We showed that kinship is important in the social system of a solitary species, suggesting the
358 potential for kin selection. Specifically, we found that the spatial distribution of the solitary
359 bush Karoo rat was not random but followed kin-based matriline. Females lived closer to and
360 overlapped more with female kin than with nonkin. We also found variation in social
361 organization, with few small groups, which always consisted of close kin and most often
362 closely related females. Our study adds to more recent studies indicating that solitary living
363 is not primitive and simple and that solitary species might have more complex social
364 structures than recognized (Baker et al., 2021; Elbroch, Levy, Lubell, Quigley, & Caragiulo,
365 2017; Makuya & Schradin, 2024a, 2024b; Meshriy et al., 2011; Roex, Mann, Hunter, & Balme,
366 2022).

367

368 Bush Karoo rats are mainly solitary but do show some deviation, leading to intraspecific
369 variation in social organization. Ours is the first peer-reviewed study describing the social
370 organization of bush Karoo rats. Unpublished data indicate that in other populations, group
371 living in the bush Karoo rat might be more common than in our study population (Do Linh San
372 et al., 2016), indicating the possibility for variation in social organization within and between
373 populations.

374

375 At our field site, groups rarely formed. These were always kin groups, as predicted, most often
376 consisting of a mother and her adult daughter(s), and sometimes sisters. Males were more
377 often solitary than females, and few of them lived together with their mother or sister. In
378 contrast to our prediction, groups were not more often found during the nonbreeding season
379 than the breeding season, even though the data indicate that they might be more common
380 at the end of the breeding season (Fig. 2), which warrants future studies. In striped mice
381 studied on the same field site, one main factor leading to solitary living is reproductive
382 competition, through female infanticide of another female's pups (Schradin et al., 2010a). In
383 the few bush Karoo rat groups, we observed either no reproduction taking place or only one
384 female reproduced, such that reproduction competition played no role. Group formation in
385 bush Karoo rats could best be explained by the delayed dispersal of females reaching
386 adulthood during the end of the breeding season, which should be studied in more detail in
387 the future.

388

389 Population density was not significantly related to solitary living as we had predicted. In our
390 current study, sufficient free territories were available for most female bush Karoo rats to
391 disperse and start solitary living. The small territories of these central place foragers, as seen
392 from the daily range data, might be one explanation for the lack of association between
393 population density and solitary living. In contrast, the sympatric striped mice have larger
394 home ranges and are more likely to form groups when population density is high (Schoepf &
395 Schradin, 2012; Schradin et al., 2010a; Schradin, Pillay, & Bertelsmeier, 2019). The striped
396 mice study generated more data collected over several more years than we collected in our
397 current study (8 years versus 5 years). Future analyses on a larger data set for bush Karoo rats
398 over more years considering population density and additional cofactors such as predation
399 pressure, food availability and availability of lodges might help us to understand when groups
400 form. It is possible that during years with very high population density, we might find more
401 and even larger groups.

402

403 Nonrandom spatial structures of amicably interacting individuals have been described for
404 crocodiles (Baker et al., 2021; Baker et al., 2023) and sharks (Anderson et al., 2021; Mourier,
405 Vercelloni, & Planes, 2012). In solitary felids and rodents this is known to depend on kinship
406 (Meshriy et al., 2011; Roex et al., 2022). In our study, female bush Karoo rats had significantly
407 more nonkin than kin neighbours, although the mean values were very similar (Fig. 3a). This
408 might simply be because, overall, a female had many more nonkin than kin in the population.
409 However, female bush Karoo rats lived closer to kin than to nonkin neighbours. This spatial
410 kinship structure is similar to that of the giant kangaroo rat, *Dipomys ingens*, which formed
411 female kin groups with increasing population density (Meshriy et al., 2011) and woodchucks,
412 *Marmota monax*, which lived closer to kin and shared home ranges (Maher, 2009). The spatial
413 kinship pattern in the bush Karoo rat seems to be related to females dispersing from their
414 natal lodge to unoccupied lodges close by. There are fitness benefits of living near kin and
415 familiar neighbours (Siracusa et al., 2021). An individual might be able to increase its inclusive
416 fitness by associating and collaborating with closely related conspecifics, even in solitary
417 species, such as alerting each other to predators (warning calls) or by social tolerance allowing

