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1 **Behavioural correlates of group size and group persistence in the African ice rat *Otomys***  
2 ***sloggetti robertsi***

3

4 Running head: Group size and persistence in ice rats

5

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25

26 **Abstract**

27 The relationship between group size and fitness has attracted much interest, with many  
28 attempts made to detect an optimal group size. Group size is determined by the benefits and  
29 costs influencing group formation, which also influences whether groups persist or fail. We  
30 investigated whether group size is associated with success (individual survival and  
31 reproductive output) in the African ice rat *Otomys sloggetti robertsi*. Ice rats form mixed-sex  
32 plural-breeding colonies that trade-off the benefits of huddling below-ground against within-  
33 colony resource competition above-ground. We measured behavioural correlates of  
34 individual success in summer and winter, focusing on energy saving (basking), acquisition  
35 (foraging) and use (burrow maintenance, distance travelled for foraging) behaviours. We  
36 predicted that 1) individuals in larger colonies would forage and travel more to find food  
37 because of greater within-colony competition for resources; 2) individuals in larger colonies  
38 would bask less than individuals in smaller colonies because of the greater energy savings  
39 generated from huddling in larger groups; and 3) burrow maintenance would be greater in  
40 smaller colonies because fewer individuals engage in this task. We showed that colonies  
41 succumbed or persisted as a group (i.e. most individuals present or all absent). In particular,  
42 in both seasons, individuals in smaller groups ( $\leq 5$  individuals) were more likely to fail, while  
43 those in larger groups ( $\geq 12$  individuals) were more likely to persist. The persistence of  
44 colonies was positively predicted by foraging and negatively by basking. Foraging was  
45 greater in larger colonies and burrow maintenance was greater in smaller colonies. While  
46 females of larger colonies produced more offspring in total, reproductive output (per capita  
47 offspring production) was not correlated with colony size. Individual ice rats in larger

48 colonies accrued fitness benefits, which were predicted, proximally, by greater foraging and  
49 possibly energy savings in larger huddling groups.

50

51 **Keywords:** Ecological constraints, Group size, Reproductive output, Social behaviour,  
52 Sociality, Thermoregulation

53

#### 54 **Statement of Significance**

55

56 What proximally determines the relationship between group size, individual success and  
57 colony persistence? In ice rats, individuals in larger groups persist, which is correlated with  
58 more foraging. Larger groups possibly enjoy the benefits of huddling in larger groups, which  
59 are rechannelled into energy-intensive activities. Groups failed or persisted as a unit.

60 Investigating the behavioural correlates between group size and persistence provides insight  
61 into the proximal underpinnings of this relationship.

62

#### 63 **Introduction**

64 The relationship between group size and the fitness of individuals within the group has  
65 generated much interest in the socio-ecological literature (Brown 1982; Rasa 1989; McGuire  
66 et al. 2002; Silk 2007; Creel and Creel 2015; Markham et al. 2015; Mumme et al. 2015). In  
67 territorial species, group size provides a measure of the resource holding potential (RHP,  
68 Parker 1974; Gilbert et al. 1995) of a group to acquire and/or defend resources (e.g. green  
69 wood hoopoe *Phoeniculus purpureus*, Radford 2003; wood ants *Formica rufa*, Batchelor and  
70 Briffa 2011; Batchelor et al. 2012). Larger groups have greater RHP (McComb et al. 1994;  
71 Kinnaird et al. 2002), and derive other benefits, such as greater energy savings through

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72 huddling (Bazin and MacArthur 1992; Gilbert et al. 2010), and a reduction of predation risk  
73 (Dehn 1990; Parrish and Edelstein-Keshet 1999).

74       However, larger groups might be disadvantageous for the constituent members when  
75 resources, for example, change as a function of extrinsic factors (e.g. season) or as larger  
76 groups suffer the consequences of faster resource depletion and an inability to locate  
77 additional resources (the ecological constraints model, Emlen 1982, 1994; Hatchwell and  
78 Komdeur 2000), leading to skewed fitness within the group (Snaith and Chapman 2007). An  
79 optimal group size for a population or species is the size that maximizes the overall fitness of  
80 the group, and balances the advantages of group living against the costs of sharing resources  
81 and potentially depleting them (Brown 1982; Rasa 1989). Detecting optimal group sizes has  
82 been unfruitful because of the dynamic variation in extrinsic (e.g. resources, predation) and  
83 intrinsic factors (e.g. diet, social organization) influencing group size, and because groups  
84 sometimes exceed a predicted optimal size, potentially related to intrinsic factors reducing  
85 dispersal (Silk 2007), when individual fitness is higher at smaller group sizes (e.g. dwarf  
86 mongooses *Helogale parvula*; Rasa 1989). Instead, a refocus on the dynamic variation  
87 between the costs and benefits of sociality might provide a better understanding of the  
88 relationship between group size and individual fitness.

89       Group size is said to be linked to the benefits and costs of individuals that ultimately  
90 shape group formation (Silk 2007). Group-living is hypothesized to arise when net fitness  
91 benefits accrued by individuals (Krause and Ruxton 2002), such as reduced predation risk  
92 (Gilchrist 2004; Lacey 2004; Hodge 2005; Silk 2007) or metabolic requirements (e.g.  
93 huddling, Hayes 2000), exceed the costs incurred, such as reproductive marginalization of  
94 some members of the group (Schradin et al. 2009) or reproductive suppression (Saltzman et  
95 al. 2006). These benefits and costs vary dynamically within and between populations,

96 differentially affecting individuals (Armitage 1987; Pollock 1994), and possibly the success  
97 of the group (Foster et al. 2002; Liker and Bókony 2009). Therefore, group size could be  
98 constrained by the trade-offs between benefits and costs for individuals within a group. For  
99 example, individuals of larger huddling groups derive more energy savings than individuals  
100 from smaller groups (e.g. African striped mice *Rhabdomys pumilio*, Scantlebury et al. 2006)  
101 but might also face greater competition for mates and food (e.g. brown capuchin monkeys  
102 *Cebus apella*, Janson 1988) and be vulnerable to predation risk (due to increased  
103 conspicuousness or decreased vigilance, Roberts 1996; Silk 2007) than smaller groups.  
104 Individuals in smaller groups might have lower competition for resources but nonetheless  
105 defend smaller territories or home ranges (Tschinkel et al. 1995). Moreover, larger group  
106 sizes are predicted to have lower short-term fitness for plural breeding species without  
107 communal care compared to singular breeders (Ebensperger et al. 2012), while the fitness  
108 benefits of group-living might only be observed over the long-term (Solomon and Hayes  
109 2009; Dugdale et al. 2010).

