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The bind of the burrow: trade-offs between refuge and foraging shape space use in Kalahari meerkats

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The understanding of habitat selection in wild vertebrates has been heavily influenced by observations of preferred foraging areas. However, foraging is only one of many ways animals interact with their environment, and preferences for habitat features that support resting, breeding and safety, along with trade-offs between these needs, remain underexplored. These trade-offs are likely to be particularly acute in complex environments where these needs are met in different locations. Using long-term data on group movements and individual life histories, we examine how preferences for foraging areas and burrow sites shape space use in Kalahari meerkats, *Suricata suricatta*. Meerkats rarely dig new sleeping and breeding burrows and must use those abandoned by other species, potentially generating trade-offs in daily space use if overnight refuges are far from optimal foraging areas. We show that space use is strongly anchored by burrow location, with burrows in white-sand habitats, particularly those in dry riverbed and pan habitats, preferred year-round while also being associated with low burrow switching rates. In contrast, foraging habitat preferences varied seasonally, with white-sand habitats often being disfavoured during foraging. Individuals also gained less weight in both wet and dry seasons when their morning foraging was concentrated in these habitats. As a result, meerkats faced a trade-off between optimal burrow locations and productive foraging grounds, which was reflected in faster, longer and more energetically costly travel when moving through or waking up in white-sand areas. Our results suggest that changes in the distribution or abundance of key burrow-constructing species in desert environments may have cascading effects on the many secondary burrow users that depend on them for survival and reproduction. More broadly, our results highlight that refuge availability can impose strong ecological constraints on animals and may restrict behavioural plasticity under environmental change, particularly if productive foraging areas shift.

Animals interact with their environment in diverse ways, and the habitats they select must provide the resources and conditions needed for survival and reproduction (Huey, 1991; Matthiopoulos et al., 2015; Mayor et al., 2009; Morris, 2003). Studies of habitat selection often emphasize access to food, and while foraging can clearly drive patterns of habitat use, it is only one of many functions that habitats serve. Animals also depend on refuges, breeding sites and resting areas, among other habitat features, and their movements and habitat use will often reflect trade-offs between these competing needs (Cowlishaw, 1997; Godvik et al., 2009; Mayor et al., 2009; Mysterud & Ims, 1998; Wilson et al., 2012).

Among the nonforaging resources that animals rely on, refuges such as burrows, dens, tree cavities or rock crevices, are especially critical for many species (Hansall, 1993; Nilsson, 1984). They provide safety from predators (Ebensperger & Blumstein, 2006; Reichman & Smith, 1990), protection from climatic extremes (Buffenstein, 1984; Milling et al., 2018; Pinkert et al., 2025; Williams et al., 1999) and

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secure sites for rearing young (Noonan et al., 2015; Wolff & Peterson, 1998) or storing food (Baroni et al., 2021). Because suitable refuges are often spatially discrete, they can exert a disproportionate influence on patterns of movement, territoriality and local population density (Camp et al., 2017; Macdonald & Johnson, 2015; Newton, 1994). For example, sleeping burrows or denning sites have been shown to constrain home ranges across mammals including carnivores, rodents, mustelids and marsupials (Eide et al., 2001; Evans, 2008; Pomilia et al., 2015; Rosalino et al., 2005), and in primates specifically, sleeping site selection frequently shapes space use in ways that reflect strong tensions between antipredator considerations and foraging needs (Chapman, 1989; Hamilton, 1982; Markham et al., 2016). Comparable constraints are also well documented in birds that depend on tree cavities for nesting, where limited availability of suitable sites can strongly restrict breeding opportunities and habitat use (Wiebe, 2011).

Collectively, such findings suggest that trade-offs between preferred sheltering and feeding habitats are common. However, because most studies of habitat selection rely solely on spatial data collected by GPS-tracking devices, the behavioural drivers and energetic costs of these trade-offs are often unclear. Spatial data reveal where animals move, but they only indirectly indicate the behaviours that generate those movements, meaning that mechanisms of habitat choice (and any associated trade-offs) are typically inferred rather than demonstrated. Incorporating additional behavioural or energetic data into habitat selection studies therefore offers the potential for a richer and more ecologically grounded understanding of animals' movement decisions (Kays et al., 2015; Nathan et al., 2008).

Secondary burrow or cavity users provide particularly clear examples of how refuge availability can impact space use and create trade-offs with access to other resources. Unlike primary excavators, who can create their own sleeping or nesting sites and may therefore be able to position themselves optimally relative to food resources (Macdonald et al., 2004), secondary users depend on structures created by other species (Andersen et al., 2021; Desmond & Savidge, 1996; Di Blanco et al., 2020; Whittington-Jones et al., 2011) or by natural processes. As a result, the availability and placement of suitable refuges are largely beyond their control and may not coincide with their foraging needs.

Here, we examine how the selection of burrow and foraging habitats influences the space use and movement patterns of meerkats, *Suricata suricatta*, in the Kalahari. Meerkats are secondary burrow users and, in the Kalahari Desert, typically occupy burrows excavated by springhares, *Pedetes capensis*, Cape ground squirrels, *Geosciurus inauris*, and Cape porcupines, *Hystrix africaeaustralis*, which they tend to renovate rather than dig them themselves (Fig. 1). They are diurnal, desert-adapted mongooses that live in family-structured groups in which reproduction is skewed towards a dominant breeding pair (Clutton-Brock et al., 2006; Clutton-Brock & Manser, 2016). Each night, groups retreat to one of many sleeping burrows within their home range (Gall et al., 2017; Strandburg-Peshkin et al., 2020), typically using the same burrow for up to a week before switching. Burrows also serve as natal den sites during the first 3–4 weeks of pup development, when dedicated babysitters remain underground with pups while the rest of the group forages (Clutton-Brock et al., 2001). During the day, groups move cohesively throughout their home range and forage mainly on surface- and shallow-dwelling invertebrates (Doolan & MacDonald, 1996; Jubber et al., 2025), occasionally making use of bolt holes and burrows in response to predators (Manser & Bell, 2004). Except under exceptional circumstances, meerkats obtain all the water they need from their food, so unlike many Kalahari mammals, their space use is not constrained by surface water (Lovegrove, 2021).

Our study focuses on the meerkat population at the Kuruman River Reserve in the Kalahari Desert, which has been continuously monitored for over three decades (Clutton-Brock & Manser, 2016). Because the population is habituated to close human observation, groups can be tracked at high spatial resolution (Kranstauber et al., 2020) and individuals can be weighed multiple times daily (Thorley, Duncan, Manser, & Clutton-Brock, 2025). This unique combination of data provides a rare opportunity to directly measure foraging returns and quantify the energetic consequences of space use decisions in a wild vertebrate population.

