MOVEMENT PATTERNS AND HABITAT USE BY NAMIB GOLDEN MOLES (*EREMITALPA GRANTI NAMIBENSIS* BAUER AND NEITHAMMER, 1959).

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Abstract

Linnaeus first documented the existence of Golden Moles (*Chrysochloridae and Afrosoricida*) in 1758 but little is currently known about the biology of most of the species. Namib Golden Moles (*Eremitalpa granti namibensis*) are small, blind insectivorous mammals that inhabit the Namib Desert dunes. They are a subspecies of Grant's Golden Mole, with the other subspecies, *Eremitalpa granti granti,* found south of the Orange River. These free-ranging small mammals consume a wide variety of predominantly sand-dwelling invertebrates, with termites (*Psammotermes allocercus silvestri*) making up more than 95% of the diet by biomass. In this study my primary aim was to investigate habitat use and foraging behaviour of a subpopulation of Namib Golden Moles (*E.g. namibensis*) within the Namib Sand Sea by following their tracks over a full calendar year at a single site. My secondary aim was to compare mole movement patterns and habitat use at the main study site with two other nearby sites that differ in habitat. I hypothesised that movement and habitat use will be non-random and influenced by the local distribution of prey resources namely, vegetation hummocks and dune slip faces. I further predicted that movement patterns would show seasonal variation linked to changes in ambient and sand surface temperatures. I followed mole tracks in the early morning for 3 to 14 consecutive days each month at the main study site and compared a subset of these data with two other sites in a single season. Along each track, I recorded GPS waypoints were the mole emerged, dipped its head into the sand to listen (head-dip), foraged (sand-swimming) and rested. I recorded both the microhabitat type (dune phase) and broad habitat (hummock or open) for each foraging and resting GPS waypoint. The area of each microhabitat available at each study site and the density of vegetation were calculated from drone images in QGIS using NGRDI and Field calculator respectively. Manly's alpha (α_r) index was used to determine microhabitat and hummock preference. Home ranges were estimated using a 95% Kernel Density Estimation and were compared monthly and between the three sites. Key measures of movement and foraging behaviour were estimated for each mole track at all sites and the averages were compared monthly within the main site and for a single season between sites. Significant differences in movement and behaviour were evident both within the main site across months and between sites within summer. Track length was shortest but straightest with the lowest number of head dips at the main site which had the least hummocks and the most open habitat. Moles preferred to both rest and forage on or close to hummocks at all sites and preferred large hummocks. Within dune habitat moles preferred avalanche bases and slip faces both of which are associated with higher prey density. Moles also preferred to forage and rest in large hummocks and the mean number of hummocks visited each day increased with track length and the number of head dips per track but decreased with track straightness. The best predictors of track length were season and sand surface temperature with track length being highest in summer and increasing with sand surface temperature. The results support previous findings that Namib Golden Moles have larger home ranges (mean = 5.08 ha) and move greater daily distances than other mole species, and furthermore that they both head dip and swim in the sand to first detect and secondly increase their chances of encountering prey. Novel findings include that mole track length is mostly affected by seasonal changes in sand surface temperature, and they resort to shorter, straighter and mostly under-sand movement in winter. Together these findings reveal how the Golden Moles foraging behaviour has evolved in response to an environment where resources are sparse and patchily distributed and their movement patterns are effective in encountering areas of high prey concentration while minimising energy output.

Introduction

Spatio-temporal patterns of habitat use are an important component of a species behavioural ecology (Garshelis, 2000, Nathan *et al.*, 2008; Torres, *et al.*, 2017) which can help conservationists to determine high-priority areas or strategies to enhance ongoing or planned conservation efforts (Wastell & Mackessy 2011; Croak *et al.,* 2013; Kong *et al*., 2018). Habitat use is broadly defined as the way an animal uses the physical and biological resources in a habitat (Krausman, 1999) and includes foraging, seeking cover, nesting, escaping predators, denning, and other life-history traits. Habitat use by small mammals is a function of various factors, including predation risks, energetic costs associated with food acquisition, micro-environmental conditions and social factors including population densities, competition and mate acquisition (Milling, *et al*., 2017; Mcdonald, *et al*., 1997; Yahner, 1986; Kuyper, 1985). Individuals are expected to select suitable habitats where they can have access to shelter with appropriate thermal, hydric, and structural conditions, as well as sites with high prey abundance and access to sexual partners, and those with fewer competitors and predators (Scheffers, *et al.,* 2014; Mole, 2007; Martin, 2001).

Although Linnaeus first documented the existence of Golden Moles (*Chrysochloridae and* Afr*osoricida*) in 1758, little is currently known about the biology of most of the species. This is due in large part to their specialized habitat requirements and restricted distributions, often in remote areas; cryptic and trap-shy nature; factors which together make them difficult to study (Bronner, 1995). Chrysochlorids are small fossorial, insectivorous mammals, endemic to sub-Saharan Africa (Asher *et al.*, 2010), with a markedly southern African centre of diversity (Bronner & Bennett, 2005). Their fur ranges from blackish to pale greyish yellow; the name Chrysochloridae refers to their iridescent sheen of green, blue, violet or copper when viewed in light. The family is divided into nine genera and twenty-one species (Asher *et al.*, 2010), and they form part of an ancient African radiation of mammals (Afrotheria) that diverged from other mammals 90-110MYA.

The Afrotheria include the hyracoids (hyraxes), proboscideans (elephants), sirenians (sea cows), macroscelidids (sengis or elephant shrews), tubulidentates (aardvarks), and tenrecs (Fokey *et al*., 2016). Despite similarities due to convergent evolution, their phylogenetic origins are very different to other fossorial mammals commonly called moles such as the True Moles (Talpidae, Eulipotyphla) of the northern hemisphere, the Marsupial Moles

(Notoryctidae, Notoryctemorphia) of Australia, and the Mole-Rats (Bathyergidae and Heterocephalidae, Rodentia) of Africa (Asher *et al.*, 2010).

Golden moles have four digits on their front feet while other 'moles' have five (Bronner & Bennett, 2005). All Golden Moles have compact fusiform or lozenge-shaped bodies, short and powerful forelimbs containing pick-like claws, and are tailless (although internal caudal vertebrae are present), blind and lack pinnae (Bronner & Bennett, 2005). Golden moles also display a high degree of structural conformity, including three forearm long bones, hyoid-mandible articulation and hypertrophied malleus, which are rarely seen elsewhere among living mammals (Asher *et al.*, 2010).

Eremitalpa granti (Broom, 1907) is the smallest of all species in the family Chrysochloridae (Bronner & Bennett, 2005). The upper parts of its body are pale greyish yellow with an iridescent, silvery sheen and the underparts are paler than the upper parts with a slightly more intense yellow tinge (Skinner and Smithers, 1990). It also has a thick pad in front of the heel on the hind foot (Roberts, 1951). The muzzle ends in a hard leathery pad that protects its nostrils and assists in sand displacement and excavation (Bronner & Bennett, 2005). Its mouth is ventral (Perrin & Fielden, 1999). Its skull resembles that of *Chrysochloris asiatica* but is smaller, broader, and has no temporal bullae (Roberts, 1951). It can be differentiated from other species by having a well-developed fourth claw on the front foot (Perrin & Fielden, 1999) and unlike *C. asiatica*, *E. granti*'s first premolar is single rooted (Roberts, 1951).

Two subspecies of *E. granti* are recognised based on differences in skull dimensions and hair length (Meester, 1964): Grant's Golden Mole (*Eremitalpa granti granti* Broom, 1907) known from south of the Orange River in South Africa; and Namib Golden Moles (*Eremitalpa granti namibensis* Bauer and Niethammer, 1959, Figure 1) from Namibia. *E.g. namibensis* have shorter, broader skulls and shorter hair than *E.g. granti* (Meester, 1964). Namib Golden Moles also differ from Grant's Golden Moles and other Golden Moles, in their ability to burrow or 'swim' in loose sands without forming permanent burrows (Rathbun & Rathbun, 2007). The Namib Golden Mole is endemic to Namibia, specifically to the Namib Desert (Maree & Bronner, 2016), while Grant's Golden Mole is confined to the west coast of South Africa (Perrin & Fielden, 1999). Recent cytogenetic data (Gilbert, *et al*. 2008) and ongoing phylogenetic analyses based on molecular, cytogenetic and morphological characters indicate that the subspecies are highly divergent and may represent cryptic species. The Orange River is probably the barrier that divides these two groups, blocking the flow of genes and thus leading to differentiation through geographic isolation (Maree & Bronner, 2016).

Figure 1.1. The Namib Golden Mole (*E.g. namibensis*) on the dune sand in Namibia (photo by Fogden and Fogden, n.d).

The Namib Golden Mole is widely distributed in the Namib dunes, from the Kuiseb River southward to the Orange River (Maree & Bronner, 2016). Their foraging behaviour has evolved directly in response to an environment where resources are sparse and patchily distributed and their movement patterns are effective in encountering areas of high prey concentration while minimising energy output (Fielden *et al.*, 1990a). They consume a wide variety of predominantly sand-dwelling invertebrates (Perrin & Fielden, 1999), with termites (*Psammotermes allocercus silvestri*) making up more than 95% of the diet by biomass (Fielden *et al.*, 1990a). Clumps of *Stipagrostis* grass that occur as vegetated hummocks are a common source of these prey (Fielden *et al.*, 1990a). Namib Golden Moles are known to feed underground (Holm, 1969) as well as on the surface (Fielden *et al*., 1990a).

Namib Golden Moles exhibit both physiological and behavioural mechanisms to thermoregulate and reduce demands for energy and water (Seymour *et al.*, 1998). These include low metabolic rate, an extremely labile body temperature, kidneys that produce relatively concentrated urine, and extensive foraging above ground at night that avoids the high-energy cost of burrowing and extreme day temperatures (Fielden *et al*., 1990b; Seymour *et al*, 1998; Rathbun & Rathbun, 2007). A low metabolic rate reduces energy expenditure (Fielden *et al*., 1990b) and may be a consequence the aridity of the environment they live and may represent adaptation to arid environment (Bennett & Spinks, 1995). A lower body temperature allows the golden mole to increase their activity range without spending unnecessary energy to maintain a typical eutherian temperature (Bennett & Spinks, 1995).

Namib Golden Moles avoid extreme temperatures by resting in favourable microclimates within the sand column during the day (Fielden *et al*., 1990b). This they do without any problems associated with respiration as air diffusion in the dry sand is good (Seymour & Seely, 1996). In addition, a low metabolic rate can be viewed as an adaptation to reduce gaseous exchange where the absolute amount of available air is limited by diffusion rates through sand as well as to balance water needs (Fielden *et al*., 1990a). Namib Golden Moles obtain water from their invertebrate prey (water content varies between 63-80%), buffer water loss through concentrating urine and employing both behavioural avoidances of extremely high temperatures and torpor to reduce water loss associated with thermoregulation (Fielden *et al*., 1990c). They possess simple kidneys with a single elongated renal papilla to allow for efficient water absorption (Fielden *et al*., 1990c).

1.1. Literature review on *Eremitalpa granti namibensis* – the Namib Golden Mole

Most of the research on this species has explored habitat use and/or movement behaviour under both laboratory observations, and surface tracking and/or radio tagging in the field. Holm (1969) pioneered studies on the behavioural ecology of Namib Golden Moles in a terrarium and by following their tracks in the field. Fielden (1989) expanded on this research with studies on the adaptive biology and ecology of both captive and free ranging Namib Golden Moles. Her study included feeding ecology, daily movements and home range, activity phasing, thermoregulation and water metabolism. Rathbun and Rathbun (2007) subsequently used radio tags to detect and map movement patterns and habitat use by free ranging Namib Golden Moles.

Multiple studies have shown that the population densities of Namib Golden Moles are generally low but stable (Fielden 1991; Seymour *et al.* 1998; Perrin & Fielden 1999). Fielden, (1991) estimated population density to be between 0.17 and 0.19 moles per hectare while Perrin & Fielden (1999) estimated it to be between 0.014 and 1.19 moles per hectare based on sand-tracking data in one study area over 10 years. The large variation in mole density was attributed to differences in prey abundance that in turn was linked to differences in vegetation and precipitation at different field sites and in different years (Seymour *et al*., 1998).

According to Fielden (1991), Namib Golden Moles are solitary and confined to relatively constant home ranges that are used in a circumscribed but nomadic fashion, but which are not necessarily spatially exclusive with varying degrees of range overlap between neighbours. Fielden (1991) who observed moles for 2–5 days a month for an entire year reported a mean home range area of 4.63 ha (n=8) with males having generally larger home ranges (range: 3.10–12.30 ha) than females (range: 1.80–4.59 ha). However, a later study by Rathbun and Rathbun (2007), using radio tags, found smaller home ranges with an average of 0.16 ha (n=6) and a range of 0.11–0.56 ha for males and 0.05–0.09 ha for females. Fielden (1991) also suggested that home ranges may temporally overlap but the incidence and extent of such overlap were difficult to determine. Fielden (1991) observed that tracks of individuals hardly crossed. Even when track crossing did occur, there was no evidence of direct interaction between the two individuals concerned, suggesting that such crossings are separate in time (Fielden, 1991).

Fielden *et al.* (1990a) found the number of patches encountered by an individual to be dependent on the length of the foraging path leading to the suggestion that Namib Golden Moles forage until they are satiated (Fielden *et al.*, 1990a). Fielden *et al.* (1990a) also found that the maximum daily movement distance was about 550 m at one site which was 60 km from the coast (Gobabeb field station – see Figure 2.1 in the Methods) and 200 m at a site called 'the Far East', a 130 km from the coast. An earlier study by Holm (1969) reported average daily foraging distances of up to 4800 m in the dune system, with a maximum of about 5800 m as opposed to 300 m in the more vegetated riverbed. Rathbun and Rathbun (2007), however, reported shorter daily movement (average of 13 m with a range of 0–82 m). Both Fielden *et al.* (1990a) and Holm (1969) suggested the differences were attributed to variation in prey distribution, which in turn was linked to variation in the distribution of vegetation. Prey were more abundant in the riverbed (Holm, 1969) and at the Far East site (Fielden *et al.,* 1990a) and consequently foraging tracks were shorter at these sites. Rathbun and Rathbun (2007) also noted a significant variation in distance moved between individuals, but their data did not allow them to assess the contributing factors. Extrinsic factors like weather and surface conditions and intrinsic factors such as sex, age, size and reproductive status are also known to affect the movement of animals (Nathan *et al.,* 2008).

In attempting to explain discrepancies between studies, Rathbun and Rathbun (2007) suggested that their radio tags, which were glued onto the fur of moles, might have adversely affected their movement and behaviour. They further suggested that previous studies relying only on the tracks of individual moles may have overestimated their movement and home ranges by confusing tracks that cross one another. It is my suggestion that Rathbun and Rathbun (2007) are likely to have underestimated the daily distance moved and home ranges of moles as their study was of short duration (only two months) and confined to winter with low maximum ambient temperatures (<26°C) at which *E. g. namibensis* typically becomes less active and occasionally torpid. Furthermore, their study was done at a site (Die Duine) with higher precipitation, more vegetation and thus presumably greater prey densities than those in the Namib dunes, factors which are predicted to result in smaller home ranges and shorter daily movements (Holm, 1969; Fielden, 1991; Fielden, *et al*, 1990a, 1992).

Foraging paths of Namib Golden Moles consist of straight sections of walking on the surface, punctuated by small depressions (dips/head-dips, see below for more details) marking the point where the mole briefly submerged its head into the sand (Fielden *et al.*, 1990a; Seymour *et al.*, 1998). When prey is detected below the surface, the mole typically reverts to a more tortuous subsurface locomotion commonly referred to as ‘sand-swimming’ (Fielden *et al.*, 1990a; Seymour *et al.*, 1998). Surface tracks consist of uniformly spaced footprints, indicating a near constant speed (Seymour *et al.*, 1998). Tracks typically change direction after a head-dip that occurs on average about every 3–5 m (Seymour *et al.*, 1998). Sand-swimming is typically observed just before and/or after the mole emerges or returns to rest and is concentrated around the base of plants as well as in areas with high termite concentrations (Fielden *et al.*, 1990a). In areas of high vegetation density, sand-swimming becomes more prevalent and may occasionally comprise the entire diel foraging path (Fielden *et al.*, 1990a). The energetic cost of sand-swimming is estimated to be 26 times higher than the cost of surface locomotion (Seymour *et al.*, 1998), so it seems likely that this foraging mode is employed only in patches of high prey return, though there are no data to evaluate this theory. Moreover, individuals which are particularly at risk to predation may resort to sand-swimming in open habitats with little vegetative cover to avoid detection by above-ground predators. No detailed study has been done on the probability of sand-swimming relative to the spatial variability and availability of different habitat types.

Head-dipping is known to be important for prey detection, but it is not clearly understood (Fielden *et al.*, 1990a). Fielden *et al.* (1990a, 1992) observed the strongly onward-going nature of the foraging paths, which often bypassed some plants within a meter or less of a dip and concluded that encounters with food patches are purely stochastic events and that Namib Golden Moles are only able to detect vegetation and/or prey over a very short distance. However, Narins *et al.* (1997) rejected this conclusion, arguing that Namib Golden Moles foraging is indeed sensory-guided, and they are sensitive to seismic vibrations generated by prey activities and plants moving in the wind.

Narins *et al.* (1997), showed head-dipping and subsequent directional movement was consistent with the moles' perception of seismic vibrations, suggesting that Namib Golden Moles might be able to detect low-frequency seismic vibrations generated by the wind blowing over grass hummocks, allowing them to navigate towards termite nests often associated with the grass roots. They also recorded low amplitude clicks, scratches, and pops, within about one metre of the hummocks, believed to be generated by termites and other animals within the sand. Narins *et al.* (1997) linked the observed increase in the frequency of head dips to the detection of these prey-generated signals. However, more measurements are needed to confirm these suggestions (Narins *et al.*, 1997). A laboratory study by Lewis *et al.* (2006) found that the movement patterns of eight individuals were influenced by vibrations with two individuals moving directly towards a vibration source. These findings suggest that the movement patterns of Namib Golden Moles may be determined at least partly by the distribution of 'noisy' vegetation patches (and associated invertebrate prey), but this has yet to be conclusively demonstrated in the field. Fielden *et al.* (1990a) found that Namib Golden Moles were equally likely to turn left or right relative to the direction of the preceding move, but they did not explore the overall trend in direction of movement.

Namib Golden Moles were originally thought to be only active during the night (Holm, 1969) but later studies reported limited activity during the day as well (Rathbun & Rathbun, 2007; Fielden *et al.*, 1992). Daytime activity was recorded mostly during summer and was largely restricted to sand-swimming behaviour, while night-time activity was dominated by surface locomotion (Fielden *et al.*, 1992). Rathbun & Rathbun, (2007) also found that Namib Golden Moles change position within their sleeping site by at least one metre during the day. According to Fielden *et al.* (1992), sand-swimming is independent of surface temperature, while surface locomotion is temperature constrained. In the terrarium, during the day, Namib Golden Moles shift their positions when the temperature rises above 25°C (Holm, 1969). Furthermore, Rathbun and Rathbun (2007) found that on occasion Namib Golden Moles remain inactive for two or more consecutive days (max 11 days). Torpor is important for moles to save energy and water (Fielden *et al.*, 1990b) especially when resources are scarce. Some animals also undergo torpor to avoid harsh environmental conditions but the data on which variables (e.g., extreme heat or cold) are most likely to trigger torpor remain poorly understood (Fielden *et al.*, 1990c).

