

**Ecological relationships between the armadillo lizard,  
*Cordylus cataphractus*, and the southern harvester termite,  
*Microhodotermes viator***

by

Cindy Shuttleworth

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at the University of Stellenbosch



Supervisor: Professor P. le Fras N. Mouton

Co-supervisor: Professor J. H van Wyk

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*Declaration:* I, the undersigned, hereby declare that the work contained in this thesis is my own original work and that I have not previously in its entirety or in part submitted it at any university for a degree.

*Signature:* \_\_\_\_\_

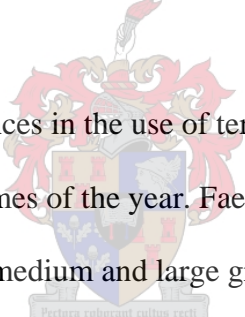
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## ABSTRACT

The role of the southern harvester termite, *Microhodotermes viator*, and several climatic parameters in the distribution of the group-living lizard, *Cordylus cataphractus*, was investigated. *Microhodotermes viator* is considered the most important prey item of *C. cataphractus* and termitophagy as the causative agent in the evolution of group-living in this species. One would therefore expect a high degree of correspondence in the ranges of *C. cataphractus* and *M. viator*. As climate will also play a role in the distribution of any species, various climatic variables were investigated to determine their influence on the distribution of *C. cataphractus*. Species distributions were visualized using the minimum polygon technique and the degree of overlap was determined using standard geographic information systems (GIS) techniques. A total of 53 *C. cataphractus* localities were investigated for the presence of termites. The climatic limits of the geographical distribution of *C. cataphractus* were investigated by means of three models, namely Classification Trees, General Discriminant Analysis and Logistic Regression. The range of *C. cataphractus* was completely included within the range of *M. viator*. *Microhodotermes viator* was included in the diet of *C. cataphractus* at 73 % of the localities sampled within the lizard's range. The current geographical range of *C. cataphractus* is mainly correlated with two climatic factors, namely the low summer rainfall and high monthly solar radiation. The restricting role of both these factors can be directly linked to the group-living nature of *C. cataphractus*. If termitophagy were the overarching cause of group-living in *C. cataphractus*, then one would expect a close relationship between termite density and lizard density and termite

density and lizard group size. I investigated these relationships at both a local and regional scale. For the local scale study, 25 quadrats of  $25 \times 25$  m were plotted at a selected site, and for the regional scale study, ten  $35 \times 35$  m quadrats at sites throughout the lizard's range were used. In each quadrat, a range of variables were recorded, the most important of which were lizard density, lizard group sizes, termite foraging port density, distance to nearest termite foraging ports, vegetation height and vegetation cover. I found that the density of termite foraging ports determines *C. cataphractus* density. Vegetation height and cover affects crevice selection by *C. cataphractus* groups, probably because an unobstructed view is necessary to locate termite activity at foraging ports.



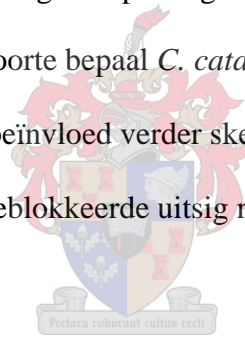
I also investigated possible differences in the use of termites by different sized groups of *C. cataphractus* during different times of the year. Faecal samples, collected once a month at Eland's Bay from small, medium and large groups from January 2005 to December 2005, were analysed for the presence of termite head material. I found that large groups fed on termites to a greater extent than small groups during certain times of the year and there was a general tendency for this phenomenon throughout the year.

The results collected in this study indicate that the southern harvester termite, *M. viator*, plays a central role in the ecology of the group-living lizard, *C. cataphractus*.

## UITTREKSEL

Die rol van die suidelike grasdraertermiet, *Microhodotermes viator*, en verskeie klimaatsparameters in die verspreiding van die groeplewende akkedis, *Cordylus cataphractus*, is ondersoek. *Microhodotermes viator*, word as die mees belangrikste prooi item van *C. cataphractus* beskou, en termietofagie as die oorsaaklike agent in die evolusie van groeplewendheid in hierdie spesie. 'n Mens sal dus 'n hoë graad van ooreenstemming in die verspreiding van *C. cataphractus* en *M. viator* verwag. Klimaat sal ook 'n groot rol in die verspreiding van 'n spesies speel, en daarom is verskeie klimaatsveranderlikes ondersoek om hulle invloed op die verspreiding van *C. cataphractus* te bepaal. Spesiesverspreidings is gevisualiseer deur gebruik te maak van die minimum veelhoek tegniek en die graad van oorvleueling is bepaal deur standard geografiese informasiesisteen (GIS) tegnieke. 'n Totaal van 53 *Cordylus cataphractus* lokaliteite is ondersoek vir die aanwesigheid van termiete. Die klimaatsbeperkings van die geografiese verspreiding van *C. cataphractus* is ondersoek deur middel van drie modelle, naamlik Klassifikasiebome, Algemene Diskriminante Analise en Logistieke Regressie. Die verspreiding van *C. cataphractus* is heeltemal ingesluit binne die verspreiding van *M. viator*. *Microhodotermes viator* was aanwesig in die dieet van *C. cataphractus* by 73 % van die lokaliteite wat ondersoek is binne die akkedis se verspreiding. Die huidige geografiese verspreiding van *C. cataphractus* word hoofsaaklik deur twee klimaatsfaktore bepaal, naamlik die lae somerreënval en hoë maandelikse sonstraling. Die beperkende rol van beide hierdie faktore kan direk gekoppel word aan die groeplewende geaardheid van *C. Cataphractus*.

As termietofagie die hoofrede vir groeplewend in *C. cataphractus* is, dan sal 'n mens 'n noue verwantskap tussen termietdigtheid en akkedisdigtheid en termietdigtheid en akkedisgroeppgrootte verwag. Ek het hierdie verwantskappe op beide 'n plaaslike en regionale skaal ondersoek. Vir die plaaslike skaal studie, het ek 25 kwadrante van 25 × 25 m geplot by 'n spesifieke lokaliteit, en vir die regionale skaal studie het ek tien 35 × 35 m kwadrante geplot by lokaliteite regoor die akkedis se verspreiding. In elke kwadrant is 'n reeks veranderlikes versamel, waarvan die mees belangrikste akkedisdigtheid, akkedisgroeppgroottes, termietvoedingspoortdigtheid, afstand aan naaste termietvoedingspoort, plantegroeihoogte en plantegroeibedekking was. Ek het gevind dat die digtheid van termietvoedingspoorte bepaal *C. cataphractus* digtheid. Plantegroeihoogte en -bedekking beïnvloed verder skeurseleksie deur *C. cataphractus* groepe, waarskynlik omdat 'n ongeblokkeerde uitsig nodig is om termietaktiwiteit by die voedingspoorte waar te neem.



Ek het ook moontlike verskille tussen die gebruik van termiete deur verskillende groeppgroottes van *C. cataphractus* tydens verskillende tye van die jaar ondersoek. Fekale monsters van klein, medium en groot groepe is eenkeer per maand, vanaf Januarie 2005 tot Desember 2005, by Elandsbaai versamel en vir die aanwesigheid van termietkopmateriaal geanaliseer. Ek het gevind dat groot groepe sekere tye van die jaar meer termiete eet as klein groepe, en dat daar 'n algemene tendensie vir hierdie fenomeen deur die jaar was.

Die resultate van hierdie studie dui aan dat die suidelike grasdraertermiet, *M. viator*, 'n sentrale rol in die ekologie van die groeplewende akkedis *C. cataphractus* speel.



*Dedication:*

To my love and darling husband, Kelvin.....and my precious son, Jonathan.

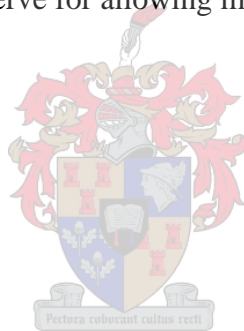




## ACKNOWLEDGEMENTS

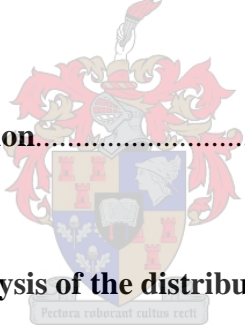
- I would firstly like to thank my husband, Kelvin for believing in me and supporting me through both the highs and lows of writing up a thesis. Thanks that I could always depend on you being available to go to the field with me when no one else could.
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## PREFACE

This study is part of ongoing research that is currently being conducted on the lizard family Cordylidae by the Vertebrate Functional Biology Group at the Department of Botany and Zoology of the University of Stellenbosch. This study will focus on a group-living member of the genus *Cordylus*, namely *Cordylus cataphractus*.

The work contained in this thesis consists of a general ecological study on the relationship between the group-living armadillo lizard, *Cordylus cataphractus* and its main prey source the southern harvester termite, *Microhodotermes viator*. *Cordylus cataphractus* is a unique species due to the fact that grouping behaviour is so strongly manifested. The relationship between termitophagy and group-living have been questioned in previous studies (Effenberger 2004, Mouton *et al.* 2005), and my research questions focus on this relationship and its impacts on the biology of *C. cataphractus*.

My thesis is structured as follows. Chapter 1 is a general introduction providing background information on my study as a whole focusing specifically on group-living in animals including lizards. This chapter also provides background information on *Cordylus cataphractus*. Chapter 2 encompasses a geographical analysis of the distribution of *Cordylus cataphractus*. Chapter 3 includes an analysis of density data collected from field sampling of various *C. cataphractus* populations. Chapter 4 consists of an annual faecal analysis of a specific *C. cataphractus* population.

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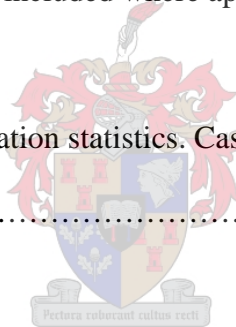
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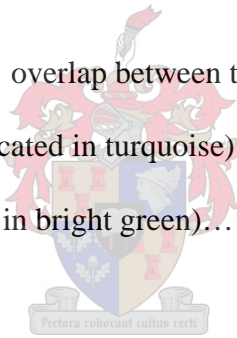


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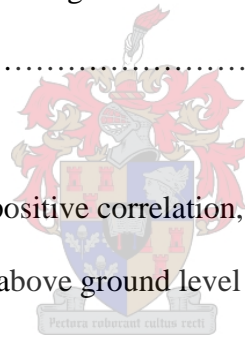
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# CHAPTER 1:

## GENERAL INTRODUCTION

Historically, it has been thought that reptilian social structures tend to be simple in nature and as a result studies on reptiles have lagged behind compared to those conducted on mammals and birds. In the light of recent findings, opinions have been re-evaluated in this regard. We have now come to an understanding that reptiles exhibit complex social behaviours, such as long-term monogamy (Bull 1988; Bull *et al.* 1998) and individual recognition by means of chemoreceptive systems (Steele & Cooper 1997; Bull *et al.* 1999, 2000; Whiting 1999). One form of social behaviour in reptiles that has received some attention in the literature is the tendency of some species to form aggregations (Gregory 1982; Cooper *et al.* 1985; Cooper & Garstka 1987; Amr *et al.* 1997; Lemos-Espinal *et al.* 1997; Ashton 1999; Mouton *et al.* 1999). Aggregating behaviour is thought to be driven by the appeal of patches of habitat to individuals. These habitats are usually limited in supply or of unusually high quality (Kearney *et al.* 2001).

The majority of animals spend a portion or part of their lives within a group. A group can be defined as “any set of organisms, belonging to the same species, which remain together for a period of time, interacting with one another to a distinctly greater degree than with other conspecifics” (Wilson 1975). A group can vary in both size and level of complexity. Group-living is a phenomenon found to occur from fish and amphibian species, which commonly form temporary spawning aggregations, to some birds, mammals and insects that spend their whole lives in large, highly ordered societies (Pulliam & Caraco 1984).

The majority of lizards live solitary lives, though temporary aggregations have been described in several species. Winter aggregations are known to occur in temperate zone species of *Eumeces*, *Urosaurus* and *Sceloporus* (Neill 1948; Worthington & Sabath 1966; Weintraub 1968; Ruby 1977). These aggregations have been found to have reproductive, feeding and thermoregulatory functions as they serve as mechanisms whereby certain activities take place. Mating (Pope 1937; Hoofien 1962), gestating (Graves & Duvall 1993; Seburn 1993) and nesting (Rand 1967; Bock & Rand 1989) aggregations can be associated with reproduction. Feeding aggregations have also been described (Vitt 1974; Arnold & Wassersug 1978). Sheltering (Hoofien 1962; Myres & Eells 1968) and basking (Hoofien 1962; Myres & Eells 1968) aggregations are found to have a thermoregulatory function. These temporary aggregations are also thought to have a possible anti-predatory (Vitt 1974) or water conserving function (Pope 1937; Myres & Eells 1968).



Only a few lizard species form long-term or permanent aggregations. Group-living lizards include, amongst others, several species of the Australian scincid genus *Egernia* (Bull *et al.* 2000). In the gidgee skink, *Egernia stokesii*, up to 16 individuals can be found to form stable social aggregations and share the same rock crevice for several years (Main & Bull 1996; Bull *et al.* 2000). The viviparous skink, *Tiliqua rugosa*, has been found to exhibit long-term pair-fidelity (Bull 1994). Stable aggregations have also been reported for the agamid, *Stellio caucasius* (Panov & Zykova 1995), the iguanid, *Sceloporus mucronatus mucronatus* (Lemos-Espinal *et al.* 1997), and females of *Liolaemus huacahuasicus* (Halloy & Halloy 1997). Unlike temporary aggregations, the stable aggregations of the species mentioned above also occur during the summer months, which suggest that these aggregations have functions other than those of thermoregulation and reproduction.

Graves & Duvall (1995) reviewed grouping behaviour in squamates and concluded that such aggregations occur as the result of either a limitation of resources like refuge sites (ecological constraints) or mutual attraction of conspecifics (philopatry), i.e., individuals within a group find it beneficial being in close proximity to conspecifics. Although, it should be noted, that these two causes are not necessarily mutually exclusive. Emlen (1994) also supports ecological constraints and philopatry as two possible causes for the evolution of group-living.

An individual's chances of surviving to reproduce may be improved in a number of ways by associating with conspecifics. The benefits of group-living can be divided into two categories: anti-predator effects and feeding benefits. According to Bertram (1978) there are five different ways in which associating in a group might help an individual avoid predation. Groups tend to be much scarcer than single individuals and therefore the chance of a predator missing a group is greater than for a single individual. The second way group-living may help an individual is in the detection of predators. The greater the numbers of detectors in a group the greater are the chances of early detection. The advantages of cohesive grouping in the detection of predators have been observed in red-billed weavers (Lazarus 1979) and meerkats (MacDonald 1986). The third benefit of group-living with regard to avoiding predation is deterring predators. A group of individuals may pose a greater threat to a predator than a single individual. In a less direct way, predators may be deterred by the lower capture success they might acquire with aggregated prey. Another benefit from living in groups is predator confusion. When groups of prey scatter the predators become confused and may find it difficult to track one individual. And the fifth benefit of group-living is the reduction of individual risk. This is also known as the "dilution effect", whereby the predator has a number of victims to

choose from, and the probability of any one individual being selected is the reciprocal of the group size (Barnard 1983). The benefits of group-living, such as, mating success, predator protection and defence against intruders have been observed in lizards (Stamps 1988).

According to Bertram (1978), the second category into which the benefits of group-living can be divided, is feeding benefits. There are various way in which associating in a group may benefit an individual with regard to feeding. Firstly, less time is spent within a group scanning for predators; therefore there will be more time to feed. Another benefit from group-living is finding better feeding areas. A group can cover a larger area when searching for food. Thirdly, individuals benefit from a group because members of the group provide each other with local information about food, observed in some lizard species (Stamps 1988). Group foraging has been observed in many bird species, e.g., gannets fish in groups (Nelson 1980), as well as black-headed gulls (Göttmark *et al.* 1986). Mammals such as lions, hyenas and Cape hunting dogs are also known to hunt in groups (Manning & Dawkins 1992). There is a number of other ways in which being in a group may influence an animal's survival prospects. Other feeding benefits, for instance, include increased efficiency in prey size selection and an increased opportunity to optimise return times to previously depleted but renewing food supplies (Barnard 1983).

In some cases group formation may improve thermal regulation (Barnard 1983). Winter aggregations in lizards are associated with a thermoregulatory function as observed in *Sceloporus jarrovi* (Ruby 1977) and *Urosaurus ornatus* (Worthington & Sabath 1966).

Group-living has its advantages, but then there are also disadvantages. Being near other individuals means increased competition for food, increased risk of disease transmission and greater conspicuousness to predators, therefore being in a group may increase the amount of interference an animal experiences in its feeding activity (Manning & Dawkins 1992). Grouping behaviour may also indirectly influence breeding success. A possible penalty of breeding in stable, cohesive groups is the potentially high risk of inbreeding (Manning & Dawkins 1992). In some group-breeding species, offspring cannibalism by group members constitutes an additional cost (Manning & Dawkins 1992). The behaviour that will be favoured by natural selection will be the one that favours the reproductive interests of the individual in the long run (Manning & Dawkins 1992).

The family Cordylidae, which is endemic to Africa, is predominantly comprised of rupicolous species, which are solitary in nature (Mouton & Van Wyk 1997). This family is divided into four genera: *Platysaurus*, *Cordylus*, *Pseudocordylus* and *Chamaesaura* (Lang 1991). Members of the genus *Platysaurus* (flat lizards), which are strictly rupicolous, have been reported to be gregarious in nature, and may be found in groups consisting of one male and up to 10 females and sub-adults sharing the same retreat (Broadley 1978; Branch 1998). Most members of the genus *Cordylus* are solitary and territorial in nature and are found to occur in both dense and diffuse colonies (Branch 1998). Yet, within this genus we do find three species, which tend to exhibit permanent grouping behaviour, namely *C. peersi* (Branch 1998), *C. macropholis* (Branch 1988; Mouton *et al.* 2000a), and *C. cataphractus* (Peers 1930; Mouton *et al.* 1999; Visagie 2001; Visagie *et al.* 2002).