Using two decades of high-resolution movement and life-history data, we first quantified habitat selection at both landscape and local scales, distinguishing between areas used for sleeping burrow sites and those used for foraging. We then investigated the behavioural and energetic consequences of habitat choice by examining habitat-specific effects on burrow fidelity, group movement speeds, foraging track lengths and foraging success. These complementary measures allowed us to test whether meerkat groups face trade-offs between occupying habitats optimal for shelter versus those that maximize foraging returns, and to understand the mechanisms driving these

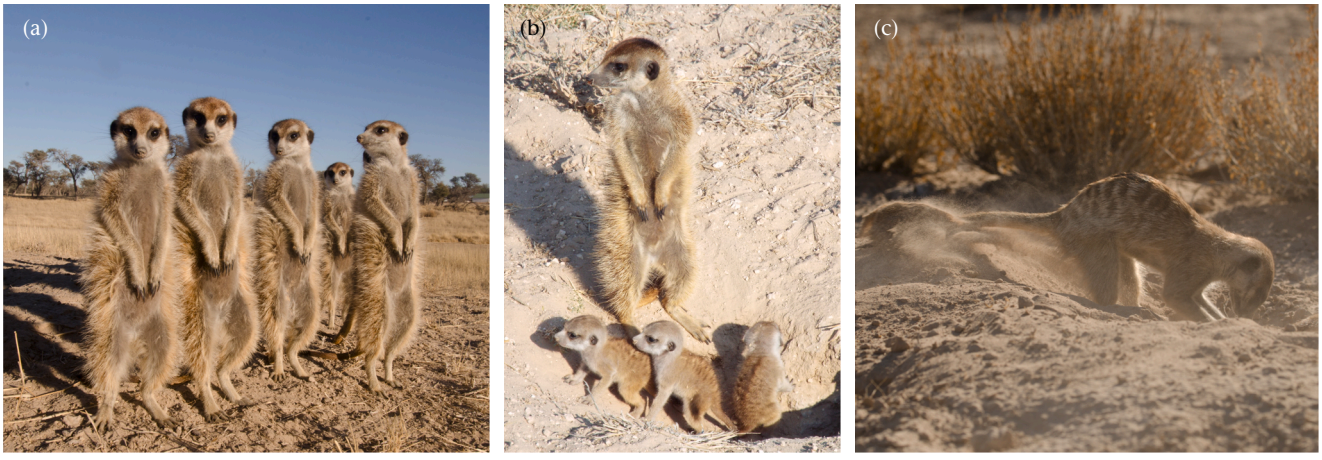

Figure 1. Meerkats use burrows as sleeping sites, thermal refuges and natal dens. (a) Meerkats sunning themselves at the entrance of a sleeping burrow on a cold winter morning before departing to forage. Groups retreat underground at night and during hot midday periods. (b) During early pup development, young remain underground under the care of babysitters while the rest of the group forages. (c) Although meerkats do not excavate their own burrows, they occasionally renovate entrances. Images (a) and (c) were taken by Kyle Finn; image (b) was taken by the first author (J.T.).

decisions. By comparing the Kalahari's wet and dry seasons, we also identified when such trade-offs were most pronounced.

METHODS

The Habitat Types

The meerkat population at the Kalahari Research Centre in South Africa (26°58′S, 21°49′E) has been continuously studied since 1993 (Clutton-Brock & Manser, 2016). The reserve is situated on the Kuruman River, which remains dry year-round except during rare, extreme rainfall events that cause flooding once every few decades. The climate features hot summers, cold winters and significant diurnal temperature variations year-round (Thorley, Duncan, Gaynor, et al., 2025). Annual rainfall is low (mean ± SD = 297.4 ± 135.3 mm, range 115–705 mm during 1998–2023), with most precipitation falling during October–April, which we refer to as the 'wet season'.

The vegetation in and around the field site is best described as southern Kalahari duneveld (Mucina & Rutherford, 2006). Although duneveld dominates the landscape at large scales, the study area encompasses a range of finer-scale habitat types that are characteristic of the broader Kalahari region (M. W. van Rooyen et al., 2008) and that are closely related to the underlying soil (T. H. van R. ooyen. van Rooyen, 1984). Following earlier research by Harrison et al. (2021), we classified these habitats into four types based on vegetation structure and soil composition (Supplementary Fig. S1). For clarity, we use functional habitat names throughout this study to make the classification easier for readers to follow, with more vegetation-focused descriptions in Supplementary Table S1:

(1) Low shrubland: calcareous white-sand areas dominated by dense dwarf shrub thickets, particularly *Rhigozum trichotomum*, with a limited grass layer.

(2) Riverbed and pans: open calcareous white-sand habitats associated with the dry Kuruman River channel, river terraces, drainage lines and scattered pans. Vegetation is generally sparse, with the riverbed and pans supporting open grass and dwarf shrub communities, while the river terraces contain a stronger woody component dominated by *Vachellia erioloba* and *Senegalia mellifera*, with occasional *Ziziphus mucronata* within the riverbed.

(3) Low duneveld: red-sand habitat characterized by a well-developed perennial grass layer with scattered trees and shrubs, especially *Vachellia* species, forming an open savannah structure.

(4) High duneveld: high duneveld plains on red sand dominated by perennial grasses, particularly *Stipagrostis amabilis.* Woody plants are sparse, with occasional shrubs such as *Grewia flava* and sporadic *V. haematoxylon* trees.

The Study Population

Meerkat groups were visited three to four times per week throughout the project's history, both in the morning and afternoon. Observers typically arrived at the sleeping burrow before any meerkats emerged and remained with the group throughout the morning foraging period. After emerging from the burrow each morning, meerkats typically bask for up to 90 min before beginning to forage. Groups forage together for 3–4 h, after which activity declines either due to satiation or because high temperatures force them to seek shade (Habicher, 2009). In the evening, observers arrived approximately 1 h before the group's return to a burrow, which may differ from the one used the previous night. We monitored an average (± SD) of 13.5 ± 7.6 groups per month (range 6–21 groups) comprising 214.5 ± 59.4 known individuals (range 101–359) .

During observation periods, data were collected on behavioural and life history traits including social and reproductive status, health and the expression of several cooperative behaviours (Clutton-Brock & Manser, 2016). Burrow use and group composition were also recorded.

Individuals were identified using unique, nontoxic dye marks applied regularly by researchers with a long paintbrush. For permanent identification, all habituated individuals over the history of the project were also implanted with passive integrated transponder (PIT) tags (Identipet, Johannesburg, South Africa) at approximately 1–2 months of age (~2250 individuals). PIT tagging enabled reliable re-identification of individuals that temporarily left the study area or moved between social groups. Animals were captured by approaching individuals on foot and gently picking them up by hand. Captured individuals were briefly placed into a cloth handling bag and restrained manually while being positioned dorsally for processing. PIT tags (8 × 2 mm) were implanted subcutaneously between the shoulder blades using a sterile, single-use 12-gauge needle. The entire capture and tagging procedure typically took only a few minutes per individual. Following implantation, individuals were immediately released at the site of capture and rejoined their social group.