110         Demonstrating the benefits and costs of group-living, and consequently group size, is  
111 empirically difficult, because the benefits and costs might have been precursors to group  
112 formation (Silk 2007) or emerge as a consequence of the success of individuals in a group. A  
113 practical solution is to record the behaviours of the group members because these behaviours  
114 will change as a consequence of, and in response to, the changing benefits and costs incurred  
115 by each individual. For example, resource competition can lead to greater aggression,  
116 increasing the motivation to disperse (e.g. toque macaques *Macaca sinica*, Dittus 1988),  
117 thereby decreasing group size. In contrast, cooperative hunting and meat sharing in  
118 chimpanzees *Pan troglodytes* leads to group sizes remaining stable (Boesch 1994).

119 We studied whether the success of individuals in a group is related to group size in the  
120 African ice rat *Otomys sloggetti robertsi*. We define successful individuals as those that have  
121 greater fitness (survival and greater reproductive output). Ice rats are medium-sized ( $\pm 130$ g),  
122 diurnal, strictly herbivorous murid rodents, endemic to the high-altitude ( $>2000$ m) alpine and  
123 sub-alpine grasslands of the Drakensburg and Maluti Mountains of southern Africa (Rowe-  
124 Rowe and Meester 1982), exposing them to some of the coldest temperatures in southern  
125 Africa (Richter 1997). However, ice rats exhibit poor physiological adaptations (Richter et al.  
126 1997), including an absence of hibernation and torpor (Willan 1990), and limited  
127 morphological adaptations (Richter 1997; Schwaibold and Pillay 2003; Rymer et al. 2007) to  
128 their harsh environment. Instead, they display behavioural adaptations, such as sun-basking  
129 (Schwaibold and Pillay 2006) and group huddling (Hinze et al. 2013), to save energy.

130 Ice rats live in multi-male, multi-female colonies (kinship unknown) of between 4 to 17  
131 adult individuals (Hinze et al. 2013), which jointly construct a complex underground burrow  
132 system with 1-2 nesting chambers (Willan 1990; Hinze et al. 2006, 2013). Burrows provide  
133 refuge against lethal temperatures above-ground but are also prone to collapse (Grab and  
134 Deschamps 2004; Mokotjomela et al. 2009). Group-living is driven by a need to huddle  
135 below-ground (Hinze et al. 2013) and not predation risk, since predators of ice rats are  
136 virtually absent in our study site due to low prey availability and local extirpation of predator  
137 populations by the local Basotho peoples (Willan 1990; Hinze and Pillay 2006; Schwaibold  
138 and Pillay 2006). During the entire study period, only two instances of predation on ice rats  
139 was observed, both by jackal buzzards *Buteo rufofuscus* (Hinze 2005). While larger colonies  
140 have greater RHP (Hinze et al. 2006), all colonies exhibit a unique daily socio-spatial  
141 dichotomy driven by thermoregulation needs (i.e. huddling below ground) and intense  
142 resource competition (as indicated by agonistic interactions, such as boxing and chasing)

143 among individuals in a colony for limited preferred food plants above-ground; Schwaibold  
144 and Pillay 2010; Hinze et al. 2013) throughout the year. Because groups of different sizes  
145 occur over small spatial scales under similar environmental conditions (Hinze et al. 2006;  
146 Schwaibold and Pillay 2010), and because its unique sociality demonstrates distinct costs and  
147 benefits of group-living (Hinze et al. 2013), the ice rat is a suitable model for studying the  
148 relationship between group size and individual success.

149 Ice rats are plural breeders (Hinze 2005) without communal nursing (evidence from  
150 captive studies; Willan 1990). Females have small litters (mean 1.44, range 1-2) of nipple-  
151 clinging offspring (Willan 1990), constraining young to suckle from the mother exclusively.  
152 Plural breeding without communal nursing can lead to competition among females for  
153 resources (Silk 2007), which might partially explain the above-ground competition for  
154 resources (Hinze et al. 2013). Colony members are also highly intolerant of strangers, which  
155 reduces the probability of emigration into existing colonies, resulting in spatial segregation of  
156 colonies (Hinze et al. 2013). New colonies form in vacant areas by dispersing sexually  
157 mature adults from existing colonies (Willan 1990).

158 The social thermoregulatory hypothesis states that animals will huddle to reduce  
159 energetic costs associated with thermoregulation (Edelman and Koprowski 2007) and  
160 predicts that huddling will result in greater energy savings in larger than small groups  
161 (Scantlebury et al. 2006; Schradin et al. 2006). However, Canals et al. (1989) suggested that,  
162 in small rodents, group sizes above five individuals do not accrue incremental energy saving  
163 advantages. Therefore, we asked whether the trade-off between the benefits of group  
164 huddling and the costs of competing for food influenced individual success in different sized  
165 ice rat colonies. We recorded behaviours of ice rats in summer and winter, focusing on  
166 common above-ground behaviours involved in energy saving (sun basking), energy



167 acquisition (foraging) and energy use (burrow maintenance and distance travelled for  
168 foraging), which would influence individual success.