Namib Golden Moles are known to use the dune base, dune slope, and occasionally dune-crest and sandy-river-bed habitats within the Namib Desert (Fielden, 1989). Results from radio-tagged Namib Golden Moles show that 73.8% of confirmed locations were on upper dunes, 18.8% on dune slopes (edges) and 7.4% on the flats between dune lines (Rathbun and Rathbun, 2006). Moreover, Fielden *et al.* (1991) found that most individuals rested underneath plants and only a few rested in open areas, but they did not assess characteristics of these resting areas such as the plant species, plant size or substrate type and temperatures, all of which may be important to the moles when selecting resting sites. Rathbun and Rathbun (2007) found Namib Golden Moles to be associated with a variety of different plants in accordance with their relative abundance, including Ostrich Grass (*Cladoraphis spinosa*), Long Bushman Grass (*Stipagrostis ciliata*), Grey Bush (*Hermannia minimifolia*), Gha Grass (*Centropodia glauca*), Bushy Bushman Grass (*Stipagrostis lutescens*) and Dune Grass (*Stipagrostis sabulicola*). No sharing of resting sites by individuals was observed (Fielden *et al.*, 1991) and the excavation of resting sites revealed no evidence of permanent burrows or nest chambers (Fielden *et al.,* 1991).

Fielden *et al.* (1990a) highlighted the importance of return time to specific resting sites (time between successive visits to a site (Cody, 1971)), especially in an environment where food is sparsely distributed. Fielden *et al.* (1990a) expected moles to utilize their home ranges in a way that the average return time to patches would have evolved as a balance between allowing prey to accumulate and preventing loss of that prey to other moles. A similar pattern of balancing return time with nectar replenishment in flowers and potential competitors was observed in hummingbirds (Gill & Wolf, 1977). The limited data on return times at Gobabeb suggest a minimum of three days between revisits to a given food patch (Fielden *et al.* (1990a).

1.2. Aims and hypotheses

The main aim of this study was to investigate habitat use and foraging behaviour of a subpopulation of Namib Golden Moles (*E.g. namibensis*) within the Namib Sand Sea near the Gobabeb-Namib Research Institute. Given the paucity of long-term studies, my primary objective was to follow the tracks of multiple Namib Golden Moles over a full calendar year at a single site. The secondary objective was to compare the mole movement patterns and habitat use at the main study site with two other nearby sites that differ in both vegetation density and the availability of different microhabitats. By comparing these sites in a single season, I sought to explore how foraging behaviour is influenced by broad scale habitat types.

Given that Namib Golden Moles are poor thermoregulators that need to maximize food intake to balance their energy and water needs using a predominantly fossorial (i.e., energetically expensive) locomotory mode in arid resource-poor environments, I hypothesized that for a local subpopulation:

> H_0: movements are purely nomadic and that patterns of habitat/resource use are stochastic and independent of environmental characteristics over both localized space and time.
>
> H_{a-} - that movement and habitat use will:
>
> - be non-random and influenced by the local distribution of resources namely, vegetation patches (and the associated prey) and
> - show seasonal variation linked to changes in ambient and sand surface temperatures.

Given that the distribution of prey is closely linked to vegetation hummocks (Fielden *et al.,* 1990a; Holm 1969), I expected Namib Golden Moles to move longer distances and to have larger home ranges at the site with lowest vegetation density. Mean daily track length, mean displacement, the mean number of head-dips per track and home range size are also expected to vary seasonally due to a predicted decline in food availability and the low ambient and sand surface temperatures in winter (Vonshak, *et al*., 2009; Fielden *et al.,* 1992; 1990b; Robinson & Seely, 1980). Sand-swimming is expected to be more frequent in proximity to vegetation where prey abundance is higher (Fielden *et al.,* 1990a) as well as in winter when the ambient and sand surface temperatures are often too cold for surface activity (Fielden *et al.,* 1992). Namib Golden Moles are expected to revisit specific vegetation patches (hummocks) less often at sites with higher vegetation density. Encounter rates with hummocks are expected to increase with track length, track tortuosity and head-dipping frequency. Moles are not predicted to show any directional preference when leaving their sleeping sites and the tracks of different moles are expected to intersect more frequently in areas with higher vegetation density where tracks are more tortuous, and the density of moles is predicted to be higher (Thompson & Gese, 2013) and during mating season.

Materials and methods

2.1. Study area

The main study site is Station Dune (23º 34’52” N and 15º 03’ 10” E), south of the Kuiseb River and southeast of the Gobabeb-Namib Research Institute. The study site covers an area of approximately 3.70 km^2 with an estimated perimeter of 11.40 km.

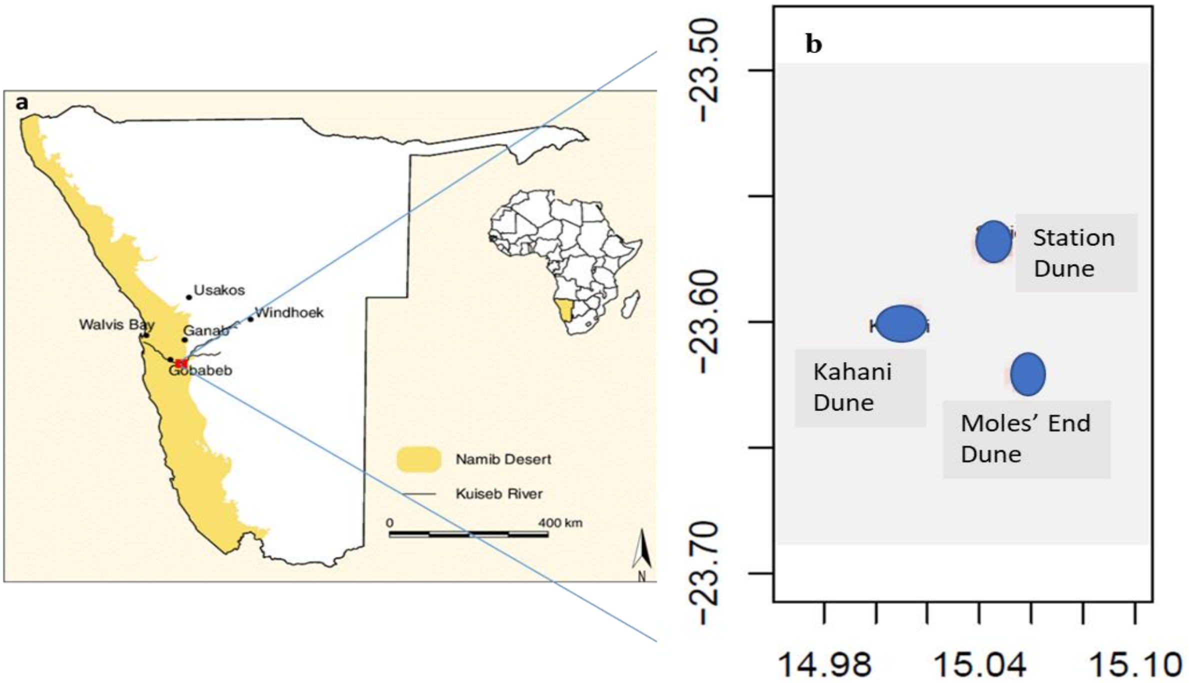


Figure 2.1. a) Map showing the relative position of Namibia in Africa (inset) and the study sites within Namibia and (b) a map showing the relative positions of the three study sites, Station Dune (main study site), Kahani Dune and Moles’ End Dune with a scale indicating the number of tracks followed at each site.

Figure 2.1 c). A high-resolution drone image showing the relative position of the study area at Station Dune (inset) just south of the Gobabeb-Namib Research Institute and the Kuiseb River.

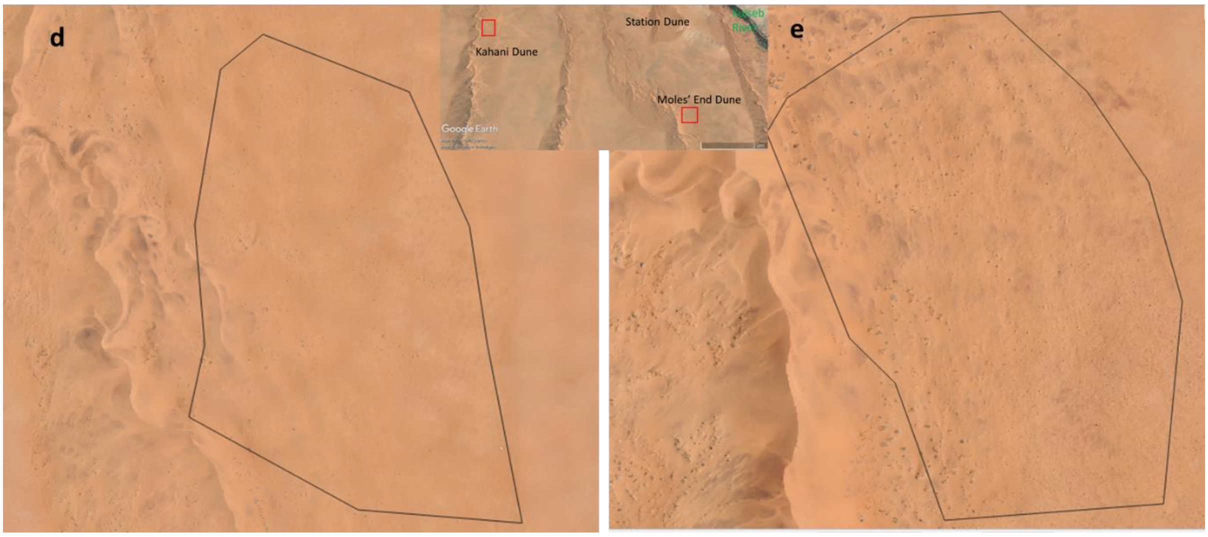


Figure 2.1 d) and e). Lower resolution drone images showing the relative position of the study area at Kahani (d) and Moles' End dunes (e).

2.1.1. Topography and vegetation

Station Dune (Figure 2.1c) is a linear dune comprising a chain of interconnected linear micro- or barchan dunes. Each linear micro-dune consists of the windward and leeward slope, a crest and a dune base. The leeward slope is further divided into the upper slip face, and the lower plinth with the avalanche or slip face base between the two. Barchan micro-dunes lack the slip face and have a brink, which may be the highest point (Robinson and Seely, 1980). The dominant vegetation type in the dune fields is dune grass (*Stipagrostis sabulicola)*, mostly located on dune bases and lower slopes. !Nara plants (*Acanthosicyos horridus*), leaf succulent (*Trianthema hereroensis*) and grasses such as *Centropodia glaucum*, *Stipagrostis lutescens* and *Cladoraphis spinosa* are also found in the dune fields. The slip face is devoid of vegetation but supports organisms that feed on windblown organic detritus (Figure 2.2 b) that accumulates at its base (Robinson and Seely, 1980).

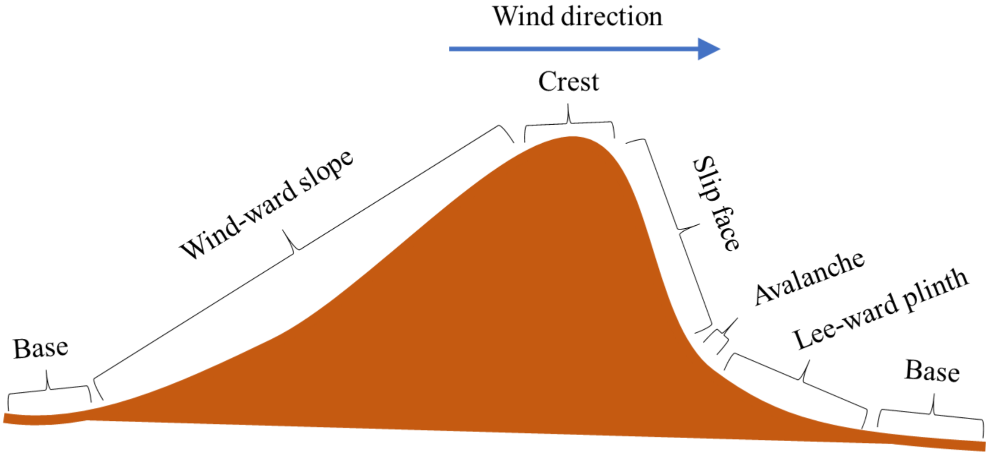


Figure 2.2a. Basic linear dune zones.

Figure 2.2b. Wind brown detritus (circled) accumulated at the avalanche base of a dune at the Station Dune site.

2.1.2. Climate

Gobabeb receives an average of 27 mm of rainfall and about 36 days of fog per year (Fielden, 1989). Rainfall occurs throughout the year with a peak between January and March (Gamble, 1980, Schulze, 1969). Fog has been recorded in every month but is more frequent and intense from September to October (Schulze, 1969, Spirig, *et a*l, 2019). The strong easterly to south-easterly wind dominates from May to August while, weaker winds from the north, northwest and southwest prevail from September to April (Robinson and Seely, 1980). In winter the mean ambient temperature is 18.5°C with a minimum of less than 3°C, while the mean summer ambient temperature is 22.8°C with a maximum of just above 40°C (Robinson and Seely, 1980). Dune surface temperature also varies along different phases of the dune at different times of the day as well as with different times of the year (Robinson and Seely, 1980). In summer the maximum dune surface may exceed 70°C but remains less than 65°C for most days while winter surface temperatures are generally 20°C lower (Robinson and Seely, 1980).

2.2. Data collection

Surface tracking was conducted at the northern end of the Station Dune, adjacent to the Kuiseb River for a maximum of 14 consecutive days a month, between September 2020 and August 2021. Two weeks was considered sufficiently long to provide robust monthly estimates of daily movement patterns, return times and inactivity periods (e.g., torpor lasts for 11 days) (Rathbun and Rathbun, 2007) in addition to variation in home range size and habitat use. Data collected earlier by Fielden *et al.* (1990a) at Gobabeb suggested that the return time to sleeping and foraging sites takes more than three days, while my preliminary observations at the study site found the return time to be about 4-6 days. To prevent double counting of individual moles I stopped data collection if the tracks of an individual were confused with that of another. This occurred on approximately 16% of the tracks that were followed and resulted in data being truncated for select individuals in certain months.

Tracking commenced in the early morning before the wind obscured the tracks. Tracks were followed, and route- marked with the GPS from the point of emergence to the final resting point. GPS waypoints were taken from where the mole first emerged from the previous night's resting point, where it dipped its head into the sand (head-dip, Figure 2.3), where it submerged (sand-swimming, Figure 2.3) as well as where it ended the day's activity (new resting point). Small marker flags were used to mark the resting points to make it easier to find them the next day. Resting sites and assumed foraging events (i.e., sand swimming) were further recorded on a standard data sheet (Appendix 1) and included information on both microhabitat (dune zones) and broad habitat type viz., vegetation hummock or open area. Microhabitats were broadly categorised into five categories based on topography, sand hardness and stability and vegetation cover (Table 2.1, Figure 2.4). Vegetation hummocks were categorised into four categories based on the dominant plant species and the size of the hummock (Table. 2.2). Intersections of individual tracks, indicating a possible interaction, were also recorded. Wind direction and strength, precipitation and temperature for the night before (18:00-05:00) were obtained from the nearby Gobabeb weather station. Surface tracking was further conducted for a period of one to two weeks at two other dunes, Kahani and Moles' End, which are about 7 and 8.5 km from Gobabeb – Namib Research Institute, respectively.

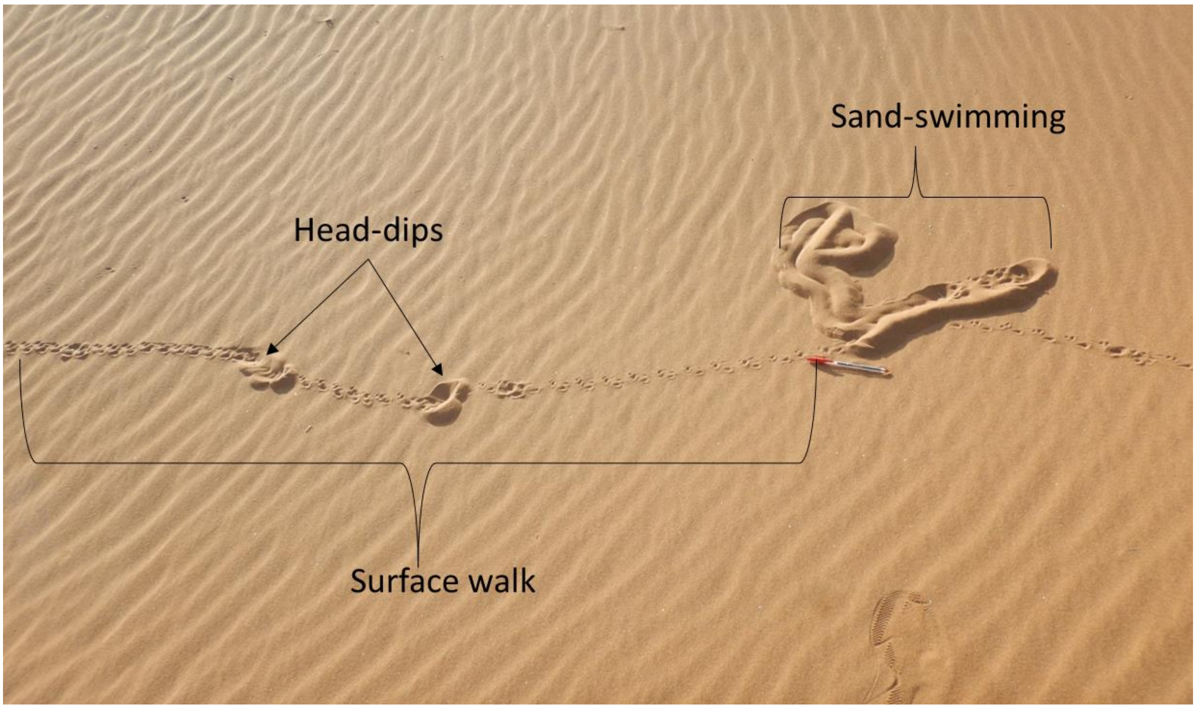


Figure 2.3. A track of a Namib Golden Mole showing a section of sand-swimming and surface walking with head-dips. A BIC ballpoint pen is shown next to the sand swimming for scale.

Table 2.1 A description of the different microhabitats (dune zones) within the study area

Microhabitat	**Description**
Base	The flat lower part of the dune is characterised by generally hard and stable sand and high vegetation cover.
Slope	The gentle wind-ward slope and the lee-ward plinth. Both are characterised by stable sand which may be hard or soft and medium vegetation cover
Crest	The highest point of the dune. The sand is generally soft and stable with little to no vegetation.
Slip face	The steep upper part of the leeward slope is characterised by soft sliding/falling sand and devoid of vegetation
Avalanche base	The juncture of the slip face and the leeward plinth. Rich in organic matter that falls from the slip face. The sand is generally hard with little vegetation.

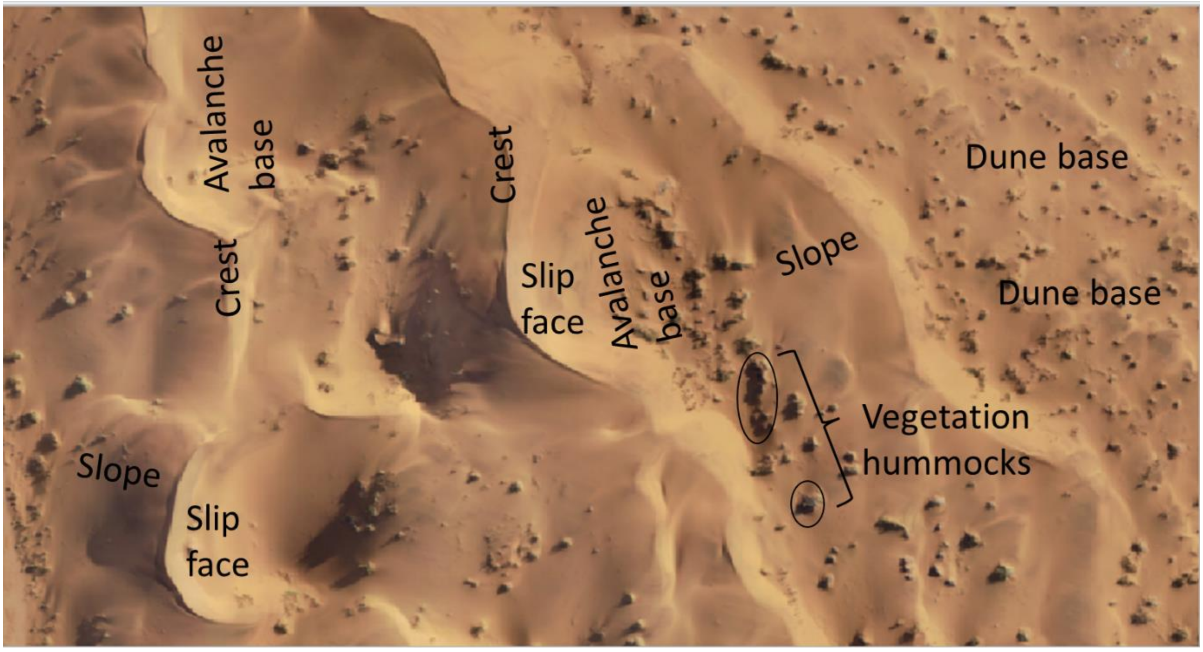


Figure 2.4. A drone image showing different microhabitats (labelled) within the Station Dune.