Most individuals were weighed at the start and end of each visit by coaxing them onto electronic scales (Sartorius TE4100, ± 1 g) in return for small amounts of water or hard-boiled egg (typically <1 g per individual). To estimate foraging returns, we used the morning weight gain, which we calculated as the difference between pre- and postforaging morning weights divided by the time between measurements. The average (± SD) rate of morning weight gain was 6.23 ± 5.06 g/h.

During morning foraging sessions, observers tracked group movements using hand-held Garmin GPS devices. They recorded the group's central location approximately every 15 min from the time they left the burrow. Between May 2002 and December 2023, 13 030 morning tracks from 61 meerkat groups were recorded, totalling 161 116 GPS fixes after data cleaning based on distance and speed thresholds, following Kranstauber et al. (2020). From these foraging tracks we calculated the movement speed of groups and travel path lengths. Movement speed was calculated as the speed between successive GPS fixes ('steps'), with groups moving at an average (± SD) speed of 217.5 ± 193.8 m/h (N = 143 922 steps). Path lengths were calculated as the summed distance of all movement steps on a given morning; the average path length was 601.1 ± 278.2 m (N = 12 710 paths). Home ranges were estimated separately using all foraging locations collected during both morning and afternoon sessions. Estimates were calculated using rolling 3-month windows, including only periods in which a group had been visited at least 20 times (Thorley, Duncan, Gaynor, et al., 2025). We calculated home ranges as the 95% autocorrelated kernel density estimate (AKDE) of all locations using the 'ctmm' package (Fleming & Calabrese, 2023). We retained estimates relating to four discrete quarterly periods of the year.

We conducted all our analyses in R version 4.4.2 (R Core Team, 2024) using the specified packages. To ensure consistency across analyses, all data sets were restricted to the same date range (May 2002–December 2023). For each statistical model, we evaluated habitat differences by estimating pairwise contrasts of the marginal means using the 'emmeans' package (Lenth, 2024). We consistently compared habitat differences within each season, and for some analyses, we also compared differences across seasons for each habitat type.

Characterizing Habitat Selection

We used the morning foraging tracks to investigate habitat selection at both the landscape and local scale. At the landscape scale, we fitted resource selection functions (RSF, Boyce & McDonald, 1999), while at the local scale, we used step selection analyses to estimate habitat selection during group movements (Avgar et al., 2016). Both methods follow a use–availability framework, comparing locations that were used by meerkat groups to those that were available; within the home range for RSFs, and within the movement step for step selection analyses. By applying these complementary methods, we aimed to understand the extent to which the different habitats were selected as areas for sleeping burrows and for foraging throughout the year.

Landscape-scale habitat selection for sleeping burrows and foraging areas

For the RSF, we started by selecting a random point from each morning track so that each track contributed the same amount of information to the sampling procedure. These points were then used to estimate the spatial extent of each group in each season (home ranges usually expand during the wet season). To do this, we created a nonconvex boundary around all selected points for each group and season and applied a 500 m buffer to account for possible movement beyond observed locations. Within each buffered extent, we randomly sampled 19 available locations per used location to represent the available habitat. Used locations were then chosen as either (1) the first GPS point of the day or (2) a randomly selected GPS point between 1 and 4 h into foraging. This distinction allowed us to model habitat selection for burrow use versus foraging areas separately, in two models. The first location of the day is normally taken very near to the sleeping burrow (median = 13.8 m) and therefore reflects burrow habitat selection, whereas later points represent periods of intensive foraging and inform on landscape-scale foraging preferences (Supplementary Fig. S2).

The two RSFs were modelled as downweighted Poisson regressions (Renner et al., 2015) using the 'sdmTMB' package (Anderson et al., 2025). Habitat type was included as a fixed effect in interaction with the season, and group identity was included as a random intercept. To account for residual spatial autocorrelation and unmeasured spatial structure in habitat use, we combined all spatial extents into a single mesh and incorporated the mesh as a stochastic partial differential equation (SPDE) effect (Lindgren et al., 2011), which provides a computationally efficient Gaussian random field approximation for modelling continuous spatial dependence. Model coefficients were interpreted as log use:availability ratios and exponentiated to estimate the relative selection intensity of the habitats (Avgar et al., 2017; Fieberg et al., 2021).

Local-scale habitat selection during foraging

For the step selection analysis, we selected all morning tracks lasting between 1 and 4 h, and where consecutive GPS fixes were taken at intervals of 10–20 min (mean ± SD = 14.6 ± 1.8 min, with 80.1% of intervals equal to 15 min). Tracks lasted an average (± SD) of 165.6 ± 24.8 min. As step-selection functions require regular sampling intervals we interpolated tracks to 15 min intervals, which represented the highest median interval in the data set. Following interpolation, 120 011 movement steps were available for the step selection analysis (i.e. consecutive fixes from a single track), coming from 12 866 morning tracks. For each observed movement step, we generated 19 random steps using the 'amt' package (Signer et al., 2019), drawing from the observed distributions of step lengths (gamma distribution) and turn angles (von Mises distribution) pooled across all groups.

Used and available steps were then analysed using the Poisson regression described by Muff et al. (2020), which is equivalent to a mixed-effects conditional logistic regression model. Briefly, each observed step and its associated random steps were assigned to a unique stratum, which was fitted as a random intercept with a large, fixed variance. Habitat selection was estimated by including the habitat class at the end of the movement step as a categorical fixed effect, in addition to uncorrelated, group-specific random slopes for each habitat type to allow each group to have its own habitat selection parameters. The models were fitted using the 'glmmTMB' package (Brooks et al., 2017). We fitted separate models for the two seasons of the year. As with the RSF, model coefficients were exponentiated to reflect relative selection intensity.

Quantifying the Behavioural and Energetic Costs of Habitat Selection Trade-offs

Habitat effects on burrow switching

If meerkat groups are selective in their choice of habitat for sleeping burrows or foraging areas, this raises questions about the mechanisms driving these preferences. Focusing first on burrow use, we hypothesized that groups would be less likely to switch burrows in the habitats that they favoured for sleeping burrows. To explore this possibility, we identified all cases where the location of a group's sleeping burrow was known on consecutive nights, recovering 41 654 such events. Of these, 13 194 were switches (31.6%), implying that groups switch burrows once every 3 days, on average. The average (± SD) distance moved between burrows was 620.8 ± 468.5 m.

We analysed the probability of burrow switching (0/1) using a generalized linear mixed effects model with binomial error distribution, implemented in the 'glmmTMB' package. Fixed effects included an interaction between habitat type and the season, alongside other predictors that we expected to be important a priori: linear and quadratic terms for group size, a three-level categorical term for pup presence (pups being babysat at the burrow, foraging with the group or absent) and a categorical term for breeding season (i.e. study year), defined as each discrete annual cycle from October of year t to September of year $t + 1$. We also included an interaction between pup presence and season to allow for seasonal differences in the effect of pups. Group identity and the burrow identity were included as random intercepts. Pups were defined as all individuals younger than 90 days old.

