Thesis master

RESOURCE PARTITIONING BETWEEN TWO SYMPATRIC AUSTRALIAN SKINKS, *EGERNIA MULTISCUTATA* AND *EGERNIA WHITII*

STEPHEN BELLAMY

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Declaration

This is to certify that this thesis does not incorporate, without acknowledgement, any material previously submitted for a degree or diploma in any university; and that to the best of my knowledge and belief it does not contain any material previously published or written by another person except where due reference is made in the text.

Stephen Bellamy

August, 2006

Abstract

When species compete for resources, in a stable homogeneous environment, there are two possible outcomes. The first is that one species will out-compete the other and exclude it from the environment. This is known as the competitive exclusion principle. The second is that both species will manage to coexist. Coexistence can only occur if the species' niches are differentiated such that interspecific competition is minimised, or eliminated. This outcome is known as resource partitioning.

Two closely related Australian skink species of the *Egernia* genus, *Egernia multiscutata* and *Egernia whitii,* are abundant and sympatric on Wedge Island in South Australia's Spencer Gulf. The species are morphologically very similar and appear to have very similar life histories and habitat requirements. Ostensibly, they would compete for limiting resources in this environment.

This thesis is the first investigation into resource partitioning in this previously unstudied model organism. I report the results of multi-faceted investigations into the coexistence of the skinks, *E. multiscutata* and *E. whitii* on Wedge Island and the evidence for, and mechanisms of, any facultative resource partitioning between them.

Study methods involved a transect survey of most of Wedge Island to determine the species' distributions and any evidence for resource partitioning; a morphological comparison to investigate any potential competitive advantages of either species; a habitat choice experiment to establish retreat-site preferences in the absence of interspecific interference; and, a series of staged dyadic encounter experiments to investigate interspecific competitive interactions.

Resource partitioning was evidenced by differential distributions of the species among substrates containing the elements required for permanent refuge shelters. This partitioning was not mediated by avoidance of particular substrates but by the presence of the opponent species, combined with attraction to suitable substrates. Asymmetries in some morphological characters were found to confer a potential competitive advantage to *E. multiscutata* in agonistic encounters with *E. whitii*. Both species were found to have the same refuge site preferences when interference competition was experimentally removed. This result was not concordant with observed resource partitioning in the field and suggests that the habitat choices of both species are modified by the presence of the opponent species. Analyses of staged dyadic encounter experiments showed that *E. multiscutata* was more likely to gain greater access to a contested habitat resource and more likely to exclude *E. whitii* from the resource than *vice-versa*. Nevertheless, the outcome of competitive interactions was not completely deterministic and there was some tolerance of co-habitation. *E. multiscutata*'s competitive advantage was attributable largely to its greater mass and head dimensions relative to snout to vent length. However, differential behavioural responses to the threat of larger opponent size also played an important part in resource partitioning between the species.

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Proverbs 3 (New International Version)

[5]“Trust in the Lord with all your heart
and lean not on your own understanding;

[6]In all your ways acknowledge him,
and he will make your paths straight.”

Amen.

Foreword

The data chapters of this thesis are written as independent manuscripts suitable for publication in refereed journals with only minor modification. Therefore it was not possible to avoid some degree of redundancy, particularly in the chapter introductions.

Originally this study was conceived as an investigation into dispersal patterns and behaviour in *Egernia multiscutata* and *Egernia whitii* on Wedge Island using molecular techniques. Much of the fieldwork was carried out on this basis.

Unfortunately a change in supervision and resources meant that it was no longer possible to complete the original research plan during the course of my candidature. Therefore, in collaboration with a new supervisory panel, I altered the project focus from dispersal to resource partitioning and adapted work already done accordingly.

TABLE OF CONTENTS

CHAPTER 1

General introduction - resource partitioning

Research question

Mackenzie *et al.* (1998) describe two possible outcomes if two species compete for resources in a stable, homogeneous environment. The first is that one species will out-compete the other, eventually excluding it from the environment. This outcome is known as the competitive exclusion principle. The second is that both species will manage to coexist. However coexistence can only occur if the species' niches are in some way differentiated such that interspecific competition is minimised or eliminated. This outcome is known as resource partitioning.

Two species of the Australian skink genus *Egernia*, *E. multiscutata* and *E. whitii,* are sympatric on Wedge Island in South Australia's Spencer Gulf. The two species are so morphologically similar that it is difficult for an inexperienced observer to distinguish between them. Ostensibly they appear to have very similar activity patterns and habitat requirements, including a generalist diet (Greer 1989; Cogger 2000; Chapple 2003; Greer 2005). Yet both species persist in this environment, sometimes in very close proximity with each other. Does this coexistence challenge the competitive exclusion principle, or is there some form of resource partitioning between these species? If so, what is the mechanism of resource partitioning?

This thesis reports the results of investigations into the coexistence of the sympatric skinks, *E. multiscutata* and *E. whitii* on Wedge Island and the evidence for, and mechanisms of, any facultative resource partitioning between them.

Background

There is a long history of studies on competitive exclusion in the scientific literature beginning with Gause (1934) and supported by a range of theoretical, field and experimental studies and model systems, including crustaceans (Bovbjerg 1969), phytoplankton (Richerson *et al.* 1970), fishes (Zaret and Rand 1971), mammals

(Brown 1971), amphibians (Jaeger 1971), birds (Terborgh 1985), viruses (Feng and Velasco-Hernandez 1996), and reptiles (Shine 1977; Reinert 1984; Langkilde *et al.* 2003).

Notwithstanding the prediction of the competitive exclusion principle, similar species are often found to coexist in the wild (Hambright and Zohary 2000). Studies, such as those above, demonstrate resource partitioning as the means by which such coexistence occurs.

Resource partitioning can be observed in numerous taxa on a number of axes such as food differentiation (Shine 1977; Bootsma *et al.* 1996; Ray and Sunquist 2001; Garcia and Arroyo 2005), morphology (Renaud and Millien 2001; Kassam D. *et al.* 2004), physiological adaptations (Huey 1991; Bollmann *et al.* 2002; Klok and Chown 2003), diurnal and seasonal activity patterns (Albrecht and Gotelli 2001; Hatano *et al.* 2001; Kocàrek 2001; Wahungu *et al.* 2004), differential behavioural responses, such as feeding behaviour (Inouye 1978; Werner and Sherry 1987), antipredator behaviour (Werner and Sherry 1987; Lingle *et al.* 2005), habitat selection (Mac Nally 1985; Arlettaz 1999) and use of habitat and micro-habitat complexity (Pianka 1966; Petren and Case 1998; Howard and Hailey 1999; Stewart *et al.* 2002), dispersal behaviour (Bonnet *et al.* 1999; Hokit *et al.* 1999; Harrison *et al.* 2001), mutual tolerance/intolerance or cooperation (Sushma and Singh 2006), flexible behavioural responses to interspecific interactions (Langkilde *et al.* 2004; Stapley and Keogh 2004) and responses to temporal environmental dynamics (Dickman *et al.* 1999; Harrison *et al.* 2001; Fox *et al.* 2003; Chesson *et al.* 2004). However it is likely that there will be more than one cause (possibly interacting) of resource partitioning such as those reviewed for a range of amphibians and reptiles by Toft (1985) and among sympatric arboreal mammals by (Sushma and Singh 2006).

Reptiles as a model system

Studies using reptilian fauna as model organisms have made significant contributions towards a more general understanding of ecology, including resource partitioning (e.g. Schoener 1968; Shine 1977; Reinert 1984; Leal and Fleishman 2002). Such studies may compliment, or challenge, conventional precepts developed from studies utilizing ‘high-energy’ model systems (Huey *et al.* 1983). Many lizard genera contain a large number of species, with a variety of life-history traits, upon which comparative studies can be undertaken. Caribbean *Anolis* species, in particular, have been well established over several decades as an ideal model system for studies as diverse as sexual selection (Trivers 1976), sexual dimorphism (Schoener 1967), convergent evolution (Losos 1992), adaptive radiations (Irschick *et al.* 1997; Glor *et al.* 2004), physiology (Menaker and Wisner 1983; Summers and Greenberg 1995), population dynamics (Schoener and Schoener 1980), behaviour (Leal and Rodriguez-Robles 1997; Leal 1999), locomotor performance (Losos 1990; Irschick 2000) and interspecific competition and resource partitioning in sympatric species (Schoener 1968; Talbot 1979; Pacala and Roughgarden 1982; Leal and Fleishman 2002).

Like their Caribbean counterparts, the Australian environment and its reptile fauna have long been recognised as providing useful models for most, if not all, terrestrial ecological concepts due to their unusually diverse nature (Heatwole and Taylor 1987). Pianka (1966) proposed that the independently evolved Australian reptile fauna would provide strong tests of resource partitioning interpretations when compared and contrasted with North American reptile fauna. Subsequently he used both Australian and North American reptile species to emphasise the importance of niche relationships in structuring lizard communities (Pianka 1973).

Many studies have continued to use Australian herpetofauna to investigate some aspects of resource partitioning, including trophic partitioning (James 1991), microhabitat separation (Pianka and Pianka 1976), weather related population dynamics (Dickman *et al.* 1999), reproductive biology (Shine 1986), social relations and interspecific competition (Downes and Bauwens 2004; Langkilde *et al.* 2004) and shelter site selection (Downes and Shine 1998; Shah *et al.* 2004; Webb *et al.* 2004).

Recent evidence of family structure within stable aggregations of the Australian skink, *Egernia stokesii* (Gardner *et al.* 2001), combined with known stable aggregations in other *Egernia* species, has enhanced the scope of lizards as a model system and focused attention on the *Egernia* genus (Chapple 2003). This includes studies on aspects relating to resource partitioning, such as site fidelity (Stow and Sunnucks 2004), social organisation and home range (Shah *et al.* 2003; Osterwalder *et al.* 2004; Fuller *et al.* 2005), habitat use and shelter site selection (Downes and

Shine 1998; Langkilde *et al.* 2003; Langkilde and Shine 2005) and interspecific competition (Langkilde and Shine 2004).

Langkilde *et al.* (2003) compared retreat site attributes between three broadly sympatric *Egernia* species (and two *Eulamprus* species) in a high altitude environment. They found that although there were some significant relative differences (relating to incident radiation), the species behaved remarkably alike, showing significant preferences for the same shelter-site attributes. This suggested the potential for intensified interspecific competition. The authors recommended that comparative studies, particularly at lower altitudes, would have great potential for investigating the factors that determine spatial distributions of organisms in the wild.

Milton and Hughes (1986) investigated habitat selection by two closely related sympatric *Egernia* species from southern Queensland. They reported no evidence that competition between the sympatric species restricted habitat preferences, suggesting human disturbance may have had some impact on their current distributions. However similar studies with other species, where human impacts are minimal, would be useful in investigating resource partitioning.

This study takes a multi-faceted approach to investigating resource partitioning in a previously unstudied model system (i.e. sympatric *E. multiscutata* and *E. whitii*) in a manner that is more comprehensive than any previous Australian studies. The results allow a broader understanding of resource partitioning principles and add to the knowledge of a genus that is of current scientific focus.

Study model

Study species

Within the *Egernia* genus there are six generally recognized species groups, one of which is the *whitii* group (Chapple 2003). Two species of the *whitii* group, *E. whitii* and *E. multiscutata* are the subjects of this study.

E. multiscutata and E. whitii are morphologically very similar. The main diagnostic characters between the species are the relative widths of their interparietal and frontal scales (Cogger 2000) and differences in the number of sharp keels on the sub-digital lamellae (Coventry and Robertson 1980). Snout to vent length (SVL) is regarded as the standard measure of length for lizards (Cogger 2000). Adult *E. multiscutata* SVL is reported by Chapple (2003) to range from 80-95 mm (*op. cit.* Store 1968; Store 1978; Cogger 2000) and for *E. whitii* 80-110 mm (*op. cit.* Hickman 1960; Rawlinson 1974; Milton 1987; Wilson and Knowles 1988; Cogger 2000). *E. whitii* populations show a decrease in SVL with increasing latitude as described by Bellamy (2006) *op. cit.* (Hickman 1960; Milton 1987; Chapple 2005). There are no reported geographic variations in SVL for *E. multiscutata* (Store 1968). Descriptions of lizard head dimensions do not seem to be routinely reported or standardised in the published literature, making comparisons difficult. However head dimensions have been reported in some *Egernia* species, usually with respect to sexual dimorphism, for example, (Clemann *et al.* 2004, *Egernia coventryi*), (Arena and Wooler 2003, *Egernia kingii*), or comparative feeding analysis (Brown 1991, *E. cunninghami, E. saxatilis, E. whtii*). Chapple (2005) reported head width for one adult population of *E. whitii* ranging from 10.72 mm to 13.87 mm and head length ranging from 18.38 mm to 22.48 mm with significant sexual dimorphism in both dimensions. Bellamy (2006) also found sexual dimorphism in head length and head width for *E. whitii* from Wedge Island. I have been unable to find published data for *E. whitii* head depth or for *E. multiscutata* head dimensions.

Most *Egernia* species, including *E. whitii,* are reported to be diurnal (Cogger 2000) and both of the study species appear to have generally similar life-history traits and activity patterns (Chapple 2003).

Egernia species, are regarded as generalist and opportunistic feeders (Greer 1989; Brown 1991), their diets containing insects and other invertebrates (Chapple 2003). They are notable for including plant material in their diet, its proportion increasing with increasing body size (Brown 1991). *E. multiscutata* and *E. whitii* have been observed to include berries and invertebrates in the field on Wedge Island (personal observations).

Both *E. whitii* and *E. multiscutata* are reported to be predominantly burrowing species whose habitats are frequently associated with rocky areas and encompass coastal heath, open forests and open woodlands (Cogger 2000; Donnellan *et al.* 2002; Chapple and Keogh 2006). Such habitats are found on Wedge Island (Robinson *et al.* 1996). *E. multiscutata,* which is a more desert-adapted species, is considered by some to be an obligate burrower, its presence generally first identified by locating its burrow systems (Coventry and Robertson 1980; Wilson and Knowles

1988; Chapple 2003) whereas *E. whitii* is regarded as either a facultative burrower or saxicolous depending on habitat suitability (Chapple 2003). *E. multiscutata* is reported to construct large complex burrows with several entrances, whereas *E. whitii* burrows are generally less complex (Donnellan *et al.* 2002; Chapple 2003).

Egernia species are noted for having strong attachments to permanent retreat sites such as rock crevices, hollow logs, dead trees and burrows (e.g. Greer 1989; Chapple 2003). Retreat sites may be constrained by various habitat parameters such as substrate, vegetation, presence or absence of competing species (Langkilde and Shine 2004) and the presence or absence of conspecifics (Stamps 1988).

E. multiscutata and *E. whitii* are both reported to live in small stable social aggregations (Hickman 1960; Coventry and Robertson 1980; Milton and Hughes 1986; Bruyn 1994; Chapple 2003). The evolution of social aggregations may be influenced partly by retreat-site constraints (Chapple and Keogh 2006).

Field site

Wedge Island lies 38 km west of mainland Yoke Peninsula in South Australia's Spencer Gulf (35° 09' S, 136° 27' E) and has been separated from the South Australian mainland for approximately 9,000 years (Robinson *et al*, 1996). Land area is 947 hectares (maximum dimensions approximately 5 km long and 1-1½ km wide). Two-hundred metre high cliffs rise from the sea on the southern shores. From this elevation the topography rapidly tapers to sandy beaches on the northern shore. The island has a temperate Mediterranean climate with hot, dry summers and cool, wet winters. There is no permanent standing water on the island but there is an inactive well and there are rainwater storage tanks attached to three holiday houses and sheds.

The island has no permanent human population and contains a mosaic of remnant woodland, coastal heath, salt marshes, rocky patches, sandy substrates and vegetated sand dunes. There are no snakes on Wedge Island (a common predator of skinks) but there are several species of raptors which would be potential predators. The island is free from pest species such as rabbits, cats, dogs and foxes (Robinson *et al.* 1996).

The distribution ranges of the study species, *E. multiscutata* and *E. whitii* overlap in South Australia (Cogger 2000) where they are abundant on some offshore islands. Wedge Island's absence of feral predators and competitors, lack of a permanent human population and abundance of the two sympatric *Egernia* species provides a unique opportunity for resource partitioning studies.

Study scope

The first objective of this study was to determine if there was any observable evidence of resource partitioning between the study species on Wedge Island. One commonly accepted means by which resource partitioning of species can be readily identified is through their patterns of distribution among differentiated habitats (e.g. Reinert 1984; Howard and Hailey 1999). Resource partitioning of habitats may be evidenced by the species' use of a range of parameters (e.g. Jaeger 1971; Talbot 1979; Mac Nally 1985; Stewart *et al.* 2002; Fox *et al.* 2003; Vessby and Wikelius 2003; Namgail *et al.* 2004; Martin and Possingham 2005). Chapter 3 reports on field investigations into habitat differentiation between *E. multiscutata* and *E. whitii* as observed by their distribution patterns on Wedge Island and by analyses of a range of habitat parameters including the presence of the competing species.

Although the study species are reported to have very similar overall size in terms of snout-to-vent length (reviewed by Chapple 2003) my initial investigations suggested that *E. multiscutata* may be slightly larger than *E. whitii* in some morphological characters. Chapter 4 reports on the comparison of these characters and their potential importance in the outcome of agonistic interactions and hence their implications for resource partitioning.

The strong attachment of each of the study species to permanent retreat sites and their predominantly burrowing behaviour (Greer 1989; Cogger 2000; Chapple 2003; Greer 2005), when combined with the outcome of habitat partitioning analyses (Chapter 3), suggested that refuge sites (or retreat sites) would be of primary importance as a parameter for investigating resource partitioning. The first experimental investigation into this parameter was to determine what the refuge site preferences of each of the species were when other potentially confounding factors were removed. The results of this investigation are reported in Chapter 5.

The second experimental investigation into refuge partitioning was to establish which, if any, of the study species would gain greater access to a contested refuge site in staged dyadic encounters. The results of this investigation are reported in Chapter 6.

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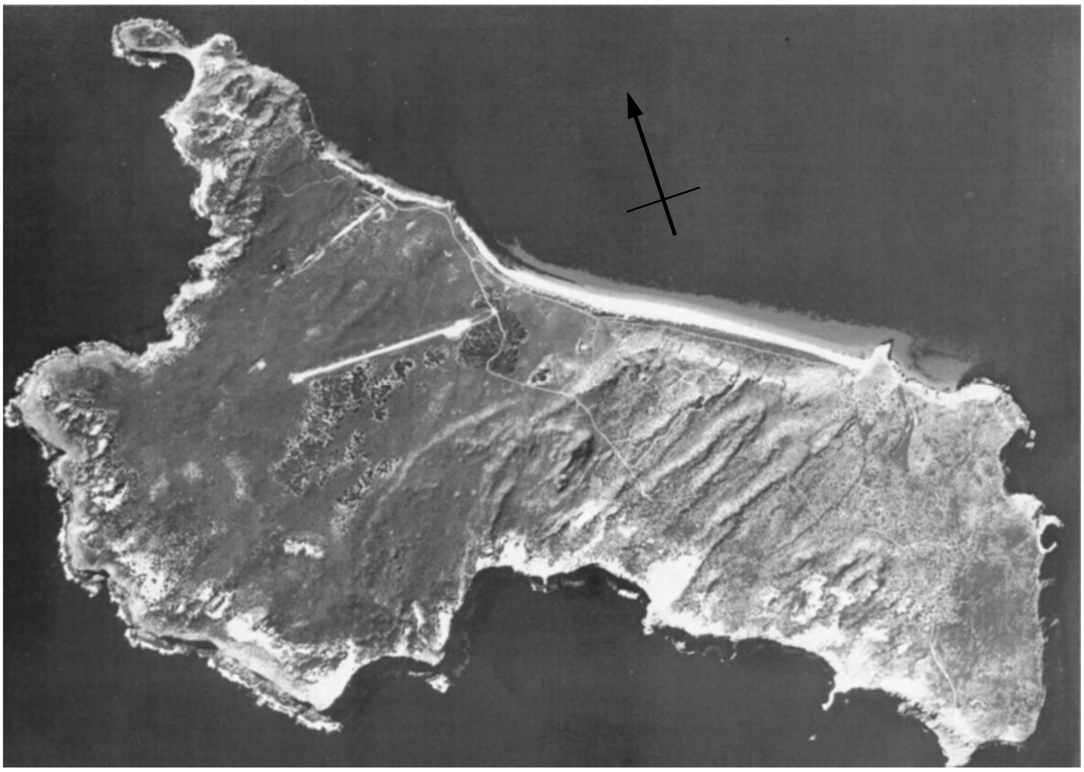
CHAPTER 2

General methods

Overview

The overall objective of this project was to investigate aspects of resource partitioning between the sympatric lizard species, *E. whitii* and *E. multiscutata*. I undertook a field study component over three seasons, from March 2001 to December 2003, on Wedge Island in South Australia's Spencer Gulf (Figure 1) and a series of laboratory experiments at Flinders University.

Figure 1: Aerial photograph, Wedge Island, South Australia



Photography supplied by MAPLAND, Environmental and Geographic Information, Department for Environment and Heritage. Used with permission, Licence number 2002/005

Field studies

The major field undertaking was a transect survey of the island. The main objective of the survey was to describe and analyse the distribution, habitat settlement choices and the extent of any habitat niche separation of the two study species.

Specimens of the two species were captured to establish laboratory colonies for experimental purposes.

Study species

E. multiscutata and *E. whitii* are morphologically very similar with similar snout to vent lengths (SVL), ranging from 80-110 mm (Chapple 2003). The main diagnostic characters between the species are the relative widths of their interparietal and frontal scales (Cogger 2000) and differences in the number of sharp keels on the sub-digital lamellae (Coventry and Robertson 1980). Figure 2 is a photograph of *E. multiscutata* and Figure 3 is a photograph of *E. whitii*. A detailed description of the study species and their ecology is given in Chapter 1.

Figure 2: Photograph of *E. multiscutata*

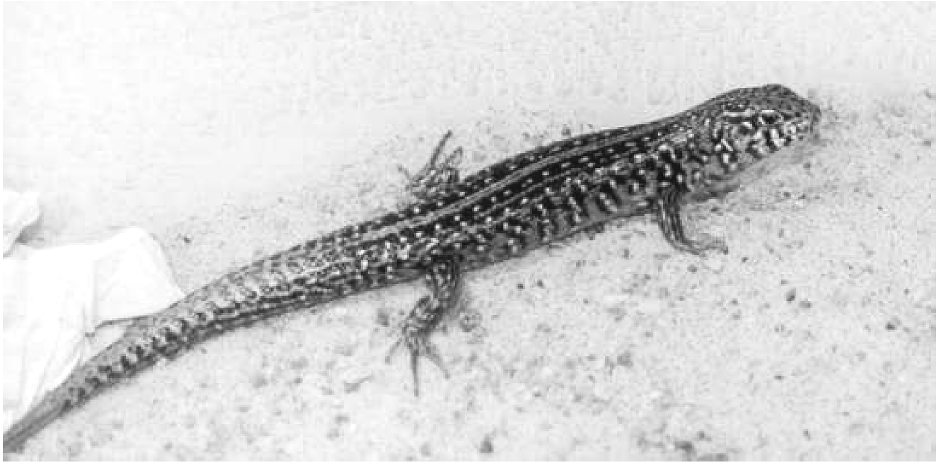


Figure 3: Photograph of *E. whitii*

Study site description

Wedge Island (35° 09' S, 136° 27' E), lies 38 km west of mainland Yorke Peninsula in South Australia’s Spencer Gulf. It is 947 hectares in area and is approximately 5 km long and 1-1 ½ km wide (Figure 1).

Since 1858, following European settlement, and until recently, the island was used for various pastoral pursuits. Consequently much of the original woodland has been cleared but some healthy patches of *Melaleuca lanceolata* (Dryland Tea-tree) woodland persist in areas where the substrate is covered with loose and embedded rocks that presumably made it unsuitable for grazing pasture. There are large areas of coastal heath and vegetated sand dunes and there are salt marshes in an inland drainage depression in the island’s north-west. Relatively flat cliff-top platforms with embedded, loose and exfoliating rocks exist around approximately ¾ of the island's perimeter. The rest of the island has generally sandy, sandy-loam or loam soils with occasional loose or embedded rocky patches.

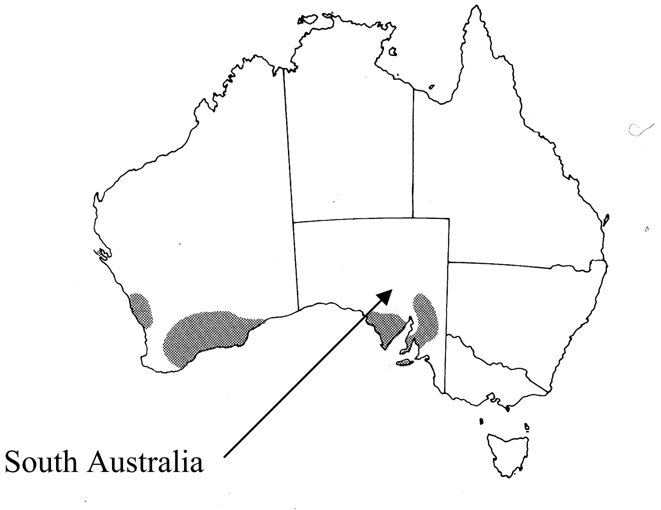
A number of invasive weed plants have been introduced to the island. The most notable, *Lycium ferocissimum* (Boxthorn), has invaded large patches of previously cleared land. An active eradication programme is in place to control this weed.

Since the early 1990s the island has been cleared of all domestic grazing animals and there are now no permanent human inhabitants or pastoral activities. The original homestead is used as a holiday house, as are the only two other houses on the island.

Wedge Island has avoided the introduction of common pest animals such as rabbits, cats and dogs and current management practices preclude the introduction of any domestic or non-native fauna and flora. However, several endangered non-endemic native mammal species have been introduced by the Department for Environment and Heritage (Robinson *et al.* 1996).

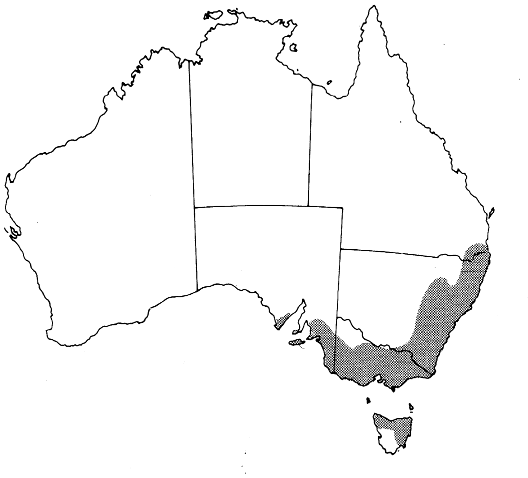
Although Wedge Island is logistically difficult to access for field studies, the absence of feral predators and competitors, the lack of a permanent human population and the abundance of reptiles make it an ideal site for herpetological study. Twelve lizard species have been recorded on the island, including eight members of the Scincidae (skink) family to which the *Egernia* genus belongs. The distribution ranges of *E. multiscutata* and *E. whitii* overlap in South Australia (Figures 4 and 5) and both species are abundant on Wedge Island (Robinson *et al.* 1996; Cogger 2000). More information regarding the field site is given in Chapter 1.

Figure 4: Distribution of *E. multiscutata*



(Cogger 2000 Page 468)

Figure 5: Distribution of *E. whitii*



(Cogger 2000 Page 474)

Transect methods

North-south transects were carried out at 200 m intervals across the whole island except for a section of the northern peninsula which contained a breeding colony of burrowing *Pelagodroma marina* (White-faced Storm-petrels). It was not possible to survey this area without causing considerable damage to the nesting site.

GPS coordinates, vegetation structure, substrate description, weather conditions and presence/absence or captures of *Egernia* species were recorded at ten-metre intervals, or resource plots, along the transects. *Egernia* sightings/captures and changes in vegetation structure or substrate were also recorded as they occurred within the ten-metre resource plots. Measurements of skink morphology were taken for every capture. GPS coordinates were recorded for all captures. More details of the transect methods and sampling techniques are discussed in Chapter 3.

Laboratory studies

A series of observations and experiments were carried out at Flinders University, utilizing *E. whitii* and *E. multiscutata*. The objectives of these experiments were to study the behaviour of the species and develop an ethogram, observe their diurnal activity patterns, determine the refuge choice preferences of each species when the opponent species was absent, and to determine if the presence of the opponent species modified refuge behaviour in a competitive situation, that is, did resource partitioning occur in this dimension?

Laboratory colonies

E. whitii and *E. multiscutata* colonies were established in the Animal Care Unit (ACU) of Flinders University using skinks collected on Wedge Island. All of the *E. multiscutata* were captured in March, 2001 and the *E. whitii* were captured over three field seasons from 2001 to 2003. The skinks were captured and held under permit numbers A23436 9 and Y24440 1 issued by the South Australian Department for Environment and Heritage (DEH) and approval number E 176 issued by Flinders University Animal Ethics Committee.

Specimens used in this project comprised a sub-set of 51 *E. whitii* selected from the laboratory colony of 98 and 20 *E. multiscutata*, being the total laboratory colony of this species.

The number of *E. multiscutata* held was optimised at 20 for logistical and ethical reasons. There was insufficient space available in the laboratory to hold more than this combined number of specimens. The use of a larger number of *E. whitii* contributed towards maintaining novel encounters between individuals of the two species. *E. whitii* were selected as the larger group for two reasons; (i) *E. whitii* were required for another project and could, with judicious use, be shared between the two projects (ii) Capturing *E. multiscutata* in the field caused more ecological impact because their burrows, which are quite extensive and used by other individuals, generally had to be destroyed during capture, whereas *E. whitii* could often be captured by lifting and replacing rocks.

