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Ecomorphology, microhabitat use, performance and reproductive output in tropical lygosomine lizards.

PhD thesis, James Cook University.

Ecomorphology, Microhabitat Use, Performance and Reproductive Output in Tropical Lygosomine Lizards

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Thesis submitted for the degree of Doctor of Philosophy
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Declaration

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma at any university or other institution of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given

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Preface

The following is a list of publications arising from work related to, or conducted as part of this thesis to date:

HOEFER, A.M., B. A. GOODMAN, AND S.J. DOWNES (2003) Two effective and inexpensive methods for restraining small lizards. *Herpetological Review* **34**:223-224.

GOODMAN, B.A., G.N.L. PETERSON (2005) A technique for sampling lizards in rocky habitats. *Herpetological Review* **36**: 41-43.

GOODMAN, B. A. (2006) Costs of reproduction in a tropical invariant-clutch producing lizard (*Carlia rubrigularis*). *Journal of Zoology* (London) **270**: 236-243.

GOODMAN, B. A. (2006) The effects of maternal size on clutch traits in a tropical invariant-clutch lizard, *Carlia rubrigularis* (Scincidae). *Amphibia-Reptilia* 27: 505-511.

GOODMAN, B. A. (IN PRESS) Divergent morphologies, performance and threat behaviours in two tropical rock-using lizards (*Reptilia: Scincidae*). *Biological Journal of the Linnean Society*.

Chapter 3 - GOODMAN, B. A. (IN PRESS) Microhabitat separation and niche overlap among five assemblages of tropical skinks. *Australian Journal of Zoology*.

Chapter 5 - GOODMAN, B. A., A. K. KROCKENBERGER and L. SCHWARZKOPF (IN PRESS) Master of them all: performance specialisation does not result in trade-offs in tropical lizards. *Evolutionary Ecology Research.*

GOODMAN, B. A., L. SCHWARZKOPF (IN REVIEW) Divergent egg-size relationships in invariant-clutch producing arboreal and saxicolous *Cryptoblepharus* skinks. *Amphibia-Reptilia*.

GOODMAN, B. A. and J. L. ISAAC (IN REVIEW) Evidence of convergent evolution in tropical rock-using lizards. *Biology Letters.*

Chapter 4 - GOODMAN, B. A. (IN REVIEW) Intersexual relationships between microhabitat use, body shape and morphology in tropical Lygosomine (Reptilia: Scincidae) lizards. *Journal of Evolutionary Biology*.

Acknowledgments

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Despite the fact that I began working on these acknowledgments within a month of arriving in north Queensland and beginning my PhD research project. A large amount of what I felt back then remains true to this day. This is simply because many of the people responsible for this achievement had an influence on me and my life, long before I even contemplated the idea of a career in science, let alone a PhD research project. For this reason I thank all of my family, in particular my parents Rod and Bev and my siblings Dean and Narelle; I could never have done it without you!

Perhaps the strangest admission is that at some stages I felt as though I had some level of divine guidance in my biological interests, particularly those of reptiles and frogs. To this end, I’m referring to my grandfather Alex “Dad Brown”, whose passion for all forms of life, but specifically insects, took him to both Cairns and Magnetic Island in the 1930’s in an effort to examine some of Australia’s tropical butterflies and moths. He passed on several years before my birth, unable to tell me of his interests, so there must be some genetic predisposition for my interests in natural history. Certainly, our conversations would’ve converged on many a likely topic. Thus, perhaps his trek to northern Queensland some 70 years before played a subconscious role in my decision to choose James Cook University in Cairns, but one can never be sure about such things!

The various pieces of equipment (animal house, racetrack, cage heating racks, thermal gradient cages, modifying plastic lizard boxes) designed, constructed and transported were a huge task, without the help of Andrew Krockenberger, Andrew Marsh, Phil Turner, Callum McCulloch, Luciano Incao, Jamie Seymour, Charles Hatcher, Peter Grabau and Rod Armstrong would probably never have come to fruition. A huge number of other people accompanied and assisted me with field work during various phases of the project including, Ben Silberschmidt, John Roth, Doug Maclure, Nigel Carr, Stewart Warboys, Dean Goodman, Dan Munroe, Peter Pauls, Jillian Randle, Dan Salkeld, Julia Scott, Darrell Kemp, Julian Colomer, Paul Drake, Scott Griffin, Patricia Turner, Kris Kupsch, Rolf Nilsson, Lewis Roberts, Peter Douch, John Hill, Michael Anthony [I apologise to those whose names are not here!!]

Obtaining radiographs of several hundred live lizards was a phenomenal effort and I am indebted to the staff of Cairns Breast Clinic, in particular Wendy Waters, Daryl Short and Chris Thompson who provided considerable amounts of their own time to radiograph my lizards, usually at short notice, free of charge.

In addition, I thank many people with whom I formed good friendships over the course of my candidature. Darrell Kemp provided much needed encouragement during an ‘uncertain’ early stage. Charles Hatcher, Darrell Kemp, Garry Werren (RIP mate!), Stuart Worboys, Darren Peck, Robin Spencer and Callum McCulloch were all great company for a chat over a beer or two. While still living in Cairns my stays in Townsville were always made more enjoyable and comedic by another lizard worker, Dan ‘the-flying-man’ Salkeld. And after moving to Townsville, leaving, and returning again, several members of the Townsville crew made this experience even more enjoyable including Euan Ritchie, Jen Martin, Stephen Williams, Yvette Williams, Carryn Mannicom, Brad Evans, Jane de Gabriel, Ben Moore, Matt Symonds, Sam

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This thesis is dedicated to the loving memory of Emily 'Nana' Brown

“No feature so uniquely characterizes life as the process of evolution….it is the mechanism that sets apart functional analyses of biological systems from attempts to understand inanimate or man-made structures. Thus, a complete understanding of organismal design by nature should involve a functional analysis, a historical analysis, and an ecological analysis” (Wainwright and Reilly, 1994)

Abstract

Ecomorphology is the study of correlations between morphology and habitat(s) in organisms. If morphology is tightly correlated with habitat, then differences in morphology should directly affect fitness via their effect on performance within specific habitats. Despite the generality of this approach, clear correlations between habitat use, morphology, and performance have been established for few vertebrate groups. Furthermore, no study has examined whether correlations between habitat use and morphology may affect fitness via an effect on reproductive output. This thesis examines the relationships between microhabitat use, morphology, performance and reproductive output among scincid lizards from tropical north east Australia.

My examination of microhabitat use, temporal activity and size for 21 skink species from five assemblages (Alligator Creek, Cairns, Chillagoe, Cooktown and Mt. Bartle Frere), revealed that species separated along two gradients of structural microhabitat use: one that ranged from large rocks to leaf litter, and a second that ranged from closed habitats (high in leaf litter, ground cover, undergrowth, proximity to vegetation and increased canopy cover) to open habitats (low in all these characteristics). Species used microhabitats non-randomly, with species from the same ecotype (arboreal, generalist, litter-dwelling, rock-using) clustering in multivariate ecological space. Despite considerable niche overlap, null-model comparisons revealed only one assemblage (Chillagoe) had greater niche overlap than expected by chance. Assemblages with more species occupied smaller niche space, indicating species packing, however, species with more diverse niches were less evenly packed. Most species overlapped in activity time and size, suggesting that structural microhabitat is the dominant axis decreasing competitive interactions, allowing coexistence within these assemblages of tropical skinks.

Sexual differences in morphology were examined for 18 skink species that occupy a range of habitats. Phylogenetic analyses revealed that females from rocky environments evolved longer limbs and shorter abdomens compared to those from leaf litter. In males, use of rocky habitats was correlated with the evolution of a flatter, shorter body. The use of more open habitats was correlated with an evolutionary increase in limb length and a decrease in abdomen length in females, and an increase in limb length in males. Phylogenetic comparisons among generalist, leaf-litter and rocky habitat species revealed that males from rocky habitats were flatter than generalist and leaf-litter species, with females less stockier than males. Selection for body flattening in females appears constrained, or weaker than for

males, presumably due to the antagonistic effect of fecundity selection to maximize space for eggs. The more extreme flattening of male lizards from rocky habitats may assist locomotor performance, male-male contests or the use of refugia.

Phylogenetic analyses of males from 18 species revealed a tight positive correlation between sprinting and climbing ability, and climbing and clinging ability. There was no trade-offs among these performance traits, such as that observed in studies of arboreal lizards. Morphologically derived species were better at sprinting, climbing and clinging, which are presumably sufficiently similar tasks for scincid lizards that no trade-offs were observed. Although biomechanical models predict that flatness should enhance climbing speed, there was no evidence that a flat body assisted in climbing in this study. Similarly, biomechanical models predict that long limbs should enhance jumping ability, but no such correlation was observed in my study.

Five conceptual models of lizard locomotion relating to habitat use and morphology (limb length) were examined using 18 species of skink. Both differences and similarities between the sexes in the relationships between microhabitat use and performance were observed. Male and female skinks both responded to increased habitat openness by evolving greater sprint speeds. However, males in open habitats also had faster climbing speeds, and better clinging ability than those from closed habitats; enhanced clinging ability is likely beneficial for increased climbing speed, or correlated selection on these two traits. While these relationships were in the same direction, they were less robust or non-significant for females. Intersexual differences in performance resulting from natural selection for improved locomotor function in particular habitats may be eroded in females by sexual selection (e.g., for increased fecundity). Moreover, specialized leaf-litter dwelling species had poor performance at all performance traits examined, suggesting that these traits were not relevant to specialisation to a leaf litter habitat, or that selection on these traits is relaxed as there is more reliance on crypsis.

Body flattening was negatively correlated with abdominal volume, such that flatter species had lower abdominal volumes. Abdominal volume was strongly correlated with reproductive output (RCM), and flatter species had lower reproductive output. Thus, body shape determines reproductive output by imposing a constraint on clutch mass. The tight correlation between abdominal shape and both RCM and habitat, suggests changes in body shape are adaptive and may have a functional role (e.g., using rock-crevices). Thus, adaptive changes in morphology can influence fitness without affecting performance. This study shows that for this group of Lygosomine lizards there is a clear evolutionary pathway between clutch mass and body shape, with body shape acting as a constraint on clutch mass and therefore, reproductive output.

Structural microhabitat use provides the dominant axis separating and allowing coexistence among this group of diurnal tropical skinks in northeast Australia. Morphological adaptation in this group of tropical lizards to two habitat gradients and in response to three categories of habitat use has led to convergence in morphology and performance, however, sexual differences were detected. The increased use of rocky and/or open habitats by species has led to evolutionary increases in running speed, climbing speed and cling ability, with performance of females lagging behind that of males. These sexual differences in morphology appear to be the result of the antagonistic effects of natural selection for performance, offset by sexual selection that affects the sexes differently. Finally, adaptive changes in morphology and body shape in response to these habitats have led to changes in reproductive output.

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Chapter 1: General Introduction

CHAPTER 1

General introduction

What do ecomorphological relationships tell us about adaptation?

All organisms are adapted to their current environment, and one of the most pervasive patterns in nature is the way unrelated organisms from similar habitats display similar traits (Darwin, 1859; Bock and Von Wahlert, 1965). For example, sunbirds, hummingbirds and honeyeaters all live in habitats with nectar available, and all use different mechanisms to obtain this nectar as food (Paton and Collins, 1989). In turn, nectar feeders may drive the co-evolution of floral variation and speciation in plants. In the geographically widespread flower genus *Aguilegia*, interspecific variation in floral traits related to mating and sexual isolation, also select for species-specific pollinators (Hodges and Arnold, 1994). In many cases, phylogenetically disparate species show convergence in morphology that correlates with specific habitats, vegetation configurations, and functional roles (Karr and James, 1975; Williams, 1983; Langerhans et al., 2006; Melville et al., 2006). Convergence among morphological structures in unrelated organisms from similar habitats, and the evolution of continuous morphological differences in response to habitat gradients, has frequently been used as strong evidence of adaptation (Lewontin, 1978; Williams and Peterson, 1982; Harvey and Pagel, 1991; Lauder, 1996). Thus, examining the link between an organisms' functional morphology and its environment may be used to provide insights about adaptation (Arnold, 1983; Emerson and Arnold, 1989; Wainwright and Reilly, 1994).

Historically, ecological morphologists attempted to infer an organism's ecology using only its morphology (Williams, 1972; Jaksic et al., 1980; Ricklefs and Travis, 1980). These studies investigated differences in morphology in the absence of ecological and performance information in an attempt to expose potentially adaptive traits, but this approach provides no information on whether an organism experienced a benefit from that trait (e.g. Jaksic et al., 1980; Pianka, 1986; See also, Garland and Losos, 1994, Miles, 1994 for further discussion). However, while much can be inferred solely from morphology, a more powerful test of the potential adaptive nature of specific morphological traits can be obtained by assessing whether specific traits increase the functional capability of an organism (Arnold, 1983; Garland and Losos, 1994). Thus, the correlation between an organisms' phenotype and its ecology is the result of natural selection for optimal performance at ecologically relevant tasks (Ricklefs and Miles, 1994; Miles, 1994).

Investigations of organismal performance were focussed by the approach advocated by Arnold (1983), which was a statistical treatment of a laboratory and field based program mephasized by Bock (1977; 1980). Arnold proposed that variation in an organism's functional morphology (e.g., morphology, physiology, biochemistry) should result in variation in performance that directly affects an organisms' fitness in a given environment (Arnold, 1983; Garland and Losos, 1994). Thus, the natural range of variation among species or populations provides the raw materials upon which natural selection operates. Studies seeking to link ecology and morphology via performance in specific environments (ecomorphology) provide a powerful test of adaptive hypotheses (Gould and Lewontin, 1979; Arnold, 1983; Losos, 1990a; Irschick and Losos, 1998). Thus, it is reasonable to expect species inhabiting similar niches would also exhibit similar morphological traits, and evidence from several groups (e.g., Anoles, East African cichlids, Darwin's finches) supports this prediction (Schluter, 2000).

It is now generally accepted that groups of species do not represent independent data that is appropriate for analyses using conventional statistical techniques (Cheverud et al., 1985; Felsenstein, 1985, 1988). Consequently, it is imperative that interspecific comparative analyses are conducted within a phylogenetic framework (Harvey and Pagel, 1991; Blomberg et al., 2003). Indeed, recent vigour and renewed interest in ecomorphology have been stimulated by advances in both analysis of comparative data (Felsenstein, 1985, 1988; Harvey and Pagel, 1991), and molecular techniques, which have increased the availability of phylogenies suitable for conducting comparative tests (Blomberg et al., 2003).

Goals of ecomorphology and additions to Arnold's paradigm

Ricklefs and Miles (1994) highlight 3 distinct goals for studies of ecomorphology. These include: (i) the inference of ecological patterns based on a species' morphology, as determined by measuring (ii) the correlation between the organism's ecology and morphology, and (iii) using the inferences developed in (1) to investigate and test the functional relationship between morphology and ecology to describe the performance and behaviour of the organism. More recently, however, a number of modifications and additions have been made to Arnold's original paradigm that enable testing of additional hypotheses. These changes include considering (i) the influence of behaviour on performance and fitness outcomes from specific morphologies, and (ii) a consideration of the effect of habitat and interspecific interactions on morphology, performance and behaviour (Figure 1.1). The addition of behaviour to the conceptual model enables an assessment of the way morphology may limit performance by limiting an organism's behavioural options and *vice versa*. Adding habitat use and specialization for a range of habitats to the model allows us to predict relationships between morphology and habitat use among species (Karr and James, 1975; Moermond, 1979). Considering interspecific interactions takes into account how competition may modify a species' habitat use (Schoener, 1975; Losos and Spiller, 1999; Melville, 2003). Intersexual differences in habitat use may also result from the competing roles of natural and sexual selection (Andersson, 1994; Olsson et al., 2002). Males and females may diverge in morphological features, suiting them to different aspects of the environment (Shine, 1986; Butler et al., 2000; Butler and Losos, 2002). Natural selection should favour the phenotype that enhances performance, such that in the absence of constraints, the most 'fit' morphology should evolve within a population (Garland and Losos, 1994). Given that different morphological traits function best in specific habitats, natural selection should lead to the evolution of the most suitable morphology within a given environment (Darwin, 1859; Fisher, 1930; Endler, 1986). Further, selective environments vary considerably with habitat and over time, and morphological characters tend to evolve most rapidly in those lineages displaying recent habitat changes (McPeek, 1995). As a result, closely related species occupying structurally divergent habitats are predicted to display the most pronounced morphological shifts, providing the best model systems in which to examine adaptive changes in morphology in response to divergent or novel environments (Baum and Larson, 1991; Losos and Miles, 1994).

A central premise of the ecomorphological paradigm is that changes in an organisms' morphology indirectly affect fitness by directly affecting performance (Arnold, 1983). However, changes in morphology may affect fitness without directly affecting performance (Garland and Losos, 1994; Figure 1.1). In this scenario, changes in morphology have direct fitness consequences without affecting either of the intermediate stages of performance or behaviour (Figure 1.1). Garland and Losos (1994) offer one possible example of how this may occur, in the case where an organism that typically relies on a specific colour pattern for crypsis is born with drastic changes in external pigmentation (e.g., albinism). If albinism is uncorrelated with other changes in morphology or performance, then a reduction in fitness may occur because of an increased risk of predation due to increased visibility (Garland and Losos, 1994). Clearly, while this example offers a test of how variation in the degree of albinism affects the probability of predation, and therefore fitness, the ability to extend this approach to an interspecific comparative study of the maladaptive effects of albinism is more problematic. More informative would be a comparative examination of how interspecific changes in morphology, correlate with an ecological or environmental gradient, and how these changes affect performance and fitness via survivorship and reproductive success (Arnold, 1983). For example, a phylogenetic comparison of 16 tadpole species along a gradient of predator exposure revealed a positive relationship between the risk of predation and the amount of predator-induced morphological plasticity (Van Buskirk, 2002). An increase in exposure to predators induces an increase in tail depth and a reduction in tail length, and these predator-induced changes may provide a functional benefit for swimming escape performance (McCollum and Leimberger, 1997; Van Buskirk and McCollum, 2000), or the larger tail may act to deflect a lethal attack away from the tadpole’s head (Hoff and Wassersug, 2000; Van Buskirk et al., 2003). Consequently, cases where adaptations or morphological change occurs in response to an ecological or environmental gradient provide an opportunity to examine how changes in ecomorphological relationships may lead to changes in fitness.

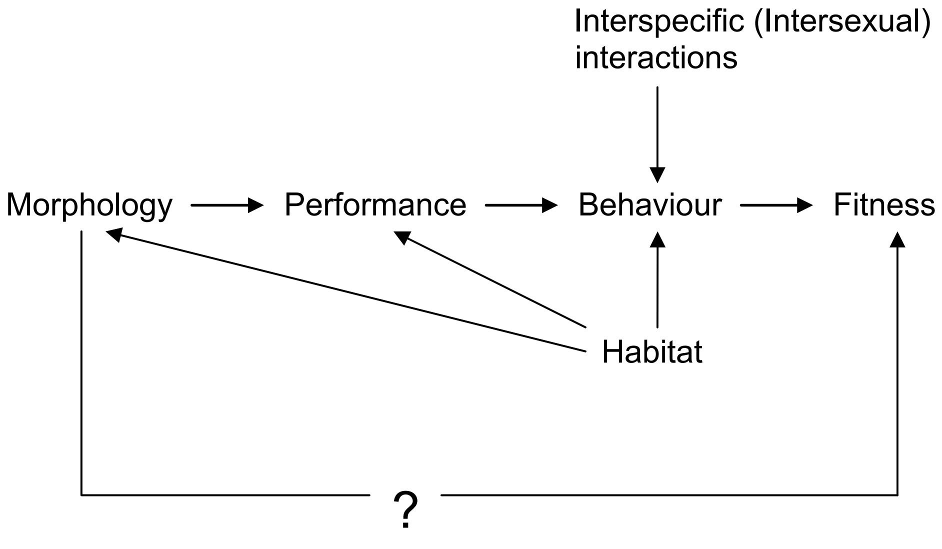


Figure 1.1. An expansion of Arnold’s paradigm incorporating several factors likely to affect key aspects of the paradigm. The path marked by a question mark proposes the conceptual and empirical possibility of a direct pathway from morphology to fitness (from Garland and Losos, 1994).

Why lizards are good subjects for ecomorphological studies

The link between morphology and habitat has been examined extensively in the squamate reptiles, a group which include a diverse range of taxa and exhibit a wide array of ecologies, morphologies and phylogenetic origins (i.e., lizards; Moermond, 1979; Pianka, 1986; Losos, 1990a; Miles, 1994; Vanhooydonck and Van Damme, 1999; Irschick and Vanhooydonck, 2002; pit-vipers; Martins et al., 2001; Sanders et al., 2004). Moreover, lizards have received considerable attention from an ecomorphological perspective (Losos, 1990a; Miles, 1994; Vanhooydonck and Van Damme, 1999; Melville and Swain, 2000), presumably because of the ease with which meaningful performance and morphological traits can be measured in this group (Garland and Losos, 1994; Bonine and Garland, 1999). Also, the members of this group display a broad range of ecologies and microhabitat use, with closely related specific often show contrasting microhabitat preferences.

Morphology and performance relationships

Performance measures

The main goal of ecomorphological studies is to establish the link between performance and morphology, and between performance and fitness. However, to establish these links requires the use of ecologically relevant measures of performance. Thus, obtaining a biologically meaningful assessment of whole organismal performance requires selection of the most ecologically relevant measures of performance to the organism to be studied (Arnold, 1983; Garland and Losos, 1994; Wainwright, 1996). Maximal sprint speed (Garland and Losos, 1994; Andrews et al., 2000; Miles, 2004) and endurance capacity (Garland et al., 1990; Garland, 1994; Bonine and Garland, 1999; Miles et al, 2000; Miles, 2004) have been examined and are related to survival (Christian and Tracy, 1981; Garland and Losos, 1994; Bonine and Garland, 1999; Miles et al, 2000; Warner and Andrews, 2002) and dominance in male lizards (Robson and Miles, 2000). Furthermore, sprint speed is heritable (Tsuji et al., 1989; Vanhooydonck et al., 2001) and highly repeatable (Huey and Dunham, 1987). Effective performance at tasks such as climbing perches and running on inclines (Huey and Hertz, 1982, 1984a; Losos, 1990a; Vanhooydonck and Van Damme, 2001), clinging (Losos, 1990a; Irschick et al., 1996; Zani, 2000; Irschick et al., 2005a), gliding (Marcellini and Keefer, 1976; Losos et al., 1989, Shine et al., 1998; McGuire and Dudley, 2005), sand-diving (Arnold, 1994, 1995), jumping (Losos et al., 1989; Losos 1990a; Lailvaux et al., 2004; Toro et al., 2004) and swimming (Gans, 1977; Webb, 2004; Webb et al., 2006) have all been used to define ecomorphological patterns and fitness gradients, measure costs of reproduction and putative adaptive benefits of traits for species from a range of habitats and ecologies.

Antagonistic natural selection that operates on species from contrasting substrates are likely to favour the evolution of substantial differences in locomotor function (Cartmill, 1985; Losos, 1990a; Zaaf and Van Damme, 2001). Therefore, a different set of morphological traits are expected to be favoured by selection in species specialised for fulfilling a specific locomotor task compared to species that use a wide range of varied substrates. Moreover, the different and opposing forces placed on climbing species or species that occupy vertical substrates, compared to species that occupy horizontal habitats, suggests substantial differences should exist between these locomotor modes (Cartmill, 1985; Losos, 1990a; Zaaf and Van Damme, 2001). Biomechanical models predict that species from open habitats or that run on level surfaces should gain the majority of propulsive force from the hind-limbs (Cartmill, 1985; Pounds, 1988; Losos, 1990b; Melville and Swain, 2000), and should have long hind limbs to enable longer strides, presumably with a long floating phase (the period when the limbs are free from the substrate; Van Damme et al., 1998; Vanhooydonck and Van Damme, 2001; Vanhooydonck et al., 2002). Further, to reduce internal inertia, the distal limb elements should be long and light in runners (Vanhooydonck and Van Damme, 2001) and the fore-limbs of such species should be considerably shorter than the hind-limbs, to prevent interference with the long, rapidly cycling hind limbs (Snyder, 1954; Zaaf and Van Damme, 2001). The body should be flattened laterally in running species to allow lateral body flexion to maximise stride length (Van Damme et al., 1997). This contrasts with climbing species from arboreal habitats, which should have short limbs, to keep the centre-of-mass close to the substrate, broadening the support base, and reducing the possibility of toppling sidewards from the perch. Climbing species should have fore-limbs and hind-limbs of equivalent length in order to perform equal length strides (Arnold, 1998; Vanhooydonck and Van Damme, 2001). In perch climbing species, both the fore-limbs and hind-limbs should be similar lengths and the distal and proximal elements in both limbs should be of similar length in order to grip perches securely (Moermond, 1979; Vanhooydonck and Van Damme, 2001). In addition, the body should be dorsoventrally flattened to lower the centre of gravity (Van Damme et al., 1997). The effects of gravity on climbers should be further reduced by having short, heavy, distal limb elements (Van Damme et al., 1997).

