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2   Burrow usage patterns and decision-making in meerkat groups
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24   **Short title:**
25   Burrow decisions in meerkats
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Data Accessibility Statement
Analyses reported in this article can be reproduced using the data and code provided as Supplementary Material to this article.

Burrow usage patterns and decision-making in meerkat groups

TITLE

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ABSTRACT

Choosing suitable sleeping sites is a common challenge faced by animals across a range of taxa, with important implications for the space usage patterns of individuals, groups, and ultimately populations. A range of factors may affect these decisions, including access to resources nearby, shelter from the elements, safety from predators, territorial defense, and protection of offspring. We investigated the factors driving patterns of sleeping site use in wild Kalahari meerkats (*Suricata suricatta*), a cooperatively breeding, territorial mongoose species that forages on scattered resources and makes use of multiple sleeping sites (burrows). We found that meerkat groups used some burrows much more often than others. In particular, large burrows near the center of the territory were used more often than small and peripheral burrows, and groups even more biased toward central burrows when rearing pups. Meerkats also used their sleeping burrows in a non-random order. When they changed sleeping burrows, they moved disproportionately to nearby burrows but did not always select the closest burrow. Burrow decisions also reflected responses to short-term conditions: rates of switching burrows increased after encounters with predators and when resources were depleted, while group splits were associated with a reduced probability of switching. The group's dominant female appeared to have disproportionate influence over burrow decisions, as groups were more likely to switch burrows when her foraging success was low. Our results link behavioral and movement

ecology to show that a multitude of environmental and social factors shape daily group

decisions of where to spend the night.

INTRODUCTION

Choices about when and where to move are among the most important decisions animals

make (Nathan et al. 2008), affecting their safety from predators (Fortin et al. 2005; Basille

et al. 2015), access to resources (Cowlishaw 1997; Polansky et al. 2013), energy

expenditure (Wall et al. 2006) and social interactions (Croft et al. 2008). Studying how

animals make movement decisions can give insights into their habitat and social

preferences (Fortin et al. 2005; Nathan et al. 2008; Strandburg-Peshkin et al. 2017),

cognitive capacities (Noser and Byrne 2007; Janmaat et al. 2014; Polansky et al. 2015), and

how they manage tradeoffs associated with different options (Cowlishaw 1997). One type

of decision faced almost universally across animal taxa is the choice of where to rest

(Christian et al. 1984; Reichard 1998; Day and Elwood 1999). Many species spend a large

proportion of their lives at sleeping sites, and in some cases also rear their young there,

suggesting that these choices can have important implications for survival and

reproduction. As a consequence, animals are expected to be selective in the sleeping

locations they choose, and potentially to use them in a strategic order (e.g. alternating

among sleep sites to avoid detection by predators). Previous work suggests that a variety of

factors can drive sleeping site selection including predation avoidance (Hamilton 1982; Di

Bitetti et al. 2000), availability or depletion of resources nearby (Janmaat et al. 2014),

maintenance of social cohesion and bonds (Chapman 1989), thermoregulation (Smith et al.

2007), and avoidance of parasites (Hausfater and Meade 1982; Butler and Roper 1996;

Roper et al. 2002). Moreover, the distribution of adequate sleeping sites across a landscape

can play an important role in constraining daily ranging patterns and even social structure

(Hamilton 1982; Boinski et al. 2000). Studying how animals select sleep sites thus provides

a link between movement and behavioral ecology, and can serve as a window into both the proximate drivers of behavior and the mechanisms that shape population-level distribution patterns.

Here we explore the question of what drives group decisions regarding sleeping site usage in meerkats (*Suricata suricatta*), a cooperatively breeding mongoose species. Meerkats live in stable groups of 2 – 50 individuals (Doolan and MacDonald 1997; Clutton-Brock and Manser 2016), which remain cohesive throughout the day and range within fiercely defended territories of approximately 2 – 5 km² (Manser and Bell 2004; Kranstauber et al. 2019), foraging on distributed prey items buried in the sand (Doolan and Macdonald 1996). Groups spend the night in burrows, underground structures typically consisting of multiple entrances linked by tunnels, that can persist over many years (Manser and Bell 2004). Burrows are an important resource for meerkats, providing shelter from the elements and protection from predators (Manser and Bell 2004). Additionally, meerkats rear their young at burrows, with pups only emerging from underground 3-4 weeks after birth (Doolan and MacDonald 1997; Clutton-Brock and Manser 2016). When they do not have burrow-dependent pups, meerkat groups use a number of burrows distributed throughout their territory (Manser and Bell 2004), returning to the same burrows at varying intervals. This raises questions as to what drives burrow usage patterns, and how groups arrive at the decision of which burrow to use on any given night.

To investigate the drivers of burrow usage decisions in meerkats, we analyzed 20 years of data on the burrow usage of a population of wild meerkats in the Kalahari Desert, South

Africa. We first characterized the overall usage rate of different burrows by each group during each year to determine whether and how meerkats are selective in the burrows they use. We then tested whether the physical structure, surrounding habitat, and position of burrows influenced the rate at which they were used, and examined transitions between burrows to determine whether meerkats use them in a random order or not. We next examined how breeding affects burrow usage decisions by comparing burrows used when rearing pups to those used outside of breeding periods. Finally, we assessed the support for different short-term drivers of burrow decisions, including predation, resource depletion, and inter-group conflict.

METHODS

Study site and data collection

Behavioral observations of meerkat groups

We used data from a long-term study of meerkats located at the Kuruman River Reserve in the Northern Cape of South Africa. All meerkats within the study population were fitted with transponders, dye-marked for individual recognition in the field, and habituated to human observation from within < 1 m (Jordan et al. 2007). Regular data collection at the study consisted of following meerkat groups on foot for 3 hours in the morning, starting when they emerged from their sleeping burrow, as well as for 1.5 – 2 hours in the evening, until they reached their sleeping burrow, with data collected ad libitum on their demographics, life history, social behavior, and anti-predator behavior (further descriptions given below). Meerkats were also weighed up to three times daily by enticing

them onto a portable scale using water or a small piece of hardboiled egg. Weights were taken once in the morning prior to foraging, once in the middle of the day, and once in the evening before meerkats went below ground in their sleeping burrows. Sleeping burrows were recorded both in the morning when the meerkats emerged, and in the evening when they went below ground. Each burrow was assigned a unique identifier, and its position (latitude/longitude) recorded. Details of data collection on life history, behavior, and weights can be found elsewhere (Clutton-Brock et al. 1999; Clutton-Brock et al. 2006; Clutton-Brock et al. 2008). All research activities were approved by the University of Pretoria Ethics Committee.

Burrow properties

To complement the data from the long-term study, we also characterized the physical properties and habitat surroundings of burrows used by meerkats at the same study site. Data on burrow properties were collected between 10 June 2019 and 20 August 2019. We measured 207 of the 210 burrows that had been used in the past year (8 June 2018 - 7 June 2019) on at least two occasions by any of the eleven meerkat groups under study at the field site during that period.

