

# Territoriality and home-range dynamics in meerkats, *Suricata suricatta*: a mechanistic modelling approach

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## Summary

1. Multiple approaches exist to model patterns of space use across species, among them resource selection analysis, statistical home-range modelling and mechanistic movement modelling. Mechanistic home-range models combine the benefits of these approaches, describing emergent territorial patterns based on fine-scale individual- or group-movement rules and incorporating interactions with neighbours and the environment. These models have not, to date, been extended to dynamic contexts.

2. Using mechanistic home-range models, we explore meerkat (*Suricata suricatta*) territorial patterns, considering scent marking, direct group interactions and habitat selection. We also extend the models to accommodate dynamic aspects of meerkat territoriality (territory development and territory shift).

3. We fit models, representing multiple working hypotheses, to data from a long-term meerkat study in South Africa, and we compare models using Akaike's and Bayesian Information Criteria.

4. Our results identify important features of meerkat territorial patterns. Notably, larger groups do not seem to control larger territories, and groups apparently prefer dune edges along a dry river bed.

5. Our model extensions capture instances in which 1) a newly formed group interacts more strongly with its parent groups over time and 2) a group moves its territory core out of aversive habitat. This extends our mechanistic modelling framework in previously unexplored directions.

**Key-words:** advection-diffusion models, habitat selection, partial differential equations, social carnivores, space use, spatial patterns

## Introduction

To survive and procreate, individuals must perform a suite of relevant activities – avoid predators, forage, compete with conspecifics and search for mates – all within a limited spatial context. Individuals' space-use decisions, and the resulting spatial patterns, affect all these activities (Clutton-Brock & Harvey 1978; Lima & Dill 1990). Answers to associated questions – what drives patterns, how are environmental and social factors involved, and how do patterns change over time? – are critical to understanding ecological processes.

In general, spatial patterns arise from animals moving in and interacting with their environment (Börger, Dalziel

& Fryxell 2008). For many of the carnivora, this takes the form of joint territory defence by social groups (Macdonald 1983). The distinction between home range (utilized area) and territory (defended area) breaks down, and the pattern of space use becomes that of a 'defended home range' (Börger, Dalziel & Fryxell 2008). Territorial interactions may involve physical violence or may be mediated by nonviolent cues that carry information about implied threats (Gosling & Roberts 2001). Often, individuals use scent marks to indicate territory ownership (Peters & Mech 1975; Bowen & McTaggart Cowan 1980; Jordan, Cherry & Manser 2007), and they commonly avoid (Peters & Mech 1975; Bowen & McTaggart Cowan 1980) and 'overmark' (Peters & Mech 1975; Jordan 2007) foreign scent marks, thus reinforcing territorial patterns without recourse to direct aggression.

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For territorial carnivores, mechanistic home-range models (Lewis & Murray 1993; Moorcroft & Lewis 2006) can be used to connect fine-scale movement behaviour to emergent spatial patterns and offer direct links between models and data. In developing these models, Lewis & Murray (1993) initially incorporated scent marking, over marking and scent-mark (SM) avoidance behaviours into random-walk movement models. Further improvements have used terrain- and resource-sensitive movement rules to capture stable patterns in spatially variable environments (Moorcroft, Lewis & Crabtree 1999, 2006). For species that do not rely on direct or cue-mediated conspecific interactions to form home ranges, other work has sought to explain home-range formation based on different mechanisms, *e.g.* movement costs, resource depletion and memory (Mitchell & Powell 2004; Fagan *et al.* 2013).

Huxley (1934) first described animal territories as 'elastic discs', centred on the territory holder and expanding or contracting depending on surrounding population pressure. Many previous mechanistic home-range models for territorial carnivores have accorded well with this concept, assuming that territories respond to conspecific interactions while remaining anchored around a temporally constant localizing centre (Potts & Lewis 2014). In reality, territories are likely to change over time, developing as an individual or group establishes a home range, and as home ranges shift in space, responding to surrounding population pressure or habitat availability (*e.g.* Potts, Harris & Giuggioli 2013). Past incarnations of mechanistic home-range models have not attempted to capture these processes.

Here, we modify the Lewis–Murray model and apply it to a population of wild meerkats, *Suricata suricatta*, studied by the Kalahari Meerkat Project (KMP). Our aim was to understand the spatial distribution of meerkat groups in their habitat, paying attention to interactions with other groups, possible effects of group size, and the influence of habitat features. We also extend the Lewis–Murray model to examine processes of territory development and territory shift. This simultaneously offers relevant insight into meerkat territoriality and extends the mechanistic modelling framework in new directions.

#### STUDY SPECIES AND SITE

Meerkats are social carnivores inhabiting southern Africa at approximate densities of 7–17 individuals km<sup>-2</sup> in groups of up to 50 individuals (Young 2003; Bateman *et al.* 2013). Within each group, a socially dominant pair largely monopolises breeding and subordinates assist in pup rearing, predator vigilance and territory defence (Clutton-Brock *et al.* 1999). Each day, group members forage together in close association, mainly consuming arthropods and small vertebrate prey (Doolan & Macdonald 1996). At night, groups return to a sleeping burrow, usually switching burrows every few days (Young 2003; Manser & Bell 2004).

Meerkat groups defend territories against conspecifics (Young 2003; Jordan, Cherry & Manser 2007). Direct interactions take multiple forms: stereotyped 'war dance' displays, chases, fights and violent burrow excavations, in order of increasing severity (Jordan, Cherry & Manser 2007; Drewe, Madden & Pearce 2009). Group size confers benefits in these instances: greater group-size disparity increases the chance that the smaller group will flee and decreases the chances of a physical fight (Young 2003).

Meerkats mark their territories using urine, faeces and anal gland secretions (Jordan 2007). Overmarking is common, and defaecation often occurs at shared latrine sites (Jordan 2007; Jordan, Cherry & Manser 2007; Mares *et al.* 2011). While shared latrines occur at boundaries between territories, latrines appear more dense within territory cores and are used most heavily in the breeding season; latrines have, therefore, been implicated in mate defence (Jordan, Cherry & Manser 2007; but see Mares *et al.* 2011).

Both sexes periodically disperse in same-sex coalitions, attempting to found new groups (Young 2003; Bateman *et al.* 2013), with larger dispersal-group size associated with increased chances of successfully joining a new group (Young 2003). Group formation is little-studied, however, and territory development in new groups remains unexplored.

Established group territories can be relatively stable over years, but shifts do occur (Gall 2012). Moorcroft, Lewis & Crabtree (1999, 2006) showed in coyotes, *Canis latrans*, how group removal could alter neighbouring territories. With meerkats, territories sometimes appear to shift farther than could reasonably be explained by similar reconfiguration. Meerkats may move their territories in response to conspecific interactions, scent marks or habitat features, such as periodically dense sour grass, *Schmidtia kalahariensis*. Meerkats seem to avoid sour grass, which appears to impede their movement and foraging efficiency and grows in previously overgrazed areas of the KMP study site (pers. comm., T. P. Flower, field site manager, 2004–2007).

The KMP study site consists of ranchland on and near the Kuruman River Reserve (26°58'S, 21°49'E), near Van Zylsrus, South Africa. The site includes a regionally typical mix of habitats: a stretch of the dry Kuruman river, nearby herbaceous 'flats', and sparsely vegetated dunes. Details pertaining to the site are available elsewhere (Young 2003).

#### Mathematical models

Mechanistic home-range models, derived from a spatially biased random-walk process, take the form of systems of partial differential equations (PDEs; see Moorcroft & Lewis 2006 for derivations). Early models (Holgate 1971; Okubo 1980) generated stable patterns by balancing spatial diffusion and attraction to a 'localizing centre' (a den site or core foraging area; Moorcroft, Lewis & Crabtree 1999). Lewis & Murray (1993) incorporated territorial

scent-marking behaviours to produce realistic patterns (see Moorcroft, Lewis & Crabtree 1999), and Moorcroft and Lewis incorporated habitat selection behaviours (see Moorcroft, Lewis & Crabtree 2006). Because the models describe spatial probability ('utilization') distributions, representing the probability of finding a focal group at any point in space at a given time, they can be directly tied to data. Thus, mechanistic home-range models connect underlying movement processes, territorial behaviour, resource selection and spatial utilization patterns (Moorcroft & Lewis 2006; Moorcroft & Barnett 2008), making important progress towards a general understanding of home-range behaviour (Börger, Dalziel & Fryxell 2008).