Performance relationships and trade-offs

Organisms are influenced by physical, physiological and ecological constraints, which cause trade-offs, in the ways resources are allocated, or in the direction and extent that evolution can procede. Thus, trade-offs result from one trait being coupled with a cost or decline in an associated trait (Partridge and Harvey, 1988; Begon et al., 1990). From an evolutionary perspective, trade-offs constrain the simultaneous evolution of two or more traits (Stearns, 1992).

In order to maximise biomechanical efficiency, our expectation is that specialized runners and climbers may differ in their morphological design (Kramer, 1951; Kardong, 2005; Cartmill, 1985; Losos et al., 1993), to the point that adaptation for one of these tasks should result in a trade-off in performance for the other, as is suggested by the ‘jack of all trades is master of none’ model (Huey and Stevenson, 1979; Futuyma and Moreno, 1988; Van Damme et al., 1997). In theory, specialist species should outperform generalist species at a few performance tasks, but be unable to maintain a similar high level of performance across a wider range of tasks, and vice versa. However, while early attempts to find evidence of evolutionary trade-offs often failed (Moreno and Futuyma, 1988), there have been few studies that rigorously address this question (but see Vanhooydonck et al., 2001a; Caley and Munday, 2003).

Possessing long parasagittal limbs may be beneficial for sprinting on horizontal surfaces because they enable longer strides and help keep the body off the surface of the ground. Body flattening should be lateral in runners, as this facilitates the lateral flexibility needed to maximise stride length, but should be dorsoventral in climbers to lower the centre of gravity. Research shows, however, there is likely to be fundamental biomechanical differences between species that climb on narrow perches and species that climb broad surfaces (compared to the stance of the lizard), such as large rocks and boulders (Van Damme et al., 1997, Vanhooydonck and Van Damme, 2001; Zaaf and Van Damme, 2001). While both performance tasks are classified as climbing, they require vastly different morphological traits. Arboreal anoles and chameleons that use narrow perches typically possess short fore and hind limbs of similar length that maintain the centre of gravity directly above the perch (Losos, 1990a; Losos et al., 1993), whereas, lacertids that climb on broad rocky surfaces possess long hind-limbs and relatively short forelimbs (Vanhooydonck et al., 2001). Thus, in the single study that examined *broad* inclined climbing, there was no trade-off between sprinting and climbing (Vanhooydonck and Van Damme, 2001). Thus, trade-offs between sprinting and climbing on perches may be the exception rather than the rule for the majority of lizard groups, because they occupy broad, inclined substrates. Thus, additional data on performance are required to test the ideas of performance specialisation and trade-offs.

Intersexual differences in morphology

Sexual selection increases the fitness of each sex indirectly by enhancing the opportunites for mating success (Darwin, 1871; Andersson, 1994; Isaac, 2005), and may cause morphological divergence between sexes despite ecologically mediated natural selection. Like most organisms, lizards often show intersexual differences in body size and shape (Andersson, 1994; Butler et al., 2000; Butler and Losos, 2002; Olsson et al., 2002), and in particular, two aspects of lizard body plans that display differences between the sexes are the greater relative size of the head in males and the greater relative length of the inter-limb region of the body in females (Olsson et al., 2002; Schwarzkopf, 2005). Sexual selection has long been proposed as the causal mechanism for these differences (Darwin, 1871; Andersson, 1994). The relatively larger heads, benefits males in bouts of intrasexual combat (Huyghe et al., 2005; Lappin and Husak, 2005). In females, selection for increased fecundity is correlated with an increase in inter-limb length, causing an increase in the amount of abdominal space available for the production of a clutch or litter (Dunham et al., 1988; Forsman and Shine, 1995; Olsson and Shine, 1997; Olsson et al., 2002). In the past, correlative investigations of habitat use and morphology have often involved only males (Losos, 1990a; Vanhooydonck and Van Damme, 1999; Kohlsdorf et al., 2001), or have used pooled data for both sexes (Jaksic et al., 1980; Miles, 1994; Melville and Swain, 2000; Zaaf and Van Damme, 2001). An obvious shortcoming with this approach is that selection may operate differently on individuals of each sex in different habitats, or individuals of different sexes may differ in morphology which may affect habitat use, and therefore, the relationship between habitat and morphology in members of each sex. Therefore, studies should investigate the ecomorpholgical relationships of the sexes independently (Herrel et al., 2002; Isaac, 2005). In lizards, there are differences in the degree of sexual-size dimorphism and in the microhabitats occupied by males and females (Schoener, 1967; Hebrard and Madsen, 1984; Butler et al., 2000; Butler and Losos, 2002; Losos et al., 2003a; See also Irschick et al., 2005). Moreover, functional constraints may pre-adapt one sex for using some habitats over others (Schoener, 1967; Temeles et al., 2000; Butler and Losos, 2002). For example, the degree of body flattening in female lizards may be reduced, due to the need to produce a clutch or litter, which may preclude the use of certain aspects of the habitat (e.g., crevices, inclined surfaces). Several studies have found differences in body shape of anoles from different habitats (Butler and Losos, 2000; Losos et al., 2003a). However, the way such differences in body shape affect performance or fecundity within the context of the habitat occupied has not been investigated.

Ecology and trade-offs in reproductive output

Organisms display considerable variation in reproductive output, with natural selection favouring traits that maximise life-time reproductive success of an individual. Reproductive output is determined by the trade-off between the costs associated with current versus future reproductive expenditure, as determined by historical, physiological and morphological/anatomical constraints (Williams, 1966; Hirshfield and Tinkle, 1975; Stearns, 1992; Roff 2002). Thus, the amount of resources allocated to reproduction remains a fundamental component of an organisms' life history and has attracted considerable attention from life-history theoreticians (Dunham et al., 1989; Stearns, 1992; Roff, 2002). One of the key determinants of reproductive output in lizards is body shape (Kaplan and Salthe, 1979; Shine, 1992; Qualls and Shine, 1995; Du et al., 2005a).

Lizard body shape and reproductive output

Early workers noted that lizard groups could be divided into species with a high 'RCM' (RCM = clutch mass / maternal post-oviposition mass; Shine, 1980), a stout body form, a 'sit-and-wait' mode of foraging, and predator evasion via crypsis, and species with low RCM, streamlined body, an 'active' mode of foraging, and which use flight for predator evasion (Vitt and Congdon, 1978). While it has long been suggested that RCM, body shape and associated escape and foraging behaviours are determined by phylogenetic origin, early in the evolutionary history of a species group (Perry, 1999) exceptions do occur. For instance, foraging mode varies considerably within the family Lacertidae (Perry, 1999) and Scincidae (Cooper, 2000), and can vary among species within a single genus (e.g., *Mabuya;* Scincidae; Cooper, 2000; Cooper and Whiting, 2000) and with both resource type and abundance (Greeff and Whiting, 2000). Therefore, an examination of the relationship between body shape and reproductive output requires a clade of lizards, preferably with close phylogenetic relationships, similar foraging modes, and substantial variation in body shape and habitat use.

Many studies suggest that costs of reproduction are correlated with RCM (Shine and Schwarzkopf, 1992; but see Olsson et al., 2000; Goodman, 2006a; Appendix II), i.e., species with a lower RCM may be favoured by selection if such individuals experience greater survivorship and life-time reproductive success (Vitt, 1981; Shine and Schwarzkopf, 1992). In several lineages of snakes, marine species produce smaller clutch masses, carried in a more anterior position than in terrestrial snakes, presumably because it improves swimming performance (Shine, 1988). Thus, reproductive material may fill only a proportion of the maximum available space, rather than all of it (Shine, 1988; Shine, 1992; Qualls and Shine, 1995). Despite numerous studies of variation in reproductive output, there have been are few tests of whether adaptation to a particular lifestyle or ecology can constrain reproductive output.

The importance of habitat use

An organism's fundamental niche, defined as those resources used in the absence of predators or competitors, may differ from its realized niche, observed when predators and competitors are present, so there is a need to identify a species' niche breadth and overlap under field conditions. Moreover, organisms typically exhibit morphological and/or physiological adaptations to the habitats and microhabitats they occupy (Losos, 1990a; Irschick and Garland, 2001). Thus, fitness is likely to be reduced if individuals are forced to occupy microhabitats to which they are less well adapted (Huey, 1991; Downes, 2001). In lizards, because shifts in microhabitat can cause reduced performance (Waldschmidt and Tracy, 1983), these shifts may also reduce survival (Arnold 1983, Huey, 1991; Kiesecker and Blaustein, 1998). Even subtle shifts in microhabitat use may lead to reduced fitness (Arnold, 1983; Huey, 1991). Thus, because spatial structure is invoked as the dominant axis providing separation and coexistence of sympatric species it is necessary in ecomorphology studies to determine a species' habitat requirements and use (Pianka, 1969a, 1986; Schoener, 1974; Toft, 1985).

Why more studies of lizards are required

Despite the body of work conducted on lizards, and while various interspecific studies have identified a relationship between morphology and ecology (Losos, 1990a; Miles, 1994; Melville and Swain, 2000, 2003; Kohlsdorf et al., 2001), other studies have been more equivocal (e.g., Jaksic et al., 1980; Leal et al., 2002; Schulte et al., 2004; Warner and Shine, 2006). In many cases, comparisons have been conducted on groups that are morphologically and ecologically specialised for specific habitats (e.g., *Anolis*; Losos, 1990a; Irschick and Losos, 1998, 1999), or have used groups restricted to a single genus or clade (*Phrynosomtidae*, Miles, 1994; *Niveoscincus*, Melville and Swain, 2000, 2003). Thus, there is a need to examine lizards from groups containing species that display a broader range of habitat use, and are from a broader phylogenetic range.

Microhabitat use of skinks from tropical north-east Australia

In Australia, the Scincidae occupy a wide range of habitats and show considerable morphological variation in response to different environments and habitats (Greer, 1989; Cogger, 2000). Despite the ecological and morphological diversity (Cogger, 2000; Pianka and Vitt, 2003), detailed descriptions of microhabitat use for the majority of Australia's tropical skink species are lacking (Ingram and Covacevich, 1990, Cameron and Cogger, 1992; Cogger, 2000). Moreover, within each of the genera *Carlia, Cryptoblepharus*, *Eulamprus*, *Lampropholis* and the monotypic *Techmarscincus jigurru*, there is at least one species that is restricted to rock habitats. Each of these rock-dwelling (saxicoline) species share a similar suite of morphological traits that are, presumably, adaptive for rock use (Ingram and Covacevich, 1978; Ingram and Rawlinson, 1981; Ingram and Covacevich, 1989). These morphological features include a dorsoventrally flattened body and head, and relatively long limbs and digits. As morphology is predicted to evolve rapidly in species or lineages that have made substantial shifts in habitat (McPeek, 1995), such differences in morphology may be expected. Indeed, current theory suggests that this body plan is a derived condition (Greer, 1989), as in all genera there are only a few species specialised for rock use. Moreover, sexual dichromatism (most noticeable in breeding males) is absent in the few rock-dwelling species (Greer, 1989; Ingram and Covacevich, 1989). Presumably, the dark body colour and lack of sexual dichromatism is adaptive in rock-using habitats because it reduces visibility of foraging lizards to predators (Greer, 1989). Nonetheless, whether this is actually the case remains untested. This study will use species from these genera to test hypotheses relating to microhabitat use, ecomorphology, performance, and trade-offs between performance and reproductive output.

Relevance and aims of this study

The aims of this project were to:

(1) Describe the microhabitat use of each taxon, and,

(2) Determine relationship(s) between microhabitat use and morphology for individuals of both sexes in this group of morphologically disparate skinks.

(3) Test whether species that were more dorsoventrally flattened had enhanced performance on rock compared to less flattened species.

(4) Determine whether there was a trade-off between sprinting and climbing and sprinting and clinging.

(5) Determine relationships between performance and gradients of microhabitat openness and substrate use

(6) Establish whether abdominal volume and reproductive output (i.e., clutch mass) was decreased in flatter species compared to those with robust body morphology.

Thesis Structure

My thesis is organised into the following chapters: Chapter 2 gives a general description of the species examined, the study sites and a brief summary of current knowledge of the life-history traits and ecology of these species in north-east Queensland. Chapter 3 describes the microhabitat separation and niche overlap among species from each of the sites examined. Chapter 4 considers intersexual differences in morphology and microhabitat use in 18 species of tropical skink, while Chapter 5 examines whether performance specialisation in one measure of performance leads to a trade-off in other, contrasting performance measures. Chapter 6 examines intrasexual correlations between two ecological gradients of microhabitat use and four separate measures of performance. Chapter 7 investigates whether changes in abdominal shape and volume (flattening) in response to a gradient of rock use causes a reduction in reproductive output. Chapter 8 is a general discussion of the results of my study, and summarises the main findings of the thesis and considers their relevance to adaptive processes and to contemporary theories in evolution and ecology. Appendix I is a paper in press describing a study that investigated divergence in morphology, performance, and escape behaviour in two closely related tropical rock-using lizards (*Reptilia: Scincidae*) from the genus *Carlia*. Appendix II is a published paper that investigated the effects of reproduction on locomotor performance in the lizard *Carlia rubrigularis*.

CHAPTER 2

General Materials and Methods

Study species

This study focussed on 18 species representing five genera from the scincid sub-family Lygosominae, including: *Carlia*, *Cryptoblepharus*, *Eulamprus*, *Lampropholis* and the monotypic genus *Techmarscincus* (formerly *Bartleia*). Many of these genera are predominantly tropical, however two are mainly temperate to sub-tropical in distribution (e.g., *Eulamprus, Lampropholis*; Greer, 1989; Cogger, 2000). Species were selected from each genus that displayed a broad degree of among-species ecological and morphological trait variation (Ingram and Rawlinson, 1981; Greer, 1989; Ingram and Covacevich, 1989, 1988; Cogger, 2000), with an effort to include congeners that occupied divergent habitats. Species were selected based on the microhabitat categories they used, as indicated in the literature (Ingram and Covacevich, 1978, 1989; Ingram and Rawlinson, 1981; Cogger, 2000), or from my own data. In addition, the robustness of the habitat categories occupied was determined quantitatively as part of Chapter 3 where four habitat categories were identified, including arboreal, leaf-litter dwelling, and rock-using; a fourth category (generalist) was used for species that used numerous, different substrates (Table 2.1).

Table 2.1. Habitat categories for 18 of the skink species examined in this study.

Arboreal	Generalist	Rock-using	Leaf-litter
Cryptoblepharus virgatus	*Carlia jarnoldae* *Carlia longipes* *Carlia pectoralis* *Carlia rostralis* *Carlia storri* *Eulamprus quoyii*	*Carlia mundivensis* *Carlia rococo* *Carlia scirtetis* *Cryptoblepharus litoralis* *Eulamprus brachysoma* *Lampropholis mirabilis* *Techmarscincus jigurru*	*Carlia laevis* *Carlia rubrigularis* *Carlia rhomboidalis* *Lampropholis robertsi*

All field work and species examined in this study were within the tropical-equatorial climatic zone of north-east Queensland, Australia, with five study sites situated between Townsville and Cooktown (Figure 2.1) (Ingram and Covacevich 1990, Cameron and Cogger, 1992; Cogger, 2000). This region is important because of its high endemism and biodiversity, and has the highest species diversity relative to the total area occupied, for members of the skink genus *Ctenotus* (James and Shine, 2000). In addition, this region also has a high species-diversity of scincids (Cogger and Heatwole, 1981). The number of species investigated at each site ranged from two to eight species (Table 2.1).

Figure 2.1. Coastal open monsoonal *Malaleuca* sp. forest with a sparse cover of leaf-litter (Left) and boulder piles of Black Mountain (Right) situated 25 km south of Cooktown.

Descriptions of study sites

Alligator Creek – Cape Bowling Green Bay National Park [30 – 60 m ASL]

This site is woodland dominated by bloodwood, poplar gum, Moreton Bay ash and ironbark (*Eucalyptus* spp.), with an understory of grasses, grasstrees, and cycads. Along the creek-line are several species of palms, casuarinas, and callistemon, with Kapok (*Bombax ceiba*) in rockier areas. The most abundant skink species and the species sampled from this site included: *Carlia pectoralis, Carlia rhomboidalis*, *Eulamprus quoyii* and *Lampropholis mirabilis*. Several other lizard species were occasionally observed at this site (Table 2.1). The majority of individuals were collected from dry riparian habitat or associated she-oak (*Casuarinae* sp.) open woodland, usually in dry river beds with numerous exposed boulders. *Eulamprus brachysoma* was sampled from granitic outcroppings and boulders.

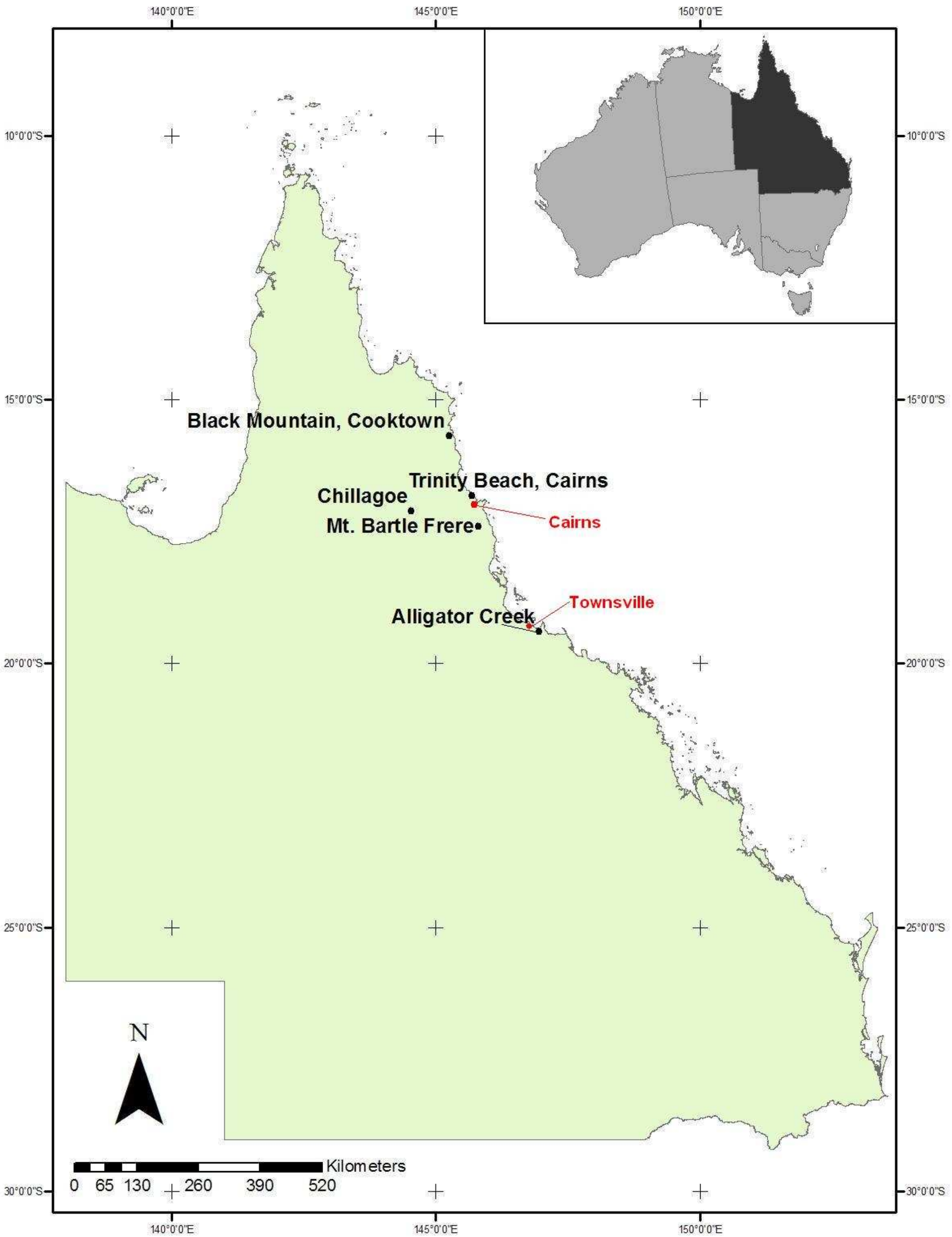


Figure 2.2. Map showing the position of the five study sites (indicated by black dots) and their proximity to the two major cites of Townsville and Cairns (indicated by red dots) in north-east Queensland, Australia.

Black Mountain – Cooktown [4 – 40 m ASL]

Black Mountain consists of a jumbled pile of black granitic boulders covering an area of 6.8 km^2 within the Black Trevethan Range (Werren and Trenerry, 1990; Borsboom, 2006). The main part of the mountain rises from near sea level to an elevation of 470 m. The majority of the habitat consists of large, exposed black boulders (Wells 1975; Figure 2.1) with sporadic patches of the fig *Ficus obliqua* var. *obliqua*, which grows in isolated sites (Werren and Trenerry, 1990). The habitat surrounding the mountain is dominated by open woodlands composed of *Eucalyptus* and *Corymbia,* including Poplar or Cabbage Gum (*Eucalyptus platyphylla)*, Darwin stringybarks, ironbarks and bloodwoods. The understorey is a medium to thick covering of leaf-litter and grass. *Carlia scirtetis* is restricted to the boulders of Black Mountain (Coavacevich, 1980), and was observed and sampled from around the edge up to elevations of 120 m (Borsboom, 2006); *E. brachysoma* was observed at this site. *Carlia longipes* was observed and sampled from the edge of Black Mountain and the open woodlands (dominated by *Eucalyptus* and *Corymbia*) surrounding the mountain. Additional individuals of *C. longipes* were observed and sampled from coastal open monsoonal *Malaleuca* sp. forest and open woodlands with a sparse cover of leaf-litter and grass.

Chillagoe [330 – 360 m ASL]

This site consisted of a series of rocky outcrops and associated open woodlands 3.5 – 4.5 kilometres west of the township of Chillagoe. This habitat consists of limestone *(karst)* formations and outcrops in combination with granitic boulders surrounded by open woodland consisting predominantly of trees of the genus *Eucalyptus* sp. (*Eucalyptus papuana*) and *Acacia* sp. (Figure 2.3). The most common trees occurring on and close to the rock outcrops are helicopter trees (*Heliconius* sp.) and deciduous trees including, *Gyrocarpus americanus* and Bottle tree (*Brachychiton australe*), with a dense evergreen crown of ebony (*Maba humilis*). Deciduous vine thicket and rubber vine (*Cryptostegia grandiflora*) also occurs here. The species observed and sampled at this site included *Carlia mundivensis* and *Carlia rococo*. *Carlia jarnoldae* were collected from the adjacent areas of savannah, open woodland. Several other lizard species were also seen at this site (Table 2.1).

Table 2.2. Locations, geographical position, habitats, vegetation and species observed at each of the five sites used in this study.

