DENSITY-DEPENDENT EFFECTS ON BODY SIZE, PHILOPATRY, AND DISPERSAL IN THE DAMARALAND MOLE-RAT (*FUKOMYS DAMARENSIS*)

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ABSTRACT

Population density may exert changes in a variety of behavioural and physiological characters in animals. However, the effects of density-dependence and dispersal are poorly studied in subterranean rodents due to the difficulties involved in observing such effects in wild populations. Using the cooperative breeding Damaraland mole-rat (*Fukomys damarensis*) as a model species, the effects of population density on body size, growth rates, group size, recruitment, philopatry and dispersal were investigated at two sites (one with low density and one with high density) in the Northern Cape of South Africa. Group size, litter size and the probability of recapture were independent of population density. However, individual body size, recruitment, dispersal rate and dispersal distance were density-dependent. Individuals were significantly larger, juveniles exhibited a significantly higher growth rate, and juvenile recruitment was significantly greater when population density was low. At higher densities, significantly more individuals were lost between capture events which may be indicative of increased rates of dispersal. Mean dispersal distances in mole-rats were reduced at higher densities and increased at lower densities. While both sexes dispersed equally, males were significantly more likely to join an established colony and females created new burrow systems. In addition, four times as many single females were found when population density was low. The apparent differences in the study populations may be attributed to variable annual rainfall or food availability. The greater annual rainfall at the high-density site may provide better habitat conditions and therefore result in an increase in the population density and an increased dispersal rate due to the relaxed ecological constraints such as reduced energetic costs to burrowing. However, the larger body size found at the low-density site may indicate that the available food at that location is of better quality. This study revealed that mole-rats were able to disperse over 1km and therefore a much larger study area would be required in capture-mark-recapture studies to ensure the recapture of the majority of dispersers. Lastly, a surprising find of this study was that females may survive a solitary existence for over two years while awaiting the arrival of a mate.

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CHAPTER 1 - Introduction

1.1 Evolution of Sociality and Cooperative Breeding

The formation of individuals into social groups occurs in nearly every major taxon, but varies widely in number, structure, and degree of cohesion (Krause and Roxton 2002, Safran et al. 2007). Group living occurs frequently in birds and mammals with a wide range of social organizations from colonial to cooperative breeding (Lack 1968, Brown 1978, Greenwood 1980, Mares and Lacher 1987, Clutton-Brock 1989, Emlen 1991). Sociality may be seasonal due to variations in climate (Madison 1984, Kunz and Lumsden 2003), availability of nesting locations (Mares and Lacher 1987, Kerth 2008), or breeding opportunities (Lack 1968, Le Boeuf and Reiter 1988). Alternatively, sociality may be a permanent adaptation to ecological constraints (Jarvis et al. 1994, Armitage 2007). A social group has been defined as the persistence of interactions among group members for a significant portion of an individual's lifetime (Wilson 1975, Jennions and Macdonald 1994). Social groups are therefore identified based on spatial and social interactions among group members during the breeding period (Lacey and Sherman 2007).

The reasons for group formation has been a long-standing puzzle in ecology and evolutionary biology because there is wide variation within and among groups across different taxa in the costs and benefits incurred by individuals (Danchin and Wagner 1997, Safran et al. 2007). Aggregations can act as information centres when group members gather and individuals with prior knowledge of resource locations lead others lacking knowledge to those resources as seen in bats (Wilkinson 1992), rats (*Rattus* spp., Berdoy and Drickamer 2007), and ravens (*Corvus corvax*, Marzluff et al. 1996). In extreme climates, huddling in groups can decrease energetic costs through sharing body heat, even raising the ambient air temperature of the den (e.g. bats, Speakman and Thomas 2003, Altringham and Senior 2005; and marmots (*Marmota* spp.), Armitage 2007). Larger group size reduces the risks of starvation through increased foraging efficiency (Lovegrove and Wissel 1988), defense of food resources (Creel and Creel 2002, Vucetich et al. 2004), or the ability to secure difficult prey through cooperative hunting (Wyman 1967, Kruuk 1972, Schaller 1972, Creel and Creel 2002). Reproductive benefits include assistance with birthing from other females (Tavolga and Essapian 1957, Kunz et al. 1994), reduced inter-birth intervals and increased rates of infant growth (Mitani and Watts 1997), increased probability of juvenile survival (Oates 1977; Rasa 1987; Campagna et al. 1992; König 1994; Clutton-Brock et al. 1999a; Canestrari et al. 2008), or reducing the occurrence of infanticide (Packer et al. 1990, Manning et al. 1995) thereby ensuring continued survival of the family group. The effects of predation are also lessened through dilution effects when predators can only select a single individual out of the herd (Hamilton 1971), through hindering predators to capture prey (Caro 2005), or providing better group defense and vigilance (Vine 1973, Treisman 1975, Rasa 1987, McGowan and Woolfenden 1989, Clutton-Brock et al. 1999b). However increased group size could also increase predation risk because larger groups are more conspicuous to predators (Vine 1973, Wittenberger and Hunt 1985, Lindström 1989, Balmford and Turyaho 1992). As group size increases so does the territory and home-range area which can lead to high energetic costs of movement (McNab 1963, Schoener 1968, Clutton-Brock and Harvey 1977). Additional costs for group living includes increased risk of disease (Gascoyne et al. 1993) and higher parasite loads (Wilkinson 1985, Brown and Brown 1986, Hoogland 1995). However the primary costs to individuals are the result of the increase in competition among group members, which can lead to increased aggression between conspecifics (Dunbar 2010). With more group members, the occurrence of feeding interference increases which in turn causes a reduction in individual foraging efficiency (Jarman 1979, Selman and Goss-Custard 1988, Treves 2000), as well as reduced growth rates (Clutton-Brock et al. 1982, Young et al. 2015, Zöttl et al. 2016b). Additionally, intra-sexual competition increases with group size, resulting in reproductive interference between group members and reduced fecundity and juvenile survival, especially among subordinate females (Hoogland 1995, Young et al. 2006). Lastly, in extreme cases, if competition increases beyond a certain point large groups may fission into smaller ones (Lefebvre et al. 2003).

Sociality evolves from either related or unrelated individuals occupying a shared territory (Emlen 1995, 1997). The evolutionary factors important for the evolution of sociality are varied among taxa, but include predator vigilance and protection (Crook 1964, Rasa 1987, McGowan and Woolfenden 1989, Clutton-Brock 1999, Alexander et al. 1991), foraging efficiency (Jarvis and Sale 1971, Jarvis and Bennett 1993, Frame et al. 1979, Zimen 1976), and the distribution or variability of resources (Crook 1964, Slobodchikoff 1984, Mares and Lacher 1987, Lovegrove and Wissel 1988). Crook (1964) found that sociality in African weaver birds (*Ploceus* spp.) varied by habitat, distribution of food resources, nesting sites and predation levels. Mares and Lacher (1987) found the vast majority of mammals occupying rocky habitats were social due to the limited availability of den sites in those areas. Armitage (2007) suggested that sociality in marmots evolved due to the necessity of juveniles hibernating with their parents to survive harsh winters. The evolution of sociality in social African mole-rats (*Heterocephalus, Cryptomys, Fukomys*) has been suggested to arise from the patchy distribution of food resources in arid environments combined with limited opportunities for dispersal (Jarvis et al. 1994).

Different types of social groups are defined by which individuals within the group reproduce and the degree of social interactions between individuals (Vehrencamp 1983; Brown 1987; Clutton-Brock 1998; Reeve et al. 1998). Coloniality represents one end of the spectrum of sociality in birds and mammals where all adult females raise their offspring independently and social bonds between individuals, such as allogrooming, are absent or limited (Alexander 1974). The formation of colonies is often seasonal for the purpose of breeding as seen in elephant seals (*Mirounga angustirostris*, Le Boeuf and Reiter 1988) and many birds (Lack 1968), or for hibernation as in some species of bats (McCracken and Wilkinson 2000). Coloniality is most common in birds, where 13% of all species (the vast majority of those being marine birds) form dense aggregations in typically secluded and protected locations with each breeding pair defending their territory from neighbours (Lack 1968). In some species, such as gulls (*Larus argentatus* and *L. delawarensis*), individuals will cooperate to drive off predators, but otherwise exhibit no further cooperative behaviour (Ewins 1991). The largest aggregations of mammals are found in bats, with some colonies consisting of several million individuals (Kerth 2008). Many species of bats roost colonially for reasons beyond predator defense, including limited availability of suitable roosting sites, thermoregulatory benefits in temperate climates, or to facilitate information sharing regarding foraging sites (Speakman and Thomas 2003, Altringham and Senior 2005, Kerth 2008). The genetic composition and stability of colonies, and therefore social behaviour varies between bat species (McCracken and Wilkinson 2000). As with birds, some bat species do not exhibit any mutual behaviour between individuals, while other species exhibit a range of social and even cooperative behaviours, from allogrooming to food sharing in vampire bats (*Desmodus rotundus*; for review see Kerth 2008).

Long lived species in which juveniles delay dispersal are characterized by having stable multigenerational family groups comprising mostly related individuals (Jarvis et al. 1994, Burda et al. 2000, Solomon 2003, Kerth 2008). Kin groups are not temporary aggregations, but evolved from both polygynous and monogamous mating systems where one sex disperses and the other remains in the natal territory (Greenwood 1980, Dobson 1982, Koenig et al. 1992, Solomon 2003). Dispersal in this context is natal dispersal where an individual leaves the natal (i.e. – birth) territory and establishes itself in a new territory (Greenwood 1980). Conversely, philopatry is the act of staying in the natal area past the point of weaning (Waser and Jones 1983). Subordinates delay dispersal if their chances of survival and independent reproduction are low. Thus, under such conditions, subordinates are expected to remain until the costs for dispersal are lessened, even if they exhibit reproductive suppression (Koenig et al. 1992; Keller and Reeve 1994; Emlen 1995, 1997). In birds, males tend to be philopatric and females are the primary dispersers, while in mammals the roles are reversed because females can reap greater potential benefits from philopatry and dispersal is more costly (Greenwood 1980, Solomon 2003, Koenig and Dickinson 2004). As a result, cooperative groups typically exhibit a sex-bias towards the philopatric sex because that sex receives greater benefits and incentives to exhibit helping behaviour to the resident breeders (Hamilton 1964, Woolfenden and Fitzpatrick 1990, Emlen 1997, Reeve et al. 1998, Clutton-Brock et al. 2002). For example in vervet monkeys (*Chlorocebus pygerythrus*), infant survival increases if the mother participated in caring for another female's infant before the birth of her first offspring (Fairbanks 1990).

The formation of groups from related individuals is necessary for the evolution of cooperative behaviour (Hamilton 1964, Emlen 1994) because individuals are more likely to provide assistance to kin than non-kin (Emlen and Wrege 1988, Hoogland 1995, Russell and Hatchwell 2001). Communal breeding societies evolved mostly from polygynous mating systems where related individuals utilize a communal site for breeding and parental care of offspring is shared between reproductive females (Lukas and Clutton-Brock 2012). In cooperative breeding societies, parental care can be shared between reproductive females, but the major difference between communal breeding societies is that cooperative breeders are assisted by non-breeding helpers that remain with the group to assist rearing the young (i.e. - their siblings or cousins) produced by other group members (Emlen and Vehrencamp 1983; Brown 1978, 1987). Parental care by individuals other than the mother is common when groups are composed of related females (Lee 1987, Norris and Schilt 1988, Manning et al. 1995, Ruckstuhl and Ingold 1998, Clutton-Brock et al. 2000). In bats (Kunz et al. 1994) and dolphins (Tavolga and Essapian 1957) other females provide birthing assistance to a pregnant female in the group. Rodents do not differentiate between different offspring, often combining litters and sharing nursing responsibilities (König 1994, Hoogland 1995, Hayes 2000). Many primates will carry another female's offspring thereby allowing the mother to forage (Mitani and Watts 1997). Other cooperative behaviour may occur between group members, such as sentinel behaviour and alarm calling (Rasa 1987; McGowan and Woolfenden 1989; Clutton-Brock et al. 1999b; Seyfarth and Cheney 1997; Manser 1999, 2001; Caro 2005; Blumstein 2007), or even attacking predators (Kobayashi 1996, Graw and Manser 2007). It is likely that the antipredator advantages of sociality facilitated the evolution of communal breeding in mammals (Hoogland 1995, Altringham and Senior 2005). In the absence of such risks, communal societies would not likely have evolved (Ylönen and Brown 2007).

In cooperative breeding systems, helpers remain past maturity and are often offspring of the reproductive pair, though could be unrelated immigrants (Clutton-Brock et al. 2001a, Burland et al. 2002) and, as a result, kinship between group members is often high (Burland et al. 2002, Cornwallis et al. 2010, Lukas and Clutton-Brock 2012). Additionally, it is suggested that the large litter size exhibited by many cooperative breeders facilitates the need for helpers to assist with offspring care (Smaldino et al. 2013).

This hypothesis may explain why cooperative breeding is not present in cetaceans even though many display cooperative hunting (Clutton-Brock 2016). Cooperative breeding societies in both birds and mammals evolved from monogamous mating systems where breeding is usually restricted to a single pair as seen in Florida Scrub Jays (*Aphelocoma coerulescens*; Woolfenden and Fitzpatrick 1990) and naked mole-rats (*Heterocephalus glaber*, Jarvis et al. 1994). However, in the plural breeding banded mongoose (*Mungos mungo*), multiple reproductive females are present and the ancestral monogamous state appears to have been replaced with a polygynous mating system (Cant et al. 2001). The presence of helpers has been attributed to a decrease in body mass loss in the dominant female during pregnancy, reductions in inter-birth intervals, increased survival of offspring and increased vigilance against predators (Rasa 1987; McGowen and Woolfenden 1989; Solomon 1991; Clutton-Brock et al. 1999a, b; Sanchez et al. 1999; Langen 2000; Clutton-Brock et al. 2001b; Russell et al. 2003; Hodge et al. 2008). Many of the same mutualistic behaviours observed in communal breeders can occur in cooperative breeders including allo-parental care (Moehlman and Hofer 1997, Creel and Creel 2002, Russell 2004), group foraging (Lovegrove and Wissel 1988), cooperative hunting (e.g. African wild dogs (*Lycaon pictus*), Creel and Creel 2002), predator vigilance and alarm calls (e.g. dwarf mongoose (*Helogale parvula*), Rasa 1987; Florida Scrub Jays, McGowan and Woolfenden 1989; and meerkats (*Suricata suricatta*), Manser 1999, 2001; Clutton-Brock et al. 1999b), and predator defense (e.g. banded mongoose, Rood 1983; and meerkats, Graw and Manser 2007). Additionally, group members can take turns babysitting young at the burrow while the rest of the group forages (Clutton-Brock 2000), protecting pups from predators (Clutton-Brock et al. 1999a), and provide food for pups (Rood 1978, Moehlman 1979, Sillero-Zubiri 1994, Brotherton et al. 2001) or the lactating female (Moehlman 1979, Malcolm and Marten 1982). In some other social organizations, group behaviour is coerced by dominant individuals (Frank 1995, Cant and Johnstone 2009), while in cooperative societies subordinate helpers assist with cooperative behaviour without aggressive actions from higher ranking individuals (Riehl and Frederickson 2016). In a wide range of cooperatively breeding birds, low adult mortality due to safe nest locations (i.e. – cavity or ledge nesting) combined with a stable climate has been shown to be the key factor predisposing species of certain phylogenetic lineages to cooperative breeding (Arnold and Owens 1999). Cooperative breeding is maintained by direct fitness benefits to individuals by group augmentation, general reciprocity or group selection (Kokko et al. 2001, Nowak 2006, Wilson and Wilson 2007) and kin selection and indirect fitness benefits (Hamilton 1964, Brown 1987, Emlen 1991). In cooperative herpestids, it is likely that predator vigilance ensures that helpers remain in the group (Doolan and Macdonald 1997, Creel and Waser 1997), while in callitrichids the energetic burden on the reproductive female to care for twin offspring facilitated the need for recruiting helpers (French

1997, Tardif 1997). Dominants may also offer “staying incentives” to subordinates in the form of breeding opportunities (Clutton-Brock 1998, Cant et al. 2001), though these incentives decrease as reproductive suppression increases due to ecological constraints (as seen in singular breeding social mole-rats (*Fukomys damarensis* and *Heterocephalus glaber*); Bennett et al. 1996, Bennett et al. 1999).

Many species of cooperative breeders exhibit reproductive suppression of subordinate group members, including social mole-rats (Bennett et al. 1999), meerkats (O’Riain et al. 2000a), dwarf mongoose (Creel and Waser 1997), wild dogs (Creel and Creel 2002), and callitrichids (French 1997). In *Clethrionomys* voles, the age of sexual maturity in females is delayed while in their mother’s territory and must disperse in order to reproduce (Carter and Roberts 1997, Solomon and Getz 1997). Additionally the absence of unrelated males will prevent females from reproducing (Carter and Roberts 1997, Cooney and Bennett 2000). Lastly, the presence of the dominant female alone appears to suppress the reproductive capabilities of subordinate group members (Carter and Roberts 1997, Beehner and Lu 2013), possibly through agonistic behaviours because hormone levels increase when she is removed (French et al. 1984, Faulkes and Abbott 1997). These processes are not mutually exclusive and a combination of mechanisms may be required to prevent subordinate reproduction. Anovulation in subordinate Damaraland mole-rats (*Fukomys damarensis*) appears to be caused by a combination of both the presence of the dominant female and inbreeding avoidance (Bennett et al. 1996, Cooney and Bennett 2000, Molteno and Bennett 2000). Similarly, in tamarins (*Leontopithecus* and *Saguinus*), both the absence of unrelated males and presence of dominant females prevent ovulation (French 1997). Although the mechanisms for reproductive suppression vary between species, many exhibit reduced levels of lutenizing hormone (LH) as a result (French 1997, Bennett et al. 1999, O’Riain et al. 2000a, Creel and Creel 2002) or even reduced ovaries (Faulkes and Abbott 1997). The decrease in LH causes a reproductive block preventing ovulation which can be alleviated upon the introduction of an unrelated male or the removal of the dominant female (Bennett et al. 1999, Cooney and Bennett 2000, Molteno and Bennett 2000).

Lifetime reproductive success in cooperative breeders is influenced by a number of factors including, but not limited to, the degree of ecological constraint on non-reproductive individuals preventing independent breeding, the group’s productivity if the subordinate stays within the group, and the chances of a subordinate to fight and depose a dominant breeder (Keller and Reeve 1994). Long reproductive tenure of dominant females combined with the suppression of subordinates suggests that cooperative breeding facilitated exponential increases in female fecundity (Clutton-Brock 2009). For example, a reproductive female naked mole-rat could potentially produce several hundred offspring in her 25 or more years of life (Hauber and Lacey 2005, Dammann and Burda 2007) and dominant female meerkats can produce over 80 surviving offspring (Clutton-Brock et al. 2006). The life span of subordinates is significantly reduced compared to those of dominant individuals further limiting their lifetime reproductive success compared to breeding individuals (Clutton-Brock et al. 2006, Dammann and Burda 2007). Direct fitness for the breeders is expected to increase with group size, but decrease for non-reproductive group members since subordinates are forced to live together due to ecological or extrinsic factors which limit dispersal (Lacey and Sherman 1997, Lacey 2004, Safran et al. 2007). Reproductive success of breeding females is strongly correlated with the number of helpers in dwarf mongooses (Rood 1990), wild dogs (Creel and Creel 2002), and meerkats (Clutton-Brock et al. 2001b). In African mole-rats, the sporadic rainfall, hard soil, and arid environment constrain non-reproductive group members to remain in the group by limiting the opportunities for dispersal and independent breeding (Jarvis et al. 1994). However, life time reproductive success in subordinates has been shown to increase in conjunction with the relaxation of ecological constraints since there are more opportunities for helpers to disperse and breed independently (Spinks et al. 2000b, Young et al. 2010). When breeding opportunities arise in subordinates, they can be targeted with aggression by the dominant female, as seen in meerkats (Clutton-Brock et al. 1998, Clutton-Brock et al. 2006), tamarins (French 1997), and naked mole-rats (Lacey and Sherman 1991). This aggression can increase as group size increases (e.g. banded mongoose, Cant et al. 2010), in the presence of unrelated males (e.g. Damaraland mole-rats, Cooney and Bennett 2000), or if a subordinate becomes pregnant, leading to abortion or eviction from the group (e.g. meerkats, Clutton-Brock et al. 1998, Young et al. 2006, Young 2009).