Börger, Dalziel & Fryxell (2008) commented that a truly mechanistic model should be able to recreate observed patterns without fixing a localizing centre *a priori*, also noting that applications of Lewis–Murray-type models have been largely restricted to stable patterns. We attempt to address some concerns regarding fixed localizing centres and exclusively stable patterns.

We developed a set of competing mechanistic home-range models to describe meerkat groups' home-range utilization distributions and how they change over time. The general form of these models relates short-term territorial changes to concurrent random and directed movement – arising from underlying 'biased random walks' – via a system of PDEs. For each group,  $i$ , changes to the utilization distribution are described by:

$$\frac{\partial u_i(\mathbf{x}, t)}{\partial t} = \underbrace{\nabla^2 [u_i(\mathbf{x}, t) D(\mathbf{x}, t)]}_{\text{diffusive (random) movement}} - \underbrace{\nabla \cdot [u_i(\mathbf{x}, t) C_i(\mathbf{x}, t)]}_{\text{advective (directed) movement}} \quad \text{eqn 1}$$

where variables and parameters are given in Table 1.  $\nabla$  indicates a spatial derivative, ( $\partial/\partial x$ ,  $\partial/\partial y$ ). Given appropriate forms of  $D(\mathbf{x}, t)$  and  $C_i(\mathbf{x}, t)$ , (1) can produce stable patterns at equilibrium [when  $\partial u_i(\mathbf{x}, t)/\partial t = 0$ ], maintained by a balance between diffusion and advection. We chose forms for  $D(\mathbf{x}, t)$  and  $C_i(\mathbf{x}, t)$  to represent different hypotheses about meerkat space use.

Meerkats exhibit an array of territorial behaviours beyond those previously studied using models of the type outlined by (1). We formulate new models designed to capture direct group interactions, territory development and territory shift, while employing some existing mechanistic models (scent marking, habitat selection and terrain avoidance). We provide a brief description of each model later, starting with existing models and proceeding to our new models. For more details, see Appendix S1. Table 2 provides a summary of the models we use.

#### SCENT MARKING

The Lewis–Murray model describes diffusive group movement, scent-marking, overmarking, foreign SM avoidance

and SM decay (Lewis & Murray 1993). We also consider the possibility that SM deposition occurs in proportion to group size (Moorcroft & Lewis 2006). Suppressing space and time dependence, our SM model is as follows:

$$\frac{\partial u_i}{\partial t} = d\nabla^2 u_i - \underbrace{\nabla \cdot \left[ u_i c \hat{\mathbf{v}}_i(\mathbf{x}) \sum_{j \neq i} p_j \right]}_{\substack{\text{advection, directed away from} \\ \text{conspecific scent marks,} \\ \text{towards localising centre}}}, \quad \text{eqn 2a}$$

$$\frac{\partial p_i}{\partial t} = \underbrace{u_i N_i \left[ 1 + m \sum_{j \neq i} p_j \right]}_{\text{scent mark deposition}} - \underbrace{p_i}_{\text{scent mark decay}}. \quad \text{eqn 2b}$$

In the SM model, when a group encounters foreign scent marks, it biases its movement towards a localizing centre. While this pattern may be most applicable for central-place foragers, it corresponds broadly to the behaviour observed in multiple social carnivores (Moorcroft & Lewis 2006). The localizing centre represents a less-than-mechanistic aspect of the models we use, and other authors have explicitly modelled processes, such as memory, that can produce similar behaviour (*e.g.* Van Moorter *et al.* 2009). For our purposes, we consider the assumption of a localizing centre to be a phenomenological description of attraction to a territory core or den site (in the breeding season; Turbé 2006).

#### HABITAT SELECTION

To account for habitat-specific patterns of space use, we employed modifications (Moorcroft, Lewis & Crabtree 2006), which represent a tendency for animals to move more slowly and spend more time in favourable habitat. Such features seem reasonable, as meerkats have been reported to move quickly between profitable foraging patches, in which they move more slowly (Doolan & Macdonald 1996). This modification affects  $D(\mathbf{x}, t)$  and  $C_i(\mathbf{x}, t)$ , so that for the SM model:

$$D(\mathbf{x}, t) = \left( e^{-\alpha_h h(\mathbf{x})} \right) d, \quad \text{eqn 3a}$$

$$C_i(\mathbf{x}, t) = \left( e^{-\alpha_h h(\mathbf{x})} \right) c \hat{\mathbf{v}}_i(\mathbf{x}) \sum_{j \neq i} p_j. \quad \text{eqn 3b}$$

The modification is comparable for the other models we present (For details, see Appendix, Moorcroft & Lewis 2006).

By considering several habitat predictors, we compared related hypotheses concerning habitat selection. Prey availability and predation risk differ between the

**Table 1.** Symbols used in models. Where applicable, variables and parameters are nondimensionalized as in Lewis & Murray (1993) and Moorcroft, Lewis & Crabtree (2006)

| Symbol <sup>a</sup>              | Interpretation  |
|----------------------------------|---|
| $\mathbf{x}$                     | Spatial location, $(x,y)$ , rescaled so that $x$ and $y \in [0,1]$  |
| $t$                              | Time  |
| $u_i(\mathbf{x},t)$              | Two-dimensional utilization distribution (a probability density function) for group $i$ at location $\mathbf{x} = (x,y)$ and time $t$       |
| $D_i(\mathbf{x},t)$              | Spatial diffusion rate, describing the tendency for group $i$ 's location to become less certain over time, if movement were left unchecked |
| $C_i(\mathbf{x},t)$              | Velocity of group $i$ 's advective flux (directed movement), which in practice serves to check diffusive group movement                     |
| $d$                              | Diffusion constant  |
| $c$                              | Advection constant  |
| $p_i(\mathbf{x},t)$              | Intensity of group $i$ 's scent marks at $\mathbf{x}$ and $t$   |
| $\hat{\mathbf{v}}_i(\mathbf{x})$ | Unit vector directed from $\mathbf{x}$ towards group $i$ 's localizing centre   |
| $\chi_i(t)$                      | Location of group $i$ 's localizing centre at time $t$  |
| $N_i$                            | Number of individuals, over 2 months of age, in group $i$   |
| $m$                              | Rate of overmarking, relative to the base scent-marking rate  |
| $\alpha_h$                       | Sensitivity to habitat features, $h(\mathbf{x})$  |
| $h(\mathbf{x})$                  | Habitat features: elevation, sand type or change in sand type   |
| $\kappa$                         | Exponential coefficient determining rate at which interaction strength of parent and daughter groups approaches normal level                |
| $t_0$                            | Time at which a daughter group forms from dispersing coalitions   |
| $A_i(\mathbf{x},t)$              | Group $i$ 's aversion to a given location at time $t$ , assumed proportional to $ C_i(\mathbf{x},t) $                                       |
| $\gamma$                         | Rate of localizing-centre movement, down aversion gradient  |
| $\alpha_r$                       | Strength of movement away from sour grass in river bed habitat  |
| $r(\mathbf{x})$                  | River bed habitat on the Kuruman River Reserve (used as a proxy for growth of sour grass during late 2007 and early 2008)                   |

<sup>a</sup>Note that symbols in bold face represent vectors.