Field site	Latitude, Longitude	Habitat	Species
Alligator Creek	19°32' S, 146°58' E	Rocky riparian zones dry open forest, granite outcrops	*Carlia jarnoldae, Carlia pectoralis, Carlia rhomboidalis, Carlia vivax*, Eulamprus brachysoma, Eulamprus quoyii, Lampropholis mirabilis, Morethia taeniopleura, Varanus tristis**
Black Mountain, Cooktown	15°40' S, 145°15' E	Granite boulder jumbles, open coastal monsoonal forest (*Malaleuca* sp.), granitic outcroppings	*Carlia jarnoldae, Carlia longipes, Carlia scirtetis, Carlia storri*, Cryptoblepharus virgatus**, Ctenotus nullum*, Eulamprus brachysoma*
Chillagoe	17°06' S, 144°32' E	Dry open woodland, dry vine thicket, limestone castes, granite and limestone combination outcrops	*Carlia jarnoldae, Carlia mundivensis Carlia rococo, Carlia schmeltzii*, Carlia vivax*, Cryptoblepharus virgatus**, Eulamprus brachysoma, Varanus panoptes*, Varanus storri**
Mt. Bartle Frere	17°23' S, 145°48' E	Granitic outcroppings, closed high-altitude tropical cloud forest, monsoon vine forest-rainforest	*Carlia rubrigularis*, Eulamprus frerei*, Lampropholis robertsi, Techmarscincus jigurru*
Trinity Beach, Cairns	16°80' S, 145°68' E	Rocky intertidal zone, mosaic closed tropical rainforest, coastal open monsoonal forest (*Malaleuca* sp. and *Eucalyptus* sp.)	*Carlia laevis, Carlia rostralis, Carlia rubrigularis, Carlia storri, Cryptoblepharus litoralis, Cryptoblepharus virgatus, Ctenotus spaldingi, Egernia frerei, Lamprophollis coggeri, Saproscincus basiliscus*, Saproscincus tetradactyla*, Varanus scalaris*, Varanus varius**

(*) – Data limitations precluded the use of this species in this study, (**) – Individuals observed only from altitudes below 1300 m at this site.

Figure 2.3. Rocky-limestone (*Karst*) outcrop (Left) and open woodland habitat 4 km east of Chillagoe (Right).

Mt Bartle Frere – Wooroonooran National Park [1400 – 1620 m ASL].

Both *L. robertsi* and *T. jigurru* were sampled at this site, which consists mainly of simple notophyll and microphyll (rainforest 1, 2; Webb and Tracey, 1981) cloud forest, with a medium ground covering of leaf litter. Occasional exposed and unexposed boulder fields occur at elevations above 1300 m ASL (Figure 2.4). *T. jigurru* was sampled from boulder fields, with the occasional individual observed within forested areas away from rocks. *Lampropholis robertsi* were collected from leaf-litter microhabitat in the region of the west summit (altitude 1450 m ASL), with a cover of rushes and grasses, and reduced trees. *Eulamprus frerei* were also observed in the region of the boulder field habitat; *C. rubrigularis* were only observed at elevations below 1300 m.

Figure 2.4. Exposed rock outcrop (Left) and closed simple notophyll and microphyll woodland and unexposed rock outcrops (Right) on Mt. Bartle Frere.

Trinity Beach – Cairns [0 – 20 m ASL]

The Cairns site provided a mosaic of habitats including rocky inter-tidal zone, dry open forest and a combination of wet-schlerophyll and rainforest. The rocky inter-tidal zone consists of free-standing rocks, rock piles and bed rock, which merged into monsoonal dry open forest with an *Acacia* sp. and *Eucalyptus* sp. overstory and a sparse understorey of grass and low shrubs. Habitat use and sampling of *Cy. litoralis* was conducted in the rocky-intertidal zone habitat, while *Cy. virgatus* was observed and sampled from trees in the dry open forest, and occasionally from rocks in syntopy with *Cy. litoralis*. Habitat use descriptions and sampling of *C. rostralis* and *C. storri* was conducted in monsoonal open forest. The rainforest habitats at this site consisted of tropical mesophyll vineforest (rainforest 1, 2; Webb and Tracey, 1981), where the species *C. laevis* and *C. rubrigularis* were sampled. Several other lizard species were also seen at this site (Table 2.1).

General skink biology

Activity and diet

In general, most members of the Lygosominae are diurnally active shuttling heliotherms, with species from hotter environments tending to be posturing heliotherms (Greer, 1989; Hutchinson, 1993). In many cases, however, lizards may compensate for extreme temperature conditions by modifying their habitat use or by behaviourally changing basking frequency and activity times (Ingram and Covacevich, 1980; Hertz and Huey, 1981; Greer, 1989). The members of the genera examined as part of this study are primarily insectivorous carnivores (Brown, 1983; Heatwole and Taylor, 1987). However, while it is well known that many larger skink species consume vegetable matter and fruit (Greer, 1989; King, 1996; Chapple, 2003) cases of herbivory in smaller species are less well known. During the reproductive season both adult and sub-adult *C. scirtetis* consume a diet that is high in figs (Goodman, 2004), which is unusual for a skink weighing less than 5 grams (King, 1996). Little is known about the selectivity and proportions of invertebrate taxa consumed by skinks from the wet-dry tropics.

Relatively little work has been conducted on the life history and seasonality of reproduction in members of the genera *Carlia*, *Cryptoblepharus*, *Eulamprus, Lampropholis* and *Techmarscincus* in north-east Queensland. However, all members are oviparous with the exception of *Eulamprus* which are all viviparous (James and Shine, 1985; Greer, 1989)

Reproduction in tropical skinks

Females

In north-east Queensland, egg production in most *Carlia* coincides with the start of the wet season (November – February), which appears typical for the genus (Wilhoft and Reiter, 1965; Whittier, 1993), and may be driven by seasonal changes in total solar radiation (Clerke and Alford, 1993). However, not all *Carlia* show this pattern. In *C. rubrigularis*, a species with a prolonged reproductive season (July – April), some females are reproductive outside the period of peak egg production (November – February). This difference may be an adaptation for the seasonally invariable rainforest habitat of this species (Wilhoft, 1963).

Reproduction in six species of *Carlia* from the Alligator River region of the Northern Territory spans from October to April, which is a longer period than *Carlia* from north-east Queensland (James and Shine, 1985). *Cryptoblepharus plagiocephalus* from the NT reproduced year-round (James and Shine, 1985), whereas egg production in *Cy. virgatus* from Townsville was restricted to the period August – January (Clerke and Alford, 1993), suggesting the existence of regional differences. Finally, there is some evidence of multiple clutch production in members of *Carlia* and *Cryptoblepharus* (James and Shine, 1988).

Like their congeners from southern Australia (e.g., Rohr, 1997), populations of *Eulamprus quoyii* in north-east Queensland reproduce during the tropical summer–wet-season (Caley and Schwarzkopf, 2004) with individuals producing up to two broods per season (L. Scharzkopf, pers. comm.).

Members of the genus *Lampropholis* show a similar pattern to that of *Carlia,* with egg production in *L. delicata* commencing slightly earlier (September) than in *Carlia* from this region and continuing through until March in populations north of Townsville, with a shorter period of egg production in populations from more temperate regions (i.e., Brisbane to Tasmania; Forsman and Shine, 1995). Shea (1987) reports *T. jigurru* is oviparous with four, shelled, oviducal eggs found in a preserved specimen sampled in early November, suggesting that at least some individuals are reproductive during the wet-season in this species.

Males

In males, much work has shown a seasonal peak in reproductive activity in males, as in females, for *C. longipes* (as *Leiolopisma fuscum*; Wilhoft and Reiter, 1965). Similarly, male *Carlia* from the NT were reproductive from November – February or March, suggesting a wet-season mating period in this region (James and Shine 1985). This contrasts with *C. rubrigularis* that shows little variation in testis mass across seasons, suggesting long reproductive season similar to that of females

(Wilhoft, 1963a, b). Interestingly, work on *C. pectoralis* (Clerke and Alford, 1993) and *Cy. plagiocephalus* (James and Shine, 1988; Clerke and Alford, 1993) suggests that males of some species are capable of year-round reproduction.

Thus, almost all species used in this study are wet-season breeders, with some differences in the reproductive patterns of latitudinal variation in species from different tropical regions, and in species from specific habitats (e.g., rainforest). In general, male reproductive activity typically matched that of their female conspecifics, and in many cases appears dependent on both region and species, with some species capable of year-round reproduction. Like other skinks with extended reproductive seasons (Henle, 1989), some females produce multiple clutches within a reproductive season (James and Shine, 1988).

The effect of an invariant clutch size

Fundamental differences have been observed between lizards from the tropics and temperate zones, namely that tropical lizards have smaller clutch sizes and lower relative clutch mass (James and Shine, 1988). Much of this difference is no doubt due to the large number of invariant-clutch-size producing species that occur in the tropics (James and Shine, 1988). The production of an invariant or ‘fixed’ clutch size (i.e., one or two egg clutches) is best known for lizards of the families Gekkonidae and Polychrotidae (Fitch, 1970), but is also reported for the genera *Carlia* and *Cryptoblepharus* of the family Scincidae (James and Shine, 1988; Greer, 1989; Goodman, 2006a, b).

In most squamate reptiles, as in most organisms, clutch size increases with an increase in body size (Dunham et al.,1988), such that as additional resources or space becomes available, females are able to increase the number of offspring or eggs they produce (Shine, 1992). In many cases, this increase in clutch size is accompanied by a decrease in egg size and vice versa (Stearns, 1992; Bernardo, 1996). Thus, the inability for invariant-clutch species to allocate additional resources to the production of more eggs presents a challenge to life-history theoreticians (Stearns, 1992, 2000; Ebert, 1994). An investigation of reproduction and maternal size-egg size relationships in the species *C. rubrigularis* revealed that while egg size increased with maternal size there was no evidence that females in better condition allocate more resources to reproduction (Goodman, 2006c). Work on geckos provides both similar and contrasting outcomes (Doughty, 1996; Doughty and Thompson, 1998), with egg size and energy content increasing with maternal size in some species (Doughty, 1996; Doughty and Thompson, 1998), but not in others (Doughty, 1997). Thus, anticipating how changes in abdominal volume and body size affect reproductive output and egg size in invariant-clutch species may be taxon dependent.

Lizard sampling and captive maintenance

All measurements were taken from live individuals collected by hand, with the aid of baited sticky traps or with pit-fall traps modified for rocky habitats (Goodman and Peterson, 2005). In the laboratory, all individuals were maintained separately in a plastic container of one of three sizes for small (SVL < 45 mm, 350L x 130W x 100H mm), medium (SVL 45–75 mm, 350 x 230 x 100 mm) or large individuals (SVL > 75 mm, 550 x 360 x 305 mm). Each container consisted of a substrate of moist potting mix (to a depth of 8-10mm), a bark refuge, and water bowl, and was placed on a rack with a heating element positioned at one end that produced a thermal gradient within each box (range 23–45°C) that spanned the preferred body temperature range of the genera examined (Goodman, unpub. data; Greer 1980, 1989). Containers were heated from 0800 to 1800 hr and dropped to 23°C ± 2°C when the heating was switched-off. The photoperiod matched local tropical conditions and was produced by standard overhead flourescent lighting on from 0700 – 1900 hr. All captive lizards were fed a combination of live *Tenebrio* larvae and crickets dusted with mineral supplement (Repti-cal®) *ad libitum*.

Morphological measurements

All measurements were taken from live animals by first cooling each individual to 18 ± 1 ºC for a minimum of one hour. The sex of each individual was recorded and the following morphological traits were measured directly using digital callipers (± 0.01 mm); snout-vent length, inter-limb length, head width, head length, head height, tail length (if regenerated both the original and regenerated tail portions), pectoral height, pectoral width, pelvis height and pelvis width. Body mass was measured using a Sartorius BP 210 s model digital balance (± 0.001 g). In addition, each individual was radiographed prior to release at its site of capture to provide high precision measurements of all skeletal elements. Radiograph measures were taken by first cooling each individual (as above) before securing it to a plexiglass plate (450 × 340 × 3 mm) using 3M™ Micropore Surgical tape (Hoefer *et al.,* 2003). Metal staples (12.9W × 6.2H mm) fixed to the surface of each plate provided a size reference. Lizards were radiographed at two power intensities depending on the lizard's size; small-medium species (SVLs 30–75 mm) were radiographed at an exposure of 22 kV and 18 mA. Species with SVLs > 75 mm were radiographed at an exposure of 24 kV @ 20 mAs. All skeletal measurements were taken directly from radiographs using digital callipers (± 0.01 mm) viewed on a light table at 20X magnification. Repeated measures of radiographed staples and actual staple dimensions were used to scale a correction factor for all the skeletal measurements. All direct and radiograph measurements were taken three times and the average used in analyses.

Performance measures

Sprint speed

Prior to conducting performance trials, each individual was transferred in its container to a constant-temperature heating chamber set to 32°C (30°C for *Eulamprus*), where individuals were allowed to acclimate for at least 1 hour prior to each performance trial. This temperature range is within the field active body temperature range of members of these genera (Goodman, unpublished data). Only one performance trait was recorded per day, with at least one day between consecutive performance trials. Sprint speed was determined using a 2-m horizontal racetrack with a series of infra-red sensors positioned at 100-mm intervals along the entire length of the track. The surface of the racetrack was course particle size sandpaper that provided excellent traction. Speed was the time elapsed between successive breaks of sensors 500 mm apart. A trial commenced when a single lizard was removed from the incubator and placed at the start of the racetrack and encouraged to sprint using an artist’s paintbrush. Each lizard was raced with at least one hour between successive trials and each trial was rated as either “good” or “poor”. A trial was rated as “poor” if an individual jumped along or out of the raceway, turned 180º and ran in the opposite direction along the raceway, or simply stopped and refused to run the full length of the raceway. Trials were rated “good” if individuals ran relatively constantly (i.e. only paused momentarily) whilst running along the entire length of the raceway.

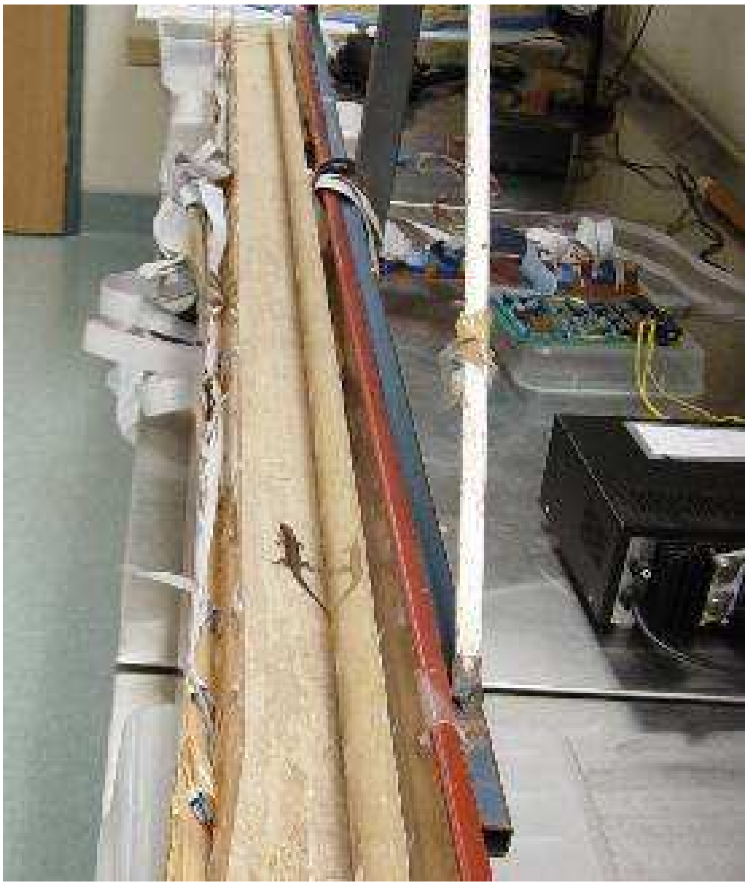


Figure 2.5. Apparatus used to measure sprint speed. Speed was determined by infrared sensors positioned at 100 mm intervals along the entire length of the 2-m raceway.

Climbing ability

Climbing ability was measured as for sprint speed except with the racetrack placed on a 70° angle; only individuals that produced two or more “good” climbing trials were used in analyses. Both sprinting and climbing used the maximum 0.5 m interval as the measure of speed.

Clinging ability

Cling performance was measured using a 5-g (for small *Carlia* and *Lampropholis*), 60-g (large *Carlia*, *Cryptoblepharus*, *Lampropholis*, *Techmarscincus*) or 300-g (the two *Eulamprus* species) Pesola™ spring-balance connected to a 25-cm length of fine gauge nylon fishing line (5 kg) with a slipknot noose tied to one end (Losos, 1990a; Zani, 2000). Trials were conducted by placing each individual on a flat, horizontal board covered with medium-course grain sandpaper. Each lizard was attached to the spring-balance by placing the noose around the mid-body just anterior to the pelvis, such that the line connecting the spring-balance was parallel to

Figure 2.6. Apparatus used for the measurement of climbing speed. The raceway was placed on a 70° angle and lizards were encouraged to run the entire length without stopping.

the lizards' body axis (Irschick et al., 1996; Zani, 2000). For each trial, a lizard was placed on the test surface and force was applied at a constant horizontal speed (0.3 ms^{-1}) in a posterior direction until each lizard was dislodged from the surface (Losos, 1990a; Zani, 2000). Trials were conducted on each individual and graded as "good" or "poor" depending on whether an individual maintained a posture with outstretched limbs with the ventral surface in contact with the test surface; a minimum of two "good" trials were obtained for each individual.

Jumping ability

Jump distance was measured by placing each individual onto a circular podium (25 cm high X 13 cm wide at top) positioned in the centre of a circular arena (130 diameter X 35 cm high) lined with sand to a depth of 5 cm. Individuals were encouraged to jump by lightly tapping the base of the tail using an artist's paintbrush. Jump distance was recorded as the maximal radial distance between the landing point of a lizard and the base of the podium. Individuals that did not jump within 15 seconds were returned to their box and placed back in the constant temperature chamber to acclimate for another hour before being re-tested. Three jumps were recorded for each individual.

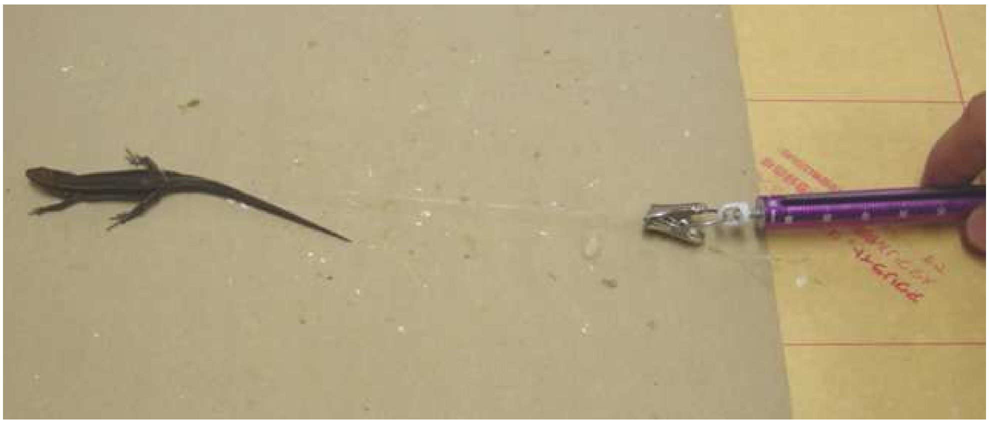


Figure 2.7. Cling ability was measured using a Pesola spring-balance, with each lizard placed on medium-course grain sandpaper.

Figure 2.8. Jump distance was measured as the maximum radial distance a lizard could jump from a circular podium.

The phylogenetic affinities within this group of skinks

The phylogenetic hypothesis used in this study (Figure 2.9) was based on the current ‘best estimate’ phylogenetic relationships of the molecular (Stuart-Fox et al., 2002), immunological (Hutchinson et al., 1990) and morphological relationships for members of the Scincid sub-family Lygosominae (Ingram and Covacevich, 1989). Supra-generic positions of genera were based on the phylogenetic relationships reported in Reeder (2003). Additional information on putative phylogenetic relationships were taken from Hutchinson et al., (1990) and Greer (1989) for *T. jigurru* (as *Leiolopisma jigurru*). While the position of *E. quoyii* was provided within Reeder (2003), the position of *E. brachysoma* was inferred from the close relationships and inclusion within the *E. murrayi* species group (Greer, 1989). The position of *Cryptoblepharus* was based on the intergeneric basis that the most primitive members of this genus are closely related to *Emoia* (Greer, 1974).

A recent molecular phylogeny of the genus *Carlia* (rainbow skinks) failed to fully resolve many of the relationships within this genus and proposed *Lygisaurus* should be synonymised with *Carlia* where they form a small clade nested within the overall *Carlia* phylogeny (Stuart-Fox et al., 2002). Indeed, the addition of sequences from several new *Carlia* species failed to enhance the phylogenetic relationships (Couper et al., 2005), and the presence of unresolved polytomies within the genus *Carlia* likely reflects a rapid (explosive) speciation event that probably occurred from the mid-Miocene onwards (Stuart-Fox et al., 2002). This scenario fits well with several other phylogeographic studies of vertebrates from north-east Queensland (Joseph et al., 1993; Moritz et al., 1997; Schneider et al., 1998), that likely resulted from sudden changes in climate and habitat, such as decreased temperature, increased aridification and a concurrent reduction in tropical-rainforest from north-east Queensland (Couper et al., 2005). The species in this study formerly within *Lygisaurus* (i.e., *Carlia rococo* and C. *laevis*), were placed in this sub-clade, several other arrangements were also used in analyses. The position of *C. scirtetis* was based on evidence from morphological traits shared with the species *C. coensis* and *C. mundivensis*, with additional analyses performed with this species placed in other phylogenetic arrangements.

The uncertainty of some of the phylogenetic positions of species prompted the use of several alternative phylogenetic arrangements in order to assess the robustness of results. These included re-doing the phylogenetic analyses with: i) *T. jigurru* as the sister taxon of *Lampropholis* + *Carlia* and as the sister taxon of *Cryptoblepharus* + *Lampropholis* + *Carlia*, ii) members formerly within *Lygisuarus* (e.g., *C. laevis*, *C. rococo*) as outgroup to *Carlia*, and, iii) *C. scirtetis* placed in different locations among the *Carlia* (A. Greer and G. Zug, pers. comm.). All phylogenetic analyses were conducted using the 'best estimate' phylogeny in addition to various permutations of this arrangement, both with and without polytomies treated as 'hard' (Purvis and Garland 1993; Garland and Diaz-Uriarte 1999). However, the use of all other phylogenetic arrangements did not qualitatively change the outcome of analyses, so I report values only for analyses performed using the phylogeny with 'hard' polytomies in the following chapters. As branch length information was not available for most of the species used in this study, branch lengths were set to unity. Several studies have shown that setting branch lengths to unity produces results that are robust and reliable (Diaz-Uriarte and Garland, 1998).