169       Because larger colonies have greater RHP, as also occurs in other species (e.g. Parker  
170 1974; McComb et al. 1994; Gilbert et al. 1995; Kinnaird et al. 2002), we predicted that  
171 individuals in larger colonies would be more successful (survival and reproductive output)  
172 than those of smaller colonies, particularly in winter, when food is limiting and temperatures  
173 are low (Schwaibold and Pillay 2010). Based on the absence of predators, within-colony  
174 competition for resources and the benefits of huddling, we made three predictions about the  
175 behaviours of ice rats. 1) In comparison to smaller groups, individuals in larger colonies  
176 would forage and travel more to find food because of greater within-colony competition for  
177 resources. 2) Individuals in larger colonies would bask less than those in smaller colonies  
178 because of the greater energy savings accrued from huddling in larger groups (e.g. striped  
179 mice; Scantlebury et al. 2006; Schradin et al. 2006) and a reduced time needed to passively  
180 warm up (i.e. sun basking) on emergence from the burrow in the morning. Alternatively, if  
181 groups of 4-5 individuals accrue the greatest benefits from huddling (Canals et al. 1989),  
182 smaller colonies should show reduced basking compared to larger colonies. 3) Burrow  
183 maintenance is energetically costly but a requirement for maintaining burrow integrity in ice  
184 rats, so we expected greater attention to burrow maintenance in smaller colonies. It is likely  
185 that each individual would have expended more energy and time maintaining the burrow in  
186 smaller colonies, whereas in larger colonies, individuals could expend less energy and lower  
187 their own maintenance behaviour (Ebensperger and Bozinovic 2000), given the greater  
188 number of individuals, an idea akin to the group vigilance or ‘many eyes’ hypothesis  
189 (Roberts 1996).

190

191 **Materials and methods**

192 *Study area*

193 Field work was conducted from 2000 to 2006 at a site in the Sani Valley, Maluti Mountains,  
194 Lesotho (29°33' S, 29°14' E; elevation: 2800m). Temperatures are characteristically low  
195 (mean winter minimum and maximum: -0.6 °C, 12.4 °C; mean summer minimum and  
196 maximum: 9.9 °C, 20.6 °C; Hinze et al. 2013) and precipitation, often in the form of snow  
197 year-round, is high (mean annual precipitation: 1200mm, Killick 1963). Vegetation is  
198 characteristically short (< 20cm), interspersed with bushes and shrubs year-round, and  
199 abundant flowering herbs in summer (Schwaibold and Pillay 2010).

200

201 *Colonies*

202 All colonies studied were located within or on the edges of several wetlands (Hinze and  
203 Pillay 2006). Colonies were identified during pilot studies using *ad libitum* behavioural  
204 observations. A colony was defined as all individuals using a communal burrow system  
205 (Hinze et al. 2006) and occupying an exclusive above-ground area around the burrow system  
206 (Hinze et al. 2013). A total of 120 colonies were selected for study in early winter (May and  
207 June) and early summer (November and December). The colonies ranged in size from 4 to 17  
208 individuals (Supplementary Table 1), identified by all resident adults. We selected colonies in  
209 which individuals were present at least two months prior to sampling, which meant that they  
210 were well established to cope with the harsh winter and to reproduce in summer (Schwaibold  
211 and Pillay 2006).

212 Different colonies were studied in each season (identified by the absence of marked  
213 individuals; see below) because sampling occurred over several years. To ensure  
214 independence of colonies and observations, only colonies greater than 50m apart were

215 selected for study. Ice rats construct burrows in both organic and mineral soils, but since  
216 organic soils are more complex and stable (Hinze et al. 2006), we selected only colonies that  
217 burrowed in organic soils. In addition, only colonies that had an intact burrow system  
218 throughout the study and for which all adult individuals were successfully trapped and  
219 marked (see below) were used in the final analyses (n = 91 colonies). The occupants of the  
220 remaining 29 colonies abandoned their burrow systems due to tunnel collapse. Because of our  
221 criteria for colony selection (present two months prior to study), we could not select an even  
222 distribution of colony classes, and instead the frequency of colonies sizes grouped into  
223 smaller, mid-range and larger classes (see Results).

224

225

#### 226 *Trapping and marking*

227 Because our study involved focal animals in the field, blind recording of individuals was not  
228 possible. Ice rats within colonies were live-trapped during their peak activity period (summer:  
229 05h00-11h00 and 13h30-17h30; winter: 08h00–15h00; Hinze and Pillay 2006) in metal traps  
230 (26 x 9 x 9 cm) baited with mixed fruits and vegetables (e.g. apple, cucumber, lettuce,  
231 spinach), placed around burrow entrances in a colony; we placed 2 traps around each burrow  
232 entrance in a colony and continued trapping until all adults were caught and marked, which  
233 was achieved within a week.

234 Traps were monitored from a short distance away and trapped animals were removed as  
235 soon as possible (within 5-10 min) to minimize stress. Individuals were weighed (nearest 1g)  
236 and their sex recorded. Adults were each fitted with a uniquely coloured plastic cable tie neck  
237 band (length 200mm, width 4.7mm; Hinze et al. 2013) to facilitate identification from a  
238 distance. Ice rats show strong site fidelity, remaining in their colonies and rarely dispersing,

10

239 and have a low rate of collar loss (< 1%, Hinze 2005), which meant that we could reliably  
240 establish the identity of a colony and its individuals. Bands did not interfere with movement  
241 or cause harm (Hinze 2005) and were removed at the end of the study. We also recorded  
242 when newly weaned offspring (juveniles) emerged aboveground 2–4 weeks after birth. They  
243 were recognized by their smaller body size.

244

#### 245 *Behavioural observations*

246 60 hours of behavioural observations (2 h daily over 5 non-consecutive days each week for 6  
247 weeks) were conducted per colony per season after individuals had been trapped and marked.  
248 Observations were made during peak ice rat morning activity times (summer: 06h00–11h00;  
249 winter: 08h00–11h00), coinciding with seasonal variations in sunrise. Observations were  
250 made only on sunny, clear days in both seasons, because ice rats spend little time above  
251 ground during poor weather conditions (Hinze and Pillay 2006). Observations were made  
252 from a vantage point approximately 3–5m from a colony. Ice rats were easily observed  
253 because of the short vegetation and they rapidly habituated to the presence of observers  
254 (within 5 min), so there was no need for our concealment during observations (Schwaibold  
255 and Pillay 2006).