Natal dispersal has received some attention in mole-rats (Braude 2000, Hazell et al. 2000, Spinks et al. 2000b, Young et al. 2010). However, sample sizes of dispersing individuals recaptured in other burrows remain small and there are many unanswered questions. How long do subordinate individuals, particularly females, remain in the natal group? How frequently does natal dispersal occur? How far can they travel when searching for a new territory? Where do they go after leaving, do they join established groups, build a new burrow, or do they occupy existing empty burrows? Young et al. (2010) provides some data on distances traveled while dispersing but only for five individuals. This study provides a larger sample of known dispersing individuals as well as distances traveled while dispersing. No studies to date have further addressed the role of population density on demographics, dispersal rates or distances traveled while dispersing. This study endeavours to fill those knowledge gaps. The primary aims of this study were to better understand how new groups were formed. I wanted to answer these questions while also determining how population density effects dispersal tendency, rates, and distances traveled by using two populations of differing population density.

1.2 Study Species – Damaraland mole-rat

African mole-rats (Family Bathyergidae) are a group of specialized subterranean Hystricognath rodents endemic to sub-Saharan Africa living in elaborately excavated burrow systems (Bennett and Faulkes 2000). Mole-rats feed predominantly on geophytes (the underground storage organ of a plant) and in some cases grasses (Bennett and Faulkes 2000). The family is divided into six genera with at least 20 species exhibiting a range of breeding strategies from solitary to eusocial (Bennett and Faulkes 2000, Faulkes et al. 2004, Ingram et al. 2004, Kock et al. 2006). The genera *Heliophobius, Bathyergus,* and *Georhychus* are solitary and occur in more mesic habitats (greater than 400mm of rainfall per year) in east-central and southern Africa (Bennett and Faulkes 2000). The monotypic genus *Heterocephalus*, the naked mole-rat (*H. glaber*) from the arid horn of Africa, occurs in large groups (over 290 individuals) with high levels of inbreeding and generational overlap (Sherman et al. 1991, Jarvis and Sherman 2002), but in the natural environment exhibit strict outbreeding (S. Braude, pers. comm.). The remaining two genera (*Cryptomys* and *Fukomys*), represent half of the species in the family (Ingram et al. 2004, Kock et al. 2006) and exhibit a range of cooperative breeding strategies (Bennett and Faulkes 2000). The highly social species mostly occur in xeric environments (less than 400mm of rain per year) which suggests that environmental conditions require cooperation and communal living for a species to survive, thereby facilitating the evolution of cooperative breeding (Jarvis et al. 1994, Bennett and Faulkes 2000). In these eusocial species reproduction is restricted to a single female and the offspring remain within the colony to assist with the foraging and rearing of subsequent generations (Sherman et al. 1991, Jarvis and Bennett 1993, Bennett and Faulkes 2000).

The current extant genera in the family likely originated in East Africa some 40-48 million years ago (mya) during the Miocene with the divergence of *Heterocephalus* from the common ancestor. Shortly after it is suggested that *Heliophobius* subsequently diverged and spread south (Faulkes et al. 2004). Rifting and volcanic eruptions in present day Kenya and Tanzania in the early Miocene in addition to climatic and vegetation changes funneled the ancestral mole-rats further south through a corridor of fluctuating environmental conditions along the eastern side of the continent while preventing expansion to the west (Honeycutt et al. 1991). During the middle Miocene (22-26 mya), the genera *Bathygerus* and *Georychus* split from the common ancestor to colonize the coastal regions of South Africa. *Fukomys* and *Cryptomys* finally diverged from the common ancestor approximately 14-17 mya. While *Cryptomys* remained primarily in South Africa, the genus *Fukomys* spread north as far as central Africa radiating into at least 13 distinct species (Ingram et al. 2004). Due to the high diversity in the latter two genera, sociality likely enabled rapid expansion into new available habitats and allowed for speciation (Faulkes et al. 2004, Faulkes and Bennett 2007).

The ancestral mating system in the family is likely monogamous, but there is debate regarding whether the ancestral condition was solitary or social, since monogamy occurs in both organizations and sociality could equally be a shared or a derived state (Burda et al. 2000, Faulkes and Bennett 2007). The three social genera *Heterocephalus*, *Cryptomys* and *Fukomys* are separated from each other by the three solitary genera, with the latter two social genera have most recently evolved (Ingram et al. 2004). The justification for solitariness stems from the fact that the majority of subterranean rodents are solitary and fossil evidence shows extinct taxa have a large body size like most of the extant solitary species (Faulkes and Bennett 2007). However, there are some species of social mole-rats which are of comparable size to the solitary species, such as the giant mole-rat (*Fukomys mechowii)* which is larger than *Georychus* and *Heliophobius* (Burda et al. 2000). Additionally a large portion of Hystricognaths (80%) are social (Kleiman 1974), including two of the closest relatives in the families Hystricidae (Old World porcupines) and Petromuridae (dassie rats; Nedbal et al. 1994), and the solitary state found in some bathyergids could be a derived trait as in some bees and wasps that have lost sociality (Wcislo and Dunfath 1997). Based on the current phylogeny within the family there is support for both scenarios (Ingram 2004, Burda et al. 2000, Faulkes and Bennett 2007).

The aridity food distribution hypothesis (AFDH) has been put forward to explain how the evolution of sociality may have arisen in the African mole-rats (Jarvis et al. 1994). The hypothesis implies that solitary females are unlikely to raise their offspring without assistance. By being social and delaying dispersal until conditions are favorable, all individuals assist with cooperative activities (foraging, pup rearing, tunnel maintenance, and colony defense) gaining many direct and indirect benefits as a result (Jarvis et al. 1994, Jarvis et al. 1998, Faulkes and Bennett 2013). Philopatry and delayed dispersal are common in the social genera *Heterocephalus*, *Cryptomys* and *Fukomys* whose colony members exhibit a slower offspring development rate than those of the solitary species (Bennett et al. 1991). Philopatry is positively correlated with the competition for breeding positions and availability of territories, hence the long tenure of breeding individuals in social mole-rats further drives the propensity for philopatry and delayed dispersal (Jarvis and Bennett 1993, Kokko and Lundberg 2001).

The Damaraland mole-rat is a highly social species occurring in the red Kalahari arenosols of southern Africa in groups of up to 41 individuals with a single reproductive female and up to three reproductive males, while non-reproductive individuals assist with pup care, foraging, burrow excavation, and colony defense (Jarvis and Bennett 1993, Bennett and Jarvis 2004). Large colonies can occupy a territory between 1.0-1.3 hectares (Lovegrove 1989; N. C. Bennett and J. U. M. Jarvis, unpublished data). Unlike the common mole-rat (*Cryptomys hottentotus*), they are aseasonal breeders and litters are born throughout the year after a gestation period of ca. 80-90 days with a mean litter size of 2.8 offspring (Bennett and Jarvis 1988, Bennett et al. 1999). They occur in sandy soil areas of thornveld savannah and grassland habitats from northeastern Namibia through Botswana and into northwestern South Africa (Bennett and Jarvis 2004). This region has distinct wet and dry seasons where during the wet season (November to April) nearly all the yearly rain falls (200-400mm) in heavy sporadic thunderstorms (Rooyen et al. 1990, Jarvis and Bennett 1993, Clutton-Brock et al. 1999a). A minimum of 25mm of rain is required to soften the soil to promote digging which enables tunnel expansion and dispersal (Jarvis et al. 1994).

Damaraland mole-rats can be considered eusocial (Jarvis and Bennett 1993). The classic definition of eusocial societies requires reproduction to be limited to a small portion of the group (and remainder effectively sterile), an overlap of generations, and cooperative brood care (Michener 1969, Wilson 1975). Under this definition many cooperative monogamous vertebrate species could be considered eusocial (dwarf mongooses, Creel and Waser 1991; African wild dogs, Malcolm and Marten 1982; Florida Scrub Jays, Woolfenden and Fitzpatrick 1990). A more stringent definition was put forth limiting eusociality to species with a definitive caste system where individuals exhibit marked changes in their morphology and irreversible sterility (Crespi and Yanega 1995). Based on the definition of Michener (1969) and Wilson (1975), Damaraland mole-rats are eusocial, but based on the definition of Crespi and Yanega (1995) they are considered cooperative breeders. Unlike naked mole-rats which will readily inbreed, the Damaraland mole-rat is an obligate outbreeder, avoiding inbreeding in favour of breeding with an unrelated partner (Bennett et al. 1996, Molteno and Bennett 2000). Therefore, it has always been assumed that colonies are composed of the reproductive pair and all other individuals are their offspring from subsequent generations (Jarvis and Bennett 1993). However, more recent evidence has shown that colonies often contain individuals (mostly males) unrelated to the reproductive pair (Burland et al. 2004).

Subordinate individuals in a colony exhibit a marked reproductive suppression maintained by a combination of inbreeding avoidance (Jarvis and Bennett 1993, Cooney and Bennett 2000), social inhibition via dominance control (Clutton-Brock 1998, Molteno and Bennett 2000, but see Cooney and

Bennett 2000), interference with mating attempts (Cooney 2002), and possibly other as yet unknown methods (Faulkes and Bennett 2007). Non-reproductive females exhibit a clear physiological block to reproduction, where ovulation is blocked at the ovary due to reduced secretion of LH (Bennett et al. 1996, Molteno and Bennett 2000). This suppression remains until an unrelated male presents himself, or dispersal occurs, likely triggered by increased rainfall (Rickard and Bennett 1997, Molteno and Bennett 2002, Young et al. 2010). In captive colonies, non-reproductive females removed from the presence of the reproductive female will begin to spontaneously ovulate providing support that anovulation is likely a form of dominance control by the reproductive female (Molteno and Bennett 2000). Cooney and Bennett (2000) believe that dominance control has little effect due to the fact that non-reproductive individuals avoid breeding with different sex colony members in the absence of the dominant female. Unrelated individuals of both sexes (including transient immigrants) are frequent in a wild population, providing evidence that non-reproductive females are presented with opportunities to mate with extra-colony members and inbreeding avoidance alone is not enough to maintain reproductive skew (Burland et al. 2004). When foreign male intruders are introduced to a colony, dominant males will prevent copulation with resident females by attacking the intruder to interrupt sexual solicitations (Cooney 2002). Non-reproductive males while not exhibiting reproductive suppression to the extent of females do have an increased frequency of immature sperm (Maswanganye et al. 1999). Immigrant females are rare in established colonies limiting the mate choice of males while they remain with the colony (Hazell et al. 2000, Burland et al. 2002, Burland et al. 2004). As a result, males must disperse from the colony to gain any direct fitness benefits. While female reproduction is regulated though physiological suppression by dominance control, males refrain from breeding with female colony members likely due to inbreeding avoidance alone (Bennett 1994, Cooney and Bennett 2000).

Direct observations of dispersal events in mole-rats are rare (O'Riain et al. 1996; Hazell et al. 2000; K. Finn, pers. obs.) and recapture of known dispersers is uncommon (Jarvis and Bennett 1993, Spinks et al. 2000b, Young et al. 2010). Due to the arid environment and sporadic rainfall where they occur, dispersal is limited to a few months out of the year following heavy rains that have softened the soil thereby reducing the energetic costs associated with digging (Jarvis and Bennett 1993, Molteno and Bennett 2002, Young et al. 2010). Damaraland mole-rats can disperse up to 430m (Young et al. 2010) from their natal colony by travelling both above and below ground (Jarvis and Bennett 1993, Hazell et al. 2000), but it is unknown if one method is preferred over the other or if greater dispersal distances are possible. Only one account documents above ground dispersal in Damaraland mole-rats where predominantly large males were found along a concrete canal in Namibia (Hazell et al. 2000). Burland et al. (2004) showed that males will readily disperse from their natal group to join established colonies and are more likely to find a potential mate in the process. Female dispersal in mole-rats may be controlled by the lowering of hormonal suppression following heavy rains triggering readiness to mate with immigrant males (Molteno and Bennett 2000, Young et al. 2010). Female immigrants to established colonies are rare due to the xenophobic nature of mole-rats (Jarvis and Bennett 1993; Cooney 2002; Burland et al. 2004; K. Finn, pers. obs.). Occasionally, cohorts of one sex or mixed sexes will form to disperse either joining an established colony or forming a nascent colony respectively, but these observations are rare (Jarvis and Bennett 1993; K. Finn, pers. obs).

CHAPTER 2: Study Sites and General Methods

2.1 Study Sites

The study was conducted at two field sites in the Northern Cape province of South Africa (Figure 1). The first site was the Kalahari Research Centre (KRC) and surrounding farmland, located 27km west of Van Zylsrus (26°58’S, 21° 49’E). The second location was the Tswalu Kalahari Reserve (Tswalu), a 104,000 hectare private nature reserve 55km south of Van Zylsrus (27°26’S, 22°16’E). The combined total size for KRC was approximately 910 hectares and Tswalu was approximately 140 hectares. The landscape of the KRC comprises arid thornveld with vegetated red sand dunes covered in grasses (*Eragrostis*, *Aristida*, *Stipagrostis*, and *Schmidtia* spp.), bushes (*Acacia [Senegalia] mellifera, Rhigozum trichotomum*, *Grewia flava*, and *Lycium cinereu*), and scattered trees (*Acacia [Vachellia] erioloba, Acaia [Vachellia] haematoxylon,* and *Boscia albitrunca*; Leistner 1967, Clutton-Brock 1999a). While the area in Tswalu lacked the typical rolling dunes found further north, the red sand and vegetation was similar to that in the KRC, except there were more black thorn acacia, but few other trees. Additionally, two geophytes the gemsbok cucumber (*Acanthosicyos naudinianus*) and eland’s bean (*Elephantorrhiza elephatina*) were present at both sites which provided the primary food resources for the study species (Jarvis et al. 1998, Voigt et al. 2014).

The summers (October – April) in the region are very hot with a mean maximum daily temperature of 34.0°C (range 17.9 – 44.2°C) and a mean minimum of 15.1°C (range -2.1 – 28.9°C). During winter (May – September) the mean minimum daily temperature is 3.1°C (range -11.6 – 18.7°C) and a mean maximum of 25.0°C (range 8.7 – 39.2°C). Throughout the year the soil surface temperature can be as much as 10°C above the ambient air temperature and maintain that temperature for over five hours during summer, but at depths inhabited by mole-rats (0.3m – 2m) the temperatures stay between 15 – 35°C (Bennett et al. 1988).

The majority of the mean annual rainfall results from sporadic heavy thunderstorms in summer between December and March. The KRC received an average of 255mm per year (averaged over 2009-2016, range 120-420mm) with 213mm falling during 2013-2014, 187mm in 2014-15, and 188mm in 2015-16. Tswalu has a higher rainfall pattern compared to the area to the west of Van Zylsrus receiving 357mm per annum (averaged over 1998-2016, range 195-681mm) with 327mm in 2013-14, 206mm in 2014-15, and 229mm in 2015-16.

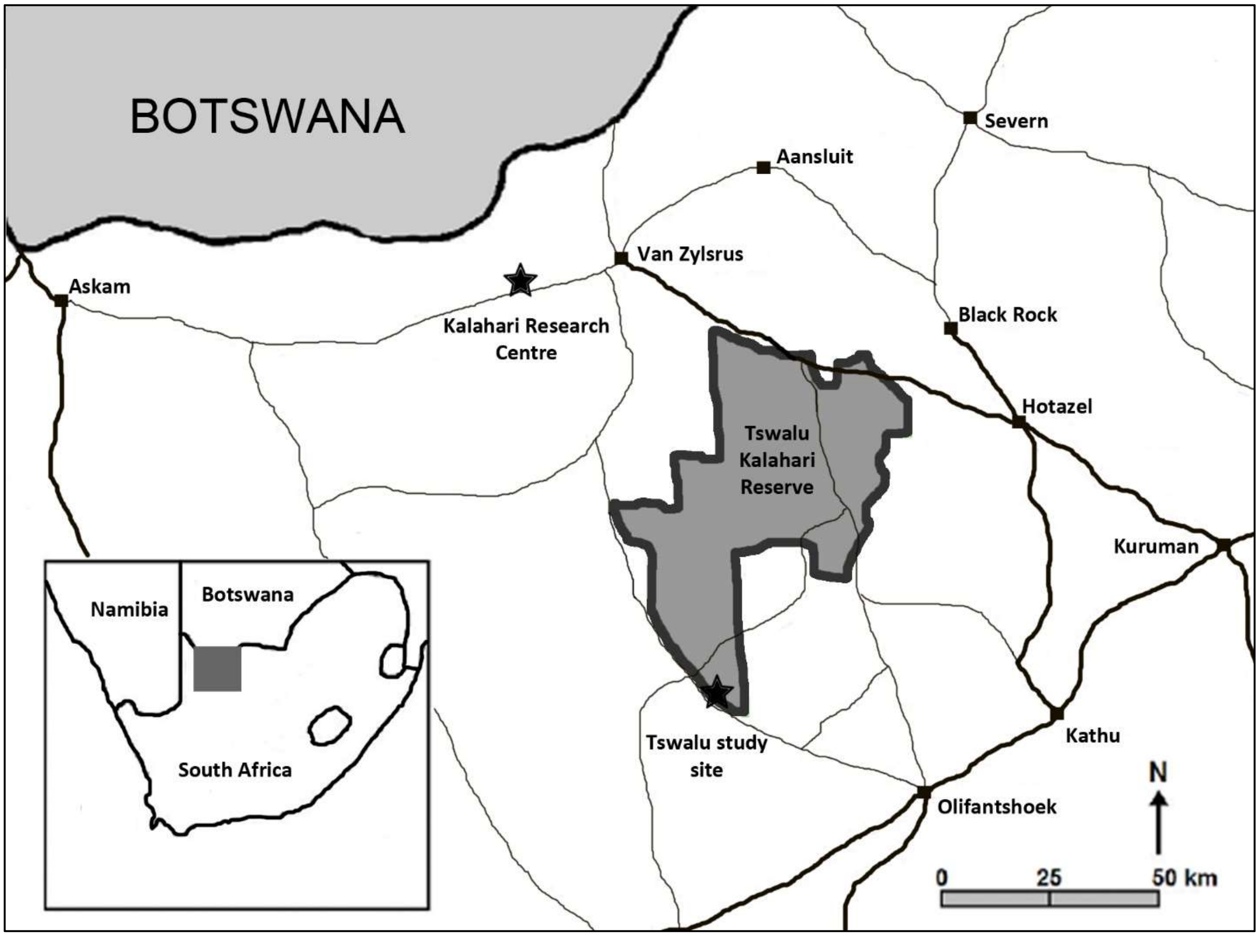

Figure 1: Study sites in the Northern Cape, South Africa. The Kalarhari Research Centre near Van Zylsrus was one location where mole-rats were studied. The other location at Tswalu Kalahari Reserve farther south receives more annual rainfall. The vegetation and soil structure is similar between the two locations with red Kalahari arenosols and scattered bushes and trees.