*Cordylus cataphractus* is endemic to the west coast of South Africa, and occurs from the Orange River in the north, extending south along the coast and adjacent coastal inland



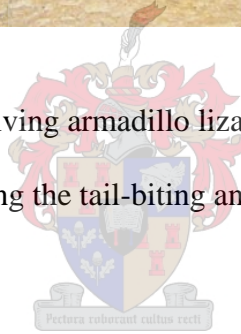
down to Piketberg, and inland as far as Matjiesfontein in the western Karoo (Mouton 1987, 1988). The vegetation types within the distribution range of *C. cataphractus* ranges from semi-desert in the north, to Namaqualand Coastal Belt, a subdivision of Succulent Karoo that consists predominantly of mesemb shrubs, along the coastal regions, and Succulent Karoo inland at Matjiesfontein (Acocks 1988). *Cordylus cataphractus* is found to occur predominantly in sandstone outcrops belonging to the Table Mountain Group, as granite outcrops seem to be unsuitable for use as refuges by this lizard species, possibly because granite does not fracture as readily and deeply enough as sandstone (Loveridge 1944).

The species is well known for its tail-biting behaviour (Figure 1). When threatened, an individual rolls into a tight ball and firmly grasps its tail in its mouth, thereby protecting its soft under parts, described in detail by Peers (1930) and Mouton *et al.* (1999). This is the reason why this lizard has received the common name, “armadillo lizard”.

*Cordylus cataphractus* has a heavily armoured morphology and is slow-moving and sluggish in nature (Losos *et al.* 2002). The entire body of *Cordylus cataphractus* is covered by rugose scales, some keeled, especially on the neck, legs and tail. The tail comprises whorls of large, rugose, serrate, strongly keeled, spinose scales above and along the lateral line. The head shields, which are found to be broader in males, are strongly rugose, with five to six rugose occipitals of which the outermost is pointed and directed obliquely backwards (Loveridge 1944). A slight degree of sexual dimorphism does occur in *Cordylus cataphractus*, with males being larger than females and males typically having a broader head (Mouton *et al.* 1999). According to Loveridge (1944), adult colouration is generally yellowish-brown (on a rare occasion chocolate-brown) on the head and back, with an even or mottled arrangement of these colours. The ventral gular region is yellow to



**Figure 1:** The group-living armadillo lizard, *Cordylus cataphractus*, displaying the tail-biting antipredatory behaviour.



light yellow with ventriculated, spotted, or veined black markings. The belly is clouded with dark brown or greenish-black streaks and spots (Loveridge 1944). Loveridge (1944) found variation in colour in relation to the environment where *C. cataphractus* occurred, which may indicate populational differences within the species.

Boie (1828) first described *Cordylus cataphractus*. Peers (1930), FitzSimons (1943) and Loveridge (1944) supplied the earliest information available on this species. Ecological studies conducted on *Cordylus cataphractus* started with general observations and descriptions by Peers (1930) and Rose (1950). Mouton *et al.* (1999) conducted studies on group structure within this species and found that groups may contain more than one adult male, one to a few adult females, and a few offspring. For example, in their study, they found one group contained seven adult males and only three adult females (Mouton *et al.* 1999).



*Cordylus cataphractus* is found to occur naturally in groups (Peers 1930; Mouton *et al.* 1999) and laboratory experiments have indicated that its grouping behaviour is the result of mutual conspecific attraction and not because of limited shelter availability (Visagie *et al.* 2005). It occurs in groups on a year round basis, and the grouping tendency is not restricted to any particular season or time of day.

#### *Causes of group-living in Cordylus cataphractus*

There are clear indications that group-living in *Cordylus cataphractus* has disadvantages. In a study conducted by Mouton *et al.* (2000c), stomach content data showed that there was a significant difference in the proportions of individuals with empty stomachs between

group-living and solitary individuals. This may indicate that competition among group members for prey items may be high and that competition may increase to an even greater degree in the dry season. There should thus be distinct advantages to living in groups, offsetting the disadvantages. A number of theories have been put forward as to why *C. cataphractus* tends to occur in groups.

1. Shortage of suitable crevices: *Cordylus cataphractus* and the two other *Cordylus* species that display some degree of grouping behaviour, *C. peersi* and *C. macropholis*, are endemic to the arid western coastal regions of southern Africa (Branch 1998). *Cordylus macropholis* is also the only terrestrial *Cordylus* species occurring in the western half of South Africa. Changes in availability of suitable rocky habitat along the coast due to rises in sea level may have forced the ancestor of this species to become terrestrial (Mouton *et al.* 2000c). The ancestor of *C. cataphractus* could have had to cope with similar changes in microhabitat availability in the coastal regions, forcing individuals to share available rock crevices and eventually resulting in permanent grouping behaviour in the species (Mouton *et al.* 1999).

Today, *Cordylus cataphractus* occurs over a large geographical area, including extensive mountainous areas where suitable crevices cannot be an ecological constraint anymore. Why has the species not reverted back to a solitary lifestyle? There must be some very distinct advantages to living in a group, keeping this behaviour enforced.

2. Reduced predation risk. An individual has a smaller chance of being detected in a group and a greater chance of detecting a predator due to the “dilution effect” and the “many eyes” hypothesis (Lima 1995; Lanham & Bull 2004). Yet, in a study conducted by Berry

(2002) little support was found for this hypothesis in *C. cataphractus*. The ‘safety in numbers’ hypothesis was tested on this species in a field study. Two findings support the hypothesis: Firstly, a positive correlation existed between group size and the distance that lizards perched from their crevice, and, secondly, lizards from large groups re-emerged from their crevice sooner following a predation threat than did lizards from small groups. Two other findings were equivocal: Individual vigilance, as indicated by head movement rate, seemed higher in large groups than in small ones, and group size generally did not seem to influence the distance at which lizards fled when approached by a human predator.

3. Clumped prey resources. According to Effenberger (2004), termitophagy (termite feeding) may be a key factor in the group-living behaviour of *Cordylus cataphractus*. Effenberger (2004) suggested that the ancestor of *C. cataphractus* was a solitary-living species, occurring in the arid western regions of South Africa. Termites became an increasingly important component in the diet of the ancestral form due to competition with other species or general food shortages in the semi-desert environment where it occurs. Predation pressure resulting from feeding out in the open led to the evolution of heavy armour, which in turn, affected the general mobility of the species and led to a reduction in activity outside the crevice. At some stage, juveniles did not have to disperse from their mother’s shelter crevice anymore, because of reduced competition for food at the crevice. Likewise, during the mating season, visiting mates did not have to leave after the mating period, because of reduced competition for food at the crevice. By staying at the mate’s refuge permanently, the mate-finding excursions could eventually be eliminated. Individuals that got lost during foraging excursions could potentially join any group. Fine-tuning to group-living occurred by gradually lowering metabolic rate (Mouton *et al.* 2000b) and fecundity (Flemming & Mouton 2002). Preliminary data suggested that a low

metabolic rate may be an important component of the group-living behaviour of *Cordylus cataphractus*, but requires further study (Mouton *et al.* 2000b). Termitophagy allows individuals to live in groups, as competition for prey items in the vicinity of the home crevice will be much less. Further, group-living will also put a limit on juvenile dispersal and the search for mates. Both these activities may have a high predation impact in this species, due to its heavily armoured morphology.

### *Termitophagy*

Termites have been reported as an important prey item for many animal species (Abensperg-Traun & Steven 1997). Specialization on ants and termites for food (myrmecophagy) is found to occur in a limited number of mammalian species (Redford 1987). Termite specialists among lizards include Australian agamid species, Australian gecko species such as *Diplodactylus conspicillatus*, *D. pulcher* and *Rhynchoedura ornata* (Pianka 1986), Australian skink species such as *Ctenotus ariadnae*, *C. grandis* and *C. pantherinus*, the Kalahari lacertid species *Pedioplanis lineoocellata*, *P. lugubris*, *P. namaquensis*, *Meroles suborbitalis*, *Heliobolus lugubris* (Huey & Pianka 1981), the Kalahari gecko, *Ptenopus garrulus* (Huey, Pianka & Vitt 2001), and the North American teiid *Cnemidophorus tigris* (Pianka 1966).

Colonies of social insects (termites, ants, bees and wasps), represent a concentrated source of energy, and therefore serve as a potentially rewarding food item for predators (Abensperg-Traun & Steven 1997). One factor that affects the selection of prey by termite-eating predators is relative abundance of the prey item (Abensperg-Traun & Steven 1997).

It has been found that termite abundance tends to decrease from arid to mesic regions (Matthews 1976; Stafford Smith & Morton 1990).

It has been found in previous studies that the southern harvester termite, *Microhodotermes viator*, is possibly the most important source of prey in the diet of *Cordylus cataphractus* (Mouton *et al.* 2000c). The southern harvester termite can be found throughout the South Western Cape in South Africa. It is known to construct permanent subterranean storage chambers connected to various foraging ports and a single hive (Coaton & Sheasby 1974; Annecke & Moran 1982). The soil mounds that form on the soil surface tend to become compacted when not removed by the elements, thereby forming hard, dome-shaped moundlets (Uys 2002). This species tends to be found in soils with high clay content (Picker *et al.* 2002). *Microhodotermes viator* can be found in a range of vegetation types, but prefers open veld and avoids fynbos on sandstone (Picker *et al.* 2002). Its diet consists mainly of small sticks and twigs (Uys 2002). Large numbers of these termites emerge during temperate weather conditions (Coaton & Sheasby 1974).

*Cordylus cataphractus* is listed as Vulnerable in the South African Red Data Book for Amphibians and Reptiles (Mouton 1988). It is very popular as a pet and the illegal pet trade poses a serious threat to this species. Because it lives in groups and is sluggish in nature, it is easily collected.

## Problem statement and objectives

The main aim of my study was to determine the role that termitophagy plays in the group-living behaviour displayed by *Cordylus cataphractus*. The following working hypothesis was formulated for the study: *The southern harvester termite, Microhodotermes viator, is an essential dietary component of Cordylus cataphractus*. From this, the following predictions were made:

- a) The range of *C. cataphractus* will be included in the range of *M. viator*.
- b) *Microhodotermes viator* will be included in the diet of *C. cataphractus* throughout the range of the latter.
- c) *Cordylus cataphractus* populations will exhibit high density in areas where termites are abundant.
- d) *Cordylus cataphractus* groups will be larger in areas where termites are abundant.
- e) Group size will be correlated with distance from nearest termite foraging port, with large groups occurring in close proximity to termite foraging ports.
- f) Height of crevices above ground-level will correlate with termite density, in areas of low-density crevices will be selected higher to increase field of vision.
- g) The height of crevices will also correlate with vegetation height.
- h) Group sizes will be smaller in areas with greater vegetation cover than in areas with little cover, as larger groups will need a more open field of vision to locate termite foraging ports.
- i) Termites will form a higher proportion of the diet for individuals from large groups.

Because of its heavy morphology and resultant vulnerability to aerial predation, *C. cataphractus* would be expected to occur in areas where solar radiation is high and

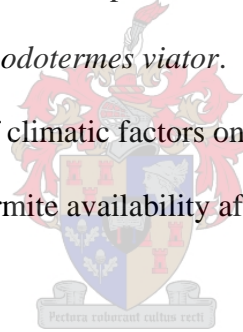


reduced basking times are required. To further reduce vulnerability to aerial predation, times of peak food availability will coincide with the mating period in *C. cataphractus*, thus avoiding two activity peaks. Two further predictions, not directly following from the hypothesis were therefore also tested in this study:

- j) The distribution of *C. cataphractus* will be influenced by solar radiation, with this lizard preferring areas with high solar radiation.
- k) The distribution of *C. cataphractus* will be influenced by rainfall, with this lizard preferring areas with a winter rainfall to a summer rainfall.

The study therefore has the following objectives:

- (1) To determine the degree of correspondence between the ranges of *Cordylus cataphractus* and *Microhodotermes viator*.
- (2) To investigate the role of climatic factors on the distribution of *C. cataphractus*.
- (3) To determine whether termite availability affects population density and group size in *C. cataphractus*.
- (4) To determine whether termite availability affects lizard crevice selection.
- (5) To determine whether vegetation height and cover affect crevice selection in *C. cataphractus*.
- (6) To determine the relationship between group size and termite utilization in *Cordylus cataphractus*.



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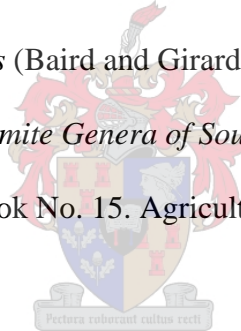
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**CHAPTER 2:**  
**GEOGRAPHICAL ANALYSIS OF THE DISTRIBUTION OF**  
***CORDYLUS CATAPHRACTUS***

**Introduction**

The armadillo girdled lizard, *Cordylus cataphractus*, is a group-living lizard endemic to the dry western regions of southern Africa (Mouton *et al.* 2000b). It occurs from the Orange River in the north, along the coast and adjacent coastal inlands down to Piketberg in the south, and inland as far as Matjiesfontein in the western Karoo (Mouton 1987, 1988). It is one of only a few lizard species permanently living in groups. Groups can consist of up to 60 individuals (Visagie 2001; Effenberger & Mouton 2006), but groups of two to six are the most common (Peers 1930; Branch 1998; Mouton *et al.* 1999).

The southern harvester termite, *Microhodotermes viator*, appears to be the most important prey item of *C. cataphractus* (Mouton *et al.* 2000b). Effenberger (2004) and Mouton *et al.* (2005) proposed that the heavy reliance on termites as a food source was responsible for the evolution of group-living in this species. If termitophagy is the proximate cause of group-living in *C. cataphractus*, as suggested by Effenberger (2004) and Mouton *et al.* (2005), one would expect a high degree of correspondence in the ranges of *C. cataphractus* and *M. viator*. While *C. cataphractus* is restricted to the arid western parts of South Africa, *Microhodotermes viator* has a much wider range (Coaton & Sheasby 1974). It is clear that even if the presence of this termite species is an important determinant of the range of *C. cataphractus*, there must also be other determining factors restricting *C. cataphractus* to only a subsection of the range of the termite.

Topography usually has an indirect effect on plant or animal distribution by determining microclimate, of which some parameters, e.g. monthly minimum temperature, have a direct effect on species survival and can thus impose strong distributional limits. Yet, according to Guisan & Hofer (2003), models fitted with climatic predictors proved superior to those fitted with topographical predictors. Topography is certainly a proxy for important environmental features other than climate, but in their study explained less variance than climate alone. Their results further suggest that the distributional limits of most reptile species are strongly associated with climatic, predominantly temperature-related factors.

Several studies have indicated that the intensity of environmental temperatures may influence activity levels of lizards (Magnusson *et al.* 1985; Haigen & Fengxiang 1995).

The following climatic variables have also been indicated as cues for reptile activity:

rainfall (Whitford & Creusere 1977), solar radiation (Van Damme *et al.* 1987),

supplemental water (Jones & Ballinger 1987), and prey availability following rain

(Reynolds 1982). Colli *et al.* (2003) found that in seasonal habitats lizard reproduction can be correlated with rainfall, because of the influence of rainfall on arthropod abundance.

*Cordylus cataphractus* is a comparatively sluggish cordylid (Losos *et al.* 2002), its sluggish nature probably related to its heavy armature and very low resting metabolic rate (Mouton *et al.* 2000c). Due to the sluggish nature of this lizard one would expect that activity out in the open would be restricted to a minimum. Solar radiation is important for lizards, as they need the energy obtained from the sun to carry out basic functions (Bogert 1949; Huey 1982). In the case of *C. cataphractus*, solar radiation may have an even greater influence on the distribution of the species, because of competition for basking sites within

the group. Extended basking times may result in high aerial predation. Mouton and Flemming (2001) found that heliothermic, rock dwelling cordylids living in cold environments are all fast runners, and a fast retreat into a crevice is the only means of escaping attacks by aerial predators. Because of the constraints of its morphology and of living in groups, *C. cataphractus* will probably not survive in areas of low solar radiation.

Arthropod abundance is greatly determined by rainfall (Reynolds 1982). Therefore one would expect the distribution of *C. cataphractus* to be indirectly influenced by rainfall, especially by the rainfall season. This is due to the fact that the rainfall season largely determines when arthropod abundance will peak, which ultimately would influence the annual peak in lizard activity.

In this study, I investigated the relationship between *Cordylus cataphractus* and *Microhodotermes viator* by determining the degree of correspondence in their distribution ranges. As climate also plays a role in the distribution of most species, I also investigated the influence of various climatic factors on the distribution of *C. cataphractus*. The results of this analysis should allow an evaluation of the possible impacts of global climate change on this Red Data lizard species. The following predictions were evaluated:

- (1) The range of *C. cataphractus* will be included in the range of *M. viator*.
- (2) *Microhodotermes viator* will be included in the diet of *C. cataphractus* throughout the range of the latter.
- (3) The distribution of *C. cataphractus* will be influenced by rainfall, with this lizard preferring areas with a winter rainfall over areas with a summer rainfall.
- (4) The distribution of *C. cataphractus* will be influenced by solar radiation, with this lizard preferring areas with high solar radiation.

## Materials and Methods

### *Locality data*

Locality data for *Cordylus cataphractus* were obtained from the CapeNature Biodiversity Database, which includes presence data from various institutions, including Port Elizabeth Museum, Transvaal Museum, SA Museum Cape Town, Ellerman Collection at the University of Stellenbosch and Cape Nature Conservation Records. Absence data was obtained from survey records of the Ellerman Collection and each absence data point was verified by the collector. *Microhodotermes viator* locality data were obtained from the literature (Coaton & Sheasby 1975).