256 Every 3 minutes, we used instantaneous scan sampling (Martin and Bateson 1986) to  
257 record the behaviour of each individual within a colony (identified via neck bands) directly,  
258 resulting in 1200 sampling intervals over each 6-week period (i.e. 40 sampling points x 5  
259 days x 6 weeks) per season. Ice rats in a colony synchronize their aboveground activity  
260 (Hinze and Pillay 2006), such that data obtained using this sampling technique represented  
261 the general activity of individuals in the colony. The behaviour scores were then converted as  
262 a per capita measure to account for differences in colony size and hence the number of

11

263 individuals scored per colony.

264 All aboveground behaviour was recorded as absence or presence. However, to address  
265 the aims of the study, the frequency counts of only the three most common aboveground  
266 behaviours were analysed on the basis of their prevalence (Hinze and Pillay 2006;  
267 Schwaibold and Pillay 2006). These included: i) basking (the individual orientated its back to  
268 the sun's rays, withdrew its limbs, tucked in its head and remained motionless aboveground;  
269 Willan 1990; Rymer et al. 2007); ii) foraging (searching, handling, and ingesting food); and  
270 iii) burrow maintenance (cleaning out and re-tunnelling of burrow entrances). Other  
271 behaviours, such as social interactions (both amicable and agonistic), were extremely rare  
272 above-ground (see also Hinze et al. 2013) and were not considered in the analyses. The  
273 maximum distances travelled by ice rats during foraging were estimated in the following  
274 way: we first measured the relative distances between all burrow entrances (colonies ranged  
275 between 4-32 entrances) and the centres of local food-plant patches prior to observations.  
276 When an ice rat emerged from a burrow, we noted from which burrow it emerged and the  
277 patch of food plants it visited. This information was then plotted on a schematic diagram of  
278 the colony and distance travelled was estimated using the average body length of an adult  
279 ( $\pm 15$  cm). No individual travelled more than 1m from burrow entrances to forage  
280 (Schwaibold and Pillay 2010).

281

### 282 *Individual success*

283 To establish individual success, colonies were revisited three months after observations  
284 (August-September for winter samples and March-April for summer samples). Colonies were  
285 identified by the presence of colony markers (see below). The three-month sampling interval  
286 was within the 1-2-year longevity of free-living ice rats (Hinze 2005). We selected a 3 month

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287 interval to coincide with seasonal changes in environmental conditions. Colonies were  
288 revisited for 3-5 consecutive days, depending on colony size, when we recorded the numbers  
289 of marked individuals still present and the number of additional (unmarked) individuals that  
290 immigrated into the colony or were sub-adult philopatric young. The maximum number of  
291 adults observed in the 3-5 days of sampling was considered to be the total number of adults  
292 present in that colony. In colonies where one or more previously marked individuals were  
293 absent, we searched for them in a 500 m radius to establish whether or not any had dispersed.  
294 Colonies that were occupied by all new, unmarked individuals or were unoccupied (with  
295 intact burrows) were scored as absent.

296       During summer checks, we also recorded the number of newly weaned offspring that  
297 were present above-ground, which would have represented the last litters born in the austral  
298 summer in February and March (Hinze 2005). Like the number of adults, the maximum  
299 number of juveniles observed during 3-5 days was considered to be the total number of  
300 juveniles present in that colony. Ice rats have small litters with a short inter-litter interval (38-  
301 49 days, Willan 1990). Juveniles were always closely associated (physically and spatially)  
302 with the mother (which was marked), including many instances of nipple-clinging even after  
303 weaning (Hinze 2005). Adult ice rats never overlap spatially aboveground in a colony, so we  
304 could accurately determine the number offspring per female. Because of the bias of larger  
305 colonies having more breeding females and a greater number of offspring, we also calculated  
306 the per capita reproductive output (i.e. number of offspring per female) to assess colony level  
307 reproductive success in terms of the proportion of offspring produced by the breeding adult  
308 females present.

309

310 *Other factors influencing colony size and individual success*

311 Several other factors could have potentially influenced colony size and individual success.  
312 These included the surface area occupied by a colony (colony area), the associated number of  
313 discrete food plant patches, the number of burrow entrances, the adult sex ratio of a colony  
314 and environmental temperature during sampling.

315 The area occupied by a colony, number of discrete food patches and number of burrow  
316 entrances could have potentially influenced food access and hence foraging, total distance  
317 travelled for foraging, and burrow maintenance (Schwaibold and Pillay 2006). Therefore,  
318 colony area was calculated using the 95% minimum convex polygon (MCP) method in  
319 Ranges6 (Kenward et al. 2002) as described by Hinze et al. (2013). Briefly, we demarcated  
320 each colony into 4x4m grid squares using coloured pegs (30 cm high) based on pilot  
321 observations of the behaviour of adults; the number of squares varied based on the size of,  
322 and area occupied by, the colony (Hinze et al. 2013). We recorded the position of all  
323 individuals in a colony every 1 h during the 60 h of behavioural sampling, noting their  
324 position within a quarter square on the grid. Locations taken greater than 35 min apart are not  
325 auto-correlated (Hinze et al. 2013). The data from all individuals in a colony were plotted on  
326 a schematic diagram, which was used to generate the convex polygons. Since two or more ice  
327 rats rarely occupied the same square (< 3%) at the same time, we excluded the rare  
328 occurrences of more than one ice rat occupying the same square from the data set.

329 Food patches were identified as described by Schwaibold and Pillay (2010). Briefly, we  
330 recorded where ice rats foraged within the colony, the areas where all individuals foraged  
331 regularly, and where the dominant food type (i.e. wetland sedges and herbaceous shrubs) was  
332 located; the number of food patches also provided a proxy for food quality and thereby  
333 territory quality (Schwaibold and Pillay 2010). The number of burrow entrances was counted  
334 when the colony was delineated using the markers.

