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

Running head: Group size and persistence in ice rats

Neville Pillay[1*] and Tasmin Lee Rymer[1,2,3]

[1] School of Animal, Plant and Environmental Science, University of the Witwatersrand, Private Bag 3, WITS 2050, Johannesburg, South Africa

[2] College of Science and Engineering, James Cook University, P. O. Box 6811, Cairns, QLD 4870, Australia; E-Mail: Tasmin.Rymer@jcu.edu.au

[3] Centre for Tropical Environmental and Sustainability Sciences, James Cook University, P. O. Box 6811, Cairns, QLD 4870, Australia

***** Author to whom correspondence should be addressed; E-Mail: Neville.Pillay@wits.ac.za

Tel.: +27-11-717-6459; Fax: +27-11-717-6494.

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Abstract

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

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

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

Statement of Significance

What proximally determines the relationship between group size, individual success and colony persistence? In ice rats, individuals in larger groups persist, which is correlated with more foraging. Larger groups possibly enjoy the benefits of huddling in larger groups, which are rechannelled into energy-intense activities. Groups failed or persisted as a unit. Investigating the behavioural correlates between group size and persistence provides insight into the proximal underpinnings of this relationship.

Introduction

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

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

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

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

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

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

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

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

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

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

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

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

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

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Materials and methods

Study area

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

Colonies

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

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

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

Trapping and marking

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

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

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

Behavioural observations

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

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

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individuals scored per colony.

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

Individual success

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

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

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

Other factors influencing colony size and individual success

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

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

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

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

Statistical analyses

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

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

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

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

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

Results

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

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

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

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

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

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

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

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

Discussion

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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Ethical approval: Our study was approved by the Animal Ethics Screening Committee of the University of the Witwatersrand (2000/12/2a, 2000/21/2a). All protocols complied with the current laws and regulations in South Africa and all applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

References

Armitage KB (1987) Social dynamics of mammals: reproductive success, kinship and individual fitness. Trends Ecol Evol 2:279-284

Armitage KB, Schwartz OA (2000) Social enhancement of fitness in yellow-bellied marmots. P Natl Acad Sci USA 97:12149-12152

Arnold W (1988) Social thermoregulation during hibernation in alpine marmots (*Marmota marmota*). J Comp Physiol B 158:151-156

Bacon PJ, Ball F, Blackwell P (1991) Analysis of a model of group territoriality based on the resource dispersion hypothesis. J Theor Biol 148:433-444

Batchelor TP, Briffa M (2011) Fight tactics in wood ants: individuals in smaller groups fight harder but die faster. Proc R Soc Lond B 278:3243-3250

Batchelor TP, Santini G, Briffa M (2012) Size distribution and battles in wood ants: group resource-holding potential is the sum of the individual parts. Anim Behav 83:111-117

Bazin RC, MacArthur RA (1992) Thermal benefits of huddling in the muskrat (*Ondatra zibethicus*). J Mammal 73:559-564

Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. J R Stat Soc B. 57:289–300

Boesch C (1994) Cooperative hunting in wild chimpanzees. Anim Behav 48:653-667

Brown JL (1982) Optimal group size in territorial animals. J Theor Biol 95:793-810

* This is the Accepted Version of a paper published in the journal Behavioural Ecology and Sociobiology: Pillay, N. & Rymer, T. L. 2017. Behavioural correlates of group size and group persistence in the African ice rat *Otomys sloggetti robertsi*. Behavioural Ecology and Sociobiology, 71, 62.

Canals M, Rosenmann M, Bozinovic F (1989) Energetics and geometry of huddling in small mammals. J Theor Biol 141:181-189

Carr GM, Macdonald, DW (1986) The sociality of solitary foragers: a model based on resource dispersion. Anim Behav 34:1540-1549

Creel S, Creel NM (2015) Opposing effects of group size on reproduction and survival in African wild dogs. Behav Ecol 26:1414-1422

Crofoot MC, Wrangham RW (2010) Intergroup Aggression in primates and humans: the case for a unified theory. In: Kappeler PM, Silk JB (eds) Mind the Gap – Tracing the Origins of Human Universals. Springer, Heidelberg, pp 171-195

Dehn MM (1990) Vigilance for predators: detection and dilution effects. Behav Ecol Sociobiol 26:337-342

Dittus WPJ (1988) Group fission among wild toque macaques as a consequence of female resource competition and environmental stress. Anim Behav 36:1626-1645

Dugdale HL, Ellwood SA, Macdonald DW (2010) Alloparental behaviour and long-term costs of mothers tolerating other members of the group in a plurally breeding mammal. Anim Behav 80:721-735

