Population structure and predation in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt).

by

Charmaine Dawn Theron

Submitted in partial fulfilment of the requirements for the degree

MSc Research: Entomology

In the Faculty of Natural and Agricultural Sciences

University of Pretoria

Pretoria

(2013-12-18)

Supervised by:

Prof. Christian Pirk[1,2]

Dr Fredrik Dalerum[1,3]

1. Department of Zoology and Entomology
2. Social Insect Research Group
3. Centre for Wildlife Management

I, Charmaine Dawn Theron declare that the thesis, which I hereby submit for the degree MSc: Entomology at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

SIGNATURE: ....

DATE: ....

Summary

Little information is available on the termite species in southern Africa, especially *Trinervitermes trinervoides* (Sjöstedt). This is an endemic, non-detrimental harvester termite that performs vital ecosystem functions in the semi-arid grassland ecosystem of southern Africa. *T. trinervoides* is the only termite species that does not compete with grazers for foraging material since they harvest litter grass. *T. trinervoides* are highly eusocial, mound-building, nasute termites. The ability to construct mounds has facilitated colonies in obtaining a population of thousands of individuals. Nevertheless it is unclear if *T. trinervoides* is monodomous (single mound) or polydomous (several mounds). The large population sizes in terms of individuals per mound and mound density of *T. trinervoides* have allowed for predator specialisation. In southern Africa the most destructive predator of *T. trinervoides* is the aardvark, *Orycteropus afer* (Pallas). In order to determine the impact of predation from the aardvark, the social structure of *T. trinervoides* first has to be understood. Using aggression as a proxy for nestmate recognition I found that each *T. trinervoides* colony occupies a single mound. The aggression structure was uniform across the population and most likely driven by resource competition. Aardvark predation risk was highest in the wet season, but predation severity was also uniform across the population. Predation from the aardvark may be driving *T. trinervoides* social structure towards monodomy in this area. Polydomy may decrease colony survival as resources are spread throughout a wide area. Furthermore this study reveals that large scale studies are important in ecological studies as small scale studies over emphasise variance in data that is reduced on a large scale.

Acknowledgements

I would like to thank the NRF for funding this project, DeBeers for the use of their property and Prof. Elisa Cameron for securing funding. I would like to thank the following people for their support in the field: David and Courtney Marneweck, Matthieu Packet, Jonatan Borling, and the staff of Benfontein Game Farm. I would like to thank to the following people for their constructive input towards the final write-up of my thesis: Liz Archer, Hanna Grace Thomas, Lydia Belton and Gordon Ringani. I would also like to thank my parents; Paul and Louise and my partner Hardus for the moral support; and many thanks to Hanna Grace Thomas and Daniel Swanepoel for the beer. Thank you to everyone that helped with this project, it is always appreciated, after all I am human.

Table of contents

List of figures

List of Tables

List of Supplementary Information

Note: Chapters II and III were written for separate publication in the appropriate international journals.

Chapter I

General Introduction:

In group living animals a social structure can be regarded as a group of individuals amongst which there is brood care and division of labour (Michener 1969; Wilson 1971; Lin & Michener 1972). The two main factors that are believed to contribute to the evolution of sociality is parental care and the poor success of young in finding a mate and rearing offspring (Andersson 1984). Insects, among other taxa, exhibit a wide range of social structures, due to the large numbers of species present, and highly cohesive colony structures are particularly frequent in this taxon (Reviewed by Andersson 1984; Ross & Keller 1995; Wilson & Hölldobler 2005). There are various levels to which social structures have evolved. The definitions below are taken from Lin & Michener (1972). The most primitive social structure is the semi-social structure in which a female would have a nest and accept other individuals of the same generation (siblings) and there is some division of labour among them, joiners to these nests may leave and found a nest of their own at any point if the resources allow. This is found in Hymenoptera such as the halictine bees (for example *Augochloropsis sparsilis*), and *Bombus* at a certain stage of development (Michener 1974). In eusocial structures there are overlapping generations within the colony and division of reproductive labour where the queen reproduces and the daughters are non-reproductive workers. The main function of daughters in a nest is to forage and construct brood cells. In primitive eusocial structures there is no morphological difference between the queen and workers. The workers are able to lay eggs but this is either suppressed or self-regulated (Wheeler 1986; Ratnieks 1988). Highly evolved eusocial structures such as those in ants and termites the workers are morphologically distinct from the queen and can be fully sterile. This brings about the formation of the worker caste, they are not able to reproduce and are bound to serve the queen for the benefit of their genetics.

Nestmate recognition is important to colonies, as it prevents non-kin from benefiting from colony membership. The mechanism of recognition is based on cues that are genetic (Beye *et al*. 1998) or environmental (such as diet: Liang & Silverman 2000; or nesting material: Breed *et al*. 1988; Stuart 1988) derivatives or a mixture of both (gestalt: Wagner *et al*. 2000; Pirk *et* *al*. 2001). A colony gestalt is a scent unique to a colony at a specific point in time. The gestalt is formed by using a combination of cues from individuals throughout the colony forming a unique scent with the queen(s) normally playing a significant role (Hölldobler & Wilson 1990). A colony gestalt is used in small to medium sized colonies where successive queens contribute to colony reproduction, or in slave-making species that "adopt" an invaded colony's workers (Reviewed by D'Ettorre & Heinze 2001). The continuous change in the cues results in the colony forming a common scent that is passed from worker to worker throughout the colony. The colony gestalt is learned by workers and used to discriminate nestmates from non-nestmates. Besides colony gestalt there are two other potential models to describe learning in nestmate recognition: common label acceptance and foreign label rejection (Lacy & Sherman 1983; Pirk *et al.* 2001). The former states that individuals will be accepted by a guard worker if any similarity is detected in the recognition cues, whereas with the latter, individuals will be rejected based on any dissimilarity detected in recognition cues. When using common label acceptance, environmental homogeneity does not provide enough variance for nestmate recognition, as such other common but unique cues must be used, like gentically derived cues. When using foreign label rejection, high genetic and environmental heterogeneity provides enough unique cues to a colony that either may be used for nestmate recognition.

Termites are highly eusocial and reproduction is fully diploid where the colony consists of a permanent king with one or multiple queens (Bartz 1979). The caste structure in termites differs from bees in that they have a worker and a soldier caste. The evolution of a permanently sterile worker caste provides for definitive division of labour in a nest/colony. The queen is the only reproductive of the colony and the workers micro-manage the colony (building, foraging, tending to brood, etc.), the soldiers provide protection to the colony, the queen and foraging parties. Termites are ecologically important insects to an ecosystem since they recycle nutrients transforming previously unavailable minerals into important nutrients that plants and animals are able to assimilate (Coventry *et al*. 1988; Dangerfield *et al*. 1998). Termites mostly feed on dead plant matter, converting things like dead trees, undigested grass in faeces or other indigestible fibres into compounds that can be used by surrounding living organisms in various manners (Scholtz & Holm 1985). A large number of termite species are considered pests as they either digest structural timber or out-compete grazers for foraging material (Sands 1961a; Ohiagu & Wood 1976; Scholtz & Holm 1985).

Many termite species live in nest-like structures with an above ground portion known as the mound. Termite mounds may take various forms and contain a highly variable portion of the structure expanse below ground (Harris 1956; Scholtz & Holm 1985). Termite mounds are constructed by workers using a mixture of saliva and soil which when dried is similar to concrete, this provides the colony protection against predators, such as ants, spiders, lizards, birds and mammals (Scholtz & Holm 1985; Richardson & Levitan 1994). The mound provides protection from extreme environmental conditions such as large temperature fluctuations, aridity, wind and rain (Adam 1993). The queen and brood are most sensitive to extreme environmental conditions and are therefore situated at the centre of the mound, where temperature and humidity fluctuates the least (Korb & Linsenmair 2000; Adam 1993).

Termite mounds are used as food storage facilities as they provide a controlled environment for long term food storage (Kruuk & Sands 1972; Adam *et al*. 2008). The mound is also a major contributing factor to the development of large colony sizes, where thousands of individuals contribute towards the success of the colony. The disruption of this micro-climate could be severe enough to cause the death of the exposed brood and the collapse of the colony (Taylor 1963). A termite colony may consist of a single mound (monodomous) or multiple mounds (polydomous). In monodomous colonies all the resources for the colony are maintained within a single mound and nestmate recognition cues do not extend beyond the mound (Pirk *et al*. 2001; Dillier & Wehner 2004). In polydomous colonies one mound contains the breeding pair and the brood and satellite mounds are used to store foraging materials or act as a shelter for foraging parties (Sands 1961b; Ohiagu & Wood 1976; Holway & Case 2000). Polydomous species are able to dominate territories far greater than monodomous species and attain much greater colony sizes due to the presence of these satellite mounds (Levings & Traniello 1981).

In southern Africa there are a number of harvester termite families. The Hodotermitidae are characterised by the large serrated mandibles and compound eyes, the cuticles are black with pigmentation, allowing them to forage in daylight. The nests are subterranean and they cut living grass, making them a major rangeland pest in southern Africa. Only two species are known to occur in southern Africa; *Hodotermes mossambicus* and *Microhodotermes viator*. The Termitidae comprise the majority of termite species (190) in southern Africa (Scholtz & Holm 1985). Little to no information, apart from personal observations, is available on the majority of the species as they feed on decaying plant matter, apart from specific species in the Macrotermitinae and Nasutitermitinae subfamilies. The Macrotermitinae are fungus growing termites, growing fungus on harvested grass for nutrients. There are five genera in southern Africa, a few species are well known for the large size of their mounds, but very little is known about this subfamily. The Macrotermitinae harvester species cover the entire range of mound construction from subterranean to 4m high chimneys (Scholtz & Holm 1985; Turner 1994). All species are mandibulate. The Nasutitermitinae are also abundant in southern Africa, however research has only been done one species, *Trinervitermes trinervoides* the snouted harvester termite, as it was thought to be a major pest to rangeland.

The genus *Trinervitermes* (Termitidae: Nasutitermitinae) are specialised grass-feeding termites that build epigeal mounds. These mounds range in height 49.59±1.08 cm (Mean±SE); with above ground surface area estimated at 10396.38±457.33 cm^2 (Mean±SE). *T. trinervoides* have been suggested to be both monodomous and polydomous (Coaton 1948; Nel & Malan 1974; Adam *et al*. 2008). The few studies done on this genus show that all species are detrimental to rangeland and have the ability to outcompete grazers for resources, save for one species: *Trinervitermes trinervoides* (Sands 1961a; Adam *et al*. 2008). These two extensive studies (Sands 1961a; Adam *et al*. 2008) have shown that *T. trinervoides* do not cut standing grass but utilise recumbent grass, that is grass that is broken off from the main stem. There is very little information available about this species due to the non-competitive nature with grazers (see below) resulting in less economical interest to investigate the species, however from the literature available I was able to gather some information. *T. trinervoides* is a grass harvesting, mound building termite endemic to southern Africa (Adam *et al*. 2008). They have a highly eusocial colony structure consisting of a permanent king, a single queen, workers and soldiers (Michener 1969; Scholtz & Holm

1985; Queller & Strassmann 1998; Miura 2004; Inward *et al*. 2007). All workers and soldiers are permanently sterile and fully diploid therefore workers and soldiers are both male and female (Miura 2004). Gene dispersal takes place through the dispersal of primary reproductives (alates), no evidence for colony fission has been found (Adam & Mitchelle 2009). Adam & Mitchelle (2009) have shown that it takes three years for a mound to propagate above ground. *T. trinervoides* as being part of Nasutitermes soldiers have well developed frontal glands, giving the head a pointed shape, producing noxious chemicals called terpenes (Nel 1968; Prestwich *et al*. 1976; Prestwich 1979; Richardson & Levitan 1994). These chemicals have been shown to have detrimental effects on the liver and kidneys if ingested in high concentrations in mammals and acts as a neurotoxin in invertebrates (Budavari *et al*. 1989). Most predators avoid Nasutitermes species as a main constituent of their diets, but can be tolerated in low concentrations (Richardson & Levitan 1994). *T. trinervoides* is ecologically important for nutrient cycling in the environment, transforming previously unavailable minerals into important nutrients that plants and animals are able to assimilate (Coventry *et al*. 1988; Dangerfield *et al*. 1998). *T. trinervoides* feed on grass that is left behind after ungulate feeding, this eliminates resource competition between them and ungulates. *T. trinervoides* digest this grass, not with the aid of intestinal symbionts, but produce their own cellulase enzyme (Potts & Hewitt 1973; Scholtz & Holm 1985; Slaytor 1992). By feeding on this grass *T. trinervoides* convert an inaccessible resource into proteins and minerals. These minerals provide nutrients back into the soil for plant assimilation (Brossard *et al*. 2007), where the termites will provide dietary proteins for many insectivores (Redford & Dorea 1984).

The large population sizes of *T. trinervoides* colonies have allowed large mammal species to specialize on them as prey, despite the small body size of individual termites (Redford & Dorea 1984; Willis *et al*.1992; Taylor *et al*. 2002), namely The Cape pangolin (*Manis temminckii* Smuts); The aardwolf, (*Proteles cristata* Sparrman) and the aardvark (*Orycteropus afer* Pallas). The Cape pangolin is a weak digger and thus feeds on surface roaming ants and termites (Swart *et al*. 1999). Due to the behavioural ecology of *T. trinervoides*, ants contribute 97% of the diet in the wet season and *Hodotermes mossambicus* is preferred in the dry season (Swart *et al*. 1999). The aardwolf is also a weak digger and feeds mostly on termite foraging parties (Richardson 1987; Taylor & Skinner 2000). The aardwolf is part of the Hyaenidae family, which may predispose it to tolerance of harmful chemicals like terpenes and has been shown to have a 90% dietary composition of *T. trinervoides* throughout the year (Richardson 1987). The aardvark (*Orycteropus afer* Pallas) is the only predator of *T. trinervoides* that is able to dig into the mounds; feeding on workers, soldiers, alates and brood/immatures (Melton 1976; Taylor *et al*. 2002). Aardvark does not rely exclusively on *T. trinervoides* for nutrients as it consumes the highly abundant ant species in the wet season (Willis *et al*. 1992). In the dry season these ant species all remain in their nests below ground, which are too energetically expensive to dig into, and therefore the aardvark consumes more *T. trinervoides* (Willis *et al*. 1992). Aardvark predation on a termite mound has both direct and indirect effects on a colony since the digging exposes large portions of the colony to external environment, removes individuals from the colony and exposes the colony to secondary predation from other insectivores, like the aardwolf (Sheppe 1970; Taylor & Skinner 2000; Taylor & Skinner 2001).

When predation removes a large number of individuals from the colony the colony structure is disrupted, processes within the colony are interrupted as soldiers appear at the sight of disturbance in large amounts to defend the colony (Willis *et al*. 1992). Predation events also remove a large amount of forage reserves, in winter this could cause a colony to starve. Repeated predation within a habitat over extended periods of time will deplete the workforce, thereby slowing the nutrient cycling thereby depleting the energy returned to the system. Aardvark predation may also have an impact on the termite social structure in an area by potentially weakening the interactions between neighbouring colonies causing population fragmentation (Fraser *et al*. 1995).

The literature provides contradicting evidence as to whether *T. trinervoides* is monodomous or polydomous. Determining this will provide us with the spatial extent of the population structure of this species. This also provides insight on the much lacking social structure of this species. The effects of predation on the social structure of a species provides insight to the ability of a population to resist stochastic events, i.e. population stability. The social structure and population stability of a species is used to determine the area of importance for conservation enclosures. For efficient conservation and ecosystem management of this area and other areas the population structure and the effects of predation on *T. trinervoides* needs to be quantified. In this project I first quantified the social structure of *T. trinervoides*, I then analysed the various aspects of aardvark predation on the population. This research project provides quantitative information on *T. trinervoides* population and how they are affected by predation; it also contributes information that is greatly lacking from literature that can be used in future studies and inferences towards conservation.

References:

Adam R.A. 1993: Aspects of the biology of the harvester termite *Trinervitermes trinervoides* (Sjöstedt) (Isoptera: Termitidae). Ph. D. thesis. University of the Orange Free State, South Africa.

Adam, R.A. & Mitchell, J.D. 2009: Energetics and development of incipient colony formation of the harvester termite, *Trinervitermes trenervoides* (Sjöstedt) (Termitidae, Nasutitermitinae). Insectes Sociaux **56**, 21-27.

Adam, R.A., Mitchell, J.D. & van der Westhuizen, M.C. 2008: Aspects of foraging in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt) (Termitidae: Nasutitermitinae). African Entomology **16**, 153-161.

Andersson, M. 1984: The evolution of eusociality. Annual Reviews of Ecological Systematics **15**, 165-189.

Bartz, S.H. 1979: Evolution and eusociality in termites. PNAS, U.S.A. **76**, 5764-5768.

Beye M., Neumann P., Chapuisat M., Pamilo P. & Moritz R.F.A. 1998: Nestmate recognition and the genetic relatedness of nests in the ant *Formica pratensis*. Behavioural Ecology Sociobiology **43**, 67-72.

Breed, M.D., Williams, C.R. & Fewell, J.H. 1988: Comb wax mediates the acquisition of nest-mate recognition cues in honey bees. PNAS, USA **85**, 8766-8769.

Brossard, M., Lopéz-Hernández, D., Lepage, M. & Leprun, J.C. 2007: Nutrient storage in soils and nests of mound-building *Trinervitermes* termites in Central Burkina Faso: consequences for soil fertility. Biology and Fertility of Soils **43**, 437-447.

Budavari S., O’Neil M.J., Smith A. & Heckelman P.E. 1989: The MERK index, eleventh ed. MERK and Company, Inc. Rahway, New Jersey, 10100.