335 The ratio of adult females to males in each colony was calculated, because greater  
336 foraging rates are expected for females in summer to meet the energetic demands imposed by  
337 pregnancy and lactation (Schwaibold and Pillay 2006). Since ice rat behaviour is influenced  
338 by environmental temperature (Hinze and Pillay 2006; Schwaibold and Pillay 2006), a  
339 Tinytag<sup>TM</sup> data logger (manufactured by Gemini data loggers, UK), calibrated at the start of  
340 each observation session and connected to a probe 5cm above the ground (the height at which  
341 ice rats were active), recorded temperature every 5 min. Data were used to calculate mean  
342 ambient temperature per colony per season.

343

#### 344 *Statistical analyses*

345 All analyses were performed using R Studio (version 0.99.489; <https://www.rstudio.com>). All  
346 tests were two-tailed probability values throughout, and statistical significance was accepted  
347 when  $\alpha \leq 0.05$ .

348 We initially screened the dataset for redundancy and auto-correlations. We tested for  
349 multi-collinearity among the continuous predictors, including colony size, using the variance  
350 inflation factor (VIF) in car package and visualized the relationship using principal  
351 components analysis (FactoMineR package). Colony size, colony area, number of burrows  
352 and the number of discrete food patches (Supplementary Table 1) were highly auto-  
353 correlated, which we also confirmed using a multiple regression analysis of colony size vs.  
354 the other 3 variables ( $r^2 = 0.83$ ;  $p < 0.001$ ). In particular, colony size and the number of  
355 discrete food patches (i.e. a proxy of territory quality) were highly significantly correlated  
356 (linear regression:  $r^2 = 0.80$ ;  $p < 0.001$ ), indicating that colony size statistically represented  
357 territory quality. We therefore retained three predictors: colony size, adult sex ratio (arcsine  
358 square-root transformed) and mean ambient temperature per colony during observations, in

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359 the analyses. Year of sampling as a random factor was omitted from the main analysis  
360 because its variance component (VarCorr package) was close to zero in all tests. The  
361 behaviours and distance travelled met the assumptions of normality (Shapiro-Wilk test, Q-Q  
362 plots).

363 We conducted four separate analyses. 1) To analyse the relationship between colony size  
364 and colony persistence, we recorded individual ice rat survival using the number of resident  
365 adults present. However, we found that individuals in colonies mostly persisted or failed as a  
366 group, rather than some individuals succumbing (see Results). Therefore, we created a  
367 binomial category of colony presence or absence. We used a logistic regression (glm2 and car  
368 packages, quasibinomial family, logit link function) to analyse whether colony persistence  
369 was predicted by season (fixed factor), colony size and their interaction. We used a likelihood  
370 ratio test to assess model fit (i.e. reject/accept the null hypothesis; Anova package). 2) We  
371 next analysed whether colony persistence was predicted by the three behaviours (basking,  
372 foraging, burrow maintenance), distance travelled, and their interaction with season, sex ratio  
373 and ambient temperature (all continuous predictors) using logistic regression (quasibinomial  
374 family, logit link function). We initially ran model selection to achieve a minimal adequate  
375 model (MuMIn package which considers logistic analyses), using a combination of first and  
376 second order effects variables. Based on the greatest AICc value, we analysed only the three  
377 behaviours, distance travelled, their interaction with season, and adult sex ratio. A likelihood  
378 ratio test was used to assess model fit. Data are reported as  $\beta$ -estimate coefficients (reported  
379 as  $\beta$ -estimate  $\pm$  SE) and as the Wald  $\chi^2$  statistic of the final algorithm iteration for each fixed  
380 output variable. 3) Since colony size was a predictor of colony persistence, and to address the  
381 aims of our study, we analysed the linear relationship between colony size and each  
382 behaviour per season separately (lme4 package). To correct for the multiple comparisons of

383 each behaviour, we adjusted p values using the Benjamini and Hochberg (1995) method. 4)  
384 We analysed the relationship between the number of juveniles and colony size in summer  
385 using a linear regression model (lme4 package) for the total number of young per colony  
386 (number of females per colony included as continuous predictor) and per-capita young per  
387 female.

388

## 389 **Results**

390 In summer, 35 of 45 (78%) colonies were still present compared to 29 of 46 (63%) colonies  
391 in winter. Colonies, and their constituent individuals, showed extremely high site fidelity  
392 because all colonies that were present still occupied the same demarcated areas three months  
393 later. Generally, we found that colonies failed or persisted as a unit (i.e. all individuals  
394 disappeared or all marked individuals were present, except for four (two per season) colonies  
395 that persisted. Specifically, in winter, two colonies of 4 individuals lost one individual each,  
396 and, in summer, two colonies (10 and 12 individuals respectively) also lost one individual  
397 each. Of the colonies that failed, we located only one collared male (original colony size =  
398 11) that had immigrated into a new unmarked colony (new colony size = 6) in winter. None  
399 of the study colonies gained additional adults through immigration or philopatric sub-adults.  
400 Many of the colonies that failed had collapsed burrow systems (n = 16; 62%) but we could  
401 not tell whether this was the cause or the outcome of colony failure. Hereafter, we consider  
402 colony persistence as a proxy of individual success.

403 For persistence of colonies, a likelihood ratio statistic indicated that the final model  
404 deviated significantly from a null model ( $\chi^2_3 = -36.62$ ,  $p < 0.001$ ). The persistence of colonies  
405 was significantly influenced by colony size but not season and season x colony size  
406 interaction (Table 1). Larger colonies were significantly more likely to persist than smaller

17

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407 colonies in winter and summer (Fig. 1). The smallest colonies (median = 5) were most likely  
408 to fail, while colonies of 12 or more individuals were most likely to succeed (Fig. 1). Colony  
409 size was auto-correlated with the number of food patches in a principal components analysis  
410 (see methods), which we used as a proxy for food quality.

