THE EFFECTS OF COASTAL LOWLAND INSTABILITY: MELANISM IN *CORDYLUS POLYZONUS* AND TERRESTRIALITY IN *CORDYLUS MACROPHOLIS*

CARA JULIA NIEUWOUDT

Department of Zoology, University of Stellenbosch

(With 13 text figures and 14 tables)

Thesis presented in partial fulfillment of the requirements for the Degree of Master of Science at
the University of Stellenbosch

Supervisor: Prof. P. Le F. N. Mouton
Co-supervisor: Dr. A. F. Flemming

DECEMBER 2001

DECLARATION

I the undersigned hereby declare that the work contained in this thesis is my own original work and has not previously in its entirety or in part been submitted at any university for a degree.

Signature Date

SUMMARY

It has been suggested that rapid environmental change along the Western Cape coastal lowland has had a profound bearing on the evolution of cordylid populations in this region. To test a hypothesis on the evolution of melanism in the cordylid lizard, *Cordylus polyzonus,* the genetic relationship among melanistic, turquoise and brown morphotypes in this species was examined with allozyme electrophoresis. No polymorphic loci were found. No evidence was found that the melanistic population was genetically distinct from the other colour morphotypes. The results suggest that the studied melanistic population, is not a relict of a previously bigger melanistic population, but simply an ecotype within a larger gene pool.

In the second section, some aspects of the ecology of the terrestrial lizard, *Cordylus macropholis* were investigated. Implications of a proposed hypothesis on habitat transition in this species, due to sea-level events, are discussed. Three complementary methods were used to investigate habitat selection in *C. macropholis* in a natural area of Strandveld Succulent Karoo vegetation. First, the sighting frequency of lizards in distinct plant categories was compared to the relative availability of the habitats. Except for one case, all sightings of lizards were made in *Euphorbia caput-medusae* plants, the least available habitat category. Second, the habitat preference of *C. macropholis* in terms of shelter quality was examined. Given a choice of three shelter-types, both adult and juvenile lizards gave preference to *E. caput-medusae*, followed by rock crevices and plant debris. Prey availability in *E. caput-medusae* plants was also found to be consistent with prey items in the stomachs of *C. macropholis* at two independent sampling times. Results indicated that *C. macropholis* shows a distinct preference for the relatively scarce refuge, *E. caput-medusae*.

Given the preference for such a scarce resource, one might expect *C. macropholis* to compete for potential mates that aggregate in these plants. To test this assumption, sex ratio, social structure, male spatial patterns and male social behaviour during the mating season were studied. Repetitive sampling of two populations revealed highly female-biased sex ratios. Sex ratio was found to relate positively to population density, as is the case in many polygynic lizard species. However, the composition of aggregations pointed to a monogamous mating structure for this species. In individual plants, segregation among adult males, and between adult males and juvenile males was significantly higher within the reproductive season than outside. Adult males also maintained a uniform spatial distribution within the reproductive season. Moreover, staged encounters indicated that adult males behaved aggressively among themselves and toward juvenile males, during the mating season. The data suggest that adult *C. macropholis* males are territorial and that less dominant males may be excluded from *E. caput-medusae* plants to habitats where their chances of survival may be lower.

By implication, one might predict that grouping behaviour in *C. macropholis* is not well manifested and that movement of individuals among plants is high. This assumption was validated by analyzing the size and stability of groups, as well as movement patterns among plants. The size of aggregations within *E. caput-medusae* plants ranged from one to 14 individuals. Grouping was a year-round phenomenon, but aggregations exhibited a low degree of long-term social structure. Site fidelity was low, with females showing significantly higher site fidelity than males. Movement of individuals in and out of a marked population was high. Results suggested no differential movement patterns between the sexes. The data confirmed that aggregation behaviour and high degree of movement in *C. macropholis* are the result of mutual competition for a limited plant resource.

OPSOMMING

Daar is voorgestel dat snelle omgewingsveranderinge aan die Wes-Kaap se kuslaagland, 'n noemenswaardige effek op die evolusie van gordelakkedis-populasies in die gebied gehad het.

In die eerste deel van die ondersoek, is die genetiese verwantskap tussen melanistiese, turkoois en bruin kleurmorfotipes in *Cordylus polyzonus* met behulp van ensiem-elektroforese bepaal. Die doel was om 'n hipotese vir die evolusie van melanisme in die spesie te toets. Geen polimorfiese lokusse is gevind nie. Daar was geen genetiese verskille tussen die melanistiese populasie wat bestudeer is, en die turkoois of bruin populasies nie. Dit suggereer dat die melanistiese populasie nie 'n oorblyfsel is van 'n eens groter melanistiese populasie nie, maar dat dit eerder 'n ekotipe is in 'n groter geenpoel.

In die tweede gedeelte van die ondersoek, word enkele aspekte aangaande die ekologie van die terrestriële gordelakkedis, *Cordylus macropholis*, ondersoek. Die implikasies van 'n voorgestelde habitatsoorgang in die spesie as gevolg van omgewingsveranderinge, word bespreek.

Habitatseleksie deur *C. macropholis*, in 'n natuurlike area binne die Sukkulente Strandveld Karoo-bioom, is ondersoek met behulp van drie metodes. Eerstens, is die frekwensie van akkedisse soos waargeneem in onderskeie plant-tipes, vergelyk met die relatiewe beskikbaarheid van die plant-tipes. Behalwe vir een geval, is alle akkedisse waargeneem in *Euphorbia caput-medusae* plante, die skaarsste van alle plant-tipes in die omgewing. Tweedens, is habitat keuse in terme van skuiling ondersoek. 'n Keuse van *E. caput-medusae* plante, sandsteenskeure en plantmateriaal is aan *C. macropholis* gestel. Beide volwasse en jong akkedisse het 'n voorkeur getoon vir *E. caput-medusae* plante, gevolg deur klipskeure en plantmateriaal. Derdens, is bepaal dat prooibeskikbaarheid in *E. caput-medusae* plante ooreenstem met die maaginhoude van *C. macropholis* gedurende twee verskillende tye. Dit is dus getoon dat *C. macropholis* 'n duidelike voorkeur het vir die relatiewe skaars skuiling, *E. caput-meduae*.

Weens hierdie spesifieke voorkeur, is dit te wagte dat kompetisie vir potensiële maats, wat saamgroepeer in die plant, sterk mag wees. Om hierdie aanname te toets, is die geslagsverhouding en sosiale sisteem van *C. macropholis*, asook die ruimtelike verspreiding van mannetjies en hulle gedrag binne die teelseisoen, bestudeer. Herhaalde studies het 'n geslagsverhouding sterk ten gunste van wyfies getoon. Die geslagsverhouding het positief gekorreleer met populasie-digtheid, soos wat die geval is in baie poligame spesies. Samestellings van groepe akkedisse, het egter 'n monogame sosiale struktuur gesuggereer. Segregasie tussen volwasse mannetjies en tussen volwasse mannetjies en jong mannetjies binne plante, was aansienlik hoër gedurende die teelseisoen as buite die teelseisoen. Volwasse mannetjies het ook 'n uniforme ruimtelike verspreiding getoon gedurende die teelseisoen. 'n Laboratorium-eksperiment het verder aangetoon dat volwasse mannetjies, gedurende die teelseioen, nie net aggressief teenoor mekaar optree nie, maar ook teenoor onvolwasse mannetjies. Data stel dus voor dat volwasse mannetjies territoriaal is. Minder dominante mannetjies mag uitgesluit word van *E. caput-medusae* plante en verdryf word na areas waar hulle kanse op oorlewing minder mag wees.

By implikasie, is dit te wagte dat groepgedrag in *C. macropholis* nie sterk gemanifesteer is nie en dat beweging van individue tussen plante aansienlik is. Die aanname is geëvalueer deur die grootte en stabiliteit van groepe in plante te monitor. Groepgrootte in *E. caput-medusae* plante het gewissel van een tot 14 individue. Groepgedrag is regdeur die jaar opgemerk, maar groepe het min tekens van langtermyn sosiale strukture getoon. Getrouheid aan spesifieke plantlokasies was laag, hoewel wyfies meer getrou was aan spesifieke plantlokasies as mannetjies. Beweging van individue in en uit die gemerkte populasie was hoog, maar resultate het geen differensiële bewegingspatrone vir die twee geslagte aangetoon nie. Die data bevestig dat groepgedrag en hoë mate van beweging in *C. macropholis*, die resultaat is van kompetisie vir 'n skaars hulpbron.

ACKNOWLEDGEMENTS

I would like to thank the following people who all contributed towards the completion of this thesis:

My supervisor, Prof. P. Le Fras N. Mouton, for his valuable guidance and encouragement.

Dr. A. F. Flemming, my co-supervisor, for his interest and assistance with statistical analysis.

All the people who assisted me in the field: Annemarie du Toit, Randal Albertus, James Dabrowski, Johan Hayes, Martin Purves, Niel Retief, Alex Searby, Louise Visagie.

Ernst Swart, for his helpful assistance in the laboratory.

Mandi Alblas and Mari Sauermann, for their technical assistance.

All the farmers in the study area, for permission to collect and to work on their premises. A special word of thanks to Herman and Kitta Burger who accommodated me on their farm, Steenboksfontein.

Prof. David Ward, for help with statistical data analyses.

Dr. Henk Geertsema, without his help the sorting and identification of the gut contents of lizards could not have been completed.

The Civil Engineering Faculty, for use of their land surveying equipment.

The Foundation for Research and Development (FRD), for the masters' busary.

My parents, for their continued support and interest.

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AN INTRODUCTION TO THE WESTERN CAPE COASTAL LOWLAND REGION: ENVIRONMENTAL HISTORY AND BIOGEOGRAPHY

Introduction

The Cape Fold Mountains and the region west of it, in the Western Cape, South Africa, boast a high endemism of vegetation and lower vertebrates (Deacon, 1983). This suggests that the long-term evolution and development of this area have been complex. Physiographically, the area is comprised of the Cape Fold Mountains and the bordering coastal lowland area to the west, the latter being characterized by level plains generally lacking orographic features of high altitude. Adjacent to the lowlands are the coastal strip and extending continental shelf that have been variously exposed in the past through changing sea levels (Baxter & Meadows, 1999). Consequently, the coastal region has been subjected to rapid environmental change (Baxter & Meadows, 1999).

Tankard (1976) suggests that between 47 000 and 25 000 BP a sea level maximum occurred at *ca.* –20 meter. With the advance of the Last Glacial Maximum (LGM) the sea level had dropped even further until it had reached a minimum of –130 m at 17 000 to 18 000 BP. Following the LGM there was a rapid rise leading up to the Holocene, with an initial transgression to within a meter or two of the modern level around 8000 BP (Baxter & Meadows, 1999). This was followed by a rapid regressive phase around 6500 BP, during which the sea level fell by at least three or four meters. A third oscillating phase occurred during which the sea level transgressed toward its maximum extent (*ca.* +4 m) sometime around 4000 BP. Following 3500 BP, there was a substantial regression, probably to below the present level, followed by a minor recovery at 1500 BP (Baxter & Meadows, 1999).

The present climate of the coastal strip is strongly influenced by the northflowing Cold Benguela Current, resulting in sea temperatures ranging from 8-14 °C (Brown & Jarman, 1978). Cooler temperatures along the immediate coast (ET = 14 - 15 °C) are a direct effect of this current, whereas temperatures of the coastal lowland are somewhat higher (ET = 15 – 16 °C) (Stuckenberg, 1969). In addition, there are upwelling zones of even colder waters from the ocean depths (Andrews & Hutchings, 1980). Accordingly, the incidence of fog along the coastline is high as wind from the warmer part of the ocean blows across the cool belt near the shore (Meigs, 1966; cited in Mouton & Oelofsen, 1988). However, the warmer temperatures of the adjacent interior and the general absence of land breezes prevent advective sea fog from reaching inland areas far from the coast (Badenhorst, 1990).

Information on climatic changes during the Late Pleistocene and Holocene suggests that present climatic conditions at zones of cold upwelling prevailed more widespread during past stages. From *ca.* 40 000 BP cool moist conditions led up to the LGM that ranged from about 25 000 – 17 000 BP. At 18 000 BP the LGM reached its peak with low-lying areas being subjected to essentially cooler and wetter conditions (Meadows & Baxter, 1999). Indications are that the Benguela Current was colder at that time and that its effect on the coastal lowland was more pronounced (Tankard, 1976). Additionally, with the lowering of the sea level and the exposure of the continental shelf at the time, the Benguela Current and cold upwellings would in effect have been located closer to the shore (Tankard, 1976). Thus, the incidence of fog and low stratus clouds at the coastal strip were presumably much higher and because of the low temperatures in the adjacent lowland, may have prevailed further inland than what is presently the case.

Following 16 000 BP, a rapid amelioration of the climate took place (Deacon, 1983; Deacon & Deacon, 1986) with a renewed onset of humidity which came to an end at about 11 000 BP (Vogel, 1985). Finally, the Holocene was divisible into two periods: the first half associated with dry conditions and the highest temperatures recorded for the Holocene, followed by a second half with temperatures around those of the present, but with more moisture availability than at present (Baxter & Meadows, 1999).

It is evident that these sea level events and climate changes should not only have had a profound bearing on the paleogeography of the Western Cape Coast (Baxter & Meadows, 1999), but also on the evolution of biota within this region.

The evolution of melanism in cordylid lizards in the southwestern Cape

One of the major aims of both ecology and evolutionary biology is to explain the distribution of organisms. There is considerable evidence that biotic distributions are orderly and not random, and this leads the biogeographer to seek a common causal nexus underlying observed patterns (Nelson & Platnick, 1981; cited in Cracraft, 1988).

There is a distinct clustering in distribution of melanistic cordylid species/populations in the southwestern coastal regions of southern Africa (Mouton, 1985, 1986; Mouton & Oelofsen, 1988; Mouton & Van Wyk, 1995). Such melanistic taxa in this region include *Cordylus peersi*, *C. niger*, *C. oelofseni*, *C. coeruleopunctatus*, *C. polyzonus*, *Pseudocordylus capensis* and *P. nebulosus*. Invariably these melanistic taxa occur in the form of small, isolated populations which are geographically restricted to zones of upwelling of cold water and fog, or orographic fog and cloud cover. The occurrence of melanistic forms in insular or peripheral populations, characterized by relatively cool environments, are well-documented worldwide (Badenhorst, 1990; Pearse & Pogson, 2000). Although the selective agent for the evolution of melanism remains uncertain, an increased efficiency of heat absorption at lower temperatures, particularly in areas where sunshine hours are limited, is considered to be an important selective advantage (see Pearse & Pogson, 2000). Melanism in ectotherms increases the capacity to utilize radiant heat and thus allows for longer activity periods and higher reproductive success (Gibson & Falls, 1979; Andrén & Nilson, 1981; Forsman & Ås, 1987).

Although the majority of melanistic cordylid species in the southwestern Cape are monotypic, Mouton & Oelofsen (1988) identified at least two complexes of closely related melanistic and non-melanistic forms. In both complexes the melanistic populations occur as isolated populations in cool enclaves, which are geographically separated by non-melanistic morphotypes. The fact that the melanistic species, *C. niger* and *C. oelofseni* share several non-adaptive characters, even though they are geographically separated by a closely related non-melanistic species, *Cordylus cordylus* (Figure 1.1), led Mouton & Oelofsen (1988) to conclude that a large melanistic population once occurred throughout the southwestern Cape. Furthermore, they concluded that this melanistic population later became fragmented and persisted as relict populations in presently suitable refugia. In the light of the high concentration of melanistic taxa along the southwestern coastal areas, as well as the particular distribution of melanistic populations within the area, Mouton & Oelofsen (1988) suggested that Late Quaternary climatic changes were instrumental in the evolution of melanism, rather than biotic or other factors.

They postulated that due to the thermoregulatory advantage of dark skin in cold environments (Norris, 1967; Porter, 1967; Pearson, 1977; Rice & Bradshaw, 1980), melanism in the taxa under question evolved in response to the adverse climatic conditions brought about by the Cold Benguela Current during the LGM. Subsequently, with the amelioration of the climate the range of the melanistic populations retracted, until they were isolated to present day cooler enclaves where they can persist in environmental conditions to which they have adapted to. An electrophoretic analysis of relationships in the *niger-oelofseni-cordylus*-complex has confirmed the relictual nature of *C. niger* and *C. oelofseni* (Brody, Mouton & Grant, 1993) and seems to underscore the proposed model of Mouton & Oelofsen (1988) on the evolution of melanism in this complex. At present, however, there still is uncertainty regarding the taxonomic status of melanistic populations within the other polymorphic cordylid complex, *Cordylus polyzonus*. As in the case of *C. cordylus*, melanistic populations occur in the Saldanha-Langebaan and Elands Bay-Lamberts Bay areas on the west coast (Mouton & Oelofsen, 1988; Cordes, Mouton & Van

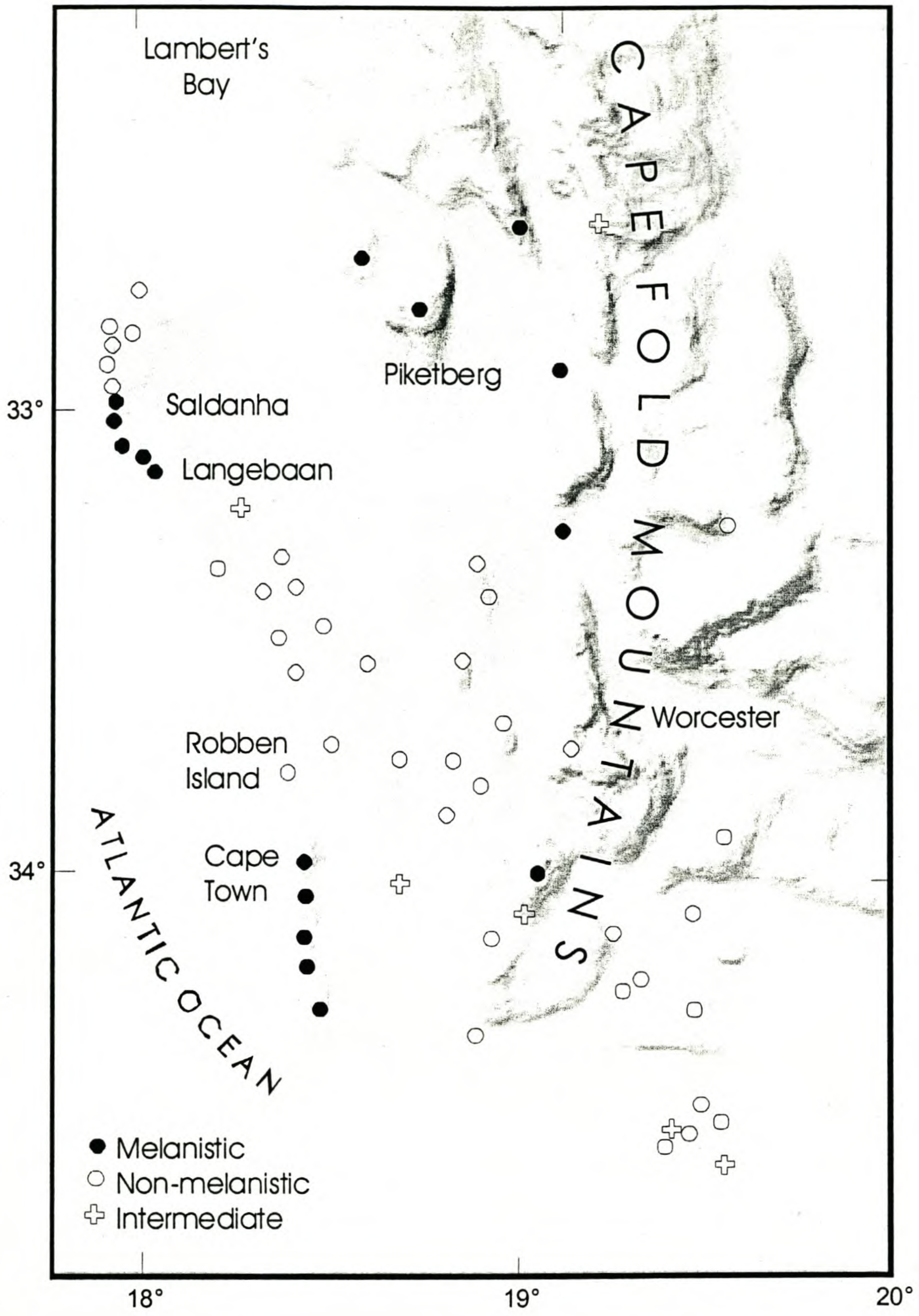

Figure 1.1 Geographical distribution of melanistic, non-melanistic and intermediate populations in the *Cordylus cordylus*-complex in the Western Cape, South Africa, south of 32°30'S and west of 19°30'E (adapted from Mouton, 1987).

Wyk, 1996), while populations of turquoise, brown, and vermillion forms occur in the adjacent inland areas (Figure 1.2) (Mouton & Oelofsen, 1988). Furthermore, some non-adaptive headshield characters were found to vary geographically with melanism (Badenhorst, 1990). The question thus remains whether the melanistic populations within the *C. polyzonus*-complex represent a separate gene pool from that of the non-melanistic forms or simply ecotypes within a larger gene pool.

The aims of the present study were the following:

1. To obtain further information on gene expression in liver and muscle tissues in the genus *Cordylus*. Gene expression in *C. polyzonus* was compared to gene expression in *Cordylus oelofseni* and other reptiles for a perspective of the evolutionary development of isozyme loci in *Cordylus*.
2. To assess the relationships among three colour morphotypes in *C. polyzonus* on the basis of isozyme data.