2.2 Mole-rat Sampling

From July 2013 to October 2016, Damaraland mole-rats (*Fukomys damarensis*) were captured at the KRC and from March 2015 to April 2016 at Tswalu. Mole-rats were captured using modified Hickman traps (Hickman 1979) baited with sweet potato (*Ipomoea batatas)* or gemsbok cucumber and placed into the burrow system of a proposed colony to be captured. The burrows were found by digging a trench perpendicular to the line of mounds until breaching the tunnel. A trap was then placed into each open tunnel and covered with sand (Figure 2).

Figure 2: Trapping methods of Damaraland mole-rats. (a) In the process of creating tunnels, mole-rats push excess sand to the surface creating a line of mounds. (b) The burrow tunnels run underneath the mounds and can be located by digging a trench between two mounds. (c) Once the tunnel is located two traps are placed in both entrances of the tunnel.

At each burrow system, two trap sites were typically established except in known large colonies, where three or four trap sites were activated to decrease the capture time. However, if the colony was known to contain only a single individual then one trapping site was opened. Each trapping site was marked using a handheld GPS unit (Garmin eTrex 10, USA). Trapping was conducted continuously throughout the year. During summer, traps were disarmed in the morning (ca. 09h00-10h00) by removing the door (which allowed mole-rats still present access to the food and potentially become habituated to using the trap as a food source) and then reactivated shortly before sunset (ca. 18h00-19h00) to prevent mortality during the heat of the day. Trapping continued throughout the night and early morning, with traps checked every one to two hours. During winter traps were checked throughout the day and disarmed overnight when temperatures could drop below freezing. Since mole-rats have poor thermoregulatory measures (Bennett and Faulkes 2000) when trapping overnight they were kept in large boxes with sand and towels which were then buried in the ground to insulate them against temperature fluctuations. Colonies were recaptured at a minimum of six month intervals to prevent damage to their tunnel system and undue stress from capture. In many cases though, the time between captures at the KRC was greater than six months, due to limited availability of assistance requiring the prioritization of certain colonies or failure to locate a colony after six months and only locating them a few months later.

Captured individuals were anaesthetized on the day of capture with a maximum of 200µl isoflurane inhalation to facilitate collecting samples and accurately measuring body morphometrics (Henry et al. 2007, Parker et al. 2008). While under anaesthesia, all individuals were implanted with a subcutaneous transponder tag (Trovan Unique, DorsetID, Netherlands) to uniquely identify them, weighed to the nearest gram (Sartorius TE4100, Germany) then measured (incisor width, incisor length, head width) using digital calipers (HM Müllner 10109, Austria) accurate to 0.01mm (Young and Bennett 2010, Young and Bennett 2013). Total body length was measured dorsally with a tape measure accurate to 1mm (Young and Bennett 2010, Young and Bennett 2013). Small pups (8-14g) were not implanted with a transponder nor measured, but were weighed. Additionally, tissue samples and blood (from individuals > 50g) were collected from all captured mole-rats for concurrent research. Captured mole-rats were housed up to 10 days in a climate controlled room at 20-25°C in artificial tunnel systems made from agricultural polyvinyl chloride (PVC) pipes with paper towel filled plastic boxes replicating a nest and provided with sweet potato and gemsbok cucumber *ad libitum* (Zöttl et al 2016a, b). Fresh water was not required since mole-rats derive all their required water from the geophytes they eat (Barnet et al. 2003, Bennett and Faulkes 2000).

If traps were inactive (i.e. – food uneaten and/or not blocked with sand) or no mole-rats captured for 48 hours after the last captured mole-rat, it was assumed all individuals present in the colony had been captured and the mole-rats were subsequently released back into their burrow as soon as possible. Prior to release, the presence of a transponder was verified in all newly marked individuals and a new transponder was implanted if the original was not located. In only a few cases (n<10) were newly implanted transponders lost from individuals while in the laboratory. Every effort was made to capture the entire colony within 7 days from the traps being activated to avoid disrupting their social structure. Having more than one active trapping location per colony, combined with trapping during the night enhanced capture success and reduced the capture time per colony (mean capture time 2.3 days ± 1.9 SD, mean time in the lab 4.0 days ± 2.0 SD, n=430; Thomas 2016; H. Thomas, pers. comm.; K. Finn, pers. obs.). In only six of 438 (KRC n=2, Tswalu n=4) capture sessions did I encounter a situation where two colonies were trapped simultaneously (determined by the presence of two reproductive females) due to multiple trapping sites per location. Occasionally (n=10) some individuals in a colony evaded capture, continually blocking the traps with sand and forcing me to extend the capture period. In these cases, after a maximum of 10 days from trap activation without capturing the elusive individual I concluded trapping and released the rest of the colony. These groups were incomplete groups and were not included in analyses. All protocols were approved by the University of Pretoria ethics committee and complied with regulations stipulated in the Guidelines for the use of Animals in Research (Permit ECO32-13).

The distance between colonies at KCR was much greater than at Tswalu. At Tswalu colonies could be as little as 5m apart, whereas at KRC the minimum distance was approximately 20m. Including colonies composed of single individuals, the mole-rat density at Tswalu was approximately 0.41 colonies/ha and 0.13 colonies/ha at KRC. Therefore, Tswalu was categorized as the “high density” site and KRC as the “low density” site. For analysis purposes I defined a colony of mole-rats as two or more individuals occurring in a single burrow system. Consequently, all subsequent colony level analyses did not include those with only single animals.

CHAPTER 3: Variations in colony attributes and individual body size between populations

3.1 Introduction

Population densities of species are shaped by the availability and distribution of resources, and ultimately the energy, available to them in their specific niches (Brown 1984, Robinson and Redford 1986). In both Neotropical and Afrotropical mammals, species with either a large body size or specific dietary preferences are generally found in low population densities, whereas smaller mammals or species with access to abundant resources are found in higher densities (Robinson and Redford 1986, Fa and Purvis 1997). The variation in habitat saturation may be attributed to food availability, and as such, density increases due to increased quantity and/or quality of diet as found in brown bears (*Urus arctos*, Stringham 1990), black bears (*Urus americanus*, Nagy and Haroldson 1990), European badgers (*Meles meles*; Kruuk and Parish 1982, Macdonald et al. 2002), naked mole-rats (*Heterocephalus glaber*, Brett 1991), ungulates (Caughley 1970), and voles (*Microtus* spp., Solomon and Getz 1997). Consequently, increased competition for available resources (food and territory) increases with population density as shown in voles (Ostfeld 1985, Wolff and Schauber 1996) and bears (Rogers 1977, Dahle and Swenson 2003). The ultimate consequence is many fundamental aspects of a species behaviour and ecology are affected by density.

In both birds and mammals, conflicting density-dependent effects on philopatry and dispersal have been observed. In the cooperative breeding Acorn Woodpecker (*Melanerpes formicivorus*), group size decreases with a reduction in population density (Trail 1980), and philopatry (and therefore group size) became enhanced with increasing habitat saturation (Stacey 1979). In Stripe-backed Wrens (*Campylorhynchus nuchalis*), juveniles were more likely to remain in their natal territories during times of high habitat saturation (Austad and Rabenold 1986), while Emlen (1982a,b) found a higher proportion of juvenile White-fronted Bee-eaters (*Meropes bullockoides)* remaining in their natal territory during seasons with low density. Dispersal rates in mammals may also be density-dependent, although there is a lack of consensus in the relationship (Gaines and McClenaghan 1980, Boutin et al. 1985, Verner and Getz 1985). In field studies on small mammals, a heightened level of dispersal was recorded in populations with high densities (Windberg and Keith 1976, Boutin et al. 1985, Spinks et al. 2000b), but more often rates were highest at low densities (Gaines and McClenaghan 1980, Jones et al. 1988, Wolff et al. 1988, McGuire et al. 1993, Getz et al. 1993, Wolff 1997, Andreassen and Ims 2001, Kokko and Lundberg 2001). Wolff (1997) attributed the inverse relationship between dispersal and density to a “social fence” in which territorial neighbours inhibit immigrants from joining the group. At low population density, it has been suggested that both a scarcity of mates as well as inbreeding avoidance may result in enhanced dispersal (Hanski 1999). Whereas at higher densities, mothers and daughters nest in close proximity to one another or occasionally communally in the same nest (Wolff 1994, Lambin and Yoccoz 1998, Solomon and Getz 1997). This tendency affects male dispersal distance, forcing them to travel further to encounter an unrelated potential mate to avoid breeding with relatives (Wolff 1994, Andreassen and Ims 2001, Lambin et al. 2001). Additionally, reduced dispersal at high densities may result from suppressed sexual maturation in species such as voles where delayed natal dispersal occurs (Clobert et al. 2004).

Large mammals and other long-lived species (*K*-selected) show most of their density-dependent changes in reproductive aspects rates in populations close to carrying capacity, while many short-lived species (*r*-selected) show most changes at lower population levels (Fowler 1981). The disparate pattern in life history trajectories may account for the differences observed between mammal species. In some birds, clutch size can be density-dependent and adjusted to match levels of competition, since a reduced clutch size may result in higher quality young (Krebs and Perrins 1978, Sinclair 1989). Chick mortality was found to be inversely density-dependent in partridges (*Perdix perdix*; Blank et al. 1967) and, as a result, during years of high density it was found to be more productive to raise fewer chicks which were heavier to increase their chances of survival, while during years of low density a strategy to raise a larger clutch of lighter chicks was preferred. In cooperative breeders, direct fitness increases with group size for the breeders, but decreases for non-reproductive group members since subordinates are forced to live together due to ecological or extrinsic factors which limit dispersal (Lacey and Sherman 1997, Lacey 2004, Safran et al. 2007). In species with long reproductive tenure, the number of young reared to weaning has been found to decrease with group size in species where dispersal is difficult and philopatry is favoured as in the tuco tucos (*Ctenomys* spp., Lacey 2004) and prairie dogs (*Cynomys ludovicianus*, Hoogland 1995). However, in species with brief tenure, the number of offspring does not vary with group size e.g. dormice (*Glis glis*, Pilastro et al. 1994) and deer mice (*Peromyscus* spp., Wolff 1994). In marmots (*Marmota flaviventris)*, reproductive rate has been shown to increase with group size in smaller groups, but started to decrease after an optimum group size was achieved (Armitage and Schwartz 2000). In many rodents, suppression of reproductive function is an adaptive response to increased population density (Brown and MacDonald 1984). The age of sexual maturity has also been shown to decrease with increasing density in many ungulate species such as red deer (*Cervus elaphus*, Albon et al. 1983), roe deer (*Capreolus capreolus*, Gaillard et al. 1992), reindeer (*Rangifer tarandus*, Skogland 1985), and bighorn sheep (*Ovis canadensis*, Jorgenson et al. 1993) as well as the carnivores: European badgers (Rogers et al. 1997), black bears (Nagy and Haroldson 1990), and brown bears (Stringham 1990).

Density may even affect mating systems (Kokko and Rankin 2006). In white footed mice (*Peromyscus leucopus*), some voles, and giant kangaroo rats (*Dipodomys ingens*), monogamous pair-bonds form when population density is low, while at higher densities promiscuity appears to the more common strategy (Mineau and Madison 1977, Kleiman 1977, Lambin and Krebs 1991, Randall et al. 2002). It is likely that multiple mating in high density situations is a female reproductive strategy used to reduce infanticide by males (Wolff 1989). Males will also defend females at low density due to the decrease in competitors and then switch to a non-defense scenario where multiple males form hierarchies of dominance to "share" breeding opportunities (Davis 1958, Ims 1987, Wolff 1989). In sciurids breeding rights are determined by agonistic interactions between resident males (e.g. *Sciurus* spp., Farentinos 1972, Thompson 1977, Wauters et al. 1990, Koprowski 1993), or sometimes nonaggressive displacements (e.g. Cape ground squirrels (*Xerus inarus*), Waterman 1995), and breeding success is strongly correlated with dominance (Sherman 1976, Dunford 1977, Waterman 1998).

Density dependent effects on the physiology of individuals has been studied extensively for large mammals (for review see Fowler 1987 and Saether 1997). In many species of ungulates, high population density results in a reduction in body mass (red deer: Clutton-Brock et al. 1982, Bonenfant et al. 2002; feral donkeys (*Equus asinus*): Choquenot 1991; reindeer: Klein 1968; roe deer: Gaillard et al. 1996), growth rate (Choquenot 1991, Leberg and Smith 1993), home range size (roe deer: Vincent et al. 1995), and survival (red deer: Clutton-Brock et al. 1985, Albon et al. 2000, Gaillard et al. 2000; soay sheep (*Ovis aries*): Milner et al. 1999; African buffalo (*Syncerus caffer*): Sinclair 1974). In carnivores, high population density has been linked to smaller home range size (Nagy and Haroldson 1990, McLoughlin et al. 2000, Dahle and Swenson 2003), declines in fecundity (Macdonald et al. 2002), and smaller body sizes (Macdonald et al. 2002).

In contrast, the effects of population density on subterranean rodents has been relatively poorly studied. Only one study, undertaken on common mole-rats (*Cryptomys hottentotus*) by Spinks et al. (2000a, b), related differences in population density, body mass, recruitment, individual loss and dispersal patterns to food availability and the amount and periodicity of rainfall at two distant locations. Spinks et al (2000a, b) found that with increasing rainfall the total available energy from geophytes increased causing a related increase in population density as well as mean body size, recruitment and dispersal rates. It has also been shown that body size varies with location in the naked mole-rat (*Heterocephalus glaber*, Jarvis 1985) and by colony size (Brett 1991, Zöttl et al. 2016). Previous studies have suggested that geophyte distribution and density may bring about an increase in colony size and body mass (Jarvis 1985, Brett 1991, Spinks 1998, Spinks et al. 2000a). Population density is often assumed to be positively correlated with food availability (as a measure of habitat quality), but this assumption can be misleading (Van Horne 1983). Therefore, it may be difficult to tease apart the effects of density and habitat quality on individual and group level dynamics. Due to their xenophobic nature, each mole-rat colony is effectively independent from its neighbours and it is unknown if the actions of one colony affect neighbouring colonies. No studies to date have investigated the effects of population density on group size, body size, recruitment, individual loss and dispersal in Damaraland mole-rats (*Fukomys damarensis*). It would thus be of interest to determine if the population density of an area (as opposed to the density within a burrow) has an effect on both body size and group level attributes.

Using two populations of wild Damaraland mole-rats with markedly different population densities, this chapter aimed to test whether (i) population density exerts differential effects on colony attributes (group size, number of offspring per litter, colony attrition and recruitment) and (ii) whether population density affects individual body size and growth of colony members. An in-depth analysis of two data-sets from capture-mark and recapture studies on Damaraland mole-rats was undertaken to test for correlations between colony size and colony attrition (i.e. – loss of individuals due to death or dispersal) at each site. A comparison of the relative differences between litter sizes and recruitment was also undertaken to determine if these attributes were affected by colony density. The differences in body mass, morphometrics, and growth rates of individuals between the two sites were compared to test for effects of density on body size and growth rates.

Based on the studies by Spinks et al. (2000a, b), I expected that colony attrition and recruitment would be density dependent, increasing at the higher density site. A positive relationship between colony size and attrition (i.e. - where more animals are lost as colony size increases), was predicted at both sites (*sensu* Spinks et al. 2000b). Additionally, I predicted that recruitment would be enhanced in larger colonies, since it has been shown that long established reproductive females are more successful at raising litters (Bennett and Faulkes 2000). Based on the findings of Spinks et al. (2000a, b) I believed that individuals in the high-density site would have a greater body size and mass than the low-density site and, as a result, colony biomass would be greater at the high-density site.

3.2 Methods and Data Analyses

All statistical analyses were performed with R version 3.2.4 (R Core Team 2016). Means are reported as mean ± SD. Colony size and within colony sex ratios (males: females) were compared using Wilcoxon rank-sum tests. The inter-site difference in original colony biomass was tested with a Wilcoxon rank-sum test and intra-site differences in biomass between capture events were tested with a Kruskal-Wallis test. The number of single females found at each site was compared between the two sites by using a Fisher’s exact test. Litter size was calculated by counting the number of individuals <85g in a cohort of a similar size at first and second capture, then taking the average among cohorts. A mass of 85g was selected arbitrarily based on observations of body mass profiles over multiple trapping sessions since some individuals would maintain a body mass of around 90-100g between captures and therefore it was unclear whether individuals of 90g or more were actually from the same or a previous litter (K. Finn, pers. obs.). Additionally, in the rare cases where a reproductive female gave birth to a litter in the lab, that litter was also included.

The inter-site differences in colony litter size, recruitment (number of new pups born between trapping events), recruitment rate and attrition rate were tested with Wilcoxon rank-sum tests. Braude (1991) outlined methods for assessing the gain and loss of individuals over time by calculating the recruitment and attrition rates. The recruitment rate is a measure of juveniles born per individual colony member between trapping sessions:

$$\text{Recruitment rate} = \frac{\text{(number of new juveniles at time A+1)}}{\text{(Colony size at time A)}}$$

The attrition rate is a measure of the number of individuals lost per individual colony member between trapping sessions:

$$\text{Attrition rate} = \frac{\text{(number of individuals at capture A - number of individuals recaptured at A+1)}}{\text{(Colony size at A)}}$$

Additionally, I calculated the recapture rate, the number of individuals recaptured out of the original colony size between trapping sessions (Braude 1991):

$$\text{Recapture rate} = \frac{\text{(number of captures at A+1 that were previously captured at A)}}{\text{(Colony size at A)}}$$

Since some colonies were captured at different time intervals between recaptures, each rate was divided by the number of six month intervals (the time between trapping sessions divided by 180) between A and A+1. While the attrition and recapture rates are related, it is important to note the differences. The attrition rate is the percentage of animals missing from the colony at the second capture event, while recapture rate is the percentage of individuals remaining in the colony. Due to the correction for time between capture events, these two values may not always sum to 100 percent. The correlation between colony attrition and colony size was tested using a Spearman Rank Correlation tests for the two sites. The same test was preformed to test for correlations between colony recruitment and colony size.

While under anaesthesia (see section 2.2 Mole-rat Sampling) animals were measured using the parameters selected by Young and Bennett (2010). Total length (TL) was measured dorsally from the tip of the nose to the end of the tail with a measuring tape accurate to 1mm. The remaining morphometrics were measured with digital calipers accurate to 0.01mm. Head width (HW) was measured from left to right between the ears to standardize the procedure between observers. Upper incisor total width (TW) was measured across the base of both incisors. Left and right upper incisor lengths (LL and RL respectively) were measured as the greatest distance between the gum and the tip of the tooth. Animals were weighed using an electronic scale (accurate to 1g) at capture and again prior to release, and body mass was the average between the two values. Since body mass is a poor indicator of age (Bennett et al. 1990), growth data from long-term captive animals at KRC of known age (M. Zöttl, unpublished data) were used to determine the minimum total length of adults in order to classify individuals into adult and juvenile age categories (Jarvis and Bennett 1993, Bennett and Faulkes 2000). I determined the inflection point along the line (ca. 15cm) and used this value to assign age categories to animals in my study. All individuals under 15cm total length were considered juveniles and those above were categorized as adults.

To narrow down which body measurements (body mass, TW, LL, RL, HW, and TL) to analyze, a principal component analysis (PCA) was performed to determine which of these factors best explained the variation in individual size. All inter-site comparisons of body mass and morphometrics were performed with Wilcoxon rank-sum tests. To prevent Type I error, a Bonferroni Correction was applied to the results. Intra-site body size differences between sexes and inter-site differences in body size were compared for both juvenile and adult mole-rats using Wilcoxon rank-sum tests. The inter-site growth rate was compared between trapping events using Wilcoxon rank-sum tests. To calculate the growth rate for each measurement, the value at first capture was subtracted from the measured value at second capture, and the difference divided by the number of months between capture.

