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

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

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

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

In mammals, solitary species are characterized by males and females only meeting for courtship and mating, and offspring leaving their mother in the period between weaning and the end of puberty (Makuya & Schradin, 2024a). Examples of solitary species are some shrews (Valomy et al., 2015), and large predators, such as black bears, *Ursus americanus* (Kovach & Powell, 2003) and leopards, *Panthera pardus* (Rafiq et al., 2020). Solitary living is often assumed to be an adaptation to sparsely distributed food that cannot be shared (Dalerum, 2007; Makuya & Schradin, 2024a; Nowak & Wilson, 1999). While individuals of solitary species do not share the same home range and sleeping sites, they do interact with conspecifics (Makuya & Schradin, 2024a). For example, the solitary puma, *Puma concolor*, has complex social networks with individualized relationships (Elbroch & Wittmer, 2012). Many solitary

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species do not have a random distribution but display a kin-based spatial structure, although this has rarely been studied.

The spatial structure of solitary species can change by season (Johansson et al., 2018). In particular, males of solitary species increase their home ranges more than females during the breeding season to overlap with many females to increase their reproductive success (Dillon & Kelly, 2008). Females might change their home ranges seasonally as a response to changes in resource availability (Potts & Lewis, 2014). For example, home range sizes of female striped mice (*Rhabdomys* spp.) vary with the seasonal availability of food (Schradin, Schmohl, et al., 2010). The impact of season and sex on home range size is well understood in group-living species (Schradin, Schmohl, et al., 2010; Stamps, 1994) but not much is known about solitary species. Studying variation in home range size of solitary species will provide an indication of their intraspecific variation in social organization (IVSO), particularly among the females.

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

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

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

METHODS

Study Species

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

Study Site and Study Period

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

Sampling Regime

Trapping and marking of bush Karoo rats

Trapping was conducted at lodges that showed signs of being occupied (fresh faeces, active runways, rats observed). The field site was divided into four to six areas, with one to two areas trapped at the same time by two teams (Fig. 1). All lodges within one area were trapped for three consecutive days before moving on to the next area. Traps were set in the morning before sunrise, checked after 45 and 90 min and then left closed during the hottest times of the day. In the afternoon, traps were set 45 min before sundown, checked after sundown and then left closed during the night. We used a combination of foldable Sherman traps (https://shermantraps.com/) and locally produced heavy metal traps of the Sherman style. Traps were baited with a combination of bran flakes, salt and sunflower oil and rebaited each morning and afternoon. They were arranged around the entrances of the lodges and along runways. No injuries due to trapping were recorded. The details of trapped rats were recorded, including their weight to the nearest 0.1 g, reproductive status and lodge number. Bush Karoo rats were removed from the traps in a plastic ziplock bag and weighed with the bag, before being taken out for inspection and then released at their lodge. Then the weight of the plastic bag was subtracted from the total weight. We marked individuals with metal band ear tags with a unique reference number for later identification (National Band and Tag Co., Newport, KY, U.S.A.; Schoepf & Schradin, 2012). To aid in visual identification during observations, individuals were marked with nontoxic hair dye (Inecto Rapido, Pinetown, South Africa), in combinations (females: head and chest/sides/back; males: hindquarters and chest/sides/back). Age was estimated from body mass at first capture, using a species-specific growth curve validated by our field data (Pillay, 2001). The bush Karoo rats were classified according to their age, with pups being up to 2 weeks old and weighing less than 30 g (weaning is at 14 days; Pillay, 2001), juveniles being 2–6 weeks old and weighing between 30 and 70 g, and adults being older than 6 weeks and weighing more than 70 g, when both sexes can start reproduction (Pillay, 2001).

Determination of kinship

Relatedness between individuals was assessed from trapping records and observations. Pups and juveniles that were trapped at a