Terrestriality in the genus C*ordylus*

The majority of species within the genus *Cordylus* are rupicolous and are restricted to southern Africa, where they typically occur in montane or highland situations (see Mouton & Van Wyk, 1997). Most of the species in this clade have restricted ranges, the warmer climates of the present interglacial apparently restricting them to cooler enclaves (Mouton & Van Wyk, 1997). However, at least six species within the genus have terrestrial lifestyles and are considered to be derived forms, their terrestrial lifestyles representing reversals (Herselman, 1991). With the exception of one species, *Cordylus giganteus*, these terrestrial forms are restricted to temperate low-lying regions (Branch, 1998). *Cordylus tasmani*, *C. giganteus*, *C. tropidosternum*, *C. jonesi* and *C. ukingensis* are all restricted in their distribution to the eastern half of southern Africa, while *C. macropholis* (Figure 1.3) is the only terrestrial species that occurs in the western half.

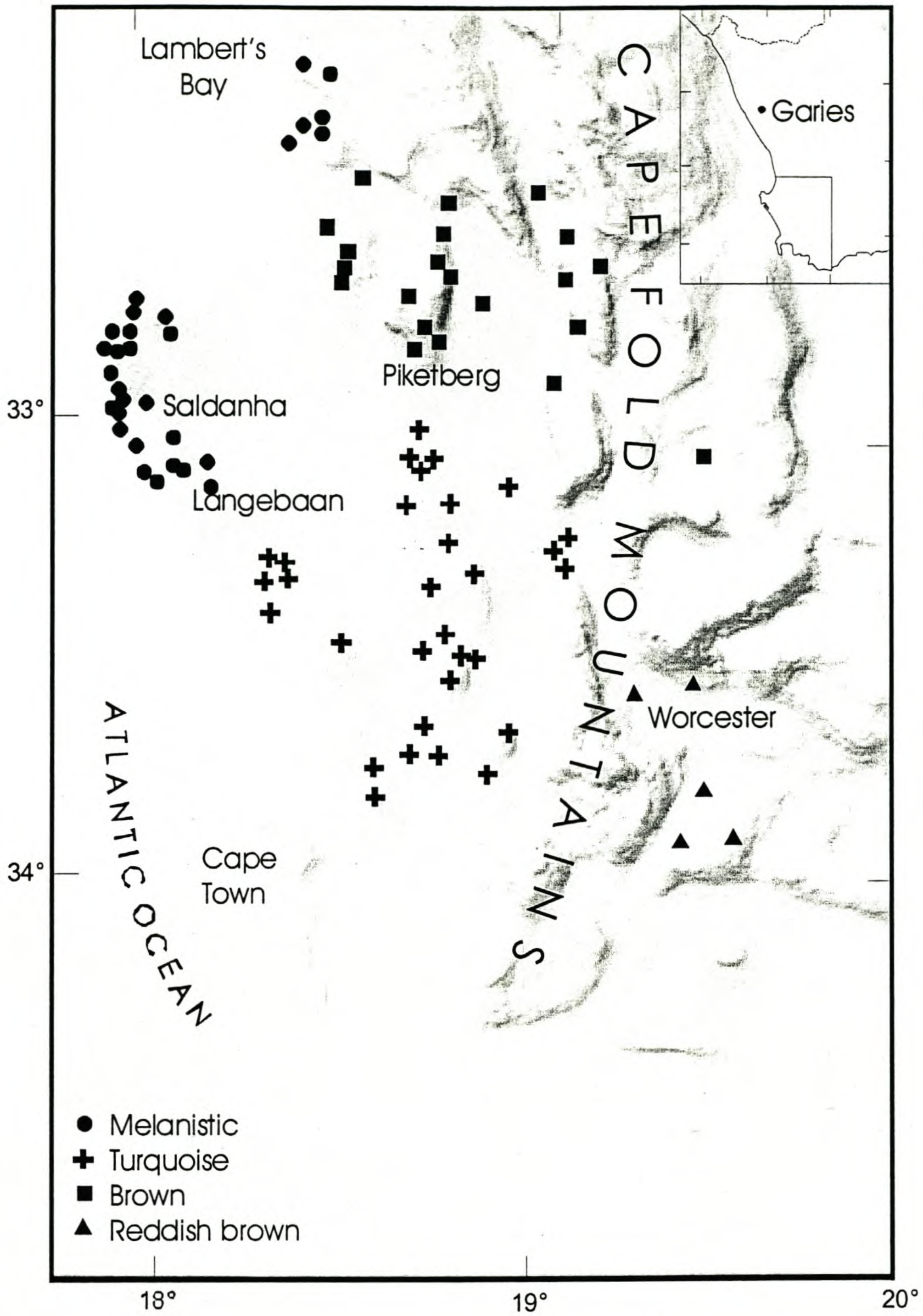

Figure 1.2 Geographical distribution of different colour morphs in the *Cordylus polyzonus*-complex in the Western Cape, South Africa, south of 32°30'S and west of 19°30'E (adapted from Badenhorst, 1990).

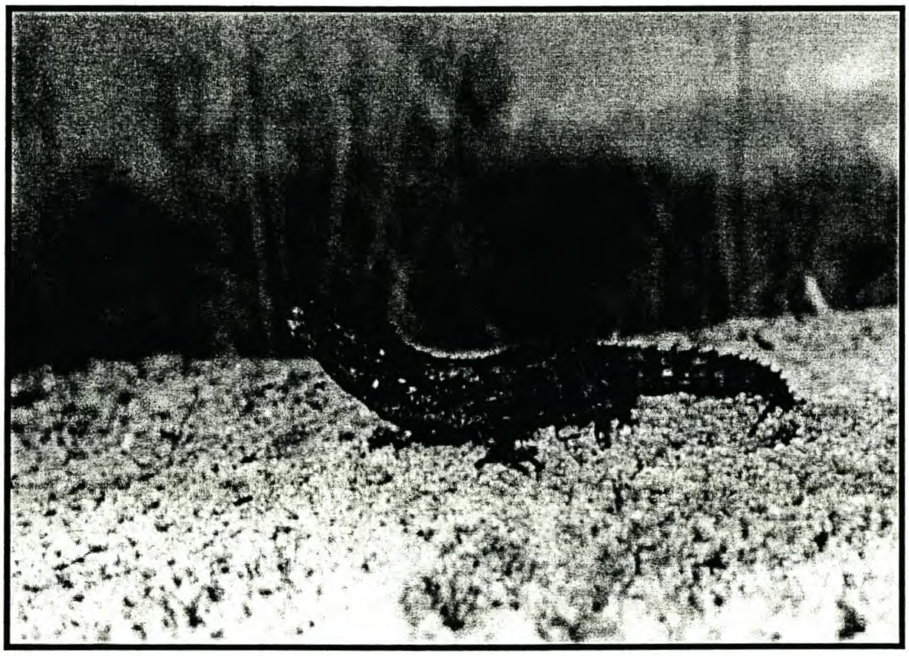

Figure 1.3 Photograph of *Cordylus macropholis*.

This species' range stretches along the western coastal lowland of southern Africa from Saldanha in the south to Kleinzee in the north (Figure 1.4) (Branch, 1998), its distribution being congruent with the Strandveld Succulent Karoo biome (Low & Rebelo, 1996).

A proposed model for the evolution of terrestriality in *Cordylus macropholis*

Molecular phylogeny of the family Cordylidae depicts a close relationship between *Cordylus macropholis* and the rupicolous species *C. cordylus*, with genetic distances that separate them being less than that usually measured between subspecies (Brody, 1991; Frost *et al.*, 2001). Based on this information and its particular restricted distribution, indications are that the terrestrial species *C. macropholis*, evolved from a rupicolous ancestor. Mouton, Flemming & Kanga (1999) consider sea level events to have played an important role as a selective force for the transition from a rupicolous to a terrestrial habitat in this species. The rapid transgression of the sea level after the Last Glacial Maximum (LGM) greatly diminished suitable rocky habitat along the coast. Subsequently, the rupicolous ancestor was probably faced with two options. Either it had to disperse into the sandy plains of the coastal lowland and to adapt to a terrestrial lifestyle, or it had to succumb to the rising sea level. Furthermore, it can be argued that the specific climatic parameters accompanying the transgression may have been an important aspect that allowed for the invasion of the terrestrial habitat. In cold climates lizards typically increase their basking times (Huey & Webster, 1976; Hertz, 1981; Hertz & Huey, 1981; Van Damme *et al.*, 1989) and will do so in open areas where basking is more effective (Hertz, 1981; Adolph, 1990). A rupicolous lifestyle for the ancestor of *C. macropholis* would thus have been beneficial and in agreement with the cooler conditions prevailing during the LGM. With the amelioration of the climate after the LGM, however, the environment became warmer. This would have allowed for shorter basking times as well as the invasion of a more closed habitat, such as the vegetation of the lowland coastal plains.

Figure 1.4 Distribution of *Cordylus macropholis* in South Africa as indicated by the shaded area (adapted from Branch, 1998).

Additionally, the vegetation of the coastal environment itself may have facilitated the transition. *Cordylus macropholis* shows a strong association with the succulent plant, *Euphorbia caput-medusae* (Figure 1.5) (Branch, 1998; Mouton *et al.*, 2000). Although it is unknown whether the first appearance of this plant coincided with the sea level transgression, it certainly offered habitat features that closely resemble that of a rock habitat. The long cylindrical branches lie heavily stacked on one another providing multiple shelter options to both lizards and invertebrate prey (Bauwens, Castilla & Mouton, 1999). Furthermore, these plants are reported to provide superior opportunities for thermoregulation compared to that of other available shrub habitats (Bauwens *et al.*, 1999). However, these plants are limited in availability, covering less than five percent of the surface area (Bauwens *et al.*, 1999).

Considering the proposed sequence of habitat transition in *C. macropholis* and the current limited availability of these plants, certain predictions can be made regarding the ecology of these lizards, two aspects being of particular interest. Firstly, *C. macropholis* exhibits a highly female-biased sex ratio (Mouton, Flemming & Searby, 1998; Bauwens *et al.*, 1999; Mouton, Flemming & Nieuwoudt, 2000) and secondly, individuals are known to aggregate in *E. caput-medusae* plants. If aggregation behaviour in *C. macropholis* is related to a shortage in preferred habitat, one might predict aggregations to be stable. Accordingly, a low degree of movement of lizards among plants is to be expected. Likewise, a preference for a habitat that may attract multiple mates, will result in competition and possibly a polygamous mating system (see Emlen & Oring, 1977). By implication, one might predict that the skewed sex ratio observed in *C. macropholis* may be due to the differential movement of the sexes among plants or to intrasexual competition (see Stamps, 1983).

Given the limited information on the ecology of this species (Mouton *et al.*, 1998; Bauwens *et al.*, 1999; Mouton *et al.*, 2000), the aim of the present study was thus twofold: firstly, to gain basic insight into the ecology of this species and secondly to evaluate this information against the

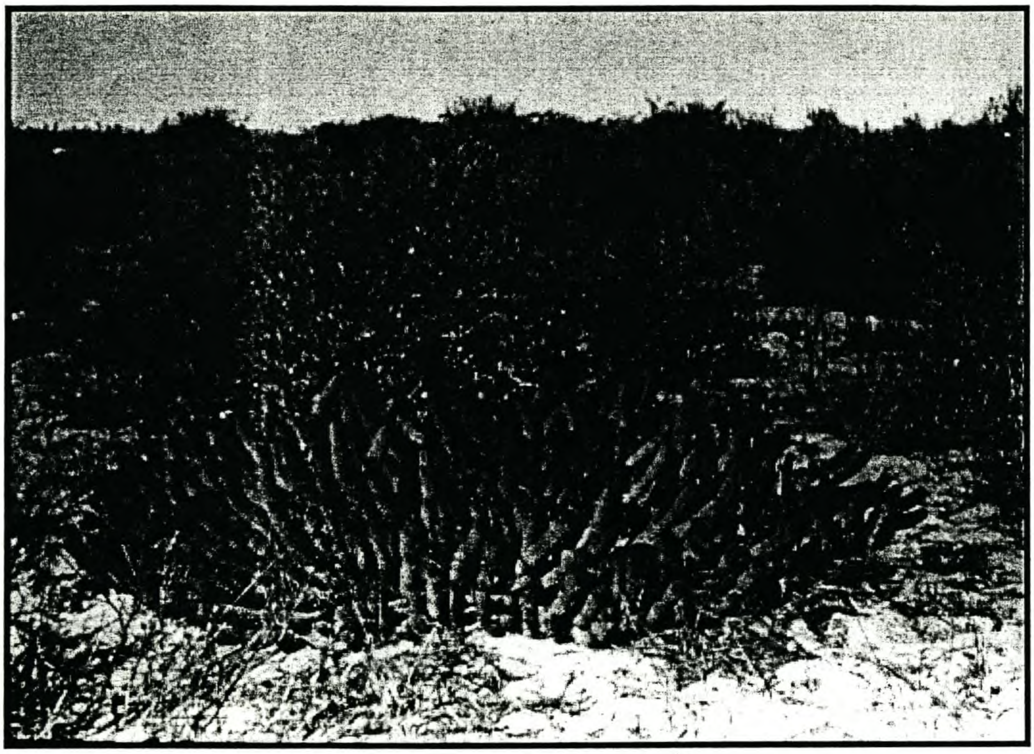

Figure 1.5 Photograph of a full-grown *Euphorbia caput-medusae* plant.

implications of the habitat transition hypothesis. The primary goals of this study were thus as follows:

1. To determine the preferred habitat of *C. macropholis*.
2. To reassess the female-biased sex ratio reported for *C. macropholis*.
3. To examine the stability of aggregations within *E. caput-medusae* plants and movement patterns among plants.
4. To study the social structure of aggregations, male spatial patterns and male social behaviour during the mating season, and to evaluate the effect of competition for limited resources on these factors.

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AN ELECTROPHORETIC ANALYSIS OF *CORDYLUS POLYZONUS* COLOUR MORPHS IN THE WESTERN CAPE PROVINCE

Abstract

Gene expression in the muscle and liver tissue of *Cordylus polyzonus* was examined to identify enzyme products that would resolve well enough to assess the genetic structure of the colour morphotypes. The number of presumptive loci controlling specific enzyme systems in *C. polyzonus* was found to be consistent with comparative data from *C. oelofseni*, except for the silencing of one locus that may have occurred in Aldolase. Proteins encoded by 33 presumptive loci were analysed by starch-gel electrophoresis for three populations representing the melanistic, turquoise and brown colour morphotypes of *C. polyzonus*. The aim was to determine whether or not the melanistic population is genetically distinct from other non-melanistic adjacent populations in order to test a hypothesis on the evolution of melanism in this species. No genetic differences either within or between populations were found. No polymorphic loci were found. The results suggest that the melanistic form in *C. polyzonus* is simply an ecotype within a larger gene pool.

Key words: melanism, allozymes, Cordylidae

INTRODUCTION

Although melanism may be a fixed trait for a given species, particularly in reptiles and insects (Majerus, 1998), many cases of intraspecific melanistic morphs have been described (Crisp, Cook & Hereward, 1979; Forsman & Ås, 1987; King, 1988; Gvozdik, 1999). Kettlewell (1973) defined melanism as the condition in which some individuals in a polymorphic species' population appear darker than normal because of an increase in epidermal pigments, collectively known as melanins. The increase of efficiency for heat-absorption at cooler temperatures and crypsis are the two main selective advantages put forth to account for the maintenance of melanistic morphs within natural populations (Pearse & Pogson, 2000).

At least two complexes of closely related melanistic and non-melanistic forms have been identified within the family Cordylidae (Mouton & Oelofsen, 1988), with melanistic populations showing a distinct clustering in the southwestern coastal regions of southern Africa (Mouton, 1985, 1986; Mouton & Oelofsen, 1988; Mouton & Van Wyk, 1995). Melanistic forms in the *Cordylus cordylus*-complex occur at distinct locations along the coast and western section of the Cape Fold Mountains, and are separated by a non-melanistic form that occurs mainly in the coastal lowlands (Mouton, 1987)(see Figure 1.1). The coastal melanistic populations are associated with zones of upwelling of cold water in the Atlantic ocean, while montane melanistic populations occur at localities where there is a high incidence of orographic fog and cloud cover (Badenhorst, Mouton & Van Wyk, 1992). Melanistic populations in this complex share some seemingly non-adaptive scale characters, such as 10 longitudinal rows of ventrals, a subocular scale reaching the lip, and separated prefrontal scales. Alternatively, the non-melanistic form has 12 longitudinal rows of ventral scales, a median subocular that doesn't reach the lip and prefrontal scales that are in contact. Furthermore, a few populations, with intermediate character suites, have also been identified and are almost invariably located in close proximity to melanistic populations or occur in peninsular situations. Mouton & Oelofsen (1988) therefore rejected the possibility that melanistic populations represent local adaptations to similar conditions of limited solar radiation.

Mouton & Oelofsen (1988) concluded that melanistic populations are closest relatives and relics from a once larger melanistic population. They proposed that due to the thermoregulatory advantage of a dark skin in cold environments (Norris, 1967; Porter, 1967; Heatwole, 1976; Pearson, 1977), an ancestral population evolved melanism in response to adverse weather conditions that prevailed during the Last Glacial Maximum. They further suggested that this melanistic population fragmented with the amelioration of the climate, to remain in suitable cooler enclaves. Subsequently, a warm-adapted, non-melanistic form dispersed into the area to occupy areas left vacant by the contracting melanistic form. In the process, melanistic populations not effectively isolated in penisular or insular situation along the coast or at high altitudes in the mountains, were swamped by the inmoving form, thus explaining the occurrence of several populations with mixed character suites.

Supporting the hypothesis of Mouton & Oelofsen (1988), an electrophoretic analysis of the relationships within the *C. cordylus*-complex by Brody, Mouton & Grant (1993) confirmed that the coastal melanistic and montane melanistic populations in the *C. cordylus* complex represent gene pools separate from the non-melanistic one. Lower levels of heterozygosity observed in the two melanistic forms than in the non-melanistic form, confirmed the suggested relictual nature of the former. Based on the consistency of differences in the scale characters and the nature of the contact zone north of Saldanha, Mouton & Van Wyk (1990) elevated the coastal melanistic form, formerly treated as a subspecies of *C. cordylus* (FitzSimons, 1943), to a full species, *C. niger*. They also described the montane melanistic form as a separate species, *C. oelofseni*.

Cordylus polyzonus is another polymorphic species within the family that exhibits melanistic and non-melanistic forms. Isolated melanistic populations are confined, as in the case of *C. cordylus*, to zones of upwellings of cold water (Badenhorst *et al.*, 1992). Populations of turquoise, brown, and vermillion forms replace the melanistic form in the adjacent inland areas

(Mouton & Oelofsen, 1988) (see Figure 1.2). Furthermore, an analysis of geographical variation in external morphological characters of *C. polyzonus* revealed a pattern similar to that recorded for the *C. cordylus*-complex in the same area (Mouton, 1987). Melanistic populations are characterized by a high incidence of a few, seemingly non-adaptive scale characters, with intermediate non-melanistic populations in close geographical proximity (Badenhorst, 1992). The question arises whether the melanistic populations of *C. polyzonus* represent a separate gene pool from the non-melanistic populations of this species as in the case of *C. cordylus*.

The first aim of this study was to analyze and compare the genetic structure of melanistic and non-melanistic populations of *C. polyzonus* by means of allozyme electrophoresis. At present, however, the only data available on electrophoretically detectable isozymes in this genus, are that of *C. oelofseni* (Brody, 1991). The second aim of this study was therefore to develop further information on the evolutionary development of isozyme loci within the genus by comparing gene expression in *C. polyzonus* to that in other reptiles and vertebrates.

MATERIALS AND METHODS

Collection Site

Standard noosing techniques were used to collect twenty melanistic specimens from the Saldanha Bay area (32°59'00"S/17°52'42"E) and twenty turquoise specimens from Klipberg on the farm Kraalbosdam (33°20'07"S/18°21'45"E) during March 1999. Another twenty specimens (brown form) were collected from a locality near Garies (30°33'20"S/17°58'50"E).

Electrophoresis

Specimens were caught and kept alive until arrival at the laboratory where they were frozen and stored at -70°C until processed. Muscle from the femoral area of the hind limb and liver tissue were removed and homogenized with a metal rod in equal volumes of extraction buffer (0.01 M Tris EDTA-NADP$^+$ pH 7.0). Tissue homogenates were kept at -70°C and centrifuged for 5 minutes at 14 000 rpm prior to electrophoresis. Homogenate was applied to filter paper wicks and loaded onto 13 % starch gels (Sigma Chemicals). Subsequently, the gels were subjected to constant amperage of 40 mA for 3-5 hours under refrigeration (6°C).

Standard histochemical staining techniques were used to visualize bands on the cut inner surface of the gel (Shaw & Prasad, 1970). Enzyme systems are referred to by upper case letters (eg. LDH) and follows recommendations of the Nomenclature Committee of the International Union of Biochemistry (1984). For multiple locus enzyme systems, locus designations followed Fisher, Shaklee, Ferris & Whitt (1980) and Buth (1984). Loci were assigned a number relative to their mobility. Number one was the most anodal. The fastest moving or most common allele was assigned the value of 100.

RESULTS

Among the 19 enzymes examined, 30 loci resolved clearly (Table 2.1), but all were found to be monomorphic in all three populations sampled. Thus, both the melanistic and non-melanistic populations investigated, lacked allozyme differentiation. The number of loci expressed in the two tissues investigated, and which could be adequately resolved were 27 (liver) and 3 (muscle).

To place gene expression in *Cordylus polyzonus* into an evolutionary context compared to other Reptilia, a brief description of gene expression is given and compared to that observed in other reptiles where such data exist. In these comparisons the tuataras (*Sphenodon* spp.) represent the only living form of the order Rhyncocephalia and are the closest relatives of squamates (Murphy & Matson, 1986). The alligator, *Alligator mississippiensis,* is a representative of the reptilian order Crocodylia. The various snakes and lizards are representatives of the order Squamata and are considered to be evolutionary advanced (see Brody, 1991).

Although the phylogeny of the lizard family Cordylidae greatly remains unresolved, *Cordylus oelofseni* represents an evolutionary advanced form within this family (Frost *et al.*, 2001). It is

Table 2.1 Enzymes and electrophoretic conditions used in the analysis of *Cordylus polyzonus* populations. Mitochondrial and supernatant loci are denoted by M- and S- prefixes, respectively.