Habitat effects on foraging success, speed of movements and morning track lengths

To investigate the mechanisms underlying foraging habitat selection, we analysed how habitat type influenced three complementary aspects of meerkat foraging behaviour: the rate of morning weight gain, group movement speeds and total morning track lengths. Each metric captures a different aspect of how habitat might affect foraging decisions and thus energetic outcomes. Morning weight gain, measured by the change in weight of adults (individuals >1 year of age) between morning and afternoon, offered a direct measure of foraging success. Movement speed served as an indicator of foraging intensity, with slower speeds assumed to reflect more intensive foraging. While reduced movement speeds may indicate higher prey encounter rates, they are also likely to be influenced by factors such as perceived or realized predation risk. Movement speed should therefore be considered an integrated behavioural metric. Track length reflected the total distance travelled during a morning foraging

session, providing information on the spatial extent of foraging effort.

All three foraging-associated metrics were analysed using linear mixed effects models and were fitted in the 'nlme' package (Pinheiro & Bates, 2000; Pinheiro et al., 2024), allowing us to account for temporal autocorrelation in the data sets. The models shared a common fixed effects structure aligned with the burrow-switching model, incorporating terms for the interaction between habitat type and season, linear and quadratic effects of group size, pup presence (and its interaction with season) and breeding year. We assessed the residuals for spatial autocorrelation using Moran's I (Moran, 1950), and in each case, the value was close to zero, indicating no meaningful residual spatial structure (beyond that already captured by the model terms).

For the weight gain model, we identified the dominant habitat type encountered across the morning as the habitat variable, the habitat in which the group spent most of its time (N = 44 983 records from 1674 individuals in 58 groups). The dominant habitat type frequently matched the habitat of the sleeping burrow used the previous night (56.7% of cases; permutation test: $P < 0.001$). Additional fixed effects included sex and linear and quadratic terms for individual age. We used a continuous autoregressive correlation structure of order 1 (corCAR1) to model the correlation between consecutive observations within individuals, defined by the number of days since each individual's first observation. Random effects included individual identity nested within group.

For the movement speed model (N = 143 922 steps), the habitat type at the start of each movement step served as the habitat variable. We additionally included linear and quadratic terms for time spent foraging. A first-order autoregressive correlation structure (corAR1) was applied to model autocorrelation among speeds recorded at ~15 min intervals. Group identity and date (nested within group) were included as random effects. We also fitted a Gamma-distributed models for movement speed, being bounded at zero and right-skewed, and this produced quantitatively similar results. We retained the Gaussian model as it allowed incorporation of temporal autocorrelation structure, with all predictions remaining within biologically realistic bounds.

In the track length model (N = 12 710 tracks), we analysed track lengths with respect to the sleeping burrow habitat to assess whether groups starting in different habitat types travelled further. A linear variable for total tracking time was included. A continuous first-order autoregressive correlation structure (corCAR1) was included to account for temporal autocorrelation in path lengths recorded on successive days within groups. Group identity was included as a random effect.

Ethical Note

All the long-term data used in this study were collected under permits granted by the ethics committee of the University of Pretoria (EC047-16, EC010-13, SOP029-12) and adhered to the standards outlined in the ASAB/ABS Guidelines for the treatment of animals in behavioural research and training (ASAB Ethical Committee/ABS Animal Care Committee, 2012). To minimize the impacts of our research on animal welfare, efforts were made to habituate all individuals to our presence, which allowed the collection of weights and behavioural data without direct handling. PIT tag implantation and dye marking were performed by experienced personnel following standard procedures designed to minimize discomfort. Handling times were brief, and no immediate behavioural or physiological effects were observed following PIT tagging or dye application.

RESULTS

Landscape-scale Habitat Selection for Sleeping Burrows and Foraging Areas

Meerkat groups displayed distinct preferences between habitats used for sleeping burrows and those used for foraging. At the population level, habitat preferences for sleeping burrows were strong and consistent throughout the year, following the order: riverbed and pans > low shrubland > low duneveld and high duneveld (Fig. 2c, Supplementary Tables S2–S3). Assuming equal habitat availability, meerkat groups were 1.57–2.07 times more likely to select riverbed and pans over low shrubland, 5.59 to 5.95 times more likely to select riverbed and pans over low duneveld, and 6.81 to 7.76 times more likely to select riverbed and pans over high duneveld, depending on the season ($P < 0.001$ for all pairwise contrasts).

Although the riverbed and pans were most frequently used for sleeping burrows, the greater availability of low duneveld meant that it was used more often than low shrubland, despite lower selection intensity (Table 1). Burrows in high duneveld areas were rarely used, with only 4.9% of first daily GPS locations (our proxy for burrow habitat) occurring in this habitat. Probability of use was similarly low, estimated at 0.037 (wet season) and 0.045 (dry season). The dominant role of the riverbed and pans in shaping long-term burrow use, and the broader influence of sleeping burrow locations on space use, is illustrated by plotting two decades of ranging data across the study site (Fig. 2b), which reveals a persistent spatial anchoring to these white sand areas and limited representation of high duneveld in home ranges (Fig. 3).

Foraging habitat preferences at the landscape scale were weaker and more variable throughout the year (Fig. 2d, Supplementary Tables S4–S5). The resource selection functions revealed one consistent pattern: low shrubland was consistently avoided, with significant underselection in all pairwise contrasts ($P < 0.05$). During the dry season (May–September), meerkat groups also showed a relative preference for high duneveld (RSF contrast ± SE = 0.23 ± 0.07, $t = 3.37$, $P = 0.004$) and low duneveld (contrast ± SE = 0.18 ± 0.04, $t = 3.53$, $P < 0.001$) over riverbed and pans. In contrast, during the wet season (October–April), selection among high duneveld, low duneveld and riverbed and pans was more evenly distributed (all pairwise contrasts: $P > 0.80$), suggesting reduced habitat discrimination while foraging. Consequently, the probability of using high duneveld and low duneveld for foraging was considerably higher than for burrow placement (Table 1).

Local-scale Habitat Selection during Foraging

At the local scale, foraging habitat selection broadly mirrored the landscape-scale results (Supplementary Fig. S3, Table S6). The step selection analysis of group movement paths indicated that low shrubland was consistently avoided in both seasons. In the dry season, selection for riverbed and pans was also lower than high duneveld (contrast ± SE = −0.16 ± 0.07, $z = 2.40$, $P = 0.077$) and low duneveld (contrast ± SE = −0.17 ± 0.05, $z = 3.53$, $P = 0.002$). In the wet season, selection for high duneveld declined so that low duneveld, and riverbed and pans were more selected; however, only model contrasts with low shrubland were significant (riverbed and pans versus low shrubland: 0.12 ± 0.02, $z = 4.88$, $P < 0.001$; low duneveld versus low shrubland: 0.15 ± 0.04, $z = 3.94$, $P < 0.001$). The analysis also found substantial variation between groups in their foraging habitat selection (Supplementary Fig. S3b).