### *Presence of termites*

A total of 53 *Cordylus cataphractus* localities were investigated for the presence of termites (Figure 2.1). Stomach contents of *C. cataphractus* within the Ellerman Collection of Stellenbosch University were analysed from 26 localities for the presence of termites. Together with the stomach content data, each site where *C. cataphractus* was found during the current study (27 localities) was investigated for the presence of termites. The presence of termites was determined either by lizard scat analysis, the presence of termite foraging ports, or the sighting of active termites.

### *Climate analysis*

Climatic data were obtained for all localities where *C. cataphractus* were recorded to date, as well as adjacent localities where the lizard was found not to occur. The climatic data set was obtained from the South African Atlas of Agrohydrology and Climatology (Shulze 1997). These data were in the form of ESRI Shape Files, from which the climatic data for

each locality were extracted. Climatic data included mean annual precipitation (MAP); mean annual temperature (MAT); solar radiation per month (SOL01-12); mean daily minimum temperature (TMIN01-12); mean daily maximum temperature (TMAX01-12); potential evaporation (APAN01-12); and median rainfall (RAIN01-12). From the above mentioned variables the following climatic variables were derived and used in the analyses: MAP, MAT, average monthly solar radiation, average monthly TMIN, average monthly TMAX, average monthly APAN, average monthly RAIN, average daily summer rainfall, average daily winter rainfall and the ratio of winter rainfall over summer rainfall, where a value greater 1.0 indicates winter rainfall and less than 1.0 summer rainfall. A topographical variable, namely altitude (ALT), was also included.

The climatic predictors of the geographical distribution of *Cordylus cataphractus* were investigated by means of three models, in order to test the congruence of the dataset via different statistical methods. The three methods, which were used, were Classification Trees (CART), General Discriminant Analysis (GDA) and Logistic Regression. CART and GDA models do not rely on *a priori* hypotheses about the relation between independent and dependent variables. The CART method consists of recursive partitions of the dimensional space defined by the predictors into groups that are as homogeneous as possible in terms of response. The tree is built by repeatedly splitting the data, defined by a simple rule based on a single explanatory variable. At each split the data are partitioned into two exclusive groups, each of which is as homogeneous as possible (Thuiller *et al* 2003). A GDA determines which variables discriminate between two or more naturally occurring groups, i.e., it can be used to determine which climatic variables are the best predictors of the distribution of *C. cataphractus*.

In CART and GDA a random sample of 60 % of the database was selected as a training data set to calibrate the models and the remaining 40 % was used for the testing data set to evaluate the resulting models predictions (Fielding & Bell 1997).

Lastly, presence and absence data for *C. cataphractus* were also regressed against the climatic variables using a logistic regression. Logistic regression determines the relationship between several independent or predictor variables and a dependent variable, i.e., this method allows a comparison between localities where the species occurs (presence represented by 1) and where it does not occur (absence represented by 0). The equation for the logistic regression model can be stated as  $y = b_0 / \{1 + b_1 * \exp(b_2 * x)\}$  (Statistica 7.1).

#### *Data analysis*

Species distributions were visualized using the minimum polygon technique and the degree of overlap was determined using standard geographic information systems (GIS) techniques. The computer programme ESRI: Arc View GIS 3.2 was used to carry out all GIS techniques (Redlands, CA, USA). Datasets were analysed using the Statistica 7.1 computer package. The proportion of *C. cataphractus* sites containing termites was compared to those not containing termites using a Z-test. The level of significance was set at  $P < 0.05$ .

## Results

### *Range overlap*

The range of *Cordylus cataphractus* was completely included within the range of *Microhodotermes viator* (Figure 2.2).

### *Presence of termites*

Of the 53 *C. cataphractus* sites sampled, 38 (73 %) were positive for termite presence in either stomach contents or faecal samples of the lizards ( $z = 2.691$ ;  $P = 0.007$ ). It should be noted that lizards from 11 of the 53 localities from where stomach contents were analysed had empty stomachs, therefore at less than 10 % of the localities from where lizard stomach contents could be obtained the contents did not include termite material.

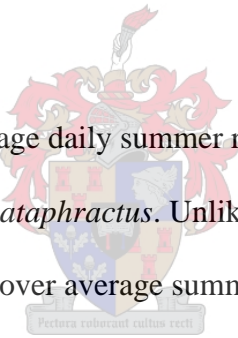
### *Climate analysis*

All three models provided generally good results for predicting the distribution of *Cordylus cataphractus*. The Classification Tree predicted 88 % of the presence of *C. cataphractus* correctly and 83 % of the absences. The General Discriminant analysis performed slightly better predicting 92 % of the presence of *C. cataphractus* correctly and 87 % of the absences. And lastly the logistic regression performed just as well predicting 93 % of the presence of this lizard species correctly and 86 % of the absences.

In all three models the most significant climatic variables were average monthly solar radiation and average daily summer rainfall. CART yielded average monthly solar radiation as the most important predictor of the distribution of *C. cataphractus*. According to this model *C. cataphractus* prefers areas with average monthly solar radiation greater



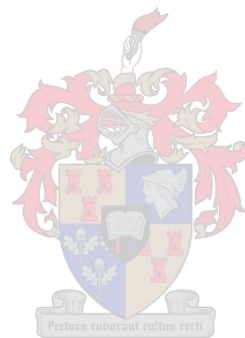
than  $22.32 \text{ MJ.m}^{-2}.\text{day}^{-1}$ . Average daily summer rainfall was the second most important predictor of the distribution of *C. cataphractus*. This lizard prefers areas with an average daily summer rainfall less than 9.33 mm. This model predicted a 95 % absence of *C. cataphractus* in areas where average daily summer rainfall reached values greater than 9.33 mm. Average monthly solar radiation in combination with average daily summer rainfall predicted 81 % of *C. cataphractus* presence. *Cordylus cataphractus* prefers areas with an average monthly solar radiation greater than  $22.32 \text{ MJ.m}^{-2}.\text{day}^{-1}$ , together with an average daily summer rainfall less than or equal to 9.33 mm. Similarly the model predicted a 71 % absence of *C. cataphractus* when average monthly solar radiation was less than or equal to  $22.32 \text{ MJ.m}^{-2}.\text{day}^{-1}$  and average daily summer rainfall was less than or equal to 9.33 mm.



The GDA (Table 2.1) yielded average daily summer rainfall as the most important predictor of the distribution of *C. cataphractus*. Unlike in the first model the GDA yielded the ratio of average winter rainfall over average summer rainfall, i.e., whether this lizard is predominantly a winter rainfall species, as the second most important determinant of its distribution. Average monthly solar radiation was the third most important predictor. A best subsets regression was carried out, which determined that the first three variables were the most important predictors in the distribution of *C. cataphractus*, with the addition of more variables not yielding a substantially better fit to the model.

Finally the logistic regression supported the GDA and also found average daily summer rainfall to be the most significant predictor of the distribution of *C. cataphractus*. Average monthly solar radiation was the second most important predictor. Unlike the first two models, the logistic regression found average daily winter rainfall as the third most

important predictor of the distribution of *C. cataphractus*. And lastly the ratio of average winter rainfall over average summer rainfall was the fourth most significant predictor of the distribution of *C. cataphractus*. All four of the above variables had  $P$  values  $< 0.05$  and the 95 % confidence interval around the odds ratios did not include the value 1.0 and can therefore be considered as good predictors of the distribution of *C. cataphractus* (Table 2.2). Yet it should be noted that average daily summer rainfall and average monthly solar radiation are better predictors than the other two variables, namely average daily winter rainfall and ratio. Though significant, the last two variables are marginal as 1.0 lies just outside their 95 % confidence intervals.



## Discussion

The finding that the distribution range of *C. cataphractus* completely falls within the range of *M. viator* and that the termite was included in the diet of the lizard at the majority of sites investigated; lend support to the suggestion that *M. viator* is a key species in the diet of *C. cataphractus* and an important determinant of its range. Swart *et al.* (1999) found a similar relationship between the Cape Pangolin (*Manis temninckii*) and the ant species (*Anoplolepis custodiens*). Like *M. viator*, *A. custodiens* is a fairly widespread and a relatively abundant species. The Cape Pangolin is, however, not found throughout the range of its prey source, *A. custodiens*. Swart *et al.* (1999) concluded that the range of the Cape Pangolin might be limited due to the activity patterns of *A. custodiens*, as temperature plays a major role in ant activity. The ants escape the cold by hibernating deep below the soil surface. If the temperature remains cold for long periods of time the ants will remain deep underground, out of reach of the shallow-digging Cape pangolin. In this situation pangolins would be left without their primary food source for extended periods during winter in these regions, and this is probably the reason that the pangolin's range does not extend into these temperate regions (Swart *et al.* 1999). A similar decrease in termite activity during cold winters may take place throughout the range of *M. viator*, thereby limiting the current distribution of *C. cataphractus* to areas within the termite's range, where the termite is active most of the year. Climate may therefore play an important indirect role in determining the range of *C. cataphractus* by affecting the availability of its main prey source, but this aspect will need further investigation.

The results obtained in this study indicate that the geographical range of *Cordylus cataphractus* is mainly determined by two climatic variables, namely average daily

summer rainfall (or the absence of summer rain), and average monthly solar radiation, i.e., sufficient levels of solar radiation. The variable that had the best correlation with regards to the presence of *C. cataphractus* was a low average daily summer rainfall, indicating that this species prefers areas with very little or no summer rain. Together with a low average daily summer rainfall *C. cataphractus* also prefers areas with a high average daily winter rainfall, which indicates that this species is predominantly a winter rainfall species. If *C. cataphractus* was a summer rainfall species then this lizard would have experienced two activity peaks per annum, namely one for feeding during late summer when invertebrate prey availability peaks, and one for mating during spring (see Flemming & Mouton 2002). Visagie (2001) found that in the Graafwater area *Cordylus cataphractus* activity peaks during late winter to spring, coinciding with a peak in invertebrate prey and also being the time when mating takes place. A single peak in annual activity may be the optimum situation for this species, as overall exposure to aerial predation will be lessened considerably.



The second most important climatic variable, which showed the best correlation with regards to the distribution of *C. cataphractus*, was found to be average monthly solar radiation. Ectotherms, including reptiles, have a requirement for a high body temperature and rely on solar radiation for energy (Bogert 1949; Huey 1982). All members of the genus *Cordylus* are heliothermic baskers (Mouton & Van Wyk 1997), and they thus utilize direct solar radiation to obtain preferred body temperatures during times of activity. Sufficient solar radiation may be a problem in the case of *C. cataphractus* as competition for basking sites among group members and the fact that individuals always stay close to the crevice during general maintenance behaviour (Visagie 2001), may prevent many individuals from using available solar radiation optimally. Therefore this species will need a certain level of

solar radiation to meet its energy requirement and will not be able to survive in areas where levels of solar radiation are low. Individuals spend most of their time in close proximity to their home crevice. During the summer months (December - February) activity levels are extremely low (Visagie 2001), and most individuals remain inside the crevice for extended periods of time (Mouton & Flemming 2001).

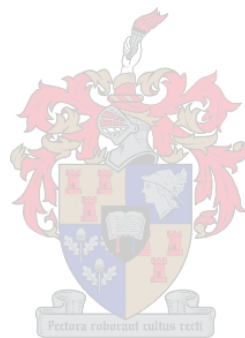
Lizards from higher elevations and thus colder climates spent more time basking in the open than those species that are found at lower elevations (Mouton & Flemming 2001).

*Cordylus cataphractus* will not be able to survive in cold areas, as solar radiation will be a limiting factor. It is thus not surprising that *C. cataphractus* is mainly a lowland species, occurring in flat areas and along the foothills of mountains (personal observations).

According to the predictions of Midgley *et al.* (2001), part of the Western Cape may lose a significant portion of its current winter rainfall due to global warming. Such a shift in rainfall patterns may seriously affect the range of *Cordylus cataphractus*, which is presently restricted to the winter rainfall area.

Various other factors may further determine the distribution of *Cordylus cataphractus*, such as geology and vegetation. This study is just a small step into the understanding of this species current distribution. Therefore it should be noted that the conclusions made in this study were based on climatic variables alone, but future studies are necessary to determine which set of abiotic and biotic factors determine the distribution of this species, which could be better used in predictive models of this species' range and the effects which global warming may have on it.

In conclusion, the distribution of *Cordylus cataphractus* is in part determined by the presence of termites and climatic factors, of which the absence of summer rain indicated by a low average daily summer rainfall and average monthly solar radiation had the greatest influence.



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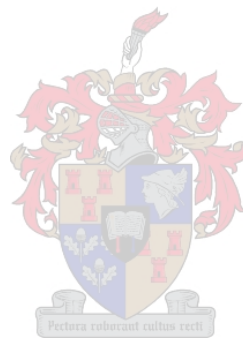
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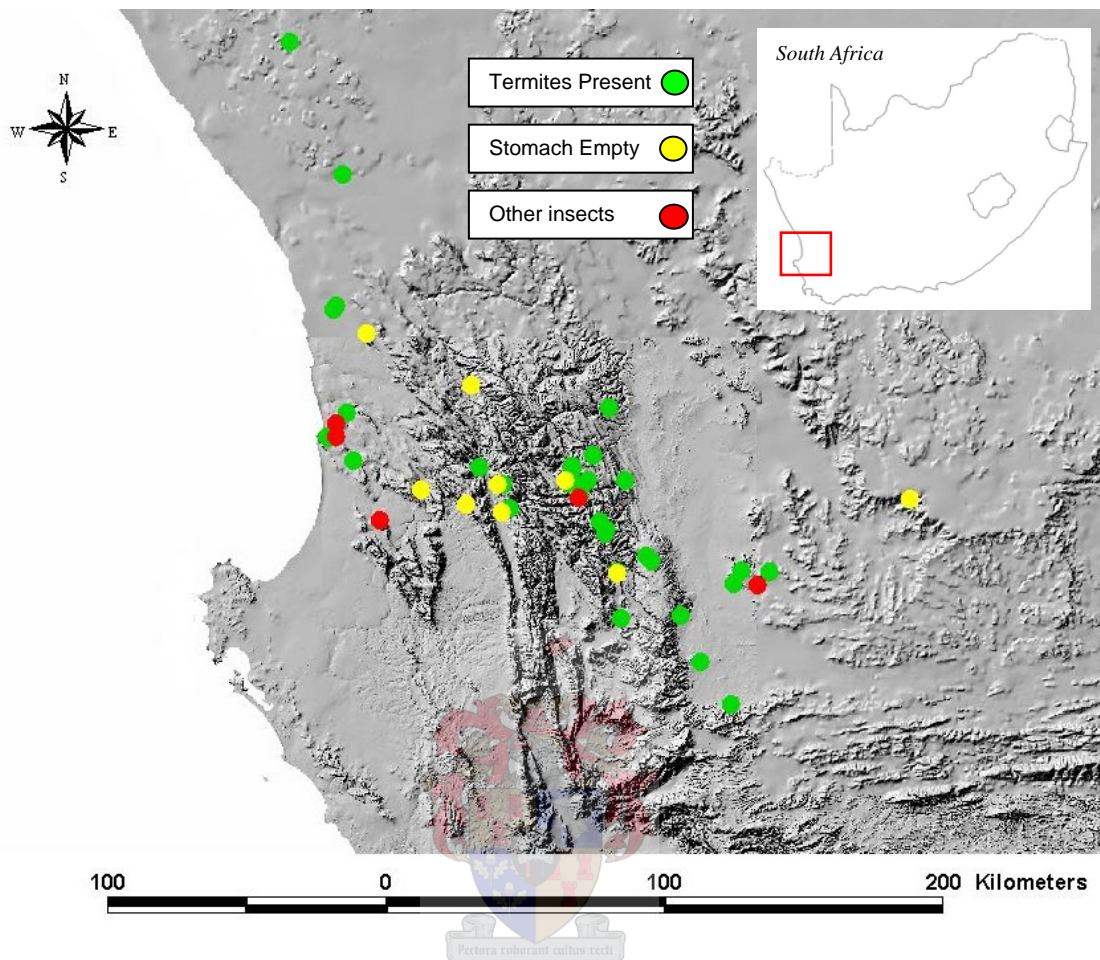
**Table 2.1** – Results obtained in the GDA, listing the three most important predictors of the distribution of *Cordylus cataphractus*

	<b>Test</b>	<b>Value</b>	<b>F</b>	<b>p-level</b>
<b>Intercept</b>	Wilks	0.77	48.22	< 0.001
<b>Summer Rainfall</b>	Wilks	0.97	4.62	0.033
<b>Ratio</b>	Wilks	0.97	5.08	0.026
<b>Average solar radiation</b>	Wilks	0.81	36.71	< 0.001