Body size and growth rates of the reproductive individuals were compared between the two locations using Wilcoxon rank-sum tests. Reproductive females are easily recognized by having prominent nipples and a perforate vagina (Bennett and Faulkes 2000, Burland et al. 2004). The reproductive male was assumed to be the heaviest individual in the colony, since in most cases I was unable to confidently determine the presence of abdominal testes (Jarvis and Bennett 1993, Bennett and Faulkes 2000). By comparing the ratio of the fourth lumbar vertebra length to the zygomatic arch width between individuals O'Riain et al. (2000b) and Henry et al. (2007) have shown that reproductive female naked mole-rats exhibit a distinct elongated body shape compared to both reproductive males and non-reproductive females. Young and Bennett (2010) found a similar pattern in Damaraland mole-rats using the ratio of body length to head width. Thus, I compared the intra-site variation in body elongation between non-reproductive and reproductive individuals.

3.3 Results

During the course of the study, I captured 683 mole-rats from 51 colonies at the KRC (low-density site) and 548 mole-rats from 57 colonies at Tswalu (high-density site). The mean colony size was similar at the two sites (df = 106, means: KRC 8.91 ± 5.7 and Tswalu 8.96 ± 5.3, p = 0.11; Figure 3) as well as the mean biomass (df=106, means: KRC 871.9 ± 566.9g and Tswalu 793.5 ± 506.2g, p = 0.48). The sex ratios within colonies were slightly male-biased and similar between the locations (df = 22, means: KRC 1.5 ± 1.3 and Tswalu 1.3 ± 1.2, p = 0.27). Both locations exhibited comparable litter sizes (df = 106, means: KRC 2.6 ± 1.2, Tswalu 2.5 ± 1.0, p = 0.51). Additionally, I found a significantly higher proportion of single individuals inhabiting isolated burrows at the low-density site than at the high-density site (KRC: two males, 47 females; Tswalu: two males, nine females; df=1, p < 0.01; Figure 3). Some of the single individuals at the low-density site (n = 15) had been recaptured in the same general location for over one year and, of those, four have been recaptured for approximately two years.

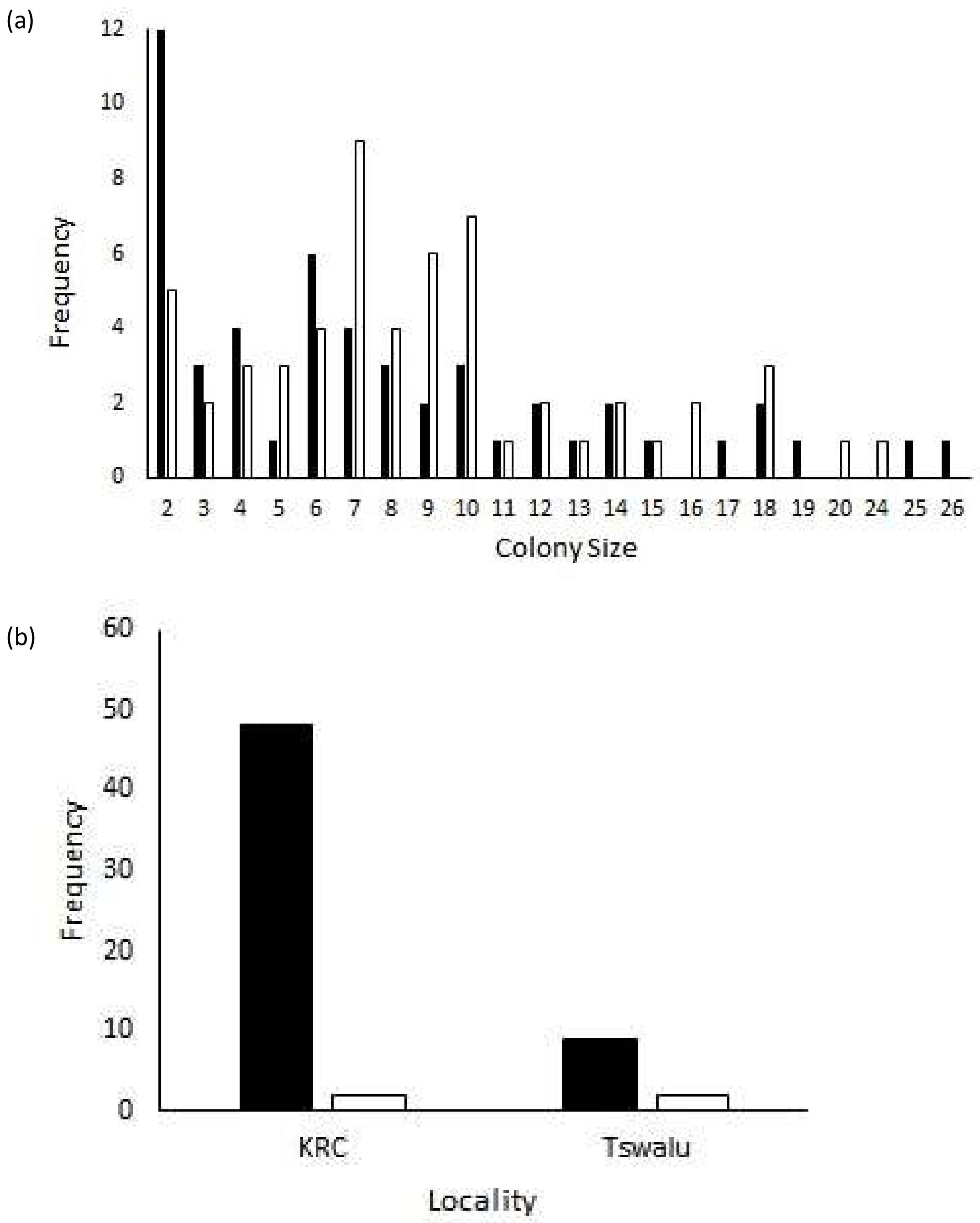

Figure 3: Damaraland mole-rat frequency of colony sizes at a low-density site (Kalahari Research Centre, KRC, n = 51) and high-density site (Tswalu Kalahari Reserve, Tswalu, n = 57). (a) Shows colonies of mole-rats consisting of at least one reproductive female and one reproductive male at KRC (black bars) and Tswalu (white bars). (b) Number of single males (white bars) and females (black bars) found inhabiting isolated burrows at KRC and Tswalu.

Of all the colonies initially captured, and which I attempted to recapture (KRC n = 40, Tswalu n = 47), 85% at both locations were relocated and recaptured (Fisher exact test, df = 1, KRC n = 34, Tswalu n = 40, p = 1.0). The colony biomass remained similar between capture events at both sites (KRC: df = 39, p = 0.47; Tswalu: df = 46, p = 0.47). Similarly, the recapture rate between trapping sessions did not differ significantly between locations (df = 86, means: KRC 0.45 ± 0.3 and Tswalu 0.50 ± 0.3, p = 0.41) and was not significantly affected by colony size (KRC: df = 39, r = -0.06, p = 0.65; Tswalu: df = 46, r = -0.01, p = 0.94). A significantly higher mean recruitment rate over time was found at the low-density site (df = 106, means: KRC 0.44 ± 0.6 and Tswalu 0.12 ± 0.3, p < 0.01) with a mean of 1.5 ± 1.6 males and 1.6 ± 1.7 females per litter between trapping events compared to the high-density site (df = 106, means: 0.38 ± 0.6 males and 0.49 ± 0.8 females, p < 0.01). The colony attrition rate was significantly higher at the high-density site (df = 106, mean: KRC 0.28 ± 0.3 and Tswalu 0.42 ± 0.3, p = 0.03). The attrition and recruitment rates at the low-density site were strongly correlated with colony size (KRC attrition rate: df = 50, r = 0.48, p < 0.01; recruitment rate: df = 50, r = -0.62, p < 0.01; Figure 4), while at the high-density site there was no correlation between either attrition or recruitment and colony size (Tswalu attrition rate: df = 56, r = 0.04, p = 0.79; recruitment rate: df = 56, r = -0.17, p = 0.28; Figure 4).

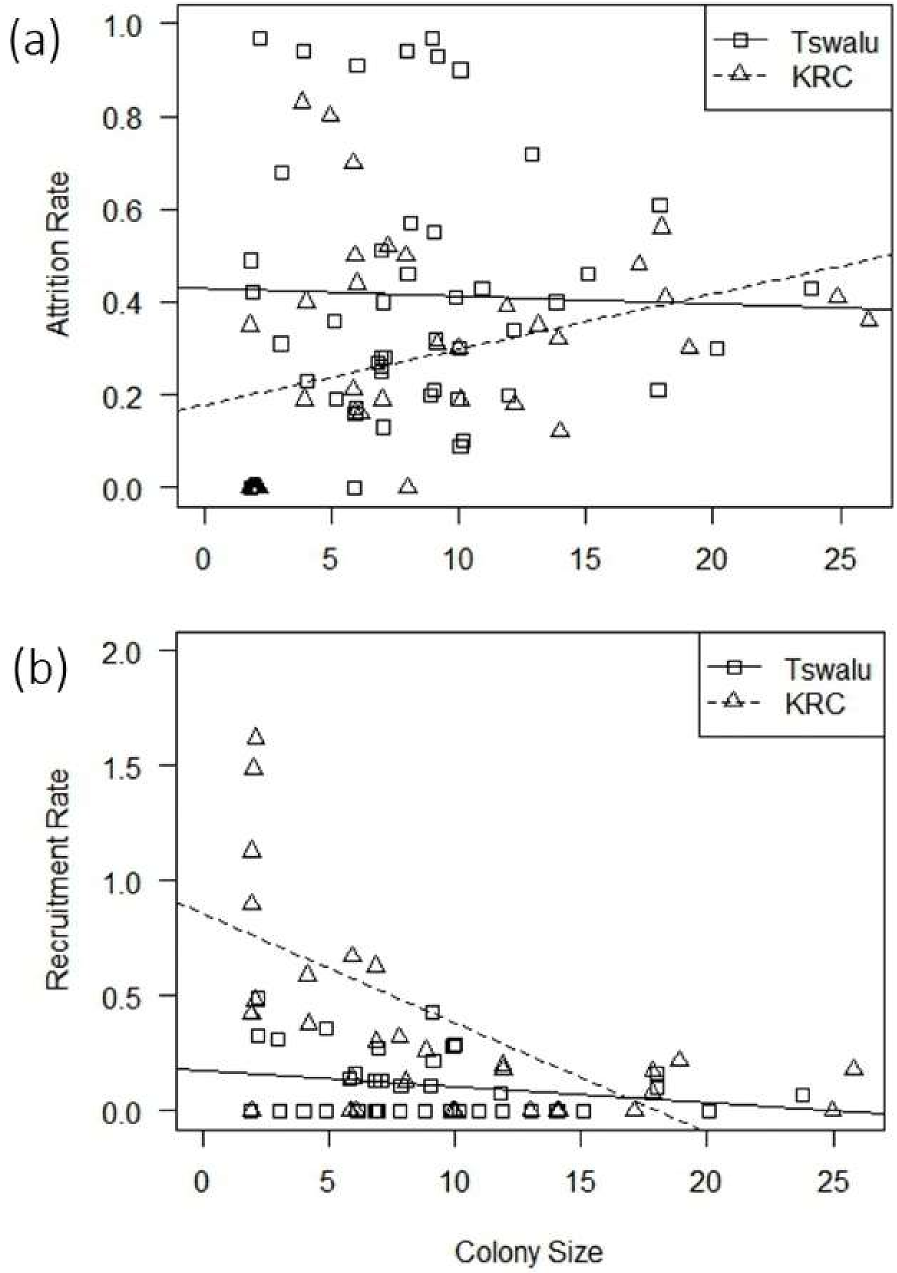

Figure 4: Effects of colony size on attrition and recruitment rates between Kalahari Research Centre (KRC) and Tswalu Kalahari Reserve (Tswalu). The KRC is a site of low population density, while Tswalu has a high population density. (a) The attrition rate represents the rate at which animals were lost due to dispersal or mortality in a colony during the time between capture events. (b) The recruitment rate represents the rate of new juveniles being born in the colony between capture events.

The results from the PCA showed that incisor length did not affect body size (Table 1). Removing body mass from the analyses revealed only slightly different results (Table 2). Based on these results, body mass, tooth width (TW), head width (HW), and total length (TL) were used to compare body size between locations.

Table 1: Results of a Principal Component Analysis (PCA) of body size in Damaraland mole-rats with sexes and localities pooled. Abbreviations: body mass (Mass), head width from ear canal to ear canal (HW), total length from snout to tail tip (TL), upper incisor width across both incisors (TW), upper left incisor length from tip to gum (LL), upper right incisor length from tip to gum (RL).

	Mass	**HW**	**TL**	**TW**	**LL**	**RL**
Standard Deviation	38.25	1.18	0.87	0.69	0.28	0.17
Proportion of Variance	0.9981	0.00096	0.00052	0.00032	0.00005	0.00002
Cumulative Proportion	0.9981	0.99909	0.99960	0.99993	0.99998	1.00000

Table 2: Results of a Principal Component Analysis (PCA) of body morphometrics excluding body mass in Damaraland mole-rats with sexes and localities pooled. Abbreviations: head width from ear canal to ear canal (HW), total length from snout to tail tip (TL), upper incisor width across both incisors (TW), upper left incisor length (LL), upper right incisor length (RL).

	HW	**TL**	**TW**	**LL**	**RL**
Standard Deviation	5.04	0.88	0.71	0.28	0.17
Proportion of Variance	0.9488	0.02857	0.01862	0.00286	0.00113
Cumulative Proportion	0.9488	0.97739	0.99601	0.99887	1.00000

There were no significant differences in the measured features of juveniles between the sexes, therefore the morphometric values of juveniles were pooled for further analyses. There were significant intra-site differences between the body sizes of male and female adults (Table 3). Juvenile mole-rats at the high-density site were significantly larger than those at low-density site, while only adult females were significantly larger at the low-density site; adult males were larger at the low-density site, but not significantly so (Table 4). There were significant differences in the growth rates of juvenile males and females at the two locations. Overall, juveniles had a significantly greater growth rate across all measured features in the KRC than at Tswalu (Table 5). There were no significant differences in the growth rates of adult females between locations. However, males had higher growth rates at KRC than at Tswalu (Table 6).

Table 3: Intra-site mean body size comparisons of juvenile and adult Damaraland mole-rats. Results are from Wilcoxon rank-sum tests comparing mean body morphometrics and mass with a Bonferroni correction. The Kalahari Research Centre (KRC) is a site of low population density while Tswalu Kalahari Reserve (Tswalu) has a high population density. Individuals were measured and weighed while under anaesthesia to ensure accuracy of measurements. Abbreviations: body mass (Mass), head width from ear canal to ear canal (HW), total length from snout to tail tip (TL), upper incisor width across both incisors (TW).

	Juveniles			**Adults**		
	Males	**Females**	**p-value**	**Males**	**Females**	**p-value**
KRC						
TW (mm)	3.88	3.91	0.67	6.01	5.73	<0.01*
HW (mm)	20.48	20.37	0.72	27.36	25.70	<0.01*
TL (cm)	13.07	13.08	0.88	18.16	17.75	<0.01*
Mass (g)	54.68	54.12	0.77	126.49	112.85	<0.01*
Tswalu						
TW (mm)	4.16	4.15	0.84	6.14	5.63	<0.01*
HW (mm)	20.67	20.60	0.85	27.24	24.98	<0.01*
TL (cm)	13.52	13.52	0.70	17.99	17.34	<0.01*
Mass (g)	59.16	58.64	0.97	122.04	104.54	<0.01*

* denotes significant differences

Table 4: Juvenile and adult mean body size comparison of Damaraland mole-rats between the Kalahari Research Centre (KRC) and Tswalu Kalahari Reserve (Tswalu). The KRC is a site of low population density, while Tswalu has a high population density. Results are from Wilcoxon rank-sum tests comparing mean body morphometrics and mass with a Bonferroni correction. Individuals were measured and weighed while under anaesthesia to ensure accuracy of measurements. Abbreviations: body mass (Mass), head width from ear canal to ear canal (HW), total length from snout to tail tip (TL), upper incisor width across both incisors (TW).

	KRC	Tswalu	p-value
Juveniles			
TW (mm)	3.89	4.15	<0.01*
HW (mm)	20.43	20.63	0.613
TL (cm)	13.07	13.52	<0.01*
Mass (g)	51.52	55.19	0.02*
Adult Males			
TW (mm)	6.01	6.14	0.05
HW (mm)	27.36	27.24	0.98
TL (cm)	18.16	17.99	0.32
Mass (g)	126.49	122.04	0.30
Adult Females			
TW (mm)	5.73	5.63	0.07
HW (mm)	25.70	24.98	<0.01*
TL (cm)	17.75	17.34	<0.01*
Mass (g)	112.85	104.54	<0.01*

* denotes significant differences

Table 5: Juvenile male and female mean growth rates compared between the Kalahari Research Centre (KRC) and Tswalu Kalahari Reserve (Tswalu). The KRC is a site of low population density while Tswalu has a high population density. The growth rate was calculated by dividing the difference between capture events in a measured feature by the number of months between captures. Individuals were measured and weighed while under anaesthesia to ensure accuracy of measurements. Abbreviations: body mass (Mass), head width from ear canal to ear canal (HW), total length from snout to tail tip (TL), upper incisor width (TW).

	KRC	Tswalu	p-value
Males			
TW (mm/month)	0.22	0.13	<0.01*
HW (mm/month)	0.71	0.38	<0.01*
TL (cm/month)	0.55	0.31	<0.01*
Mass (g/month)	7.29	4.13	<0.01*
Females			

TW (mm/month)	0.17	0.11	<0.01*
HW (mm/month)	0.45	0.31	<0.01*
TL (cm/month)	0.43	0.29	<0.01*
Mass (g/month)	5.15	3.32	<0.01*

* denotes significant differences

Table 6: Adult male and female mean growth rates at the Kalahari Research Centre (KRC) and Tswalu Kalahari Reserve (Tswalu). Results are from Wilcoxon rank-sum tests with a Bonferroni correction. The KRC is a site of low population density while Tswalu has a high population density. The growth rate was calculated by dividing the difference between capture events in a measured feature by the number of months between captures. Individuals were measured and weighed while under anaesthesia to ensure accuracy of measurements. Abbreviations: body mass (Mass), head width from ear canal to ear canal (HW), total length from snout to tail tip (TL), upper incisor width (TW).

	KRC	**Tswalu**	**p-value**
Males			
TW Rate (mm/month)	0.09	0.05	<0.01*
HW Rate (mm/month)	0.31	0.06	<0.01*
TL Rate (cm/month)	0.17	0.06	<0.01*
Mass Rate (g/month)	3.84	2.00	0.01
Females			
TW Rate (mm/month)	0.03	0.03	0.81
HW Rate (mm/month)	0.07	0.12	0.11
TL Rate (cm/month)	0.08	0.07	0.86
Mass Rate (g/month)	1.57	1.89	0.41

* Denotes significant differences

The reproductive males at KRC had a comparable mean TW (6.61 at each site, p = 0.95), a greater, but not significant HW (29.41 compared to 28.86, p = 0.11), but a significantly larger TL (19.2 compared to 18.7, p < 0.01) and body mass (151.5 compared to 141.0, p < 0.01) than those at Tswalu. Reproductive females at the KRC were significantly larger in all morphometric measurements and body mass (TW p < 0.01, HW p < 0.01, TL p < 0.01, body mass p = <0.01; Figure 5). Reproductive females had a significantly higher elongation index than non-reproductive females (reproductive females 7.01, non-reproductive females 6.6, p = 0.02). The elongation index of both reproductive and non-reproductive females did not differ between locations (reproductive females p = 0.91, non-reproductive females p = 0.36). No significant differences were found between the growth rates of reproductive individuals from the two locations, across all measurements, however males at the high-density site did grow at a higher rate but not significantly so (Table 7).