Ebensperger LA, Bozinovic F (2000) Communal burrowing in the hystricognath rodent, *Octodon degus*: a benefit of sociality? Behav Ecol Sociobiol 47:365-369

Ebensperger LA, Correa LA, León C, Ramírez-Estrada J, Abades S, Villegas Á, Hayes LD (2016) The modulating role of group stability on fitness effects of group size is different in females and males of a communally rearing rodent. J Anim Ecol 85:1502-1515

Ebensperger LA, Rivera DS, Hayes LD (2012) Direct fitness of group living mammals varies with breeding strategy, climate and fitness estimates. J Anim Ecol 81:1013-1023

* This is the Accepted Version of a paper published in the journal Behavioural Ecology and Sociobiology: Pillay, N. & Rymer, T. L. 2017. Behavioural correlates of group size and group persistence in the African ice rat *Otomys sloggetti robertsi*. Behavioural Ecology and Sociobiology, 71, 62.

Edelman AJ, Koprowski JL (2007) Communal nesting in asocial Abert's squirrels: the role of social thermoregulation and breeding strategy. Ethology 113:147-154

Emlen ST (1982) The evolution of helping. I. An ecological constraints model. Am Nat 119:29-39

Emlen ST (1994) Benefits, constraints and the evolution of the family. Trends Ecol Evol 9:282–285

Foster KR, Fortunato A, Strassmann JE, Queller DC (2002) The costs and benefits of being a chimera. Proc R Soc Lond B 269:2357-2362

Gettinger RD (1984) Energy and water metabolism of free-ranging pocket gophers, *Thomomys bottae*. Ecology 65:740-751

Gilbert C, McCafferty D, Le Maho Y, Martrette J-M, Giroud S, Blanc S, Ancel A (2010) One for all and all for one: the energetic benefits of huddling in endotherms. Biol Rev 85:545-569

Gilbert P, Price J, Allan S (1995) Social comparison, social attractiveness and evolution: how might they be related? New Ideas Psychol 13:149-165

Gilchrist JS (2004) Pup escorting in the communal breeding banded mongoose: behaviour, benefits, and maintenance. Behav Ecol 15:952-960

Glaser H, Lustick S (1975) Energetics and nesting behaviour of the northern white-footed mouse, *Peromyscus leucopus noveboracensis*. Physiol Zool 48:105-113

Grab SW, Deschamps CL (2004) Geomorphological and geoecological controls and processes following gully development in alpine mires, Lesotho. Arctic Antarct Alpine Res 36:49-58

Hatchwell BJ, Komdeur J (2000) Ecological constraints, life history traits and the evolution of cooperative breeding. Anim Behav 59:1079-1086

* This is the Accepted Version of a paper published in the journal Behavioural Ecology and Sociobiology: Pillay, N. & Rymer, T. L. 2017. Behavioural correlates of group size and group persistence in the African ice rat *Otomys sloggetti robertsi*. Behavioural Ecology and Sociobiology, 71, 62.

Hayes LD (2000) To nest communally or not to nest communally: a review of rodent communal nesting and nursing. Anim Behav 59:677-688

Hinze AJ (2005) Social behaviour and activity patterns of the African ice rat *Otomys sloggetti robertsi*. PhD Dissertation, University of the Witwatersrand, South Africa

Hinze A, Pillay N (2006). Life in an African alpine habitat: diurnal activity patterns of the ice rat, *Otomys sloggetti robertsi*. Arctic Antarct Alpine Res 38:540-546

Hinze A, Pillay N, Grab S (2006) The burrow system of the African ice rat *Otomys sloggetti robertsi*. Mammal Biol 7:356-365

Hinze A, Rymer T, Pillay N (2013) Spatial dichotomy of sociality in the African ice rat. J Zool Lond 290:208-214

Hodge SJ (2005) Helpers benefit offspring in both the short and long-term in the cooperatively breeding banded mongoose. Proc R Soc Lond B 272:2479-2484

Janson CH (1988) Food competition in brown capuchin monkeys (*Cebus apella*): Quantitative effects of group size and tree productivity. Behaviour 105:53-76

Judge DS, Carey JR (2000) Postreproductive life predicted by primate patterns. J Geront 55A:B201-B209

Kenward R, South A, Walls S (2002) Ranges 6. Anatrack Ltd, Dorset, UK

Killick DJB (1963) An account of the plant ecology of the Cathedral Peak area of the Natal Drakensberg. Botanical Survey of South Africa, Memoir No. 34. Republic of South Africa, Government Printer, Pretoria

Kinnaird MF, O’Brien TG, Nurcahyo A, Prasetyaningrum M (2002) Inter-group interactions and the role of calling among siamangs. XIXth Congress of the International Primatological Society, Beijing, China

Krause J, Ruxton GD (2002) Living in groups. Oxford University Press, New York

* This is the Accepted Version of a paper published in the journal Behavioural Ecology and Sociobiology: Pillay, N. & Rymer, T. L. 2017. Behavioural correlates of group size and group persistence in the African ice rat *Otomys sloggetti robertsi*. Behavioural Ecology and Sociobiology, 71, 62.

