

**SOCIAL STRUCTURE AND SPATIAL-USE IN A GROUP-LIVING LIZARD,
*CORDYLUS CATAPHRACTUS***

by

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Thesis presented in partial fulfilment of the requirements for the degree of

The crest of Stellenbosch University, featuring a shield with various symbols, topped by a crown and flanked by two lions.

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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:.....

Date:.....



ABSTRACT

There is overwhelming evidence that the Armadillo Lizard, *Cordylus cataphractus*, forms permanent aggregations, and that termites are possibly the most important component of the diet of this species. In addition, the spinose morphology and defensive tail-biting behaviour displayed by this lizard species strongly imply that individuals move away from the crevice, where they are more vulnerable to predation. Therefore the aim of this part of the study was to investigate whether *C. cataphractus* harvest termites at the termite foraging ports and to discuss the likely ecological implications of termitophagy for this species. A quadrat at the Graafwater study site, including several crevices housing *C. cataphractus* groups, was measured out. All the foraging ports of the subterranean harvester termite (*Microhodotermes viator*) present in the quadrat, were located and their positions recorded in respect to the distance from the nearest crevice housing lizards. The presence of *C. cataphractus* tracks at the foraging ports was used to verify whether individuals visited specific termite foraging ports. Tracks were found at foraging ports located at an average distance of 6.1 m, but were also located at foraging ports up to 20 m from the nearest crevice. The results strongly support the hypothesis that *C. cataphractus* individuals move away from the crevice to feed on termites. Termitophagy and the heavy armature of *C. cataphractus* appear to be key factors in the group-living behaviour of this species. Termitophagy allows individuals to live in groups as competition for food at the home crevice will be limited. The

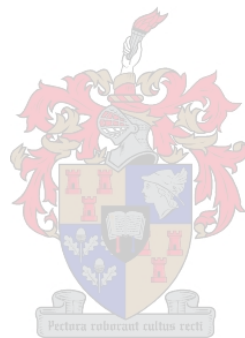
heavy armature of *C. cataphractus* renders it clumsy and slow-moving, compared to other cordylids. Group-living will, however, eliminate juvenile dispersal and mate-searching excursions, activities which, in the light of the heavy morphology of the species, may result in high predation impact.

The global objective of the study was to investigate social structure and space-use in *Cordylus cataphractus*. For the correct interpretation of data on the latter, it was necessary to first establish an ethogram for the study animal. Members of a multi-male group located at the Graafwater site, including all age-sex classes, were observed in the field by telescope, for a total of 102 hours. All individuals were observed to predominantly display maintenance behavioural act systems, however, agonistic act systems were also observed. Aggression levels were determined for the respective agonistic behavioural acts observed. Males were highly aggressive and displayed the most aggression (67.42 %). Females and sub-adults displayed aggression for 34.97 % and 37.75 % of the total observation time, respectively. Juveniles did not display aggression at all. Mating behaviour was also observed and described. An ethogram was thus established for the first time for *C. cataphractus*, and was compared to the ethograms available for a few other cordylids.

The spatial distribution of individuals within a population has an important impact on the social structure that ensues. Living in a group imposes several pressures on the individual and competition for mates is one. The main aim of the study was to determine the space-use of all the

individuals included in a multi-male *Cordylus cataphractus* group (n = 55), to elaborate on the mating system. Specific focus was on the adult males and females of the multi-male group, because, ultimately, the manner in which individuals, particularly the adult males and females, utilise space, determines the mating system. The mating system is an important aspect of social structure. A two-dimensional grid pattern was delineated at a free-living, multi-male group's crevice, situated at the Graafwater study site, to be able to plot the position of each individual during observations. All marked individuals, that were visible, were scanned through a telescope and their respective positions were recorded at 30-minute intervals. Arcview 3.2 Geographical Information Software was used to create a computerised model replicate of the two-dimensional grid pattern at the crevice, and to graphically depict the recorded positions for each individual. The space-use of males overlapped greatly with the space-use of females ($66.12 \pm 31.81 \%$), but a 0 % overlap in space-use was observed among adult males. The space-use of sub-adults and juveniles overlapped highly among one another, as well as with the space-use of adult males and females. The results showed conclusively that adult male *C. cataphractus* are territorial, defending specific sites at the crevice. The territory of each male included in the multi-male group incorporated at least one female. The space-use of several females incorporated the space-use of two or more males. Males were observed to mate with one or more females, and one female was observed to mate with two different males on more than one occasion. Thus the evidence strongly suggests

that *C. cataphractus* males display typical territorial polygyny whereas females may be promiscuous.



UITTREKSEL

Daar is oorweldigende bewyse dat die pantsergordelakkedis, *Cordylus cataphractus*, permanent in groepe bly en dat termiete waarskynlik die belangrikste komponent in die dieet van hierdie spesie is. Die stekelrige morfologie en die stert-byt beskermingsgedrag is verder sterk aanduidings dat hierdie akkedisse tyd weg van hul klipskeure spandeer waar hulle meer gevoelig vir predasie is. Die doelwit van die eerste deel van die studie was om te bepaal of *C. cataphractus* termiete by die voedingspoorte van die termietneste oes en verder ook om die moontlike ekologiese implikasies wat termitofagie vir die spesie inhou, te bespreek. 'n Kwadraat was by die Graafwater studielokaliteit uitgemeet om verskeie akkedisgroepe in te sluit. Al die voedingspoorte van die suidelike grasdraer termiet (*Microhodotermes viator*) binne die kwadraat is gevind en die afstande na die naaste klipskeur wat akkedisse huisves, is vir elke voedingspoort bepaal. Die teenwoordigheid van *C. cataphractus* spore in die sand by die voedingspoorte was gebruik om besoeke aan spesifieke voedingspoorte te bevestig. Spore is by voedingspoorte gemiddeld 6.1 m vanaf die naaste akkedisgroep gevind, maar tot so ver as 20 m vanaf die naaste akkedisgroep. Die resultate verleen sterk ondersteuning vir die hipotese dat *C. cataphractus* individue op termiete weg van hul klipskeur af voed. Termitofagie en die swaar pantser van *C. cataphractus* is waarskynlik sleutelfaktore in die groeplewe-gedrag van die spesie. Termitofagie laat groeplewe toe omdat kompetisie vir voedsel by die klipskeur beperk sal wees. Die swaar pantser van *C. cataphractus* het tot gevolg dat die spesie

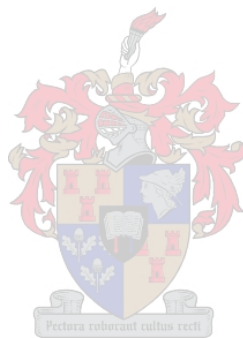
lomp en stadig is in vergelyking met ander gordelakkedis. Groeplewe sal egter natale spreiding en maatsoek-ekskursies, aktiwiteite wat in die lig van die lompheid van die spesie swaar predasie impak tot gevolg kan hê, uitskakel.

Die oorhoofse doelwit van die studie was om die sosiale struktuur en spesifiek ruimtebenutting by *C. cataphractus* te ondersoek. Vir korrekte interpretasie van data oor lg. was dit egter eers nodig om 'n etogram vir die studiedier saam te stel. Lede van 'n multi-mannetjie groep, wat alle ouderdomsgrootte klasse ingesluit het, is by die Graafwater studielokaliteit m.b.v. 'n teleskoop vir 'n totaal van 102 uur dopgehou. Al die individue in die groep het oorwegend instandhoudings-handelingsisteme vertoon, alhoewel agonistiese handelingsisteme ook vertoon is. Aggressievlakke is vir die verskeie agonistiese gedragshandelings bepaal. Mannetjies was hoogs aggressief en het die meeste aggressie vertoon (67.42 %). Wyfies en subvolwassenes het aggressie vir 34.97 % en 37.75 % van die totale observasietyd respektiewelik getoon. Jong individue het geen aggressie getoon nie. Paringsgedrag was ook waargeneem en beskryf. 'n Etogram is dus vir die eerste keer vir *C. cataphractus* opgestel en is ook vergelyk met etogramme van ander gordelakkedis.

Die ruimtelike verspreiding van individue binne 'n populasie het 'n belangrike invloed op die sosiale struktuur wat daaruit voortvloei. Om in 'n groep te lewe, plaas verskeie drukke op die individue binne die groep en

kompetisie vir maats is een hiervan. The hoofdoelwit van die studie was om die ruimtebenutting van al die individue binne 'n multi-mannetjie groep van *C. cataphractus* ($n = 55$) te bepaal en om die paringsstelsel in so 'n groep te ondersoek. Die spesifieke fokus was op die volwasse mannetjies en wyfies, omdat die paringsstelsel deur die wyse waarop volwasse individue ruimte benut, bepaal word. Die studie is by die Graafwater studielokalisiteit gedoen. Die oppervlak buite 'n klipskeur wat deur 'n multi-mannetjie groep bewoon word is opgedeel in sektore om die kartering van die posisies van die individue tydens observasietye moontlik te maak. Al die individue is vooraf met verfkodes langs die kant van die kop gemerk en op gegewe observasiedae is individuele posisies elke 30 min aangeteken. *Arcview 3.2 Geographical Information Software* was gebruik om 'n tweedimensionele, gerekenariseerde replikaat van die klipskeur en onmiddellike omgewing te skep en om die waargenome posisies van individue grafies voor te stel. Die ruimtebenutting van mannetjies het grootliks met dié van wyfies ooreenstem, terwyl zero ooreenstemming tussen mannetjies waargeneem is. Ruimtebenutting van subvolwasse en jong individue het ook grootliks onderling ooreenstem en ook met dié van volwasse mannetjies en wyfies. Die resultate toon duidelik aan dat volwasse mannetjies territoriaal is en dat spesifieke standplase rondom die klipskeur verdedig word. Die territorium van elke volwasse mannetjie het of 'n gedeelte of die hele ruimtebenutting van ten minste een volwasse wyfie ingesluit. Ruimtebenutting van verskeie wyfies het met dié van twee of selfs meer mannetjies ooreenstem. Mannetjies is waargeneem om met meer as een wyfie te paar en ten minste een wyfie het met meer as een

mannetjie gepaar. Die resultate dui dus sterk daarop dat *C. cataphractus* mannetjies tipies terroitoriale poligenie vertoon terwyl wyfies weer promisku is.



DEDICATION

“The blood of the dragon, we are told, is the
‘most precious Medicine upon Earth’:
For this blood drives away all disease
in the bodies of metals,
of men and of beasts.
From it the Sages derive their science,
And through it they attain the
Heavenly Gift,
which is called the Philosopher’s Stone.”

P. Marshall
Philosopher’s Stone



...to those who have lived and carry on living...

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Finally, I would like to acknowledge the symbolism of *Cordylus cataphractus*. One symbol of original perfection is the circle: "...the famed serpent Ouroboros, making a circle with his tail in his mouth and enclosing the principle: 'One the All' ...more than any other symbol, the Ouroboros, of course, symbolises the Philosopher's Stone."

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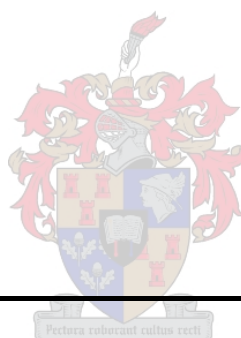
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CHAPTER 1

GENERAL INTRODUCTION

1.1 A BRIEF OVERVIEW OF SOCIAL STRUCTURE

1.1.1 Defining Social structure

Social structure is defined as the relationships of conspecifics with one another, and includes communication, competition, mate acquisition, dominance and parental care (Whitehead 1997). Social structure is greatly influenced by the mating system, which in turn is affected by various ecological aspects (Emlen & Oring 1977), for example, foraging mode, reproductive mode, morphology and space-use.

Social structure is not to be confused with sociality. Sociality is a culminating aspect of social structure normally displayed in group-living species (Wilson 2000; Chapple 2003), and refers to a group of individuals belonging to the same species that organise themselves in a cooperative manner, that is, forming a society (Wilson 2000). Sociality has established itself among species of most taxa and several species have in due course formed highly developed societies, to the point where there is a division of labour, cooperative care of offspring, overlapping generations, and only certain group members being active reproductives (Lanham 2001). For instance, in the orders Hymenoptera (ants, bees and wasps) and Isoptera (termites), social castes are formed in which a rare form of sex determination - haplodiploidy - manifests itself, where unfertilised eggs produce males and fertilised eggs produce females (Gullan & Cranston 1994). Ultimately, sterile female castes revolving around one fertile female

are formed, and this type of society is named a eusocial society (Krebs & Davies 1993). Jarvis (1981) showed that eusociality not only manifests itself in a haplodiploid genetic system, but also in the diploid mammals, for example the Naked Mole-rat (*Heterocephalus glaber*) and the Damaraland Mole-rat (*Cryptomys damarensis*) (Jarvis *et al.* 1994).

Each society signifies a particular group-living strategy used within that species under specific prevalent environmental conditions (Wcislo 1997). Eusocial systems have been considered the climactic point of social evolution (Wilson 1975) but, sociality, quasi sociality, and sub-sociality have, however, arisen independently numerous times in other species (Crespi & Choe 1997). Eusocial societies should therefore not be considered as signifying a higher level of evolution, but possibly as an intricate design suited for the respective environmental pressures experienced by the species in question.

Many aspects of an animal's social structure can be predicted on the basis of an understanding of a restricted set of environmental variables (Emlen & Oring 1977). In effect, ecological constraints impose limits on the degree to which sexual selection can operate (Emlen & Oring 1977). Bearing inclusive fitness of the individual in mind, we should expect a strong competitive element in many aspects of reproductive behaviour. Whilst introducing the theory of sexual selection, Darwin (1871) was clearly aware of intraspecific competition. Evidently, the more limiting one sex is the greater the resulting sexual selection in that species (Emlen & Oring 1977). Sexual selection is intense in highly polygamous species and only slight in monogamous species, hence, the greater the potential for

monopolising multiple mates, the greater should be the potential intensity of sexual selection and the tendency for polygamy, and vice versa (Emlen & Oring 1977). In nature, as critical resources become unevenly distributed, the potential for obtaining additional mates increases (Emlen & Oring 1977). This is because some individuals may be more capable of controlling larger quantities of resources than others.

Ultimately, simply stated, the social structure of a species may largely depend on intraspecific and interspecific competition, and mating success, which in turn are driven by environmental and genetic variables.

1.2 SOCIAL STRUCTURE IN REPTILES

1.2.1 General

Reptiles have long been considered behaviourally 'simple' in comparison to other vertebrates, and in reviews of social structure, reptiles have thus largely been neglected (Hughes 1998). The most well-documented aspect of social structure in reptiles, more so in lizards, has been territoriality (Stamps 1977). Territorial lizards are known to characteristically display intraspecific aggressive behaviour towards intruding conspecifics (Carpenter & Ferguson 1977; Stamps 1977). Normally a male defends an area containing a specific resource(s), normally basking, shelter and perch sites, food, and occasionally, females (Stamps 1977; 1983a). The total area that an individual makes use of to complete all necessary activities (e.g. feeding), is termed its home-range (Rose 1982; Perry & Garland 2002). The extent to which the home-ranges of males and females of a species overlap is important because it largely

determines access to mates (Rose 1982). The manner in which members of the same sex use space thus largely determines the mating system (hence, social structure) that manifests itself (Stamps 1977). Hence, mechanisms underlying reproductive success are the most likely determinants of the mating system that will ensue (Emlen & Oring 1977).

1.2.2 Aggregation behaviour

Brattstrom (1974) showed that aggregation behaviour in lizards might result in a shift in the type of social structure that ensues. Different socio-ecological strategies appear to have evolved on numerous occasions among an array of lizard lineages (Chapple 2003), although permanent aggregation behaviour in reptiles is rare. Much research has been and is currently being done on the Australian scincid genus *Egernia*, which contains several gregarious rock-dwelling and ground-dwelling species (Bull *et al.* 2000; Chapple 2003). *Egernia stokesii* is a fine example of a rock-dwelling, group-living lizard that lives in stable aggregations (family groups of up to 17 individuals) for several years (Main & Bull 1996; Bull *et al.* 2000; Chapple 2003). However, stable aggregations have been reported only for a few lizard species, amongst others: the agamid, *Stellio caucasicus* (Panov & Zykova 1995), the iguanid, *Sceloporus mucronatus mucronatus* (Lemos-Espinal *et al.* 1997), females of *Liolaemus huacahuasicus* (Halloy & Halloy 1997), several *Egernia* species (reviewed by Chapple 2003), and of course the subject of this study, *Cordylus cataphractus* (Mouton *et al.* 1999). The aggregation behaviour displayed by these species differs from temporary aggregation behaviour since aggregations also occur during the

summer months, suggesting that these aggregations have more than just thermal or reproductive functions.

In most cases, aggregations in reptiles are non-social, seasonal (temporary) and generally associated with either thermoregulation (e.g., winter aggregations in temperate species; Myres & Eels 1968; Ruby 1977; Elfstrom & Zucker 1999) or reproduction (reviewed by Graves & Duvall 1995). Feeding aggregations have also been described (Vitt 1974). Females of many species need to increase their body temperatures when gravid and aggregating may help to facilitate this (Schwarzkopf & Shine 1991). The Western Whip snake (*Hierophis viridiflavus*) forms aggregations of gravid females that return back to the same site annually, and no non-gravid females or males are present (Capula & Luiselli 1995). Bock & Rand (1989) showed that nesting aggregations are important in egg hatching success in the green iguana. Wikelski (1999) showed the importance of aggregations in the Marine Iguana in respect to increased thermoregulation and curbing of parasite loads. Myres & Eels (1968) reported more effective thermoregulation in aggregations of boa constrictors during the winter season.

One might argue that especially since some seasonal aggregations are associated with reproduction, there are bound to be an abundance of social interactions, thereby rendering the aggregation a social aggregation. For our purposes of discussion a social aggregation is regarded to be a group of individuals that permanently group together and are thus enforced to continuously interact among one another.

Lekking behaviour may result in aggregation behaviour. Normally, lekking behaviour entails a large aggregation of males, in which each male secures an area that it uses to attract a female, often by additionally putting on displays for the females (Andersson 1994). Lekking behaviour, which is common in birds (e.g. Ruffs) and mammals (Widemo & Owens 1999), is, however, unusual in reptiles, being displayed by only a few species, e.g., the Marine Iguana, *Amblyrhynchus cristatus* (Wikelski *et al.* 1996). Males of this species establish territories on intertidal rock-outcrops in fairly close proximity, thus all together they essentially form a cluster of territories (leks) that attract aggregations of females during the breeding season (Wikelski *et al.* 1996).

Assuming that permanent group-living behaviour requires more complex social behaviour in comparison to solitary-living behaviour, the fact that *C. cataphractus* is a diurnal, visually-orientated species (Mouton *et al.* 2000b) gives credence to the postulation by Brattstrom (1974). He states that diurnal, visually-orientated lizards are more likely to exhibit more complex social behaviour, more so than other reptile species. The notion that non-visually orientated species lack behavioural complexity may not be proper (Schwenk 1995; Torr & Shine 1996; Lanham 2001). Each species has a particular life history, physiology, morphology and behavioural repertoire specific to its environment, therefore aspects and complexity of social structure manifested in species will differ.