418 them to share food sources (Dobson, Viblanc, Arnaud, & Murie, 2012; Griffiths & Armstrong,
419 2001; Viblanc, Saraux, Murie, & Dobson, 2016; Viblanc et al., 2022; Walmsley et al., 2023).
420 This can have significant fitness benefits as shown in Columbian ground squirrels, *Urocitellus*
421 *columbianus*, which, overall, have more weaned offspring when they have female kin
422 neighbours (Viblanc et al., 2016). Solitary animals may lose some of the direct benefits of
423 group living (Makuya & Schradin, 2024a), and forming a kinship spatial structure could be a
424 strategy to reduce such costs (Makuya & Schradin, 2024b).

425

426 When individuals derive benefits from close kin, they increase their inclusive fitness, which
427 often occurs in pair- and group-living species (Ferriere & Michod, 2011; Gardner & West,
428 2014; Hamilton, 1964a; Hamilton, 1964b). That the ranges of close female kin of solitary
429 species overlap more than those of nonkin might be a result of living closer to each other,
430 which indicates higher tolerance between close kin. Such situations might then enable some
431 collaboration, as described for other solitary mammals (Elbroch & Wittmer, 2012; Lührs &
432 Kappeler, 2013; Meshriy et al., 2011). Future studies should test whether closely related bush
433 Karoo rats share important foraging grounds and whether they might collaborate in territorial
434 defence of areas with resources. While individuals overlap in space, they may not always
435 overlap in time, which can be confirmed by studying the fine scale interactions of individuals
436 (Schlägel et al., 2019). Kin selection might provide a basis for understanding the social system
437 of solitary species with a kin-based spatial structure, although this has been largely ignored in
438 the literature.

439

440 GPS dataloggers have been used in several large mammal studies to assess their spatial
441 structure, such as in cougars, *Puma concolor*, and fossas, *Cryptoprocta ferox*, where this
442 technique revealed previously unknown relationships, often influenced by kinship (Elbroch et
443 al., 2017; Lührs & Kappeler, 2013). By using mini-GPS for the first time in a small rodent to
444 determine spatial structure, we found that the ranges of bush Karoo rats overlapped more
445 with their kin than with their nonkin neighbours. Large carnivores that display territorial
446 defence have greater overlap in spatial ranges when food availability is low (Nams et al.,
447 2023). In our study, season did not significantly influence range overlap, but we cannot
448 exclude this possibility (see Fig. 4b). However, we found that bush Karoo rats had larger
449 ranges in the wet, breeding season than in the dry, nonbreeding season. This is surprising,
450 since more food is available in the wet season, and one might expect bush Karoo rats to
451 instead extend their home ranges in the food-poor dry season. In the wet breeding season,
452 females might have to forage over larger areas to obtain both energy and protein-rich food
453 necessary for breeding. The shrubs into which lodges are built offer some food (leaves) even
454 in the dry season. Smaller ranges in the dry season might help save energy, as occurs in the
455 synoptic striped mouse which also has smaller home ranges in the dry season (Schradin et al.,
456 2010b). Finally, our GPS data confirmed that the spatial structure in the solitary bush Karoo
457 rat is not random but is influenced by kinship.

458

459 While solitary living has long been regarded as an ancestral and primitive trait, recent
460 comparative studies indicate that solitary living might be a derived state in mammals, and an
461 adaptation to specific environments (Makuya & Schradin, 2024a). However, studying solitary

462 living is important to understand mammalian social evolution (Clutton-Brock, 2021; Makuya
463 & Schradin, 2024a). Multiple studies using modern network analysis indicate that even
464 solitary mammals (social organization) might have complex social interactions with their
465 neighbours (social structure; Elbroch & Wittmer, 2012; Lührs & Kappeler, 2013; Meshriy et
466 al., 2011). Our study adds to evidence uncovering the social complexity of solitary mammals.
467 It provides insight into the importance of kinship in a solitary species and shows that
468 intraspecific variation in social organization can also occur in a primarily solitary species. Our
469 observations of female kin structure and the rare occurrence of female kin groups indicate
470 the possibility of evolution leading to social groups.