Coaton, W.G.H. 1948: *Trinervitermes* species- the snouted harvester termites. Union of South Africa, Dept of Agriculture Bulletin **261**, 1-19.

Coventry, R.J., Holt, J.A. & Sinclair, D.F. 1988: Nutrient cycling by mound building termites in low fertility soils of semi-arid tropical Australia. Australian Journal of Soil Research **26**, 375-390.

D'Ettorre, P. & Heinze, J. 2001: Sociobiology of slave-making ants. Acta Ethologica **3**, 67-82.

Dangerfield, J.M., Mccarthy, T.S. and Ellery, W.N. 1998: The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. Journal of Tropical Ecology **14**, 507-520.

Fraser, D.F., Gilliam, J.F. & Yip-Hoi, T. 1995: Predation as an agent for population fragmentation in a tropical watershed. Ecology **76**, 1461-1472.

Harris W.V. 1956: Termite Mound Building. Insectes Sociaux **3**, 261-268.

Holway, D.A. & Case, T.J. 2000: Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. Animal Behaviour **59**, 433-441.

Inward, D., Beccaloni, G. & Eggleton, P. 2007: Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biology Letters **3**, 331-335.

Korb J. & Linsenmair K.E. 2000: Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? Insectes Sociaux **47**, 357-363.

Kruuk H. & Sands W.A. 1972: The aardwolf (*Proteles cristatus* Sparrman) as a predator of termites. African Journal of Ecology **10**, 211-227.

Lacy, R.C. & Sherman, P.W. 1983: Kin recognition by phenotype matching. The American Naturalist **121**, 489-512.

Levings, S.C. & Traniello, J.F.A. 1981: Territoriality, nest dispersion and community structure in ants. Psyche **88**, 265-319.

Liang D. & Silverman J. 2000: "You are what you eat": Diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, *Linepithema humile*. Naturwissenschaften **87**, 412-416.

Lin, N. & Michener, C.D. 1972: Evolution of Sociality in Insects. The Quarterly Review of Biology **47**, 131-159.

Melton, D.A. 1976: The biology of aardvark (Tubulidentata-Orycteropodidae). Mammal Rev **6**, 75-88.

Michener, C.D. 1969: Comparative social behaviour of bees. Annual Review of Entomology **14**, 299-342.

Michener, C.D. 1974: The social behaviour of the bees: A comparative study. Harvard University Press, Cambridge, Mass.

Miura, T. 2004: Proximate mechanisms and evolution of caste polyphenism in social insects: From sociality to genes. Ecological Research **19**, 141-148.

Nel J.J.C. 1968: Aggressive behaviour of the harvester termites *Hodotermes mossambicus* and *Trinervitermes trinervoides* (Sjöstedt). Insectes Sociuax **15**, 145-156.

Nel, J. J. C. & Malan, E. M. 1974: The distribution of mounds of *Trinervitermes* trinervoides in the central Orange Free State. Journal of the Entomological Society of South Africa **37**, 251-256.

Ohiagu, C.E. & Wood, T.G. 1976: A Method for measuring rate of grass-harvesting by *Trinervitermes geminatus* (Wasmann) (Isoptera, Nasutitermitinae) and observation on its foraging behaviour in Southern Guinea Savanna, Nigeria. Journal of Applied Ecology 13, 705-713.

Pirk, C.W.W., Neuman, P., Moritz, R.F.A. & Pamilo, P. 2001: Intranest relatedness and nestmate recognition in the meadow ant *Formica pratensis* (R.). Behav. Ecol. Sociobiol. **49**, 366-374.

Prestwich G.D. 1979: Chemical defence by termite soldiers. Journal of Chemical Ecology **5**, 459-480.

Prestwich G.D., Tanis S.P., Pilkiewicz F.G., Miura I. & Nakanishi K. 1976: Nasute Termite Soldier Frontal Gland Secretions. 2. Structures of Trinervitene Congeners from *Trinervitermes* Soldiers. Journal of the American Chemical Society **98**, 6062-6064.

Queller, C.D. & Strassmann J.E. 1998. Kin Selection and Social Insects. BioScience 48, 165-175.

Ratnieks, F.L.W. 1988: Reproductive harmony via mutual policing by workers in eusocial hymenoptera. The American Naturalist **132**, 217-236.

Redford, K.H. & Dorea, J.G. 1984: The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. Journal Zoology London **203**, 385-395.

Richardson, P.K.R. & Levitan, C.D. 1994: Tolerance of aardwolves to defence secretions of *Trinervitermes trinervoides*. Journal of Mammalogy **75**, 84-91.

Richardson, P.K.R. 1987: Aardwolf: The most specialized myrmecophagous mammal? South African Journal of Science **83**, 643-646.

Ross, K.G. & Keller, L. 1995: Ecology and evolution of social organisation: Insights from fire ants and other highly eusocial insects. Annu. Rev. Ecol. Syst. **26**, 631-656.

Sands, W.A. 1961a: Foraging behaviour and feeding habits in five species of *Trinervitermes* in West Africa. Entomolgia Experimentalis et Applicata **4**, 277-288.

Sands, W.A. 1961b: Nest structure and size distribution in the genus *Trinervitermes* (Isoptera: Termitidae, Nasutitermitinae) in West Africa. Insectes Sociaux **8**, 177-188.

Scholtz, C. H. & Holm, E. 1985. Insects of Southern Africa. Butterworth Publishers (PTY) LTD, Durban, South Africa.

Sheppe, W. 1970: Invertebrate predation on termites of the African savanna. Insectes Sociaux **17**, 205-218.

Slaytor, M. 1992: Cellulose digestion in termite and cockroaches: What role do symbionts play? Comparative Biochemistry and Physiology Part B: Comparative Biochemistry **103**, 775-784.

Stuart R.J. 1988: Collective cues as a basis for nestmate recognition in polygynous leptothoracine ants. Proceedings of the Natural Academy of Sciences, USA 85, 4572-4575.

Swart, J.M., Richardson, P.R.K. & Ferguson, J.W.H. 1999: Ecological factors affecting the feeding behaviour of pangolins (*Manis temminckii*). Journal of Zoology London **247**, 281-292.

Taylor W.A., Lindsey P.A. & Skinner J.D. 2002: The feeding ecology of the aardvark *Orycteropus afer*. Journal of Arid Environments **50**, 135-152.

Taylor, W.A. & Skinner, J.D. 2000: Associative feeding between Aardwolves (*Proteles cristatus*) and Aardvarks (*Orycteropus afer*). Mammal Rev **30**, 141-143.

Taylor, W.A. & Skinner, J.D. 2001: Associative feeding between Ant-eating Chats, *Myrmecocichla formicivora*, and Aardvarks, *Orycteropus afer*. Ostrich **72**, 199-200.

Turner, J.S. 1994: Ventilation and thermal constancy of a colony of a southern African termite (*Odontotermes transvaalensis*: Macrotermitinae). Journal of Arid Environments **28**, 231-248.

Wagner, D., Tissot M., Cuevas W. & Gordon D.M. 2000: Harvester ants utilise cuticular hydrocarbons in nestmate recognition. Journal of Chemical Ecology **26**, 2245-2257.

Willis, C.K., Skinner, J.D. & Robertson, H.G. 1992: Abundance of ants and termites in the False Karoo and their importance in the diet of the aardvark *Orycteropus afer*. African Journal of Ecology **30**, 322-334.

, E.O. & Hölldobler, B. 2005: Eusociality: Origin and consequences. PNAS **102**, 13367-13371.

Wilson, E.O. 1971: The insect societies. Harvard University Press, Cambridge, Massachusetts, USA. pp x+ 548.

Chapter II

Nestmate recognition and aggression in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt, 1911)

This chapter is intended to be submitted to Ethology and therefore was formatted according to Ethology author guidelines

Abstract:

Most insect social structure research is done on highly social insects such as wasps, ants and bees. *Trinervitermes trinervoides* is the most abundant, non-detrimental termite species in southern Africa, and due to this fact is neglected in research. Colony spatial structure must be determined first in order for future studies to asses population stability and importance of this species to conservation of ecosystems. *T. trinervoides* colonies live in mounds housing thousands of workers and soldiers, and are also used to store foraging materials for the dry season. Studies on closely related *Trinervitermes* species indicate that *T. trinervoides* could occupy multiple mounds per colony. In this study I used aggression tests between individuals from different mounds to determine the spatial scale of colonies. There were low levels of aggression between individuals from the same mound and the significant increase in aggression over distance from immediate neighbouring mounds up to 5000 metres provides evidence that each colony occupies a single mound. There was an overall positively significant increase in aggression over distance between mounds on a large distance scale (mounds 5-5500 metres apart). However, there was an opposite effect of distance on aggression between mounds on a small distance scale (mounds 5-360 metres apart). The highest levels of aggression observed were between immediate neighbouring mounds suggesting there was a large amount of resource competition between directly neighbouring mounds. Factors influencing aggression on a large distance scale may be the Dear Enemy Phenomenon or the genetic structure of the population. The Dear Enemy Phenomenon states that individuals with an established territory will display reduced aggression towards immediate neighbours passing through the territory compared to individuals from further away, as they may potentially usurp the territory. The genetic structure of individuals can be used to differentiate nestmates from non-nestmates, and termite colony success is increased through inclusive fitness, genetically different individuals are detrimental to inclusive fitness. The different relationships between aggression and distance across spatial scales suggest that there are multiple factors influencing the social structure of this species.

Introduction:

In eusocial insects a colony consists of a group of related individuals where the workers and soldiers are mostly sterile and the only way they can increase their fitness is through inclusive fitness, which involves raising siblings (Queller & Strassmann 1998). Each colony separates itself from other colonies to prevent non-related individuals from benefiting from their labour, and thus prevents increasing the fitness of non-related individuals. Individuals recognise members from their own colony using cues that may be determined by genetics (Beye *et al*. 1998), environment (such as diet: Liang & Silverman 2000; or nesting material: Breed *et al*. 1988; Stuart 1988), or both (Wagner *et al*. 2000; Pirk *et al*. 2001). The consequences of genetic and environmental variability on the importance of different recognition mechanisms depend on the recognition process the organism is following. For instance, if the process follows the common label acceptance principle, environmental homogeneity will not provide enough variance for environmental cues to be used for recognition. Whereas foreign label rejection will not work where there is high amounts of genetic or environmental heterogeneity, as any point of dissimilarity will result in individuals being rejected as nestmates.

Termites (Family: Termitidae) are highly eusocial insects with a fully diploid system, containing a king and queen and sterile workers and soldiers (Michener 1969; Scholtz & Holm 1985; Queller & Strassmann 1998; Miura 2004; Inward *et al*. 2007). The worker caste takes on colony maintenance and brood care duties and the soldier caste defend and protect the colony (Noirot 1985; Miura 2001). Many termite species live in nest-like structures with an above ground portion known as mounds (Fig. 2.1). Termite mounds may take various forms and contain a highly variable portion of the structure expanse below ground (Harris 1956; Scholtz & Holm 1985). Termite mounds produce a very controlled environment with a specific micro-climate, since termites are sensitive to fluctuations in humidity and temperature (Korb & Linsenmair 2000). The disruption of this micro-climate could be severe enough to cause the death of the exposed brood and the collapse of the colony. A termite colony may consist of a single mound (monodomous) or multiple mounds (polydomous). In monodomous colonies all the resources for the colony are maintained within a single mound and nestmate recognition cues do not extend beyond the mound. In polydomous colonies one mound contains the breeding pair and the brood and satellite mounds are used to store foraging materials or act as a shelter for foraging parties (Sands 1961; Ohiagu & Wood 1976; Holway & Case 2000).

Trinervitermes trinervoides (Sjöstedt) is a grass harvesting termite that feeds on recumbent grass (e.g., bent grass or grass that is no longer connected to the tussock; Adam *et al*. 2008). They are therefore dependent on other herbivores to provide them with a food source, but the large size of the colonies as well as their often high abundances makes them ecologically important, particularly in terms of nutrient recycling. The large extreme temperature fluctuations in large parts of their range has caused *T. trinervoides* to form mounds as an adaptation to cope with temperature extremes (Ohiagu & Wood 1976; Smith & Yeaton 1998). However, the population structure of this termite species is still poorly known, for instance, it is not clear if *T. trinervoides* is monodomous or polydomous throughout their range. A monodomous colony would support a smaller territory than a polydomous colony, which may have implications on the social structure. Monodomous colonies support smaller colony sizes compared to polydomous colonies which can use satellite mounds for soldiers, workers and food storage (van Wilgenburg & Elgar 2007, Flanagan *et al*. 2012). However if predation is density dependent then polydomous colonies will have a higher predation risk than monodomous colonies (Holling 1959).

Aggression between colonies may be affected by various factors, such as resource competition, space limitation and the Dear Enemy phenomenon. Due to *T. trinervoides* being dependent on ungulates for resources and the often high mound densities there may be high levels of resource competition (Hairston *et al*. 1960), and therefore high levels of aggression towards immediate neighbouring colonies. Therefore one could expect a higher aggression level between neighbours than between members of distant colonies. With increase in population density within a particular area, contact between neighbouring colonies will be more frequent (Hairston *et al*. 960). One could expect to see density dependent aggression, with higher aggression levels in more densely populated areas. On the other hand, the weak flying ability of the alates may result in a high degree of genetic relatedness over smaller spatial scales, which would generate the opposite prediction, since genetic relatedness is negatively correlated with aggression (Pirk *et al*. 2001). Another option would be that aggression is influenced by the Dear Enemy-phenomenon, i.e. individuals selectively directing their aggression towards specific individuals that are perceived as a greater threat. The selective aggression is displayed as reduced aggression towards immediate neighbours, since borders between the neighbours are established and constant border fight might be too costly, and colony members display increased aggression towards more distant individuals. The threat perceived by immediate neighbours towards one territory is minimal, as they already have territory of their own, compared to the threat from a more distant individual, who may be in search of territory (Heinze *et al*. 1996; Husak & Fox 2002).

In this study I used aggression between individuals as a proxy for nestmate recognition to determine the spatial extent of *T. trinervoides* colonies. The relationship between aggression and distance between mounds is used to provide insight into the spatial structure of a population of *T. trinervoides* in central South Africa.

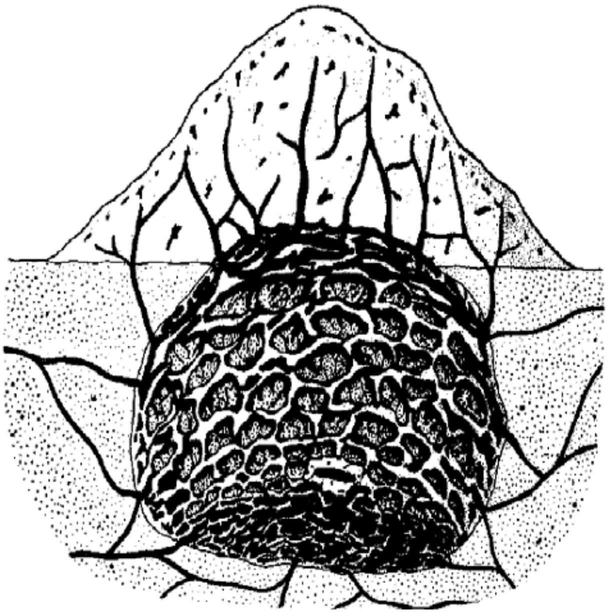


Fig. 2.1. A graphical representation of a cross section through a *T. trinervoides* mound (picture taken with permission from Scholtz & Holm 1985).

Materials and Methods:

Study site:

I conducted the study on Benfontein Game farm, an 11,000ha farm near Kimberley on the Free State and Northern Cape border in central South Africa (28°50`S, 24°50`E). The summer day-time temperatures range between 28-33 °C, and fall to between 10-12 °C in the winter. Rainfall in the wet season ranges from 28-73mm, and 7-8mm in the dry season, with an annual rainfall of 420mm (The South African Weather Service).The climate is semi-arid (Dean & MacDonald 1994), but landscape structures formed by a prehistoric lake (Morris 2013) cause the farm to hold some water after high levels of precipitation.

Mound selection and collection of termites:

I sampled mounds in groups of six mounds, and each such group is henceforth referred to as a cluster. Each cluster was selected based on a stratified random design but constrained to areas with visibly dense mound population. Clusters were selected so that the sample areas did not overlap. There were eight clusters selected to sample variation in aggression across a small distance scale (i.e. within 500 meters, close distance clusters 1-8). For each of the eight close clusters a sample of six mounds was selected as follows: a central mound was chosen at random and the other mounds were chosen by taking the closest mound within distance categories: the closest mound within 20m; closest between 20-40m; closest between 40-80m, closest between 80-150m, closest mound after 150m. The minimum distance between two mounds was 5m and the maximum distance was 340m. One cluster was selected to sample variation across a large distance scale (2-6 km, far distance cluster 9). The large distance scale consisted of four mounds selected to represent a reference point for extrapolation of social structure over the scale of the entire farm. These four mounds came from the opposite points of the farm (North, East, South and West) and were separated by distances ranging from 2000 to 5500m (Fig 2.2).

Each mound was partially dug up, taking a section of the above ground portion large enough to fill a 25l container 5cm below the rim. Each section contained a large number of workers and soldiers. These plastic containers were then transported to an indoor laboratory, where they were left to settle for at least 12 hours before any tests were performed.