**Table 2.** Summary of mechanistic home-range models used in this paper. The core partial differential equation models balance random diffusive movement against directed movement towards a 'localizing centre', or territory core, to generate stable patterns

|  | Model (abbreviation)  | Summary   | Equation | References                         |
|--|-----------------------|---|----------|------------------------------------|
| Core models                              | Scent marking         | Mechanistic partial differential equations (PDE) home-range model based on signal-mediated interactions between social groups | (2)      | Lewis & Murray (1993)              |
|  | Direct interaction    | Mechanistic PDE home-range model based on direct interactions between social groups   | (6)      | This paper                         |
| Habitat-interaction models               | Habitat selection     | Modification whereby groups spend more time in more desirable habitat   | (3)      | Moorcroft, Lewis & Crabtree (2006) |
|  | Terrain avoidance     | Modification whereby groups actively move away from less desirable habitat  | (4)      |                                    |
| Territorial dynamics models <sup>a</sup> | Territory development | Modification to allow increasing interaction strength between parent and newly formed daughter groups                         | (7)      | This paper                         |
|  | Territory shift       | Modification to allow territory relocation through movement of a group's territory core towards less aversive habitat         | (8)      |                                    |

<sup>a</sup>Territorial dynamics modifications assume the processes generating dynamic changes to home-range patterns operate on longer time-scales than those generating home-range patterns themselves.

low-lying river bed/flats and adjoining elevated dunes, and past evidence indicates associated differences in meerkat foraging success and space use (Manser & Bell 2004; Turbé 2006). Lacking direct estimates of prey availability or risk, we chose plausible correlates, considering (i) elevation, (ii) sand type (red 'ferrous' vs. pale 'clay' sand) and (iii) a sand-type 'edge' measure, as candidates for  $h(\mathbf{x})$ . (i) and (ii) correlate with regions of dunes and river bed/flats, while (iii) represents the interface between the two (see Appendix S1 for details). We note that we did not identify the potential importance of edge habitat until

after fitting the territory-development models (see Discussion), but there is *a priori* reason to consider this habitat type, as meerkats have been shown to prefer the dune/river bed interface seasonally (Turbé 2006).

#### TERRAIN AVOIDANCE

In the period during which we fit the territory-shift model (see Methods), meerkat groups seemed to avoid a region of river bed within the Kuruman River Reserve (T. P. Flower, pers. comm.). This may have been due to

extensive sour grass growth in the area, whereas sour grass was kept in check by high grazing pressure on the adjoining ranches. To accommodate this feature of meerkat space use, we adapted the terrain-avoidance modification of Moorcroft, Lewis & Crabtree (2006), allowing groups to actively move away from areas of dense sour grass, included by proxy as sand type in the reserve-specific area of river bed. For the SM model without habitat selection,

$$C_i(\mathbf{x}, t) = c\hat{v}_i(\mathbf{x}) \sum_{j \neq i} p_j - \alpha_r \nabla r(\mathbf{x}), \quad \text{eqn 4}$$

#### DIRECT GROUP INTERACTIONS

As an alternative to the SM model, we considered the possibility that home ranges result from direct interactions with neighbouring groups (for previous models incorporating this concept, see Stamps & Krishnan 1999; Morrell & Kokko 2005). We model the situation in which groups use experience of aggressive interactions to avoid regions used by other groups (not just regions in which they interact with other groups), so that

$$C_i(\mathbf{x}, t) = \underbrace{c\hat{v}_i(\mathbf{x}) \sum_{j \neq i} \frac{N_j}{N_i + N_j} u_j}_{\substack{\text{velocity of movement directed} \\ \text{away from regions of space} \\ \text{use by foreign groups,} \\ \text{towards localising centre}}} \quad \text{eqn 5}$$

The full model, without habitat selection, becomes as follows:

$$\frac{\partial u_i}{\partial t} = d\nabla^2 u_i - \nabla \cdot \left[ \underbrace{u_i c\hat{v}_i(\mathbf{x}) \sum_{j \neq i} \frac{N_j}{N_i + N_j} u_j}_{\substack{\text{advection, directed away from} \\ \text{space used by foreign groups,} \\ \text{towards localising centre}}} \right], \quad \text{eqn 6}$$

which we refer to as the direct-interaction (DI) model.

Again, we allow for group size to affect interactions, assuming that groups avoid regions of space in proportion to the size advantage of competing groups there. We measure a group's size advantage in a given interaction as the proportion of interacting meerkats it represents, which correlates well with whether a given group wins an intergroup interaction (Pearson's correlation coefficient = 0.53; see Young 2003). To remove the group-size effect, we simply remove the  $N_j/(N_i + N_j)$  term from the model.

#### TERRITORY DEVELOPMENT

New meerkat territories form when same-sex coalitions of dispersers from 'parent' groups join and establish 'daughter' groups. New breeding groups must often carve out home ranges from already populated habitat, and groups regularly form from dispersing coalitions of nearby origin, so that newly formed groups are at times

situated next to the natal groups of their founders (KMP, long-term observation). Before forming new groups, dispersers can go through a period of 'floating' (Peters & Mech 1975; Young 2003), and newly formed meerkat groups often make wider use of space than established groups.

Although parent and daughter groups at times engage in violent direct interactions (Drewe, Madden & Pearce 2009), other behavioural evidence suggests how each group's avoidance of the other's territory may build up gradually over time. Meerkats often fail to recognize group members by sight; when individuals return to their group after being separated they risk an aggressive war dance (usually reserved for hostile intergroup interactions) until in close proximity, where individuals can use scent or other cues to aid recognition (KMP, long-term observation). It is thus conceivable that direct interactions between a new group and its parent group could become aggressive before scent cues or mental maps adapt to the realities of local group compositions. A new group's territory might thus emerge slowly, as its members come to recognize the territory or scent marks of a progenitorial group as foreign.

We suggest a model in which the strength of interaction between parent and daughter groups is time dependent, exponentially approaching the population-wide level from an initial state of complete tolerance. We modified the DI model without group-size dependence so that

$$C_i(\mathbf{x}, t) = c\hat{v}_i(\mathbf{x}) \left[ \sum_{j \notin \{i, K_i\}} u_j + \sum_{j \in K_i} u_j (1 - e^{-\kappa(t-t_0)}) \right], \quad \text{eqn 7}$$

where  $K_i$  is the set of kin groups (*i.e.* parent or daughter groups) for group  $i$ .

#### TERRITORY SHIFT

At times, meerkat territories seem to drift in space (KMP long-term observation). This is a phenomenon discussed by other authors (Doncaster & Macdonald 1991; Moorhouse & Macdonald 2005) and a feature of recent individual-based territory models (Potts, Harris & Giuggioli 2013). Potts, Harris & Giuggioli (2013) developed a SM-based territorial interaction model that did not incorporate a localizing centre, in which territories drifted in the environment (and home ranges emerged) as a result of SM decay leading to shifts in territorial boundaries. If social carnivores are indeed drawn to a territory core, as our models describe, we argue that a localizing centre which responds to habitat conditions and group interactions may better capture space-use patterns.

Here, we suggest a phenomenological model for home-range movement whereby a group's idealized localizing centre moves in response to the same stimuli that generate advection. In the model, we allow a group to move its home range away from areas of high conspecific avoidance or poor habitat to areas associated with lower advection speed. We consider that this tendency would be

averaged across the group's utilization distribution (*i.e.* weighted according to habitat use), and that greater average differences in advection speed would generate faster movement of the home-range centre, so that

$$\frac{d\bar{x}_i(t)}{dt} = -\gamma \bar{\nabla} A_i(t), \quad \text{eqn 8}$$

where

$$\bar{\nabla} A_i(t) = \int \int_{\Omega} u_i \nabla A_i(\mathbf{x}, t) d\mathbf{x} d\mathbf{y} \propto \int \int_{\Omega} u_i \nabla (|C_i(\mathbf{x}, t)|) d\mathbf{x} d\mathbf{y}$$

over  $\Omega$ , the domain of interest.