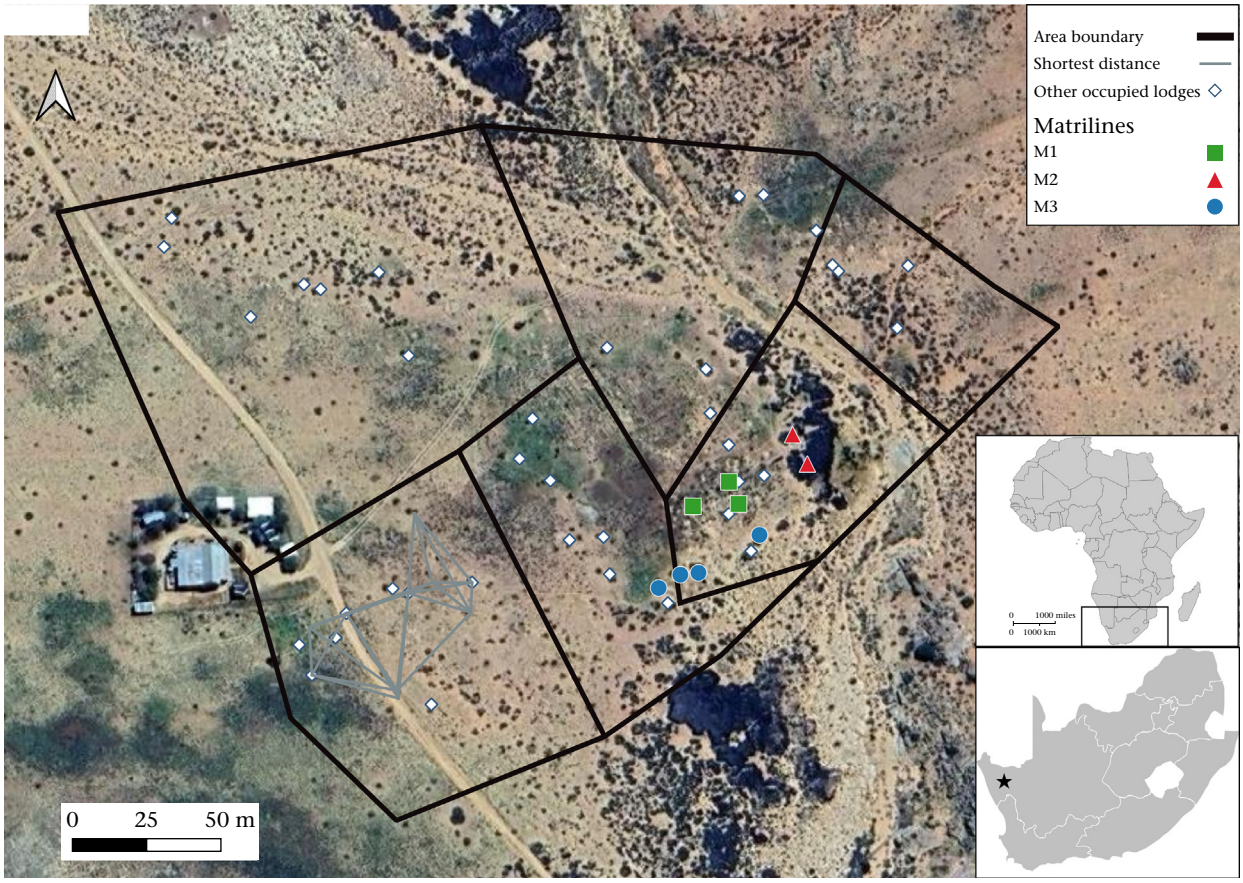

Figure 1. Satellite image of the field site (star in insert map). The black polygons are the boundaries of the six trapping areas within the field-site that we demarcated for trapping purposes. In one trapping area we show an example of matrilines in part of the study site for August 2022. Symbols and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

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

Determination of reproduction

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

Behavioural observations in the field

Focal observations were conducted five times a week at lodges with evidence of being occupied by bush Karoo rats to determine occupancy of lodges (which individuals were present) and to identify when pups emerged and juveniles/young adults dispersed. The morning observations started 5 min before the sun started shining on the lodges and lasted for 30 min; afternoon observations started 25 min before the sun stopped shining on the lodges. Lodges were usually observed on 2 days a month. The lodges that contained juveniles or a pregnant female were monitored more than twice in a month. The behaviours recorded during the observations included activities (e.g. foraging and feeding), lodge building and social behaviours including the following groups of behaviour: (1) amicable behaviours (i.e. grooming, body contact); (2) social investigation (i.e. sniffing); and (3) aggression (i.e. chasing, fighting). Behavioural data will be presented elsewhere.