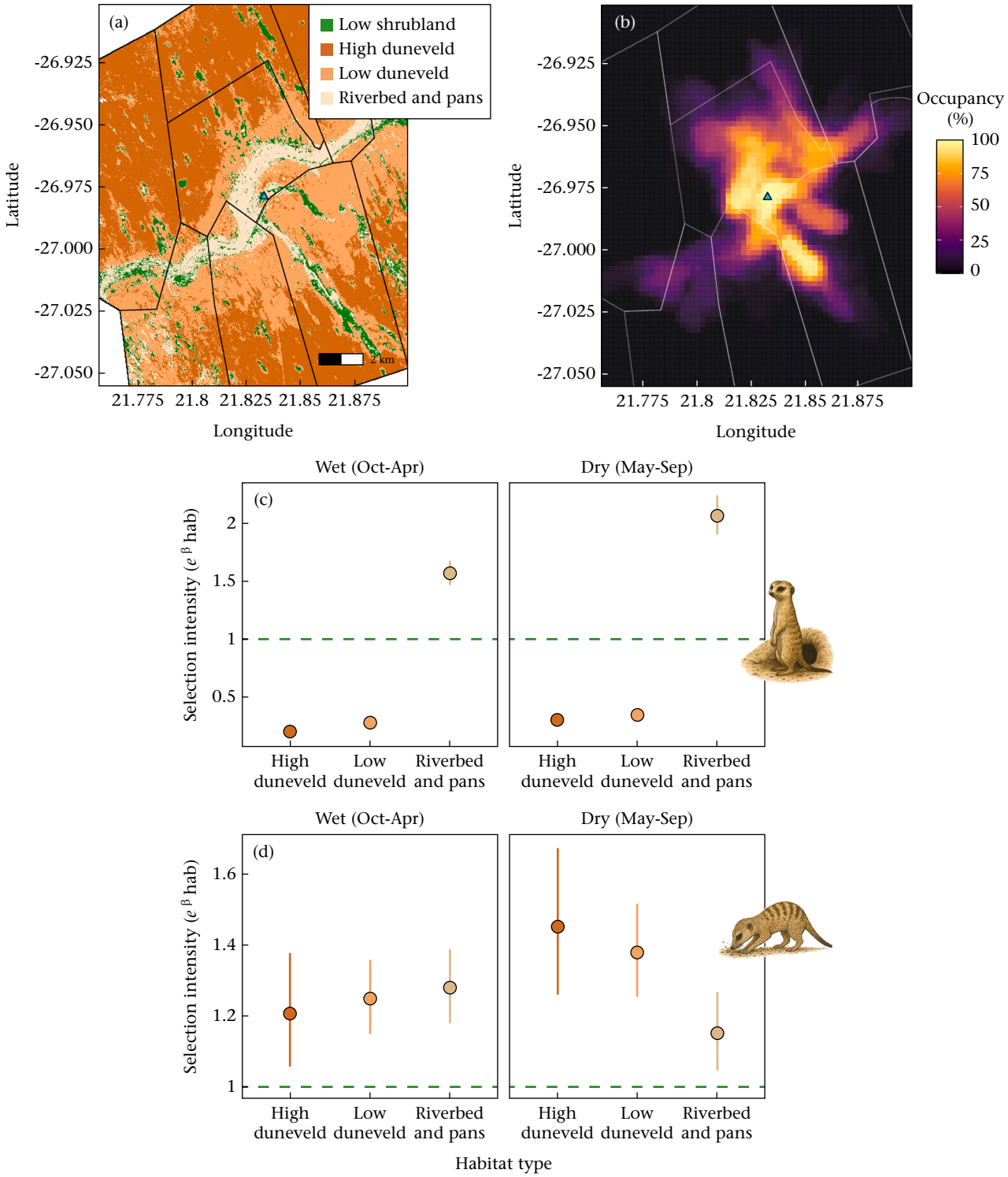

Figure 2. Habitat selection by meerkat groups at the Kuruman River Reserve (2002–2023). (a) The four main habitat types in and around the reserve, with the central farmhouse noted by the blue triangle. (b) The percentage use of space by established meerkat groups. Here the % occupancy refers to the percentage of periods for which each pixel overlapped the home range (95% autocorrelated kernel density estimate) of at least one meerkat group. Periods were treated as rolling 3-month windows ($N = 260$ periods, $N = 1062$ group home ranges). Habitat selection at the landscape scale, estimated through resource selection functions for (c) burrows and (d) foraging areas. The selection intensities of the different habitat classes in wet and dry seasons are presented relative to the reference category of low shrubland (dashed green line). Values above the line indicate selection, whereas values below indicate avoidance. Points represent the model-predicted means ± 95% confidence intervals.

Habitat Effects on Burrow Switching

The probability of meerkat groups switching burrows from one night to the next varied with both habitat type and season (Fig. 4a, Supplementary Tables S7–S8). Across both seasons, groups were consistently more likely to switch burrows in low duneveld. In the dry season, the probability of burrow switching was significantly higher in low duneveld than in riverbed and pans (contrast ±

Table 1
Estimated probability of use (POU) and availability of the different habitats for sleeping burrows and areas of foraging in different periods of the year

Season	Habitat class	Sleeping burrow habitat POU	Foraging habitat POU	Habitat availability
Dry season	Low shrubland	0.132	0.085	0.110
	High duneveld	0.045	0.138	0.123
	Low duneveld	0.218	0.558	0.523
	Riverbed and pans	0.605	0.218	0.244
Wet Season	Low shrubland	0.166	0.090	0.110
	High duneveld	0.037	0.120	0.121
	Low duneveld	0.221	0.535	0.525
	Riverbed and pans	0.576	0.255	0.244

Probability of use was estimated by multiplying selection intensities from resource selection functions by the relative availability of each habitat type. Relative availability was defined as the proportion of habitat types within the available points generated for the resource selection functions (within each group's home range plus a small buffer). The wet season spans October–April and the dry season May–September. Cases where totals do not equal 1 are due to rounding to three significant figures.

SE = 0.19 ± 0.07, $z = 2.61$, $P = 0.045$). This pattern was more pronounced in the wet season, when switching in low duneveld was significantly higher than switching in riverbed and pans (contrast ± SE = 0.24 ± 0.07, $z = 3.65$, $P < 0.001$) and low shrubland (contrast = 0.26 ± 0.08, $z = 3.18$, $P = 0.008$). In contrast, the probability of burrow switching in high duneveld did not differ significantly from other habitats in either season, with wider confidence intervals likely reflecting the smaller sample of burrows in high duneveld.

Burrow-switching probability was also strongly associated with babysitting. Groups were significantly less likely to switch burrows when pups were being babysat (~10%) compared to when pups were foraging with the group or absent (~40%; Supplementary Table S7, Fig. S4b). In all cases, burrow switching was more frequent during the wet season, even though babysitting occurred more often then (34% of observations) than in the dry season (20%).