411 For the behaviours, a likelihood ratio statistic indicated that the final model deviated  
412 significantly from a null model ( $\chi^2_9 = -38.32$ ,  $p < 0.001$ ). The frequency of basking, foraging  
413 and season\*basking and season\*foraging were significant correlates of colony persistence  
414 (Table 1). The frequency of basking was significantly greater in winter (Fig. 2). The  
415 frequency of basking was slightly lower in colonies that persisted in winter compared to those  
416 that failed, but there was no difference between colonies that were present and failed in  
417 summer (Fig. 2). In both seasons, foraging frequencies were significantly greater in colonies  
418 that persisted (Fig. 2). In colonies that failed, the frequency of foraging was significantly  
419 greater in winter (Fig. 2). Importantly, colonies that persisted displayed lower basking and  
420 greater foraging in both seasons. Similarly, colonies that failed always displayed lower  
421 basking than foraging, although there was little variation in the frequency of basking or  
422 foraging across seasons (Fig. 2).

423 The frequency of burrow maintenance, the distance travelled, the interaction of both  
424 these behaviours with season, and sex ratio were not significant predictors of colony  
425 persistence (Table 1). The continuous data are summarised in Table S1 (supplementary data).

426 We compared the relationship between frequencies of behaviour by colony size in each  
427 season (Fig. 3). Basking showed a small but not significant increase by colony size in winter,  
428 whereas, in summer, there was a small, although non-significant, decrease by colony size  
429 (Table 1). In contrast, foraging was positively and significantly correlated with colony size in  
430 both seasons (Table 1; Fig. 3). Burrow maintenance by individuals significantly decreased

431 with increasing colony size in winter and approached significance in summer (Table 1; Fig.  
432 3). As a result of this finding, we also compared total burrow maintenance scores (i.e. by all  
433 members in a colony) against colony size and found a weak positive correlation in both  
434 seasons (winter:  $r^2 = 0.29$ ,  $F_{1,43} = 12.64$ ,  $p < 0.001$ ; summer:  $r^2 = 0.32$ ,  $F_{1,43} = 29.25$ ,  $p <$   
435  $0.001$ ), indicating that total investment in burrow maintenance was greater in larger than  
436 smaller colonies. The distance travelled showed a slight increase by colony size in both  
437 seasons, although this was not statistically significant (Table 1; Fig. 3).

438 Colony size and the number of females per colony (Table 1) were significant predictors  
439 of the number of juveniles per colony. Larger colonies produced significantly more offspring  
440 ( $r^2 = 0.74$ ,  $F_{2,32} = 97.71$ ,  $p < 0.001$ ; Fig. 4a), which reflected the positive correlation between  
441 female numbers and colony size. The largest colonies produced 3-4 times more offspring than  
442 the smallest colonies (Fig. 4a). In contrast, colony size did not predict per capita young  
443 (Table 1), indicating no relationship between colony size and the number of young per female  
444 ( $r^2 = 0.03$ ,  $F_{1,33} = 0.99$ ,  $p = 0.325$ ; Fig. 4b).

445

## 446 **Discussion**

447 We studied the relationship between group size and individual success (i.e. survival and  
448 reproduction) in the semi-fossorial African ice rat. Ice rats show a unique spatial social  
449 dichotomy: individuals in colonies huddle belowground at night, accruing thermoregulatory  
450 benefits (Hinze and Pillay 2006), but colony members compete for limited food resources  
451 aboveground during the day, a cost of group-living (Hinze et al. 2013). We expected that  
452 larger colonies were more likely to be present over time than smaller colonies, particularly in  
453 winter. We also studied the observable behavioural correlates of individual success. We  
454 predicted that individuals in larger colonies would engage more in foraging and travelling

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455 (energy intense), and show reduced basking (passive warming) and reduced burrow  
456 maintenance (energy intense).

457 Our intention was to measure the number of surviving individuals in each colony to  
458 assess the fitness benefits accrued by different sized colonies. Yet, individual success was  
459 tied to group persistence because groups were either present or absent. While we could not  
460 definitively confirm the fate of individuals of colonies that disappeared, our systematic  
461 searches in the relatively open alpine habitat of ice rats produced no evidence of any of the  
462 individuals that disappeared, barring one individual, suggesting that emigration is limited.  
463 This indicates that colonies failed as a group, rather than individuals disbanding and  
464 emigrating into new colonies. In particular, larger colonies were more likely to persist than  
465 smaller colonies.

466 The complete demise of social groups has been reported in prairie voles *Microtus*  
467 *ochrogaster*, which was attributed to predation pressure (McGuire et al. 2002). However, ice  
468 rats at our study site have very low incidences of natural predators (Willan 1990; Hinze and  
469 Pillay 2006; Schwaibold and Pillay 2006), and therefore predation can be discounted as a  
470 potential explanation for colony failure. Although one individual was found to have  
471 dispersed, generally group territoriality in ice rats limits dispersal into existing colonies  
472 (Hinze et al. 2013) and there was no evidence of other individuals dispersing into vacant  
473 areas, suggesting a general reluctance to disperse, even if suitable vacant areas were  
474 available. Theoretical and empirical studies show that groups remain together, even  
475 exceeding the projected optimum number of individuals (Silk 2007). Similarly, individual ice  
476 rats remained in their colonies for unknown reasons, even when colony failure was imminent.

477 The social thermoregulation hypothesis maintains that huddling creates energy savings  
478 (Edelman and Koprowski 2007), particularly in larger groups (e.g. Alpine marmots *Marmota*

479 *marmota*, Arnold 1988; southern flying squirrels *Glaucomys volans*, Stapp et al. 1991; grey  
480 partridge *Perdix*, Putaala et al. 1995; striped mice, Scantlebury et al. 2006; Schradin et al.  
481 2006). Canals et al. (1989) postulated that the optimal huddling group size for small rodents  
482 is 4-5. Yet, a median colony size of 5 ice rats was more likely to fail. We predicted that the  
483 energy savings from huddling in larger groups could be used to offset energy acquisition  
484 activities, as reported in white-footed mice *Peromyscus leucopus* (reduce their daily energy  
485 expenditure by 29% via huddling; Glaser and Lustick 1975). Consequently, passive energy  
486 acquisition via basking should have been lower in larger groups (Vickery and Millar 1984)  
487 and the benefits of huddling on group persistence would have been more pronounced in  
488 winter. However, we found that individuals of smaller groups did not bask more than those of  
489 larger groups. Basking showed marginal changes in magnitude and an inconsistent  
490 relationship with colony size and persistence (i.e. the basking vs colony size relationship did  
491 not vary seasonally and individuals of persisting colonies showed a small reduction in  
492 basking frequency). Nonetheless, huddling could have other advantages, such as providing  
493 energy savings that could be rechannelled into other activities, such as foraging.