471

472 <H2>Conclusion

473 The evolution of sociality can only be explained by including studies on solitary species
474 (Clutton-Brock, 2021; Makuya & Schradin, 2024b). Several years of field data showed that
475 bush Karoo rats are mainly solitary, yet their spatial organization is influenced by kinship.
476 Solitary species may miss out on the benefits gained by group-living species (Makuya &
477 Schradin, 2024a), but the costs of solitary living can be reduced by having a kin-based spatial
478 structure. The groups we observed consisted of close kin, and these groups likely formed as
479 a result of delayed dispersal. This is a potential starting point for the evolution of group living.
480 In conclusion, our study supports the notion that kinship and kin selection might be important
481 in solitary species.

482 Data Availability

483 Data are uploaded as supplementary files.

484 Declaration of Interest

485 The authors declare that they have no conflicting interests.

486

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497

498 Supplementary Material

499 Supplementary material associated with this article is available in the online version at doi

500

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708

709 **Appendix**

710

711 **Tables**

712 **Table 1.** Observed forms of social organization in bush Karoo rats

Social organization	Definition
Solitary living	<p>Only one adult bush Karoo rat was trapped and observed at a lodge.</p> <p>We differentiated between solitary males and solitary females.</p> <p>Mother families, i.e. one mother with one or more offspring that were not adult, were also considered to be solitary living.</p>
Sibling pairs	Adult sister and adult brother
Female groups	Two or more adult females were trapped and observed at one lodge together
Mother and adult son	Adult female with her adult son

713 Pups: less than 2 weeks old; juveniles: 2 - 6 weeks; adults: > 6 weeks old.

714

715 Table A1. Results of the generalized linear mixed-effects models to identify whether
 716 population density and the season have an impact on the percentage of solitary females in
 717 the bush Karoo rat

Predictors	Estimates	95% Confidence Interval	<i>P</i>
(Intercept)	99.4	90.68 – 108.1	< 0.001
Population density	-0.43	-0.96 – 0.09	0.116
Season (nonbreeding)	0.895	-5.36 – 3.43	0.691
Random effects σ^2 /ICC	37.21/0.386		
Marginal R^2 /conditional R^2	0.41/0.039		

718 σ^2 : variance of the random effect 'ID'; ICC: intraclass coefficient of variation. The marginal R^2
 719 considers only the variance of the fixed effects, while the conditional R^2 takes both the fixed
 720 and random effects into account. Factors in bold type indicate significant predictors. %
 721 Solitary living = season + population density + (1|year)

722

723

724

725 Table A2. Results of the linear mixed-effects models to identify which relationship category
 726 predicts the number of neighbours a rat has

Predictors	Estimates	95% Confidence Interval	<i>P</i>
(Intercept)	0.61	0.45 – 0.74	< 0.001
Relationship (nonkin)	0.11	0.02 – 0.199	< 0.01
Season (nonbreeding)	0.1	-0.098 – 0.293	0.35
Random effects σ^2 /ICC	0.40/0.198		
Marginal R^2 /conditional R^2	0.011/0.207		

727 σ^2 : variance of the random effect 'ID'; ICC: intraclass coefficient of variation. The marginal R^2
 728 considers only the variance of the fixed effects, while the conditional R^2 takes both the fixed
 729 and random effects into account. Factors in bold type indicate significant predictors. Number
 730 of neighbours = relationship (kin versus nonkin) + (1 | Focal ID) + (1 | Month)

731

732

733 Table A3. Results of the linear mixed-effects models to identify which relationship category
 734 predicts the distance to the nearest neighbour

Predictors	Estimates	95% Confidence Interval	<i>P</i>
(Intercept)	8.89	7.98 – 9.79	< 0.001
Relationship (nonkin)	10.35	9.68 – 11.02	< 0.001
Season (nonbreeding)	-0.44	-1.17 – 0.28	0.23
Random effects σ^2 /ICC	28.79/0.509		
Marginal R^2 /conditional R^2	0.321/0.667		