1.2.3 Social behaviour

At the most basic level, social behaviour comprises discrete behavioural acts that are controlled by a particular set of locomotory sequences (Carpenter & Ferguson 1977). Many social behavioural acts have been described in lizards and are used in the context of resource defence, aggression, mating and courtship (Carpenter & Ferguson 1977). Behavioural acts also vary according to the spatial distribution of individuals in a population. These types of distributions are classified as free-ranging, defence of home range, and site-defence (Stamps 1977). Social behaviour in lizards (type, diversity, frequency) is strongly linked to the mating system (Fox *et al.* 2003), and there is an important relationship between the social structure, morphology and habitat of lizards (Ruddock 2000).

The social structure of a population is continuously influenced by, and influences, aspects of species' biology (Wilson 1975). Thus, various correlations can be made between social structure and aspects of a species' biology (Whitehead 1997).

1.2.4 Correlates of social structure

There are six distinct correlates of social structure, namely reproductive mode, foraging mode, communication mode, habitat, spatial use, and morphology (Ruddock 2000).

Two reproductive modes occur among lizards, oviparity (egg-laying) and viviparity (live-bearing). These modes have widespread implications. Garland & Losos (1993) reported that movement in gravid viviparous

females is impaired, and energy reserves are drained during reproduction. Guillelte (1993) states that viviparity also results in increased basking times to facilitate the development of embryos. Hence, constraints are imposed on movements, making a territorial social structure more appropriate (Ruddock 2000). Cooper *et al.* (1990) have shown that viviparity is closely associated with a sit-and-wait foraging mode, which in turn is more compatible with a territorial social structure.

Foraging modes have been classified into two distinct categories, namely, sit-and-wait foraging and a widely-foraging. Sit-and-wait foragers wait for food items to pass them by, whilst widely-foraging species actively pursue their prey (Huey & Pianka 1981). The foraging mode imposes constraints on the social structure of a lizard; for instance, sit-and-wait foraging allows territorial species to spend more time between foraging attempts relatively inactive and in roughly the same position, allowing the lizard to survey its territory concurrently (Ruddock 2000). Logically, the home-ranges of sit-and-wait foragers are normally smaller, in comparison to those of active foragers (Huey & Pianka 1981). Foraging mode is envisaged to be coupled with many different aspects of lizard biology, in particular, prey chemical discrimination (Cooper 1995), reproductive mode (e.g., Mouton & Van Wyk 1997), and social behaviour (e.g., Ruddock 2000).

The communication mode of lizards entails a complex system of behavioural acts, including a wide variety of visual displays (Carpenter & Ferguson 1977), as well as various glands that are used for chemical communication. Some lizard species are more visually-orientated as

opposed to being chemically-orientated, and it seems that these two orientation types, although they both serve a purpose of individual recognition, are related to different territorial defence types (Ruddock 2000). Territory defenders usually show a large array of colour patterns and displays, whereas site defenders usually lack this (Fox, McCoy & Baird 2003). Site defenders generally seem to rely on chemical communication (Stamps 1977). Although generalisations can be made about the different levels of occurrence of communication mode in the different lizard families, it must not be forgotten that lizards often make use of both visual and chemical communication (Stamps 1977). It is the degree of use that may differ.

Another important factor determining social structure is habitat type. Baird *et al.* (1997) showed that the nature of the immediate surroundings affects the conspicuousness of displays and thus, the potential for a certain social structure to evolve. Stamps (1973) reported that social structure might differ within a species as a result of varying habitat type. The abundance and distribution of resources, such as food, have also been shown to affect the spatial distribution of lizards and are important in the evolution of social structure (Ruddock 2000). Distribution of food has been postulated to greatly influence social structure, where an even food distribution results in territorial systems, and an uneven food distribution causes clumping and as a result dominance hierarchies are expected to arise (Brown & Orians 1970). Torr & Shine (1996) showed that when resources are abundant they do not have to be defended so intensely and this may result in a non-territorial system. Thus, it is

important to keep in mind that an organism, thereby also its social structure, may be under intense selective pressure by the habitat the organisms lives in (Ruddock 2000).

Spatial-use and distribution patterns have been studied quite extensively in lizards and are strongly indicative of the type of social structure. Brattstrom (1974) reported that there is a density dependent relationship between territory and hierarchy; hierarchies are established typically under crowded conditions. Social structure is regularly described by space-use data. Three distinct scenarios exist: if males and females have a low home-range overlap then this suggests territoriality (Rose 1982); large overlap between male and female home-ranges suggests the presence of a dominance hierarchy. Exceptions do, however, occur, for instance, extensive home-range overlap can also occur even if the lizards are territorial (Eifler & Eifler 1998).

Differences in morphology between the sexes of a species are described by the term sexual dimorphism. Factors including intrasexual selection among males, and resource partitioning between males and females strongly influence sexual dimorphism in size and colouration. Stamps (1983a) has proposed a model for polygyny in lizards. The model predicts that male-male competition is more intense in territorial species as opposed to non-territorial species, and it also shows by comparison that territorial lizards display greater sexual dimorphism. The presence of sexual dimorphism in a species is normally associated with territoriality and a polygynous mating system, yet once again there are exceptions of non-territorial species that are sexually dimorphic (Ruddock 2000), for

instance, larger males also sometimes mate guard. Morphology can also impose constraints on the social structure of a species, since body size largely determines the home-range size that can be maintained by a lizard, even though maintenance may also depend on other variables, for instance energetics (Rose 1982).

1.2.5 The Various Types of Social Structure in Lizards

Interactions between individuals; content, quality and temporal patterns of interactions; and content, quality and patterning of relationships, are three levels of description of social structure proposed by Hinde (1976). Each ecological correlate is an aspect of social structure and accordingly, social structure can be assessed on various different levels. The various levels of social structure pertain to the ecological correlates discussed above. Spatial-use studies have been especially useful in determining the prevalent mating system in various lizard species (Stamps 1977; Lemos-Espinal *et al.* 1997; Ruddock 2000).

In the African genus *Cordylus* social structure and behaviour has, to date, only been partially investigated in four species: *C. cordylus* (Wirminghaus 1990; Ruddock 2000), *C. giganteus* (Ruddock 2000), *C. macropholis* (Nieuwoudt *et al.* 2003), and *C. cataphractus* (Mouton *et al.* 1999). *Cordylus cataphractus* presents us with an opportunity to investigate the social structure in a reptile that displays permanent group-living behaviour. Permanent aggregating behaviour, as mentioned before, is rare among lizards and unusual among reptiles in general.

1.3 OBJECTIVES OF STUDY

Cordylus cataphractus is a rock-dwelling lizard that presents the strongest manifestation of permanent grouping behaviour (Fig. 1.1) among all lizard species (Mouton *et al.* 1999). It is the only sit-and-wait foraging lizard species to display permanent grouping behaviour. Other lizard species that display grouping behaviour are generally either herbivores or widely-foraging species (Mouton *et al.* 2000b). *Cordylus cataphractus* is endemic to the hot, arid western coastal regions of South Africa, inhabiting sandstone outcrops along the sandy coastal plains. Groups of up to 40 individuals have been encountered occupying a single rock crevice (Mouton *et al.* 1999; Visagie 2001).

The grouping behaviour in this species has been shown to be a result of mutual conspecific attraction and not because of limited shelter availability (Visagie *et al.* 2004). The male-biased size sexual dimorphism portrayed in *C. cataphractus* strongly suggests that sexual selection is at hand (Mouton *et al.* 1999). The intensity of sexual selection, in turn, will predictably determine the potential social structure in this lizard species. Therefore, questions about the underlying social mechanisms that ensure access to mates and maintenance of social structure in a permanent group-living scenario, arose.

The objectives of this study were: i) To determine the mating system of *C. cataphractus*. The mating system highlights the social structure of a species. To achieve this first objective, the social behaviour and space-use of individuals in a multi-male group of *C. cataphractus* were determined. ii) To evaluate the ecological consequences of termitophagy in *C.*

cataphractus. Termitophagy has been shown to result in specific ecological consequences among lizards (Perry & Pianka 1997). I specifically wanted to evaluate the role of termitophagy in the permanent grouping behaviour displayed by this species. This objective was achieved by determining how far individuals move away from the crevice to forage on termites.

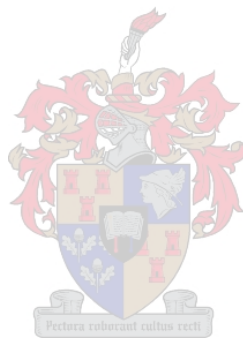
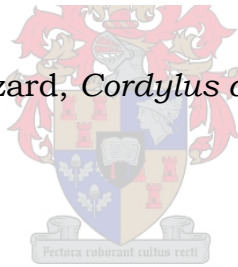




Fig. 1.1. The group-living lizard, *Cordylus cataphractus*



CHAPTER 2

THE STUDY ANIMAL

Cordylus cataphractus

2.1 CLASSIFICATION AND DESCRIPTION

Cordylus cataphractus (Fig. 2.1) was described by Boie (1828). Peers (1930), FitzSimons (1943) and Loveridge (1944) contributed valuable subsequent information on the species. It belongs to the Cordylidae family, which is endemic to regions of Sub-Saharan Africa (Branch 1998). Largely resembling a dragon-like serpent, this relatively small lizard has evolved a spiny morphology, and as a result, it is heavily armoured, thickset, slow-moving and can easily be captured by hand. If threatened away from the crevice, the lizard takes its tail in its mouth, forming a ball of spines, with the very spinose tail and limbs protecting the soft underside of the body (Peers 1930; Mouton *et al.* 1999). According to the description by Loveridge (1944), the entire body 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, broader in males, are strongly rugose, with five to six rugose occipitals of which the outermost is pointed and directed obliquely backwards. *Cordylus cataphractus* is slightly sexually dimorphic, with males being larger than females and males typically having a broader head (Mouton *et al.* 1999).

Adult colouration is normally yellowish-brown (occasionally chocolate-brown) on the head and back, with an even or mottled

arrangement of these colours (Loveridge 1944). The ventral gular region is yellow to light yellow with ventriculated, spotted, or veined black markings. The belly is clouded with dark brown or greenish-black streaks and spots (Loveridge 1944). *Cordylus cataphractus* also boasts a level of phenotypic plasticity in terms of colour in relation to its environment. Loveridge (1944) reports that individuals, transferred from their arid habitat to a moister area located on the Cape Peninsula, underwent “striking colour changes”, although it was not clear whether diet, humidity or temperature were factors prompting such changes.

Cordylus cataphractus is best known for its distinctive anti-predatory behaviour to which it owes its common name, the Armadillo Lizard (Rose 1950). Locally, it is often referred to as ‘skurwejantjie’. Overseas, this lizard is sometimes also referred to as the ‘miniature sungazer’, stemming most likely from the common name for similar looking ‘sungazer’ (*Cordylus giganteus*), which is endemic to the Free State, South Africa. These two lizard species look morphologically very similar, barring that *C. giganteus* is almost double the size of *C. cataphractus*, and lives in self-constructed underground burrows (Ruddock 2000). Phylogenetically, *C. giganteus* was earlier reported to be the sister species to *C. cataphractus* (Herselman 1991). Frost *et al.* (2001) provide the most recent description of the molecular - phylogenetic relationships for the family Cordylidae, and from their results it is clear that *C. cataphractus* and *C. giganteus* are not closely related species.

2.2 FAMILY HISTORY OF *C. CATAPHRACTUS*

The historical transformation in cordyliform lizards included eco-physiological and behavioural adjustments in prey chemical discrimination ability, reproductive mode, foraging mode, and preferred substrate (Mouton & Van Wyk 1997). The Cordyliformes is a clade divided into the Gerrhosauridae and Cordylidae families (Lang 1991), of which the cordylids are endemic to the southern sub-continent of Africa and the gerrhosaurids occur both in Africa and Madagascar (Mouton & Van Wyk 1997). The Cordylidae was initially partitioned into four genera: *Chamaesaura* (grass lizards), *Cordylus* (girdled lizards), *Platysaurus* (flat lizards), and *Pseudocordylus* (crag lizards) (Loveridge 1944; Branch 1998). The cordylid phylogeny is still in its infancy although an inclusive understanding of its near outgroups and monophyly has been established earlier by Estes *et al.* (1988). Lang (1991) provided the most comprehensive reconstructed phylogeny for the cordylid family. Frost *et al.* (2001) state that although Lang's (1991) paper is informative of the morphological variation and the first taxonomic outgroup, Gerrhosauridae, it is only a beginning point for the understanding of phylogenetics in the group. By including molecular data into the character database containing primarily morphological traits (Lang 1991; Harvey & Gutberlet 1995), some new conclusions were reached. It was suggested that *Chamaesaura* and *Pseudocordylus* be transferred to the genus *Cordylus* to render a monophyletic taxonomy, and it was concluded that *Platysaurus* is the sister taxon to all the remaining cordylids (Frost *et al.* 2001).

Viviparity has evolved in the *Cordylus-Pseudocordylus-Chamaesaura* clade, as an adaptation to cold climates, evident in the temperate and highland distribution of extant species (Mouton & Van Wyk 1997). *Platysaurus*, which retained the oviparous plesiomorphic mode, has a predominantly lowland, subtropical distribution (Mouton & Van Wyk 1997). In the genus *Cordylus* there has also been a shift from the more widely-foraging mode, typical in the gerrhosaurids, to a more sedentary sit-and-wait foraging mode (Loveridge 1944). In addition to utilising rocks as refuge, lizards in a cold climate could utilise the heat from the rocks to facilitate thermoregulation, and a more sedentary foraging-mode would allow an individual to spend the majority of its time near its crevice-refuge basking on the rocks. Rocks would predictably also provide vantage points from which to spot prey.

In summary, there has been considerable morphological and physiological transformation in the family Cordylidae as a consequence of cold climates many years ago (Mouton & Van Wyk 1997). As a result, extant members of the genus *Cordylus* are viviparous, rock-dwelling, sit-and-wait foraging, relatively stocky lizards that vary greatly in degree of spinosity (Branch 1998).

2.3 SOCIAL STRUCTURE IN THE CORDYLIDAE

Social structure within Cordylidae has been poorly studied. Only a few behavioural studies have been executed (e.g., *Cordylus Cordylus* (Wirminghaus 1990; Cooper *et al.* 1996), *Platysaurus broadleyi* (Whiting 1999), *Cordylus giganteus* (Ruddock 2000), *Cordylus macropholis*

(Nieuwoudt *et al.* 2003). It is therefore difficult to make sound conclusions regarding social behaviour displayed in this family. The rock-dwelling lifestyle, sit-and-wait foraging mode, and a viviparous reproductive mode of the majority of cordylids (Mouton & Van Wyk 1997; Branch 1998), suit a territorial social structure, as is evidenced by sexual dimorphism displayed by most species (Mouton *et al.* 1999). Body morphology varies greatly among cordylid species, ranging from heavily armoured *C. cataphractus* to snake-like *Chamaesaura* (Branch 1998), which greatly influences the social behaviour of the lizards. Cooper & Van Wyk (1994) reported that prey-chemical discrimination (PCD) might be absent in the family. However, glandular epidermal structures are present in the cordylids, with considerable variation between species and between populations of the same species (Van Wyk & Mouton 1992). These glands are most likely used in social chemical communication, and studies investigating the glandular-chemical communication aspect of social structure are presently underway.

2.4 DISTRIBUTION, CLIMATE AND HABITAT

Cordylus cataphractus is distributed throughout the western extremes of South Africa (Fig. 2. 1.), from the Orange River in the north, stretching south along the coast and adjacent coastal inlands down to the Piketberg Mountains, and inland as far as Matjiesfontein in the Karoo (Loveridge 1944; Mouton *et al.* 1987; Mouton 1988; Branch 1998). The distribution of *C. cataphractus* falls predominantly within the winter rainfall region of South Africa. During summer, the rainfall figures attain a

maximum of 125 mm, but are normally less than 62.5 mm, and during winter the figures can range from 62.5 mm up to 250 mm (Acocks 1988). The vegetation types range 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 at Matjiesfontein (Acocks 1988). Granite outcrops seem to be unsuitable for use as refuges by *C. cataphractus*, as opposed to sandstone outcrops, possibly because granite does not fracture as readily and deeply enough (Loveridge 1944). Each fissure is normally inhabited by one group, which may persist for several seasons (Loveridge 1944; Mouton *et al.* 1999). Loveridge (1944) claims that although *C. polyzonus* occurs on the same hills as *C. cataphractus* there is no association between the two.

2.5 PREVIOUS RESEARCH AND CONSERVATION STATUS

Inquiries into the ecology of *C. cataphractus* started with general observations and descriptions by Rose (1950) and Peers (1930). Peers (1930) assumed that *C. cataphractus* forms family groups that, typically as in other group-living lizard species (e.g., *Egernia* spp. reviewed in Chapple 2003), include one adult male, one to a few adult females, and a few offspring. Mouton *et al.* (1999) showed that this was not the case in all *C. cataphractus* groups. Groups may contain more than one adult male. For example one group sampled contained seven adult males and only three adult females (Mouton *et al.* 1999). Flemming & Mouton (2002) established that female *C. cataphractus* only give birth to one live young per year in comparison to the 2-9 in other cordylids. *Cordylus*

cataphractus displays typical sit-and-wait foraging behaviour, analogous to other species in the family (Cooper *et al.* 1997; Mouton *et al.* 2000b). In light of the Armadillo Lizard being a sit-and-wait forager, it was postulated that living in groups might require certain behavioural, morphological, and physiological adaptations to meet energetic demands (Visagie 2001). Visagie (2001) subsequently reported that these lizards do indeed display very low activity levels during the hot summer months in comparison to the sympatric solitary-living cordylid species, which was indicative of an energy saving behaviour. Mouton *et al.* (2000a) investigated metabolic activity in *C. cataphractus* to contribute to the limited information on metabolic rate in the family Cordylidae, and in hope to be able to compare metabolic rates of group-living species with solitary-living species, in a phylogenetic perspective, in the future. The resting metabolic rate of *C. cataphractus* was reported to be very low for its size.

Cordylus cataphractus is listed as Vulnerable in the South African Red Data Book for Amhíbians 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.



Fig. 2. 1. Map depicting the distribution range of *Cordylus cataphractus* in South Africa (after Branch 1998).

2.6 GENERAL MATERIALS & METHODS

2.6.1 Study Site

The study site was situated on a farm in the Graafwater district (3218BA), Western Cape, South Africa. The site was located on a hill-slope, strewn with sandstone outcrops (Fig. 2.2). The population density of *C. cataphractus* at this site is high, with group sizes varying from just a few individuals per group, to large groups of up to 30 individuals (Mouton *et al.* 1999). For a description of the habitat, refer to section 2.4. Rain falls mainly in winter along the west coast and rainfall figures range from 50-150 mm. The summer is usually dry with rainfall figures easily falling below 50 mm. The aridity is, nonetheless, relieved by regular sea mists that are characteristic of the coastal regions (Acocks 1988).