Housing of laboratory colonies

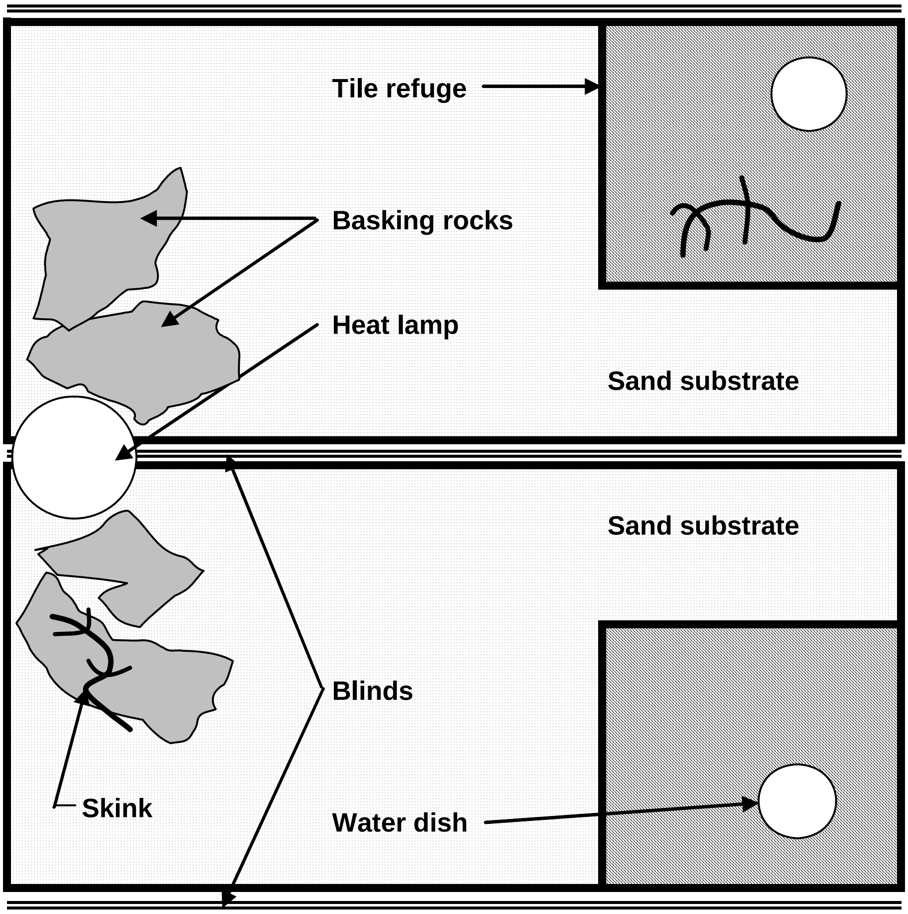
The skinks were either housed separately, in pairs as captured in the field, or as parent/offspring (lab–born) family groups. Other *E. whitii* were held in larger familiar groups as captured in the field but these were not utilized in this study.

Enclosures for specimens of both species selected for this study were rectangular glass terraria 600 mm long x 305 mm wide x 300 mm high. The terraria were positioned in pairs on shelves in 25°C constant temperature rooms on a 12 hr light/dark cycle. A 120 W heat-lamp was positioned centrally above each pair of tanks 450 mm above the shelf level. The heat lamp was on for eight hours per day, nominally 9:00 am to 5:00 pm, creating a basking site temperature of 34°C. These conditions approximated the summer season in the field. Plain cardboard blinds surrounded each tank so that there was no visual contact between unfamiliar skinks.

Diet included crickets, mealworms, Wombaroo® reptile supplement, egg and a variable mixture of frozen peas or frozen mixed vegetables (cooked as per packet instructions) watermelon, spinach, broccoli and banana. A constant supply of drinking water was provided in Petri dishes.

The terraria were landscaped with a sand substrate approximately five millimetres deep. In each tank two basking rocks were placed side by side under the heat lamp. Besides providing basking sites these rocks also provided potential shelter in the crevices between them and under irregular convex areas at their base. However the main refuge shelter was constructed from concrete tiles, 190 mm long x 190 mm wide x 30 mm thick, placed on top of two supports. These supports were '**L**' – shaped PVC angle sections approximately 90 mm long. The angles were inverted to create triangular supports. Each 'leg' of the L-shape was 25 mm long and 2 mm thick. The refuges were positioned at the end of the tanks in the corner opposite the heat lamp abutting two of the walls. This arrangement created a potential refuge the full area of the tile and 19 mm high. However the skinks could modify the actual refuge area by moving the sand substrate. Figure 6 shows the general arrangement of 'home' enclosures.

Figure 6: Diagrammatic plan layout of laboratory colony enclosures



Handling of skinks and equipment during experiments

Skinks were captured by hand from their home terraria for use in the experimental trials. To avoid unnecessary handling the skinks were immediately placed into clear plastic containers with tightly-fitting lids and air holes drilled in the sides. The container's dimensions were 175 mm long x 120 mm wide x 55 mm high. A settling period of one hour was normally allowed in the temporary containers prior to commencement of the trials. Variations from this procedure are described individually for each experiment in the relevant chapters of this thesis.

The skinks were introduced into their experimental arenas by placing the plastic containers in the arena and removing the lids to allow the skinks to escape.

I wore Latex® examination gloves during capture and all subsequent handling. Gloves were changed between skinks to avoid any cross-contamination of odours. All test arenas and other smooth-surfaced experimental paraphernalia were thoroughly cleaned with 70% alcohol between replicate trials. Refuge tiles were thoroughly washed in hot water and detergent, rinsed and allowed to dry between each replicate. Clean sand substrate was also used for each replicate.

Experimental procedures

Experiments were conducted in novel glass arenas of identical size to the 'home' enclosures but landscaped in a manner appropriate for each investigation. Details of each experimental setup are described in the relevant chapters. The only variation from this general procedure was the recording of diurnal activity patterns. These observations were gathered from the skinks' 'home' enclosures.

Experiments were filmed and recorded onto VHS video cassettes for later viewing. This avoided unnecessary observer influence on the skinks during the course of the trials. Each skink was allowed at least two-weeks to rest between uses to avoid any habituation to experimental techniques or familiarity with other skinks. Video tapes were viewed either at normal speed or frame by frame as required. Often, sections of the tapes had to be viewed repeatedly to record all of the behaviour, especially interactions between skinks.

Observations were logged onto time-stamped electronic data files developed specifically for this project. Each change of status of the skinks' behaviour was entered into a single-column against the appropriate time-stamp. Data were then automatically generated and summarised in variables in these computer files using Boolean logic, built-in functions and arithmetic and comparison operators. Automatic data validation checks were carried out during data entry using logical functions and conditional formatting. Data summaries were also cross-validated using comparison operators and conditional formatting.

Behaviours, such as basking, refuging and escaping, were recorded as durational events while others, such as tongue-flicks and tail-lashes, were recorded as spike events. These are indicated in the results section in the relevant chapter and in the ethogram in Chapter 6. Data from the computer files were copied into files in the statistical analysis program, SPSS® version 11.5 for Windows for analyses.

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CHAPTER 3

Habitat differentiation between *Egernia whitii* and *Egernia multiscutata* on Wedge Island

Abstract

Two Australian skink species of the *Egernia* genus, *E. multiscutata* and *E. whitii,* are sympatric on Wedge Island in South Australia’s Spencer Gulf. Conventional ecological theory holds that where

species compete for resources in a stable environment coexistence can only occur if there is partitioning of the resources. Here I ask whether resource partitioning is evident on Wedge Island?

A survey involving 47,170 meters of transects covering most of Wedge Island was carried out. Data were analysed using Chi squared analyses and logistic regression. The results demonstrated resource partitioning between the study species on Wedge Island as evidenced by the differential distribution of the species among substrates containing different habitat parameters, particularly those which provide the resources for permanent refuge shelters. This partitioning was not mediated by avoidance of those habitat features occupied by the opponent species but by the presence of the opponent species, combined with an attraction to suitable substrates.

Introduction

Background

Mackenzie *et al.* (1998) describe two possible outcomes if two species compete for resources in a stable, homogeneous environment. The first is that one species will out-compete the other, eventually excluding it (the so-called 'competitive exclusion principle'). The second is that both species will manage to coexist. The authors assert that such coexistence can only occur if the species' niches are in some way differentiated, that is, their resources are partitioned in such a way that interspecific competition for them is weak or non-existent.

There is a long history of studies on competitive exclusion in the scientific literature beginning with Gause (1934) and supported by a range of theoretical, field, and experimental studies and model systems, including crustaceans (Bovbjerg 1969), phytoplankton (Richerson *et al.* 1970), fishes (Zaret and Rand 1971), mammals (Brown 1971), amphibians (Jaeger 1971), birds (Terborgh 1985), viruses (Feng and Velasco-Hernandez 1996), and reptiles (Shine 1977; Reinert 1984; Langkilde *et al.* 2003).

Notwithstanding the prediction of the competitive exclusion principle, similar species are often found to coexist in the wild (Hambright and Zohary 2000). Studies, such as those above, demonstrate or propose resource partitioning as the means by which such coexistence occurs. Species coexistence can manifest resource partitioning in a variety of forms and can be mediated by a range of proximate or ultimate causes, such as food differentiation (Bootsma *et al.* 1996; Garcia and Arroyo 2005), morphology (Renaud and Millien 2001; Kassam D. *et al.* 2004), physiology (Huey 1991; Bollmann *et al.* 2002; Klok and Chown 2003), diurnal and seasonal activity patterns (Albrecht and Gotelli 2001; Hatano *et al.* 2001; Kocàrek 2001), differential behavioural responses, such as feeding behaviour (Werner and Sherry 1987) or antipredator behaviour (Werner and Sherry 1987; Lingle *et al.* 2005) and temporal environmental dynamics (Harrison *et al.* 2001). However it is likely that there will be more than one cause (possibly interacting) of resource partitioning such as those reviewed for a range of amphibians and reptiles by Toft (1985) and among sympatric arboreal mammals (Sushma and Singh 2006).

One commonly accepted means by which resource partitioning of species can be readily identified is through their patterns of distribution among differentiated habitats or refuge sites (Reinert 1984; Howard and Hailey 1999). Resource partitioning of habitats may be evidenced by the species' use of a range of parameters such as: soil type or substrate (Jaeger 1971; Mac Nally 1985), topography (Stewart *et al.* 2002; Vessby and Wikelius 2003), vegetation succession, vertical stratification, or structure (Talbot 1979; Fox *et al.* 2003; Namgail *et al.* 2004; Martin and Possingham 2005) and retreat site use (Shah *et al.* 2003; Shah *et al.* 2004; Webb *et al.* 2004).

Analyses of habitat-use parameters may give an indication of the mechanisms of resource partitioning such as discussed by McCollin (1998) with respect to habitat selection of birds at forest edges, and by Arlettaz (1999) with respect to sympatric bat species.

Studies using reptilian fauna as a model organism have made a significant contribution towards a more general understanding of ecology, often complimenting or challenging conventional precepts developed from studies utilizing 'high-energy' model systems (Huey *et al.* 1983). Many lizard genera contain a large variety of species upon which comparative studies can be undertaken. Caribbean *Anolis* species, in particular, have been well established over several decades as an ideal model system for studies as diverse as sexual selection (Trivers 1976), sexual dimorphism (Schoener 1967), convergent evolution (Losos 1992), adaptive radiations (Irschick *et al.* 1997; Glor *et al.* 2004), physiology (Menaker and Wisner 1983; Summers and Greenberg 1995), population dynamics (Schoener and Schoener 1980), behaviour (Leal and Rodriguez-Robles 1997; Leal 1999), locomotor performance (Losos 1990; Irschick 2000) and interspecific competition and resource partitioning in sympatric species (Schoener 1968; Talbot 1979; Pacala and Roughgarden 1982; Leal and Fleishman 2002).

Like their Caribbean counterparts, the Australian environment and its reptile fauna have long been recognised as providing useful models for most, if not all, ecological concepts due to their unusually diverse nature (Heatwole and Taylor 1987). Pianka (1966) proposed that the independently evolved Australian reptile fauna would provide strong tests of resource partitioning interpretations when compared and contrasted with North American reptile fauna. Subsequently he used both Australian and North American reptile species to emphasise the importance of niche relationships in structuring lizard communities (Pianka 1973).

Many studies have continued to use Australian herpetofauna to investigate aspects of resource partitioning, including trophic partitioning (James 1991), microhabitat separation (Pianka and Pianka 1976), weather related population dynamics (Dickman *et al.* 1999), reproductive biology (Shine 1986), social relations and interspecific competition (Downes and Bauwens 2004; Langkilde *et al.* 2004; Langkilde and Shine 2004) and shelter site selection (Downes and Shine 1998; Shah *et al.* 2004; Webb *et al.* 2004).

Recent evidence of family structure within stable aggregations of the Australian skink, *Egernia stokesii* (Gardner *et al.* 2001) has enhanced the scope of lizards as a model system and focused attention on the *Egernia* genus (Chapple 2003). This includes studies on aspects relating to resource partitioning, such as site fidelity (Stow and Sunnucks 2004), social organisation and home range (Shah *et al.* 2003; Osterwalder *et al.* 2004; Fuller *et al.* 2005), habitat use and shelter site selection (Downes and Shine 1998; Langkilde *et al.* 2003; Langkilde and Shine 2005) and interspecific competition (Langkilde and Shine 2004).

Milton and Hughes (1986) investigated habitat selection by two closely related sympatric *Egernia* species from southern Queensland. They reported no evidence that competition between the sympatric species restricted habitat preferences, suggesting human disturbance may have had some impact on their current distributions. However similar studies with other species, where human impacts are minimal, would be useful in investigating resource partitioning.

Langkilde *et al* (2003) compared retreat site attributes between three broadly sympatric *Egernia* species (and two *Eulamprus* species) in a high altitude environment. They found that although there were some significant relative differences (relating to incident radiation), the species behaved remarkably alike, showing significant preferences for the same shelter-site attributes. This suggested the potential for intensified interspecific competition. The authors recommended that comparative studies, particularly at lower altitudes, would have great potential for investigating the factors that determine spatial distributions of organisms in the wild.

This study uses two sympatric skink species of the *Egernia* genus, *E. multiscutata* and *E. whitii* (a model system that has not previously been used) to determine if there is any interspecific resource partitioning, as described by habitat parameters, and to investigate the determinants of such partitioning.

Model system

Field site

Wedge Island lies 38 km west of mainland Yoke Peninsula in South Australia's Spencer Gulf (35° 09' S, 136° 27' E) and has been separated from the South Australian mainland for approximately 9,000 years (Robinson *et al*. 1996). Land area is 947 hectares (maximum dimensions approximately 5 km long and 1-1½ km wide). Two-hundred metre high cliffs rise from the sea on the southern shores. From this elevation the topography rapidly tapers to sandy beaches on the northern shore.

Wedge Island has a temperate Mediterranean climate with hot, dry summers and cool, wet winters. Although the island has a pastoral history it has been cleared of all domestic grazing animals since the early 1990s and there are now no permanent human inhabitants or pastoral activities (Robinson *et al.* 1996). The island has avoided the introduction of common pest animals such as rabbits, cats and dogs and current management practices prohibit the introduction of any domestic or non-native fauna and flora. Twelve lizard species have been recorded on Wedge Island, including eight members of the Scincidae (skink) family to which the *Egernia* genus belongs (Robinson *et al.* 1996).

The distribution ranges of the study species, *E. multiscutata* and *E. whitii* overlap in South Australia (Cogger 2000) where they are abundant on some offshore islands. Wedge Island's absence of feral predators and competitors, lack of a permanent human population and abundance of the two sympatric *Egernia* species provide a unique opportunity for resource partitioning studies.

Study species

Within the *Egernia* genus there are six generally recognized species groups, one of which is the *whitii* group (Chapple 2003). Two species of the *whitii* group, *E whitii* and *E multiscutata* are the subjects of this study.

E. multiscutata and *E. whitii* are morphologically very similar with similar snout to vent lengths (SVL), ranging from 80-110 mm (Chapple 2003). There was no significant interspecific difference in the SVL of Wedge Island adult specimens (Chapter 4). However, mass and head dimensions were significantly larger in *E. multiscutata* (Chapter 4). The main diagnostic characters between the species are the relative widths of their interparietal and frontal scales (Cogger 2000) and differences in the number of sharp keels on the sub-digital lamellae (Coventry and Robertson 1980).

Most *Egernia* species, including *E. whitii,* are reported to be diurnal (Cogger 2000). Laboratory observations confirm that this is true for both *E. whitii* and *E. multiscutata* (Chapter 5). Both species appear to have generally similar life-history traits and activity patterns (Chapple 2003).

Egernia species, are regarded as generalist and opportunistic feeders (Greer 1989; Brown 1991), their diets containing insects and other invertebrates (Chapple 2003) and notably, plant material, its proportion increasing with increasing body size (Brown 1991). *E. multiscutata* and *E. whitii* have been observed feeding on berries in the field on Wedge Island (personal observations).

Both *E. whitii* and *E. multiscutata* are predominantly burrowing species whose habitats are frequently associated with rocky areas and include coastal heath, open forests and open woodlands (Cogger 2000; Donnellan *et al.* 2002; Chapple and Keogh 2006) such as found on Wedge Island (Robinson *et al.* 1996). *E. multiscutata,* which is a more desert-adapted species, is considered by some to be an obligate burrower whereas *E. whitii* is regarded as either a facultative burrower or saxicolous depending on habitat suitability (Chapple 2003). *E. multiscutata* is reported to construct large complex burrows, whereas *E. whitii* burrows are usually less complex (Donnellan *et al.* 2002; Chapple 2003). The presence of *E. multiscutata* is generally first identified by locating their burrow systems (Coventry and Robertson 1980; Wilson and Knowles 1988; Chapple 2003).

Egernia species are noted for having strong attachments to permanent retreat sites such as rock crevices, hollow logs, dead trees and burrows (e.g. Greer 1989; Chapple 2003). *E. multiscutata* and *E. whitii* are both reported to live in small stable social aggregations (Hickman 1960; Coventry and Robertson 1980; Milton and Hughes

1986; Bruyn 1994; Chapple 2003). The evolution of social aggregations may be influenced partly by retreat-site constraints (Chapple and Keogh 2006). Retreat sites may be constrained by various habitat parameters such as substrate, vegetation, presence/absence of competing species (Langkilde and Shine 2004) and the presence or absence of conspecifics (Stamps 1988). This strong attachment to retreat sites, or refuges, makes the various habitat parameters that may affect them important for analyses (e.g. Downes and Shine 1998; Langkilde and Shine 2004; Langkilde and Shine 2005).

Methods

Overview

I conducted a transect survey of Wedge Island during the skinks' activity season in 2002. The objectives were to determine if a variety of categorical (viz. substrate type and the presence of the other skink species) and interval (foliage height diversity) parameters influenced the distribution of the two study species on Wedge Island.

Survey scope

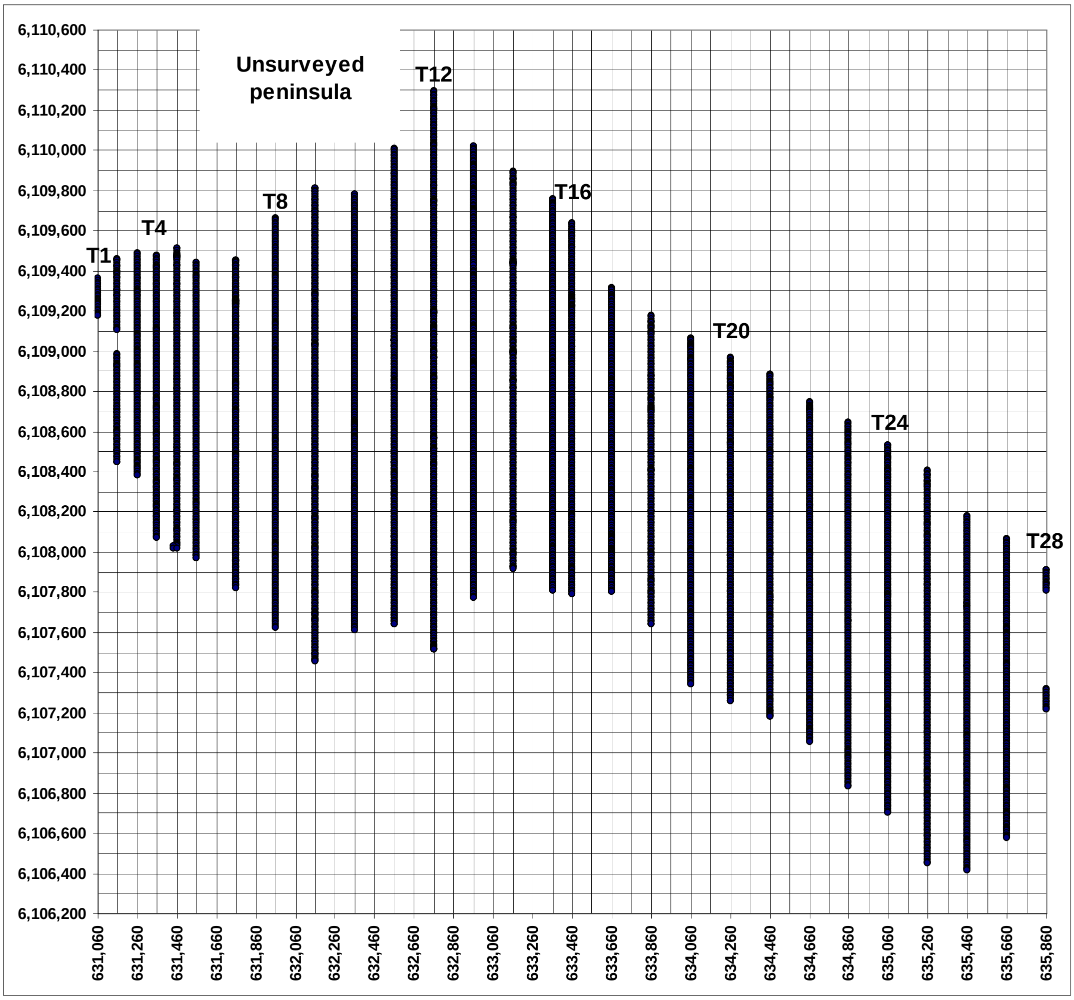
The survey was conducted in the months of April, August, September and December, 2002 and involved a total of 31 survey days. Twenty-eight north-south transect lines (T1 to T28) were established at 200 m or 100 m eastings across the entire island (Figure 1).

The only section of the island that was not surveyed was a small peninsula on the north coast (Figure 1). The substrate of this peninsula was mostly vegetated sand dunes with rocky platforms atop the coastal cliffs. The dunes were honeycombed with the burrows of *Pelagodroma marina* (White-faced Storm-petrel) making it impossible to survey the area without collapsing the burrows. *E. multiscutata* were observed to make use of these burrows as temporary refugia while traversing the area. Refer to Chapter 2, Figure 1 for an aerial photograph of Wedge Island showing the small northern peninsula.

Transect 1 (T1) and Transect 28 (T28) were established on eastings as close as practicable to the cliff-edges at the western and eastern boundaries of the island respectively. The interruptions to transects T2 and T28 were the result of the intrusion of bays into the coastline. For logistical reasons the 28 transects were surveyed in haphazard order.

Transects T1-T6 were surveyed at 100 m eastings rather than 200 m eastings. This generated three extra transects that were intended to substitute for an equivalent distance through similar habitat from the unsurveyed peninsula. The fixed eastings of transects T1 and T28 at the western and eastern extremities of the island plus the additional 100 m transects between T1 and T6 resulted in a 100 m separation between T15 and T16. The total distance of linear transects for the survey was 47,170 m.

Figure 1: North-south survey transects, Wedge Island, South Australia shown on a 100 m grid reference



Sampling methods

Overview

I used a hand-held Garmin® GPS 12 Personal Navigator® (GPS) to establish the starting coordinates for each transect. The course was set and maintained using a hand-held magnetic compass and line-of-sight to prominent landscape features, such as trees, along the transect lines. Headings were either due south or due north. Position was checked regularly using the GPS.

Sampling

General: I surveyed the transects on foot, recording visual observations along the way. Preliminary investigations showed that skink sightings and captures for both species were scarce when temperatures exceeded 30°C or if there was steady rain.

Therefore no sampling was attempted if the rain was steady or the temperature was above 28°C (mean survey temperature was 20.0°C).

At the start of each transect I logged the date, start time and start coordinates (using the GPS) and I recorded descriptions of habitat parameters such as substrate and vegetation structure as well as the presence or absence of the study species. I checked regularly to ensure that the maximum desirable survey temperature was not exceeded during sampling and paused sampling if rain occurred.

To optimise sampling effort in the field, data for all parameters in the study transect were initially recorded as contiguous with the previous observations in each particular transect until an observed change in status was encountered. At this point I recorded the new description, along with all other parameters. However for analyses the 'notional' sampling units were 10m linear resource plots (resource plots) along the transects. These notional resource plots were automatically generated from the field data in an electronic database subsequent to collection (see details under the 'Data handling' subheading below).

Substrate: Seventeen substrate categories were initially defined and recorded during the survey. These are described in Table 1 of the data handling and analyses section. Each observed change of substrate type encountered was recorded along with its GPS coordinates and all other parameters. These initial substrate descriptions were subsequently grouped into broader substrate categories with similar characteristics (see Data handling and analyses section below).

Vegetation: In the field survey I described each vegetation life-form and stratum, that is, trees, shrubs, hummock grasses and herbaceous layer according to Specht and Specht's percentage projective foliage cover (Specht and Specht 1999). This method is logistically simple to estimate in a remote field situation since minimal equipment is required. Specht and Specht (1999) use the height and life-form of the vegetation stratum and the 'shade', or the percentage projective foliage cover that it casts on the ground to produce a textual description of the vegetation. I added a numerical grid reference to this to facilitate efficient field recording and electronic data manipulation. For example; trees between 5 m and 10 m tall that project 40% shade cover on the ground would be classed as "low open-forest" using the Specht and Specht's (1999) textual method and '3,2' using my numerical grid method (Table 1).

Although the adapted Specht and Specht's (1999) method was efficient in the field survey it did not facilitate statistical analysis well, since no scale is implied for various strata. Therefore I converted these data into a foliage height diversity index for statistical analyses (see details under Data handling and analyses below).

Table 1: Description of percentage projective foliage cover for each vegetation life-form and stratum.

		Projective foliage cover, %			
Life form and height of stratum		**100-70** **1**	**70-30** **2**	**30-10** **3**	**<10** **4**
Trees > 30m	**1**	Tall closed-forest	Tall open-forest	Tall woodland	-
Trees 10 – 30m	**2**	Closed-forest	Open-forest	Woodland	Open-woodland
Trees 5 10m	**3**	Low closed-forest	Low open-forest	Low woodland	Low open-woodland
Trees < 5m	**4**	Very low closed-forest	Very low open-forest	Very low woodland	Very low open-woodland
Shrubs > 2m	**5**	Closed-scrub	Open-scrub	Tall shrubland	Tall open-shrubland
Shrubs 0.25 – 2m					
Sclerophyllous and semi-sclerophyllous	**6**	Closed-heathland	Heathland	Open-heathland	Sparse-heathland
Non-sclerophyllous	**7**	Low closed-scrub	Low open-scrub	Low shrubland	Low open-shrubland
Shrubs < 0.25m					
Sclerophyllous and semi-sclerophyllous	**8**	-	-	Dwarf open-heathland (fell-field)	Dwarf sparse-shrubland (fell-field)
Non-sclerophyllous	**9**	-	-	Dwarf open-shrubland	Dwarf sparse-shrubland
Hummock grasses	**10**	-	Dense hummock grassland	Hummock grassland	Open hummock grassland
Herbaceous layer					
Graminoids & grass	**11**	Closed (tussock) grassland	(Tussock) grassland	Open (tussock) grassland	Sparse (tussock) grassland
Sedges	**12**	Closed-sedgeland	Sedgeland	Open-sedgeland	Sparse sedgeland
Herbs	**13**	Closed-herbland	Herbland	Sparse-herbland	Open-herbland
Ferns	**14**	Closed-fernland	Fernland	-	-
Reeds and rushes	**15**	Closed-reedland	Reedland	-	-

Adapted from Specht and Specht (1999)

Species' presence/absence: *Egernia* species were recorded as present if evidence of their existence could be confidently identified within visual distance of the observer's position on the transect line. Consequently some sightings, captures and other evidence of their presence were, in the strictest sense, slightly 'off-transect'. The mean off-transect distance for presence observations was 1.0 m, well within the accuracy of the GPS measurements. Absences were recorded if no continued evidence of *Egernia* species was observed.

I used a suite of characters as an aid to differentiation between the study species. On Wedge Island 40% of captured *E. multiscutata* were plain colour morphs, whereas no plain colour morphs of *E. whitii* were found. *E. multiscutata* were generally found to have vertically-banded patterning of the supralabial and infralabial scales, whereas *E. whitii* generally had horizontal banding of these scales (Chapter 2, figures 2 and 3). With experience the differences in mass and head dimensions (Chapter 4) became very apparent in the field. In combination with the previously mentioned characters, close association of the skinks with the characteristic burrows of *E. multiscutata* was also an additional identifier (Coventry and Robertson 1980; Wilson and Knowles 1988; Chapple 2003). Where any doubt existed about the identification of a specimen it was either captured and identified using Cogger's diagnostic key (Cogger 2000, pp 454 - 456) or recorded as absent.

Every observed presence of each species was recorded along with all other parameters at the observation site. This potentially produced multiple records within each resource plot. However any multiple recordings were aggregated to one record for each resource plot prior to analyses (see 'Data handling and analyses' subheading below).

E. multiscutata were recorded as present in a resource plot if a specimen was seen or captured or if their active characteristic burrow entrances were present (Coventry and Robertson 1980; Wilson and Knowles 1988; Chapple 2003). Burrow entrances were considered to be active if they were clear of debris and had fresh tracks around them. There were only 24 captures of *E. multiscutata* since they usually retreated into their burrow systems upon approach. Capture of this species was achieved by digging them out of their burrows. Capture of larger numbers would have resulted in undesirable widespread destruction of habitat in a broad-acre survey.

E. whitii were recorded as present if a specimen was seen or captured and identified. Capture of *E. whitii* was relatively easily achieved (184 captures) by lifting rocks and grabbing the specimens by hand. However it was not possible to record them as present by their active burrow systems alone (usually shallow burrows under loose rocks) since these burrows could potentially have been made by other lizard species such as *Ctenophorus fionii* and *Nephrurus milii*, both of which were found under rocks in co-habitation with *E. whitii*. Therefore the sampling method was potentially biased towards *E. multiscutata* in terms of species density. However this bias was reduced by the aggregation of observations into one presence or absence record for each species in each resource plot prior to analyses.

Data handling and analyses

Grid reference positions for each change of landscape feature and observed presence of skinks was measured with the GPS. The resultant data were recorded into survey-specific logbooks.

The logbook data were transcribed into electronic data files in Microsoft® Office Excel 2003 (Excel) format. Field data transcribed into the Excel files were structured within 10 m notional resource plots. The start and finish coordinates of these were automatically generated from the starting coordinates of the transect in question. In this way the notional sampling unit became the 10 m resource plot.

All parameters in the resource plots in the Excel files were automatically recorded as being the same as the previous record until a change in status was observed. Separate records were generated for each presence/absence of the two study species and each change in habitat parameter. Therefore there was the potential for multiple habitat descriptions and presence/absence observations within a single resource plot with each habitat description being mutually exclusive data points. This resulted in a total of 4,717 resource plots containing 5,271 individual records.