Aggression tests:

There are multiple ways to evaluate the extent of a colony, for instance by using genetic markers (Queller and Goodnight 1989; Thompson & Herbert 1998; Pirk *et al*. 2001; Vargo 2003), by radioactive isotope labelling (Suárez & Thorne 1999; Adam *et al*. 2008), by following foraging tunnels between mounds, and by conducting aggression tests (Nel 1968; Pirk *et al*. 2001; Suárez *et al*. 2002). Aggression tests rely on individuals showing increased aggression to non-colony members compared to colony members. They have been used on ants (Morel *et al*. 1990; Gordon & Kulig 1996; Beye *et al*. 1998, Stuart & Herbers 2000; Wagner *et al*. 2000; Pirk *et al*. 2001; Suárez *et al*. 2002; Chapuisat *et al*. 2005; Buczkowski 2012; Tindo *et al*. 2012), bees (Kukuk *et al*. 1977), wasps (Singer & Espelie 1992) and a few termite species (Nel 1968; Levings & Adams 1984; Binder 1987; Adams 1991; Polizzi & Forshler 1998). These studies have shown highly variable levels in the aggression of different species, where some could be categorised into a few different levels whereas others seemed to have an all or nothing response in a fight situation.

I recorded aggression tests by introducing soldiers from different mounds to each other in arena where interactions could be recorded. The arenas were small, round plastic containers 5cm deep (25ml) and provided no grip for the termites, to prevent them from climbing out. Each interaction test consisted of a piece of mound (~14cm^3) covered in soldiers and a single introduced termite from a different mound. The introduced termite was identified by a dot of yellow paint on the front of the head. Termites from all mounds were tested reciprocally against each other. Each mound was represented by 10 individual intruders, and no intruder was used twice. Termites introduced back into the incipient colony were used as a control. The interactions were recorded with a Sony CamCorder on a tripod for five minutes to allow sufficient time for interactions. If no contact was made between the intruder and any other termite after three minutes it was recorded as no interaction occurring.

The videos of the interactions were observed for behavioural studies using VLC 2.0. VLC is a free and open source multi-media player that is made by the VideoLAN Organisaiton. The behavioural description given below for the aggressive interactions and in Appendix A have never been published for this species, for this reason I include the information here for future studies on behavioural aspects of this and other species. *T. trinervoides* has nasute soldiers, which have an elongated rostrum with an enlarged frontal gland which gives the head a pointed shape (Prestwich 1979). The nasute soldiers use the production of a sticky, pungent fluid ejaculated from the frontal gland as a form of colony defence (Nel 1968; Prestwich *et al*. 1976; Richardson & Levitan 1994). Aggression was therefore observed as a visible event of terpene production (Nel 1968; Richardson & Levitan 1994), or when the behaviour typically associated with terpene production was observed. The typical behaviour of terpene production was classified as a termite facing the general direction of the "intruder" from a stand still position making a sudden downward drop of the head while simultaneously moving the entire body backwards without moving the feet. The downward drop of the head may or may not be accompanied by a side-to-side movement of the head. The event of an aggressive action towards another termite was recorded regardless of the size of the terpene drop produced. This method was used because in the videos you cannot always see the visible production of terpenes even if they were produced. The number of aggressive interactions towards the "intruder" was recorded for each video and used for analyses. For further behavioural descriptions see Appendix A.

I performed a pilot study prior to this to test the effects of the mound soil, paint, natural and artificial light on the behaviour of the termites. From this brief pilot study I did not notice that the paint had any noticeable effect on termite behaviour. However I noticed changes when working at night under artificial light conditions. Using this I only performed the behavioural tests during the day. The absence of mound soil and crumbling the mound soil for an even surface also made a noticeable change in the behaviour. For this reason unmodified pieces of the mound soil was included when performing behavioural tests. Additionally if the paint was affecting the behaviour this would be visible in the controls. This is why the results were compared to the controls and not to absolute zero.

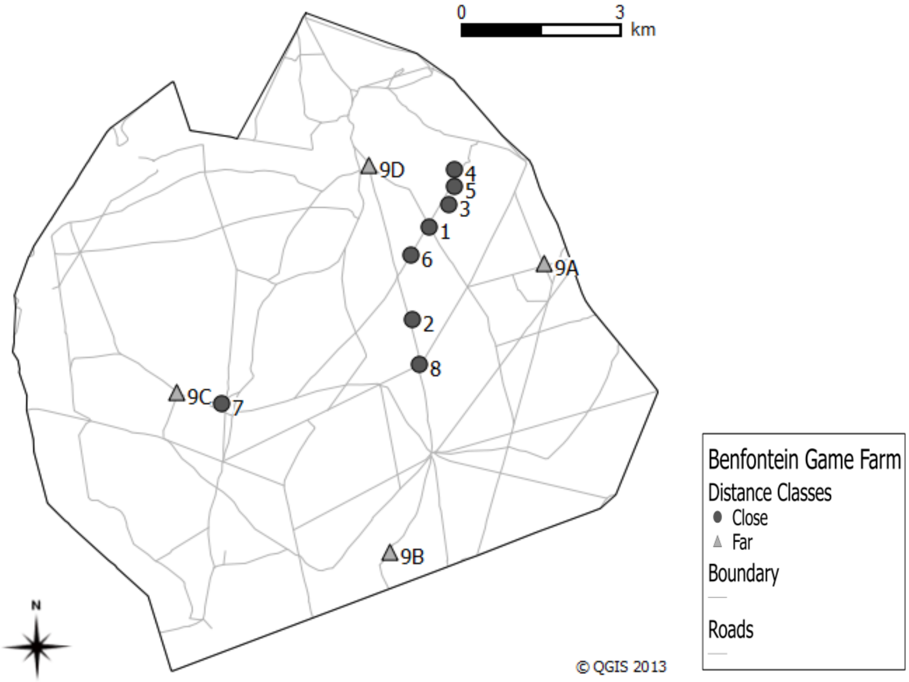


Fig. 2.2. The map of Benfontein Game Farm representing the eight clusters done on a small scale (Close-dots) numbered 1-8, and the one cluster done on a large scale (Far-triangle) numbered 9. Each one of the round dots from 1-8 represent an area from where six mounds were sampled.

Data analysis:

The data were grouped according to the distance classes, where the controls were in the same distance class, all reciprocal mound tests within 500m in the close distance class and the mound tests over 2000m in the far distance class. I used a generalized mixed linear model fitted with a Laplace approximation, with a Poisson error distribution and a log link function to evaluate the effect of distance class on aggression levels, defined as the number of aggression events. Tukey contrasts were used to compare the effects between the close and far distance classes relative to the controls, and secondly the close and far distance classes were compared to each other. Results reported are given with adjusted p-values. I similarly evaluated the effect of distance between mounds on aggression within the close distance class using a generalized mixed linear model, with a Poisson error distribution and a log link. In this model, I used the raw pair-wise distances between mounds as a continuous fixed effect predictor and aggression levels as defined above as the response variable. In both models I fitted the identity of the home and intruder mound each nested within the sample cluster as a random effect structure. Data were analysed using R v2.15.1 (http://www.r-project.com), using lme4 package v0.999999-0 (Bates *et al*. 2012) and post-hoc tests were done using multcomp package v1.2-15 (Horthorn *et al.* 2013).

Results:

A total of 2918 tests were performed. There was a significant effect of distance class on aggression levels (χ^2=4191.5,df=2 p<0.001), with aggression levels being higher between termites from mounds in the close (z=44.454, p<0.001) and far (z=16.182, p<0.001) distance class compared to termites from the same mound (Fig. 2.3). However, there were no significant difference in aggression levels between termites from mounds in the close and far distance class (z=-1.793, p=0.157). Within mounds from the close distance class (i.e. mounds within 500 meters apart), there was a weak but significant negative relationship between the distance between mounds and aggression levels (β=-8.959x10-4, z=-6.745, p<0.001) (Fig. 2.4).

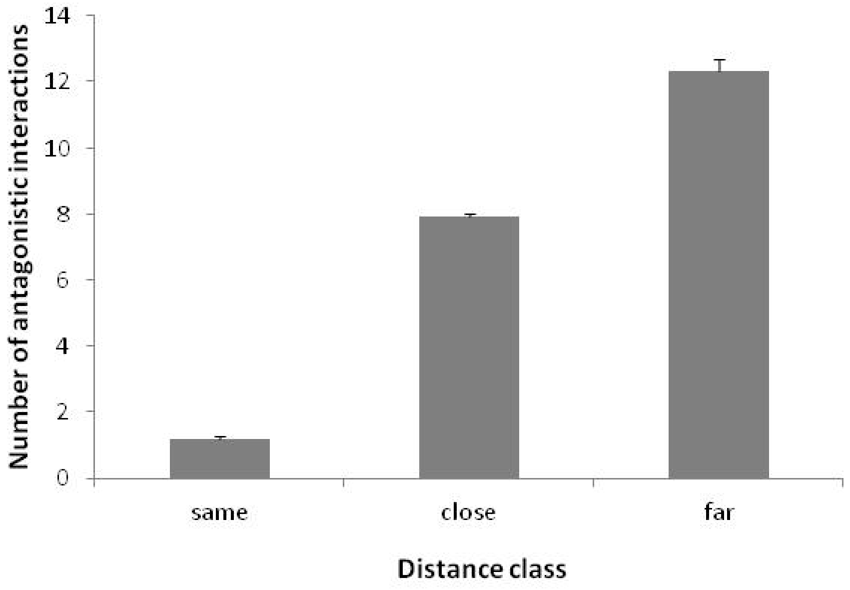


Fig. 2.3. Mean number of antagonistic interactions (±S.E.), recorded as terpene production or the behaviour associated therewith, between *T. trinervoides* individuals from the same mound (same), mounds within 500m apart (close) and mounds between 2000-5500m apart (far). The data represented in the Same and Close distance class represent the mean aggression within a

cluster averaged over the eight clusters. Data represented in the Far group is the average between mound pairs of a single cluster. The error bars show the average standard error for each cluster averaged for each distance class. Aggression levels in the Close (z=44.454, p<0.001) and Far (z=16.182, p<0.001) distance class were significantly higher than Same distance class. However there was no significant difference between Close and Far distance classes (z=-1.793, p=0.157).

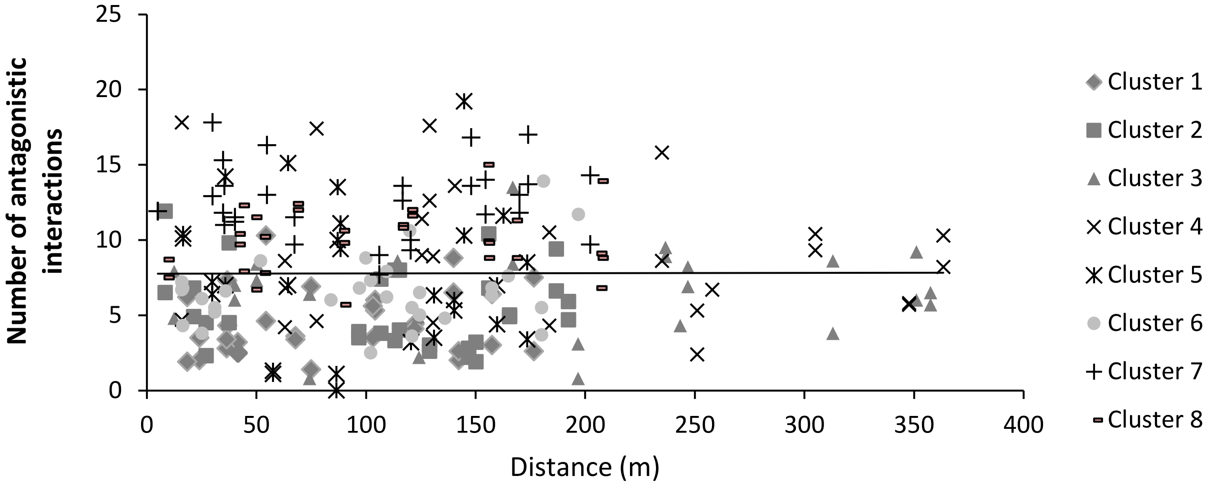


Fig. 2.4. The effect of distance between mounds on the mean number of antagonistic interactions, recorded as terpene production or the behaviour associated therewith, between *T. trinervoides* individuals from mounds within 500m apart. Each data point represents the mean aggression of individuals for each pairwise comparison. The fitted line shows a significant but weak negative relation (β=-8.959x10-4, z=-6.745, p<0.001) between mounds over distance.

Discussion:

In this study there was a clear and significant increase in aggression between the control group and the remainder of the pair wise mound comparisons. The distances between these pair wise comparisons were as small as 5m and as great as 340m, and the aggression was significantly lower in the controls than the close by neighbours. These results suggest that a colony only occupies one mound, and support Adam *et al.* (2008) who treated a few selected colonies with radioactive isotopes (^{131}I). Sands (1961) stated that termite social structure is a response to environmental requirements. In West Africa there are five *Trinervitermes* species co-occurring and as a result there are various social structures present. *T. carbonarius* is monodomous and shows preference for moister climates, where mounds are larger than in drier areas. *T. ebenerianus* is facultative polydomous and sometimes shares mounds with other *Trinervitermes*. spp. in the area. *T. oeconomus* and *T. auriterrae* show no evidence for grass storage in mounds and are often found cohabitating with other termite species. *T. suspensus* prefer to occupy abandoned mounds, and are known to store substantial amounts of grass therein. *T. geminatus* is a polydomous species, building low domed mounds, in a high rainfall area in West Africa (Ohiagu & Wood 1976). Harris (1956) showed that *Macrotermes* are monodomous, but the mound shape changed with changing environmental conditions within each species.. Very little information is available about *T. trinervoides*, and comparing these results within the genus where aggression tests have been used show that there is variation in social structure throughout the genus. These results also show that aggression tests can be used as a standalone method, especially in restricted budget projects.

There was no significant difference in the aggression levels between the close and far pair wise comparisons. This result suggests that non-nestmates receive the same levels of aggression throughout the population, irrespective of the physical distances between colonies. Very little information is available about the flight distances of any termite alates, but they are known throughout to be very weak flyers. The poor dispersal ability of these reproductives may cause a genetic substructure in the population. The poor dispersal would cause nearby colonies to have a large amount of genetic similarity, with distant mounds to have the least genetic similarity. The process used for cue recognition is either common label acceptance or foreign label rejection. Common label acceptance means that any similarity in a cue would lead to acceptance. Foreign label rejection means that any dissimilarity in a cue would lead to rejection (Pirk *et al*. 2001). If the common label acceptance process was used there would have to be sufficient heterogeneity in environment or genetic based cues to separate colonies within a space of 5m. Due to a potential low rate in genetic change over this distance, with common label acceptance in use lower levels of aggression would be displayed to more genetically similar individuals. However the aggression levels are the same over these distances, showing evidence for foreign label rejection process.

The aggression on a small scale shows the highest level of aggression between neighbouring mounds. The foraging territories of neighbouring colonies may greatly overlap (Adam *et al*. 2008). The weak, but significant, decrease in aggression levels over distance suggests that aggression levels may be influenced by foraging competition. *T. trinervoides* does not cut standing but recumbent grass (Adam *et al*. 2008) and is thus dependent on other herbivores, such as ungulates, to provide them with food. Coupled with the large sizes of colonies, up to thousands of individuals per colony, and the often small distances between colonies, down to as little as 5m, a high level of resource competition between neighbouring colonies could be expected. Aggressive interactions are energetically costly to individuals as well as to the colony (Marler & Moore 1989). Increased interactions with other colonies would result in increased aggressive interactions and decreased foraging time. Colonies lose thousands of workers and soldiers during these interactions (Levings & Adams 1984). With decreased demographics and reduced resource intake a colony will be weakened. This may cause a population to self destruct, however behavioural adaptations have shown colonies to actively avoid one another to prevent such mortalities (Nel 1968).

I did not find any evidence in this population to support “The Dear Enemy Phenomenon”, with reduced aggression towards recognised close neighbours and increased aggression towards individuals from further areas (Fisher 1954 taken from Rosell & Bjørkøyli 2002; Temles 1994). The only encounters two colonies have with each other in this species are during foraging and alate dispersal. A display of aggression during foraging would be expected more than aggression during alate dispersal when reproductives are in search of a counterpart with different genetics. The “Dear Enemy Phenomenon” is thought to have been recorded in many eusocial ant species where foraging areas greatly overlap (Heinze *et al*.

1996; Langen *et al*. 2000). However there were too many unknown contributors in these studies towards nestmate recognition to confirm the presence of the "Dear Enemy Phenomenon".

Our results suggest that this species uses the foreign label rejection process for nestmate recognition. This is the process of recognition used in social structures whereby a single common and unique cue is used to distinguish nestmates from non-nestmates and rejection of non-nestmates is based on any dissimilarity from this cue. This makes it harder for non-nestmates, even if they share genetic similarities, to join the colony. This also provides the colony with great resistance to social parasites. Many studies (e.g. Beye *et al*. 1998; Breed *et al*. 1988; Stuart 1988; Liang & Silverman 2000; Wagner *et al*. 2000; Pirk *et al*. 2001) have focused on the basis for recognition (genetics, environment or cuticle hydrocarbons) and not on the process.

Conclusion:

Our results strongly suggest that each mound is a colony. Over a spatial scale of kilometres there was no significant increase in aggression over distance, suggesting population structure may be uniform across this spatial scale. There was a weak but negative relationship between aggression and distance over the scale of a few hundred metres, suggesting that resource competition may be an important factor in determining aggression levels between neighbours.

References:

Adam, R.A., Mitchell, J.D. & van der Westhuizen, M.C. 2008: Aspects of foraging in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt) (Termitidae: Nasutitermitinae). African Entomology **16**, 153-161.

Adams, E.S. 1991: Nest-mate recognition based on heritable odors in the termite Microcerotermes arboreus. PNAS. USA. **88**, 2031-2034.