Lacey EA (2004) Sociality reduces individual direct fitness in a communally breeding rodent, the colonial tuco-tuco (*Ctenomys sociabilis*). Behav Ecol Sociobiol 56:449-457

Liker A, Bókony V (2009) Larger groups are more successful in innovative problem solving in house sparrows. P Natl Acad Sci USA 106:7893-7898

Macdonald DW, Carr GM (1989) Food security and the rewards of tolerance. In: Standen V, Foley R (eds) Comparative Socioecology: the Behavioural Ecology of Humans and Animals, Vol. 8. Blackwell Scientific, Oxford, pp 75-99

Markham AC, Gesquiere LR, Alberts SC, Altmann J (2015) Optimal group size in a highly social mammal. P Natl Acad Sci USA 112:14882-14887

Martin P, Bateson P (1986) Measuring Behaviour. An Introductory Guide. Cambridge University Press, New York

McComb K, Packer C, Pusey A (1994) Roaring and numerical assessment in contests between groups of female lions, *Panthera leo*. Anim Behav 47:379-387

McGuire B, Getz LL, Oli MK (2002) Fitness consequences of sociality in prairie voles, *Microtus ochrogaster*: influence of group size and composition. Anim Behav 64:645-654

Mokotjomela T, Schwaibold U, Pillay N (2009) Does the ice rat *Otomys sloggetti robertsi* contribute to habitat change in Lesotho? Acta Oecol 35:437-443

Mokotjomela T, Schwaibold U, Pillay N (2010) Population surveys of the ice rat *Otomys sloggetti robertsi* in the Lesotho Drakensberg. Afr Zool 45:225-232

Mosser AA, Packer C (2009) Group territoriality and the benefits of sociality in the African lion, *Panthera leo*. Anim Behav 78:359-370

Mumme RL, Bowman R, Pruett MS, Fitzpatrick JW (2015) Natal territory size, group size, and body mass affect lifetime fitness in the cooperatively breeding Florida Scrub-Jay. Auk 132:634-646

* This is the Accepted Version of a paper published in the journal Behavioural Ecology and Sociobiology: Pillay, N. & Rymer, T. L. 2017. Behavioural correlates of group size and group persistence in the African ice rat *Otomys sloggetti robertsi*. Behavioural Ecology and Sociobiology, 71, 62.

Oli MK, Armitage KB (2003) Sociality and individual fitness in yellow-bellied marmots: Insights from a long-term study (1962-2001). Oecologia 136:543-550

Parker GA (1974) Assessment strategy and the evolution of fighting behaviour. J Theor Biol 47:223-243

Parrish JK, Edelstein-Keshet L (1999) Complexity, pattern, and evolutionary trade-offs in animal aggregation. Science 284:99-101

Pollock GB (1994) Social competition or correlated strategy? Evol Ecol 8:221-229

Putaala A, Hohtola E, Hissa R (1995) The effect of group size on metabolism in huddling grey partridge (*Perdix perdix*). Comp Biochem Physiol B 111:243-247

Radford AN (2003) Territorial vocal rallying in the green woodhoopoe: influence of rival group size and composition. Anim Behav 66:1035-1044

Rasa OAE (1989) The costs and effectiveness of vigilance behaviour in the Dwarf mongoose: implications for fitness and optimal group size. Ethol Ecol Evol 1:265-282

Richter TA (1997) Does the southern African ice rat (*Otomys sloggetti*) show morphological adaptation to cold? J Zool Lond 242:384-387

Richter TA, Webb PI, Skinner JD (1997) Limits to the distribution of the southern African ice rat (*Otomys sloggetti*): Thermal physiology or competitive exclusion? Funct Ecol 11:240-246

Roberts G (1996) Why individual vigilance declines as group size increases. Anim Behav 51:1077-1086

Rowe-Rowe DT, Meester J (1982) Habitat preferences and abundance relations of small mammals in the Natal Drakensberg. S Afr J Zool 17:202-209

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Rubenstein DR (2011) Spatiotemporal environmental variation, risk aversion, and the evolution of cooperative breeding as a bet-hedging strategy. P Natl Acad Sci USA 108:10816-10822

Rymer TL, Kinahan AA, Pillay N (2007) Fur characteristics of the African ice rat *Otomys sloggetti robertsi*: Modifications for an alpine existence. J Therm Biol 32:428-432