Determination of Social Organization

We used a combination of trapping and behavioural observations to assess the social organization (i.e. group size and composition) of each adult bush Karoo rat for every month they were observed in the study site. We identified four forms of social organization (Table 1). Because lodges occupied by bush Karoo rats showed clear signs of use such as collected plant material, active runways and fresh faeces, we were certain that we had trapped at all occupied lodges on the field site (bush Karo rats on our field site always live in a lodge). The open habitat (no trees, low-growing shrubs) ensured we did not miss a lodge and we continuously surveyed the field site for occupied lodges. If we did not trap a bush Karoo rat at a lodge with an indication of occupancy within the

Table 1
Observed forms of social organization in bush Karoo rats

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

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

normal trapping regime of 3 days, we continued trapping and also observed the lodge, to ensure that trap-shy individuals were trapped and marked. Our behavioural observations confirmed that bush Karoo rats trapped at a lodge also inhabited that lodge, although some inhabited several neighbouring lodges. Apart from roaming males, we very rarely observed any bush Karoo rats at a lodge that they did not inhabit.

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

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

Monthly Determination of Neighbours and Distance Between Neighbours

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

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

We ran an LME to test for a difference in the distance between the closest kin versus nonkin neighbour. For every female, we took the mean distance to the kin neighbours and the mean distance to the nonkin neighbours such that each focal rat had a maximum of two neighbour values per month for the analyses. This was done to control for pseudoreplication. We included relationship (kin versus nonkin) and season as fixed effects and the ID of the focal rat and the year as random effects:

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

Mini-GPS Dataloggers

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

versus nonkin) were used as fixed predictors and the ID of the rat was a random effect. This was followed by an LMM to assess the influence of the season and relationship on the overall overlap between ranges. The models we used were:

$$DRS = season + (1|ID)$$

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

Statistical Analysis

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

Ethical Note

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

RESULTS

Social Organization

Most adult female and adult male bush Karoo rats were solitary (mean ± SD % solitary: females: 96.6 ± 10.26%; males: 98.9 ± 2.97%; Fig. 2). Adult groups made up a small percentage of the population and consisted of adult female kin (mother and adult daughter or sisters, 6.6 ± 9.5% of all social units), mother and adult son (0.32 ± 0.93%) and sibling pairs (brother and sister, 0.13 ± 0.66%; Fig. 2). In total, we observed 97 groups in 23 of the 51 months of study, with a group size of two or three individuals (2.2 ± 0.397). Of these, 50 groups consisted of a mother and one ($N = 31$ groups) or two ($N = 19$ groups) daughters and 31 of two ($N = 28$ groups) or three ($N = 3$ groups) sisters. We observed 12 groups consisting of a mother and her adult son and four groups of a sister and brother. For the groups consisting of two or three females, none of the females bred in 65 groups (end of the breeding season), one bred in seven groups and both females bred in five groups. There were no significant effects of season (LME; $t_{46} = 0.4$, $P = 0.69$; Table A1) or population density (LME; $t_{48} = -1.6$, $P = 0.116$; Table A1) on the percentage of solitary living females.

Spatial Structure

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

Daily Range Size and Overlap

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

DISCUSSION

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

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

At our field site, groups rarely formed. These were always kin groups, as predicted, most often consisting of a mother and her adult daughter(s), and sometimes sisters. Males were more often solitary than females, and few of them lived together with their mother or sister. In contrast to our prediction, groups were not more often found during the nonbreeding season than the breeding season, even though the data indicate that they might be more common at the end of the breeding season (Fig. 2), which warrants future studies. In striped mice studied on the same field site, one main factor leading to solitary living is reproductive competition, through female infanticide of another female's pups (Schradin, König, & Pillay, 2010). In the few bush Karoo rat groups, we observed either no reproduction taking place or only one female