The recorded projective foliage cover values were automatically converted into a foliage height diversity index (FHDI) in the Excel spreadsheets using the formula $(-\ \Sigma/i\ \mathrm{P}_i \log_e \mathrm{P}_i)$ where P_i is the proportion of the total foliage that occurs in the i^{th} vegetation stratum (MacArthur and MacArthur 1961). The 'P' values were converted from the Specht and Specht (1999) adapted numerical grid reference into four strata chosen to represent, trees, shrubs, herbs and grasses. Using the FHDI rather than

Specht and Specht's (1999) projective foliage cover facilitated statistical analyses in that increased FHDI values directly represented increased diversity in the vegetation structure.

All data were transferred from Excel spreadsheets to the statistical analysis program SPSS® version 11.5 for Windows (SPSS) for analyses. Since the base unit chosen for analysis was the 10 m resource plot it was necessary to aggregate the records upon transfer to the SPSS data files. Each resource plot thus contained a single record that potentially had multiple data points for separate non-exclusive dichotomous categorical (0 or 1) substrate parameters and for the presence/absence of each species. Mean values were used for aggregated FHDI. For example, one resource plot record may have both species' present and more than one type of substrate with a mean value for FHDI. The number of individual records was thereby reconciled with the number of resource plots and reduced to 4,717.

Substrate types: Seventeen different substrate types were identified and recorded as categorical variables during the transect survey. However these were later grouped and recoded into five separate substrate variables which reflected broader substrate characteristics with similar features. These similarities were defined by the presence of sand, loam, rocks, rocky platforms and areas which were *a priori* considered inhospitable, such as vehicular tracks, swamps and the airstrip (Table 2). Any resource plot could potentially contain more than one substrate thus the five separate substrate variables were not necessarily mutually exclusive.

For the purpose of logistic regression analyses (refer to 'Determinants of distribution' sub-heading below) the five separate substrate variables were recoded into a new predictor variable, 'Substrat'. Substrat is a 'dummy' categorical variable containing six possible mutually-exclusive categories. The substrat variable enabled the odds-ratios of the predictor variables to be assessed against the substrate 'inhospitable' which was set as the reference category. The first 5 categories in the nominal substrat variable have the same description as the substrate variables 1-5 in Table 2. However 'substrat' also contains a 6th category, 'complex'. 'Complex' represents any combinations of the substrate numbers 1 to 5 and is used to codify any resource plots where two or more different substrate types were found within a single plot. 'Complex' was used for preliminary investigations into the distribution of the individual species and the concurrent presence of both species, including the possible effects of substrate transitions.

Table 2: Recorded substrate types and their recoded descriptions used for statistical analyses

Recorded substrate number	Substrate description	Recoded substrate variables	
		Independent predictor variables not exclusive within a resource plot	**'Substrat' with 'dummy' variables** mutually exclusive within a resource plot
1	Sea	**1. Inhospitable**	**1. Inhospitable** (reference category)
5	Blow out in sand dunes		
15	Samphire swamp		
16	Vehicular tracks and airstrip		
2	Beach, including vegetated areas	**2. Sand / loam**	**2. Sand / loam**
3	Low sand dune		
4	High sand dune		
6	Sandy soil		
8	Loamy soil		
17	Sand mounds with loose rocks on an embedded rocky platform	**3. Rock / sand**	**3. Rock / sand**
7	Sand with loose rocks		
13	Sand mounds on rocky platform		
9	Loam with embedded rocks	**4. Rock / loam**	**4. Rock / loam**
10	Loam with loose rocks		
11	Rocky platform with embedded rock	**5. Rocky platform**	**5. Rocky platform**
12	Rocky platform with loose rocks		
14	Cliff-top		
		Any combination of 1-5	**6. Complex**

Logistic regression analyses: Since the two dependent variables (presence/absence of each species) and the majority of the predictor variables were categorical, Logistic regression was chosen as the primary means of analysing the survey data (Pallant 2002).

I used the forced entry method (Pallant 2002) with the presence/absence of each species analysed in turn as the dependent variable individually while the other species was included as a predictor variable.

The analyses used the aggregated SPSS data file for 10 m resource plots using the 'dummy' predictor variable 'Substrat' with its substrate categories. However the dummy variable 'complex' was omitted from analyses since its value did not reflect a specific independent habitat type. Consequently the number of resource plots was reduced in these analyses from 4,717 to 4,617. Substrate category 'inhospitable' was selected and set as the reference category for odds-ratio comparisons. The predictor variable, 'FDHI' (foliage height diversity index), is continuous with higher values representing greater complexity.

Results

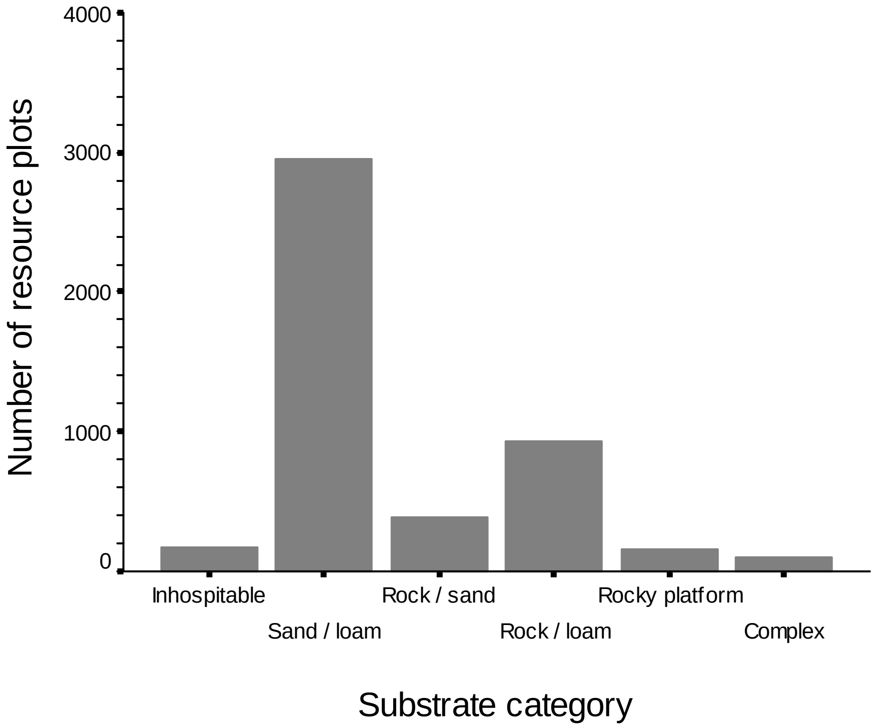
Preliminary data investigations

In this section I present the results of SPSS descriptives statistics used to identify the distributions of the two study species at the time of the survey, along with their relationship to habitat parameters, each other and expected distributions.

Frequency of habitat types

Figure 2 shows the number of resource plots that contained each of the substrate categories for the variable 'substrat' shown in Table 2 of the methods section.

Figure 2: Number of resource plots containing each substrate category



The most common substrate category on Wedge Island was ‘sand / loam’ which was found in 62.7% of all resource plots. This substrate includes all of the non-rocky areas that contain sandy or loamy soils.

‘Rock / loam’ was the next most common with 19.8% of resource plots containing this substrate. Many of the areas with residual woodland had rock / loam substrates.

‘Rock / sand’ was found in 8.3% of resource plots. This substrate was usually found along drainage lines in the vegetated dunes where water run-off had eroded the topsoil. Consequently it was quite distinct from rock / loam and was not grouped with it.

‘Rocky platform’ was only found in 3.4% of resource plots. This substrate occurred in a narrow strip along the tops of coastal cliffs around approximately $^{2}/_{3}$ of the island and often contained loose as well as embedded rocks. Sand dunes frequently abutted this substrate.

‘Inhospitable’ substrate was found in 3.8% of resource plots. ‘Inhospitable’ includes all of those areas, such as tracks and swamp, which were considered *a priori* to be unlikely habitats for skinks. Nevertheless there was some skink occupancy in these areas, particularly where burrow systems had an exit at the margin between edge-vegetation and tracks.

'Complex' substrates, that is, more than one substrate category, were found in 2.1% of resource plots.

The two most common substrates, 'sand / loam' and 'rock / sand' were also more contiguous in their distributions than the other substrates. The mean number of contiguous resource plots containing 'sand / loam' substrate was 33, *SE* = 3.55 (a linear distance of 330 m) and 24, *SE* = 3.61 for 'rock / loam'. The mean number of contiguous resource plots containing the remaining substrates was 10, *SE* = 1.72 for 'rock / sand', 8, *SE* = 2.24 for 'rocky platform', 4, *SE* = 0.77 for 'inhospitable and 1, *SE* = 0.01 for 'complex'. 25% of 'sand / loam' and 15% of 'rock / loam' substrate occurrences were found in patches where 50 resource plots or more (a linear distance of at least 500m) abutted each other. None of the other substrates were found to be contiguous in resource plots over the same distance.

The mean distance, or gaps, between patches of the various substrates on the same transect was: 17 m, *SE* = 2.03 for 'sand/ loam', 45 m, *SE* = 3.96 for 'complex', 83 m, *SE* = 11.23 for 'inhospitable', 92 m, *SE* = 13.95 for 'rock / loam', 116 m, *SE* = 27.21 for 'rock / sand', and 442 m, *SE* = 244.12 for 'rocky platform'.

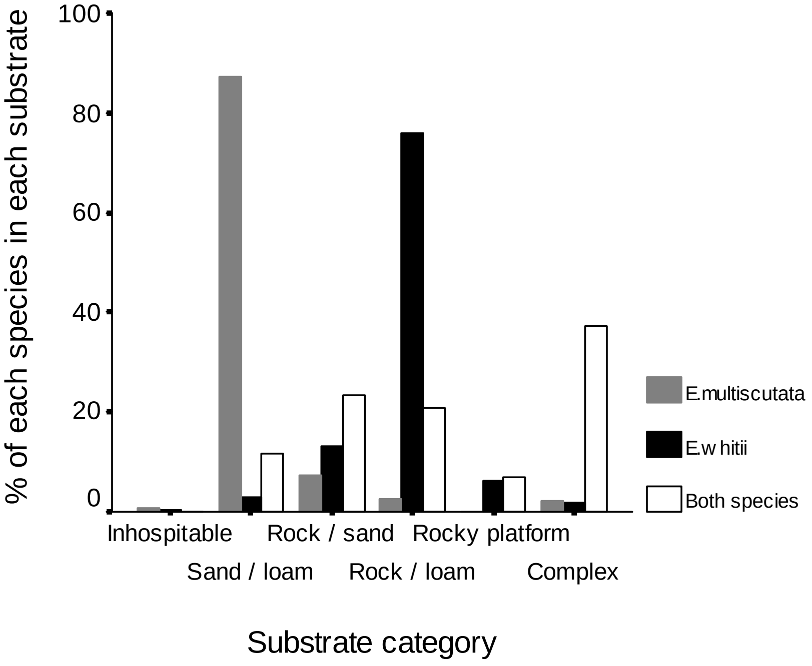
Distribution of the two *Egernia* species

Overview: Of the 4,717 surveyed resource plots 2,285 were occupied by *E. multiscutata* exclusive of other *Egernia* species and 745 exclusively by *E. whitii*. Forty-three resource plots were co-occupied by *E. multiscutata* and *E. whitii*. Therefore there was a total of 3,073 occupied resource plots and 1,644 that were unoccupied by either species. The combined total number of resource plots containing each species was 2,328 for *E. multiscutata* and 788 for *E. whitii*.

Substrate occupancy: Figure 3 shows the percentage of all individuals of each species recorded during the survey that occupied each of the six mutually exclusive substrate categories. It also includes those instances when both species occurred concurrently within a resource plot.

There was apparent partitioning between the two species in terms of 'sand / loam' and 'rock / loam', substrates in which the majority of skinks were found. Both species were present concurrently in some resource plots containing each of the substrate categories other than 'inhospitable'.

Figure 3: Percentage of each or both species occupying each substrate category



Eighty-seven percent of all observed *E. multiscutata* occurred in resource plots containing 'sand / loam' substrate, whereas 76% of *E. whitii* were found in resource plots containing 'rock / loam' substrate. In each case there were very low proportions of the opponent species. The ratios of the percentages of all observed individuals of the predominant species to the secondary species within these substrates were 29:1 for 'sand / loam' and 30:1 for 'rock / loam'.

Resource plots containing *E. whitii* were also found in all of the other substrates. The proportions of *E. whitii* in each substrate were: 'inhospitable' (<1%), 'sand / loam' (3%), 'rock / sand' (13%), 'rocky platform' (6%) and in 'complex' (2%), that is, where there was more than one substrate within a resource plot.

Resource plots containing *E. multiscutata* were also found in all other substrates. The proportions of *E. multiscutata* in each substrate were: 'inhospitable' (<1%), 'rock / sand' (7%), 'rock / loam' (2.5%), 'rocky platform' (<1.0%) and in 'complex' (2%) substrates.

Resource plots containing both species concurrently were found in all substrates except 'inhospitable'. The proportions of substrates where both species were present were: 'sand / loam' (12%), 'rock / sand' (23%), 'rock / loam' (21%), 'rocky platform' (7%) and 'complex' (37%).

Comparison of expected and actual substrate occupancy: The values reported above are for an uneven distribution of resource plots per Figure 2. To investigate the distribution of *Egernia* species more thoroughly and overcome the problem of the uneven distribution of resource plots I carried out a cross-tabulation investigation in SPSS. I compared the expected number of resource plots containing each species for each substrate category (i.e. assuming no resource preferences) with the actual distribution as observed in the field survey. The results are presented in Figure 4(a) and 4 (b) for individual species and in Figure 5 where both species were present concurrently.

Figure 4(a): Expected and actual numbers of resource plots containing *Egernia multiscutata* in each substrate category.

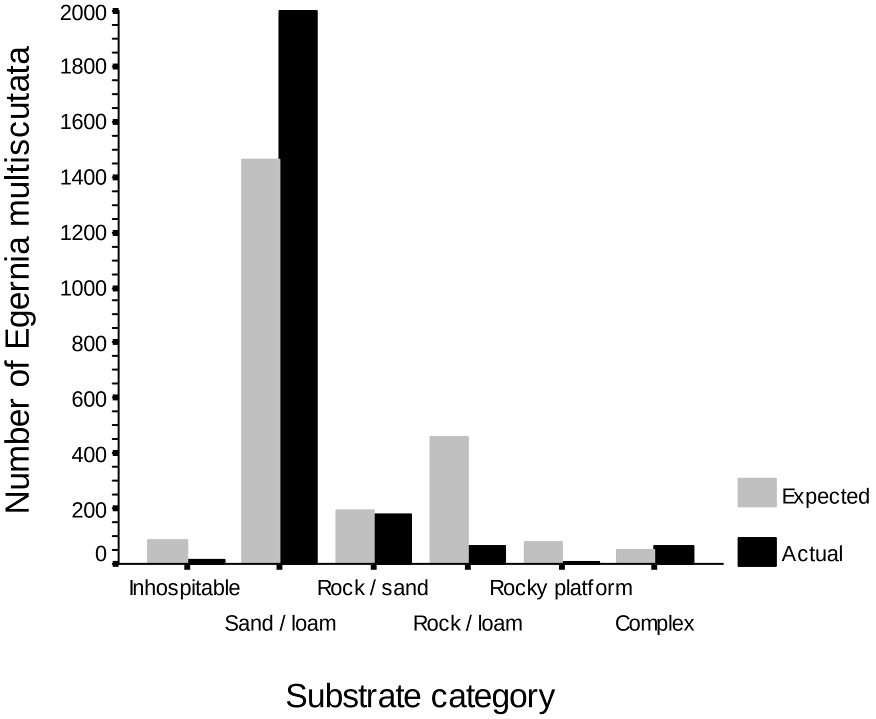
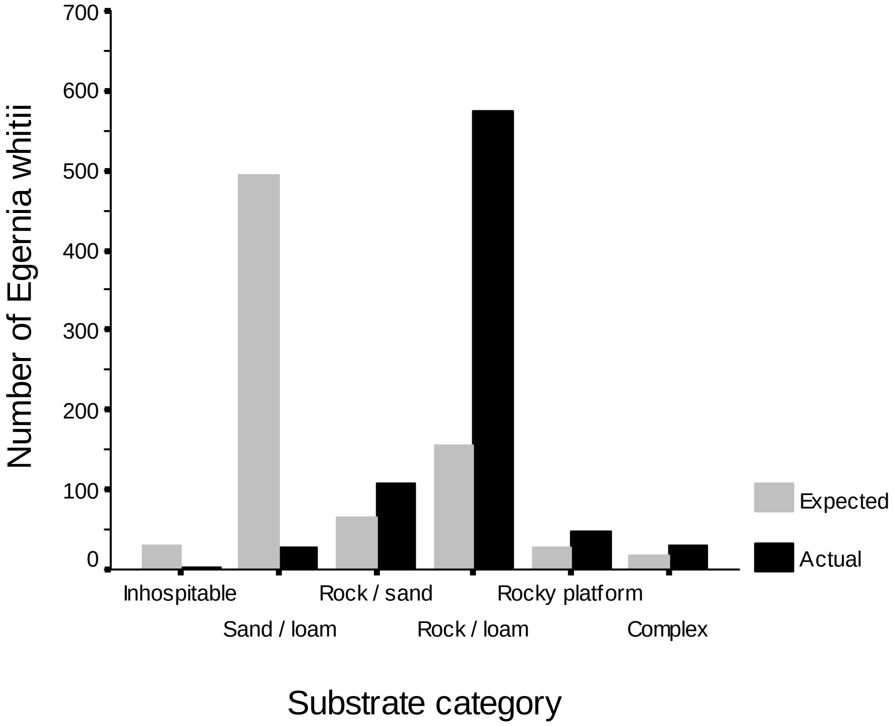


Figure 4(b): Expected and actual numbers of resource plots containing *Egernia whitii* in each substrate category.



Comparisons between the ‘actual’ resource plots containing each of the species with the ‘expected’ values show that on many occasions the actual distributions of the two species varied considerably from expectations for random assortment.

Not surprisingly resource plots containing each of the species were under-represented in the ‘inhospitable’ substrate category compared with random assortment, for *E. multiscutata* ($\chi^2_1 = 96.4$, $P<0.001$) and for *E. whitii* ($\chi^2_1 = 28.0$, $P<0.001$). This suggests that the *a priori* estimation of substrates unsuitable for habitation was substantially justified.

Comparison of the ‘actual’ values for the two species in Figures 4 (a) and (b) support the earlier indication that there was some resource partitioning between them in terms of ‘sand / loam’ and ‘rock / loam’ substrate categories. In the substrate category ‘sand / loam’ resource plots containing *E. multiscutata* were significantly over-represented ($\chi^2_1 = 1155.6$, $P<0.001$) compared with expected values (Figure 4 (a)), whereas *E. whitii* were significantly under-represented ($\chi^2_1 = 1410.5$, $P<0.001$) compared with expected values (Figure 4 (b)). Conversely, resource plots containing *E. multiscutata* were significantly under-represented ($\chi^2_1 = 785.1$, $P<0.001$) in the ‘rock / loam’ substrate category (Figure 4 (a)), whereas resource plots containing *E. whitii* were significantly over-represented ($\chi^2_1 = 1747.0$, $P<0.001$) (Figure 4 (b)).

The distribution of the two species in ‘sand / loam’ and ‘rock / loam’ substrates may be an indication that some degree of competitive exclusion occurred between the two species. However they could equally be due to different ultimate substrate preferences between the two species rather than proximate competitive interactions. In either case, neither species fully occupied the resource plots in these substrates to the exclusion of the other.

Resource plots containing *E. whitii* were significantly over-represented ($\chi^2_1 = 40.1$, $P<0.001$) within the ‘rock / sand’ substrate whereas those containing *E. multiscutata* were very close to expectation ($\chi^2_1 = 1.02$, $P = 0.314$).

E. multiscutata was significantly under-represented ($\chi^2_1 = 119.6$, $P<0.001$) in the ‘rocky platform’ category whereas *E. whitii* was significantly over-represented ($\chi^2_1 = 22.5$, $P<0.001$) in this substrate. This substrate description did not include areas with sandy soil that would be suitable for the typical *E. multiscutata* burrow systems (Coventry and Robertson 1980) but it did include loose rocks under which skinks could shelter. However sand dunes, which would be suitable for extensive burrows, sometimes abutted the 'rocky platform' resource plots

Resource plots containing each of the species were significantly over-represented in the 'complex' substrate category, for *E. multiscutata* ($\chi^2_1 = 9.1$, P = 0.003) and for *E. whitii* ($\chi^2_1 = 12.2$, P<0.001). On 38.5% of occasions 'complex' substrates occurred where 'sand / loam' and 'rock / loam substrates abutted, each being the most frequently selected habitat of one of the species. On these occasions it was more likely that each of the species would be present due to the proximity of their selected habitats.

Results from a cross-tabulation investigation into expected and actual presence of both species occurring concurrently within a single resource plot are shown in Figure 5.

Figure 5: Expected and actual numbers of resource plots concurrently containing both *Egernia* species in each substrate category.

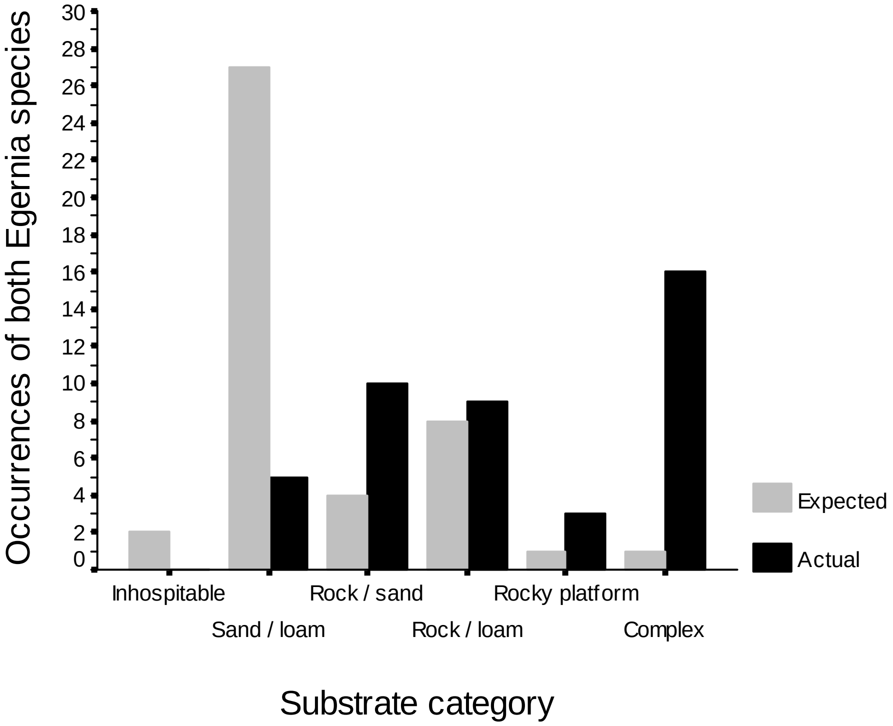


Figure 5 shows that there was concurrent presence of both species within at least some single resource plots for all substrates except 'inhospitable'.

In the 'sand / loam' substrate the actual number of resource plots containing both species concurrently was significantly lower than expectation

($\chi^2_1 = 119.6$, P = 0.003). This may indicate that *E. multiscutata*, which was the main occupier of this substrate (refer to Figure 4 (a)), excluded *E. whitii* to a large degree. However it may also indicate that this substrate was non-preferred by *E. whitii* and hence more available to *E. multiscutata*.

In each of the remaining substrates containing resource plots where both species were present concurrently the actual values were significantly higher than expectation, for rock / sand ($\chi^2_1 = 33.5$, P<0.001), for rock / loam ($\chi^2_1 = 13.5$, P<0.001), for rocky platform ($\chi^2_1 = 5.7$, P = 0.017) and for complex ($\chi^2_1 = 230.5$, P<0.001).

Concurrent presence of the species is an indication that they were sympatric and able to live in close proximity without one species completely excluding the other. However the total number of resource plots where concurrent presence occurred was very small compared with the number of occupied resource plots (43 out of 3,073 occupied plots). Therefore in the majority of cases the skinks appear to have partitioned the habitat resources but with some tolerance in resource use.

This section has presented the distribution of the study species on Wedge Island at the time of the survey. In the following section I investigated some possible determinants of these distributions.

Determinants of distribution

Overview

I carried out logistic regression analyses to investigate the distribution relationships more thoroughly and determine to what degree the various habitat parameters and the presence of the other species affected the odds of the study species being present in a resource plot.

Presentation of results

The results are presented in tabular form in Tables 3 (a) & (b) and 4 (a) & (b). In the first section of the tables, (a), the contribution of the independent variables towards the predictive ability of the model is assessed using the Wald test (Tabachnick and Fiddel 2001). The Wald statistic and its corresponding significance level test the significance of each independent variable on the dependent variable while controlling for other variables and is the ratio of the logistic coefficient, B, to its standard error squared. Variables with significance values of less than 0.05 contribute significantly in the model.

The logistic coefficient, B, in section (a) is analogous to the B values in multiple regression analyses. Negative B values indicate that an increase in the independent variable will result in a decreased probability of the presence of the species under study. Positive B values indicate an increased probability of the species' presence.

The odds ratio values in section (a) represent the proportional change in the odds of the presence of the dependent variable for a unit increase in the independent predictor variable, while controlling for the other predictor variables (Pallant 2002).

For the continuous predictor variable, FHDI (foliage height diversity index), the odds ratio represents the proportional change in odds for a unit increase in the index (on a scale of 1.00 to 10.00 for FHDI).

For the dichotomous categorical predictor variables 'e.mpres' and 'e.wpres' (presence of the competing species) the odds ratio represents the proportional change in odds when the competing species is present compared with when it is absent.

The predictor variables, 'sand / loam', 'rock / sand', 'rock / loam' and 'rocky platform' are dichotomous categories in the 'dummy' variable 'substrat'. The substrate category 'inhospitable' is set as a reference category and therefore not used as a predictor. 'Complex' substrate is excluded since it does not represent a specific independent habitat description. For the substrate variable the odds ratios represent the proportional change in the odds of the dependent species presence when the predictor variable is present compared with when it is absent relative to the reference category.

Odds ratios greater than one indicate increased odds of the study species' presence. Ratios less than one indicate decreased odds of the study species' presence. The more the odds ratio values diverge from one the greater the effect of the independent variable. I also report the 95% CI for the odds ratio. These are the range of values within which we can be 95% confident the reported odds ratio falls. The reported odds ratios are only one of a possible range of values since the 95% CI values can vary widely. Therefore in the text I refer to relative changes and directions of the odds ratios rather than absolute values.

Section (b) of the tables incorporates the Hosmer and Lemeshow Goodness of Fit Test and the overall correct classification of cases for presence and absence of the dependent variable (species). The Hosmer Lemeshow test gives an indication of the improved performance of the model once the predictor variables are included. The Hosmer-Lemeshow test is the most reliable goodness-of-fit test available in SPSS (Pallant 2002). Poor model fit is indicated by a significance value of less than 0.05.

Results of logistic regression analyses

The results of logistic regression analyses using the aggregated SPSS data file are presented in Table 3 (a) & (b) for *E. whitii* and Table 4 (a) & (b) for *E. multiscutata*.

Each species was analysed as the dependent variable individually with the other species used as an independent variable.

Egernia whitii:

Table 3 (a): Logistic regression Wald statistic and odds ratio results for *E. whitii* using the aggregated data file. Refer to 'Presentation of results' above for an explanation of the tables.

Independent Variable	B	S.E.	Wald	Sig.	Odds ratio	95% C.I. for Odds ratio Lower	Upper
FHDI	-0.01	0.03	0.25	0.620	0.99	0.94	1.04
Sand / loam	0.72	0.74	0.93	0.330	2.05	0.48	8.75
Rock / sand	4.23	0.73	33.74	<0.005	68.89	16.52	287.35
Rock / loam	5.08	0.72	49.61	<0.005	160.77	39.11	660.85
Rocky platform	3.62	0.73	24.42	<0.005	37.30	8.88	156.70
E.mpres	-2.36	0.22	119.77	<0.005	0.09	0.06	0.14

N=4,617 df=1

Table 3 (b): Logistic regression goodness of fit and overall correct classification results for *E. whitii*. Refer to 'Presentation of results' above for an explanation of the tables.

Hosmer – Lemeshow Goodness of Fit Chi-square	df	Sig	Classification of cases Overall correct classification, %
52.46	8	<0.005	89.3

Predictive value of independent variables: The significance values in Table 3 (a) show that the foliage height diversity index (FHDI) and 'sand / loam' substrate did not make a significant contribution towards the predictive ability of the model for the presence of *E. whitii*. The variables influencing the presence of *E. whitii* in the model were the remaining three substrate categories and the presence of *E. multiscutata*.

Effect of substrates: When controlling for the other predictor variables the odds ratios for each of the significant substrate categories were all greater than one. Therefore the likelihood of *E. whitii* presence was increased by the presence of these substrates relative to the 'inhospitable' substrate. The substrate with the largest effect was 'rock / loam' followed by 'rock / sand' then 'rocky platform'. These results are consistent with the results shown in Figure 4 (b).

Effect of *E. multiscutata*: The B value for the independent variable, 'e.mpres' indicates that the presence of *E. multiscutata* had a negative effect on the presence of *E. whitii*. The odds ratio for this variable was 0.09. Another way to express this is to take the reciprocal of the odds ratio (1/0.09 = 11.11), that is, the odds of the presence of *E. whitii* were approximately 11 times less likely in the presence of *E. multiscutata* when controlling for other variables. While cause and effect cannot be directly attributed from this analysis the results suggest the possibility that competitive exclusion occurred on some occasions with *E. multiscutata* excluding *E. whitii*. This interpretation is consistent with the apparent partitioning of substrate settlement choices observed in Figure 3.

Model fit: The overall correct classification of cases for the presence and absence of *E. whitii* in the resource plots was 89% (Table 3 (b)). Only one case was misclassified as present when in fact it was absent. All other misclassified cases were predictions for absence when in fact they were present.

The significance of the Hosmer-Lemeshow Goodness of Fit Test was <0.005, indicating a poor model fit. Nevertheless the predictive effects of the parameters studied were still significant and concordant with data presented in Figures 3, 4 (a), 4 (b) and 5.

It is likely that the poor fit was due to the model's tendency to misclassify cases of actual absence for both species. There are probably several parameters that potentially would have improved the model fit but were not recorded or analysed during the survey. Examples could include the presence or absence of predators, vegetation species and patch fragmentation (Jellinek *et al.* 2004), proximity of individuals of the same species, proximity of other species, dimensions and distribution of preferred habitat, ambient weather conditions and suitability of dispersal pathways (Stow *et al.* 2001). Sampling error would also erode the model fit (Mackenzie *et al.* 2004).

Egernia multiscutata:

Table 4 (a): Logistic regression Wald statistic and odds ratio results for *E. multiscutata* using the aggregated data file. Refer to 'Presentation of results' above for an explanation of the tables.