A typical sleeping burrow is a network of contiguous holes connected by underground tunnels (see Figure S1 for example photos). Because it was not possible to measure the internal structure of a burrow without specialized imaging equipment, we focused on properties observable from above ground. These included its length, width, and number of holes (entrances). Holes were considered part of a burrow if they extended below ground

farther than an observer could see, and if they were less than 5 m away from the nearest other hole (similar to the "chain rule" used to delineate social groups in other studies (Whitehead 2008)). The length of the burrow was defined as the distance between the two most separated holes, and the width was defined as the largest distance perpendicular to the long axis defined by these two most separated holes. All distances were measured using a DME 300XL Laser Rangefinder. The number of holes was counted exactly if less than 30 and estimated to the nearest 5 if greater than 30. Because length, width, and number of holes were found to be highly correlated (Figure S2), we chose to use length as a proxy for overall burrow size in subsequent analysis. To incorporate information on burrow shape and density of holes, we computed the aspect ratio (width divided by length, giving an indication of how circular vs. oblong a burrow is) as well as an estimated hole density (number of holes divided by the estimated burrow area assuming a roughly elliptical shape, i.e. π x length x width).

In addition to the dimensions of the burrow itself, we classified the surrounding habitat of each burrow into one of six categories (flats, pans, dunes, riverbed, river banks, and shrub land) and visually categorized the density of vegetation covering the burrow based on an ordinal scale (from 0 = none to 7 = high). In measuring vegetation levels, we focused only on shrubs and did not include grasses, which are highly seasonal. We also measured the distance of the burrow from the center of the group's range, with the center defined as the mean position (easting and northing) across all burrows used during that year.

Data processing

We combined data on burrow usage with demographic data, meerkat weights and ad libitum behavioral data collected during the same period to analyze burrow usage patterns and the relative importance of different factors in driving burrow decisions. All analyses except those involving measurements of burrow properties (see above) incorporate data collected over the period 18 June 1996 – 9 December 2017.

Burrow usage over time: We compiled a dataset of burrows used on each date by each group from long-term observational data. We combined data from four sources: observations of burrows used by each group in the morning (source 1) and evening (source 2), as well as observations of the times meerkats emerged from the burrow (source 3) and when they returned (source 4), where in the last two sources burrow identity was also logged by observers in a separate data table. Agreement among these 4 sources was relatively high (85% – 97%, depending on which pair of the 4 sources are compared), and discrepancies could either be driven by meerkat groups changing burrows after observers left or by observer errors in recording the burrow identity. When sources disagreed, we selected either the burrow recorded in the majority of sources or (if there was a tie), we prioritized morning observations over evening observations, and observations from the table of burrow times over observations of only the burrow identity. Using these rules, we produced a single dataset giving the burrow selected by each observed group, each evening.

Demographic data: Demographic data from the same data collection period was used to assess the demographic factors that may play a role in meerkat groups' burrow choices.

These factors included the *presence of burrow-dependent pups* (present or absent), the *pregnancy status of the dominant female* (pregnant or non-pregnant), and the *pregnancy status of subordinate females* (at least one pregnant or none pregnant). A group was considered to have burrow-dependent pups in the period between the birth of a litter and when the last litter member was observed to begin foraging with the group. In the case of pups that were lost before emerging from the burrow for the first time, or died after emergence, these events were either observed or their dates estimated by observers in the field based on the last time pups were seen or when the group left a birth burrow. In these cases, the group was considered not to have burrow-dependent pups after the date of death of the last litter member.

Foraging success: Meerkat fractional weight gain or loss was used as a proxy for foraging success on a given day. We assessed an individual's fractional weight gain on a given day by subtracting its morning weight from its evening weight, then normalizing the difference by dividing by the morning weight. (Note that using absolute weight gain gave no qualitative differences to the results.) To test whether the decision to switch burrows is driven by the foraging success of dominant individuals or by the foraging success of all group members, we considered the possible effects of *weight gain of dominant female*, *weight gain of dominant male,* and *median weight gain of subordinates*.

Behavioral data: Because events on the day of burrow selection may affect subsequent burrow choice decisions, we also incorporated information from ad libitum behavioral observations on a given day into our analysis. For each day when behavioral observations

were made, we measured the *alarm rate* (number of predator alarms observed divided by observation time), as well as determining whether the group had a *group split* during the day (at least one split or no split), and whether the group had an *inter-group interaction* with another group, or not. Predator alarm events were identified and recorded at the group level when at least 50% of the group responded to a predator or perceived threat (responses to alarm calls range from briefly looking in the direction of the perceived threat to fleeing down a bolt hole). Group splits were defined as times when two or more subgroups of mixed sex were spatially separated by at least 100 m for at least 15 minutes. Inter-group interactions occurred when two or more groups of at least 3 individuals were in proximity and interacted with one another.

Analyses

How often are different burrows used?

To characterize the overall patterns of burrow usage by meerkat groups, we first assessed the number of burrows typically used by meerkat groups within a one-year period (thus covering all seasons). To account for differing numbers of observations, we plotted the number of unique burrows used by the group as a function of the number of observations, observing a flattening-out of this curve after approximately 150 observations. We therefore estimated the number of unique burrows typically used by computing the median, inter-quartile range, and 95% range of unique burrows used by groups only in years where more than 50% of observations were available (at least 183 days). This subsample represented 100 group-years of data distributed across 25 unique groups. To examine whether the number of unique burrows used varied seasonally, we performed a similar analysis in

which we computed the number of unique burrows used by a given group within each month as a function of the number of observations. To enable valid comparisons across months, we excluded months in which burrow-dependent pups were present with groups from the analysis.

To investigate whether meerkats were selective in their burrow use, preferring specific burrows over others, we examined the extent to which burrows were used equally or unequally often. We used Lorenz curves, a popular method for assessing inequality often used in economics (Lorenz 1905), to visualize the extent to which meerkats used burrows at unequal rates. For each group during each year, we first ranked the burrows from least to most used, then plotted the cumulative fraction of burrow usage vs. the fraction of burrows composing that usage. This procedure produces a diagonal line if all burrows are used equally, and as the inequality of usage increases, the curve departs more and more from the diagonal. We also computed the Gini coefficient (a measure of the level of inequality, ranging from 0 for equal distributions to 1 for highly unequal distributions) for each group during each year. As in the analysis above, only years for which at least half of all observations were available were used.

What physical, habitat, and spatial properties are associated with frequent burrow use?
To investigate what makes particular burrows attractive to meerkat groups and others not, we fit conditional logistic regression models relating the frequency of burrow usage to the properties of burrows and their surroundings, as well as their locations within the groups' home ranges. Conditional logistic regression models assume that an entity (here a meerkat

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group) chooses a single option (here the burrow used on a given night) out of a set of possible options (here the set of all burrows used by the group during that year). Each option is characterized by a set of features (e.g. burrow length, hole density, etc.), and coefficients are fit to predict the probability of a given option being chosen as a function of these features. The coefficients fitted for each feature are a measure of how much, and in what direction, that feature predicted the decision outcome (Thurfjell et al. 2014), thus giving information about what features of burrows meerkats "prefer". Here, we fitted separate models for each meerkat group using the *clogit* function in the R package *survival*, and used the following features as predictors: burrow length (a proxy for overall size), aspect ratio (a measurement of burrow shape), density of entrances (holes), habitat type, density of vegetation covering the burrow, and distance from the center of the range. Although data from the same group are not independent, we can draw inferences about the population-wide burrow preferences of meerkats by looking for consistent preferences across groups. We assessed whether meerkats showed consistent preference patterns by comparing the fitted coefficient values across groups for each feature. If meerkats showed consistent preferences in a certain direction, we would expect coefficient values to be either consistently above or consistently below 0 across groups. Because habitat type is a categorical variable, we used the fitted coefficients to generate a preference ranking for each group (from highest to lowest fitted coefficient). We then quantified the inconsistency of habitat preferences by counting up the number of inconsistent rankings of pairs of habitat types (e.g. dunes was ranked higher than flats in one group and lower in another) across all groups, and dividing by the total number of possible pairs. To assess whether rankings were more consistent than expected by chance, we compared these inconsistency

fraction values to a randomized null model in which the ranks for each habitat type were shuffled within each group.