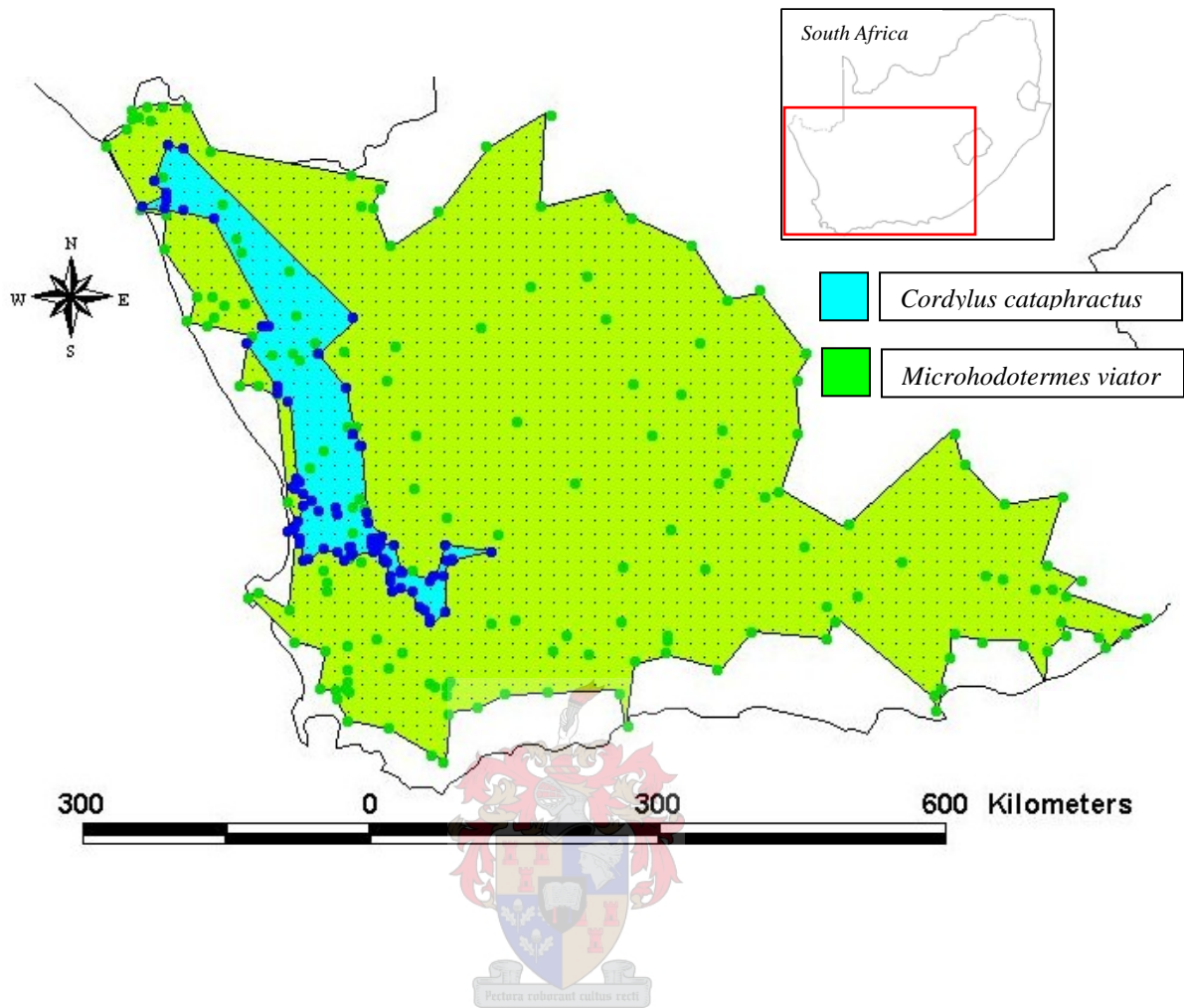


**Table 2.2** – Results obtained in a logistic regression analysis, with the first four climatic variables being the significant predictors of the distribution of *Cordylus cataphractus*

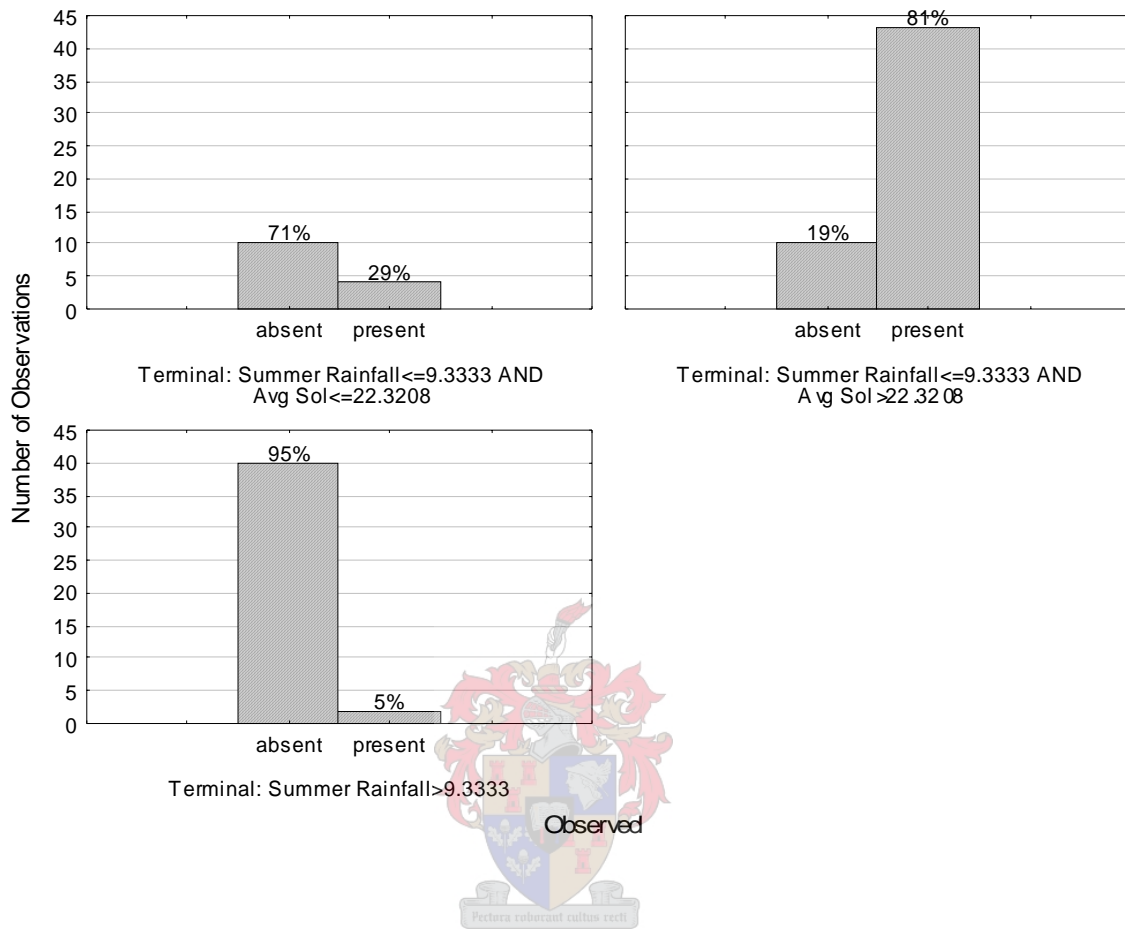
	<b>Estimate</b>	<b>Standard Error</b>	<b>p-level</b>	<b>Wald statistic</b>	<b>p-level</b>	<b>Odds ratio</b>
<b>Summer rainfall</b>	-0.99	0.23	0.00003	18.05	0.000022	0.37
<b>Average solar radiation</b>	3.32	1.46	0.24	5.14	0.023	27.70
<b>Winter rainfall</b>	0.096	0.044	0.029	4.85	0.028	1.10
<b>Ratio</b>	-0.51	0.24	0.032	4.65	0.031	0.060
<b>Avg Min</b>	2.31	1.39	0.098	2.76	0.097	10.055
<b>Avg Max</b>	-2.27	1.40	0.11	2.63	0.10	0.10
<b>Avg APAN</b>	-0.054	0.047	0.25	1.32	0.25	0.95
<b>ALT</b>	-0.0006	0.0016	0.71	0.14	0.71	0.99



**Figure 2.1** – Map indicating the 53 *Cordylus cataphractus* localities, which were checked for the presence of the southern harvester termite, *Microhodotermes viator*, with localities where the termite was present indicated in green, where lizard stomachs were empty in yellow and where lizard stomachs contained other insect material in red.



**Figure 2.2** – Map indicating 100 % overlap between the distribution of the armadillo lizard, *Cordylus cataphractus* (indicated in turquoise) and the southern harvester termite, *Microhodotermes viator* (indicated in bright green).



**Figure 2.3** – Results obtained in the Classification Tree analysis.



**CHAPTER 3:**  
**THE EFFECT OF TERMITE ABUNDANCE ON POPULATION  
DENSITY, GROUP SIZE AND CREVICE SELECTION IN THE  
ARMADILLO LIZARD, *CORDYLUS CATAPHRACTUS***

**Introduction**

The armadillo lizard, *Cordylus cataphractus*, is one of few lizard species permanently living in groups (Mouton *et al.* 1999; Visagie *et al.* 2005; Costandius *et al.* 2006). Groups can consist of up to 60 individuals (Visagie 2001; Effenberger & Mouton 2006), but sizes of two to six are the norm (Peers 1930; Branch 1998; Mouton *et al.* 1999). *Cordylus cataphractus* is a heavily built, spiny lizard, which is relatively sluggish compared to other cordylids (Peers 1930; Branch 1998; Losos *et al.* 2002). It also displays the peculiar antipredatory behaviour of gripping its spiny tail in its mouth and rolling into a tight ball when threatened (Mouton *et al.* 1999).

The southern harvester termite, *Microhodotermes viator*, is the most important prey item of *C. cataphractus* (Mouton *et al.* 2000). Effenberger (2004) and Mouton *et al.* (2005) suggested that the heavy reliance on termites as a food source was the causative agent in the evolution of group-living in this species. To harvest termites, the lizards need to visit the termite foraging ports, which can be considerable distances away from the lizard's home crevice (Effenberger 2004). The heavy armour and the tail-biting antipredatory behaviour of *C. cataphractus* probably evolved in response to predation pressure by terrestrial predators during these visits (Mouton *et al.* 2005). Due to their heavy armour, these lizards have low sprinting abilities (Losos *et al.* 2002) and are therefore particularly vulnerable to aerial predation during general

maintenance behaviour around the rock crevice, such as basking. Grouping behaviour possibly evolved to lessen the effects of aerial predation by taking advantage of predation reduction effects of living in groups ('many eyes' and 'dilution' effects; Lima 1995; Lanham & Bull 2004). Termitophagy will facilitate group-living by alleviating competition for food among group members at the home crevice.

If termitophagy is the overarching cause of group-living in *C. cataphractus*, as suggested by Effenberger (2004) and Mouton *et al.* (2005), one would expect a close relationship between termite density and lizard density and also termite density and lizard group size. Like other cordylids, *C. cataphractus* is a typical sit-and-wait forager, lacking prey chemical discrimination ability (Mouton *et al.* 2000). One would therefore expect that termite activity at the foraging ports of a termite nest will have to be seen by the lizards from the crevice refuge before individuals will venture out to these ports to harvest the termites. The height above ground level of the available perches at the refuge rock should be important, as it will determine the field of vision of the lizard. One would expect that in areas where termite density is low, lizards will select crevices high above ground level to increase their field of vision and to improve the chances of seeing active termites. Likewise, one would also expect a close correlation between vegetation height and crevice height above ground level.

In this study I investigated the relationship between termite abundance and *C. cataphractus* abundance and termite abundance and lizard group size. I also investigated the effects of termite abundance and vegetation height on crevice selection by *C. cataphractus*. If significant correlations between these parameters are found, it will provide some support for the hypothesis that termitophagy is the overarching cause of group-living in *C. cataphractus*, as proposed by Effenberger (2004) and Mouton *et al.* (2005). My study was conducted at a local as well as a regional scale.

## Materials and Methods

### *Study sites*

Local scale: A study site was selected at Eland's Bay, along the West Coast of South Africa. The site included a range of rocky outcrops of Table Mountain Sandstone (Figure 3.1). The area has a Mediterranean climate with an average annual rainfall of 275 mm of which an average of 70 % falls in the winter (Burgers 1995). The vegetation types include Langebaan Dune Sandveld and Leipoldville Sand Fynbos (Mucina *et al.* 2005).

Regional scale: Ten study sites were selected throughout the range of *Cordylus cataphractus* (Figure 3.2). These sites represented a variety of habitats, from coastal lowland to inland montane areas, from succulent Karoo vegetation to Mountain Fynbos, and from areas with annual rainfall as low as 50 mm (e.g., the Tankwa region (Low & Rebelo 1996)) to areas with annual rainfall above 250 mm (e.g., the Brandwacht and Lambert's Bay regions (Low & Rebelo 1996)). In the south, the geology of the coastal lowlands is characterized by deep dune sand with highly calcareous areas and sandstone outcrops, whereas, inland within the Fynbos Biome, it consists mostly of quartzitic sandstone with shale and conglomerate lenses (Low & Rebelo 1996). The geology in the Succulent Karoo Biome is dominated by siltstone and shale, yet granites and sandstones are also present (Low & Rebelo 1996).

### *Data collection*

At the Eland's Bay site, twenty five 25 m x 25 m quadrats were plotted along a 1.4 km transect. At each of the ten sites selected for the regional scale study, a 1225 m<sup>2</sup> quadrat (in most cases a 35 m x 35 m square) was plotted to include the maximum number of lizard groups possible. During surveys, all crevices within each quadrat were carefully inspected and at those crevices where lizards were found, special care was taken to record all lizards in the

group. It was therefore sometimes necessary to open crevices with a crow bar, but in all such cases, damage to crevices was kept to a minimum. For each *C. cataphractus* group found, I measured the height of the crevice above ground level and also the height of the highest vantage point at the refuge rock. Vegetation height at the site was taken as the mean of at least two persons' estimations of the general vegetation height. Vegetation cover, expressed as a percentage of surface area, was again estimated by at least two persons and the mean value taken. In each case, I was one of the people making the estimation, and the other estimation was made by one of two fellow field workers.

At the Eland's Bay site, the 25 quadrats were all selected with a surplus of crevices available within each so that crevice availability did not play a major role in determining lizard density. In the regional analysis, this was not possible to achieve, and I had to take differences in crevice availability into account. For each quadrat, I determined the total number of lizards it could accommodate by estimating and adding the numbers of lizards individual crevices could house. I used crevice saturation, i.e., the number of lizards recorded as a percentage of the maximum number of lizards a quadrat could accommodate, had all the available crevices been filled to capacity, as an indicator of lizard density.

In this study, the density of termite foraging ports was recorded rather than termite density as measurement of actual subterranean termite density is extremely difficult (Gibson 2001). Furthermore, *Microhodotermes viator* concentrates its foraging at the foraging ports (Coaton & Sheasby 1974) and when harvesting termites, *C. cataphractus* therefore targets the foraging ports (Effenberger 2004). Termite foraging port density should thus be a good surrogate for termite density. Termite foraging port density was determined by plotting three randomly selected 10 × 10 m squares within each quadrat. Three to four people walked the 10 × 10 m

squares, flagging all potential foraging ports. The potential ports were then rechecked for authenticity. The foraging ports of *M. viator* were in most cases easily identified by their oval shape and the concentration of dry plant material around them (Figure 3.3). Sometimes plant material was absent and the port opening blocked, making them more difficult to find. Termite foraging port density for the site was taken as the mean of the densities calculated for the three 10m x 10m squares and was expressed as number of ports per square meter. At Eland's Bay, the mean distance from the crevice to the five nearest termite foraging ports were recorded for each lizard group.

The fieldwork in this study was conducted under Western Cape Nature Conservation Permit No: 001 – 201 - 00016, issued to Prof. P. le F. N. Mouton.

#### *Data analysis*

Data were tested for normality and homogeneity of variances using the Kolmogorov-Smirnov test, with Lilliefors' correction (Sokal & Rohlf 1981). Pearson's product moment and Spearman Rank Order correlations were used to test for possible correlations. Data were square root transformed where applicable. All statistical analyses were conducted using the programs SigmaStat 3.0 and Statistica 6.0. The level of significance was set at  $P < 0.05$ .



## Results

### *Local scale*

The mean values of all the parameters recorded at the Eland's Bay site, are listed in Table 3.1 and the correlation values in Table 3.2. No correlation was found between lizard density and termite foraging port density, lizard group size and port density, lizard density and vegetation height, and lizard group size and vegetation height. Lizard group size was, however, positively correlated with the mean distance to the five nearest termite foraging ports (Figure 3.4), as well as to the distance to the first nearest termite foraging port (Figure 3.5).

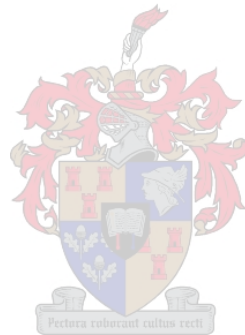
Significant correlations were also found between mean height of lizard crevice above ground level and termite density (Figure 3.6), mean highest vantage point of the crevices containing groups above ground level and termite density (Figure 3.7), mean height of the lizard crevice above ground level and vegetation height (Figure 3.8), and the mean highest vantage point and vegetation height (Figure 3.9). Mean crevice height was correlated with vegetation cover (Figure 3.10) and the mean highest vantage point of the crevice above ground level was also correlated with vegetation cover (Figure 3.11). There was a positive correlation between lizard density and group size (Figure 3.12).

### *Regional scale*

The mean values of all the parameters recorded at the 10 sites in the regional analysis, are listed in Table 3.3 and the correlation values in Table 3.2. No correlation was found between mean crevice height and termite foraging port density, mean crevice vantage point and termite foraging port density, crevice height and vegetation height, crevice height and vegetation cover, crevice vantage point and vegetation height and crevice vantage point and vegetation cover.

Crevice saturation was positively correlated with termite foraging port density across the 10 study sites (Figure 3.13). Although the relationship between mean lizard group size and termite foraging port density across the sites was not statistically significant, there was a distinct positive tendency in the data. Crevice saturation and mean lizard group size were, however, positively correlated (Figure 3.14).

Both crevice saturation and mean lizard group size were negatively correlated with vegetation height across the study sites (Figure 3.15 and Figure 3.16). I also found that termite foraging port density was negatively correlated with vegetation height (Figure 3.17).



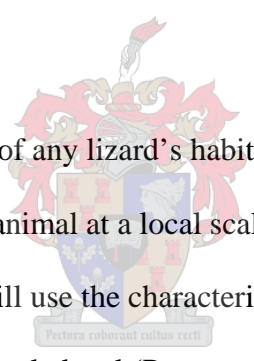
## Discussion

Some of the results obtained in this study point to a very close relationship between the group-living lizard, *Cordylus cataphractus*, and the southern harvester termite, *Microhodotermes viator*. Not only does the correlation between lizard abundance and termite foraging port abundance that I recorded at a regional scale, show that *M. viator* abundance may regulate *C. cataphractus* density, but the correlations between vegetation cover/height and crevice characteristics also show that conditions allowing the optimal harvesting of the termites may be of prime importance.