Independent						95% C.I. for Odds ratio	
Variable	B	S.E.	Wald	Sig.	Odds ratio	Lower	Upper
FHDI	0.24	0.02	204.78	<0.005	1.28	1.23	1.32
Sand / loam	2.64	0.30	79.19	<0.005	13.94	7.80	24.90
Rock / sand	2.08	0.32	42.93	<0.005	8.03	4.31	14.96
Rock / loam	0.02	0.33	0.00	0.96	1.02	0.54	1.93
Rocky platform	-0.27	0.51	0.28	0.61	0.76	0.28	2.08
E.wpres	-2.33	0.22	114.74	<0.005	0.10	0.06	0.15

N=4,617 df=1

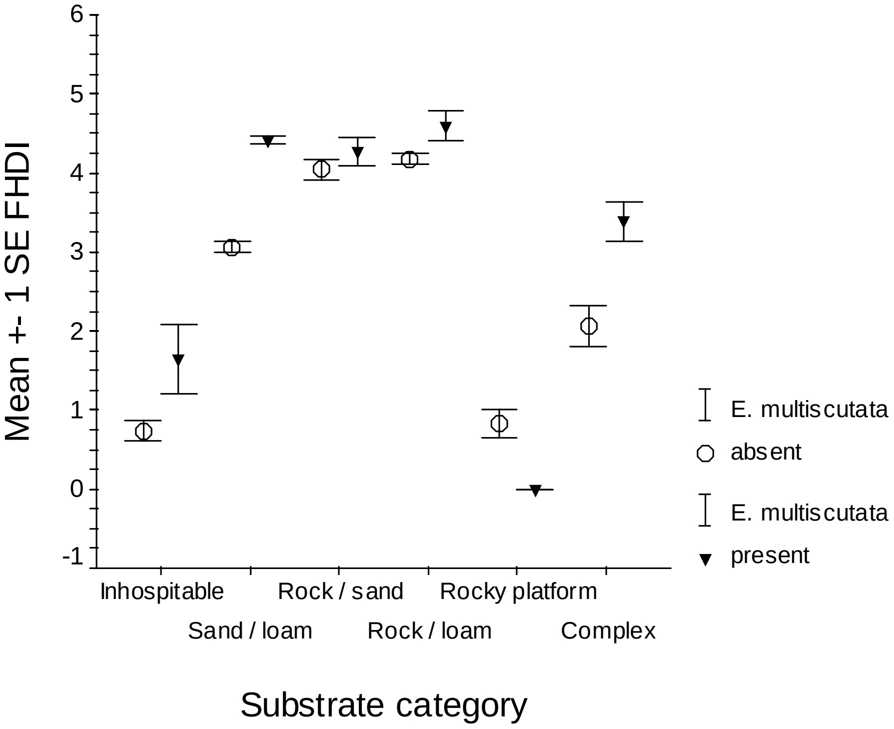
Table 4 (b): Logistic regression goodness of fit and overall correct classification results for *E. multiscutata*. Refer to 'Presentation of results' above for an explanation of the tables.

Hosmer – Lemeshow Goodness of Fit			Classification of cases
Chi-square	df	Sig	Overall correct classification, %
157.43	7	<0.005	73.2

Predictive value of independent variables: The significance values in Table 4 (a) show that neither 'rock / loam' nor 'rocky platform' had a significant effect on the presence of *E. multiscutata* when other variables were controlled for. The variables influencing the presence of *E. multiscutata* in the model were foliage height diversity index (FHDI), the remaining two substrate categories and the presence of *E. whitii*.

Effect of foliage height diversity: Unlike *E. whitii,* there was a positive effect of FHDI on the presence of *E. multiscutata,* at least in the range found at the study site, as indicated by the positive B value in the table. When the other predictor variables were controlled for the odds ratio shows that for each unit increase in FHDI the odds of the presence of *E. multiscutata* were increased. Figure 6 shows *E. multiscutata* presence at increased FHDI for all substrate categories other than ‘rocky platform’, where foliage was typically very sparse.

Figure 6: Mean foliage height diversity index (FHDI) compared with *E. multiscutata* presence/absence for each substrate category.



Effect of substrates: Figure 4 (a) showed that *E. multiscutata* was present in each of the substrate categories, albeit at lower frequencies in some when compared with random sorting. However, when all of the other predictor variables were controlled for the Logistic regression analysis showed that only ‘sand / loam’ and ‘rock / sand were significant relative to ‘inhospitable’ substrate, each having a positive effect on the presence of *E. multiscutata*, Table 4 (a). The odds ratios show that the larger of these substrate effects was for ‘sand / loam’, followed by ‘rock / sand’. ‘Rock / sand’ also had a positive effect on *E. whitii* presence. These analyses support the results of preliminary investigations shown in Figure 3.

Effect of *E. whitii:* There was a significant effect of the variable, 'e.wpres' on the presence of *E. multiscutata* when all other variables were controlled for. The odds ratio for this variable was less than one and the B value was negative, indicating reduced odds of the presence of *E. multiscutata* in presence of *E. whitii*. The reciprocal of the odds ratio of 0.10 is 10.0. This was comparable with the effect of *E. multiscutata* on the presence of *E. whitii*. These results suggest that for each species there were behavioural responses to the presence of the other species that may be an exclusion process resulting in resource partitioning

Model fit: The overall correct classification of cases for the presence and absence of *E. multiscutata* in the resource plots was 73.2% (Table 4 (b)). As with the results for *E. whitii* only one case was misclassified as present when in fact it was absent. All other misclassified cases were predictions for absence when in fact they were present.

The significance of the Hosmer-Lemeshow Goodness of Fit Test was <0.005 indicating a poor model fit. This could be due to the model's tendency to misclassify absences as noted above and the fact that there are probably several missing parameters that would be significant predictors as discussed in the *E. whitii* results section.

Discussion

Frequency of habitat types

Of the six substrate types described in the Wedge Island survey, two, ‘sand / loam’ and ‘rock / loam’, were present in the majority of all resource plots (approximately 83%). Of these two, ‘sand / loam’ was three times more common than ‘rock / loam’ (Figure 2).

Resource plots containing ‘sand / loam’ and ‘rock / loam’ were more contiguous in their distributions than those containing any of the other substrate types. Unlike other substrates they frequently had contiguous patches extending more than 500 linear metres. ‘Sand / loam’ also had the shortest distance between patches, $\bar{x} = 17$ m, $SE = 2.03$, whereas ‘rock / loam’ had a much greater distance between patches, $\bar{x} = 92$ m, $SE = 13.95$. This increased distance may have a negative effect on *E. whitii*’s vulnerability during dispersal from one resource habitat to another, (e.g. Bonnet *et al.* 1999; Stow *et al.* 2001) and impact on its distribution (Diego-Rasilla and Pérez-Mellado 2003).

Distribution of the two Egernia species

Differences in habitat quality could be expected to impact on the spatio-temporal distribution of species (Wiens 2001). For example, (Vickery *et al.* 1994) found that different bird species had different sensitivities to habitat area. Boundaries between patches of favourable habitat are also known to create differential dispersal impediments to species (Haddad 1999). In addition, differences in habitat characteristics (Langkilde *et al.* 2003), outcomes of competitive interactions between (Langkilde and Shine 2004) and among (Akin 1998) species and different ultimate preferences in habitat type between the species may render some resource plots more habitable than others. Consequently the actual distribution of the species is not likely to be random and this was the case on Wedge Island where broad scale habitat partitioning was observed.

Substrate occupancy

Approximately 65% of the 4,717 surveyed resource plots were occupied by *Egernia* species at the time of survey. *E. multiscutata* occupied approximately 74% of these exclusive of *E. whitii* and 24% were occupied by *E. whitii* exclusive of *E. multiscutata*. The remaining 2% of occupied resource plots were co-occupied by the two study species (Figure 3).

Co-occupancy within resource plots suggests a degree of niche overlap in which co-existence could occur. However, Figure 3 shows that the two most common substrate types were broadly partitioned between the two *Egernia* species. *E. whitii* primarily occupied resource plots containing 'rock / loam' substrate (approx. 76% of all *E. whitii* occurrences) whereas *E. multiscutata* primarily occupied resource plots containing 'sand / loam' substrates (approx. 87% of all *E. multiscutata* occurrences). In each case the ratios of the percentages of the predominant species to the secondary species in these two substrates was much higher than for the other substrates (30:1 for 'rock / loam' and 29:1 for 'sand / loam'). These results give a clear indication of substrate resource partitioning between the two species and are concordant with the reported obligate burrowing behaviour of *E. multiscutata* (in sandy substrates) and *E. whitii*'s flexible facultative borrowing or saxicolous behaviour (Chapple 2003). It may be that *E. whitii*'s tendency towards saxicolous behaviour on Wedge Island is an indication that its distribution is limited by the presence of *E. multiscutata*'s rather than by its range of preferred substrates.

The difference in the rate of substrate occupancy between the study species may be partially an artefact of the sampling method since *E. multiscutata* presence could be reliably recorded from the presence of its characteristic burrow systems, whereas *E. whitii* presence could not (Coventry and Robertson 1980; Wilson and Knowles 1988; Chapple 2003). Nevertheless, 'sand / loam' substrate was far more prevalent than other substrates. If resource plots containing this substrate were at least as favourable as others in terms of habitat resources, then it is likely that the species better adapted to its acquisition, and recruitment within it, would be the more abundant (Hokit *et al.* 1999).

Expected and actual substrate occupancy

When allowing for the uneven distribution of substrates, preliminary investigations showed that the actual frequency of resource plots containing each of the study species differed from the null-hypothesis random distribution expectations for all of the substrate*species combinations except for *E. multiscutata**rock / sand (refer to

Figures 4 (a), 4 (b) and 5 and sub-heading “Comparison of expected and actual substrate occupancy:” above for Chi-squared analyses). This is an indication that there was a mechanism, or mechanisms, causing non-random sorting of the species across the various resource plots.

Deviations from null-hypothesis expected distributions of the species were greatest in resource plots containing ‘sand / loam’ substrate, where *E. multiscutata* was the primary species (Figure 4 (a)) and ‘rock /sand’ substrate, where *E. whitii* was the primary species (Figure 4(b)), in each case either indicating exclusion of the opponent species or non-preferred habitat for the opponent species.

Each of the study species was present in significantly greater than expected numbers in resource plots containing ‘complex’ substrates. ‘Complex’ substrates frequently occurred where ‘sand / loam’ and ‘rock / loam’ substrates overlapped. Therefore it was likely that the associated populations of the two species would be brought into close proximity simply due to their presence in their preferred substrates. By definition ‘complex’ substrates have more elements in them than other substrates. This structural complexity may be more productive in terms of food resources (e.g. August 1983) and may allow closer proximity with other skinks whilst avoiding direct interaction (e.g. Schoener 1968; Petren and Case 1998). However ‘complex’ substrates were only found in 2.1% of resource plots, making them unavailable to skinks in the broader scale.

The frequencies of resource plots containing each of the study species were lower than would be expected for ‘inhospitable’ substrate (Figures 4 (a) and 4 (b)). This is in accordance with this substrate’s *a priori* definition and should not be considered surprising.

E. multiscutata was present in lower than expected numbers of resource plots containing the remaining substrates (Figure 4 (a)) except rock / sand, where it was present in expected numbers, whereas *E. whitii* was present in greater than expected numbers (Figure 4 (b) for all remaining substrates. This may be an indication that interactions between the species are a mechanism of partitioning of the habitat resources. *E. whitii* is possibly more adapted to settlement in a broader range of substrates than *E. multiscutata* due to its exclusion by *E. multiscutata* from the most common substrate, ‘sand / loam’. Alternatively, the results could also suggest that

E. multiscutata was less able to access other substrates due to the prior residency of *E. whitii* and is therefore adapted to concentrate in ‘sand / loam’ substrates.

Both species were present concurrently in representative resource plots for all substrates except ‘inhospitable’ (Figure 5). The number of plots with concurrent presence was significantly higher than expected for all of the remaining substrates other than ‘sand / loam’ (primarily *E. multiscutata* territory) where it was significantly lower than expected by random sorting. In ‘rock / loam’ substrates (where *E. whitii* was most prevalent) the concurrent presence of both species was significantly higher than expected by random sorting. These results may be an indication that *E. multiscutata* was more likely to encroach on the territory of *E. whitii* than *vice versa*.

Determinants of distribution

The effects of each of the potential predictor variables on the presence/absence of each species was analysed using logistic regression while controlling for the other variables. The predictor variables were, FHDI, the presence of the other species and each of the substrate types, except for ‘complex’. These were compared with the effect of ‘inhospitable’ substrate. ‘Complex’ was not a unique substrate since it represented any combination of the other substrates. Generally all of these predictor variables had either a positive or negative effect on the presence of one or the other species.

Effect of foliage height diversity (FHDI)

Egernia whitii

Increases in foliage height diversity had no significant effect on the presence of *E. whitii* (Table 3 (a)). This was a little surprising since *E. whitii* has previously been reported to prefer areas with a well developed canopy and shrub layers (Milton and Hughes 1986) and increased structural complexity would be expected to be more productive in terms of food resources (August 1983). However the odds-ratios for the effects of the various substrates indicate that the presence of suitable rocks for refuge sites was the overriding requirement, regardless of FHDI. The result may be an indication of *E. whitii*’s habitat selection flexibility (Chapple 2003).

Egernia multiscutata

Foliage height diversity index had a positive effect on the presence of *E. multiscutata* when controlling for other variables (Table 4 (a)). This effect occurred across all substrates except 'rocky platform' where vegetation was typically sparse (Figure 6) and where *E. multiscutata* were only present in a small number of resource plots (Figure 3 and 4 (a)). *E. multiscutata* burrow entrances were almost always observed to be associated with shrubs in sand at the perimeter of the foliage canopy and this was concordant with previously reported burrow descriptions (Coventry and Robertson 1980; Chapple 2003). It is likely that the roots of shrubs reinforce the sand burrows against collapse and provide cover for predator avoidance.

Effect of substrates

On *Egernia whitii*

All of the substrates other than 'sand / loam' had a positive effect on the presence of *E. whitii* (Table 3 (a)) indicating *E. whitii*'s habitat flexibility. The relative magnitude of the odds-ratio for 'rock / loam' substrate indicates that it was by far the most attractive substrate for occupancy by *E. whitii* This was concordant with *E. whitii*'s reported saxicolous behaviour (Chapple 2003). Importantly, 'sand / loam' substrate, while not having a positive effect on the presence of *E. whitii,* did not have a negative effect either. That is, while controlling for the effect of the presence of the competitor species 'sand / loam' of itself was not a deterrent to settlement, hence it is not surprising that *E. whitii* would be found in this substrate on some occasions.

On *Egernia multiscutata*

Of the analysed substrates only 'sand / loam' and 'rock /sand' had a significant effect on the presence of *E. multiscutata* when the other variables were controlled for. Each of these two had a positive effect, the larger of which was 'sand / loam'. This result supports the notion of *E. multiscutata* being primarily adapted to habitats containing 'sand / loam'. *E. multiscutata* is considered to be an obligate burrower (Chapple *et al.* 2004) for which it would appear to require a sandy substrate, at least in its range on Wedge Island. While there was no significant effect of 'rock / loam' (*E. whitii*'s preferred substrate) on the presence of *E. multiscutata,* neither was there a negative effect.

On both species

'Rock / sand' substrate was unique in having a significantly positive effect on the presence of each of the species (Tables 3(a) and 4(a)). However the proportion of the total number of *E. whitii* in this substrate was almost double that of *E. multiscutata* (Figure 3). 'Rock / sand' substrate may supply sufficient habitat cues to attract settlement of both species (i.e. sand for *E. multiscutata* and rocks for *E. whitii*) (Downes and Shine 1998; Stamps 2001). This result may be an indication that rock / sand was highly contestable and that *E. multiscutata* was less successful in acquiring it. However it may be that acquisition of this uncommon substrate (Figure 2) is less critical to *E. multiscutata* than to *E. whitii* and from a risk/benefit viewpoint less optimal to defend (Stamps 1977).

Effect of competing species

Effect of *E. multiscutata* on *E. whitii* presence

The presence of *E. multiscutata* had a significantly negative effect on the presence of *E. whitii* (approximately 11 times less likely, Table 3 (a)). This is a clear indication that interactions between the species are a proximate mechanism which could result in resource partitioning between them (Downes and Shine 1998; Langkilde *et al.* 2003; Langkilde and Shine 2004). One possible explanation for this outcome is interspecific asymmetries in head size and mass (Chapter 4) which may endow *E. multiscutata* with a competitive advantage in agonistic encounters. It would appear from the results that either *E. whitii* was avoiding direct competition with *E. multiscutata* by selecting habitat in which *E. multiscutata* was not present, or *E. multiscutata* was overtly excluding *E. whitii* from its presence.

Effect of *E. whitii* on *E. multiscutata* presence

The presence of *E. whitii* had a significantly negative effect on the presence of *E. multiscutata* (approximately 10 times less likely, Table 4 (a)). This was very similar to the effect of *E. multiscutata* on *E. whitii* and again is a clear indication that interactions between the species result in resource partitioning (Downes and Shine 1998; Langkilde *et al.* 2003; Langkilde and Shine 2004). Possible interpretations could include that either *E. multiscutata* was avoiding direct competition with *E. whitii* on a risk/benefit (Stamps 1977) basis by selecting habitat in which *E. whitii* was not present, or that *E. whitii* was overtly excluding *E. multiscutata* from its presence.

General considerations

The results of this survey and analyses show a marked habitat resource partitioning between the study species. This differentiation is mainly between sandy substrates (*E. multiscutata*) and rocky substrates (*E. whitii*) and is largely concordant with previously reported habitat preferences for both species but indicative of some constraints on the distribution of both species. There is also some overlap of the species in most substrates, indicating some tolerance of close proximity, possibly on a risk/benefit basis. Analyses also indicate that interspecific interactions between the species are a likely mechanism of the observed partitioning.

Experimental studies using this model system and in which morphological asymmetries, habitat preferences and interspecific competition are investigated would be very useful in gaining a more complete understanding of resource partitioning between these species on Wedge Island.

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CHAPTER 4

Morphological comparisons between *Egernia whitii* and *Egernia multiscutata*

Abstract

Larger size is generally considered to confer a competitive advantage in agonistic interactions between species. Morphological characters that are known to influence the outcome of competitive interactions in lizards are snout to vent length, head size, and mass.

The Australian skinks *Egernia multiscutata* and *Egernia whitii* are sympatric on Wedge Island in South Australia's Spencer Gulf. They are morphologically very similar and are reported to have very similar snout to vent lengths. Here I compare a range of morphological characters between adult specimens of both species to assess if there are any interspecific morphological asymmetries with the potential to confer a competitive advantage in agonistic encounters.

A two-sample Kolmogorov-Smirnov test showed that there was no significant interspecific difference in snout to vent length. However, univariate analyses of variance showed that, relative to snout to vent length, *E. multiscutata* had significantly greater mass, head length, head depth and head width than *E. whitii*. These results suggest that *E. multiscutata* has a potential competitive advantage in agonistic encounters with *E. whitii*. This potential advantage may contribute to resource partitioning and the distribution patterns of the species on Wedge Island.

Introduction

Conventional ecological theory holds that two sympatric species with the same resource requirements will not co-exist in a stable, homogeneous environment unless there is some form of niche separation, or resource partitioning, between them (Mackenzie *et al.* 1998). Such resource partitioning would be mediated through the exclusion of one, or both, species from preferred elements of their fundamental niche via competitive interactions (the so-called 'competitive exclusion principle') (Gause 1934).

Resource partitioning between sympatric species has been demonstrated in numerous taxa on a variety of axes, such as food partitioning (Shine 1977; Bootsma *et al.* 1996; Ray and Sunquist 2001; Garcia and Arroyo 2005), physiological adaptations (Huey 1991; Bollmann *et al.* 2002; Klok and Chown 2003), diurnal and seasonal activity patterns (Albrecht and Gotelli 2001; Hatano *et al.* 2001; Kocàrek 2001; Wahungu *et al.* 2004), behavioural differences such as, feeding behaviour (Inouye 1978; Werner and Sherry 1987), antipredator behaviour (Werner and Sherry 1987; Lingle *et al.* 2005), habitat selection (Mac Nally 1985; Arlettaz 1999) and use of habitat and micro-habitat complexity (Pianka 1966; Petren and Case 1998; Howard and Hailey 1999; Stewart *et al.* 2002), dispersal behaviour (Bonnet *et al.* 1999; Hokit *et al.* 1999; Harrison *et al.* 2001), mutual tolerance/intolerance or cooperation (Sushma and Singh 2006), flexible behavioural responses to interspecific interactions (Langkilde *et al.* 2004; Stapley and Keogh 2004), responses to temporal environmental dynamics (Dickman *et al.* 1999; Harrison *et al.* 2001; Fox *et al.* 2003; Chesson *et al.* 2004) and morphology (Renaud and Millien 2001; Kassam D. *et al.* 2004).

It is likely that there will be more than one single cause of resource partitioning (Toft 1985; Sushma and Singh 2006) but interspecific competition is recognized as a primary mediator (Schoener 1968; Talbot 1979; Pacala and Roughgarden 1982; Langkilde *et al.* 2004; Langkilde and Shine 2004).

A major contributor to the outcome of interspecific competitive interactions is interspecific asymmetry in the size of morphological characters (Melville 2002; Kassam D. *et al.* 2004; Langkilde and Shine 2004). These asymmetries can be readily observed in field populations and may be an adaptive outcome of competitive displacement (Melville 2002). Characters with the potential to deliver combative advantages in lizards include snout to vent length (Langkilde and Shine 2004), head size, particularly head depth (Herrel *et al.* 2001; Verwaijen *et al.* 2002), which in turn affects bite force, and mass (Huyghe *et al.* 2005). Bite force (mediated by head size) and, to a lesser extent, mass have been demonstrated to be the most important predictors of the outcome of fights in lizards (Huyghe *et al.* 2005).

Wedge Island lies 38 km west of mainland Yoke Peninsula in South Australia's Spencer Gulf (35° 09' S, 136° 27' E) (Robinson *et al.* 1996 p 777). The island is approximately 947 hectares in area and is within the overlapping distribution ranges of two sympatric skink species of the *Egernia* genus, *E. multiscutata* and *E. whitii* (Robinson *et al.* 1996; Cogger 2000).

Wedge Island's absence of feral predators and competitors, lack of a permanent human population and abundance of the two sympatric *Egernia* species provide a unique opportunity for resource partitioning studies.

E. multiscutata and E. whitii are morphologically very similar. The main diagnostic characters between the species are the relative widths of their interparietal and frontal scales (Cogger 2000) and differences in the number of sharp keels on the sub-digital lamellae (Coventry and Robertson 1980). Snout to vent length (SVL) is regarded as the standard measure of length for lizards (Cogger 2000). *E. multiscutata* SVL is reported by Chapple (2003) to range from 80-95 mm (*op. cit.* Store 1968; Store 1978; Cogger 2000) and for *E. whitii* 80-110 mm (*op. cit.* Hickman 1960; Rawlinson 1974; Milton 1987; Wilson and Knowles 1988; Cogger 2000). *E. whitii* populations show a decrease in SVL with increasing latitude as described by Bellamy (2006) *op. cit.* (Hickman 1960; Milton 1987; Chapple 2005; Bellamy 2006). There are no reported geographic variations in SVL for *E. multiscutata* (Store 1968). Descriptions of lizard head dimensions do not seem to be routinely reported or standardised in the published literature, making comparisons difficult. However head dimensions have been reported in some *Egernia* species, usually with respect to sexual dimorphism, (e.g. Arena and Wooler 2003, *Egernia kingii*; Clemann *et al.* 2004, *Egernia coventryi*), or comparative feeding analysis (Brown 1991, *E. cunninghami, E. saxatilis, E. whtii*). Chapple (2005) reported head width for one adult population of *E. whitii* ranging from 10.72 mm to 13.87 mm and head length ranging from

18.38 mm to 22.48 mm with significant sexual dimorphism in both dimensions. Bellamy (2006) also found sexual dimorphism in head length and head width for *E. whitii* from Wedge Island. I have been unable to find published data for *E. whitii* head depth or for *E. multiscutata* head dimensions.

Analyses of a transect survey undertaken on Wedge Island demonstrated resource partitioning on the basis of habitat substrate and, to a lesser degree, vegetation structure. However the results also show that the habitat choice of both species was negatively affected by the sympatric opponent, indicating an effect of competitive interactions (Chapter 3).

Aim

The aim of this investigation is to assess the potential of any interspecific asymmetries in morphological characters between *E. multiscutata* and *E. whitii* on Wedge Island to influence the outcome of interspecific agonistic interactions and resource partitioning.

Methods

Sampling methods

I collected morphometric data from field-captured *E. multiscutata* and *E. whitii* on Wedge Island in South Australia's Spencer Gulf (see Chapters 1 and 2 for field site details).

Specimens of *E. multiscutata* were haphazardly captured in March 2001. Specimens of *E. whitii* were captured between March 2001 and December 2002, either haphazardly, or during a transect survey on Wedge Island (Chapter 3).

Morphometric data collected included: mass, snout to vent length (SVL), head length, head depth, head width, tail length, regenerated tail length and combined hind leg and foot length (leg/foot). Attempts were made to sex the specimens by everting the hemipenes but this was largely unsuccessful except where a positive male ID was made. However, where positive sexual identification of captured specimens was possible the ratio of males to females was 1:1 for *E. multiscutata* (18 individuals) and 1:1 for *E. whitii* (32 individuals) (Bellamy 2006). The sex ratio of *E. whitii* is concordant with the sex ratio of South Australian Museum off-shore specimens of

E. whitii examined by Robyn Bellamy (97 specimens) (Bellamy 2006) and the 1:1 ratio of field captured specimens reported by Chapple and Keogh (2006) (78 specimens).

Snout to vent length is generally used as a diagnostic character indicating overall size in lizards (Cogger 2000). Overall length, including the tail, is a less reliable indicator since tails can be absent or in various stages of regrowth following autotomy. I therefore used SVL as the most reliable measure of the comparative sizes of the skinks. SVL is defined by (Cogger 2000, page 777) as "the distance between the tip of the snout and the anterior opening of the vent measured along the vertebral line or its equivalent". Tail length was measured from the anterior opening of the vent to the tip of the tail. Regenerated tail length is the regrown section of the tail. The regenerated section was identified by discontinuities in scale pattern and was measured from the tip of the regenerated tail to the observed discontinuity. Combined hind leg and foot length was measured from the groin to the tip of the longest toe with the leg extended, not including the toe nail (Cogger 2000, page 203). Head length was taken from the tip of the snout to the lower part of the ear opening. Head width was measured transversely in line with the interparietal scale. Head depth was also measured in line with the interparietal scale in the vertical plane.

I used a dial calliper to measure head dimensions and I recorded the data to the nearest millimetre. Snout to vent length, tail length, regenerated tail length and combined hind leg and foot length were measured by holding the extended specimen, or its leg/foot, or tail, flat along a steel rule with one millimetre discrimination. Mass was recorded to the nearest 0.1 g using an electronic scale.

Only adult specimens were used for interspecies morphological comparisons. Adults were defined by SVLs greater than or equal to 74 mm for *E. whitii* which was determined to be the smallest Wedge Island adult (13 years of age) by skeleto-chronology (Bellamy 2006). This length coincided with the smallest SVL of the captured *E. multiscutata*.

The resultant data set included 185 specimens of *E. whitii* and 23 specimens of *E. multiscutata*. The between-species difference in sample size was due to *E. multiscutata's* tendency to refuge in extensive burrow systems in the field. Capturing *E. multiscutata* invariably involved the destruction of the burrow systems and this negative effect was minimised during captures, resulting in few live captures for *E. multiscutata*. *E. whitii* specimens on the other hand tended to refuge under moveable rocks and therefore could easily be returned to their intact capture locations.

Results

Table 1 Morphometric data from field captured specimens (Wedge Island), including mean mass (in grams), SVL, tail length, regenerated tail length, combined hind leg and foot length, head length, head width and head depth (all in mm).

Species	N	Mass	SVL	Tail length	Regenerated tail length	Hind leg	Head length	Head width	Head depth
E. multiscutata	23	15.77 (0.6)	81.1 (0.9)	103.7 (4.1)	44.0 (6.9)	31.0 (0.49)	18.4 (0.19)	14.2 (0.15)	12.4 (0.21)
E. whitii	185	12.97 (0.2)	81.7 (0.3)	111.5 (1.6)	29.9 (2.1)	28.5 (0.12)	17.1 (0.07)	12.0 (0.07)	10.7 (0.06)

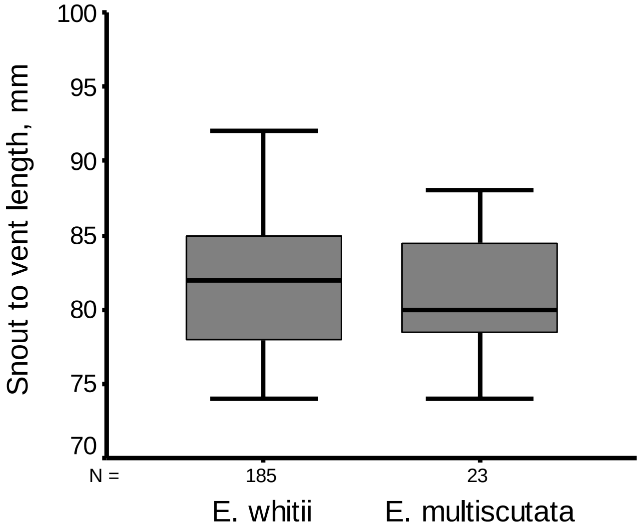
Standard errors are given in parentheses

Snout to vent length:

I conducted preliminary analyses comparing the snout to vent lengths of *E. whitii* and *E. multiscutata*. The box plot (Figure 1) gives an early indication that the SVLs were very similar for the two species with a trend for *E. whitii* to be marginally larger than *E. multiscutata*.

Since the sample was truncated (SVL cut-off dimension = 74 mm) I compared the SVLs of the two species using a two-sample Kolmogorov-Smirnov test with SVL as the dependent variable and species as the grouping variable. The Kolmogorov-Smirnov test is sensitive to any differences in distribution, not just central tendency. The species' SVL were not significantly different, $Z = 0.722$, $P = 0.675$.