Bates, D., Meachler, M., & Bolker, B. 2012: Linear Mixed-Effects Models Using S4 classes; lme4 package for R. URL: http://lme4.r-forge.r-project.org/.

Beye M., Neumann P., Chapuisat M., Pamilo P. & Moritz R.F.A. 1998: Nestmate recognition and the genetic relatedness of nests in the ant *Formica pratensis*. Behavioural Ecology and Sociobiology **43**, 67-72.

Binder, B.F. 1987: Intercolonial aggression in the subterranean termite *Heterotermes aureus* (Isoptera: Rhinotermitidae). Psyche **95**, 123-137.

Breed, M.D., Williams, C.R. & Fewell, J.H. 1988: Comb wax mediates the acquisition of nest-mate recognition cues in honey bees. PNAS, USA **85**, 8766-8769.

Buczkowski, G. 2012: Colony spatial structure in polydomous ants: complimentary approaches reveal different patterns. Insectes Sociaux **59**, 241-250.

Chapuisat, M., Bernasconi, C., Hoehn, S. & Reuter, M. 2005: Nestmate recognition in the unicolonial ant Formica paralugubris. Behaviuoral Ecology **16**, 15-19.

D'Ettorre, P. & Heinze, J. 2001: Sociobiology of slave-making ants. Acta Ethologica **3**, 67-82.

Dean, W.R.J. & MacDonald, I.A.W. 1994: Historical changes in stocking rates of domestic livestock as a measure of semi-arid and arid rangeland degradation in the Cape Province, South Africa. Journal of Arid Environments **26**, 281-298.

Flanagan, T.P., Letendre, K., Burnside, W.R., Fricke, G.M. & Moses, M.E. 2012: Quantifying the effect of colony size and food distribution on harvester ant foraging. PloS ONE doi: 10.1371/journal.pone.0039427.

Gordon M.G. & Kulig A.W. 1996: Founding, Foraging, and Fighting: Colony size and the spatial distribution of harvester ant nests. Ecology **77**, 2393-2409.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. 1960: Community structure, population control and competition. American Naturalist 94, 421-425

Harris W.V. 1956: Termite Mound Building. Insectes Sociaux **3**, 261-268.

Heinze J., Foitzik S., Hippert A. & Hölldobler B. 1996: Apparent Dear-Enemy Phenomenon and environment-based recognition cues in the ant *Leptothorax nylanderi*. Ethology **102**, 510-522.

Holling, C.S. 1956: The components of predation as revealed by a study of small mammal predation on the European pine sawfly. Can. Entomology **91**, 293-320.

Holway, D.A. & Case, T.J. 2000: Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. Animal Behaviour **59**, 433-441.

Horthorn, T., Bretz, F., Westfal, P., Heiberger, R.M. & Schuetzenmeister, A. 2013: Simultaneous Inference in General Parametric Models; multcomp package for R. URL: http://www.crcpress.com/product/isbn/9781584885740

Husak J.F. & Fox S.F. 2002: Adult male collard lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. Animal Behaviour **65**, 391-396.

Inward, D., Beccaloni, G. & Eggleton, P. 2007: Death of an order: a comprehensive molecular phylogenetic study confirms that termites are eusocial cockroaches. Biology Letters **3**, 331-335.

Korb J. & Linsenmair K.E. 2000: Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? Insectes Sociaux **47**, 357-363.

Kukuk, P.F., Breed M.D., Sobti, A. & Bell, W.J. 1977: The contributions of kinship and conditioning to nest recognition and colony member recognition in a primitively eusocial bee, *Lasioglossum zephyrum* (Hymenoptera: Halictidae). Behavioural Ecology and Sociobiology **2**, 319-327.

Langen T.A., Tripet, F. & Nonacs, P. 2000: The red and the black: habituation and the dear-enemy phenomenon in two desert *Pheidole* ants. Behavioural Ecology and Sociobiology. **48**, 285-292.

Levings, S.C. & Adams, E.S. 1984: Intra- and interspecific territoriality in *Nasutitermes* (Isoptera: Termitidae) in a Panamanian mangrove forest. journal of Animal Ecology **53**, 705-714.

Liang D. & Silverman J. 2000: “You are what you eat”: Diet modifies cuticular hydrocarbons and nestmate recognition in the Argentine ant, *Linepithema humile*. Naturwissenschaften **87**, 412-416.

Lin, N. & Michener, C.D. 1972: Evolution of Sociality in Insects. The Quarterly Review of Biology **47**, 131-159.

Marler, C.A. & Moore, M.C. 1989: Time and energy costs of aggression in testosterone-implanted free-living male mountain spiny lizards (*Sceloporus jarrovi*). Physiological Zoology **62**, 1334-1350.

Michener, C.D. 1969: Comparative social behaviour of bees. Annual Review of Entomology **14**, 299-342.

Miura, T. 2001: Morphogenesis and gene expression in the soldier-caste differentiation of termites. Insectes Sociaux **48**, 216-223.

Miura, T. 2004: Proximate mechanisms and evolution of caste polyphenism in social insects: From sociality to genes. Ecological Research **19**, 141-148.

Morel, L. Vander Meer, R.K. & Lofgren, C.S. 1990: Comparison of nestmate recognition between monogyne and polygyne populations of *Solenopsis invicta* (Hymenoptera: Formicidae). Ann. Entomol. Soc. Am. **83**, 642-647.

Morris, D. 2013: Proposed Blackwood Solar Energy Facility on Portion 1 of Padamsfontein 1593, south east of Kimberley, in the Tokologo Local Municipality, Free State: Scoping Phase heritage input. McGregor Museum, Department of Archaeology, accessed online at: http://savannahsa.com/documents/5525/Appendix%20G%20-%20Heritage%20scoping%20report.pdf on 2013-11-13 12:52pm

Nel J.J.C. 1968: Aggressive behaviour of the harvester termites *Hodotermes mossambicus* and *Trinervitermes trinervoides* (Sjöstedt). Insectes Sociaux **15**, 145-156.

Noirot, C., 1985. The caste system in higher termites. In: Caste Differentiation in Social Insects (J.A.L. Watson, B.M. Okot-Kotber and C. Noirot, eds.), Pergamon Press, New York. pp. 75–86.

Nowak, M.A., Tarnita, C.E. & Wilson E.O. 2010: The evolution of eusociality. Nature **466**, 1057-1062.

Ohiagu, C.E. & Wood, T.G. 1976: A Method for measuring rate of grass-harvesting by *Trinervitermes geminatus* (Wasmann) (Isoptera, Nasutitermitinae) and observation on its foraging behaviour in Southern Guinea Savanna, Nigeria. Journal of Applied Ecology **13**, 705-713.

Pirk, C.W.W., Neuman, P., Moritz, R.F.A. & Pamilo, P. 2001: Intranest relatedness and nestmate recognition in the meadow ant *Formica pratensis* (R.). Behavioural Ecology and Sociobiology. **49**, 366-374.

Polizzi, J.M. & Forschler, B.T. 1998: Intra- and interspecific agonism in *Reticulitermes flavipes* (Kollar) and *R. virginicus* (Banks) and effects of arena and group size in laboratory assays. Insectes Sociaux **45**, 43-49.

Prestwich G.D. 1979: Chemical defence by termite soldiers. Journal of Chemical Ecology **5**, 459-480.

Prestwich G.D., Tanis S.P., Pilkiewicz F.G., Miura I. & Nakanishi K. 1976: Nasute Termite Soldier Frontal Gland Secretions. 2. Structures of Trinervitene Congeners from *Trinervitermes* Soldiers. Journal of the American Chemical Society **98**, 6062-6064.

Queller, D.C. & Goodnight, K.F. 1989: Estimating Relatedness Using Genetic Markers. Evolution **43**, 258-275.

Queller, D.C. & Strassmann, J.E. 1998: Kin Selection and Social Insects. BioSciences **48**, 165-175.

R Core Team. 2013: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Richardson, P.K.R. & Levitan, C.D. 1994: Tolerance of aardwolves to defence secretions of *Trinervitermes trinervoides*. Journal of Mammalogy **75**, 84-91.

Rosell, F. & Bjørkøyli, T. 2002: A test of the dear enemy phenomenon in the Eurasian beaver. Animal Behaviour **63**, 1073-1078.

Sands, W.A. 1961: Foraging behaviour and feeding habits in five species of *Trinervitermes* in West Africa. Entomolgia Experimentalis et Applicata **4**, 277-288.

Scholtz, C.H. & Holm, E. 1985: Insects of Southern Africa. Butterworth Publishers (PTY) LTD, Durban, South Africa.

Singer, T.L. & Espelie, K.E. 1992: Social wasps use nest paper hydrocarbons for nestmate recognition. Animal Behaviour **44**, 63-68.

Smith F.R. & Yeaton R.I. 1998: Disturbance by the mound-building termite, *Trinervitermes* trinervoides, and vegetation patch dynamics in a semi-arid, Southern African grassland. Plant Ecology **137**, 41-53.

Stuart R.J. 1988: Collective cues as a basis for nestmate recognition in polygynous leptothoracine ants. Proceedings of the Natural Academy of Sciences, USA **85**, 4572-4575.

Stuart, R.J. & Herbers, J.M. 2000: Nest mate recognition in ants with complex colonies: within and between-population variation. Behavioural Ecology **11**, 676-685.

Suarez, A.V., Holway, D.A., Liang, D., Tsutsui, N.D. & Case, T.J. 2002: Spatiotemporal patterns of intraspecific aggression in the invasive Argentine ant. Animal Behaviour **64**, 697-708.

Suárez, M.E. & Thorne, B.L. 1999: Rate, amount, and distribution pattern of alimentary fluid transfer via trophallaxis in three species of termites (Isoptera: Rhinotermitidae, Termopsidae). Annals of the Entomological Society of America **93**, 145-155.

Temles, E.J. 1994: The role of neighbours in territorial systems: when are they ‘dear enemies’? Animal Behaviour **47**, 339-350.

Thompson, G.J. & Herbert, P.D.N. 1998: Population genetic structure of the Neotropical termite *Nasutitermes nigriceps* (Isoptera: Termitidae). Heredity **80**, 48-55.

Tindo, M., Mbenoun Masse, P.S., Kenne, M., Mony, R., Orivel, J., Doumtsop Fotio, A., Fotso Kuaté, A., Dijiéto-Lordon, C., Fomena, A., Estoup, A., Dejean, A. & Foucaud, J. 2012: Current distribution and population dynamics of the little fire ant supercolony in Cameroon. Insectes Sociaux **59**, 175-182.

van Wilgenburg, E. & Elgar, M.A. 2007: Colony structure and spatial distribution of food resources in the polydomous meat ant Iridomyrmex purpureus. Insectes Sociaux **54**, 5-10.

Vargo, E.L. 2003: Hierarchical analysis of colony and populaiton genetic structure of the eastern subterranean termite, *Reticulitermes flavipes*, using two classes of molecular markers. Evolution **57**, 2805-2818.

VLC media player. URL: http://www.videolan.org/vlc/index.html

Wagner, D., Tissot M., Cuevas W. & Gordon D.M. 2000: Harvester ants utilise cuticular hydrocarbons in nestmate recognition. Journal of Chemical Ecology **26**, 2245-2257.

Wilson, E.O. 1971: The Insect Societies. Harvard University Press, Cambridge.

Wilson, E.O. 1976: A social ethogram of the neotropical arboreal ant *Zacryptocerus varians* (Fr. Smith). Animal Behaviour **24**, 354-363.

Appendix A

This is the first full behavioural description given for this species. This provides insight into the behaviour outside of aggression and can be used to further understand the social structure of this species and can also be used for comparison with other species to provide insight into the evolution of social structures in insects. The shaking behaviour observed by *T. trinervoides* soldiers had an unknown cause, this behaviour has only been published once in regard to ants by Wilson (1976).

Behavioural descriptions:

Standing: A termite is not moving any of its legs at all, when the movement of the legs does not cause the termite to move more than a body length in any direction, or if the movement of the termite did not last longer than 3 seconds continuously (see micro movements).

Walking: A termite walks in any direction for more than 3 seconds uninterrupted. A 3 second margin was used because of the large number of micro movements made by a termite.

Micro movements: A termite places one of its legs forward, leans on that leg and then moves back to its original position, or readjust its footing, or turns slightly, these movements only last a fraction of a second, and may occur for any amount of time, but do not lead to the vector movement of the termite in any direction in that space of time. When a walking termite stops and performs any of these micro movements it interrupts the walking action, so only once a termite has been walking for 3 seconds was it recorded as walking.

One-way antennating: A termite makes contact with any part other than the antennae of another termite using its antennae.

Reciprocal antennating: A termite makes contact with the antennae of another termite using its own antennae.

Soldier Aggression/ terpene production: The typical behaviour of terpene production was classified as a soldier facing the general direction of the “intruder” from a stand still position making a sudden downward drop of the head while simultaneously moving the entire body backwards without moving the feet. The downward drop of the head may or may not be accompanied by a side-to-side movement of the head as well. The event of an aggressive action towards another termite was recorded regardless of the size of the terpene drop produced.

Misfire: The action of terpene production may occur without the production /ejaculation of the terpenes. This was a regular occurrence and was also seen as aggression towards a termite.

Worker Aggression: Workers of this genus still have strong mandibles used for cutting grass. Workers attacking intruder soldiers aim for the soft exoskeleton just behind the head, once this has been reached by the worker the soldier is easily decapitated since the workers are often larger than the soldiers.

One-on One : A single termite approaches the “intruder” and it will either first make antennal contact with it before ejaculating terpenes over it, or it will immediately ejaculate terpenes over it without prior antennal contact. The intruder may reciprocate with terpene ejaculation towards the aggressor.

Group Attack: A single “intruder” may at any point be surrounded by multiple termites. All or some of these may ejaculate terpenes onto the “intruder”. The terpene ejaculation is not very accurate and in this case will often end up covering a fellow nestmate as well as the “intruder”. The group is a fluid structure with termites joining and leaving at any time. Some of the termites make antennal contact with a group member when joining the group and it may/ may not join the attack. The group structure did not appear to have any effect on the movement of the “intruder”.

Chasing: The “intruder” will move away from the defender and the other termites will follow and continue the attack. This could end at any moment and is not delimited by the amount of terpene present on the termite or the moving ability.

Shaking: A termite soldier in a standing position shakes its body vigorously along the anterior-posterior axis. This action was observed both in the field and in the lab and did not immediately appear to attract any attention from other termites. Wilson (1976) observed that in *Zacryptocerus varians*, ‘turtle ants’, the workers would jitter, moving the thorax up and down rapidly by pumping their legs. The methods used here were not sufficient to determine the exact purpose of this shaking behaviour.

On Back: When a termite is upside down the majority of the ventral surface is visible and it requires the use of another object, termite, or uneven surface to return to the upright position again. Most commonly in situations when termites are upside down they kick their legs vigorously in the air with one leg being held flat against the surface in an attempt to get back over.

Helping: A termite assists another termite from being in the upside position to the upright position again. Helping behaviour was observed between kin and non-kin alike and there were also observations of co-incidental helping between non-kin. A termite moving past another termite, on its back, in close proximity, would tolerate the other termite making use of a nearby limb as leverage to turn itself over again. However when the termite on its back is covered in terpenes and makes use of this passer-by they would often end up getting entangled due to the sticky nature of the terpenes (see sticky ball).

A sticky ball: An “intruder” on its back would make use of any termite passing by to help itself over. The “intruder” would usually be covered in terpenes and thus become stuck to the helper. A nearby nestmate would then ejaculate terpenes on the entangled termites, as they stumbled around, thereby entangling more nestmates and subsequently making a large ball of entangled termites. In the lab this resulted in several termites losing limbs and others dying of exhaustion.

Chapter III:

Spatial and temporal variation in aardvark (*Orycteropus afer*) (Pallas) (Tubulidentata:Orycteropodidae) predation on the mounds of the harvester termite, *T. trinervoides,* (Sjöstedt) (Isoptera:Termitidae).

This chapter is intended to be submitted to Ethology and therefore was formatted according to Ethology author guidelines

Abstract:

In the harsh semi-arid climate of southern Africa dietary resources are strongly correlated with the seasons. Myrmecophages are dependent on ants and termites for dietary proteins, fat and water. Ants and termites are vital in these habitats for nutrient cycling, such as the harvester termite *Trinervitermes trinervoides*. There are a number of mammalian myrmecophages that predate on *T. trinervoides*. The aardvark, *Orycteropus afer*, is the only one capable of digging into the mound, exposing the entire colony to external environmental conditions and secondary predation. Predation events on *T. trinervoides* mounds have an effect on colony and population structure. In this study the predation frequency and severity were quantified between the seasons and habitats. The direction from which aardvark attacks were based was also quantified. There was a seasonal difference in the rate of predation on the mounds. The rate of predation did not differ between the habitats. The severity of attacks did not change significantly over the seasons or habitats. The attack direction did not deviate from uniform over the seasons or habitats. The aardvark is an influential predator of *T. trinervoides*. In the wet season predation is higher due to the reduced energy costs of digging into the mound. In the dry season the mounds are hard and animals are in energy deficit and more energy is required to dig into the mounds in the dry season compared to the wet season. This study provides quantitative data that is missing for future studies on the influence of aardvark predation on the persistence of a termite colony, the influence of secondary predation on a colony, and the implications of these factors on the social structure of *T. trinervoides*.