Habitat Effects on Foraging Success

The rate of morning weight gain varied with habitat and season, with groups generally gaining weight faster when the dominant portion of their morning was spent in high duneveld and low duneveld rather than in low shrubland, or in riverbed and pans (Fig. 4b, Supplementary Tables S9–S10). These differences were present in both seasons, although the magnitude and the significance of the contrasts varied. In the dry season, weight gain was higher in high duneveld compared to all other habitats (all contrasts $P \leq 0.044$; Supplementary Table S10), and in low duneveld versus riverbed and pan habitat (contrast ± SE = 0.35 ± 0.08 g/h, $t = 4.36$, $P < 0.001$). In the wet season, low duneveld and high duneveld again supported higher weight gain rates, with significant contrasts between high duneveld and both low shrubland (contrast ± SE = 0.40 ± 0.13 g/h, $t = 3.15$, $P = 0.009$) and riverbed and pans (contrast ± SE = 0.72 ± 0.08 g/h, $t = 9.47$, $P < 0.001$) and between high duneveld and both low shrubland (contrast ± SE = 0.55 ± 0.19 g/h, $t = 2.84$, $P = 0.023$) and riverbed and pans (contrast ± SE = 0.86 ± 0.17 g/h, $t = 5.20$, $P < 0.001$).

The rate of morning weight gain also varied with individual- and group-level factors (Supplementary Fig. S5, Table S9). Females gained weight faster than males (estimate ± SE = 0.57 ± 0.07 g/h, $t = 8.07$, $P < 0.001$), and weight gain followed a nonlinear age pattern, increasing with age before declining in older individuals (linear estimate ± SE = 0.48 ± 0.05 g/h, $t = 10.12$, $P < 0.001$; quadratic estimate ± SE = −0.15 ± 0.02 g/h, $t = -8.38$, $P < 0.001$). Individuals also gained more weight when pups were being babysat (all contrasts: $P < 0.001$), while group size had little effect (linear estimate ± SE = 0.08 ± 0.05 g/h, $t = 1.65$, $P = 0.098$; quadratic estimate ± SE = −0.00 ± 0.03 g/h, $t = 1.65$, $P = 0.66$).

Habitat Effects on Speed of Group Movements and Morning Track Lengths

Across both seasons, groups moved fastest through the white sand habitats (Fig. 4c, Supplementary Tables S11–S12). These differences were most pronounced during the dry season, when groups moved between 29.8 and 34.7 m/h faster in riverbed and pans and in low shrubland compared to low duneveld or high duneveld, corresponding to a 14.1–16.8% increase in speed ($P < 0.001$ in all contrasts). In the wet season, when movement speeds were generally higher, the contrasts between the habitats were smaller but still significant. Groups moved significantly faster shortly after leaving the burrow in the morning (linear estimate ± SE = −35.16 ± 0.56, $t = 62.47$, $P < 0.001$; quadratic estimate ± SE = 9.04 ± 0.54, $t = 16.58$, $P < 0.001$), when dependent pups were being babysat (pairwise contrasts: $P < 0.001$; Supplementary Table S11), and in larger groups (linear estimate ± SE = 16.85 ± 1.27, $t = 13.30$, $P < 0.001$; quadratic estimate ± SE = −3.65 ± 0.61, $t = 5.98$, $P < 0.001$; Supplementary Fig. S6).

Meerkat groups also covered longer distances over the course of the morning when emerging from sleeping burrows in riverbed and pans or in low shrubland habitat, although effect sizes were sometimes small and not always statistically significant (Fig. 4d, Supplementary Tables S13–S14). This pattern was strongest in the wet season, when track lengths from low shrubland burrows were longer than those from low duneveld (contrast ± SE = 43.3 ± 9.2 m, $t = 4.70$, $P < 0.001$), high duneveld (contrast ± SE = 44.1 ± 16.8 m, $t = 2.62$, $P = 0.044$) and from riverbed and pans (contrast ± SE = 22.6 ± 7.9 m, $t = 2.87$, $P = 0.021$), while those from riverbed and pans burrows also exceeded those from low duneveld burrows (contrast = 20.7 ± 7.7 m, $t = 2.70$, $P = 0.035$).

A similar, but less marked, pattern occurred in the dry season, with groups emerging from low duneveld burrows covering shorter distances than those from low shrubland (contrast ± SE = −35.9 ± 11.1 m, $t = 3.22$, $P = 0.007$) or riverbed and pans (contrast ± SE = −26.9 ± 8.7 m, $t = 3.10$, $P = 0.010$). Track lengths were positively associated with group size (linear estimate ± SE = 48.4 ± 3.7, $t = 13.00$, $P < 0.001$; quadratic estimate ± SE = −10.8 ± 1.8, $t = 5.99$, $P < 0.001$; Supplementary Table S13, Fig. S7a) and were reduced when dependent pups were present, and especially when pups were foraging with the group (pairwise contrasts: $P < 0.001$; Supplementary Table S13, Fig. S7b). Morning tracks were longer during the wet season, in line with the higher movement speeds at this time.

DISCUSSION

Our study shows that meerkat space use in the Kalahari is shaped more strongly by the distribution of suitable burrow

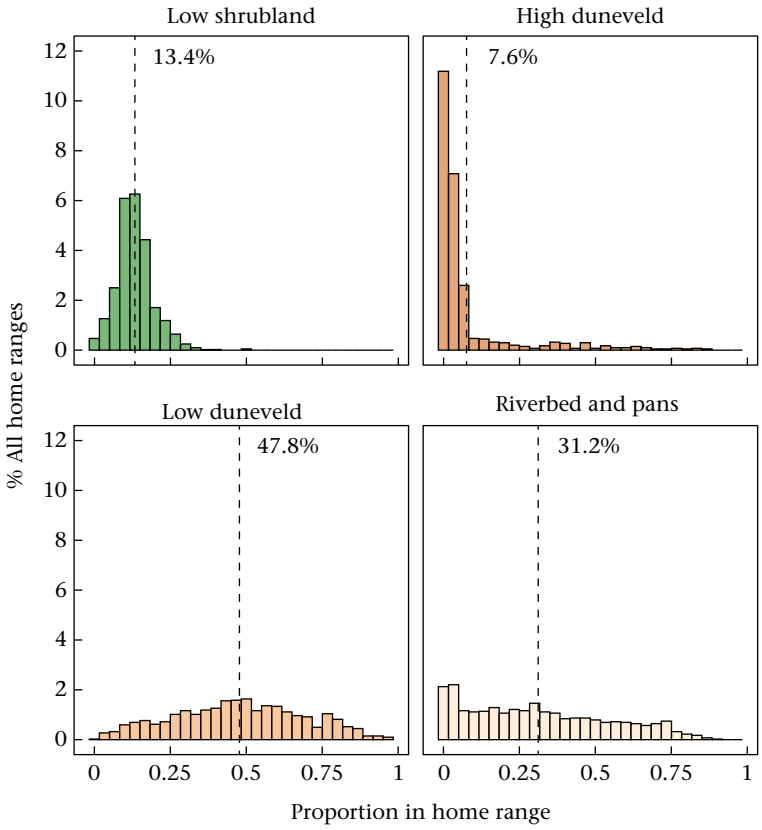

Figure 3. The percentage of each home range in the different habitat types. The histograms display the overall percentage of all home ranges, with the mean percentage in each case noted by the vertical line and the text. Home ranges were estimated as the 95% autocorrelated kernel density estimate (AKDE) of morning movement tracks in discrete 3-month windows.