## Methods

In an attempt to gain initial insight, we chose distinct time periods to examine stable territorial patterns, territory development and territory shift. We did this so that relevant processes were plausibly tractable, even though they occurred within an often complex and dynamic context. During period one (1 January 2003 to 31 December 2003), groups were relatively stable. During period two (1 July 2004 to 31 December 2005), a new group formed from dispersing propagules of two adjacent groups. During period three (15 June 2007 to 14 February 2008), an existing group's home range shifted in space.

### DATA COLLECTION AND PROCESSING

During the relevant periods, researchers made weekly (and often daily) visits to habituated groups of meerkats. Visits occurred while meerkats were foraging, either before or after their midday period of inactivity. During these visits, researchers collected detailed life history information and recorded spatial group locations using handheld Global Positioning System (GPS) units. We used data on population size and structure to generate group-size measurements [number of individuals older than 2 months (Bateman *et al.* 2013), averaged over census counts made every 2 months]. To reduce spatial autocorrelation, we resampled one GPS point from each observation session.

We used satellite-imaging data to generate standardized maps of elevation, sand type and interface between sand types (details in Appendix S1). We refer to these three candidates for habitat features,  $h(\mathbf{x})$ , as DEM, SAND and EDGE, respectively (see Fig. S1, Supporting information for representations of the versions used in period one models).

### MODEL FITTING AND COMPARISON

For a given model form, parameter combination and set of localizing centres, we numerically approximated meerkat home-range distributions (Appendix S1). Conveniently, these distributions are probability density functions and can be used directly to calculate the likelihood of empirical observations, given the model. By convention, we use the negative log likelihood, summed across all relocations for appropriate groups in each timestep:

$$-\ln(\mathcal{L}) = \sum_{T \in \mathbf{T}_p} \sum_{i \in \mathbf{G}_p} \sum_{l \in \mathbf{L}_{p,i}^T} [-\ln(u_i^T(\mathbf{x}_l))], \quad \text{eqn 9}$$

where  $\mathcal{L}$  is the likelihood of the observed data, for the given model;  $\mathbf{T}_p$  and  $\mathbf{G}_p$  are the sets of timesteps and groups, respectively, used for fitting;  $\mathbf{L}_{p,i}^T$  is the set of GPS relocations for group

$i$ , during timestep  $T$ ;  $u_i^T$  is the home-range distribution for group  $i$  in timestep  $T$ ;  $\mathbf{x}_l$  is the position of the  $l^{\text{th}}$  relocation for group  $i$  in timestep  $T$ . We fit each model by numerically optimizing parameters to minimize (9).

In period one, we modelled stable home-range patterns over 12 months considering this period as a single long timestep. We fit sixteen candidate models (Table S1, Supporting information), as described previously and outlined in Table 2. For further details, see Appendix S1.

When implementing the territory-development and territory-shift models (in periods two and three, respectively), we made a quasi-equilibrium assumption that home-range patterns equilibrate quickly relative to the dynamic processes that alter home ranges (territory development and shift). Biologically, this translates to the assumption that groups make use of their territories, thereby generating spatial patterns, on a shorter timescale than that at which underlying determinants of space-use change. Mathematically, we approximate continuous change by allowing stable home ranges to change step-wise, according to discretized changes in group interaction strength or location of their home-range centres. We chose timestep lengths to allow convenient and efficient model fitting, while offering reasonable descriptions of processes that occur in continuous time; this was a judgement call that we made to balance realism with practical modelling considerations. We did not expect to characterize precisely the processes of territory development and shift, using only a single observation of each process, so we do not consider the effect that timestep length has on parameter estimates. As an approximation of the true dynamic processes, we assumed that parameter values held throughout entire timesteps, changing discretely between successive timesteps according to the relevant model. This meant that each equilibrated home-range distribution arising from the models was associated with a set of empirical observations recorded over several weeks. See Appendix S1 for details.

Although the SM model provided the best fit to data in period one (see Results), the DI model fit was very similar (Fig. S3, Supporting information). The DI model was also much faster to fit, as scent marks in the discretized SM model take considerable computation time to equilibrate. We therefore used the DI model to investigate territory development and territory shift, as the inclusion of multiple timesteps itself increased the time required for each model fit. Because of their poor performance in period one, we did not include group size or elevation in the candidate model sets for periods two and three. Further consideration of these variables will be an important avenue to explore in future work.

To model territory development, we focused on three groups during period two: initially adjacent groups GG and Y and their daughter group, CD, formed at the beginning of October 2004. Our candidate model set (Table S2, Supporting information) included models with the territory-development modification and models in which all groups interacted at full strength throughout. For each timestep in period two, we simulated models as for period one, allowing interactions between parent and daughter groups to increase between timesteps according to the discretized version of (7). See Appendix S1 for details.

To model territory shift in period three, we focused on group CD's range shift to the northeast of the study site. Our candidate model set (Table S3, Supporting information) included models with and without the territory-shift modification (to describe CD's territory shift) and the terrain-avoidance modification.

To compare models in each period of interest, we used Akaike's Information Criterion (AIC; Akaike 1973) and the Bayesian Information Criterion (BIC; Schwarz 1978). AIC penalizes model complexity, irrespective of data set size, while BIC penalizes model complexity taking data set size into account. Bayesian derivations of both AIC and BIC are possible, and the prior assumptions implicit in using AIC turn out to be stronger than those explicit in using BIC (Kass & Raftery 1995; Bolker 2008): AIC-based model selection makes assumptions about model complexity prior to model fitting, while the use of BIC makes no such assumptions (Link & Barker 2006). As a result, AIC tends to favour complex models, with the effect exacerbated with large data sets (Kass & Raftery 1995; Link & Barker 2006). BIC may, therefore, be a good criterion for model comparison with large data sets, although opinion is divided (*e.g.* Burnham & Anderson 2002). Given the size of our data set and the low to moderate complexity of our models, we present both criteria, which are minimized for 'best' models. Between models, AIC and BIC differences of less than two provide weak evidence that the minimum-information-criterion model is better, while differences of more than 10 provide strong evidence (Burnham & Anderson 2002; Bolker 2008).

#### STATISTICAL SOFTWARE

We performed model optimization and data manipulation using R 2.15.0 (R Development Core Team 2012). To improve speed, we discretized PDEs in the C programming language and interfaced compiled code with R. We then incorporated spatial information and other model features, fitting parameter values with R's *optim* optimizer. See Appendix S1 for details.

## Results

We fit mechanistic home-range models, describing territorial patterns in meerkat social groups. We considered models based on scent marking and direct interactions that incorporated habitat selection, and we extended the DI model to investigate territory development and territory shift.

#### STABLE TERRITORIES

The model that best described stable meerkat home-range patterns was the SM model, (2), without dependence on group size ( $N_i$  set to one, for all  $i$ ) and with  $h(\mathbf{x}) = \text{EDGE}$  (Table S1, Supporting information). The model describes space use influenced by neighbouring groups and concentrated along the edges of the river bed and flats habitats (Fig. 1).

Akaike's Information Criterion and BIC gave similar results. In general, models without group size performed better than those with group size, and sand-type edge was a better predictor of space use than was sand type itself, which was in turn better than elevation (Table S1, Supporting information). While models that included scent marking performed better than the DI models (6), the best SM model and the best DI model produced

extremely similar results (Fig. S3, Supporting information). SM models described utilization distributions that were slightly more flat-topped and steep-sided.

Although all models captured the general pattern of space use where groups were tightly packed in the river bed, and group spacing is determined empirically in the model, incorporation of habitat features greatly improved the fit within groups' home ranges (Fig. S4, Supporting information).

#### TERRITORY-DEVELOPMENT MODEL

Territorial patterns in the 15 months after group CD formed were best captured by a model (7) in which interactions between GG and CD and between Y and CD (parent and daughter groups) increased over time (Table S2, Supporting information). Again, EDGE performed better than SAND in predicting space use (Table S2, Supporting information). The model produced a pattern whereby CD's use of space initially overlapped that of Y and GG (Fig. 2) – a pattern clearly present in the data but absent from the model without a gradual increase in interaction strength (compare Fig. 2 to Fig. S5, Supporting information).