Table 2.2. A description of the different sized vegetation hummocks categories within the study area.

Vegetation hummocks	**Description**
Small hummock	A single tussock or cluster of *S. sabulicola* grasses that have formed a hummock with an average spread of ≤1 m
Medium hummock	A cluster of *S. sabulicola* grasses that have formed an intermediate-sized hummock with an average spread of>1 but ≤ 2 m
Big hummock	A cluster of *S. sabulicola* grasses that have formed a large hummock with an average spread of> 2 m
Others (name)	Plants of all sizes that are not of *S. sabulicola* species

Although I intended to sample five moles for fourteen days a month for a full calendar year at Station Dune, this was not always possible with strong winds sometimes obliterating all tracks and access to the study site occasionally prevented when the Kuiseb River flowed. Thus, the months of April (last half), May and June (first half) were not sampled because of strong wind, while the last half of December and the whole of January were not sampled as the Kuiseb River was flowing. Since moles were not marked, and there was a high probability that I was following the same moles that I previously followed in the previous sessions, a possible total of 56 moles were tracked. That is 40 at Station Dune (main study site), nine of which were tracked in October/September), four in November, ten in February, five in March, two in June, five in June/July (28 June –04 July) and five in August. I did not intend to compare seasons at either of the other two sites but rather included them as a snapshot comparison (in one season) with the main study site. I sampled 11 individuals at Moles' End, six of which were followed in November 2021 and five in April 2022. I followed five individuals at Kahani Dunes in December 2021. All moles were tracked for between three and 14 days except the two moles tracked in June, which were only tracked for two days and were thus excluded from some analyses.

2.3. Data analyses

2.3.1. Weather

I calculated the monthly average temperatures (sand surface and ambient) and precipitation (fog and rain) for all nights (18:00-05:00) that preceded tracking during the study. Camera traps set up around their sleeping sites revealed that moles typically start moving after 18:00 (under the sand) but only come to the surface around 20:00. Furthermore, fresh tracks in the morning after fog indicate that they are active until around 5:00.

2.3.2. Data extraction

GPS data from surface tracking were superimposed onto a high-resolution drone image of Station Dune using QGIS to visualise the movement of the Namib Golden Moles across the study area. The number of hummocks encountered by each mole per day was then determined in addition to the number of hummocks visited more than once by the same individual and the time elapsed between successive visits. GPS data were further viewed using the Basecamp software, where the length of tracks, net displacement and trend direction were estimated. The number of head-dips and the number and length of sand-swims per track were obtained from GPS data recorded on the standard data sheet (Appendix1).

The vegetation density of the three study sites was determined using the Normalized Green-Red Difference Index (NGRDI) in QGIS. The extent of each study site was determined by drawing a polygon around the area where the moles were active. I estimated the area covered by each vegetation hummock at Station Dune using the QGIS Field calculator after which I derived a diameter for each hummock that was used to classify hummocks into different size categories. The extent of the different microhabitats o Station Dune were estimated by drawing polygons around each microhabitat and then calculating their area using the QGIS Field calculator.

2.3.3. Exploratory analyses and comparisons of foraging behaviour

Descriptive statistics (mean, standard deviation, median, and range) of track length, net displacement, number of head-dips per track, number and total length of sand-swimming per track, and number of grass hummocks encountered were calculated for each mole track at all sites. Track length is the total distance (m) covered by an individual mole in single night of foraging, from one sleeping site to the next. Net displacement is the straight-line distance (m) between the two sleeping sites after a night of foraging. The frequency with which moles dipped their heads was calculated by dividing the number of head-dips by the total track length. Sand-swimming length was calculated by summing all of the individual sand swims recorded for each track. Sand–swimming frequency was calculated as the number of sand-swims per track. The number of hummocks encountered is the sum of all hummocks the mole tracks pass through.

In addition to the above variables, track straightness (i.e., how straight or tortuous the track is) was calculated by dividing the net displacement with track length. The percentage of sand-swimming was calculated as a percentage of the total length of sand-swimming over the total length of each track. Each of these variables were then averaged to compare between months at the main site and within a single season between sites using either ANOVA (with post-hoc Tukey test) or Kruskal-Wallis (with Post-hoc Dunn test) based on whether the data are normally distributed or not.

Track length is the most reliable variable to measure and an important metric when exploring an animal's spatial ecology. I used a Generalised Linear Model ('GLM') to assess which variables (season, vegetation density, mean sand surface temperature and mean ambient temperature) best explain Namib Golden Moles' track length. All predictor variables were tested for correlation using the Pearson's product- moment correlation test: Sand surface temperature was found to be highly correlated to air temperature and season (i.e., r >0.7, Appendix 2). As a result, it was not included in the same model structures with air temperature and season and two model structures were run, with one excluding sand surface temperature while the other excluding the ambient temperature and season. I fitted GLMs specifying a Gaussian distribution and the identity link function. Full diagnostic plots of fitted models showed signs of non-constant variance, suggesting appropriate model fit (Appendix 3). As this was an exploratory analysis, I considered all possible GLM permutations and selected the most parsimonious model according to Bayesian Information Criterion (‘BIC’: Neath and Cavanaugh, 2012). Models with Δ BIC < 2 were considered equally plausible.

I used Spearman correlation coefficients to explore the relationship between track length, track straightness, number of head-dips and the frequency of visiting vegetation hummocks as well as to investigate whether the frequency of re-visitation to specific hummocks influences the time it takes to return to that hummock. Furthermore, I used the ANOVA test to compare the number of hummocks reused and the return time between Station Dune, Kahani and Moles’ End using only data from October/November and December.

2.3.4. Possible interactions

Given that Namib Golden Moles are solitary and only associate during mating (Fielden, 1991), I explored whether the frequency with which tracks intersect varies with time of year using an ANOVA test. Similarly, an ANOVA test was used to compare the frequency of track intersections between the three study sites using only data from October/November and December to explore possible effects of habitat type on this behaviour.

2.3.5. Movement direction

The mean circular trend direction (from emerging to resting point) for each track at Station Dune study site was calculated using the R package “circular”. Track trend directions were first converted to circular before the mean was calculated.

2.3.6. Home ranges

Home ranges were estimated using 95% Kernel Density Estimation (KDE), with h = “h ref”. KDE was chosen because it is more accurate than other methods such as minimum convex polygon and fractional dimension (Powell 2000). Home range sizes of moles tracked at Station Dune in October/November were first compared to those tracked at Kahani and Moles’ End in November and December using a Kruskal-Wallis (KW) test. Home range sizes of individuals tracked at Station Dune were further compared monthly, between February, March, June/July, August, September and October/November using a Kruskal-Wallis test. To determine whether the home range sizes were biased toward individuals that were tracked for a longer period, I used the Spearman correlation coefficient to explore the relationship between home range sizes and the tracking periods.

2.3.7. Habitat use and preference

Manly's alpha (α_r) index was used to determine the preference between open area and vegetation hummocks, between different microhabitats as well as between different categories of vegetation hummocks for resting and foraging behaviour at Station Dune:

$$\alpha_r = \frac{ri}{ni} \frac{1}{\sum(rj/nj)}$$

where *ri,rj* is how much Namib Golden Moles used the microhabitat or hummocks category *i* or *j* and *ni,nj* is the availability of microhabitat or hummocks category *i* or *j* within the study area. Availability of vegetation hummocks was estimated by calculating the area covered by all hummocks and then subtracting it from the area of Station Dune study site to get the area of uncovered or open area. Microhabitat availability was calculated by the total area covered by each microhabitat as a proportion of the total area of all microhabitats at the study site. Availability of different classes of vegetation hummock was estimated by the total number of each category as a proportion of the total number of all categories in the study area. To estimate resting microhabitats and vegetation use, I counted the number of times individuals slept in each microhabitat and around each hummock category. Foraging behaviour was calculated as the number of sand-swims recorded in each microhabitat and hummock category.

Results

3.1. Weather

Air and sand surface temperature peaked in the month of April, which is the autumn and was lowest in the spring months of August and September. Most of the precipitation was in the form of fog which was highest in the summer months of November and December. Rainfall (0.1 mm) was recorded in the month of February only.

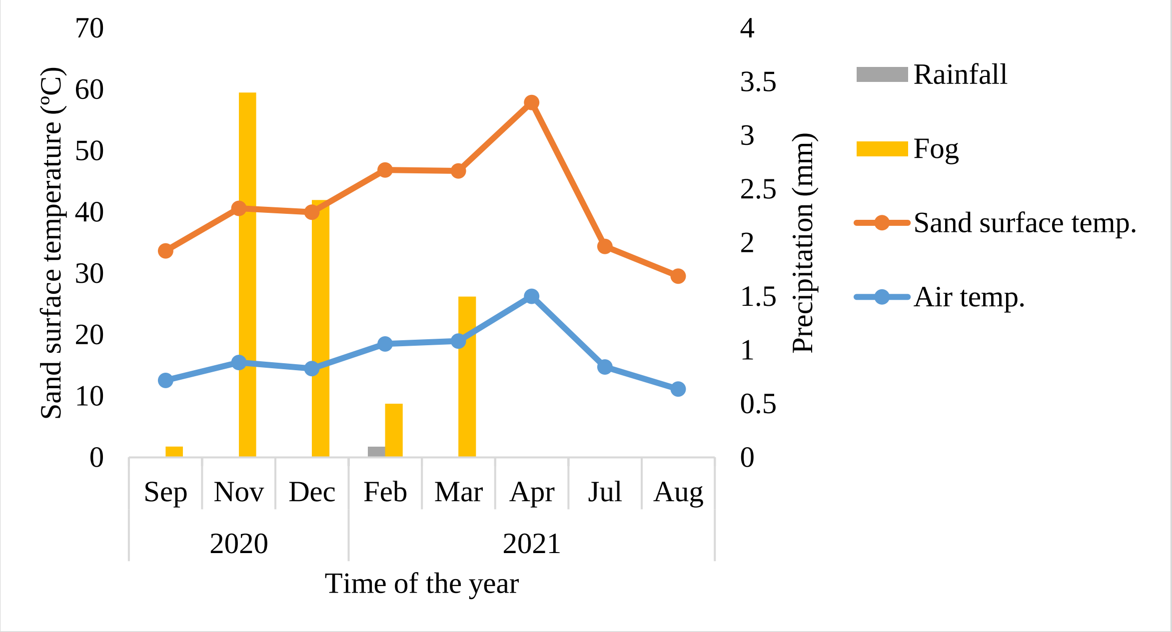


Figure 3.1. Composite graph showing the average monthly temperature of the sand surface and air, and the total monthly precipitation from fog and rainfall recorded for all nights (18:00-05:00) that preceded tracking during the study (September 2020-August 2021).

3.2. Hummock density

Hummock density was higher at Moles' End (0.85 hummocks/m^2) compared to Kahani (0.04 hummocks/m^2) and Station Dune (0.00055 hummocks/m^2).

Table 3.1. Vegetation densities at the three study sites.

Sites	Area (m^2)	No. of hummocks	Density (hummocks/m^2)
Station Dune	596049	3294	0.00055
Moles' End	203531	173564	0.85
Kahani	314641	13264	0.04

3.3. Descriptive statistics of foraging tracks

On average, across all sites Namib Golden Moles moved 265 m (±17.98), with a net displacement of 94 m (±5.21) (Table 3.2). Each track has on average 216 (±27.32) head dips and included an average of 7 (±0.63) sand swims covering an average distance of 20 m (±1.58). Moles visited an average of 12 (±1.13) vegetation hummocks per night. See Appendix 11 for the descriptive statistics of foraging tracks per site.

Table 3.2. Summary statistics of foraging tracks of all individual moles tracked.

	N	Minimum	Maximum	Mean	Std. Error	Std. Deviation	Median
Track length (m)	56	8.80	607.25	264.72	17.98	134.57	261.8
Net displacement(m)	56	6.40	200.67	94.07	5.21	39.02	90.02
No. of head dips/track	54	1.83	1170.46	216.31	27.32	200.79	151.75
No. of sand-swims/track	56	0.80	22.38	7.34	0.63	4.71	5.75
Sand swimming length (m)	56	3.20	56.33	20.24	1.58	11.82	18.41
No. of hummocks encountered/track	56	0.80	34.40	12.29	1.13	8.47	8

3.3.1. Comparison of track length, net displacement and track straightness between study sites.

The mean track length (ANOVA: H= 9.98, df=2, p<0.01, Figure 3.2a) and track straightness (ANOVA: H= 5.72, df=2, p=0.02, Figure 3.2c) varied significantly between sites. A post hoc Tukey test revealed significant differences in track length between Station Dune and Moles' End (p=0.02), and Kahani (p<0.01). The straightness also varied significantly between Station Dune and Moles' End (p=0.01). There was no significant difference in mean track length between Moles' End and Kahani (p= 0.29) as well as in straightness between Kahani and Station Dune (p=0.10), and Moles' End (p=0.55). There was no significant difference in net displacement (Kruskal Wallis (KW): H= 3.25, df=2, p=0.20, Figure 3.2b), between the three sites.

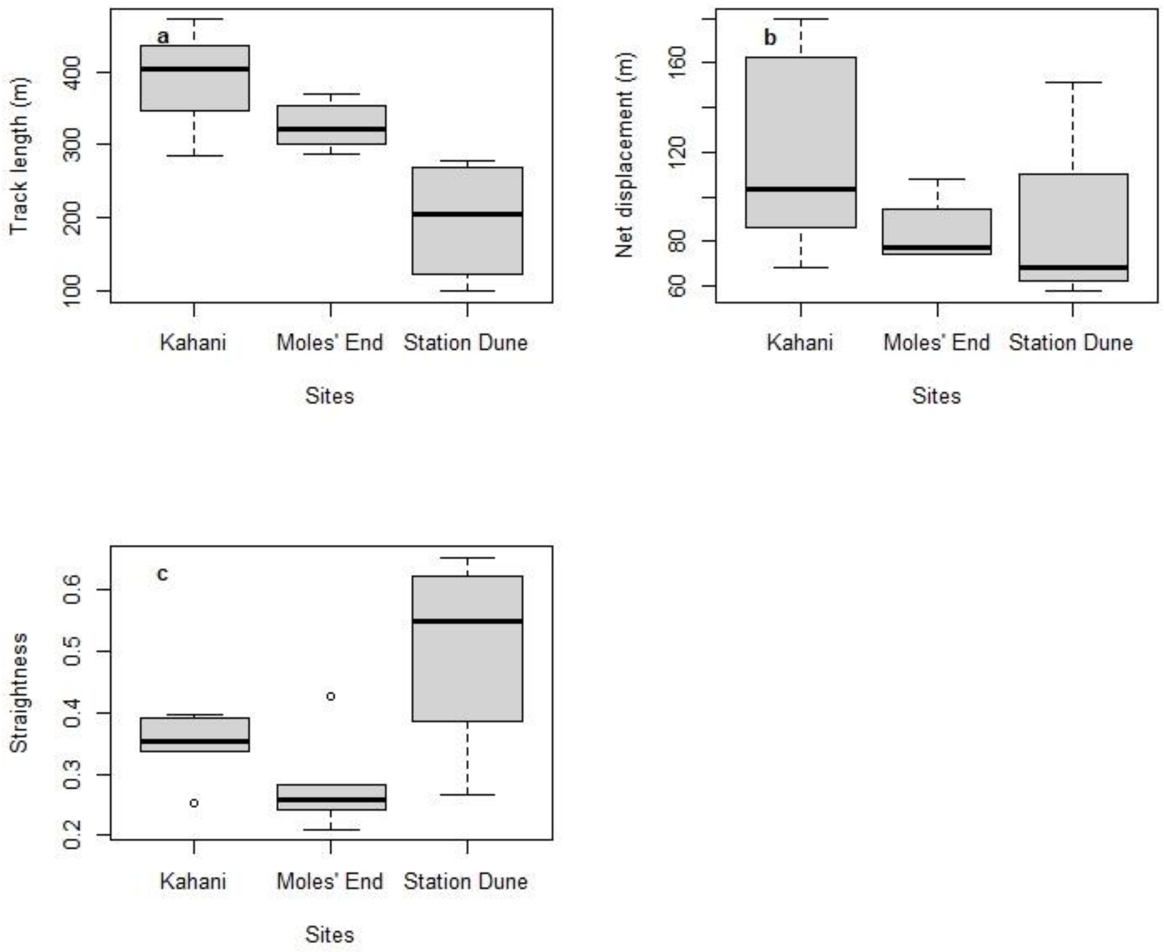


Figure 3.2. Box and whisker plots showing the mean, standard deviation and outliers of the a) track length (m), b) net displacement (m) and c) straightness of Namib Golden Moles' foraging tracks at Station Dune (4), Moles' End (6) and Kahani (n=5) in summer (November 2020 to April 2021).

3.3.2. Temporal variation in track length, net displacement and straightness at Station Dune.

The mean track length (KW: H=22.61, df=5, P<0.01) and displacement (ANOVA: H=3.003, df=5, P=0.02, Figure 3.3a) varied significantly with month. A post hoc Dunn test revealed significant differences in track length between the month of August which had the lowest average and, February (highest, p<0.01), March (p<0.01), September (p=0.01), November (p=0.049); February and July (p<0.01), November (p=0.04); as well as July and March (p=0.01), while a post hoc Tukey test revealed a significant difference in displacement between September and August (p=0.01) see Appendix 4. a &b). The mean straightness also varied significantly with month (ANOVA: H=14.19, df=5, p<0.01, Figure 3.3b), with significant differences between February which had the lowest levels of straightness and September (p<0.01), August (p<0.01), July (p<0.01) as well as between July and March (p<0.01) (Appendix 4c).

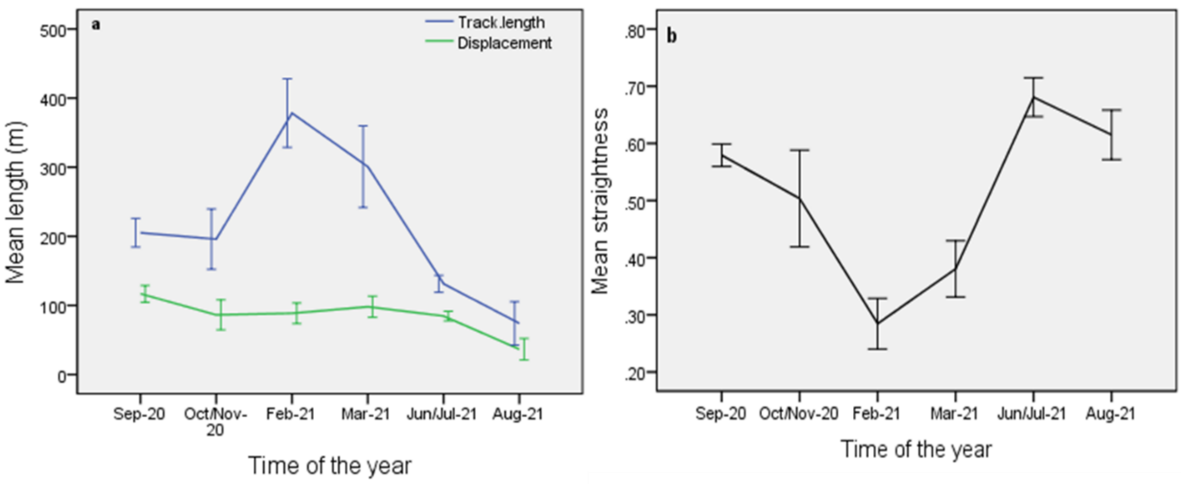


Figure 3.3. Line graph with error bars (SE) showing the monthly mean of a) the total length (m), net displacement (m) and b) straightness of Namib Golden Moles tracks throughout the year at Station Dune.