494 As predicted, foraging frequency was positively correlated with colony size and,  
495 importantly, colony persistence was also associated with greater foraging frequencies. We  
496 suggest that the greater foraging in larger colonies is related to intense within-colony  
497 competition for food, as seen in mountain gorillas *Gorilla beringei* (Watts 1985). We also  
498 expected greater travelling to find food but travel frequencies did not vary with colony size,  
499 perhaps because ice rats never travel far (maximum 1 m) to forage (Schwaibold and Pillay  
500 2010).

501 Individuals of larger colonies showed lower levels of burrow maintenance compared to  
502 those of small colonies, particularly in winter. Ice rat burrows are shallow (Willan 1990,

503 Hinze et al. 2006), and burrow maintenance is important for maintaining the integrity of  
504 burrow systems that are prone to collapse from soil erosion (Grab and Deschamps 2004) and  
505 livestock trampling (Mokotjomela et al. 2009). In addition, burrows provide quick below-  
506 ground access to food patches, thereby reducing exposure to lethal lower temperatures above-  
507 ground, particularly during winter (Schwaibold 2005). Burrow maintenance requires great  
508 energetic investments by individuals (dependent on soil type, size and structure of the burrow  
509 system, Gettinger 1984), redirecting behaviours and energy from foraging and reproduction.  
510 For example, pocket gophers *Thomomys bottae* increase energy expenditure by 360-3400  
511 times during burrowing (Gettinger 1984). There was a (weak) positive association between  
512 colony size and total investment by all ice rat colony members in burrow maintenance,  
513 however, indicating that in smaller colonies, each individual would have expended more  
514 energy and time maintaining the burrow, whereas in larger colonies, individuals shared in  
515 maintenance costs and would have saved energy (Ebensperger and Bozinovic 2000).

516 Both foraging and burrowing had weak predictive relationships with colony size, ranging  
517 from 18% to 35%, indicating that the variance in the relationship could be explained by other  
518 factors. We offer three explanations, which need further consideration. 1) A possible  
519 stochastic explanation might be the non-random distribution of the colony size classes in  
520 small, mid-range and larger bins, which was unavoidable in our study of free-living ice rats.  
521 2) For foraging behaviour, the location (clumped vs. scattered), size of food plant patches  
522 (small vs. large; Schwaibold and Pillay 2010), and food quality could influence feeding rates  
523 of individuals that competitively exclude other individuals from patches. If so, individuals in  
524 larger colonies, for example, could show reduced foraging when plant patches are small,  
525 clumped, and/or of high quality, whereas individuals in smaller colonies could show higher  
526 foraging rates in small, scattered and/or poor quality plant patches. 3) For burrowing, ice rats

527 construct burrow systems in organic and mineral soils (Hinze et al. 2006), and while we  
528 selected colonies in the more stable organic soil, it is possible that soil type, integrity and  
529 proximity to wetland drainage (Hinze et al. 2006) could influence burrow maintenance  
530 independent of colony size.

531 Group size is inversely related to per capita offspring number in several mammal species  
532 with plural breeding females without communal breeding, such as yellow-bellied marmots  
533 *Marmota flaviventris* (Armitage and Schwartz 2000) and tuco-tucos *Ctenomys sociabilis*  
534 (Lacey 2004), which is largely related to resource competition (Silk 2007). However,  
535 individuals of larger groups do not necessarily have greater fitness (Ebensperger et al. 2012),  
536 at least in the short-term, although plural breeding may confer long-term direct fitness  
537 benefits (Solomon and Hayes 2009; Dugdale et al. 2010). In accordance with a meta-analysis  
538 by Ebensperger et al. (2012), we found that per capita reproduction was not related to colony  
539 size in ice rats, suggesting that individuals of larger groups do not necessarily have greater  
540 reproductive fitness in the short term. However, we did find that larger ice rat groups  
541 collectively produced more young and were more likely to persist, which suggests lifetime  
542 reproductive success could be greater in individuals of these larger colonies, as seen in  
543 Japanese macaques *Macaca fuscata* (Crofoot and Wrangham 2010) and new world monkeys  
544 *Cebus* sp. (Judge and Carey 2000).

545 Our reproduction output data are consistent with those of Ebensperger et al. (2016), who  
546 found that social stability can modulate fitness of degus *Octodon degus*, particularly of  
547 females which can form socially stable groups, producing more offspring that survive to  
548 weaning. Weaned ice rat offspring would have increased the maximum colony size to 13 for  
549 smaller colonies and up to 32 for larger colonies. Such inflated numbers likely put additional  
550 strain on diminishing resources and, given the high site fidelity of colonies and potential



551 competition among females for food (as suggested for other plural breeding species without  
552 communal nursing, Silk 2007), it is apparent that individuals of persisting colonies secured  
553 sufficient food to meet the energy requirements of adults and offspring. Indeed, Rubenstein  
554 (2011) suggested that large group sizes buffer the effects of environmental variation in  
555 temporally variable habitats where resources are heterogeneously distributed across the  
556 landscape.