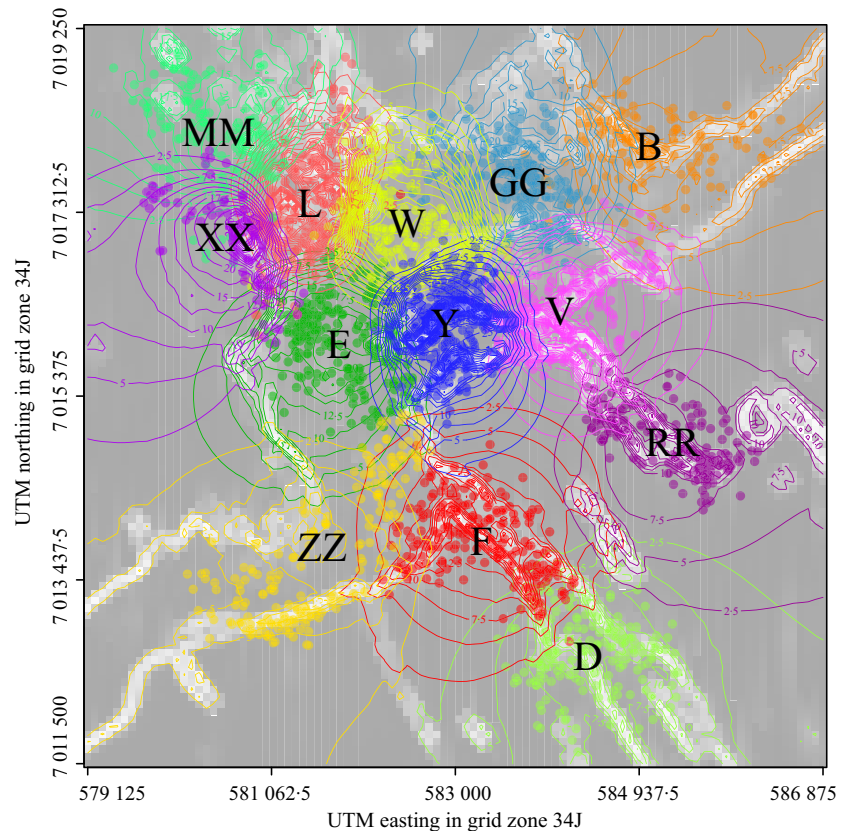
#### TERRITORY-SHIFT MODEL

The territory-shift model (8) including terrain (as a proxy for sour grass) avoidance best described changes in group CD's space use, performing better than models with a static localizing centre (Table S3, Supporting information). While  $h(\mathbf{x}) = \text{EDGE}$  generated the absolute minimum AIC and BIC values,  $h(\mathbf{x}) = \text{SAND}$  generated a fit that is statistically equivalent (Table S3, Supporting information).

The best models captured many features of CD's space use, presenting a description whereby patterns changed as a result of both changes in the set of surrounding groups and shifts in CD's localizing centre (Fig. 3). The disappearance of GG and V, and the appearance of KU, shifted CD's space use about its localizing centre, and the localizing centre tended to move away from neighbouring groups into less crowded habitat. The model incorporating SAND provides a broadly similar description (Fig. S6, Supporting information).

## Discussion

Mechanistic home-range models, fit to space-use data, successfully described meerkat home ranges based on interactions with neighbouring groups and habitat selection patterns. These models provided particularly good descriptions of stable space-use patterns for groups from the core of the study area (to which models were fit; Fig. 1), and modifications to the basic models captured features of dynamic patterns in periods of territory establishment and territory shift (Figs 2 and 3).



**Fig. 1.** Stable meerkat home-range distributions at the Kalahari Meerkat Project, South Africa, between 1 January and 31 December 2003. Contour lines represent individual groups' utilization distributions, produced by the Lewis–Murray scent-marking model (see text), without group-size dependence and incorporating movement in relation to sand-type edge habitat. Points represent GPS relocations of actual meerkat groups. Group codes (black text) show the location of groups' relocation centroids, used as localizing centres in the model.

#### SCENT MARKING

Our results suggest that meerkat groups use scent marking to mediate territorial interactions. Caution would be prudent in drawing conclusions, however, as untested model formulations, involving memory or other feedbacks, might generate similar stable patterns. That said, scent cues are clearly important in meerkat behaviour, and scent marking has been implicated in meerkat mate guarding and territory defence (Jordan 2007; Jordan, Cherry & Manser 2007; Mares *et al.* 2011). For dominant males, which must guard against cuckolding and group takeovers by foreign males (Mares, Young & Clutton-Brock 2012), scent marking for mate guarding and for territory defence may manifest in very similar ways (Mares *et al.* 2011). With respect to faecal marking, dominant male meerkats engage in the most mark deposition and inspection (Jordan 2007; Mares *et al.* 2011), and groups' responses may be strongly influenced by these males' behaviour (Mares *et al.* 2011).

Observed patterns of scent marking are consistent with those we would expect if our best models are accurate. In a time frame that largely overlapped with period one, Jordan, Cherry & Manser (2007) found that latrine use was not concentrated on home-range borders, consistent with our best model's prediction of a low overmarking rate (consider Fig. S3, Supporting information).