3.3.4. Predictors of track length

The most parsimonious GLMs (Table 3.3) retained season (z=5.76, P<0.01, Table 3.4) and sand surface temperature (z=5.72, P<0.01, Table 3.4) as significant predictors of the track length with longer tracks in warm summer and shorter tracks in colder winter (Figure 3.4).

Table 3.3. Model selection value for the top six generalised linear models (with Gaussian distribution and the identity link function) with the track length as the response variable and the covariates: season, vegetation density and the average sand surface and ambient temperature.

Model	**BIC**	**ΔBICc**
Track length= $\beta_0 + \beta_1$Season	668.9	0.00
Track length= $\beta_0 + \beta_1$Sand surface temperature	669.2	0.00
Track length= $\beta_0 + \beta_1$Sand surface temperature + vegetation density	672.7	3.52
Track length= $\beta_0 + \beta_1$Season + Vegetation density	672.7	3.83
Track length= $\beta_0 + \beta_1$Season + Ambient temperature	672.9	3.96
Track length= $\beta_0 + \beta_1$Season + Ambient temperature + Vegetation density	676.6	7.68

Table 3.4. Summary statistics of the top two most parsimonious GLMs (BICs =668.9 and 669.2) for the effect of a) season and b) average sand surface temperature on the length of Namib Golden Moles' tracks.

Variable	Estimate	Std. Error	Z	P
Intercept	151.10	24.79	6.095	1.36e-07
Season	177.36	30.80	5.760	4.60e-07

Variable	Estimate	Std. Error	Z	P
Intercept	-252.72	91.89	-2.75	0.00818
Sand surface temperature	20.94	3.66	5.72	5.32e-07

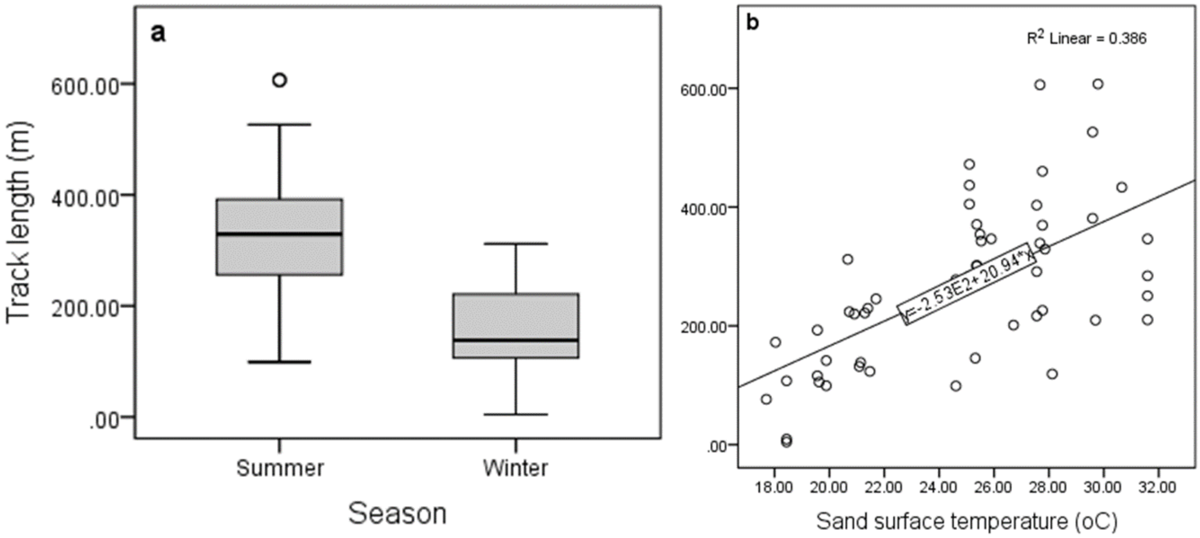


Figure 3.4. a) Box and whisker plots showing the mean, standard deviation and outliers of the track length in summer and winter. b) A regression showing the significant relationship between Namib Golden Moles track length and the average sand surface temperature of the night on which tracks were made.

3.3.5. Spatial and temporal variation in head-dipping behaviour

Moles dipped their heads in the sand at an average rate of 0.79 times per meter, with a range between 0 and 4.10 and a median of 0.62. The frequency of head-dips varied significantly between the three study sites (ANOVA: H=8.51, df=2, p=0.01, Figure 3.5a), with low frequency at Station Dune compared to Moles' End ($p<0.01$) and Kahani (p=0.04). The frequency of head-dips also varied significantly with month (KW: H=20.39, df=6, $p<0.01$, Figure 3.5b). A post hoc Dunn test shows a significant difference in frequency of head-dips between August and, February ($p<0.01$), March ($p<0.01$), June (p=0.01), July (p=0.04) (see Appendix 5).

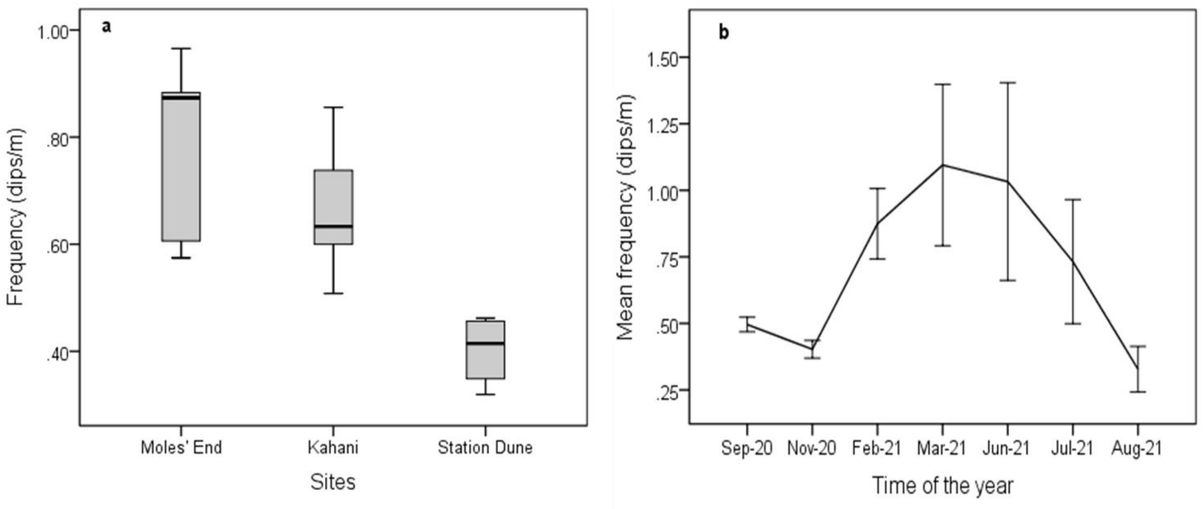


Figure 3.5. a) Box and whisker plot showing the mean, standard deviation and outliers of the number of head-dips per meter for Namib Golden Moles at Station Dune (n=4), Kahani (n=5) and Moles' End (n=5). b) A line graph with error bars (SE) showing the monthly mean number of head-dips per meter at Station Dune.

3.3.6. Spatial and temporal variation in sand-swimming behaviour

The mean number of sand-swims per track (KW: H=10.35, df=2, p=0.01), the mean total length sand-swims per track (ANOVA: H = 5.17, df=2, p=0.02) and the mean percentage of sand-swims per track (ANOVA: H=8.51, df=2, p=0.01) varied significantly between the three sites (Figure 3.6a), with more sand-swims recorded at Moles' End compared to Station Dune (p<0.01) and Kahani (p=0.01) and shorter swims at Kahani compared to Moles' End (p=0.02). There was no significant difference in the mean number of sand-swims between Station Dune and Kahani (p=0.33) as well as in the mean total length of sand-swims between Kahani and Station Dune (p=0.09) and Kahani and Moles' End (p=0.88). A post hoc Tukey test revealed that the mean percentage of sand-swims at Kahani varied significantly from that of Station Dune (p=0.04) and Moles' End (p=0.28).

The mean number of sand-swimming events per track varied significantly between the different times of the year (KW: H=13.21, df=5, p=0.02, Figure 3.6b), with more swims recorded in March compared to August (p=0.03). There was no significant difference between the other months (see Appendix 6a.). There was no significant difference in the mean length of sand-swims (KW: H=4.64, df=5, p=0.46, Figure 3.6b), but the mean percentage of sand-swimming per track differed significantly (KW: H=21.47, df=5, p<0.01, Figure 3.6b) and was lower in February compared to June/July (p=0.038) and August (p<0.01). See appendix 6 b. for the month-to-month comparisons of the mean percentage sand-swimming.

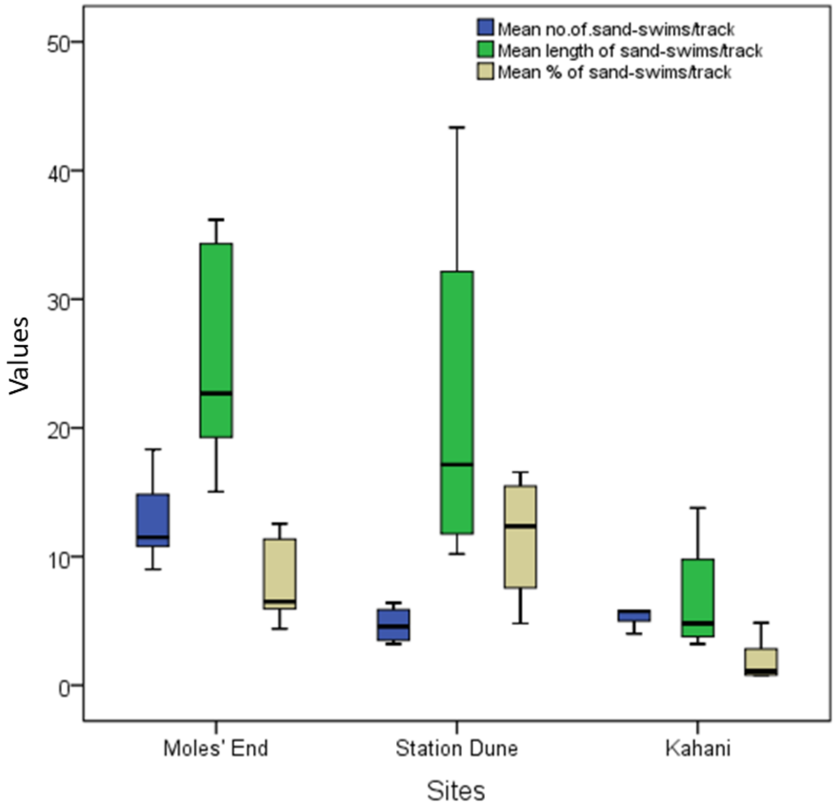


Figure 3.6a. Box and whisker plots showing the mean, standard deviation and outliers of the number of sand-swims per track, length of sand-swims (m) and percentage of each that was sand-swimming for Namib Golden Moles at Station Dune (n=4), Kahani (n=5) and Moles' End (n=6) in the summer.

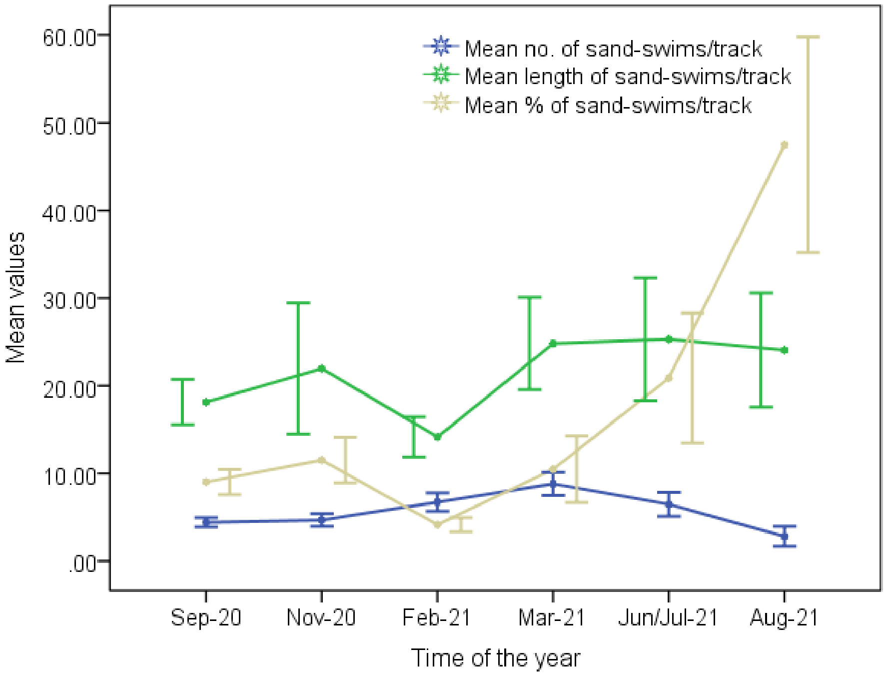


Figure 3.6b. Line graph with error bars (SE) showing the monthly mean number of sand-swims per track, mean length of sand-swimming (m) and the mean percentage of sand-swims per track for Namib Golden Moles at Station Dune from September 2020 to August 2021. SE not centred on data points to avoid overlaps.

3.3.7. Variation in visits to hummocks

The mean number of hummocks visited varied significantly between the three sites (ANOVA: H=14.6, df=2, p<0.01, Figure 3.7a), as well as between months (KW: H=12.27, df=5, p=0.03, Figure 3.7b). The number of hummocks visited was significantly lower at Station Dune compared to Moles' End (p<0.01) and Kahani (p<0.01). There was no significant difference between Moles' End and Kahani (p=0.91). More hummocks were visited in February 2021 compared to August 2021 (p=0.014) but there were no differences between the other months (see Appendix 7 for the month-to-month comparisons).

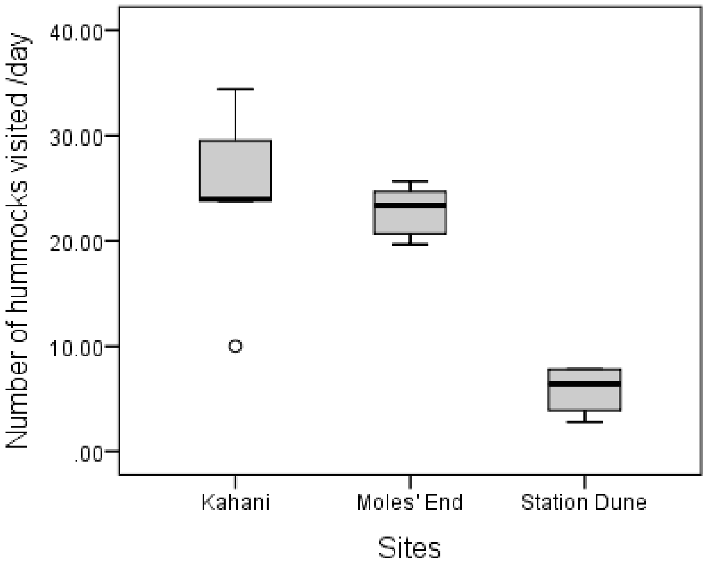


Figure 3.7a. Box and whisker plot showing the mean, standard deviation and outliers of the number of hummocks visited per day by Namib Golden Moles at Station Dune, Moles' End and Kahani.

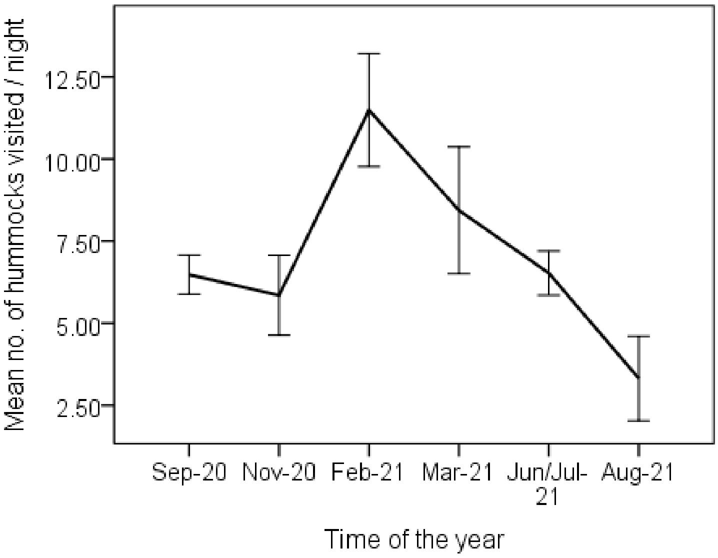


Figure 3.7b. A line graph with error bars showing the monthly mean number of hummocks visited per day by Namib Golden Moles at the Station Dune between September 2020 and August 2021.

3.3.7.1. Relationship between hummock encounter rate and track length, track straightness, and head-dipping frequency

The mean number of hummocks encountered correlated positively with mean track length (test stat rho = -0.83, p<0.01, n= 56, Figure 3.8a), negatively with track straightness (rho=0.54, p<0.01, n=56, Figure 3.8b) and positively with the frequency of head-dips (rho=0.58, p<0.01, n=54, Figure 3.8c).

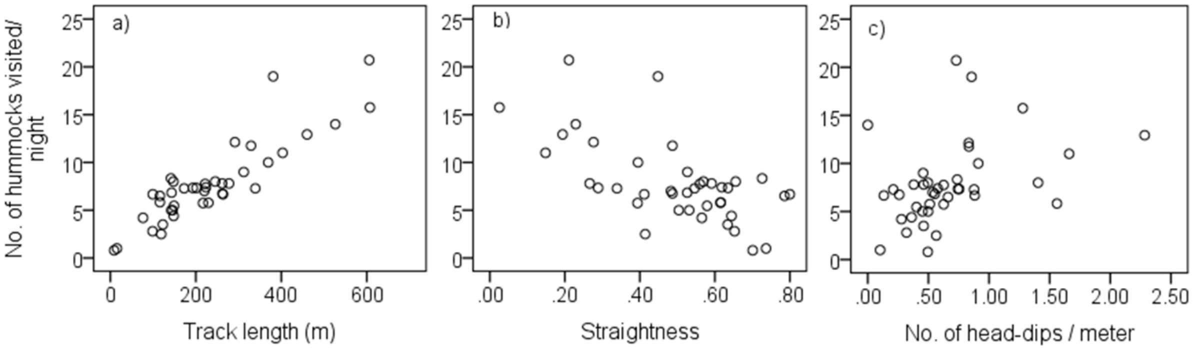


Figure 3.8. Scatter plots showing the relationship between the mean number of grass hummocks encountered and a) total track length, b) track straightness, and c) head-dips frequency for individual moles across all sites.

3.3.7.2. Number of hummocks reused and return time

Namib Golden Moles visited an average of 12 hummocks per day of which an average of two (or 18%) had been previously visited by the same mole within the previous seven days (the average number of days moles were followed) and with an average return time to any given hummock of about two days. There was no significant difference in the mean number of hummocks re-visited (ANOVA: H=0.95, df=2, p=0.42, Figure 3.8a) and the mean return time (ANOVA: H=1.16, df=2, p=0.20, Figure 3.8b) between the three sites. Spearman correlation test also revealed a weak negative correlation between the number of revisits and return time (rho= -0.12, p=0.01, n= 56, Figure 3.9).