Enzyme	Enzyme commission number	Locus abbreviation	Buffer*
Aspartate aminotransferase	2.6.1.1	*s-Aat*	TC
		m-Aat	TC
Aldolase	4.1.2.13	*ALD*	TC
Adenylate kinase	2.7.4.3	*Ak-1*	TC
		Ak-2	TC
Creatine kinase	2.7.3.2	*CK*	RW
Esterases	3.1.1.1	*Est-1*	TC/MF
Glucose phosphate isomerase	5.3.1.9	*GPI*	RW
Glucose-6-phosphate dehydrogenase	1.1.1.49	*G6pd-1*	TC
		G6pd-2	TC
Glutamate dehydrogenase	1.4.1.3	*GLUD*	TC
Glyceraldehydephosphate dehydrogenase	1.2.1.12	*GAP*	TC
Isocitrate dehydrogenase	1.1.1.42	*Idh-1*	TC
		Idh-2	TC
Lactate dehydrogenase	1.1.1.27	*Ldh-1*	MF/TC
		Ldh-2	MF/TC
Malate dehydrogenase	1.1.1.37	*s-Mdh*	TC
		m-Mdh	TC
Malic enzyme	1.1.1.40	*Me-1*	TC
		Me-2	TC
Mannose phosphate isomerase	5.3.1.8	*MPI*	MF
6-Phosphogluconate dehydrogenase	1.1.1.44	*Pgd-1*	TC
		Pgd-2	TC
Phosphoglucomutase	2.7.5.1	*Pgm-1*	MF/RW
		Pgm-2	MF/RW
Peptidases:			
Leucyl-glycyl-glycine tripeptidase	3.4.1.1	*Pep-B*	MF
L-leucyl-tyrosine dipeptidases	3.4.13.11	*Dip-1*	MF
		Dip-2	MF
		Dip-3	MF
Sorbitol dehydrogenase	1.1.1.14	*SDH*	TC

* RW: pH 8.1, Lithium hydroxide 0.06 M, Boric acid 0.3 M (Ridgway, Sherburne & Lewis, 1970)

MF: pH 8.7, Tris 0.18 M, Boric acid 0.1 M, NaEDTA 0.004 M (Markert & Faulhaber, 1965)

TC: pH 8.6, Tris 0.661 M, Citric acid 0.083 M (Charlesworth, 1972) presently the only species, within this family, for which electrophoretic data are available (Brody, 1991).

Aspartate Aminotransferase (*AAT* 2.6.1.1)

Two zones of banding were observed in *C. polyzonus*. Both isozymes were more prominent in the muscle tissue than in the liver. The bands were interpreted as reflecting the mitochondrial (*m-Aat*) and supernatant (*s-Aat*) forms of this enzyme, respectively. Brody (1991) also identified a supernatant and a mitochondrial form in *C. oelofseni*. Two loci were also reported by Dessauer & Densmore (1983) in the alligator, *A. mississippiensis,* and by Hofman, Maxson & Arntzen (1991) in the family Chamaeleonidae.

Aldolase (*ALD* 4.1.2.13)

A single locus, migrating cathodally from the origin, was observed in the muscle tissue of *C. polyzonus*. Milton (1990) also reported one locus in the Australian skink, *Egernia whitii*. Two loci were, however, reported by Brody (1991) in *C. oelofseni* and by Dessauer & Cole (1984) in the whiptail lizard, *Cnemidophorus tigris*.

Adenylate kinase (*AK* 2.7.4.3)

One presumptive locus of this monomeric enzyme was strongly expressed in the muscle tissue. Brody (1991) identified one locus which was expressed in all tissues, but stated that it was expressed most in muscle tissue.

Creatine kinase (*CK* 2.7.3.2)

The product of one locus of this dimeric enzyme was detected in muscle tissue. Usually the products of two loci are detected in the Reptilia, a muscle type, encoded by *Ck-A* and a brain type, encoded by *CK-C* (Fisher *et al.*, 1980; Murphy & Matson, 1986). In *C. oelofseni*, Brody (1991) also reported the strong expression of one locus in muscle tissue.

Esterase (*EST* 3.1.1.1)

Two loci were observed and could be resolved for routine use in liver tissue. Seven loci were identified in *C. oelofseni* of which none was sufficiently resolved for routine use (Brody, 1991). Three esterase loci were reported for the tuatara and for *Crotalus viridis viridis* (Murphy & Crabtree, 1985; Murphy & Matson, 1986). One esterase locus was also identified in liver tissue of the lizard genus *Petrosaurus* (Iguanidae) (Aguilars-S, Sites & Murphy, 1988).

Glucosephosphate isomerase (*GPI* 5.3.1.9)

One locus was expressed in muscle tissue as a cathodally migrating band. This corresponds to expression in *C. oelofseni* (Brody 1991), *Petrosaurus* (Aguilar-S *et al.*, 1988), *Nerodia fasciata* (Serpentes: Colubridae) (Lawson, Meier, Frank & Moler, 1991) and *A. mississippiensis* (Dessauer & Densmore, 1983).

Glucose-6-phosphate dehydrogenase (*G6PD* 1.1.1.49)

One cathodally and one anodally migrating locus were detected in liver tissue. Two loci were also observed in *A. mississippiensis* (Dessauer & Densmore, 1983). Brody (1991) and Milton (1990), however, reported only one locus for *C. oelofseni* and *E. whitii* respectively.

Glutamate dehydrogenase (*GLUD* 1.4.1.3)

The product of a single locus was observed. One locus was also expressed in *C. oelofseni* (Brody, 1991) and in *Crotalus viridis viridis* (Murphy & Crabtree, 1985). Two loci were identified by Hofman *et al.* (1991) in the family Chamaeleonidae.

Glyceraldehyde-3-phosphate dehydrogenase (*GAP* 1.2.1.12)

One locus was detected in liver tissue. Two loci were expressed in *C. oelofseni*, one in muscle, the other in brain tissue (Brody, 1991). A similar distribution of expression was observed in the tuatara in which *Gap-A* was expressed only in skeletal muscle and *Gap-B* was expressed in brain tissue (Murphy & Matson, 1986).

Isocitrate dehydrogenase (*IDH* 1.1.1.42)

The products of two loci were observed on the gel. Brody (1991) identified two loci in *C. oelofseni*. *Idh-1* was expressed in all tissue examined, but was strongest in liver, whereas *Idh-2* was expressed exclusively in liver tissue. Two loci, *M-Idh-A* in muscle and *S-Idh-A* in liver, were also expressed in the genus *Petrosaurus* (Iguanidae) (Aguilar-S *et al.*, 1988). The expression of a single locus seems to be restricted to the more basal reptiles, such as the tuatara (*Sphenodon punctatus*) and some North American species of *Eumeces* (Murphy, Cooper & Richardson, 1983).

Lactate dehydrogenase (*LDH* 1.1.1.27)

Two lactate dehydrogenase loci were expressed in liver tissue. This is in accordance with the findings of Milton (1990) where two loci were also expressed in the liver tissue of the Australian skink, *E. whitii*. Brody (1991) observed the expression of one locus in skeletal muscle (*Ldh-A*) and the other (*Ldh-B*) in heart tissue of *C. oelofseni*.

Malate dehydrogenase (*MDH* 1.1.1.37)

The products of two loci were identified. Brody (1991) stated that one locus encodes for the cytoplasmic form and the other for the mitochondrial form. Mitochondrial enzymes usually migrate more slowly than supernatant forms or migrate cathodally from the origin (Murphy & Crabtree, 1985). One zone of banding was observed migrating cathodally and was interpreted as being the product of the mitochondrial locus (*m-Mdh*).

Malic enzyme (*ME* 1.1.1.40)

Two loci were expressed in liver tissue. This is in accordance with the expression of *Me-1* and *Me-2* in *C. oelofseni* and *Crotalus viridis viridis* (Brody, 1991; Murphy & Crabtree, 1985).

Mannosephospate isomerase (*MPI* 5.3.1.8)

This monomeric enzyme was encoded by a single locus and was expressed strongly in liver tissue. The expression of a single locus has been reported for many other reptiles (Murphy & Crabtee, 1985; Milton, 1990; Brody, 1991; Hofman *et al.*, 1991).

6-Phosphogluconate dehydrogenase (*PGD* 1.1.1.44)

Two loci of this dimeric enzyme were expressed in liver tissue of *C. polyzonus*. Brody (1991) reported the expression of only a single locus in *C. oelofseni*, but a variable number of loci have been reported in other Squamata (Sites & Greenbaum, 1983; Murphy & Crabtree, 1985).

Phosphoglucomutase (*PGM* 2.7.5.1)

Two loci of this monomeric enzyme were expressed in *C. polyzonus*. Two loci were also expressed in *Cordylus oelofseni* (Brody, 1991). The expression of only one locus has been reported for the Chamaeleonidae (Hofman *et al.*, 1991), the prairie rattlesnake (*Crotalus v. viridis*) and in *A. mississippiensis* (Dessauer & Densmore, 1983; Murphy & Crabtree, 1985).

Tripeptidase (*PEP*-B 3.4.1.1)

The products of a single locus were detected with the tripeptide LEU-LEU-GLY as a substrate and it was strongly expressed in liver tissue. Similar expression was reported in *C. oelofseni* (Brody, 1991).

Dipeptidase (*Dip-1*, *Dip-2*, *Dip-3* 3.4.13.11)

Four presumptive loci were identified with LEU-TYR as a substrate. Brody (1991) reported the expression of four loci in *C. oelofseni*, while Milton (1991) reported the expression of only one locus in *E. whitii*. The number of loci expressed seem to vary and several dipeptidase isozymes have been reported in reptiles (Dessauer & Cole, 1984; Murphy & Crabtree, 1985).

Sorbitol dehydrogenase (*SDH* 1.1.1.14)

One locus was expressed in liver tissue. In *C. oelofseni,* the single enzyme of this locus is expressed in kidney, duodenum and liver (Brody, 1991). The expression of only one locus has been found in anurans and other higher land vertebrates (Duellmann & Hillis, 1987).

DISCUSSION

The number of loci that encode the expression of particular enzyme systems may vary within particular taxonomic groups (Murphy & Crabtree, 1985). This information may be useful in comparative genetic studies to determine relationships between taxa as well as the evolutionary advancement between the different reptile taxa (Brody, 1991). For instance, the primitive condition in *Alligator mississippiensis* is highlighted by the expression of two loci of the enzymes, *G6PD* and *G3PD*, compared to only one locus in more advanced reptiles. Similarly tissue specific gene expression for two enzymes, *ALD* and *GLUD*, in the western whiptail lizard, *Cnemidophorus tigris*, highlights the advanced evolutionary state of this reptile. Brody (1991) also reported on the possibly advanced condition of *Cordylus oelofseni* in the expression of the SOD enzyme. Two loci are expressed in other squamate reptiles (Dessauer & Cole, 1984; Dessauer & Densmore, 1983) and even three in the ancient reptiles (Murphy & Matson, 1986). However, only one locus was expressed in *C. oelofseni*, which may indicate the silencing of one locus and therefore may represent a derived evolutionary state (Murphy & Crabtree, 1985).

The number of presumptive loci controlling specific enzyme systems in *C. polyzonus* (Table 2.1) was found to be consistent with comparative data from *C. oelofseni*, except in two cases. I found only a single locus expressed for *ALD*, whereas two were expressed in *C. oelofseni*. In *Cnemidophorus tigris Ald-1* expression was restricted to neural tissue (Dessauer & Cole, 1984). It is therefore possible that this locus went undetected in this study as I did not examine these tissues. However, Brody (1991) found both *Ald-1* and *Ald-2* expressed in a variety of tissues of *C. oelofseni*, including liver and muscle tissues. It is thus possible that one locus has been silenced in *C. polyzonus*, but re-runs of variable duration and buffer combinations are recommended to exclude the possibility of failed detection of a possible second locus.

Two loci were observed for *G6PD*, as opposed to only one being detected in *C. oelofseni* (Brody, 1991) and most other lizards (Dessauer & Cole, 1984; Murphy & Matson, 1986). However, the one cathodally migrating locus observed in *C. polyzonus* probably corresponds to a band also observed by Brody (1991) and termed 'Nothing dehydrogenase' (*NDH*).

Allozyme data do not support a scenario for *C. polyzonus* similar to that proposed by Mouton and Oelofsen (1988) for the *C. cordylus*-complex, namely that a melanistic population was for some time isolated in the Saldhanha-Lambert's Bay-Piketberg region, that it attained certain scale characters through genetic drift before fragmenting into smaller populations, and that an expanding, non-melanistic form eventually came into contact with the melanistic variant, swamping those melanistic populations not suitably isolated. The complete lack of allozyme differentiation between adjacent melanistic and non-melanistic *C. polyzonus* populations observed in this study, may be interpreted as indicating that the different colour morphs are simply ecotypes within one large gene pool. This is supported by the ontogenetic colour change in juveniles of the melanistic form of *C. polyzonus*, whereas there is no ontogenetic color change in *C. niger* and *C. oelofseni*, the hatchlings being melanistic at birth (Badenhorst, 1990). The colour morphs within the complex may thus represent adaptations to local ecological conditions and sufficient time may not have elapsed for colour to become genetically fixed. The different melanistic populations are therefore not relictual forms, but may suggest that melanism have arisen several times independently in the *C. polyzonus*-complex. As these populations are restricted to coastal locations of relatively cooler conditions and limited solar radiation (see Badenhorst, 1990), the selective agent responsible for the melanistic form could be temperature. Thermal melanism is considered to confer a selective advantage in cooler conditions if darker lizards can absorb heat more efficiently and thereby increase there activity season and reproductive success (Pearse & Pogson, 2000). The mutations involved in producing the darker phenotype are likely to differ among the independent melanistic populations, resulting in slightly different appearances of melanism (Pearse & Pogson, 2000). One way to test the hypothesis on parallel evolution of melanism in *C. polyzonus*, would therefore be to compare melanism among the different populations by means of darkness scores (see Pearse & Pogson, 2000).

The genetic similarity among the populations seems in disagreement with the marked morphological variation among populations and the presence of certain scale characters in the melanistic *C. polyzonus* populations in the Saldanha and Lambert's Bay areas. Both these populations are characterized by a higher incidence of three particular scale characters compared to the non-melanistic forms (Badenhorst, 1990). However, the relatively low incidence of the three character states at the localities where they have been recorded, indicates that they are not under strong environmental control. Under such conditions, these states would have been absent either in all individuals, or present in all individuals and Badenhorst (1990) concluded that they have arisen through genetic drift in a small gene pool. Rising sea-levels during the Holocene may have played an important role in isolating and restricting small populations to areas of relatively higher elevation, such as Saldanha, Platberg and Lambert's Bay (see Figure 1.2).

Cordylus polyzonus has an extensive distribution range (Branch, 1998) and one would have expected much higher genetic variability, as the overall levels of genetic variability should, under some assumption (Kimura, 1983), be positively correlated with the size of a species' range (Aguilars-S *et al.*, 1988). Brody *et al.* (1993) also reported low levels of heterozygosity in other species of the Cordylidae family. The low variability in *Cordylus niger* and *C. oelofseni*, however, is in accordance with the limited ranges of both, with *C. cordylus* showing a relatively higher variability that is correlated with its relatively larger distribution range.

Reduced heterozygosity has been observed in a number of mammal species (Sage & Wolff, 1986), amphibians (Highton & Webster, 1976) and reptiles (Sattler & Guttman, 1976) in North America and has been ascribed to serial recolonizations of recently unglaciated territory during the post-Pleistocene (Sage & Wolff, 1986). Populations at the edge of a rapid range expansion are the products of successive founding events and generally tend toward the loss of genetic variability (Nei, Maruyama & Chakraborty, 1975). Genetic invariability may also be the result of strong stabilizing selection over an extended period of time if the environment remained stable (Ridley, 1996). In the view of the late Holocene sea-level events in the southwestern Cape (Hendey, 1983; Mouton & Oelofsen, 1988; Baxter & Meadows, 1999), the lack of genetic variability in *C. polyzonus* may be the result of a rapid range expansion from the bottlenecks following these events during the Holocene. Alternatively, these populations in the Western Cape may be at the edge of a fluctuating range-expansion of a population that has been subjected to stabilizing selection in a more stable inland environment. Furthermore, the presumably small home ranges of this lizard and discontinuous rock habitat in the coastal lowland may promote inbreeding, which may further result in a loss of heterozygosity (see Gorman *et al.*, 1975).

The lack of genetic variability found, however, may represent a lack of data. It may be that polymorphisms are present in these populations, but in such low frequencies that the sample size was inadequate to detect variation. It is also questionable whether protein electrophoresis is the most appropriate method when investigating relationships within this species. Another method, like restriction mapping of mitochondrial DNA, may be more useful in separating more closely related populations (Rose & Selcer, 1989).

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HABITAT SELECTION IN THE GIRDLED LIZARD, *CORDYLUS MACROPHOLIS*

Abstract

I used three complementary methods to study habitat selection in *Cordylus macropholis* in a natural area of Strandveld Succulent Karoo vegetation. First, the sighting frequency of lizards in distinct plant categories was compared to the relative availability of the plants. Except for one case, all sightings of lizards were made in *Euphorbia caput-medusae* plants, the least available habitat category. Second, the habitat preference of *C. macropholis* in terms of shelter quality was examined. Given a choice of three shelter types, both adult and juvenile lizards gave preference to *E. caput-medusae*, followed by rock crevices and plant debris. I also studied prey availability in *E. caput-medusae* plants as a cue for habitat selection by *C. macropholis*. The standing crop of available arthropod prey in *E. caput-medusae* plants was found to be consistent with prey items in the stomachs of lizards at two independent sampling times.

Key words: shelter preference, diet, terrestrial lizard, Cordylidae

INTRODUCTION

The large-scaled girdled lizard, *Cordylus macropholis*, is endemic to a small area along the west coast of southern Africa (see Figure 1.4) (Branch, 1998). It is the only one of the six terrestrial species in the predominantly rupicolous family Cordylidae, that occurs in the western half of southern Africa (Mouton, Flemming & Nieuwoudt, 2000), suggesting evolution from a rupicolous ancestor (see also Frost *et al.*, 2001). It is a diurnal, heliothermic lizard (Branch, 1998) that, like the other species in the genus, is believed to feed mainly on arthropod prey while following a sit-and-wait foraging strategy (Cooper, Whiting & Van Wyk, 1997). It is relatively small (adult snout-vent length: 58-75 mm) and occurs in a variety of habitats, ranging from limestone cracks to plants and associated dry matter (Branch, 1998). Despite its seemingly ubiquitous presence in the different habitats, it is generally considered to exhibit strong preference for the succulent plant, *Euphorbia caput-medusae* (Branch, 1998; Mouton *et al.*, 2000). However, no quantitative data exist on the presence of *C. macropholis* in the different available habitats. Mouton *et al.* (2000) reported high densities of this lizard in *E. caput-medusae* plants, with aggregations of up to nine individuals in individual plants. Moreover, Bauwens, Castilla & Mouton (1999) observed that *C. macropholis* greatly restricts its activities to these plants. These authors concluded that *E. caput-medusae*, where present, is the preferred habitat type of *C. macropholis* as these plants are superior to other plant habitats in terms of shelter and prey resources.

This paper reports on habitat selection of *C. macropholis* in an area of natural Strandveld vegetation along the west-coast of southern Africa. I combined three approaches to study habitat preference. First, I evaluated lizard presence in different plant habitats relative to each habitat's availability. Second, I examined habitat preference in terms of shelter quality. Third, I attempted to evaluate prey availability in *E. caput-medusae* plants in relation to the diet of *C. macropholis*. I determined whether the arthropod community available to lizards in these plants is consistent with the stomach contents of *Cordylus macropholis*.

MATERIALS AND METHODS

The study was conducted between May and October 2000. The study area was located just north of Lambert's Bay (32°07'S, 18°19'E, Western Cape Province, South Africa). It is a winter rainfall region with rainfall ranging from 50–150 mm per annum (Acocks, 1988). The habitat is representative of the Strandveld Succulent Karoo biome (Low & Rebelo, 1996). It is characterized by the predominance of mesembs (eg. *Ruschia* spp.) ranging from stemless dwarfs to shrubs 2.5 m high (Acocks, 1988). Succulents and semi-succulents, such as *Zygophyllum morgsana* (skilpadbos), *Euphorbia mauritanica* and *E. burrmannii* are also common, and are interspersed with grasses like *Ehrharta calycina* and *Tribolium hispidum*. *Euphorbia caput-medusae* plants were also present, but in densities of less than *ca*. 1 plant per 10 m^2 (Bauwens *et al*., 1999).

Resource Abundance

The survey was conducted on a sunny afternoon during November 2000. I demarcated an area of 30 x 30 m and made observations while systematically searching the area. I wanted to determine what microhabitats the area has to offer, the relative abundance of each microhabitat in the area, and to what extent *C. macropholis* utilizes the different habitats. I recognized five possible habitat type categories in terms of the amount of shade and shelter provided: 1) Semi-succulent shrubs, < 1 m high that provide moderate to good shade, but moderate shelter (mainly *Zygophyllem meyeri*); 2) thorny shrubs, that provide poor to moderate shade and good shelter (*Galenia* spp.); 3) grasses, providing poor shade and shelter; 4) succulents, that provide moderate shade and shelter (mainly *Euphorbia* spp. excluding *E. caput-medusae*); and 5) *Euphorbia caput-medusae* plants. The availability of these microhabitats were estimated by recording their frequency in the 30 x 30 m area.

Shelter Choice

A field experiment was carried out during September 2000 in an area of natural vegetation within the range of *Cordylus macropholis* (for description see Bauwens *et al.*, 1999). Nine moderately sized *E. caput-medusae* plants were selected. Around each of these, a triangular enclosure was constructed using strips of hardboard (200 × 30 × 0.35 cm). The circumference of the enclosure was *ca*. 600 cm and built to house the *E. caput-medusae*-plant in one corner. The following were placed in the remaining corners: a pile of limestone rocks providing sufficient crevices for retreat, and a pile of leaf litter and plant debris. The latter was selected as to be representative of the available shelter options under other dominant plants in the area. The distance between shelters did not exceed one meter (Figure 3.1).