Introduction:

In an ecosystem there are interactions between organisms, such as predators and prey, and these interactions have implications on other organisms in the ecosystem (Jones *et al*. 1994; Schmitz *et al*. 1997; Schmitz & Suttle 2001). Keystone species activity has a disproportionate effect on the distribution patterns, stability and integrity of a community through time relevant to their biomass in the system (Paine 1969a; Bond 1993). Species that have a large influence on an ecosystem through their biomass or abundance are known as dominant species (Steneck 2005). In many ecosystems it is evident that some species are more important than others in shaping the ecosystem, whether it is quantitatively or qualitatively (Dalerum *et al*. 2012; Dalerum 2013). In southern Africa the importance of many species to the functioning of its ecosystem is unknown. With little information published about the ecosystem functions in this area, to develop these links, I start by looking at some of the aspects of aardvark predation on termite mounds.

Insects play a significant role within many ecosystems (Swank *et al*. 1981; Rosenberg *et al*. 1986; Losey & Vaughan 2006), especially social insects like ants or termites that may become more abundant than any other species, leading them to dominate a particular habitat (Eggleton *et al*. 1995; Plowes *et al*. 2007). Termites are ecologically important species to an ecosystem since they recycle nutrients transforming previously unavailable minerals into important nutrients that plants and animals are able to assimilate (Coventry *et al*. 1988; Dangerfield *et al*. 1998). Termites mostly feed on dead plant matter, converting things like dead trees, undigested grass in faeces or other indigestible fibres into compounds that can be used by surrounding living organisms in various ways (Scholtz & Holm 1985). The Macrotermitinae (Termitidae) convert vegetation by growing fungus on the harvested material (Scholtz & Holm 1985). This is then used in two different ways; the fungus provides nutrients for the soil and thus vegetation, and the fungus is consumed by the termites providing them with proteins (Fittkau & Klinge 1973). All other termites eat plant matter, and digestion of cellulose occurs with the aid of intestinal symbionts, except in Termitidae (Scholtz & Holm 1985). Termitidae, such as *Trinervitermes trinervoides*, are capable of producing their own cellulase enzymes allowing digestion of plant cellulose without the aid of intestinal symbionts (Potts & Hewitt 1973; Scholtz & Holm 1985; Slaytor 1992), *T. trinervoides* feed on grass that is left behind after ungulate feeding, which eliminates resource competition between them and ungulates. By feeding on this grass *T. trinervoides* convert an inaccessible resource into proteins and minerals. These minerals return nutrients back into the soil for plant assimilation (Brossard *et al*. 2007), where the termites will provide dietary proteins for many insectivores (Redford & Dorea 1984).

In semi-arid ecosystems such as those found in southern Africa, rain, temperature extremes and nutrition are major driving factors behind ecosystem functions (Western 1975; Brouwer *et al*. 1993; Lima *et al*. 2002). Moderate to low rainfall in summer months provide enough water for plant growth and some perennial lake formation (Brouwer *et al*. 1993). Day time temperatures in summer may exceed 40°C (South African Weather Service), resulting in the majority of small mammals, predators and some insects being nocturnal. In winter the water sources often dry up, vegetation dies back and night time temperatures often fall below zero (South African Weather Service). The majority of insects at this time will hibernate within their nests, often below ground. Nocturnal feeders may even shift to crepuscular or even diurnal feeding patterns to avoid leaving dens at night when it is coldest. In the dry, cold winter months (3 months) with limited resources animals are in energy deficit and lose a large portion of body fat (Torbit *et al*. 1985). Animals rely on the few resources available to them and may also resort to a seasonal shift in diet (Williams *et al*. 1997, Taylor *et al*. 2002).

T. trinervoides are social termites that form large colonies. These colonies consists of a king, queen, workers and nasute soldiers and seasonal reproductives (alates; Michener 1969, Scholtz & Holm 1985). In a colony the workers are responsible for feeding all individuals in the colony, maintaining the colony and caring for the brood (Franks 1987). *T. trinervoides* colonies are able to reach population sizes of thousands (Adam 1993). *T. trinervoides* colonies occupy nests in the form of mounds (Scholtz & Holm 1985). Mounds provide defence against predators and an area of food storage thereby allowing social colonies to reach large population sizes. *T. trinervoides* mounds (Fig 3.1) have an above ground portion known as the epigeal portion, with the royal chamber for the king and queen and the brood chamber for the eggs and immatures in the centre of the mound (Scholtz & Holm 1985; Adam 1993). The mound has a hard external shell connected to the centre by a system of galleries. Mounds are constructed by workers using a mixture of saliva and soil, which when dried forms a hard, sturdy structure similar to concrete (Melton 1976). The hard exterior shell provides protection from predators and extreme climatic conditions experienced in southern Africa (Sheppe 1970; Adam 1993). However a mound is easily detected by predators and due to the large number of individuals present in a mound the colony is not able to mobilise to escape predation. *T. trinervoides* have a small body size and individual activity depends on environmental conditions (Casey 1976). A termite mound reduces temperature fluctuations of the internal environment, providing a more stable environment for the brood development and activities within the mound (Adam 1993; Frazier *et al*. 2006). *T. trinervoides* have been suggested to be both monodomous and polydomous (Coaton 1948; Nel & Malan 1974; Adam *et al*. 2008). However, in chapter II I found behavioural support for a monodomous structure in this study area. Therefore, predation events on *T. trinervoides* mounds are likely to have dramatic effects on the termite colonies. The microclimate within the mound may cause an uneven distribution of termites within the mound as they follow the optimum temperature through the mound. Ant and termite species build mounds to allow maximum sun exposure, creating a temperature gradient within the mound (Grigg 1973). These temperature gradients within the mound may cause an uneven distribution of termites within the mound.

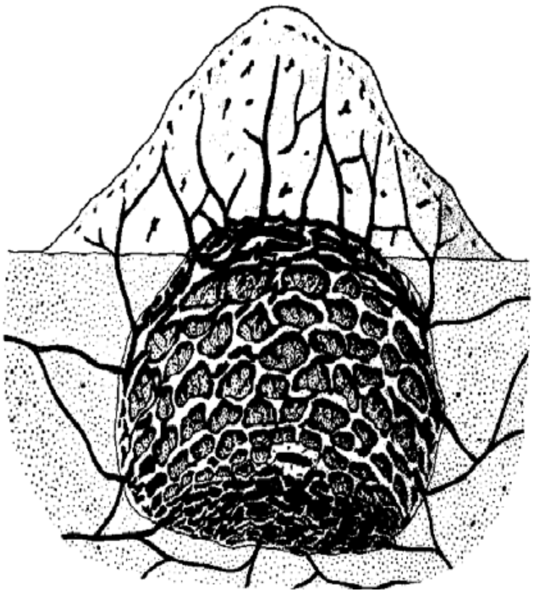


Fig 3.1. A pictoral representation of a termite mound, showing the above ground (epigeal), below ground, central galleries and tunnels. Taken with permission from Scholtz & Holm (1985).

Myrmecophages are animals that consume ants and termites, and are dependent on these insects to provide a portion of necessary dietary proteins and fats (Redford & Dorea 1984; Willis *et al*. 1992). The large population sizes of *T. trinervoides* colonies have allowed three large mammal species to specialize on them as prey despite the small body size of individual termites (Redford & Dorea 1984; Willis *et al*. 1992; Taylor *et al*. 2002); namely the Cape pangolin (*Manis temminckii*, Smuts); the aardwolf, (*Proteles cristata*, Sparrman) and the aardvark (*Orycteropus afer*, Pallas). The Cape pangolin is a weak digger and thus feeds on surface roaming termites (Swart *et al*. 1999). The aardwolf is also a weak digger and feeds mostly on termite foraging parties (Richardson 1987; Taylor & Skinner 2000). The aardvark is the only predator of *T. trinervoides* that is able to dig into the mounds feeding on workers, soldiers, alates and brood/immatures (Melton 1976; Taylor *et al*. 2002). Taylor *et al*. (2002) found that aardvark feed more on *T. trinervoides* in the winter than in the summer. This could be explained by greater food limitation. However the dietary composition of *T. trinervoides* in aardvark diet has been shown to be higher in summer (Willis *et al*. 1992). This could be due to higher seasonal abundances of insects in general or the rain softening the mounds making easier access to the termites.

Aardvark predation events on termite mounds have direct demographic effects on the colonies by removing individuals, and cause structural mound damage with subsequent increased vulnerability to secondary attacks from other opportunistic myrmecophages (Sheppe 1970; Taylor & Skinner 2000) and other insectivores (Taylor & Skinner 2001). These structural damages also expose areas of the mound to external environmental extremes (Melton 1976). When holes are made in the mound the mound is repaired by workers while the soldiers surround them for protection (Harris 1956), unless the damage is severe which may force the colony to move to another mound. The cost between repairing the destroyed mound and moving the entire colony to an empty mound would both be great and heavily dependent on colony strength and the amount of time taken to perform these tasks. Damage to the colony in winter would also expose the colony to severe cold which could kill a large portion of the colony and potentially the queen. If termites move to a new mound they must locate an empty one whilst carrying the queen and brood. Chances of predation during this level of exposure are also high. Although there is some information published about the feeding ecology of the aardvark it is unclear which factors are predicted directly by *T. trinervoides*, for example will the micro-climate in the mound influence termite distribution within the mound to such an extent that it would influence the feeding patterns of the aardvark?

In this study I assessed *T. trinervoides* mounds to determine if there was an effect of season or habitat on aardvark predation risk and predation severity. I also aimed to determine if the micro-climate within the mound would influence the predation habits of the aardvark. *T.*

trinervoides may be a keystone species to this ecosystem. Using these results to determine the effects of predation on the termite population will provide insight to stability of this ecosystem.

Materials and methods:

Study site:

The study was conducted on Benfontein Game farm, an 11, 000ha farm close to Kimberley on the Free State and Northern Cape border in central South Africa (28°50`S, 24°50`E). Benfontein lies within a semi-arid zone (Dean & MacDonald 1994), but due to the presence of landscape structures formed by a prehistoric lake (Morris 2013), the farm holds water in the northern areas after high levels of precipitation. For seasonal comparisons the wet season was defined as September-April and the dry season as May-August. The summer day-time temperatures range between 28-33 °C, and fall to between 10-12 °C in the winter. Rainfall in the wet season ranges from 28-73mm, and 7-8mm in the dry season, with an annual rainfall of 420mm (The South African Weather Service).

Termite mound monitoring:

The study area was classed into four different habitat types; grassland, savannah, shrub and pan. Six sites were designated to each habitat type, and spread evenly throughout the farm. The sites on the farm were chosen using a quasi-random design for a concurrent pit-fall survey. All termite mounds were selected within a 100m radius of each pit-fall site for monitoring, making up in total 183 mounds being monitored. Some sites did not have any living mounds within the 100m radius and were thus not used in this study, which left mounds around a total of 16 sites being monitored (Fig. 3.2). Each mound was tagged by putting a steal ring though it with a label attached and a piece of reflective tape, and its coordinates recorded. The mounds were observed once a month, or as close to this frequency as possible. Because of logistic constraints the time between visits ranged from 4-9 weeks. The pan habitat was badly affected by high levels of rainfall, which made data collection from this habitat impossible for large parts of the study. The pan habitat consisted of 13 mounds at the beginning of the study. Similarly, the savannah habitat was not favoured by the termites so that only a total of seven mounds were monitored in this habitat. This compared to the grassland and shrubland habitats which had 74 and 42 mounds monitored respectively. Sites without active mounds could not be replaced with other sites as there would have been an overlap in sites or sites would have been clustered within a specific area, resulting in uneven data representation.

At the first monitoring event the size and azimuth of existing attack holes were taken along with photographs of each attack hole. The diameter and the height of each mound were also measured. In subsequent monitoring events, the size and azimuth of any new attack holes were recorded. Predation risk for each mound was calculated as the total number of observed predation events divided by the total number of months a mound was observed. Each hole made in an observation mound was counted as a predation event, so if multiple holes were observed in the mound each was recorded and counted as a separate predation event. If the mound was abandoned before the end of the study, the number of observation months was counted until the month in which the mound was observed to no longer be active. This controlled for the fact that the mounds could have died in between observation periods. Predation severity of each mound was calculated by using the perpendicular diameters of the attack holes to calculate the surface area of the hole. The diameter of the mound was used to calculate the spherical surface area of the mound, the value was halved since a mound would represent half a sphere level with the ground. A ratio was then calculated by dividing the surface area of the attack hole by the surface area of the mound.

There was a formation of a lake due to high levels of continuous rainfall from November 2010 up to April 2011. The lake dried up enough for vehicle access in August 2011, after which the study sites were checked following 10 months of inaccessibility. The formation of the lake on the farm resulted in the death of all the termite mounds situated in the pan area (P6 lost 9 of 12 mounds, SH4 lost both mounds, P3 lost the one mound), save the few that were above the water line (P6 F, I, J, L). There were only two out of the six possible sites in the Pan that had living mounds to be observed therefore calculating the variance for this habitat type resulted in high error. The Savannah habitat sites only had seven mounds over two sites (one site had one mound) making data for this habitat type sparse and highly variable and only one predation event occurred in the dry season, the error calculation for this site was also very high (see Addendum). Due to the irregularities the Pan and Shrub data were removed for analyses of microclimate effects.

Data analysis:

Predation risk was analysed using a generalized linear mixed-effects model, with restricted maximum likelihood and binomial error distributions, to evaluate the effects of season on predation risk within the various habitats. In the model I specified habitat and season as fixed effect and mound identity as a random effect structure. Fixed terms were evaluated with sequential likelihood ratio tests. Predation severity was analysed using a logit transformation on the hole:mound ratios as this provides an increase in power and more interpretable results especially when including random effects structure into the model (Warton & Hui 2011). Predation severity was analysed using a linear mixed-effects model, with restricted maximum likelihood. In the model I specified direction, habitat and season as fixed effects and sampling month, mound and site as random effects. Fixed terms were evaluated with conditional F-tests.

The Rayleigh's test was used to test if the azimuth data collected for each predation event deviated from uniform direction within each habitat between the seasons.

Data were analysed using R v3.0.1. (http://www.r-project.org), including the user provided packages lme4 package v0.999999-0 (Bates *et al*. 2012), nlme (Pinheiro *et al*. 2013) and circular (Agostinelli & Lund 2011).

The Addendum shows maps of each site, showing which mounds were predated over the study period of 24 months, showing that some mounds were not predated on at all, while others were predated on, some repeatedly. This helps interpret data showing the non deviation from normality in predation within a site and across habitats.

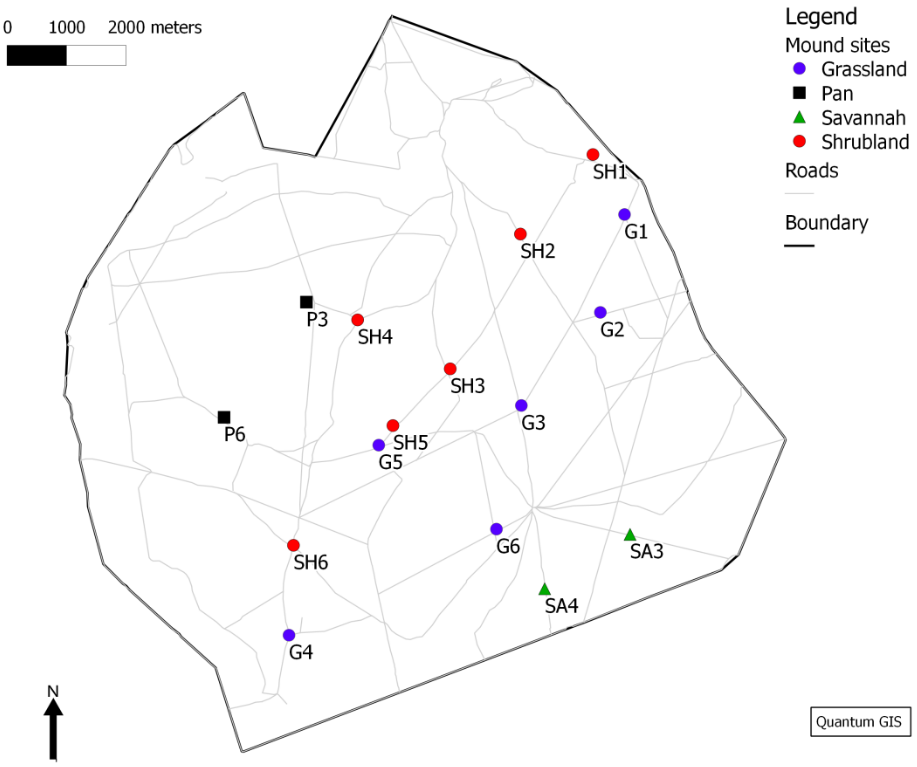


Fig 3.2. The layout of Benfontein Game Farm with the various sites where termite mounds were monitored for the 23 month period. Only the central point is shown for each site, Grassland (G1-6 : mean no. of mounds ±SE; 12.333±1.256), Savannah (SA3-4 : mean no. of mounds ±SE; 1.167±0.980), Shrub (SH1-6 : mean no. of mounds ±SE; 7.50±1.360), Pan (P3-6 : mean no. of mounds ±SE; 2.667±1.978)

Results:

There was a significant effect of season on monthly predation risk (χ^2_1=22.822, p=1.777x10^{-6}), with a higher predation risk during the wet season (Mean=0.061 ± SE=0.007) compared to the dry season (Mean=0.0242 ± SE=0.009; Fig 3.3). There was no significant effect of habitat on monthly predation risk (χ^2_3=4.470, p=0.215) and there was no interaction between habitat and season (χ^2_3=0.528, p=0.913). The grassland habitat had the most predation events with 65 in the wet season and 11 in the dry. The shrub habitat had 25 predation events in the wet season and 4 in the dry season; the pan habitat had 17 predation events in the wet season and 1 in the dry season; and the savannah habitat had 6 predation events in wet season and 1 in the dry season. There was no significant effect of habitat ($F_{2,9}$=0.486 p=0.630), season ($F_{1,25}$=1.177 p=0.288) or attack direction ($F_{7,25}$=0.988 p=0.463), on predation severity. The attack direction of the predation holes showed no deviation from a uniform direction within habitats and within the wet and dry seasons (Table 3.1).