2.6.2 Meteorological data

The temperature was recorded at 30-minute intervals for the duration of the daily observational period. A brief note on the general climate was made concurrently. The light intensity and temperature were recorded with Hobo H8 data loggers programmed to take readings at 30-minute intervals, and the temperature probes were positioned at the crevice refuge prior to the commencement of observations. The data loggers recorded the microclimate in the immediate surrounding of the refuge. Rainfall and additional climate data for the Graafwater district (31°55' S, 18°30' E, 100-200 m above sea-level) were obtained from the South African Weather Service.



Fig. 2.2. The typical environment of *C. cataphractus* individuals distributed in the Succulent Karoo vegetation belt.



2.6.3 Study Group

A large group including more than 10 individuals was selected. The total number of individuals in the group was not known upon selection, but data presented by Effenberger (2001), confirmed that the large group included at least three adult males, several females, and was easily observable from a distance, from all directions (ensuring little disturbance by the observer). From two hides stationed at nearly opposing vantage points, the entire immediate peripheral area outside the crevice could be observed. Owing to the flat topography of the base rock upon which the crevice is situated and the fact that the majority of the immediate surroundings of the crevice received sun, depending on the time of day, provided several basking areas (in full view by the observer) for the lizards.

2.6.4 Marking of individuals

Individuals were captured using a 5–20 m extendable catching pole that had a noose tied at the tip, which was used to lasso the lizards and lift them from the crevice. This method was used to minimise the disturbance at the crevice during the capturing process, because the marking procedure would inevitably impose stress on the individuals. The lizards were captured, marked and released immediately thereafter. Marking persisted for several days to include the majority of the group. Fifty-five individuals were captured, sexed and marked. The *C. cataphractus* group was divided into four age-sex classes, including: six adult males, 16 adult females, 16 sub-adults, and 17 juveniles. The adult lizards were sexed by examining the femoral and generation glands located

on the ventral aspect of the lower thigh region of the hind legs. Adult males display well-developed femoral glands, located on the ventral anterior margin of the thigh, and possess a generous number of generation glands, located on the lower ventral aspect of the thigh. Adult males also show a pronounced hemi-penal bulge at the base of the tail, located below the cloacal region. Females do not have such well-developed femoral glands and possess extremely few if any generation glands. Sub-adults and juveniles cannot be sexed externally with enough certainty, since the glands in individuals of these two age-classes are still not pronounced enough. Therefore, snout-vent length (SVL) measurements were also used to indicate age-sex class. Size class indicators were used to confirm age class, namely: *adults*: SVL > 95 mm, *sub-adults*: SVL ≤ 95 mm (Mouton *et al.* 1999), *juveniles*: SVL ≤ 75 mm (Flemming & Mouton 2002). Living alongside *C. cataphractus* in the same crevice, were two *Cordylus polyzonus* (cordylid) and three *Pachydactylus b. bibronii* (nocturnal gecko) individuals, the crevice thus sporting an astonishing total of 63 resident individuals. These other species were not considered in the study.

In the following chapters the ecology of *C. cataphractus* is addressed in direct relation to the evidence presented in previous studies, and the social behaviour, space-use and mating system are investigated for the first time.

CHAPTER 3

TERMITOPHAGY AND THE EVOLUTION OF GROUP-LIVING IN *CORDYLUS*

CATAPHRACTUS

3.1 INTRODUCTION

3.1.1 General

There is overwhelming evidence that the Armadillo Lizard, *Cordylus cataphractus*, forms permanent aggregations (Mouton *et al.* 1999; Visagie 2001; Visagie *et al.* 2002; Visagie *et al.* 2004). Furthermore, the species shows other unique features, which seem to be related to group-living, and if so, which suggest that the species already had a long history of group-living. Not only has it, for example, an exceptionally low resting metabolic rate for its size (Mouton *et al.* 2000a), but it also displays extremely low fecundity compared to other cordylids (Flemming & Mouton 2002). While the advantages of group-living are normally obvious in most group-living scenarios, it is not so in the case of *C. cataphractus*. Berry (2002) could not find any clear evidence that the species may benefit from a reduced predation risk through its group-living lifestyle. Flemming & Mouton (2002) reason that delayed dispersal of neonates in this slow-moving lizard may be beneficial, but taking into account that juveniles have to compete for resources with adults in the group, this advantage is probably negated. Also, delayed neonate dispersal does not explain why adults should stay together.

There is, on the other hand, a clear indication of the costs of group-living in *C. cataphractus*. The significant difference in the proportions of individuals with empty stomachs between group-living and solitary individuals that Mouton *et al.* (2000b) found in their analysis of stomach contents in this species, for example, suggests that competition among group members for food may be high, especially during the dry season. Visagie (2001) reported that members of a large group sit further from the crevice than individuals in smaller groups, most likely due to increased competition for resources among group members of larger groups.

Why then does *C. cataphractus* prefer to live in groups? The causative agents for the evolution of group-living in species are in general difficult to determine, but two broad categories can be identified. These are a) ecological constraints, where groups form due to a shortage of resources such as refuge sites, and b) philopatry, where individuals gain by being in close proximity to conspecifics (Emlen, 1994). Mouton *et al.* (1999) suggest that changes in the availability of suitable rocky habitat along the west coast of South Africa, resulting from rises in sea level, may have forced individuals to share available rock crevices and eventually resulting in permanent grouping behaviour in the species. Today, the species occurs over a large geographical area, including extensive mountainous areas where suitable crevices cannot be an ecological constraint anymore. Why is the species not forced to revert back to a solitary lifestyle? The aim of this study was to investigate the possible causative agents of group-living in *C. cataphractus* and also to

identify those factors that keep group-living enforced. There is reason to believe that termitophagy (termite feeding) and associated antipredator behaviour may be key factors in the group-living behaviour of this species. I therefore first provide some background on antipredator behaviour and diet, and highlight those factors that point to the importance of termitophagy.

3.1.2 Antipredatory behaviour

Some of the outstanding features of *Cordylus cataphractus* are its spiny armature and its tail-biting behaviour (Fig. 3.1). Tail-biting behaviour in reptiles is described as a defensive behaviour; a threatened individual will take its tail in its mouth to form a ball shape, protecting its soft underparts whilst also becoming cumbersome-to-handle prey (Carpenter & Ferguson 1977). Mouton *et al.* (1999) reported that, although tail-biting behaviour is not unique to *C. cataphractus* within the family Cordylidae, in the wild all *C. cataphractus* individuals immediately bite their tails upon handling, whereas the other tail-biting cordylids only occasionally do so. *Cordylus cataphractus* seldom tries to bite the collector instead of its tail. The lizard remains in a curled up, tail-bitten position until it senses that the danger has abated (Mouton *et al.* 1999). The tough osteodermate scales of the dorsal body, together with the sharp spines on the tail, body and limbs, form an effective barrier protecting the soft underparts of the lizard from predators (Mouton *et al.* 1999).



Fig. 3.1. A spiny morphology and tail-biting behaviour together are an effective predator deterrent.



Since all *C. cataphractus* individuals display tail-biting behaviour, the indication is that individuals are geared to defend themselves away from the crevice. Firstly, tail-biting behaviour would prove pointless inside the crevice for the reason that there is little space for manoeuvring into a ball shape. Secondly, *C. cataphractus* displays extremely low activity levels and when active, spends most of its time within centimeters of the crevice opening into which it quickly disappears when danger threatens (Mouton *et al.* 1999; Visagie 2001; Losos *et al.* 2002). It does not bite its tail and roll into a ball in such close proximity of the refuge (pers. obs.).

Mouton *et al.* (1999) are of the opinion that the spiny armature and tail-biting behaviour of *C. cataphractus* are clear indications that, although slow runners, individuals regularly venture some distance away from their crevices. They point out the resemblances between *C. cataphractus* and ant-specialists such as *Moloch horridus*, the Australian Thorny Devil, and *Phrynosoma* species from America. All are slow-moving, extremely spiny and occur in arid environments.

Moloch horridus, for example, is an obligate ant specialist, eating virtually nothing else (Pianka & Pianka 1970). The feeding rate for an individual has been estimated at 24 to 45 ants per minute, and large numbers of ants are eaten per meal, ranging from 675 up to 2 500 prey items (Pianka 1997). *Moloch horridus*, which feeds in the open for long periods, boasts cryptic colouration, sharp spines and a false head that provide

protection against predators. The false head is a spiny knob-like appendage on the back of the neck of the lizard. When threatened the lizard tucks its real head down between its forelegs, leaving the spiny false head in the position of the real head (Pianka & Pianka 1970). This would make it difficult for most predators to handle and swallow. Mouton *et al.* (1999) reason that *C. cataphractus* could be an opportunistic feeder and that individuals could regularly move away from their shelters to feed on termites out in the open, hence the strong resemblances with the above-mentioned ant specialists.

3.1.3 Foraging mode and diet

Despite being a group-living species, *C. cataphractus* behaves like a strict sit-and-wait forager, similar to other members of the genus *Cordylus* (Mouton *et al.* 2000b). Cooper *et al.* (1997) investigated foraging mode within the Cordyliformes, and reported that the cordylids are predominantly extreme sit-and-wait foragers. However, there is evidence of plasticity in foraging mode within the genus *Platysaurus* (Cooper *et al.* 1997; Greeff & Whiting 2000). Both foraging mode and prey chemical discrimination appear to be stable across most lizard families, in that active foragers typically chemically discriminate their prey whereas sit-and-wait foragers do not (Garland & Losos 1993; Cooper 1994; Cooper & Van Wyk 1994). Cooper & Van Wyk (1994) showed that chemical prey discrimination is absent in *Cordylus cordylus*. Mouton *et al.* (2000b) showed that prey chemical discrimination is also absent in *C. cataphractus*. Thus both these studies

support the general consensus that sit-and-wait foragers lack prey chemical discrimination. This stability is probably true for the entire family Cordylidae (Mouton *et al.* 2000b).

Stomach content analysis revealed that *C. cataphractus* is a generalist feeder, with the southern harvester termite *Microhodotermes viator* as possibly the most important prey item in its diet (Mouton *et al.* 2000b). *Microhodotermes viator* is distributed throughout the South-Western Cape and builds permanent underground storage chambers connected to a number of foraging ports and to a single hive (Coaton & Sheasby 1975; Annecke & Moran 1982). These termites emerge in great numbers during temperate weather conditions, and are regularly active, harvesting (foraging), on warm moonlit nights (Coaton & Sheasby 1975; pers. obs.). FitzSimons (1943, p.442) remarks that after spring rains allate termite individuals emerge in large swarms, and that *C. cataphractus* individuals 'feed ferociously' on the termites. His observation underscores the findings of Mouton *et al.* (2000b). We thus know that *C. cataphractus* eats termites, but we do not know how it harvests the termites. Being a sit-and-wait forager that stays close to its crevice, does it only eat those termites that venture really close to the crevice? Or does it, as its heavy armour and tail-biting behaviour seem to suggest, move considerable distances away from the crevice to harvest termites active on the surface at the termite nest's openings (foraging ports)? The immediate aim of this study was to find proof that *C. cataphractus* harvests termites at the termite nest-discs, in other

words that it moves away from the crevice to do this. With this proof in hand, I then discuss the significance of termitophagy in the evolution of group-living behaviour in this species.

3.2 MATERIALS & METHODS

A quadrat with an area of 6000 m² was demarcated at the Graafwater study site to include several crevices containing *C. cataphractus* groups, as well as several termite nest-discs (nest-disc = termite nest area, which on the surface can be located by locating foraging ports and soil dumps). The quadrat was thoroughly searched and all termite nest-disc areas and associated foraging ports, as well as all the crevices containing lizards, were mapped. Foraging ports, rather than soil-dump mounds (see Coaton & Sheasby 1975) were focused upon since termite surface activity is high at the foraging ports while individuals are busy harvesting. The distance from the midpoint of each crevice containing lizards, to the closest nest-disc area was measured and recorded as the nearest nest-disc distance (NND). The NND underestimates, rather than overestimates, the distance travelled by an individual from a crevice to a nest-disc area.

Lizard tracks made by all the other predominant lizard species at the site, namely *C. polyzonus*, *Meroles knoxii* and *Pachydactylus bibronii* were examined and differentiated from the track made by *C. cataphractus*. Similar-sized lizards were observed and photo's of the tracks were taken and

closely examined. The sand around each termite nest-disc area, more specifically the foraging ports, was brushed to be able to clearly see any tracks left by visiting lizards. Readings were taken at 08h00 and 18h00. Taking a reading entailed inspecting the brushed sand for *C. cataphractus* tracks at all nest-disc areas in the quadrat. If *C. cataphractus* tracks were present, the nest-disc area was scored one and if not, it was scored zero. Any other animal tracks present were identified and noted. The termite nest-disc areas were monitored over five days of temperate to warm climatic conditions in November 2003. This is incidentally the month when grasses emerge and the termites are normally highly active at the study site (pers. obs.).

3.3 RESULTS

The termite nest disc areas, numbers of associated foraging ports and nearest nest-disc distances are listed in Table 3.1. The results show that *C. cataphractus* visit termite nest disc areas, as tracks were present at termite nest disc areas up to 20 m away from the nearest crevice (Fig.3.2). Individuals ventured an average distance of 6.10 m from the crevice. Certain tracks could also be followed from a foraging port several meters back to the crevice from which the individual ventured.

Table 3.1. The number of termite nest-disc areas located in the quadrat together with the number of surrounding foraging ports, and the nearest nest-disc distances (NND)

Nest-Disc area number	NND (m)	Number of surrounding foraging-ports
1	4.60	3
2	5.60	20
3	5.70	6
4	6.10	1
5	6.10	0
6	6.20	14
7	7.00	3
8	7.10	3
9	7.20	5
10	10.20	6
11	11.10	2
12	12.50	6
13	13.00	8
14	14.60	10
15	16.70	11
16	19.20	5
17	19.30	15
18	23.20	7
19	24.50	0
20	24.90	7
21	31.50	4
22	34.20	4
23	35.00	4
24	37.60	7
25	47.10	1
26	52.50	6
-		Total = 158

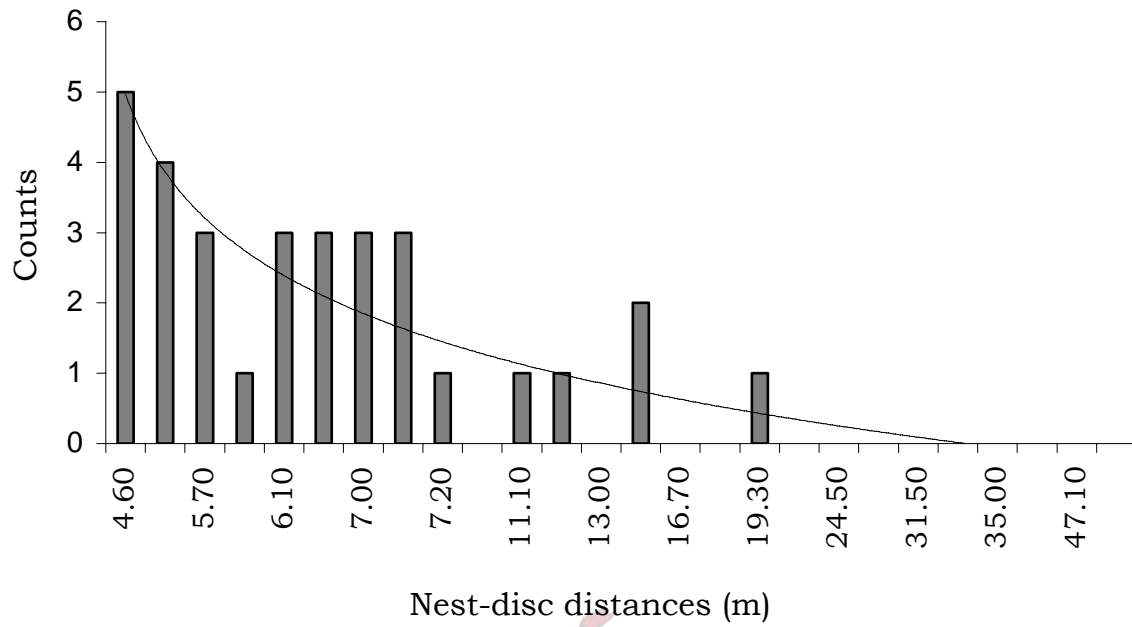


Fig. 3.2. Histogram depicting distances travelled by *C. cataphractus* individuals that visit termite nest-disc areas to forage on termites.

Other tracks encountered at the termite nest-disc areas, included those of the sand lizard, *Merolus knoxii*, the angulate tortoise, *Chersina angulata*, and the karoo robin, *Erythropygia coryphaeus*. Another track encountered was that of the yellow mongoose (*Cynictis penicillata*), a termite specialist feeder (Skinner & Smithers 1990), and one of the potential small mammal predators at the study site preying on *C. cataphractus*.

3.4 DISCUSSION

The results of this part of the study show that *Cordylus cataphractus* individuals visit termite nests considerable distances away from their rock shelters. Together with the stomach content data of Mouton *et al.* (2000b), there is thus convincing evidence that *C. cataphractus* harvest termites away from their rock shelters. How often specific individuals leave their shelters to harvest termites and how long they stay away from their rock shelters is not known at present.

3.4.1 Plasticity in foraging mode

Cordylus cataphractus exhibits the typical characteristics of an extreme sit-and-wait forager (Mouton *et al.* 2000b). It has a the stocky built (Cooper *et al.* 1997; Branch 1998) and spends a limited amount of time moving (Mouton *et al.* 2000b) – immobility being the primary defence mechanisms of sit-and-wait foraging species (Vitt & Price 1982). *Cordylus cataphractus* is

generally slow-moving and is easily captured by hand in the open (FitzSimons 1943). Widely foraging lizards, on the other hand, normally boast a more streamlined body and high agility to facilitate evasion of predators (Schoener 1971, Greene 1988). *Cordylus cataphractus* furthermore lacks prey chemical discrimination ability and is highly visually orientated, a clear indication that it is, like other cordylids, a typical sit-and-wait forager (Mouton *et al.* 2000b).

Despite the complex relationships between the ecological correlates of foraging mode (e.g., morphology, sensory mode, relative clutch mass), certain species may display a level of plasticity in foraging mode (i.e., marked change in foraging velocity) in response to food availability (Norberg 1977). Huey & Pianka (1981) showed that the foraging velocity of the sit-and-wait foraging Kalahari gecko, *Ptenopus garrulus*, did indeed increase with an increase in food availability (after summer rain storms when swarms of allate termite reproductives emerged). The Namib Desert lacertid, *Meroles anchietae*, is another fine example of an arid land lizard that displays flexibility in foraging mode. During periods of wind this lizard sit-and-wait forages on seeds and invertebrates carried by the wind, and during wind-calm periods *M. anchietae* forages widely for prey (Robinson & Cunningham 1978). It seems that it may be advantageous to have a flexible foraging mode in unpredictable arid environments.

A model by C. Janson predicts that predators favour sit-and-wait foraging energetically when the prey is highly mobile (Huey & Pianka 1981).

Huey & Pianka (1981) conclude, however, that foraging mode within species may not be as flexible as is assumed in some of the foraging models, since active and sit-and-wait foragers may differ vitally in life history traits. Although, should such a shift occur, constraints on a flexible foraging mode would likely be non-symmetrical and thus from an energy point of view, a shift would most likely occur from a widely foraging to a sit-and-wait foraging mode rather than vice versa (i.e., the likelihood of a widely foraging species shifting to a sit-and-wait foraging mode is greater than the opposite) (Huey & Pianka 1981).