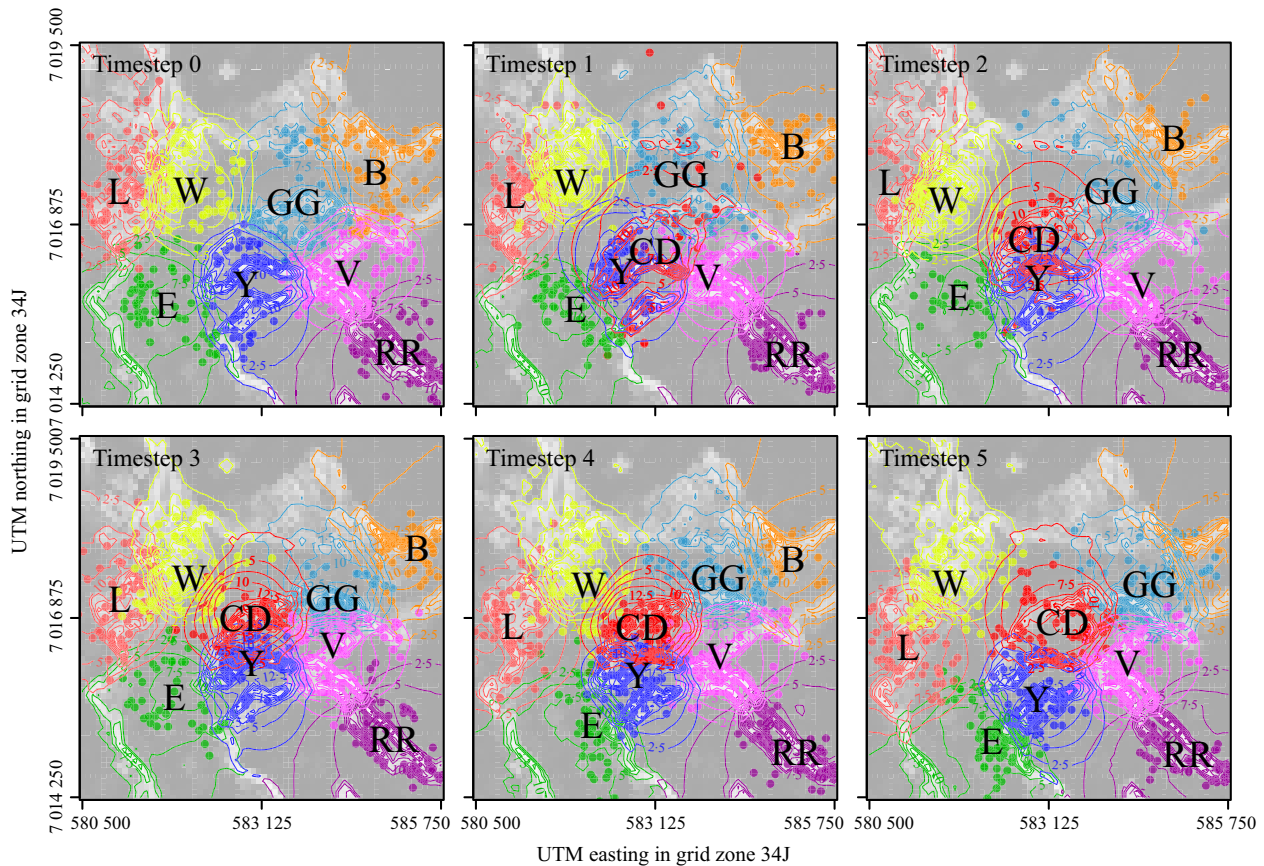
#### GROUP SIZE AND ESTABLISHMENT

The lack of evidence for a direct group-size effect was somewhat surprising, given the benefits associated with group size in meerkats' intergroup interactions (Young 2003). Future work may detect group-size effects taking different functional forms or in other phases of territorial interactions. Our result, however, offers further circumstantial evidence that scent marking, performed disproportionately by a single dominant male in each group, mediates territorial interactions. Past work confirms that, while all individuals scent mark to some extent, group size and composition have little effect on overall rates of faecal marking (Jordan 2007).

Territorial group-size independence is also consistent with the observation that meerkat mean group size closely tracks population density (Bateman *et al.* 2013). Group size seems to fluctuate within relatively consistent territories. Data from foxes, *Vulpes vulpes*, suggest a close analogue: pairs calibrate territory size to resource availability in bad years, with group size increasing, rather than territory size shrinking, in years of plenty (Lindström 1989). In fact, establishment of territories based on food availability in poor conditions, and maintenance of those territories even in good conditions, may be a common pattern in the carnivora (Macdonald 1983).

Although group size appears not to influence territory size directly, our model of group establishment suggests a mechanism whereby large groups might benefit from their





**Fig. 2.** Territory development in meerkat group CD. Contour lines show utilization distributions, as described by a direct-interaction home-range model (see text) in which interaction strength of CD with Y and GG (its parent groups) starts at zero in timestep 1 and increases through timestep 5. Groups spend more time at interfaces between sand types (white background). Timesteps are 3 months each, starting 1 July 2004 and ending 31 December 2005. Points represent group GPS relocations. Group codes (black text) show the location of groups' relocation centroids, used as localizing centres in the model.

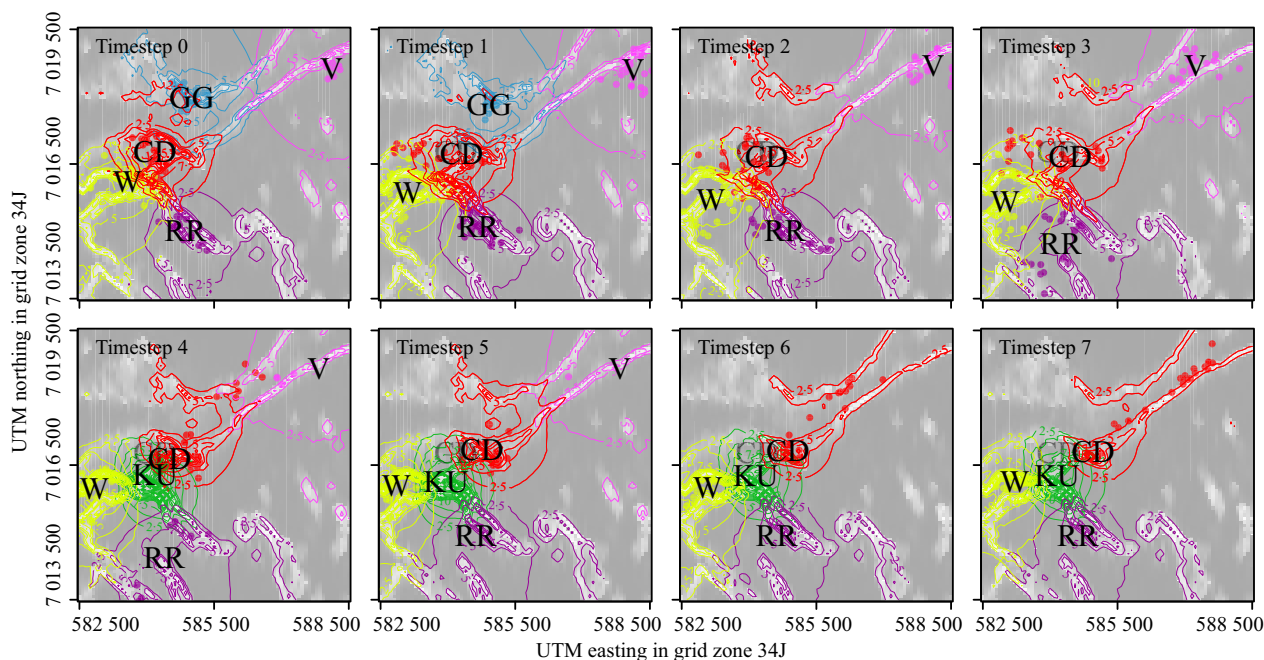
size. Larger meerkat groups tend to produce more numerous and larger dispersing coalitions, and therefore have the potential to establish more new groups (Young 2003; Bateman *et al.* 2013). If our model is broadly correct, it presents a mechanism by which related groups could 'carve out' territory. Even if parent and daughter groups do not actually tolerate each other *per se* (violent interactions certainly occur; Drewe, Madden & Pearce 2009), the resulting influence on surrounding groups may be the same. Elevated density of overlapping groups (Fig. 2) could push neighbouring groups out of an area, helping to avail habitat for the newly formed group. Breeders might thus help to ensure that their progeny gain access to adequate habitat.

#### HABITAT SELECTION AND SEASONAL PATTERNS

From our models, habitat type is clearly an important factor in determining meerkat space use. At a local scale, evidence suggests that meerkats prefer regions at the interface between clay-sand flats and ferrous-sand dunes (Figs 1–3). Notably, the inclusion of sand type (the next best predictor of stable space use; Table S1, Supporting information)

produced ambiguous results: in the stable-territory models, groups showed a preference for clay sand, but in territory-development models, groups showed the opposite preference (Tables S1 and S2, Supporting information; territory-shift models must balance habitat preference with movement preference, so do not allow such clear interpretation). This has at least two potential explanations. First, annual conditions could have affected patterns: 2003 was a particularly dry year, while 2004/2005 was wet, and sour grass growth (as in 2007/2008) or prey availability in the river bed may have played a role. Secondly, model constraints and differences in spatial domain may have led to misidentification of conflicting 'sand-type preference' in relevant models fit to data from different periods, when true preference is for edge habitat. In fact, this observation is what led to our consideration of edge habitat in the first place (as reported in the Mathematical models section).

At a broad scale, meerkats seem to prefer the river bed region to surrounding habitat (Clutton-Brock *et al.* 1999); though at a finer scale, they have been shown to seasonally prefer dune edges to the river bed itself (Turbé 2006). Levels of both foraging success and predation risk likely affect this pattern. The river bed and flats offer more 'bolt



**Fig. 3.** Territory shift in meerkat group CD. Contour lines show utilization distributions, as described by a direct-interaction home-range model, in which CD's localizing centre moves down the average advection-speed gradient (see text for details) from one timestep to the next. Timesteps are 1 month, starting 15 June 2007 and ending 14 February 2008. Groups spend more time at interfaces between sand types (white background). Points represent group GPS relocations. Group codes (black text) show the location of localizing centres, determined (except for CD) by the centroid of each group's GPS data in the corresponding timestep. Grey 'CD's show the initial location of group CD's empirically determined localizing centre (in timestep 0).

hole' refuges than do the dunes (Manser & Bell 2004) and may offer lower levels of predation risk (Turbé 2006). At a local scale, meerkats seem to prefer less productive, but less risky, flats habitat during the dry season, when foraging necessitates risk-prone digging, but they move to dune edges in the wet season, when an abundance of surface prey facilitates less risky, and highly profitable, foraging there (Turbé 2006).