One day prior to the start of the experiment, fifty-four *C. macropholis* were hand-collected from a location south of Lambert's Bay (32°07'S, 18°19'E, Western Cape Province, South Africa). Lizards with a snout-vent-length (SVL) range of 50-72 mm were used. To ascertain whether the choice of shelter varied with lizard size, data were compiled into arbitrarily defined size categories of juvenile and adult lizards. A SVL of 58 mm was taken as the size at sexual maturity (see Mouton *et al.*, 2000).

The group of individuals for each of the nine enclosures was composed in accordance with the natural occurring sex ratio of 2:1 (female:male) (Mouton *et al.*, 2000). The group composition was as follows: two adult females, one adult male, two juvenile females and one juvenile male. In three enclosures, the corner housing an *E. caput-medusae* plant was partitioned off using plastic strips (30 cm wide). In another three enclosures, the rock piles were partitioned off and in the remaining three, the plant debris. A group of lizards was placed in the partitioned section and allowed three days to settle in their ascribed shelter. After the settling period the partition was removed and the lizards were free to move to the other shelter options; all three shelters now located in a common enclosure. Four days after the partition had been removed, the enclosures were searched early in the morning. The distribution of each group of lizards among the three

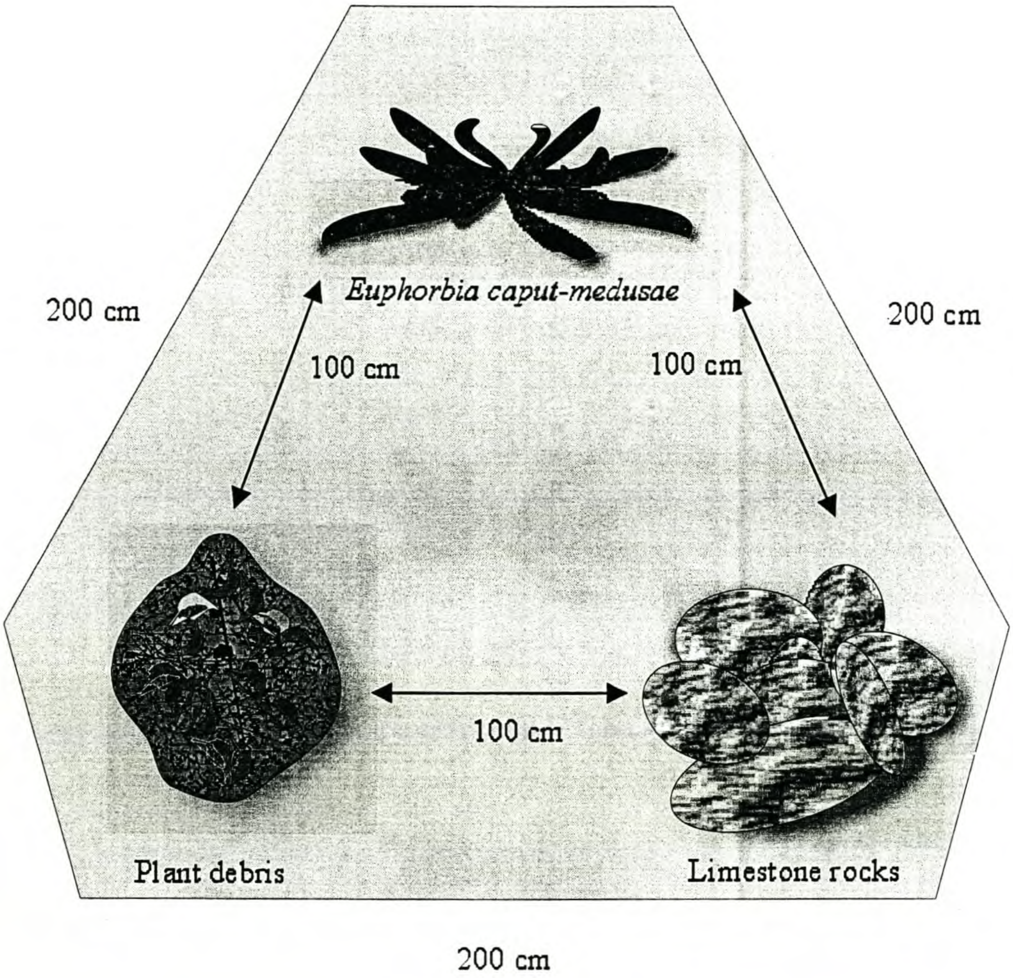

Figure 3.1 Diagram of the construction and placement of shelters in the experimental enclosure.

shelter options was noted.

Chi-square goodness of fit distribution was used to test the frequency counts to the expected frequency of lizards under the null hypothesis that the numbers in each shelter option, was directly proportional to its availability. The chi-square test of independence was used to test for independence between size category and shelter choice. A significance level of 0.05 or less was taken to imply rejection of the null hypothesis.

Food Availability

Twenty *C. macropholis* were hand-collected from *E. caput-medusae* plants at a location south of Lambert's Bay (32°07'S, 18°19'E, Western Cape Province, South Africa). Lizards were collected once during June 2000 ($N = 13$) and once during September 2000 ($N = 7$). Following sacrifice of the lizards by injection with Euthenaze, the stomachs were removed and the contents stored in 70 % ethyl alcohol. Stomach contents were examined under a dissecting microscope and prey items classified to the level of order or family. Food availability in terms of quantity and diversity within the plants was measured by hand-collecting all visible arthropods present in the plants ($N = 13$) which the lizards were collected from. These samples were stored in 70 % ethyl alcohol and later sorted to the level of family.

I analyzed diet composition and prey availability using two measures: (1) the relative abundance (percentage) of total prey items, and (2) the relative incidence (percentage) of one or more prey items of a particular prey taxon in the stomach contents. The non-parametric Mann-Whitney *U*-test was used to test for differences between the two sampling times in the number of prey orders. Differences between the two sampling times in abundance of prey taxa in the stomach contents, and the availability of prey in the field were analysed using contingency tables. Simpson's diversity index (D) was used to determine periodical changes in dietary diversity:

$$D = 1 - \Sigma(\varphi_i)^2$$

where φ_i is the relative abundance of each prey taxa in the stomach contents. This index ranges from 0 (low diversity) to a maximum of $(1 - 1/S)$, where S is the number of prey taxa (Krebs, 1985).

Ivlev's (1961) log Q index as modified by Jacobs (1974) was specifically designed for comparing selectivity with the availability of prey types in the environment. I used Spearman rank correlation to determine the correlation between electivity scores and prey availability to reduce the possible effects of sampling bias in estimating prey availability (see Pérez-Mellado *et al.*, 1991).

RESULTS

Resource Abundance

I searched a total of 1015 plants and found a total of 19 lizards. I observed lizards in only two habitat categories within the 1080 m^2 area. The availability of microhabitats in the study site and the observed number of lizards in each category are summarized in Table 3.1. Only one lizard was observed in a semi-succulent plant, *Zygophyllum meyeri*. This plant was, however, located less than five meters away from an *Euphorbia caput-medusae* plant. Lizards seem to avoid thorny shrubs, grass and other succulent plant species.

Shelter Choice

Of 54 lizards used in the experiment, nine escaped from the enclosures during the settling stage of the experiment. Thus, the effective sample size for each shelter type at the start of the experiment was as follows: 14 in *Euphorbia*-plants, 13 in rock shelters and 18 in plant debris. Nine remained in the *Euphorbia*-plants, six remained in rock shelters and four remained in plant debris. Although a larger proportion of lizards remained in the *Euphorbia*-plants, the difference in distribution among shelters was not significant ($\chi^2 = 5.3$, $\nu = 2$, $P > 0.05$). Of the 26 lizards that moved away from their initial shelters, 18 chose "*Euphorbia*-plants", six chose "rock

Table 3.1. Frequency of microhabitat categories and the observed frequency of *C. macropholis* found in each type.

Habitat category	% of total vegetation cover	Number of lizards
Semi-succulents	62.4	1
Thorny shrubs	5.3	-
Grass	23.7	-
Succulents	6.2	-
E. caput-medusae	2.4	18

shelters" and two chose "plant debris". Movement in the number of lizards towards the distinct shelter categories differed significantly ($\chi^2 = 16.0$, $\nu = 2$, $P < 0.005$).

Examination of the data by size class showed a random pattern of habitat choice. Of the lizards that ranged from 50-58 mm, 15 chose "*Euphorbia*-plants", four chose "rock shelters" and two chose "plant debris". Of the lizards that ranged from 58.1-70 mm, 12 chose "*Euphorbia*-plants", eight chose "rock shelters" and four chose "plant debris". There was no significant difference in the distributions among the three shelter options ($\chi^2 = 2.15$, $\nu = 2$, $P > 0.50$). Thus, there was no correlation between the choice of habitat and lizard size.

Diet and Food Availability

Diet composition.— I recorded nine invertebrate families from the stomach samples ($N = 13$) obtained during June. Stomachs contained a mean of 3.5 ± 0.4 prey numbers and a mean of 2.5 ± 0.3 prey families. A total of nine invertebrate families were also recorded from the stomach samples ($N = 7$) obtained during September. Stomachs contained a mean of 4.3 ± 0.9 prey numbers and a mean of 2.7 ± 0.4 prey families. There were no significant differences in the number of prey families (Mann-Whitney *U*-test: $z = 0.244$, $P = 0.807$) or in the total number of items per stomach between June and September samples (Student's t-test: $t = 0.75$, $df = 9$, $P = 0.47$). Simpson's diversity index of the relative abundance of prey taxa suggests that stomach samples collected during June, contained a higher diversity of prey taxa than those samples collected during September (Table 3.2).

Formicidae was the most dominant family with respect to both relative abundance and relative incidence in stomach samples during June (Table 3.2), followed by Tenebrionidae, Coccinellidae and Pentatomidae. During September the most important group with respect to both relative abundance and relative incidence, was Tenebrionidae, comprising 47.2 % of the diet, followed by Melyridae and Formicidae (Table 3.2). A positive rank correlation between relative

Table 3.2 Relative abundance, and relative incidence of various prey taxa, number of prey items, number of lizards examined, prey taxon diversity, and rank correlation between relative abundance and relative incidence (r_s) for *C. macropholis* during June and September 2000.

Prey taxon	June 2000		September 2000	
	% abundance	% incidence	% abundance	% incidence
Coleoptera				
Tenebrionidae	20.0	38.5	47.2	71.4
Curculionidae	4.4	15.4	5.6	14.3
Chrysomelidae	2.2	7.7	8.3	42.9
Melyridae	6.7	23.1	13.9	42.9
Coccinellidae	17.8	53.8	2.8	14.3
Histeridae	2.2	7.7	-	-
Scarabaeidae	-	-	5.6	28.6
Hymenoptera				
Formicidae	28.9	53.8	11.1	28.6
Hemiptera				
Pentatonidae	15.6	46.2	-	-
Cercopidae	-	-	2.8	14.2
Pycodidae	2.2	7.7	2.8	14.2
No. of prey items	45		36	
No. of lizards examined	13		7	
Diversity	0.813		0.730	
r_s	0.935		0.918	

abundance and relative incidence of prey items existed for both sampling times (Table 3.2; $P < 0.01$). This indicates that the most frequently eaten prey was also encountered in a large proportion of the stomachs examined and excludes the possibility of biasing the results with the consideration of prey types consumed sporadically in large amounts by only a few individuals.

Food availability and electivity.— The relative abundance of arthropod families collected in the *Euphorbia caput-medusae* plants is shown in Table 3.3. Ten taxa were collected using the method of visual inspection. This method however failed to sample important invertebrate orders that were present in the stomach samples of *C. macropholis*, namely Melyridae and Coccinellidae. Tenebrionidae and Formicidae were the most abundant arthropods collected from the plants (Table 3.3).

Although the abundance of Curculionidae and Chrysomelidae in the diet of *C. macropholis* was low (Table 3.2), the electivities in these families were the highest (Table 3.4). For the other taxa, including the important prey taxa, such as Tenebrionidae and Formicidae, electivity scores were close to zero or negative. There was a significant negative correlation between electivity of the different prey families and their relative abundance in the environment ($r_s = -0.955$, $P < 0.01$). This indicates that lizards did not select prey families in proportion to their relative abundance in the plants.

Variation in diet composition and prey availability.— The analysis was restricted to the two major taxa (Tenebrionidae and Formicidae) for which pooled periodical contribution to the diet fluctuated between 48 and 59 % (Table 3.5). The relative abundance of Formicidae and Tenebrionidae in the diet exhibited variation between the June and September samples, but these fluctuations were not significant (*Z*-test, Tenebrionidae: $P = 0.11$, Formicidae: $P = 0.054$). The relative contribution of Tenebrionidae was highest during September, whereas the relative

Table 3.3 The relative abundance (%) of invertebrate families from *E. caput-medusae* plants sampled during June and September 2000 from the Lambert's Bay area.

Invertebrate Family	June 2000	September 2000
Blattidae	68.7	89.3
Tenebrionidae	5.6	1.3
Formicidae	18.5	4.4
Curculionidae	1.6	-
Chrysomelidae	0.4	-
Pycodidae	0.4	-
Pentatomidae	0.4	1.9
Reduvioidae	-	1.9
Isopoda	-	0.6
Diplopoda	-	0.6
Total no. items	249	159

Table 3.4 Relative abundance of prey items collected from *E. caput-medusae* plants and electivity for *C. macropholis*.

Prey taxon	% abundance	electivity
Tenebrionidae	25.4	-0.194
Formicidae	64.2	-1.034
Curculionidae	1.5	0.494
Chrysomelidae	1.5	0.494
Pycodidae	1.5	0.110
Pentatomidae	6.0	0.108

contribution of Tenebrionidae was highest during September, whereas the relative contribution of Formicidae was the highest during June (Table 3.5). The relative abundance of both prey groups in the *E. caput-medusae* plants fluctuated considerably between sampling times (*Z*-test, both $P < 0.05$), both groups being more abundant during the June-sample (Table 3.5).

DISCUSSION

Resource Abundance

Cordylus macropholis occupied only a limited range of available microhabitats in the Strandveld Succulent Karoo vegetation type. Except for a single case, all sightings were made in the plant *Euphorbia caput-medusae* only, despite the fact that alternative microhabitats were present in greater abundance. Lizards seem to exhibit a strong preference for *Euphorbia caput-medusae* plants, despite its relative low abundance in the area. Quantitative data of this study therefore confirms reports by Mouton *et al*. (2000) and Bauwens *et al*. (1999) on the favored association of these lizards with *E. caput-medusae* plants relative to other plants in the environment.

The structural features of an environment may be a key stimulus for lizards in habitat selection (Heatwole, 1977; Schoener, 1977). Vegetation structure may affect avoidance of predators (Stamps, 1983), thermoregulation (Christian, Tracy & Porter, 1983) or foraging (Karasov & Anderson, 1984). *Euphorbia caput-medusae* can be considered a good quality habitat as its structure contributes favorably to all the above-mentioned variables. Cylindrical branches (2-6 cm diameter), covered with tubercles, radiate from a low central stem (see Figure 1.5) and may attain lengths of up to *ca*. 150 cm. These lie heavily stacked on one another in irregular piles, leaving spaces for shelter between layers of branches and between the central stem and the branches (Bauwens *et al*., 1999). Additionally, the milky sap of this plant is considered poisonous (Jacobsen, 1960) and may be a contributing factor in providing protection against predators. In contrast to occupation of many other plant habitats, *C. macropholis* is not faced with a trade-off between thermoregulatory behaviour and predator avoidance (see Huey &

Table 3.5 Variation for the five major families in relative abundance in the stomachs of *Cordylus macropholis*, and relative abundance in the plants during June and September 2000.

	June 2000	September 2000
Tenebrionidae		
Relative abundance (%)		
Plants	5.6	1.3
Stomachs	20	47.2
Formicidae		
Relative abundance (%)		
Plants	18.5	4.4
Stomachs	28.9	11.1
Melyridae		
Relative abundance (%)		
Plants	-	-
Stomachs	6.7	13.9
Coccinellida		
Relative abundance (%)		
Plants	-	-
Stomachs	17.8	2.8
Pentatomidae		
Relative abundance (%)		
Plants	0.4	1.9
Stomachs	15.6	-

Slatkin, 1976; Huey, 1982). Thermal conditions under *E. caput-medusae* cover are conducive to the body temperatures of lizards exposed at the surface and lizards may remain under plant cover for long periods during the day (Bauwens *et al.*, 1999). Furthermore, *E. caput-medusae* plants are home to a variety of invertebrate prey (see elsewhere) and may provide patches of food, as structurally complex habitats have been hypothesized to contain higher number of invertebrate prey (see Strijbosch, 1988). As members of the genus *Cordylus* are considered to follow a sit-and-wait foraging strategy (Cooper, 1995; Cooper, Whiting & Van Wyk, 1997), this clumped distribution of prey may be a great resource to *C. macropholis*.

As the physical structure of *E. caput-medusae* is unique in its environment (pers. obs.), it may allow for habitat specific recognition. This may permit habitat separation or the shift of *C. macropholis* individuals to these relative scarce refugia. Potentially this may lead to crowding and competition among individual *C. macropholis* lizards. Especially during the mating season, dominant males may establish territories within and around plants, which may result in the relegation of subordinate males to lower quality habitats. Consequently, these repelled individuals may be exposed to higher predation risk, which may ultimately result in a female-biased sex ratio due to increased male mortality.

Castilla & Bauwens (1992) also showed that the range of habitats occupied by lizards may reflect the size of their home range or degree of movement. Therefore the limited use of available vegetation habitats by *C. macropholis* suggests that it restricts most of its activities to *E. caput-medusae* plants and that home ranges are probably small (see also Bauwens *et al.*, 1999). However, the degree of movement among plants seems to be high over relatively longer time periods (pers. obs.). Frequent intraspecific contact and social interactions because of crowding, may greatly determine the length of occupancy of a plant by any single individual. Furthermore, it is important to consider that although *E. caput-medusae* plants are perrenial, these microhabitats are far less permanent than those presented by rock crevices for instance. Subsequently, lizards are forced to shift to other refugia when habitat quality declines.

During the survey we recorded one lizard in *Zygophyllum meyeri*. This plant provides moderate shade and dense plant debris at the base of the stem, and was reported to be an alternative habitat to that of *E. caput-medusae* (H. Louw, pers. comm.). However, the *Z. meyeri* plant was located less than five meters away from an *E. caput-medusae* plant and it is therefore possible that the sighted lizard was only passing through a "sub-optimal" habitat.

Shelter Choice

Lizards often have latent behavioural patterns that permit them to occupy a broader range of habitats to that which they prefer (Heatwole, 1977). It is therefore important when studying habitat selection behaviour, not only to ascertain the preferred habitat type, but also the flexibility in behaviour. *Cordylus macropholis* exhibited a preference for *Euphorbia caput-medusae* plants, but also chose to use the other two shelter-options provided in this study. Lizards presumably use these plants more frequently than other habitats, as was also indicated by the field survey (see elsewhere), but may inhabit other shelters if *E. caput-medusae* becomes unavailable or if absent in the environment. *Euphorbia caput-medusae* plants may cover less than five percent of area surface in the biome and populations may be spaced far apart (Bauwens *et al.*, 1999; pers. obs.). During dispersion, lizards may therefore have to make use of alternative shelter types in the environment, such as scattered limestone rocks or vegetation that offer safe retreats. Interesting is the seemingly higher preference for rock shelters than that of plant debris, despite its relatively lower availability in the environment (pers. obs.). Furthermore, it is expected that the morphology of *C. macropholis* will enable it to better exploit plant debris, as a tubular body and shortened legs will facilitate utilization of a dense medium to an optimum (see Heatwole, 1977; Garland & Losos, 1994). This selection behaviour may possibly be explained by a phylogenetic constraint.

It is widely accepted that *C. macropholis* may have evolved from a rupicolous ancestor (Mouton, Flemming & Kanga, 1999; Frost *et al.*, 2001). Sea level events in the low lying coastal area are believed to have forced the ancestor to become terrestrial as a result of the fluctuating availability of suitable rocky habitat. *Euphorbia caput-medusae* plants would have been a suitable choice of habitat as its structure strongly resembles that of a rocky habitat in its geometric configuration, a factor identified as an important stimulus in habitat selection (see Heatwole, 1977). The variable orientation of the long tubercular branches, as in the case of stony surfaces, may facilitate postural adjustments of lizards to increase net radiation intake, whereas the branches lying laterally on the ground enhance heat gain through conduction. Furthermore, the stacked branches provide sheltered "crevices". This similarity in features between habitats, may have selected for selection behaviour to remain conserved despite the transition.

In many lizard species, adult and juvenile individuals occupy different habitats (Martín & López, 1998). These differences are ascribed to different needs of adults and juveniles in biophysical properties of the habitat (Paulissen, 1988; Law, 1991); morphological differences (Moermond, 1979) and agonistic interactions and predator avoidance (Mellado, 1980; Carrascal, Díaz & Cano, 1990 cited Martín & López, 1998). My study showed that juvenile *C. macropholis* lizards exhibited the same preference for *E. caput-medusae*, despite their smaller size that would permit them to utilize structurally different habitats to that of adults (see Moermond, 1973). This suggests that the selection behaviour manifests at an early age and underscores the possibility of phylogenetic constraints in the behaviour of *C. macropholis*. Alternatively, learning may take place at an early age as young are born within these plants (pers. obs.) and may make use of conspecifics as cues in habitat selection (see Kiester, 1979).

Diet and Food Availability

Lizards that follow a sit-and-wait foraging strategy will encounter and consume fairly active prey (e.g. ants, centipedes), whereas actively foraging lizards eat less active prey (e.g. termites, caterpillars) (Huey & Pianka, 1981). The large proportion of active prey (Formicidae and

Tenebrionidae) present in the diet of *Cordylus macropholis*, supports the hypothesis that this species follows a sit-and-wait foraging strategy. Other important groups in the diet included pentatomids, coccinnelids and melyrids.