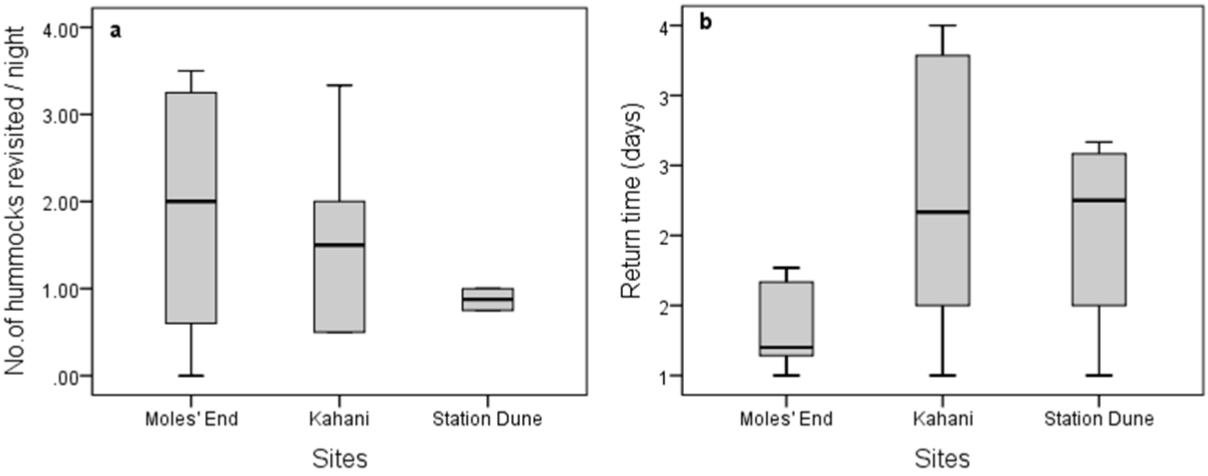


Figure 3.8. Box and whisker plots showing the mean, standard deviation and outliers of a) the number of hummocks revisited per individual/day and b) the return time (days) from the last visit by Namib Golden Moles at Station Dune (n=4), Moles' End (n=6) and Kahani (n=5).

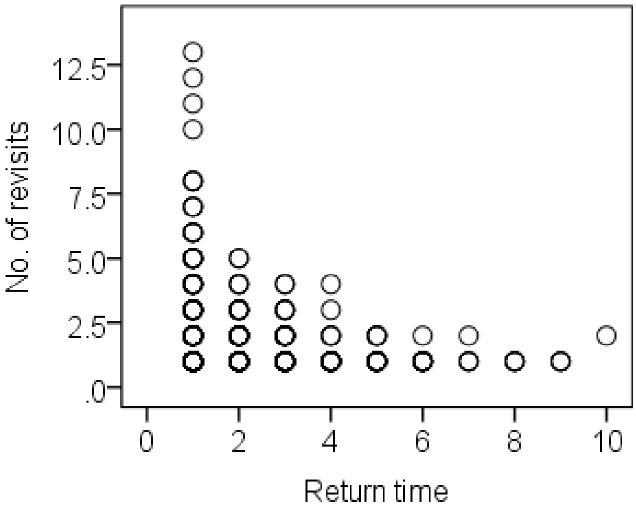


Figure 3.9. Scatter plot showing the relationship between the number of times Namib Golden Moles revisited a hummock and the time (days) it took to return to that hummock.

3.4. Track intersections

The mean number of intersecting Namib Golden Moles' tracks across all sites was 0.57 (±0.08) with a median of 0.40 and a range between 0.00 and 3.25. There was no difference in the mean number of intersections between the three study sites (ANOVA: H=1.81, df=2, p=0.21, Figure 3.10a). However, the mean number of track intersections at Station Dune varied with months of the year (KW: H=18.45, df=5, p<0.01, Figure 3.10b), with more intersections recorded in September 2020 compared to June/July 2021 (p=0.03) and August 2021 (p<0.01). There was no significant difference in the number of intersections between September, November, February and March (both p>0.05, see Appendix 8).

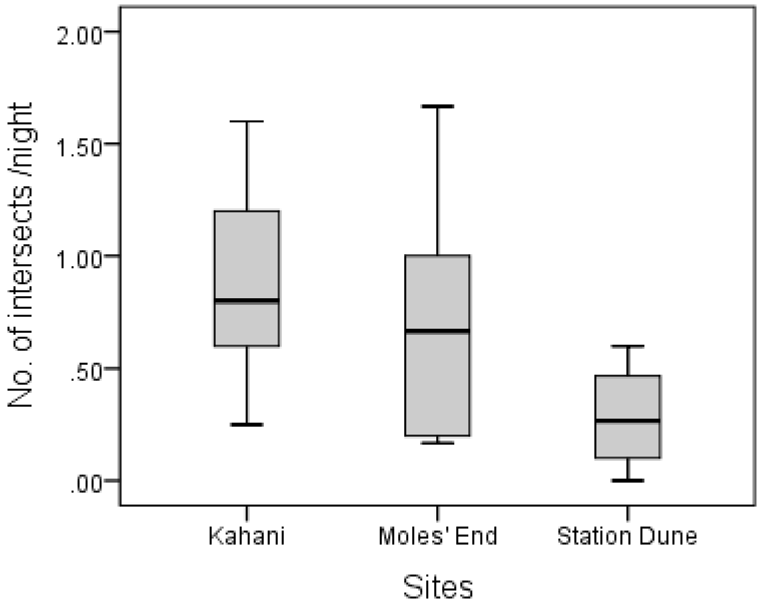


Figure 3.10a. Box and whisker plot showing the mean, standard deviation and outliers of the mean number of Namib Golden Moles’ tracks that intersected at the three study sites between November and December 2020.

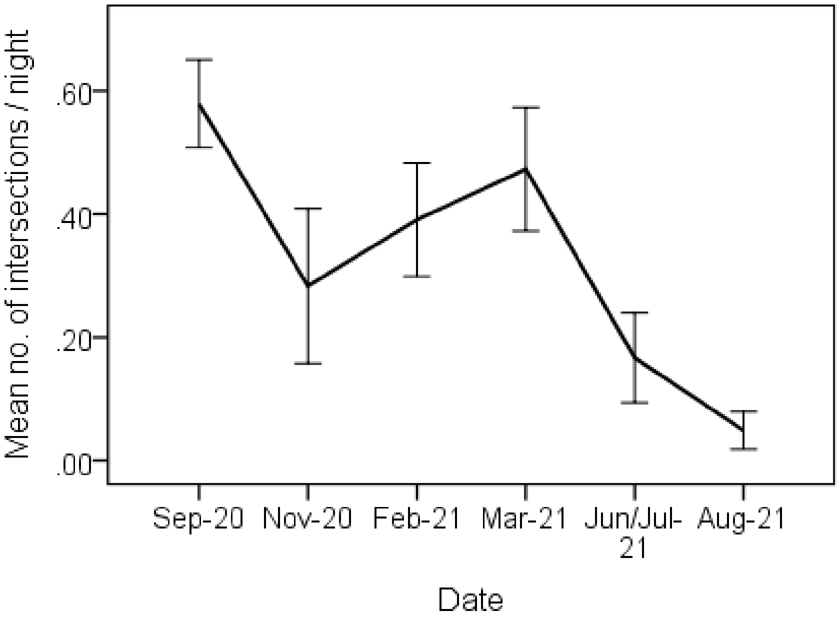


Figure 3.10b. Line graph with error bars (S.E) showing the monthly mean number of Namib Golden Moles’ tracks intersections at the Station Dune between September 2020 and August 2021.

3.5. Days with no activity

Inactivity was recorded for nine moles, of which five were inactive for just one day, one was inactive for five consecutive days, while the other three were inactive for at least two non-consecutive days within a tracking period (Table 3.5).

Table 3.5. Inactivity patterns for individual moles in different months across all sites. Data include the number of nights each mole was inactive and whether they were consecutive or non-consecutive nights. The ambient and sand surface temperature on the night of inactivity is provided with an average for multiple inactive nights.

Mole ID	Month and year	No. of tracking days	No. of nights inactive	Air temperature (°C)	Sand surface temperature (°C)
3	Sep 2020	14	1	14.23	22.06
6	Sep 2020	13	1	9.74	19.18
9	Sep 2020	5	1	12.43	22.19
27	Feb 2021	5	1	19.86	29.31
36	Mar 2021	14	2 (non-consecutive)	20.01	28.00
47	Jul 2021	7	1	16.99	20.37
52	Aug 2021	10	4 (non-consecutive)	10.85	18.10
53	Aug 2021	10	2 (non-consecutive)	11.02	18.13
54	Aug 2021	10	5 (consecutive)	10.23	17.70

3.6. Movement direction

Moles moved in all directions relative to their starting point, (circular mean direction=43) but the most likely direction was North (Figure 3.11).

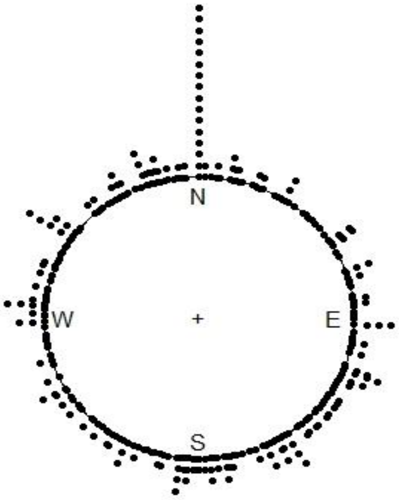


Figure 3.11. Circular plot showing the daily directionality of movement of Namib Golden Moles after emerging from their sleeping site.

3.7. Home ranges

The home range size of Namib Golden Moles ranged between 0.02 and 17.09 hectares, with an average of 5.08 hectares (±0.56, n=54, Appendix 9). There was no correlation between home range size and the number of tracks obtained for an individual throughout the study (rho=0.26, p=0.06, n=54), nor a difference in mean home range size between the three sites (KW: H=4.93, df=2, p=0.09, Figure 3.12a). The statistical test further revealed no significant difference in the mean home range size at Station Dune between different months of the year (KW: H=10.95, df=5, p=0.05, Figure 3.12b).

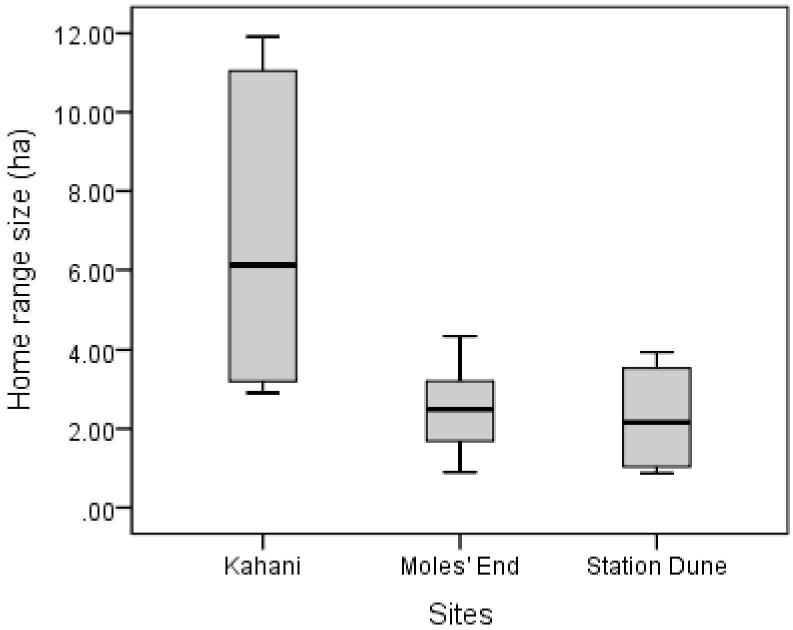


Figure 3.12a. Box and whisker plot showing the mean, standard deviation and outliers of home ranges size of Namib Golden Moles tracked at Station Dune (n=4), Moles' End (n=6) and Kahani (n=5) in October/November and December 2020.

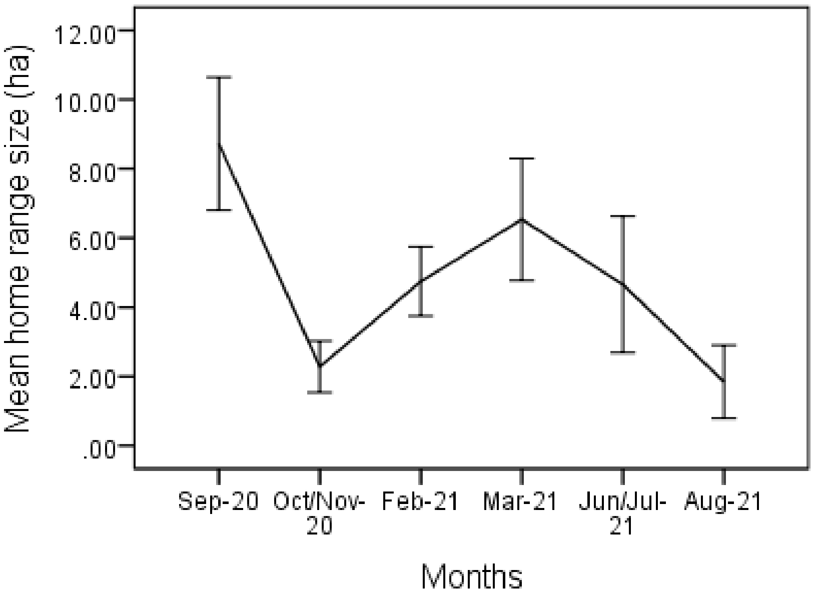


Figure 3.12b. Line graph with error bars (SE) showing the monthly mean home range size of Namib Golden Moles between September 2020 and August 2021 at Station Dune.

3.8. Habitat use and preference

Moles mostly used hummocks for resting and foraging compared to open areas (Figure 3.13). However, the proportion of foraging around vegetation and in open areas differed between sites, with an almost equal proportion at the Station Dune compared to Kahani and Moles' End where they were mostly foraging around vegetation (Figure 3.13a). The use of vegetation and open areas for foraging was similar at Kahani and Moles' End. The proportion of resting also differed markedly between the three sites, with Moles' End showing a higher percentage of resting in vegetation compared to Kahani and Station Dune but little difference between Station Dune and Kahani (Figure 3.13b). Manly's alpha index revealed that Namib Golden Moles showed a strong preference toward hummocks for both resting (α=0.99, Table 3.6a) and foraging (α=0.96, Table 3.6b) compared to open areas (α=0.01 and 0.04).

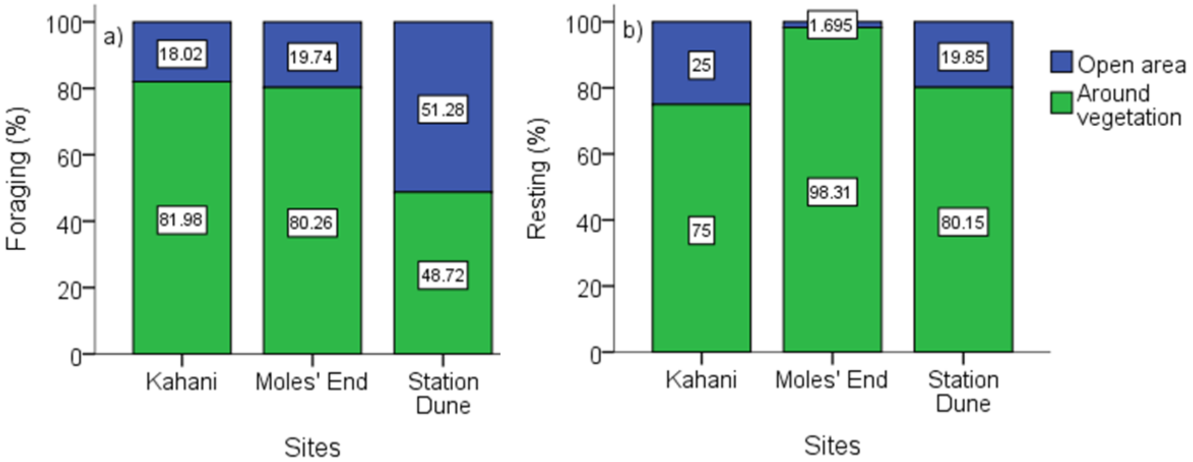


Figure 3.13. Bar graphs showing the percentage number of times Namib Golden Moles a) foraged and b) rested around grass hummocks and open areas across the three study sites.

Table 3.6 (a). The number of times Namib Golden Moles used either open areas or hummocks for resting relative to the availability of the habitat and the Manly's α_r index.

Habitat	**Number of times used**	**Availability**	**Manly's alpha (α_r)**
Open area	29	0.95	0.01
Hummocks	226	0.05	0.99

Table 3.6 (b). The number of times Namib Golden Moles used either open areas or hummocks for resting relative to the availability of the habitat and Manly's αr index.

Habitat	**Number of times used**	**Availability**	**Manly's alpha (α_r)**
Open area	592	0.95	0.04

Hummocks	839	0.05	0.96

3.8.2. Resting microhabitats

The frequency of resting varied across microhabitats (Figure 3.14) with the dune base being used more than the avalanche base, and the crest. The slip face, avalanche base, slope and the crest were all used at a similar frequency. However, Manlys’ alpha index, (Table 3.7) that incorporates the availability of microhabitats, shows that Namib Golden Moles prefer the avalanche bases (α=0.39) and slip faces (α=0.37) for resting compared to the dune bases (α=0.13), slopes (α=0.07) and crests (α=0.04).

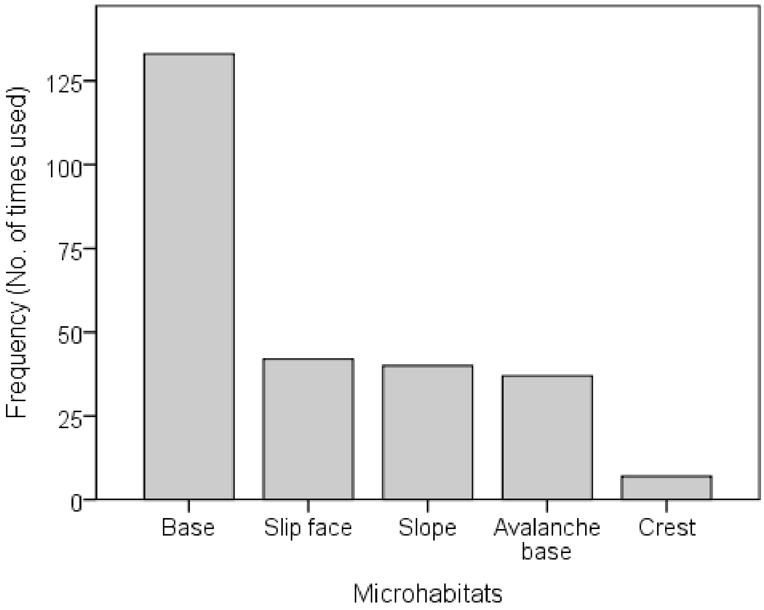


Figure 3.14. Bar graph showing the number of times Namib Golden Moles used different classes of microhabitats (dune zones) for resting at the Station Dune.

Table 3.7. The number of times Namib Golden Moles used different microhabitats for resting relative to their availability and Manly’s α_r index

Microhabitat	**Number of times used**	**Availability**	**Manly’s alpha (αr)**
Dune base	133	0.53	0.13
Slip face	42	0.06	0.37
Slope	40	0.28	0.07
Avalanche base	37	0.05	0.39
Crest	7	0.09	0.04

3.8.3. Dimensions of resting hummocks

The frequency of resting (Figure 3.15) differed across different hummock categories with big hummocks used more than small hummocks and medium hummocks. ‘Others’ was the least used. Manly’s alpha index (Table 3.8) revealed that Namib Golden Moles prefer big hummocks (α=0.52) for resting compared to medium α=0.22) and small hummocks (α=0.26).