Saltzman W, Ahmed S, Fahimi A, Wittwer DJ, Wegner FH (2006) Social suppression of female reproductive maturation and infanticidal behaviour in cooperatively breeding Mongolian gerbils. Horm Behav 49:527-537

Scantlebury M, Bennett NC, Speakman JR, Pillay N, Schradin C (2006) Huddling in groups leads to daily energy savings in free-living African four-striped grass mice, *Rhabdomys pumilio*. Funct Ecol 20:166-173

Schradin C, Schneider C, Yuen CH (2009) Age at puberty in male African striped mice: the impact of food, population density and the presence of the father. Funct Ecol 23:1004-1013

Schradin C, Schubert M, Pillay N (2006) Winter huddling groups in the striped mouse. Can J Zool 84:693-698

Schwaibold UH (2005) Foraging biology and habitat use of the southern African ice rat, *Otomys sloggetti robertsi*. PhD Dissertation, University of the Witwatersrand, South Africa

Schwaibold U, Pillay N (2003) The gut morphology of the African ice rat, *Otomys sloggetti robertsi*, adaptations to cold environments and sex-specific seasonal variation. J Comp Physiol B 173:653-659

Schwaibold U, Pillay N (2006) Behavioural strategies of the African ice rat *Otomys sloggetti robertsi* in the cold. Physiol Behav 88:567-574

* This is the Accepted Version of a paper published in the journal Behavioural Ecology and Sociobiology: Pillay, N. & Rymer, T. L. 2017. Behavioural correlates of group size and group persistence in the African ice rat *Otomys sloggetti robertsi*. Behavioural Ecology and Sociobiology, 71, 62.

Schwaibold U, Pillay N (2010) Habitat use in the ice rat *Otomys sloggetti robertsi*. S Afr J Wildl Res 40:64-72

Silk JB (2007) The adaptive value of sociality in mammalian groups. Philos T Roy Soc B 362:539-559

Sitch S, Huntingford C, Gedney N et al (2008) Evaluation of the terrestrial carbon cycle, future plant geography and climate-carbon cycle feedbacks using five dynamic global vegetation models (DGVMs). Glob Change Biol 14:2015-2039

Solomon NG, Hayes LD (2009) The biological basis of alloparental behaviour in mammals. In: Bentley G, Mace R (eds) Substitute Parents: Biological and Social Perspectives on Alloparenting in Human Societies. Berghahn Books, Herndon, Virginia, USA, pp 13-49

Snaith TV, Chapman CA (2007) Primate group size and interpreting socioecological models: Do folivores really play by different rules? Evol Anthropol 16:94-106

Stahler DR, MacNulty DR, Wayne RK, von Holdt B, Smith DW (2013) The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. J Anim Ecol 82:222-234

Stapp P, Pekins PJ, Mautz WM (1991) Winter energy expenditure and the distribution of southern flying squirrels. Can J Zool 69:2548-2555

Tschinkel WR, Adams, ES, Macom T (1995) Territory area and colony size in the fire ant *Solenopsis invicta*. J Anim Ecol 64:473-480

Vickery WL, Millar JS (1984) The energetics of huddling by endotherms. Oikos 43:88-93

Watts DP (1985) Relations between group size and composition and feeding competition in mountain gorilla groups. Anim Behav 33:72-85

Willan K (1990) Reproductive biology of the southern African ice rat. Acta Theriol 35:39-51

Young AJ, Jarvis JUM, Barnaville, J, Bennett NC (2015) Workforce effects and the evolution of complex sociality in wild Damaraland mole rats. Am Nat 186:302-311

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List of tables and figures

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

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

Fig. 2 The frequencies of basking and foraging in the ice rat *Otomys sloggetti robertsi* in the Maluti Mountains, Lesotho, in colonies that were present (y) or failed (n) in winter (grey boxes; n = 46) and summer (white boxes; n = 45). Medians (dark horizontal bars), 1st and 3rd interquartiles (boxes), 95% CI (whiskers) and outliers (dots) are shown. Frequencies were calculated as the per capita score for each colony

Fig. 3 The relationship between ice rat *Otomys sloggetti robertsi* colony size in the Maluti Mountains, Lesotho, and the frequency of behaviours: basking, foraging and burrow maintenance, and the distance travelled in winter (n = 46) and summer (n = 45). The linear regression equation and adjusted r^2 are shown for only foraging and burrow maintenance per season because the relationship was (or had a tendency to be) significant. Frequencies were calculated as the per capita score for each colony

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Fig. 4 The reproductive output of female ice rats *Otomys sloggetti robertsi* in colonies of different sizes (n = 91) in the Maluti Mountains, Lesotho, showing a) the total number of young and b) per capita young by females. The linear regression equations and adjusted r^2 values are shown in each panel

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