Qualitative data on the number of prey items and prey taxa in the stomach contents of *C. macropholis* suggest that foraging did not decrease from one sampling time to another. Both these samples were, however, collected during the wet season and it is likely that reduced feeding may take place during the generally drier, summer season. Another terrestrial cordylid species, *Cordylus giganteus*, is known to exhibit seasonally reduced feeding (Van Wyk, 2000). More quantitative data are needed, however, to verify whether periodical depression in feeding also occurs in *C. macropholis*.

If the relative abundances of invertebrates in the *Euphorbia caput-medusae* plants reflect their availability to the lizards, the results indicate that the diet of *C. macropholis* and prey availability in the microhabitat is consistent. The two major groups, (Formicidae and Tenebrionidae) contributing to the diet at both sampling times, were also abundant in the plants. Although the contribution of these two groups to the diet did not change dramatically, their relative availability in the plants did. The negative correlation between electivity of the different prey families and their relative abundance in the environment indicates that lizards did not select prey in proportion to their relative abundance in the plants. It may indicate that lizards consume the minimal proportions of certain prey types or nutrients to obtain a balanced diet (see Pèrez-Mellado *et al.*, 1991). This may be confirmed by the high relative diversity of prey families in the diet of *C. macropholis*. Prey items such as Chrysomelidae and Melyridae are visiting insects that are most likely attracted to *E. caput-medusae* plants.

Data suggest that the *E. caput-medusae* habitat, to which *C. macropholis* seem to restrict itself, provide a constant source of prey. I conclude that this feature may be an important cue to a sit-and-wait forager, such as *C. macropholis*, in the selection of relatively scarce refugia as preferred habitat.

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SEX RATIO, SOCIAL STRUCTURE AND SPACING PATTERNS IN *CORDYLUS MACROPHOLIS*

Abstract

Sex ratio, social structure and male spatial patterns were studied in *Cordylus macropholis*, a terrestrial lizard that inhabits the succulent *Euphorbia caput-medusae*. Repetitive sampling of two populations revealed highly female-biased adult sex ratios that also extended to younger age-classes. Sex ratio was found to relate positively to population density, as is the case in many polygynic lizard species. However, group composition pointed to a monogamous mating structure. In individual plants, segregation among adult males, and between adult males and juvenile males was significantly ($P < 0.05$) higher within the reproductive season than outside. Adult males appear to maintain a uniform spatial distribution among plants within the reproductive season. The female-biased sex ratio observed for *C. macropholis* in *E. caput-medusae* plants may be the result of territorial behaviour. Territorial exclusion may lead to the spill over of males to habitats of lesser quality, where survival is expected to be lower.

Key words: female-biased sex ratio, density, territoriality, grouping behaviour

INTRODUCTION

The sex ratio of vertebrates usually is 1:1 at birth, apparently because natural selection favours those parents that equally invest into offspring of each sex (Fisher, 1930; see also Maynard-Smith, 1978; Charnov, 1979). A 1:1 sex ratio has been reported for many lizard populations (Turner, 1977; Fellers & Drost, 1991; Mouton, Flemming & Kanga, 1999), but sex ratio can also be variable among species (Schoener, 1983) or dynamic within the same species through time (Schoener & Schoener, 1980; Barbault, 1986). Departures from a 1:1 ratio among adult lizards are commonly ascribed to differential survival rates among the sexes (Stamps, 1983), which in turn are generally associated with population social structure (Stamps, 1983). In a polygynic species, for example, males may stand a greater predation risk than females because of increased conspicuousness during courtship behaviour and territorial defense (Stamps, 1983; Andrews & Nichols, 1990).

Among taxa with genotypic sex determination, sex ratio may deviate from 1:1 at birth. Such cases have been described for mites and insects (Hamilton, 1967; Werren, 1980), mammals (Cockburn, Scott & Dickman, 1985) and even reptiles (Madsen & Shine, 1992). This phenomenon is, however, usually restricted to small populations where dispersal is limited, so that siblings have to compete with each other either for mating opportunities or for resources (see Hamilton, 1967).

There appears to be clear dichotomy among cordylid lizards as far as sex ratios are concerned (Mouton, Flemming & Kanga, 1999). Adult sex ratios of close to 1:1 have been described for *Cordylus cataphractus*, *C. polyzonus* and *Pseudocordylus melanotus*, whereas highly female-biased ratios have been recorded for *C. niger*, *C. cordylus*, *C. giganteus* and *C. macropholis* (see Mouton *et al.*, 1999). Although territorial behaviour has been described for lizards of the genus *Cordylus* (Wirminghaus, 1990; Cordes, Mouton & Van Wyk, 1995), little information exists on the social structures within this clade and how it might relate to variation in sex ratio. Some *Cordylus* species are sexually dimorphic in size (Cordes *et al.*, 1995; Mouton, Flemming &

Nieuwoudt, 2000). As the degree of sexual dimorphism may be indicative of the degree of sexual selection (Stamps, 1983), one might expect some of these species to display a polygamous social structure. Thus far, a polygamous social system has only been suggested for the gregarious species, *Cordylus cataphractus* (Mouton *et al*., 1999).

Species of the genus *Cordylus*, which is endemic to Africa, are generally rupicolous (Mouton & Van Wyk, 1997). They all are diurnal, insectivorous sit-and-wait foragers (Cooper, 1995; Cooper, Whiting & Van Wyk, 1997). Reproduction takes place seasonally, with winter/spring ovulation, followed by gestation in late summer or autumn (Van Wyk 1989, 1991; Flemming & Van Wyk, 1992, Flemming, 1993; Van Wyk & Mouton, 1996).

I investigated sex ratio in *Cordylus macropholis*, as well as group social structure and spacing patterns of adult males. A population survey by Mouton *et al*. (2000) outside the reproductive season revealed a highly female-biased sex ratio in this terrestrial species that, as does *C. cataphractus*, form aggregations. Groups of up to nine individuals may shelter in the succulent *Euphorbia caput-medusae* plant, but no adult males were found to share a plant shelter (Mouton *et al*., 2000). If males are territorial, there should be little intrasexual overlap of home ranges, especially during the reproductive season.

I evaluated the extent and variability of the sex ratio in two *C. macropholis* populations. Subsequently, I investigated whether the composition of aggregations gives any indication of social structure. I hypothesized that if a female-biased sex ratio does exist in this species, that it may relate to male territorial behaviour. Accordingly, one would expect male segregation to be higher within the reproductive season than outside; and adult males to maintain home ranges. Subsequently, I compared the frequency of males found together in plants, between seasons and also examined variation in their spatial distribution within and outside the reproductive season.

MATERIALS AND METHODS

Study Area

The study area was located in the vicinity of Lambert's Bay (32°07'S, 18°19E) in the Western Cape, South Africa. The general area falls within the western arid zone of South Africa, which is characterized by a desert-like climate (Schulze & McGee, 1978). Low & Rebelo (1996) described the vegetation as Strandveld Succulent Karoo.

I delimited a 4.2 ha area at Site A, which was situated just north of Lambert's Bay and another area (1.7 ha) at Site B just south of the village. Site B was the same site as that used previously for studies on *Cordylus macropholis* (Bauwens, Castilla & Mouton, 1999; Mouton *et al.*, 2000). Both sites were located in two natural areas where the succulent plant, *Euphorbia caput-medusae* is abundant. The sites were approximately 200 m from the coast and separated from it by low, vegetation-covered dunes parallel to the coast.

I visited Site A during February, May, August and November of 2000, while Site B was visited during May 1999 and March 2000. During each visit, I collected lizards by hand while systematically searching all *E. caput-medusae* plants within the demarcated areas for a period of three days. Each captured lizard was returned to the plant where it was first collected.

Population density

I calculated the population density (number of lizards/ha) for each sample by dividing the number of lizards captured by the total sampling area (Site A: 4.2 ha; Site B: 1.7 ha). I considered the sampling method as an accurate measure of determining the population size within the demarcated area, as I was at all times able to remove all lizards present within an *E. caput-medusae* plant. Moreover, previous habitat surveys revealed no lizards in plants other than *E. caput-medusae* plants (see Chapter 3).

Sex ratio

I collected all *C. macropholis* individuals from *E. caput-medusae* plants at sites A and B, irrespective of size and sex. The snout-vent-length (SVL) of each lizard was taken with a digital caliper to the nearest 0.01mm. The lizards were sexed by checking for the presence or absence of hemipenes and the number of femoral glands (see Mouton *et al.*, 2000). Only the smallest individuals were difficult to sex with confidence. The minimum size at sexual maturity for both sexes was taken as 58 mm (see Mouton *et al.*, 2000). The sex ratio was calculated for adults (≥ 58 mm SVL) and juveniles (< 58 mm SVL) for each sampling period. The differences in numbers found were tested using the Chi-Square test (Zar, 1984).

Social structure and male segregation

To analyze social structure I investigated group composition at Site A. I defined groups as aggregations of lizards found in *E. caput-medusae*. Only cases in which it was possible to remove all lizards from a plant were considered for group composition analysis. The lizards were sexed, measured and returned in their original groups to the plants from which they were collected. Data from mark-recapture studies on these populations revealed a high degree of movement among *Euphorbia*-plants (unpublished data). I therefore treated aggregations sampled at different periods as independent groups. I pooled data obtained from the February and May samples and from the August and November samples to represent data outside and within the reproductive season. Differences in the type of structures observed were compared using the Z-test for proportions (Zar, 1984).

Male spatial patterns

Cordylus macropholis prefers *Euphorbia caput-medusae* plants, where they occur, as shelter to other substrates in this environment (unpublished data). Moreover, other authors suggested that this species restricts most of its daily activities to a single *E. caput-medusae* plant (Bauwens *et* *al*., 1999). For this study I therefore considered a single *E. caput-medusae* plant to constitute the home range or possibly a core area within the home range of a specific individual that inhabits such a plant.

To determine the possibility of range defense by adult males, I investigated adult male spatial patterns at Site A during February 2000 and late August 2000. I chose these periods to facilitate the comparison of spatial distribution outside and inside the reproductive season.

I delimited an area of *c*. 17 000 m^2 at Site A in which I mapped the locations of all *E. caput-medusae* plants within this area by using standard land surveying equipment.

To determine the density of adult males (> 58 mm SVL) within the area, all *Euphorbia caput-medusae* plants were systematically searched during the sampling periods. The geographical location of each plant that housed an adult male was recorded and the spatial pattern was estimated by using an index of aggregation (Krebs, 1989):

$$\mathrm{R} = \mathrm{r}_{A} / \mathrm{r}_{E} = \text{Index of aggregation}$$

where r_A is the mean distance to the nearest neighbour and r_E is the expected distance to the nearest neighbour. When $R = 1$, the spatial pattern is random, when clumping occurs R approaches zero, and in a regular pattern R approaches an upper limit around 2.15. A value of $|z| < 1.96$ was accepted as significant deviation from these R-limits.

RESULTS

Density and sex ratio

The mean (± SD) density of *Cordylus macropholis* at Site A was 38.1 ± 9.9 lizards/ha, but ranged from 25.7 lizards/ha to 47.1 lizards/ha over the sampling periods (Table 4.1). Mean (± SD) population density at Site B was 77.1 ± 0.8 lizards/ha, a significantly higher density than at Site A ($t = -7.7623$, $df = 3$, $P = 0.002$).

Table 4.1 Densities of *Cordylus macropholis* (number/ha).

Site and sample	Total
Site A	
February 2000	34.5
May 2000	47.1
August 2000	45.2
November 2000	25.7
Site B	
May 1999	77.6
March 2000	76.5

Figure 4.1 shows the size distribution of lizards captured at the two sites during this study. Only lizards over 45 mm SVL were plotted by sex, as smaller individuals could not be sexed with confidence. It is evident that the sample at Site A contained more females than males in all the size-classes (Figure 4.1a). The sex ratio of *C. macropholis*, considering all lizards sampled at this site, was significantly ($P < 0.001$) female-biased for adults (female:male = 1.67, $\chi^2 = 11.3$, $n = 179$), but not significantly ($P > 0.05$) different from 1:1 for juveniles (female:male = 1.37, $\chi^2 = 1.7$, $n = 71$). At Site B, females were more common than males in five of the six size-classes (Figure 4.1b). The population sex ratio of all adult lizards deviated significantly ($P < 0.001$) from 1:1 (female:male = 2.32, $\chi^2 = 16.3$, $n = 103$). The sex ratio for juveniles were also significantly female-biased (female:male = 1.57, $\chi^2 = 3.5$, $n = 77$). Figure 4.1 (b) shows that although there was no significant ($P > 0.05$) deviation from 1:1 in the smallest size-class (female:male = 0.67, $\chi^2 = 6.0$, $n = 15$), a significant ($P < 0.05$) female-bias apparently sets in at size-classes over 50 mm SVL (female:male = 1.93, $\chi^2 = 4.5$, $n = 44$).

Table 4.2 lists the following sex ratios for the different sampling periods: adult females/adult males, juvenile females/juvenile males, and all females/all males. The sex ratios (females:males) of all females to all males, and of adult females to adult males were at all times significantly female-biased. Among adults at Site A, the sex ratio ranged from 1.63 outside of the reproductive season to 2.75 within the reproductive season. Variation at Site B was slightly less (2.2 to 2.36), possibly due to fewer samples. The sex ratio (females:males) for juveniles was significantly female-biased during May 2000 and August 2000, whilst during the other periods the ratio did not differ from 1:1.

Figure 4.2 shows the relation between sex ratio and density for all individuals from Site A and Site B. All three sex ratios calculated for individuals from both Sites A and B, correlated positively with total population density (Table 4.3). Correlation coefficients were generally low, but somewhat higher for juveniles than for either all individuals or adult individuals.

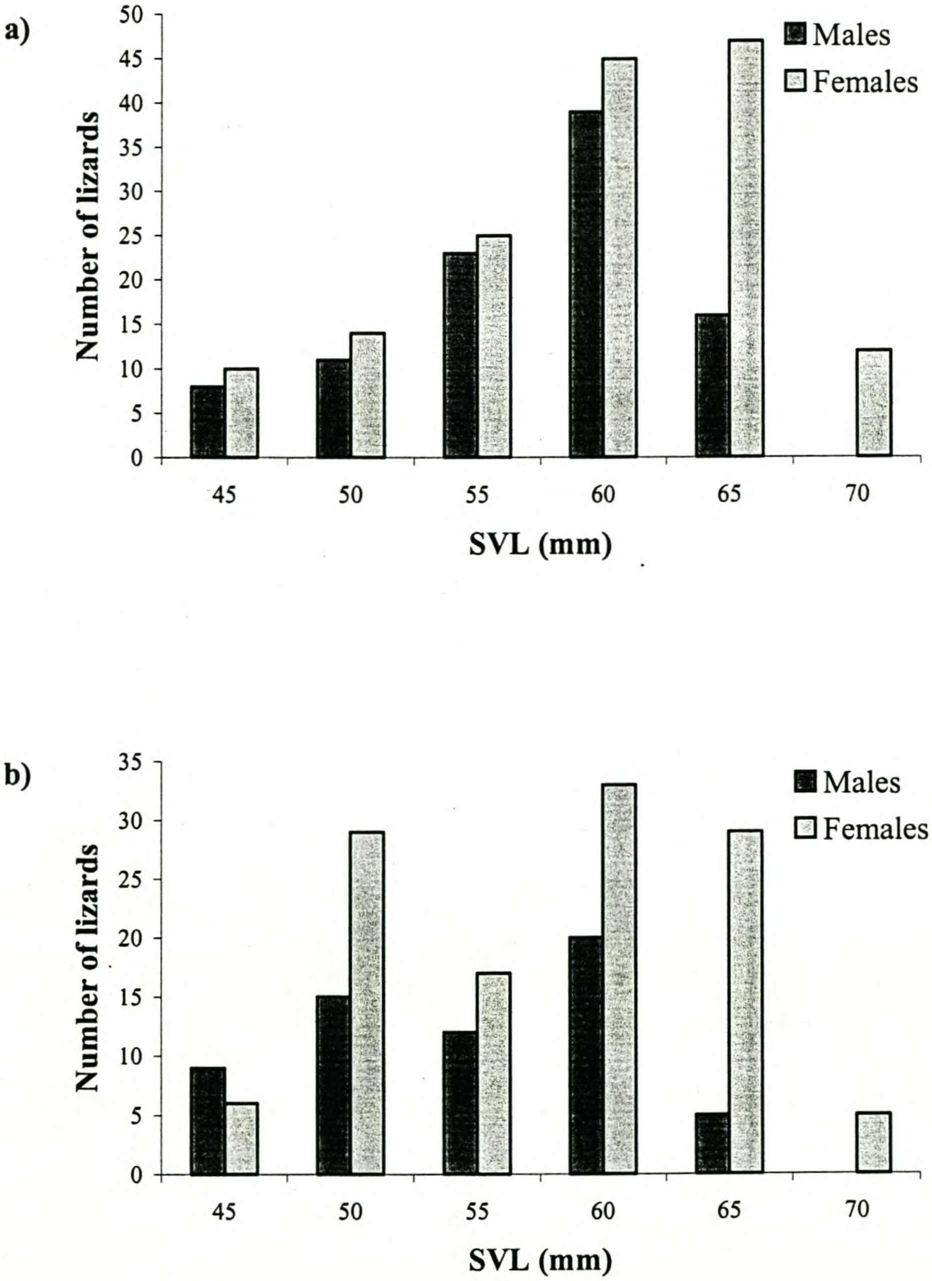

Figure 4.1 Size distribution of *Cordylus macropholis* from populations at Site A (a) and Site B (b). Snout-vent-length (SVL) at initial capture of all lizards caught from 1999 through 2000. Each size-class represents a range of 5 mm SVL. Lizards with SVL < 45 mm were not included in this analysis.

Table 4.2 Sex ratios in *Cordylus macropholis*.

	all	adult	juvenile
	all	adult	juvenile
Site A			
February 2000	1.59*	1.63*	1.5
May 2000	1.79*	1.71*	1.92*
August 2000	1.84*	1.82*	1.86*
November 2000	2.18*	2.75*	0.8
Site B			
May 1999	1.84*	2.2*	1.52
March 2000	2.02*	2.36*	1.67

*$P < 0.05$

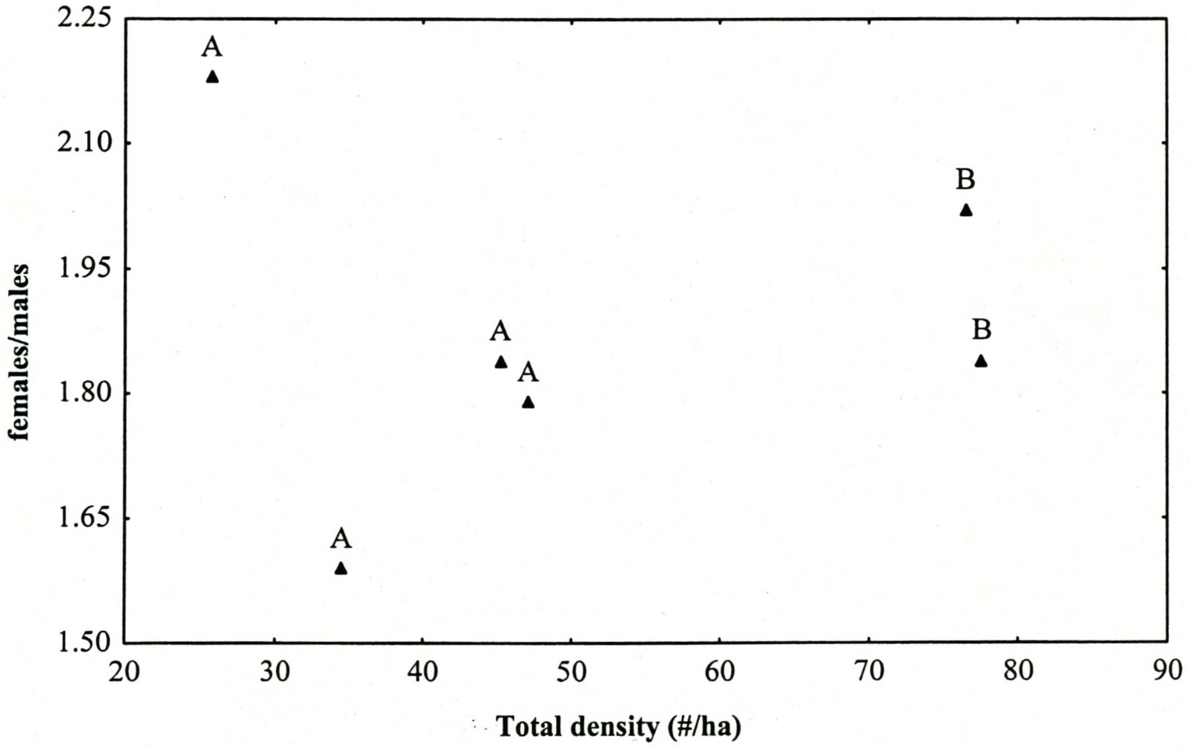

Figure 4.2 Relation between sex ratio and density for *Cordylus macropholis* from the two sites (A and B).

Table 4.3 Pearson correlation coefficients between sex ratio and total density.

	all all			adult adult			juvenile juvenile		
	N	*r*	*P*	*N*	*r*	*P*	*N*	*r*	*P*
All	6	0.013	NS	6	0.084	NS	6	0.512	NS
Site A	4	-0.514	NS	4	-0.760	NS	4	0.911	NS

Social structure and male segregation

Analysis of adult group social structure was based on 127 observations where two or more adult individuals shared an *Euphorbia caput-medusae* plant. A structure comprised of a single male and female with a varying number of juveniles (0-9 individuals) predominated. Fifty-five percent ($N = 35$) of all adult groups ($N = 64$) outside of the reproductive season displayed this structure. This number increased to 65 % ($N = 41$) of all adult groups ($N = 63$) within the reproductive season. This increase was, however, not significant (Z-test, $P > 0.05$). Cases where single adult males shared a plant with more than one female were less frequent during both the reproductive (22 %) and non-reproductive season (23 %).