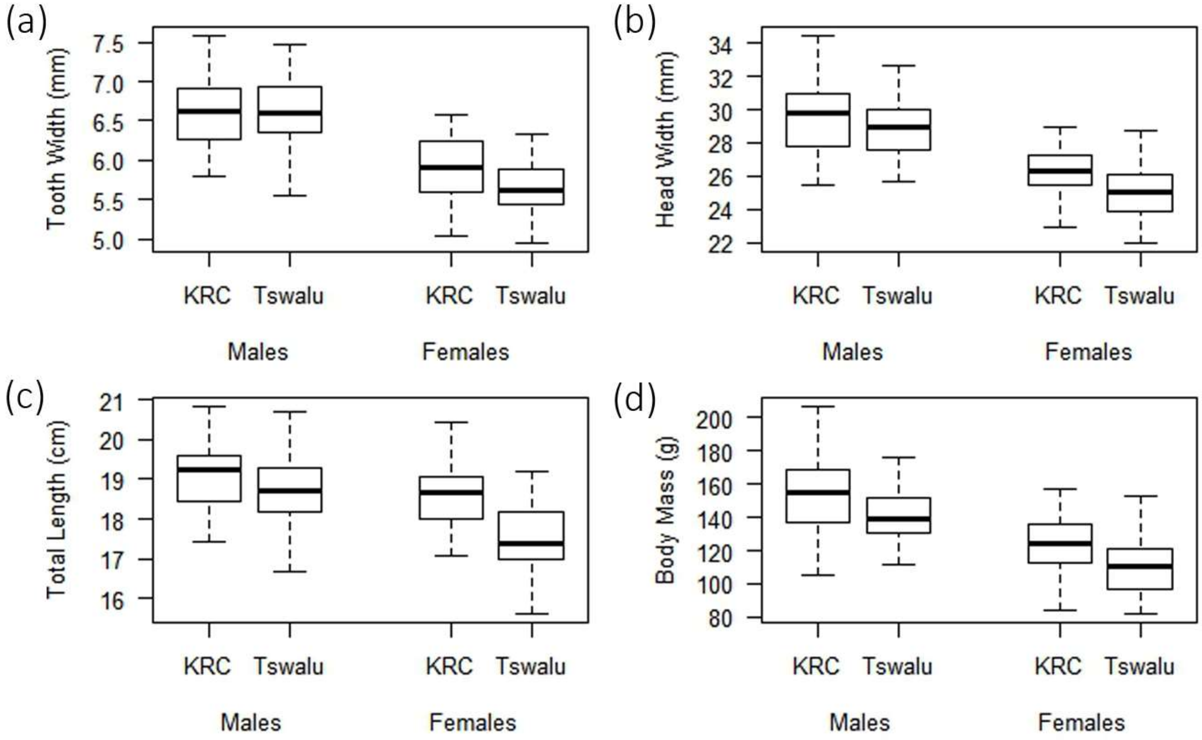

Figure 5: Body measurements and body mass of reproductive individuals at Kalahari Research Centre (KRC) and Tswalu Kalahari Reserve (Tswalu). The KRC is a site of low population density, while Tswalu has a high population density. Individuals were measured (cm) and weighed (g) while under anaesthesia to ensure accuracy of measurements. (a) Tooth width was measured across the upper incisors. (b) Head width was the greatest distance between the ears. (c) Total length was measured from snout to tail tip. (d) Body mass was the mean between the body mass at capture and at release.

Table 7: Growth rates of reproductive males and females at the Kalahari Research Centre (KRC) and Tswalu Kalahari Reserve (Tswalu). The KRC is a site of low population density, while Tswalu has a high population density. Results are from Wilcoxon rank-sum tests with a Bonferroni correction. The growth rate was calculated by dividing the difference between capture events in a measured feature by the time between captures. Individuals were measured and weighed while under anaesthesia to ensure accuracy of

measurements. Abbreviations: body mass (Mass), head width from ear canal to ear canal (HW), total length from snout to tail tip (TL), upper incisor width (TW).

	KRC	Tswalu	p-value
Queens			
TW Rate (mm/month)	0.00	0.00	0.22
HW Rate (mm/month)	-0.03	-0.03	0.91
TL Rate (cm/month)	0.01	0.03	0.25
Mass Rate (g/month)	0.34	0.49	0.99
Reproductive males			
TW Rate (mm/month)	0.01	0.01	0.35
HW Rate (mm/month)	0.02	-0.08	0.36
TL Rate (mm/month)	-0.01	0.01	0.14
Mass Rate (g/month)	0.24	0.71	0.06

* Denotes significant differences

3.4 Discussion

Group size is regulated by recruitment, attrition, and the duration of juvenile philopatry (Jarvis and Bennett 1993, Burda et al. 2000). In naked mole-rats (Brett 1991), colony size was suggested to be density-dependent, while in Damaraland mole-rats group size was suggested to be based on geophyte availability (Lovegrove and Painting 1987). In the common mole-rat, colony size was not found to differ either by population density, rainfall, or geophyte availability (Spinks et al. 2000a, b). In this study group size between the two sites was comparable despite differences in colony recruitment and attrition rates as well as density and rainfall, corresponding with the findings of Spinks et al. (2000a, b).

The number of young reared to weaning has been found to decrease with group size in species with long reproductive tenure where dispersal is difficult and philopatry is favoured (Hoogland 1995, Lacey 2004). The results of this study show a similar trend was present in Damaraland mole-rats (which exhibit both long reproductive tenure and significant constraints to dispersal; Bennett and Faulkes 2000), recruitment rate was negatively correlated with group size at the low-density site. An inverse relationship between juvenile recruitment and density is expected in rodents, when density is high pregnancy rates remain high, while juvenile recruitment into the group decreases (Spinks et al. 2000b, Wolff et al. 2002, Krebs 2003). While I was unable to quantify the pregnancy rates of reproductive females, the frequent occurrence of colonies without new juvenile recruits at the high-density site leads me to believe that colony recruitment does decrease with increasing population density. A decrease in juvenile recruitment could result from reductions in litter sizes, survival, or the number of females breeding (Wolff et al. 2002). In this study decreased litter sizes can be ruled out as a cause since the mean litter size was comparable between the two sites. High density has been found to cause increased levels of corticosterone and decreased testosterone in greater gerbils (*Rhombomys opimus*), a rodent living in large social groups (Rogovin et al. 2003a, b) and social stress has been linked to decreased survival rates in areas of high population density (Sapolsky 1983, Wingfield et al. 1990). Additionally, juvenile infanticide by neighbouring conspecifics to the nest is a significant source of juvenile mortality in other rodents (Sherman 1981, Hoogland 1995, Blumstein 1997, Agrell et al. 1998) and increases with population density (Labov et al. 1985, Mappes et al. 1995, Wolff and Schauber 1996). Therefore the absence of juveniles cannot be attributed to a single definitive cause in this study, but it appears to be density dependent.

At the high-density site I observed a greater rate of individuals lost due to mortality or dispersal. It is difficult to attribute the percentage loss of individuals to dispersal or other mortality in field studies since estimates of dispersal rates are difficult to obtain (Krebs et al. 2007). Density-dependent predation has been observed in desert gerbils (*Gerbillus* spp., Ylönen and Brown 2007) providing evidence for higher mortality in arid environments due to predation. Previous studies in terrestrial rodents, such as banner-tailed kangaroo rats (*Dipodomys spectabilis),* have suggested that dispersal rates decrease when fewer potential new territories are available due to competition for resources, hindering dispersal and resulting in increased philopatry (Gaines and McClenaghan 1980, Wolff 1997, Wolff et al. 1988, Jones et al. 1988, Andreassen and Ims 2001). While there are some similarities in the spatial ecology of terrestrial desert rodents and mole-rats (see Jones et al. 1988), the subterranean niche provides safe refuge from predators, but significant constraints to dispersal in arid environments (Bennett and Faulkes 2000). Spinks et al. (2000a, b) found that common mole-rats exhibited a higher attrition rate at a location with greater population density and attributed this increase to a higher dispersal rate instead of a higher mortality rate due to the scarcity of subterranean predators. The positive relationship between density and attrition found in this study are more akin to the findings for the common mole-rat, instead of terrestrial rodents. Additionally, the higher annual rainfall at the high-density site in this study may ease the ecological constraints on burrowing allowing for increased opportunities for dispersal, which was suggested by Spinks et al. (2000b) in common mole-rats. The higher attrition rate observed in this study at the high-density site may indicate that more individuals dispersed in this study than was observed, but succumbed to predation before locating a territory or dispersed beyond the boundaries of the study site.

This study reported a significantly higher number of single individuals at the arid location which exhibited a lower population density. These results are not surprising given that a higher population density increases the probability of dispersing individuals locating a mate, as predicted by the dispersal threshold hypothesis (Koenig et al. 1992). The aridity food distribution hypothesis (AFDH, see Section 1.2 Study Species) implies that single individuals are not able to survive long periods between rainfall events in arid environments without the assistance of conspecifics due to the increased costs of foraging (energy expenditure and predation risk; Jarvis et al. 1994). In the arid Kalahari region the period between sufficient rainfalls may be two or three years, while in areas with a higher annual rainfall (such as Tswalu) the period can be six months. The results of this study have shown that single females are able to persist for long periods (>2 years in some cases) at the arid, low-density site without the assistance of conspecifics. This conclusion appears to contradict the AFDH (Jarvis et al. 1994) and Spinks et al. (2000b) who suggested that the lowered geophyte density in arid areas will have seriously reduced foraging efficiency in single individuals. However, in all cases where a male joined a single female, instead of leaving after copulation, as seen in the solitary species (Bennett and Faulkes 2000), the male remained. While a single animal may locate enough food to survive, a female alone suffers a high reproductive cost to her fitness by waiting a prolonged period without mating and may therefore only have a short window to locate a mate before succumbing to starvation.

At both locations significant sexual dimorphism in the body size of adults was observed, which supports previous work (Young and Bennett 2013). At the low-density site reproductive females were significantly larger overall and reproductive males were significantly longer than at the high-density site. This result is contradictory to the results of Spinks et al. (2000a, b) who found that body mass decreased with reduced population density at the arid site and attributed this result to an energy saving adaptation in the presence of a reduced geophyte food density. One of two scenarios are possible: 1) greater density caused increased intra-colony competition between individuals or 2) habitat quality was actually greater at the arid location than the more mesic one. Due to the similarity in colony sizes between the two locations, intra-colony competition can be ruled out as a cause of the disparity in body size. In naked mole-rats (Jarvis 1985) and common mole-rats (Spinks 1998, Spinks 2000b) it has been proposed that individual body size is reduced in habitats of low geophyte quality or density. While a vegetation analysis was not undertaken, more gemsbok cucumbers (*Acanthosicyos naudinianus*) were located while capturing mole-rats at the arid low-density site (K. Finn, pers. obs.). Additionally, the greater population density at the mesic site may result in a reduction in the total available food sources over time. If this observation is representative of the overall geophyte density and distribution it would corroborate the previous studies

(Jarvis 1985, Spinks 1998, Spinks et al. 2000a), indicating that body mass in mole-rats may be affected more by habitat quality than population density. However, without a detailed survey of the geophyte density and distribution (based on recommendations by Jarvis et al. 1998) at the locations, the relationship between habitat quality, population density, and body size in Damaraland mole-rats is only speculation.

The conflicting body size of adults and juveniles found in this study is important to highlight. At the low-density site even though adults were larger, juveniles were significantly smaller. Spinks et al. (2000a) found that both juveniles and adults exhibited a reduced body mass in the arid less dense habitat. No matter which site has a reduced body size, it would be reasonable to assume the body sizes of adults and juveniles would be expected to scale in a similar fashion. Therefore, I believe that my result is more of a statistical artefact from basing age on a set body length at both populations, rather than an effect of density or resource quality. Other studies have relied on body mass to separate individuals into age classes (Spinks et al. 2000a, Dammann et al. 2011) even though younger individuals might actually be heavier than older individuals (Bennett et al. 1990, Bennett and Navarro 1997). I endeavoured to develop a method based on total length (TL) which may be a more accurate predictor of age (M. Zöttl, unpublished data). However, my attempt to differentiate adults and juveniles using a criteria besides body mass still requires development.

In this study, adult males exhibited a significantly higher rate of growth at the lower density site, while there were no differences in the growth rates of adult females between sites. Male ungulates have been shown to be more sensitive to limited food availability than females when population density fluctuates due to their larger size and higher growth rates (Clutton-Brock et al. 1985, Kjellander et al. 2005). Inferior habitat quality in the high-density site may account for the reduced growth rates of adult males observed at that site. Recent studies on Damaraland mole-rats have shown that males require more time than females to reach maximum body mass (Young et al. 2015, Zöttl et al. 2016b). The findings of this study would account for the differences in growth rates between the sexes. Additionally, Zöttl et al. (2016b) found that juveniles exhibit a reduced growth rate in large groups. Due to the similarity in group size between the two populations in this study, the difference in juvenile growth rates between the two sites must be caused by another factor. Better quality habitat at the low-density site could account for the increased growth rates observed in this study.

The comparison of body elongation between reproductive and non-reproductive females support previous studies (O’Riain 2000b, Henry et al. 2007, Young and Bennett 2010) that reproductive females have a greater body length for their skull width than non-reproductive females. The growth rates of reproductive females were similar at the two locations and reduced compared to non-reproductive females. Interestingly the reproductive males at the high-density site exhibited a significant increase in body mass between trapping events. The reduced growth rates of reproductive compared to non-reproductive females at both locations confirms that the reproductive individuals are the oldest individuals in the group (Bennett et al. 1990, Jarvis and Bennett 1993) and have already reached a plateau in their growth curve. However, the increased rate of growth in the reproductive males at the high-density site compared to low-density site is surprising, especially in light of the increased growth rate overall of adult males at the low-density site. It is possible that the reproductive males at the high-density site were newly dominant animals still growing or recent immigrants gaining body mass that was lost during dispersal. If either case were true, then it would appear that dominance tenure in males may be greatly reduced at the higher density site.

This study aimed to determine the presence of density-dependent relationships in colony attributes (colony size, number of offspring per litter, colony attrition and recruitment) and individual body size and growth rates. These colony attributes were compared between two populations of Damaraland mole-rats with varying density, Tswalu Kalahari Reserve (high-density site) and Kalahari Research Centre (low-density site). Increased attrition rates and reduced recruitment of juveniles, where many colonies did not recruit a single juvenile in six months, were observed at the higher density site. On the contrary, at the low-density site I observed a lower attrition rate, a greater recruitment rate and an increase in the number of single females. Spinks et al. (2000a, b) concluded that geophyte density and distribution as opposed to population density explained the variation between sites. If population density affected mole-rats more than habitat quality, it would be expected that body size would be affected the same way in both Damaraland and common mole-rats. Since body size was found to be greater at the arid lower density site, it would appear that differences in habitat quality is the most reasonable cause for differences in body size, while the other results of this study could potentially be density dependent. An interesting question remains to be answered, what causes density fluctuations in mole-rat populations?

CHAPTER 4: Density related effects on philopatry and dispersal between populations

4.1 Introduction

Reproductive competition is a central tenet to the evolution of societies, though the exact mechanism is debated (Clutton-Brock 2004, Carranza 2010, Cornwallis and Uller 2010, Tobias et al. 2012). Intra-sexual competition leads to the evolution of different behavioural strategies in males and females based on the different costs and benefits for either sex (Leturque & Rousset 2004). Most rodent mating systems are polygynous, leading to high competition between males compared to females, therefore males might benefit more than females by dispersing to areas with less competition for mates (Dobson 1982). The competition between females for environmental resources (food and nesting areas) has been suggested to drive the evolution of female dispersal, whereas availability of mates drives male dispersal (Dobson 1982, Lurz et al. 1997, Nunes et al. 1997).

Dispersal is the act whereby individuals leave their natal (i.e. – birth) group, or birth site and establish themselves in a new location (Stenseth and Lidicker 1992). Sex-biased dispersal is influenced by nomadism (Dobson 1982), longevity (Waser and Jones 1983) and breeding systems (Pusey 1987, Solomon 2003, Koenig and Dickinson 2004). Females are the primary dispersers in birds, while male dispersal is more common in mammals (Greenwood 1980, Pusey 1987). Polygynous rodents generally exhibit male-biased dispersal, while in monogamous rodents both sexes will disperse (Greenwood 1980, Dobson 1982, Busch et al. 2000, Nunes 2007). Dobson (1982) suggested that competition for mates may have acted in conjunction with inbreeding avoidance in shaping male-biased dispersal in rodents. However, in monogamous societies both sexes would be required to disperse to avoid breeding with same sex parents (Dobson 1982, Busch et al. 2000). In subterranean rodents, both sexes will disperse, from non-breeding juveniles and sub-adults (Family Geomyidae) to all individuals present in the population (Family Ctenomyidae and Bathyergidae; Busch et al. 2000, Spinks et al. 2000b). In the common mole-rat (*Cryptomys hottentotus hottentotus*), Spinks et al. (2000b) found that non-breeding individuals of both sexes were the primary dispersers in arid locations while both non-breeding and breeding individuals dispersed in mesic locations. Burland et al. (2004) showed males will readily disperse from their natal group to join established colonies and are more likely to find a potential mate in the process. Female immigrants to established colonies are rare due to the xenophobic nature of mole-rats (Jarvis and Bennett

1993; Spinks et al. 2000b; Cooney 2002; K. Finn, pers. obs.), but have been observed singly occupying isolated burrows (Jarvis and Bennett 1993; K Finn, pers. obs.).

Under certain conditions individuals delay dispersal leading to the condition referred to as philopatry (Koenig et al. 1992). Philopatry is the act of remaining within the natal group past an individual's potential for independence (Solomon 2003). Group living appears to have evolved due to the harsh environmental conditions which require the need for extended parental care (Barash 1974, Armitage 2007). It has also been proposed that the patchy distribution of limited resources (either food or shelter) in the environment promotes philopatry and consequently the development of sociality in a number of rodents, as observed in prairie dogs (*Cynomys* spp., Slobodchikoff 1984), African mole-rats (*Heterocephalus*, *Cryptomys*, *Fukomys*, Jarvis et al. 1994), tuco tucos (*Ctenomys* spp., Lacey 2004), and rock dwelling species (Mares and Lacher 1987). By delaying dispersal various forms of cooperative behaviour evolve (Waser 1988), such as communal care of young, group foraging or hunting, and territory defense (Lewis and Pusey 1997, Creel and Creel 2002). Individuals assist with cooperative activities benefiting the entire group and gain many direct and indirect benefits as a result (Koenig et al. 1992, Solomon 2003). Secondary benefits to delayed dispersal include increased vigilance (McGowan and Woolfenden 1989, Clutton-Brock et al. 1999), more efficient exploitation or defense of resources (Bednarz 1988, Lovegrove and Wissel 1988), larger territory sizes leading to a higher probability of obtaining a territory in the future through territory budding (Woolfenden and Fitzpatrick 1990), and increased reproductive success or survival of related individuals (Brown 1987; Mumme et al. 1989, Koenig and Mumme 1990, König 1994).