Similar close relationships between termites and lizards have been reported elsewhere. In a study conducted by Morton & James (1988) on the Australian lizard fauna, for example, it was found that as termite abundance and diversity declined, lizard diversity also declined. In another study, James (1991) related some of the observed differences in ecology and behaviour between *Ctenotus pantherinus* and other species of *Ctenotus* to the specialization of the former on termite prey. In Australia termites are abundant in spinifex grasslands (Morton & James 1988) and according to James (1991) termites will most probably be available at times when other invertebrates, which rely on green herbage, are not, due to the fact that termites are able to sufficiently survive xeric conditions. As a result of obtaining such a regular food supply such as termites, *C. pantherinus* may be able to maintain sufficient body condition to reproduce in years when the low densities of other invertebrate prey prevents other species of *Ctenotus* from accumulating enough fat reserves to reproduce. James (1991) concluded that the relative “immunity” of *C. pantherinus* to the rise and fall of invertebrate prey availability might account for this species’ more stable activity and population densities, and higher juvenile survival rates.



The density of *C. cataphractus* at any given locality will be the net result of a wide range of determining factors, including climatic ones as found in Chapter 2. The effect of termite foraging port density on lizard density and group size may thus to a large degree be obscured by the effects of these other factors. In this regard, the positive tendency in the data that I recorded in my analysis of the influence of termite port density on group size, may also be considered an indicator of the close relationship between *C. cataphractus* and *M. viator*. Yet, it should be noted that this correlation yielded a very low  $r$  value and for future studies, a dataset including lizard groups with greater variation in group size and with more large groups should yield a better understanding on the relationship between lizard group size and termite abundance.

The image is a faint watermark of a university crest, likely from the University of Cambridge, centered on the page. It features a shield with various symbols, topped with a crown and a crest, and a motto scroll below. The crest is rendered in a light, semi-transparent style.

Vegetation is an important aspect of any lizard's habitat as it interacts with the morphology, physiology, and behaviour of the animal at a local scale, which in turn may have further implications on how the animal will use the characteristics of a specific landscape at a microscale, mesoscale and macroscale level (Porter *et al.* 2002). The effect of vegetation height and cover on crevice selection by *C. cataphractus* indicates that it may be important for the lizards to see termite activity from the refuge crevice before going out to harvest the termites. Like other cordylids, *C. cataphractus* is a typical sit-and-wait forager relying on vision to detect prey (Cooper *et al.* 1997; Mouton *et al.* 2000). Although its heavy armour would provide some protection against terrestrial predators when going out to harvest termites, one would expect excursions to be as brief as possible, i.e., following the shortest route to and from the foraging ports and spending the shortest possible time at the ports. Although vegetation cover may provide protection during foraging excursions, it will at the

same time impair vision. Throughout the distribution range of *C. cataphractus* along the arid western parts of South Africa, vegetation cover is sparse.

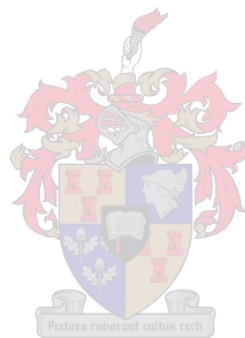
*Cordylus cataphractus* also includes other invertebrate prey in its diet besides the southern harvester termite (Mouton *et al.* 2000). In the group situation, there should thus be competition among group members for these additional prey items that venture close to the crevice. Mouton *et al.* (2000), for example, found a larger proportion of individuals with empty stomachs in large groups than in small groups. One would therefore expect that high termite abundance or high termite availability close to a crevice would lessen intra-group competition and allow groups to be larger, larger group sizes being advantageous in terms of predation avoidance (Lima 1995; Lanham & Bull 2004). I was unable to show any correlation between foraging port density and group size in this study. A possible reason for this may be the overriding effect that crevice availability and size will have on group size.

The finding that lizards select crevices higher above ground level when termite foraging port density is high is also not one that I expected. One would have thought that lizards would select higher vantage points in areas where termite abundance is low to increase their chances of spotting termite activity. I cannot at this stage provide a logical explanation for the positive correlation between crevice height and foraging port density recorded in this study.

The positive correlation that I recorded between crevice saturation and group size is a clear indication that group size is also to some degree dictated by crevice availability. The causative agents for the evolution of sociality are usually divided into two categories, namely, ecological constraints, where groups form due to a shortage of resources, and philopatry, where individuals gain by being in close proximity to conspecifics (Emlen 1994). It is clear

from my results that the two categories are in this case not mutually exclusive, grouping behaviour may be dictated by philopatric factors, but actual group size may be determined by environmental constraints.

In conclusion, the findings of this study confirm that the southern harvester termite plays a central role in the ecology of the armadillo lizard, *C. cataphractus*, in not only dictating lizard density, but also lizard group size, and, in combination with vegetation height, crevice selection by the lizards.



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**Table 3.1** – Table containing the variables recorded in the 25 quadrats at Elandsbaai, with the means and standard errors included where applicable.

Quadrat number	No of lizards in quadrat	Mean lizard group size	Mean termite foraging port density (nr/m <sup>2</sup> )	Mean crevice height (mm)	Mean crevice top point(mm)	Vegetation height (mm)	Vegetation cover (%)
1	3	3 ± 0.0 S.E	0.03 ± 0.01 S.E	20 ± 0.00 S.E	45 ± 0.00 S.E	55	0.4
2	5	2.5 ± 0.5 S.E	0.08 ± 0.005 S.E	14 ± 6.00 S.E	55 ± 5.00 S.E	60	0.6
3	2	2 ± 0.0 S.E	0.04 ± 0.02 S.E	40 ± 0.00 S.E	60 ± 0.00 S.E	55	0.45
4	2	2 ± 0.0 S.E	0.07 ± 0.02 S.E	20 ± 0.00 S.E	30 ± 0.00 S.E	50	0.35
5	7	1.75 ± 0.48 S.E	0.9 ± 0.02 S.E	61.3 ± 15.33 S.E	103.8 ± 11.61 S.E	40	0.8
6	8	4 ± 1.00 S.E	0.14 ± 0.03 S.E	60 ± 10.00 S.E	130 ± 20.00 S.E	70	0.7
7	8	1.75 ± 0.25 S.E	0.12 ± 0.005 S.E	80 ± 33.42 S.E	117.5 ± 33.76 S.E	90	0.7
8	12	3 ± 0.71 S.E	0.20 ± 0.01 S.E	97.5 ± 17.02 S.E	132.5 ± 25.62 S.E	70	0.8
9	5	2.5 ± 1.5 S.E	0.17 ± 0.03 S.E	30 ± 20.00 S.E	70 ± 30.00 S.E	50	0.6
10	6	3 ± 1.00 S.E	0.24 ± 0.01 S.E	35 ± 25.00 S.E	85 ± 5.00 S.E	45	0.8
11	6	2 ± 0.58 S.E	0.21 ± 0.03 S.E	33.3 ± 3.33 S.E	83.3 ± 8.82 S.E	70	0.8
12	10	2.5 ± 0.5 S.E	0.27 ± 0.07 S.E	95 ± 11.9 S.E	146.3 ± 16.5 S.E	70	0.9
13	1	1 ± 0.00 S.E	0.25 ± 0.04 S.E	60 ± 0.00 S.E	100 ± 0.00 S.E	40	0.6

Quadrat number	No of lizards in quadrat	Mean lizard group size	Mean termite foraging port density (nr/m2)	Mean crevice height (mm)	Mean crevice top point(mm)	Vegetation height (mm)	Vegetation cover (%)
14	2	1 ± 0.00 S.E	0.23 ± 0.02 S.E	55 ± 35.00 S.E	75 ± 25.00 S.E	40	0.65
15	8	2.67 ± 0.67 S.E	0.16 ± 0.00 S.E	50 ± 0.00 S.E	76.7 ± 8.82 S.E	40	0.6
16	3	1.5 ± 0.5 S.E	0.17 ± 0.05 S.E	70 ± 40.00 S.E	110 ± 60.00 S.E	70	0.7
17	7	1.75 ± 0.48 S.E	0.18 ± 0.03 S.E	72.5 ± 32.76 S.E	102.5 ± 30.92 S.E	70	0.55
18	16	2.67 ± 0.92 S.E	0.18 ± 0.03 S.E	61.7 ± 14.93 S.E	98.3 ± 20.88 S.E	70	0.6
19	4	2 ± 0.00 S.E	0.11 ± 0.01 S.E	45 ± 5.00 S.E	75 ± 15.00 S.E	60	0.8
20	10	3.33 ± 1.33 S.E	0.12 ± 0.02 S.E	56.7 ± 26.03 S.E	90 ± 30.00 S.E	60	0.55
21	11	1.83 ± 0.31 S.E	0.11 ± 0.005 S.E	28.3 ± 14.47 S.E	65 ± 15.65 S.E	50	0.5
22	7	1.75 ± 0.75 S.E	0.10 ± 0.00 S.E	30 ± 9.13 S.E	55 ± 5.00 S.E	50	0.8
23	23	3.29 ± 0.52 S.E	0.29 ± 0.08 S.E	23.3 ± 5.38 S.E	48.6 ± 3.4 S.E	60	0.6
24	17	2.43 ± 0.37 S.E	0.13 ± 0.00 S.E	48.6 ± 19.57 S.E	72.9 ± 17.00 S.E	60	0.8
25	8	1.6 ± 0.25 S.E	0.6 ± 0.02 S.E	32.6 ± 14.41 S.E	56.6 ± 7.18 S.E	40	0.75



**Table 3.2** – Summary of the correlation statistics. Cases where the correlations are significant are shaded.

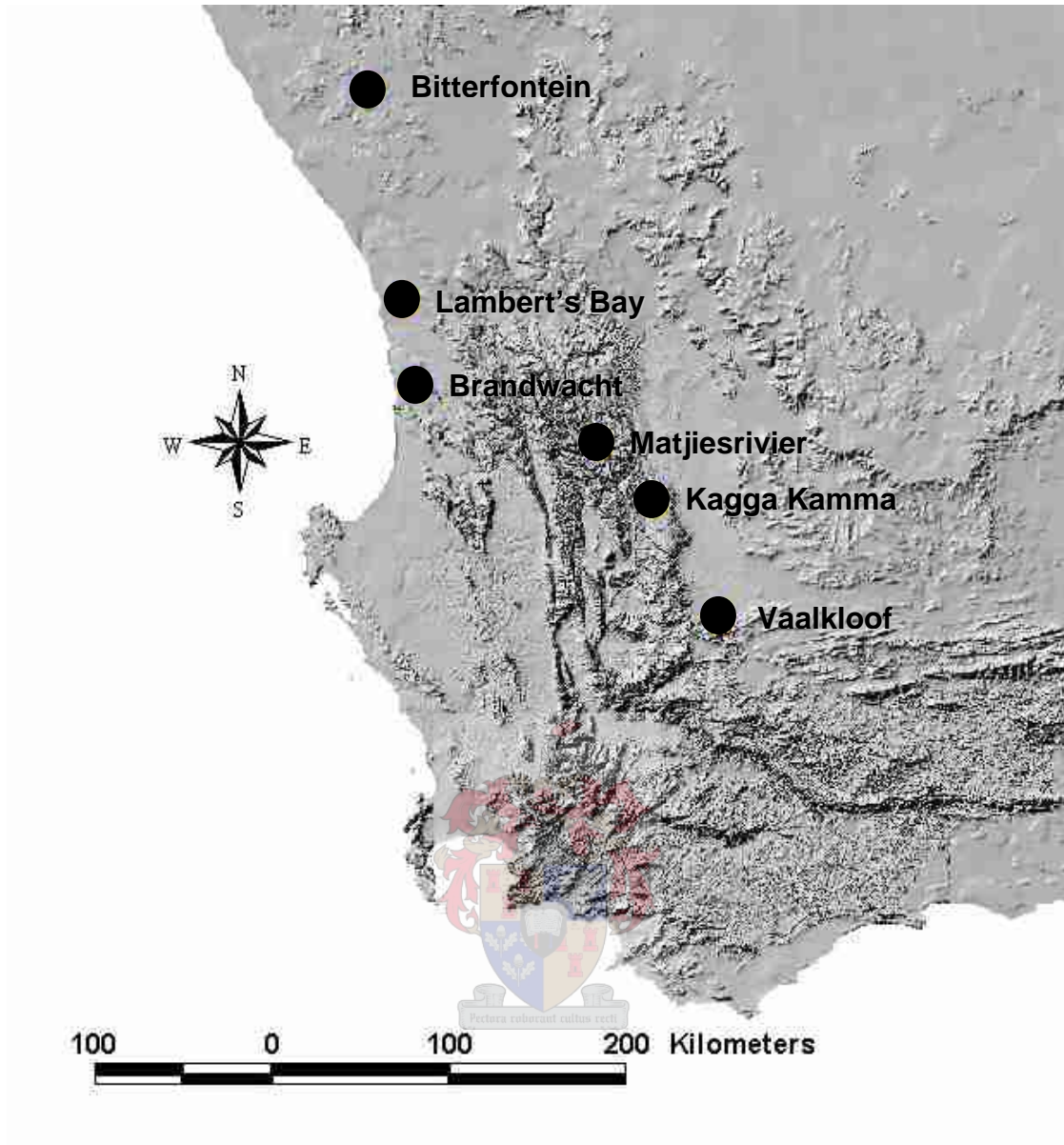
Correlations investigated	Local	Regional
Lizard density/crevice saturation & port density	$r = 0.10, P = 0.63, n = 25$	$r = 0.64; P = 0.046, n = 10$
Group size & port density	$r = -0.08, P = 0.69, n = 25$	$r = 0.60; P = 0.07, n = 10$
Lizard density & vegetation height	$r = 0.36, P = 0.08, n = 25$	$r = -0.64; P = 0.04, n = 10$
Group size & vegetation height	$r = 0.28, P = 0.18, n = 25$	$r = -0.66; P = 0.04, n = 10$
Group size & port distance	$r = 0.23, P = 0.04, n = 82$	Did not test
Crevice height & port density	$r = 0.55, P = 0.0046, n = 25$	$r = -0.37, P = 0.3, n = 10$
Crevice height & vegetation height	$r = 0.47, P = 0.02, n = 25$	$r = -0.06, P = 0.08, n = 10$
Crevice height & vegetation cover	$r = 0.44, P = 0.03, n = 25$	$r = 0.16, P = 0.67, n = 10$
Vantage point & port density	$r = 0.61, P = 0.0011, n = 25$	$r = -0.37, P = 0.3, n = 10$
Vantage point & vegetation height	$r = 0.51, P = 0.0092, n = 25$	$r = 0.04, P = 0.89, n = 10$
Vantage point & vegetation cover	$r = 0.55, P = 0.0049, n = 25$	$r = 0.12, P = 0.75, n = 10$
Crevice saturation/Lizard density & group size	$r = 0.45, P = 0.03, n = 25$	$r = 0.86; P = 0.0015, n = 10$
Port density & vegetation height	$r = 0.09, P = 0.66, n = 25$	$r = -0.72; P = 0.02, n = 10$

**Table 3.3** – Summary of the variables recorded per quadrat at the ten selected sites, with means and standard errors included where applicable.

Site	Crevice saturation (%)	Number of lizard groups	Mean lizard group size	Mean crevice height (mm)	Mean vantage point (mm)	Vegetation height (mm)	Vegetation Cover (%)	Mean termite foraging port density (#/m <sup>2</sup> )
Bitterfontein	59	4	2.5 ± 0.87 SE	187.5 ± 68.85 SE	400 ± 61.24 SE	300	0.3	0.1 ± 0.04 SE
Brandwacht	48	4	3.25 ± 0.63 SE	437.5 ± 190.80 SE	637.5 ± 343.01 SE	300	0.15	0.15 ± 0.05 SE
Kagga Kamma 1	56	7	2.14 ± 0.46 SE	472.9 ± 132.73 SE	857.1 ± 152.92 SE	700	0.5	0.03 ± 0.03 SE
Kagga Kamma 2	53	6	2.83 ± 0.83 SE	133.3 ± 16.67 SE	350 ± 40.82 SE	700	0.7	0.06 ± 0.03 SE
Lambert's Bay 1	67	15	2.13 ± 0.22 SE	130 ± 41.35 SE	410 ± 51.22 SE	300	0.5	0.2 ± 0.04 SE
Lambert's Bay 2	78	4	3.5 ± 1.32 SE	262.5 ± 94.37 SE	625 ± 131.5 SE	300	0.5	0.16 ± 0.03 SE
Lambert's Bay 3	90	5	3.6 ± 0.93 SE	50 ± 38.73 SE	450 ± 132.29 SE	400	0.2	0.11 ± 0.01 SE
Matjiesrivier 1	25	2	1 ± 0.00 SE	0 ± 0.00 SE	300 ± 100.00 SE	800	0.2	0.04 ± 0.01 SE
Matjiesrivier 2	14	2	1 ± 0.00 SE	400 ± 100.00 SE	750 ± 150.00 SE	900	0.3	0.04 ± 0.01 SE
Vaalkloof	31	5	1.6 ± 0.4 SE	630 ± 162.48 SE	850 ± 159.69 SE	400	0.5	0 ± 0.00 SE



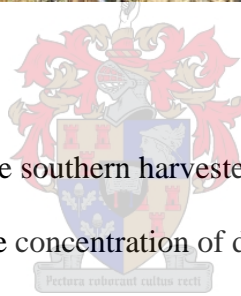
**Figure 3.1** – The study site at Eland's Bay, along the West Coast of South Africa. The site included a range of rocky outcrops of Table Mountain Sandstone.