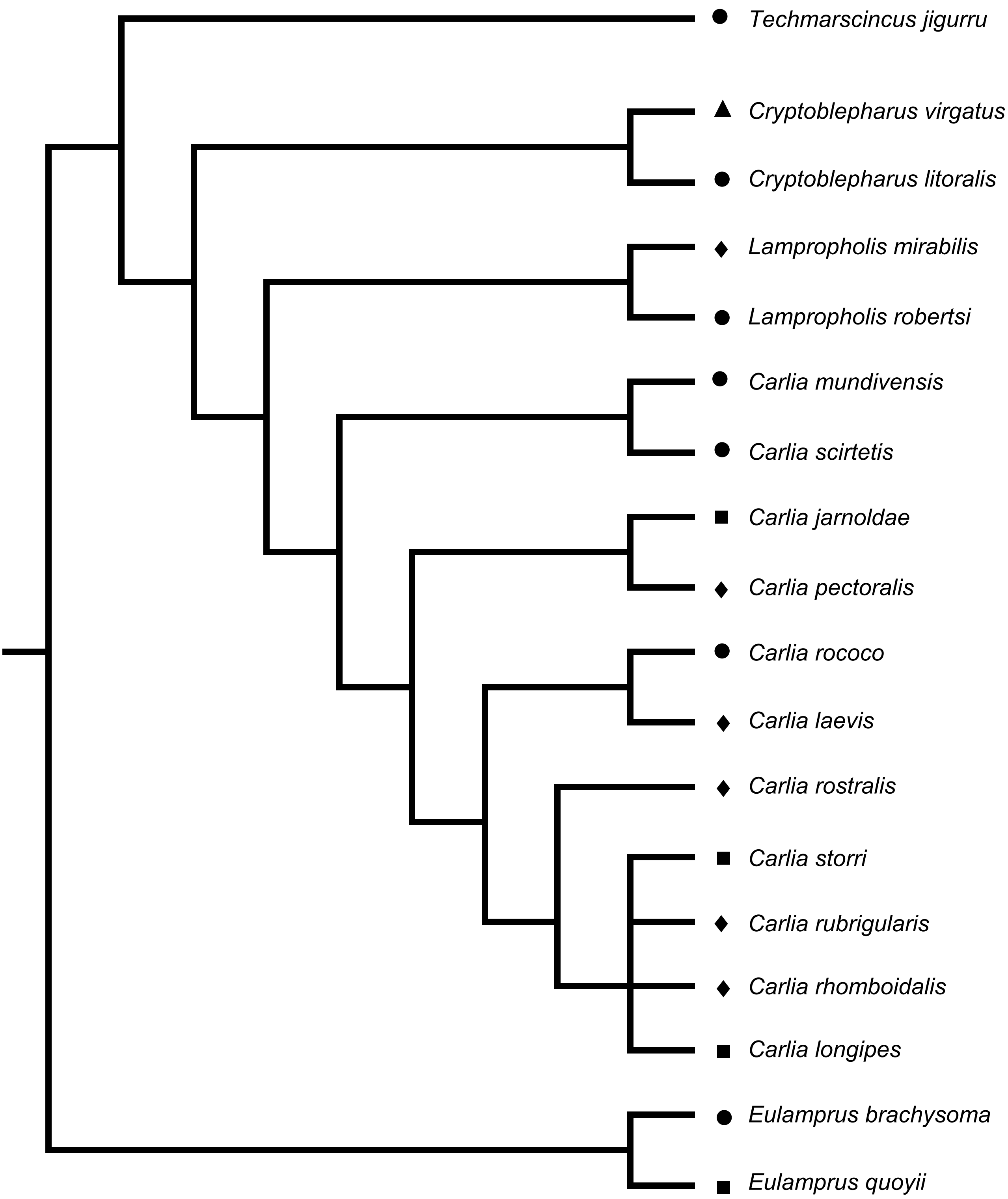


Figure 2.9. Phylogenetic relationships of the 18 scincid lizard species examined in this study. The tree represents the current 'best estimate' working hypothesis and is based on genetic (mitochondrial DNA, ND4), immunological and morphological evidence (Greer, 1974, 1989; Covacevich, 1984; Shea, 1987, Stuart-Fox et al., 2002, Reeder, 2003). Symbols indicate the four habitat types occupied by each species: triangles, arboreal; squares, generalist; diamonds, leaf-litter dwelling; circles, rock-using.

Comparative phylogenetic analyses

Related species share, to varying degrees, part of their evolutionary history and for this reason do not constitute independent data (Felsenstein, 1985; Harvey and Pagel, 1991). Consequently, use of conventional statistical inference to determine significance levels are invalid if used directly for interspecifc comparisons. The use of phylogenetic comparative methods that account for phylogenetic relationships provides a solution to this impasse. Phylogenetic comparative methods that incorporate Felsenstein's (1985) method of independent contrasts require information on the relationships between species, including correct information on the phylogenetic topology, branch lengths to estimate change in traits variance over time, character evolution that occurs by a process of Brownian motion and little within-species variation within traits of interest (Felsenstein, 1985; Harvey and Pagel, 1991).

However, while it is necessary to conduct analyses within a phylogenetic framework, whether hypotheses based on phylogenetic or conventional statistics should be considered more informative depends on whether data show evidence of significant phylogenetic signal (Freckleton et al., 2002; Blomberg et al., 2003; Garland et al., 2005). The descriptive statistic K provides one index of the amount of phylogenetic signal within a trait, based on the Brownian motion model of character evolution of a given phylogenetic tree with known topology and branch lengths (Blomberg et al., 2003). K equal to 1 indicates that a trait shows an expected amount of phylogentic signal among close relatives, whereas K-values less than 1 indicate a trait is less similar among close relatives, and therefore has less phylogenetic signal then expected. A K greater than 1 suggests there is more phylogenetic signal than expected. To test for phylogenetic signal and calculate a K statistic and P-value for tests of significance for each trait, I used the program PHYSIG.M (Blomberg et al., 2003), as implemented in the program MatLab. I performed 1000 randomizations on the current 'best-estimate' phylogeny and report K-values for all morphological and ecological traits examined in this study (Blomberg et al., 2003; Table 2.3). However, while K-values are likely to be more than 80% reliable for phylogenies consisting of 20 or more species, they are considerably less for phylogenies with fewer than 20 species. As this study consisted of 18 species, I also report P-values for significance testing of all traits as produced in PHYSIG.M to provide an additional diagnostic of whether traits display phylogenetic signal (Blomberg et al., 2003).

Prior to analyses I calculated the mean of each ecological variable for each species, except variables for refuge use, which consisted of the proportion that individuals of each species used each refuge type. The variables from all continuous ecological data were $\log_{10}$-transformed prior to analyses following the addition of 1 to account for non-normality and heteroscedasticty (Sokal and Rohlf, 1995) and all data expressed as percentages were converted to proportions. All data represented as proportions were arcsine square-root transformed prior to analyses (Quinn and Keough, 2002). For morphological data, the species mean of each trait for each sex was $\log_{10}$-transformed prior to being used in phylogenetic comparative analyses. To test for differences between sexes and among species from different habitats in limb-length and body shape, each trait was regressed against snout-vent length independently for each sex, and the residuals calculated.

For Chapters 4, 6, and 7, two complementary phylogenetic analyses were used to test for relationships between a series of ecological traits and lizard morphology, and between a series of ecological traits and performance, whereas Chapter 5 uses solely the phylogenetic independent contrasts method in analyses. First, a conventional non-phylogenetic ANOVA was conducted on each morphological trait to test for differences among discrete habitat types. However, as species values are unlikely to represent statistically independent data (Felsenstein, 1985, 1988; Harvey and Pagel, 1991) it is not possible to establish their significance based on conventional tables of critical *F*-values (Pagel, 1993). To resolve this problem, I developed a null distribution of *F*-values incorporating the phylogenetic relationships of the species using the PDSIMUL module of the program PDAP (Garland et al., 1993) using the traits means and variances as input data. The evolution of each morphological trait was simulated based on the known phylogenetic relationships for this group of species (Figure 2.9) and a null distribution of *F*-values was developed by running 1000 unbounded simulations of each trait based on the Brownian motion model of evolutionary change. Next, PDANOVA was used to conduct phylogenetic ANOVAs and ANCOVAs after assigning each species to one of three habitat categories (rock-using, leaf litter, generalist; Table 2.2). Species were assigned to a dominant habitat category (‘ecotype’) based on published descriptions of the preferred microhabitat use of each species. Habitat was used as the factor and snout-vent length as the covariate. However, because PDANOVA calculates means, variances and statistics relating to slopes (Garland et al., 1993), it was necessary to allocate the single arboreal species (*Cy. virgatus*) in this study to the rock-using scansorial habitat category for this analysis. This decision was based on the evidence that this species often climbs vertical rocks as well as trees in many of the habitats it occupies (Chapter 3). Morphological differences between habitat groups were considered significant if the non-phylogenetic *F*-value exceeded the 95th percentile (i.e., 949/1000) of the empirically-developed distribution of *F*-values.

Table 2.3. *K*– and *P*–values for female and male morphological traits. All values calculated with branch lengths set to unity. Number of mean square error values (MSE) that exceeded the original value provided for reference. All values calculated using PHYSIG.M (See Blomberg *et al.,* 2003, for details on methodology).

TRAIT	Females			Males		
	K	*P*	Number of MSE values > original MSE	*K*	*P*	Number of MSE values > original MSE
Snout-vent length	0.5128	0.023	23	0.6771	0.006	6
Inter-limb length	0.5328	0.017	17	0.7408	0.005	5
Head width	0.5665	0.002	2	0.7462	<0.001	0
Head height	0.5992	0.002	2	0.7538	<0.001	0
Body width	0.5400	0.008	8	0.7092	<0.001	0
Body height	0.5581	0.001	1	0.6637	<0.001	0
Radio-ulna length	0.5471	0.012	12	0.5782	0.004	4
Humerus length	0.5116	0.017	17	0.5949	0.003	3
Tibia-fibula length	0.4518	0.039	39	0.5131	0.011	11
Femur length	0.5148	0.017	17	0.5852	0.013	13
Fore-limb length	0.5584	0.007	7	0.5780	0.007	7
Hind-limb length	0.4853	0.013	13	0.5470	0.006	6
Tail length	0.3938	0.064	64	0.4562	0.032	32

Independent contrasts were calculated for each of the ecological and morphological data sets using PDTREE. I tested whether independent contrasts of the ecological and morphological traits conformed to the assumptions of adequate standardisation of branch lengths by testing for significant linear or non-linear trends using both statistical correlations and visual inspection of all diagnostic plots. Contrasts of trait values were checked for adequacy of standardisation by dividing the independent contrast of each trait by the standard deviation of the branch length (square root of the corrected branch lengths) for that trait (Garland et al., 1992). However, as analyses revealed there was no evidence of trends within the data ($r < 0.4$; All P-values > 0.12) branch lengths were considered adequately standardised under the Brownian motion model of evolution. The independent contrasts of the morphological data were size-corrected by regressing (through the origin) the standardised independent contrast of the trait of interest against the standardised independent contrast of snout-vent length (Garland et al., 1992). Next, principal component analyses (PCA) with Varimax rotation was performed on each of the data sets (morphological, substrate-perch, habitat openness, refuge availability) to reduce the dimensionality of the data while maximising the variance and improving interpretation of the axis loadings. A previous study has explored this approach and found no differences in the results despite differences in the methods (Zani, 2000). The broken stick method and PC axes with eigenvalues > 1.0 generally result in the retention of the same set of PC axes (Jackson, 1993). Thus, PC axes with eigenvalues > 1.0 were considered important and retained for use in subsequent analyses.

To assess the relative similarity of the position of species in microhabitat openness space, substrate use space and refuge use space with the position of species in morphological space for females and males, canonical correlations were performed separately on each data set. Scores for each set of PC axes of the independent contrasts conducted on each data set were used in the canonical correlation analyses to produce a series of phylogenetically correct canonical correlations (Miles and Ricklefs, 1984; Losos, 1990a). This approach uses the canonical correlation axes to test the null hypothesis that the i^{th} correlation axis and all that follow are zero using Bartlett's approximation of Wilks' λ, which produces a χ^2 distribution for significance testing (Miles and Ricklefs, 1984).

Chapter 3

Microhabitat separation and niche overlap among five assemblages of tropical skinks

(Accepted for publication [*Australian Journal of Zoology*])

Introduction

The modern concept of the niche is defined as the volume, in multidimensional hyperspace, in which a species can maintain a viable population (Hutchinson 1957; Pianka, 1969a, 1973; Begon et al., 1990). Spatial microhabitat occupation and use are generally considered the most important factors allowing separation and coexistence of sympatric species (Pianka, 1973, 1986; Schoener, 1974; Toft, 1985; Tilman, 1994), and niche overlap along structural environmental axes may indicate those species likely to co-occur within a habitat (Wilson, 1999). Further, because a species' fundamental niche (i.e., those resources used in the absence of predators or competitors) may differ from that of the realized niche (observed when these factors are operating), a species' niche may differ or shift substantially among habitats. Organisms typically exhibit morphological and/or physiological adaptations for the habitats they occupy (Losos, 1990a; Irschick and Garland, 2001) and fitness may be compromised if individuals are forced to occupy sub-optimal habitats (Huey, 1991; Garland and Losos, 1994). In ectotherms, such as lizards, the occupation of different microhabitats can have a powerful effect on various functions that may directly affect fitness, including thermoregulation (Huey, 1974; Huey and Stevenson, 1979; Scheers and Van Damme, 2002), home range size (Perry and Garland, 2002), diet (Perry and Garland, 2002), locomotion (Losos and Sinervo, 1989; Sinervo and Losos, 1991) and responses to predators (Snell et al., 1988; Irschick et al., 2005).

In lizards, because shifts in microhabitat can cause reduced performance which may affect survival, even subtle shifts in habitat use may lead to reduced growth rates, fitness and survival (Huey, 1991; Losos and Spiller, 1999; Melville, 2003). Moreover, conspecifics, or taxonomically closely related species, that occupy habitats with different thermal environments may display fundamental shifts in habitat use (Adolph, 1990), emphasising the intrinsic link between microhabitat use and the biology of lizards. An important distinction between temperate and tropical systems is that the increased availability and predictability of the thermal environment means tropical reptiles may be free from the need to bask for long periods or may thermoregulate passively (Shine and Madsen, 1996). Consequently, structural microhabitat use and niche breadth *per se* are likely to be of major importance for lizards from the tropics.

In Australia, the Scincidae are particularly biodiverse and occupying a wide range of habitats (Cogger and Heatwole, 1984; Greer, 1989; Pianka and Vitt, 2003). Members of the skink genus *Ctenotus* have long been recognised for the high species richness displayed in specific biomes of the arid zone (Pianka, 1969a, b; 1973; 1986; James, 1991a, b; Downey and Dickman, 1993). However, recent work has challenged this view, suggesting that the number of species for a given area is greater in tropical north-east Queensland (James and Shine 2000). Despite the high level of biodiversity and endemism of skinks from this region, detailed descriptions of microhabitat use and patterns of niche overlap are few compared to species from other regions (e.g., Pianka, 1969a, 1973; Webb, 1985; Melville and Swain, 1997, 2000). Moreover, despite increased work on reptiles from the Australian wet-dry tropics (e.g., Christian and Weavers, 1996; Schneider et al., 1999; Webb et al., 2001) none have focused on the structural niche patterns of skinks from this region. This study aims to address this lack of information by investigating the microhabitat occupation and niche patterns of 21 skink species from five assemblages by asking the following questions: (1) What structural microhabitat features separate these lizards? (2) Is there evidence of structural niche overlap within assemblages? (3) Is there evidence of temporal activity separation among co-occurring species? (4) Are co-occurring species likely to differ in body size? (5) Is there geographic variation in microhabitat use and niche overlap? (6) Is there evidence of species packing? and (7) Are assemblages of species with more specialised niches less evenly packed?

Methods

Study Species

This study compared 21 skink species from 24 populations representing seven genera within the Lygosomine sub-family; *Carlia* (11)*, Cryptoblepharus* (2), *Ctenotus* (1), *Eulamprus* (2), *Lampropholis* (3), *Morethia* (1) and *Techmarscincus* (1) (formerly the genus *Bartleia*). All are widely-foraging, insectivorous species (Taylor, 1986; Greer, 1989). The members of this sub-family occupy a range of habitat-types, including limestone outcrops, boulder-jumbles, cloud forest, open monsoon forest, rainforest (Ingram and Covacevich, 1989; Ingram, 1990; Cogger, 2000). Morphological and genetic phylogenies have been instrumental in establishing broad phylogenetic relationships among these genera (Greer, 1979; Reeder, 2003), however, a fully resolved phylogeny of all study species is currently unavailable. Species previously incorporated within the genus *Lygisaurus* are now included in *Carlia* based on a recent molecular study (Stuart-Fox et al., 2002).

Measuring lizard microhabitat occupation

Lizards from five assemblages were studied (Figure 2.2), with between 2 and 8 species examined from each location (Table 2.2). Structural microhabitat use of lizards was assessed at each site by walking haphazard transects of 100 m through all available habitat-types and recording the lizard species observed and the following variables for each observation, microhabitat (small rock < 0.5 m^3, large rock > 0.5 m^3, log, leaf-litter, grass and leaf litter, bare earth), perch angle (degrees), perch height above substrate (cm) and canopy height (m). I also recorded the percentage of each microhabitat type (small rock < 0.5 m^3, large rock > 0.5 m^3, log, leaf-litter, grass and leaf litter, bare earth), % canopy (>2 m) and % understorey vegetation (<2 m) within a 3 m radius around each lizard.

Measuring the distribution of available microhabitats

The distribution of available structural microhabitats was determined at each of the five sites by randomly sampling microhabitats along a series of 100 m linear transects that traversed all habitats. Sampled points were determined as the distance corresponding to the number of paces matching the number rolled on a six-sided dice. Terrestrial habitats (rocks, leaf-litter, bare earth, etc.) were sampled by throwing a small beanbag vertically at each sample point and recording the same variables for when a lizard was observed. Arboreal habitats (i.e., trees, perches, etc.) were sampled simultaneously at each site by sampling the nearest tree within a 5-m radius of each terrestrial habitat sample. Arboreal microhabitat data was recorded at height intervals of 30-cm from the ground corresponding to the number on the dice (i.e., 30 to 180 cm high). For the purpose of the study, I considered only heights to 180 cm owing to the difficulty of reliably observing small arboreal skinks at heights greater than that of the average adult human. For arboreal habitats I recorded an identical set of variables as to those recorded for the terrestrial habitats.

Structural microhabitat use and niche overlap

Indices of niche overlap (Pianka's) were calculated for each species from raw data of the proportions that lizard's used all available substrate types using the program 'Ecological Methodology' (Krebs, 2002).

Pianka's niche overlap:

$$O_{jk} = \frac{\sum_{i}^{n} p_{ij}\ p_{ik}}{\sqrt{\sum_{i}^{n} p_{ij}^{2}\ \sum_{i}^{n} p_{ik}^{2}}}$$

where

O_{jk} = Pianka's measure of niche overlap between species j and species k

p_{ij} = Proportion resource i is of the total resources used by species j

p_{ik} = Proportion resource i is of the total resources used by species k

n = Total number of resources states

Lizard sampling and body size

All measurements were taken from live individuals collected by hand, with the aid of baited sticky traps or with pit-fall traps modified for rocky habitats (Goodman and Peterson, 2005). For each adult individual captured, I measured snout-vent length using digital callipers (± 0.01 mm).

Statistical Analyses

For multivariate analyses of structural microhabitat use, all continuous structural microhabitat variables were $\log_{10}$-transformed prior to analyses, following the addition of 1, to improve non-normality and heteroscedasticty (Sokal and Rohlf, 1995). Percentages were converted to proportions and were arcsine square-root transformed prior to analyses (Quinn and Keough, 2002). A principal components analysis (PCA) using Varimax rotation on the correlation matrix was performed to reduce the 16 continuous habitat variables to a smaller number of variables explaining more of the variation within the raw data (Tabachnick and Fidell, 1989). Factor scores with eigenvalues greater than 1.0 were considered important (Jackson, 1993) and retained for use in subsequent analyses. PC axes with eigenvectors greater than 0.5 were considered significant and indicative of a correlation between the PC axis and the original variable (Tabachnick and Fidell, 1989). All variables were tested for the assumptions of normality and heteroscedasticity prior to further statistical analyses. Lizards from each assemblage were allocated to one of four ecotype (arboreal, generalist, rock-using, litter-dwelling, rock-using) based on the substrate used most frequently (Ingram and Rawlinson, 1981; Ingram and Covacevich, 1988, 1989; Cogger, 2000; Goodman unpublished data). The first two PC axes describing the multivariate structural microhabitat (niche) position and overlap was analysed by calculating Euclidean distance, and represents the centroid value of species in multidimensional ecological space. Euclidean distance was then used to calculate nearest neighbour distances (NND) for species in each assemblage. Species packing was assessed using mean NND and the standard deviation of the NND (SDNND) taken from a distance matrix for species from each assemblage. Mean NND provides an index of species dispersion in ecological space, while SDNND gives an index of the evenness of species packing in ecological space (Ricklefs at al., 1981; Winemiller, 1991). To account for differences in the number of individuals encountered within an assemblage on niche specialization, I calculated the distance from the species centroid to the centroid of the entire assemblage (Shenbrot et al., 1991; Winemiller, 1991). This measure represents the microhabitats used by a species as a distance from the centre of the ecological gradients used by the entire assemblage, and therefore, represents an index of ecological specialization. Pearson correlations were used to compare relationships between NND, mean CD and mean NND. Niche packing was examined using one-way analysis of variance (ANOVA); it was necessary to exclude assemblages with fewer than three species from this comparison. The proximity of species from a stream was assessed by measuring 'distance from water' for species at Alligator Creek.

The program ECOSIM Version 7.0 (Gotelli and Entsminger, 2001) was used to assess whether species within an assemblage displayed greater niche overlap then expected by chance using two randomization algorithms. The RA3 algorithm retains the niche breadth of each species, but randomizes the resource states that are actually used. This corresponds to a simple reshuffling of each row of the matrix, with the amount of specialisation of each species retained, but allowing potential use of other resource states. The RA4 algorithm retains the niche breadth of each species, but fixes zero states to observed values, such that only non-zero values are reshuffled within each row. Comparisons of the performance of RA3 and RA4, indicate RA3 is superior in detecting non-random overlap patterns. While RA4 maintains the structure of the real data, it may be prone to Type II errors as it often fails to detect non-randomness (Winemiller and Pianka, 1990). I present results for both algorithms as patterns significant with RA4 are likely to be robust (Winemiller and Pianka, 1990). Significance levels of multiple comparisons were adjusted using sequential Bonferroni correction (Quinn and Keough, 2002). All analyses were performed using JMP Version 4.0.2 (SAS Institute, Inc. Cary NC) and STATISTICA version 6.0 (StatSoft, Inc. Tulsa OK), with the level of statistical significance set to alpha ≤ 0.05.

Results

What structural microhabitat features separate this group of lizards?

A total of 1679 lizards were observed during this study. A PCA conducted on the ecological data from all sites was used to determine the ecological positions of each species. The first three factors in this PCA accounted for 56.35 % of the variation in the raw data. The first PC axis was negatively correlated with species that occupied habitats dominated by a high proportion of rock coverage, particularly large rocks (rocks > $0.5m^3$), a perch angle greater than zero and high height above the substrate, and was positively correlated with species that occupied substrates of leaf litter. The second PC axis described a gradient that increased with the amount leaf litter and % ground cover (Table 3.1). In general, species that occupied similar structural microhabitats clustered as groups with little overlap among other groups (Figure 3.1). PC1 separated rock-using species and the single arboreal species from leaf litter and generalist species. PC2 separated arboreal from rock-using species and leaf litter from generalist species (Figure 2). All four of the ecotype classes differed significantly in their position in structural ecological space (All *P's* < 0.0001).

Table 3.1. Principal components axes of the structural microhabitat variables for 21 species of tropical skinks.

Variable	PC1	PC2	PC3
Microhabitat	0.842	0.161	0.131
Perch Angle	-0.664	0.048	0.142
Height above substrate	-0.788	-0.136	-0.150
Canopy Height	0.562	0.509	0.467
% Canopy	0.234	0.452	0.722
% Undergrowth	0.172	0.555	-0.138
%Total Ground Cover	0.726	0.556	0.162
% Rock < 0.5 m3	0.205	-0.444	-0.078
% Rock > 0.5 m3	-0.860	-0.348	-0.304
% Logs	0.263	0.017	0.561
% Leaf Litter cover	0.568	0.707	0.171
% Bare Earth	0.545	-0.260	0.072
% Total Rock cover	-0.812	-0.486	-0.341
Distance to Nearest Vegetation	-0.414	-0.445	0.092
Nearest Vegetation Height	0.134	0.128	0.569
Distance to refuge	0.124	-0.458	0.016
Eigenvalue	6.271	1.432	1.312
% of total variance	39.196	8.952	8.198

To explore the relationship between the structural microhabitats used by lizards and those available at each of the five sites, separate PCAs were conducted on species microhabitat use and null data from each of the five sites. The PCA of the structural microhabitat data for the first three PC axes for Alligator Creek, Cooktown, Chillagoe, Mt. Bartle Frere and Cairns, explained 54.97, 61.03, 63.41, 61.26 and

60.03 % of the total variation in the raw data, respectively. For each of these PCAs, negative scores correlated strongly with areas of habitat dominated by large rocks (rocks > 0.5m^3), whereas positive scores correlated with a high proportion of leaf litter and total ground cover. There were slight differences among sites in the structural microhabitat variables correlated with the second PC axis. At Alligator Creek, positive scores were correlated with an increase in the number of small rocks and negative scores were correlated with increased ground cover and leaf litter on PC axis two (Figure 3.2A). At Cooktown, positive scores on PC axis two were correlated with increased percentage undergrowth and small rocks and negatively with distance to nearby vegetation (Figure 3.2B). At Chillagoe, PC axis two described a positive gradient of increase in percentage canopy (Figure 3.2C). PC axis two for Mt Bartle Frere consisted of a positive gradient that described an increase in vegetation height and distance to vegetation (Figure 3.2D). At Cairns, positive scores on PC axis two were correlated with perch angle and perch height above substrate and negatively with larger rock microhabitats with distance to nearby vegetation (Figure 3.2E). In all cases, species selected structural microhabitat features that were significantly different from the available structural microhabitats (Table 3.2).