Differences in dispersal patterns observed between populations or species may be attributable to an interaction of factors such as population density, timing of dispersal, fitness of dispersers, distribution of available resources and environmental variability (Koenig et al. 1992). In cooperative breeding birds, the availability of vacant territories affects the probability of dispersal (Koenig and Mumme 1987, Kokko and Ekman 2002). If density is low, an individual born in the highest-quality territory should disperse and breed independently, since fitness gains would be higher than remaining philopatric. Conversely, if the density is high, the fitness gains are higher when remaining in high-quality habitats (Koenig et al. 1992). If a limiting resource is non-consumable, time-dependent, or renewable, resource depletion is likely to be low and the probability of delayed dispersal and group living is high (Waser 1988). The availability of vacant territories is more important for females due to the fact that they require a safe burrow or nest in which to raise their young with sufficient food availability in the habitat (Dobson 1981). The distribution of resources influences the distribution of females, which in turn affects male dispersal rates and the subsequent distances moved due to the fact that males need to monopolize multiple partners. Natal philopatry is likely to be found in species in which territory quality is highly predictable over time (Waser 1988, Powell 1989, Zack 1990, Stacey and Ligon 1991). Cooperative breeders are non-migratory (Brown 1974) and are found in habitats where resources do not show marked seasonal fluctuations (Ford et al. 1988).

The estimates of dispersal rates and dispersal distances in mammals are difficult to obtain from field studies (Krebs et al. 2007). There is a lack of consensus to the relationship between dispersal rates and population size (Gaines and McClenaghan 1980, Boutin et al. 1985, Verner and Getz 1985). Large mammals and other long-lived species (*K*-selected) are expected to show most of their density-dependent changes in vital rates at population levels quite close to carrying capacity, while many short-lived species (*r*-selected) show most density dependence at lower population levels (Fowler 1981). Early models (Krebs 1978, Lidicker 1975, Stenseth 1983, Tinbergen et al. 1987), predicted that dispersal rates are highest during increasing population density, and lowest during both peak and declining density. When habitats are saturated it is more difficult for individuals to establish a territory. However, field studies have shown dispersal rates to decrease with increasing habitat saturation in rodents (McGuire et al. 1993, Getz et al. 1993, Jones et al. 1988, Wolff 1997, Kokko and Lundberg 2001, Solomon 2003) as well as increase when habitat saturation is high (Windberg and Keither 1976, Boutin et al. 1985, Spinks et al. 2000b). The disparity in life history trajectories could account for the differences observed between mammal species. Wolff (1997) attributed the inverse relationship in density-dependent dispersal to a "social fence" in which territorial neighbours inhibit immigrants from joining the group. At high densities mothers and daughters will nest in close proximity to one another or occasionally communally in the same nest (Wolff 1994, Solomon and Getz 1997, Lambin and Yoccoz 1998). This tendency affects male dispersal distance, forcing them to travel further to encounter an unrelated potential mate and avoid breeding with relatives (Wolff 1994, Andreassen and Ims 2001, Lambin et al. 2001). Although dispersal distances can be highly variable and dependent on the degree of habitat saturation and available territories or partners (Swingland 1982, Lambin et al. 2001), dispersal distances in mammals generally appear to be related to diet type and body size (Van Vuren 1998, Sutherland et al. 2000). In a study comparing dispersal distances of numerous birds and mammals with a range in life history traits, dispersal distances were found to increase with an increase in either body mass or diet restriction (Sutherland et al. 2000). In other words, small mammals (or birds) with a wide herbivorous diet have the shortest dispersal distances while large carnivores exhibit the greatest distances.

Dispersers incur costs to survival and/or fecundity and these costs in turn increase with distance travelled (Bengtsson 1978, Jones 1988). Koenig et al. (1992) proposed the delayed dispersal threshold model to explain the factors influencing dispersal: the risks associated with dispersal, probability of successful establishment in a suitable territory, the probability of securing a mate, and the likelihood of independent reproduction. Due to the harsh living conditions burrowing rodents face, there are significant costs associated with dispersal: high predation risk due to limited visual acuity (Kott et al. 2010), high energy expenditure while digging through densely packed sand (Lovegrove 1988, Jarvis et al. 1998), the necessity to build up fat reserves to sustain themselves until a suitable territory is located (Spinks et al. 2000b), and the potential for lethal aggression from conspecifics during prospective immigration since mole-rats are characteristically xenophobic (Spinks et al. 2000b, Cooney 2002). Offspring may delay dispersal until they are of sufficient size to effectively survive emigration and win these contests for territory and breeding rights (Solomon 2003). Mole-rats occurring in arid environments disperse only during the wet season (November to April) when rain sufficiently softens the soil and lowers the energetic costs associated with dispersal (Jarvis et al. 1994, Jarvis et al. 1998, Molteno and Bennett 2002, Young et al. 2010). Therefore the dispersal rates in subterranean rodents are presumed to be low (Lacey et al. 2000).

The ability to directly observe dispersal events is rare in subterranean rodents (O’Riain et al. 1996; Hazell et al. 2000; K. Finn, pers. obs.) and recapture of known dispersers is uncommon (Jarvis and Bennett 1993, Spinks et al. 2000b, Young et al. 2010). Therefore little is known about their preferred mode of dispersal, the presence of sex-bias in dispersal, triggers for dispersal, the frequency of dispersal cohorts and dispersal distances. Both sexes will disperse from the natal territory in subterranean rodents (Busch et al. 2000, Spinks et al. 2000b), however, Hazell et al. (2000) showed that the majority of dispersers in Damaraland mole-rats (*Fukomys damarensis*) are adult males and that dispersers were heavier than other colony members. Female dispersal in mole-rats may be controlled by the lowering of hormonal suppression during periods of heavy rain allowing for readiness to mate with immigrant males (Molteno and Bennett 2002, Young et al. 2010). Single females have been observed in the wild to emigrate from their natal colony, presumably to wait for a potential mate (K. Finn, pers. obs.). Males may voluntarily disperse from their natal colony to become integrated into an established colony (Burland et al. 2004) or locate a single female to establish a nascent colony (NC Bennett, pers. comm.; K. Finn, pers. obs.), but the exact impetus for male dispersal is unknown (Clutton-Brock 2016). Occasionally, cohorts of one sex or mixed sexes will form to disperse either joining an established colony or forming a nascent colony by isolation respectively, but these observations are rare (Jarvis and Bennett 1993; K. Finn, pers. obs.). Spinks et al. (2000b) found that loss of individuals from a colony was positively correlated with colony size and proposed a colony size threshold, above which inclusive fitness is no longer maximized so it is in an individual's best interests to disperse.

Damaraland mole-rats are ideal candidates for dispersal studies because individual colonies occupy a small area for extended periods, have a limited window of dispersal, and presumably have relatively short dispersal distances (Jarvis et al. 1994, Bennett and Faulkes 2000, Young et al. 2010). In addition, all animals can potentially be marked in an area to track their inter-colony movements over time (Jarvis and Bennett 1993, Young et al. 2010, this study). Therefore, this thesis set out to better understand the movement of individuals between colonies and determine if density affects the rate and success of individual dispersal. Furthermore, size- and sex-biased dispersal was investigated in order to ascertain if this process is operational at either of the populations under study as suggested by Hazell et al. (2000). The understanding of dispersal distances and patterns can unravel the relationship between dispersal and mortality for mark-recapture studies. Additionally, estimating the number of successfully migrating individuals can greatly assist with estimates on annual colony attrition due to natural non-dispersal related mortality.

Using two populations of wild Damaraland mole-rats with markedly different population densities, this study aims to test whether (i) population density affects dispersal and philopatry as suggested by the dispersal threshold model; and (ii) whether population density exerts a differential effect on philopatry in male and female mole-rats. In-depth analyses of two data-sets from capture-mark and recapture studies on Damaraland mole-rats were undertaken to compare differences in body size and dispersal tendencies at the two sites. First, a comparison of the relative differences between morphological measurements, body mass, and growth rates were undertaken to determine if these attributes are affected by colony density. To test for evidence of sex-biased dispersal, the number of known dispersers of each sex was compared within and between sites. Furthermore, the relationship between philopatrics (individuals staying in the group), dispersers, and lost individuals was analyzed with a series of body mass and growth rate comparisons. These tests determined if dispersing individuals were heavier prior to emigration than individuals who chose to stay at home, and whether dispersers were of a similar body mass to individuals that were lost between captures. Finally, a comparison between the mean dispersal distances travelled by each sex was investigated in relation to the density of animals in a unit area.

Based on the findings of Hazell et al. (2000), I predicted a male bias in dispersal patterns at both sites. I also believed that there would be more dispersers at the high-density site (Tswalu) due to the increased colony density and therefore a greater probability of dispersing individuals locating a receiving colony to join as found in Spinks et al. (2000a, b). Relatedly, there should be a lower proportion of lone females at Tswalu due to the higher density and limited availability of open territories. Due to the high density at Tswalu and relatively closer distances observed between colonies, I expected the mean dispersal distance to be reduced. I further predicted that the results of the three-way comparison between philopatrics, dispersers, and lost individuals would show that dispersers have a greater body mass prior to dispersal than philopatrics, and lost individuals would have a lower body mass than philopatrics.

4.2 Methods and Data Analyses

During the study, known and unknown immigrants joined established colonies between capture sessions. Known immigrants were easily identified by being marked with a transponder tag, whereas unknown immigrants were slightly harder to confidently identify (see 2.2 Mole-rat Sampling). In most cases, approximately six months had passed between captures at a colony and any unmarked individuals greater than 85g were easily identified as immigrants since it was unlikely for wild juveniles to reach 85g in six months (Bennett and Navarro 1997; Zöttl et al 2016b). When more than six months had passed between captures at a colony, individuals more than 85g could quite understandably be offspring from the dominants. In these cases, immigrant status could not be assigned to unmarked individuals with confidence, so all unmarked individuals were assumed to be offspring from litters born between capture events.

All statistical analyses were performed with R version 3.2.4 (R Core Team 2016). Testing the residuals of the data set determined that the distribution was not normal, therefore non-parametric tests were used for analysis on the data set. The presence of intra-site sex-bias in dispersers was determined using a Fisher exact test. Due to the disparity in the passage of time between the locations, it was not possible to directly compare the number of dispersers without correcting for time and the total number of individuals captured at each site. Thus, for each immigrant, the number of days transpiring since the previous capture was divided by 180 which produced the number of six month intervals between captures. The reciprocal of this value was summed to arrive at a representative value of the number of immigrants captured at a location per unit time. The total number of captures at each location was determined by combining each individual's total number of captures after the original capture. The difference in the number of dispersers out of the total population of recaptures at each site was compared between locations using a Fisher exact test. The proportion of males and females joining established colonies both within and between sites was compared using a Fisher exact test. The proportion of females becoming reproductive out of the total number of immigrant females was tested using a Fisher exact test.

For all known dispersers the estimated distance travelled (m) was measured as the shortest straight line distance from their natal colony to the new colony to the nearest metre in Map Source (Garmin, USA). The intra-site distances were compared between sexes first, and then inter-site distances were compared using Wilcoxon Matched-pairs tests. A Spearman Rank Correlation test determined if the time between captures was correlated with the distance travelled by known immigrants.

The relationships between non-reproductive dispersers (known individuals that left the natal colony and were recaptured at a different location), philopatrics (non-reproductive individuals staying with the colony between capture events), and lost individuals (individuals not recaptured at the consecutive attempt and not captured at a different location) were investigated. First the duration that non-reproductive individuals remained in their natal colony was compared between sexes within the Kalahari Research Centre (KRC; since long-term data was only available at that site) using a Wilcoxon rank-sum test. Additionally, the presence of a correlation between the duration of time non-reproductive individuals remained in the colony and colony size using a Spearman Rank Correlation test. Then the body masses of philopatric, dispersing and lost individuals were compared using a series of tests. Firstly the last recorded body mass of dispersing individuals prior to dispersal was compared to the current body mass of both philopatric and lost individuals using Wilcoxon rank-sum tests. Similarly, the most current body mass of philopatric animals was compared to the last recorded body mass of lost animals using a Wilcoxon rank-sum test. These tests determined if dispersing individuals were heavier prior to emigration than to those individuals that chose to stay, and also showed if dispersers were of a similar mass to individuals that were lost between captures. Additionally, the growth rates between capture events of philopatrics were compared to the growth rates during emigration (i.e. – the difference in the morphological measurements between leaving the natal colony and establishment in a new colony divided by the time between captures) of dispersing individuals to determine if dispersers have a steeper growth trajectory after emigrating from the natal colony.

4.3 Results

A total of 44 known and three unknown immigrants were captured at the KRC and 18 known and four unknown immigrants at Tswalu. At the KRC, 22 immigrants were male and 25 were female, whereas at Tswalu 13 were male and nine were female. Comparing the sex ratios of the dispersing individuals, no intra-site sex-bias was found in the dispersing individuals (KRC: df = 1, p=0.83; Tswalu: df = 1, p = 0.76). There was no significant difference in the number of immigrants captured over time out of the total population of recaptures (KRC n = 444, Tswalu n = 222) at each location (10.8% at KRC and 9.9% at Tswalu, df = 1, p = 0.31). The mean number of emigrants per colony at KRC was 2.2 ± 1.3, whereas it was 1.4 ± 0.6 at Tswalu. At KRC 22 marked females from long established colonies were recaptured alone in a new burrow, whereas only two were recaptured at Tswalu. Males were captured significantly more frequently as immigrants in other colonies (including burrows of a single female) than females at KRC (n = 20:1, df = 1, p < 0.01). While there was a male-biased immigration rate to established colonies at Tswalu (n = 11:4), the observed rate was not significant (df = 1, p = 0.27). The ratios of males to females joining established colonies was not significantly different between locations (df = 1, p = 0.14). I observed 12 cases (KRC = 9, Tswalu = 3), whereas dispersing males joined a single female. At both locations two single males were recaptured in isolated burrows that were likely still in the process of migrating to a new colony. Of the females that dispersed from their natal colony, three from each location became reproductively active (12% KRC and 33.3% Tswalu). The proportion of females becoming reproductive out of the total number of immigrant females was not significantly different between locations (df = 1, p = 0.34).

No significant differences were found in the distances travelled between the sexes at each location (df = 1, KRC means: males 738.6 ± 1067.3m and females 924.8 ± 1067.1m, p= 0.31; df = 1, Tswalu means: males 256.3 ± 266.7m and females 268.5 ± 224.2m, p = 0.62) so sexes were combined to test for inter-site differences in dispersal distance. Dispersing individuals from KRC travelled a significantly greater distance than those found at Tswalu (df = 1, mean 893.8m ± 941.4 and 264.9m ± 254.3 respectively, p < 0.01; Figure 6). Removing the top four outliers from the KRC sample reduced the mean dispersal distance to 593.1 ± 459.2m. The distance travelled was not correlated with the time between capture events (KRC: r = 0.06, p = 0.69; Tswalu: r = 0.05, p = 0.84).

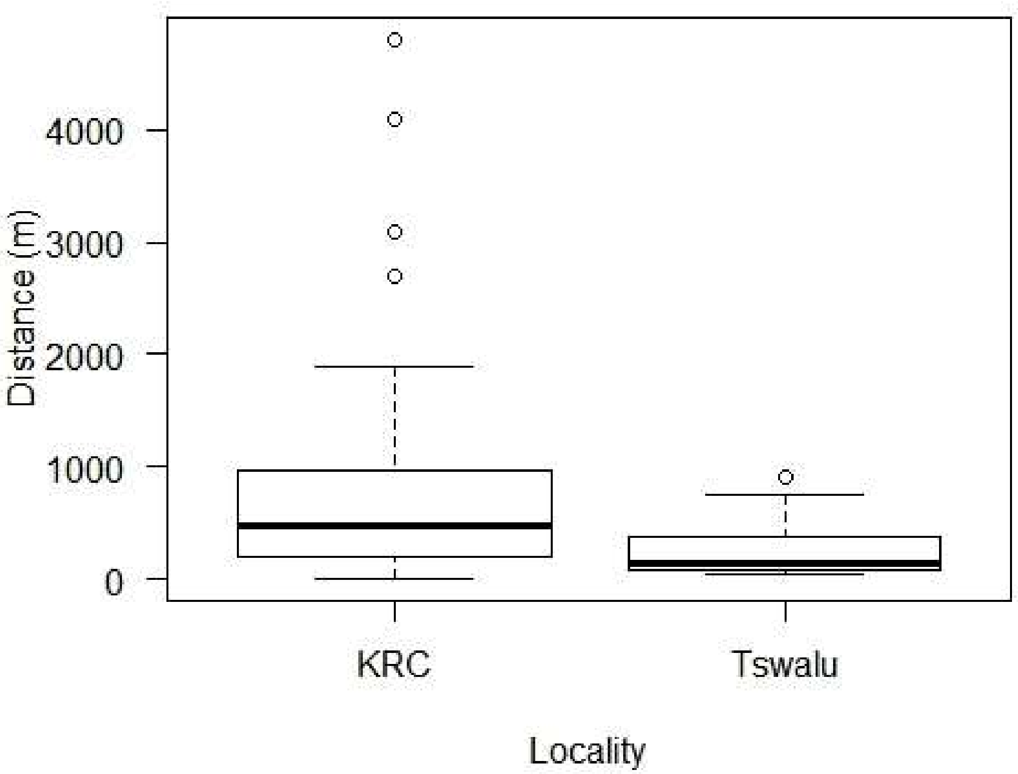

Figure 6: Distance travelled by known immigrants at Kalahari Research Centre (KRC, n = 43) and Tswalu Kalahari Reserve (Tswalu, n = 18). Distance travelled (metres) was measured as the shortest straight line distance between the closest previous trapping locations at the natal colony and the colony immigrated into. The distances travelled did not significantly differ between sexes, so they were combined for each location. The dispersal distances were log transformed for each location to remove the bias of outliers.

The length of time non-reproductive males (n = 89) and females (n = 124) remained within the group was compared using a Wilcoxon rank-sum test on the data set from KRC since the data from that location covered multiple years. Females spent a significantly longer period of time in the group than males (df = 1, means females = 406.7 ± 238.4 days and males = 354.3 ± 216.1 days, p = 0.02; Figure 7) and colony size was correlated with the duration of time non-reproductive females remained in the colony (r = -0.30, p < 0.01), but not for males (r = -0.02, p = 0.82). It must be noted that some of these non-reproductive individuals (n = 12) became reproductive within their natal colony during the intervals between trapping periods.