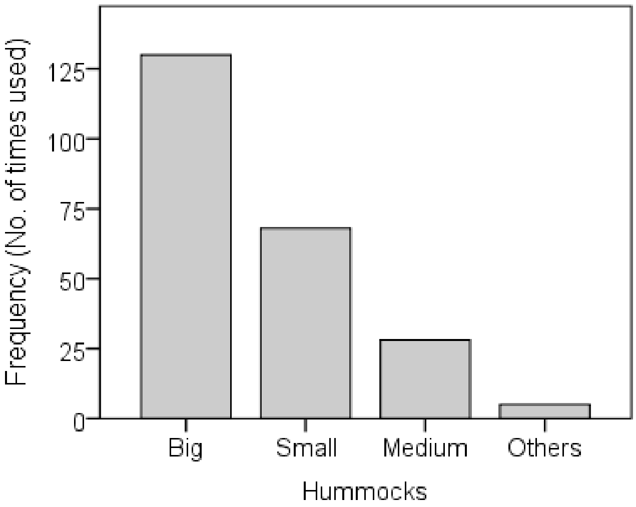


Figure 3.15. Bar graphs showing the number of times Namib Golden Moles used different vegetation hummocks categories for resting at Station Dune.

Table 3.8. The number of times Namib Golden Moles used different hummocks for resting relative to their availability and Manly's α_r index.

Hummocks	**Use (number of times)**	**Availability**	**Manly's alpha (α_r)**
Big hummock	130	0.39	0.52
Small hummock	68	0.41	0.26
Medium hummock	28	0.20	0.22

3.8.4. Foraging microhabitats

The frequency of foraging varied across different microhabitats (Figure 3.16) with the dune base used more compared to the avalanche base slip face, slope and the crest. Relative to the availability of microhabitats, Namib Golden Moles prefer to forage mostly at the avalanche bases (α=0.49, Table 3.9) and slip faces (α=0.31) and least prefer the dune bases (α=0.13), crests (α=0.03) and dune slopes (α=0.04).

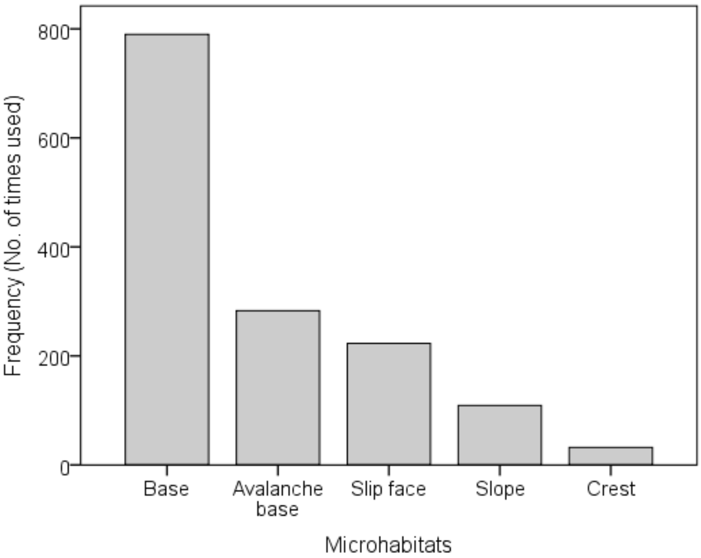


Figure 3.16. Bar graph showing the number of times Namib Golden Moles foraged on different microhabitats at Station Dune.

Table 3.9. The number of times Namib Golden Moles used different microhabitats for foraging relative to their availability and Manly's αr index.

Microhabitat	**Number of times used**	**Availability**	**Manly's alpha (αr)**
Dune base	790	0.53	0.13
Avalanche base	283	0.05	0.49
Slip face	216	0.06	0.31
Slope	116	0.28	0.04
Crest	32	0.09	0.03

3.8.5. Dimensions of foraging hummocks

The frequency of foraging varied between different classes of hummocks (Figure 3.16). Small and big hummocks were mostly used compared to medium hummocks while "others" was the least used. Manly's alpha index (Table 3.10) reveals that, Namib Golden Moles prefer to forage around small (α=0.48) and big hummocks (α=0.37) compared to medium-sized hummocks (α=0.19).

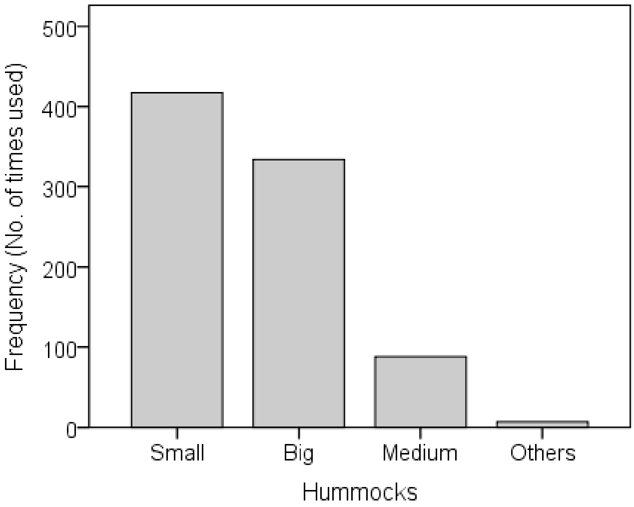


Figure 3.16. Bar graph showing the number of times Namib Golden Moles foraged around different classes of vegetation hummocks at Station Dune.

Table 3.10. The number of times Namib Golden Moles used different hummocks for foraging relative to their availability and Manly's αr index.

Hummocks	**Use (number of times)**	**Availability**	**Manly's alpha (α_r)**
Big hummock	334	0.39	0.37
Small hummock	417	0.41	0.48
Medium hummock	88	0.20	0.19

Discussion

4.1. Movement behaviour

Overall, my findings are similar to those of other studies on the movement patterns and habitat use of Namib Golden Moles in the Namib dune environment. The study confirms that Namib Golden Moles indeed have relatively larger home ranges compared to other subterranean insectivores such as *Amblysomus hottentotus, Talpa europaea, Scalopus aquaticus* and *Scapanus orarius* (Fielden, 1989). Larger home ranges than those of mesic moles reflects the scarce and patchily distributed food resources in the Namib Desert (Fielden, 1991) and is consistent with the findings for a variety of desert dwelling mammals (Fielden, 1989). Home range size in this study averaged 5.08 ha that is similar to that of Fielden (1991) (4.63 ha) but larger than that reported by Rathbun and Rathbun (2007). The latter study used VHF tracking of tagged moles to estimate home ranges, which provides a much coarser estimate of habitat use than tracks. Tracks indicate exactly where a mole moved, how it moved and how often it paused for a head dip, while VHF recordings are relatively sparse samples of where an animal is in space at select sample times. GPS positions are less accurate when using VHF tracking which relies on triangulation of the position from a distance. Additionally, VHF tracking provides no information on the mode of locomotion (i.e., surface walking versus sand swimming) or behaviour (i.e., head-dipping) of the animal. The strength of VHF tracking is the reliability of repeatedly locating the sleeping site of a given mole. There were occasions when the track I was following intersected another in such a manner that I could no longer be certain that I was following the original track. Under these circumstances (n=23), I had to abandon that mole in that month leading to unequal effort across months. While this represents a caveat of tracking spoor, I still consider it preferable to VHF tracking which is both invasive and provides limited behavioural information.

Track length in this study averaged 265 m, which is similar to that reported by Fielden (1991) (290m) but much less than the 3 miles (4500 m) noted by Holm (1969) in the dune system at Gobabeb and the 1410 m reported by Seymour, *et al*. (1998) at a site 10 km south of Gobabeb. Rathbun and Rathbun (2007) reported an average track length of only 13.8 m that once again may reflect the different method used (VHF tracking). VHF tracking provides only a small number of GPS waypoints to estimate movement rather than recording the exact movement of the animal as derived from following their spoor. While this difference readily explains why VHF derived tracks are shorter, they do not explain why net displacement in this study (94 m) was also substantially higher than that of Rathbun and Rathbun (2007) who found an average day and night displacement of 7.2 m (8.8 m during the day, 5,6 m at night). Net displacement is the distance between two sleeping sites and should be independent of the method used as it relies on estimating the distance between GPS points. This suggests that moles in Rathburn and Rathburn (2007) were moving much smaller distances than those in this and other studies.

This study also found a higher frequency of head-dips (0.78 dips/m) and sand-swims (7 swims/track) and slightly longer length of sand-swimming (20 m) compared to 0.29 dips/m and 16 m of sand-swimming reported by Seymour, *et al.* (1998). Namib Golden Moles use sand-swimming and head-dips to sample their seismic environment and detect prey (Narins, *et al.* 1997). The mean number of hummocks (12) encountered per track across all sites was slightly less than that recorded in earlier study at Gobabeb (19) but matches that recorded at the Far East site (11, Fielden, *et al.* 1990a). Sand-swimming, which is an energetically more expensive mode of locomotion was typically only used in the vicinity of vegetation and close to or on grass hummocks. Similar results were shown by Fielden, *et al.*, (1990a) who attributed this shift in behaviour to a higher prey concentration on hummocks which may offset the higher locomotory costs.

Moles moved off in every possible compass direction from their overnight sleeping sites with only a slight bias towards a northerly direction. The lack of clear directional bias in movement may reflect the scattered distribution of hummocks throughout the environment which would not favour an overall directional bias. Rather moles are predicted to move from hummock to hummock using vibrational cues of both prey and vegetation that are transmitted through the sand and detected by the large auditory bullae of the moles (Narins, et al., 1997).

Track length and displacement distance differed significantly with time of the year supporting the suggestion that weather influences the moles' movement patterns (Fielden, 1989). It may not be a coincidence that track length at Station Dune peaked in February, the same month rainfall was recorded during tracking days. Tracks were shorter in the winter months of June/July and August when sand surface temperature was lower. The GLM result shows that the length of tracks is mostly influenced by season and sand surface temperature. Rathbun and Rathbun (2007) also found shorter track lengths in winter and suggested cooler temperatures restrict movement because of thermoregulatory costs. Similarly, other heterothermic insectivorous species like bats are also known to hunt for shorter periods of time in cold weather and may completely cease foraging when the temperature falls below a certain threshold (O'Farrell & Bradley, 1970; O'Shea & Vaughan, 1977, Fielden, 1989). Furthermore, seven moles did not move for at least one night between June and September compared to only two in the other five months in which tracking was carried out. On six of these occasions the average night-time air temperature dropped below 15°C while the sand surface temperature dropped below 23°C on seven occasions. In one case in August, an individual remained inactive for five consecutive days suggesting the animal had entered torpor. Ambient and sand surface temperature on these nights averaged 13.5°C (range 11.83-15.33) and 21.7°C (range: 20.22-22.62), respectively (Table 3.3). Daytime ambient and sand surface temperature averaged 21.73°C (range: 18.67-24.23) and 26.86°C (range: 25.89-27.31), respectively. While torpor in small mammals is more likely at lower temperatures it may also reflect a lack of availability of food, or a combination of lower temperatures and food restriction, typical of winter conditions (Bennett and Spinks, 1995).

Torpor has been described in many species of the Afrotheria clade (Lovegrove and Génin, 2008; McAllan, and Geiser, 2018) and other fossorial small mammals. Data from *Amblysomus hottentotus* reveals that torpor may occur below 15°C and above 30°C (Kuyper, 1985), while *Neamblysomus julianae*, entered shallow torpor at temperatures outside the range of 12.4 to 34.4°C (Scantlebury *et al.*, 2008). *Chrysochloris asiatica* reportedly entered the state of torpor at an ambient temperature of 9°C (Bennett and Spinks, 1995). Tenrecs like *Echinops telfairi*, remined in torpor for 12 to 18 hours each day but can go into a prolonged torpor for two to four days but can also remain in shallow torpor for weeks (Lovegrove and Génin, 2008; McAllan and Geiser, 2018). Rock Elephant Shrews, *Elephantulus myurus*, entered torpor when their body temperature dropped below 15.3°C (Mzilikazi, and Lovegrove, 2004).

My results showed variation in most measures of movement behaviour, viz., track length, straightness of tracks, the frequency of head-dips, the number of sand-swims per track, sand-swimming length, the percentage of sand-swimming and the number of hummocks encountered per track of Namib Golden Moles between sites with different vegetation densities. Variation in track length contrasts with early studies where tracks were shorter in areas with higher vegetation density (Fielden *et al.*, 1990a). The generalised linear models revealed that vegetation density had little effect on track length and tracks were shorter at Station Dune despite this site having the lowest density of vegetation. According to Fielden et al., (1990a), moles are likely to continue foraging until their energy requirements have been satisfied, and hence their track length depends on the number of 'profitable' patches encountered. Analysis of foraging events at Station Dune further shows that moles were not always foraging in hummocks but also in open areas. Therefore, it is likely that Station Dune tracks were shorter because there are relatively more 'profitable' patches that may not be necessarily associated with extant grass hummocks but their remnants (i.e., roots). Net displacement distance was similar among the three study sites, suggesting that differences in track length reflect greater foraging effort by moles within a certain range (home range).

Tracks were more tortuous at the site (Moles' End) with the highest vegetation density. De Knegt, *et al*. (2007) argue that this behaviour originates from the larger number of cues (i.e., vibrations from vegetation) available to the foragers to include in their decision making. Field observation shows that most turns were after dips, suggesting that they mostly turn after detecting a vibration linked to vegetation and/or prey. Densely vegetated sites will have more hummocks in closer proximity and thus moles are predicted to turn more frequently when navigating between them relative to traversing large open areas such as in typical of Station Dune site.

Home range size varied markedly amongst individuals (0.02–17.09 ha) in this study, but I was unable to discern the potential drivers of this variation given I did not capture the animals and thus could not account for age, sex, size and reproductive state, all of which are predicted to be important factors (Nathan *et al*., 2008). Home range size in moles is mostly determined by the access and distribution of food (Mace, *et al*., 1983; Fielden, 1991). Both Fielden, (1991) and Holm (1967) found large home ranges in areas with low vegetation density. However, spatial comparisons of home range size reveal no difference between the three study sites despite having markedly different vegetation densities. Furthermore, home range sizes were similar throughout the year despite the prediction of seasonal fluctuations in prey density and availability (Fielden et al. 1991). I had also expected home ranges to vary with season due to restricted movement in winter, but it is possible that longer nights in winter balance out the smaller thermal window for foraging.

Namib Golden Moles mostly walked along the sand surface (87% of all movement), while frequently dipping their heads in the sand to detect prey (Narins *et al*. 1997). The frequency of head-dips was higher at sites with more hummocks, possibly reflecting increased levels of acoustic information that moles can use to navigate between hummocks. Fielden, *et al*. (1990a) found that the inter-dip lengths become shorter as the mole approach hummocks or in areas with a higher prey concentration, thus helping the moles to locate prey species within patches. The frequency of head-dips also varied monthly, with a decline in August and September reflecting the decrease in track length in these months due to low sand surface temperature that restricted the moles to short and (mostly) submerged movement. The occurrence of fog in October/November may also affect the head-dipping behaviour of the moles, directly by hardening the sand surface and indirectly by reducing the surface foraging activities of the moles.

Surface foraging, although riskier from a predation perspective, helps moles to cover greater distances than the comparatively safer but energetically more costly sand-swimming (Seymour *et al.,* 1998). Furthermore, sand-swimming is a more effective mode of moving locomotion for when feeding on subsurface prey than walking on the surface (Fielden *et al*., 1999a). The number of sand-swimming events peaked in March and was lowest in August, but the total length of sand-swimming tracks remains similar throughout the year. The decline in the number of sand-swimming events in August reflects the reduction of track length. During this time, several tracks were just below the sand surface causing the percentage of sand-swimming to surface foraging to increase. Switching to sand-swimming can also be viewed as a way of avoiding exposure to low ambient temperatures. According to Fielden (1989), the sand surface temperature below 16ºC may inhibit Namib Golden Moles surface activity. The sand surface temperature (18.4ºC) in August was however higher than the predicted cut-off by Fielden (1989).

Given that moles sand-swim more on mounds than in the open area, the assumption is that there is more prey on mounds and swimming represents active feeding. It was thus not surprising that the number of sand-swimming events was highest at the site with the highest hummock density (Moles' End). Despite this, the total distance moved while submerged was similar to the least vegetated site (Station Dune) as moles here tended to sand-swim less frequently but more intensively (i.e., when they encounter a hummock or an area of high prey concentration, they swim a greater distance). As expected, the number of hummocks visited per metre of track was higher at the more densely vegetated Kahani and Moles' End sites compared to Station Dune. Data from Station Dune (Figure 3.12) shows that Namib Golden moles encounter more hummocks when they move longer distances. This result is supported by the observation made by Fielden *et al*., (1999a), that the number of hummocks encountered by an individual depends on the length of the foraging path. Monthly variation in the number of hummocks visited was thus mainly due to differences in track length with month. The results from the Station Dune further show that moles have a greater chance of encountering more hummocks when moving tortuously, and when dipping their heads in the sand frequently. The higher number of hummocks encountered at Kahani and Moles' End may also be a function of their greater relative abundance. Neither the number of hummocks that were visited more than once nor the return time to hummocks differed between sites suggesting that optimal foraging rules were similar across all three sites.

In an environment where food is sparsely distributed, it is important for an animal not to search the same area more than once in short succession as prey are likely to become locally depleted (Fielden *et al*., 1999a). Revisits to hummocks were, however, independent of return time and most hummocks (53%) were revisited after only one day, while one was revisited for 13 consecutive days. Two individuals each visited the same hummocks for more than 10 consecutive days. Importantly these revisits were outside of the assumed breeding season (October and November, Roth, 2004) and thus returning to young in a den cannot explain this observation. Together these data suggest that prey within hummocks are not easily depleted within a single foraging event and that prey may readily evade moles after an initial surprise. Termites typically retreat to the safety of a deeper nest once a threat is detected (Noirot and Darlington, 2000) and thus moles may rely on regular surprise visits to capture those individuals actively foraging. Revisitation to specific hummocks suggests that moles have a mental map of their home range and select hummocks either having better returns on foraging effort and/or being safer and more thermally stable sleeping sites.

The low number of tracks that intersects with other moles supports the claim of Fielden (1991) that Namib Golden Moles show site fidelity in their movement, but not necessarily spatial exclusivity. Field observation shows no evidence of direct interaction between the moles whose tracks intersects, suggesting that they were temporally separated. Fielden (1991) also found little evidence of any direct interaction between neighbours as each mole forages in a different area of its home range each day suggesting that there may be a system of mutual avoidance. According to Fielden (1991), neighbouring individuals must be able to recognise each other for mutual avoidance to operate successfully. Scent marking has been demonstrated in other fossorial animals such as *Spalax ehrenbergi* (Gazit, *et al*., 1997), *Talpa europaea* and *Galemys pyrenaicus* but is yet to be demonstrated in *Chrysochloridae* (Fielden 1991). There was no difference in the mean number of tracks that intersected with other moles between the three sites with different vegetation densities, suggesting that vegetation densities have little effect on the territorial behaviour of Namib Golden Moles. The mean number of intersections was however different between months, with the peak in September and the lowest number in August. The peak was again just outside the estimated breeding season (October -November, Roth, 2004), but this was probably the time males start to explore new areas in search of females. The low intersection rate in colder June/July and August may be a consequence of shorter daily distances moved because of lower temperatures.

4.2. Habitat use and preference

Vegetation in the dunes of the Namib causes windblown sand to accumulate, which over time forms mounds or hummocks providing shade, shelter and food for many animals, including Namib Golden Moles (Robinson and Seely, 1980). Hummocks also provide a microhabitat for Namib Golden Moles allowing them to escape temperature extremes during summer and in winter (Fielden, *et al*, 1999b). Moles have high conductance and when resting in an uncovered open area must dig deeper to find a favourable thermal conditions (Fielden, 1989). Field observations show that black-backed jackals follow mole tracks to their sleeping sites and then attempt to dig them out. By resting amongst the plants and roots within hummocks, moles are afforded more protection from such predation efforts than those resting in the open (Fielden, *et al*, 1990b). This may also explain why moles showed a clear preference for not only resting in hummocks but for doing so in larger hummocks.