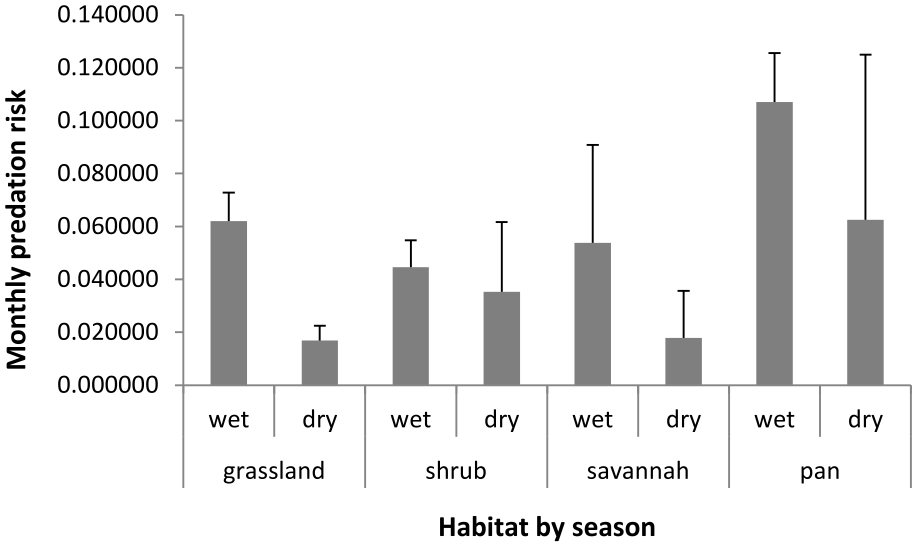


Fig. 3.3. Mean Predation probability (±SE), for *T. trinervoides* mounds by the aardvark in a semi-arid environment. The predation probability (predation.events/obs.month) shown is for each of the habitat types (Grassland; Pan; Savanna; Shrub) for the wet and dry season calculated over a 23 month observation period. The data represented here is the average predation event per month for the mounds (eg. G1A-P) within a site (eg. G1-6) averaged for the habitat (eg. Grassland). Wet season is from September-April and dry season from May-August.

Table 3.1. The predation events on the monitored mounds at Benfontein Game Farm for the wet season (September-April) and dry season (May-August) given according to the habitat of the monitored mounds and the azimuth of the predation event for the 23 month monitoring period. The Rayleigh's test result (r.bar) with the associated p-value, and the adjusted p-value for the habitats are given below.

Habitat	Grassland	Grassland	Savanna	Savanna	Shrub	Shrub	Pan	Pan
Season	Wet	Dry	Wet	Dry	Wet	Dry	Wet	Dry
N	18	0	1	1	8	1	3	0
NE	2	0	0	0	0	0	0	0
E	14	5	1	0	6	2	2	1
SE	1	0	0	0	4	0	0	0
S	20	3	2	0	4	0	1	0
SW	2	0	0	0	0	0	0	0
W	6	2	1	0	3	1	1	0
NW	1	0	1	0	0	0	0	0
Total Predation events	64	10	6	1	25	4	7	1
r.bar	0.1	0.4	0.1	1.0	0.2	0.4	0.3	1.0
p.value	0.3	0.2	0.9	0.5	0.2	0.6	0.5	0.5
p.value adjust	0.7	0.6	0.9	0.6	0.7	0.6	0.7	0.6

Discussion:

The predation risk of termite mounds by aardvark was found to be higher in the wet season than in the dry season. The concrete-like external structure of mounds is softened by rain making it easier for aardvark to dig into mounds. At the beginning of the rainy season each mound is densely packed with mature alates (Adam 1993). Alates being the primary source of reproduction for the colony have a body with high fat content (Redford & Dorea 1984). These fat reserves serve as the energy source during colony foundation. The alates of the colony disperse in swarms after the first heavy rains of the season, sometimes in synchronised swarms, thereby minimising predation (Sands 1965; Adam & Mitchelle 2009). In a study done by Adam (1993) the alates were found to be in the mound all year round in various phases of development. After high levels of rainfall expose internal galleries the alates swarm out of mound on a nuptial flight. Aardvark predation in the wet season may trigger alates to swarm if they are ready or risk being eaten. The higher predation risk in the wet season is an anomaly since there are an abundance of resources in the wet season for the aardvark and other myrmecophages. *T. trinervoides* has been shown to contribute between 18-20% of the aardvark diet during the wet season (Willis *et al*. 1992; Taylor *et al*. 2002). The rain softening the mounds in the wet season reduces the energetic cost of digging into the mounds compared to the dry season, which may explain the results observed. It has been shown that in the dry season the aardvark consume ants and termites only the amount consumed is greatly reduced (Willis *et al*. 1992)

The formation of lakes in the low lying areas of the farm resulted in some of the mounds being submerged for an extended period of time. It is not clear to what extent the water entered the mounds and underground tunnels or if the termites possess any ability to withstand this amount of saturation. However if the termite colonies were able to survive the extended period of submerging they were destroyed by aardvark sometime soon thereafter, most likely due to the fact that the mound was soft and easy to dig in for the aardvark. The softness most likely resulted in the mounds being dug up to such an extent that all termites including the queen were killed.

The lack of effect of habitat, season and predation angle to predation severity may be as a response to mound size. The mound size is a good indicator of colony population size (Adam 1993). Thus the response of predation severity to mound size may be a response to colony population size. The uniform spread of predation angles on the mounds could be caused by multiple factors. The size of the termite mound is small when compared to other mound building ants and termites (Harris 1956; Weir 1973; Schuurman & Dangerfield 1996). The development of a micro-climate in a mound is influential to the termites in the mound, mostly the queen and brood. However, this does not reflect in the predation habits of the aardvark. The mound size is also not large enough (Addendum) to be influenced by external weather conditions such as predominant rain and wind directions, which would influence the entire mound to more or less the same extent. The field site in Kimberley is a flat terrain. With the comparatively small size of the mounds there would be minimal slope effect on the temperature gradient of the mound, even distribution of rainfall over the mound and no noticeable wind-chill effects on a mound. The lack of preference in attack direction may also be as a result of the way in which the aardvark feeds: the aardvark feeds on mounds at random during roaming events (Taylor *et al*. 2002). The direction of approach is seemingly irrelevant. The aardvark digs into the centre of the mound to feed on the immatures and may even get to the queen (Adam 1993). With the easiest and nutritionally most valuable prey at the centre of the mound the direction that the aardvark digs from would make little difference. The building sites on a mound might influence the digging direction with the high concentration of workers attracting aardvark predation. However a link between building site direction and predation direction was never established.

The termite mound has a dual purpose as it provides the colony with protection from predation and at the same time provides protection from extreme environmental fluctuations. The micro-climate within a mound provides an ideal environment for termites and allows the colony to perform more efficiently throughout the seasons. When the aardvark digs into the mound the internal environment is suddenly altered. This sudden change in climate may cause a great amount of stress on the colony and even the death of brood. After the aardvark has fed on the colony, the removal of soldiers and workers leaves the colony defences weakened, and prolongs the time taken to repair the mound. The softest part of the mound is exposed and this leaves the colony vulnerable to attack from other myrmecophages, birds, spiders, lizards and beetles (Sheppe 1970; Taylor & Skinner 2000; Taylor & Skinner 2001). Continued predation on selected colonies will cause the death of a colony, and ultimately a reduction in genetic variability of the population. This will influence the population stability and may have severe ecological implications.

During the wet season in the semi-arid region of southern Africa, there are multiple species of ants and termites available for myrmecophages to feed upon (Lindsey 1999). *T. trinervoides* is the only species that builds visible epigeal mounds, whereas other ant and termite species in this area build the nest below ground with a few foraging tunnels emerging onto the surface. Ants may be found in abandoned termite mounds. Extreme temperature variations in the dry season results in the majority of ants and termites remaining in their nests below ground and living off stored forage material. *T. trinervoides* also remain within their nests and live off stored grass since the night time temperatures are far below their threshold and absence of cuticle pigmentation prevents them from foraging in the sun during the day (Hewitt *et al*. 1972; Adam *et al*. 2008). The aardvark is believed to roam randomly using hearing and smell to locate food sources, not focusing on *T. trinervoides* mounds (Melton 1976). However with the seasonal shift in feeding frequency upon these mounds, *T. trinervoides* predation is not random. The hard concrete-like external shell of the mound could lead to aardvark actively avoiding excessive digging into mounds in the dry season to conserve energy, compared to easier diggings in the wet season. In winter when animals are in energy deficit, Iexpected an increase in mound predation by the aardvark, however it appears that the energetic costs of digging into the mound are too great. The decrease in dietary composition of termites in the dry season implies that the aardvark is not exclusively dependent on *T. trinervoides* during this time (Redford & Dorea 1984, Willis et al 1992).

Conclusion:

Aardvark predation on termite mounds is higher in the wet season, but is consistent across all habitat types. The rain in the wet season could be softening the external shell of the mounds thereby reducing energetic costs involved in digging into mound. The increased predation in the wet season also exposes the colony to severe stress of external environmental temperature extremes as well as exposing the colony to increased secondary predation events. The random foraging pattern proposed by other researchers may apply to habitat types but there is a non-random predation over the seasons. Due to *T. trinervoides* being the only non-pest species in this genus there is little information available resulting only in rare fundamental research. This study provides information on a species that is vital to ecosystem functions in the semi-arid habitat of southern Africa. Future studies could use this information to assess the impact of aardvark predation on colony persistence and termite social structure, as well as the impact of secondary predation from aardvark holes, and how these factors influence ecosystem functions of semi-arid environments.

References:

Adam R.A. 1993: Aspects of the biology of the harvester termite *Trinervitermes trinervoides* (Sjöstedt) (Isoptera: Termitidae). PhD thesis. University of the Orange Free State, South Africa.

Adam, R.A. & Mitchell, J.D. 2009: Energetics and development of incipient colony formation of the harvester termite, *Trinervitermes trenervoides* (Sjöstedt) (Termitidae, Nasutitermitinae). Insectes Sociaux **56**, 21-27.

Adam, R.A., Mitchell, J.D. & van der Westhuizen, M.C. 2008: Aspects of foraging in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt) (Termitidae:Nasutitermitinae). African Entomology **16**, 153-161.

Agostinelli, C. & Lund, U. 2011: R package 'circular': Circular Statistics (version 0.4-3). URL: https://r-forge.r-project.org/projects/circular

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2012: lme4: Linear mixed-effects models using Eigen and S4. R package version 1.0-4. http://CRAN.R-project.org/package=lme4.

Bond, W.J. 1993: Keystone species. Biodiversity and Ecosystem Function, Springer study edition **99**, 237-253.

Brossard, M., Lopéz-Hernández, D., Lepage, M. & Leprun, J.C. 2007: Nutrient storage in soils and nests of mound-building *Trinervitermes* termites in Central Burkina Faso: consequences for soil fertility. Biology and Fertility of Soils **43**, 437-447.

Brouwer, J., Fussell, L.K. & Herrmann, L. 1993: Soil and crop growth micro-variability in the West African semi-arid tropics: a possible risk reducing factor for subsistence farmers. Agriculture, Ecosystems & Environment **45**, 229-238.

Casey, T.M. 1976: Activity patterns, body temperature and thermal ecology in two desert caterpillars (Lepidoptera:Sphingidae). Ecology **57**, 485-497.

Coaton, W.G.H. 1948: *Trinervitermes* species- the snouted harvester termites. Union of South Africa, Dept. of Agriculture Bulletin **261**, 1-19.

Coventry, R.J., Holt, J.A. & Sinclair, D.F. 1988: Nutrient cycling by mound building termites in low fertility soils of semi-arid tropical Australia. Australian Journal of Soil Research **26**, 375-390.

Dalerum, F., Cameron, E.Z., Kunkel, K.E. &.Somers, M.J. 2012: Interactive effects of species richness and species traits on functional diversity and redundancy. Theor. Ecol **5**, 129-139.

Dangerfield, J.M., Mccarthy, T.S. & Ellery, W.N. 1998: The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. Journal of Tropical Ecology **14**, 507-520.

Dean, W.R.J. & MacDonald, I.A.W. 1994: Historical changes in stocking rates of domestic livestock as a measure of semi-arid and arid rangeland degradation in the Cape Province, South Africa. Journal of Arid Environments **26**, 281-298.

Eggleton, P., Bignell, D.E., Sands, W.A., Waite, B., Wood T.G. & Lawton, J.H. 1995: The species richness of termites (Isoptera) under differing levels of forest disturbance in the Mbalmayo Forest Reserve, southern Cameroon. Journal of Tropical Ecology **11**, 85-98.

Fittkau, E.J. & Klinge, H. 1973: On biomass and trophic structure of the Amazonian rain forest ecosystem. Biotropica **5**, 2-14.

Flecker, A.S. 1996: Ecosystem engineering by a dominant detritivore in a diverse tropical stream. Ecology **77**, 1845-1854.

Franks, N.R. 1987: The organization of working teams in social insects. TREE **3**, 72-75.

Frazier, M.R., Huey, R.B. & Berrigan, D. 2006: Thermodynamics constrains the evolution of insect population growth rates: “Warmer is Better”. The American Naturalist **168**, 512-520.

Grigg, G.C. 1973: Some consequences of the shape and orientation of ‘magnetic’ termite mounds. Australian Journal of Zoology **21**, 231-237.

Harris, W.V. 1956: Termite mound building. Insectes Sociaux **3**, 261-268.

Jones, C.G., Lawton, J.H. & Shachak, M. 1994: Organisms as ecosystem engineers. Oikos **69**, 373-386.

Korb, J. & Linsenmair, K.E. 2000: Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? Insectes Sociaux **47**, 357-363.

Lima, M., Stenseth, N.C. & Jaksic, F.M. 2002: Food web structure and climate effects on the dynamics of small mammals and owls in semi-arid Chile. Ecology Letters **5**, 273–284.

Lindsey, P.A. 1999: The feeding ecology and habitat use of the aardvark *(Orycteropus afer)*, MSc dissertation, University of Pretoria, Pretoria, viewed 2013/11/11 < http://upetd.up.ac.za/thesis/available/etd-11162006-100552/ >

Losey, J.E. & Vaughan, M. 2006: The economic value of ecological services provided by insects. BioScience **56**, 311-323.

Melton, D.A. 1976: The biology of aardvark (Tubulidentata-Orycteropodidae). Mammal Rev **6**, 75-88.

Michener, C.D. 1969: Comparative social behaviour of bees. Annual Review of Entomology **14**, 299-342.

Morris, D. 2013: Proposed Blackwood Solar Energy Facility on Portion 1 of Padamsfontein 1593, south east of Kimberley, in the Tokologo Local Municipality, Free State: Scoping Phase heritage input. McGregor Museum, Department of Archaeology, accessed online at: http://savannahsa.com/documents/5525/Appendix%20G%20-%20Heritage%20scoping%20report.pdf on 2013-11-13.

Nel, J.J.C. & Malan, E.M. 1974: The distribution of mounds of *Trinervitermes trinervoides* in the central Orange Free State. Journal of the Entomological Society of South Africa **37**, 251-256.

Paine, R. T. 1969b: A note on trophic complexity and community stability. The American Naturalist **103**, 91-93.

Paine, R.T. 1969a: The Pisaster-Tegula interaction: Prey patches, predator food preference, and intertidal community structure. Ecology **50**, 950-961.

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & the R Development Core Team. 2013: nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-111.

Plowes, R.M., Dunn, J.G. & Gilbert, L.E. 2007: The urban fire ant paradox: native fire ants persist in urban refuge while invasive fire ants dominate natural habitats. Biological Invasions **9**, 825-836.

Potts, R.C. & Hewitt, P.H. 1973: The distribution of intestinal bacteria and cellulase activity in the harvester termite *Trinervitermes trinervoides* (Nasutitermitinae). Insectes Sociaux **20**, 215-220.

R Core Team. 2013: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Redford, K.H. & Dorea, J.G. 1984: The nutritional value of invertebrates with emphasis on ants and termites as food for mammals. Journal Zoology London **203**, 385-395.

Richardson, P.R.K. 1987: Aardwolf: The most specialized myrmecophagous mammal? South African Journal of Science **83**, 643-646.

Rosenberg, D.M., Danks, H.V. & Lehmkuhl, D.M. 1986: Importance of insects in environmental impact assessments. Environmental Management **10**, 773-783.

Sands, W.A. 1965: Alate development and colony foundation in five species of *Trinervitermes* (Isoptera: Nasutitermitinae) in Nigeria, West Africa. Insectes Sociaux **12**, 117-130.

Schmitz, J.O. & Suttle, K.B. 2001: Effects of top predator species on direct and indirect interactions in a food web. Ecology **82**, 2072–2081.

Schmitz, J.O., Beckerman, A.P. & O’Brien, K.M. 1997: Behaviourally mediated trophic cascades: effects of predation risk on food web interactions. Ecology **78**, 1388-1399.

Scholtz, C.H. & Holm, E. 1985: Insects of Southern Africa. Butterworth Publishers, Durban, South Africa.

Schuurman, G. & Dangerfield, J.M. 1996: Mound dimensions, internal structure and potential colony size in the fungus growing termite *Macrotermes michaelseni* (Isoptera: Macrotermitinae). Sociobiology **27**, 29-38.

Sheppe, W. 1970: Invertebrate predation on termites of the African savanna. Insectes Sociaux **17**, 205-218.