We did not assess seasonal changes in interaction patterns or habitat preference. Given the computational cost in fitting our models with their few parameters, we deemed this infeasible for the current study. As a result, a preference for edge habitat represents an average across seasons, although seasonal changes are not immediately apparent from data (Figs 2 and 3). Future work should focus on this aspect of space use. Specifically, seasonal and interannual fluctuations in the rain-limited environment, as well as seasonal breeding-related behaviours, may play important roles. Analysis of prey availability and risk across habitat types and climatic conditions would be valuable (e.g. see Moorcroft, Lewis & Crabtree 2006).

Notably, breeding status can change territorial patterns (e.g. jackals, *Canis mesomelas* and *Canis adustus*, Lovelidge & Macdonald 2001; shrews, *Sorex araneus*, Wang & Grimm 2007). For meerkats, babysitting of pups at the natal burrow necessitates central-place foraging during the breeding season, while more fluid movement patterns are possible at other times (Turbé 2006). Also, when males prospect for extra-group matings, often during peak

female fertility (Young, Spong & Clutton-Brock 2007), they sometimes seem to draw their groups with them towards neighbouring groups (Mares *et al.* 2014). As prospecting is related to male dispersal (Young 2003), such a process may also be able to explain some range shifts, if groups are drawn by dispersing male coalitions.

#### TERRITORY SHIFT

From our model of territory shift, it appears that factors affecting movement patterns within a territory may also partly explain shifts in territory location. Our approach starts to address one of the major criticisms of many mechanistic home-range models – that territorial patterns rely on a focal point chosen *a priori*, even if estimated from data (Börger, Dalziel & Fryxell 2008). Our models were, however, unable to capture dramatic shifts in localizing centre, and much of the change in model patterns resulted from altered local interactions, as surrounding groups formed and disappeared – a process that has been noted previously (Moorcroft, Lewis & Crabtree 2006).

Factors we did not consider could influence group movement. For example, the availability of sleeping burrows, which are most dense in the river bed, flats and low dunes (Manser & Bell 2004; Turbé 2006), could influence coarse-scale habitat selection. Also, even if group size does not obviously affect stable territorial patterns, large groups do have advantages in group interactions (Young 2003) and seem to have more scope to position or

reposition their home ranges by forcing other groups out of desirable habitat (T. P. Flower, pers. comm.).

Our model aligns with the concept of territorial drift (Doncaster & Macdonald 1991; Moorhouse & Macdonald 2005), but the mechanistic underpinnings in our models differ from those previously proposed (Potts, Harris & Giuggioli 2013). Here, home-range shifts occur because of a change in the location of a territory core, instead of as a result of drifting territorial boundaries that result from SM decay (Potts, Harris & Giuggioli 2013). Although the inclusion of a localizing centre in our models is, at least in part, phenomenological, it may effectively summarize active home-range positioning. If this is the case, home-range shifts could occur as we have hypothesized, in response to conspecific and habitat cues, or, for example, if groups are drawn to new habitat by prospecting male coalitions. Our approach expands on the elastic disc analogy of Huxley (1934) by allowing the anchor, around which the disc may expand or contract, to shift. Whether such a model is most accurate, or whether home-range patterns more closely resemble more ephemerally anchored elastic discs (as proposed by Potts, Harris & Giuggioli 2013), should be the subject of future research.

We note that some localizing centres for period three, in which we modelled territory shift, were based on sparse or imputed data (see Appendix S1). While we did have data for the focal group, for which we calculated likelihoods, this could still have affected inference.

#### MODELLING CONSIDERATIONS

Any mechanistic model used with real data must be anchored in observation. Because a mechanistic home-range model's chosen localizing centre and the centroid of its resulting home-range distribution do not necessarily coincide, the centroid of relocation data is not, inherently, the most representative choice of localizing centre (e.g. placing group ZZ's localizing centre further to the northeast might have produced a more realistic fit: Fig. 1). The use of the relocation centroid represents, however, a convenient and robust simplifying assumption that has produced good empirical results (Moorcroft, Lewis & Crabtree 1999, 2006; this study).

The concept of a localizing centre is, itself, a simplification. Except perhaps when young pups remain at their natal burrow (Turbé 2006), meerkats do not have a clear single point of attraction in their home ranges. The idea of a core foraging area (Moorcroft, Lewis & Crabtree 1999) could apply, but, in reality, the multiple burrows within each meerkat group's home range may serve as multiple attraction points (Don & Rennolls 1983).

Memory processes likely play an important role in space-use patterns (Fagan *et al.* 2013). Van Moorter *et al.* (2009) proposed a home-range model in which movement from any given location relies on a 'dynamic attractor field' incorporating the 'utility' of multiple locations and both working and reference memory of already-visited

locations. Their model can produce stable home ranges without the need for territorial interactions, a characteristic that may be necessary for studying meerkat space use in sparsely populated habitat (e.g. group CD in the latter timesteps of period three: Fig. 3, and peripheral groups generally). More broadly, movement decisions depend on individual state, phenotype and experience, but our current understanding of how animals integrate multiple sources of information is rudimentary (Morales *et al.* 2010). The use of memory in movement models has, so far, been a largely theoretical exercise, but its addition to mechanistic home-range models for use with empirical data is plausible (Morales *et al.* 2010; Fagan *et al.* 2013).

#### FURTHER IMPLICATIONS AND FUTURE WORK

Multiple approaches have been used to study spatial patterns, among them resource selection analysis, mechanistic movement models and statistical home-range models. Our approach has incorporated aspects of each, informed by behavioural knowledge, to take advantage of a rich empirical data set and extend existing models. In the future, the potential to unify behavioural, spatial, demographic and evolutionary aspects of population dynamics into coherent models (e.g. Lewis & Moorcroft 2001; Haydon *et al.* 2008) presents exciting possibilities (Börger, Dalziel & Fryxell 2008).

Future work will aim to explore further details of meerkat territoriality, such as seasonal patterns and territory movement. Ultimately, we hope to link knowledge of spatial patterns with work on group dynamics and dispersal to gain further insight into the ecological and evolutionary processes at play for this cooperative breeder.

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#### Data accessibility

The data can be accessed at <http://hdl.handle.net/10402/era.38956>.

#### References

- Akaike, H. (1973) Information theory and an extension of the maximum likelihood principle. *Second International Symposium on Information Theory* (eds B.N. Petrov & F. Csaki), pp. 268–281. Akadémiai Kiadó, Budapest.
- Bateman, A.W., Ozgul, A., Nielsen, J.F., Coulson, T. & Clutton Brock, T.H. (2013) Social structure mediates environmental effects on group size in an obligate cooperative breeder, *Suricata suricatta*. *Ecology*, **94**, 587–597.
- Bolker, B.M. (2008) *Ecological Models and Data in R*. Princeton Univ. Press, Princeton.