Are meerkats more selective about burrow usage during periods when they have burrow-dependent pups?

To determine whether meerkats become more selective in their burrow usage when they rear pups, we compared the burrows selected during periods when burrow-dependent pups were present (*pup burrows*) to those selected when they were not (*non-pup burrows*). We first computed the usage rate of a given burrow by a group during a given year during times when no burrow-dependent pups were present. We then generated the distribution of these usage rates for pup burrows and non-pup burrows separately. If these histograms were to align, it would indicate that meerkats are equally selective of their burrows when they are rearing pups as compared to when they are not. In contrast, if the histogram for pup burrows were more weighted toward large values compared to the histogram for non-pup burrows, it would indicate that burrows that are generally more frequently used (as assessed during non-pup periods) are disproportionately chosen as pup burrows, suggesting increased selectivity. We also tested whether pup burrows were more centrally located within group ranges than non-pup burrows. To do so, we first computed the distance of each burrow from the range center (i.e. the mean position of all burrows used in the past year), then ranked and normalized these distances between 0 and 1 within each group to account for range size differences. Finally, we computed and visually compared the distribution of these normalized distances for pup-burrows vs. non-pup burrows.

Do meerkats use burrows in a random order?

In addition to making choices about which burrows to use, meerkat groups must also decide in what order to use them, raising questions as to what factors govern this order. To address this question, we started by investigating whether meerkat groups used burrows in a random order or whether their usage showed non-random patterns. To do so, we used a network-based approach that allowed us to test whether rates of transition between burrows used on consecutive nights differed from that expected based on a null model that preserved their overall usage rates. We first constructed a 'burrow transition network' (Figure 1) for each group during each year, with nodes representing burrows and edges representing transitions between them. Edge weights e_{ij} represent the number of times that meerkats spent a night in burrow i (the *source node*) followed by a consecutive night in burrow j (the *sink node*). Self-transitions were excluded in these computations in order to focus solely on transitions among burrows, and data from periods where pups were present at the burrow were also excluded.. Edge weights were then normalized by dividing each edge by its out-degree (i.e. the total number of transitions away from burrow i), such that each edge weight could be interpreted as the probability of moving to burrow j given that the group was at burrow i on the previous night.

Using this network, we determined whether certain transitions between pairs of burrows were over-represented and others under-represented, compared to a randomized null model in which the overall usage of each burrow in each group-year was preserved. To perform this comparison, we computed the variance of all edge weights in the burrow transition networks described above, and took the mean edge weight variance across all

group-years as a test statistic. We compared this value to the same test statistic computed for randomized null networks. Null networks were constructed by randomly selecting 1000 pairs of consecutive burrow observations and swapping the *sink nodes* between them (and ensuring that no self-connections were created in the process). This permutation results in the same total amount of usage for each burrow as both source and sink (i.e. preserves in-degree and out-degree), but randomizes the extent to which certain sources and sinks are associated with one another. If the variance of edge weights in the real data is higher than the variance of edge weights in the randomized null model, this indicates that the order of burrow usage is non-random.

To determine what might drive non-random patterns of usage, we next tested whether meerkats are more likely to transition to nearby burrows within their range compared to random burrows. To do so, we compared the distribution of distances between consecutively used burrows in the real data to the distribution of distances generated by the null model described above. We also investigated whether meerkats simply transition to the nearest burrow when they switch by computing the distribution of distances to the nearest other burrow used by the group during that year.

What factors affect group decisions to return to the same burrow or switch burrows?
In addition to being driven by the overall properties of sleep sites and their spatial distribution, decisions about where to spend the night may also reflect short-term behavioral responses to current environmental and social conditions. To determine which short-term factors play an important role in burrow decision-making, we used logistic

regression models to predict whether a meerkat group returned to the current burrow (1) or switched to a different burrow (0) on a given evening. For this analysis, we used only records for which burrow data was available on two consecutive nights. If consecutively occupied burrows were less than 30 m apart, this was also coded as a 'return'. This threshold was chosen to be consistent with the methods of the long-term study, where burrows within 30 m of one another are considered the same because they might be connected underground. To reduce noise in the estimation of overall burrow usage rates, we limited our analysis to years in which at least 90 observations of consecutive night pairs were available. Because the presence of pups dramatically increases the probability of return, we also excluded nights when burrow-dependent pups were present from this analysis. This resulted in 27,179 observations, representing 221 group-years from 35 unique groups.

Using multi-model inference, we assessed the relative importance and model averaged effect size and direction of different factors in predicting the outcome of these burrow decisions. Multi-model inference is an approach that allows one to draw inferences from a set of fitted models, rather than fitting only one model or searching for the "best" model (Grueber et al. 2011). Here, logistic regression models were fitted for each possible combination of predictors, and each predictor's *importance score* was derived based on a weighted measure of the AIC scores of models in which that predictor was present. Predictors that were more often present in models with low AIC scores (i.e. the models with greater empirical support) achieved higher importance scores. Ranking the predictors by importance score thus gives an aggregate indication of how important each factor was in

predicting the outcomes of group burrow decisions. We report these importance scores as well as the model averaged coefficients. Fixed effects used in the models are given in Table 1. Because the natural ranges of different variables differed, we standardized all non-categorical predictors by subtracting the mean and dividing by the standard deviation (z-score transformation). We included group-year (i.e. each combination of meerkat group and observation year) as a random effect to control for differences among groups in different years. Prior to performing fits, we assessed multi-collinearity across all continuous predictors (max value = 1.57), and found that it did not exceed the recommended maximum of 5 (Chatterjee and Hadi 2012). Models were fitted using the R packages *MuMIn* and *lme4*, with the *dredge* function used to fit all possible models and the *model.avg* and *importance* functions used to compute model averaged coefficients and importance scores respectively.

In an additional set of analyses, we computed the probability directly from the data that meerkat groups returned to the previous night's burrow, as a function of each of the above variables. This served as a complementary analysis to the model fitting approach described above, as these probability computations do not rely on any model assumptions (such as the specific functional form of the fitted model), but also do not allow incorporation of multiple factors simultaneously. In addition, we note that the complete set of predictors was only available for 20% of samples in our dataset (5443 observations). For example, because meerkat groups were not observed every day, in many instances predictors relying on observational data were not available. In the above multi-model inference analysis, we used only data for which all predictors were available to enable valid model comparisons.