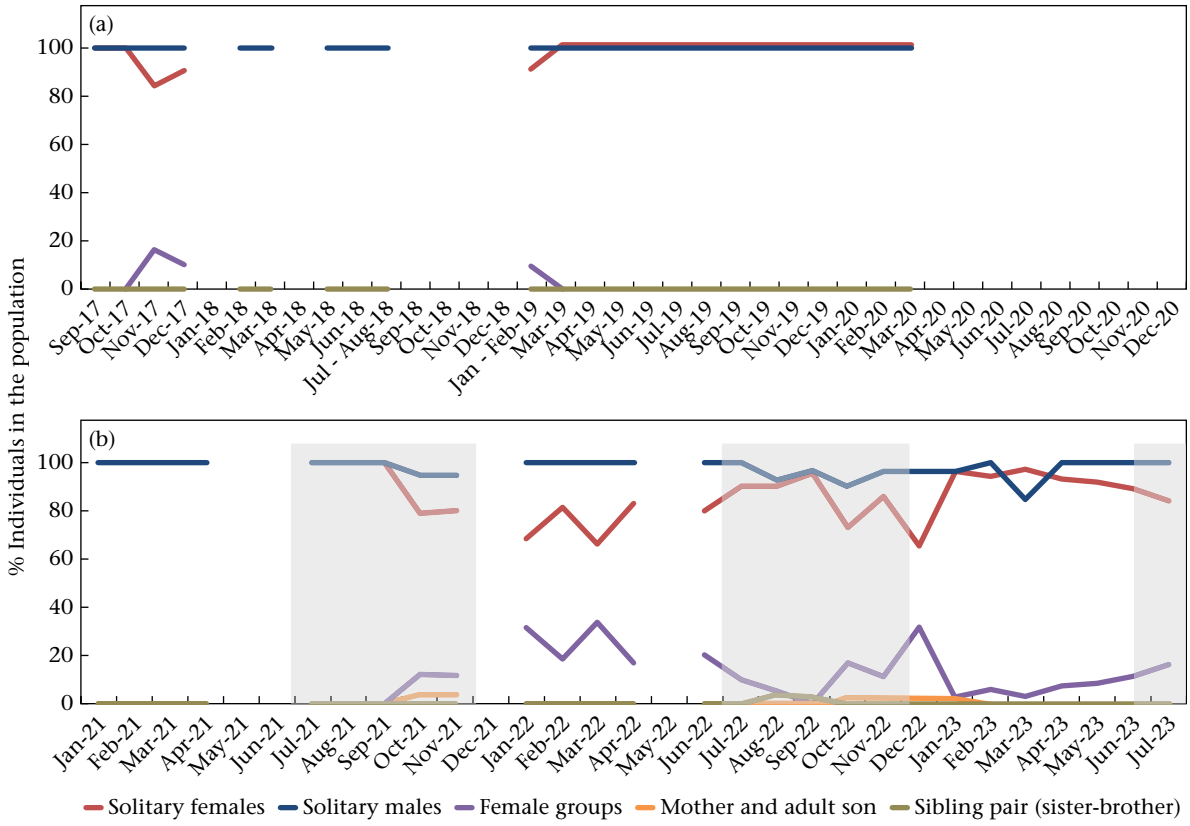

Figure 2. Distribution of social units in bush Karoo rats in 7 years. (a) September 2017 – December 2020; (b) January 2021 – July 2023. The breaks in the lines are from periods when no data were collected, for example due to the covid lockdown (March to December 2020). The definitions for the different social units are given in Table 1. The grey boxes indicate the wet, breeding season in winter/spring. The number next to the respective month refers to the year (i.e. Sept-17 = September 2017).