Huey *et al.* (2001) report that the vast majority of lizard species are generally in positive energy balance irrespective of foraging mode. Notably, several species of diurnal termite specialists were found to be in positive energy balance, with a low incidence of empty stomachs. With specific reference to arid environments, widely foraging species needed almost double the amount of energy for their daily activities in comparison to sit-and-wait foraging species, but did attain a net energy gain of 1.5 times more than that of a sit-and-wait foraging species (Huey & Pianka 1981). Clearly, a shift from a sit-and-wait foraging mode to a widely foraging one would be energetically very demanding with respect to the eco-morpho-physiological aspects of an individual. An increase in foraging velocity also increases the chance of encountering predators consequently augmenting the overall risk of predation (Andrews 1979; Huey & Pianka 1981; Perry & Pianka 1997).

With regard to the evidence that *C. cataphractus* moves away from the crevice, although it is a sit-and-wait forager, one might argue that this lizard also forages widely, and that it thus essentially displays flexibility in foraging mode. To emphasize this, harvester termites are relatively (over a large scale) non-mobile, spatially and temporally distributed (i.e., sporadic clumped distributions) (Wilson & Clark 1977; Coaton & Sheasby 1975), and thus are characteristically a prey item pursued by widely foraging species (Huey & Pianka 1981; Huey, *et al.* 2001). Most probably, however, *C. cataphractus* does not conduct searches for termites, but spot the termite foraging ports from the crevice. In the arid environment where the species occur, visibility will probably be good at most times.

3.4.2 Optimal foraging

When predators themselves are exposed to predation pressure from higher trophic levels, the element of risk must be considered and time-minimising behaviour is expected over energy-maximising behaviour (Krebs & Davies 1993). From the seventies onward, vehement arguments about Optimal Foraging Theory (OFT) have been presented (Perry & Pianka 1997). Schoener (1971) introduced two measures of foraging success that remain in use, 1) maximisation of energy intake rate and 2) minimisation of time needed to obtain nourishment. That is if foraging success is 'assumed commensurate with fitness' (see review by Perry & Pianka 1997). Assuming that it is, if the potential diet consists of (n) prey types ranked by profitability,

the optimal forager should: 1) always include the most profitable prey in its diet, even if the item is rare enough to not have a significant contribution to the total net caloric intake, and 2) beginning with the individually most profitable type of prey, continue to include types in its diet until the profitability of a type falls below the net caloric intake of the diet without that type (Schoener 1971; Krebs 1978). Termites may rank as the most profitable prey item on the prey list of *C. cataphractus*, as was indicated by the stomach content analysis. Termites are small and numerous, therefore, predictably presenting a lizard with little handling time as well as little time needed to obtain many prey items (e.g., *Moloch* feeding on ants, mentioned earlier).

Cordylus cataphractus individuals that venture away from the crevice to feed on termites must eventually return to the crevice, hence, ultimately making a round trip between the nest and the food patch. Central Place Foraging theory (CPF) was used in the past to assess the energy requirements of individuals travelling away from the nest, to obtain a resource, and then bringing it back to the nest (e.g., food for young) (Andersson 1981). The CPF theory specifies that the animal must return to a central place after foraging about, and basically stipulates that the energy cost is for a round trip (Orians & Pearson 1979). Central place foraging theory could be applicable to *C. cataphractus* since, as shown by Landahl (1997), the conclusions can be generalised to accommodate predator populations foraging out of refuges, not necessarily out in all directions, and

additionally to infer the effects of their foraging behaviour on prey distributions within habitats.

An investigation into the energetics of *C. cataphractus* directly related to the intake of specific prey items deems necessary before further conclusions can be made about foraging success within this species. In future studies, the use of an OFT model, incorporating CPF theory, as presented by Landahl (1997) may prove invaluable for measuring foraging success and monitoring energy budgeting displayed by this species. The foraging success in *C. cataphractus* clearly differs among individuals (Mouton *et al.* 2000b), and so an investigation into the foraging success of individuals would give further insight into the amounts of energy fluctuating through an individual and in turn the group.



3.4.3 Other termitophagous lizard species

Many lizard species include termites in their diets, but termites appear to be a more important prey item among gekkotans and autarchoglossans than among iguanians, and among desert lizards than among Neotropical lizards (Pianka & Vitt 2003). Many fossorial forms are termite specialists, for example, *Typhlosaurus*. Several desert-living lizards, for example, species from the family Lacertidae (in particular Kalahari lacertids) display termitophagy. Termites, beetles and ants constitute major prey items in all major desert-lizard systems, and termites were reported to assume a disproportionate role in the Kalahari Desert (Pianka 1986).

After heavy summer rains in arid environments, when termites send out their allate reproductives in great abundance, virtually every species of lizard eats nothing but termites (even lizard species that normally never feed on termites) (Pianka 1986). Nonetheless, the majority of termite specialists are ground-dwelling active foragers rather than rock-dwelling sit-and-wait foragers, since active foragers have a higher chance of finding a more sporadic and clumped prey source (Huey & Pianka 1981).

3.4.4 Advantages of termitophagy

Food specialization on termites is economically feasible, because these social insects are generally clumped and hence constitute a concentrated food supply (Huey & Pianka 1981). Lizards can eat their fill at one spot, thereby cutting down on total movement and also on total foraging time. Reductions in movement and foraging time will decrease predator impact on the species. Termites are no less nutritious than other insect prey, in fact the allates are considered highly nutritious (Redford & Dorea 1984; Van der Westhuizen *et al.* 1985). Termites are an abundant and easy prey source in arid environments, and therefore should be a profitable prey item even though there is no significant difference in nutrition content in comparison to other insects. The fact that allate termite reproductives are considered highly nutritious underscores the evidence that most lizards living in arid environments capitalise on this rich food source when the opportunity arises.

3.4.5 Disadvantages of termitophagy

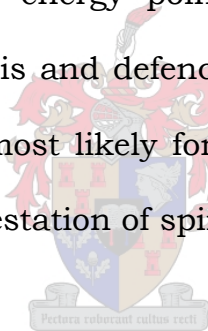
Termites are spatially and temporally unpredictable prey. Moreover, foraging activity and allate releases may occur at night and thus, diurnal lizards may not be able to take full advantage of this food source. For example, during the hot summer months in the arid Kaokoveld of Namibia, termite foraging activity is limited predominantly to temperate moonlit nights (Coaton & Sheasby 1975). *Cordylus cataphractus* is a diurnal lizard.

In light of the evidence that worms usually heavily parasitize *Moloch horridus* individuals, Pianka (1997) reports that the parasitic nematode worms probably exploit ants and termites as intermediate hosts and various lizard species as their final hosts. Therefore being a termite specialist may result in a higher parasite load. Increased parasite loads have been reported to be a cost in permanently group-living species (Lanham 2001). Therefore in *C. cataphractus*, being a termite specialist may accentuate the problem of parasite load in a group-living scenario.

3.4.6 Consequences of termitophagy

Termitophagy requires *C. cataphractus* individuals to regularly venture considerable distances away from their crevices. In the arid western parts of the country where *C. cataphractus* occurs, this means that individuals will be out in the open, where vegetation cover will provide little or no protection

against predators. Theoretically, this predation pressure can have two opposite evolutionary outcomes: a) the species may evolve good sprinting abilities so that individuals can outrun potential predators, or b) the species may evolve armature or behavioural strategies to deter predators from eating the lizards. In the case of *C. cataphractus*, high sprinting ability will probably be inefficient as an antipredator mechanism, because individuals may need to run several meters back to their shelters, which may be considerable distances away. Lizards that feed in the open and are fast runners, are normally not rock-dwelling and will run to the closest shelter offered. Therefore from an energy point of view, one would expect *C. cataphractus* to rely on crypsis and defence, not evasive behaviour (see also section 3.4.1.). Hence, it is most likely for this reason that *C. cataphractus* displays such a strong manifestation of spinosity and tail-biting behaviour.



3.4.7 Termitophagy and group-living

Termitophagy and the heavy armature of *C. cataphractus* appear to be key factors in the group-living behaviour of this species. Termitophagy allows individuals to live in groups as competition for food at the home crevice will be limited. The heavy armature of *C. cataphractus* renders it clumsy and slow-moving, compared to other cordylids. Group-living will eliminate juvenile dispersal and mate-searching excursions, activities which, in the light of the heavy morphology of the species, may result in high predation impact. Group-living offers the opportunity of increased vigilance via the

many eyes hypothesis and the dilution effect (Hamilton 1971), which in the case of *C. cataphractus* with its heavy armature, may be particularly beneficial. The many eyes model is explained within the group size effect (Lima 1995). As group size increases individual vigilance decreases. Lima (1995) stresses that *collective detection* is essential to the many eyes model or else benefits to group members will be negated. As mentioned earlier, Berry (2002), however, failed to find a clear advantage of a reduced predation risk by grouping behaviour in *C. cataphractus*.

3.4.8 Secondary effects of group-living

Despite the fact that termitophagy may relieve competition for food in the group-living situation, the unpredictability of this food source will require *C. cataphractus* to source other invertebrate prey when termites are not available. There will thus always be some degree of competition for food in the group-living situation, which, through natural selection, will result in further adaptations to group-living. When resources are limited, neonates will compete with each other for food and larger, more competitive neonates will have an advantage. Natural selection will thus favour increased neonate size, which will reduce the number of offspring that can be produced. The very low fecundity and large neonate size recorded for *C. cataphractus* (Flemming & Mouton 2002), therefore in all likelihood represents a secondary effect of group-living. Likewise, a low resting metabolic rate (Mouton *et al.*

2000a) may be a further secondary effect of group-living to lessen the effects of competition for food in the group-living situation.

3.4.9 Evolutionary scenarios

Two largely overlapping, evolutionary scenarios for the evolution of group-living behaviour in *Cordylus cataphractus* are proposed. The scenarios are not mutually exclusive.

a) Termitophagy the initial driving force: The ancestor 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 as explained above. The heavy armour affected the general mobility of the species and led to a reduction in activity levels 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 and fecundity.

b) Limited shelter availability the initial driving force: The initial driving force was not termitophagy, but limited shelter availability. Along the arid west coast of South Africa, rising sea levels and/or shifting sand dunes resulted in limited rocky habitat available for this rock-dwelling species. Individuals were thus forced to share available crevices. Because of competition for food, members of a group had to venture further from the crevice to obtain food. Individuals started to include termites in the diet and this soon became the most important prey item, thereby alleviating competition for food at the home crevice. The species evolved heavy armour to facilitate foraging on termites in the open, away from the crevice. Termitophagy resulted in the further strengthening of group-living behaviour.

3.4.10 Further predictions

If termitophagy plays such a key role in group-living in *C. cataphractus* as advocated here, then this species should be termitophagous throughout its range. Despite the species' low metabolic rate, individuals should find it difficult to survive in groups if termites do not form a major part of their diet. The heavy body armour should largely prevent the species from leading a solitary lifestyle as neonate dispersal and mate-finding excursions will increase predation impact dramatically. One would predict that groups would be smaller and population density lower in areas with low termite abundance.

CHAPTER 4

SOCIAL BEHAVIOUR OF *CORDYLUS CATAPHRACTUS*

4.1 INTRODUCTION

The behavioural repertoire of lizards has been used to facilitate answering various complex questions (Torr & Shine 1994). Owing to the diverse habitat-specific circumstances that lizards are exposed to, they show great behavioural and morphological diversity; yet lizard behaviour is relatively stereotypical and best understood among all reptiles (Carpenter & Ferguson 1977). It is thus possible to compile a list of behavioural acts (i.e., an ethogram) that can be divided into a dichotomy of agonistic and non-agonistic actions (Carpenter & Ferguson 1977). At the most basic level, behaviour is broken down into individual behavioural acts. Each act is the most basic movement produced by a particular set of muscular actions or motor sequences (Carpenter & Ferguson 1977). An act system is a combination of behavioural acts relayed together, and some acts may form part of more than one act system (for a detailed explanation of act systems in lizards see Carpenter & Ferguson (1977)).

Clearly, studies of social behaviour may prove useful in assessing the social relationships among individuals. Social behaviour in lizards is strongly linked to the mating system (Stamps 1977). Hence, a significant relationship often exists between the habitat, morphology and social structure of lizards (Stamps 1983). Sexual dimorphism, for instance, is greatest in highly territorial species and is largely due to sexual selection and intra-specific niche divergence (Stamps 1983a; Shine 1989). Focus in

social behaviour studies may be directed on agonistic actions because agonistic social behaviour ultimately serves for defence of resources (Parker 1974). Agonistic social behaviour (aggression) may be mediated by dominance hierarchies, but is often distinctly the result of competition for resources among conspecifics and particularly of territorial encounters (Martins 1994). Martins (1994) also highlights that aggression is graded in intensity, from less aggressive displays to highly aggressive combat.

Cordylid lizards are predominantly sedentary, sit-and-wait foraging, rock-dwelling species (Mouton & Van Wyk 1997). Therefore, especially in terms of field studies, the potential for observing daily maintenance activity and social behaviour is great, because individuals tend to spend most of their time completing daily tasks at their refuge. Little is known, however, about cordylid behaviour. In terms of an ethogram, behavioural data are only available for *Cordylus cordylus* (Wirminghaus 1990), *C. giganteus* (Ruddock 2000), and *C. macropholis* (Nieuwoudt *et al.* 2003). Whiting (1999) investigated the dear enemy phenomenon in *Platysaurus broadleyi*. Mouton *et al.* (1999) speculate that the male-biased sexual dimorphism evident in *C. cataphractus* is largely a result of sexual selection.

Sexual selection has been demonstrated to be a powerful agent that influences the evolution of social behaviour in many phylogenetically diverse vertebrates (Andersson 1994; Wade 1995). Gross (1996) recently determined that sexual selection may also be responsible for variation in social behaviour within each sex. On the whole, it is still widely appreciated that sexual selection can result in marked differences in the

social behaviour displayed by males and females (Trivers 1972). Males are more likely to be the sex that competes intensively for access to mates (Baird *et al.* 2003). Thus, particularly in the male sex, sexual selection may result in asymmetries in both behaviour and morphology that are important in competitive contests for mates (Andersson 1994). As was pointed out in Chapter 3, *C. cataphractus* males in a multi-male group are expected to compete for access to mates. Intrasexual male competition for mates often results in selection for agonistic behaviour patterns (Shine 1989; Hews 1990). Therefore, the objective in this part of the study was to establish an ethogram for *C. cataphractus*. An ethogram is a prerequisite for the analysis of the social structure in permanent multi-male groups (see Chapter 5).

4.2 MATERIALS & METHODS

The general materials and methods are described in Chapter 2.

4.2.1 Procedure

Field observations were carried out during the breeding season, from September until the end of November 2002. Lizards were monitored on days when lizard activity was rife, from when they became active in the morning (\pm 10h00) until activity abated in the evening (\pm 18h00). Observations were completed through a telescope positioned in a hide about 50 m from the crevice.

4.2.2 Behavioural acts

Very little is known about the behaviour of *Cordylus cataphractus* and therefore behavioural acts were in this study described and recorded for the first time for this species. Focus was on the social behaviour displayed by *C. cataphractus*, but all behavioural acts were monitored. Behavioural acts were recorded at 30-minute intervals using the scan-sampling method (Martin & Bateson 1986). Recording all visible members in the multi-male group took up to 10 min, therefore readings commenced 5 min prior to and ended 5 min after the 30-min interval point. Each social behavioural act and interaction was recorded over a total of 102 hours of field observation time. All distinct behavioural acts by all age-sex classes were identified and described. Once a coherent index was produced of all the displayed social behaviours, the behavioural acts, as summarised in Ruddock (2000) for *Cordylus giganteus* and the framework for *C. cordylus* (Wirminghaus 1990), were used as a basis to produce the ethogram for the study animal.

4.2.3 Frequency and context

Behavioural acts were expressed as counts. It was thus possible to calculate the frequency (proportion) of behavioural act systems elicited by each observed (marked) individual. Since behavioural observations were at 30-minute intervals and not continuous, the behavioural frequencies presented are not a time budget. It was not always possible to observe all individuals in the multi-male group at all times. Therefore, certain individuals may have a higher 'percentage sighted' than others, and so the

frequency of a behavioural act system inevitably differs from individual to individual. Thus, the frequency of behavioural act systems displayed by an individual was calculated proportionally to the total observation time for that specific individual. Initially, for indexing, social behaviours were divided into agonistic and non-agonistic actions. Subsequent to the indexing, further evaluation was carried out in accordance with the behavioural frameworks available for the other cordylids to determine the context of the respective behaviours elicited. Where comparison with other cordylids was not possible, the review of stereotyped lizard behaviour by Carpenter & Ferguson (1977) was used to evaluate the context of the behaviour.

4.2.4 Frequency of agonistic behavioural acts

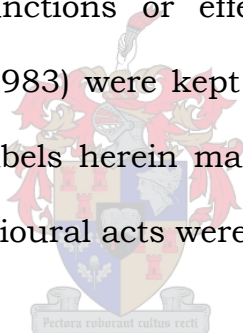
To determine the frequency of agonistic behavioural acts during an encounter, for descriptive purposes only, intruder-resident trials were staged at seven single-male groups using a randomised block method. The objective of these trials was to determine the frequency (proportion) of the different agonistic acts displayed by residents of the crevice towards the intruder and to establish an aggression level table for future use in behavioural studies on the study animal. The intruder was tethered to a heavy hand-sized rock, within 30 cm of the crevice. The lizard was covered by a cotton bag, which was then removed by the observer from a distance, using a drawstring to slip off the bag thus exposing the intruder to the residents of the group. A trial was monitored from the time a resident appeared until the resident chased the intruder and the intruder chose to

flee or for a base time of 10 minutes. Behavioural acts displayed by the resident were focused on, since behavioural acts displayed by the intruder would undoubtedly be affected by the stress imposed by handling and the introduction procedure.

4.3 RESULTS

4.3.1 Behavioural repertoire

The social repertoire of *C. cataphractus* could distinctly be divided into agonistic and non-agonistic social behaviour. Adults characteristically performed the behavioural acts described, unless stated otherwise. The difficulties of assigning functions or effects to behaviours based on observational data (Slater 1983) were kept in mind while the labelling of acts was completed. The labels herein mainly have a heuristic purpose. The following discrete behavioural acts were discerned:



Agonistic Behaviour

FACE OFF – the individual initiating an encounter fixes its gaze on the opponent, either at a slight distance (roughly up to 30 cm) away or face-to-face.

PUSHING – the head region (specifically the snout) is used to nudge or push an adversary.

FACE-OFF CIRCLING – the head-to-tail movement of two individuals in a semi-circular or circular path while presenting themselves laterally.

BODY TILT – the body is tilted on its longitudinal axis to the left or right. This behaviour is also referred to as the arched body-tilt.

ARCHED BACK – an individual raises its back dorsally, higher in the centre along the longitudinal axis, producing an arch effect.

TAIL FLICKING – the tail is thrashed in a brisk wave-like manner at the opponent (usually directed at the head region).

BITE – an individual bites the hind-leg, foreleg, tail, head or flank of its opponent. A bite may be held for a long duration, accompanied by violent jerking, when aggression levels escalate.