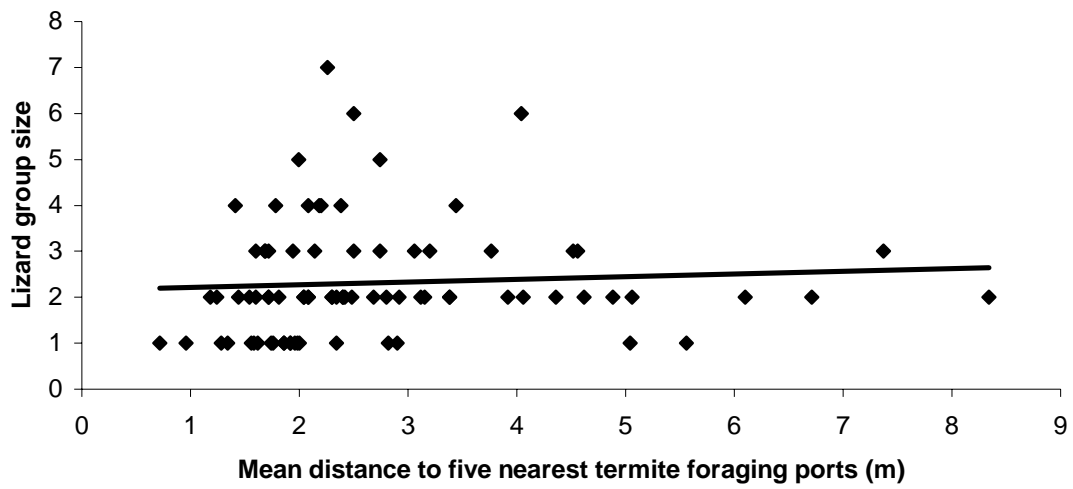


**Figure 3.2** – Map indicating the location of the ten regional study sites, namely Brandwacht (1), Bitterfontein (1), Kagga Kamma (2), Lambert's Bay (3), Matjiesrivier (2) and Vaalkloof (1), where *Cordylus cataphractus* was sampled, with number of quadrats at site indicated in brackets.



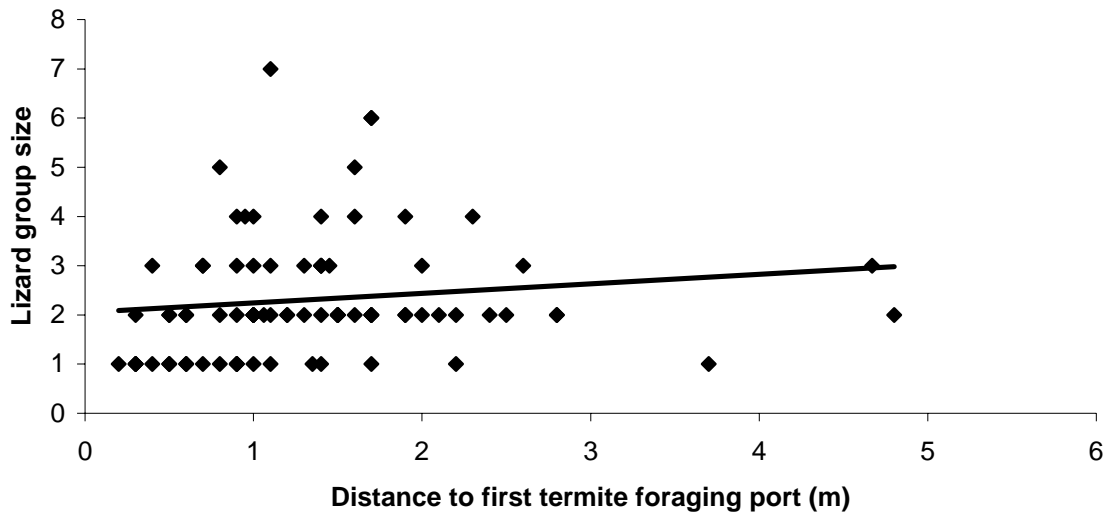
**Figure 3.3** – A foraging port of the southern harvester termite *Microhodotermes viator*, easily identified by its oval shape and the concentration of dry plant material around it.





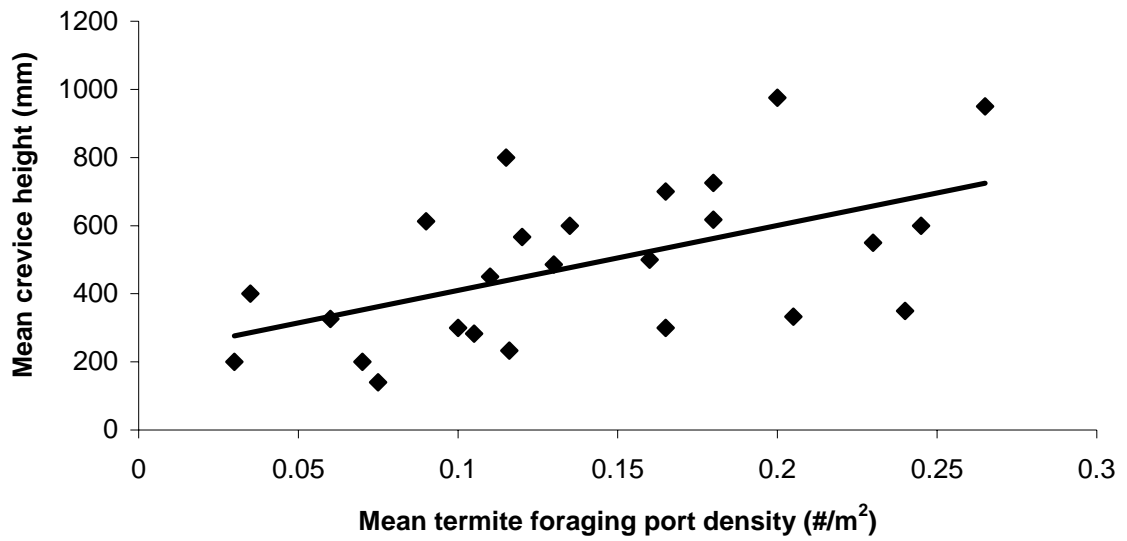
**Figure 3.4** – Graph indicating a positive correlation, at the local scale, between lizard group size and mean distance to five nearest termite foraging ports ( $r = 0.23$ ,  $P = 0.042$ ,  $n = 82$ ).





**Figure 3.5** – Graph indicating a positive correlation, at the local scale, between lizard group size and the distance to the first nearest termite foraging port ( $r = 0.28$ ,  $P = 0.010$ ,  $n = 82$ ).

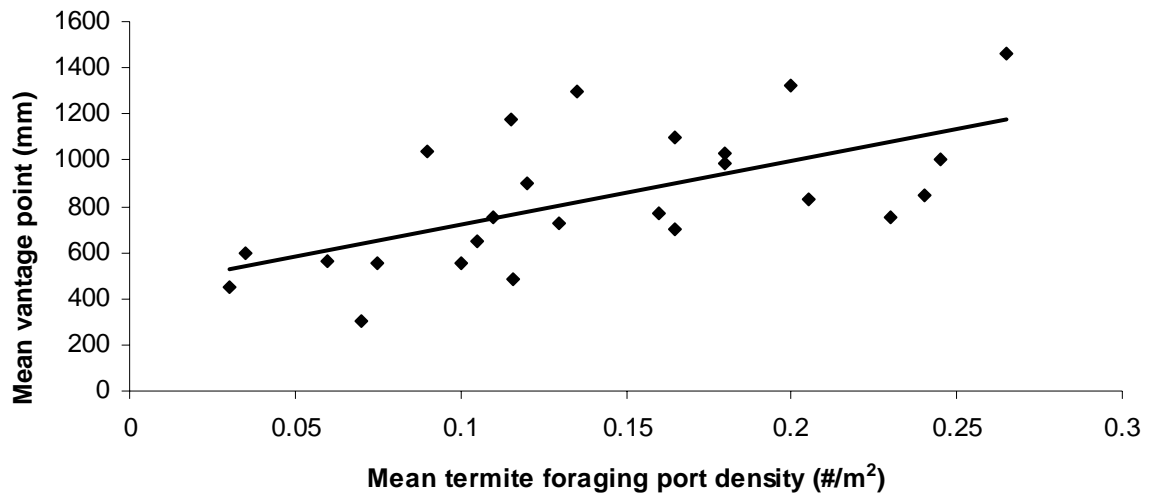




**Figure 3.6** – Graph indicating a positive correlation, at the local scale, between mean height of lizard crevice above ground level and mean termite foraging port density ( $r = 0.55$ ,  $P = 0.0046$ ,  $n = 25$ ).

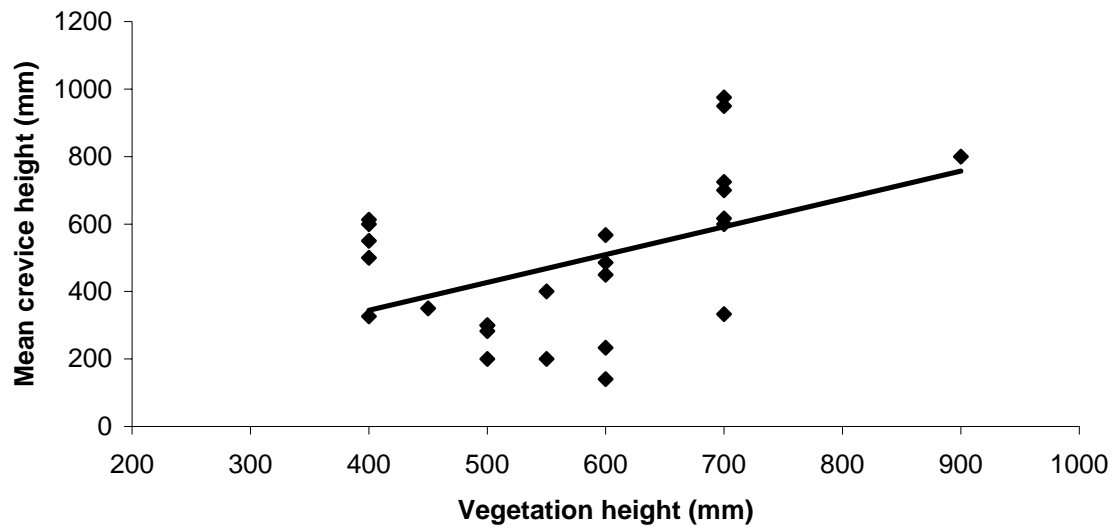






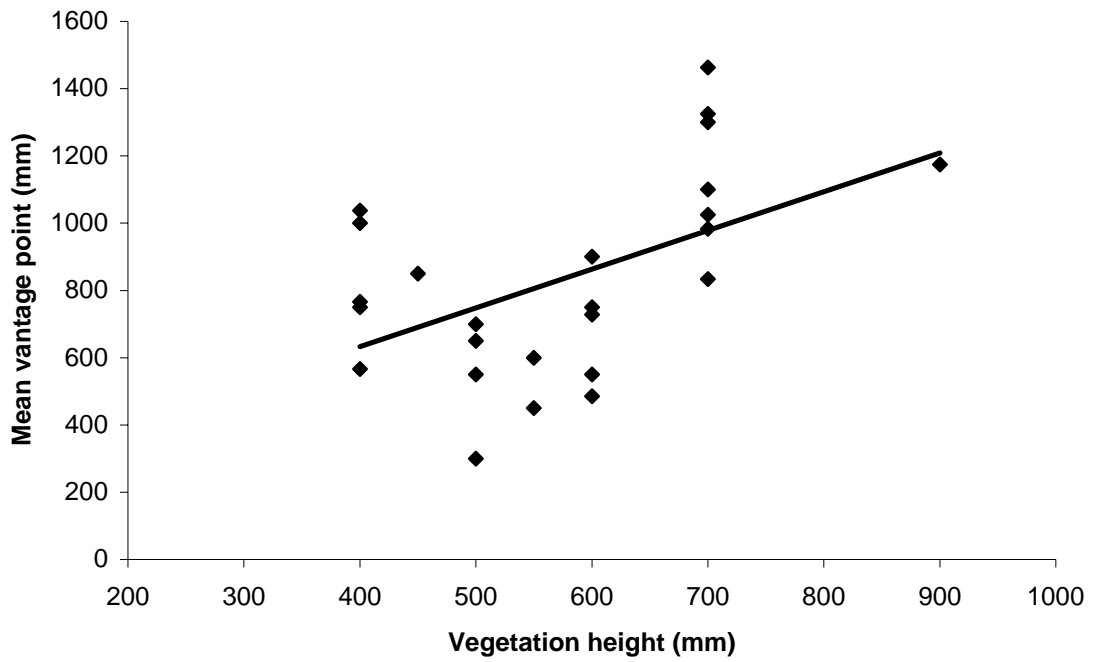
**Figure 3.7** – Graph indicating a positive correlation, at the local scale, between mean vantage point of lizard crevice above ground level and mean termite foraging port density ( $r = 0.61$ ,  $P = 0.0011$ ,  $n = 25$ ).



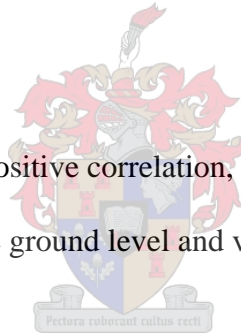


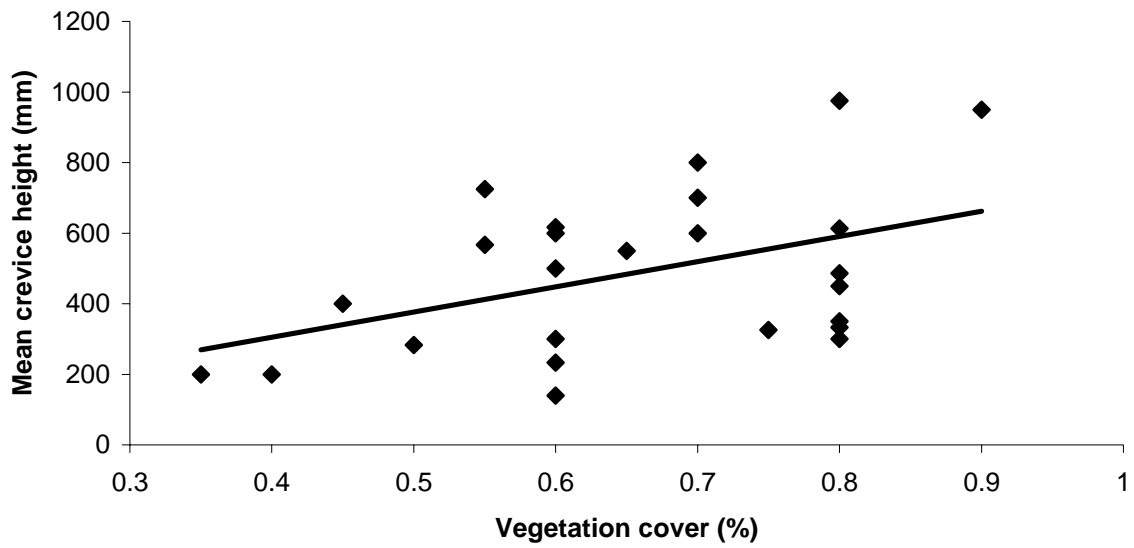
**Figure 3.8** – Graph indicating a positive correlation, at the local scale, between the mean height of the lizard crevice above ground level and vegetation height ( $r = 0.47$ ,  $P = 0.018$ ,  $n = 25$ ).





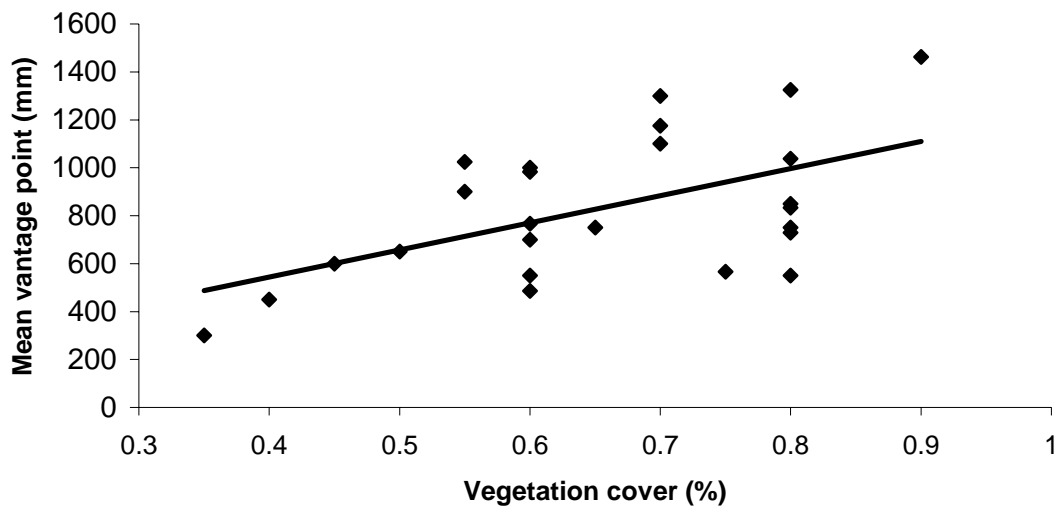
**Figure 3.9** – Graph indicating a positive correlation, at the local scale, between the mean vantage point of the crevice above ground level and vegetation height ( $r = 0.51$ ,  $P = 0.0092$ ,  $n = 25$ ).