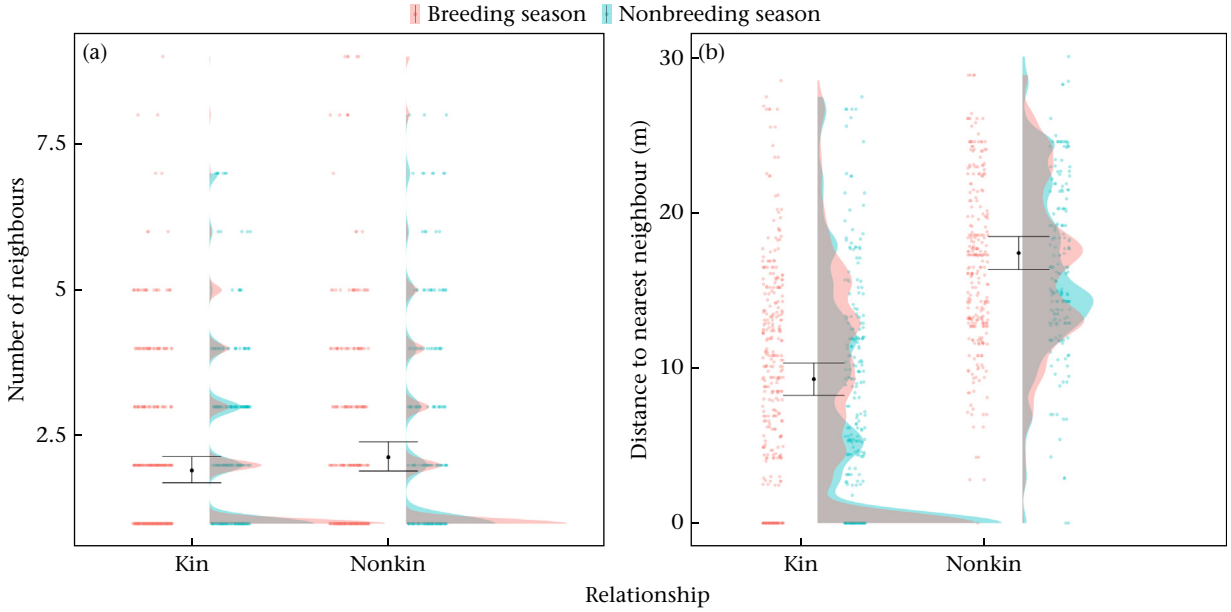

Figure 3. (a) The number of female neighbours by kinship ($P < 0.01$) and (b) the mean distance to the nearest neighbour in relation to kinship ($P < 0.001$) in bush Karoo rats, for both seasons. Points represent individual values (kin: $N = 556$; nonkin: $N = 444$). The black point is the model estimate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

reproduced, such that reproduction competition played no role. Group formation in bush Karoo rats could best be explained by the delayed dispersal of females reaching adulthood during the end of the breeding season, which should be studied in more detail in the future.

Population density was not significantly related to solitary living as we had predicted. In our current study, sufficient free territories were available for most female bush Karoo rats to disperse and start solitary living. The small territories of these central place foragers, as seen from the daily range data, might be one explanation for the

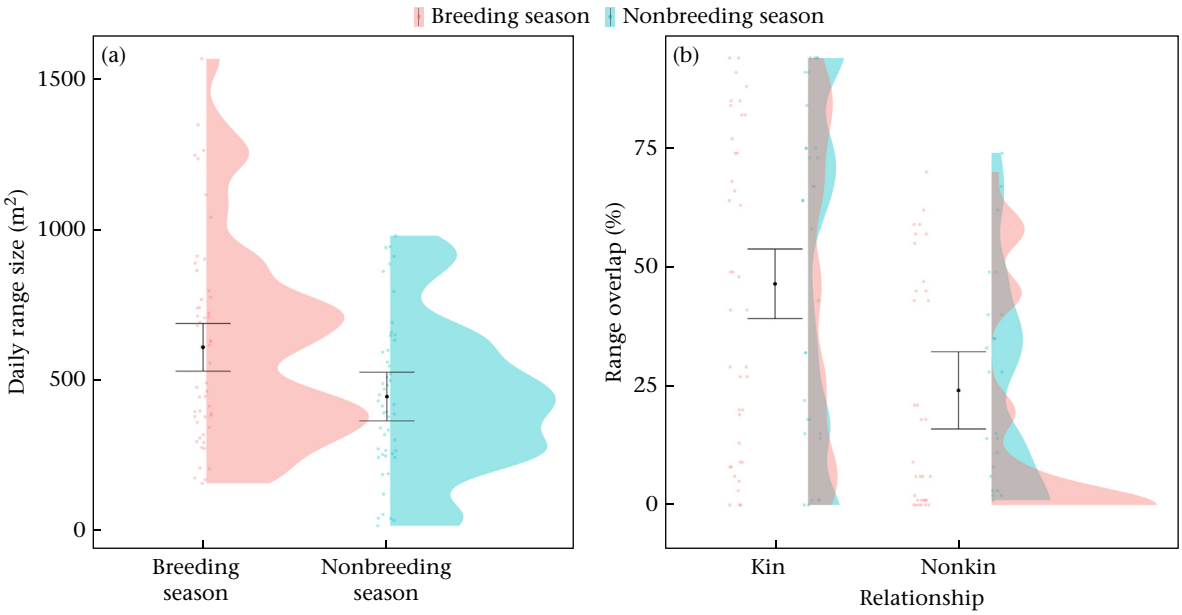

Figure 4. Seasonal comparison of (a) daily range size (nonbreeding: $N = 59$; breeding: $N = 81$) and (b) overlap (nonkin: $N = 54$; kin: $N = 72$) in bush Karoo rats. The black point is the model estimate and the error bars are the confidence intervals of the model. The half-violin plot shows the raw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

lack of association between population density and solitary living. In contrast, the sympatric striped mice have larger home ranges and are more likely to form groups when population density is high (Schoepf & Schradin, 2012; Schradin, König, & Pillay, 2010; Schradin et al., 2019). The striped mice study generated more data collected over several more years than we collected in our current study (8 years versus 5 years). Future analyses on a larger data set for bush Karoo rats over more years considering population density and additional cofactors such as predation pressure, food availability and availability of lodges might help us to understand when groups form. It is possible that during years with very high population density, we might find more and even larger groups.