CHASE – an opponent is chased over a distance longer than that of the body length of the individual carrying out the chase.

FULL RAISE – lizard raises itself off the ground by extending all four legs.

ENGORGED THROAT – the skin under the throat is slightly expanded, making the neck area look larger.

TAIL WAGGING – tail is wagged slowly or briskly from side-to-side in a sweeping manner.

Non-agonistic behaviour

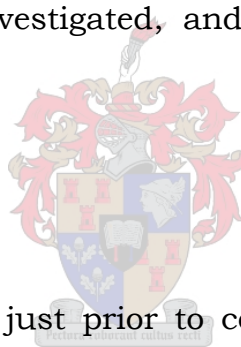
Submissive

HEAD BOBBING – the head is moved up and down rapidly without the shoulders or forelegs moving.

CROUCH – the individual keeps/presses its entire trunk close to the substrate.

Investigative

TONGUE FLICKING – the individual fully extrudes its tongue from mouth towards the area being investigated, and may in many circumstances touch the substrate.



Mating

COURTSHIP – the male will, just prior to copulation, begin to bite at the hind-legs, tail, or flank of the female. These bites are less aggressive and may be held for a few minutes, but usually are of short duration.

COPULATION – the male maintains a bite to the head region of the female while sliding his tail and one hind-leg under the tail of the female, so that the cloacal apertures lie opposite each other and copulation can take place. The other hind-leg is used for stability by holding onto the dorsal aspect of the posterior end of the female, positioning it over the base area of the tail.

TWITCHING – after copulation, both males and females display a series of violent twitches.

CLOACAL SCRAPING – an individual drags the vent region of its body over the ground, with the tail slightly arched.

HIND-LEG DRAGGING – the male can be seen dragging its hind legs with the ventral aspect of the thigh region pressed firmly against the substratum.

4.3.2 Frequency and context

Behavioural acts were divided into two contextual situations, namely maintenance and social behaviour. Maintenance behaviour was further sub-divided into three act systems, namely general, inner-margin, and outside behavioural act systems. Social behaviour was further sub-divided into the following act systems: investigation, submission, aggression, and mating (Table 4. 1).

General maintenance included foraging and hind-leg dragging behaviour. Unfortunately, in many instances, it was not possible to observe individuals foraging and actually taking a prey item, even though the behaviour of the individual was indicative of a foraging attempt. Therefore, only when an individual was clearly seen taking a prey item, was it recorded as foraging. Adults were not observed to take prey at the crevice during recordings, but sub-adults and juveniles were.

For logistic purposes, I termed *inner-margin* behaviour as types of *rest* behaviour since individuals on many occasions had closed eyes or just

remained in the shade or both. I termed *outside* behaviour as types of *bask* behaviour outside the crevice, since individuals were continually positioning themselves in relation to the sun. Inner-margin maintenance behaviour included all behavioural acts other than social behaviour at the inner-margin of the crevice, where individuals were still visible and did not retreat into the crevice completely. Inner-margin behaviour typically included *rest* behaviour where an individual was observed to lie flat with open or closed eyes; *semi-elevated rest* where an individual sat with its upper body raised by extending its forelegs, and eyes kept open; and *fully elevated rest* where an individual was observed to fully raise its body by extending all four legs and eyes kept open.

Behavioural acts outside the crevice predominantly took place within 0 - 30 cm from the refuge and included *bask* behaviour where an individual was observed to lie flat, and eyes were kept open or closed; *semi-elevated bask* behaviour where an individual sat in the sun with its upper body raised by extending its forelegs, eyes kept open; and *fully elevated bask* behaviour where an individual was observed to fully raise its body by extending all four legs, eyes kept open. It is important to note that both fully elevated rest and bask behaviour were not observed in a social context and therefore must not be confused with *full raise* aggressive behaviour that was observed in a social context. Both *inner-margin* and *outside* behavioural acts may well be categorised as thermoregulatory behaviour, but without sequential evidence of temperature fluctuations in direct relation to the lizard's behaviour, it is

safer to omit from assigning a thermoregulatory purpose to these non-social maintenance act systems.

In the social context, investigative behaviour included tongue-flicking. Submissive behaviour included head-bobbing and crouching behavioural acts. Aggressive behaviour included encounter and combat behavioural acts, where encounters typically entailed aggressive display and encounter behaviours (Table 4.3). Mating behaviour included courtship and copulation (Table 4.1).

Certain behavioural acts were displayed more than other acts, and differences were apparent in the proportion of behavioural acts displayed by the various age-sex classes (Table 4.1). A One Way ANOVA was used to compare the data. The data are percentages and were therefore transformed prior to testing, using the Arcsine transformation. In the social context, a One Way ANOVA showed that there was a significant difference in aggressive behaviour among the age-sex classes (One Way ANOVA: $df = 3$, $H = 18.296$, $P < 0.001$). The Dunn's multiple comparison procedure was used to isolate the groups that differ. Adult males showed a significantly greater proportion of aggressive behaviour than juveniles ($Q = 3.216$, $P < 0.05$), but adult males did not elicit a significantly different proportion of aggression than adult females ($Q = 2.104$, $P > 0.05$), and sub-adults ($Q = 2.468$, $P > 0.05$). Sub-adults displayed little aggression (1.64 %) and juveniles were not observed to elicit any aggression. Sub-adults and juveniles did, however, display the highest proportion of submissive behaviour. Females displayed little aggression (1.93 %) and even less submissive behaviour (1.36 %). No significant difference was

found in the proportion of submissive behaviour displayed by all age-sex classes (One Way ANOVA: $df = 3$, $H = 2.493$, $P = 0.477$). However, juveniles did display a high proportion of submissive behaviour, which incidentally entailed 100 % of their social behaviour (Table 4.1, Summary).

Where general maintenance behaviour is concerned, males were the only age-sex class to display hind-leg dragging behaviour (6.08 %). No significant difference was found in maintenance behaviour between the respective age-sex classes (One Way ANOVA: $df = 3$, $H = 1.382$, $P = 0.710$). Males also displayed flat *bask* behaviour frequently, and together with the females, displayed a high proportion of *semi-elevated bask* behaviour in comparison to the sub-adults and juveniles. Males were observed to elicit *fully elevated bask* behaviour less often (0.22 %) than both females (0.75 %) and sub-adults (0.98 %), while juveniles abstained from displaying this behaviour. Juveniles did elicit a very high proportion of *rest* behaviour (45.06 %) in comparison to the other age-sex classes (Table 4.1). *Semi-elevated rest* and *fully elevated rest* behavioural acts were also displayed more frequently by juveniles than by the other age-sex classes.

A significant difference was found in *outside* behaviour between the age-sex classes (One Way ANOVA: $df = 3$, $F = 4.288$, $P = 0.009$). Adult males and females, as well as sub-adults, displayed significantly higher proportions of *outside* behaviour than the juveniles (Holm-Sidak: $t = 2.159$, $P = 0.036$; $t = 3.429$, $P = 0.001$; $t = 2.178$, $P = 0.034$, respectively). Overall, males were observed to elicit maintenance behaviour for a total of 88.52 % of the time (Table 4.2). Out of this total, the majority of the time (59.34 %) was spent eliciting *outside* behaviour. Females were observed to

spend a total of 94.48 % eliciting maintenance behaviour, 62.80 % of this behaviour included *outside* behaviour, and 5.52 % of the time included social behaviour (Table 4.2). Sub-adults displayed maintenance behaviour for 95.41 % of the total time observed of which a majority of 51.78 % was *outside* behaviour (Table 4.2). Juveniles, on the other hand, displayed a marked difference in comparison to the adults and sub-adults by also predominantly displaying maintenance behaviour, 93.99 % of the time, however, only 32.66 % of this behaviour was *outside* behaviour (Table 4.2). A significant difference was observed between *inner-margin* behaviour (One Way ANOVA: $df = 3$, $F = 5.990$, $P = 0.001$). The Holm-Sidak multiple comparison method showed that adult males, adult females, as well as sub-adults displayed a significantly lower proportion of *inner-margin* behaviour in comparison to the juveniles ($t = 3.387$, $P = 0.001$; $t = 3.600$, $P < 0.001$; $t = 2.335$, $P = 0.024$ respectively). Investigative behaviour was only recorded for sub-adults (1.11 %) and foraging maintenance behaviour only for sub-adults (0.25 %) and juveniles (0.35 %) (Table 4.2). As could be expected only the sexually mature adults displayed mating behaviour.

Table 4. 1. Frequency of behavioural acts per act system divided into two contextual situations – maintenance and social behaviour. The table lists the proportion of behavioural act systems and their respective behavioural acts displayed out of a 100 % context for each of the main act systems (maintenance and social act systems, respectively) (i.e., a 200 % total, see Summary).

			Males	Females	Sub-Adults	Juveniles
Maintenance	General	Feeding	0.00	0.00	0.26	0.37
		Hind-leg dragging	6.08	0.00	0.00	0.00
	Inner-margin	Rest	20.19	21.40	29.39	45.06
		Semi-elevated rest	2.87	10.00	13.94	16.30
		Fully elevated rest	3.82	2.12	2.29	3.65
	Outside	Bask	44.54	42.42	40.17	24.71
		Semi-elevated bask	22.28	23.31	12.97	9.91
		Fully elevated bask	0.22	0.75	0.98	0.00
	Total		100.00	100.00	100.00	100.00
Social	Investigation	Tongue-flicking	0.00	0.00	25.57	0.00
	Submission	Head-bobbing	0.00	24.61	36.68	100.00
	Aggression	Encounter	47.17	28.00	37.75	0.00
		Combat	20.25	6.97	0.00	0.00
	Mating	Copulating	32.58	40.42	0.00	0.00
Total			100.00	100.00	100.00	100.00
SUMMARY						
Maintenance	General	-	6.08	0.00	0.26	0.37
	Inner-margin	-	26.88	33.52	45.62	65.01
	Outside	-	67.04	66.48	54.12	34.62
Social	Investigation	-	0.00	0.00	25.57	0.00
	Submission	-	0.00	24.61	36.68	100.00
	Aggression	-	67.42	34.97	37.75	0.00
	Mating	-	32.58	40.42	0.00	0.00
Total			200.00	200.00	200.00	200.00

4.3.3 Frequency of agonistic behavioural acts

Twelve intruder-resident trials were staged, using seven adult males (intruders) of varying size, and seven single-male groups. To account for sample size, certain individuals were used in more than one trial but no one individual was introduced to the same single-male group twice. Several days were left in between trials where the same individual was used again. In all trials the resident male in the single-male groups emerged to fend off the intruder. Face-off and biting behaviour were displayed on two-thirds of the occasions, being the predominant agonistic acts displayed by the resident males (16.0 % respectively). Pushing (14.0 %), chasing (12.0 %), tail-wagging (aggressive) and tongue-flicking (10.0 %) behaviour followed closely. Face-off circling was displayed on a third of the occasions (8.0 %) and the agonistic full raise and body-tilt behavioural acts were only elicited 4.0 % of the time. An engorged throat, arched back and tail-flicking were only displayed on a quarter of the occasions (2.0 %). An ethogram listing the aggressive social behaviours displayed during social interactions was established and levels of aggression were assigned to the various agonistic acts (Table 4.3).

From six observed unstaged social encounters between two male members in the multi-male group (total, $n = 6$), it was clear that resident males reacted aggressively towards other resident males that were moving through or pausing in their area of space-use. All encounters ended with the resident male evicting the intruder ($n = 6$). Three of the observed encounters were between Male 1 and Male 2, who were incidentally neighbours (see Chapter 5).

Face-off and face-off circling agonistic behaviours were the predominant responses elicited during an encounter between two resident males ($n = 4$) in the multi-male group. Body-tilting and chasing behaviour were displayed during 50 % of the encounters ($n = 3$), and full raise and arched back agonistic displays were only elicited during a third of the encounters ($n = 2$). Thus far the only mentioned behaviours that were considered highly aggressive are body-tilting and chasing agonistic acts. (see Table 4.3). Only during one encounter was biting behaviour actually observed ($n = 1$) and no tail-flicking ($n = 0$), another highly aggressive behaviour, was elicited. Male aggression towards either a female, sub-adult or juvenile was normally in the form of bites to the flank of the individuals, but only on a few occasions.



Table 4.2. Frequency of behavioural acts per act system divided into two contextual situations – maintenance and social behaviour. The table depicts the proportion of behavioural act systems displayed out of a 100 % context, including both the main act systems.

		Males	Females	Sub-adults	Juveniles
MAINTENANCE	General	5.38	0.00	0.25	0.35
	Inner-margin	23.80	31.68	43.63	61.33
	Outside	59.34	62.80	51.78	32.67
SOCIAL	Investigation	0.00	0.00	1.11	0.00
	Submission	0.00	1.36	1.59	5.66
	Aggression	7.74	1.93	1.64	0.00
	Mating	3.74	2.23	0.00	0.00
Total		100.00	100.00	100.00	100.00

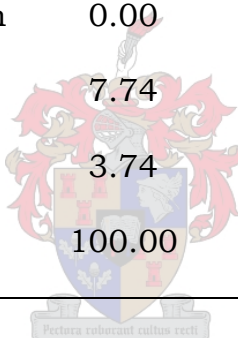


Table 4.3. Aggressive social behaviour as displayed by *C. cataphractus* individuals during social encounters. Two types of tail-wagging were elicited, namely: submissive (subm.), and aggressive (aggr.) tail-wagging behaviour.

Behavioural Acts	Aggression	Aggression	Behavioural Type
	Level	Score	
Head-bobbing	0	-1	Display
Crouch	0	-1	Display
Tail-wagging (subm.)	1	0	Display
Tongue-flicking	2	1	Investigative
Face-off	3	2	Display/Encounter
Tail-wagging (aggr.)	3	2	Display/Encounter
Full raise	4	3	Display/Encounter
Engorged throat	4	3	Display/Encounter
Arched back	4	3	Display/Encounter
Pushing	5	4	Encounter
Face-off circling	5	4	Encounter
Body tilt	6	5	Encounter
Chasing	6	5	Combat
Tail-flicking	7	6	Combat
Biting	8	7	Combat

4.4 DISCUSSION

4.4.1 Behavioural repertoire

There are many similarities in behavioural acts among the four cordylid species for which data are available. The majority of behavioural acts displayed by *C. cataphractus* are stereotyped behaviours as listed in the review of lizard behaviour acts by Carpenter & Ferguson (1977).

The head-rubbing behaviour described for *C. cordylus* was reported to be a distinct agonistic display behaviour used during social encounters, but head-rubbing was also observed after foraging (Wirminghaus 1990). Head-rubbing was observed only during maintenance behaviour for *C. cataphractus* after every successful foraging attempt, but not during social encounters. Head-rubbing was elicited by all the age-sex classes, and is thus likely to serve a maintenance cleaning purpose since it has no evident social purpose. Head-rubbing was not recorded for *C. giganteus*, nor for *C. macropholis*, although it must be kept in mind that the focus was solely on determining social behavioural acts in the studies on the latter two species. It is therefore possible that both the latter mentioned cordylids also display head-rubbing behaviour after foraging.

Many of the display behaviours described for *C. cordylus* by Wirminghaus (1990), were not observed in *C. cataphractus*, *C. giganteus* and *C. macropholis*. For example, horizontal bob-threats, angled bob-threats, and contorted threats were only observed in *C. cordylus* (Wirminghaus 1990). Jerky display movements however, represented by a shuffle-walk, head-shaking shuffle-walk, and head-shake in *C. cordylus*, are also elicited by *C. giganteus* and *C. macropholis* as agonistic display

behavioural acts. Jerky movements were absent during social encounters in *C. cataphractus*. As Carpenter & Ferguson (1977) point out, many behaviours may be carried out accompanied by jerky movements, but the jerky movement as such is not necessarily an individual behavioural act. For instance, a *C. cataphractus* individual may display an arched body-tilt towards its opponent while face-off circling around his opponent in a staccato fashion, yet another individual may display the arched body-tilt and face-off circling, but not in a staccato fashion, yet both excite the same response by the opponent (pers. obs.). The importance of the elicited behaviour thus lies in the arched body-tilt and face-off circling behaviour, and not in the jerky movement. Therefore, 'jerky movement' as an act was considered an ambiguous description and was not considered as a distinct behavioural act for *C. cataphractus*.

Body-tilting was another agonistic display behaviour elicited by both *C. cordylus*, and *C. cataphractus*. In both these cordylids, this behavioural act often accompanied face-off circling, especially if the encounter was escalating in aggression (refer to Table 4.3). Body-tilting was not reported in *C. giganteus* and *C. macropholis*.

The full-raise behaviour described for *C. cataphractus* is a display behaviour used during agonistic encounters as described for *C. giganteus*, but has also been recorded for individuals performing maintenance behavioural acts at the inner margins and outside the crevice (*fully elevated rest* and *bask* behaviour, refer to Table 4.1). This suggests that full-raise (or fully elevated) behaviour may have an alternative function. In *C. cordylus* a fully elevated (body raised on all four legs extended) posture

is adopted, while displaying thermoregulatory behaviour (Wirminghaus 1990). *Cordylus cataphractus* individuals were observed to fully raise themselves and remain standing in that posture for several minutes, with no evidence of any social context. On really hot summer days, full-raise behaviour was also utilised to press the dorsal part of the lizard's body to the roof of the crevice. Wirminghaus (1990) observed the same behaviour for *C. cordylus* and states that it is positive heliothermic basking. Incidentally, full-raise behaviour is not considered an agonistic behaviour in *C. cordylus* as it is for *C. giganteus* (Ruddock 2000) and for *C. cataphractus*.

Two highly aggressive behaviours were reported for all four of the cordylid species. According to the review by Carpenter & Ferguson (1977), biting behaviour can be considered as the most aggressive response during a social encounter. Both biting and face-off circling agonistic behaviours described for *C. cataphractus*, were also described for *C. cordylus*, *C. giganteus*, and *C. macropholis*. Face-off circling behaviour was described as head-off circling for *C. cordylus* (Wirminghaus 1990) and circling for *C. giganteus* (Ruddock 2000), but they are essentially identical to the agonistic face-off circling behaviour described for *C. macropholis* (Nieuwoudt *et al.* 2003) and now for *C. cataphractus*. Biting behaviour was often accompanied by tail-flicking. Tail-flicking was observed in *C. giganteus* and was rated as highly aggressive. Tail-flicking was absent in both *C. cordylus* and *C. macropholis*. This highly aggressive behaviour is not unique to the cordylids, and is displayed, for instance, by agamids and lacertids (Carpenter & Ferguson 1977). However, both *C. cataphractus* and

C. giganteus have an exceptionally spinose morphology, with heavily spinose tails. Tail-flicking behaviour in these two cordylid species seems to be rather appropriate, as flicking a heavily spinose tail as opposed to a smooth tail, into the head region of ones opponent, will predictably be more effective during combat.

Agonistic chasing behaviour, as described in this study for *C. cataphractus*, was only described for *C. cordylus*. In both species chasing behaviour follows biting behaviour and is graded as highly agonistic. The absence of chasing behaviour in the ethograms of *C. giganteus* and *C. macropholis* is dubious, since chasing behaviour is normally one of the culminating behaviours of a combat act system in many lizard species (Carpenter & Ferguson 1977).