Figure 1: Comparison of snout to vent lengths (SVL) for adult, field-captured *E. multiscutata* and *E. whitii*



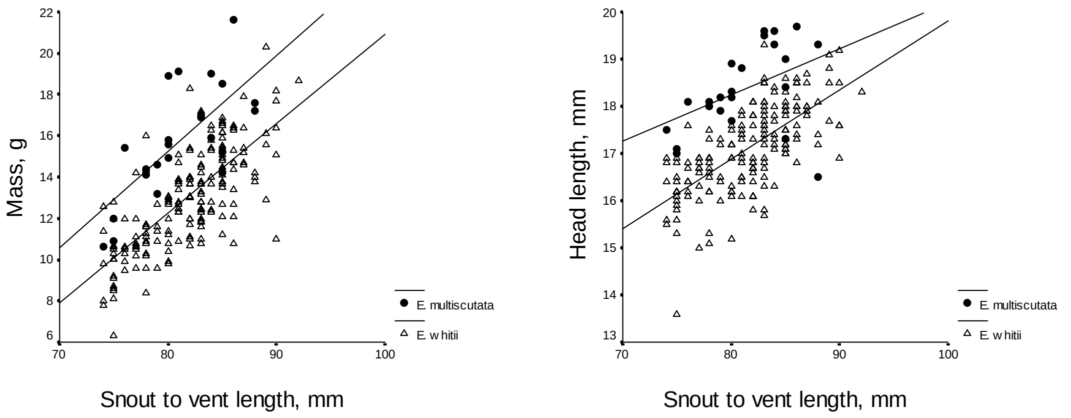
Other morphological characters relative to SVL:

Having established that there was no significant between-species difference in the SVL of the samples in the study I investigated the within-species and between-species relationships between SVL and other recorded morphological characters (Figures 2 a) – f)). Regenerated tail length is not shown since tail autotomy is an event resulting from external influences rather than a function of the overall size, or growth, of the skinks.

Generally, all of the recorded morphological characters increased in size with increasing SVL. Slopes for the relationships of the various morphological measurements regressed on the SVL appeared similar for both species.

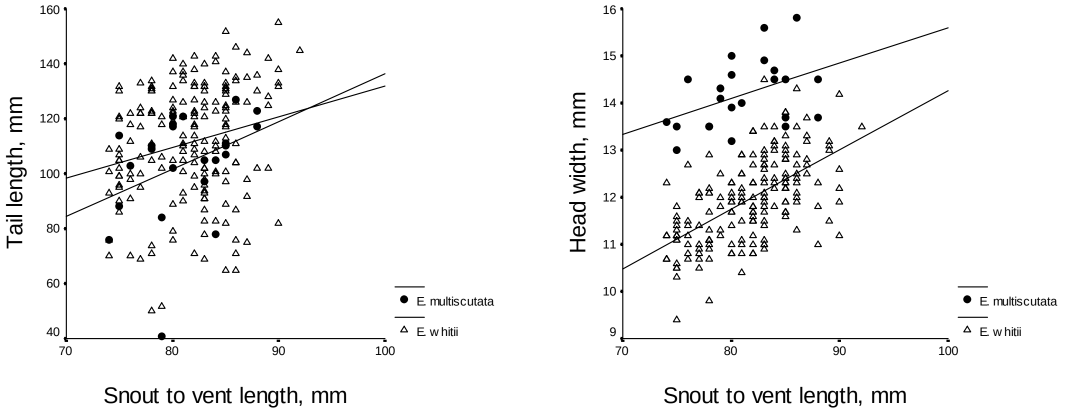
In all stages of growth (as defined by SVL) all character dimensions of the sampled specimens, with the exception of tail length, were larger for *E. multiscutata* than for *E. whitii*. Under ideal circumstances the expectation would be that intact tail length would be a function of growth in SVL. However, actual tail length on most occasions was partially a function of tail autotomy since 78% of *E. multiscutata* and 70% of *E. whitii* showed evidence of tail regeneration.

Figure 2: Between-species comparisons between selected morphological characters and snout to vent lengths for *E. whitii* and *E. multiscutata*.



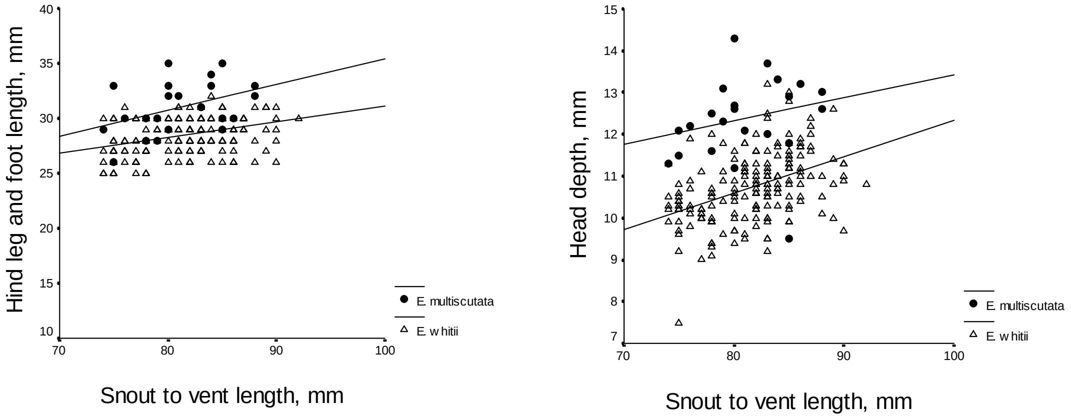
a) Mass

d) Head length



b) Tail length

e) Head width



c) Hind leg and foot length

f) Head depth

Interaction effects:

I conducted a univariate analysis of variance for each morphological character to test for species * SVL interaction effects using species as the fixed factor and SVL as the covariate. The results of these analyses are presented in Table 2. The Levene's test is included to check for violation of the assumption of equality of variance. Significance values <0.05 indicate that this assumption was violated.

Table 2: Species * Snout to vent length interaction effects on morphological characters for *E. multiscutata* and *E. whitii*.

				Levene's test of equality of error variances	
Dimension	**F**	**d.f.**	**Sig.**	**F**	**Sig.**
Mass	0.121	1	0.729	0.787	0.376
Tail length	0.301	1	0.584	2.513	0.114
Regenerated tail length	0.546	1	0.461	0.563	0.454
Head length	1.684	1	0.196	0.333	0.564
Head width	1.615	1	0.205	0.272	0.602
Head depth	0.563	1	0.454	0.908	0.342
Hind leg and foot length			*N/A*	5.235	0.023

The Levene's tests indicated that the assumption of equality of variance was violated when testing for the interaction effect on combined hind leg and foot length which was subsequently excluded from analyses. Variances were not significantly different for all other relationships.

The species * SVL interactions were not significant for any of the remaining dependent variables. Therefore the between-species effects were analysed without the interaction effect while controlling for the effect of SVL. Table 3 shows the between-species results of these univariate analyses of variance for each morphological character.

Table 3: Univariate analyses of variance for morphological comparisons between *E. multiscutata* and *E. whitii*

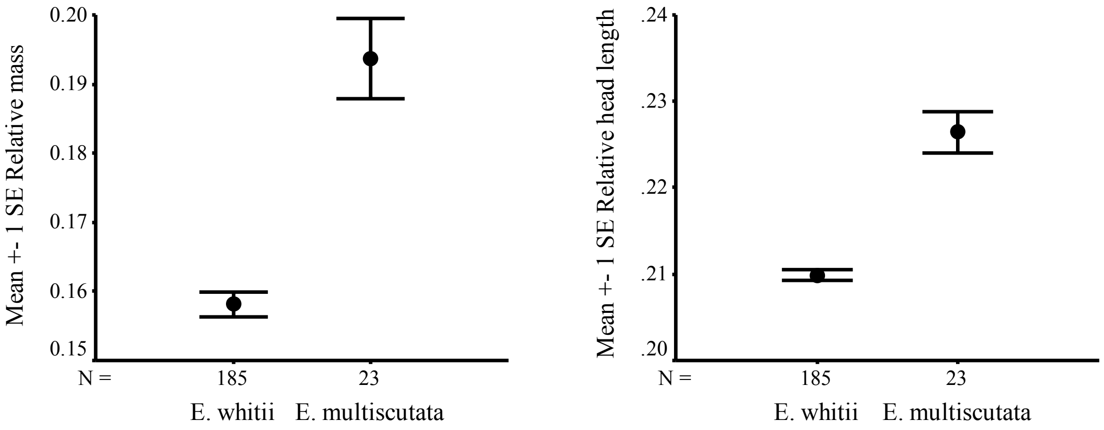
Dimension	F.	d.f.	Sig.
Mass	64.472	1	<0.0005
Tail length	2.543	1	0.112
Regenerated tail length	5.321	1	0.022
Head length	72.957	1	<0.0005
Head width	202.302	1	<0.0005
Head depth	97.659	1	<0.0005

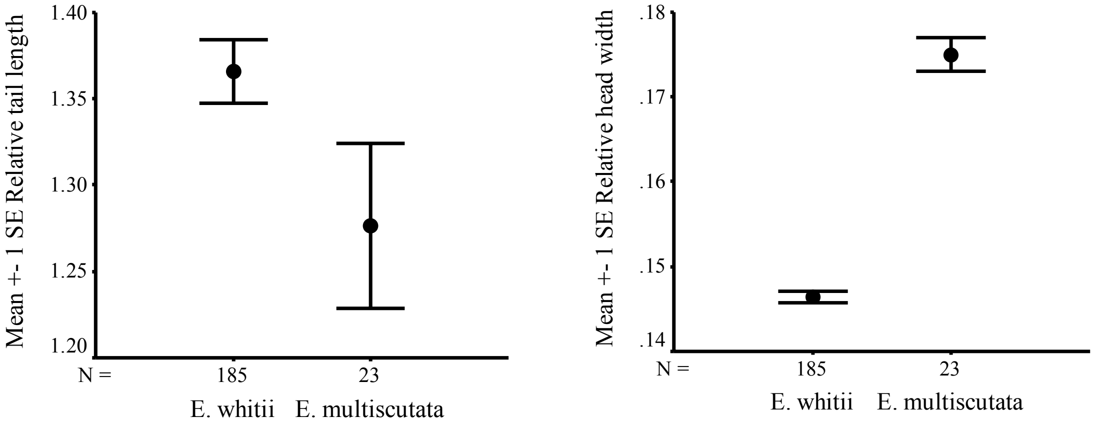
The results demonstrate that there was a highly significant between-species difference in mass and head dimensions relative to SVL. Although there was no significant difference in tail length between the species there was a trend for *E. whitii* to have longer tails relative to SVL (Figure 3 b). The problem of comparing tail lengths has been outlined previously. However there was a significant between-species difference in regenerated tail length with *E. multiscutata* having greater loss than *E. whitii*. The proportion of specimens with tail loss was similar between the species' samples, 78% for *E. multiscutata* and 70% for *E. whitii*.

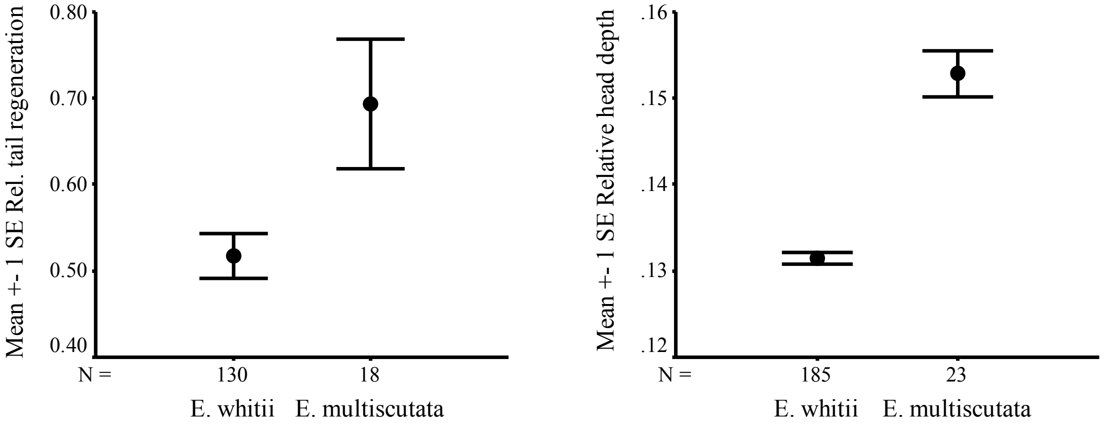
The direction of the between-species morphological differences is shown in Figure 3 a) – f) where all morphological characters are presented as a ratio of SVL.

The results confirm that relative to SVL *E. multiscutata* was larger than *E. whitii* for all of the significant between-species morphological characters except regenerated tail length.

Figure 3: Between species comparisons of selected morphological characters relative to SVL for *E. whitii* and *E. multiscutata* as a ratio of SVL.


a) Relative mass
d) Relative head length


b) Relative tail length
e) Relative head width


c) Relative tail regeneration length
f) Relative head depth

Discussion

Mean SVL for *E. whitii* was 81.7 mm which is concordant with the latitudinal SVL cline discussed by Bellamy (2006) and the size range summarised by Chapple (2003). Mean SVL for adult *E. multiscutata* was 81.1 mm which falls at the lower end of the range as summarised by Chapple (2003).

There was no significant difference in SVL between the sampled study species (Figure 1, sub-heading '*Snout to vent length'* in the results section above), suggesting no evidence of character displacement in this dimension as found in other sympatric skink species (Melville 2002). Therefore if either species were to gain a size-mediated competitive advantage it would have to be on other morphological characters relative to SVL.

Figure 2 shows that for both species, mass, head length, head width, head depth, combined hind leg and foot length and, to some degree, tail length all increased in size proportionally with SVL. Importantly in terms of competitive interactions, all of the characters were larger for *E. multiscutata* than *E. whitii*, except for tail length. These asymmetries were highly significant for mass and head dimensions when taking into account species*SVL interaction effects and controlling for SVL. There was also a significant difference in regenerated tail length with *E. multiscutata* having a greater length of regenerated tail. This may be due to phylogenetic differences in the ease of tail autotomy (e.g. Van Sluys *et al.* 2002). However it may also be an indication that the observed habitat resource partitioning of the species on Wedge Island (Chapter 3) entails increased predation risk to *E. multiscutata*, resulting in greater tail autotomy (e.g. Cooper Jr *et al.* 2004) and its potential associated costs, such as, reproductive success (Martin and Salvador 1993), energetic and locomotor costs (McConnachie and Whiting 2003; Lin *et al.* 2006) and subsequent behavioural modifications (Cooper 2003). Greater combined hind foot and leg length might confer a digging advantage; however there was no significant difference between the species in this dimension (Table 2).

Head size has been shown to affect bite force (Huyghe *et al.* 2005) and gape size (Langkilde and Shine 2005) in lizards. Open mouth displays (gape size), which often precede bites, are known to elicit submissive responses from the smaller specimens in staged experimental encounters between sympatric skink species (Langkilde and Shine 2005). Similarly, larger head size and bite force have been shown to confer a competitive advantage and dominance in lizards (López and Martín 2002; Huyghe *et al.* 2005), as does greater mass (Downes and Shine 1998; Huyghe *et al.* 2005).

These results suggest that *E. multiscutata* has a potential competitive advantage in agonistic encounters with *E. whitii* due to its larger mass and head size (Huyghe *et al.* 2005). This potential advantage may contribute to the observed resource partitioning of the species on Wedge Island (Chapter 3, e.g. Langkilde *et al.* 2004; Langkilde and Shine 2004).

While there was no evidence of character displacement in SVL in either of the study species in sympatry on Wedge Island, it is possible that there is character displacement in head dimensions and mass. Routine collection and publication of standardised morphological character data in lizards would be helpful in advancing investigations into aspects of interspecific competition.

Future experiments using staged dyadic encounters between *E. multiscutata* and *E. whitii,* where an essential resource is contested, would provide a useful test of the competitive advantage of larger mass and head dimensions in these species.

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CHAPTER 5

Refuge choice experiment

Abstract

Australian skinks of the genus *Egernia* are noted for their strong attachments to permanent retreat sites. *E. multiscutata* and *E. whitii* are reported to have similar life-histories, a similar suite of habitat preferences, and are sympatric on Wedge Island in South Australia’s Spencer Gulf. They show evidence of resource partitioning of habitat in the field, with *E. multiscutata* primarily present in sand / loam substrates and *E. whitii* primarily present in rock / loam substrates. In this study I experimentally presented the species with a choice of refuges, either using an existing ‘rock’ refuge or constructing their own sand burrow, to investigate the refuge preference of *E. multiscutata* and *E. whitii* in the absence of proximate interspecific interactions.

Independent-samples t-tests showed that there was no significant interspecific difference in the choice of refuges. The majority of specimens of both species initially chose the ‘rock’ refuge, and both ultimately chose to construct their own burrow refuge overnight. These results suggest that the habitat choices of the two species on Wedge Island are modified by interspecific interactions with the opponent species.

Introduction

Two skink species of the genus *Egernia, E. multiscutata* and *E. whitii,* are abundant and sympatric on Wedge Island in South Australia’s Spencer Gulf (Chapter 3, Robinson *et al.* 1996).

Theory (e.g. Gause 1934; Mackenzie *et al.* 1998) and empirical observations for a wide range of species (e.g. Bovbjerg 1969; Brown 1971; Jaeger 1971; Zaret and Rand 1971; Terborgh 1985; Feng and Velasco-Hernandez 1996), including reptiles (e.g. Schoener 1968; e.g. Shine 1977; Reinert 1984; Leal and Fleishman 2002) generally concur that when species compete for resources in a stable environment coexistence can only persist if there is some form of resource partitioning. If this general principle is to be supported among Wedge Island taxa, resource partitioning should be evident between *E. multiscutata* and *E. whitii*.

Resource partitioning may be readily observed on a number of axes such as, morphological asymmetries (e.g. ; Kassam *et al.* 2004), diet (e.g. Garcia and Arroyo 2005), activity patterns (e.g. Albrecht and Gotelli 2001; Kocàrek 2001) and habitat selection (Stewart *et al.* 2002; Namgail *et al.* 2004). The axes may be manifold and interrelated (Toft 1985).

Egernia multiscutata and *E. whitii* are morphologically very similar species with very little reported interspecific difference in snout to vent length (SVL), the standard measure of skink size (Cogger 2000; Chapple 2003). Investigation into interspecific dimorphism between Wedge Island specimens confirmed that there was no significant difference in SVL between *E. multiscutata* and *E. whitii* (Chapter 4). However, there were significant differences in mass and head dimensions (Chapter 4) which may endow *E. multiscutata* with a competitive advantage over *E. whitii* (Herrel *et al.* 2001; Verwaijen *et al.* 2002; Huyghe *et al.* 2005).

Most Australian skinks, including *Egernia* species, are generalist and opportunistic feeders (Greer 1989; Brown 1991), their diets containing insects and other invertebrates (Chapple 2003). However members of the *Egernia* genus are noted for the inclusion of plant material in their diets, its proportion increasing with increasing body size (Brown 1991). I have personally observed *E. multiscutata* and *E. whitii* feeding on berries in the field on Wedge Island. Both species were successfully maintained on identical diets, including invertebrate and vegetable matter, in the laboratory (Chapter 2). I did not consider food niche differentiation to be a primarily important axis of resource partitioning investigations in these species.

Most *Egernia* species, including *E. whitii* are reported to be diurnal (Cogger 2000). *E. multiscutata* and *E. whitii* appear to have generally similar life-history traits and activity patterns (Chapple 2003). In laboratory observations both study species maintained similar diurnal activity patterns and remained in refuge shelters throughout the night (see 'Preliminary investigations' sub-heading in the results section below). Such similarities in activity patterns suggest that this would not be a likely avenue for resource partitioning.

Field investigations on Wedge Island revealed a marked differentiation in the distribution of the study species. *E. multiscutata* generally inhabited sandy substrates whilst *E. whitii* generally inhabited rocky/loam substrates. The presence of both species overlapped on occasions, mainly in areas containing both rock and sand (Chapter 3). This suggested that habitat differentiation would be a productive avenue for further investigation of resource partitioning.

Although *E. multiscutata* may be an obligate burrower and *E. whitii* is considered to be saxicolous (Chapple 2003), both are reported to be burrowing species whose habitats are frequently associated with rocky areas and include coastal heath, open forests and open woodlands (Cogger 2000; Donnellan *et al.* 2002).

Egernia species are noted for having strong attachments to permanent retreat sites such as rock crevices, hollow logs, dead trees and burrows (e.g. Greer 1989; Chapple 2003). This strong attachment makes retreat sites, or refuges, an ideal habitat parameter for experimental study (e.g. Downes and Shine 1998; Langkilde and Shine 2004; Langkilde and Shine 2005).

On Wedge Island *E. multiscutata* was almost always found to be associated with sand burrows and *E. whitii* with shorter, less complex burrows under loose rocks (Chapter 3). This is generally consistent with previously reported observations for burrow use (Milton and Hughes 1986; Donnellan *et al.* 2002; Chapple 2003) but suggests that *E. whitii*'s burrowing activity may be somewhat restricted compared with the more complex burrowing activity described by Chapple (2003), Chapple and Keogh (2006) (*op. cit.* Wilson and Swan 2003) and those found in sandy substrates as described by Greer (1989). Similarly, *E. multiscutata* may not have expanded into its full range of habitat parameters and potential distribution range by avoiding rocky areas that could otherwise comprise part of its habitat (Cogger 2000). Both species were found to be less likely to be present when the opponent species was present on Wedge Island (Chapter 3).

The observed resource partitioning on Wedge Island (Chapter 3), along with the potential competitive advantage to *E. multiscutata* of interspecific morphological asymmetries (Chapter 4) and the apparent restriction of *E. whitii*'s burrowing activity (Chapple 2003; Chapple and Keogh 2006) and possible restriction of *E. multiscutata* range expansion, combine to suggest that habitat partitioning may be due, at least in part, to a proximate mechanism mediated by species interactions rather than simply by ultimate differential habitat preferences of the study species.

This study seeks to investigate the refuge preferences of *E. multiscutata* and *E. whitii* in the absence of proximate interspecific interactions.

Methods

Overview

I conducted a refuge choice experiment using 18 individuals of each of the two study species, *E. whitii* and *E. multiscutata,* to determine if: 1) there were any differences in the refuge choices of the two species when placed in novel arenas that were free from interspecific influences, and 2) if one species had a greater propensity to burrow than the other.

The choices of refuge shelter presented were designed to simulate potential shelters available in the skinks' natural field site and included a built tile shelter or a mound of compacted sand, with a 'pilot' burrow entrance, in which the skinks could construct a burrow (see details under the heading, 'Experimental arenas' below).

Initial choice of refuge would be an indication of the importance of loose rock substrate in a field situation where the species' found themselves in unfamiliar territory with an immediate imperative to find shelter, such as when avoiding predation or during dispersal transience (Weisser 2001; Wiens 2001).

Overnight refuge choice would be an indication of the species' preferred settlement habitat. Between-species differences in preferred overnight refuge may indicate a proximate behavioural mechanism that allows non-agonistic resource partitioning. Alternatively, uniform choice of overnight refuge may indicate that the preferred resource is contestable in a field situation where the species are sympatric, such as on Wedge Island.

Preliminary investigations

Prior to the commencement of the refuge choice experiment I conducted preliminary investigations into the diurnal activities of the two study species in their 'home' enclosures to gather information that would facilitate appropriate experimental design and procedures.

Eight specimens of each species were video-taped for a 24 hour period (using infrared for night-time filming). I reviewed the tapes later, logging each change of behaviour onto electronic data files in Microsoft® Office Excel 2003 format to investigate their gross activity patterns such as, time spent in refuge behaviours, basking, resting and moving (refer to ethogram in Chapter 6 for more details of skink behaviours). In particular I wanted to determine if the skinks were active overnight or if they rested in a refuge overnight.

These preliminary investigations were not carried out under controlled experimental conditions since the species were housed in individual enclosures in separate rooms whose light/dark and heat-lamp cycles were not perfectly synchronised. Therefore no statistical comparisons are presented for these investigations in this paper. However sample graphical representations are shown in the results section as an aid to interpretation of the refuge choice experimental results.

Test specimens

The skinks used in the refuge choice experiment were selected from laboratory colonies housed in the Animal Care Unit (ACU) of Flinders University. These colonies were established from adult skinks that were captured on Wedge Island in South Australia’s Spencer Gulf. For more details of test specimens and field site refer to Chapters 1 and 2.

Housing conditions for laboratory colonies

Laboratory populations were usually housed in rectangular glass terraria 600 mm long x 305 mm wide x 300 mm high. Lighting conditions in the terraria approximated summer conditions in the field. Blinds were positioned between terraria so that there could be no visual contact between unfamiliar skinks. Refugia in the ‘home’ terraria were of similar design to those in the experimental arenas and the skinks were habituated to this type of refuge for at least six months prior to the experiment. For more details on the housing conditions for laboratory colonies refer to Chapter 2.

Experimental arenas

The experimental trials were carried out in novel glass arenas 600 mm long x 305 mm wide x 300 mm high, similar to the glass tanks in which the skinks were normally housed.

The objective of the experiment was to present the skinks with a choice of two potential refuge shelters that simulated the potential refuge shelters available to the species’ on Wedge Island (Chapter 3, Robinson *et al.* 1996) using materials that were familiar to the skinks in their ‘home’ enclosures (Chapter 2). The options presented were: 1) a built refuge shelter created from concrete tiles similar to the shelters in their ‘home’ terraria and which simulated rock shelters in the field, 2) a compacted sand mound in which the skinks could create their own refuge shelter by burrowing and which simulated sand substrates in the field.

To create the choice of shelter sites, one end of the arena was divided longitudinally by a clear PVC ‘T’- shaped divider. The cap of the ‘T’, which was 290 mm long, was positioned against the end of the arena and the shaft of the ‘T’ divided the arena centrally for 350 mm of its 600 mm length. The height of the divider was 130 mm and the thickness of the PVC was 5 mm.

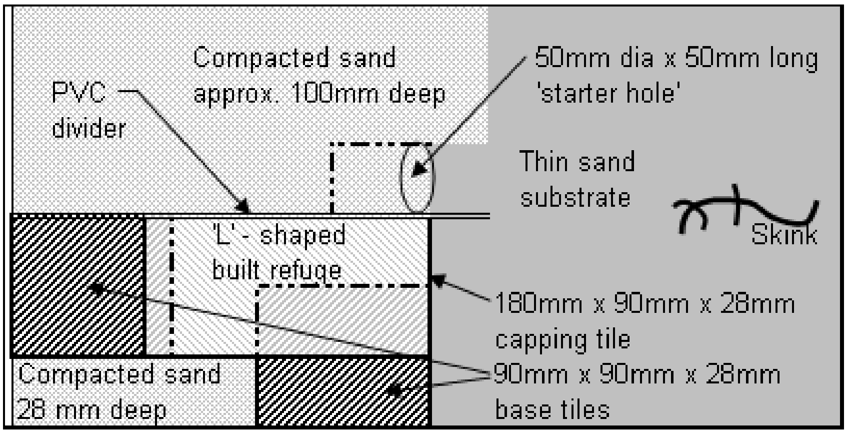
On one side of the divider I constructed a refuge shelter by positioning two concrete tiles 90 mm x 90 mm x 28 mm thick on a sand substrate approximately 5 mm thick. Another tile 180 mm x 90 mm x 28 mm was positioned on top so that the two tiles made an ‘L’- shaped refuge shelter 50 mm wide by approximately 23 mm high. The ‘toe’- end of the ‘L’ was blocked off with compacted sand so the refuge shelter was only open at one end (see Figure 1).

On the other side of the divider I made a mound of compacted sand approximately 100 mm deep suitable for the skinks to dig their own refuge burrows. I made a 50 mm diameter x 50 mm long ‘pilot’ burrow entrance (not long enough for a suitable refuge without modification) so that the skinks were presented with two openings immediately adjacent each other on either side of the PVC divider, one in the sand and the other in the built tile refuge shelter (Figure 1)

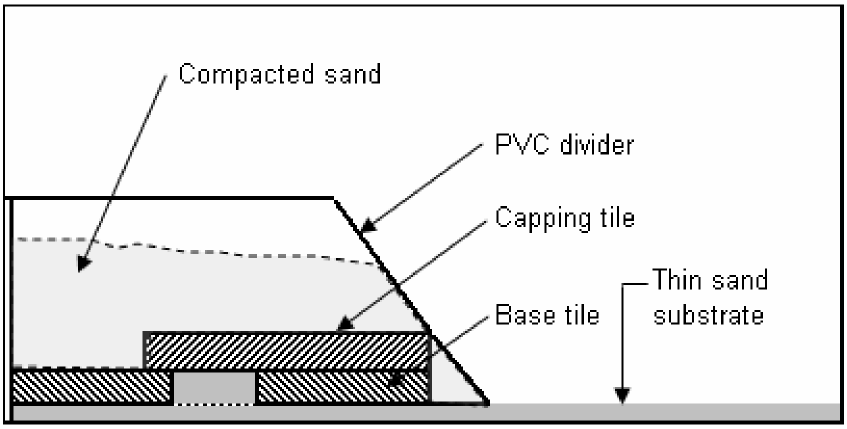
A 120 W heat-lamp was positioned 450 mm above the base level at the end of the arena opposite the refuge shelters. A supply of drinking water was provided in Petri dishes but feeding was withheld and animal care workers were excluded from the room for the duration of the trials. Blinds were positioned around all sides of the arenas so that external stimuli were uniform. No other landscape features were present.

A video camera was centrally positioned 450 mm above the top of each test arena so that the whole of the arena was in the field of view. The observations were recorded directly onto VHS video cassette tapes.

Figure 1: Diagrammatic layout of substrate choice experimental arena



Plan view



Side view

Handling of skinks and equipment

Handling of skinks and cleaning of test arenas and equipment was carried out in accordance with the methods described in Chapter 2.

Experimental procedure

I conducted 18 substrate choice experiment replicates for each of the two study species. All trials were commenced between 10:00 am and 11:30 am of the first day and terminated as soon as practicable after the lights and heat lamps had automatically switched on the following morning.

For each replicate the positions of the built refuge and the sand mound were randomly allocated to the left or right of the arena. One hour prior to the trials the skinks were removed from their home tanks and placed into clear plastic containers with tightly-fitting lids and air holes drilled into the sides. The containers' dimensions were 175 mm long x 120 mm wide x 55 mm high. These were then placed within the test arenas to ensure that immediate external influences among the test specimens prior to the experiment were uniform.

Trials commenced by starting the video recorder and releasing the skinks into the test arenas, at which stage I left the room to minimise observer influence. I returned just prior to 'lights-out' to set the cameras to infrared. The following morning I stopped the trials and returned the specimens to their 'home' terraria.

I measured the height, width, length and number of changes in direction (bends) of any sand burrows that the skinks had constructed and calculated the burrow volume. I reviewed the video tapes to record the initial choice of refuge shelter and the ultimate overnight refuge shelter settlement choice of the specimens.

Initial refuge choice was determined by recording the first potential shelter (i.e. built tile refuge or pilot hole in the sand) that the specimens attempted to access after their release into the test arena. Overnight refuge choice was determined to be the last shelter that the specimens settled in after the heat lamp went out and just prior the lights-out.

Data were transcribed into the statistical analysis program SPSS® version 11.5 for Windows (SPSS) for analyses.