However, because computing probabilities directly from empirical data does not rely on such model comparisons, we were able to take advantage of larger subsets of the available data when computing probabilities directly. Thus, this second set of analyses served both to confirm the results of the model fitting approaches above, and to enable probability estimates to be computed over the full set of available data for each predictor.

RESULTS

How often are different burrows used?

Meerkat groups (n=25) used a median number of 26 unique burrows each year (Inter-quartile range = 19-32, Range = 6 – 65, Figure S3a). The distribution of burrow usage was highly unequal, with only a small fraction of all burrows receiving the majority of usage (Figure 2). Quantifying the level of inequality using the Gini coefficient yielded a median value of 0.31 (Inter-quartile range = 0.24 – 0.38, Range = 0.07 – 0.54), which corresponds to the most frequently chosen 20% of burrows receiving about 75% of all usage. The number of unique burrows used was relatively consistent across different months of the year, however it was slightly reduced in winter as compared to summer months (Figure (Figure S3b-c).

What physical and habitat properties are associated with frequent burrow use?

Conditional logistic regression models revealed that meerkats preferentially used larger burrows and burrows closer to the center of their ranges (Figure 3). Across the eleven groups analyzed, distance from range center showed a consistent negative effect on the probability that a given burrow was selected, whereas burrow length showed a

consistently positive effect (with the exception of one group). In contrast, the fitted

coefficients for aspect ratio, density of entrances, and vegetation density did not show a

consistent direction across groups. Similarly, the fitted coefficients for habitat type did not

show a consistent ranking across groups (Figure S4). These results suggest that meerkats

did not show strong consistent preferences related to these factors.

Are meerkats more selective about burrow usage during periods when they have burrow-

dependent pups?

When rearing pups, meerkats disproportionately selected burrows that otherwise showed

high use (Figure 4a). These pup burrows were on average closer to the center of the

group's home range than non-pup burrows (Figure 4b). When burrow-dependent pups

were present, meerkats returned to the same burrow as they had used the previous night

93% of the time, as compared to 62% when pups were not present (Figure S5a). Moreover,

the probability of returning to the same burrow sharply decreased for pup ages of 20 – 40

days, coinciding with the time that pups typically begin foraging with the group (Figure

S5b).

Do meerkats use burrows in a random order?

Analysis of burrow transitions confirmed that meerkats did not use burrows in a random

order (permutation test, P < .01). Meerkats transitioned more often between burrows that

were close together (Figure 5): consecutively-used burrows were on average 512 m apart

(median = 512 m, IQR = [335 m, 766 m]), smaller than what would be expected based on

the null model of random usage within a year (median = 763 m, IQR = [457 m, 1185 m]).

However, meerkats also did not always move to the nearest burrow, as distances to the nearest burrow were much smaller than distances to the next burrow used (Figure 5).

What factors affect group decisions to return to the same burrow or switch burrows?
The overall usage rate of a burrow was the strongest predictor of whether meerkats returned to the same burrow on a given evening, in terms of both importance score and effect size (Table 1). The rate of predator alarms during foraging also appeared to play a role (Table 1), with meerkats being less likely to return to the same burrow when many alarms were given during that day (Figure 6a). Furthermore, meerkats were more likely to return to the same burrow on days when group splits occurred (Table 1; Figure 6b), and when the dominant female's weight gain was high (Table 1; Figure 6d-f). In contrast, the weight gain of the dominant male and the median weight gain of subordinate members of the group had low importance scores and effect sizes (Table 1; Figure 6d-f). The association of weight gain with burrow returns does not appear to be driven by pregnancy, as we found that this association was stronger when the dominant female was not pregnant (Figure 6e-f).

DISCUSSION

Meerkat groups showed clear preferences in the sleeping burrows they used. The majority of the time, they used a small proportion of all burrows, and in particular chose burrows in the center of their territory (Figure 2; Figure 3). Disproportionate use of central sleeping sites has also been found in other territorial species (Zhang 1995; Smith et al. 2007), however this pattern is not universal (Singhal et al. 2007). Choosing sleep sites located at

the center of a group's range might offer more flexibility to move in different directions, potentially providing benefits for both territory defense and resource acquisition. On the other hand, it has also been argued that peripheral sleep sites may offer early detection of territorial incursions and/or early access to the resources of neighboring groups (Day and Elwood 1999), thus the role of sleep site positioning in relation to territory and resource defense remains unclear. However, the notion that meerkats protect the center of their territory more than the boundaries is consistent with earlier findings that groups tend to locate their latrines in central areas (Jordan et al. 2007). Finally, an alternative explanation for the pattern of central burrow use that cannot be ruled out is that meerkats tend to center their ranges around particularly suitable burrows, or that their territory-restricted movement simply leads them to encounter central burrows more often.

The tendency to use central burrows became even more pronounced when rearing pups (Figure 4b). This preference could allow them the greatest flexibility in ranging for both resource acquisition and territory defense during times when the group is restricted to a single burrow for multiple weeks. Using central burrows could also minimize the potential for conflict with neighboring groups, which can sometimes lead to pup mortality. Regardless of the underlying factors driving burrow selection, the strong preference expressed towards specific, highly used burrows during pup rearing periods (Figure 4a) is consistent with preferences for specific nest and den-site features shown in other species (Theuerkauf et al. 2003; Cunningham et al. 2016), and suggests that the choice of burrows could be important to meerkat reproductive success.

Apart from preferring central burrows, meerkats also showed a clear and consistent bias toward using larger burrows more often than smaller burrows. Larger burrows could allow more pathways to escape in the event of a predator attack, and it is also possible that large size could correlate with other important and unmeasured structural properties of burrows underground, such as their depth and structural stability. In contrast to the clear preference regarding burrow size, meerkats did not show consistent preferences regarding burrow shape (aspect ratio), density of entrances, vegetation cover, or habitat type (Figure 3; Figure S4), suggesting that these factors may not strongly influence burrow decisions. However, this result must also be interpreted with caution because the lack of consistent preferences for these other factors does not necessarily mean that meerkats do not have preferences in these dimensions. Here we limited our analysis to comparing usage rates among burrows that were actually used by meerkat groups, thus we have not addressed what makes certain structures suitable for use as burrows in the first place. Studies across a range of species (Hamilton 1982; Christian et al. 1984; Chapman 1989; Reichard 1998; Day and Elwood 1999) have shown that animals tend to select for certain physical features when choosing sleep sites, and also that the surrounding habitat can play an important role. An earlier study of meerkat ranging patterns (Bateman et al. 2014) found evidence that they concentrated their space use along the edges of the river bed habitats, and a visual examination of the locations of burrows throughout the landscape (Figure 1) does suggest that burrows may be more heavily concentrated in these edge regions. However, future work linking habitat measurements, ranging patterns, burrow usage, and characterization of unused burrows is required to give a clearer picture of what features of

burrows make them suitable for use, and to disentangle the link between burrow distribution and group ranging patterns.