Walk-over behaviour was described for *C. giganteus* as an agonistic behaviour during encounters (Ruddock 2000). This behavioural act was not described for *C. cataphractus* because it was observed in only one aggressive encounter. Future behavioural studies on the study animal might keep this in mind.

Tail-wagging behaviour in *C. cataphractus* was elicited in two different contexts, a submissive and aggressive context, respectively. The same was reported by Ruddock (2000) for *C. giganteus*. Tail-wagging was also described for *C. macropholis*, but only in an aggressive context. However, a lateral tail-wag or tail-twitch was described for *C. cordylus* and *C. macropholis*. The lateral tail-wag was regarded as a submissive behaviour in both species. The size of the lizards may influence their behaviour (Carpenter & Ferguson 1977) and therefore a 'twitching' tail movement

may be more prominent in a smaller species whereas a wavelike undulation may be more prominent in a larger heavier lizard, as is the case in both *C. cataphractus* and *C. giganteus*.

Agonistic display behaviours that entailed engorging the throat region, arching the back, and raising the body on all fours seem to be restricted to *C. cataphractus* and *C. giganteus*, the larger of the four mentioned cordylid species. Larger lizard species are expected to display more fervently (Carpenter & Ferguson 1977; Stamps 1983a, 1994). The evidence therefore strongly suggests that the similarities in agonistic behaviour displayed by *C. cataphractus* and *C. giganteus* may be attributed to the fact that they are larger lizards than *C. cordylus* and *C. macropholis*.

On the whole, the social behaviour of *C. cataphractus* is very similar to that of *C. giganteus*, but nonetheless includes several behavioural acts displayed by *C. cordylus* and *C. macropholis* as well. On the other hand, new behaviours have been described for the study species. These behaviours include pushing, crouching, courtship, copulation, twitching, cloacal-rubbing and hind-leg dragging. Although these behaviours have not been described for *C. cordylus*, *C. giganteus*, and *C. macropholis*, some are likely to be present. The reason being that behavioural observations were made on free-living *C. cataphractus* individuals, and did not entail staged social events.

4.4.2 Frequency and context

In a maintenance context, it is clear that individuals from all age-sex classes spend more time displaying maintenance act systems in comparison to social act systems. The results show that males spend a great proportion of the time outside, albeit in close proximity of the crevice, as do females and sub-adults, although the latter two do so to a lesser extent than the males. The fact that males spend so much of their time displaying outside maintenance behaviour, as well as general maintenance, strongly suggests that males need to monitor space outside the crevice (Fox *et al.* 2003). The hind-leg dragging behaviour was only displayed by males and is strongly indicative of territorial marking, as is the case, for example, in the desert iguana (Alberts 1992). Males also spent more time in a semi-elevated posture, which could be indicative of the fact that males prefer to remain in a posture that gives them better perspective of their immediate surroundings. Females also remained in a semi-elevated posture outside the crevice for more of the time in comparison to sub-adults and juveniles. Yet, when residing at the inner-margins, juveniles remain in a semi-elevated position more of the time than do the adults. This suggests that when adults are sitting outside the crevice they rely heavily on vision to avoid predators and food. This is also true for the juveniles, only juveniles spend the majority of their time at the inner-margins and therefore it seems logical that they will display semi-elevated behaviour since they also need to keep an eye out for passing prey items. The difference is that adults forage more from an *outside* position.

Wirminghaus (1990) reported that agonistic encounters in *C. cordylus* were limited to less agonistic threat displays predominantly among males. For instance, highly aggressive combat, where biting was involved, was infrequent in comparison to threat displays. In *C. macropholis*, however, higher levels of aggression seem to be frequent in encounters among males (Nieuwoudt *et al.* 2003). In *C. giganteus*, females were reported to be the slightly more aggressive sex, in which aggressive responses often escalated to combat, showing that intruders were tolerated to a very marginal extent (Ruddock 2000).

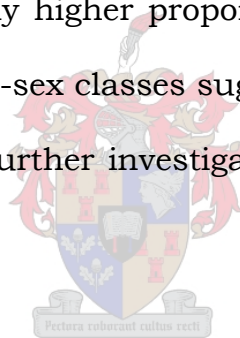
In a social context, *C. cataphractus* males were clearly the more aggressive of the sexes. The fact that during staged-encounters, biting and face-offs were the two predominant behaviours, followed by pushing, chasing and tail-wagging (aggressive), suggests that the study animal is highly aggressive, and does not allocate much time or energy into display behaviour. Aggression in *C. cataphractus* seems to be predominantly directed by males more specifically towards other males. To underscore this, males were only on a few occasions observed to display aggression towards females, sub-adults or juveniles. The evidence also shows that aggressive behaviour is displayed far less frequently than maintenance behaviour. This may mean that since *C. cataphractus* inhabits arid regions, it is of greater importance to allocate energy to maintenance activities, such as feeding as opposed to social activities, and therefore social activities are restricted, particularly to the male sex.

In comparison to other lizard species, the social behaviours displayed by *C. cataphractus* and the contexts thereof are representative of males

belonging to territorial species, competing for access to mates (Carpenter & Ferguson 1977). Carpenter & Ferguson (1977) report that in the agamid, *Agama agama*, the males also present themselves laterally, together with face-off circling agonistic acts. Tails are lashed at the opponents face and as the opponent tries to retreat it is bitten or chased. *Cordylus cataphractus* also displays social behaviour analogous to certain species of gekkonids. The engorged throat, arched back, face-off, and face-off circling are typical during agonistic encounters of *Lygodactylus picturatus keniensis* (Carpenter & Ferguson 1977). The head-bobbing and crouching behaviour displayed predominantly by *C. cataphractus* juveniles is analogous to the behaviour displayed by the Ashy Gecko (Regalado 1997) in a submissive social context, and not a courtship context as is the case in a number of other lizards, e.g., some *Sceloporus* species (Carpenter & Ferguson 1977). Furthermore, some of the agonistic acts displayed by *C. cataphractus* are also displayed by lacertids, for example, the engorged throat, arched back, full raise and biting behaviour displayed by *Lacerta agilis* (Carpenter & Ferguson 1977). Courtship and mating behaviour in *C. cataphractus* is very similar to that described for iguanids and more so, the agamids (Carpenter & Ferguson 1977).

The fact that the majority of social activities are restricted to the male sex in *C. cataphractus*, underscores the speculation mentioned at the beginning of this chapter that the sexual dimorphism in this species may partially be a result of sexual selection, which in turn may be responsible for variation in social behaviour within each sex. It also confirms the widely appreciated fact that sexual selection can result in marked

differences in the social behaviours displayed by males and females (Trivers 1972). In conclusion, the social behaviour repertoire of *C. cataphractus* is similar to other territorial diurnal lizards. All the social behaviours displayed by the study animal are typical stereotyped behaviours as described by Carpenter & Ferguson (1977), in particular for the agamids and lacertids. The gherrosaurids are the skink-like ancestors of the Cordylidae and so we may expect much behaviour to be stereotyped among the families. The agonistic actions were characteristic of intraspecific aggressive behaviour by lizards (Carpenter & Ferguson 1977). *Cordylus cataphractus* shows little display behaviour during agonistic actions, but the significantly higher proportion of aggression in males in comparison to the other age-sex classes suggests that males are defending a resource. This warrants further investigation into the mating system of this species.



CHAPTER 5

SPACE-USE BY MEMBERS OF A MULTI-MALE GROUP IN THE GROUP-LIVING LIZARD, *CORDYLUS CATAPHRACTUS*.

5.1 INTRODUCTION

Ecological factors may strongly influence the spatial distribution of individuals and the ability of one sex to gain access to the other (Emlen & Oring 1977). Spatial distribution of individuals within a population has an important impact on the social structure that ensues (Brattstrom 1974). Brattstrom (1974) showed that when the territorial free-living iguanid, *Ctenosaura hemilopha*, was exposed to crowded laboratory conditions, it adopted a hierarchical social structure. This 'social structure shift' has also been shown to be true for other lizard species, for example the night-living lizard, *Xantusia henshawi*, and the gecko, *Phyllodactylus xanti* (Brattstrom 1974). Hence, a density dependent relationship exists between territoriality and hierarchy (Brattstrom 1974; Stamps 1977). Stamps (1977) though, states that in nearly all saurians some territoriality is displayed.

5.1.1 Variations in patterns of space-use

Lizards have been reported to display wide-ranging inter- and intraspecific variation in patterns of space-use (Stamps 1983a; Fox *et al.* 2003), and therefore may particularly be considered for studies of factors that affect home-range size (Perry & Garland 2002). Interpreting the

home-ranges of individuals in a population may prove especially useful in elaborating on the social structure that is established within that population. A home-range is the entire area (space) within which an individual moves, and variation in home-range size is to be expected between species, habitat, and years (Rose 1982). Competition for food (Milstead 1970) and mates (Andrews 1971) are the two most frequently cited objectives in home-range defence, where typically males in a population partition space to succeed in one or both of these objectives. The inclusion of mainly these two resources within an individual's home-range is now considered fundamental (Perry & Garland 2002). Home-ranges are considered important for mating success, because, for example, 1) the likelihood of a male mating with a female should decrease as the number of males' home-ranges overlapping with that particular female increases, and 2) a male's mating success should increase as the number of females within his home-range increases (Stamps 1977; Rose 1982).

There are basically three main variations in territoriality that can be considered (Stamps 1977): i) *Home-range defence*, where much or all of the home-range is defended, and it is an all-purpose territory. ii) *Specific-site defence*, where a small site or area within the home-range is defended, and it is a definite-purpose territory. iii) *Non-territorial*, where individuals of a species defend no portion of the home-range.

Ultimately, the manner in which individuals, particularly the adult males and females, utilise space, determines the mating system (Emlen & Oring 1977). For simplicity, mating systems may be divided into two

groups, polygynous and non-polygynous systems, although this dichotomy is really a reduction from a continuum (Stamps 1983a). Territorial polygyny is widespread in lizards and more importantly, there is extensive variation in the degree of polygyny (Stamps 1983a).

5.1.2 Social structure in *Cordylus cataphractus*

The fact that the group-living armadillo lizard, *Cordylus cataphractus*, displays two group extremes, single-male and multi-male groups, suggests that a 'social structure shift' may exist, warranting further investigation. Perry & Garland (2002) mention that group-living individuals may share a home-range (i.e., extensive home-range overlap among members of a group). The single-male *C. cataphractus* groups typically include one adult male, one or more adult females, possibly a few sub-adults, and juveniles (Mouton *et al.* 1999). Multi-male groups normally include two or more adult males, and a few to several adult females, sub-adults and juveniles (Mouton *et al.* 1999). In the family Cordylidae, territoriality has been described for a few species, including, *Platysaurus broadleyi* (Whiting 1999), *C. giganteus* (Ruddock 2000) and *C. cordylus* (Ruddock 2000). As in the majority of cordylids (Cooper *et al.* 1997; Losos *et al.* 2002), *C. cataphractus* remains close to its crevice refuge most of the time (Mouton *et al.* 1999; Visagie 2001) and is a sit-and-wait forager (Mouton *et al.* 2000b). Therefore, predictably there would be extensive home-range overlap among members of a *C. cataphractus* group, even more so in multi-male groups that normally include many individuals.

Living in a group imposes several pressures (Chapter 3) and competition for mates is one. Sexual selection is normally considered a prime causal factor of sexual differences in body size, head size and body colouration (Stamps 1983). Other causal factors include natural selection (Anderson & Vitt 1990) and a range of environmental processes (Stamps 1993). In particular reference to a multi-male group, the fact that *C. cataphractus* displays male-plus sexual dimorphism in head size and body size, suggests that the sexual dimorphism displayed in this species may likely be due to the forces of sexual selection, specifically male-male competition for access to females (Mouton *et al.* 1999). Mouton *et al.* (1999) speculate that the composition of the smaller groups may hint at some degree of polygyny, and that sexual dimorphism in body and head size is normally greatest in territorial species with a polygynous mating system. In general, the larger the male the better chance he has of winning fights against rival males and patrolling a larger territory (Stamps 1983).

5.1.3 Aims of study

The objective of this part of the study was to investigate the social structure in a *C. cataphractus* multi-male group. By elaborating on the extent of space-use at the crevice by members in a multi-male group, where *C. cataphractus* individuals spend most of their time, important conclusions may be reached pertaining to the mating system. *Cordylus cataphractus* may in fact display a 'social structure shift' as reported above for other species. Assuming that a *C. cataphractus* male from a

single-male group displays territoriality, as groups become larger conditions will become more crowded, and thus one might expect either a dominance hierarchy (a 'social structure shift' – Brattstrom 1974) or specific-site defence to establish itself in a multi-male group (Stamps 1977).

As in other diurnal sit-and-wait foragers, *C. cataphractus* also has a high visual-orientation (Mouton *et al.* 2000b). As opposed to a widely foraging mode that relies on prey chemical discrimination and thus a low visual-orientation, a high visual-orientation that accompanies a sit-and-wait foraging mode is especially conducive to successful territorial defence (Stamps 1977). Since territoriality has been reported in other cordylids (examples mentioned above) and *C. cataphractus* groups typically include at least one male and a few females (Mouton *et al.* 1999), the indications are that *C. cataphractus* males are territorial.

Therefore, I predicted that males in a multi-male group would partition space at the crevice to gain access to females. A low degree of overlap in space-use between members of the same sex has been regarded as indirect evidence of territoriality (Rose 1982). Hence, male members of the group were predicted to have a low level of overlap and females a higher level of overlap. Males were also predicted to use larger areas on average in comparison to females, since the larger the area defended by a male the greater the chance of incorporating more females into his territory (Stamps 1977, 1983a).

5.2 MATERIALS & METHODS

The general materials and methods and selection of the multi-male study group are described in Chapter 2.

5.2.1 Observational procedure

The perimeter of the crevice was measured and divided into equivalent sections (Fig. 5.1., 5.2.). These vertical sections were further sub-divided into four horizontal, circumferential distance-from-crevice zones encompassing the entire crevice, at 0-30, 31-60, 61-90 and >91 cm, respectively, creating a 2D-grid system. A neighbouring small rock crevice, 1 m south-west of the main study crevice, was included in the grid-pattern, because individuals from the study group regularly used space at the small rock (no other group besides the study group utilised space at the neighbouring small rock). Non-toxic, long-lasting, water-based paint was used to demarcate the respective sections and zones. This grid system made it possible to record the position of an individual outside and at the inner margins of the crevice mouth.

All marked individuals, that were visible, were scanned through a telescope and their respective positions were recorded at 30-minute intervals. This observation procedure is in accordance with the scan sampling method (Martin & Bateson 1986) and is not to be confused with the instantaneous sampling method (Martin & Bateson 1986).



Fig. 5.1. Delineated vertical and horizontal grid lines.





Fig. 5.2. Delineated vertical and horizontal grid lines.



5.2.2 Observational period

Observations were carried out on days when lizard activity was rife. Daily observations commenced when individuals became active in the mornings and continued until the majority of lizards had retreated to their refuge for the night. The observational window period spanned over the breeding season, from the beginning of September 2002 until and including November 2002. Unfortunately, *C. cataphractus* remains inactive during much of the non-breeding season (Visagie 2001) thus making it impossible to collect a coherent spatial data set as for the breeding season. The September-November 2003 breeding season was used to collect additional spatial data.

5.2.3 Data analysis

The Geographical Information Software (GIS) package Arcview Ver. 3.2 was used to create a computerised two-dimensional grid system that simulates the immediate surroundings of the crevice, to scale. The data points were plotted and the minimum convex polygon procedure (Rose 1982) was used to determine the space used by each respective individual. Each polygon represents a certain area and hence, the total space-use by each individual could be calculated as well as the percentage overlap (and for that matter non-overlap) of space-use among individuals. The number of females who's space-use overlapped with a male's space-use could be determined as well as the number of males that overlapped with a female.

How to regard the data with respect to *overlap* and *non-overlap*, needed careful attention. For logistic purposes, I assigned terms to the

various overlap and non-overlap possibilities. *Overlap* may be the time spent by an individual in a polygon also frequented by others, but not necessarily at the same time (termed - Overlap Type 1) or *overlap* may be the time spent by an individual in a polygon at the same time as another individual (this was termed - Overlap Type 2). Further, *non-overlap* may be the time spent in a polygon frequented by other members of the group but not at the same time (termed - Non-overlap Type 1) or *non-overlap* may be the time spent by an individual in a polygon that is not frequented by any other individual at all (this was termed - Non-overlap Type 2). For the purpose of this study, to be able to determine *space-use* as the *area used by an individual at the crevice*, Overlap Type 1 and Non-Overlap Type 1 were considered. Overlap Type 2, for instance, would be indicative of an encounter at that location between two individuals, rather than reflecting space-use for either of the individuals. Data on percentage overlap were transformed using the Arcsine transformation and subsequently tested for normality (Lillifor's test) and homogeneity of variance (Levene's test) (Zar 1984). The overlap data were then analysed using the One Way ANOVA to test for significant differences between overlap percentages among the respective age-sex classes, more specifically between adult males and females.

Pearson's Product Moment Correlation was used to investigate the relationships between adult male SVL and territory size, as well as adult male SVL and the number of females whose space-use overlapped. This was done to determine whether larger males have larger territories, and thus access to more females.

5.3 RESULTS

5.3.1 Space-use

Space-use data for 51 marked individuals in the multi-male group were obtained, including six adult males, 15 adult females, 14 sub-adults, and 16 juveniles. No data were obtained for four of the 55 originally marked individuals, one adult female, two sub-adults, and one juvenile. These individuals were never seen outside the crevice throughout the observation period and might have left the group. Each adult male utilised a specific area at the crevice and each male spent most of the time in this area or at the inner margins of the crevice directly adjacent to this area (Fig. 5.3). Males 5 and 6 were the only two males to frequent two alternative locations at the crevice. Figure 5.3 shows that Male 5 utilised an area between Males 1 and 4, as well as an area between Males 3 and 4. The figure shows that Male 6 utilised an area on top of the roof of the crevice, adjacent and to the right of the vertical fissure through the rock, as well as an area at the neighbouring small crevice, situated south-west of the main crevice. There was considerable variation among males in total space-use, with an average size of $7\,905.5 \pm 4\,309.5 \text{ cm}^2$ (Table 5.1.). The majority of males utilised space further than the 0-30 cm zone, for example, male 2 used the 61-90 cm zone to a large extent (Fig. 5.3).

Males, on occasion, used the vertical fissure as a throughway to the roof of the crevice. The correlation of male SVL with the total space-use per male showed no significant correlation between the variables (PPM Correlation: $r^2 = -0.251$, $P > 0.05$). The space-use map generated for males at the beginning of the following breeding season (2003), showed that the

same male individuals were found using the same areas again. The exception was Male 6 who was, at the time of the 2003 observations, only using the area on the roof of the crevice, and not his alternative area at the neighbouring small crevice (Fig. 5.4).