Data on the spatial segregation among adult males were based on 127 observations for adult aggregations. Cases where two or more adult males shared a plant were infrequent. Of the 64 adult aggregations observed outside of the reproductive season, only 12.5 % ($N = 8$) comprised of such adult male-male combinations. This number decreased significantly to 3 % ($N = 2$) of all adult aggregations ($N = 63$) counted within the reproductive season ($P < 0.05$).

Outside the reproductive season, 28 % ($N = 23$) of adult/juvenile groups ($N = 82$) were comprised of single adult males that shared a plant with one or more juvenile males. Some adult males shared the same plant shelter with juvenile males within the reproductive season ($N = 12$). This was, however, a significant decrease from the number, of these types of combinations, observed outside the reproductive season ($P < 0.05$).

Male spatial patterns

Data on the spacing of males were obtained from the distribution of 18 adult males among *Euphorbia caput-medusae* plants within the area that I had demarcated at Site A. Fifty-eight *E. caput-medusae* plants were recorded and mapped within the demarcated area. These plants were randomly spaced ($R = 0.91$, $|z| = 1.35$) and I therefore considered it not to be a confounding or limiting factor in the observed spacing of male lizards. Furthermore, either females or juveniles or both also occupied all of these plants, which indicated its potential to function as shelter.

The spacing pattern of the adult males among these plants outside the reproductive season was random (R = 0.91, $|z|$ = 0.66), with nearest neighbouring distances to other adult males that averaged 14.1 m. During the mating season adult males inhabited *E. caput-medusae* plants in such a pattern that spaced them on average 16.0 m from their nearest adult male neighbour. The distribution pattern of the adult males during this period showed a slight tendency toward a uniform pattern away from randomness, although the deviation was not significant (R = 1.04, $|z|$ = 0.33).

DISCUSSION

Underscoring data by Mouton *et al.* (2000), my results suggest that the female-biased population sex ratio recorded for *Cordylus macropholis* is not due to sampling error. Factors such as active predation, large home range size and divergent activity patterns among the sexes often complicate the estimation of sex ratio in populations of lizards (Stanner & Mendelssohn, 1987; Van Sluys, 2000). However, despite some variation, successive sampling in *C. macropholis* revealed a female-bias, which suggests that estimates were not confounded by seasonal variation in activity patterns of the sexes. Moreover, I was able to sample all lizards from *Euphorbia caput-medusae* plants, therefore the calculated ratio was not based on estimates, but on absolute numbers.

The 1:1 ratio observed in the smallest size-classes suggests that there are no between-sex differences at birth. Evidently, the female-biased ratio observed is the result of events that influence the persistence of males within the population. Population social structure commonly causes sexual differences in survival or persistence rates. In a polygynic species, for instance, male survival is usually lower than that of females, because of increased predation risk due to territorial and courtship behaviour (Stamp, 1983). For some polygynic bird and lizard populations, males are seemingly regulated by territorial behaviour whereas females are regulated by habitat features to such an extent that the population sex ratio is often correlated with habitat quality (see Schoener & Schoener, 1980). Better quality habitats usually house denser populations with a higher number of females (Schoener & Schoener, 1980). This seems to be the case in *C. macropholis*, where a more skewed female-biased sex ratio was positively related to a higher density at Site B. Accordingly, the female-biased ratio recorded for *C. macropholis* may be correlated with the quality of habitat at sampling sites. Sampling from areas where *E. caput-medusae* plants are less abundant or absent may reveal sex ratios closer to 1:1. *Euphorbia caput-medusae* plants are, however, considered better quality microhabitats to other plants in the environment (Bauwens *et al*., 1999). It offers numerous hiding places among its tuberculate stems (Mouton *et al*., 2000) and also a clumped supply of invertebrate prey that also utilizes the plant as shelter (unpublished data). Such features may attract both males and females, but territorial behaviour may prevent males from clumping in these plants and may lead to a "spill-over" to other habitats of lesser quality. The few observations of adult male-male combinations within *E. caput-medusae* plants, and especially the high segregation inside the reproductive season, seem to support this.

Territorial behaviour is expected to be more intense during the reproductive season as the competition for mates increase. Thus, the even more skewed female-biased ratio, observed at Site A during the reproductive season, possibly reflects stronger competition among males at this time. Larger males may exclude less dominant males from *E. caput-medusae* plants. Shelter and foraging opportunities may be much lower outside of *E. caput-medusae* plants, and may give rise to lower survival rates in these expelled males. This may ultimately result in the loss of males in the adult size-classes as observed for the sampled population.

The existence of territorial behaviour in *C. macropholis* is also suggested by adult male spatial patterns. The presence of territories is generally indicated by a relatively uniform distribution of home ranges in space (Davies, 1978), as is the case in *C. macropholis* males during the reproductive period. Furthermore, adult males have been observed to act aggressively towards one another during this period (see Chapter 6).

Aggressive behaviour, however, may not occur amongst adult lizards only. Adult males in *Sceloporus jarrovi* display aggressively toward juveniles, despite their small size and presumably reduced competitive status (Ruby & Baird, 1993). Possible evidence for similar agonistic interactions among juvenile and adult males in *C. macropholis*, comes from data on increased segregation between these size-classes outside and within the reproductive season. Furthermore, my data on the size-class distribution for the population at Site B, show a female biased ratio for size-classes as young as 45-50 mm SVL. This is similar to findings by Mouton *et al.* (2000) and suggests that juvenile males may also be excluded from quality habitat territories. The reason for this is unclear, but may relate to the reduction of competition in dense populations where visibility is low. Adult males may follow a strategy to expel all other males from their territories, irrespective of their competitive status at that stage, as they risk not being able to exert dominance over these intruders at a later stage. Moreover, visual constraints may hinder residents in encountering intruders at a later stage.

If mortality in juvenile males is indeed due to territorial defence by adult males, the latter should, however, be able to discriminate between juvenile males and females, despite sexual immaturity at this age. The answer to this may lie in the presence of generation glands in neonates of *C. macropholis*. Although the function of generation glands is still unclear, they are thought to function in association with the femoral glands in territorial marking (Cooper & Van Wyk, 1996). In cordylid species examined to date, these glands usually begin to differentiate with the onset of spermatogenic activity, but in *C. macropholis* these gland are already active at birth (Mouton, Flemming & Searby, 1998). Generation glands of neonates are histologically similar to that of adults, but instead of multiple mature glandular generations, possess only two. However, juvenile individuals, sized 49 mm SVL, were shown to possess multiple mature glandular generations within the same order as those of adult individuals. More data on the differentiation of these generation glands are needed, however, to confirm if the onset of mature glandular generations are concurrent with the onset of higher mortality in juvenile males.

Noteworthy is the fact that the only other two known cordylid species that also display active generation glands at neonatal age, namely *Cordylus tasmani* and *Cordylus tropidosternum*, are also terrestrial (Mouton *et al.*, 1998). More data on territorial behaviour and sexual discrimination for these species are, however, needed to determine in what way the presence of active generation glands in neonates is related to their terrestrial lifestyle.

The composition of groups within *E. caput-medusae* plants, both within and outside of the reproductive season indicate that cases of polygyny are probably common (23% of adult groups). Despite the potential of the *E. caput-medusae* habitat to attract multiple mates, the poor visibility within the habitat probably places constraints on the economic defensibility of more than one female. Accordingly, I observed both outside (55 %) and within the reproductive season (65 %), more cases where groups consisted of an adult pair with a varying number of juveniles. This points to a monogamous mating structure, as has been observed for some other *Cordylus* species (see Burrage, 1974; Van Wyk, 1992).

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AGGREGATION BEHAVIOUR AND MOVEMENT PATTERNS IN *CORDYLUS MACROPHOLIS*

Abstract

Aggregation behaviour and movement were studied in *Cordylus macropholis*. The size of aggregations within *Euphorbia caput-medusae* plants ranged from one to 14 individuals. Grouping was a year-round phenomenon and groups were generally larger during autumn/winter than during spring/summer. Groups exhibited a low degree of long-term social structure, but most groups comprised an 1:1 adult sex ratio (male:female). Site fidelity was low, with females showing significantly ($P < 0.05$) higher site fidelity than males. Movement of individuals in and out of the population was high. There was, however, no significant ($P > 0.05$) difference between the proportion of males and females that moved in or out of the population, either outside or within the reproductive season. Females covered slightly greater distances than males outside of the reproductive season, whereas males covered slightly greater distances than females within the reproductive season. The results suggest that aggregation behaviour and high degree of movement in *C. macropholis* are the result of mutual competition for a limited plant resource. The results do not confirm differential movement patterns between the sexes.

Key words: grouping behaviour, social structure, site fidelity

INTRODUCTION

The formation of aggregations is common in squamates and may occur for a number of reasons (Graves & Duvall, 1995). Individuals may concentrate in a relatively small area to lay eggs (Lynch, 1966; Palmer & Braswell, 1976), nest (Rand, 1968, Burger, 1993), or sleep (Boersma, 1982). Many lizard species form winter aggregations that are considered to have a thermoregulatory function during times of lesser activity (Vitt, 1974; Boykin & Zucker, 1993). Year-round grouping behaviour, however, is less common among lizards and has been reported only for a few species (Johnston, Lanham & Bull, 1997; Lemos-Espinal *et al*., 1997).

With the exception of the genus *Platysaurus*, most members of the family Cordylidae are solitary forms (Mouton, Flemming & Kanga, 1999). However, one species within the genus *Cordylus* has been described as gregarious, namely *Cordylus cataphractus* (Mouton *et al*., 1999). Grouping behaviour in this species seems to be a year-round phenomenon and up to 30 individuals may share a rock crevice. Most groups are comprised of an adult pair or one adult male, with a varying number of females and juveniles, indicating that grouping in this species probably has a social function. Mouton *et al*. (1999) suggested that a shortage of suitable rocky habitat might have been a proximate reason for grouping in this species. The western coastal region of southern Africa, to which this species is endemic (Branch, 1998), was subjected to sea level transgressions and regressions (Baxter & Meadows, 1999). This may have resulted in a fluctuating availability of suitable habitat and may have forced individuals to share available rock crevices, until permanent grouping behaviour was eventually established in this species (Mouton, Flemming & Kanga, 1999).

In the light of these sea level events, one might expect other closely-related species that share the same geographical area, to show similar aggregation behaviour (see Vrba, 1985). This seems to be the case in *Cordylus macropholis*, a relatively small-sized lizard with adult size ranging from 60-77 mm snout-vent length (Branch, 1998). It is the only terrestrial species, in the predominantly rupicolous family Cordylidae, that is endemic to the western half of South Africa

(Mouton, Flemming & Nieuwoudt, 2000), indicating evolution from a rupicolous ancestor (see Frost *et al.*, 2001). Bauwens, Castilla & Mouton (1999) termed this species an extreme microhabitat specialist that restricts most of its activities to the succulent plant, *Euphorbia caput-medusae*. In a survey conducted during winter, Mouton *et al.* (2000) found aggregations of up to nine individuals of *C. macropholis* within individual plants of this species. No information exists on the stability of these aggregations or on movements of individuals among plants. Despite reports of low above-ground activity by Bauwens *et al.* (1999), a highly female-biased ratio reported for *C. macropholis* (Mouton *et al.*, 2000) suggests extensive movement among plants. Skewed sex ratios are often associated with divergent activity patterns between the sexes (Stamps, 1983). For example, males actively seek females during the reproductive season. This increases the risk to predation and may result in differential mortality of males (Stamps, 1983).

In order to test a hypothesis on the functional significance of grouping behaviour in *C. macropholis*, I report on the stability and nature of aggregations. Additionally, I test the prediction that the female-biased ratio in *C. macropholis* is the result of differential activity patterns between the sexes. The study specifically addressed the following questions: (1) Is aggregation, like in the case of *C. cataphractus*, a year-round phenomenon in *C. macropholis*? (2) Are aggregations relatively stable and do they have a social significance? (3) Do males move more than females, either among aggregations, or into and out of a marked population? (4) Do males cover greater distances than females?

MATERIALS AND METHODS

Study area

Fieldwork was carried out near Lambert's Bay (32°07'S, 18°19'E) in the Western Cape, South Africa. The general area is included in the Namaqualand Coastal Belt, a subdivision of the Succulent Karoo (Veld Type no. 31a; Acocks, 1988), that includes vegetation of low altitude, hot arid areas. Rainfall ranges from 50-200 mm per annum, but aridity is reduced by sea mists.

The area bears vegetation of predominantly mesembs, ranging from stemless dwarfs to 2.5 m high shrubs. The most common shrubs found in the area are *Galenia africana* and *Zygophyllum morgsana*, whilst the perrenial grass *Cladoraphis cyperoides* is also abundant. The succulent plant, *Euphorbia caput-medusae*, is less common and cover *ca.* 5 % of the area (see Bauwens *et al.*, 1999). This plant has cylindrical succulent branches (2-6 cm diameter), covered with tubercles, that radiate from a low, central stem. Branches range from 10-20 cm in young plants, but can attain lengths of up to *ca.* 150 cm in old plants. In the younger plants branches remain upright, but in older plants branches lie on the ground and on top of each other in irregular piles. *Cordylus macropholis* shelters in spaces between layers of branches and between the central stem and the branches (Figure 5.1).

I delimited a 4.2 ha area (Site 1), just north of Lambert's Bay and another area (1.7 ha), Site 2, just south of the village where I carried out a mark-recapture study. I visited Site 1 during February, May, August and November 2000, and Site 2 during May 1999 and March 2000. During each visit, I collected lizards by hand while systematically searching all *E. caput-medusae* plants within the demarcated areas for a period of three days. Lizards were marked individually by toe-clipping and released to their original location, noting sex and snout-vent-length (to nearest 0.1 mm).

Toe-clipping was considered the most effective method for long-term identification of animals as *C. macropholis* is too small to allow attachment of radio-transmitters, and because the skin is shed, paint or dye would be ineffective. Recapture results indicate that the long-term survival of the lizards was not affected. In total 594 lizards were marked and 417 were recaptured.

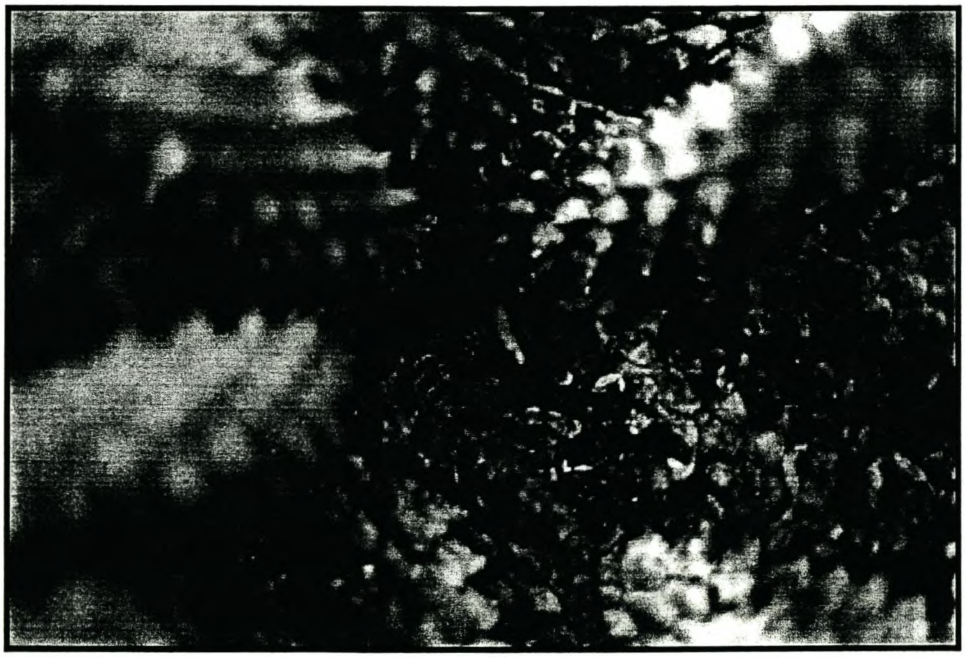


Figure 5.1 Photograph of *C. macropholis* sheltering among the branches of an *Euphorbia caput-medusae* plant.

Group size and composition

Groups were defined as aggregations of lizards found in individual *E. caput-medusae* plants. I systematically searched all *E. caput-medusae* plants at Site 1 during each visit to determine the size of aggregations. The composition of aggregations was noted by determining the sex, snout-vent-length and identity of each individual. I only considered cases for group analysis where it was possible to remove all lizards successfully from a plant. After the necessary data were recorded, I returned all lizards as a group to the plant they were collected from.

Movement

The location of each *E. caput-medusae* plant within the delimited study plots was mapped by use of standard land surveying equipment. This allowed the investigation of movements of marked lizards during the study periods.

During each visit, I systematically searched all mapped *Euphorbia*-plants within the delimited areas for lizards, after which the lizards' precise positions, in relation to the plants could be mapped.

For analysis of movement, lizards at Site 2 were marked during May 1999 and recaptured ten months later during March 2000. This period included the summer mating season. Lizards at Site 1 were marked and recaptured over three, shorter three-month periods. These were: (1) February-April, which was inclusive of the birth and neonatal period for juveniles; (2) May-July, inclusive of the winter period of expected lesser activity and; (3) August-November, inclusive of the mating season.

Data analysis

All data analyses were conducted using Statistica for Windows (Statsoft, Inc. 2000). A significance level of $\propto = 0.05$ was used for all statistical tests. Data were tested for normality and homogeneity of variance using Kolmogorov-Smirnov and Levene's tests respectively (Sokal

& Rolf, 1981). When data were not normally distributed, appropriate non-parametric tests were used.

RESULTS

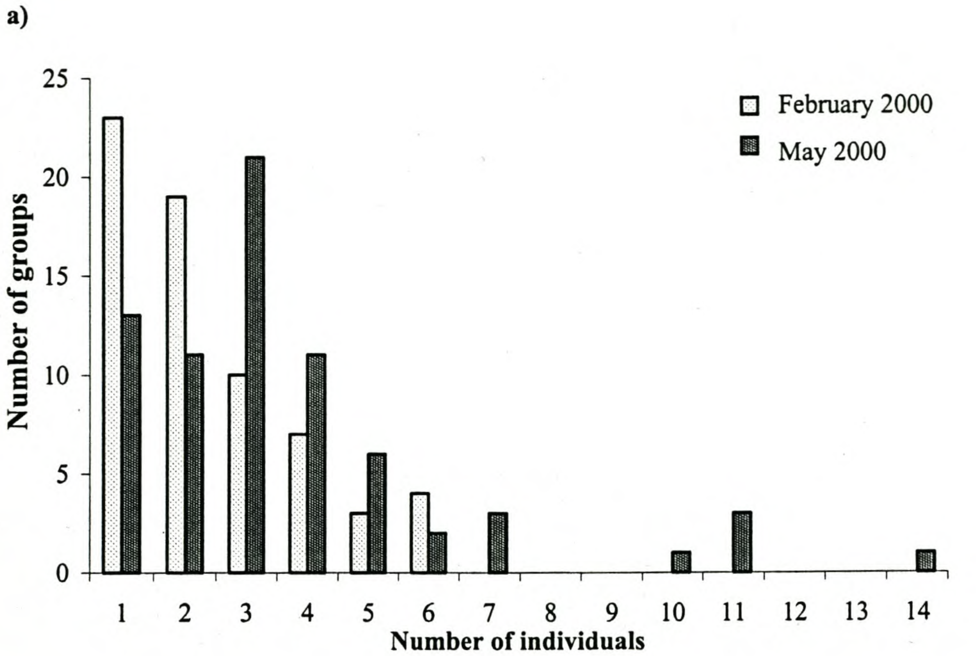
Group size and composition

In 322 groups observed throughout the four sample periods at Site 1, numbers ranged from one to 14 (Figure 5.2). The mean group size for the February, May, August and November samples are shown in Figure 5.3 and differed significantly (Kruskal Wallis, $H_{(3,320)} = 52.6$, $P < 0.05$). Mean group size during November was significantly smaller than that recorded for February, May and August. Mean group size for May was significantly larger than for the other samples ($F_{(3,316)} = 18.0$, both $P < 0.05$).

Of the individuals occurring singly ($N = 114$), 55 % were adult females, 14 % adult males and 31 % juveniles. Where groups comprised of two or more individuals, a mixed structure of adults and juveniles predominated, whereas only a few aggregations involved either juveniles only, or adults only (Table 5.1).

Aggregations where adults were observed together, were recorded for February, May, August and November, but were more frequent during the November sample (Table 5.1). The ratio of males to females within these adult aggregations, ranged from 2 males: 1 female to 1 male: 4 females (Figure 5.4). The ratio did not differ significantly among the respective sampling periods, with the mode for all periods being 1 adult male: 1 adult female per group (Table 5.2)(Kruskal Wallis, $H_{(3,110)} = 2.4$, $P = 0.49$).

Only six cases were observed, predominantly during the March-August period, where the composition of aggregations in plants had remained intact between sampling periods (Table 5.3). Such groups were relatively small (range: 2-4 individuals) with structures that comprised of adult/juvenile combinations. Only one group's structure (one adult male and one juvenile female) had stayed intact for longer than three months and up to a period of nine months.