In areas where vegetation hummocks are scarce, moles tend to forage more in open areas. This was evident at Station Dune, where foraging events were equally distributed between hummocks and open areas but resting was almost always in hummocks despite constituting only 5% of the total habitat at the study site. Importantly hummocks are not the only source of prey and Fielden et al. (1990a) showed that prey availability does not correlate significantly with hummock size. Termite casts, which indicate termite presence, have been found in open areas were roots are apparent (likely old mounds that have lost their vegetation and hence superstructure) and in which moles routinely engage in swimming behaviour (Fielden *et al*, 1990a). Narins *et al.* (1997) suggested that moles can detect low amplitude vibrations generated by insects and may thus be able to detect termite activity when foraging in open areas.

Habitat use patterns at Station Dune site reveal that Namib Golden Moles prefer the avalanche base and slip face for both foraging and resting even though there is minimal vegetation in both microhabitats. Both the slip face and avalanche base collect wind-blown detritus (Robinson and Seely, 1980) which supports a diverse faunal community upon which the Golden Moles may feed. Wind-blown organic detritus is a crucial source of nutrition in several dune communities (Robinson and Seely, 1980). Softer, unstable sand of the slip face makes it easier for the Golden Moles to swim in the sand to access these insects and other prey items. Dune bases by contrast typically have abundant fixed vegetation and more than half of all foraging events recorded at Station Dune were at the dune base around vegetation hummocks. The crest and the leeward slope (especially the upper plinth) are known to be low in organic matter (le

Roux, 1970; Robinson and Seely, 1980) with less vegetation and hence prey. These habitats are thus avoided by Golden Moles when foraging in dunes.

4.3. Conclusions, limitations and recommendations

The findings of this study broadly support previous research on Namib Golden Moles living in the dunes of Namibia. Vegetated hummocks are critical components of this landscape providing moles with both a refuge and foraging site. Moles preferred to sleep in large hummocks, mostly travel above ground when moving between them and are more likely to both rest and sand swim in proximity to or on hummocks. Navigating to mounds appears to be achieved through detecting either noise emitted by invertebrates foraging on vegetative matter or vibrations transmitted by vegetation when the wind blows (Narins et al. 1996). Sand-swimming in open areas with evidence of old root systems suggests that moles can detect insects in the absence of above ground vegetation.

Home range size and mean track length, displacement and head dipping rates were all similar to a previous study by Fielden et al. (1990a) with moles having straighter tracks with fewer head dips in more open areas. Despite this the proportion of each track that was comprised of sand-swimming, a behaviour assumed to reflect active foraging, was similar across sites. Furthermore, the displacement distance, home ranges size, the number of times moles revisit certain hummocks, the return time to these hummocks and the number of tracks intersected each other were similar across the three sites despite having different densities of hummocks. Together these results suggest that broad scale habitat type does not exert marked effects on the movement and foraging patterns of moles. It is possible that while moles at Station Dune have less access to hummocks, they have greater access to prey at the slip face and avalanche base of dunes where plant debris accumulates and supports a diverse faunal community.

The study revealed clear temporal variation in most of the movement variables measured, including the mean length of foraging path, mean displacement distance, straightness of the track, the mean number of head-dips, the mean number and percentage of sand-swimming, the number of hummocks visited and the number of tracks intersecting those of other moles all varied seasonally. Only home ranges, the length of sand-swimming, the number of hummocks revisited and return time to specific hummocks did not differ seasonally.

A clear limitation of this study was the inability to reliably identify and hence obtain repeated movement metrics on the same moles. My results are confounded by pseudo-replication given I could not be sure I was measuring the same or different moles in each month. An obvious solution to this is to capture and mark individuals to enable routine identification. However, moles are extremely sensitive to vibrations caused by movement and tracking moles that have been tagged with VHF transmitters or a microchip requires routine disturbance of moles in their natural habitat. These disturbances in addition to the invasive procedures associated with the capture, handling and attaching or inserting of foreign objects may all impact the natural behaviour of moles (Rathburn and Rathburn 2007). Given the main objective of this study was to understand natural movement patterns both over time and in different areas I considered these methods inappropriate.

References

Aldredge, J., 2009. Factors Affecting Breeding Territory Size And Placement Of The Florida Grasshopper Sparrow (*Ammodramus Savannarum Floridanus*). *Electronic Theses and Dissertations, 2004-2019*. 4042. Retrieved, January 24, 2023, from https://stars.library.ucf.edu/etd/4042.

Asher, R.J., Maree, S., Bronner, G., Bennett, N.C., Bloomer, P., Czechowski, P., Meyer, M. and Hofreiter, M. 2010. A phylogenetic estimate for Golden Moles (Mammalia, Afrotheria, Chrysochloridae). *BMC evolutionary biology*, *10*(1), 69.

Bennett, N.C. and Spinks, A.C., 1995. Thermoregulation and metabolism in the Cape golden mole (Insectivora: *Chrysochloris asiatica*). *Journal of Zoology*, *236*(3), 521-529.

Bronner, G n.d., *Golden Moles*, IUCN Afrotheria Specialist Group, viewed 14 November 2019, <https://www.afrotheria.net/golden-moles>

Bronner, G.N. & Bennett, N.C. 2005. *Order Afrosoricida*. In *The Mammals of the Southern African Subregion, 3rd ed*. J. D. Skinner and C. T. Chimimb, Eds. Cape Town: Cambridge University Press,

Cody, M.L. 1971. Finch flocks in the Mohave Desert. *Theoretical Population Biology*, *2*(2), 142-158.

Croak, B.M., Crowther, M.S., Webb, J.K. and Shine, R., 2013. Movements and habitat use of an endangered snake, *Hoplocephalus bungaroides* (Elapidae): implications for conservation. *PloS one*, *8*(4).

De Knegt, H.J., Hengeveld, G.M., Van Langevelde, F., De Boer, W.F. and Kirkman, K.P., 2007. Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology*, *18*(6), 1065-1072.

Fielden, L.J., Perrin, M.R. and Hickman, G.C. 1990a. Feeding ecology and foraging behaviour of the Namib Desert Golden Mole, *Eremitalpa granti namibensis* (Chrysochloridae). *Journal of Zoology*, *220*(3), 367-389.

Fielden, L.J., Waggoner, J.P., Perrin, M.R. and Hickman, G.C. 1990b. Thermoregulation in the Namib Desert Golden Mole, *Eremitalpa granti namibensis* (Chrysochloridae). *Journal of Arid Environments*, *18*(2), 221-237.

Fielden, L.J. 1991. Home range and movements of the Namib Desert Golden Mole, *Eremitalpa granti namibensis* (Chrysochloridae). *Journal of Zoology*, *223*(4), 675-686.

Fielden, L.J., Hickman, G.C. and Perrin, M.R. 1992. Locomotory activity in the Namib Desert Golden Mole *Eremitalpa granti namibensis* (Chrysochloridae). *Journal of Zoology*., *226*, 329-344.

Fielden, L. J. 1989. Selected aspects of the adaptive biology and ecology of the Namib Desert Golden Mole *(Eremitalpa granti namibensis).* Ph.D. dissertation, University of Natal, Pietermaritzburg, Natal, South Africa.

Foley, N.M., Springer, M.S. and Teeling, E.C. 2016. Mammal madness: is the mammal tree of life not yet resolved?. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *371*(1699), .20150140.

Fogden M. and Fogden P. n.d. Grant's Golden Mole (*Eremitalpa granti*) hunting at night, Namib Desert, Namibia. *Minden Pictures*. Retrieved, January 24, 2023, from *https://www.mindenpictures.com/stock-photo-grant-s-golden-mole-eremitalpa-granti-hunting-at-night-namib-desert-naturephotography-image00510447.html*

Garshelis, D.L. 2000. Delusions in habitat evaluation: measuring use, selection, and importance. *In Research Techniques in Animal Ecology: Controversies and Consequences*. Columbia University Press, New York. 111-164.

Gasc, J.P., Jouffroy, F.K., Renous, S. and Blottnitz, F.V. 1986. Morphofunctional study of the digging system of the Namib Desert Golden Mole (*Eremitalpa granti namibensis*): cinefluorographical and anatomical analysis. *Journal of Zoology*, *208*(1), 9-35.

Gazit, I., Terkel, J. and Zuri, I., 1997. Effect of scent-marking in delaying territorial invasion in the blind mole-rat *Spalax ehrenbergi*. *Behaviour*, *134*(11-12), pp.867-880.

Gilbert, C., Maree, S. and Robinson, T.J. 2008. Chromosomal evolution and distribution of telomeric repeats in Golden Moles (Chrysochloridae, Mammalia). *Cytogenetic and genome research*, *121*(2), 110-119.

Gregory, T. 2016. Home range estimation. *The International encyclopedia of primatology*,1-4.

Holm, E. 1969. Contribution to the knowledge of the biology of the Namib Desert Golden Mole *Eremitalpa granti namibensis* Bauer & Niethammer 1959. *Scientific Papers of the Namib Desert Research Station*, *1971*(41), 37-42.

Jackson, C.R., Setsaas, T.H., Robertson, M.P., Scantlebury, M. and Bennett, N.C., 2009. Insights into torpor and behavioural thermoregulation of the endangered Juliana's golden mole. *Journal of Zoology*, *278*(4), 299-307.

Kong, D., Luo, W., Liu, Q., Li, Z., Huan, G., Zhang, J. and Yang, X. 2018. Habitat use, preference, and utilization distribution of two crane species (Genus: Grus) in Huize National Nature Reserve, Yunnan–Guizhou Plateau, China. *PeerJ*, *6*, 5105.

Krausman, P.R. 1999. Some basic principles of habitat use. *Grazing behaviour of livestock and wildlife*, *70*, 85-90.

Kuyper, M.A., 1985. The ecology of the golden mole *Amblysomus hottentotus*. *Mammal Review*, *15*(1), .3-11.

Ie Roux, G. J., 1970. The microbiology of sand-dune ecosystems in the Namib Desert. M.Sc. Thesis, University of Stellenbosch, Stellenbosch, South Africa.

Lewis, E.R., Narins, P.M., Jarvis, J.U., Bronner, G. and Mason, M.J. 2006. Preliminary evidence for the use of microseismic cues for navigation by the Namib Golden Mole. *The Journal of the Acoustical Society of America*, *119*(2), 1260-1268.

Lovegrove, B.G. and Génin, F., 2008. Torpor and hibernation in a basal placental mammal, the Lesser Hedgehog Tenrec *Echinops telfairi*. *Journal of Comparative Physiology B*, *178*(6), .691-698.

Macdonald, D.W., Atkitnson, R.D.P. and Blanchard, G. 1997. Spatial and temporal patterns in the activity of European moles. *Springer-Verlag*, 109, 88-97.

McAllan, B.M. and Geiser, F., 2018. Torpor During Reproduction in Mammals and Birds: Balancing Energy Expenditure for Survival. *Life Sciences*.

Maree, S. and Bronner, G.N. 2016. *A conservation assessment of Eremitalpa granti granti*. In The Red List of Mammals of South Africa, Swaziland and Lesotho. Child MF, Roxburgh L, Do Linh San E, Raimondo D & Davies-Mostert HT, Eds. South Africa. South African National Biodiversity Institute and Endangered Wildlife Trust.

Martin, T.E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts. *Ecology*, *82*(1), 175-188.

Meester, J. 1964. Revision of the Chrysochloridae I. the desert Golden Mole *Eremitalpa Roberts*. *Scientific Papers of the Namib Desert Research Station*, *1964*(26), 1-8.

Milling, C.R., Rachlow, J.L., Johnson, T.R., Forbey, J.S. and Shipley, L.A. 2017. Seasonal variation in behavioral thermoregulation and predator avoidance in a small mammal. *Behaviuoral Ecology 28* (5), 1236-1247.

Mole, G., 2007. A Quantitative Habitat Description for Juliana's. *The Ecology and Conservation of Juliana's Golden Mole (Neamblysomus julianae)*, .25.

Mzilikazi, N. and Lovegrove, B.G., 2004. Daily torpor in free-ranging rock elephant shrews, Elephantulus myurus: a year-long study. *Physiological and Biochemical Zoology*, *77*(2), .285-296.

Nathan, R., Getz, W.M., Revilla, E., Holyoak, M., Kadmon, R., Saltz, D. and Smouse, P.E. 2008. A movement ecology paradigm for unifying organismal movement research. *Proceedings of the National Academy of Sciences*, *105*(49), 19052-19059.

Narins, P.M., Lewis, E.R., Jarvis, J.J. and O'Riain, J. 1997. The use of seismic signals by fossorial southern African mammals: a neurotheological gold mine. *Brain Research Bulletin*, *44*(5), 641-646.

Neath, A.A. and Cavanaugh, J.E., 2012. The Bayesian information criterion: background, derivation, and applications. *Wiley Interdisciplinary Reviews: Computational Statistics*, *4*(2), 199-203.

Noirot, C. and Darlington, J.P., 2000. Termite nests: architecture, regulation and defence. In *Termites: evolution, sociality, symbioses, ecology*. *Springer, Dordrecht*. 121-139.

Oosthuizen, M.K., Robb, G., Harrison, A., Froneman, A., Joubert, K. and Bennett, N.C., 2021. Flexibility in body temperature rhythms of free-living natal mole-rats (*Cryptomys hottentotus natalensis*). *Journal of Thermal Biology*, *99*, 102973.

Perrin, M.R. and Fielden L.J. 1999. *Eremitalpa granti*. *Mammalian Species 629*, 1–4

Powell, R.A., 2000. Animal home ranges and territories and home range estimators. *Research techniques in animal ecology: controversies and consequences*, *442*, 65-110.

Rathbun, G.B. and Rathbun, C.D., 2007. Habitat use by radio-tagged Namib Desert Golden Moles (*Eremitalpa granti namibensis*). *African journal of ecology*, *45*(2), 196-201.

Robinson, M.D. and Seely, M.K. 1980. Physical and biotic environments of the southern Namib dune ecosystem. *Journal of Arid Environments*, *3*(3), 183-203.

Roberts, A. 1951. The mammals of South Africa. *The Mammals of South Africa*. The Trustees of the Mammals of South Africa Book Fund. Johannesburg, South Africa

Roth, J. 2004. "*Eremitalpa granti*" (Online). *Animal Diversity Web*. Retrieved, September 13, 2022, from https://animaldiversity.org/accounts/Eremitalpa_granti/

Scantlebury, M., Lovegrove, B.G., Jackson, C.R., Bennett, N.C. and Lutermann, H., 2008. Hibernation and non-shivering thermogenesis in the Hottentot golden mole (*Amblysomus hottentottus longiceps*). *Journal of Comparative Physiology B*, *178*(7), 887-897.

Scheffers, B.R., Edwards, D.P., Diesmos, A., Williams, S.E. and Evans, T.A., 2014. Microhabitats reduce animal's exposure to climate extremes. *Global change biology*, *20*(2), 495-503.

Schulze, B.R., 1969. The climate of Gobabeb. *Scientific Papers of the Namib Desert Research Station*, *1969*(38), 5-12.

Seymour, R.S. and Seely, M.K. 1996. The respiratory environment of the Namib Desert Golden Mole. *Journal of Arid Environments*, *32*(4), 453-461.

Seymour, R.S., Withers, P.C. and Weathers, W.W. 1998. Energetics of burrowing, running, and free-living in the Namib Desert Golden Mole (*Eremitalpa granti namibensis*). *Journal of Zoology, 244*(1), 107-117.

Skinner, J. D., and Smithers R. H. N. 1990. *The mammals of southern African sub-region*. University of Pretoria, Pretoria, 771.

Spirig, R., Vogt, R., Larsen, J.A., Feigenwinter, C., Wicki, A., Franceschi, J., Parlow, E., Adler, B., Kalthoff, N., Cermak, J. and Andersen, H., 2019. Probing the fog life cycles in the Namib desert. *Bulletin of the American Meteorological Society*, *100*(12), 2491-2507.

Thompson, C.M. and Gese, E.M., 2013. Influence of vegetation structure on the small mammal community in a shortgrass prairie ecosystem. *Acta Theriologica*, *58*(1), 55-61.

Torres, L.G., Orben, R.A., Tolkova, I. and Thompson, D.R. 2017. Classification of Animal Movement Behavior through Residence in Space and Time. *PLoS ONE* 12(1): e

Wastell, A.R., and Mackessy, S.P. 2011. Spatial Ecology and Factors Influencing Movement Patterns of Desert Massasauga Rattlesnakes (*Sistrurus catenatus edwardsii*) in Southeastern Colorado. *Copeia* (1), 29-37.

Von Mayer, A., O'Brien, G. and Sarmiento, E.E. 1995. Functional and systematic implications of the ear in Golden Moles (Chrysochloridae). *Journal of Zoology*, *236*(3), 417-430.

Vonshak, M., Dayan, T. and Kronfeld-Schor, N., 2009. Arthropods as a prey resource: patterns of diel, seasonal, and spatial availability. *Journal of Arid Environments*, *73*(4-5), 458-462.

Yahner, R.H., 1986. Microhabitat use by small mammals in even-aged forest stands. *American Midland Naturalist*, 174-180.

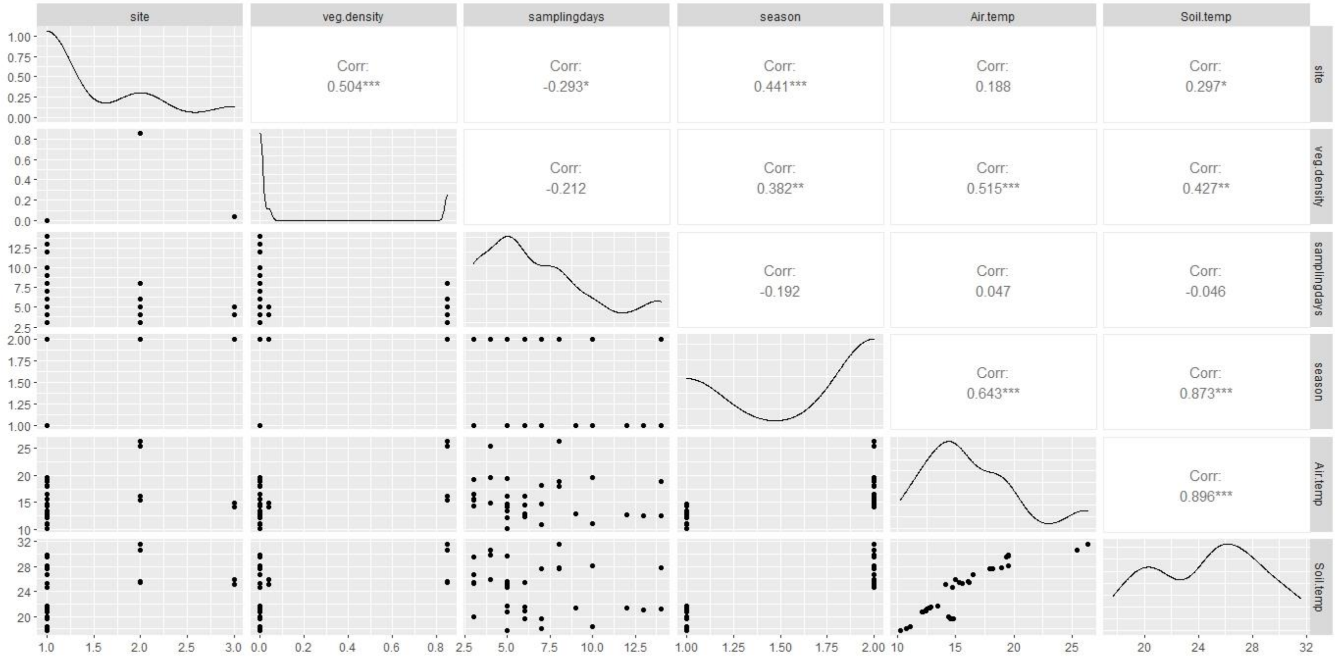
Appendices

Appendix 1-Field datasheet

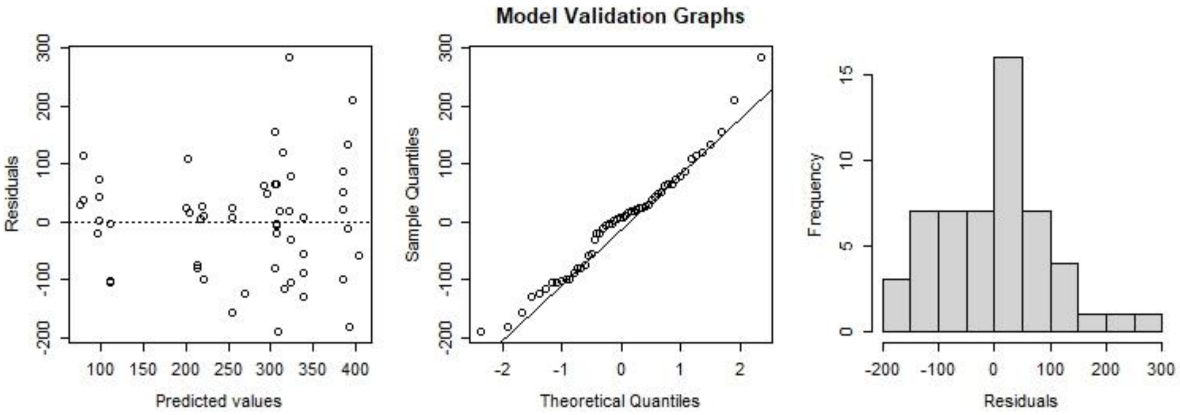
Date		**Temperature (°C)**	
Time		**Fog (mm)**	
Wind Speed (m/s)		**Rain (mm)**	
Wind direction (deg)		**Cloud cover (%)**	

Mole NO	**GPS Points ↓**	**Activities (emerge, rest, swim, head-dip, turn)**	**Swimming Length/distance to the next vegetation (m)**	**Microhabitat (Crest, slip face, windward slope, base, avalanche)**	**Soil hardness (soft, hard)**	**Soil stability (stable, sliding)**	**Vegetation (open area, single grass, big hummock, small hummock, medium hummock, Others)**	**Comments (tortuosity, other animal tracks, compacted crusty material, detritus, etc**

Appendix 2. Correlation (Pearson correlation coefficient) between variables thought to predict the Namib Golden Mole track length



Appendix 3. Model validation graph for top generalised liner model (GLM) on Namib Golden Mole track length showing residual versus predicted values spread (left), sample versus theoretical quantile spread (middle) and distribution of data (right).