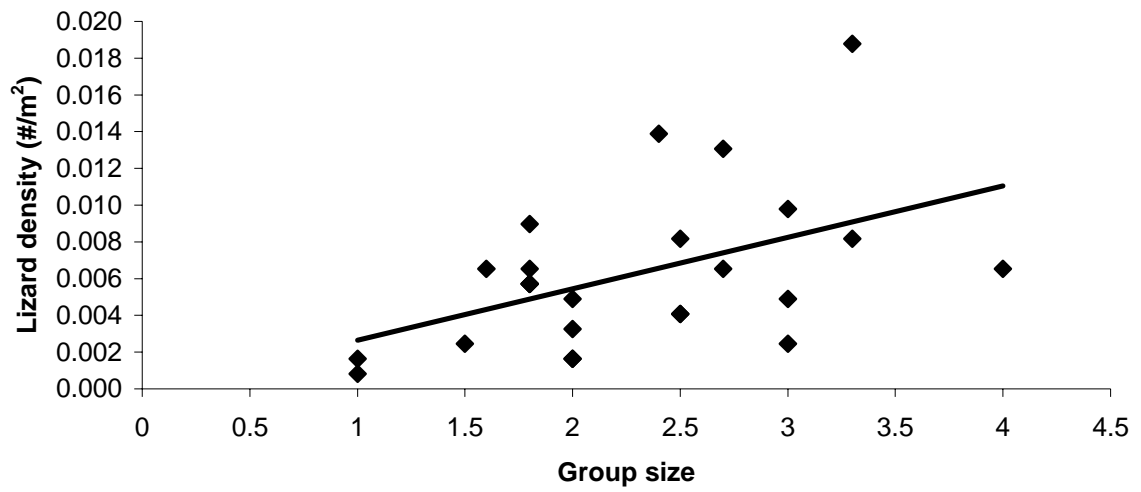
**Figure 3.10** – Graph indicating a positive correlation, at the local scale, between the mean height of the lizard crevice above ground level and vegetation cover ( $r = 0.44$ ,  $P = 0.027$ ,  $n = 25$ ).



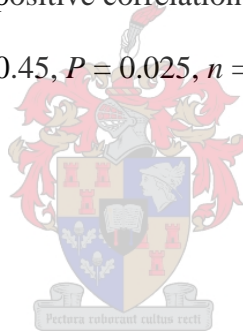


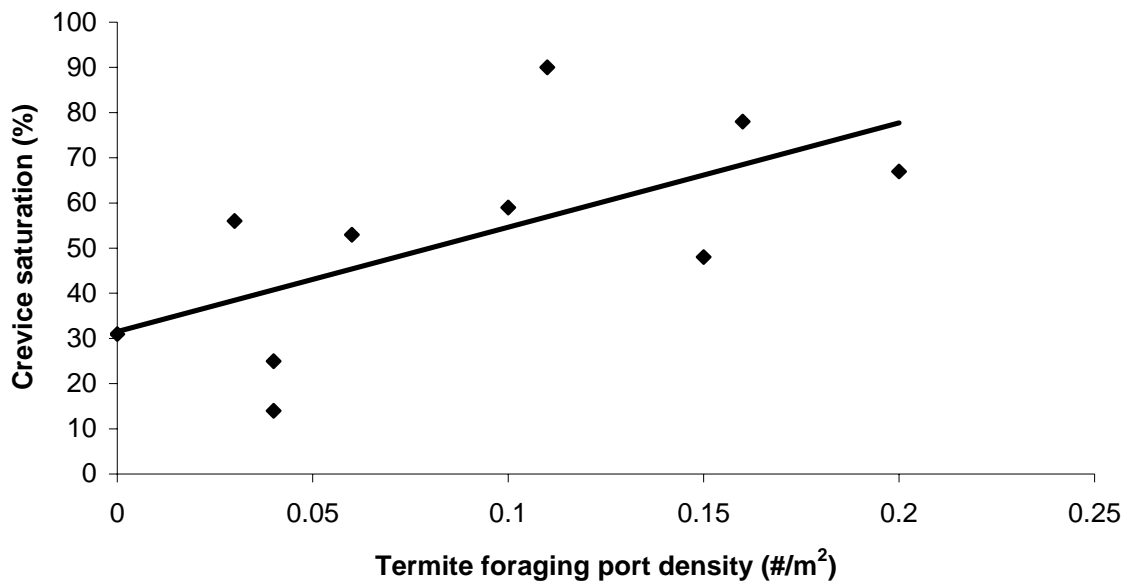
**Figure 3.11** – Graph indicating a positive correlation, at the local scale, between the mean vantage point of the crevice above ground level and vegetation cover ( $r = 0.55$ ,  $P = 0.0049$ ,  $n = 25$ ).



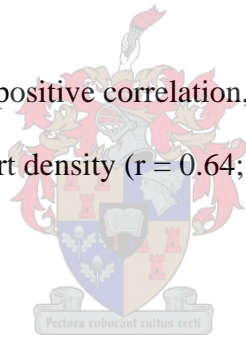


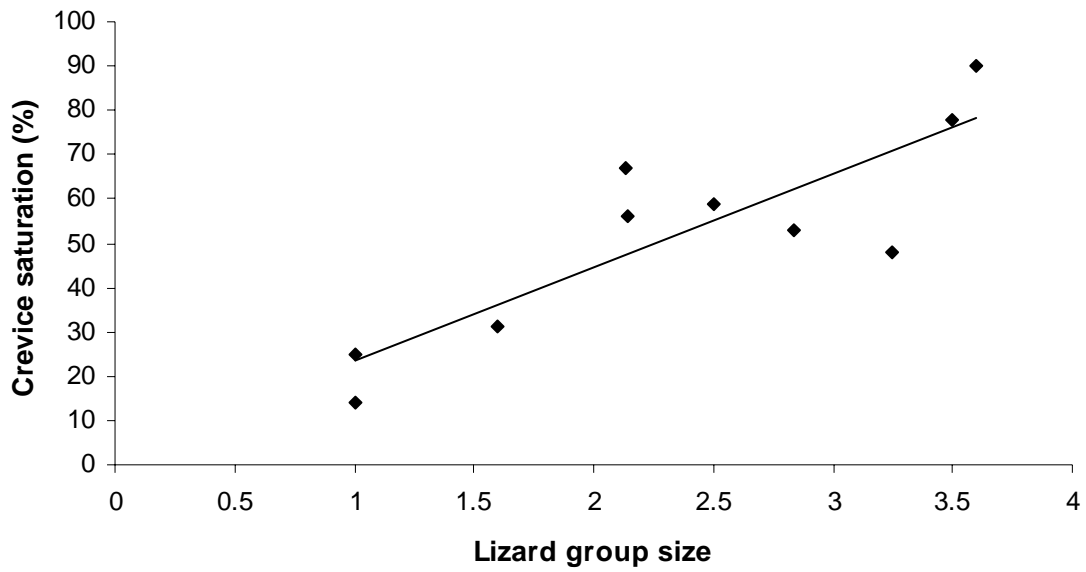
**Figure 3.12** – Graph indicating a positive correlation, at the local scale, between lizard density and lizard group size ( $r = 0.45$ ,  $P = 0.025$ ,  $n = 25$ ).



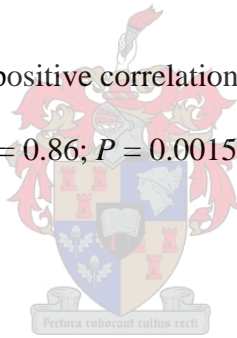


**Figure 3.13** – Graph indicating a positive correlation, at the regional scale, between crevice saturation and termite foraging port density ( $r = 0.64$ ;  $P = 0.047$ ,  $n = 10$ ).

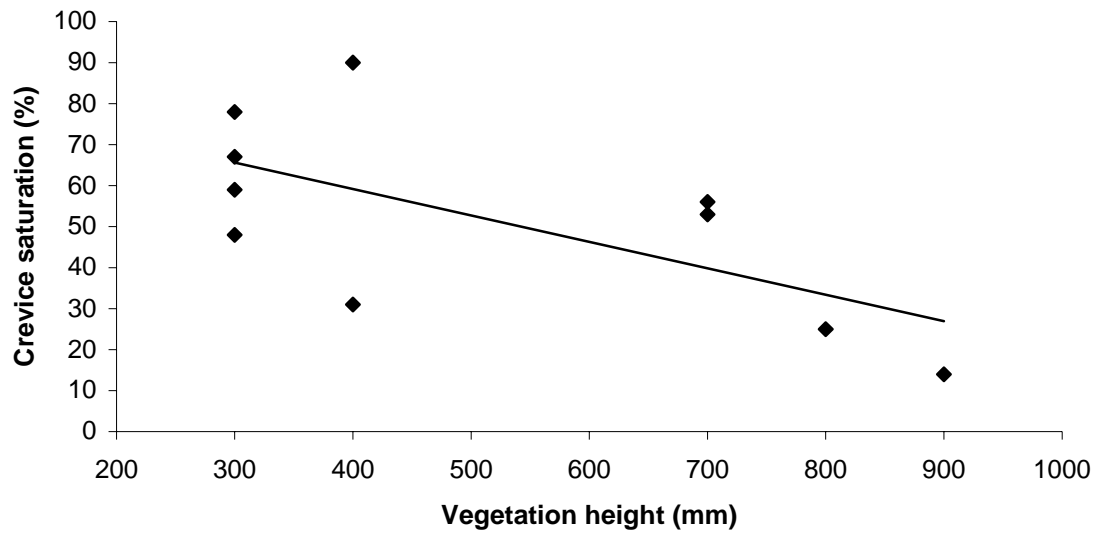




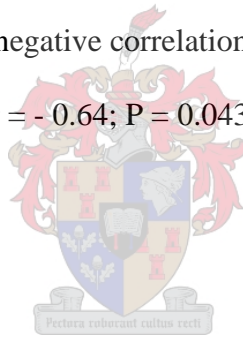
**Figure 3.14** – Graph indicating a positive correlation, at the regional scale, between crevice saturation and lizard group size ( $r = 0.86$ ;  $P = 0.0015$ ,  $n = 10$ ).

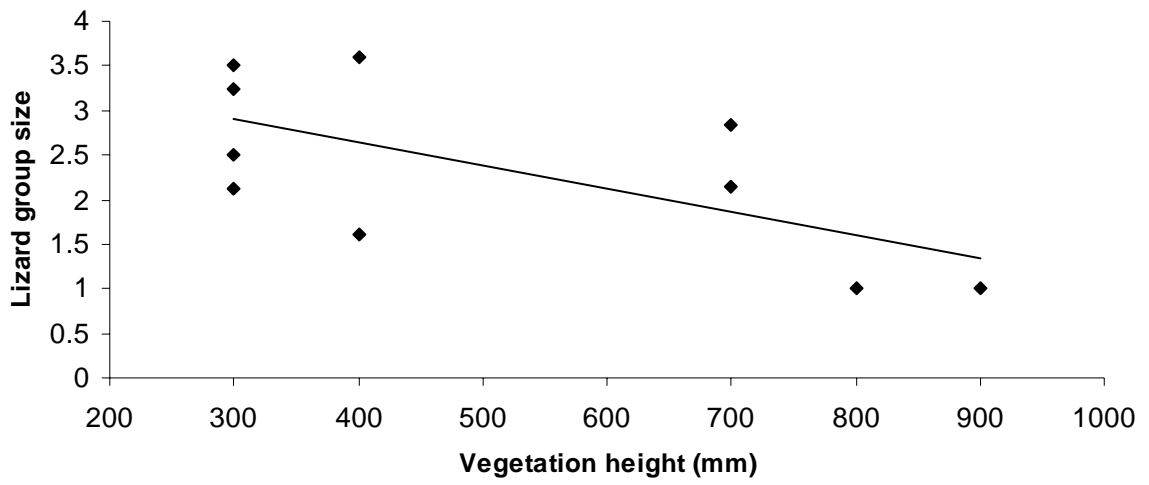




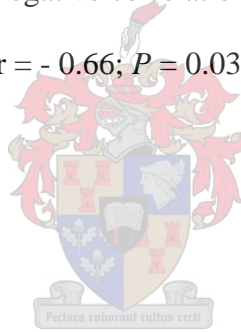


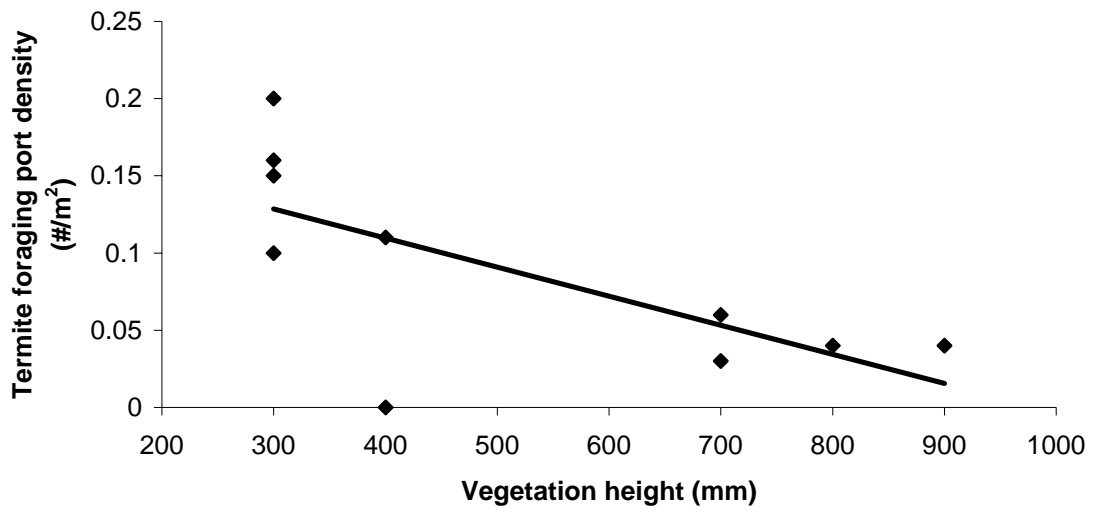
**Figure 3.15** – Graph indicating a negative correlation, at the regional scale, between crevice saturation and vegetation height ( $r = -0.64$ ;  $P = 0.043$ ,  $n = 10$ ).



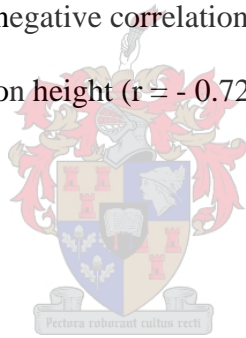


**Figure 3.16** – Graph indicating a negative correlation, at the regional scale, between lizard group size and vegetation height ( $r = - 0.66$ ;  $P = 0.037$ ,  $n = 10$ ).





**Figure 3.17** – Graph indicating a negative correlation, at the regional scale, between termite foraging port density and vegetation height ( $r = -0.72$ ;  $P = 0.016$ ,  $n = 10$ ).



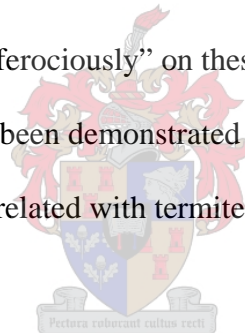
**CHAPTER 4:**  
**GROUP SIZE AND TERMITE UTILIZATION IN THE**  
**ARMADILLO LIZARD, *CORDYLUS CATAPHRACTUS***

**Introduction**

Because of their clumped nature, colonies of social insects (termites, ants, bees and wasps), represent a concentrated source of energy, that are potentially rewarding and economically feasible food sources for lizard predators (Huey & Pianka 1981; Abensperg-Traun & Steven 1997). A lizard can feed at one spot and become satiated within a short period of time, thereby reducing energy expenditure and exposure to predators. Ant and termite alates, in particular, as well as their larval and pupal stages, have a substantially higher fat content than other castes (Redford 1984) and are nutritionally very valuable (Swart *et al.* 1999).

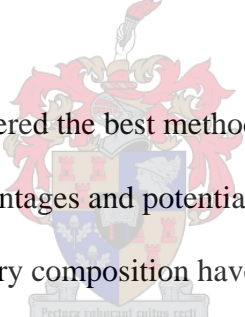
Although termitophagy is common among lizard species, it tends to be more common among gekkotans and autarchoglossans than among iguanians, and among desert lizards than among Neotropical species (Pianka & Vitt 2003). Termite specialists include fossorial forms in the family Scincidae and several desert-living lizards, especially species from the family Lacertidae (Pianka & Vitt 2003). Pianka (1986), however, reported that after heavy summer rains in arid environments, when termites send out their alate reproductives in great abundance, virtually every species of lizard eat nothing but termites.

The armadillo lizard, *Cordylus cataphractus*, is an arid zone autarchoglossid from South Africa that relies on the southern harvester termite, *Microhodotermes viator*, as its main food source (Mouton *et al.* 2000; Effenberger 2004). Unlike most other termite species occurring within the range of *C. cataphractus*, *M. viator* emerges in great numbers during the day during temperate weather conditions (C. Shuttleworth, pers.obs.), and is also regularly active on warm moonlit nights (Coaton & Sheasby 1974). During activity, it forms dense concentrations at the foraging ports of the hives (Figure 4.1) and it is here where it is harvested by *C. cataphractus* (Effenberger 2004). FitzSimons (1943) also remarked that after spring rains alate termite individuals emerge in large swarms, and that *C. cataphractus* individuals “feed ferociously” on these. The close relationship between *M. viator* and *C. cataphractus* has been demonstrated in Chapter 3, where it was found that *C. cataphractus* density is correlated with termite abundance.



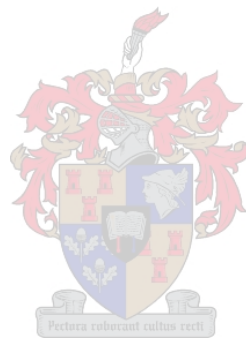
Dependence on a specific food resource should ultimately result in evolutionary shifts in behaviour and morphology to optimise the use of that resource. *Cordylus cataphractus* permanently lives in groups, a behaviour that is not common among insectivorous, sit-and-wait foragers (Mouton *et al.* 2000). It has been suggested that termitophagy was the driving force in the evolution of group-living in *C. cataphractus* (Effenberger 2004; Mouton *et al.* 2005). The heavy armour and tail biting antipredatory behaviour displayed by this species is linked to predation pressure when harvesting termites out in the open, some distance away from the crevice refuge. The heavy armour and resultant reduced agility (Losos *et al.* 2002), however, renders this species vulnerable to aerial predation

during general maintenance behaviour at the crevice refuge (Mouton & Flemming 2001), where it spends the greatest proportion of its activity time (Visagie 2001). Group-living may have evolved to reduce aerial predation, by taking advantage of predation reduction effects of living in groups ('many eyes' and 'dilution' effects; Lima 1995; Lanham & Bull 2004). Termitophagy should be an essential component of group-living, without it competition for food among group members should be too severe for the group to exist for an extended period of time. It also follows that the use of termites as food should be more pronounced in large *C. cataphractus* groups than in small ones. The aim of this study was to investigate possible differences in the use of termites by different sized groups of *C. cataphractus* during different times of the year.