735 σ^2 : variance of the random effect 'ID'; ICC: intraclass coefficient of variation. The marginal R^2
 736 considers only the variance of the fixed effects, while the conditional R^2 takes both the fixed
 737 and random effects into account. Factors in bold type indicate significant predictors. Distance
 738 = relationship (kin versus nonkin) + season + (1 | Focal ID: Month) + (1 | Neighbour ID: Month)

739

740

741 Table A4. Results of the linear mixed-effects models to identify whether season influences
 742 daily range size

Predictors	Estimates	95% Confidence Interval	<i>P</i>
(Intercept)	445.94	365.17 – 526.71	< 0.001
Season (breeding)	163.75	57.01 – 273.09	< 0.01
Random effects σ^2 /ICC	18,276/0.213		
Marginal R^2 /conditional R^2	0.073/0.271		

743 σ^2 : variance of the random effect 'ID'; ICC: intraclass coefficient of variation. The marginal R^2
 744 considers only the variance of the fixed effects, while the conditional R^2 takes both the fixed
 745 and random effects into account. Factors in bold type indicate significant predictors. Home
 746 range size = season + relationship + (1|ID)

747

748

749 Table A5. Results of the linear mixed-effects models to identify whether season influences
 750 daily range size overlap

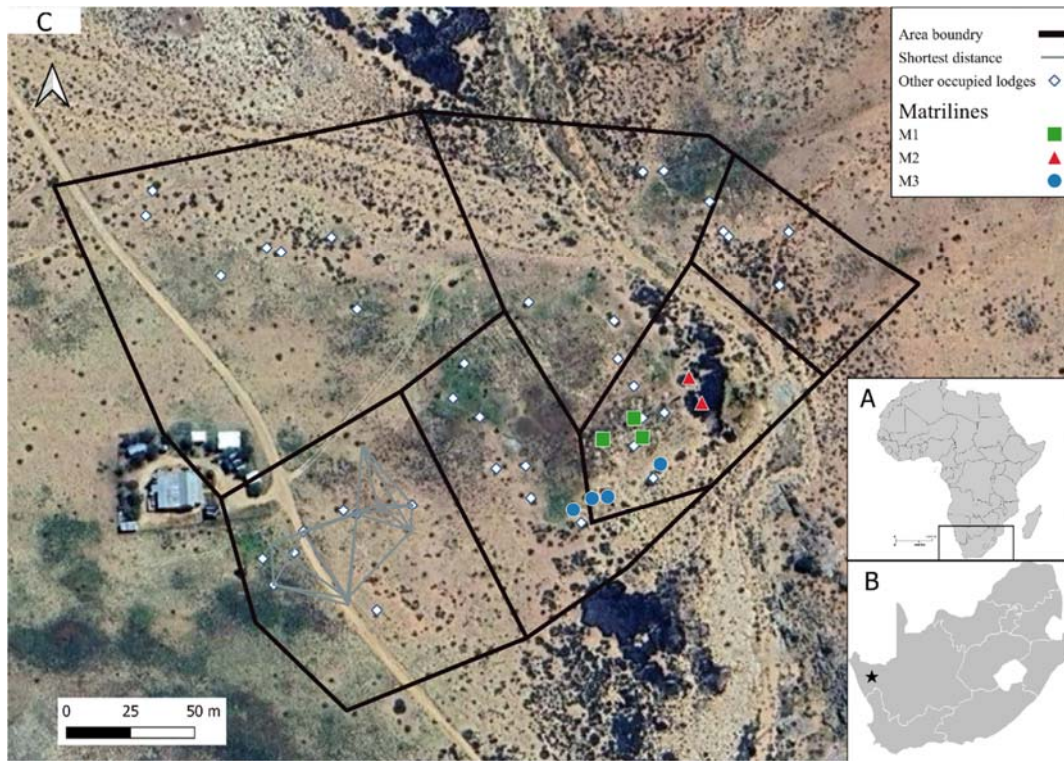
Predictors	Estimates	95% Confidence Interval	<i>P</i>
(Intercept)	49.34	40.26 – 58.42	< 0.001
Relationship (nonkin)	-22.41	-31.98 – -12.8	< 0.001
Season (nonbreeding)	-4.96	-14.69 – 4.79	0.32
Random effects	195.0/0.223		
σ^2 /ICC			
Marginal R^2 /conditional R^2	0.132/0.326		