557 In ice rat colonies, the area occupied and the number of food plant patches (i.e. a proxy  
558 of territory quality) correlated positively with colony size, indicating that larger groups may  
559 be able to dominate limiting food resources compared to smaller groups, a phenomenon also  
560 observed in other social species, such as wolves *Canis lupis* (Stahler et al. 2013). The greater  
561 RHP of larger ice rat groups, and the additive influences of energy savings through huddling  
562 and energy gains through increased foraging and energy saved by sharing burrowing  
563 maintenance (especially in winter), suggests that larger groups are more successful at  
564 territorial defense, as seen in lions *Panthera leo* (Mosser and Packer 2009). While we did not  
565 test colony dominance of resources in this study, a previous study of ice rats indicated intense  
566 aggression between individuals from different colonies (Hinze et al. 2013). This suggests that  
567 larger ice rat colonies actively defend high quality food patches, rather than larger groups  
568 forming passively in response to larger food patches, as suggested by the resource dispersion  
569 hypothesis (Carr and Macdonald 1986; Macdonald and Carr 1989; Bacon et al. 1991).  
570 Furthermore, high site fidelity suggests that colony location, possibly in synergy with colony  
571 size, is a critical determinant of the success of individuals, since sites must sustain the colony  
572 for long periods, particularly during energetically demanding times.

573 Three important general patterns emerged from our study. 1) Individuals in smaller  
574 colonies of  $\leq 5$  individuals were most vulnerable to failure. While other studies have shown

575 that the lower and higher extremes in group size experience disadvantages (e.g. baboons  
576 *Papio cynocephalus*, Markham et al. 2015), our study does not provide an optimal group size,  
577 and instead shows that ice rat colonies of > 12 individuals are most likely to succeed. Many  
578 of the colonies that failed had collapsed burrow systems, but we could not tell whether this  
579 was the cause or the outcome of colony failure. Similarly, we do not know whether colonies  
580 fail because they are initiated by inherently less competitive individuals or because of  
581 extrinsic (e.g. colony location) or some other intrinsic (e.g. disease) factors. 2). Group-living  
582 and individual success is the outcome of the net benefits to individuals within the group, with  
583 individuals leaving or joining groups to maximize their own individual fitness (e.g. yellow-  
584 bellied marmots, Oli and Armitage 2003). Yet, the persistence of ice rat colonies was an all-  
585 or-nothing phenomenon, with adults remaining in their colonies regardless of their imminent  
586 failure. Willan (1990) proposed that the intense aggression by sexually active adult ice rats  
587 most likely reduces the chance of emigration, and that new colonies are established by young  
588 individuals in an unoccupied area in the vicinity of the parental burrow. Thus, future  
589 individual success is likely to be determined at the outset when groups form. Individuals of  
590 colonies which later fail were either unable to detect when colony collapse is imminent, or,  
591 even if they could detect changes, remain in their groups because of the benefits, such as  
592 huddling (i.e. making the best of a bad situation). 3) Persisting colonies had high individual  
593 survival. Higher survival rates of ice rat populations have been attributed to rising minimum  
594 ambient temperatures in the Lesotho highlands (Mokotjomela et al. 2009, 2010), associated  
595 with environmental change. Rising temperatures could have a positive influence on plant  
596 productivity (Sitch et al. 2008), reducing potential resource competition. As a result, while  
597 individuals of smaller colonies may still have had to offset lost social thermoregulatory

598 benefits, the buffering effects of higher ambient temperatures could promote greater survival  
599 of individuals (Mokotjomela et al. 2009, 2010) and colony persistence.

600 Ours is one of only a few mammal studies to investigate the proximate factors of survival  
601 and reproduction in relation to group size. The behavioural variations in foraging and burrow  
602 maintenance by colony size demonstrate shifts in motivational priorities between individuals  
603 in different colony size classes. In ice rats, behavioural rather than physiological adaptations  
604 to cold temperatures have influenced the evolution of their unusual social system. Group size  
605 positively predicted individual success, which we suggest is linked to the thermoregulatory  
606 benefits obtained from huddling in larger groups, despite competition for food within  
607 colonies. Individuals of larger colonies increased energy acquisition through increased  
608 foraging, which might explain colony persistence. While females of larger colonies that were  
609 present did not have greater per capita reproductive success, we predict that better survival  
610 and potentially a greater lifetime reproductive success are potential emergent benefits of  
611 individuals in larger ice rat groups. Future studies must consider the competitive attributes of  
612 individuals that form colonies, directly measure the energy savings achieved by ice rats  
613 through huddling, and assess differences in life histories of young produced by females in  
614 different size colonies to understand the relationship between colony size and fitness (Young  
615 et al. 2015).

616

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620

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623 the current laws and regulations in South Africa and all applicable international, national,  
624 and/or institutional guidelines for the care and use of animals were followed.

625

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811 **List of tables and figures**

812

813 **Table 1** Predictors and correlates of colony persistence and colony size, and reproductive  
814 output of ice *Otomys sloggetti robertsi*. Fixed, continuous predictors are provided for the  
815 different analyses. Significant effects are indicated in bold

816

817 **Fig. 1** The absence (n) or presence (y) of ice rat *Otomys sloggetti robertsi* colonies in the  
818 Maluti Mountains, Lesotho, as a function of colony size in winter (grey boxes; n = 46) and  
819 summer (white boxes; n = 45). Medians (dark horizontal bars), 1<sup>st</sup> and 3<sup>rd</sup> interquartiles  
820 (boxes), 95% CI (whiskers) and outliers (dots) are shown

821

822 **Fig. 2** The frequencies of basking and foraging in the ice rat *Otomys sloggetti robertsi* in the  
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825 interquartiles (boxes), 95% CI (whiskers) and outliers (dots) are shown. Frequencies were  
826 calculated as the per capita score for each colony

827

828 **Fig. 3** The relationship between ice rat *Otomys sloggetti robertsi* colony size in the Maluti  
829 Mountains, Lesotho, and the frequency of behaviours: basking, foraging and burrow  
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831 regression equation and adjusted  $r^2$  are shown for only foraging and burrow maintenance per  
832 season because the relationship was (or had a tendency to be) significant. Frequencies were  
833 calculated as the per capita score for each colony

834

835 **Fig. 4** The reproductive output of female ice rats *Otomys sloggetti robertsi* in colonies of  
836 different sizes (n = 91) in the Maluti Mountains, Lesotho, showing a) the total number of  
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838 values are shown in each panel