Is there evidence of structural niche overlap within these assemblages?

In general, while the within assemblage, among-species niche overlap (Pianka's) was relatively high, there were relatively few pair-wise comparisons where species exhibited no significant difference in structural microhabitat overlap (Table 3.3A–3.3D). The comparisons of observed and simulated niche overlap revealed that only lizards from Chillagoe overlapped significantly more than expected (Table 3.4A.), with results identical for both randomization algorithms (RA3 and RA4). There were no differences between observed and expected niche overlap variance among species from assemblages (Table 3.4B). However, comparisons of two-dimensional niche overlap among species pairs within each assemblage revealed some exceptions. At Alligator Creek, there was no difference in the two-dimensional structural microhabitat positions of *C. jarnoldae* and *E. quoyii*, *C. jarnoldae* and *M. taeniopleura*, *C. pectoralis* and *M. taeniopleura* and *E. brachysoma* and *L. mirabilis* (Table 3.3A).

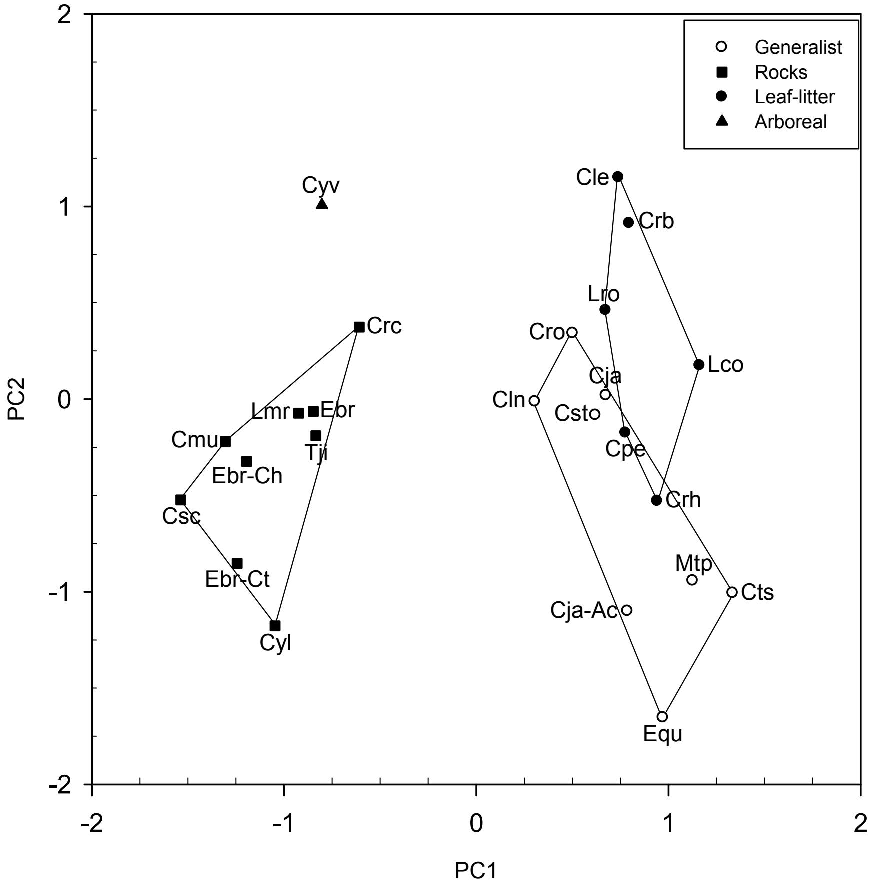
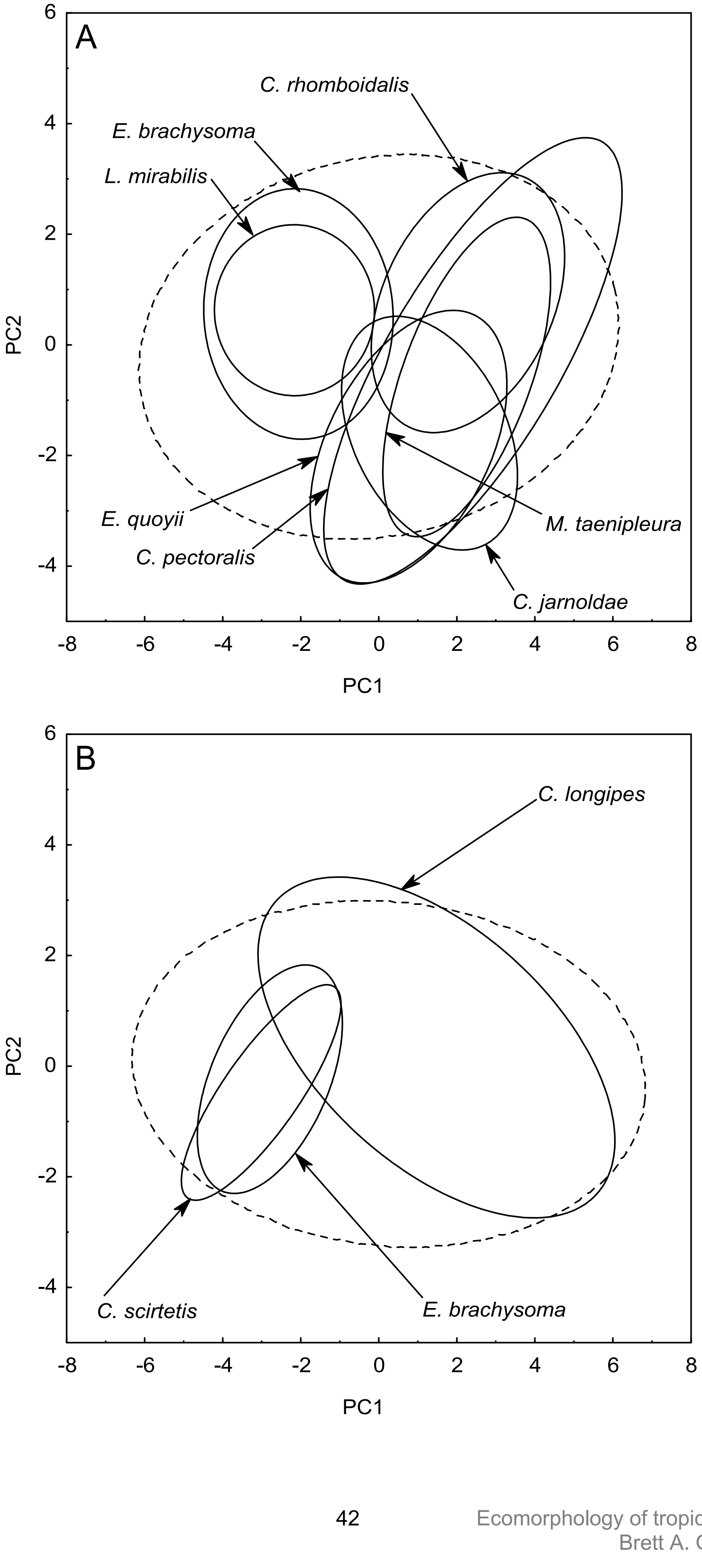
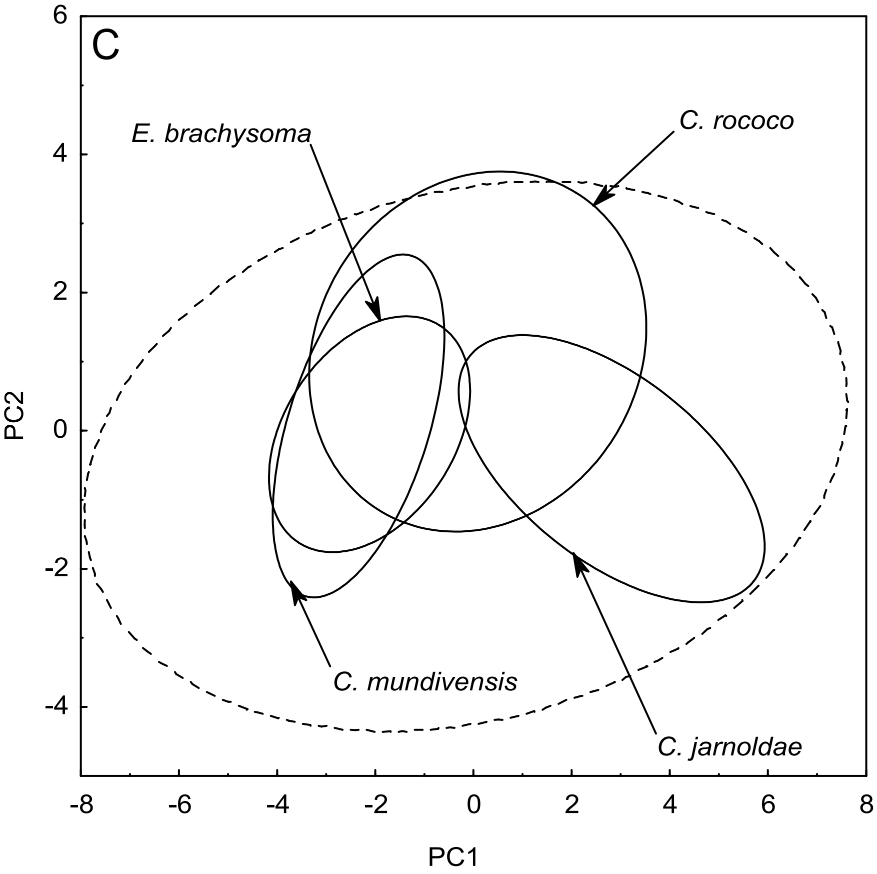
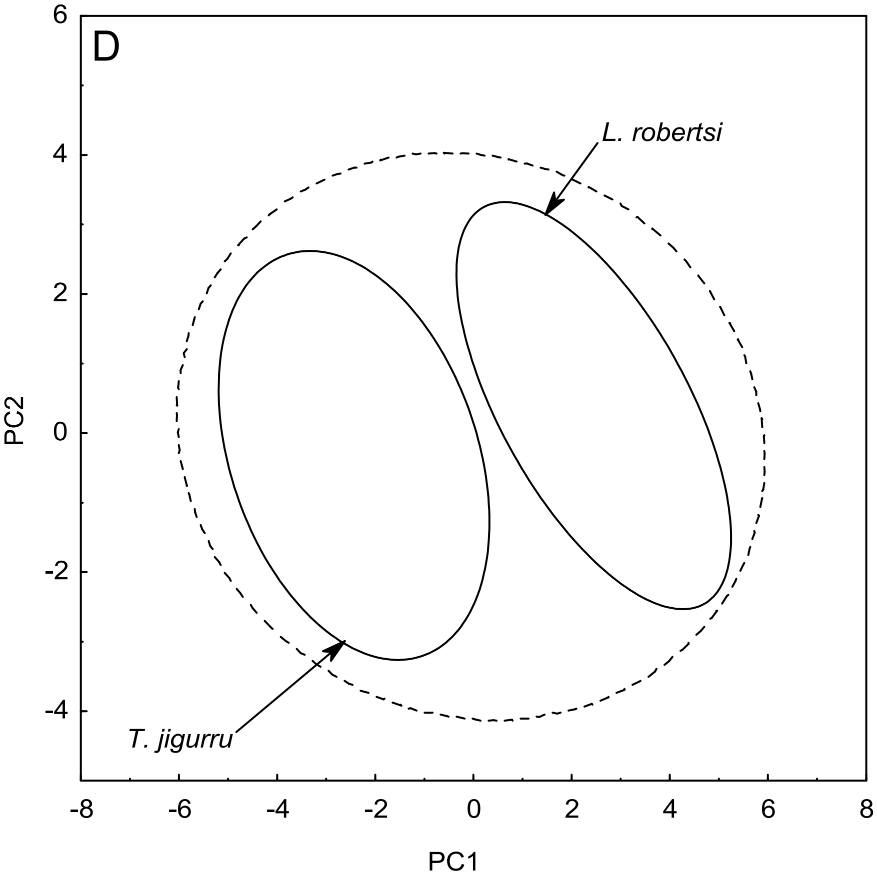


Figure 3.1. Position of 21 tropical scincids representing 24 populations in two-dimensional ecological space based on principal components scores. PC1 describes a gradient of microhabitat occupation with negative scores indicating species correlated with the occupation of habitats dominated by a high proportion of rock coverage, particularly large rocks (rocks > $0.5m^3$), and was positively correlated with species that occupied substrates consisting of leaf litter. The second PC axis described a gradient that was inversely related to the distance from the nearest potential refuge. Species abbreviations; *Carlia jarnoldae*-Alligator Creek (Cja-Ac), *Carlia jarnoldae*-Chillagoe (Cja), *Carlia laevis* (Cle), *Carlia longipes* (Cln), *Carlia mundivensis* (Cmu), *Carlia pectoralis* (Cpe), *Carlia rhomboidalis* (Crh), *Carlia rococo* (Crc), *Carlia rostralis* (Cro), *Carlia rubrigularis* (Crb), *Carlia scirtetis* (Csc), *Carlia storri* (Cst), *Cryptoblepharus litoralis* (Cyl), *Cryptoblepharus virgatus* (Cyv), *Ctenotus spaldingi* (Cts), *Eulamprus brachysoma*-Alligator Creek (Ebr), *Eulamprus brachysoma*-Chillagoe (Ebr-Ch), *Eulamprus brachysoma*-Cooktown (Ebr-Ct), *Eulamprus quoyii* (Equ), *Lampropholis coggeri* (Lco), *Lampropholis mirabilis* (Lmr), *Lampropholis robertsi* (Lro), *Morethia taeniopleura* (Mtn), *Techmarscincus jigurru* (Tji).

Despite the similarity in structural microhabitat use of *C. jarnoldae* and *E. quoyii*, *E. quoyii* typically occupied microhabitats closer to water (Kruskall-Wallace test; χ^2 = 35.00, P < 0.0001). In addition, there were substantial size differences among these species (Figure 3.4; see below).


A
C. rhomboidalis
E. brachysoma
L. mirabilis
E. quoyii
C. pectoralis
M. taenipleura
C. jarnoldae
PC2
PC1
6
4
2
0
-2
-4
-8
-6
-4
-2
0
2
4
6
8
B
C. longipes
C. scirtetis
E. brachysoma
PC2
PC1
6
4
2
0
-2
-4
-8
-6
-4
-2
0
2
4
6
8


C
6
4
2
0
-2
-4
PC2
-8
-6
-4
-2
0
2
4
6
8
PC1
E. brachysoma
C. rococo
C. mundivensis
C. jarnoldae


D
6
4
2
0
-2
-4
PC2
-8
-6
-4
-2
0
2
4
6
8
PC1
L. robertsi
T. jigurru

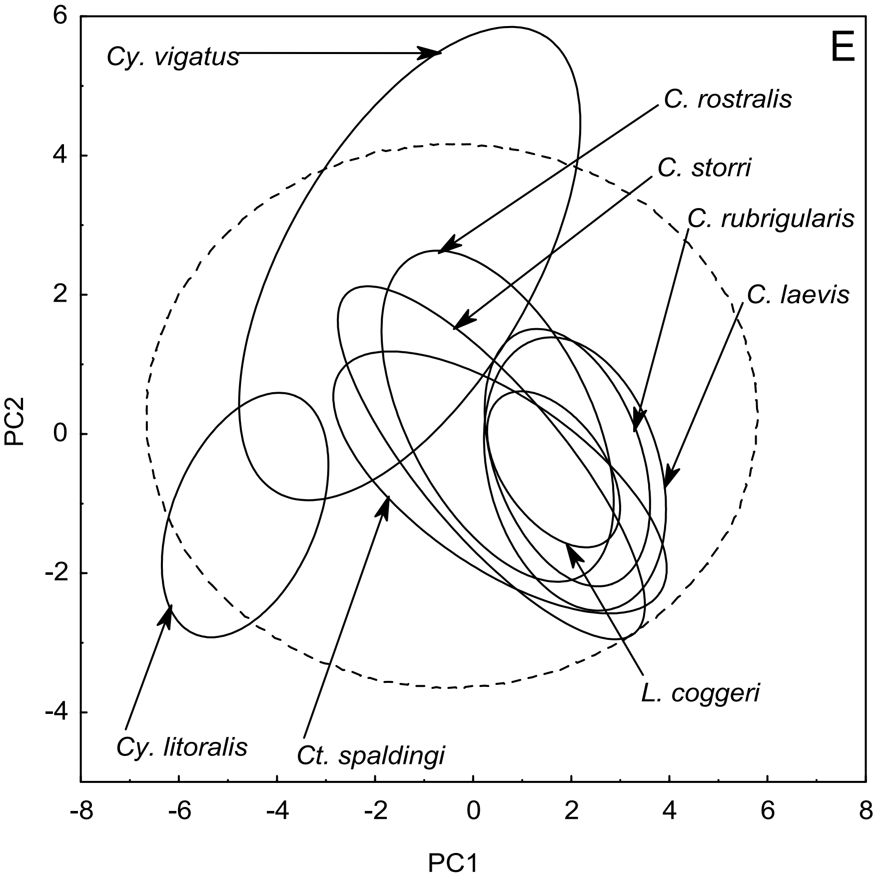


Figure 3.2. Null habitat and actual habitat use of skink species from A. Alligator Creek, B. Black Mountain, C. Chillagoe, D. Mt. Bartle Frere, and. E. from Cairns, Qld. Elipses with solid lines represent species; elipses with broken lines represent the available habitat at each site. Elipses are 95 % confidence elipses.

At Cairns, there was no difference in the two-dimensional structural ecological space occupied by the species-pairs, *C. laevis* and *C. rubrigularis*, *C. laevis* and *L. coggeri*, *C. rostralis* and *C. storri*, and between *C. storri* and *Ct. spaldingi* (Table 3.3B); however, in many cases body size differed between species (Figure 3.4; see below). Similarly, at Chillagoe there was no difference in the two-dimensional structural ecological position of the rock-using species-pairs of *C. mundivensis* and *E. brachysoma* (Table 3.3C). There was no significant difference in the two-dimensional structural microhabitat position of *C. scirtetis* and *E. brachysoma* at Cooktown (Table 3.3D). At Mount Bartle Frere, *L. robertsi* and *T. jigurru* occupied significantly different structural ecological space (Figure 3D; $F_{1, 144}$ = 153.73, P < 0.0001).

Is there evidence of temporal activity separation among co-occurring species?

There was considerable overlap in the activity of species from each assemblage, with most species active throughout the day. There was evidence that some species became less active during the middle (13:01–15:00) of the day (Figure 3.3). There was also species-specific differences when some species were most

Table 3.2. Statistical results of comparisons of structural microhabitat occupation and available structural microhabitat of species from each of the five sites used in this study. Parentheses show sequential Bonferroni adjustment of significance levels for multiple table-wise comparisons.

SPECIES	*F**	*P*
Carlia jarnoldae-Alligator Creek	23.07	<0.0001 (α < 0.002)
Carlia jarnoldae-Chillagoe	51.28	<0.0001 (α < 0.008)
Carlia laevis	60.70	<0.0001 (α < 0.001)
Carlia longipes	31.10	<0.0001 (α < 0.016)
Carlia mundivensis	29.83	<0.0001 (α < 0.008)
Carlia pectoralis	36.34	<0.0001 (α < 0.002)
Carlia rhomboidalis	49.65	<0.0001 (α < 0.002)
Carlia rococo	35.11	<0.0001 (α < 0.008)
Carlia rostralis	12.24	<0.0001 (α < 0.001)
Carlia rubrigularis,	146.47	<0.0001 (α < 0.001)
Carlia scirtetis	94.07	<0.0001 (α < 0.016)
Carlia storri	7.55	<0.0001 (α < 0.001)
Cryptoblepharus litoralis	304.37	<0.0001 (α < 0.001)
Cryptoblepharus virgatus	294.34	<0.0001 (α < 0.001)
Ctenotus spaldingi	12.64	<0.0001 (α < 0.001)
Eulamprus brachysoma-Alligator Creek	26.67	<0.0001 (α < 0.002)
Eulamprus brachysoma-Chillagoe	9.98	<0.0001 (α < 0.008)
Eulamprus brachysoma-Cooktown	26.27	<0.0001 (α < 0.016)
Eulamprus quoyii	60.05	<0.0001 (α < 0.002)
Lampropholis coggeri	32.76	<0.0001 (α < 0.001)
Lampropholis mirabilis	94.85	<0.0001 (α < 0.002)
Lampropholis robertsi	52.07	<0.0001 (α < 0.025)
Morethia taeniopleura	15.97	<0.0001 (α < 0.003)
Techmarscincus jigurru	43.86	<0.0001 (α < 0.025)

*Tests are squared Mahalanobis distances with sigma-restricted parameterization.

active, with some species most active late in the afternoon (*E. brachysoma*-Chillagoe, *E. brachysoma*-Cooktown, *Cy. litoralis, C. rococo, C. rhomboidalis*), while other species were more active early in the day (*C. mundivensis*, *T. jigurru*; Figure 3.3).

Table 3.3A. Niche overlap (Pianka's) and percentage overlap (in parentheses) of seven tropical diurnal skink species from Alligator Creek north-east Queensland.

Species	*C. pectoralis*	*C. rhomboidalis*	*E. brachysoma*	*E. quoyii*	*L. mirabilis*	*M. taeniopleura*
C. jarnoldae	0.712* (58)	0.433* (41.5)	0.200* (17.1)	0.857 (69.1)	0.486* (37.4)	0.330 (32.5)
C. pectoralis	—	0.929* (79.0)	0.115* (22.9)	0.582* (56.2)	0.265* (32.7)	0.889 (68.3)
C. rhomboidalis		—	0.123* (21.4)	0.407* (39.4)	0.156* (17.9)	0.983* (79.5)
E. brachysoma			—	0.147* (22.9)	0.943 (79.7)	0.014* (5.6)
E. quoyii				—	0.344* (39.6)	0.269* (24.7)
L. mirabilis					—	0.035* (5.6)

*Denote species that occupy significantly different ecological space following sequential Bonferroni correction. Species-overlaps in ecological space tested using pairwise comparisons of Mahalanobis (D^2) distance.

Table 3.3B. Niche overlap (Pianka's) and percentage overlap (in parentheses) of eight tropical diurnal skink species from Cairns north-east Queensland.

Species	*C. rostralis*	*C. rubrigularis*	C. storri	*Ct. spaldingi*	*Cy. litoralis*	*Cy. virgatus*	*L. coggeri*
C. laevis	0.772* (52.1)	0.977 (85.7)	0.840* (65.5)	0.849* (61.5)	0.014* (2.2)	0.009* (6.2)	0.826 (68.6)
C. rostralis	—	0.789* (55.0)	0.939 (78.7)	0.821* (61.2)	0.150* (24.0)	0.070* (12.3)	0.672* (41.1)
C. rubrigularis		—	0.872* (66.1)	0.919* (66.2)	0.021* (3.6)	0.009* (7.6)	0.884* (69.5)
C. storri			—	0.886 (65.4)	0.160* (25.8)	0.055* (12.3)	0.765* (55.7)
Ct. spaldingi				—	0.083* (16.5)	0.018* (6.2)	0.852 (65.4)
Cy. litoralis					—	0.115* (14.9)	0.013* (2.2)
Cy. virgatus						—	0.006* (5.7)

Table 3.3C. Niche overlap (Pianka's) and percentage overlap (in parentheses) of four tropical diurnal skink species from Chillagoe north-east Queensland.