The use of many different burrows and the lack of a specific order are both consistent with predation and/or resource depletion being drivers of burrow usage decisions, as has been found for sleeping site decisions in other systems (Hamilton 1982; Zhang 1995; Di Bitetti et al. 2000). Over the long term, using multiple sleep sites in a non-predictable order could prevent predators from learning specific locations that animals typically occupy (Boinski et al. 2000). Moreover, the negative effect of alarm call rate on the probability of returning to the same burrow we found in meerkats (Figure 6a; Table 1) suggests that they can alter their exposure to short-term predation pressure changes by becoming more likely to switch sleep sites when perceived predation risk is high. Our results also support a role of resource depletion in driving burrow switches in the short-term, as groups became more likely to switch burrows when foraging success, as quantified via weight gain, was low, in particular the dominant female's foraging success (Figure 6d-f; Table 1). We were unable to address whether parasite avoidance may also drive burrow alternation (as been hypothesized in primates (Hausfater and Meade 1982)), due to lack of data on parasite load. However, meerkats could also potentially solve this issue by alternating the locations that they choose to occupy within a given burrow, which would be particularly effective in larger burrows.

Beyond the influences discussed above, sleep site selection could also be driven by social factors (Hamilton 1982; Chapman 1989). Here, we did not detect an effect of inter-group

encounters on the probability of switching burrows (Table 1; Figure 6c). This could indicate that inter-group encounters have only a transient effect on movement patterns, rather than extending to burrow decisions later in the day. However, a more thorough investigation of this issue, for example incorporating the locations and outcomes of inter-group encounters and the detailed trajectories of the two interacting groups, could shed more light on this issue. Although no clear effect of inter-group interactions on sleep site usage was found, our results do suggest that within-group coordination could play a role. The finding that groups were likely to return to the same burrow on days when the group split (Table 1; Figure 6b) suggests that burrows could play a role in aiding group coordination by serving as meet-up locations in cases where individuals become isolated from one another. The use of sleeping sites as a coordination mechanism has been suggested for other species (Chapman 1989), however as group splits are relatively rare in meerkats (occurring on only 2.8% of all days we analyzed), such coordination seems unlikely to be a major driver of burrow usage patterns in this system.

Although many of the drivers of movement are likely to be consistent across group members, individual differences in preferences can also create conflicts of interest within social groups (Conradt and Roper 2010). Earlier findings give differing perspectives on the level of decision-sharing within meerkat groups, suggesting that in this species movement decisions may range from shared to unshared depending on context (Gall et al. 2017). Theoretical models show that decisions about timing versus direction are fundamentally different due to the fact that intermediate outcomes are more likely to be viable in timing decisions than in spatial decisions, leading to differing predictions for the expected level of

decision-sharing in different scenarios (Conradt and Roper 2009; Conradt and Roper 2010). Our results suggest that the dominant female influenced the (spatial) decision of whether to return or switch burrows, with groups more likely to switch burrows when her foraging success was low (Figure 6d-f; Table 1). In contrast, an earlier study of the *timing* of burrow returns found that the decision of when to return to the burrow was better predicted by the mean weight gain of subordinates than by the weight gain of dominants (Gall et al. 2017). These findings raise the intriguing possibility that temporal and spatial decisions may be controlled by different mechanisms in this system. More generally, our results highlight that studying decision-making regarding sleep sites in social species can help reveal the processes underlying group decision-making, particularly when the costs and benefits of differ sleeping sites vary consistently across group members.

Taken together, our analysis of natural burrow usage patterns in meerkats suggests that a multitude of factors including predation, reproduction, resource depletion, and the need to coordinate, can all play a role in driving these daily decisions. However, manipulative experiments will be important to firmly establish causal relationships between these factors and burrow decisions. For example, dominant and subordinate foraging success could be manipulated via feeding, or perceived predation pressure could be increased via presentations of artificial predators. Such manipulations could also give insight into how different factors are weighed against one another in different contexts, while examining the fine-scale movements and behavior of all individuals within moving groups would help to tease apart the dynamics of how these decisions arise. Given the widespread importance of sleeping sites for many species, investigating how these decisions are made across different

contexts, populations, and species can allow us to uncover much about the behavioral and ecological determinants of individual and group decision-making. Moreover, revealing the factors governing sleep site decisions is often also crucial to understanding animal ranging and spatial distribution patterns. Studying patterns of sleep site selection thus affords a link between movement and behavioral ecology, and has the potential to shed much light on the lives of animals across multiple spatial and temporal scales.

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TABLES

Table 1. Predictors used in models of burrow choice, as well as fitted model coefficients and normalized importance scores. Rows are ranked by the predictor's importance score. Further information on model fits can be found in Table S1 and Figures S6-S7.

Feature	Type	Description	Model avg coefficient	Importance score
Burrow usage rate	Continuous	Percentage of time the previous night's burrow was used in the past year (a proxy for burrow quality)	0.514	0.186
Alarm rate	Continuous	Number of predator alarms divided by hours of observation time on that day	-0.092	0.181
Group split	Binary	Whether or not a group split was observed	0.429	0.162
DF weight gain	Continuous	Difference between evening and morning weight for the dominant female of a group	0.186	0.143
DF pregnancy status	Binary	Whether the dominant female of a group was pregnant	-0.053	0.101
Sub pregnancy status	Binary	Whether any of the subordinates in a group was pregnant	-0.014	0.062
DM weight gain	Continuous	Difference between evening and morning weight for the dominant male of a group	0.001	0.056
Sub weight gain	Continuous	Mean difference between evening and morning weight for the subordinates in a group	-0.003	0.056
Inter-group interaction (IGI)	Binary	Whether or not an inter-group interaction was observed on that day	0.003	0.052

FIGURES LEGENDS

Figure 1. Visualization of burrow usage across different groups (represented by different colors) in the year 2013. Points indicate the locations of burrows, with larger points corresponding to more frequently used burrows. Lines represent transitions between burrows on consecutive evenings. Line width corresponds to the number of transitions (in either direction) observed between two burrows, normalized by the total number of transitions for each group. For clarity, only lines where at least two transitions were observed are shown. Note that edge weights in the burrow networks we analyzed were slightly differently defined, and also incorporated the direction of the transition (i.e. directed weighted networks, see Methods).

Figure 2. Unequal distribution of burrow use. (a) Lorenz curves (individual lines) for all group-years with at least half of burrow observations present. The curves show the fraction of burrow usage (y-axis) made up by the fraction of least popular burrows (x-axis). The strong deviation from the diagonal (dotted line) indicates a highly unequal distribution.

Figure 3. Meerkats prefer large burrows closer to the center of their home ranges. Plots show fitted coefficients (x-axis of each plot) for each burrow feature based on conditional logistic regression models fitted separately for each group (y-axis). Points show maximum likelihood coefficient values, and error bars show 95% confidence intervals. Fitted coefficients for habitat effects are shown in Figure S4.

Figure 4. Meerkats are more selective when choosing burrows for rearing pups, and choose burrows closer to the center of their home range. (a) Comparison of the overall distribution of burrow usage rate for burrows used during periods when burrow-dependent pups were present (pup burrows; red solid line) compared to those used when they were not (black dashed line). To avoid the bias induced by the long periods spent at the same burrow when pups are present, burrow usage rate for each burrow (x-axis) was here computed using only data from when burrow-dependent pups were not present. The histograms were then computed by counting how many pup burrows (red line) and non-pup burrows (black line) fall within a given range of usage rates. If meerkats were not more selective in their burrow choices in the presence of pups, the two distributions would be expected to align. (b) Distribution of normalized distances from the home range center of the set of burrows used when burrow-dependent pups were present (pup burrows; red solid line) or absent (non-pup burrows; black dashed line). Note that to avoid a bias toward pup burrows being in the center, here home range centers were computed using data only from non-pup periods.