Appendix 4(a). Monthly comparison of track length- Post-hoc Dunn's test

	chi2	Z	P	P.adjusted	comparisons
1	22.60487	-3.92015	4.42E-05	4.42E-05	Aug-21 - Feb-21
2	22.60487	-0.7096	0.238976	0.238976	Aug-21 - Jul-21
3	22.60487	3.513868	0.000221	0.000221	Feb-21 - Jul-21
4	22.60487	-2.92155	0.001741	0.001741	Aug-21 - Mar-21
5	22.60487	0.546634	0.292315	0.292315	Feb-21 - Mar-21

6	22.60487	-2.44603	0.007222	0.007222	Jul-21 - Mar-21
7	22.60487	-1.65778	0.048681	0.048681	Aug-21 - Nov-20
8	22.60487	1.749607	0.040093	0.040093	Feb-21 - Nov-20
9	22.60487	-1.11134	0.13321	0.13321	Jul-21 - Nov-20
10	22.60487	1.096683	0.13639	0.13639	Mar-21 - Nov-20
11	22.60487	-2.3005	0.01071	0.01071	Aug-21 - Sep-20
12	22.60487	1.88042	0.030025	0.030025	Feb-21 - Sep-20
13	22.60487	-1.72171	0.042561	0.042561	Jul-21 - Sep-20
14	22.60487	1.012221	0.155716	0.155716	Mar-21 - Sep-20
15	22.60487	-0.28471	0.387934	0.387934	Nov-20 - Sep-20

Appendix 4(b). Monthly comparison of displacement- Post-hoc Tukey test

	Date.diff	Date.lwr	Date.upr	Date.p.adj
Jul-21-Aug-21	47.9515	-18.4852	114.3882	0.273888
Nov-20-Aug-21	49.70286	-26.41	125.8157	0.379218
Feb-21-Aug-21	51.96179	-10.1841	114.1076	0.145613
Mar-21-Aug-21	61.44247	-10.3174	133.2023	0.128951
Sep-20-Aug-21	80.12627	16.84004	143.4125	0.00657
Nov-20-Jul-21	1.751361	-69.3649	72.86761	1
Feb-21-Jul-21	4.010289	-51.9045	59.92511	0.999928
Mar-21-Jul-21	13.49098	-52.9457	79.92768	0.989346
Sep-20-Jul-21	32.17478	-25.0048	89.35439	0.542197
Feb-21-Nov-20	2.258929	-64.8663	69.38412	0.999998
Mar-21-Nov-20	11.73962	-64.3732	87.85242	0.997029
Sep-20-Nov-20	30.42342	-37.7589	98.60576	0.757242
Mar-21-Feb-21	9.480687	-52.6652	71.62654	0.99718
Sep-20-Feb-21	28.16449	-23.9678	80.29681	0.584859
Sep-20-Mar-21	18.6838	-44.6024	81.97004	0.946065

Appendix 4c. Monthly comparison of straightness- post-hoc Tukey test

	Date.diff	Date.lwr	Date.upr	Date.p.adj
Mar-21-Feb-21	0.09568	-0.08902	0.280384	0.627084
Nov-20-Feb-21	0.218759	0.019255	0.418262	0.024798
Sep-20-Feb-21	0.294557	0.139614	0.4495	2.64E-05
Aug-21-Feb-21	0.330244	0.145539	0.514948	7.24E-05
Jul-21-Feb-21	0.396113	0.229927	0.562298	3.66E-07
Nov-20-Mar-21	0.123079	-0.10314	0.349294	0.577577
Sep-20-Mar-21	0.198877	0.010783	0.386971	0.033148
Aug-21-Mar-21	0.234564	0.021286	0.447842	0.024193
Jul-21-Mar-21	0.300433	0.102975	0.49789	0.000761
Sep-20-Nov-20	0.075799	-0.12685	0.278444	0.865883
Aug-21-Nov-20	0.111485	-0.11473	0.337701	0.674253
Jul-21-Nov-20	0.177354	-0.03401	0.388719	0.143056

Aug-21-Sep-20	0.035687	-0.15241	0.223781	0.992189
Jul-21-Sep-20	0.101555	-0.06839	0.2715	0.476942
Jul-21-Aug-21	0.065869	-0.13159	0.263326	0.912447

Appendix 5. Monthly comparison of head-dips- post-hoc Dunn's test

	chi2	Z	P	P.adjusted	Comparisons
1	20.38466	-2.95966	0.00154	0.00154	Aug-21 - Feb-21
2	20.38466	-1.71957	0.042755	0.042755	Aug-21 - Jul-21
3	20.38466	1.009848	0.156284	0.156284	Feb-21 - Jul-21
4	20.38466	-2.2643	0.011778	0.011778	Aug-21 - Jun-21
5	20.38466	-0.31165	0.377654	0.377654	Feb-21 - Jun-21
6	20.38466	-0.96442	0.167417	0.167417	Jul-21 - Jun-21
7	20.38466	-3.16179	0.000784	0.000784	Aug-21 - Mar-21
8	20.38466	-0.62548	0.265829	0.265829	Feb-21 - Mar-21
9	20.38466	-1.44222	0.07462	0.07462	Jul-21 - Mar-21
10	20.38466	-0.12579	0.449947	0.449947	Jun-21 - Mar-21
11	20.38466	-0.11113	0.455756	0.455756	Aug-21 - Nov-20
12	20.38466	2.623069	0.004357	0.004357	Feb-21 - Nov-20
13	20.38466	1.510094	0.06551	0.06551	Jul-21 - Nov-20
14	20.38466	2.101434	0.017801	0.017801	Jun-21 - Nov-20
15	20.38466	2.869833	0.002053	0.002053	Mar-21 - Nov-20
16	20.38466	-1.05527	0.14565	0.14565	Aug-21 - Sep-20
17	20.38466	2.253298	0.01212	0.01212	Feb-21 - Sep-20
18	20.38466	0.894536	0.185517	0.185517	Jul-21 - Sep-20
19	20.38466	1.670439	0.047416	0.047416	Jun-21 - Sep-20
20	20.38466	2.529861	0.005705	0.005705	Mar-21 - Sep-20
21	20.38466	-0.85544	0.196155	0.196155	Nov-20 - Sep-20

Appendix 6(a). Monthly comparison of the number of sand-swims- post-hoc Dunn's test

	Comparison	Z	P.unadj	P.adj
1	Aug-21 - Feb-21	-2.437	0.01481	0.192528
2	Aug-21 - Jul-21	-2.03118	0.042236	0.506837
3	Feb-21 - Jul-21	0.295165	0.767868	0.767868
4	Aug-21 - Mar-21	-3.08458	0.002038	0.030576
5	Feb-21 - Mar-21	-1.12477	0.260687	1
6	Jul-21 - Mar-21	-1.30054	0.193415	1
7	Aug-21 - Nov-20	-1.05549	0.291203	1
8	Feb-21 - Nov-20	1.059411	0.289413	1
9	Jul-21 - Nov-20	0.767885	0.442556	1
10	Mar-21 - Nov-20	1.852682	0.063928	0.703208
11	Aug-21 - Sep-20	-0.94769	0.343288	1

12	Feb-21 - Sep-20	1.754643	0.07932	0.793204
13	Jul-21 - Sep-20	1.311123	0.189816	1
14	Mar-21 - Sep-20	2.549895	0.010776	0.150858
15	Nov-20 - Sep-20	0.298617	0.765232	1

Appendix 6(b). Monthly comparison of percentage of sand-swimming- post-hoc Dunn’s test

	Comparison	Z	P.unadj	P.adj
1	Aug-21 - Feb-21	4.372865	1.23E-05	0.000184
2	Aug-21 - Jul-21	1.569394	0.116556	0.815894
3	Feb-21 - Jul-21	-2.99545	0.00274	0.038366
4	Aug-21 - Mar-21	2.353358	0.018605	0.223257
5	Feb-21 - Mar-21	-1.65544	0.097835	0.782679
6	Jul-21 - Mar-21	0.972523	0.33079	1
7	Aug-21 - Nov-20	1.829845	0.067273	0.605458
8	Feb-21 - Nov-20	-1.97364	0.048423	0.48423
9	Jul-21 - Nov-20	0.492283	0.622519	1
10	Mar-21 - Nov-20	-0.38892	0.697334	1
11	Aug-21 - Sep-20	2.460569	0.013872	0.180332
12	Feb-21 - Sep-20	-2.22578	0.026029	0.286316
13	Jul-21 - Sep-20	0.899881	0.368184	1
14	Mar-21 - Sep-20	-0.20789	0.835317	0.835317
15	Nov-20 - Sep-20	0.241199	0.809401	1

Appendix 7. Monthly comparison of the number of plants visited- post-hoc Dunn’s test

	Comparison	Z	P.unadj	P.adj
1	Aug-21 - Feb-21	-3.31151	0.000928	0.013919
2	Aug-21 - Jul-21	-1.73459	0.082814	0.91095
3	Feb-21 - Jul-21	1.619533	0.105333	0.947993
4	Aug-21 - Mar-21	-2.205	0.027454	0.384361
5	Feb-21 - Mar-21	0.765395	0.444036	1
6	Jul-21 - Mar-21	-0.64708	0.517581	1
7	Aug-21 - Nov-20	-1.15423	0.248406	1
8	Feb-21 - Nov-20	1.757084	0.078904	0.946843
9	Jul-21 - Nov-20	0.385125	0.700145	1
10	Mar-21 - Nov-20	0.92466	0.355143	1
11	Aug-21 - Sep-20	-1.69068	0.090898	0.908978
12	Feb-21 - Sep-20	1.895168	0.05807	0.754913
13	Jul-21 - Sep-20	0.14417	0.885367	0.885367
14	Mar-21 - Sep-20	0.80955	0.418199	1

15	Nov-20 - Sep-20	-0.28079	0.778869	1

Appendix 8. Monthly comparison of the mean number of track intersections per day- post-hoc Dunn’s test

	Comparison	Z	P.unadj	P.adj
1	Aug-21 - Feb-21	-2.33102	0.019752	0.237029
2	Aug-21 - Jul-21	-0.86841	0.385169	1
3	Feb-21 - Jul-21	1.558956	0.119007	0.952055
4	Aug-21 - Mar-21	-2.73241	0.006287	0.081735
5	Feb-21 - Mar-21	-0.8241	0.409884	1
6	Jul-21 - Mar-21	-2.08293	0.037258	0.409834
7	Aug-21 - Nov-20	-1.43546	0.151156	1
8	Feb-21 - Nov-20	0.530443	0.595805	0.595805
9	Jul-21 - Nov-20	-0.72505	0.468423	1
10	Mar-21 - Nov-20	1.14068	0.254003	1
11	Aug-21 - Sep-20	-3.64461	0.000268	0.004017
12	Feb-21 - Sep-20	-1.64563	0.09984	0.898556
13	Jul-21 - Sep-20	-3.02484	0.002488	0.034827
14	Mar-21 - Sep-20	-0.54635	0.584826	1
15	Nov-20 - Sep-20	-1.78047	0.074999	0.749988

Appendix 9. Tracking dates, home range area (ha), site and the total number of days each individual was tracked.

Tracking dates	**Mole ID**	**H.R. area (ha)**	**Site**	**Total no. of days**
14/09/2020-18/09/2020	M1	8.178372	Station Dune	5
14/09/2020-19/09/2020	M2	16.01524	Station Dune	6
14/09/2020-27/09/2020	M3	7.730117	Station Dune	14
14/09/2020-25/09/2020	M4	17.09148	Station Dune	12
15/09/2020-19/09/2020	M5	5.316444	Station Dune	5
15/09/2020-27/09/2020	M6	4.456447	Station Dune	13
19/09/2020-27/09/2020	M7	4.142297	Station Dune	9
19/09/2020-23/09/2020	M8	14.44885	Station Dune	5
21/09/2020-26/09/2020	M9	1.144164	Station Dune	6
31/10/2020-02/11/2020	M10	0.869493	Station Dune	3
31/10/2020-04/11/2020	M11	3.940724	Station Dune	5
31/10/2020-04/11/2020	M12	1.198513	Station Dune	5
31/10/2020-04/11/2020	M13	3.12374	Station Dune	5
07/11/2020-12/11/2020	M14	4.34582	Moles’ End	6
08/11/2020-12/11/2020	M15	3.204783	Moles’ End	5
10/11/2020-12/11/2020	M16	1.688006	Moles’ End	3
10/11/2020-12/11/2020	M17	2.631437	Moles’ End	3

10/11/2020-12/11/2020	M18	2.34366	Moles’ End	3
10/11/2020-12/11/2020	M19	0.897372	Moles’ End	3
01/12/2020-05/12/2020	M20	11.04973	Kahani	5
01/12/2020-04/12/2020	M21	2.90724	Kahani	4
01/12/2020-05/12/2020	M22	3.198257	Kahani	5
01/12/2020-05/12/2020	M23	11.91399	Kahani	5
01/12/2020-05/12/2020	M24	6.121038	Kahani	5
09/02/2021-12/02/2021	M25	2.922553	Station Dune	4
09/02/2021-11/02/2021	M26	4.757546	Station Dune	3
09/02/2021-13/02/2021	M27	1.635951	Station Dune	5
09/02/2021-11/02/2021	M28	7.893529	Station Dune	3
18/02/2021-25/02/2021	M29	2.89449	Station Dune	8
18/02/2021-25/02/2021	M30	4.425032	Station Dune	8
18/02/2021-24/02/2021	M31	9.89269	Station Dune	7
18/02/2021-25/02/2021	M32	2.724597	Station Dune	8
18/02/2021-24/02/2021	M33	9.23182	Station Dune	7
22/02/2021-24/02/2021	M34	1.068069	Station Dune	3
16/03/2021-29/03/2021	M35	1.858476	Station Dune	14
16/03/2021-29/03/2021	M36	10.06347	Station Dune	14
16/03/2021-29/03/2021	M37	9.88927	Station Dune	14
16/03/2021-23/03/2021	M38	8.108456	Station Dune	8
20/03/2021-29/03/2021	M39	2.760127	Station Dune	10
03/04/2021-10/04/2021	M40	5.320913	Moles’ End	8
03/04/2021-10/04/2021	M41	4.526917	Moles’ End	8
03/04/2021-10/04/2021	M42	2.644181	Moles’ End	8
03/04/2021-10/04/2021	M43	8.552443	Moles’ End	8
07/04/2021-10/04/2021	M44	2.85087	Moles’ End	4
15/06/2021-16/06/2021	M45	1.159474	Station Dune	2
15/06/2021-16/06/2021	M46	1.27743	Station Dune	2
28/06/2021-04/07/2021	M47	12.30463	Station Dune	7
28/06/2021-03/07/2021	M48	1.502711	Station Dune	6
28/06/2021-30/06/2021	M49	3.622947	Station Dune	3
28/06/2021-30/06/2021	M50	1.871094	Station Dune	3
28/06/2021-03/07/2021	M51	3.965676	Station Dune	6
15/08/2021-24/08/2021	M52	0.02865	Station Dune	10
15/08/2021-24/08/2021	M53	2.074453	Station Dune	10
15/08/2021-24/08/2021	M54	0.020289	Station Dune	10
16/08/2021-22/08/2021	M55	5.771966	Station Dune	7
19/08/2021-23/08/2021	M56	1.322151	Station Dune	5

Appendix 10. Sand-swimming by a Namib Golden Mole within a grass hummock.

Appendix 11. Summary statistics of foraging tracks of all individual moles tracked per site.

		Site					
		Kahani (5)		Moles-End (11)		Station Dune (40)	
		Statistic	Std. Error	Statistic	Std. Error	Statistic	Std. Error
Track length	Mean	388.8600	33.36240	318.2258	20.34301	227.4602	21.83985
	Median	405.0000		322.4000		216.7500	
	Variance	5565.248		4138.379		18602.190	
	Std. Deviation	74.60059		64.33024		136.38984	
	Minimum	284.00		210.25		8.80	
	Maximum	472.00		433.25		607.25	
Net displacemen	Mean	119.8500	21.72822	93.9733	5.61715	91.1332	6.75006

t	Median	103.2000		92.7625		87.0000	
	Variance	2360.578		315.524		1776.970	
	Std. Deviation	48.58577		17.76298		42.15413	
	Minimum	68.25		74.67		6.40	
	Maximum	179.40		120.00		200.67	
No. of head dips	Mean	228.6500	31.66301	343.4958	39.87145	182.1213	34.51497
	Median	234.7500		313.1875		116.0000	
	Variance	5012.731		15897.328		46460.043	
	Std. Deviation	70.80064		126.08461		215.54592	
	Minimum	135.50		177.00		1.83	
	Maximum	311.00		601.00		1170.46	
No. of sand swims	Mean	5.2700	.35199	14.4592	1.42288	5.5100	0.45928
	Median	5.7500		13.3125		5.3333	
	Std. Deviation	.78708		4.49955		2.86818	
	Minimum	4.00		9.00		.80	
	Maximum	5.80		22.38		12.50	
Sand swimming length	Mean	7.0670	2.04077	26.4861	2.29644	20.2021	1.98258
	Median	4.8000		26.6604		16.5400	
	Std. Deviation	4.56330		7.26198		12.38118	
	Minimum	3.20		15.04		4.93	
	Maximum	13.78		36.17		56.33	
No of plants encountered	Mean	24.3400	4.08578	22.9233	1.03538	7.6546	0.66878
	Median	24.0000		21.9792		7.2857	
	Std. Deviation	9.13608		3.27416		4.17654	
	Minimum	10.00		19.50		.80	
	Maximum	34.40		29.25		20.71	