SPECIES	*C. mundivensis*	*C. rococo*	*E. brachysoma*
C. jarnoldae	0.136* (18.8)	0.290* (39.6)	0.009* (4.8)
C. mundivensis	—	0.957* (73.2)	0.973 (81.3)
C. rococo		—	0.912* (59.2)

Table 3.3D. Niche overlap (Pianka's) and percentage overlap (in parentheses) of three sympatric tropical diurnal skink species from Cooktown north Queensland.

SPECIES	*C. scirtetis*	*E. brachysoma*
C. longipes	0.541* (28.1)	0.577* (38.6)
C. scirtetis	—	0.916 (69.6)

Do co-occurring species separate along an axis of body size?

Most of the species from the five assemblages overlapped in size. However, there were several species within an assemblage from the same ecotype that did not (Figure 3.4). Among generalist species at Alligator Creek, neither *M. taeniopleura* nor *C. jarnoldae* overlapped with *E. quoyii*. Among litter-dwelling species at Cairns, there was no size overlap between *C. rubrigularis* and *C. laevis*, and between *Ct. spaldingi* and *C. storri*.

Is there geographic variation in microhabitat use and niche overlap?

Eulamprus brachysoma and *C. jarnoldae* occurred in more than one assemblage. There was significant geographical variation in structural microhabitat use for *E. brachysoma* from Alligator Creek and Cooktown ($F_{1,\ 55} = 11.12$, $P < 0.001$), Alligator Creek and Chillagoe ($\mathrm{F}_{1,\ 52} = 4.10$, $\mathrm{P} < 0.05$) and Cooktown and Chillagoe ($F_{1,\ 41} = 3.83$, $P < 0.05$) (Figure 3.1). Similarly, there was a significant difference in the structural microhabitat use of *C. jarnoldae* from Alligator Creek and Chillagoe ($F_{1,\ 90} = 59.38$, $P < 0.001$). Despite these differences only *C. jarnoldae* displayed a significant amount of niche overlap among assemblages (Table 3.5A). That is, *E. brachysoma* showed substantial non-random shifts in microhabitat use among assemblages.

There were no differences between observed and expected niche overlap variance for these species among assemblages (Table 3.5A).

Table 3.4. Results from comparisons of A. mean niche overlap, and B. mean niche overlap variance of species from each of the five assemblages. Results from the two models RA3 and RA4 are shown. See text for descriptions of randomisation models used.

A. SITE	Model	Observed mean niche overlap	Expected mean niche overlap	$P_{\text{Obs > Exp}}$
Alligator Creek	RA3	0.394	0.337	0.179
	RA4	0.394	0.376	0.336
Cairns	RA3	0.310	0.259	0.131
	RA4	0.310	0.265	0.162
Chillagoe	RA3	0.677	0.427	0.006
	RA4	0.677	0.500	0.011
Cooktown	RA3	0.590	0.423	0.078
	RA4	0.590	0.566	0.154
Mt. Bartle Frere	RA3	0.681	0.576	0.098
	RA4	0.681	0.677	0.380

B. SITE	Model	Observed niche overlap variance	Expected niche overlap variance	$P_{\text{Obs > Exp}}$
Alligator Creek	RA3	0.116	0.090	0.121
	RA4	0.116	0.090	0.115
Cairns	RA3	0.108	0.082	0.089
	RA4	0.108	0.084	0.115
Chillagoe	RA3	0.112	0.114	0.483
	RA4	0.112	0.107	0.488
Cooktown	RA3	0.169	0.165	0.344
	RA4	0.169	0.170	0.344
Mt. Bartle Frere	RA3	0.179	0.174	0.717
	RA4	0.179	0.137	0.379

Is there evidence of species packing?

There was no difference among assemblages in NND (ANOVA: $F_{3, 17} = 8.94$, $P > 0.45$), suggesting assemblages with more species had smaller NNDs and were more packed. In accordance with this result, while the relationship between the number of species within an assemblage and mean NND fell short of statistical significance, this relationship was negative ($r = -0.79$, $P = 0.11$; Figure 3.5), suggesting spatial niche dispersion declines as the number of coexisting species within an assemblage increases.

Are assemblages with more specialised niches less evenly packed?

A comparison of mean CD was positively related to the SDNND ($r = 0.94$, $P < 0.05$), indicating that assemblages with more ecologically specialised species were less evenly arranged in structural ecological space (Figure 3.6).

Discussion

All species used available microhabitats non-randomly, with species separating according to substrate, the amount of leaf litter, ground cover, undergrowth, proximity to vegetation and amount of canopy cover. In general, species tended to have overlapping activity times, however, there were cases where co-occurring species from the same ecotype did not overlap in size. While there was significant structural niche separation between most species, within-assemblage comparisons of niche overlap using null models revealed few cases where niche overlap was greater than expected by chance. Assemblages with more species showed evidence of species packing, with assemblages consisting of a greater number of species consisting of more diverse niches which were less evenly packed.

The majority of separation in structural microhabitat use was attributed to variation in substrate type: species separated across a gradient of habitats from large rocks to leaf litter and total ground cover, and also along a gradient of increasing leaf litter, ground cover, undergrowth, proximity of vegetation and canopy cover. Several other studies have, similarly, identified the role of substrate structure and other specific microhabitat characteristics in determining the spatial arrangements of a community of lizards (Paulissen, 1988; Melville and Schulte, 2001). For example, soil particle size, the amount of rock and gravel substrate and available shelter in rodent burrows and vegetation were found to be important features describing the spatial structure of desert lizard communities in both Mexico and middle Asia (Shenbrot et al., 1991). I identified rock use, and rock size and availability as important features of

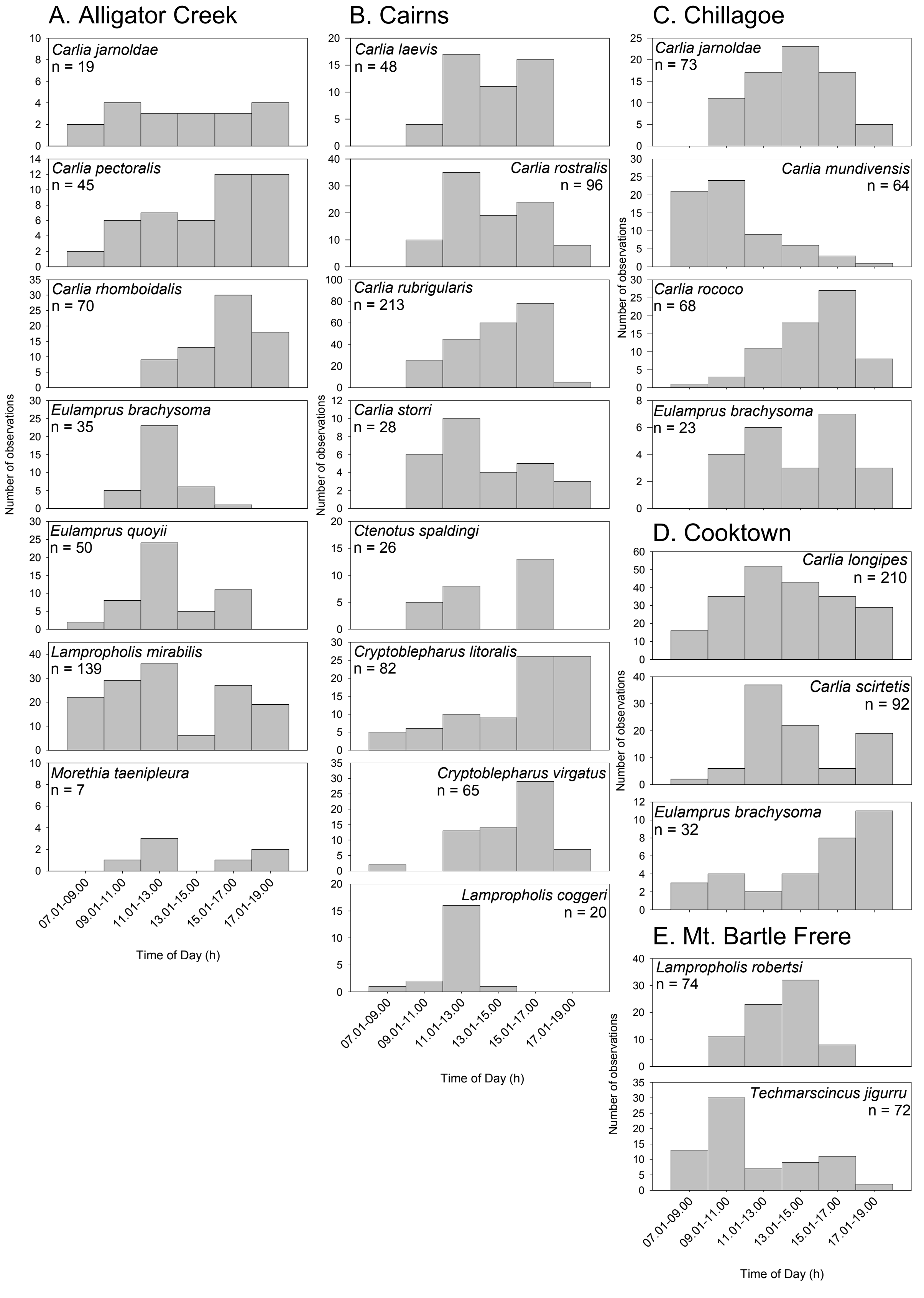


Figure 3.3. Temporal activity of 21 species of skinks from five assemblages in tropical north Queensland.

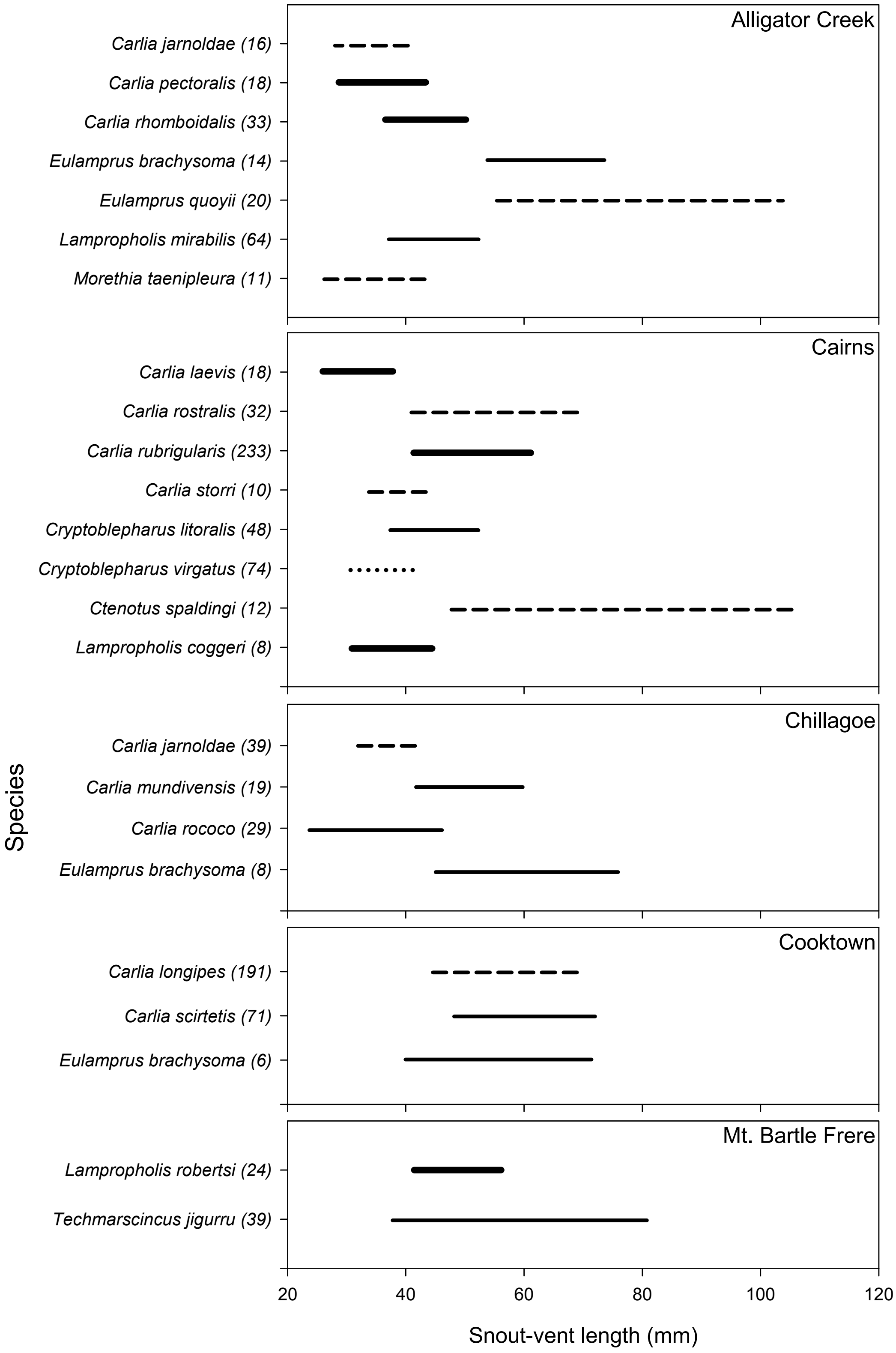


Figure 3.4. Size range of adults and sub-adults of 21 species of skinks representing 24 populations from five assemblages in tropical north Queensland. Sample sizes are in parentheses, line style indicates ecotype: dotted line–arboreal; broken line–generalist species; thick line–leaf litter-dwelling; thin line–rock-using species.

Table 3.5. Comparisons of A. mean niche overlap, and B. variance in niche overlap for *Eulamprus brachysoma* and *Carlia jarnoldae* that occurred in multiple assemblages. *E. brachysoma* occurred at Alligator Creek, Chillagoe and Cooktown. *Carlia jarnoldae* occurred at Alligator Creek and Chillagoe. See text for descriptions of randomisation models used.

A. Species	Model	Observed mean niche overlap	Expected mean niche overlap	$P_{\text{Obs > Exp}}$
Eulamprus brachysoma	RA3	0.757	0.731	0.435
	RA4	0.757	0.673	0.151
Carlia jarnoldae	RA3	0.974	0.573	0.025
	RA4	0.974	0.776	0.254

B. Species	Model	Observed niche overlap variance	Expected niche overlap variance	$P_{\text{Obs > Exp}}$
Eulamprus brachysoma	RA3	0.025	0.037	0.494
	RA4	0.025	0.047	0.635
Carlia jarnoldae	RA3	0.001	0.178	0.988
	RA4	0.001	0.093	0.989

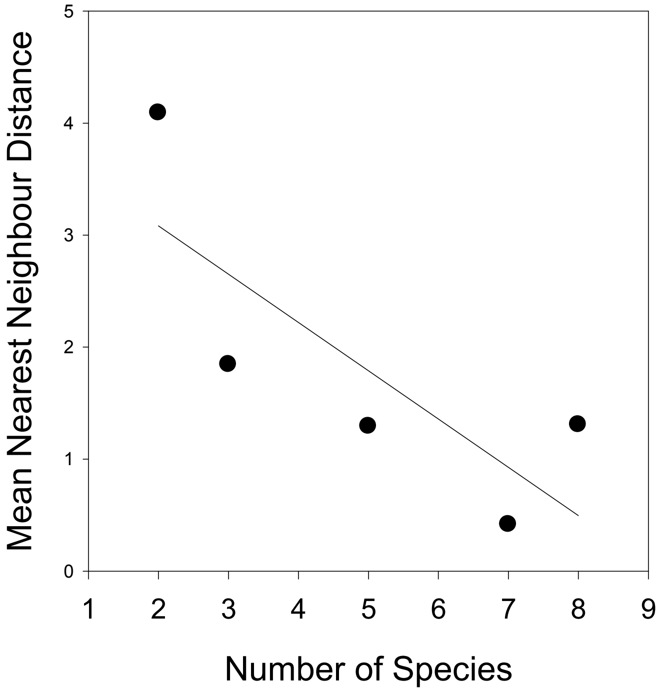


Figure 3.5. The relationship between the number of sympatric species and mean nearest neighbour distance for the five assemblages of skinks examined in this study.

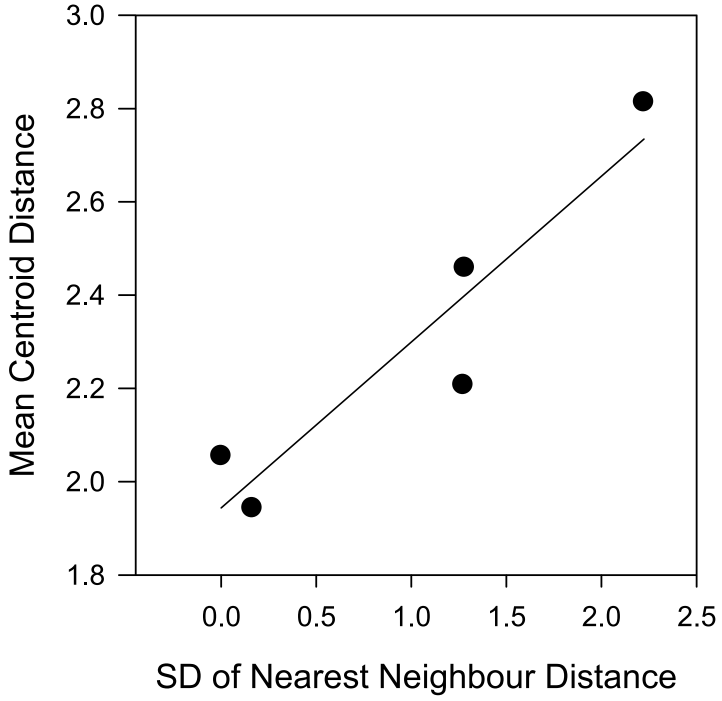


Figure 3.6. The relationship between the SD of nearest neighbour distance and mean centroid distance for the five assemblages of skinks examined in this study.

the structural microhabitats used by lizards in my study. Likewise, Howard and Hailey (1999) found significant niche separation among four lizard species from three rock outcrops in South Africa, which they attributed to the structural complexity of granite rock at each site. Published species descriptions suggest that some of the species in my study (e.g. *C. scirtetis*, *L. mirabilis*) are restricted to rocky habitats (Ingram and Rawlinson, 1981; Ingram and Covacevich, 1980; Covacevich, 1984), which may explain, to some degree, the importance of substrate type in defining the positions of species in structural microhabitat space. Further, structural microhabitat separation in species from assemblages occupying structurally complex (e.g., arboreal) habitats have been identified (Colli et al., 1992; Vitt et al., 1981; Vitt, 1991a), suggesting that variation in substrate type may be a prevailing descriptor in separating species from many lizard groups (Scheibe, 1987; Shenbrot et al., 1991; Melville and Swain, 2000; Vitt et al., 2000).

The second PC axis (Table 3.1) delineated species based on leaf litter and vegetative features. Several other studies have also identified the role of vegetative features, probably due to their role in providing shade for thermoregulation, as being of primary importance in the microhabitat use of lizards from many regions (Pianka, 1975; Paulissen, 1988; Brown and Nelson, 1993). For example, in desert habitats, which lack considerable structural complexity, shrubs and grasses were the most important microhabitats describing lizard communities (Pianka, 1975, 1986; Shenbrot et al., 1991). This suggests that for assemblages made up of more structurally complex habitats, such as those in this study, substrate cover is of greater importance, followed by vegetation features. Thus, in assemblages composed of habitats with less structural and substrate complexity, the separation provided by vegetation availability is of utmost importance for separating co-existing lizard species.

Structural microhabitat use in each assemblage of lizards in my study was non-random. A comparison of two *Carlia* species found that while both species used available microhabitat non-randomly, *C. vivax* used ground and litter cover non-randomly (Singh et al., 2002). Similarly, nine species of desert agamid from central Australia exhibited non-random selection of microhabitats, with preferences for a suite of structural and thermal characteristics (Melville and Schulte, 2001). Five species of sympatric temperate-zone skinks select thermally suitable rock crevices non-randomly, restricting themselvess to areas with minimal vegetation, close to logs and with high levels of solar exposure (Langkilde et al., 2003). In general, non-random microhabitat use indicates that lizard activity is constrained to a smaller subset of resources (Grant and Dunham, 1988). Moreover, while thermoregulation was not assessed in this study, it presumably reflects a compromise between suitable thermal and structural characteristics (Heatwole, 1977; Adolph, 1990). The greater range of thermally suitable microhabitats in the tropics (Shine and Madsen, 1996) may reduce the need for lizards to bask for long periods, and thus, place more importance on structural microhabitat use.

Microhabitat overlap was relatively high among several species, with most species showing no difference in structural microhabitat use (Table 3.3A–3.3D). In addition, overlap in temporal activity was high. In assemblages other than Chillagoe, structural microhabitat niche overlap was less than expected by chance. This suggests that, for the most part, some level of competitive interaction may be limiting species overlap within these assemblages. Another consideration is that co-existing species may actually differ along other niche dimensions (Pianka, 1973, 1986). In some cases, species from the same ecotype differed in size, which may enable coexistence. In those cases where species differ in size, gape-limited prey size may diverge. Because head size and gape width are generally considered reliable determinants of the potential prey size that can be consumed (Herrel et al., 1999; Vitt et al., 2000), cases where species differed in gape size may enable dietary divergence (Pianka 1973; Huey and Pianka, 1977). On the other hand, there was considerable size-overlap among many co-occurring species from the same ecotype, suggesting that competition for prey is likely to be high, due to the fact that similar-sized lizard species typically consume prey of similar size (Pianka, 1973; Montanucci, 1981; Vitt et al., 2000). Alternatively, species may differ in the use of other microhabitat features. For example, in addition to size, 'distance to water' is clearly an important descriptor in the niche separation of *C. jarnoldae* and *E. quoyii*. Thus, in the case of these two species, differences in both body size and structural microhabitat use are likely to reduce the degree of resource competition allowing coexistence.

Of the two species which occurred in more than one assemblage, only *C. jarnoldae* showed geographic variation in microhabitat use. This suggests that the competitive environment or the structural range of microhabitats used changes with geographic locality. There is evidence that lizards shift habitat use in the presence of larger species with similar ecologies. The skink *Niveoscincus microlepidotus* exhibits a shift in microhabitat when in sympatry with the larger species *N. greeni* (Melville, 2003). In addition, on small islands of the Caribbean, exposure of the lizard *Anolis sagrei* to a novel predator caused a shift in microhabitats from on the ground to narrow, elevated perches (Losos et al., 2003b). Thus, in some cases, shifts in microhabitat use may cause morphological or ecological plasticity. In laboratory and natural field experiments, exposure of *A. sagrei* to modified microhabitats consisting of wider perches resulted in a phenotypically plastic increase in relative limb-length (Losos et al., 1997, 2000). This suggests that both ecological and morphological changes may facilitate the coexistence of sympatric lizard species.

The volume of ecological space occupied within assemblages was inversely related to the number of co-occurring species. Scheibe (1987) found a similar case in a comparison of temperate-zone lizard communities in which NNDs and interspecific overlap in ecological and morphological space was unrelated to community size. In a comparison of the morphology of three desert lizard assemblages, Ricklefs et al., (1981) found that members of the species-rich *Ctenotus* group exhibited the lowest index of niche packing, but occupied the greatest area of morphological space. This suggests that morphological disparity among species may provide much of the necessary variation to facilitate the coexistence of many species. Indeed, how the morphology of the skinks in this study relates to assemblage size and structural microhabitat use remains unexplored.