- Börger, L., Dalziel, B.D. & Fryxell, J.M. (2008) Are there general mechanisms of animal home range behaviour? A review and prospects for future research. *Ecology Letters*, **11**, 637–650.
- Bowen, W.D. & McTaggart Cowan, I.M.T. (1980) Scent marking in coyotes. *Canadian Journal of Zoology*, **58**, 473–480.
- Burnham, K.P. & Anderson, D.R. (2002) *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer Verlag, New York.
- Clutton-Brock, T. & Harvey, P.H. (1978) Mammals, resources and reproductive strategies. *Nature*, **273**, 191.
- Clutton-Brock, T.H., Maccoll, A., Chadwick, P., Gaynor, D., Kinsky, R. & Skinner, J.D. (1999) Reproduction and survival of suricates (*Suricata suricatta*) in the southern Kalahari. *African Journal of Ecology*, **37**, 69–80.
- Don, B. & Rennolls, K. (1983) A home range model incorporating biological attraction points. *The Journal of Animal Ecology*, **52**, 69–81.
- Doncaster, C.P. & Macdonald, D.W. (1991) Drifting territoriality in the red fox *Vulpes vulpes*. *Journal of Animal Ecology*, **60**, 423–439.
- Doolan, S.P. & Macdonald, D.W. (1996) Diet and foraging behaviour of group-living meerkats, *Suricata suricatta*, in the southern Kalahari. *Journal of Zoology (London)*, **239**, 697–716.
- Drewe, J.A., Madden, J.R. & Pearce, G.P. (2009) The social network structure of a wild meerkat population: I. Inter-group interactions. *Behavioral Ecology and Sociobiology*, **63**, 1295–1306.
- Fagan, W.F., Lewis, M.A., Auger-Méthé, M., Avgar, T., Benhamou, S., Breed, G. *et al.* (2013) Spatial memory and animal movement. *Ecology Letters*, **16**, 1316–1329.
- Gall, G. (2012) *Assessments of spatio-temporal shifts in meerkats*. MSc Master's thesis, University of Zurich.
- Gosling, L. & Roberts, S. (2001) Scent-marking by male mammals: cheat-proof signals to competitors and mates. *Advances in the Study of Behavior*, **30**, 169–217.
- Haydon, D.T., Morales, J.M., Yott, A., Jenkins, D.A., Rosatte, R. & Fryxell, J.M. (2008) Socially informed random walks: incorporating group dynamics into models of population spread and growth. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **275**, 1101–1109.
- Holgate, P. (1971) Random walk models for animal behavior. *Statistical Ecology: Sampling and Modeling Biological Populations and Population Dynamics*, Volume 2 of Penn State Statistics. Penn State University Press, University Park, PA.
- Huxley, J. (1934) A natural experiment on the territorial instinct. *British Birds*, **27**, 270–277.
- Jordan, N.R. (2007) Scent-marking investment is determined by sex and breeding status in meerkats. *Animal Behaviour*, **74**, 531–540.
- Jordan, N.R., Cherry, M.I. & Manser, M.B. (2007) Latrine distribution and patterns of use by wild meerkats: implications for territory and mate defence. *Animal Behaviour*, **73**, 613–622.
- Kass, R.E. & Raftery, A.E. (1995) Bayes factors. *Journal of the American Statistical Association*, **90**, 773–795.
- Lewis, M.A. & Moorcroft, P. (2001) ESS analysis of mechanistic models for territoriality: the value of scent marks in spatial resource partitioning. *Journal of Theoretical Biology*, **210**, 449–461.
- Lewis, M.A. & Murray, J.D. (1993) Modelling territoriality and wolf-deer interactions. *Nature*, **366**, 738–740.
- Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Lindström, E. (1989) Food limitation and social regulation in a red fox population. *Ecography*, **12**, 70–79.
- Link, W.A. & Barker, R.J. (2006) Model weights and the foundations of multimodel inference. *Ecology*, **87**, 2626–2635.
- Loveridge, A. & Macdonald, D. (2001) Seasonality in spatial organization and dispersal of sympatric jackals (*Canis mesomelas* and *C. adustus*): implications for rabies management. *Journal of Zoology*, **253**, 101–111.
- Macdonald, D.W. (1983) The ecology of carnivore social behaviour. *Nature*, **301**, 379–384.
- Manser, M.B. & Bell, M.B. (2004) Spatial representation of shelter locations in meerkats, *Suricata suricatta*. *Animal Behaviour*, **68**, 151–157.
- Mares, R., Young, A.J. & Clutton-Brock, T.H. (2012) Individual contributions to territory defence in a cooperative breeder: weighing up the benefits and costs. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **279**, 3989–3995.
- Mares, R., Young, A.J., Levesque, D.L., Harrison, N. & Clutton-Brock, T.H. (2011) Responses to intruder scents in the cooperatively breeding meerkat: sex and social status differences and temporal variation. *Behavioral Ecology*, **22**, 594–600.
- Mares, R., Bateman, A.W., English, S., Clutton-Brock, T.H. & Young, A.J. (2014) Timing of predispersal prospecting is influenced by environmental, social and state-dependent factors in meerkats. *Animal Behaviour*, **88**, 185–193.
- Mitchell, M.S. & Powell, R.A. (2004) A mechanistic home range model for optimal use of spatially distributed resources. *Ecological Modelling*, **177**, 209–232.
- Moorcroft, P.R. & Barnett, A. (2008) Mechanistic home range models and resource selection analysis: a reconciliation and unification. *Ecology*, **89**, 1112–1119.
- Moorcroft, P. & Lewis, M.A. (2006) *Mechanistic Home Range Analysis*. Princeton University Press, Princeton.
- Moorcroft, P.R., Lewis, M.A. & Crabtree, R.L. (1999) Home range analysis using a mechanistic home range model. *Ecology*, **80**, 1656–1665.
- Moorcroft, P.R., Lewis, M.A. & Crabtree, R.L. (2006) Mechanistic home range models capture spatial patterns and dynamics of coyote territories in Yellowstone. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **273**, 1651–1659.
- Moorhouse, T.P. & Macdonald, D.W. (2005) Temporal patterns of range use in water voles: do females' territories drift? *Journal of Mammalogy*, **86**, 655–661.
- Morales, J.M., Moorcroft, P.R., Matthiopoulos, J., Frair, J.L., Kie, J.G., Powell, R.A. *et al.* (2010) Building the bridge between animal movement and population dynamics. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, **365**, 2289–2301.
- Morrell, L.J. & Kokko, H. (2005) Bridging the gap between mechanistic and adaptive explanations of territory formation. *Behavioral Ecology and Sociobiology*, **57**, 381–390.
- Okubo, A. (1980) *Diffusion and Ecological Problems: Mathematical Models*. Springer-Verlag, Berlin.
- Peters, R.P. & Mech, L.D. (1975) Scent-marking in wolves: radio-tracking of wolf packs has provided definite evidence that olfactory sign is used for territory maintenance and may serve for other forms of communication within the pack as well. *American Scientist*, **63**, 628–637.
- Potts, J.R., Harris, S. & Giuggioli, L. (2013) Quantifying behavioral changes in territorial animals caused by sudden population declines. *The American Naturalist*, **182**, E73–E82.
- Potts, J.R. & Lewis, M.A. (2014) How do animal territories form and change? Lessons from 20 years of mechanistic modelling. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **281**. Online early.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Schwarz, G. (1978) Estimating the dimension of a model. *The Annals of Statistics*, **6**, 461–464.
- Stamps, J.A. & Krishnan, V. (1999) A learning-based model of territory establishment. *The Quarterly Review of Biology*, **74**, 291–318.
- Turbé, A. (2006) *Foraging decisions and space use in a social mammal, the meerkat*. PhD thesis, University of Cambridge.
- Van Moorter, B., Visscher, D., Benhamou, S., Börger, L., Boyce, M.S. & Gaillard, J.M. (2009) Memory keeps you at home: a mechanistic model for home range emergence. *Oikos*, **118**, 641–652.
- Wang, M. & Grimm, V. (2007) Home range dynamics and population regulation: an individual-based model of the common shrew *Sorex araneus*. *Ecological Modelling*, **205**, 397–409.
- Young, A.J. (2003) *Subordinate tactics in cooperative meerkats: helping, breeding and dispersal*. PhD, University of Cambridge.
- Young, A.J., Spong, G. & Clutton-Brock, T. (2007) Subordinate male meerkats prospect for extra-group paternity: alternative reproductive tactics in a cooperative mammal. *Proceedings of the Royal Society of London. Series B, Biological Sciences*, **274**, 1603–1609.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Appendix S1.** Modelling details and supplementary results.