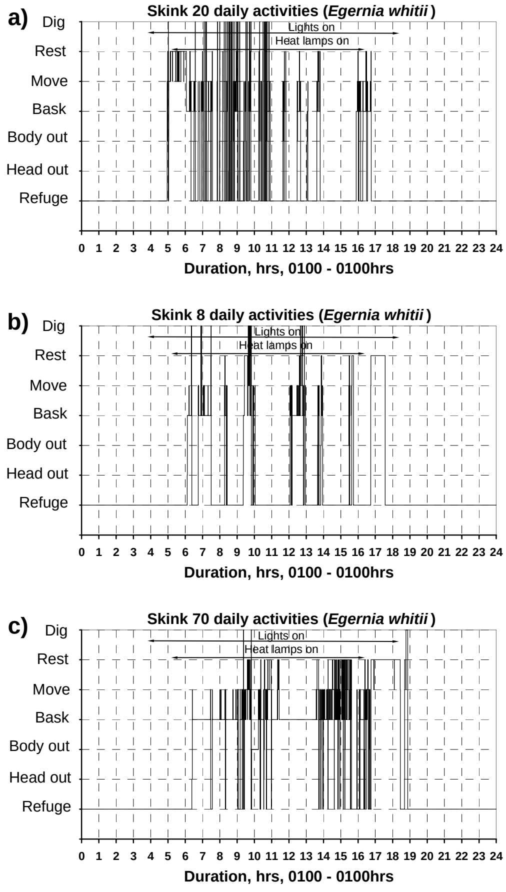
Results

Preliminary investigations

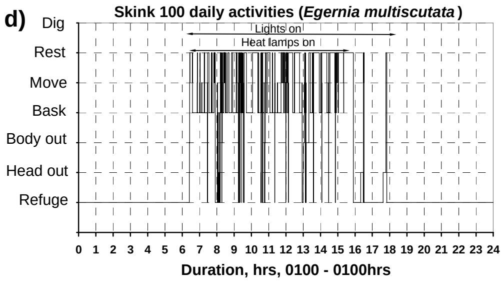
Activity patterns from the 24 hr diurnal activity investigations for representative *E. whitii* are shown in Figure 2 a), b) and c). Results for representative *E. multiscutata* are shown in Figure 2 d), e) and f).

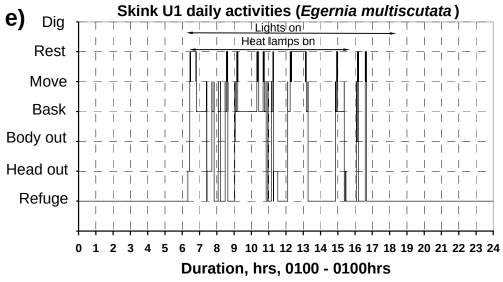
Figure 2: 24hr diurnal activity patterns for selected *E. multiscutata* and *E. whitii*. Refer to the ethogram in Chapter 6 for details of behaviours.

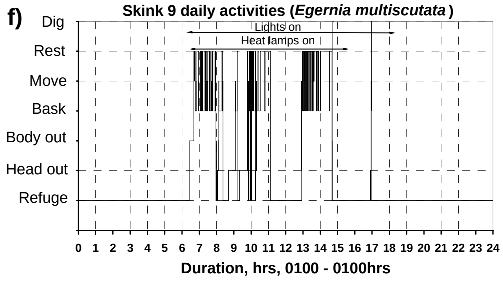
Egernia whitii



Egernia multiscutata







The activity patterns in Figure 2 are typical examples of the 16 replicates investigated. They were selected to demonstrate that the patterns appear to vary as much within species as they did between species. When no other activities, such as feeding or refuge construction were available, both species typically cycled, with varying frequency and duration, between refuge behaviours and basking behaviour with concomitant time spent moving between activities and some time resting in the open. The graphs also show that *E. whitii* appeared to spend more time digging than *E. multiscutata*. However this did not involve refuge shelter construction since their ‘home’ shelters had already been constructed prior to the investigations. Rather, this digging time shows the greater propensity of *E. whitii* to maintain a clear ‘runway’ at the entrance to the refuge shelter.

On almost every occasion the skinks settled into a refuge shelter between the time that the heat-lamps switched off and the time that the lights switched off. On only one occasion did a skink briefly emerge from the refuge after lights-out before returning to the refuge almost immediately (Figure 2 c)).

E. multiscutata tended to emerge from the refuge as soon as 'daylight' arrived whereas *E. whitii* tended to delay its emergence until about two hours after 'daylight'. However this difference may be a reflection of the very early time at which the lights came on in the *E. whitii* room during the observational period (in the preliminary investigations the species were housed in separate rooms and I was unable to synchronise the lighting regimes). The results may suggest that both species are adapted to a period of about 12-13 hours of consolidated overnight rest in a refuge shelter. This overnight refuging behaviour, combined with the times spent in the refuge during the day, are an indication of the importance of refuge resources to both species and thus their relevance for comparative investigators into the species.

In the following refuge choice experiment the knowledge gained from these preliminary investigations allows observers to determine overnight refuge settlement by recording the last choice made by each specimen just prior to 'lights-out'.

Refuge choice experiment

Overview

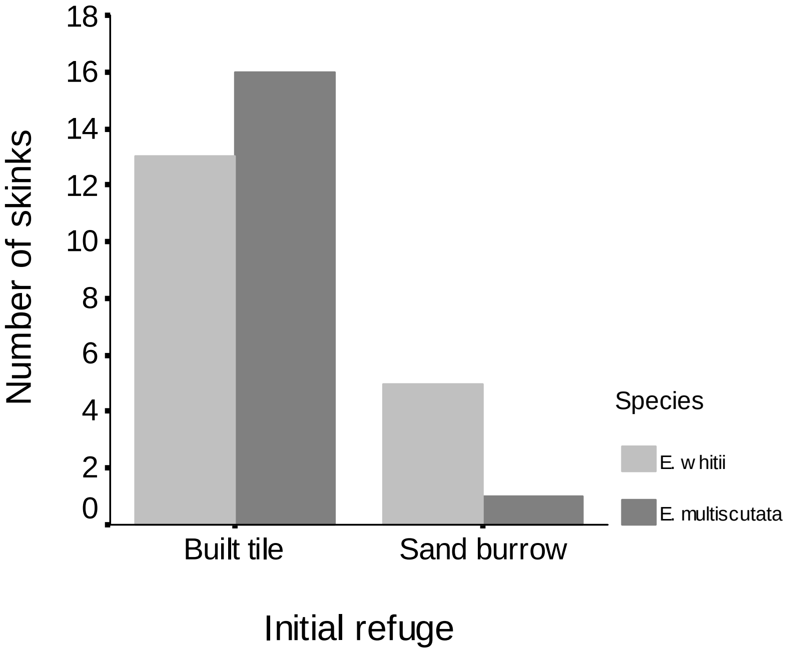
Data from the refuge choice experiment for the two study species were compared to determine if there were any between-species differences in their initial choice of refuge shelter or their ultimate choice of an overnight shelter. I also made between-species comparisons of the dimensions and complexity of skink-constructed sand burrows.

I used non-parametric techniques in SPSS to analyse the data for the two categorical refuge choice variables, initial choice and overnight choice, and independent-samples t-tests to analyse any differences in the burrow dimensions. The results are presented in the following two sections.

Initial refuge choice

Figure 3 shows the number of *E. whitii* and *E. multiscutata* that selected the built tile refuge shelter and the 'pilot' sand burrow entrance as their initial choice of shelter.

Figure 3: Number of *E. whitii* and *E. multiscutata* that selected each of the potential refuge shelters as their initial choice.

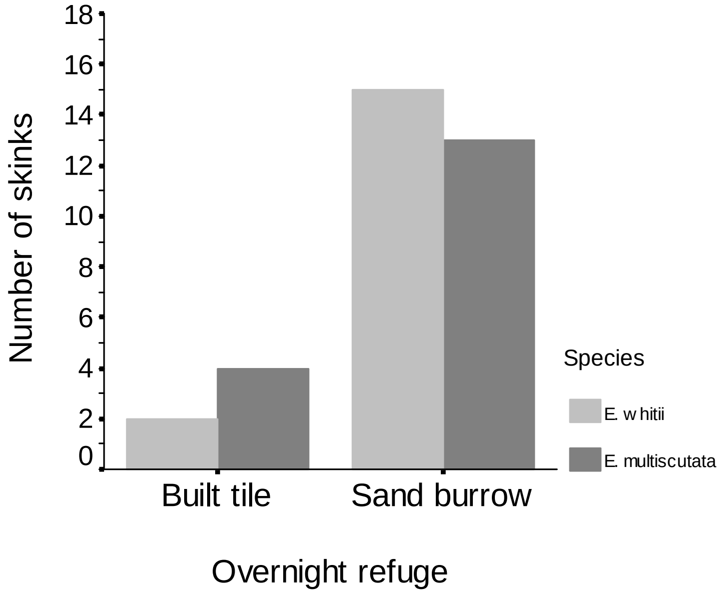


The majority of individuals in both species chose the built tile refuge shelter as their initial choice. I used a Fisher's Exact Probability Test to analyse differences in initial refuge choice between the study species. The results show that there was no significant between-species difference in the initial choice of potential refuge shelter (Fisher's Exact Test, $P = 0.177$) with both species tending to choose the built-tile refuge for initial refuge shelter. 72.2% of *E. whitii* and 94.4% of *E. multiscutata* chose the tile shelter as their first point of refuge.

Overnight refuge choice

Figure 4 shows the number of *E. whitii* and *E. multiscutata* that selected the built tile refuge or the self-excavated sand burrow as their overnight choice of shelter. One specimen of each species did not settle in a refuge shelter by 'lights-out'. These 'non-performers' were not included in the analyses.

Figure 4: Number of *E. whitii* and *E. multiscutata* that selected each of the potential refuge shelters as their overnight choice.



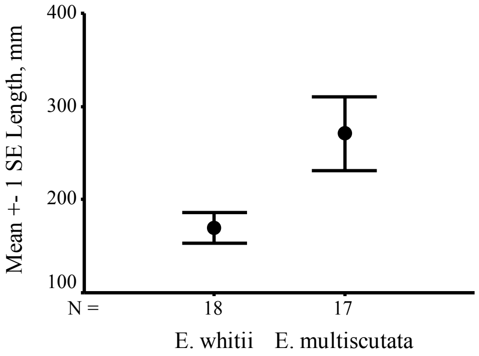
The majority of test lizards from both species chose to excavate and settle in their own sand burrow overnight and all of those individuals that chose the sand burrow as their initial choice also chose the sand burrow as their overnight refuge.

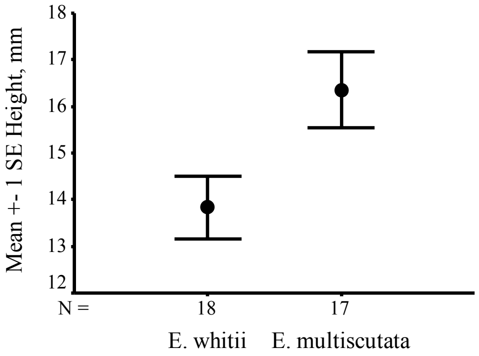
Analysis using Fisher's Exact Probability Test showed that there was no significant between-species difference in the overnight choice of refuge shelter, P = 0.656, with both species tending to choose to build their own sand burrow. 88.2% of *E. whitii* and 76.5% of *E. multiscutata* chose the sand burrow as their ultimate overnight refuge shelter.

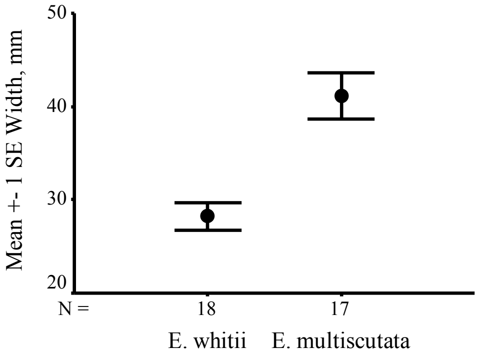
Burrow dimensions

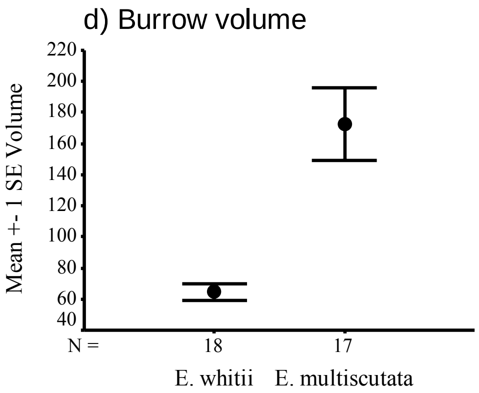
Figure 5 a) – d) compares the mean dimensions of skink-excavated sand burrows for the two species.

Figure 5: Comparison of skink-excavated sand burrow dimensions for *E. whitii* and *E. multiscutata*. Error bars represent mean standard errors


a) Burrow length


b) Burrow height


c) Burrow width



The mean dimensions for burrow a) length, b) height, c) width and d) volume were all greater for *E. multiscutata* than *E. whitii*. I conducted independent-sample t-tests to analyse these differences.

Burrow length: There was a significant between-species difference in this dimension (*E. whitii* $\bar{x} = 170.00$, *SE* = 16.67, *E. multiscutata* $\bar{x} = 270.88$, *SE* = 39.54, $t_{21.55} = -2.35$, P = 0.028). The magnitude of the differences of means was large (eta-squared = 0.143).

Burrow height: There was a significant between-species difference in this dimension (*E. whitii* $\bar{x} = 13.83$, *SE* = 0.67, *E. multiscutata* $\bar{x} = 16.35$, *SE* = 0.81, $t_{33} = -2.41$, P = 0.022). The magnitude of the differences of means was large (eta-squared = 0.149).

Burrow width: There was a significant between-species difference in this dimension (*E. whitii* $\bar{x} = 28.22$, *SE* = 1.48, *E. multiscutata* $\bar{x} = 41.18$, *SE* = 2.48, $t_{33} = -4.55$, $P < 0.0005$). The magnitude of the differences of means was large (eta-squared = 0.385).

Burrow volume: There was a significant between-species difference in this dimension (*E. whitii* $\bar{x} = 64.46$, *SE* = 5.35, *E. multiscutata* $\bar{x} = 172.63$, *SE* = 23.61, $t_{17.64} = -4.47$, $P < 0.0005$). The magnitude of the differences of means was large (eta-squared = 0.999).

Burrow complexity

Skink-constructed burrow complexity was described in terms of the number of changes in direction (bends) in the burrow. The results for the two species are shown in Figure 6.

Figure 6: Skink-constructed burrow complexity for each species.

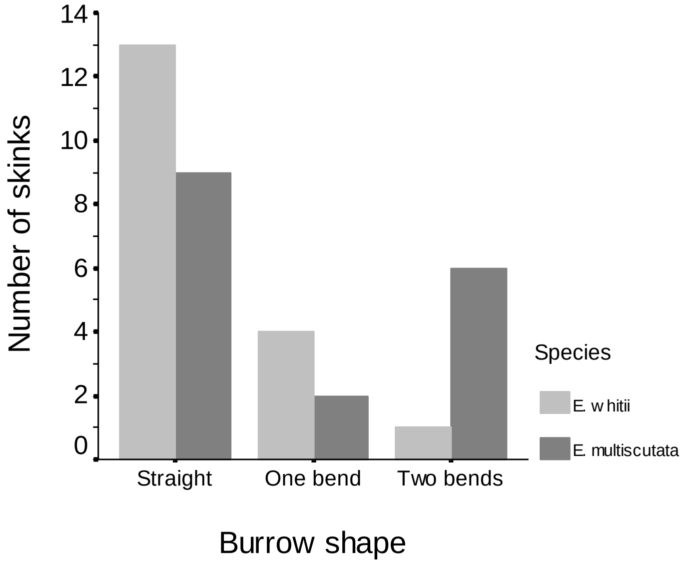


Figure 6 shows a trend for *E. multiscutata* to dig more complex burrows, that is, with two bends, than *E. whitii*. This is consistent with observations in the field where *E. multiscutata* burrows often had multiple entrances and bifurcations.

Discussion

Overall activity patterns

Preliminary laboratory investigations showed that both of the study species retreated into a refuge shelter overnight for approximately 12-13 hrs and frequently returned to the refuge for periods up to 2+ hrs at a time as part of their normal daily cycle (see ‘Preliminary investigations’ sub-heading in the results section above). This behaviour was concordant with the reported diurnal activity and their close association with a permanent refuge site for these species (Cogger 2000; Donnellan *et al.* 2002; Chapple 2003). The results indicate the importance of retreat sites in this model system and their relevance for investigations into habitat selection and resource partitioning.

Initial refuge choice

During the experimental trials the majority of both species (72% of *E. whitii* and 94% of *E. multiscutata*) chose the ‘rock’ refuge as their initial choice of shelter. There was no significant interspecific difference in this choice. This is not surprising since the skinks would have had an imperative to quickly access a refuge as an antipredator response following their pre-trial exposure and handling (e.g. Martin 2001; e.g. Amo *et al.* 2003). Under these circumstances a sand burrow would require a considerable amount of time and effort to construct, whereas loose rocks which have spaces under them can provide an instant refuge.

Analyses of the distribution of the species on Wedge Island showed that the likelihood of *E. multiscutata* presence in rocky substrate was only marginally higher than the likelihood of its presence in inhospitable substrate (Chapter 3). Given the initial choice of refuge in this study it seems likely that its restricted presence in rocky substrate on Wedge Island was due to the presence of *E. whitii*. If this is so it would potentially impact on *E. multiscutata*’s dispersal behaviour (Bonnet *et al.* 1999; Stow *et al.* 2001; Weisser 2001; Wiens 2001).

Overnight refuge choice

All of the specimens, except for one *E. multiscutata*, constructed a sand burrow before ‘lights out’ during the trial period and all of those individuals that choose the sand burrow as their initial choice also chose the sand burrow as their overnight choice. However, while all specimens chose an initial refuge shelter, one specimen of each species did not take refuge in either of the shelter options overnight. This was an unusual occurrence which had not been observed in preliminary laboratory observations. It may possibly have been due to the skinks becoming disorientated in the novel arena following the sudden onset of darkness.

For the majority of specimens, overnight choice of refuge was in self-constructed sand burrows (88% of *E. whitii* and 77% of *E. multiscutata*) rather than the existing ‘rock’ shelter. There was no significant interspecific difference in these choices. However, there was a significant difference in the extent of burrow construction, with *E. multiscutata* building longer, higher and wider burrows than *E. whitii*. These results were concordant with *E. multiscutata*’s reported burrowing habits which are known to be usually more complex than *E. whitii*’s (Coventry and Robertson 1980; Chapple 2003).

Although *E. whitii* is sometimes known to burrow in cracks in the soil and in soil at the sides of roots in trees in a similar fashion to *E. multiscutata* (Hickman 1960), it seems to be more generally saxicolous than the experimental results would suggest (Hickman 1960; Milton and Hughes 1986; Chapple 2003). Analyses of the distribution of the two species on Wedge Island, where all observed *E. whitii* refuge shelters were found under loose rocks (Chapter 3), supports the reported saxicolous behaviour of this species. The experimental results may therefore be an indication that *E. whitii* modifies its preferred refuge behaviour in response to interspecific competition from *E. multiscutata*.

One other study, which compared *E. whitii* with a morphologically very similar sympatric species (*E. modesta*), found no evidence supporting the restriction of habitat preferences in either species (Milton and Hughes 1986), but that study did not specifically analyse retreat site use. A more detailed assessment of habitat parameters may therefore have been productive in revealing habitat partitioning between the species. Among other suggestions, Milton and Hughes (1986) postulated that anthropogenic spatio-temporal disturbance may have advantaged the incursion of *E. modesta* into territory that was previously more suitable for *E. whitii*, or alternatively, that small behavioural differences observed between the species may be sufficient for them to coexist. It would seem reasonable from the combination of experimental results and the distribution of the study species on Wedge Island that subtle modifications in the refuge behaviour of both species could be consistent with their observed resource partitioning, and hence their coexistence.

General considerations

The distributions of *E. multiscutata* and *E. whitii* on Wedge Island are concordant with the previously reported apparent ultimate habitat preferences of the two species. However, there is now experimental evidence suggesting that *E. whitii*'s refuge behaviour, and hence its distribution, may be somewhat restricted by the presence of *E. multiscutata*. Similarly, comparison between *E. multiscutata*'s initial choice of refuge and its limited presence in rocky areas on Wedge Island suggest that it too may be somewhat constrained in its refuge activity. That is, there may be a proximate mechanism, mediated by behavioural responses to competitive interactions, that results in the observed habitat partitioning on Wedge Island.

Similar investigations into resource partitioning of other species and further investigations into any differences in their behavioural responses to interspecific competitive interactions would be beneficial in understanding the general the principles of coexistence in sympatric species. The experimental design may be enhanced by conducting preliminary trials to potentially improve the design of the 'rock shelter' to better simulate rock crevices in the field. For example, a different kind of potential refuge could be tested by placing a rock on a thick layer of sand or soil and allowing the specimens to choose between the two. Dimming the lights over a period of time to avoid the unnatural sudden onset of 'night' may possibly avoid temporary disorientation of the test specimens.

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CHAPTER 6

Refuge acquisition experiment

Abstract

Retreat sites, or refuges, are among the most important of habitat requirements for lizards. On Wedge Island, in South Australia's Spencer Gulf, two sympatric skink species, *Egernia multiscutata* and *E. whitii,* partition habitat resources in terms of the substrates that provide the resources for refuges. Although the species have similar snout to vent lengths, there are interspecific asymmetries in other morphological characters which have the potential to confer a competitive advantage to *E. multiscutata*. In the experimental absence of the competing species the refuge choices of *E. multiscutata* and *E. whitii* are modified from those observed in the field. In this study I use dyadic encounter experiments to focus on a single critical habitat resource to investigate whether interspecific competitive interactions are a proximate mechanism of resource partitioning between sympatric *E. multiscutata* and *E. whitii*.

Independent-samples t-tests showed that *E. multiscutata* gained significantly more time in the refuge than *E. whitii* and that *E. whitii*'s refuge behaviour was reduced by the presence of *E. multiscutata*. Pearson product-moment correlation coefficients showed that asymmetries in morphological characters gave *E. multiscutata* an advantage in competitive interactions. However differential behavioural responses to increased competitor size also gave *E. multiscutata* an advantage. Nevertheless there was some tolerance for close interspecific proximity and co-habitation such that the outcome of interactions was not completely deterministic.

Introduction

Retreat sites, or refuges, are among the most important habitat requirements of reptiles (Diego-Rasilla and Pérez-Mellado 2003). They have the potential to influence the ecology of species in a range of proximate and ultimate ways, such as predator avoidance (Martin 2001; Amo *et al.* 2003), foraging strategies (Merker and Nagy 1984; Belliure *et al.* 1996; Martin *et al.* 2003), mating opportunities (Shine *et al.* 2000; Martín *et al.* 2003), social structure (Duffield and Bull 2002), inter- and intraspecific competition (Langkilde and Shine 2004) energy use (Merker and Nagy 1984), thermal ecology (Heatwole and Taylor 1987; Polo *et al.* 2005), hibernation (Rutherford and Gregory 2003), dispersal vulnerability (Bonnet *et al.* 1999; Stow *et al.* 2001), and the distribution of species (Diego-Rasilla and Pérez-Mellado 2003).

Reptiles would be expected to optimise refuge utilization by balancing the costs and benefits of their use in a given circumstance (Cooper 1998; Downes and Shine 1998; Martin *et al.* 2003; Shah *et al.* 2003). This balance may lead to a strong association with, and fidelity to, their refuges (Beck and Jennings 2003; Milne *et al.* 2003; Shah *et al.* 2004). Members of the Australian scincid genus *Egernia* are particularly noted for having strong attachments to permanent retreat sites such as rock crevices, hollow logs, dead trees and burrows (e.g. Greer 1989; Chapple 2003).

In a stable environment, where suitable refuge sites are limited, and where the benefits of refuge shelters are high, there is likely to be competition for refuge sites (Stamps 1983). If, in addition, two species are sympatric, the competitive exclusion principle would predict that one of the species would out-compete and exclude the other unless there are some mechanisms allowing coexistence through resource partitioning (Mackenzie *et al.* 1998).

Differences in the competitive ability of species to obtain refuge sites where requirements are overlapping, may contribute to apparent differences in their ultimate habitat selection choices (Langkilde and Shine 2004; Wahungu *et al.* 2004), although interspecific competition alone is unlikely to be the sole cause of such resource partitioning (Toft 1985).

Recent research attention in Australia has focused on *Egernia* species as a model system for ecological studies (e.g. Gardner *et al.* 2001; Donnellan *et al.* 2002; Duffield and Bull 2002; Chapple 2003; Langkilde *et al.* 2003; O'Connor and Shine 2003; Chapple and Keogh 2004; Chapple *et al.* 2004; Jellinek *et al.* 2004; Langkilde *et al.* 2004; Langkilde and Shine 2004; Lanham and Bull 2004; O'Connor and Shine 2004; Osterwalder *et al.* 2004; Stow and Sunnucks 2004; Chapple 2005; Chapple and Keogh 2005; Chapple *et al.* 2005; Fuller *et al.* 2005; Chapple and Keogh 2006; O'Connor and Shine 2006).

Milton and Hughes (1986) investigated habitat selection by two closely related sympatric *Egernia* species, *E. whitii* and *E. modesta*, from southern Queensland. They reported no evidence of competition restricting habitat preferences but suggested that human disturbance may have had some impact on their current distributions. However their study focused on a range of habitat parameters that did not explicitly include permanent retreat sites.

More recent studies have shown that species within the *Egernia* genus have complex stable social systems centred around permanent retreat sites (e.g. Greer 1989; Chapple 2003; Chapple and Keogh 2006) and that they are sensitive to habitat fragmentation and disturbance where suitable refuge sites are limiting (e.g. Mac

Nally and Brown 2001; Nichols and Nichols 2003; Jellinek *et al.* 2004). It is not surprising then that competitive exclusion between sympatric *Egernia* species, with substantially overlapping retreat site requirements, have recently been found to occur in both field and laboratory studies (Langkilde *et al.* 2003; Langkilde and Shine 2004). Langkilde and Shine 2004, recommended that comparative studies using other reptile/ecosystem models are needed to determine if competitive interactions have a more general influence on habitat selection in skinks.

Within the *Egernia* genus there are six generally recognized species groups, one of which is the *whitii* group (Chapple 2003). Two species, *E. whitii* and *E. multiscutata*, which are the subjects of this study, are part of this group (Chapple 2003). Their distributions overlap in South Australia (Cogger 2000; Hutchinson 2000) where they are both sympatric and abundant on Wedge Island, in South Australia's Spencer Gulf, which is the field source of the experimental specimens (Robinson *et al.* 1996).

Both *E. whitii* and *E. multiscutata* are burrowing species whose habitats are frequently associated with rocky areas and include coastal heath, open forests and open woodlands (Cogger 2000; Donnellan *et al.* 2002) such as found on Wedge Island (Robinson *et al.* 1996). *E. multiscutata,* which is a more desert-adapted species, is considered by some to be an obligate burrower (Chapple 2003). *E. multiscutata* constructs large complex burrows, whereas *E. whitii* burrows are usually less complex (Donnellan *et al.* 2002; Chapple 2003).

A survey carried out on Wedge Island (Chapter 3) has shown that there was broad scale habitat partitioning between the study species, with *E. multiscutata* primarily settling in sandy substrates and *E. whitii* primarily settling in rocky substrates. There was considerable species overlap in substrates containing both sand and rocks (Chapter 3).

Laboratory experiments have shown that both *E. multiscutata* and *E. whitii* prefer to construct their own overnight refuges by borrowing in sand rather than use an existing novel rocky crevice (Chapter 5). However, *E. multiscutata* burrows were larger and more complex than *E. whitii* burrows in this same experiment (Chapter 5). When observed in laboratory enclosures during their normal activity cycles, both species were found to remain in their refuges overnight and maintained a close association with the refuges during daylight hours, alternating their behaviour between refuging and other activities (Chapter 5).

E. multiscutata and *E. whitii* are morphologically very similar, with the main diagnostic characters being the relative widths of their interparietal and frontal scales (Cogger 2000) and differences in the number of sharp keels on the sub-digital lamellae (Coventry and Robertson 1980). Snout to vent length (SVL), regarded as the standard measure of lizard length (Cogger 2000), is reported to range from 80-110 mm for *E. whitii* and 80-95 mm for *E. multiscutata* (Chapple 2003). SVLs of adult Wedge Island field captured specimens were not found to be significantly different between the two species (Chapter 4). However, after checking for species*SVL interaction effects and controlling for SVL, measurements of mass, head length, head width and head depth were found to be significantly larger in *E. multiscutata* than *E. whitii* (Chapter 4).

Larger size is generally presumed, and theoretically considered, to confer advantages in competitive interactions in a range of taxa, including lizards (Robson and Miles 2000; Hone and Benton 2005). Empirical data confirm that in lizards, larger size frequently leads to dominance in both intraspecific (Carothers 1981; Olsson 1992; Downes and Shine 1998) and interspecific competition (Langkilde and Shine 2004; Langkilde and Shine 2005). Differential body size, associated with habitat partitioning, has been found to be greater in sympatry than in allopatry for at least one of the sympatric scincid species (Melville 2002), indicating character displacement.

Larger head size in lizards, particularly head depth, is associated with bite force between and within species (Herrel *et al.* 2001; Verwaijen *et al.* 2002). Bite force and, to a lesser extent, mass have been demonstrated to be the most important predictors of the outcome of fights in lizards (Huyghe *et al.* 2005). It would therefore be reasonable to expect that due to its larger head size and greater mass *E. multiscutata* would gain an advantage in access to refuge sites over *E. whitii*, at least in initial interactions.

Factors other than size may also have an influence on the outcome of competitive interactions. For example, prior residency (Cooper and Vitt 1987), agonistic experience (Stuart-Fox and Johnston 2005), persistence (Stamps and Krishnan 1995;

Sih and Mateo 2001), learning (Stamps and Krishnan 1999), colouration and displays (Carpenter 1995; Langkilde and Shine 2005), cost/benefit of agonism (Stamps 1977; López and Martín 2002) and strategic behavioural flexibility (Pereira *et al.* 2003; Langkilde *et al.* 2004; Stapley and Keogh 2004).

In addition to the substrate resource partitioning found between the study species on Wedge Island, analysis of their distributions revealed that the presence of both species was significantly and negatively affected by the presence of the opponent species. While it was clear that interspecific interactions played a significant part in ultimate resource partitioning, there was no clear indication of species dominance as a proximate mechanism for such differentiation (Chapter 3).