There was also significant variation in the size of total space-use among adult females, with an average space-use size of $3\,944.1 \pm 2\,493.8$ cm² (Table 5.3.). Females predominantly frequented the 0-30 cm zone and to a large extent, the inner margins of the crevice as well. The zones further from the crevice were utilised more rarely (Fig. 5.5). Notably, certain females were more site-specific in comparison to other female members of the group. For example, Female 1 only utilised an area that coincided with the space-use of Male 3. Female 7, on the other hand, utilised space that coincided with the space-use of Male 1 and Male 2. Other females utilised several areas around the crevice, and if one compares Fig. 5.3 with Fig. 5.5, it becomes clear that the areas used by females coincided considerably with areas used by males. The space on top of the roof of the crevice was largely utilised by females. Only one female, on a regular basis, frequented the inner margins of the vertical fissure. Nonetheless, many females regularly used the vertical fissure as a throughway to the roof of the crevice. A few females also made use of the small neighbouring crevice as can be seen in Fig. 5.5).

Sub-adults also displayed marked variation in total space-use. Sub-adults utilised an area with an average total space-use size of $3\,885.7 \pm 3\,324.6$ cm² (Table 5.4.). In most cases, similar to the females, sub-adults preferred utilising space in the first 0-30 cm zone and at the inner

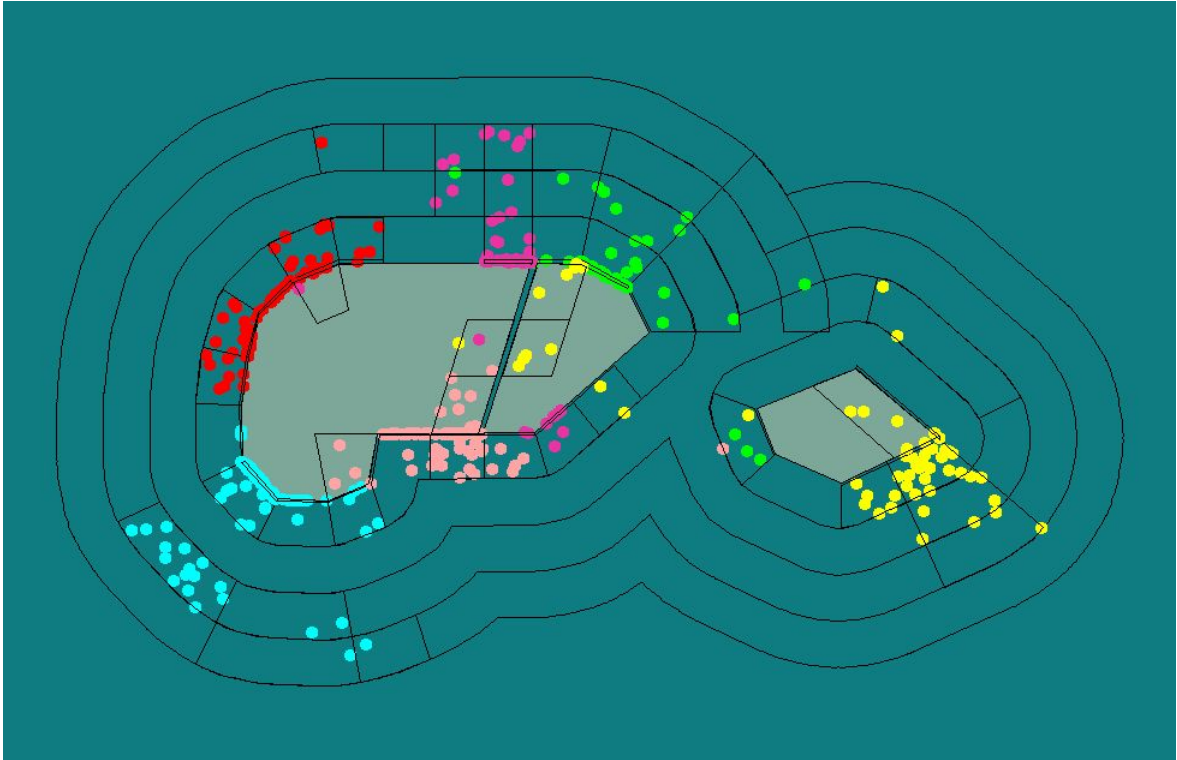


Fig. 5.3. Graphic presentation (scale 1:44) - of space-use by all six resident adult males in the multi-male group. Each coloured dot represents a different male, where red = Male 1; light blue = Male 2; light pink = Male 3; green = Male 4; dark pink = Male 5; and yellow = Male 6.



Fig. 5.4. Graphic presentation (scale 1:44) - of space-use by all six resident adult males in the multi-male group, during the following breeding season. Each coloured dot represents a different male, where the colours red = Male 1; light blue = Male 2; light pink = Male 3; green = Male 4; dark pink = Male 5; and yellow = Male 6.

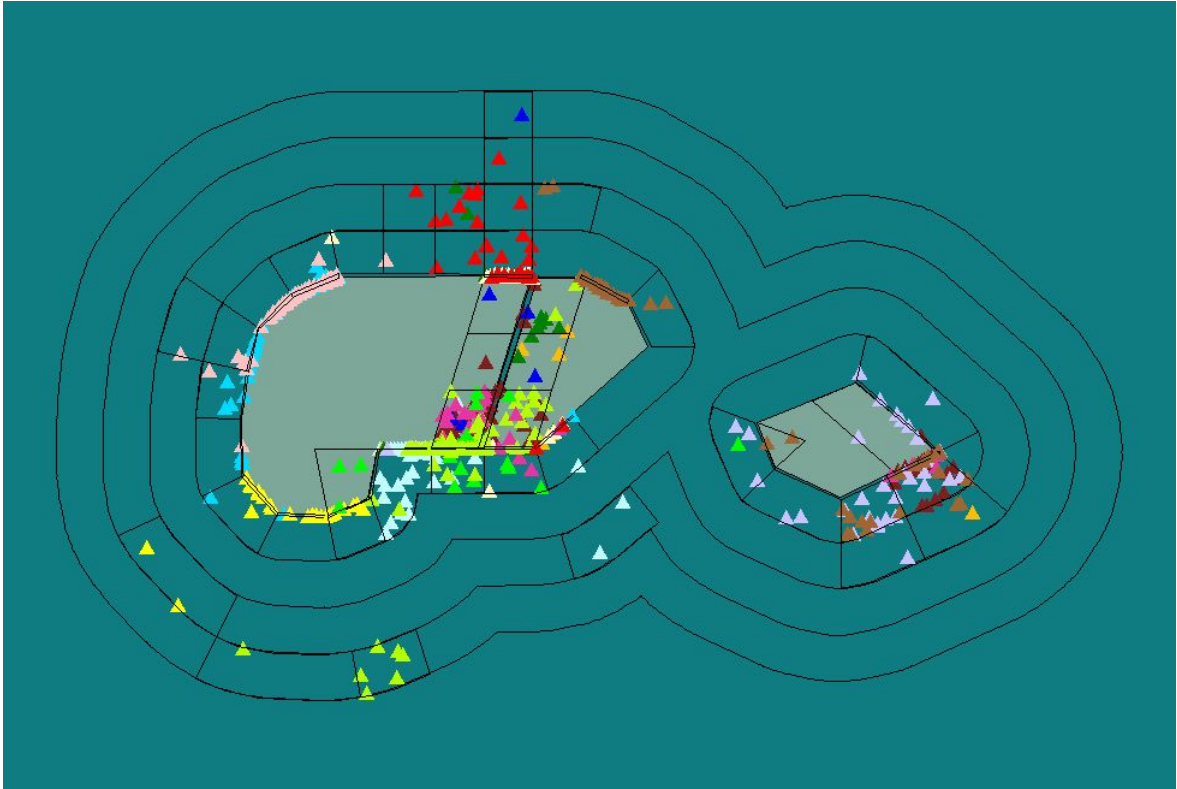
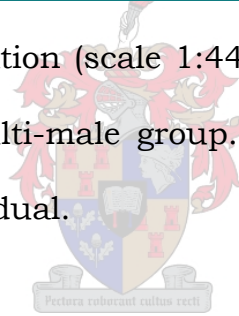


Fig. 5.5. Graphic presentation (scale 1:44) - of space-use by 15 resident adult females from the multi-male group. Each different colour triangle represents a different individual.



margins of the crevice (Fig. 5.6). Although, sub-adult individuals did frequent zones further from the crevice, including the > 91 cm zone. Sub-adults also utilised space on the roof of the crevice (adjacent to the vertical fissure). By comparing the space-use of males, females and sub-adults, it is clear that sub-adults utilised areas that coincided, quite generously, with the space-use of both males and females. However, sub-adults, together with juveniles, did utilise areas that adults did not (Fig. 5.8).

Of all the age-sex classes, the juveniles used the smallest amount of space around the crevice, predominantly only utilising the inner margins (Fig. 5.7), with an average total space-use of $1\,003.3 \pm 1\,474.3\text{ cm}^2$ (Table 5.5.). Very few juveniles ventured further than 0-30 cm away from the crevice, and in comparison to the adults and sub-adults relatively few juveniles frequented the roof of the crevice. Juveniles also seemed to congregate predominantly on one side of the crevice, even though there wasn't any distinct spatial partitioning among juveniles. A significant difference was found in the size of the total space-use among males, females, sub-adults and juveniles (One Way ANOVA: $df = 3$, $H = 24.166$, $P < 0.001$). Isolating the groups that differ, a pairwise multiple comparison procedure (Dunn's Method) showed that space-use by juveniles was significantly less in the following comparisons: juveniles and males ($Q = 4.353$, $P < 0.05$), juveniles and females ($Q = 3.559$, $P < 0.05$), and juveniles and sub-adults ($Q = 3.064$, $P < 0.05$).



Fig. 5.6. Graphic presentation (scale 1:44) - of the space-use by 15 resident sub-adult individuals from a multi-male group. Each different colour square represents an individual.

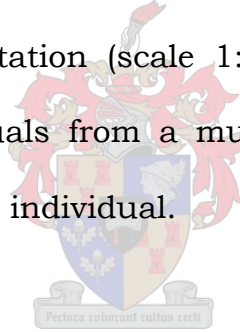




Fig. 5.7. Graphic presentation (scale 1:44) - of space-use by 16 resident juvenile individuals from the multi-male group. Each different colour cross represents a different individual.

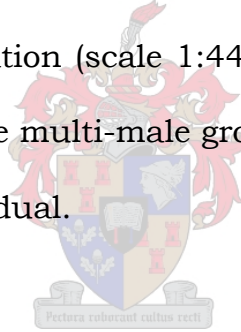
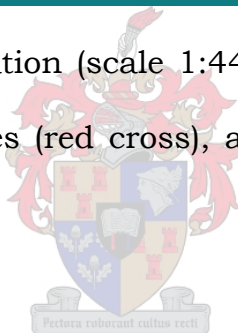




Fig. 5.8. Graphic presentation (scale 1:44) - of space-use by sub-adults (yellow square) and juveniles (red cross), and no adults frequented these areas.



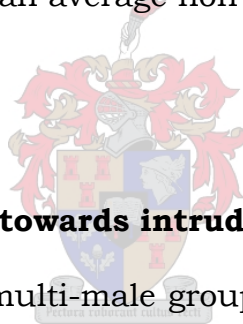
5.3.2 Overlap

To determine whether there was a significant difference between the overlap in space-use of the adult males and females, a One Way ANOVA on Ranks was carried out on the overlap data (i.e., M vs. M, M vs. FM, FM vs. FM and FM vs. M, where M = males and FM = females – Table 5.1 & 5.2). Prior to testing the data with ANOVA, the percentage overlap data were transformed using the ArcSine transformation. A significant difference was found between the male overlap and female overlap data (ANOVA: $df = 3$, $H = 17.884$, $P < 0.001$). To isolate the groups that differed, the Dunn's multiple comparison procedure was used. The overlap data show that there was zero overlap between all males, meaning that zero percent of space-use by a male overlapped with the space-use of another male in the group (Table 5.1.). The space-use of males overlapping with the space-use of females in the group was greater, however, not significantly greater than overlap among males ($66.12 \pm 31.81 \%$) ($Q = 2.518$, $P > 0.05$). The space-use of each male included at least two females within that area, ranging up to 10 females per male (e.g., Male 3, Table 5.5). No significant correlation was found between male SVL and the number of females that overlapped with a male (PPM Correlation: $r^2 = 0.371$, $P > 0.05$).

There was significantly greater space-use overlap among the females than among the males in the group ($Q = 3.150$, $P < 0.05$). On average $61.68 \pm 37.94 \%$ of the space-use by a female overlapped with the space-use of other females in the group. The space-use by a female that

overlapped with the space-use of a male ($85.67 \pm 18.15 \%$) was also significantly greater than overlap displayed among males ($Q = 4.151$, $P < 0.05$). On average the total space-use of a female overlapped with the space-use of at least one male, in most cases two males, and with eight other females (Table 5.6.).

The high values of percentage overlap for the sub-adults and juveniles strongly suggest that spatial-partitioning is absent amongst these two classes. Sub-adults did, however, show a high level of overlap with juveniles in areas that adults refrained from frequenting. Sub-adults showed an average non-overlap percentage of 18.05 %, with adults (Table 5.3.), and juveniles showed an average non-overlap percentage of 15.27 %, with adults (Table 5.4.).



5.3.3 Agonistic responses towards intruders

Male members in the multi-male group showed a significantly higher proportion of aggressive behaviour in comparison to the members from the other age-sex classes. Refer to Chapter 4 section 4.3.3. for detail on the types (level) and frequency of agonistic acts displayed during encounters between males.

5.3.4 Mating events

Eleven mating events were observed. Males were observed to mate with at least two females, with one exception (Table 5.7.). Out of the five females that were observed to mate, only Female 7 was observed to mate with more than one male (Table 5.7.). Incidentally, the female that was

observed in the majority of the mating events ($N = 4$) was Female 7 (Table 5.7). Too few mating events were observed to obtain a statistically significant trend between the sexes, in regard to the number of mating events and number of mates. Nevertheless, the results do show that males and females both mate with one or more mates.

Table 5.1. Results showing the total size of the area utilised by a male individual, and the percentage of overlap in space-use by that male with the space-use of other male (M vs. M) and female (M vs. FM) members in the multi-male group (where M = male and FM = female).

	Total area used (cm ²)	Overlap - Percentages	
		M vs. M	M vs. FM
Male 1	4099.74	0.00	78.69
Male 2	12057.09	0.00	21.75
Male 3	6128.79	0.00	100.00
Male 4	5729.83	0.00	98.74
Male 5	4874.07	0.00	41.09
Male 6	14543.22	0.00	56.45
<i>AVERAGE</i>	7905.46	0.00	66.12

Table 5.2. The total size of the area utilised by a female individual, and the percentage of overlap in space-use by that female with the space-use of other female (FM vs. FM) and male (FM vs. M) members in the multi-male group.

	Overlap -Percentages		
	Total area used (cm ²)	FM vs. FM	FM vs. M
Female 1	5605.97	67.66	67.66
Female 2	2365.44	100.00	100.00
Female 3	4570.06	100.00	100.00
Female 4	4025.36	89.16	58.36
Female 5	6549.32	79.02	61.08
Female 6	9809.15	23.24	57.33
Female 7	2417.24	8.79	97.45
Female 8	165.47	100.00	100.00
Female 9	2587.77	1.67	100.00
Female 10	3446.97	100.00	98.70
Female 11	4473.23	71.39	100.00
Female 12	1136.16	12.68	100.00
Female 13	2203.32	100.00	100.00
Female 14	2842.17	37.97	68.66
Female 15	6964.31	33.68	75.81
<i>AVERAGE</i>	3944.13	61.68	85.67

Table 5.3. The total size of the area frequented by a sub-adult individual, and the percentage overlap in space-use by that sub-adult with the space-use of other sub-adult (SA / SA), female (SA / FM) and male (SA / M) members in the multi-male group (where SA = sub-adult). The percentage of non-overlap between sub-adults and adults was calculated (SA / ADULTS).

	Area used (cm ²)	Overlap -Percentages			Non-overlap
		SA / SA	SA / M	SA / FM	SA / ADULTS
Sub-Adult 1	2304.13	100.00	100.00	2.68	0.00
Sub-Adult 2	2188.38	100.00	100.00	100.00	0.00
Sub-Adult 3	6875.26	56.91	18.12	56.91	43.09
Sub-Adult 4	14061.06	62.38	62.46	78.32	21.68
Sub-Adult 5	4301.12	98.44	67.79	95.10	4.90
Sub-Adult 6	2164.7	53.47	100.00	8.50	0.00
Sub-Adult 7	5098.16	100.00	52.23	75.27	24.73
Sub-Adult 8	4166.99	100.00	55.81	72.33	3.86
Sub-Adult 9	3613.28	72.54	100.00	100.00	0.00
Sub-Adult 10	2439.94	54.27	51.40	51.40	48.60
Sub-Adult 11	1117.03	100.00	0.00	0.00	100.00
Sub-Adult 12	1391.7	100.00	100.00	13.88	0.00
Sub-Adult 13	1941.69	55.01	100.00	7.51	0.00
Sub-Adult 14	2736.97	49.79	43.91	94.13	5.87
<i>AVERAGE</i>	3885.74	78.77	67.98	54.00	18.05

Table 5.4. The total size of the area frequented by a juvenile individual, and the percentage overlap in space-used by that juvenile with other juvenile (J / J), female (J / FM) and male (J / M) members from the multi-male group (where J = juvenile). The percentage of non-overlap between juveniles and adults was also calculated (J / ADULTS).

		Overlap -Percentages			Non-overlap
	Area used (cm ²)	J / J	J / M	J / FM	J / ADULTS
Juvenile 1	120.61	44.47	44.47	44.47	55.53
Juvenile 2	101.19	100.00	100.00	100.00	0.00
Juvenile 3	488.02	10.60	10.60	100.00	0.00
Juvenile 4	240.43	100.00	40.12	40.12	59.88
Juvenile 5	179.1	100.00	100.00	100.00	0.00
Juvenile 6	215.95	100.00	67.57	67.57	32.43
Juvenile 7	194.04	100.00	100.00	100.00	0.00
Juvenile 8	1075.09	100.00	100.00	100.00	0.00
Juvenile 9	1222.97	100.00	93.95	22.52	6.05
Juvenile 10	2309.73	100.00	93.77	55.94	6.23
Juvenile 11	323.08	100.00	55.44	55.44	44.56
Juvenile 12	2340.18	100.00	97.01	97.01	2.99
Juvenile 13	77.91	100.00	100.00	100.00	0.00
Juvenile 14	1151.32	100.00	93.92	18.03	6.08
Juvenile 15	240.83	100.00	100.00	100.00	0.00
Juvenile 16	5771.82	3.96	63.02	21.24	1.21
<i>AVERAGE</i>	1003.27	89.65	78.34	71.51	15.27

Table 5.5. The number of males (M / M) and females (M / FM) that overlap in space-use, per male.

Overlap - Numbers		
	M / M	M / FM
Male 1	0	2
Male 2	0	2
Male 3	0	10
Male 4	0	2
Male 5	0	7
Male 6	0	7
<i>AVERAGE</i>	0	5

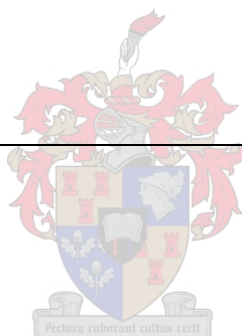


Table 5.6. The number of females (FM / FM) and males (FM / M) that overlap in space-use, per female.