Slaytor, M. 1992: Cellulose digestion in termite and cockroaches: What role do symbionts play? Comparative Biochemistry and Physiology Part B: Comparative Biochemistry **103**, 775-784.

South African Weather Service; Historical Rain Maps URL: http://www.weathersa.co.za/web/index.php/sclimate/historical-rain-maps Minimum and maximum temperatures for Northern Cape URL: http://www.weathersa.co.za/web/index.php/nc

Steneck, R.S. 2005: An ecological context for the role of large carnivores in conserving biodiversity. In: Ray, J.C., Redford, K.H., Steneck, R.S., & Berger, J. (eds) Large carnivores and the conservation of biodiversity. Island Press, Washington DC, pp 9–33.

Swank, W.T., Waide, J.B., Crossley Jr, D.A. & Todd, R.L. 1981: Insect defoliation enhances nitrate export from forest ecosystems. Oecologia **51**, 297-299.

Swart, J.M., Richardson, P.R.K. & Ferguson, J.W.H. 1999: Ecological factors affecting the feeding behaviour of pangolins (Manis temminckii). Journal of Zoology London **247**, 281-292.

Taylor, L.R. 1963: Analysis of the effect of temperature on insects in flight. Journal of Animal Ecology **32**, 99-117.

Taylor, W.A. & Skinner, J.D. 2000: Associative feeding between Aardwolves (*Proteles cristatus*) and Aardvarks (*Orycteropus afer*). Mammal Rev **30**, 141-143.

Taylor, W.A. & Skinner, J.D. 2001: Associative feeding between Ant-eating Chats, *Myrmecocichla formicivora*, and Aardvarks, *Orycteropus afer*. Ostrich **72**, 199-200.

Taylor, W.A., Lindsey, P.A. & Skinner, J.D. 2002: Feeding ecology of the aardvark *Orycteropus afer*. Journal of Arid Environments **50**, 135-152.

Torbit, S.C., Carpenter, L.H., Swift, D.M. & Alldredge, A.W. 1985: Differential loss of fat and protein by mule deer during winter. The Journal of Wildlife Management **49**, 80-85.

Warton, D.I. & Hui, F.K.C. 2011: The arcsine is asinine: the analysis of proportions in ecology. Ecology **92**, 3-10.

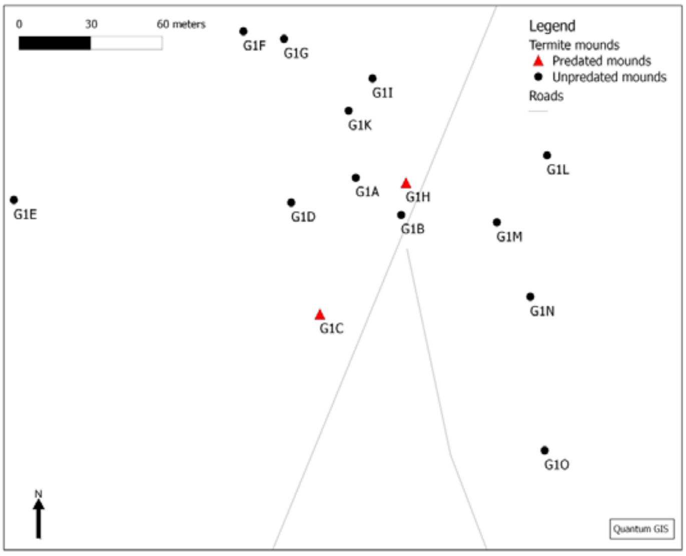
Weir, J.S. 1973: Air flow, evaporation and mineral accumulation in mounds of *Mactrotermes subhylinus* (Rambur). Journal of Animal Ecology **42**, 509-520.

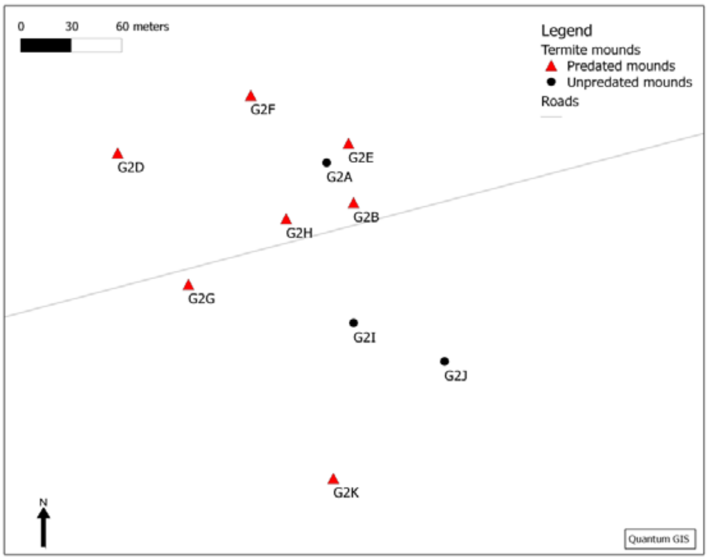
Western, D. 1975: Water availability and its influence on the structure and dynamics of a savannah large mammal community. African Journal of Ecology **13**, 265-286.

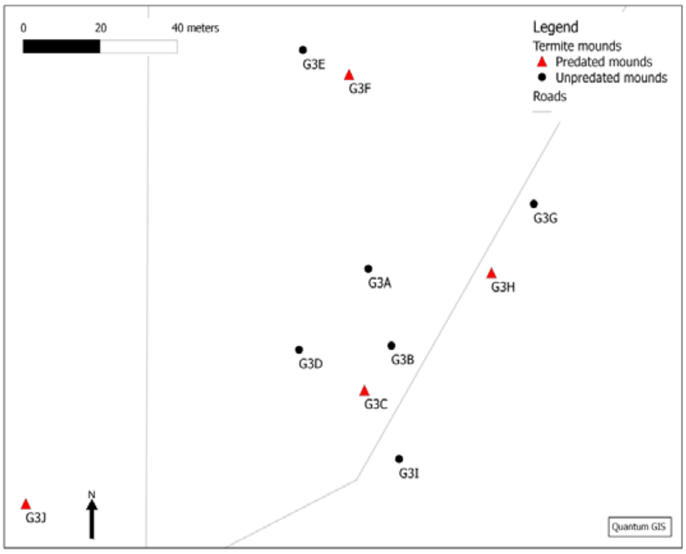
Williams, J.B., Anderson, M.D. & Richardson, P.R.K. 1997: Season differences in field metabolism, water requirements, and foraging behaviour of free-living aardwolves. Ecology **78**, 2588-2602.

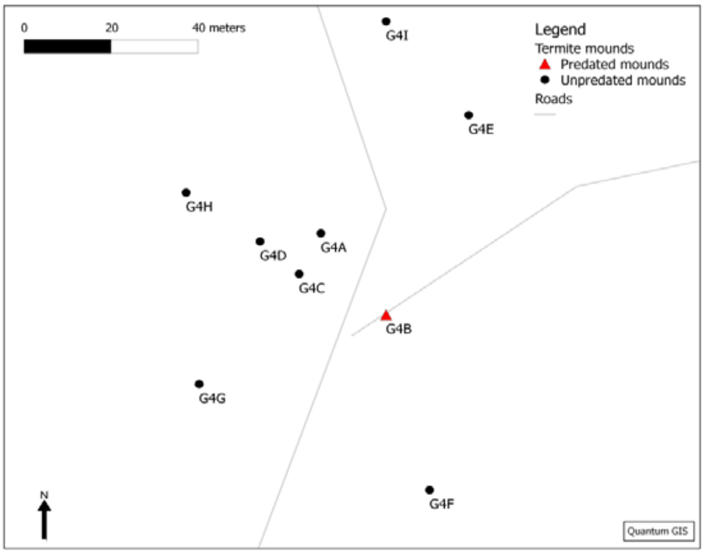
Willis, C.K., Skinner, J.D. & Robertson, H.G. 1992: Abundance of ants and termites in the False Karoo and their importance in the diet of the aardvark *Orycteropus afer*. African Journal of Ecology **30**, 322-334.

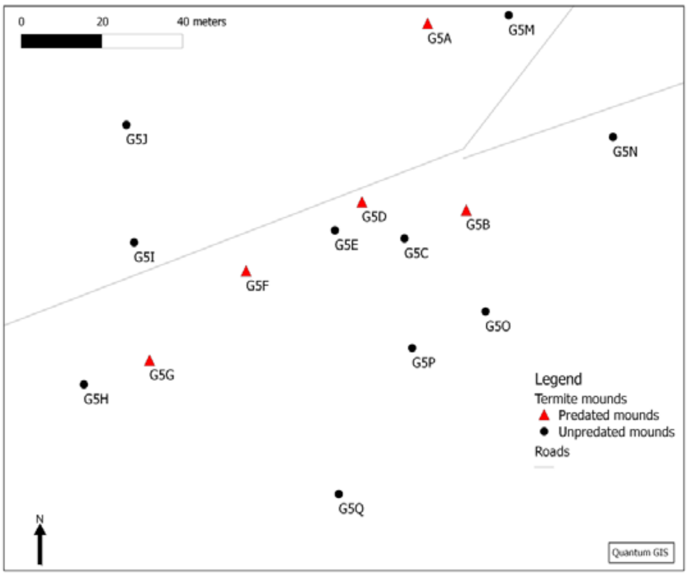
Addendum

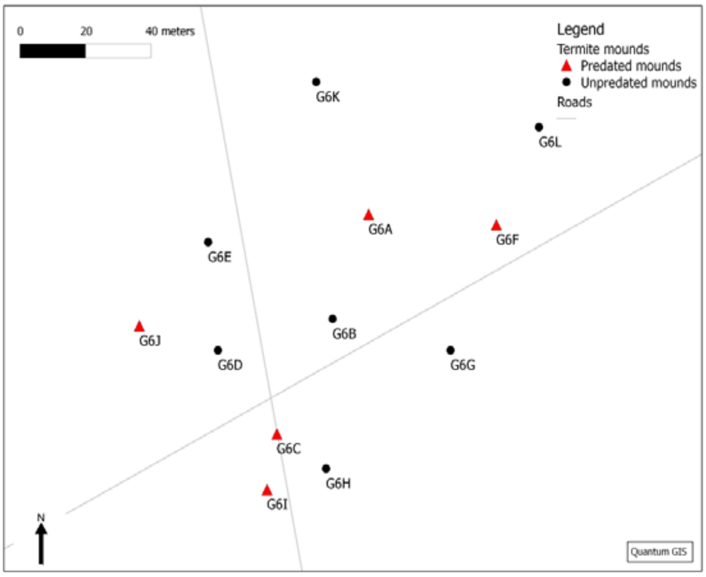

0
30
60 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
G1F
G1G
G1I
G1K
G1L
G1A
G1H
G1E
G1D
G1B
G1M
G1N
G1C
G1O
N
Quantum GIS

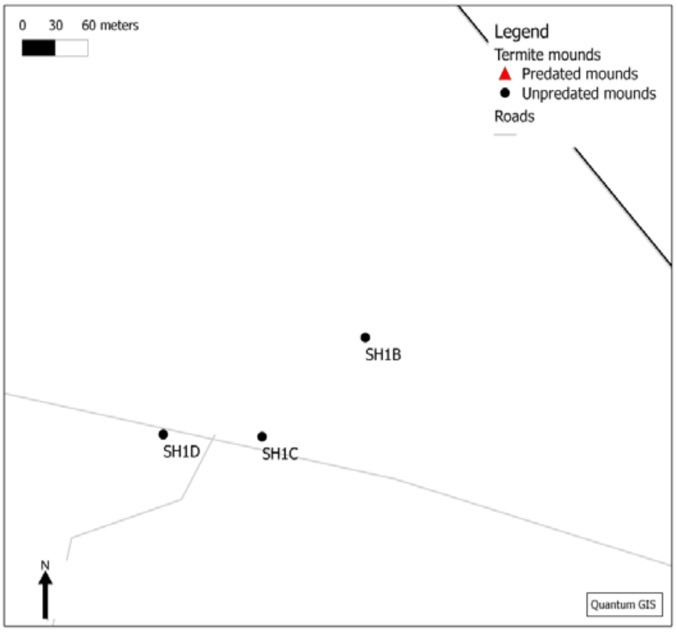

0
30
60 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
G2F
G2D
G2E
G2A
G2B
G2H
G2G
G2I
G2J
G2K
N
Quantum GIS

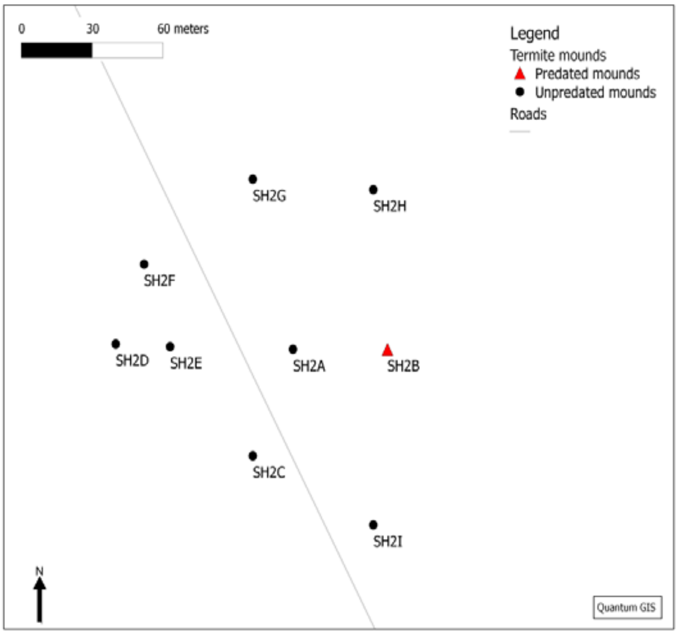

0
20
40 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
G3E
G3F
G3G
G3A
G3H
G3D
G3B
G3C
G3I
G3J
N
Quantum GIS

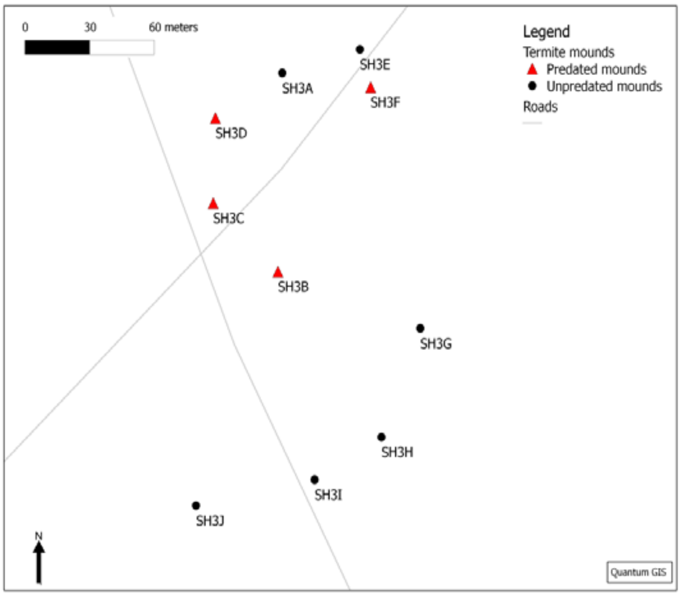

0
20
40 meters
G4I
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
G4E
G4H
G4D
G4A
G4C
G4B
G4G
G4F
N
Quantum GIS

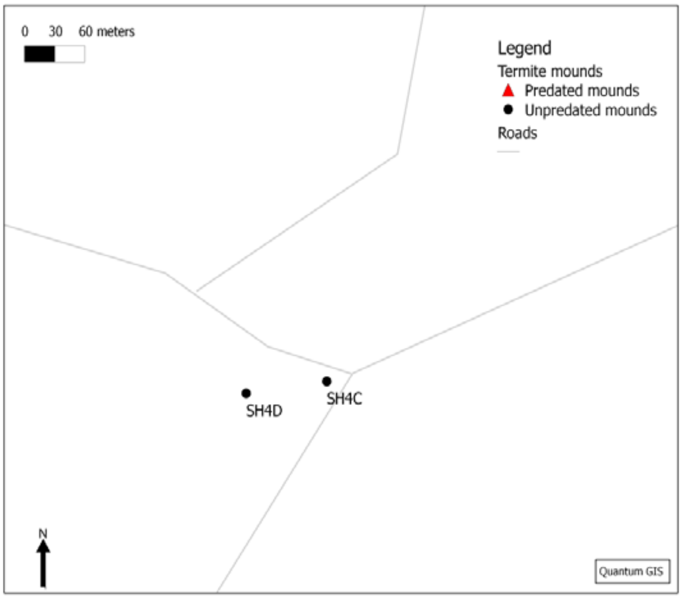

0
20
40 meters
G5A
G5M
G5J
G5N
G5D
G5B
G5E
G5C
G5I
G5F
G5O
G5P
G5G
G5H
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
G5Q
N
Quantum GIS