The Wedge Island survey assessed a number of resource parameters in evaluating habitat differentiation. The dynamics and trade-offs involved in habitat selection between sympatric species may obscure the underlying cause of partitioning. This study removes complexity by focusing on a single and critical habitat resource, refuge shelters, to experimentally investigate the proximate mechanisms of resource partitioning between sympatric *E. multiscutata* and *E. whitii* on Wedge Island.

Methods

Overview

I conducted three experimental trials involving *E. whitii* and *E. multiscutata.* One series of trials were staged dyadic encounter experiments between the two species. The aim of this series was to determine if there was any significant difference between the species' ability to acquire a refuge shelter in the presence of the other species and in the absence of potential confounding factors.

The same experimental design was duplicated as two series of singleton control experiments in which each species was tested individually in the absence of the other species. The aim of the control experiments was to determine if any observed differences between the behaviour of the species in the dyadic encounter trials arose from competitive exclusion rather than species specific differences in resource utilization.

Test specimens

The skinks used in these experiments were selected from laboratory colonies housed in the Animal Care Unit (ACU) of Flinders University. These colonies were established from field-captured skinks that naturally occur sympatrically on Wedge Island, in South Australia's Spencer Gulf. (Refer to Chapters 1 and 2 for more details of the field site and laboratory colonies). For the dyadic encounters all of the *E. multiscutata* used were field-captured adults and all but one of the *E. whitii* used were field-captured adults. The other *E. whitii* was born in the laboratory and had reached adult size by the time of this experiment. The singleton encounters used one laboratory-born individual of adult size of each species and the rest were field-captured adults.

Housing conditions for laboratory colonies

Laboratory populations of both species were normally housed in rectangular glass terraria 600 mm long x 305 mm wide x 300 mm high. A heat lamp was provided above the terraria and was on for 8 hrs per day. The terraria were kept in 25°C constant temperature rooms with a 12 hr light/dark cycle. Conditions in the terraria approximated summer conditions in the field. In addition to the heat lamp each terrarium was provided with two basking rocks, a built tile refuge, sand substrate and a water dish. Skinks were fed three times per week on a mixture of live invertebrates, vegetables and Wombaroo® reptile supplement. Blinds were positioned between terraria so that there could be no visual contact between unfamiliar skinks. For more details on the housing conditions for laboratory colonies refer to Chapter 2.

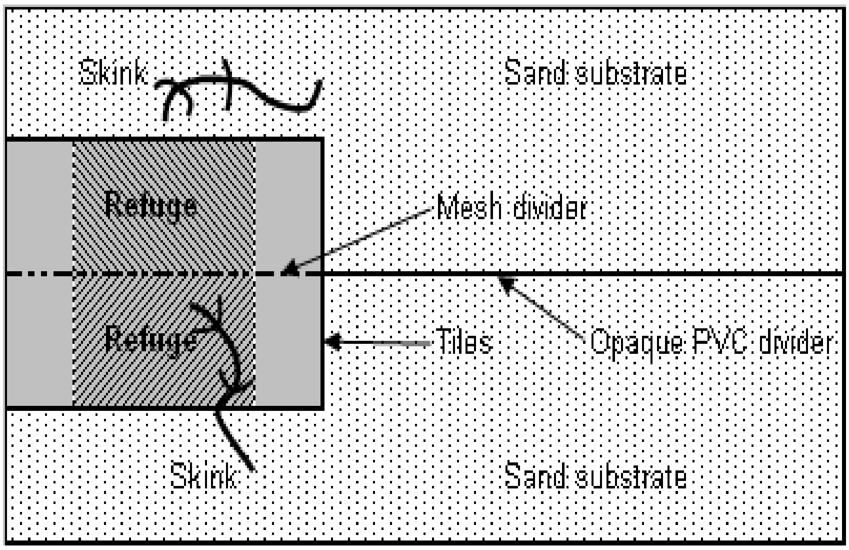
Experimental arenas

The experimental trials were carried out in novel glass arenas 600 mm long x 305 mm wide x 300 mm high, similar to the glass tanks in which the skinks were normally housed. An opaque PVC divider, 600 mm long x 300 mm high x 5 mm thick, was positioned vertically along the central length of the arena so that in plan view the arena was divided into two equal parts, each 150 mm wide x 600 mm long. One end of the divider had a notch cut out at the base 170 mm long and 25 mm high. Five millimetre square wire mesh was fixed into this notch. The divider prevented physical and visual contact and volatile-olfactory stimuli between the species for most of the length of the arena, whereas the meshed section allowed visual, olfactory and minimal physical contact while preventing serious combat and resultant injury from occurring to the skinks during the trials.

Identical refuge shelters were constructed in each side of the divided arena using the same method used in the skinks' 'home' tanks (refer to Chapter 2) except that the refuge tile was only 95 mm wide. This width frequently caused the tails of the test skinks to be exposed while they were in the refuges (when viewed from above), thus allowing observation of tail-signalling behaviour. The refuges were positioned in such a way that they were separated only by the wire mesh (Figure 1). Therefore if both skinks were to access the refuge at the same time they were forced into close physical, visual, aural and olfactory proximity with each other. A thin layer of clean sand was used as a substrate but no other landscape features were provided in the test arena. No heat lamp, food or water was provided during the trial. These arrangements greatly restricted the range of behavioural activities available to the skinks during the trials thereby reducing potential confounding factors.

A video camera was positioned centrally above each test arena 450 mm above the shelf level so that the whole of the arena was in the field of view. The observations were recorded directly onto VHS video cassette tapes.

Figure 1: diagrammatic plan layout of dyadic encounter experimental arena



Handling of skinks and equipment

Skinks were captured by hand from their home terraria for use in the experimental trials. I wore Latex® examination gloves during handling and changed them between skinks to avoid any cross-contamination of odour. All test arenas and other smooth-surfaced experimental paraphernalia were thoroughly cleaned with 70% ethanol between replicate trials. Refuge tiles were thoroughly washed in hot water and detergent, rinsed and allowed to dry between each replicate and clean sand substrate was also used for each replicate.

Experimental procedure

I performed 19 dyadic encounter trial replicates during the skinks' normal activity season, utilising all of the adult members of the *E. multiscutata* population once. Standard morphological measurements were taken of all specimens prior to commencement of the trials. Linear dimensions were measured either by Vernier callipers or steel rule and mass was measured by electronic digital scales (refer to Chapter 4 for details of standard morphological measurements).

The number of *E. multiscutata* specimens was limited by available resources in the Animal Care Unit and ethical considerations during field capture (refer to Chapter 2 for more details). Nineteen adult *E. whitii* with snout-to-vent-lengths (SVL) comparable to the *E. multiscutata* were selected from the laboratory colony of 51 individuals and paired with the *E. multiscutata* according to the closest match in this dimension. The sex of the specimens was rarely known with confidence but when available same-sex pairs were matched for the trials.

For each replicate the species' were randomly allocated to the left or right hand side of the arena. One hour prior to the trials the skinks were removed from their home tanks and placed into clear plastic containers with tightly-fitting lids and air holes drilled into the sides. The containers' dimensions were 175 mm long x 120 mm wide x 55 mm high. These were then placed on the shelves next to the test arenas in an exposed position. There were two objectives in doing this. Firstly, it ensured that immediate external influences among the test specimens prior to the experiment were uniform. Secondly, it increased the skinks' exposure to unfamiliar but uniform surroundings with the intention of heightening the imperative to seek a refuge during the trial.

Trials were commenced by starting the video recorder and releasing the two skinks into the test arena as close to simultaneously as possible, at which stage I left the room to minimise observer influence. After one hour the experiment was stopped and the skinks were returned to their normal enclosures. The one hour duration for the trials was determined following earlier pilot trials and observations in which ethograms were developed. Graphs of cumulative new behaviours observed over time in the pilot trials became asymptotic prior to one hour duration.

The procedure for singleton trials was identical with the procedure above but without the opponent species.

Data collection

Video tapes were viewed either at normal speed or frame by frame as required. Often sections of the tapes had to be viewed several times to record all of the behaviour and interactions between skinks.

Each change of behaviour was logged onto time-stamped electronic data files in Microsoft® Office Excel 2003 format. Time discrimination in these files was one second; hence there were 3,600 records for each one-hour replicate. Observer bias was avoided by automatically generating and summarising pre-defined variables using Boolean logic, built-in functions and arithmetic and comparison operators. Automatic data validation checks were carried out during data entry using logical functions and conditional formatting. Data summaries were also cross-validated using comparison operators and conditional formatting. Data from the computer files were copied into files in the statistical analysis program SPSS® version 11.5 for Windows for analysis.

Results

Ethogram

The ethogram used in these trials is shown in Table 1. This is not a comprehensive repertoire but represents only pertinent behaviours displayed during the trials. Most behaviours were recorded as durational data but some were recorded as spike-event data. Others were recorded as both durational and spike data and stored into separate variables. Data types are indicated on the ethogram

Total escaping, resting and refuging behaviour durations were recorded as component parts of their summated variables to facilitate detailed investigations.

Table 1: Ethogram developed from observations during trials.

Variable		**Description of behaviour**
(SPSS® name)	**Data type: D=durational, S=spike event**	
Total escaping time (escape)	D	The skink attempts to escape from the test arena. This includes: pressing its snout around the perimeter of the arena, attempting to climb the walls and digging at the corners, =Σ(esc1,esc2,esc3).
Escape 1 (esc1)	D	Attempting to escape via the central divider
Escape 2 (esc2)	D	Attempting to escape via the outside wall
Escape 3 (esc3)	D	Attempting to escape via ends of arena
Total resting time (rest)	D	Total time the skink spends resting in the open while not in the refuge, =Σ(rest1,rest2)
Rest 1 (rest1)	D	Time spent resting on sand substrate
Rest 2 (rest2)	D	Time spent resting on top of the refuge tile
Move (move)	D	Skinks leave the refuge or casually move around the arena.
Tongue flick (flick) (flick2)	D S	A skink rapidly flicks its tongue in and out, often several times in succession. Skinks use tongue flicks to gather chemo-sensory information
Nose (nose) (nose2)	D S	A skink positions its snout into the opening of the refuge but does not immediately enter. Interpreted as risk assessment information gathering behaviour prior to entering the refuge
Dig (dig)	D	A skink modifies the refuge substrate by digging the sand at the entrance to, or within, the refuge. It is considered part of the skink's refuging repertoire
Refuge (refuge)	D	Recorded when the skink's head and torso are wholly within the refuge up to and including the hind legs. The refuge was purposely built so that on many refuging occasions the skink's tail was exposed when viewed from above.
Head out (headout)	D	Similar to refuge behaviour except that the head of the skink is emergent. From this position the skink can quickly retreat into the refuge if threatened.
Body out (bodyout)	D	Similar to head out behaviour except that the front legs and varying degrees of the torso, up to but not including the hind legs, are emergent. Skinks can thermoregulate from this position and withdraw quickly if threatened.
Total refuge time (refuget)	D	Total time spent associated with the refuge. That is, the summation of dig, refuge, headout and bodyout variables
Tail twitch (twitch)	S	A rapid lateral twitching of the distal end of the tail. Tail twitching is regarded as a submissive signal.
Tail lash (lash) (lash2)	D S	A rapid lateral serpentine lashing of the whole tail. Tail lashing is regarded as an aggressive signal. Often employed at the approach of another skink
Excluded (excluded)	S	Entry to the refuge is denied to one species by the presence of the other species in the adjacent refuge. Logically: IF ((species1 = refuget) AND (species 2 = dig OR species 2 = nose) AND (species 2 does not then refuge) THEN (species 2 = excluded))
Evicted (evicted)	S	A skink leaves the refuge within 10 seconds of either the approach of the other species or an agonistic interaction with the other species. Logically: (i) *Approach*, IF ((species 1 = refuget) AND ((species 2 = nose OR species 2 = dig OR species 2 = refuge) AND (within 10 sec (species 1 = move OR species 1 = retreat))) THEN (species 1 = evicted)). (ii) *Agonistic interaction*, IF((species 1 = refuget) AND ((species 2 = tail lash OR species 2 = tail twitch) OR (species 1 = tail lash OR species 1 = tail twitch)) AND (((species 1 = move OR species 1 = retreat) THEN (species 1 = evicted)) OR ((species 2 = move OR species 2 = retreat) THEN (species 2 = evicted))))
Retreat (retreat) (retreat2)	D S	A skink runs away from another skink. Occurs immediately following an agonistic interaction with another skink or at the approach of another skink.
Co-refuge ratio (refprop)	D	The ratio of the time both skinks are wholly within the refuge shelter at the same time divided by the total time the subject was wholly within the refuge.

Dyadic encounters

Overview

Total durational values and occurrences of spike events for all behaviours were compared between the two species using independent samples t-tests. Significant results (P < 0.05) are presented in Table 2. Some between-species and between-treatment relationships are shown graphically in Figure 6.

Table 2: Independent samples t-tests comparison between *E. whitii* and *E. multiscutata* refuge acquisition behaviour during staged dyadic encounters

Variable	Mean Difference	t	df	Significance (2-tailed)
Escape 3	322.37	2.758	23.864	0.011
Move	180.53	2.677	36.000	0.011
Head out	-216.58	-3.011	36.000	0.005
Refuge	-775.59	-3.354	36.000	0.002
Nose (duration)	156.16	3.521	19.671	0.002
Nose (spike)	9.42	3.802	26.020	0.001
Retreat *(duration)*	8.26	3.314	18.000	0.004
Retreat (spike)	3.16	3.438	18.000	0.003
Excluded	6.00	3.758	19.590	0.001
Tail twitch†	2.79	2.230	18.000	0.039
Total escaping	412.89	2.445	26.198	0.022
Total refuging	-1042.89	-4.443	36.000	<0.001
Co-refuge ratio	0.32	3.918	26.675	0.001

- Negative sign indicates larger values for *E. multiscutata*

† Tail twitch may not be part of *E. multiscutata's* repertoire.

Generally, *E. multiscutata* obtained greater access to the refuge resource than *E. whitii* whereas *E. whitii* was engaged in more non-refuging activity. These results may be an indication that *E. whitii* refuge acquisition was modified by the presence of *E. multiscutata*.

Non-refuge behaviour

E. whitii spent significantly more time than *E. multiscutata* in 'total escaping' effort, in generally moving ('move') about the arena, nosing ('nose') the refuge and retreating ('retreat') from the presence of the opponent. Occurrences of 'nose', 'retreat', 'excluded' and 'tail twitch' spike events were also significantly higher for *E. whitii* (Table 2).

The ‘total escaping’ variable comprises three components, ‘escape 1’, ‘escape 2’ and ‘escape 3’. Escape 3 was the only contributor towards the difference in total escaping time. Escape 3 behaviour involves attempting to escape via the ends of the arena, one end being the furthest distance from the investigator at release time and the other end the furthest distance from sensory proximity to the opponent, that is, at the refuge.

E multiscutata was not observed to ‘retreat’ from *E. whitii* in any of the replicate trials but was observed to be ‘excluded’ from the refuge when *E. whitii* was present (18 times total in 7 replicates). However the incidence of ‘excluded’ was higher for *E. whitii* (132 times total in 13 replicates). There was no significant difference in the ‘evicted’ variable between the two species with these events being very rare.

There were statistically significant differences between the two species in both ‘nose’ (duration) and ‘nose’ (spike). Nose (spike) is a measure of the number of times a skink attempted to access the refuge, whereas nose (duration) is a measure of the amount of time the skink spent hesitating at the entrance to the refuge. *E. whitii* spent more time in this behaviour than *E. multiscutata*.

There was a significant difference in ‘tail twitch’ behaviour between the two species in that it was observed in *E. whitii* but not in *E. multiscutata*. I interpret tail-twitch behaviour as displaying submissive agitation as first described and subsequently interpreted for the skink *Lampropholis guichenoti* (Torr and Shine 1994; Torr and Shine 1996). Tail twitch behaviour was not observed in *E. multiscutata* during development of the ethogram. Therefore ‘tail twitch’ may not form part of its behavioural repertoire. Alternatively it may not form part of *E. multiscutata*’s inter-species signalling behaviour with *E. whitii*.

Refuge acquisition – total refuging time

Total refuging time comprises the four summated variables, ‘head out’, ‘body out’, ‘dig’ and ‘refuge’. There was a highly significant difference in total refuging time between the two species. *E. multiscutata* was the more successful species in acquiring this resource due to spending more time in two of the component variables, ‘refuge’ and ‘head out’. There was no significant difference between the species in the other components, ‘body out’ and ‘dig’ behaviour (Table 2).

Refuge acquisition – effects of specimen size

***Overview*:** Scatter-plots were used for preliminary investigations into any effects of specimen size on refuge acquisition time. After checking that the data did not violate the assumptions of normality, linearity and homoscedasticity a Pearson product-moment correlation coefficient matrix was produced to determine the strength (Pearson correlation, r) and direction (negative values = negative correlation, positive values = positive correlation) of any relationships (Table 3). Due to the possible influence of confounding interactions between an individual's own size and that of its opponent, partial correlations were carried out to further investigate any relationships (Tables 4 & 5).

For the purpose of these analyses mass was regarded as the best 'summary' indicator of overall size difference. Measurement of mass was more precise than other dimensions (refer to Chapter 4) and it is probably the quickest indicator for skinks to assess visually. Also, a negative relationship between relative mass (*E. multiscutata* mass / *E. whitii* mass) and refuging time for both species (smaller but in the same directions for other relative dimensions) allowed a more meaningful investigation into the effects of specimen size (Figure 3). Snout-to-vent lengths were not analysed since this dimension was used in the selection of test pairs. Tail length was rejected as an unreliable indicator of overall size due to the potential differential history of tail-autotomy between subjects (refer to Chapter 4).

General results: Detailed results are reported under their appropriate sub-headings but generally, Pearson product-moment correlations showed that the refuging time of both species were correlated with several of their opponent's, as well as their own, dimensions (Table 3).

Table 3: Pearson product-moment correlations between specimen size and refuge acquisition.

Dimension	*n*=19	*Egernia whitii* refuge time, *r* ‡	*Egernia multiscutata* refuge time, *r* ‡
Mass	Own	-0.023	-0.326
	Opponent's	-0.681**	0.492*
	Relative†	-0.529*	-0.614**
Head length	Own	0.053	0.024
	Opponent's	-0.467*	0.515*
	Relative	-0.241	-0.291
Head width	Own	0.145	0.041
	Opponent's	-0.268	0.643**
	Relative	-0.292	-0.399
Head depth	Own	0.218	-0.049
	Opponent's	-0.536*	0.525*
	Relative	-0.553*	-0.363

† Relative dimension = *E .multiscutata* dimension / *E. whitii* dimension

Significance		‡ Strength	
*	P<0.05	*r* = 0.10 to 0.29	small
**	P<0.01	*r* = 0.30 to 0.49	medium
***	P<0.005	*r* = 0.50 to 1.00	large

Direct effects of own dimensions: Analysis by Pearson product-moment correlation suggested that there were small correlations between *E. whitii's* own mass, as well as head dimensions, and its own refuge time. These relationships were negative for mass and positive for head dimensions but were not statistically significant (Table 3, Figure 2 (a) for mass).

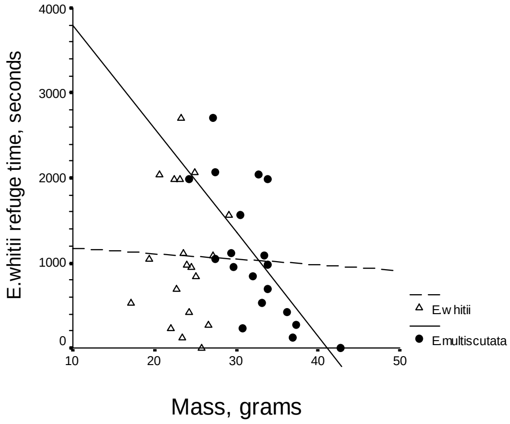
Results for *E. multiscutata* were similar to *E. whitii* with small non-significant correlations between its own head dimensions and its own refuging time. These were positive for length and width but negative for depth (Table 3). The correlation between *E. multiscutata* mass and its own refuging time was medium and negative but not statistically significant (Table 3, Figure 2 (b)).

Direct effects of opponent's dimensions: Table 3 shows that the direct relationships between the mass, the head length and the head depth of the opponent and the subject's own refuging times were medium to large and in opposite directions for the two species. There was a similar relationship for head width but with only a small effect on *E. whitii* refuge time.

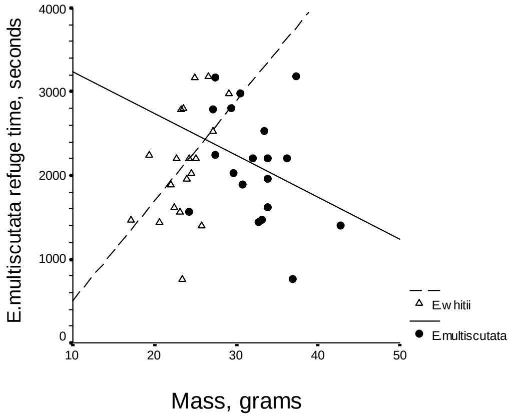
E. whitii spent less time in the refuge as *E. multiscutata* size increased, whereas *E. multiscutata* spent more time in the refuge as *E. whitii* size increased (see also Figure 2 (a) and (b) for mass).

Figure 2: Total refuging time plotted against mass. Total refuging time is plotted for each species against its own mass and the mass of its dyadic partner, both represented on the same X-axis scale.

(a) *E. whitii* total refuging time



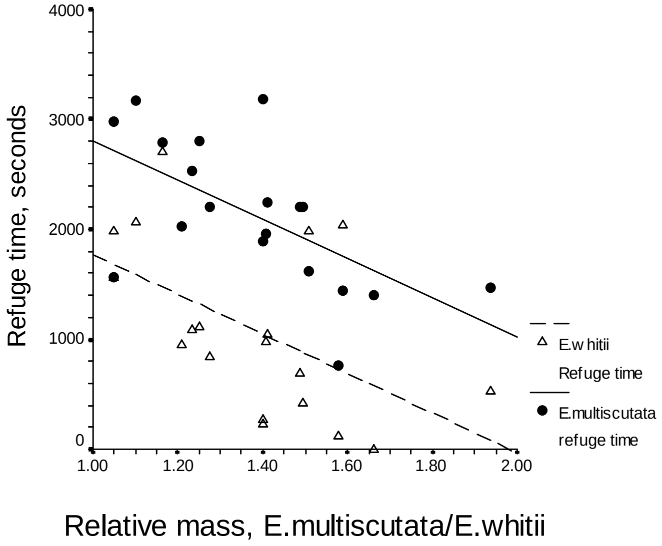
(b) *E. multiscutata* total refuging time



Effect of relative dimensions: Table 3 and Figure 3 indicate that there was a large negative relationship between relative mass (*E. multiscutata* mass / *E. whitii* mass) and total refuging time for both species, each spending less time in the refuge as *E. multiscutata* mass increased relative to *E. whitii.* This relationship was of similar strength for both species.

Relationships between refuging time and other relative dimensions were in the same directions as relative mass but of only medium to small strength, except for the effect of *E. multiscutata* head depth on *E. whitii* refuge time, which was large (Table 3).

Figure 3: Relative mass* plotted against refuging time for both species
***Relative mass = *E. multiscutata* mass / *E.whitii* mass**



Partial correlations, controlling for own dimensions: Partial correlations were used to further investigate the relationships between refuge time and the dimensions of the opponent while controlling for the subject's own dimensions (Table 4). Comparison of the zero order (Pearson product-moment) and control correlations show that, with the exception of *E. whitii* head width, the strength of the relationships increased when controlling for own dimensions (Table 4). In the case of the relationship between *E. multiscutata's* refuge time and its opponent's mass and head width the increase in strength was of a degree of significance. The different directions of the correlations between the two species suggested that they adopted different behavioural strategies from each other in contending with increased opponent size.

Table 4: Partial correlations between specimen's own refuge time and its opponent's dimensions, controlling for its own equivalent dimensions.

Dimension	Zero order/partial correlation design	*E. whitii* refuge time, *r* ‡	*E. multiscutata* refuge time, *r* ‡
Opponent's mass	Zero order	-0.681**	0.492*
	Control	-0.690**	0.602**
Opponent's head length	Zero order	-0.467*	0.515*
	Control	-0.495*	0.525*
Opponent's head width	Zero order	-0.268	0.643**
	Control	-0.262	0.647***
Opponent's head depth	Zero order	-0.536*	0.525*
	Control	-0.558*	0.528*

Significance		‡ Strength	
*	P<0.05	*r* = 0.10 to 0.29	small
**	P<0.01	*r* = 0.30 to 0.49	medium
***	P<0.005	*r* = 0.50 to 1.00	large

Partial correlations, controlling for the opponent's equivalent dimensions: Controlling for the opponent's dimensions showed that all *E. whitii* dimensions had small positive relationships with its own refuge time but these were not statistically significant (Table 5).

There were no significant Pearson product-moment correlations between any of *E. multiscutata's* head dimensions and its own refuge time (Table 5). However the medium negative correlation between *E. multiscutata's* own mass and its own refuge time, previously reported in Table 3 and Figure 2 (b), increased in strength to become statistically significant (P < 0.05) when controlling for the opponent's mass (Table 5).

Table 5: Partial correlations between specimen's own dimensions and refuge time, controlling for the opponent's equivalent dimensions.

Dimension	Zero order/partial correlation design	*E. whitii* refuge time, *r* ‡	*E. multiscutata* refuge time, *r* ‡
Own mass	Zero order	-0.023	-0.326
	Control	0.157	-0.498*
Own head length	Zero order	0.053	0.024
	Control	0.195	-0.123
Own head width	Zero order	0.145	0.041
	Control	0.134	0.104
Own head depth	Zero order	0.218	-0.049
	Control	0.284	-0.083

Significance		‡ Strength	
*	P<0.05	*r* = 0.10 to 0.29	small
**	P<0.01	*r* = 0.30 to 0.49	medium
***	P<0.005	*r* = 0.50 to 1.00	large

Refuge acquisition – co-refuging

There was some tolerance for close proximity between the species where refuge acquisition was concerned. This was assessed by the "the co-refuge ratio", that is, the proportion of the species' refuge time when they were refuging at the same time as their opponent.

An independent-samples t-test revealed a highly significant difference in co-refuge ratio between the two species (see Table 2). The mean proportion of refuging time spent co-refuging for *E. multiscutata* was 22.21% and for *Egernia whitii* it was 48.62%. That is, *E. whitii* was more likely to share refuge time with *E. multiscutata* than *vice versa*.

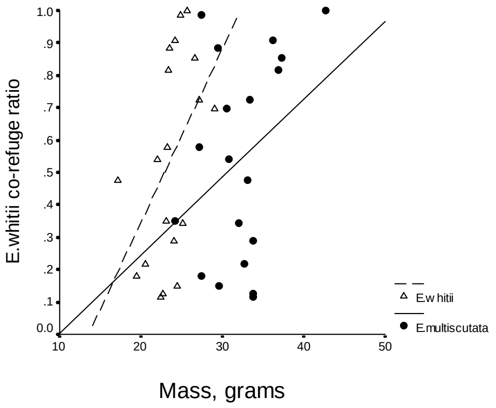
Pearson product-moment correlation coefficients between mass and co-refuge ratio are reported in the following paragraphs.

For *E. whitii*, co-refuging ratio significantly increased as its own mass increased (r = 0.47, P = 0.04) with a trend to increase as *E. multiscutata* mass increased, though not significantly (r = 0.33, P = 0.16) (Figure 4 (a)).

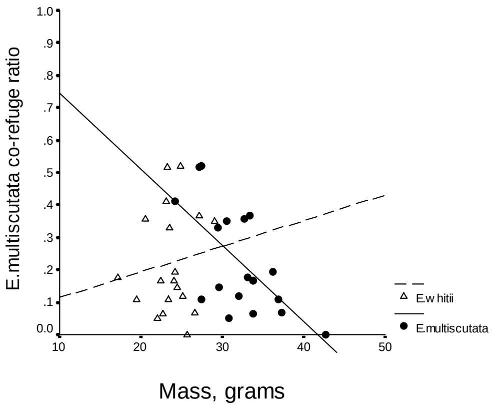
For *E. multiscutata*, co-refuging ratio significantly decreased as its own mass increased (r = -0.64, P = 0.003) with a slight trend to increase as *E. whitii* mass increased, though not significantly (r = 0.14, P = 0.58) (Figure 4 (b)).

Figure 4: Co-refuge ratio plotted against mass. Co-refuge ratio is plotted for each species against its own mass and the mass of its dyadic partner, both represented on the same X-axis scale.

(a) *E. whitii* co-refuge ratio



(b) *E. multiscutata* co-refuge ratio



Singleton encounters

Between-species comparisons

There were no significant (P < 0.05) differences between test specimens of the two species for any of the variables in the ethogram with P values ranging from 0.057 for ‘head out’ behaviour to 0.808 for ‘body out’ behaviour. This suggests that the study species had very similar patterns of behaviour when the competitor species was absent.

There was, however, a significant difference between the species in the time taken to first acquire a refuge, with *E. multiscutata* gaining access earlier than *E. whitii*, $MD = 625.67$, $t_{18.47} = 2.521$, $P = 0.021$.

Between-treatments comparisons

Independent samples t-tests indicated a number of significant differences ($P < 0.05$) between the singleton and dyadic treatments. Significant between-treatment results for *E. whitii* are shown in Table 6 (a) and for *E. multiscutata* in Table 6 (b). The varying degrees of freedom in these tables are due to whether variances were found to be homogeneous or not in the two treatments. Bonferroni adjustments were not applied to these P values. Therefore some caution should be exercised in their interpretation. Selected results are shown graphically in Figure 6 for both between-species and between-treatments.

Table 6 (a): Comparison between dydadic and singleton trials for *Egernia whitii*

Variable	Mean Difference	t	df	Significance (2-tailed)
Head out	-261.33	-2.879	8.833	0.018
Flick event	4.82	2.462	25	0.021
Nose event	12.56	3.490	25	0.002
Nose duration	186.72	4.214	19.545	<0.0005
Total refuging	-1172.14	-3.055	25	0.005

- Negative sign indicates larger values for singleton trials

Table 6 (b): Comparison between dyadic and singleton trials for *Egernia multiscutata*

Variable	Mean Difference	t	df	Significance (2-tailed)
Escape 2	100.32	2.939	18.492	0.009
Escape 3	144.92	2.063	26	0.049
Head out	-339.67	-2.763	26	0.010
Flick event	4.64	3.162	26	0.004
Nose duration	29.43	2.069	26	0.049
Total escaping	291.06	2.587	26	0.016

- Negative sign indicates larger values for singleton trials

Total refuging time was significantly higher for *E. whitii* in the singleton trials than in the dyadic trials (Table 6 (a), Figure 6 (d). This result suggests that *E. whitii* refuge acquisition time was negatively impacted by the presence of *E. multiscutata*.