Conventional measures of niche overlap are typically positively related to the number of sympatric species (Pianka, 1969a, 1973, 1974). This relationship suggests that the degree of overlap may be closely related to the number of competing species and is probably maintained by ‘diffuse competition’; the sum competitive effect of interspecific competitors (MacArthur, 1972). As such, assemblages with more intense levels of diffuse competition require greater niche separation. In a similar way, species in larger assemblages are more dispersed in ecological space. Although statistical significance was not detected, I found mean niche breadth was negatively related to the number of sympatric species, as did Pianka (1974) for *Ctenotus* assemblages. Negative relationships between the number of sympatric species and niche breadth provide support for the ‘niche overlap’ hypothesis, which predicts that the maximal amount of niche overlap should decline with an increase in the intensity of competition. Further, the number of sympatric species was negatively related to species dispersion in ecological space. Despite limiting analyses to the niche use of a clade of diurnal, widely-foraging skinks from a restricted geographic area, the relationship between the number of sympatric species and species dispersion appears fairly robust. Interestingly, such patterns are not always encountered in lizard assemblages. Shenbrot et al., (1991) found no relationship between niche breadth and the number of sympatric species in an examination of the community organisation of desert lizards from Mexico and Asia. They suggested the greater niche overlap of Asian lizards was explained by the large amount of body size differentiation observed among species in these communities. This shows that body size alone may facilitate the coexistence of some co-occurring sympatric species. In my study, however, while body size differences and subtle differences in temporal activity help reduce competitive interactions (Pianka, 1969a, 1986), differences in structural microhabitat use appears to be the main mechanism allowing coexistence within assemblages of these tropical skinks.

Chapter 4

Sexual dimorphism: the relationship between body size, body shape and microhabitat use in a lineage of tropical skinks

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Introduction

The trend for organisms to show morphological variation related to their preferred habitat has received research attention for more than two decades (Miles and Ricklefs, 1984; Miles et al., 1987; Lauder, 1996; Irschick and Losos, 1999). Substantial insight into the nature of adaptation can be gained by examining the link between an organisms' morphology and its environment (Arnold, 1983; Garland and Losos, 1994; Wainwright and Reilly, 1994). For example, because different forces affect species occupying vertical substrates compared to species that occupy horizontal habitats, substantial differences should exist in their locomotion and associated morphological traits such as limb length and body shape (Cartmill, 1985; Zaaf et al., 1999; Zaaf and Van Damme, 2001). In lizards, arboreal species have short limbs that keep their centre-of-mass close to the substrate, reducing the possibility of toppling sidewards off a perch, and fore-limbs and hind-limbs of equivalent length to produce strides of equal length and grip perches securely (Losos and Sinervo, 1989; Sinervo and Losos, 1991; but see Vanhooydonck and Van Damme, 2001).

While many empirical studies on lizards have found support for the relationship between morphology and ecology, others have been more equivocal (e.g., Leal et al., 2002; Schulte et al., 2004). For example, behavioural adjustments in locomotion may reduce or prevent selection-mediated adaptive morphological change in response to different habitats (Huey, Hertz and Sinervo, 2003; Schulte et al., 2004). Alternatively, there may be no tight correspondence between morphology and habitat, because some morphologies work well in a variety of habitats (Vanhooydonck and Van Damme, 2001). Phylogenetic history (Losos, 1995) ecological and functional constraints (e.g., life history; Vitt, 1981; Shine, 1988; Sinervo and Losos, 1989), and the contemporary and historical competitive environment may all influence a species' habitat use and morphological and physiological response to it over evolutionary time (Simpson, 1953; Schoener, 1974; Losos, 1995; Losos et al., 2003b).

Sexual selection may also cause morphological differences between sexes, independent of ecologically mediated natural selection. Like many other organisms, lizards can be sexually dimorphic in body size and shape (Andersson, 1994; Butler et al., 2000; Olsson et al., 2002; Schwarzkopf, 2005). Males commonly have larger heads, whereas females have longer inter-limb lengths (Olsson et al., 2002). In lizards, the larger heads of males increase success in male-male combat (Huyghe et al., 2005; Lappin and Husak, 2005), while longer inter-limb length in females provides space for more offspring (Olsson et al., 2002). As such, morphological studies restricted to a single sex will fail to reveal important differences between sexes, both in morphology and ecology. For example, if female lizards are less flat than males to provide room for clutch production, their ability to use crevices, or inclined surfaces may be affected. Consequently, studies should investigate ecomorpholgical relationships of each sex separately (Herrel et al., 2002). In lizards, there are differences in the degree of sexual-size dimorphism and microhabitat occupied between males and females (Butler et al., 2000; Losos et al., 2003a; Irschick et al., 2005b), but whether individuals of different sexes exhibit different morphologies in response to different microhabitats remains largely unexplored for most lizard groups (c.f., Butler et al., 2000; Butler and Losos, 2002; Losos et al., 2003a for *Anolis*; Herrel et al., 2002 for *Phrynosomatid* lizards).

While the radiation and diversification of Anoline lizards has provided evidence in support of ecomorpholgical relationships (Williams, 1983; Losos and Sinervo, 1989; Losos, 1990a; Irschick and Losos, 1999; Irschick et al., 1997), anoles as a group are restricted to arboreal habitats. A test of the ecomorphological paradigm (Arnold, 1983; Garland and Losos, 1994) and intersexual differences is required for other lineages that use a wider range of habitats. The aim of this study was to determine how morphology and intersexual differences relate to ecology in a sub-family of Australian skinks (Lygosominae) from five genera (*Carlia*, *Cryptoblepharus*, *Eulamprus*, *Lampropholis, Techmarscincus*). Species from these genera occupy a variety of microhabitat types, from trees and boulders to terrestrial leaf litter habitats, and possess a range of body shapes from long to short, and robust to flattened (Greer, 1989; Cogger, 2000). Specifically, I examined whether i) certain morphological traits (such as longer limbs, and flatter bodies) were correlated with specific microhabitat use (such as rocky habitats), and ii) whether relationships between morphology and ecology differed between the sexes.

Methods

Habitat use

SUBSTRATE USE, HABITAT OPENNESS AND REFUGE USE

Each species of skink was allocated to one of four microhabitat types based on field observeation and published data of the microhabitat most commonly used by each species (Chapter 3). Measurements of substrate use, habitat openness, and refuge use are described in Chapter 2.

SUBSTRATE USE, HABITAT OPENNESS AND REFUGE USE

Lizards were studied at five sites, with between two and six species examined from each site (Table 2.2). Observations were conducted on undisturbed lizards on clear days with adequate solar radiation. To reduce the possibility of disturbance, lizards were spotted and observed from a distance of > 6 m using 10X field binoculars (Bushnell®). Lizard substrate use, habitat openness and refuge use was assessed by walking haphazard transects of 100 m through all available habitats and recording the species observed and the following variables within a 3m radius of each individual; microhabitat type, total ground cover, total rock cover, % litter cover, % bare earth, % logs, % rock < 0.5 m^3, % rock > 0.5 m^3, height above substrate (cm), perch angle (degrees), solar exposure, canopy type, nearest vegetation, nearest vegetation height, canopy height, % canopy, % undergrowth, undergrowth type. Refuge use was determined by observing where individuals of each species typically took refuge. In cases where refuge data were not available, a species' refuge was defined as the nearest potential refuge where escape from a predator seemed likely; casual observations suggest potential refuges provide a reliable surrogate of realized refuge use. Refuge data recorded included distance to nearest refuge and the predominant refuge type used, and the proportion used of each of the following categories: tree refuge, vegetation pile, leaf litter, under rock, under log, crevice / crack. In addition, each species was categorized as one of four broad microhabitat categories (arboreal, generalist, leaf litter and rocks) based on the most common microhabitat type used (Chapter 3).

Lizard sampling and morphological measurements

All measurements were taken from live individuals. Details of lizard capture techniques, husbandry, and measurements were given in Chapter 2.

Phylogenetic analyses

Details of phylogenetic analyses and tests of phylogenetic signal and associated levels of significance (*K* statistic and *P*-value) are provided in Chapter 2. Prior to analyses I calculated the mean of each ecological variable (microhabitat type used, total ground cover, total rock cover, % litter cover, % litter cover, % bare earth, % logs, % rock < 0.5 m3, % rock > 0.5 m3, height above substrate, solar exposure, canopy type, nearest vegetation, vegetation height, canopy height, % canopy, % undergrowth, undergrowth type) for each species, except variables for refuge use (Distance to nearest refuge, Tree refuge, Vegetation pile, Leaf Litter, Under Rock, Under Log, Refuge Type, Crevice / Crack), which consisted of the proportion that individuals of each species used each refuge type. The variables from all continuous ecological data were $\log_{10}$+1-transformed prior to analyses (Sokal and Rohlf, 1995). This transformation successfully achieved normality and homoscedasticty within the data. All data expressed as percentages were converted to proportions and all proportions were arcsine square-root transformed prior to analyses (Quinn and Keough, 2002). For morphological data, the species mean of each trait for each sex was $\log_{10}$-transformed prior to being used in phylogenetic comparative analyses. Individuals of different sexes and species were different sizes, so morphological differences were confounded with size differences in comparisons. Therefore, to control for size differences when comparing limb-length and body shape between sexes and among species from different habitats, I used residuals from the regression of each trait and log-transformed snout-vent length (sexes combined).

The two complementary phylogenetic analyses were used to test for relationships between ecological traits and lizard morphology are detailed in Chapter 2. The similarity of each species in three-dimensional substrate use, microhabitat openness and refuge-use space was tested using canonical correlation (Chapter 2).

Results

Morphology

There was substantial variation in body size and shape (Table 4.1A), and in limb length and limb proportions (Table 4.1B) among species and sexes. The use of phylogenetic comparative methods was justified based on the large number of significant *K*-values for the morphological traits of males and females (Table 2.3). The PCA of size-corrected, standardised, independent contrasts of females and males explained 86.1 and 88.8 % of the variation using the first three PC axes, respectively (Table 4.2). For females, PC1 described a gradient of species with decreasing inter-limb length and increased length of the limbs and limb elements, whereas PC2 described a gradient of increasing head and body height and increasing tail length. PC3 described a gradient of increasing body and head width. In males, PC1 described a gradient of increasing length of the limbs and limb elements, whereas PC2 described a gradient of increasing inter-limb and tail length and body height. PC3 described a gradient of increasing body and head width and head height.

Substrate use, habitat openness and refuge use

The first three PC axes of the analysis of standardised independent contrasts of substrate use explained 87.6 % of the variation among these variables (Table 4.3A). PC1 described a gradient from rock users (negative loadings), that perched high above the substrate, to leaf-litter users (positive loadings) at ground level. PC2 described a gradient of species using habitats dominated by small rocks (negative) to species from habitats with a high proportion of bare earth (positive). PC3 described a gradient of species that used microhabitats of increasing structural complexity, perch angle and perch height above substrate.

The first two axes of habitat openness (Table 4.3B) accounted for 70.9 % of the variation among the variables, with PC1 describing a gradient where lizards occupied open habitats far from nearby vegetation to habitats with increasing amounts of undergrowth and canopy cover, with a high canopy. PC2 loaded strongly and positively for habitats with high nearby vegetation, and for canopy and undergrowth type and negatively for amount of solar exposure.

The first three axes for refuge use (Table 4.3C) described 79.2 % of the variation among the variables, with PC1 describing a gradient where species predominantly used trees or leaf litter as refuges (positive), to rock crevice and rock crack refuges (negative). The second PC described an increasing gradient along which species tended to be large distances from the nearest refuge and use under-rock refuges. PC3 axis described a decreasing gradient where high negative values indicated species that took refuge under logs or in vegetation piles.

In general, substrate use defined gradients of declining rock use, whereas microhabitat openness defined a gradient of increasing vegetation complexity. Refuge use primarily defined a refuge gradient ranging from crevices or crack use to tree and leaf litter refuges.

Table 4.1A. Body shape variables for 18 species of Lygosomine lizards from tropical Australia. Shown are mean values (± S.E.). Females are on first line, males on the second. Letters represent habitat category: A-Arboreal; G-Generalist; Litter-dwelling; R-Rock-using.

SPECIES		N	Snout-vent	Inter-limb	Head Width	Head Height	Body Width	Body Height	Tail Length
Carlia jarnoldae	G	14	38.34 ± 0.84	19.41 ± 0.56	5.19 ± 0.07	3.40 ± 0.07	7.68 ± 0.27	3.82 ± 0.09	48.79 ± 4.32
		12	41.16 ± 0.71	19.97 ± 0.40	5.79 ± 0.12	4.10 ± 0.21	8.35 ± 0.26	4.37 ± 0.15	54.33 ± 3.84
Carlia laevis	L	8	34.34 ± 0.71	18.20 ± 0.74	4.01 ± 0.13	2.69 ± 0.16	6.26 ± 0.18	3.02 ± 0.07	47.19 ± 2.77
		5	35.21 ± 0.28	18.14 ± 0.36	4.33 ± 0.03	2.72 ± 0.07	6.25 ± 0.14	3.10 ± 0.12	41.10 ± 3.49
Carlia longipes	G	17	57.80 ± 0.78	28.52 ± 0.46	7.77 ± 0.08	5.91 ± 0.12	12.09 ± 0.31	6.95 ± 0.12	87.88 ± 3.60
		14	61.57 ± 1.21	29.95 ± 0.78	8.57 ± 0.20	6.55 ± 0.14	12.68 ± 0.44	7.58 ± 0.23	94.79 ± 5.16
Carlia mundivensis	R	10	53.40 ± 1.83	25.66 ± 0.97	7.86 ± 0.22	5.08 ± 0.17	11.48 ± 0.38	5.77 ± 0.20	78.85 ± 4.92
		8	55.53 ± 1.82	26.86 ± 1.01	8.92 ± 0.32	5.83 ± 0.23	11.40 ± 0.41	6.27 ± 0.25	88.38 ± 3.39
Carlia pectoralis	L	6	43.25 ± 1.77	21.89 ± 1.07	5.81 ± 0.13	4.41 ± 0.15	8.92 ± 0.49	4.88 ± 0.20	69.92 ± 4.58
		10	44.45 ± 1.02	21.81 ± 0.59	6.24 ± 0.12	4.64 ± 0.10	8.43 ± 0.35	5.18 ± 0.14	74.55 ± 2.79
Carlia rhomboidalis	L	10	46.74 ± 0.87	23.81 ± 0.47	6.24 ± 0.09	4.86 ± 0.08	9.31 ± 0.30	5.43 ± 0.13	70.00 ± 2.63
		15	47.20 ± 0.93	23.09 ± 0.53	6.80 ± 0.11	4.89 ± 0.11	9.51 ± 0.31	5.50 ± 0.17	70.13 ± 3.81
Carlia rococo	R	8	35.09 ± 1.34	17.42 ± 0.80	4.55 ± 0.08	2.74 ± 0.07	7.09 ± 0.27	3.18 ± 0.12	55.13 ± 2.55
		9	39.77 ± 1.13	19.72 ± 0.72	5.22 ± 0.10	3.28 ± 0.10	7.06 ± 0.24	3.64 ± 0.13	51.83 ± 4.66
Carlia rostralis	G	8	57.73 ± 1.14	30.00 ± 0.62	7.65 ± 0.12	5.72 ± 0.12	11.85 ± 0.50	6.70 ± 0.10	85.75 ± 4.81
		8	59.89 ± 2.01	29.68 ± 1.05	8.38 ± 0.26	6.46 ± 0.24	12.71 ± 0.54	7.62 ± 0.30	97.69 ± 7.92
Carlia rubrigularis	L	11	50.25 ± 1.26	25.44 ± 0.57	6.95 ± 0.15	4.77 ± 0.15	10.83 ± 0.34	5.97 ± 0.23	67.41 ± 4.48
		13	51.79 ± 1.20	25.96 ± 0.59	7.30 ± 0.15	5.08 ± 0.16	10.56 ± 0.33	6.21 ± 0.16	71.42 ± 6.54

Table 4.1A. Continued.

Carlia scirtetis	R	16	65.35 ± 1.00	30.87 ± 0.69	9.17 ± 0.18	5.73 ± 0.10	13.68 ± 0.38	6.56 ± 0.12	90.41 ± 4.86
		16	65.08 ± 1.71	30.47 ± 0.88	9.45 ± 0.27	5.93 ± 0.17	13.00 ± 0.29	6.55 ± 0.17	92.34 ± 5.97
Carlia storri	G	5	40.52 ± 2.34	19.82 ± 1.45	5.43 ± 0.22	4.26 ± 0.15	7.94 ± 0.69	4.74 ± 0.38	71.50 ± 4.94
		5	40.72 ± 0.95	19.67 ± 0.31	5.68 ± 0.09	4.66 ± 0.07	8.26 ± 0.46	5.02 ± 0.11	78.80 ± 3.81
Cryptoblepharus	R	11	42.10 ± 1.28	22.64 ± 0.72	4.53 ± 0.11	2.79 ± 0.11	6.88 ± 0.19	3.07 ± 0.09	51.32 ± 3.29
		14	42.48 ± 0.74	21.89 ± 0.52	4.68 ± 0.08	2.97 ± 0.08	6.96 ± 0.18	3.27 ± 0.08	54.96 ± 2.75
Cryptoblepharus	A	10	37.86 ± 1.02	19.72 ± 0.81	3.98 ± 0.08	2.37 ± 0.09	6.44 ± 0.36	2.40 ± 0.10	37.35 ± 2.49
		14	36.06 ± 0.63	18.40 ± 0.34	4.07 ± 0.08	2.42 ± 0.06	5.77 ± 0.16	2.40 ± 0.06	41.00 ± 2.90
Eulamprus	R	2	56.34 ± 2.60	29.86 ± 1.08	7.32 ± 0.19	5.32 ± 0.06	11.88 ± 1.13	5.80 ± 0.08	66.25 ± 20.25
		12	68.43 ± 1.59	35.45 ± 0.99	9.53 ± 0.28	6.84 ± 0.21	13.86 ± 0.42	7.35 ± 0.24	80.25 ± 4.39
Eulamprus quoyii	G	15	102.05 ± 4.68	54.45 ± 2.82	12.80 ± 0.55	10.46 ± 0.49	21.00 ± 1.07	11.83 ± 0.59	154.73 ± 7.92
		5	103.39 ± 2.58	52.88 ± 1.75	14.04 ± 0.53	11.32 ± 0.40	20.27 ± 1.03	12.71 ± 0.51	161.60 ± 8.96
Lampropholis mirabilis	R	20	45.03 ± 1.02	22.36 ± 0.58	5.86 ± 0.09	3.71 ± 0.08	8.94 ± 0.19	4.18 ± 0.10	62.03 ± 2.31
		13	47.24 ± 0.89	23.00 ± 0.43	6.18 ± 0.09	3.97 ± 0.10	9.10 ± 0.23	4.55 ± 0.10	74.85 ± 1.79
Lampropholis robertsi	L	12	47.69 ± 0.87	26.06 ± 0.63	5.67 ± 0.08	4.04 ± 0.12	8.87 ± 0.29	4.90 ± 0.11	54.71 ± 3.53
		12	46.97 ± 0.75	25.13 ± 0.38	5.98 ± 0.14	4.21 ± 0.10	8.54 ± 0.26	5.16 ± 0.14	60.08 ± 2.71
Techmarscincus jigurru	R	4	60.65 ± 3.97	32.77 ± 2.32	6.93 ± 0.25	4.71 ± 0.09	9.92 ± 0.62	5.39 ± 0.27	115.88 ± 7.19
		10	70.43 ± 1.34	37.71 ± 0.81	8.19 ± 0.12	5.66 ± 0.09	11.47 ± 0.22	6.26 ± 0.11	107.50 ± 8.21

Table 4.1B. Length of limb elements and limbs for 18 species of Lygosomine lizards from tropical Australia. Shown are mean values (± S.E.). Females are on first line, males on the second. Letters represent habitat categories: A-Arboreal; G-Generalist; Litter-dwelling; R-Rock-using.

Species		N	Femur I	Tibia-fibula	Humerus	Radio-ulna	Fore-limb	Hind-limb
Carlia jarnoldae	G	1	6.10 ± 0.11	4.47 ± 0.09	5.09 ± 0.09	3.84 ± 0.10	14.35 ± 0.28	19.30 ± 0.28
		12	6.58 ± 0.12	4.88 ± 0.08	5.55 ± 0.11	4.09 ± 0.09	14.75 ± 0.28	19.90 ± 0.30
Carlia laevis	L	8	4.63 ± 0.03	3.05 ± 0.05	3.85 ± 0.06	2.56 ± 0.10	9.47 ± 0.23	13.46 ± 0.13
		5	4.87 ± 0.08	3.17 ± 0.06	4.04 ± 0.15	2.52 ± 0.28	9.31 ± 0.27	13.37 ± 0.34
Carlia longipes	G	17	9.35 ± 0.13	7.00 ± 0.11	7.44 ± 0.08	5.44 ± 0.09	20.97 ± 0.22	30.79 ± 0.34
		14	10.45 ± 0.21	7.94 ± 0.15	8.38 ± 0.17	6.08 ± 0.13	23.08 ± 0.36	33.47 ± 0.50
Carlia mundivensis	R	10	9.34 ± 0.29	6.67 ± 0.19	7.52 ± 0.24	5.83 ± 0.15	20.72 ± 0.62	27.45 ± 0.61
		8	9.75 ± 0.29	7.32 ± 0.27	8.05 ± 0.25	6.37 ± 0.24	21.26 ± 0.69	28.24 ± 0.84
Carlia pectoralis	L	6	6.82 ± 0.15	4.83 ± 0.13	5.48 ± 0.15	4.15 ± 0.12	15.78 ± 0.46	22.03 ± 0.54
		10	7.19 ± 0.16	5.30 ± 0.11	5.98 ± 0.12	4.27 ± 0.08	15.85 ± 0.34	22.64 ± 0.36
Carlia rhomboidalis	L	10	7.06 ± 0.11	5.25 ± 0.09	6.03 ± 0.08	4.56 ± 0.06	16.73 ± 0.24	22.60 ± 0.38
		15	7.36 ± 0.10	5.48 ± 0.09	6.18 ± 0.11	4.78 ± 0.09	16.73 ± 0.26	22.58 ± 0.34
Carlia rococo	R	8	5.55 ± 0.16	3.76 ± 0.10	4.34 ± 0.12	3.08 ± 0.16	11.07 ± 0.27	16.02 ± 0.41
		9	5.96 ± 0.10	4.15 ± 0.08	4.85 ± 0.11	3.62 ± 0.12	12.63 ± 0.34	17.16 ± 0.39
Carlia rostralis	G	8	8.91 ± 0.14	6.68 ± 0.10	7.18 ± 0.12	5.50 ± 0.12	20.29 ± 0.20	28.84 ± 0.34
		8	9.70 ± 0.17	7.32 ± 0.14	7.97 ± 0.13	6.16 ± 0.07	22.09 ± 0.19	30.69 ± 0.37
Carlia rubrigularis	L	11	7.91 ± 0.12	5.74 ± 0.16	6.72 ± 0.13	4.91 ± 0.16	18.62 ± 0.43	24.98 ± 0.43
		13	8.42 ± 0.16	6.12 ± 0.14	7.16 ± 0.15	5.25 ± 0.16	19.18 ± 0.42	25.76 ± 0.50

Table 4.1B. continued.