751 σ^2 : variance of the random effect 'ID'; ICC: intraclass coefficient of variation. The marginal R^2
 752 considers only the variance of the fixed effects, while the conditional R^2 takes both the fixed
 753 and random effects into account. Factors in bold type indicate significant predictors. Overlap
 754 = season + relationship + (1|ID)

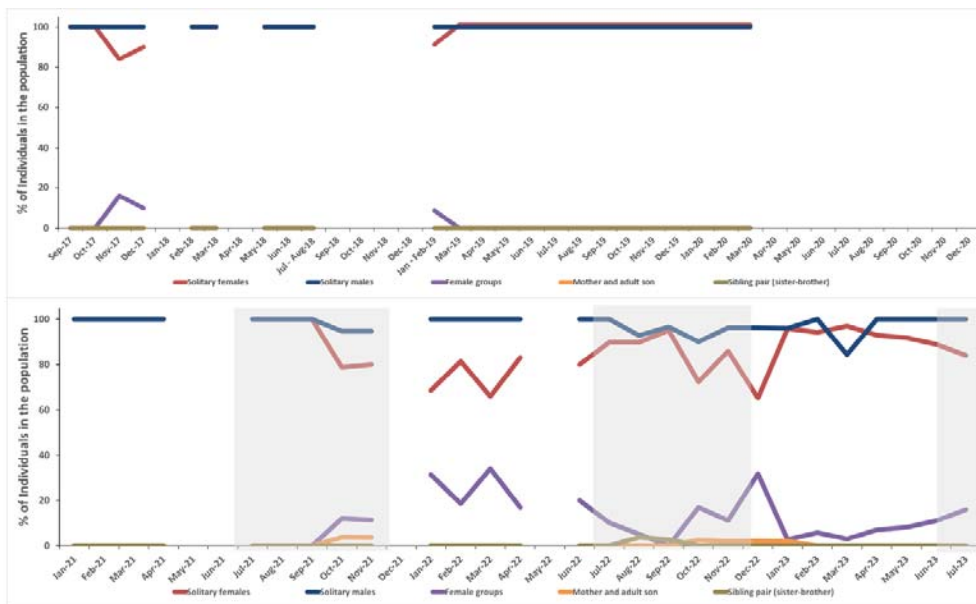
755

756

757 **Figure legends**

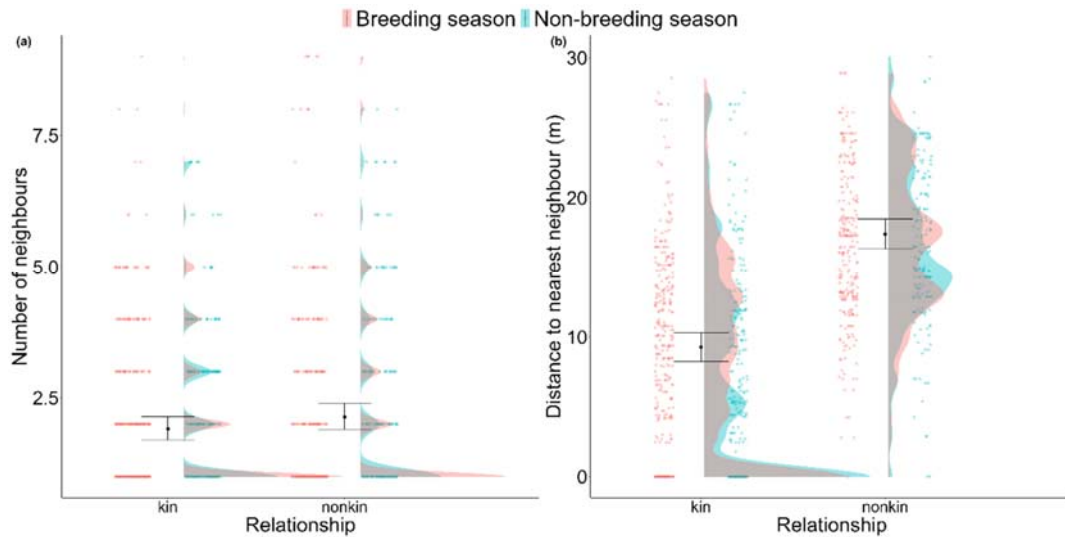


758 **Figure 1.** Satellite image of the field site (star in insert map). The black polygons are the
 759 boundaries of the six trapping areas within the field-site that we demarcated for trapping
 760 purposes. In one trapping area we show an example of matrilines in part of the study site
 761 for August 2022. Symbols and colours represent lodges that were occupied by bush Karoo
 762 rats of three different matrilines (white: rats from other matrilines). In another trapping
 763 area the grey lines represent an example of the shortest distance between the occupied
 764 lodges calculated in QGIS.
 765

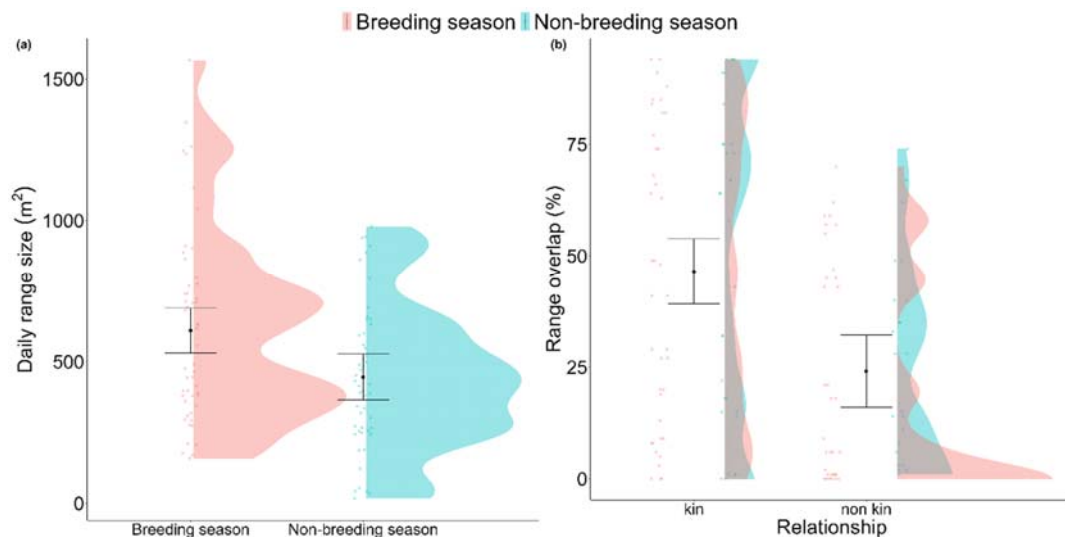


766 **Figure 2.** Distribution of social units in bush Karoo rats in 7 years. (a) September 2017 –
 767

768 December 2020; (b) January 2021 – July 2023. The breaks in the lines are from periods when
 769 no data were collected, for example due to the covid lockdown (March to December 2020).
 770 The definitions for the different social units are given in Table 1. The grey boxes indicate the
 771 wet, breeding season in winter/spring. The number next to the respective month refers to
 772 the year (i.e. Sept-17 = September 2017).



773
 774 **Figure 3.** (a) The number of female neighbours by kinship ($P < 0.01$) and (b) the mean
 775 distance to the nearest neighbour in relation to kinship ($P < 0.001$) in bush Karoo rats, for
 776 both seasons. Points represent individual values (kin: $N = 556$, nonkin: $N = 444$). The black point
 777 is the model estimate and the error bars are the confidence intervals of the model.
 778 The half-violin plot shows the raw data distribution.



779
 780 **Figure 4.** Seasonal comparison of (a) daily range size (nonbreeding: $N = 59$; breeding: $N = 81$)
 781 and (b) overlap (nonkin: $N = 54$; kin: $N = 72$) in bush Karoo rats. The black point is the model
 782 estimate and the error bars are the confidence intervals of the model. The half-violin plot
 783 shows the raw data distribution.