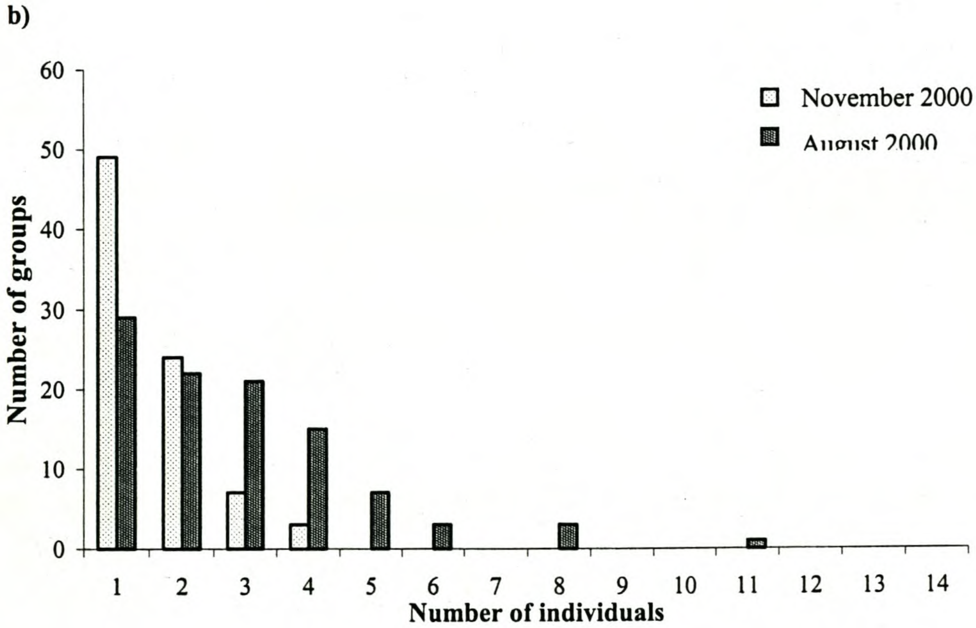


Figure 5.2 The number of individuals in aggregations of *Cordylus macropholis* observed during the respective sampling periods at Site 1.

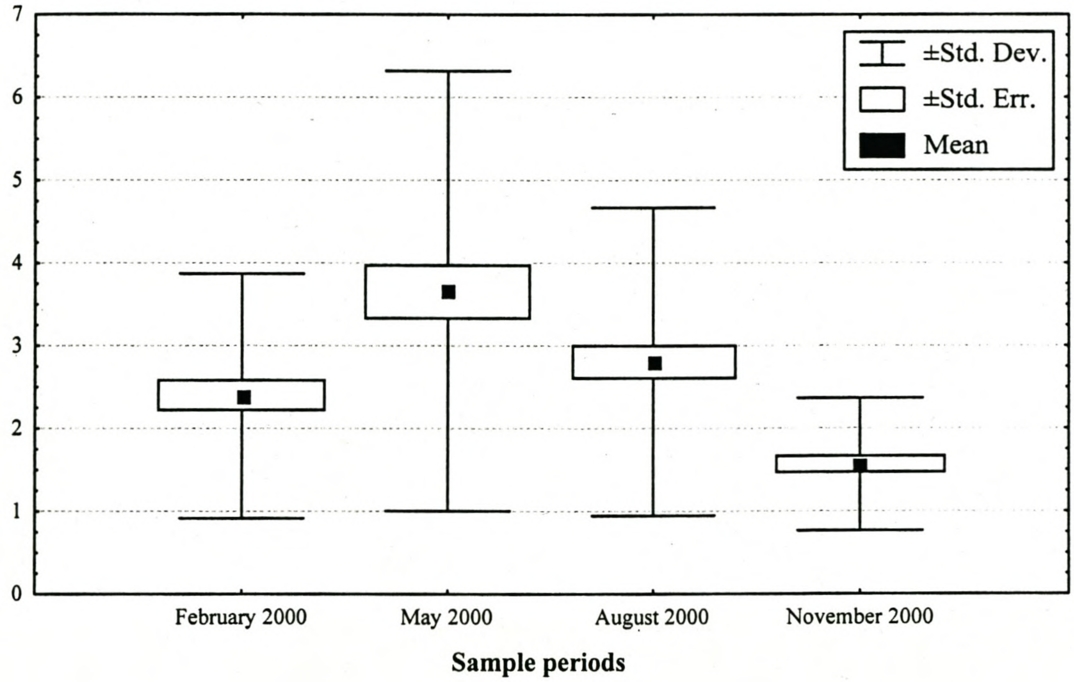


Figure 5.3 Mean group size of *Cordylus macropholis* found in *Euphorbia caput-medusae* plants at Site 1 for the respective samples.

Table 5.1 Composition of aggregations (> 2 individuals) of *Cordylus macropholis* found sheltering in *Euphorbia caput-medusae* plants ($N = 208$) at Site 1 during February, May, August and November 2000.

Composition	February	May	August	November
Adults only	10 (23.3 %)	2 (3.4 %)	7 (9.7 %)	10 (29.4 %)
Adult/juvenile combinations	32 (74.4 %)	52 (88.1 %)	55 (76.4 %)	21 (61.8 %)
Juveniles only	1 (2.3 %)	5 (8.5 %)	10 (13.9 %)	3 (8.8 %)
Total number of aggregations	43	59	72	34

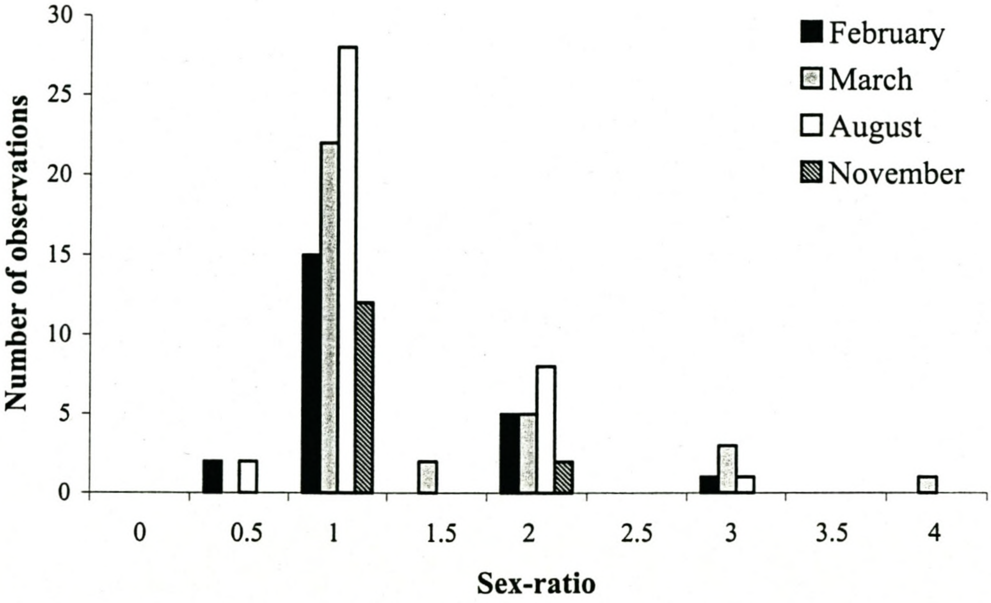


Figure 5.4 The ratio of adult females to adult males in aggregations ($N = 108$).

Table 5.2 The mean ratio of adult males:females in aggregations of *Cordylus macropholis* sampled at Site 1 during February, May, August and November 2000.

Sample period	Mean (SE)	*N*
February 2000	1.3 (0.6)	23
May 2000	1.5 (0.8)	32
August 2000	1.2 (0.5)	39
November 2000	1.1 (0.4)	14

Table 5.3 Group size and composition for *C. macropholis* groups ($N = 6$) at Site 1 that stayed intact between sampling times.

Group size	Composition	Period of time (months)
2	1AF+1J	3 (August-November)
	1AM+1J	9 (February-November)
3	1AF+2J	3 (March-August)
	1AM+1AF+1J	3 (March-August)
	3J	3 (March-August)
4	1AM+2AF+1J	3 (March-August)

Movement

I used the number of individuals that moved in and out of the marked populations at Site 1 and Site 2 as a relative index of movement. Of the 157 lizards marked during February at Site 1, 62 (39.5 %) had left and 177 (112.7 %) new individuals had entered the population when sampled three months later (May). Of the 272 marked lizards present in the population after the May-recapture, 100 (36.8 %) individuals were lost from the population when sampled three months later (August) prior to the mating season. New arrivals to the population totaled 89 (32.7 %).

During the final recapture (November), after the mating season, the marked population (N = 261) during August had decreased by 178 (62.2 %) individuals and newcomers equaled 49 (38.3 %) individuals. Females, males and neonates were lost from the population in proportions significantly greater than that gained (Z-test, $P < 0.05$ in all cases).

The marked *C. macropholis* population at Site 2 lost 104 (60.8 %) individuals over the ten month period that spanned the breeding season, whereas new arrivals in the population totaled 84 individuals (55.6 %). The difference, however, in the numbers gained and lost in the population did not differ significantly (Z-test, $P = 0.35$).

Figure 5.5 shows the proportional contribution of females, males and neonates to the numbers lost and gained from the two populations. At Site 1, the May survey revealed that a slightly greater proportion of males than females were lost from the population and a slightly smaller proportion of males than females entered the population, but these differences were not significant (Z-test, both $P > 0.05$). Neonates contributed 39 % of the total gain during this period. The number of females, males and neonates gained and lost during the May-August period did not differ significantly and males and females entered and left the population in equal proportions (Z-test, $P > 0.05$ in all cases).

During the mating season (August-November) proportionally more males than females left and entered the population, but these differences were not significant (Z-test, $P > 0.05$).

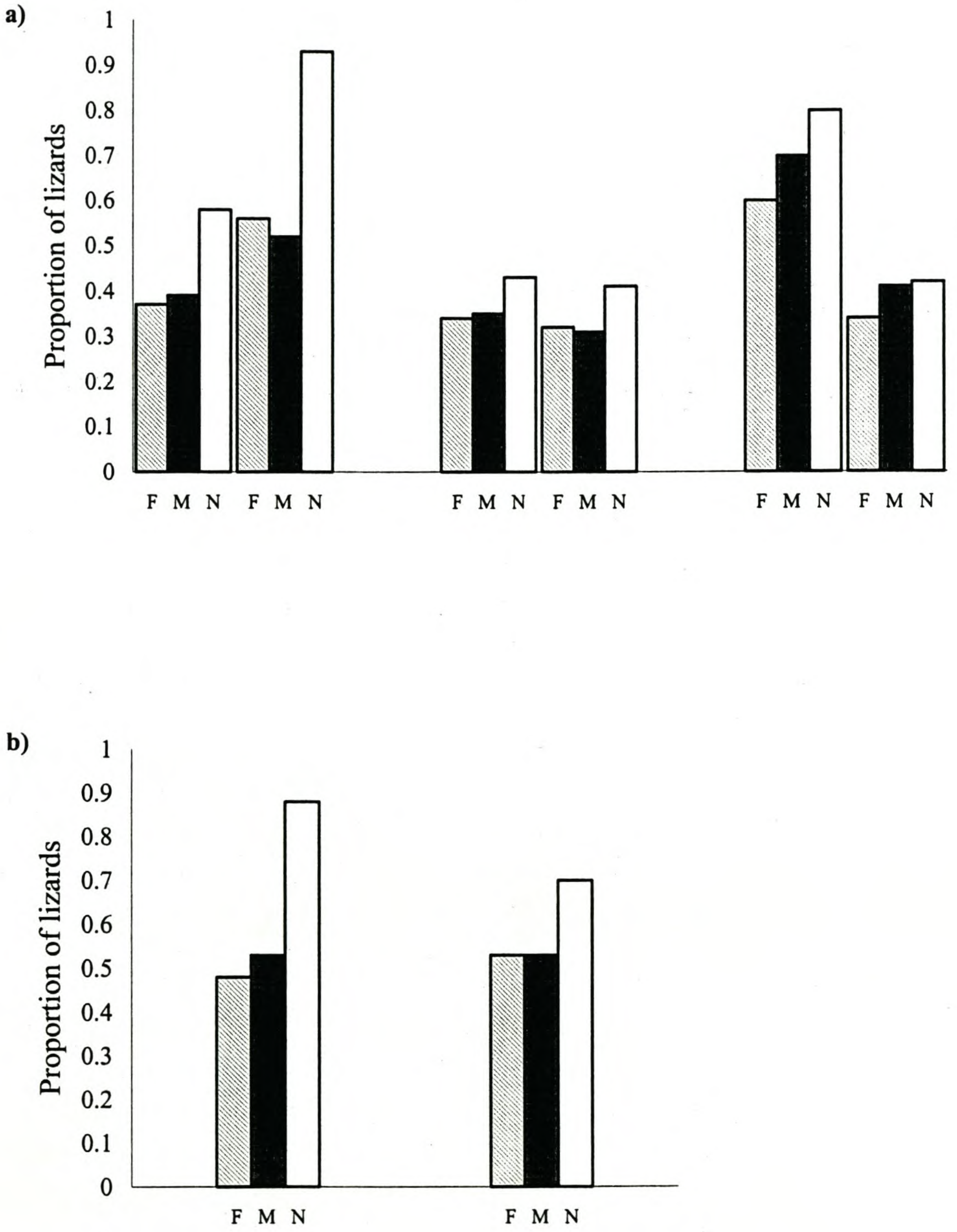


Figure 5.5 The number of individuals lost and gained from the populations of *Cordylus macropholis* at Site1 (a) and Site 2 (b). Numbers are given in proportion to the original numbers present in each category. F = females, M = males and N = neonates

Neonates left the population in significantly greater proportions compared to that of females (Z-test, $P < 0.05$), but not compared to that of males (Z-test, $P > 0.05$).

The proportion of males that was lost from the population at Site 2 was slightly higher than the proportion of females, but not significantly so (Z-test, $P = 0.60$). Males and females moved into the population in equal proportions (Z-test, $P = 1.0$). Neonates also moved into the population in similar proportions as females and males, but left the population in significantly greater proportions (Z-test, $P < 0.005$).

Straight-line distance moved

Fifty-six of the marked lizards ($N = 423$) at Site 1 were recaptured at least once in *Euphorbia caput-medusae* plants different from their original locations. Of these, 46 lizards (82 %) had traveled further than the average distance (6.3 m) to the nearest neighbouring *Euphorbia caput-medusae* plant.

Of the marked lizards ($N = 171$) at Site 2, only 22 (10 females, 11 males, 1 neonate) were recaptured in other *Euphorbia*-plants within the demarcated area after 10 months. Sixteen (73 %) of these individuals were found further away (> 5.1 m) than the average nearest neighbouring *Euphorbia*-plant.

The average distances traveled by males and females at both sites are shown in Table 5.4. Females covered greater distances than males during the long ten-month period and the two shorter periods (February-August) outside of the mating season. The average distance covered by males during the mating season, however, exceeded that of females. These differences between the sexes in the average distances moved by individuals at both sites were, however, not significant (Site 1: Mann-Whitney U-test, $Z = -1.11$, $P = 0.26$; Site 2: Mann-Whitney U-test, $Z = 0.52$, $P = 0.60$). Both males and females covered on average, greater distances during the August-November mating period (Table 5.4). However, no significant difference existed in the distances covered by either males or females during the respective three three-month periods

Table 5.4 The mean (and SE) of straight line distances (in meters) moved by male and female *Cordylus macropholis* at Site 1 for each mark-recapture period.

Sample	Males	n	Females	n
May 1999-March 2000	23.2 (28.0)	11	31.7 (32.9)	11
February 1900-May 2000	10.3 (0.76)	3	37.3 (44.7)	9
May 2000-August 2000	25.6 (32.6)	7	44.8 (39.9)	15
August 2000-November 2000	86.6 (74.5)	7	70.7 (81.9)	10

(males: Kruskal-Wallis, $H = 4.23$, $P = 0.12$, females: Kruskal-Wallis, $H = 1.83$, $P = 0.40$).

Long-term site fidelity

Lizards at Site 1 were more site-specific outside of the mating season than immediately after the mating season. Only seven (4.5 %) of the marked lizards (N = 157) at Site 1 were recaptured nine months later in the same plants that they were first captured. This number increased to 70 (44.6 %, 45 females, 21 males, 4 neonates) when recaptured after the first six months after being marked and prior to the August to November mating period. Thus, there was a significant decrease in the number of marked lizards that were found in the same plant prior to and after the mating season (Z-test, $P < 0.005$). The proportion of females to males that was recaptured in their original plants, prior to the mating season, was in accordance with the sex ratio of the population at the time when first marked ($\chi^2 = 1.2$, $df = 1$, $P = 0.266$).

Of the lizards marked ($N = 171$) at Site 2 and recaptured ($N = 67$) ten months later, only 45 (26.3 %, 31 females and 9 males, 5 neonates) were recaptured in the plants in which they were first captured. With respect to a null hypothesis of numbers being in accordance with the sex ratio present in the population when first marked, females were significantly more site specific than males (Chi-square: $\chi^2 = 3.7$, $df = 1$, $P < 0.05$).

DISCUSSION

The relatively low percentage of individuals that occurred singly (~ 36 %) in *Euphorbia caput-medusae* plants seems to suggest some degree of grouping behaviour in *Cordylus macropholis*. However, this figure is more than twice as much compared to that of singular individuals in *C. cataphractus* (15 %) and confirms reports by Mouton *et al.* (1999) that grouping is less well manifested in *C. macropholis* than in *Cordylus cataphractus*. Supporting this, is the fact that although individual *C. macropholis* aggregate within *E. caput-medusae* plants, they seldom occur within close physical proximity to each other. This, by definition, separates the grouping phenomenon observed in *C. macropholis* from that observed in *Cordylus cataphractus* (Mouton *et al.*, 1999) and a number of other species (Elfström & Zucker, 1999). In these species contact between individuals is maintained in either the head or tail regions, whereas this is not the case in *C. macropholis*.

However, similar to grouping behaviour in *C. cataphractus*, *C. macropholis* aggregates year-round which suggests that grouping is not a seasonal phenomenon as in the case of many other lizards species (e.g. Worthington & Sabath, 1966; Burns, 1970; Vitt, 1974; Ruby, 1977). The smaller aggregations observed for *C. macropholis* during November, may relate to higher activity levels among lizards during the mating season or the extension of their activity to other plants during the hotter summer months. The larger aggregations observed during May is consistent with the birth of neonates. By grouping in *E. caput-medusae* plants, the survival of juveniles may be increased and they need not to disperse until they are older.

Other advantages of grouping may include mate acquisition, increased vigilance for predator protection and resource or habitat assessment (see Stamps, 1988). For all of these reasons, animals that occur in close proximity may experience enhanced fitness, thus resulting in selection for social interaction (Allee, 1938). However, aggregations may also arise not as the result of social interaction, but because of mutual attraction to features in the environment of limited availability (Graves & Duvall, 1995). For instance, *Thamnophis* spp. may concentrate in areas of high prey availability or aggregate in areas with dense cover (see Graves & Duvall, 1995). The impermanent nature of *C. macropholis* groups, suggests that grouping in this species, is the proximate result of incidental mutual attraction to a scarce resource. *Euphorbia caput-medusae* plants are superior micohabitats to other plants in the environment, but are relatively scarce and cover less than ten percent of the total area (Bauwens *et al.*, 1999). The implications are that individuals compete for this limited resource, with resulting social interaction. One would expect high encounter rates among individuals and territorial behaviour to be common. Consequently, movement among *E. caput-medusae* plants is probably high.

This seems to be supported by the low degree of site-fidelity observed for this species and suggests that the same *E. caput-medusae* refuge may not be used over an extended period. This corresponds to the general pattern of refuge fidelity as many lizards may shift their home range either in response to food availability (Eifler, 1996) or habitat availability (M'Closkey, 1997). However, individuals that display home-range fidelity may experience greater fitness as they are familiar with food sources and refuges from predators within their home range (Greenwood & Harvey, 1982). The fact that female *C. macropholis* displayed a higher degree of site fidelity than males may therefore reflect a higher survival rate for females than for males. Female sedentary behaviour during the reproductive season is typically interpreted as an adaptation favouring predator evasion and energy conservation (Rose, 1981). Alternatively, the sedentary behaviour of females, especially over the period that included the breeding season, may be indicative of the mating structure and that females remain in specific courtship areas as such.

The low degree of social segregation and impermanence of social structures underscore that social interaction is not the source of selection for aggregation formation. As opposed to the case of *C. cataphractus*, social grouping may not have been established in *C. macropholis* as advantages normally conferred by grouping, may not be prevalent in the terrestrial habitat. Visibility in the terrestrial habitat is generally low, thus selection for group vigilance may be negligible. Similarly, mate acquisition may be less successful as visual displays and signals may be hampered although individuals may be in close proximity. Furthermore, one has to remember that *E. caput-medusae* shelters are less permanent than rock crevices for instance. Periodical degradation of shelters and fluctuating habitat quality will force groups to break down and thus select against stable social groups.

Despite the dynamic nature of aggregations, a 1:1 sex ratio (male:female) was predominant in all the aggregations that involved adult individuals, with only a few cases of more than one female per male. This seems to suggest a monogamous mating structure for *C. macropholis*.

Data on daily activity and home range of males during the mating season are lacking, however, and makes conclusion about mating system or social structure premature.

Relative activity of *C. macropholis* followed the typical pattern for temperate zone lizards in southern Africa in that adult activity peaks in the spring mating season and then continues at lower levels throughout the late-summer and winter. Late-summer activity was characterized by the appearance of young. *Cordylus macropholis* breeds in September and young are born live from March to April (Branch, 1998). Late summer activity was characterized by a net gain in adult numbers in *Euphorbia* plants, whereas spring activity exhibited a loss in adult numbers. The reason for this is not evident and may relate to a possible habitat shift during the hotter season or higher mortality.

Neonate activity was pronounced during the spring season after equaling that of adult individuals during the winter season. The meaningful number of neonates that were lost during that period suggest that dispersion was postponed until this season, as *Euphorbia*-plants probably provide safe refuge and ample food supply throughout the winter to survive.

The data showed a trend of higher loss in male numbers in the samples preceding and following the mating season, which may suggest differential activity patterns for the sexes over the mating season. No meaningful differences among the sexes in activity were, however, observed, but sample size for the period following the mating season was most likely too small. This is underscored by the fact that a similar trend was observed after the ten-month period that included a mating season. Although sample size was sufficient, events following the mating season might have obscured any significant patterns as recapture of this sample was only conducted four months after the mating season. Increased activity in male *C. macropholis* will increase their risk of being preyed upon and will result in differential mortality of the sexes (see Stamps, 1983). Data on daily activity patterns are however needed to verify whether male activity does increase during the mating season and how it relates to the observed female-biased sex-ratio.