Nonrandom spatial structures of amicably interacting individuals have been described for crocodiles (Baker et al., 2021, 2023) and sharks (Anderson et al., 2021; Mourier et al., 2012). In solitary felids and rodents this is known to depend on kinship (Meshriy et al., 2011; Roex et al., 2022). In our study, female bush Karoo rats had significantly more nonkin than kin neighbours, although the mean values were very similar (Fig. 3a). This might simply be because, overall, a female had many more nonkin than kin in the population. However, female bush Karoo rats lived closer to kin than to nonkin neighbours. This spatial kinship structure is similar to that of the giant kangaroo rat, *Dipomys ingens*, which formed female kin groups with increasing population density (Meshriy et al., 2011) and woodchucks, *Marmota monax*, which lived closer to kin and shared home ranges (Maher, 2009). The spatial kinship pattern in the bush Karoo rat seems to be related to females dispersing from their natal lodge to unoccupied lodges close by. There are fitness benefits of living near kin and familiar neighbours (Siracusa et al., 2021). An individual might be able to increase its inclusive fitness by associating and collaborating with closely related conspecifics, even in solitary species, such as alerting each other to predators (warning calls) or by social tolerance allowing them to share food sources (Dobson et al., 2012; Griffiths & Armstrong, 2001; Viblanc et al., 2016, 2022; Walmsley et al., 2023). This can have significant fitness benefits as shown in Columbian ground squirrels, *Urocitellus columbianus*, which, overall, have more weaned offspring when they have female kin neighbours (Viblanc et al., 2016). Solitary animals may lose some of the direct benefits of group living (Makuya & Schradin, 2024a), and forming a kinship spatial structure could be a strategy to reduce such costs (Makuya & Schradin, 2024b).

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

GPS dataloggers have been used in several large mammal studies to assess their spatial structure, such as in cougars, *Puma concolor*, and fossas, *Cryptoprocta ferox*, where this technique revealed previously unknown relationships, often influenced by kinship (Elbroch et al., 2017; Lührs & Kappeler, 2013). By using mini-GPS for the first time in a small rodent to determine spatial structure, we found that the ranges of bush Karoo rats overlapped more with their kin than with their nonkin neighbours. Large carnivores that display territorial defence have greater overlap in spatial ranges when food availability is low (Nams et al., 2023). In our study, season did not significantly influence range overlap, but we cannot exclude this possibility (see Fig. 4b). However, we found that bush Karoo rats had larger ranges in the wet, breeding season than in the dry, nonbreeding season. This is surprising, since more food is available in the wet season, and one might expect bush Karoo rats to instead extend their home ranges in the food-poor dry season. In the wet breeding season, females might have to forage over larger areas to obtain both energy and protein-rich food necessary for breeding. The shrubs into which lodges are built offer

some food (leaves) even in the dry season. Smaller ranges in the dry season might help save energy, as occurs in the synoptic striped mouse which also has smaller home ranges in the dry season (Schradin, Schmohl, et al., 2010). Finally, our GPS data confirmed that the spatial structure in the solitary bush Karoo rat is not random but is influenced by kinship.

While solitary living has long been regarded as an ancestral and primitive trait, recent comparative studies indicate that solitary living might be a derived state in mammals, and an adaptation to specific environments (Makuya & Schradin, 2024a). However, studying solitary living is important to understand mammalian social evolution (Clutton-Brock, 2021; Makuya & Schradin, 2024a). Multiple studies using modern network analysis indicate that even solitary mammals (social organization) might have complex social interactions with their neighbours (social structure; Elbroch & Wittmer, 2012; Lührs & Kappeler, 2013; Meshriy et al., 2011). Our study adds to evidence uncovering the social complexity of solitary mammals. It provides insight into the importance of kinship in a solitary species and shows that intraspecific variation in social organization can also occur in a primarily solitary species. Our observations of female kin structure and the rare occurrence of female kin groups indicate the possibility of evolution leading to social groups.

Conclusion

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

Author Contributions

Lindelani Makuya: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Validation, Visualization, Writing – original draft, Writing – review & editing. **Neville Pillay:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – review & editing. **Carsten Schradin:** Conceptualization, Funding acquisition, Methodology, Project administration, Supervision, Writing – original draft, Writing – review & editing.

Data Availability

Data are uploaded as supplementary files.

Declaration of Interest

The authors declare that they have no conflicting interests.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2024.06.022.

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Appendix

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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