habitat than by foraging opportunities. Using two decades of fine-scale tracking and life-history data, we found that groups consistently anchored their ranges to calcareous white sand habitats, which provided the preferred locations for sleeping burrows, despite these areas offering lower foraging returns than alternative habitats. Foraging habitat selection was more flexible and responsive to seasonal conditions but remained secondary to the spatial constraints imposed by burrows. This trade-off was evident in faster and longer tracks in riverbed and pan habitat, and in low shrubland habitat, suggesting their lower foraging value. Our results indicate that decisions about where to sleep and rear offspring play a primary, if not the main, role in shaping the movement and spatial behaviour of this arid-adapted carnivore. Given that many other species also rely on refuges that they do not construct themselves, including cavity-nesting birds and other secondary users of spatially limited shelters, such trade-offs may be more widespread than currently recognized.

Sleeping Burrow Habitat Dominates Space Use

Previous work on our population has described aspects of burrow dynamics (Dyble et al., 2019; Strandburg-Peshkin et al., 2020) and foraging habitat selection (Bateman et al., 2015; Turbé, 2006), but ours is the first study to integrate these dimensions to examine their joint influence on space use. Across seasons and years, meerkats consistently preferred burrows in white sand areas, showed lower switching probabilities there and maintained long-term associations with these patches. The reasons for higher burrow fidelity in white sand areas (including calcareous pans, flats and the dry riverbed) remain uncertain. One possibility is that soil properties in these areas allow primary excavators to construct deeper, more stable burrows with multiple entrances and larger chamber systems, providing secondary users like meerkats improved thermal buffering and greater space; the latter may be particularly important given that the average meerkat group numbers around 14 individuals (Thorley, Duncan, Manser, & Clutton-Brock, 2025). Whatever the cause, the strong association of meerkats with white sand habitats underscores the disproportionate importance of sleeping burrows in structuring their space use.

A strong reliance on refuges is common to many animals in arid environments, where alternative shelters are scarce and extreme temperatures promote belowground activity across numerous taxa (Kinlaw, 1999; Oliveira et al., 2024; Pinkert et al., 2025). Supporting this view, refuge availability strongly dictates movement in other arid-adapted species: the Australian plains mouse, *Pseudomys australis*, confines its dry season home range to cracks within specific clay habitats (Young et al., 2017); degus, *Octodon degus*, in central Chile exhibit more bursty locomotion in open areas (Vásquez et al., 2002); and desert-living baboons (*Papio ursinus*) in Namibia prioritize low-risk food patches near cliffs and trees, even when these offer poorer foraging returns (Cowlishaw, 1997). These studies underscore how refuge placement governs daily movement flexibility and home range structure.

In our own study, we incorporated behavioural, physiological and spatial data to provide a mechanistic understanding of the importance of refuges in shaping meerkat space use. While such comprehensive data sets are uncommon, requiring habituated animals and substantial human effort, the growing use of multi-sensor biologgers is enabling more integrated analyses that link

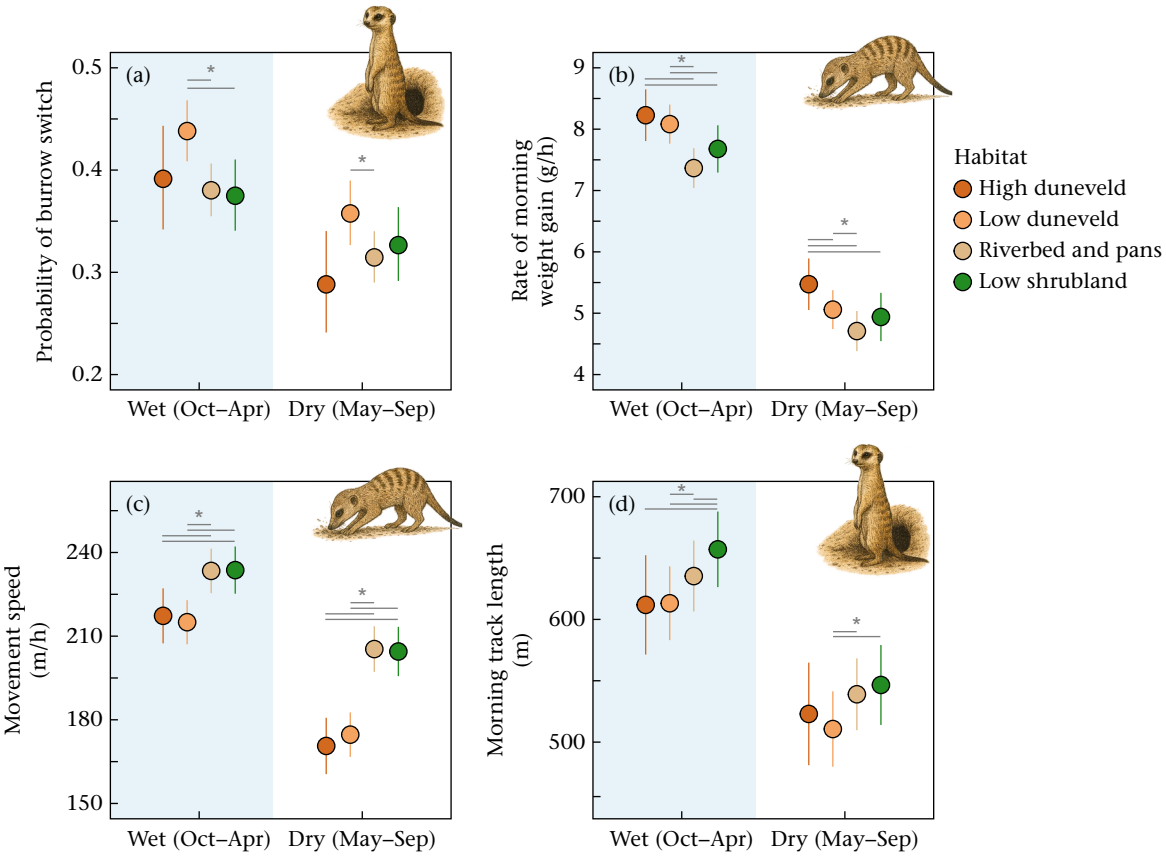

Figure 4. Effects of habitat type on burrow- and foraging-associated metrics throughout the year: (a) burrow-switching rate; (b) morning weight gain; (c) group movement speed; (d) total morning track length (travel distance). Each panel displays the model-predicted means ± 95% confidence intervals for the interaction between habitat and the season of the year. Significant within-season contrasts (*$P < 0.05$) among the habitat types are shown by the horizontal segments. The inset meerkat images indicate whether the habitat effect refers to the habitat of the previous night's sleeping burrow or the habitat while foraging. Track length is estimated for the mean track duration of 152 min.

physiology to movement behaviour (Curtin et al., 2018; Hetem et al., 2025). The application of these approaches will be especially valuable for understanding habitat selection in arid systems as warming climates intensify refuge-related constraints.