Cordylus macropholis has been described as an extreme microhabitat specialist that restricts its movement to *Euphorbia caput-medusae* plants (Bauwens *et al*., 1999). Data on long-term movement suggest that *C. macropholis* is relatively sedentary outside the mating season. Both males and females moved over distances that were less than that for, *Sceleporus graciosus*, which was described as a sedentary species (Stebbins & Robinson, 1946, cited by Fellers & Drost, 1991). However, I have to point out that the data for *C. macropholis* only represent net movement and that it may be an underestimate of total distances covered daily by individuals. Nevertheless, the covered distances exceeded that to the next nearest neighbouring *Euphorbia caput-medusae* plant. This suggests that *C. macropholis* does move considerable distances and does not necessarily restrict its activity to single plants for extended periods of time as was suggested by Bauwens *et al*. (1999).

Among lizards with similar foraging strategies there should not be a relationship between body size and home-range size (Rose, 1982). Thus, the slightly greater distances moved by female *C. macropholis* individuals outside the mating season cannot be ascribed to sexual dimorphism in size or differential energy requirements and can probably be attributed to small sample size.

The slight difference in the distances moved by both sexes in *C. macropholis* during the November-sample and other samples, is consistent with previous observations that spring activity of a species may be greater than during other seasons (Dubas & Bull, 1992). Bull (1978) suggested that this may be because temperature during this period is most optimal, or because of courtship activity. Alternatively, seasonal food availability may inversely affect home-range size in the sense that the less food available per unit area, the bigger the area over which an animal should have to forage (see Van Sluys, 1997). Qualitative data suggest that prey contribution to the diet of *C. macropholis* remained constant, although the availability of prey in *E. caput-medusae* plants may decrease during the dry season (pers. obs.). Quantitative data on foraging are, however, needed to verify whether changes in prey availability take place above the requirements of these lizards or whether lizards need to supplement food resources by visiting other *E. caput-medusae* plants.

Although there was no significant difference among the sexes in the distance moved over the mating season, the slightly greater distances moved by males follows a general tendency in lizards. Males increase activity in their search for females during the mating season or increase their home range to include more females in their territory (Stamps, 1983).

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MALE AGGRESSIVE BEHAVIOUR DURING THE MATING SEASON IN *CORDYLUS MACROPHOLIS*

Abstract

Agonistic behaviour and differences in adult male behaviour towards male and female juveniles were investigated in *Cordylus macropholis* during the mating season. Encounters were staged between adult males ($N = 7$), between adult males and juvenile males ($N = 7$) and between adult males and juvenile females ($N = 8$). Twelve behavioural acts were discerned. Tail-lashing, push-ups, shuddering, face-offs and biting were identified as aggressive acts. Adult males showed high frequencies of aggressive behaviours among each other and toward juvenile males. No aggressive behaviours were displayed toward juvenile females. The results suggest that adult males are territorial. Aggressive exclusion from territories may take place under natural conditions during the mating season. A highly female-biased sex ratio in *C. macropholis* may relate to territorial behaviour in this species.

Key words: ethogram, sex ratio

INTRODUCTION

Social behaviour in lizards is largely determined by foraging style (Stamps, 1983). Territorial behaviour is therefore often conservative to families that are diurnal and that exhibit a sit-and-wait foraging strategy, as visual orientation used in feeding may facilitate range defence and communication via displays or visible cues (Stamps, 1977). Social interaction among conspecifics and consequent behaviours may be more prevalent when individuals compete for access to mates or limited resources (Stamps, 1983; West-Eberhard, 1983). Such contests often result in agonistic behaviours, that in the case of territorial animals may lead to spatial segregation (Stamps, 1977; Akin, 1998) or even differential mortality in less dominant individuals (Stamps, 1977).

Social behaviours in lizards are generally highly stereotyped (Jenssen, 1975; Ruby, 1977), which makes it possible to compile a list (ethogram) of behavioral acts for a species. Consequently, many studies have focused on describing behavioural repertoires of lizards (Brattstrom, 1971; Greenberg, 1977; Perril, 1980; Torr & Shine, 1994) as insight in the range of behaviours exhibited by an animal is considered vital in answering more complex questions (Torr & Shine, 1994).

Anecdotal information suggests that territorial behaviour is common in cordylid lizards (FitzSimons, 1943; Loveridge, 1944; Burrage, 1974; Branch, 1998; Cooper & Van Wyk, 1994; Cooper, Van Wyk & Mouton, 1995). The majority of species in the family Cordylidae are rupicolous and considered to be sit-and-wait foragers (Cooper, 1995; Mouton & Van Wyk, 1997; Cooper, Whiting & Van Wyk, 1997). Accordingly, they spend most of their time on elevated perches where visibility is good and likely to facilitate range defence. Social behaviour in this group is of particular interest as it displays an apparent dichotomy in social systems. For instance, data suggest a polyganous mating system for some species (Mouton & Van Wyk, 1993; Mouton, Flemming & Kanga, 1999; Mouton, Flemming & Nieuwoudt, 2000), whereas other species appear to be monogamous (Burage, 1974; Van Wyk, 1992). Furthermore, a few species exhibit female-biased sex ratios (Cordes, Mouton & Van Wyk, 1995; Mouton *et al.*, 2000), whilst this is not true for other species (Mouton *et al.*, 1999). As skewed sex ratios are commonly associated with social systems (see Stamps, 1983) these differences in sex ratio may relate to this apparent dichotomy in social systems. Thus far, only two comprehensive descriptions of cordylid social behaviour have been published (Wirminghaus, 1990; Whiting, 1999).

This study examined the social behaviour of *Cordylus macropholis*, one of six terrestrial species in its genus (Mouton & Van Wyk, 1997). This species exhibits a female-biased sex ratio that extends down to smaller size-classes (Mouton *et al.*, 2000). The specific association of this species with a plant species that occurs in relatively low densities in the environment (Bauwens, Castilla & Mouton, 1999; Mouton *et al.*, 2000), makes *C. macropholis* a candidate for the formation of a territorial social system.

I investigated social behaviour in this species by means of staged encounters. Specifically I addressed the following questions: 1) Do adult males show aggressive behaviour towards one another during the reproductive season? 2) Do adult males display any sexual bias in social interactions with juveniles, despite their assumed reduced competitive state?

MATERIALS AND METHODS

Study animals

Cordylus macropholis is a relatively small-sized lizard, with adult size ranging from 60-77 mm snout-vent length (Branch, 1998). This lizard shows a strong association with the plant, *Euphorbia caput-medusae*, that offers a number of shelter opportunities among its succulent branches. Adult *C. macropholis* shows no sexual differences in colour (Branch, 1998). Females generally attain larger body sizes, but male-plus dimorphism exists for head size and tail length (Mouton, Flemming & Nieuwoudt, 2000). Reproduction in the family Cordylidae takes place seasonally, with winter/spring ovulation, followed by gestation in late summer or autumn (Van Wyk 1989, 1991; Flemming & Van Wyk, 1992, Flemming, 1993; Van Wyk & Mouton, 1996).

Lizards were captured by hand in the Lambert's Bay area (32°07'S, 18°19E) during August and early September 2000. Each lizard was marked uniquely on the dorsal surface of the head to aid identification during the experimental procedure. A snout-vent-length of 58 mm was taken as the size at sexual maturity (see Mouton *et al.*, 2000). I used 21 males (four juvenile and 17 adult) with a SVL range of 49.5-66.8 mm and seven juvenile females with a SVL range of 48.5-58.3 mm. Data on social behaviour were collected from a series of staged encounters in the laboratory. After completion the four juvenile males were sacrificed and the epididymi investigated for sperm inactivity to verify sexual immaturity.

Housing

Prior to experiments, lizards were kept separately in glass terraria under a 14L:10D photoperiod. Despite being a terrestrial species, *Cordylus macropholis* can also be found under limestone rocks (Branch, 1998) and shelters readily under ceramic tiles in laboratory conditions (pers. obs.). Each terrarium was therefore provided with a ceramic tile shelter. Food (*Tenebrio* larvae) and water were provided ad libitum.

Testing cages

During experiments lizards were kept in glass terraria, measuring 400 x 600 x 300 (high) mm. Each terrarium was divided into two equal compartments by means of a thin (35 mm) removable ply-wood partition. Each terrarium therefore housed two lizards. The two lizards that were to be staged against one another were visually isolated until the partition was removed. All sides of the terraria were also blackened out to isolate the lizards visually. Each compartment contained a ceramic tile cover and a sandy substrate. Water was provided ad libitum and lizards were fed small mealworms (*Tenebrio* sp.) daily. Homogeneous lighting was provided by eight 150 W spot-lights set on a 14L:10D. *Cordylus macropholis* is known to maintain field body temperatures around 28-30 °C (Bauwens *et al.*, 1999). Room temperature was therefore kept at 28°C during the photophase and 16°C during the dark phase.

Trial procedure

Observations were made at the end of September 2000, during the mating season. The lizards were introduced to the testing cages and allowed a period of seven to ten days to familiarize themselves with their residence. To identify and classify overt aggressive behaviour and postural displays among adult males during the mating season, I staged encounters (N = 7) between adult males. Subsequently, I investigated any sexual biases that may exist in the social behaviour between adult males and juveniles, by observing interactions between adult males and juvenile males (N = 8) and between adult males and juvenile females (N = 7).

Encounters were conducted between 09:00 to 14:00. Not more than four pairs were tested daily to minimize disturbance. Before testing, the room was darkened and the partition was removed. Subsequently, the lights were switched on, a timer was activated and the behaviour of both lizards were observed for a period of 30 minutes. To observe the behaviour unobtrusively all interactions were filmed by a video camera that was connected to a monitor in an adjacent room. This also allowed for reanalysis of the observed behaviour.

The frequencies of observed acts during 30-minute encounters were recorded. The average number of observed acts were compared between the five types of encounters. Data were tested for normality and homogeneity using Kolmogorov-Smirnov and Levene's tests, respectively (Sokal & Rolf, 1981). Where data sets were not normally distributed, Mann-Whitney U-tests were used for two-sample comparisons.

RESULTS

Behavioural acts

Lizards were observed for a total of 660 minutes. During 22 staged encounters, only 18 cases (adult male vs. adult male ($N = 5$); adult male vs juvenile male ($N = 7$); adult male vs. juvenile female ($N = 7$)) of social interaction were observed. The following behavioural acts with identifiable starting and end points were discerned and are referred to in capatilized words.

ARCHED TAIL: Distal region of tail is held flat against substrate, but proximate region is slightly arched away from the substrate, while facing away and presenting its tail to the other individual.

BITE: One lizard grasps another with its jaws.

FACE-OFF CIRCLING: Two lizards parallel to each other in a head-to-tail position, following a common circular path.

FLEE: One lizard moves rapidly away from another approaching lizard.

HEAD-NOD: A slow upward movement of the head, followed by a rapid downward movement.

LEG-WAVE: The leg is lifted from the substrate and moved in a circular manner along a vertical plane.

LUNGE: An attempt to bite another lizard.

PUSH-UPS: The body is repeatedly lifted from the substrate by straightening the front, or both the front and hind legs.

SHUDDER: Movement in short, rapid jerks while the body is inflated.

TAIL-LASH: Side-to-side undulation of the tail.

TAIL-TWITCH: Rapid vibration of the distal part of the tail.

TONGUE-FLICKING: The tongue is rapidly protruded and retracted after it has been brought into contact with another lizard.

Frequency and context of behavioural acts

The frequencies of behavioural acts were compared between the different types of encounters (Table 6.1).

TONGUE-FLICKING was the only behavioural act performed by individuals in all types of encounters. Without exception TONGUE-FLICKING occurred, at initial contact between individuals and was directed at the hind/tail region of the other lizard. Adult males placed with juvenile females displayed the highest frequency of TONGUE-FLICKING (Table 6.1).

Juveniles placed with adults were the only individuals to display HEAD-NODS. Juveniles exhibited this display in response to TONGUE-FLICKING by adult males (*N* = 7) or when in close proximity of an adult male (*N* = 2). HEAD-NODS were often given in combination with TAIL-TWITCHING (*N* = 6). When given by females (*N* = 8), HEAD-NODS elicited no response from adult males, but when given by a juvenile male (*N* = 1) it elicited a BITE-response from an adult male.

ARCHED TAIL, TAIL-TWITCH and FLEEING were displayed by juveniles placed with adult males and also by some adult males placed with other adult males. In juvenile females, ARCHED TAIL (*N* = 2) and TAIL-TWITCH (*N* = 6) were displayed in response to TONGUE-FLICKING by adult males or close male proximity, but in turn elicited no response from males. Juvenile males placed with adult males showed TAIL TWITCHING (*N* = 3) in response to TONGUE-FLICKING by adult males, that in turn elicited BITING from adults. Similarly, an ARCHED TAIL display by juvenile males was given in response to TONGUE-FLICKING by an adult male (*N* = 3) or after being BITTEN by an adult male (*N* = 2). Adult males displayed

Table 6.1 Comparison of the mean frequency (SE) of behavioural acts among five types of 30 minute encounters. The behaviour of the animal named first is listed, eg. In AM-JM the adult male's behaviour is listed. AM = adult male, JM = juvenile male; JF = juvenile female

Encounters *N*	AM-AM 10	AM-JM 7	AM-JF 7	JM-AM 7	JF-AM 7
Behavioural Act					
Tongue-flicking	0.40 (0.16)	0.71 (0.29)	1.43 (0.30)	0.86 (0.26)	0.29 (0.18)
Head-nods	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.14 (0.14))	1.00 (0.38)
Arched tail	0.20 (0.13)	0.00 (0.00)	0.00 (0.00)	0.71 (0.29)	0.29 (0.18)
Tail-twitch	0.30 (0.15)	0.00 (0.00)	0.00 (0.00)	0.57 (0.30)	0.86 (0.34)
Flee	0.30 (0.21)	0.00 (0.00)	0.00 (0.00)	0.43 (0.30)	0.14 (0.14)
Leg-wave	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.14 (0.14)	0.00 (0.00)
Push-up	0.00 (0.00)	0.57 (0.30)	0.00 (0.00)	0.43 (0.20)	0.00 (0.00)
Shudder	0.90 (0.18)	0.57 (0.30)	0.00 (0.00)	0.57 (0.30)	0.00 (0.00)
Tail-lash	0.80 (0.13)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Face-off	1.00 (0.00)	0.14 (0.14)	0.00 (0.00)	0.14 (0.14)	0.00 (0.00)
Chase	0.10 (0.10)	0.14 (0.14)	0.00 (0.00)	0.00 (0.00)	0.00 (0.00)
Lunge	0.1 (0.10)	0.00 (0.00)	0.00 (0.00)	0.14 (0.14)	0.00 (0.00)
Bite	0.80 (0.13)	0.71 (0.18)	0.00 (0.00)	0.14 (0.14)	0.00 (0.00)

ARCHED TAIL and TAIL-TWITCHING behaviour (both $N = 3$) after being bitten by another adult individual. I only observed one case where a juvenile female FLED from an approaching adult male. Juvenile males FLED more frequently than juvenile females when interacting with adult males (Table 6.1). Juvenile males FLED in response to being CHASED (N = 2) or BITTEN (N = 1) by adult males. One adult male was observed to FLEE from another approaching adult male, but no adult males ever FLED from juveniles.

LEG-WAVE was performed by one juvenile male individual after being bitten by an adult male. This behaviour was performed in conjunction with TAIL-TWITCHING and an ARCHED TAIL display.

PUSH-UP displays occurred only when adult males and juvenile males encountered each other (Table 6.1) and usually preceded SHUDDER movement.

TAIL-LASHING was observed only between adult males and never in other types of encounters (Table 6.1).

SHUDDERING, FACE-OFFS and BITING were restricted to male-male interactions and never occurred during male-female interactions (Table 6.1). Adult males, when interacting with other adult males, displayed the highest frequency of these three behavioural acts. Both SHUDDERING and FACE-OFFS either evoked, or preceded biting from individuals. When placed with juvenile males, adult males displayed FACE-OFF behaviour less frequently. However, adult males did not display significantly lower frequencies of SHUDDERING and BITING when placed with juvenile males (both $P > 0.05$). BITING was the most frequent behaviour exhibited by adult males toward juvenile males.

DISCUSSION

Suggested function of behaviours

Many of the behaviours that I observed in *Cordylus macropholis* follow a similar pattern of that described for *Cordylus cordylus* (see Wirminghaus, 1990). However, some behaviours have not been previously described for *C. cordylus* or appear in different contexts than those previously described. Subsequently, I attempt to infer the functional significance of observed behaviours based upon the context in which they occurred. However, I have to point out the incomplete nature of the compiled list of behaviours. Due to the small number of individuals observed (N = 28) and the nature of staged encounters, this study unquestionably failed to document all behaviours exhibited by *C. macropholis* under natural conditions.

Tongue-flicking usually plays an important role in chemoreception (see Cooper, Van Wyk & Mouton, 1996). As this behaviour was prevalent in all types of interactions, it may aid in species recognition or chemical discrimination between the sexes. The high frequency of tongue-flicking observed in male-female interactions suggests that tongue-flicking may be associated with mate selection.

Head-nods, arched-tail and tail-twitch behavioural displays in *C. macrophol*is were exclusively displayed by juveniles placed with adult males or by adult male individuals which were subjected to overt aggression, suggesting that these behaviours are submissive signals. Head-nodding performed by females and smaller males in response to larger males, has also been recorded in *Anolis carolensis* (Carpenter & Ferguson, 1977) and is generally accepted as being a submissive response. Similarly, I observed a leg-waving display by a juvenile in response to overt aggression from an adult male. Records for this response in other unrelated species include that of *Amphibolurus barbatus*, *Lacerta melisellensis* and *Anolis opalinus* and are generally thought to stop agonistic behaviour of the more dominant lizard (Carpenter & Ferguson, 1977).

Push-up displays in *C. macropholis* were only observed in juvenile male-adult male interactions. This suggests that this display is more prevalent when opponents are differently matched and may have an assertive function. Push-ups often evoked shuddering and biting which indicates that it probably forms part of a graded aggressive response.

Tail-lashing occurred only among adult males and was associated with aggressive behaviour (eg. biting). It has been suggested that tail-lashing may draw a predator's attention away from the lizard's body and may therefore function as a "pursuit deterrent" signal (see Torr & Shine, 1994).

Both shuddering and face-offs preceded biting responses by male individuals, which suggest that they formed part of a graded aggressive response.

General

Staged encounters indicated that adult male *Cordylus macropholis* interact aggressively during the reproductive season. This aggressive behaviour may reflect territorial behaviour and may explain distinct spatial patterns (see Chapter 4). Although up to 11 individuals inhabit a single *Euphorbia caput-medusae* plant, Mouton *et al.* (2000) reported no cases where more than two adult males shared the same plant shelter. Most groups consist of predominantly an adult pair, with varying number of juveniles, but single males may also share a plant with a varying number of females (Mouton *et al.*, 2000). Thus, it may be that such plants constitute a territory from which other males are excluded. Opposed to other plants in the environment, *Euphorbia caput-medusae* plants offer superior shelter opportunities, but are, however, a relatively scarce resource (Bauwens *et al.*, 1999). Consequently, males may compete to establish territories within these plants during the mating season as to encompass home ranges of females that also aggregate in these plants.

Agonistic encounters in the rupicolous species, *Cordylus cordylus*, often are limited to less intense threat displays such as shudder displays and passive threats and rarely involve biting (Wirminghaus, 1990). However, higher levels of aggression appear to be frequent in encounters among *C. macropholis* males. This may relate to movement patterns in this species and constraints imposed by the terrestrial environment. Visual encounters may be frequent in a rupicolous habitat and may result in one male to become familiar with another neighbouring male. If dominance has been previously established, males may avoid further overt aggression to reduce the cost of territory defence and the risk of injury (Ydenberg, Giraldeau & Falls, 1988). This phenomenon has been named the 'war of attrition' (Ydenberg *et al.*, 1988), and predicts that aggression and degree of familiarity are inversely related such that aggression will be fiercest and longest between complete strangers and lowest between familiar animals. Accordingly, low visibility in the terrestrial environment may hamper neighbour recognition in *C. macropholis*. In addition movement of these lizards among plants are high, and because the composition of groups change constantly (unpublished data), maintenance of dominant status may require sustained high levels of aggressive behaviour (see also Torr & Shine, 1996). Undoubtedly these high levels of aggression may result in injury. Mouton *et al.* (2000) reported on a high scar incidence in adult males, but whether these scars are the result of predation or intraspecific aggression remains to be confirmed.

The study showed that adult males are aggressive toward juvenile males, despite their presumed reduced competitive status. Support for the exclusion of juvenile males is suggested by the higher number of flight responses observed for juvenile males than for juvenile females. It is possible that adult males need to exclude young males from plants as they stand the risk, due to visual constraints, not to encounter them later when they do become sexually competitive. A prerequisite for this hypothesis is that males should be able to discriminate between the sexes in juvenile lizards. Pheromonal detection and the ability to discriminate among the sexes in conspecifics were reported in the closely related species, *Cordylus cordylus* (Cooper *et al.*, 1996). The femoral and possibly the generation glands on the ventral aspect of the lizards' hind legs are thought to be the source of pheromones (Cooper *et al.*, 1996). These epidermal glands are sexually dimorphic in adults and absent in juveniles in most cordylid lizards (Van Wyk and Mouton, 1992). However, Mouton, Flemming & Searby (1998) reported on the presence of active generation glands in neonates in *C. macropholis*. These glands degenerate in females as they get older, but remain active in males. Thus, the presence of these glands in juveniles may enable adult males to discriminate among males and females and to expel males even at a young age. The high frequency of tongue-flicking directed at another lizard's hind region during interactions, seems to support this hypothesis.

The aggressive exclusion of males from territories, especially at a young age, may strongly affect on the sex ratio of this species. Less suitable shelter and feeding opportunities for these excluded males may exist outside these *E. caput-medusae* plants, whereas females that are not excluded may experience increased fitness. This may lead to differential persistence rates for the sexes and may ultimately result in a female-biased sex ratio, as has been observed for two *C. macropholis* populations (see Chapter 4).

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