Figure 5. Meerkats are more likely to move to nearby burrows, however they do not always use the closest burrows. Plot shows the distribution of distances between consecutively used burrows in the real data (red circles), in a null model assuming random usage order (black diamonds), and in a null model assuming meerkats move to the nearest burrow (blue triangles).

Figure 6. Short-term social and ecological effects on burrow decisions. Plots show the empirical probability that a group returned to the burrow from the previous evening as a function of (a) predator alarm rate, (b) presence or absence of a group split, (c) presence or absence of an intergroup interaction (IGI) and (d-f) weight gain of individuals within the group. In (d-f), the % weight change of the dominant female (red triangles), the dominant male (blue diamonds), or the median % weight change of subordinate group members (black circles) is shown. These probabilities were either computed across all data (d), or separated into times when the dominant female was pregnant (e) or not pregnant (f). Error bars show 95% confidence intervals on probability estimates (Clopper-Pearson intervals; error bars in d-f are excluded for clarity). For all plots, only data from when burrow-dependent pups were not present with the group are included (N=27,179 observations from 35 groups).

Electronic Supplementary material for

"Burrow usage patterns and decision-making in meerkat groups"

CONTENTS

The electronic supplementary material includes:

1. Supplemental Figures and Tables (in this document)

2. Supplemental Data (separate files)

    a. burrow_use_clean.RData: Contains data frame with all burrow usage data for all groups

    b. burrow_selection_data.RData: Contains data frame with all consecutive burrow decisions (stay at the same burrow or go to a new burrow) as well as predictor variables (e.g. alarm rate)

    c. pup_periods.RData: Contains data frame with pup periods for each group

    d. burrow_measurements.csv: Measurements from all measured burrows

    e. burrow_usage_rates.csv: Usage rates in the past year from measured burrows

3. Supplemental Code (separate files)

    a. model_stay_or_go.R: Script to model group decisions of whether to return to a given burrow or switch to a different one (multi-model inference)

    b. burrow_probability_analyses.R: Script to compute empirical probability of staying at a given burrow as a function of various factors

    c. burrow_basic_natural_history.R: Script to compute distribution of burrow usage, centrality vs. usage, etc.

    d. birth_vs_nonbirth_burrows.R: Script for analyses comparing birth burrows to non-birth burrows

    e. burrow_network_by_group_year.R: Script to create burrow transition network and run network analyses

f. burrow_usage_vs_properties: R script to fit models relating burrow properties to usage rate

SUPPLEMENTAL FIGURES AND TABLES

Table S1. Multi-model inference results for models predicting meerkat decisions to return to the same burrow (1) or switch burrows (0). All models within Delta (AICc) < 2 of the top-ranked model are shown. Upper table gives fitted coefficients, log likelihoods, AICc scores, and Delta (AICc), and model weights. Lower table gives relative importance scores of each predictor across all models, model averaged coefficients, and standard error estimates. Model averaged coefficients were averaged over all models within Delta < 2 of the top-ranked model.

Model rank	Intercept	Burrow usage rate	Alarm rate	Group split	Dom F weight gain	Dom preg	Sub preg	Dom M weight gain	Sub weight gain	IGI	DF	Log likelihood	AICc	Delta	Weight
1	0.627	0.515	-0.091	0.424	0.174	-0.090					7	-3477.160	6968.300	0.000	0.082
2	0.592	0.513	-0.093	0.437	0.194						6	-3478.229	6968.500	0.130	0.077
3	0.605	0.513	-0.093	0.440	0.192		-0.071				7	-3477.831	6969.700	1.340	0.042
4	0.635	0.515	-0.092	0.427	0.174	-0.084	-0.056				8	-3476.916	6969.900	1.520	0.038
5	0.627	0.515	-0.091	0.420	0.197	-0.091			-0.019		8	-3477.022	6970.100	1.730	0.034
6	0.592	0.513	-0.093	0.434	0.217				-0.018		7	-3478.107	6970.200	1.890	0.032
7	0.624	0.516	-0.092	0.423	0.175	-0.091				0.030	8	-3477.106	6970.200	1.900	0.032
8	0.627	0.516	-0.091	0.425	0.167	-0.090		0.007			8	-3477.135	6970.300	1.960	0.031

	Intercept	Burrow usage rate	Alarm rate	Group split	Dom F weight gain	Dom preg	Sub preg	Dom M weight gain	Sub weight gain	IGI
Relative importance score		0.186	0.181	0.162	0.143	0.101	0.062	0.056	0.056	0.052
Model averaged coefficient	0.615	0.514	-0.092	0.429	0.186	-0.053	-0.014	0.001	-0.003	0.003
Standard Error	0.046	0.044	0.031	0.181	0.089	0.065	0.046	0.010	0.017	0.028

G31A

- Habitat: River banks
- Dimensions: 21 x 15 meters
- Holes: 35
- Vegetation cover: Medium

G185A

- Habitat: Pans
- Dimensions: 25 x 16 meters
- Holes: 35
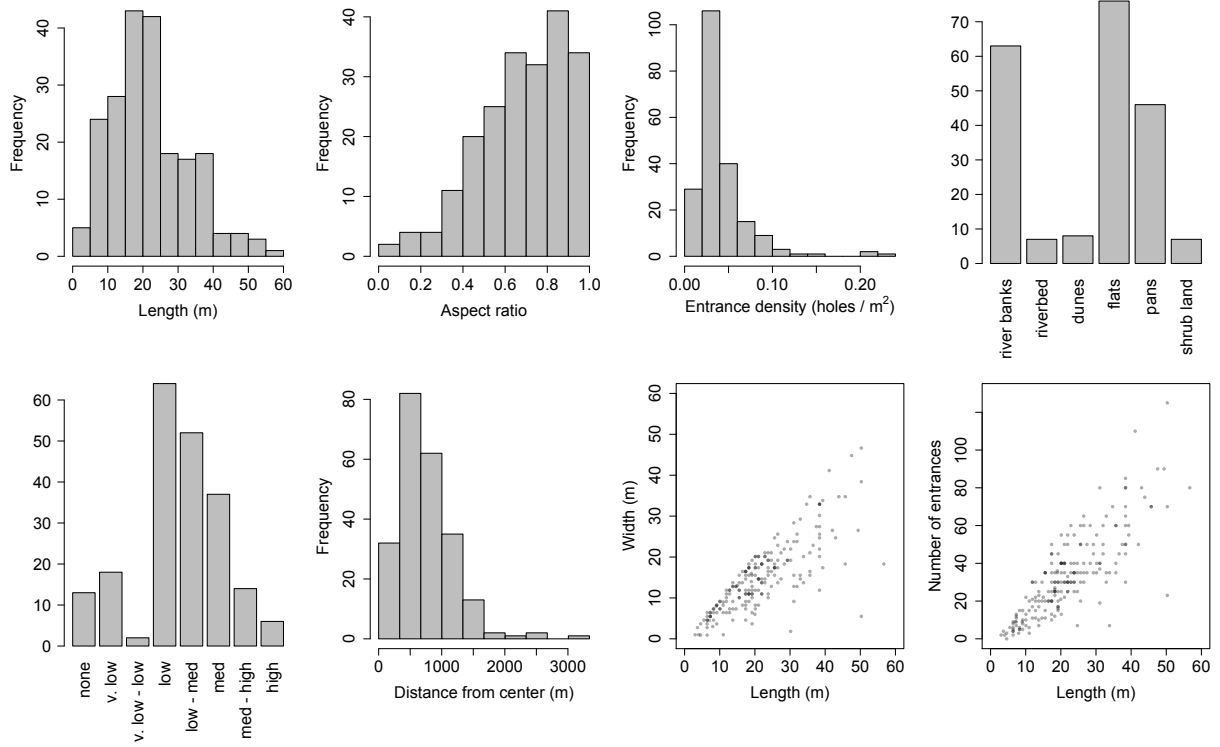- Vegetation cover: Very low