Overlap - Numbers		
	FM / FM	FM / M
Female 1	9	1
Female 2	12	3
Female 3	11	3
Female 4	11	2
Female 5	9	3
Female 6	2	2
Female 7	4	3
Female 8	7	1
Female 9	1	1
Female 11	12	2
Female 12	9	1
Female 13	9	2
Female 14	10	2
Female 15	4	1
Female 16	3	2
<i>AVERAGE</i>	8	2

Table 5.7. Eleven mating events were observed involving four males and six females.

Individual	No of Mating Events	No of Different Mates
Male 1	3	2
Male 2	3	2
Male 3	3	2
Male 5	2	1
Female 1	2	1
Female 7	4	2
Female 9	1	1
Female 12	1	1
Female 13	1	1
Female 14	2	1

5.4 DISCUSSION

The space-use data obtained in this study clearly indicate that there is a high level of spatial partitioning among the male members in a multi-male group, but that there is little or no spatial partitioning among the females, sub-adults and juveniles.

A low percentage overlap in space-use among individuals of the same sex is considered as indirect evidence that individuals of that sex are territorial (Stamps 1977; Rose 1982). The lack of overlap in space-use among *C. cataphractus* males can thus be considered as substantial indirect evidence of male territoriality in multi-male groups, in this species. The fact that males display significantly more aggressive behaviour than any of the other age-sex classes underscores the presence of intrasexual competition among males (Carpenter & Ferguson 1977, Stamps 1977). The agonistic responses by an adult male towards males that intrude into his area of space-use are also highly indicative of intrasexual, defensive, territorial behaviour (Carpenter & Ferguson 1977). If males compete for access to females through territoriality, then they should maximise behaviour associated with advertisement or defence of space from other males (Baird *et al.* 2003). Findings during the staged intruder-resident trials (see Chapter 4) showed that the male sex in both a single-male group and multi-male group was the sex to aggressively confront an intruder in all cases. The hind-leg dragging behaviour described in Chapter 4 was observed on numerous occasions in male individuals moving along the margins of their areas of space-use. I assumed that this behaviour was indicative of territorial marking, where

males most likely use the femoral glands located on the ventral margin of the thigh region for scent-marking, as was reported by Alberts & Werner (1993) for green iguanas, and Alberts (1992) for desert iguanas. Although no data were recorded in my study, individuals tongue-flicking at the substratum and other individuals have been observed several times.

The results from this part of the study also show that the males of the study group utilised the same space in the following breeding season, which suggests that individuals occupy the same space at the crevice for longer periods. Hence, it is possible that males also maintain their areas of space-use, albeit not as evidently, throughout the non-breeding season. Males that establish territories at the same time, or maintain them from breeding season to breeding season, greatly cut the costs of escalating aggression (e.g., injuries from more aggressive non-neighbour encounters) (Baird *et al.* 2003). Therefore it would be advantageous for males to mark their areas of space-use, because by scent-marking his area of space-use the male does not have to rely solely on physically letting an intruder know that the space is already occupied (Bull *et al.* 1999). The correlation results of male SVL with the total space-use per male may be misleading as the sample size (males, $n = 6$) is unfortunately too small to test these variables that show much variation. Likewise, the correlation results of male SVL with the number of females that overlapped with a male may also be misleading because of small sample size (males, $n = 6$).

The high percentage of overlap in space-use among females suggests that females have different spatial requirements, in comparison to that of males. Females usually maximise efforts to secure the resources that they

require for production and survival of eggs and offspring, rather than engaging in intrasexual competition for males (Baird *et al.* 2003). Not only does the space-use among females in a multi-male group overlap significantly more in comparison to that among males, but females do not display such a high level of aggressive behaviour as males do (see Chapter 4). The infrequent aggression observed in females typically included pushing and aggressive tail-wagging behaviour, and on occasion entailed a bite or a tail-flick. Aggression in females was directed predominantly towards other females and sub-adults, and on one occasion a male was seen being confronted by an adult female. This suggests that females are likely to limit aggressive encounters to competition among group members for resources other than mates, for example, competing for a prime basking site or vantage point (Stamps 1977, 1983b; Baird *et al.* 2003). Maximising parental investment may inevitably involve intrasexual competition for resources and/or choosing a male mate that controls high-quality resources (Baird *et al.* 2003). Thus, *C. cataphractus* females are considered to be non-territorial, however, a certain degree of dominance hierarchy is suggested as the reason for the displayed aggression among females. Further investigations are necessary to elaborate on this.

The space-use by sub-adults and juveniles was predominantly restricted to the inner margins of the crevice, especially in the juveniles. Since sub-adults showed a slightly higher average percentage non-overlap with adults in comparison to juveniles, even though the space-use by both young age classes overlapped highly with the space-use of adults, it might be that sub-adults try to avoid areas where adults are very active.

Avoiding areas of intense adult activity, may prove helpful in avoiding regular expensive aggressive encounters between, for instance, a younger sub-adult male and an adult male (Stamps 1983b). It is thus intriguing that sub-adults and juveniles particularly restricted their space-use to one area of the crevice where incidentally, the largest male, Male 1, resides. Adult male aggression towards juvenile males was described in a cordylid, *Cordylus macropholis* (Nieuwoudt *et al.* 2003), but such aggression was not distinctly evident in *C. cataphractus*. Only a very small proportion of the aggression displayed by males was towards subadults and juveniles. Nonetheless, from the data obtained in this study (see Chapter 4) it may be concluded that males do not display a highly aggressive relationship with sub-adults and juveniles. Therefore, importantly, the evidence that sub-adults and juveniles utilise space free of adults may, on the other hand, indicate the manner by which the younger age classes cope with competition for food in an opportunistic group-living scenario.

The overlap data show two important facts, namely: no male was found sharing space with another male, and the total space-use of each male coincided with the total space-use of at least two or more adult females in the multi-male group (see Table 5.5). The pairwise multiple comparisons of the adult and female overlap data support the hypothesis that adult males are territorial since there was significantly lower overlap between males in comparison to overlap between females. Male space-use that overlapped with female space-use was not significantly different, but the result was only slightly non-significant ($Q = 2.518$). This can most likely be attributed to the small sample size for adult males. Nevertheless,

there was a significant difference between female vs. male and male vs. male space-use. Thus, the prediction, that males would show little overlap with other males but greater overlap with females is supported. Together with the evidence of highly aggressive behaviour displayed by adult males, this strongly suggests that *C. cataphractus* males display territorial polygyny, where a male typically defends an area that incorporates more than one female (Stamps 1977, 1983a; Baird *et al.* 2003; Fox *et al.* 2003). Given that males only defend a specific area(s) at the crevice and their home-range is predictably quite large (Chapter 3), *C. cataphractus* males must be classified as specific-site defenders (Stamps 1977).

The fact that certain females were observed to frequent areas used by different males and a female was also observed to mate with more than one male on more than one occasion (see Table 5.7), suggests that females may switch territories during the breeding season (Tokarz 1995), or readily mate with males from adjoining territories (Trivers 1976). Hence, females may display polyandry in this species, but since only one female was observed to mate with more than one male, further investigation is needed for this to be confirmed.

The argument is that, being polyandrous increases a female's fitness with an increase in the genetic diversity of her male mates (Yasui 1998; Fedorka & Mousseau 2002). A higher survivorship of offspring is expected in polyandrous cases compared to monandrous cases, and it was suggested that polyandry might thus be maintained through genetic benefits (Fedorka & Mousseau 2002). Polyandry may be a bet-hedging strategy by females that are seeking different males to lower the

probability of mating with an infertile or lower quality male (Fedorka & Mousseau 2002). On the other hand, polyandry may be a bet-hedging strategy by females against the uncertainty of future environmental conditions, by increasing the genetic diversity of their offspring (Ridley 1993). *Cordylus cataphractus* lives in an unpredictable, arid environment where the quest for 'good genes' would be very beneficial in terms of increasing the survivorship of offspring. Hence, both suggested bet-hedging strategies for polyandry may be applicable to the study animal. Although, polyandry may increase the genetic diversity and thus, increase a female's fitness and offspring survivorship, polyandry may, on the other hand, decrease the longevity of a female by increasing the toxicity of the female's internal environment (e.g., transfer of diseases, accumulation of sperm chemicals rendered toxic in large amounts) (Trivers 1972; Fedorka & Mousseau 2002).

With respect to the type of spacing pattern displayed by *C. cataphractus*, two different exclusive occupancy type schemes were consulted. According to the classification scheme of agonistic behaviour and area defended in lizards, taken from Martins (1994), *C. cataphractus* males display defence of area Types IV and V, where a specific site is defended at the shelter (crevice), using both combat and threat behaviour. Females predominantly displayed defence of area Type VIII (no area defence, although threat behaviour present), but also displayed Type V on occasion. According to the exclusive occupancy types listed by Stamps (1977), *C. cataphractus* was classified as Type I, which specifies that adult males are not found together and nor are females (i.e. intrasexual

segregation), but other combinations of age and sex may be. The overlap data presented in this part of the study, strongly suggest that, according to the exclusive occupancy types listed by Stamps (1977), *C. cataphractus* better fits exclusive occupancy Type 2, where one adult male is normally found with one or more females, and possibly a few juveniles.

In the case of a multi-male group, one might argue that the occupancy types concluded above for the study animal are inappropriate. However, even though several adult males in a multi-male group, most likely together with several females and juveniles, essentially share a shelter site, it does not necessarily mean that they share all space at the shelter site. If for instance, several male and female *C. cataphractus* individuals did share much of the space at a communal shelter site then one would surely not conclude the exclusive occupancy types reported above. Nonetheless, the data show that *C. cataphractus* males display a high degree of spatial-partitioning in conjunction with agonistic behaviour, where the space-use of one male overlaps with the space-use of one or more females, and therefore the exclusive occupancy types reported for this species, according to the classification scheme taken from Martins (1994), deem appropriate.

Sexual selection is a powerful agent influencing the evolution of social behaviour and mating systems (Andersson 1994). Therefore, the most obvious consequence of sexual selection for variation in social behaviour is that males and females are often selected to adopt fundamentally different tactics to maximise reproductive success (Trivers 1972). The mating success of an individual ultimately determines its reproductive

success (Krebs & Davies 1993; Andersson 1994). The conclusions above with regard to the spatial patterns displayed by *C. cataphractus*, inevitably prompt further questions, particularly with respect to the mating success of individuals. Since males from both a single-male and multi-male group essentially display territorial polygyny, it goes to say that a male that manages to establish a territory potentially has access to at least one female. This has been shown to be the case for many species of territorial lizards (Stamps 1977, 1983a, 1994; Fox *et al.* 2003).

The presence of two group size extremes manifested in *C. cataphractus* poses an important question; is there a difference in mating success between the male from a single-male group and males from a multi-male group? The resident male in a single-male group potentially has access to all the females in the group, without having to compete with other resident males for access. In a multi-male group, on the other hand, the resident males have to compete amongst one another for access to females in the group. Therefore we can predict that generally the resident male in a single-male group should have a higher or more assured mating success in comparison to a male in a multi-male group. However, the space-use and overlap data presented in this part of the study do show that all the adult males in the multi-male group maintained a territory and each male had access to at least one female. In terms of a polygynous mating system males normally strive to maximise access to females and to successfully mate with as many as possible (Baird *et al.* 2003). Thus, with this in mind, a multi-male group consisting of several females increases the chance for a resident male in the group to mate with many females. Of

course there are exceptions in multi-male group compositions, where not all groups include several females, and there might be several more males than females (Mouton *et al.* 1999). Therefore, in multi-male groups, the number of females a male has access to depends on intrasexual competition with other resident males, and the number of females present in the group. In a single-male group, the number of females a male has access to, is only limited by the number of females present in the group. Further investigations are clearly necessary to elaborate on mating success in *C. cataphractus*.

Ultimately, the significance of the two group size scenarios manifested in the study animal needs to be tackled. Since, both group size extremes seem to be functioning both in a social and ecological context, the crux of the matter might have to do with careful energy budgeting in an unpredictable arid environment, by this species. From an energy point of view, the male in a single-male group will predictably maintain his mating success as long as he defends his territory against intruding males. We know that intergroup movement by individuals is relatively high in *C. cataphractus* (Visagie *et al.* 2002) therefore, it is likely that the resident males will regularly encounter individuals trying to join the group. If the male in a single-male group allows (i.e., is defeated during a challenge) another male to join the group, he will experience a decrease in mating success. Especially if the intruding male has a higher resource potential (or fighting ability) (see Leuck 1995) than the resident male, the intruder may well succeed in restricting the resident male's access to females.

In a multi-male group the resident males already have to compete amongst one another for access to females, but nevertheless, the more the number of resident males the greater the competition for space and thus automatically females. Therefore a resident male in a multi-male group would predictably also fend off intruding non-resident males from his territory. One subtle difference might be expected: the resident male from a single-male group will display a higher level of aggression towards an intruder in comparison to a male from a multi-male group. The dear enemy phenomenon (Krebs & Davies 1993) may be applicable to a multi-male group context, and thus resident males in a multi-male group will most likely display lower aggression towards group members than to intruder males from outside. Also, the inactivity by groups during the greater part of the non-breeding season (Visagie 2001) may be indicative of seasonal territoriality. One might predict that the males in a multi-male group may relax territoriality during the non-breeding season, but a male from a single-male group should not, to ensure his mating success does not decrease. Therefore one would expect a single-male group male to maintain a high level of aggression throughout the year. Seasonal territoriality has been reported in several species of lizards; for example, Ruby (1978) reported that male iguanid *Sceloporus jarrovi* display seasonal territoriality in response to the distribution of females. Fitch & Von Achen (1977) showed that activity levels of territorial males differ from season to season.

How exactly individuals are allowed to join a group is not known, and perhaps more importantly, how a single-male group becomes a multi-male

group is also unknown. The turning point may arise by an intruding male winning a fight and the resident male backs down, or in certain instances sub-adult males may be allowed to remain in the group once they have matured. Much information is still needed to elaborate on the significance of the two group size extremes in *C. cataphractus*, especially with respect to mating success.

In summary, *C. cataphractus* males have conclusively shown to be territorial by defending a specific area at the crevice – *specific-site defence*. The territories have a definite purpose, but further investigations are needed before we conclude as to what this purpose(s) may be. Males mate with more than one female and thus display territorial polygyny. Females may be polyandrous, thus signifying that the mating system in a multi-male group is a promiscuous one. Females may display a dominance hierarchy as a result of competition for resources other than mates, and sub-adults and juveniles may form part of the dominance hierarchy.

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APPENDIX

The following data set was recorded for a multi-male group of *Cordylus cataphractus* consisting of 58 individuals. Data for only 55 members of the group were recorded since three individuals, two females and a sub-adult, managed to avoid being captured (AM = adult male, AF = adult female, SA = sub-adult, and J = juvenile, SVL = snout-vent length, HS = head width).

							Caught in	
	Toeclip	Sex	SVL	HS	Colour Code	Ref. No.	Section	lost digits
1	1210	SA	88.12	22.31	YT	A1B2C1	A20-A2	
2	1220	SA	92.82	26.27	YM	A1B2C2	"	
3	1230	AF	105.82	28.7	GT	A1B2C3	"	
4	1240	SA	94.73	27.24	YB	A1B2C4	"	
5	1250	SA	87.21	23.45	YTM	A1B2C5	"	
6	1310	AF	101.25	26.02	GM	A1B3C1	"	
7	1320	AF	99.52	27.95	GB	A1B3C2	"	
8	1330	AF	112.05	30.82	GTM	A1B3C3	"	
9	1340	J	57.54	14.31	PTM	A1B3C4	"	
10	1350	J	59.28	14.35	PT	A1B3C5	"	
11	1410	SA	75.67	19.17	YTB	A1B4C1	"	
12	1420	AF	104.94	27.92	GTB	A1B4C2	"	
13	1450	AF	113.8	31.84	GMB	A1B4C5	"	C5
14	1430	J	58.26	14.58	PM	A1B4C3	"	
15	1111	SA	92.84	24.58	YMB	A1B1C1D1	"	B1
16	1440	SA	73.28	19.13	YTMB	A1B4C4	"	
17	1510	SA	76.44	22.5	Y1	A1B5C1	"	
18	1520	J	70.95	19.09	PB	A1B5C2	"	
19	1530	J	62.76	16.2	PTB	A1B5C3	"	
20	2410	AM	116.65	33.22	RT	A2B4,5C1	A12-A14	B4,5
21	1540	J	63.08	15.79	PMB	A1B5C4	"	

22	1550	J	58.88	15.16	P1	A1B5C5	"	
23	2110	J	59.71	14.39	PTMB	A2B1C1	"	
24	2120	J	70.42	18.15	P2	A2B1C2	"	
25	2130	J	71.77	18.9	P3	A2B1C3	"	
26	1112	AF	98.38	28.86	GTMB	A1B1C1D2	"	B1; D2
27	2140	J	61.36	14.36	PT1	A2B1C4	"	
28	2150	J	69.2	17.69	PTM1	A2B1C5	"	
29	2210	J	56.91	13.89	PTB1	A2B2C1	"	
30	2220	SA	76.8	19.47	Y2	A2B2C2	"	
31	2230	AF	97.64	25.98	G1	A2B2C3	A7-A11	
32	2240	AF	101.78	29.26	G2	A2B2C4	"	
33	2250	SA	90.51	24.6	Y3	A2B2C5	"	
34	2310	SA	93.39	24.74	YT1	A2B3C1	"	A2
35	2320	SA	94.1	26.1	YTM1	A2B3C2	"	
36	2330	J	72.84	19.04	PM1	A2B3C3	"	
37	2340	J	62.22	15.29	PB1	A2B3C4	"	
38	2350	J	66.46	15.68	PMB1	A2B3C5	"	
39	2141	AM	110.57	32.53	RB	A2B1C4,5D1	A15-A19	A2; C4,5; D1
40	2420	AF	105.42	28.97	G3	A2B4C2	"	
41	2430	SA	94.48	26.29	YTB1	A2B4C3	"	
42	2440	J	56.06	13.79	PTMB1	A2B4C4	"	
43	2450	AM	104.94	30.22	RM	A2B4C5	Small rock	
44	4110	AM	114.51	34.53	RTM	A4B1C1	A20-A1	A4
45	2510	AF	98.82	25.99	GT1	A2B5C1	A20-A2	
46	2520	AM	111.37	32.79	RTB	A2B5C2	A7TOP3	
47	2530	AF	96.65	27.29	GTM1	A2B5C3	A20-A2	
48	2540	SA	76.36	21.99	YM1	A2B5C4	"	
49	2550	AF	104.5	29.24	GTB1	A2B5C5	A12-A14	
50	3110	AF	99.86	29.03	GM1	A3B1C1	A20-A2	
51	3120	SA	92.89	27.14	YB1	A3B1C2	"	
52	3130	AF	99.9	27.94	GB1	A3B1C3	A7-A11	

53	3140	SA	92.82	26.57	YMB1	A3B1C4	"
54	3150	AF	98.15	28.83	GMB1	A3B1C5	"
55	2222	AM	113.7	33.44	RMB	A2,3B2C2D2	A2