Although total refuging time was slightly higher for the *E. multiscutata* singleton trials than in the dyadic trials the means were not significant ($P < 0.05$) (Figure 6 (d)). This suggests that *E. multiscutata* refuge acquisition time was not affected by the presence of *E. whitii*.

The highly significant result for *E. whitii* nose duration (that is, hesitating at the refuge entrance) shows that it spent much less time in this behaviour in the singleton trials than in the dyadic trials (Table 6 (a)). This suggests ‘hesitancy’ on the part of *E. whitii* to enter the refuge when *E. multiscutata* was present. Table 6 (b) indicates *E. multiscutata* also spent less time in this behaviour during the singleton trials than the dyadic trials (see also Figure 6 (g)). This result suggests that *E. multiscutata* was also more ‘hesitant’ in entering the refuge when *E. whitii* was present, though much less so than *E. whitii*.

Total escaping time (and its component variables, escape 2 and escape 3) was significantly higher in the dyadic trials than the singleton trials for *E. multiscutata*. The results suggest that *E. multiscutata* escape behaviour was more affected by the presence of *E. whitii* than *vice versa*, although total escaping time was higher for *E. whitii* in both treatments (Figure 6 (e)). The marginally higher total escaping time for *E. whitii* in the dyadic trials in comparison with the singleton trials was not statistically significant (Figure 6 (e)).

Significantly less time was spent in ‘head out’ behaviour for both species in the dyadic trials than in the singleton trials. For the dyadic trials the ‘head out’ position would involve the subject turning its back on the potential presence of the competing species in the other refuge shelter. The lower time spent in this position in the dyadic trials may therefore represent a greater vigilance on the part of the subject in guarding its acquisition.

Both species were recorded as having more ‘tongue flick events’ in the dyadic trials than in the singleton trials. This may be an indication that the specimens were collecting more chemosensory information due to the presence of the other species. However caution should be exercised in interpreting these data since the ‘flick events’ data could not be considered as robust as other data in the trials due to limitations in the resolution of the photographic equipment which made observation of tongue flicks difficult.

Composite results

Figure 6 (a) to (g) is a series of composite graphs, comparing mean values for selected variables, that give an overview of between-treatment and between-species experimental results. Along with the previous analyses, these graphs show that:

- 'Retreat', 'excluded' and 'evicted' events only occurred in the dyadic trials and were significantly higher for *E. whitii* (for 'retreat' and 'excluded') (Figure 6 (a) – (c)).
- 'Total refuging time' was similar for both species in the singleton trials but was significantly reduced for *E. whitii* in the dyadic trials (Figure 6 (d)).
- *E. whitii* spent more time attempting to escape than *E. multiscutata* in both treatments. However *E. multiscutata* 'total escaping' time was significantly more affected (increased) in the dyadic trials than *E. whitii's* (Figure 6 (e)).
- *E. multiscutata* spent more time in 'head out' behaviour than *E. whitii* in both treatments. However *E. multiscutata*'s behaviour was more affected (reduced) in the dyadic trials than *E. whitii*'s (Figure 6 (f)).
- 'Nose duration', i.e. hesitating at the refuge entrance, was significantly higher for *E. whitii* in the dyadic trials than in the singleton trials. *E. multiscutata*'s 'nose duration' also increased in the dyadic treatment but to a much lesser degree than *E. whitii*'s (Figure 6 (g)).

Figure 6: Selected between-treatment and between-species comparisons.

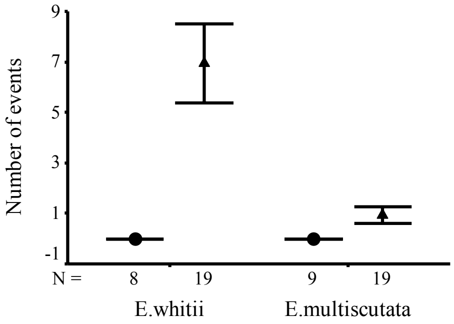
Legend

Error bars = Mean + - 1 SE

● Singleton trials

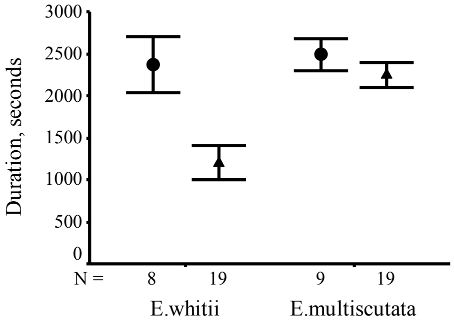
▲ Dyadic trials

(b)



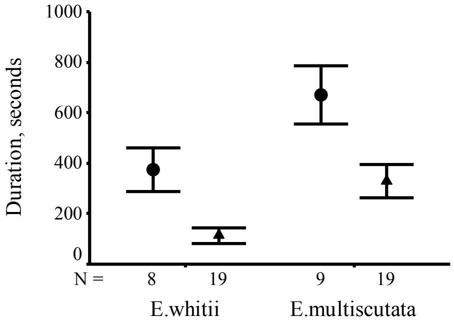
Excluded

(d)



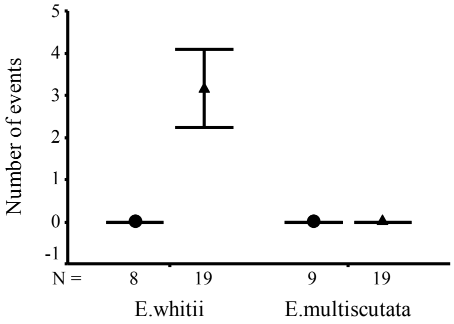
Total Refuging

(f)



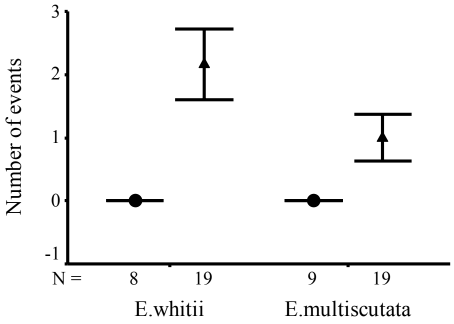
Head out

(a)



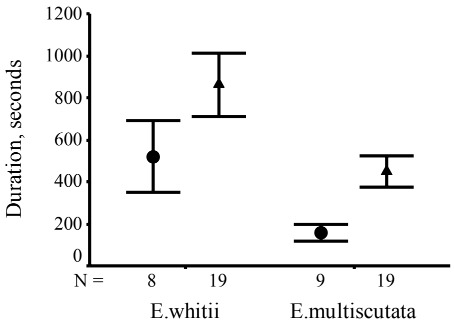
Retreat

(c)



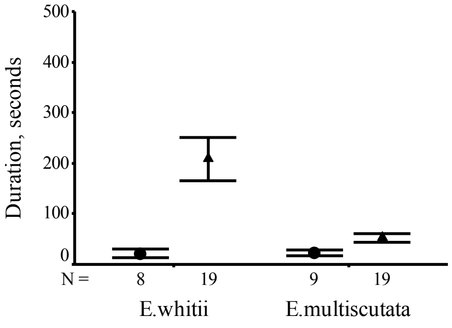
Evicted

(e)



Total escaping

(g)



Nose

Discussion

Non-refuge behaviour

Egernia whitii spent more time in all non-refuge-associated behaviour than *E. multiscutata* during dyadic trials. To some extent these results are the corollary of refuge behaviour, that is, if the skink was not refuging it had to be doing something else. Despite this, significant differences in some of these behaviours suggest differences in the strategies or responses of the study species and these are now discussed.

Escape behaviour

E. whitii spent significantly more time than *E. multiscutata* in attempting to escape from the arena in both the dyadic and singleton trials. Much of this behaviour occurred early in the trials with *E. whitii* taking significantly longer to gain entry into the refuge. Escape behaviour mostly involved getting as far away as possible from the area of close sensory proximity to the opponent (Table 2). However the fact that there was no significant difference in this behaviour for *E. whitii* between the dyadic and singleton trials suggests the behaviour was at least partly a response to the novel arena, or situation, rather than to the presence of *E. multiscutata*. In contrast, while *E. multiscutata* spent less time than *E. whitii* in escape behaviour during dyadic trials (Table 2), there was a significant increase in its time spent in this behaviour compared to the singleton trials (Table 6 (b)) and no significant between-species difference in escape behaviour during singleton trials.

These results suggest that *E. multiscutata*'s escape behaviour was modified (increased) by *E. whitii*, whereas *E. whitii*'s escape behaviour was not modified by *E. multiscutata*. The results are concordant with the findings from logistic regression analyses in Chapter 3 which indicated that the presence of *E. whitii* was a deterrent to *E. multiscutata*.

Retreat behaviour

There was a significant between-species difference in retreat behaviour in the dyadic trials (Table 2). In fact, *E. multiscutata* did not retreat from *E. whitii* in any of the replicates. Retreats by *E. whitii* occurred immediately following an agonistic interaction (e.g. tail lash or the direct approach of the other skink). This difference in behaviour would likely lead to the avoidance, or reduction, of interspecific competition in the field situation. Provided there is adaptive behavioural flexibility, this would lead to resource partitioning (Pereira *et al.* 2003; Langkilde *et al.* 2004; Langkilde and Shine 2004; Morrell and Kokko 2005).

Tail twitch

Tail twitch behaviour is considered to be submissive signalling (Torr and Shine 1994; Torr and Shine 1996) and was observed in *E. whitii* during dyadic trials but not in *E. multiscutata* (Table 2). It is possible that this behaviour is not part of *E. multiscutata*'s repertoire since it has not been reported in this species nor observed by me. Alternatively, it may not form part of its inter-species signalling behaviour with *E. whitii*. However, tail-lash behaviour (interpreted as aggressive signalling (Torr and Shine 1994)) was observed in the dyadic trials, suggesting that tail movements form part of interspecific signalling. The other obvious interpretation is that its absence may simply indicate that *E. multiscutata* did not indicate submissiveness to *E. whitii*. Further investigation into intra- and inter-specific signalling in lizards would be beneficial.

Nose behaviour

Nose behaviour represents the number and/or duration of time(s) the skink spent hesitating at the entrance to the refuge with its nose just at the opening (often tongue flicking). I have assumed that the skinks were assessing the risk/benefit of entering the refuge. *E. whitii* spent significantly more time on more occasions than *E. multiscutata* in this behaviour (Table 2). My interpretation is that *E. whitii* was more reluctant to enter the refuge when *E. multiscutata* was present than *vice versa*, suggesting *E. multiscutata* was more likely to enter an occupied refuge than *E. whitii*. Comparison with the singleton trials however, shows that the 'nose' behaviour of both species was modified by the presence of the opponent, suggesting that neither species had an absolute prerogative to access an occupied refuge. I have found no similar investigations in the current literature for comparison.

Excluded behaviour

E. whitii was excluded from the refuge significantly more often than *E. multiscutata* (Table 2). This is a clear indication that *E. whitii* was more likely to avoid agonistic interactions than *E. multiscutata*, suggesting that *E. whitii* would generally adopt an alternative strategy (such as the observed resource partitioning) in the field (Chapter 3). However *E. multiscutata* was excluded on a number (18) of occasions, indicating that *E. whitii* may sometimes gain a competitive advantage due to prior residency (Cooper and Vitt 1987) and that refuge occupation was dynamic and subject to more than just interspecific morphological asymmetry. This contention was also supported by the lack of any significant difference between the species in 'evicted' behaviour and its rare occurrence in the trials.

Refuge acquisition

Overview

Both theory (Robson and Miles 2000; Hone and Benton 2005) and empirical data (Langkilde and Shine 2004; Langkilde and Shine 2005) suggest that larger animals will tend to win initial agonistic interactions for a contested resource in paired encounters.

On Wedge Island *E. multiscutata* has been shown to be larger than *E. whitii* in head dimensions and mass, relative to snout to vent length (Chapter 4). Consequently, even though dyads in this experimental study were matched by SVL, *E. multiscutata* had a potential competitive advantage over *E. whitii* in several important combative characters (Herrel *et al.* 2001; Verwaijen *et al.* 2002; Huyghe *et al.* 2005). It is therefore not surprising that *E. multiscutata* gained significantly more time in the refuge than *E. whitii* during dyadic trials (Table 2). This result was consistent with the size-based linear interspecific dominance hierarchy previously found in experimental trials for other skink species (Langkilde *et al.* 2003).

To gain access to the refuge in the dyadic encounters the skinks would have had to either tolerate the close proximity of the opponent species or modify their temporal refuging activities so that they partitioned their refuge access on a time niche dimension (Pianka 1973; Kocàrek 2001). In fact the results suggest that both strategies occurred.

Niche partitioning

Comparisons between singleton and dyadic trials show that *E. whitii*'s time niche was modified by the presence of *E. multiscutata*, whereas there was no such modification to *E. multiscutata*'s refuging behaviour. Singleton trials, where the skinks could access the refuge free of competitive interactions, showed that there was no significant interspecific difference in the time spent in the refuge by the two study species' (see "Singleton encounters" sub-heading in the results section).

Comparisons between the singleton and dyadic trials showed that there was no significant difference in *E. multiscutata*'s refuging time between the two treatments (Table 6 (b)). However, *E. whitii*'s refuging time was significantly shorter in the dyadic trials than in the singleton trials (Table 6 (a). These results indicate that *E. whitii* reduced its refuge time in response to *E. multiscutata*, whereas *E. multiscutata* did not. This does not necessarily imply that *E. whitii* would suffer a reduction in fitness in the field. Other investigations have shown that through apparent behavioural flexibility skinks may be able to maintain 'normal' body temperature and food intake by minimising agonistic interspecific interactions (Langkilde *et al.* 2004). In one particular study *E. whitii* shelter site use was found to be suppressed more by some species in a lizard assemblage than others, with *Eulamprus tympanum*, a skink whose mass was approximately 25% less than *E. whitii*, having the least effect (Langkilde *et al.* 2003). Interspecific interactions were also found to be more intense than intraspecific interactions in the same study. It appears therefore that *E. whitii* is flexible in its behavioural responses, probably on a potential cost/benefit basis (Pereira *et al.* 2003), depending on the species, or size of individual, with which it interacts.

Proximity tolerance

The 'co-refuge ratio' shows that both species had some tolerance for close proximity of the other. *E. multiscutata* shared its refuge with *E. whitii* for about 22% of its own refuging time and *E. whitii* shared with *E. multiscutata* for about 49% of its own refuging time. This appears to be unusual in sympatric lizards and may be related to the close morphological similarity of the two species. Previous investigations have shown that within a five-species lizard assemblage (including three *Egernia* species) there was no interspecific tolerance for co-refuging, with the rank of the skinks' ability to exclude other lizards corresponding exactly to relative body size (Langkilde and Shine 2004). It is also possible that due to the experimental design in which, for ethical reasons, the skinks were separated by an open wire mesh barrier, agonistic interactions were unable to escalate to a physically damaging or even lethal level, thus altering the cost/benefit ratio. Nevertheless, skinks were frequently excluded from taking refuge in the dyadic trials confirming an effect of interspecific interactions (Table 2).

Behavioural responses to relative size

Table 3 and figures 2 (a) and (b) show that while the refuge time of both species was affected by their opponent's size, these effects were in different directions. Figure 3 shows that as the relative mass of *E. multiscutata* increased with respect to *E. whitii* both species spent less time in the refuge, to the point where *E. whitii* was excluded from the resource as the ratio approached 2:1. Such competitive exclusion is not unexpected given mass asymmetry (Huyghe *et al.* 2005). However it appears that it was not mediated by increased agonism on the part of *E. multiscutata,* since it too spent less time in the refuge as its relative size increased. Rather, it was *E. whitii*'s response to the increasing likelihood of losing agonistic interactions to a relatively larger competitor.

Figure 3 suggests that *E. multiscutata*'s refuge behaviour was also modified as *E. whitii's* relative mass increased. In this case *E. multiscutata* spent more time in the refuge, indicating a response to increased competition that was opposite that of *E. whitii*'s, that is, to stay and defend. This suggests that *E. multiscutata* had a perception of a greater threat from larger *E. whitii* with the concomitant need to invest more in holding the resource. Differences in the behaviour of the species was also confirmed in that, when controlling for the opponent's mass, *E. multiscutata* spent less time in the refuge as its own mass increased, whereas *E. whitii*'s refuge time was not affected (Table 5).

General considerations

The results of this study indicate that the most likely proximate stimulus for the observed time niche partitioning in the dyadic trials was the morphological differences between the species (as per Huyghe *et al.* 2005). Several of their opponent's as well as their own dimensions correlated with refuge time, the largest effect being due to mass (Tables 3, 4, and 5, Figs 2, 3 and 4). However the results also point to differential behavioural responses to this stimulus as the proximate mechanism of partitioning.

Some caution should be exercised in extending the experimental results to field conditions since the area of the experimental arenas was constrained by artificial boundaries. Consequently, the range of optional behavioural strategies was also constrained, for example, the option of leaving the arena in search of an alternative refuge (habitat partitioning). Nevertheless, the results were compatible with the analyses of observed broad scale habitat partitioning and co-existence observed on Wedge Island (Chapter 3).

The implications of these results are that *E. whitii* is likely to lose direct competitive interactions with *E. multiscutata*, at least in the first instance. Nevertheless the outcome of interactions was not completely deterministic, with *E. whitii* obtaining some access to the refuges in the dyadic trials. Similarly, it also persists in sympatry with *E. multiscutata* on Wedge Island. I suggest that behavioural flexibility and species specific differences in responses to interspecific competition result in habitat partitioning on Wedge Island. The outcome is that *E. whitii* is generally relegated to habitat that is non-preferred by *E. multiscutata*. However experimental results show that *E. multiscutata* must invest more time in holding the resource as its opponent size increases, suggesting that *E. whitii* poses a threat in the field situation if it is large.

For co-existence to persist on Wedge Island *E. whitii* must obtain some competitive advantage over *E. multiscutata* in habitat that contains rocks but does not contain sandy substrate (Chapter 3). In these habitats aggressive interactions may not be the most cost effective behaviour for *E. multiscutata* and an economic equity may be ‘negotiated’ such that co-existence can occur. It is possible that this outcome is mediated through the cost/benefit ratio of *E. multiscutata*’s apparent obligate burrowing behaviour, *E. whitii*’s reported saxicolous behaviour and dynamic behavioural responses to interspecific interactions. Further investigations into this relationship would be beneficial in understanding resource partitioning in sympatric species.

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CHAPTER 7

General Discussion

Research question

Two species of the skink genus *Egernia, E. multiscutata* and *E. whitii,* coexist in abundant numbers on Wedge Island in South Australia's Spencer Gulf (Robinson *et al.* 1996; Chapter 3). The species are morphologically very similar (Coventry and Robertson 1980; Cogger 2000; Chapple 2003; Chapter 4) and they are reported to have similar activity patterns, life histories, and generalist diets (e.g. Greer 1989; Brown 1991; Cogger 2000; Chapple 2003; Chapter 6). Both species are predominantly burrowers with strong attachments to permanent refuges (Greer 1989; Chapple 2003; Chapter 6). Their reported distributions suggest that they have very similar habitat requirements (Cogger 2000; Donnellan *et al.* 2002). Such interspecific similarities suggest that they are likely to compete for similar resources (e.g. Stamps 1983; Langkilde *et al.* 2003; Langkilde and Shine 2004).

The competitive exclusion principle holds that coexistence can only occur between two species that compete for resources in a stable environment if the species niches are differentiated (Mackenzie *et al.* 1998). If the competitive exclusion principle applies to the *Egernia* species on Wedge Island it should be evidenced by some form of niche differentiation, or resource partitioning. Do the sympatric skinks *E. multiscutata* and *E. whitii* on Wedge Island show evidence of resource partitioning, and if so, by what mechanism is it mediated?

Evidence for resource partitioning

Preliminary investigations of a transect survey of Wedge Island (refer to Chapter 3) showed that there was broad habitat partitioning between *E. multiscutata* and *E. whitii*. Generally, *E. multiscutata* was present primarily in sand / loam substrates and *E. whitii* was present primarily in rock / loam substrates. However each of the species was also present to a lesser degree in all of the other substrates and both species were present concurrently in 43 resource plots (out of a total of 3,073 occupied resource plots) among all except 'inhospitable' substrates (see Figure 3, Chapter 3), indicating some tolerance for close interspecific proximity.

Analyses showed that deviations from the null-hypothesis random distribution of each of the species within each of the substrates were greatest in sand / loam and rock / loam substrates. *E. multiscutata* was more prevalent than expected in sand / loam and less prevalent than expected in rock / loam, whereas *E. whitii* was more prevalent than expected in rock / loam and less prevalent than expected in sand / loam (Figure 4 (a) and 4 (b) and in-text results under the heading 'Comparison of expected and actual substrate occupancy', Chapter 3), suggesting that the species may affect each other's habitat choices. However the range of reported habitat preferences for both species encompasses both sandy substrates and rocky areas (Greer 1989; Cogger 2000; Chapple 2003). Thus, the presence of *E. multiscutata* in sandy substrates and *E. whitii* in rocky substrates was concordant with aspects of the known range of habitat preferences of both species, including *E. multiscutata*'s reported obligate burrowing habit and *E. whitii*'s flexible facultative burrowing or saxicolous behaviour (Chapple 2003). However the results also suggest that neither species appears to fully utilize its potential range of habitat preferences on Wedge Island, giving a strong indication that resource partitioning occurs. It is possible that the observed resource partitioning is facilitated to some extent by *E. whitii*'s apparently more facultative burrowing behaviour.

The results of logistic regression analyses of the transect survey data were concordant with the preliminary analyses, indicating that the odds of the presence of *E. multiscutata* were most positively affected by the presence of sand / loam substrate and the odds of the presence of *E. whitii* were most positively affected by rock / loam substrate (Chapter 3, Tables 3 (a) and 3 (b)). Importantly, the odds of the presence of each species were not significantly affected by the substrate primarily occupied by the opponent species. Therefore we can conclude that the lower than null-hypothesis expected presence of *E. multiscutata* in rock / loam and *E. whitii* in sand / loam substrates was not the result of avoidance of these substrates by the less prevalent species, at least for the habitat parameters analysed.

Logistic regression analyses also showed that the presence of each of the species was significantly negatively affected by the presence of the opponent species (Chapter 3, Tables 3 (a) and 3 (b)), indicating that resource partitioning was, at least in part, the result of proximate interspecific interactions (e.g. Downes and Shine 1998; Langkilde *et al.* 2003; Langkilde and Shine 2004).

Mechanisms of resource partitioning

The transect survey demonstrated that habitat partitioning occurs between *E. multiscutata* and *E. whitii* on Wedge Island and suggests a constrained use of the potential range of available habitat parameters for both species. Analyses indicated that this constraint was not mediated by avoidance of habitable substrates. However there was an indication that partitioning may be mediated by interspecific interactions or avoidance. Could this mechanism affect a shift from the fundamental habitat niche of either, or both, of the species such that their realised niches are sufficiently differentiated to minimise agonistic interactions and allow coexistence?

Three further questions help in investigating the question above: 1) Do either of the species have a potential ultimate competitive advantage over the other? 2) Would either species select a different habitat if the opponent species were not present? 3) Do direct interspecific competitive interactions cause the displacement of either species from essential habitat resources?

Potential competitive advantage

Asymmetries in the size of morphological characters are a major predictor of the outcome of agonistic interactions (e.g. Melville 2002; Kassam D. *et al.* 2004). The characters with the greatest potential to deliver a competitive advantage in lizards are snout to vent length, head size and mass (e.g. Verwaijen *et al.* 2002; Herrel *et al.* 2004; Langkilde and Shine 2004; Huyghe *et al.* 2005).

E. multiscutata and *E. whitii* have a similar range of snout to vent lengths (Store 1968; Milton 1987; Cogger 2000; Chapple 2003; Chapter 4). However, measurements taken from field samples on Wedge Island showed that

E. multiscutata was significantly larger in head size and mass, relative to SVL. Hence *E. multiscutata* potentially has a competitive advantage over *E. whitii* in direct agonistic interactions, including gape displays (e.g. Langkilde and Shine 2005).

Refuge choice

Egernia species are noted for their strong attachments to permanent retreat sites, or refuges (e.g. Greer 1989; Chapple 2003). Permanent refuges are known to be among the most important of habitat features for many reptiles (e.g. Martin 2001; Amo *et al.* 2003; Diego-Rasilla and Pérez-Mellado 2003; Martin *et al.* 2003; Polo *et al.* 2005). In the Wedge Island survey (Chapter 3) almost all observed skinks were associated with either a sand burrow or a shallow burrow under loose rocks. Although there was obvious partitioning of the substrates (which provide the resources for refuges) on Wedge Island, the substrate in which each of the species mainly settled was not, of itself, a deterrent for settlement by the opponent species. Was this phenomenon a result of proximate interspecific interactions, ultimate habitat preferences, or both? A substrate choice experiment, in which the competitor species was absent, was devised to investigate (Chapter5).

When given a choice between digging their own refuge burrows in sandy substrate or accessing a ready-made 'rock' burrow (simulating surface rocks with crevices underneath) the majority of individuals of both species initially chose to refuge under the 'rock' (Chapter 5, Figure 3). However the majority of individuals of both species chose to excavate their own burrows for longer-term overnight refuges (Chapter 5, Figure 4). There was no significant difference between the choices of the two species (Chapter 5). Burrow dimensions were significantly larger for *E. multiscutata* (Chapter 5, Figure 5) and their burrows were more complex (Chapter 5, Figure 6). These experimental results were concordant with the broad range of habitat parameters reportedly used by both species (Hickman 1960; Coventry and Robertson 1980; Milton and Hughes 1986; Greer 1989; Donnellan *et al.* 2002; Chapple 2003). However the results were discordant with the observed habitat partitioning on Wedge Island (Chapter 3). This clearly suggests that *E. whitii*'s preferred choice of overnight refuge is modified on Wedge Island, such that it tends towards the saxicolous end of its behavioural spectrum. No such modification of overnight refuge was observed for *E. multiscutata*. However there is so far no convincing field evidence from Wedge Island to suggest that *E. multiscutata* routinely uses loose rocks as a temporary refuge. Hence *E. multiscutata*'s initial choice of the 'rock' refuge in the experiment suggests that its behaviour in the field may also be modified by the presence of *E. whitii*. This could have implications for *E. multiscutata*'s antipredator responses (e.g. Martin 2001; Amo *et al.* 2003) and its dispersal dynamics (e.g. Bonnet *et al.* 1999; Stow *et al.* 2001; Weisser 2001; Wiens 2001). Further observations of *E. multiscutata* field behaviour, particularly during dispersal events are warranted in this area.

Refuge competition

Evidence of resource partitioning on Wedge Island, combined with the potential competitive advantage of *E. multiscutata* in agonistic interactions made possible by morphological asymmetries, suggest that *E. whitii*'s habitat choice behaviour is modified from its full potential scope when sympatric with *E. multiscutata*. Experimental results also indicate that *E. whitii*'s overnight refuge behaviour is modified in the field situation and suggest that *E. multiscutata*'s refuge behaviour may also be somewhat constrained. A further experiment (Chapter 6) investigated the outcome of direct competitive interactions for a contested essential habitat resource (refuge) to determine if competitive exclusion of either species occurred when no alternative refuge was available.

The main results of the refuge competition experiment (Chapter 6) indicated that *E. multiscutata* out-competed *E. whitii* to gain significantly more time in the refuge than *E. whitii* (Chapter 6, Table 2). *E. whitii*'s refuge time was significantly reduced from its normal refuging behaviour (that is, when *E. multiscutata* was absent), whereas *E. multiscutata*'s refuge time was not reduced by the presence of *E. whitii* (Tables 6 (a) and (b)). Direct exclusion events of each species by the other were observed but *E. whitii* was excluded significantly more often than *vice-versa* (Chapter 6, Table 2). These between-species differences were not completely deterministic however. Even though the dyadic partners were matched as closely as possible in snout to vent length, other morphological characters played a significant role in the outcome of competitive encounters. The dimensions of a specimen's opponent had a significant effect on its refuging time (Chapter 6, Tables 3, 4 and 5). Importantly, the behavioural responses of the species to their opponent's were in different directions (Chapter 6, Figure 2). As the mass of *E. whitii* increased the response of *E. multiscutata* was to spend more time in the refuge (guarding), whereas *E. whitii*'s response to increased *E. multiscutata* mass was to spend less time in the refuge (Chapter 6, Figure 2). This difference in behavioural response is critical to the outcome of agonistic interactions between the species. Nevertheless, there was some tolerance for co-habitation within the refuges, suggesting the potential for coexistence. Experiments using specimens in which *E. whitii* specimens are relatively larger than the *E. multiscutata* specimens would give more insight into the field dynamics of interspecific competition and coexistence.

General considerations

This study has produced clear evidence of resource partitioning between *E. multiscutata* and *E. whitii* on Wedge Island. This partitioning was evidenced from the differential distribution of the species among substrates containing different habitat parameters, particularly those which provide the resources for permanent refuge shelters.

Both species are known to have a similar range of habitat preferences, but *E. whitii* appears to be more flexible in its use of these features compared with *E. multiscutata*. As an obligate burrower, sandy substrates appear to be essential for *E. multiscutata*.

Habitat partitioning on Wedge Island was not mediated by ultimate interspecific differences in the avoidance of particular substrates, but mainly by the presence of the opponent species, combined with an attraction to suitable substrates.

The mechanism of habitat partitioning was shown experimentally to be not only the competitive advantage gained by the relatively larger morphological characters of *E. multiscutata,* but also the different behavioural responses of the two species to each other. *E. whitii* was more likely to retreat from, or avoid, agonistic encounters with *E. multiscutata* than *vice-versa*.

While both species are predominantly burrowers, *E. whitii*'s more flexible facultative burrowing behaviour appears to give it more options in selecting habitat. Therefore it may be adaptive for *E. whitii* to modify its settlement behaviour on Wedge Island to a narrower range of substrates where it tends to be saxicolous rather than risk potentially costly agonistic encounters with resident *E. multiscutata* in more suitable burrowing substrate. Similarly, *E. multiscutata* may direct its settlement behaviour to those substrates that provide the best resources for its obligate burrowing behaviour, while avoiding potentially costly interspecific agonistic encounters where *E. whitii* is resident.

These investigations have shown for the first time both the fact and mechanisms of resource partitioning between *E. multiscutata* and *E. whitii*.

Future studies using this model system should focus on those areas of co-residency in the distribution of the species and the dynamics of competition between specimens of various sizes, ages and sexes. The effects of prior residency should be more thoroughly investigated, as well as the effects of the presence of the opponent species on dispersal behaviour. Many *Egernia* species are known to live in stable social groups, including *E. whitii*, and possibly *E. multiscutata*. This group stability may be adaptive in terms of interspecific competition and further investigation would be warranted. Similar studies using other sympatric species would provide a more general understanding of resource partitioning and competitive exclusion.

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