G1118A

- Habitat: River bed
- Dimensions: 7 x 5 meters
- Holes: 9
- Vegetation cover: Low

G145A

- Habitat: Flats
- Dimensions: 49 x 27 meters
- Holes: 90
- Vegetation cover: Medium

**Figure S1.** Examples of measured burrows representing different habitats, sizes, and vegetation cover categories.

Figure S2. Basic information on burrow properties, including distributions of burrow (top row) length, aspect ratio, entrance density, and habitat type as well as (bottom row) vegetation density, distance from center of range, relationship between length and width, and relationship between length and number of entrances.
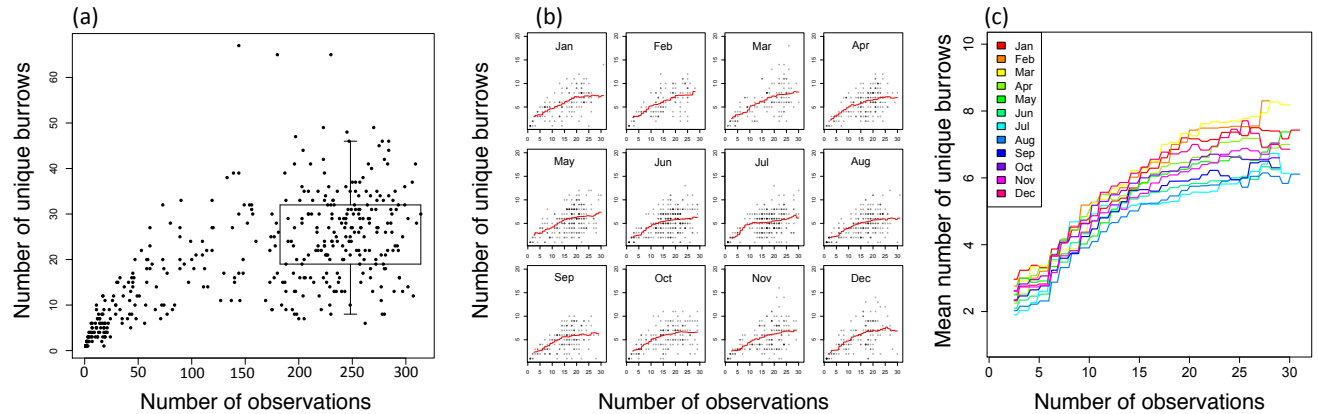
Figure S3. Number of unique burrows used by a group within a full year (a) and during each month (b-c). (a) Number of unique burrows observed in a given year for a given group vs. total number of observations. Because the curve flattens out around 150, we used only group-years in which at least 183 days (more than half a year) of data were observed in estimating the number of unique burrows groups typically use in a year. (b) Number of unique burrows used within a month vs. total number of observations for each month within the year. Here, only months in which meerkats did not have burrow-dependent pups are used in the analysis. (c) Mean number of unique burrows used within each month (colored lines) vs. number of observations, shown for easier comparison of different months to one another. Means were computed for each value on the x axis, using a sliding window of width 5 observations.
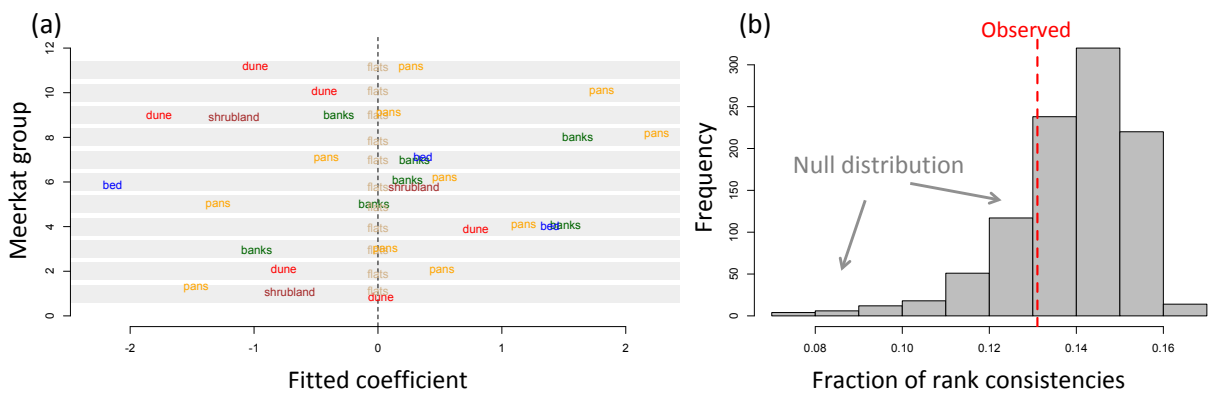
Figure S4. Meerkats did not show consistent habitat preferences when selecting burrows. (a) Coefficients from conditional logistic regression models of burrow choice (see also Figure 3). Each row shows the coefficients associated with different habitat types for a given group. Text labels are located at coefficient