Faecal content analysis was considered the best method for investigating termite utilization in this species. The advantages and potential disadvantages of using faecal content analyses to determine dietary composition have been well documented (Fox & Archer 1984; Putman 1984; Dickman & Huang 1988; Luo *et al.* 1994; Dickman 1995). The principal advantage is that numerous random samples can be collected from a population without sacrificing animals. The major problem is that both small and soft-bodied prey items may be either completely or almost completely digested, and therefore overlooked, whereas large hard-bodied prey that resist digestion are likely to be over-estimated (Dickman & Huang 1988). The sampling of stomach contents substantially reduces this problem, but it requires the destruction of the study animal (Fox & Archer 1984). *Cordylus cataphractus* is listed as a threatened species (Branch 1998; Baard *et al.* 1999) and large-scale sampling of stomach contents was not an option in this study. This

study focused on a termite species with a large chitinous head that was found undigested in faecal samples, making faecal sample analysis highly feasible.



## Materials and Methods

### *Study site*

A study site was at Eland's Bay, along the West Coast of South Africa. The site includes a range of rocky outcrops of Table Mountain Sandstone. The area has a Mediterranean climate with an average annual rainfall of 275 mm of which an average of 70 % falls in the winter (Burgers 1995). The vegetation types found in the area include Langebaan Dune Strandveld and Leipoldtville Sand Fynbos (Mucina *et al.* 2005).

### *Collection and analysis of faecal data*

At the study site, ten small *C. cataphractus* groups (1-3 individuals), five medium-sized groups (4-10 individuals), and two large groups (more than 10 individuals) were selected for study. A minimum of 20 scats was collected on a monthly basis as a representative of each category, giving a monthly total of 60 scats. A minimum of two scats per lizard group was collected monthly from the small group category, four scats per group from the medium group category and ten scats per group from the large group category.

*Cordylus cataphractus* is known to deposit scats in piles, i.e., individuals in the group defecates at a specific site (Effenberger 2001). Scats were therefore easily located. Only whole, well-preserved scats were collected using a pair of forceps. After each monthly collection, the areas around the refuge crevices were cleared of all remaining scats, so that a fresh sample could be collected the next month. Each scat that I collected was placed individually in a vial for later analysis in the laboratory. At the laboratory, the scats were dried overnight in a Memmert dry oven at 40 °C. The dry mass of each was



then determined, using a Mettler AE 200 microscale. Each scat was then teased apart under a stereomicroscope and *Microhodotermes viator* heads and mandibles were separated from the rest of the scat material. The termite heads were placed overnight in the dry oven, removed and then weighed. These samples were preserved in 70 % ethanol. The percentage termite head material per scat was determined by dividing the mass of the termite heads by the total dry mass.

### *Regional analysis*

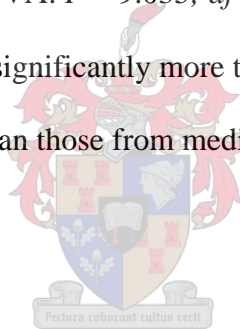
Faecal samples were collected at different times of the year from localities throughout the distributional range of *Cordylus cataphractus*. These samples were analysed under a stereomicroscope and scored for termite presence or absence. I also investigated the stomach contents of 42 *C. cataphractus* specimens in the Ellerman Collection of the University of Stellenbosch. The lizards were scored for termites present, other insect material present and empty stomachs. The faecal and stomach content data were combined to determine whether *C. cataphractus* had termites present in its diet throughout the year.

### *Data analysis*

Data were tested for normality and homogeneity of variances using Kolmogorov-Smirnov test, with Lilliefors' correction (Sokal & Rohlf 1981). Monthly scat data were compared using ANOVA. All statistics were conducted using the statistical programmes SigmaStat 3.0 and STATISTICA 6. The level of significance was set at  $P < 0.05$ .

## Results

The mean monthly percentages of termite head material in the scats of the various group categories of *C. cataphractus* are depicted in Figure 4.2. The scats of all group categories contained termites during all months of the year for which data were available. While the mean percentage of termite head material was higher in larger than in medium sized and small groups in most months, statistically significant differences were only found for two months at the end of the dry season. During March, the scats from large groups contained significantly more termite head material than both medium (ANOVA:  $F = 9.035$ ;  $df = 2$ ;  $P < 0.001$ ) and small groups (ANOVA:  $F = 9.035$ ;  $df = 2$ ;  $P = 0.008$ ), and in April, the scats from large groups contained significantly more termite head material than those from small groups, but not more than those from medium-sized groups (Dunn's Test:  $Q = 2.896$ ;  $df = 2$ ;  $P < 0.05$ ).



When pooling the annual termite utilization data of each group size category and comparing scats containing more than 50 % termite head material, large groups contained overall significantly more termite head material than small and medium groups (ANOVA:  $F = 6.397$ ;  $df = 2$ ;  $P = 0.005$ ; Fisher LSD: Large vs. Small,  $P = 0.001$ ; Large vs. medium,  $P = 0.017$ ).

When comparing termite utilization within group size categories, small groups utilized more termites in June than in April (Kruskal-Wallis:  $H = 41.54$ ,  $df = 11$ ; Dunn's Method:  $Q = 3.69$ ,  $P < 0.05$ ), September (Dunn's Method:  $Q = 4.64$ ,  $P < 0.05$ ) or November

(Dunn's Method:  $Q = 3.63$ ,  $P < 0.05$ ), and also more in July than September (Dunn's Method:  $Q = 4.046$ ,  $P < 0.05$ ). Medium groups utilized more termites in June than in September (Kruskal-Wallis:  $H = 37.20$ ,  $df = 11$ ; Dunn's Method:  $Q = 4.47$ ,  $P < 0.05$ ) or January (Dunn's Method:  $Q = 3.78$ ,  $P < 0.05$ ). Large groups utilized more termites in March than September (Kruskal-Wallis:  $H = 26.53$ ,  $df = 10$ ; Dunn's Method:  $Q = 4.44$ ,  $P < 0.05$ ), also in July than September (Dunn's Method:  $Q = 3.44$ ,  $P < 0.05$ ) and in April than September (Dunn's Method:  $Q = 3.489$ ,  $P < 0.05$ ).

Alates, which were identified by their wings and head segments, were recorded in faecal samples during the months of February (three scats), March (three scats), April (one scat), and October (seven scats), with the majority of these scats literally consisting of alates only. Rainfall peaked in May-June 2005 (38.1 mm – 39.3 mm) and August 2005 (65.8 mm) (Figure 4.2). The increase in utilization of termites in large lizard groups coincided with the onset of rain in March/April when large numbers of termites, especially alates, were present.

### *Regional analysis*

On a regional scale, i.e., excluding the Eland's Bay data, termites were present in the diet of *C. cataphractus* throughout the year, except for the months of January and November, which were inconclusive. Faecal data could not be collected for these two months. Only one lizard specimen could be obtained within the Ellerman Collection to represent January and only two lizards representing November. All three of these lizards unfortunately had empty stomachs.

Of the 42 museum specimens representing 26 localities, of which the stomach contents were analysed, seven contained southern harvester termites, 12 contained other insect material such as centipedes and beetles and the remaining 23 specimens had empty stomachs.

All of the faecal samples that were collected from a total of 23 localities throughout the range of *C. cataphractus* contained southern harvester termites.



## Discussion

In this study, I found that *Cordylus cataphractus* utilizes termites throughout the year and that individuals in large groups appear to eat proportionally more termites than individuals in small groups. These results lend some support to the hypothesis that termitophagy is an essential component of group-living in *C. cataphractus*. Without a clumped food source such as termites, intra-group competition for food will be too high to make group-living feasible. *Cordylus cataphractus* is a sit-and-wait forager (Mouton *et al.* 2000) and this foraging mode, associated with a rock-dwelling lifestyle and heliothermic basking, typically results in a high degree of territoriality and a solitary lifestyle in most other lizard species (Stamps 1983).

The finding that individuals in larger groups utilize termites to a greater extent than individuals in small groups, may be interpreted as an indication of the differences in food competition at the crevice refuge experienced in large versus small groups, and hence, differences in the need to source food away from the crevice to lessen competition. It may, however, also be an indication of differences in foraging efficiency of individuals in large versus small groups, individuals in large groups being able to locate termites more effectively than individuals in small groups. The latter possibility needs to be investigated as it may at least partly explain the group-living behaviour displayed by *C. cataphractus*.

Vrcibradic & Rocha (1998) found a high degree of similarity between the diet composition of *Mabuya frenata* and prey availability. The great variety of prey taxa

consumed by *M. frenata*, suggests that it is a generalist and opportunistic feeder, not a termite specialist per se. Representatives of a variety of insect orders were also found in the diet of *Cordylus cataphractus* throughout the year, supporting Mouton *et al.* (1999) that *C. cataphractus* is also a generalist and opportunistic feeder and not a termite specialist as such. However, the inclusion of termites in its diet may be necessary for it to survive in groups. Furthermore, its heavy build may compel it to live in groups, thus the availability of termites may be essential for this species to survive in any given area.

The apparently lower presence of termites in the scats of all three size categories of *C. cataphractus* during September may be linked to the greater availability of insects in general at the end of the rainy season (Wolda 1978; Reynolds 1982). The large amounts of alates found in the faecal samples of *C. cataphractus* individuals in February, March, April and October indicate that this species does capitalise on this nutritious caste (Redford 1984) at certain times of the year when swarming by the termite takes place. Alates within a nest can change the food value of an ant or termite colony (Redford 1987) as illustrated by the strong positive correlation between the presence of alates or prealates in a nest and longer feeding bouts by echidnas (Griffiths & Simpson 1966) and *Tamandua anteater* (Lubin & Montgomery 1981). The alate swarming season is known to extend from October through to May, and this is possibly due to low rainfall and the erratic distribution of rain over much of the arid distribution area of this termite taxon (Coaton & Sheasby 1974).

Foraging activity of termites increases during the dry season (Pinheiro *et al.* 2002) to support the production of alates that swarm at the onset of the rainy season. Colli *et al.* (2003) found that the consumption of termites by geckos was higher during the dry season. They concluded that individuals of the gecko species *Gymnodactylus geckoides amarali* might concentrate breeding, i.e., when females lay their eggs, in the dry season, because access to termites is maximized. Consumption of termites was higher in large *Cordylus cataphractus* groups during the dry season with large groups consuming significantly more termites than small groups in March and April.

Lizards that feed predominantly on termites are often widely foraging species, because termites are usually clumped and unpredictably distributed in space (Huey & Pianka 1981; Magnusson *et al.* 1985; Cooper 1994). Mouton *et al.* (2000) demonstrated that *C. cataphractus* behaves like a strict sit-and-wait forager when at the crevice, but no data are available on how it harvests termites, i.e., whether termite activity is spotted from a lookout point at the crevice or whether individuals regularly go on ‘blind’ excursions in the hope of locating active termite ports. High competition for food among group-living organisms may favour a shift from sedentary “long-wait” ambushing to more mobile “short-wait” ambushing or even to a cruising visual searcher that is a virtual active forager (Wymann & Whiting 2002). Brazilian species of the genus *Mabuya* are neither sit-and-wait foragers (Pianka 1966) nor typical active foragers. Instead, they seem to adopt an intermediate foraging strategy (Vitt 1991; Cooper 1994) and may fall in the category of “cruisers” (Regal 1978; Vitt 1995) or “proximal intensive foragers” proposed by Anderson (1993) to differentiate the foraging mode of skinks from that of the “wide-

intensive foraging” teid *Cnemidophorus tigris* (Vrcibradic & Rocha 1998). However, shifts in foraging behaviour may involve trade-offs, such as increased predation risk for lizards that normally forage close to refuges such as rock crevices. Given its sluggish nature and the sparse vegetation cover in the arid areas where it occurs, it is unlikely that *C. cataphractus* goes on ‘blind’ excursions but data are needed to confirm this.

Fossorial insects are found close to the surface in the morning and go deeper under the surface during the heat of the day (Vitt & Ohmart 1977). Visagie (2001) found that *C. cataphractus* has a bimodal activity pattern, indicating that the daily activity patterns of *M. viator* and *C. cataphractus* coincide to a large degree (Coaton & Sheasby 1974).

In conclusion, this study provides new insights of the annual feeding strategy of *C. cataphractus*. It was previously thought that *C. cataphractus* only fed on the southern harvester termite, *M. viator*, at certain times of the year, specifically when the termite was most abundant due to swarming. This study clearly shows that this termite plays a much more important role in the diet of *C. cataphractus* and it is utilized by the lizard throughout the year. I can also conclude that group size plays a role in termite utilization, as it was found that large lizard groups fed on termites to a greater degree than small groups in certain months and that there was a general tendency for this phenomenon throughout the year. This is understandable as pre-autumn and autumn feeding is important in cordylids for fat body build-up (Flemming & Mouton 2002). These fat bodies are utilized during the reproductive cycle and are especially important with regards to vitellogenesis and pregnancy (Flemming & Mouton 2002). The peak in termite



utilization by large groups in Autumn (March and April) may be associated with fat body build-up, as the amount of arthropods available around the home crevice may not be sufficient in supporting a large group's dietary needs during Autumn and therefore they need to go out and forage on termites.

*Cordylus cataphractus* is listed as Vulnerable in the South African Red Data Book for Amphibians and Reptiles (Mouton 1988). It is very popular as a pet and the illegal pet trade poses a serious threat to this species. Because it lives in groups and is sluggish in nature, it is easily collected. It is critical to understand the ecology of a species when considering conservation efforts. The southern harvester termite, *M. viator*, plays a central role in the ecology of *C. cataphractus* and thus the presence of termites should be an important factor in conservation planning with regards to this species.



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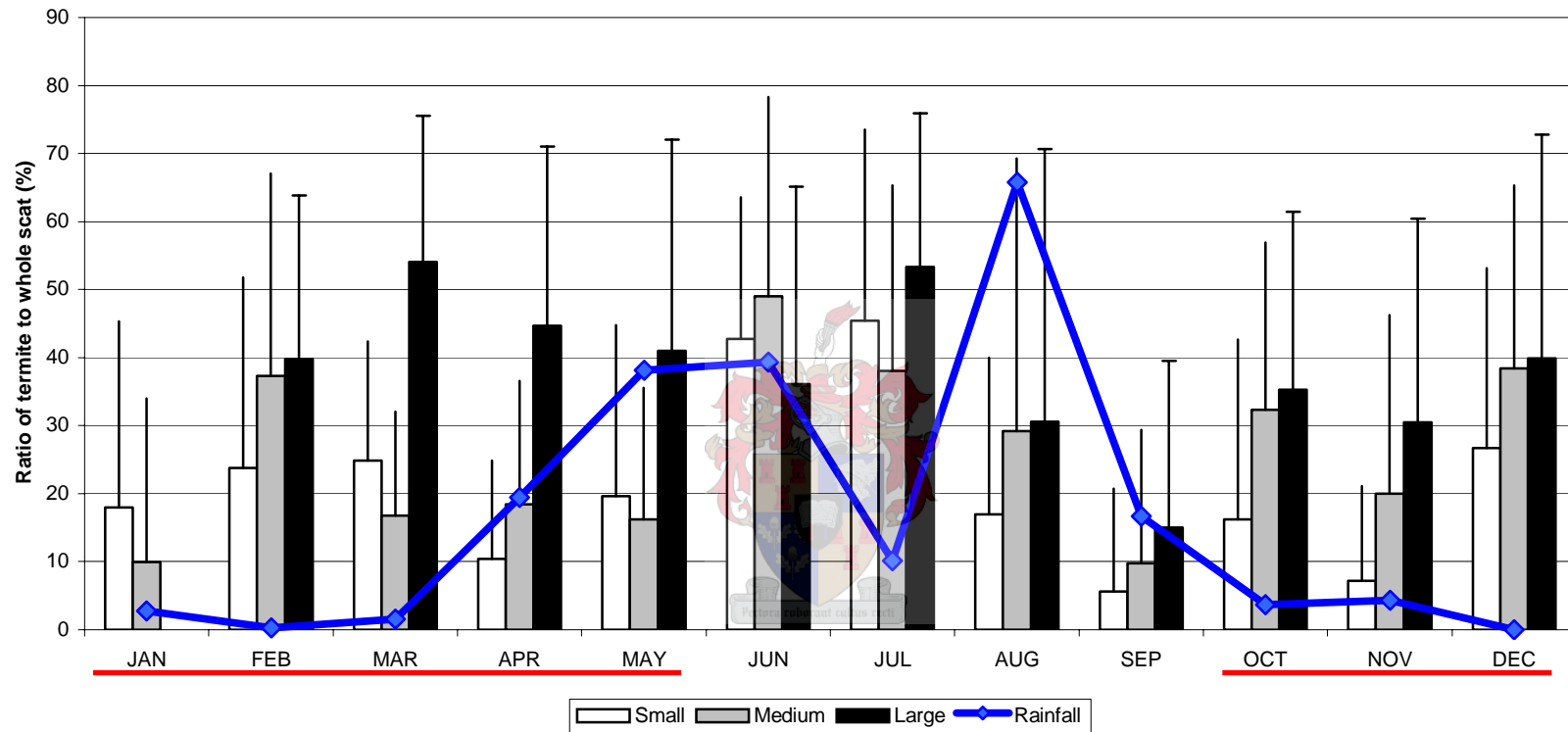
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**Figure 4.1** – The southern harvester termite, *Microhodotermes viator*, concentrates its activity at the foraging ports of the hive and it is here where it is harvested by *Cordylus cataphractus*



**Figure 4.2** – Graph indicating percentage termite head material (y-axis) versus month of the year, January to December (x-axis). With small lizard groups indicated in white, medium groups in grey and large groups in black. Total monthly rainfall (mm) is indicated in blue and termite alate season (October to May) in red.