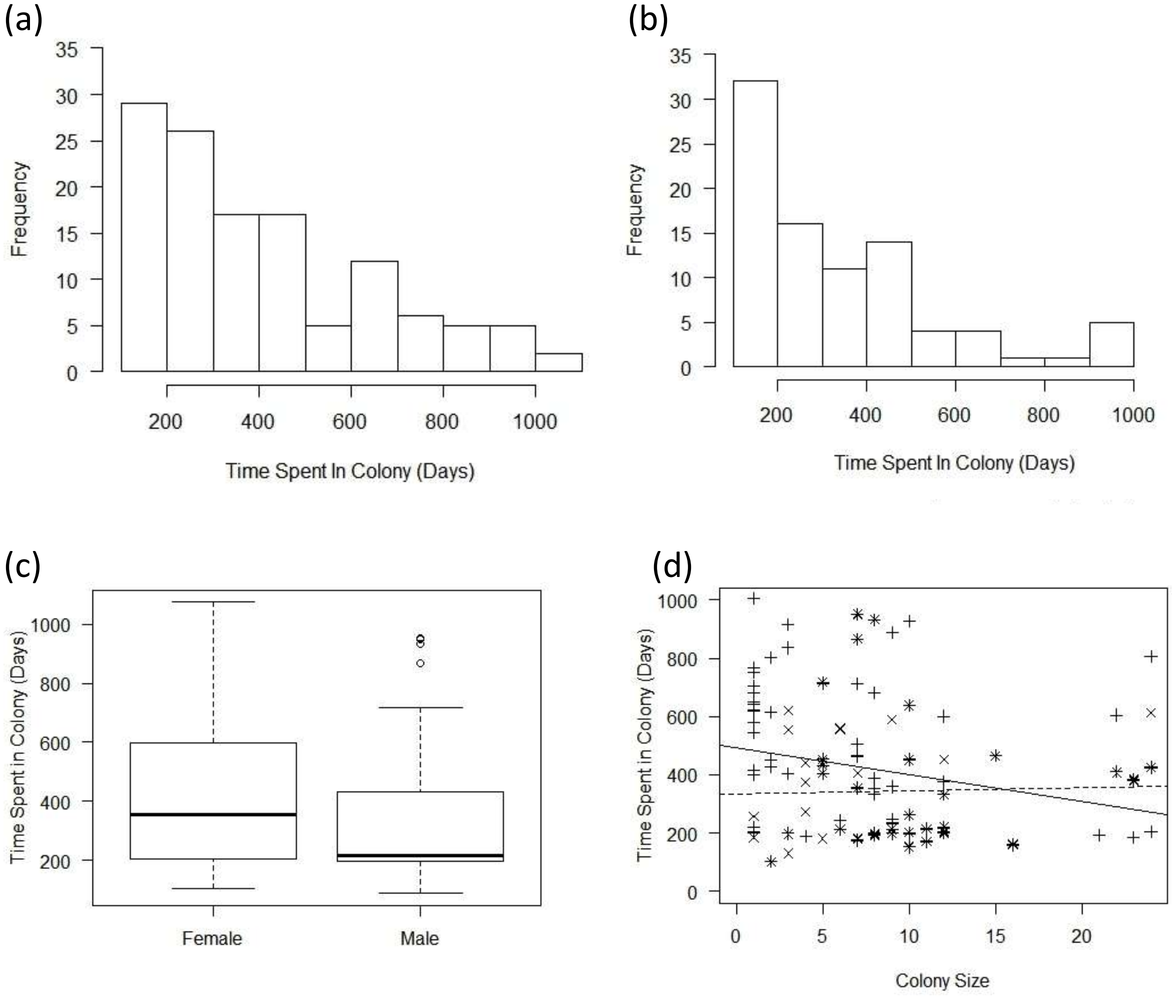

Figure 7: Comparisons between male and female philopatry in subordinate mole-rats. Subordinate individuals are those individuals that were non-reproductive at the time of first capture, but some individuals (n = 12) changed their reproductive status. The distribution of time spent in the natal colony (days) for subordinate (a) males (n = 93) and (b) females (n = 125). (c) Comparison of the median time spent in the colony (days) for females and males. (d) The duration of stay for females (+, solid line) but not for males (X, broken line) was strongly correlated with colony size.

The results of the three-way comparison among body masses of philopatric, dispersing, and lost individuals are summarized in Table 8. Male and female philopatric individuals from KRC were significantly heavier than individuals lost between capture events (df = 1, males: $p < 0.01$, females $p < 0.01$; Figure 8, Table 8), whereas at Tswalu philopatric male and female individuals were heavier, but not significantly so (df = 1, males p = 0.06, females p = 0.12; Table 8). Philopatric females at KRC were significantly heavier that dispersing females (p = 0.04; Table 8), philopatric males were heavier than dispersing males, but not significantly so (p = 0.05; Table 8). At Tswalu male dispersers exhibited a greater mean body mass than philopatrics (Table 8), but there were no significant differences between philopatric and dispersing individuals in either sex (df = 1, males p = 0.53, females p = 0.54). However, philopatric individuals exhibited greater growth rates in all measurements compared to dispersing individuals at both KRC and Tswalu study sites (Figure 9, Table 8). At KRC philopatric females showed significantly greater growth rates in all measurements and KRC philopatric males showed significantly greater growth rates in all except the HW. At Tswalu, philopatric individuals had greater growth rates than dispersing individuals, but only males exhibited significantly greater growth rates in TL and body mass. There were no significant differences in the body masses of dispersers and lost individuals from either location (KRC: df = 1, males p = 0.29, females p = 0.20; Tswalu: df = 1, males p = 0.18, females p = 0.92; Table 8).

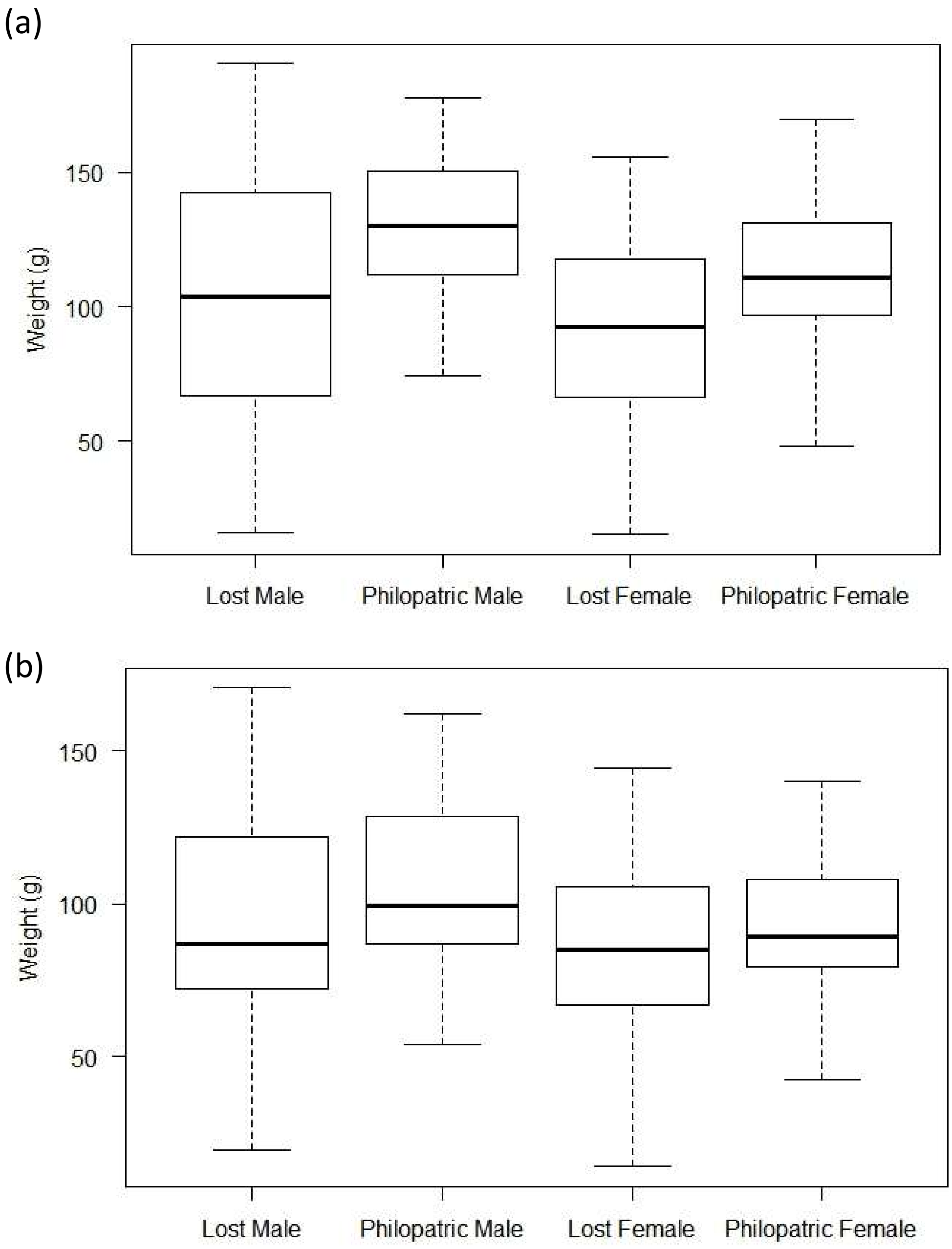

Figure 8: Comparisons of body mass between philopatric and lost Damaraland mole-rats at (a) Kalahari Research Centre (KRC, low density) and (b) Tswalu Kalahari Reserve (Tswalu, high density). “Philopatric” mole-rats are individuals that were recaptured in the same natal group. “Lost” individuals are those that were not recaptured at subsequent captures either in their natal group or any other group in the area and are assumed to have died or dispersed outside of the study site. The body mass of philopatric individuals at recapture was compared to the initial capture body mass of lost individuals using a Wilcoxon rank-sum test. Male and female philopatric individuals at KRC were significantly heavier than lost individuals, while there were no significant differences between Tswalu groups.

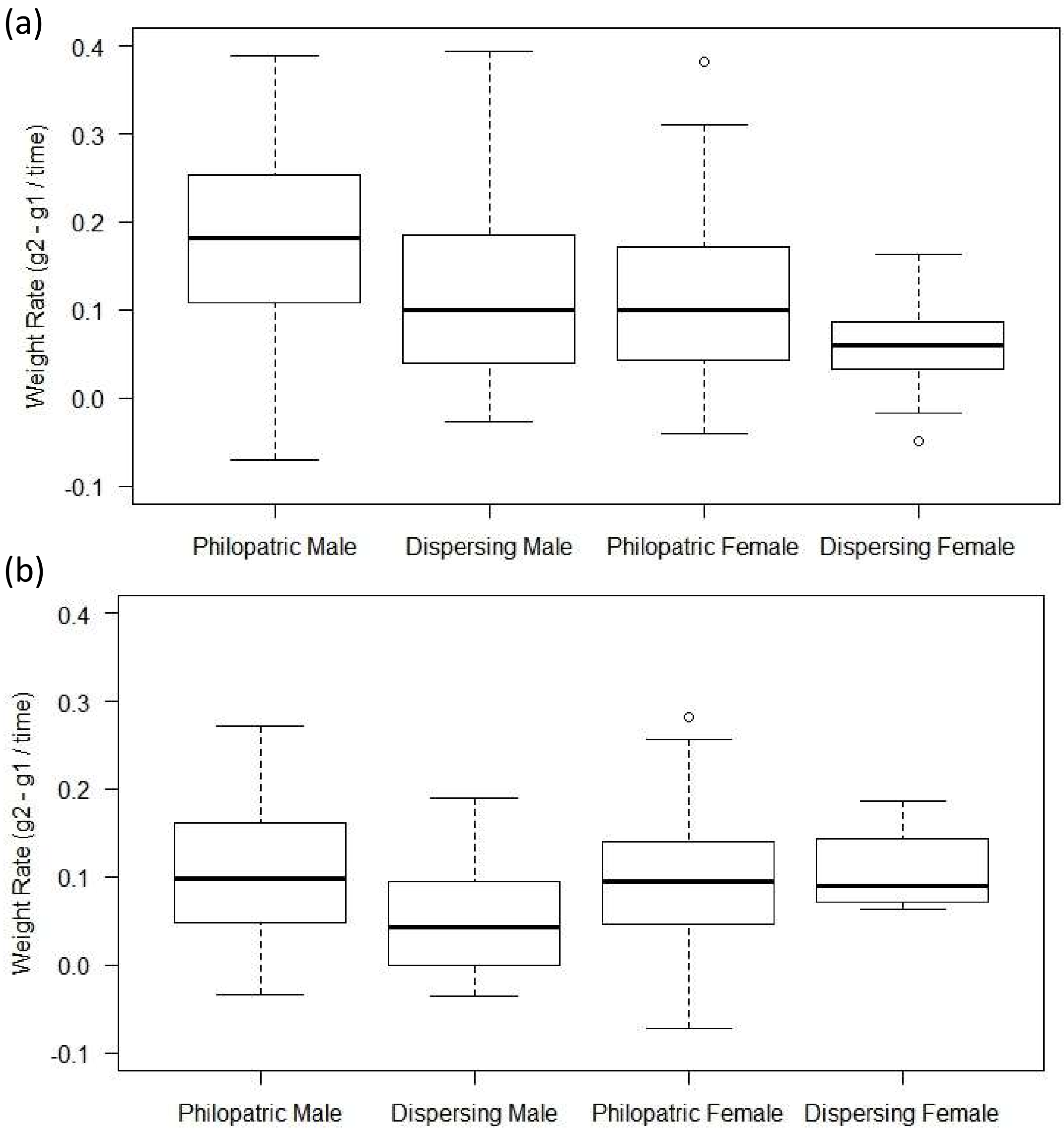

Figure 9: Comparisons between change in body mass of philopatric and dispersing Damaraland mole-rats at (a) Kalahari Research Centre (KRC, low density) and (b) Tswalu Kalahari Reserve (Tswalu, high density). The change in body mass was calculated by subtracting the body mass at initial capture from the body mass at recapture, then dividing by the time between capture events. Philopatric individuals are those that remained in their natal colony between capture events, while dispersing individuals were recaptured in another colony. The intra-sex differences between philopatric and dispersing individuals was compared using a Wilcoxon rank-sum test. At KRC philopatric males and females exhibited a significant positive growth in body mass, while at Tswalu only males showed a significant difference in the change in body mass. This positive growth in body mass of philopatric individuals serves to illustrate the cost incurred by dispersing individuals.

Table 8: Intra-site differences in mean body mass and mean growth rates of philopatric, dispersing, and lost Damaraland mole-rats. The body mass and growth rates (tooth width (TW), head width (HW), and total length (TL)) are the measure of growth over time in each between capture events. These growth rates were compared within a low-density site at the Kalahari Research Centre (KRC) and a high-density site at Tswalu Kalahari Reserve (Tswalu). Philopatric individuals were those that remained within the group between capture events. Disperser individuals were marked individuals that were recaptured as immigrants to a colony different than their natal colony. Lost individuals were those individuals that were not recaptured either in their natal colony or as immigrants to another colony. A Wilcoxon rank-sum test was used to compare the growth rates between philopatric and disperser individuals.

	Males				**Females**			
	Philopatric	Disperser	Lost	p-value	Philopatric	Disperser	Lost	p-value
KRC								
Body Mass	131.4	113.5	101.5	-	113.7	100.4	89.3	-
Body Mass Rate	0.175	0.119	-	0.02*	0.110	0.055	-	0.01*
TW Rate	0.005	0.002	-	<0.01*	0.003	0.001	-	<0.01*
HW Rate	0.016	0.011	-	0.06	0.009	-0.001	-	<0.01*
TL Rate	0.012	0.005	-	<0.01*	0.008	0.003	-	<0.01*
Tswalu								
Body Mass	105.3	111.5	95.7	-	91.7	89.0	84.6	-
Body Mass Rate	0.104	0.050	-	0.03*	0.096	0.107	-	0.75
TW Rate	0.003	0.002	-	0.08	0.003	0.003	-	0.92
HW Rate	0.007	0.002	-	0.05	0.008	0.008	-	0.95
TL Rate	0.007	0.002	-	0.02*	0.008	0.006	-	0.65

*denotes significant differences

4.4 Discussion

Natal dispersal is an important ecological process to maintain genetic diversity within a population and it reduces the effects of inbreeding depression (Ibrahim et al. 1996, Dobson 2007). Wolff et al. (1988) concluded that resource competition does not drive natal dispersal. As a consequence, dispersal may have evolved as a means to avoid inbreeding (Dobson 1982, Moore and Ali 1984, Wolff 1992). The high reproductive skew in singularly breeding Damaraland mole-rats has been shown to be affected by inbreeding avoidance (Cooney and Bennett 2000) and therefore both sexes are predicted to disperse equally. However, Hazell et al. (2000) found a tendency for male-biased dispersal in Damaraland mole-rats in Namibia, while Spinks et al. (2000a, b) found an increased dispersal rate in common mole-rats which was male-biased at high densities, but no sex-bias at low densities. This study did not find a sex-bias in the two populations, nor a relationship between dispersal rates and density. However, females were found to spend a significantly longer time than males in the natal territory at the low-density site suggesting that males do in fact disperse sooner. The limited duration of the study at Tswalu could affect the observed dispersal rates and lack of sex-bias since a slight sex-bias was present, but it was not significant. Perhaps with a longer study period a better understanding of the dispersal tendencies in the sexes would become apparent. Alternatively, the mortality of dispersing individuals may be extremely high, as has been reported in the dwarf mongoose (*Helogale parvula*), where up to 50% of males and 78% of females fall foul before establishing a new territory (Waser et al. 1994, Creel and Waser 1997), which would indicate a male-biased dispersal in capture-mark-recapture studies if dispersal rates are equal. Thus the observed dispersal frequencies reported in this study are more of a probability of successful dispersal than actual dispersal rates. Hazell et al. (2000) based their conclusions on already deceased mole-rats along a concrete canal which is likely a much more accurate measure of dispersal tendencies and mortality in subterranean rodents.

Long distance dispersal in mammals is infrequent, but maintains genetic diversity among widely separate populations (Nunes 2007). However, in males, survival rates will decrease with the distance travelled from the natal territory (Bengtsson 1978, Jones 1988) due to risks associated with unfamiliar habitats, passage through areas of relatively high predator densities, or the physiological costs of long distance movement (Waser et al. 1994, Plissner and Gowaty 1996). Dispersal distances of over 1km have been observed in white footed mice (*Peromyscus leucopus*, Maier 2002), deer mice (*Peromyscus maniculatus*, Bowman et al. 1999), yellow bellied marmots (*Marmota subflavus*, Salsbury and Armitage 1994), Belding's ground squirrels (*Urocitellus beldingi*; Sherman 1976), naked mole-rats (Braude 2000), and now Damaraland mole-rats (this study). While the mean distance travelled by mole-rats at the high-density site (Tswalu) was comparable to the mean of the distances reported by Young et al. (2010) and Braude (2000), the mean distance at the low-density site (KRC) was almost twice the maximum distance travelled. The greatest distance travelled by an individual from the low-density site was a staggering 4.8km from the natal burrow, whereas a maximum distance of only 900m was observed at the high-density site, which is twice the distance reported by Young et al. (2010). These new recorded distances serve to illustrate the short comings of capture-mark-recapture studies in mole-rats occurring by under estimating dispersal frequency in areas of less than 43 hectares (Jarvis and Bennett 1993, Spinks et al. 2000b, Young et al. 2010). Based on the maximum dispersal distances documented in this study (provided they are representative), to ensure observing all inter-colony movement a minimum area approaching 100 (1 km^2) hectares in high density locations and a daunting 2,500 (25 km^2) hectares in low density areas would be required. However, I realize the labour intensive effort required to capture mole-rat colonies in the hypothetical study areas. Therefore location sizes based on the mean dispersal distances provides a more reasonable 28 hectares and 144 hectares respectively would still account for the capture of approximately 75% of dispersing mole-rats.

Banner-tailed kangaroo rats (*Dipodomys spectabilis*) inhabit similar conditions to mole-rats, occupying large nest mounds which are costly to build, last for decades and are evenly spaced in the environment (Holdenreid 1957, Jones et al. 1988). As a result, the total number of mounds remains stable between years and unoccupied nests are available, especially in periods of low density (Jones et al. 1988). The consistent placement, longevity, and number of mounds in close proximity (ca. 50m in high density areas; Jones et al. 1988) to each other is comparable to the situation of mole-rat burrows which can also remain in the same general area for decades and can be relatively close to neighbouring territories (ca. 10-50m in high density areas; Jarvis and Bennett 1993; K. Finn, pers. obs.). Jones et al. (1988) found that dispersal distances decreased during periods of high population density and increased during periods of decreased population density, which again is the same pattern observed in this study.