values associated with each habitat type: flats, dunes, shrub land, pans, river banks ("banks"), and river bed ("bed"). Flats was taken as the reference category in model fits, and therefore was defined to have a coefficient of 0. Note that model fits only include habitat types present in each group's set of burrows used, hence not all coefficients were fitted for all groups. (b) Results of permutation test comparing consistency of habitat rankings (by coefficient value) across each group. The consistency of habitat ranks was not greater than expected by chance, indicating that meerkats do not show consistent habitat preferences (across groups) when selecting burrows.
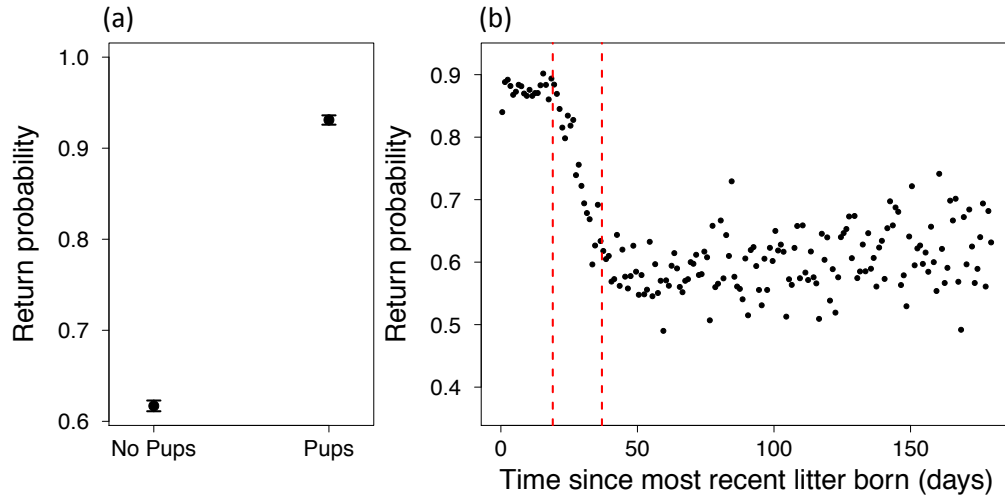
Figure S5. Effect of pups on decisions to return or switch burrows. The probability of returning to the same burrow is shown as a function of (a) the presence or absence of burrow-dependent pups and (b) the time since the most recent litter was born. Note that y-axis scales differ between plots.
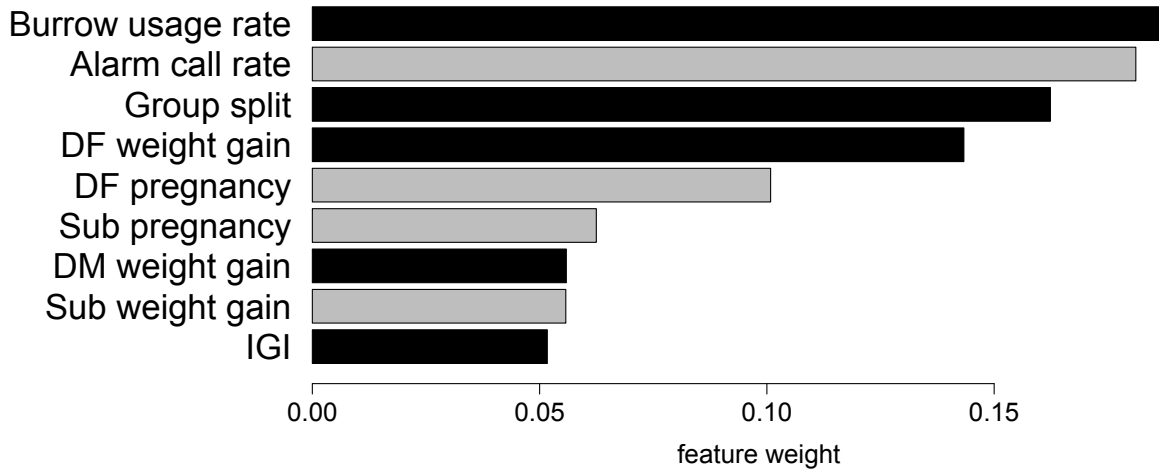
Figure S6. Relative importance weights (based on weighted AIC scores) for different features in predicting group burrow decisions. Higher feature weights indicate greater relative importance of a given feature based on multi-model inference. Definitions of features are given in Table 1. Black and grey bars indicate positive and negative effects, respectively, on the probability of returning to the same burrow.
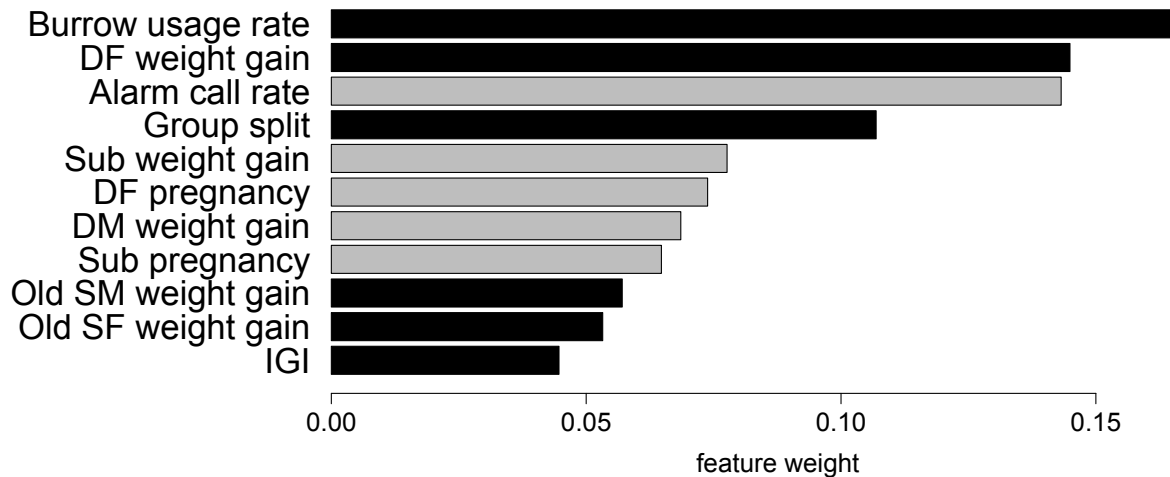
Figure S7. Additional model selection analysis incorporating the weight gain of the oldest male and female subordinates as predictors ("Old SM weight gain" and "Old SF weight gain respectively").
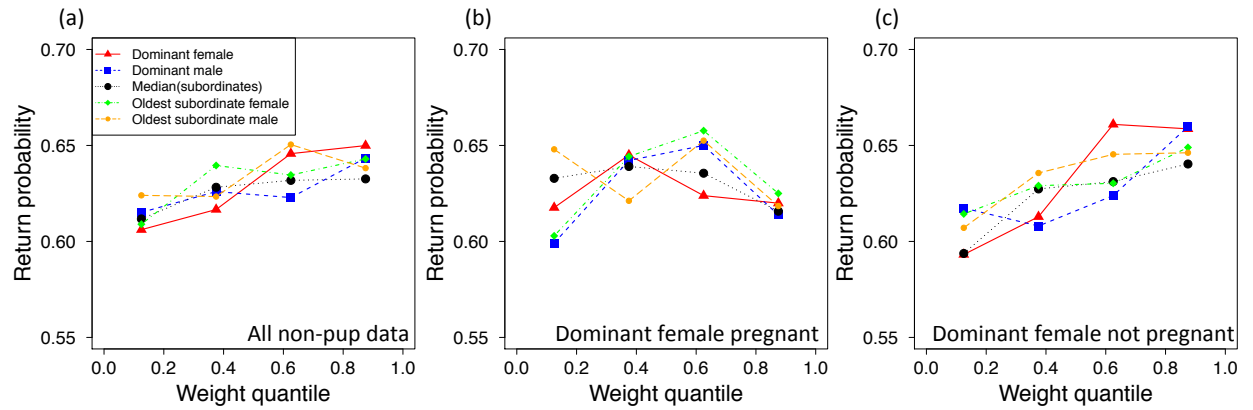
Figure S8. Additional analyses of the association of weight gain on the probability of returning to the same burrow, incorporating the oldest male and female subordinates.