Foraging Space Use Is More Flexible and Secondary

Multiple lines of evidence indicate that foraging habitat selection was weaker and more seasonally dependent than burrow site selection. Groups preferentially foraged in the red-sand habitats of low duneveld and high duneveld during the dry season, a preference that diminished in the wet season when all habitat types offered higher foraging returns. The duneveld habitats were also associated with reduced group movement speeds and higher morning body weight gains, suggesting greater prey availability or accessibility. Yet, despite these energetic advantages, groups rarely used burrows in the most productive foraging habitats and instead often travelled from preferred refuges to reach them.

While food availability likely contributes to the habitat-specific foraging decisions of meerkats, vegetation structure, predation risk and abiotic factors may also play important roles. The white sand areas at our field site are extremely open, especially in the dry season (Supplementary Fig. S1), which may increase exposure to aerial or terrestrial predators and render them less attractive foraging spots. Indeed, like many small mammals, meerkats prefer to remain close to vegetative cover while foraging (Le Roux et al., 2009). The dry riverbed also hosts most of the tall trees in the area, which provide potential perching sites for the Kalahari's many raptors, and possibly increasing vigilance demands. Conversely, the avoidance of low shrubland habitats may reflect the low permeability of areas that are densely covered by this shrub. Other landscape features, such as bolt hole density, may further influence foraging decisions, and the presence of neighbouring groups likely plays an additional role (Bateman et al., 2015; Kranstauber et al., 2020). Vegetation structure will also affect the amount of shade available, thereby influencing the local thermal conditions experienced during foraging. For example, recent work on white-browed sparrow weavers, *Plocepasser mahali*, in the Kalahari Desert demonstrates that birds in shadier home ranges can forage more efficiently at high ambient air temperatures (Whyte et al., 2026). Separating the relative contributions of food distribution, landscape permeability, predation risk and thermoregulatory constraints could be an important avenue for future research.

Energetic Trade-offs and Life-history Consequences

Our results support the idea that trade-offs between refuges and food acquisition can be pronounced in obligate secondary burrow users, which cannot relocate or modify refuges to align with food availability. Accordingly, groups with burrows in riverbed and pans or in low shrubland habitats travelled further during morning foraging bouts, and those that spent most of their time foraging in these habitats showed lower weight gains. Such reductions in daily weight gain are expected to cascade into effects on reproductive success and survival (Thorley, Duncan, Manser, &

Clutton-Brock, 2025), although the relatively small scale of white sand patches seems to allow most established groups to balance these needs effectively most of the time.

Although not explicitly tested here, we expect that the foraging–shelter trade-off becomes more difficult to manage during pup rearing, when fidelity to sleeping burrows peaks due to their role as denning sites. Groups then effectively become central-place foragers, with reduced flexibility to adjust their ranging in response to changing foraging conditions. Our long-term data further suggest that the trade-off may be intensifying, as morning foraging returns have declined over the past two decades (Supplementary Fig. S5d), mirroring concurrent declines in adult body mass (Thorley, Duncan, Gaynor, et al., 2025). Together, these patterns highlight the growing influence of climate warming and more frequent droughts on foraging success, trends that if they continue, will amplify the constraint imposed by the spatial separation of refuges and foraging habitats.

Broader Spatial and Ecological Implications

The spatial dynamics we uncovered are likely to scale beyond group ranges to also impact the connectivity of meerkat populations across the wider landscape. Much of the species' distribution lies within the arid savannah biome of the Kalahari, where duneveld predominates. In contrast, the white sand pans and dry riverbeds that provide their favoured burrow habitat occupy a much smaller fraction of the landscape (Thomas & Shaw, 1991). It is therefore unsurprising on reflection that the two major ecological studies of meerkats have been situated on the dry riverbeds of the Nossob River in the Kgalagadi Transfrontier Park (Clutton-Brock et al., 1999; Doolan & MacDonald, 1996, 1997) and the Kuruman River, sites which provide abundant sleeping burrow habitat. Although speculative, our results suggest that large portions of the Kalahari may present suboptimal habitat for meerkats, with the patchy distribution of sleeping burrow habitat constraining dispersal opportunities and potentially limiting gene flow. Population genetic studies could test this idea.

Beyond the Kalahari, meerkats also occur throughout the Nama-Karoo biome of South Africa. Whether the meerkat populations living in these areas experience similar trade-offs between burrow availability and foraging opportunities remains unknown, as even basic ecological descriptions are lacking. Comparisons across populations, including those in truly arid regions such as the Namib Desert, would clarify how landscape structure, sleeping burrow habitat and foraging preferences determine space use across the species' range.

Finally, our study highlights that shifts in the abundance or distribution of primary burrowers could disproportionately affect secondary burrow users, reinforcing the role of primary excavators as keystone species. While existing burrows may persist for some time, they are not permanent, and changes in their availability may cascade through ecosystems, much as changes in the abundance of woodpeckers in forest ecosystems can limit the numbers of secondary cavity-nesting species (Trzcinski et al., 2021). In the Kalahari, the reliance of many species on burrows is particularly concerning given recent evidence that climate change is already impacting the region's most well-known ecosystem engineer, the aardvark (Rey et al., 2017).

Conclusion

In summary, our study demonstrates that in a desert-adapted, secondary burrow-using carnivore, the spatial distribution of refuges outweighs that of foraging opportunities in shaping space use, movement and energetic outcomes. Burrows anchor home ranges and impose trade-offs that highlight the role of nonforaging habitat features in driving animal behaviour. Our findings underscore the need for habitat selection frameworks that explicitly integrate multiple resource types and consider the constraints they impose on behavioural flexibility. As environmental change reshapes the distribution of both refuges and foraging resources, understanding how species navigate these trade-offs will be essential for predicting their persistence and distribution in arid ecosystems.

Author Contributions

Jack Thorley: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Chris Duncan:** Writing – review & editing, Methodology, Investigation, Formal analysis, Conceptualization. **Annika Herdtle:** Writing – review & editing, Investigation, Formal analysis. **Marta Manser:** Writing – review & editing, Investigation, Funding acquisition, Data curation. **Dominic Cram:** Writing – review & editing, Investigation, Conceptualization. **Tim Clutton-Brock:** Writing – review & editing, Investigation, Funding acquisition, Data curation, Conceptualization.

Data Availability

Data and reproducible R code are available on GitHub (https://github.com/JThor1990/Meerkat-habitat-selection).

Declaration of Interest

The authors declare no conflicts of interest.

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Supplementary Material

Supplementary material associated with this article is available at https://doi.org/10.1016/j.anbehav.2026.123696.

The Supplementary Material has not been checked or copy-edited and the content, formatting and file functionality are the sole responsibility of the author(s).

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