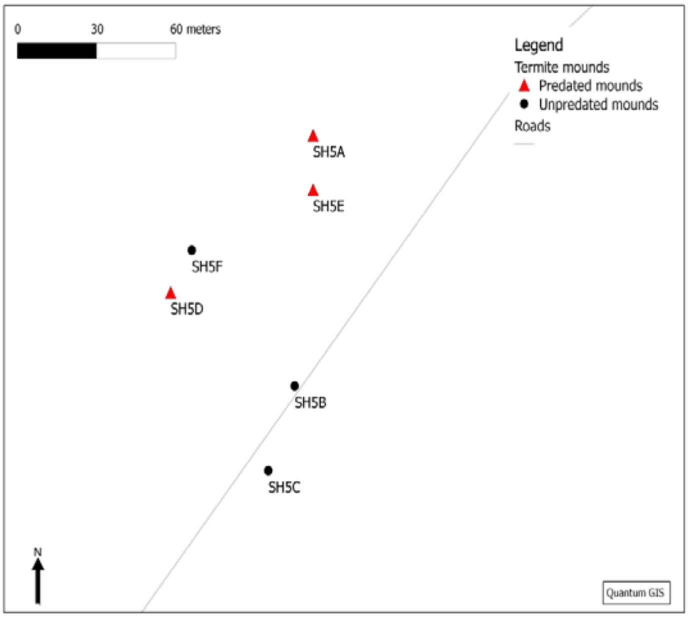

0
20
40 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
G6K
G6L
G6A
G6F
G6E
G6J
G6B
G6D
G6G
G6C
G6H
G6I
N
Quantum GIS

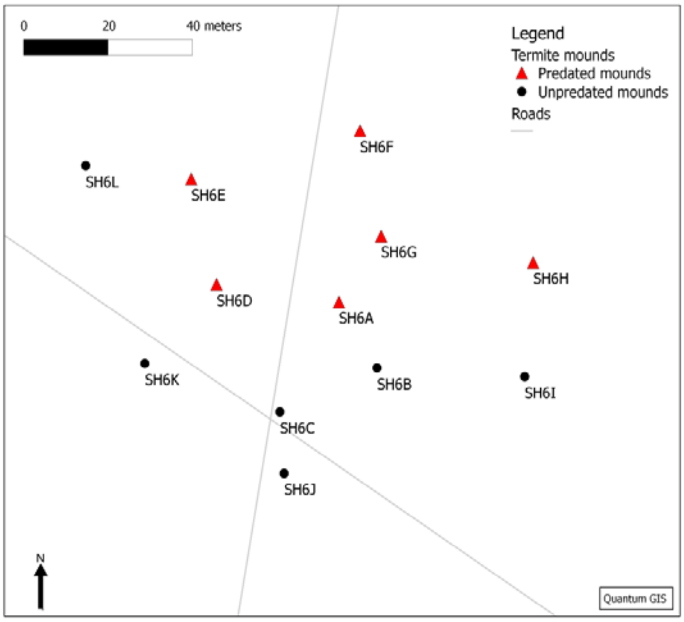

0 30 60 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
SH1B
SH1D
SH1C
N
Quantum GIS


0 30 60 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
SH2G
SH2H
SH2F
SH2D
SH2E
SH2A
SH2B
SH2C
SH2I
N
Quantum GIS


0 30 60 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
SH3E
SH3A
SH3F
SH3D
SH3C
SH3B
SH3G
SH3H
SH3I
SH3J
N
Quantum GIS


0 30 60 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
SH4D
SH4C
N
Quantum GIS


0 30 60 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
SH5A
SH5E
SH5F
SH5D
SH5B
SH5C
N
Quantum GIS


0 20 40 meters
Legend
Termite mounds
▲ Predated mounds
● Unpredated mounds
Roads
SH6F
SH6L
SH6E
SH6G
SH6H
SH6D
SH6A
SH6K
SH6B
SH6I
SH6C
SH6J
N
Quantum GIS

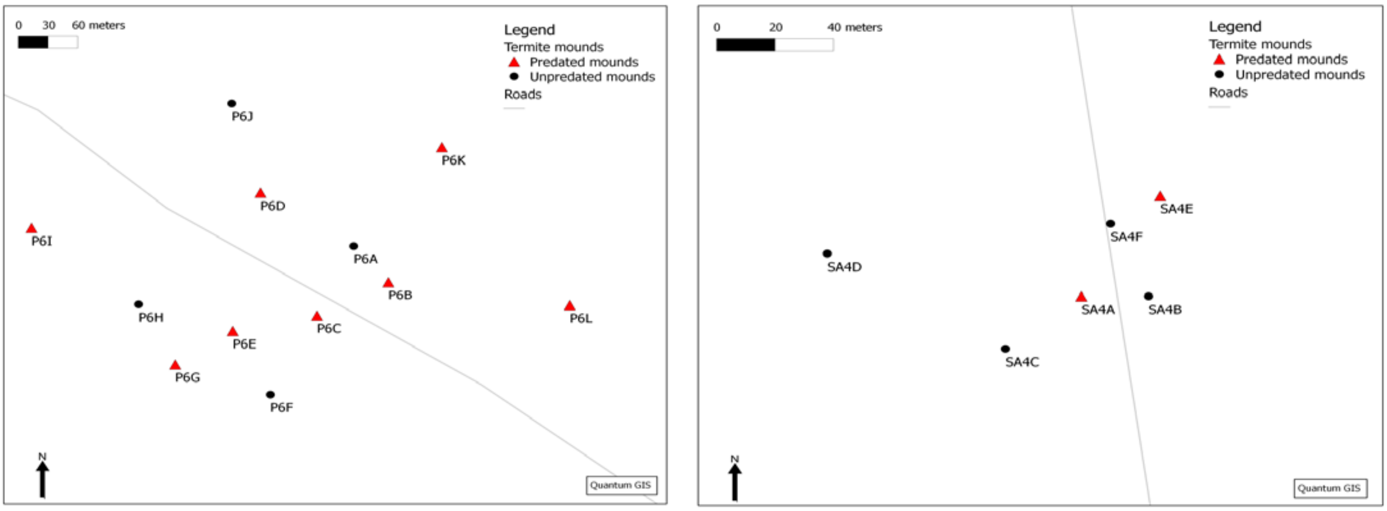
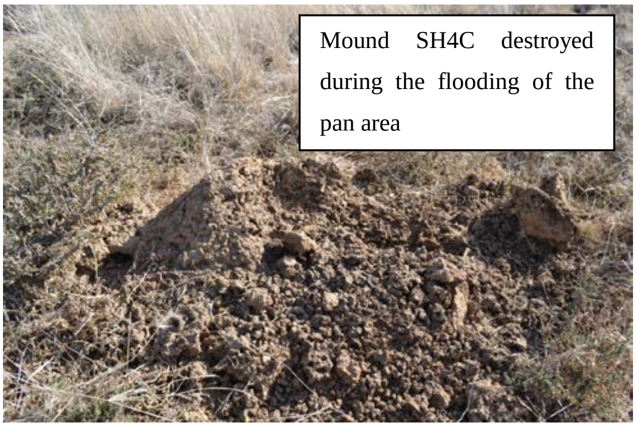


Table 3.2 The Table shows the Mean, Standard deviation (Std. Dev.) and standard error (Std. Err.) for the 126 mounds measured over the study area. Mound circumference represents the largest part of the mound. Mound volume is an estimate of half a sphere, to roughly depict above ground volume. Mound surface area also provides a rough estimate of the above ground portion of the mound.

	Height (cm)	Diameter (cm)	Mound Circum	Mound voume	Mound surface area
Mean	49.58730159	81.51587302	256.0896678	3776.339814	10396.3759
Std. Dev.	12.1169434	23.91609805	75.13463794	2073.263924	5133.478419
Std. Err.	1.079463114	2.130615356	6.693525549	184.7010304	457.3266058



Mound SH4C destroyed during the flooding of the pan area

P6E destroyed

P6B destroyed

P6C destroyed

P6D-destroyed

SH6E-destroyed

SH6G-destroyed

Chapter IV

General Discussion:

The decreased aggression levels between individuals from the same mound compared to individuals from different mounds indicate that each mound is one social unit or in other words one colony. From this I can conclude that *T. trinervoides* is a monodomous species. When comparing various studies done on social structure, using aggression tests, there was no evidence to show that a termite species is both monodomous or polydomous , suggesting that social structure is fixed within a termite species (Harris 1956; Sands 1961; Ohiagu & Wood 1976; Adam *et al.* 2008) unlike ants species where it can vary (Pirk *et al*. 2001). The aggression levels did not change significantly over the population, suggesting that the population structure may be uniform across this spatial scale with little sub-structuring. If the population structure changed between the habitats or seasons there would be a change in the aggression levels at a specific point. This also relates to the genetic structure fot he population, if there were areas of low genetic heterogeneity on a small scale intersperced with areas of high genetic heterogeneity the genetic substructure of the population would be reflected in the aggression levels. Indeed, the possible genetic substructure at this spatial scale caused by the weak flying ability of the alates did not reflect in the aggression levels. There may be a sufficient amount of genetic dispersal from surrounding colonies to prevent substructure of the population forming.

There was a weak negative relationship between distance and aggression over the small spatial scale. This shows the highest levels of aggression are towards immediate neighbouring mounds. It has been shown that foraging areas greatly overlap for this species (Adam *et al*. 2008). From this I conclude that the aggression structure of the *T. trinervoides* population in this area is strongly driven by resource competition. It is not known if these levels of aggression will persist in the field. High levels of aggression cost the colony resources and energy. It has been shown that *T. trinervoides* actively avoid aggressive interactions (Nel 1968). However, the strong uniform response towards non-nestmates suggests that maintaining colony integrity is a fundamental feature in the interactions among conspecifics. Avoiding intraspecies aggression conserves energy and population numbers, this behavioural adaptation allows the colony to direct a larger amount of resources towards colony defence and recovery from predation events from the aardvark. This study shows that in ecology extrapolation of small scale data to a population level may be highly inaccurate. Data should be collected at the population level as small scale interaction may create noise in data, which may negatively influence large scale population management. The uniform level of aggression over the population suggests that the population structure of this species is stable, with the social structure functioning uniformly over the entire population. This provides some valuable insight into the conservation of this habitat. The *T. trinervoides* population is stable, and most beneficial termite species, more information is needed on the population stability of the aardvark for effective conservation of this ecosystem.

Predation risk from the aardvark was highest in the wet season. This could be due to the rains softening the concrete-like external shell of the mound, reducing energetic costs of digging into mounds. In winter myrmecophages were thought to be dependent on *T. trinervoides* to provide the necessary dietary proteins to support them through the winter. The aardvark has been shown to decrease dietary composition of termites from 20% in summer to 13% in winter (Willis *et al*. 1992; Taylor *et al*. 2002). Even though we did not directly measure the amount of termites consumed during each predation event, this shows that in winter the aardvark may avoid digging into termite mounds due to the energetic costs, despite the guaranteed availability of resources in the mound. The increase in termites in the diet in the wet season is linked to the general increase in abundance of resources in the wet season (Lindsey 1999). In the wet season a large number of foraging parties are sent out (Adam *et al*. 2008), thus there are a reduced number of termites in the mound. This will result in a lower dietary value per mound and this may cause the aardvark to increase predation frequency on mounds. The dietary contribution of alates may fluctuate throughout the year, depending on development and mound size (larger mounds are older and have more alates; Adam 1993). Overall the low energetic costs of digging into termite mounds in summer favour predation.

With predation risk of mounds remaining consistent through the various habitats the foraging habits were not concentrated in the grassland regions, but spread evenly throughout the farm even though termite mound density is higher in grassland habitats. Termite colonies in less favourable habitats may be impacted more severely by these predation events. However due to the formation of the lake, the sporadic predation events and the few termite mounds present in these habitats, statistically this could not be determined. Less favourable habitats have a lower relative abundance of the preferred resource for *T. trinervoides* colonies. With resources harder to come by in these habitats the energetic costs to the colony to recover from each predation event will be higher. This energetic cost in turn will reduce the reproductive potential of the colony resulting in a slower genetic turnover in these habitats.

There was no effect of habitat, season or attack direction on the predation severity. The size of a termite mound is a representative of the population size of the colony (Adam 1993). The predation severity may be a direct response to mound size, and therefore population size of a colony. The uniform spread of predation angles is mostly attributable to their size. The size of *T. trinervoides* mounds is small when compared to other mound building ants and termites (Harris 1956; Weir 1973; Schuurman & Dangerfield 1996). Due to the small size of the mound the micro-climate within the mound form concentric rings or contours of a temperature gradient following the shape of the mound towards the centre (Adam 1993). The flat landscape of the study area and the small size of the mounds also prevent the development of slope effect on the mound. Despite these factors the tasks carried out by the workers within the mound may cause a temporary polar distribution of termites. Even though the termites in the mound may have a polar distribution, this is not reflected in the aardvark predation habits. This may also be influenced by various behavioural modifications from the aardvark. Aardvak attack holes went directly to the centre of the mound (pers. obs.), where the brood and queen would have been, from this perspective the angle of approach is insignificant.

In the semi-arid environment the mammals are in energy deficit in winter (Torbit *et al*. 1985) . I expected the aardvark to be dependent on *T. trinervoides* for nutrients in winter, however the dietary composition decreases in winter (Willis *et al*. 1992). This shows that the aardvark is not exclusively dependent on *T. trinervoides* in winter. However aardvark predation may facilitate other myrmecophages that are exclusively dependent on *T. trinervoides* throughout the year, such as the aardwolf. The holes made by the aardvark facilitate weaker diggers in accessing additional nutrients from the mound (Taylor & Skinner 2000; Taylor & Skinner 2001). Predation holes are also used as shelters by small mammals (bat-eared fox families; porcupines; pers. obs.) and invertebrates (ants; spiders; scorpions; beetles) through the winter. Future studies should aim to quantify the effects of secondary predation on the social structure of this *T. trinervoides* population.

The high mound density in grassland habitats results in high levels of resource competition (Hairston *et al*. 1960). Each predation event removes forage reserves from the mound. The aggression structure over the population is uniform. *T. trinervoides* are directly dependent on the ungulate population in this area, in the wet seaason, to provide foraging resources as they feed on recumbent grass (Adam *et al*. 2008). Ungulate feeding patterns may be the major factor of the aggression structure of the population of *T. trinervoides* in grassland habitats. Aardvark predation is uniform over the population. These predation events may be a driving factor of *T. trinervoides* social structure. Monodomous colonies would be selected for since polydomy would increase the predation risk of a colony. One could speculate that the survival chance is higher when investing into one nest mound rather than splitting the resources into several smaller units, which are relatively more vulnerable. Although monodomous colony structure bears the risk of putting all "eggs into one basket" it might help to reach the right colony size quicker to survive predation events compare to splitting up the resources. Predation may also be a driving factor for increased genetic diversity in the population, by removing the weaker colonies there is an increased chance of survival for new colonies. Further research about the aardvark may prove it to be a keystone species to this ecosystem and provide insight into the selection factors driving population stability.

References:

Adam R.A. 1993: Aspects of the biology of the harvester termite *Trinervitermes trinervoides* (Sjöstedt) (Isoptera: Termitidae). Ph. D. thesis. University of the Orange Free State, South Africa.

Adam, R.A., Mitchell, J.D. & van der Westhuizen, M.C. 2008: Aspects of foraging in the harvester termite, *Trinervitermes trinervoides* (Sjöstedt) (Termitidae: Nasutitermitinae). African Entomology **16**, 153-161.

Hairston, N.G., Smith, F.E. & Slobodkin, L.B. 1960: Community structure, population control, and competition. The American Naturalist **64**, 421-425.

Harris W.V. 1956: Termite Mound Building. Insectes Sociaux **3**, 261-268.

Lindsey, PA. 1999: *The feeding ecology and habitat use of the aardvark (Orycteropus afer),* MSc dissertation, University of Pretoria, Pretoria, viewed 2013/11/11 < http://upetd.up.ac.za/thesis/available/etd-11162006-100552/ >

Nel J.J.C. 1968: Aggressive behaviour of the harvester termites *Hodotermes mossambicus* and *Trinervitermes trinervoides* (Sjöstedt). Insectes Sociuax **15**, 145-156.

Ohiagu, C.E. & Wood, T.G. 1976: A Method for measuring rate of grass-harvesting by *Trinervitermes geminatus* (Wasmann) (Isoptera, Nasutitermitinae) and observation on its foraging behaviour in Southern Guinea Savanna, Nigeria. Journal of Applied Ecology 13, 705-713.

Pirk, C.W.W., Neuman, P., Moritz, R.F.A. & Pamilo, P. 2001: Intranest relatedness and nestmate recognition in the meadow ant *Formica pratensis* (R.). Behav. Ecol. Sociobiol. **49**, 366-374.

Sands, W.A. 1961: Foraging behaviour and feeding habits in five species of *Trinervitermes* in West Africa. Entomolgia Experimentalis et Applicata **4**, 277-288.

Schuurman, G. & Dangerfield, J.M. 1996: Mound dimensions, internal structure and potential colony size in the fungus growing termite *Macrotermes michaelseni* (Isoptera: Macrotermitinae). Sociobiology **27**, 29-38.

Taylor W.A., Lindsey P.A. & Skinner J.D. 2002: The feeding ecology of the aardvark *Orycteropus afer*. Journal of Arid Environments **50**, 135-152.

Taylor, W.A. & Skinner, J.D. 2000: Associative feeding between Aardwolves (*Proteles cristatus*) and Aardvarks (*Orycteropus afer*). Mammal Rev **30**, 141-143.

Taylor, W.A. & Skinner, J.D. 2001: Associative feeding between Ant-eating Chats, *Myrmecocichla formicivora*, and Aardvarks, *Orycteropus afer*. Ostrich **72**, 199-200.

Torbit, S.C., Carpenter, L.H., Swift, D.M. & Alldredge, A.W. 1985: Differential loss of fat and protein by mule deer during winter. The Journal of Wildlife Management **49**, 80-85.

Weir, J.S. 1973: Air flow, evaporation and mineral accumulation in mounds of *Mactrotermes subhylinus* (Rambur). Journal of Animal Ecology **42**, 509-520.

Willis, C.K., Skinner, J.D. & Robertson, H.G. 1992: Abundance of ants and termites in the False Karoo and their importance in the diet of the aardvark *Orycteropus afer*. African Journal of Ecology **30**, 322-334.