Female immigrants to a group are rare in cooperative breeders, but they have been observed in African wild dogs (*Lycaon pictus*, Creel and Creel 2002), banded mongooses *Mungos mungo* (Cant et al. 2001, Cant et al. 2013), and mole-rats (*Cryptomys hottentotus,* Spinks et al. 2000b; *Fukomys damarensis*, Burland et al. 2004). The low rates of female immigration could be explained by equal rates in male and female immigration into established colonies, but the majority of females fail to oust the resident dominant female and are killed, or violently expelled, as a result. In this study I found that only five of 69 (7.2%) total immigrants to established colonies were female. Of these five female immigrants two were marked juveniles (36g at Tswalu and 75g at KRC) at first capture, and three were adults (one marked and two unmarked) which became the new reproductive female. The three latter occasions all occurred at Tswalu and are worth mentioning. The first case involved a newly formed colony where a marked immigrant female was recaptured instead of the original reproductive female. The immigrant female dispersed from a colony 426m away and it was unclear whether the original female dispersed or died prior to her joining, or was killed (or evicted) by the intruder. The second case concerned a colony previously consisting of 18 individuals (10 males, 8 females) where at recapture only five males (body mass 64-140g at first capture) and one female (76g at first capture) were recaptured with an unmarked immigrant reproductive female and two new pups. It is interesting to note that the heaviest male at first capture remained the reproductive male (gaining an additional 25g since first capture), while heavier (n = 5) and lighter (n = 2) females than the one female recaptured were missing. In the first two cases, the fate of the original reproductive female was unknown. In the third case a new unmarked reproductive female was captured with a marked male from Colony 3 and in another trap a few metres away, the reproductive female of Colony 3 was recaptured. All of the mole-rats were housed together in same tunnel in the lab, but the following morning the original reproductive female was found with multiple bite wounds and huddling in a corner of the tunnel away from the nest which was occupied by the other two. What may have happened was that either the male dispersed and located a single female, or the new female invaded the colony, displaced the original female and blocked the tunnel between them isolating the original female into a separate burrow. These cases lead me to suspect that eviction (or equally likely death) of the loser in contests for breeding status may occur in wild Damaraland mole-rats. In the second case it is likely that all other females were evicted or killed by the immigrant. Increasing aggression to subordinate females by the dominant female has been shown to occur during the later stages of the dominant female's pregnancy cycle in meerkats (*Suricata suricatta*, Clutton-Brock et al. 1998) and the probability of eviction increases as relatedness decreases (Clutton-Brock 2016).

The presence of single females has been previously observed in other field studies of mole-rats (Jarvis and Bennett 1993, Young et al. 2010). Since females moving to established colonies are rare (Spinks et al. 2000b, Burland et al. 2004, Young et al. 2010, this study) it is more likely that female dispersers establish themselves in isolated burrows instead of risking the costly endeavor to overthrow the resident dominant female. The data from this study supports this suggestion since 24 marked females at both locations were recaptured alone in discrete burrows compared to five marked females recaptured in colonies that were not their natal colony. These females left their natal colony most likely by burrowing away from the colony and then blocking the tunnel behind them in the process, but possibly by dispersing long distances (>1km) above ground or utilizing a network of empty burrows of extinct colonies to facilitate safe movement over long distances underground. These three suggested methods are not mutually exclusive. The majority (75%) of the marked females in this study dispersed less than 1000m which could easily be traversed underground during the wet season when the damp soil facilitates digging. I have personally observed a single female creating a line of mounds over 300m during one month, and traveling 900m over the course of three months is achievable during the wet season. I suspect that the majority of the unmarked single females found at the initiation of this study are from the neighbouring colonies and as a result would be more closely related to colonies within 1000m. This hypothesis can be easily tested using molecular data.

In Florida Scrub Jays (*Aphelocoma coerulescens)* helper males will occupy a section of the natal territory and recruit an unrelated female mate to claim the area as their own territory, this process is referred to as “territory budding” (Woolfenden and Fitzpatrick 1978). A similar process has been observed in Damaraland mole-rats where a mixed-sex pair will occupy a marginal section of the burrow system and back block the tunnel behind them creating a new isolated burrow for themselves (Jarvis and Bennett 1993; K. Finn, pers. obs.). Two cases of territory budding were observed at the KRC and one possible case in Tswalu. The first case involved an adult non-reproductive female that had been living with the group since initial capture (29 months prior) and a male born to the reproductive female six months after initial capture. They formed an independent nascent colony on the edge of the original colony, raising one litter of offspring. The dispersing male was definitely the offspring of the reproductive female living with the colony for 23 months, while the dispersing female’s relationship to the reproductive female is unknown since she was an adult present at initial capture. The second case occurred 11 months after the removal of the original reproductive female. A male-female pair of non-reproductive individuals stayed in the area of the burrow system (13 months after separating the female became reproductive and produced a litter of four pups) while the rest of the group was captured 100m away at a new location with a previously non-reproductive female which became reproductive, a known immigrant reproductive male, and four pups. The case at Tswalu is the afore mentioned event at Colony 3 where a new reproductive female was captured with a marked male and the original reproductive female was captured a short distance away.

It is unclear whether single females were forcefully evicted, as seen in other cooperative breeders (meerkats, Clutton-Brock et al. 1998; banded mongoose, Cant et al. 2010; some primates, Pope 2000, Kappeler and Fichtel 2012), or disperse voluntarily. During the wet season when the costs of dispersal are lowered, immigrant males are more likely to join established colonies (Burland et al. 2004, Young et al. 2010; this study). In laboratory maintained colonies, increased female-female aggression has been observed after an unrelated male is introduced to a colony (Cooney et al 2000; K. Finn, pers. obs.) and territory budding can occur when an unrelated mixed sex pair isolate themselves in an unused section of the colony burrow (Jarvis and Bennett 1993; K. Finn, pers. obs.). If eviction was not the cause of females dispersing singly in the presence of immigrant males I would expect to see more colonies formed by territory budding. Since I have seen more occurrences of successfully dispersing single females (n = 24) than territory budding via mixed sex pairs (n = 2), I speculate that during the wet seasons if an unrelated male joins a colony causing increased female aggression and a subordinate female is unable to win the reproductive position, the dominant female evicts the aggressor from the colony. Alternatively the unrelated male and his selected female could block themselves into a section of the burrow and thereby completely avoid any possible aggression from the reproductive female. However, it is possible that territory budding occurs more often than observed since during capture traps are typically placed at a high concentration of mounds assumed to be relatively central to the colony's territory and only occasionally set on the periphery of colonies. Additionally subordinate females have an increased chance of eviction when they become pregnant and afterwards aborting their litter when evicted (Gilchrist 2006, Young et al. 2006, Young 2009). A small portion of the observed single females had a perforate vagina indicating that they had mated with a male, but did not have any pups present at capture, therefore if they became pregnant they must have aborted their litter during dispersal.

The comparison between the growth rates of philopatric and dispersing individuals illustrates the costs to dispersers. Dispersers gained significantly less body mass and grew slower during the search for a new territory than those individuals that chose to stay in the natal colony. The data revealed that philopatric individuals were heavier at both sites than individual that disappeared due to attrition, while there were no differences between the body mass of individuals who disappeared and the pre-dispersal body mass of those that dispersed. While it is difficult to determine the fate of individuals which went missing, it can be assumed they dispersed or succumbed to predation while in the natal colony. It has been assumed that predation rates in the burrow of subterranean rodents are low (Bennett and Faulkes 2000). These results suggest that the majority of lost individuals attempted to disperse instead of succumbing to predation or other mortality while in the natal colony.

This study attempted to test the effects of population density on dispersal patterns and philopatry in Damaraland mole-rats. Dispersal rates did not appear to be density-dependent in either population. While a sex-bias in dispersing individuals was not found at either location, non-reproductive females at KRC remained in the group significantly longer than males. Additionally, the similarity in body masses between dispersing individuals and individuals that were lost between capture events provides circumstantial evidence that a majority of the lost individuals likely dispersed. The distance travelled by dispersers from the natal group does appear to be density dependent, decreasing as the population density increases.

CHAPTER 5: Conclusion

The primary goal of this study was to expand upon the limited data available on density dependent effects on body size, growth rates, colony composition, litter size, recruitment as well as philopatry in Damaraland mole-rats (*Fukomys damarensis*) by comparing two populations of varying densities. The secondary goal of the study was to provide data on dispersal distances and immigration tendencies, which are depauperate in this species. The findings of this study reveal that colony size, biomass, litter size, recapture probability and immigration rates do not appear to be related to fluctuations in density. However, body size, growth rates, colony recruitment, colony attrition, dispersal distance and the presence of single females in the environment appear to be density dependent.

Tswalu exhibited a greater annual rainfall, a higher population density, a greater attrition rate than the more arid KRC site to the northwest. Increased annual rainfall allows for a longer period where the soil was soft enough to facilitate digging, thereby allowing for more dispersal opportunities. The greater density of mole-rats at Tswalu increased the probability of dispersing individuals finding a mate and therefore greatly reduced the dispersal distances needed to find a mate. Since mole-rats exhibit limited mortality from predation (Bennett and Faulkes 2000, Spinks et al. 2000b) it is likely that the increased rate of attrition observed at Tswalu can be attributed to increased natal dispersal. Further, the similarity in the body masses of individuals lost between capture and dispersing individuals suggests that the majority of lost individuals attempted to disperse instead of succumbing to predation or some other form of mortality while in the natal colony. If this premise holds, dispersal may occur more frequently in high density populations as indicated by the higher attrition rate. This finding is contrary to previous findings in rodents where dispersal has been found to be at its highest at low densities (McGuire et al. 1993, Getz et al. 1993, Jones et al. 1988, Wolff et al. 1988), but it is supported by Spinks et al. (2000, 2000b) who found a positive relationship between density and dispersal rates in the related common mole-rat (*Cryptomys hottentotus*).

I also found a significant difference in the behaviour of dispersers, males were more likely to join an established colony while females were more likely to establish a new burrow system by themselves. While the number of successful dispersers was comparable between locations, this result may not be indicative of the actual dispersal rates at the location due to the behavioural differences between the sexes. The chances of a mole-rat succumbing to predation during dispersal would increase with distance travelled and the time spent searching for a territory (Fretwell and Lucas 1969, Jones et al. 1988, Waser et al. 1994, Creel and Waser 1997). Though it was not significant, there were slightly more successful dispersing males at Tswalu and more females at KRC which may indicate that mortality is higher in females at Tswalu and males at KRC. Since the density was higher at Tswalu, it would be expected that dispersing males would exhibit a reduced search time for a new colony due to the close proximity of colonies (and therefore a lower mortality rate) and females would have increased search times due to the reduced probability of locating an unoccupied territory (therefore a higher mortality rate). At KRC, the relationship would be reversed females would quickly locate a vacant territory (resulting in decreased mortality risk), while males would spend longer searching for a colony due to the greater distance between colonies. Additionally, at KRC females spent a longer duration in their natal colony than males. These results may indicated the presence of a male-bias in dispersal at KRC and a female-bias in dispersal at Tswalu, and the disparity in dispersal behaviour and mortality risks resulted in the equal probabilities of successful dispersal observed in this study. Even if this proposed sex-bias was not present, a greater rate of dispersal than what was observed in this study likely occurs in both populations due to the high likelihood of predation while dispersing. The additional individuals lost between capture events at Tswalu either dispersed outside of the study site or died during emigration. The next step would be to determine the presence of a sex-bias in individuals lost between captures.

There are many ecological and behavioural similarities between arid dwelling terrestrial and subterranean rodents (Holdenreid 1957, Jones et al. 1988, Bennett and Faulkes 2000, Nevo 2007, Randall 2007). Jones et al. (1988) found that dispersal distances decreased during periods of high population density and increased during periods of decreased population density, which is essentially the same pattern observed in this study. Density-dependent predation has been observed in desert gerbils (*Gerbillus* spp., Ylönen and Brown 2007), however, this relationship is unlikely in subterranean rodents due to the safety of their occupied niche (Bennett and Faulkes 2000). If mole-rats disperse above ground, they would be at the mercy of a host of predators at both sites, but additionally by brown hyena (*Hyaena brunnea*), black-backed jackal (*Canis mesomelas*), and Eagle Owls (*Bubo* spp.) which were not typically observed at the low-density site. Previous studies in terrestrial rodents, such as banner-tailed kangaroo rats (*Dipodomys spectabilis),* have suggested that dispersal rates decrease when fewer potential new territories are available due to competition for resources, hindering dispersal and resulting in increased philopatry (Gaines and McClenaghan 1980, Wolff 1997, Wolff et al. 1988, Jones et al. 1988, Andreassen and Ims 2001). However, the subterranean niche inhabited by mole-rats likely precludes basing the decision to disperse on prior knowledge of the surrounding habitat conditions which would be gained by experimental forays as seen in other terrestrial rodents (Jones et al. 1988, Randall 2007, Nunes 2007). Although supposing the ecology of kangaroo rats and mole-rats were more similar than previously thought, and mole-rats truly exhibit a decrease in dispersal rates at higher densities, then the higher attrition rates observed at higher densities in mole-rats (Spinks et al. 2000a, b; this study) would have to be related to inter-colony mortality. Due to the intense aggression exhibited to intruders (Cooney 2002), it may be that more intrusions occur in higher density situations leading to the death of colony members or complete displacement of colonies. Therefore, perhaps in high density situations, the number of colony intrusions by neighbouring colonies increases dramatically and the greater attrition observed in common mole-rats (Spinks et al 2000) and Damaraland mole-rats (this study) is due to hyper-aggression between colonies which results in the death of combatants.

In naked mole-rats (*Heterocephalus glaber*) both males and females were unlikely to join established colonies, instead they appeared to prefer establishing a new territory by themselves and waiting for a mate to arrive (Braude 2000). The finding of this study support Jarvis and Bennett (1993) who found fewer single individuals at locations of high density (where distance between colonies could be less than 5m) since the probability of individuals locating a mate is much greater under these conditions. In Damaraland mole-rats (Burland et al. 2004, this study) and common mole-rats (Spinks et al. 2000b) males will readily join established colonies, while females rarely do so. At both sites, dispersing females were much more likely to be found in isolated burrows, therefore it is plausible that single individuals follow the same waiting game that naked mole-rats play. The exact impetus for non-reproductive individuals to leave the natal colony is unknown. It has been suggested that when unrelated males join a colony they sequester a female away from the rest of the colony by blocking the tunnel behind themselves, thereby forming a new colony via territory budding (Woolfenden and Fitzpatrick 1978, 1990), or dispersing as part of a coalition (Jarvis and Bennett 1993; K. Finn, pers. obs.). However, the few cases of territory budding and formation of coalitions observed during the course of this study lead me to believe that eviction by the dominant female may be responsible for triggering dispersal in female Damaraland mole-rats as seen in other cooperative breeders (meerkats (*Suricata suricatta*), Clutton-Brock et al. 1998; banded mongoose (*Mungos mungo*), Cant et al. 2010; and some primates, Pope 2000, Kappeler and Fichtel 2012). When an unrelated male joins an established colony there can be intense competition between females, often escalating to severe wounds (Cooney and Bennett 2000; K. Finn, pers. obs.) and in a captive situation has led to the loser hiding in a section of the tunnel to avoid contact with the aggressor (K. Finn, pers. obs.). It should be pointed out though that no marked dispersing female has shown obvious signs of participating in such a skirmish.

The higher proportion of single individuals at the low-density site provides evidence for the increased availability of territories, but reduced probability of finding a mate, when population density is low. At the low-density site, dispersers must travel over three times as far in order to locate a mate due to the widely scattered colonies. Braude (2000) speculated that single females would use chemosensory cues when creating mounds scented with their faeces or urine to attract roving males travelling above ground. In laboratory scent presentation studies individuals were able to discriminate between related and unrelated individual's odours, even if the related individual was unknown to the test subject (Heth and Todrank 2007). Above ground dispersal has been observed in naked mole-rats (Heaton 1998), giant mole-rats (*Fukomys mechowii*, Kawalika and Burda 2007) and Damaraland mole-rats (Hazell et al. 2000, Voigt et al. 2014) as well as implied in silvery mole-rats (*Heliophobis argenteocinereus*, Patzenhauerová et al. 2010). The greater maximum distances travelled by dispersers at the low density location (12 occurrences >900m) leads me to believe that above ground dispersal may occur more frequently in low density populations. Additional evidence for above ground dispersal is one case at the low-density site where a male travelled 1.6km in under 52 days with no other fresh mounds within a 100m radius of the new colony.

One possible explanation for the increased density observed at Tswalu is that higher rainfall leads to better quality habitat. Although they tend to be smaller, geophytes in mesic regions are of better quality and found in higher densities than in arid areas (Lovegrove and Painting 1987; Lovegrove and Knight-Eloff 1988, Spinks et al. 2000ba). Spinks et al. (2000b) concluded that the greater distance between geophytes in arid environments would increase foraging costs for mole-rats living at low densities and as a result, body size decreases as an energy saving mechanism. However, the increased body size of adults and increased growth rate in juveniles exhibited at the arid low-density site in this study could also be explained by better geophyte availability at that location. An alternative suggestion is that the greater population density at Tswalu may reduce the total available geophytes over time, and with the reduced amount of geophytes brings about the reduced body size observed in individuals. Whichever the case, I believe it appears that habitat quality more than population density affects individual body size in mole-rats, which corresponds to trends observed in many ungulates (Clutton-Brock et al. 1985, Kjellander et al. 2005). Additionally, the assumption that habitat quality is positively correlated with population density may break down under certain conditions (van Horne 1983). The misleading assumption of a positive habitat quality-density relationship would be expected in environments that show marked seasonality, temporal fluctuations in resources, or patchy environmental characteristics. Species that are dietary generalists show social dominance interactions, high reproductive capacity, or exhibiting high site fidelity could deviate from the expected habitat quality-density relationship (van Horne 1983). Since social mole-rat colonies also exhibit high site fidelity, occur in regions characterized by seasonal sporadic rainfall, patchy distribution of geophytes and burrows, exhibit social dominance in the form of reproductive suppression, and have a high reproductive capacity throughout the life of the reproductive female, it could be that other factors besides habitat quality affect density in mole-rats are involved. Without an in depth assessment of the local geophytes at either site, I am hesitant to suggest that habitat quality affects density.

There is interest in the relationship between body mass, population density, reproductive performance, and resource availability because life history theories predict a trade-off between mass and reproduction when resources are limited (Stearns 1992). Tests of these theories are difficult since they require long-term data sets on an individual's reproductive success and body mass under varying levels of resource availability. While the data presented here is still in its infancy, there is great potential for long term comparative work on this relationship using these two populations. The longevity of mole-rats and the varying density and body size of the two populations studied presents the perfect combination to further study density-dependent reproductive performance over time and how it relates to habitat quality. The next step after this study is to quantify the differences in geophyte biomass, distribution, and density at the two study sites to disentangle the relationship between population density, habitat quality, and individual body size. The next step would be to compare the reproductive performance of reproductive females to determine if density or habitat quality affects lifetime reproductive success. This study could be completed using a combination of counting foetuses in radiographs of pregnant free ranging females and the number of juvenile recruits found between capture events.

While much of the aspects of dispersal and movement in subterranean rodents are unknown, this study provides a large sample size of the potential distances travelled by dispersing individuals to assist future studies. An additional step would be measuring colony home range size either by telemetry (Šklíba et al. 2016) or burrow excavation (Šumbera et al. 2012, Thomas et al. 2015) to determine if it decreases with population density or colony size and then determine if home range size or colony size more affects dispersal tendency or likelihood of territory budding. Recent advances in molecular techniques have aided our understanding of dispersal patterns in these hard to study rodents by using local and regional relatedness to determine the presence of sex-bias in dispersal and gene flow between populations (Burland et al. 2004, Fernandez-Stolls et al. 2007, Stiver et al. 2007). Applying molecular based analysis on the dispersal patterns in this study could provide a better understanding of estimating dispersal rates and uncovering the presence of sex-bias more easily than reliance on capture-mark-recapture data.

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