Carlia scirtetis	R	16	13.02 ± 0.19	10.69 ± 0.15	10.78 ± 0.15	8.64 ± 0.13	30.09 ± 0.36	40.39 ± 0.48
		16	13.19 ± 0.30	10.88 ± 0.29	10.83 ± 0.23	8.52 ± 0.22	29.19 ± 0.59	39.76 ± 0.88
Carlia storri	G	5	6.60 ± 0.28	4.75 ± 0.19	5.55 ± 0.20	4.42 ± 0.28	16.02 ± 0.68	20.96 ± 0.67
		5	6.82 ± 0.21	5.07 ± 0.16	5.72 ± 0.15	4.46 ± 0.14	15.59 ± 0.51	21.64 ± 0.44
Cryptoblepharus litoralis	R	11	6.50 ± 0.14	4.67 ± 0.07	5.46 ± 0.12	4.35 ± 0.09	16.16 ± 0.31	20.52 ± 0.32
		14	6.69 ± 0.13	4.81 ± 0.09	5.72 ± 0.11	4.76 ± 0.23	16.08 ± 0.33	20.10 ± 0.28
Cryptoblepharus	A	10	5.18 ± 0.09	3.81 ± 0.11	4.89 ± 0.10	3.93 ± 0.07	13.77 ± 0.25	15.97 ± 0.27
		14	5.21 ± 0.08	3.84 ± 0.06	4.82 ± 0.07	3.91 ± 0.09	13.44 ± 0.27	15.94 ± 0.28
Eulamprus brachysoma	R	2	8.65 ± 0.35	5.92 ± 0.44	6.66 ± 0.25	5.01 ± 0.18	19.35 ± 0.82	27.39 ± 0.85
		12	10.60 ± 0.19	7.23 ± 0.14	8.34 ± 0.15	6.21 ± 0.12	22.85 ± 0.39	31.94 ± 0.58
Eulamprus quoyii	G	15	13.33 ± 0.47	9.53 ± 0.36	10.80 ± 0.42	8.02 ± 0.34	30.53 ± 1.10	44.44 ± 1.46
		5	14.46 ± 0.51	10.02 ± 0.21	11.59 ± 0.38	8.42 ± 0.27	31.16 ± 0.64	45.57 ± 0.51
Lampropholis mirabilis	R	20	7.22 ± 0.10	5.45 ± 0.08	5.70 ± 0.09	4.46 ± 0.07	15.86 ± 0.24	22.48 ± 0.27
		13	7.64 ± 0.15	5.75 ± 0.13	6.02 ± 0.11	4.90 ± 0.09	16.66 ± 0.29	23.19 ± 0.43
Lampropholis robertsi	L	12	6.29 ± 0.11	4.27 ± 0.07	5.17 ± 0.13	3.89 ± 0.07	14.25 ± 0.25	18.52 ± 0.28
		12	6.44 ± 0.09	4.33 ± 0.06	5.36 ± 0.07	4.01 ± 0.05	14.28 ± 0.15	18.60 ± 0.29
Techmarscincus jigurru	R	4	9.14 ± 0.46	6.17 ± 0.41	7.40 ± 0.47	5.41 ± 0.32	21.70 ± 0.94	28.91 ± 1.56
		10	10.74 ± 0.24	7.69 ± 0.16	8.67 ± 0.16	6.40 ± 0.15	24.28 ± 0.44	33.36 ± 0.57

Table 4.2. Principal components analysis on independent contrasts of the morphological traits for females and males of eighteen Lygosomine skink species. Component loadings greater than 0.5 are considered significant and are shown in bold face (Tabachnick and Fidell, 1989).

Morphological trait	Females			Males		
PC Axis	1	2	3	1	2	3
Eigenvalue	6.89	2.49	1.28	6.17	2.62	1.87
% Variation explained	57.37	20.78	10.66	51.41	21.86	15.56
Inter-limb length	**-0.738**	0.135	0.318	-0.104	**-0.957**	0.007
Head Width	0.465	-0.338	-0.786	0.287	-0.066	-0.912
Head Height	-0.013	**-0.916**	-0.202	-0.087	-0.068	-0.964
Body Width	0.261	-0.023	-0.937	0.480	-0.027	-0.548
Body Height	-0.150	**-0.816**	-0.392	-0.173	**-0.860**	-0.301
Femur length	**0.925**	-0.073	-0.227	**0.945**	0.031	-0.240
Tibio-Fibula length	**0.968**	0.063	-0.173	**0.989**	0.062	-0.043
Humerus length	**0.960**	0.125	-0.140	**0.929**	0.081	-0.285
Radio-ulna length	**0.944**	-0.035	-0.091	**0.935**	0.006	0.121
Fore-limb length	**0.954**	-0.058	-0.095	**0.965**	0.031	-0.107
Hind-limb length	**0.944**	-0.113	-0.153	**0.970**	-0.113	-0.145
Tail length	0.226	**-0.812**	0.273	0.210	**-0.859**	0.077

Table 4.3. Principal component axis loadings of standardised independent contrasts of ecological variables from each of the three ecological categories.

Variable	PC1	PC2	PC3
(A) Substrate Use			
Body Angle	-0.017	-0.277	0.934
Total Ground Cover	0.920	0.045	-0.287
Total Rock Cover	-0.884	-0.421	0.133
% Litter cover	0.950	-0.077	-0.282
% Bare Earth	0.245	0.824	-0.223
% Logs	0.660	0.334	0.347
% Rock < 0.5 m3	0.007	-0.963	-0.117
% Rock > 0.5 m3	-0.769	0.569	0.218
Height above substrate	-0.709	-0.080	0.554
Microhabitat type used	0.394	-0.179	-0.842
Eigenvalue	5.58	1.78	1.57
% of total variance	55.77	17.80	15.65
(B) Microhabitat Openness			
Solar exposure	-0.089	-0.811	
Canopy type	-0.584	0.539	
Nearest Vegetation	-0.765	-0.298	
Vegetation Height	0.321	0.794	
Canopy Height	0.917	0.080	
% Canopy	0.814	0.089	
% Undergrowth	0.833	0.170	
Undergrowth type	0.662	0.535	
Eigenvalue	4.05	1.62	
% of total variance	50.66	20.23	
(C) Refuge use			
Tree refuge	0.714	0.345	-0.033
Vegetation pile	0.207	-0.134	-0.786
Leaf Litter	0.715	-0.460	0.414
Under Rock	-0.085	0.778	-0.347
Under Log	0.068	0.151	-0.737
Refuge Type	0.955	-0.168	-0.199
Crevice / Crack	-0.945	-0.083	0.301
Distance to nearest refuge	0.172	0.818	0.397
Eigenvalue	2.99	1.84	1.50
% of total variance	37.43	22.96	18.77

Component loadings greater than 0.5 are considered significant (Tabachnick and Fidell, 1989).

Habitat and Intersexual differences in morphology and body shape

To test for differences in shape among habitats and sexes for the large number of morphololgical traits measured I used a Multivariate Analysis of Covariance, with sex and habitat as factors and Snout-vent length as covariate. This analysis revealed that morphology differs among habitats (Pillai's trace: F 28, 34 = 3.19, $P < 0.001$) and with sex (F 15, 15 = 2.53, $P < 0.05$). This indicates that shape differs with habitat and sex independent of size.

Conventional and phylogenetic ANOVA and ANCOVA based on simulations

Non-phylogenetic ANCOVAs identified few traits that differed among habitats between the sexes (Table 4.4). Both conventional and phylogenetic ANCOVA identified differences among habitat categories in head and body heights of males and females (Table 4.4). Post-hoc comparisons of residual head height revealed that both female and male rock-using species had significantly flatter heads (Tukey-Kramer, $P < 0.05$; Figure 4.2) than generalists species, and significantly flatter bodies than generalist and leaf litter species (Tukey-Kramer, $P < 0.05$; Figure 4.3). However, for females these differences disappeared when compared using among-habitat pairwise phylogenetic comparisons (Table 4.5). However, the differences in body flattening between litter-dwelling and rock-using species, and between body and head height between rock-using and generalist species remained significant in males after conducting pairwise among-habitat phylogenetic comparisons (Table 4.5).

Canonical correlations

FEMALES

The first canonical axis between morphology and substrate use space and for morphological and between microhabitat openness space was significant (Table 4.6). The first axis describes a negative relationship between species from habitats that perched on large rocks, with a high proportion of surrounding rocks, high above the substrate, to species that occupied perches of leaf litter with a high proportion of total ground cover (Substrate use PC 1 described 92 % of the variance in CC axis 1). This gradient was associated with a decrease in fore- and hind-limb length and in the length of the limb elements and with an increase in inter-limb length (Female Morphology PC 1 described 100% of the variance in CC axis 1). In females, the occupation of habitats dominated by large rocks caused the evolution of longer limbs and shorter bodies (Figure 4.4A). The first CC axis of microhabitat openness and morphology (Table 4.6) described an inverse relationship between species from habitats with increasing % canopy cover and % undergrowth with a high canopy

(Microhabitat openness PC 1 described 100% of the variance in CC axis 1). Again, this ecological gradient was associated with a decrease in fore- and hind-limb length and in the length of the limb elements and with an increase in inter-limb length (Morphology PC 1 described 64 % of the variance in CC1; Figure 4.4B). That is, in females, occupying open habitats is associated with an evolutionary increase in limb length and a decrease in body length (Figure 4.4B). This was the only canonical correlation that remained significant after adjusting for multiple tests.

MALES

As for females, the first CC axis for males between morphology and substrate use space and between morphology and microhabitat openness space was significant (Table 4.6). Substrate use PC 2 described 66 % of the variance in CC1, while Morphology PC 2 described 72 % of the variance in CC1. Males with flatter, shorter bodies tend to be associated with the occupation of habitats dominated by large rocks (Figure 4.4A). Microhabitat openness PC 1 described 99 % of the variance in CC1, while Morphology PC 1 described 84 % of the variance in CC1 (Figure 4.4B). In males, the occupation of open habitats is associated with an evolutionary trend for increased limb length. None of the CCs between morphology - refuge use were significant for females or males (Table 4.6).

Discussion

This group of Lygosomine lizards display differences in the correlations among differences in habitats and among differences between sexes. Species using rocky habitats had flatter bodies and heads than generalists, and had flatter bodies than species that use leaf litter. Differences in body shape appeared more extreme in males, which were more dorsoventrally flattened than females. In both sexes, species from rocky habitats tend to have increased limb length and reduced body length, with males of species from rocky habitats also having flatter bodies. A similar analysis revealed that in both sexes, species evolved longer limb length, with females showing a reduction in body length in response to increased habitat openness. These intersexual differences may be the result of sexual selection, or selection for different locomotor or reproductive function in one sex versus the other in different habitats.

Body shape and microhabitat use

Phylogenetic analyses revealed complementary patterns of morphological change in response to the three discrete habitat types and the range of continuous ecological variables examined. Specifically for males, species from rocky habitats, including the single arboreal species, had flatter bodies and heads than generalists, and had flatter bodies than species that use leaf litter (Figure 4.2, 4.3; Table 4.5). Although other studies have noted the association between body flattening and rock-use (e.g., Vitt, 1981; Vitt et al., 1997), this is the first phylogenetic comparative study to document an evolutionary change in body flattening (body height and head height) in response to the occupation of rocky habitats.

Whereas, a number of comparative studies involving lizards have found evidence for morphological differentiation in response to different substrates (Losos, 1990a; Miles, 1994; Herrel et al., 2002), including several intraspecific studies of different populations (Vitt 1981; Vitt et al., 1997; Herrel et al., 2001; Irschick et al., 2005a), others studies have not (e.g., Vanhooydonck and Van Damme, 1999; Schulte *et al.,* 2004). In my study, most species used broad, flat substrates (even leaf-litter dwellers) that differed in the level of inclination. Hence, it may be that the range of inclined surfaces encountered is more important in the evolution of a flattened morphology, and several studies have identified adaptive shifts in body shape in response to different substrates. For example, populations of *Urosaursus ornatus* (Herrel et al., 2001) and *Tropidurus hispidus* are more flattened when they occur on rocks (Vitt et al., 1997). Therefore, the evolution of dorsoventrally flattened morphology appears to be an adaptive response to the occupation of rocky habitats in lizards. Climbing species should have flat heads and bodies to assist in keeping the body close to the climbing surface, which in turn, should reduce the influence of gravity from pulling the body away from the substrate (Vanhooydonck and Van Damme, 1999, 2001; Zaaf and Van Damme, 2001). Moreover, in the *Liolaemus* group, which showed no adaptive morphological differentiation, members tended to occupy broad, horizontal substrates (Schulte et al., 2004). It may be that when the degree of substrate inclination is low, selection for morphological divergence and adaptation is reduced, as behavioural modifications become more important (Huey *et al.,* 2003). The association between flattening and rocky substrates suggests that it would be worth experimentally assessing performance of flattened species, to determine if performance is enhanced by this morphology (Herrel et al., 2002; Chapter 5).

Table 4.4. Conventional analysis of variance and phylogenetic ANOVA simulation results of the morphological traits of 18 Lygosomine skink species from three habitat types (rock-using, litter-using and generalist habitat categories). Phylogenetic simulations indicate the number of simulated *F*-values that exceeded the *F*-value for conventional non-phylogenetic analysis. *F* and *P*-values are for conventional non-phylogenetic ANCOVA with snout-vent length as the covariate and habitat type as factor. Snout-vent length was compared using conventional and phylogenetic ANOVA. Differences among habitat groups are significant if the *F*-value of the non-phylogenetic ANOVA is greater than 949 of the simulated phylogenetic *F*-values. Significant differences among habitat groups are shown in bold. Degrees of freedom for male and females are 15.

Morphological trait	Female		Male		Phylogenetic simulations	
	F	*P*	*F*	*P*	Female	Male
Snout-vent length	0.55	0.587	1.02	0.384	537/1000	494/1000
Inter-limb length	0.55	0.589	0.96	0.405	457/1000	410/1000
Head width	0.43	0.658	0.71	0.500	302/1000	407/1000
Head height	5.40	**0.017**	6.28	<**0.010**	969/1000	963/1000
Body width	0.60	0.562	2.49	0.118	360/1000	803/1000
Body height	6.30	<**0.010**	8.85	<**0.003***	964/1000	988/1000
Tibia length	0.97	0.404	0.77	0.481	512/1000	307/1000
Femur length	1.27	# 0.310	0.66	0.534	569/1000	292/1000
Radius-ulna length	1.52	# 0.252	1.96	# 0.176	622/1000	731/1000
Humerus length	0.95	0.410	0.61	0.556	541/1000	351/1000
Fore-limb length	1.26	# 0.312	1.27	# 0.310	619/1000	552/1000
Hind-limb length	0.93	0.416	0.81	0.466	530/1000	331/1000
Tail length	0.29	0.753	1.47	0.263	342/1000	846/1000

ANCOVA had significant interaction term. Compared residuals from ordinary least-squares regression of trait against snout-vent length using one-way ANOVA with habitat as factor.

*significant following sequential Bonferroni correction.

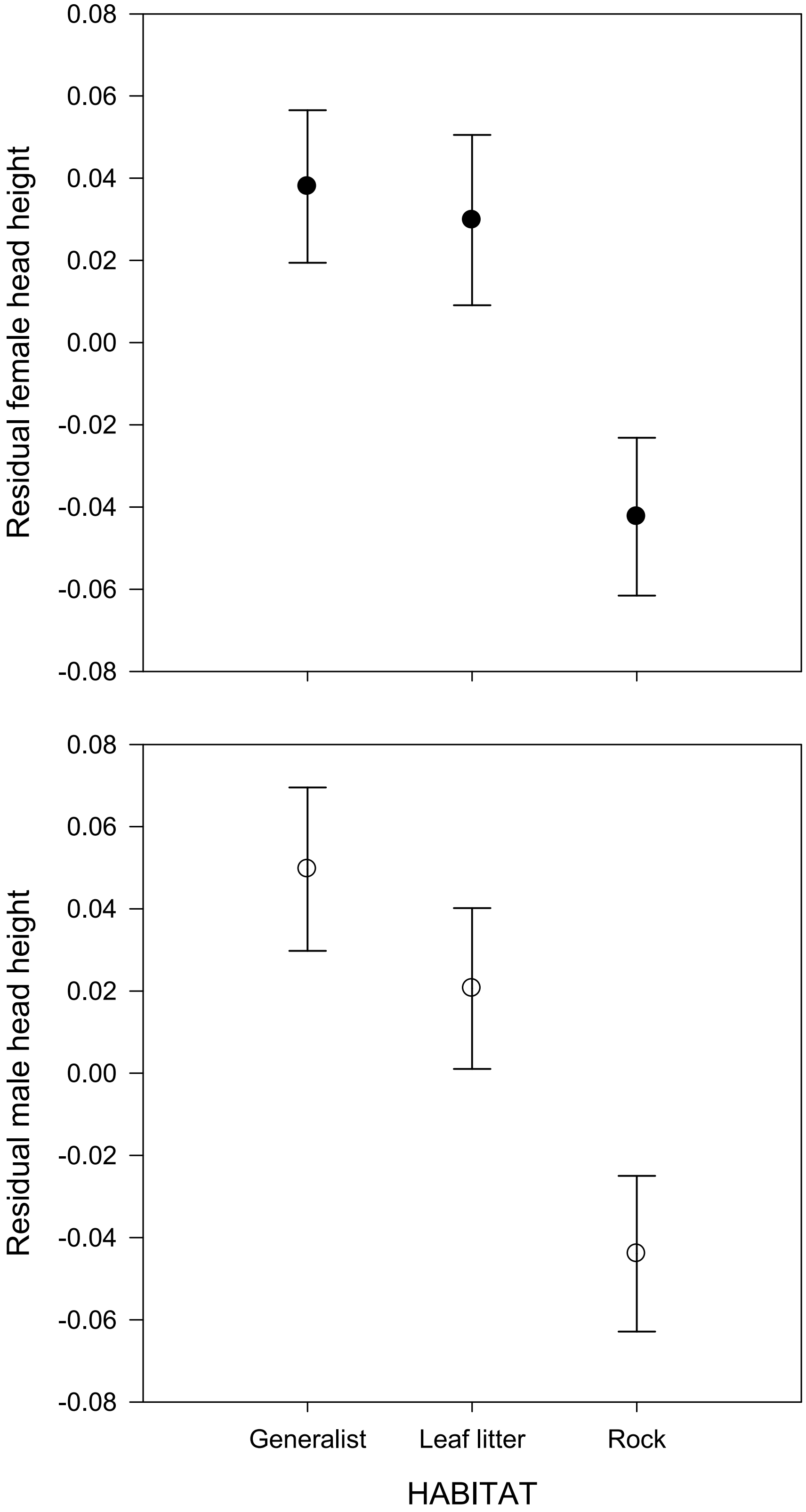

Figure 4.2. Comparisons between residual measures of head height and habitat type for 18 species of Lygosomine lizards. Analyses using conventional ANCOVA detected significant differences between habitat categories. All differences among females disappeared when analysed using pairwise phylogenetic ANOVA. Females are represented as closed symbols; males as open symbols. Shown are means and standard errors.

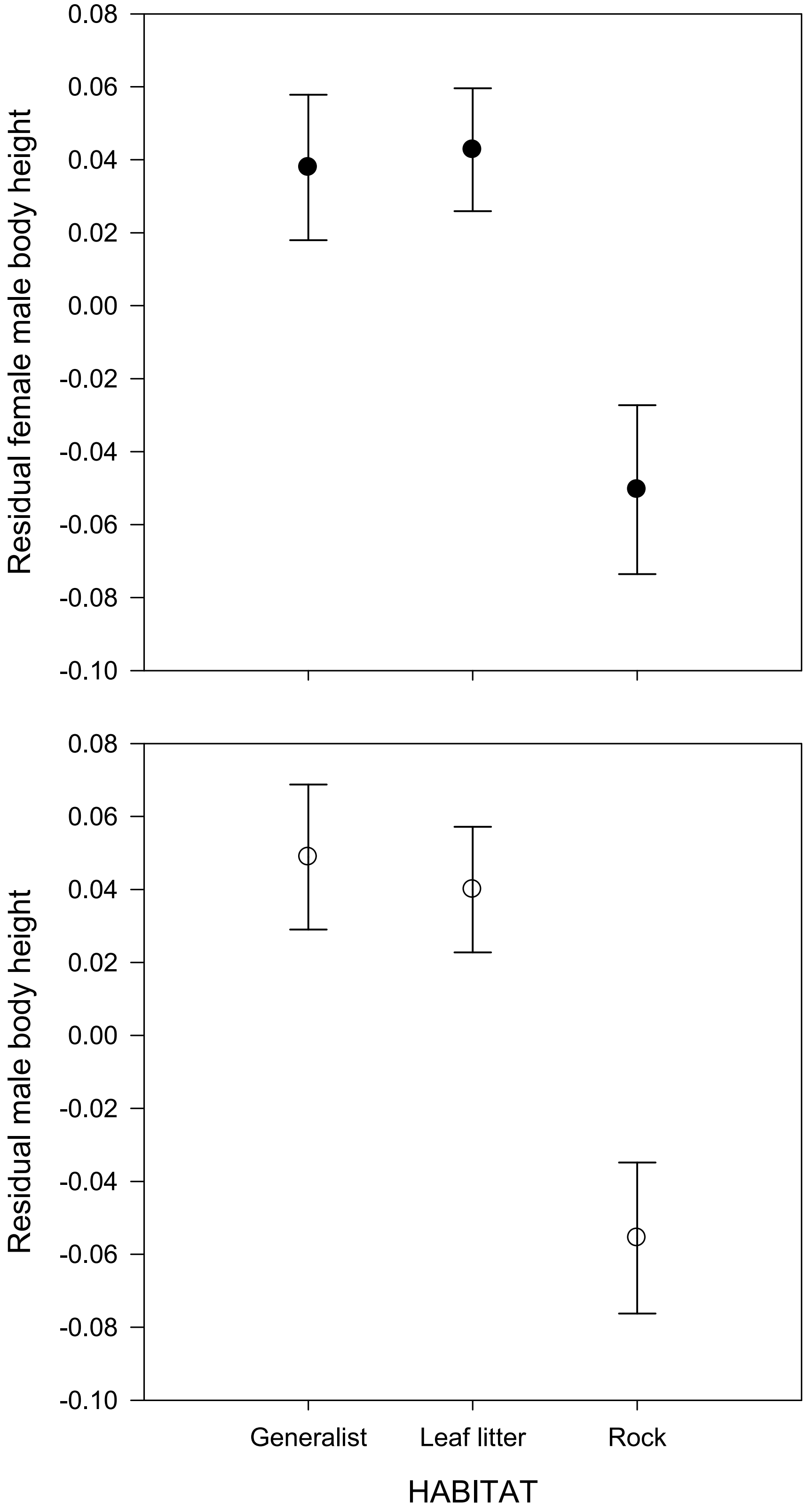

Figure 4.3. Comparisons between residual measures of body height and habitat type for 18 species of Lygosomine lizards. Analyses using conventional ANCOVA detected significant differences between habitat categories. All differences among females disappeared when analysed using pairwise phylogenetic ANOVA. Females are represented as closed symbols; males as open symbols. Shown are means and standard errors.

Table 4.5. Comparisons of head height and body height of 18 species of Lygosomine lizards from three habitats. Differences among habitats groups are considered significant (at $P < 0.05$) if the conventional *F*–value (*F*) is greater than the phylogenetically simulated *F*–value (F_{phylo}). Differences among habitat group are shown in bold. All phylogenetic simulations are 1000 unbounded evolutionary simulations.

Variable	Females			Males		
	F	*F*phylo	*P*	*F*	*F*phylo	*P*
Rock-using – Leaf-litter						
Head height	6.033	8.647	0.032	5.08	8.294	0.046
Body height	8.227	8.608	0.015	**10.31**	**8.148**	**0.008**
Rock-using – Generalist						
Head height	7.933	8.659	0.017	**10.58**	**7.889**	**0.008**
Body height	6.951	8.243	0.023	**11.56**	**7.989**	**0.006**
Leaf-litter – Generalist						
Head height	0.0857	2.866	0.777	1.083	3.409	0.328
Body height	0.0349	2.894	0.857	0.115	3.261	0.743

Table 4.6. Canonical correlations comparing the positions in morphological space of males and females compared to their position in two aspects of habitat (substrate-perch and microhabitat openness) and refuge use space.

Canonical Variable		Canonical Correlation	Canonical R^2	Canonical Redundancy	χ^2	d.f.	P
FEMALE							
Substrate use vs. morphology	CC1	0.782	0.612	0.204	17.80	9	0.035
	CC2	0.624	0.389	0.130	6.17	4	0.187
	CC3	0.027	0.001	0.001	0.01	1	0.924
Microhabitat openness vs. morphology	CC1	0.823	0.677	0.226	18.30	6	<0.006*
	CC2	0.493	0.243	0.081	3.61	2	0.164
Refuge use vs. morphology	CC1	0.781	0.610	0.203	13.57	9	0.139
	CC2	0.363	0.132	0.044	1.79	4	0.774
	CC3	0.039	0.002	0.001	0.02	1	0.889
MALE							
Substrate use vs. morphology	CC1	0.830	0.689	0.229	20.77	9	0.014
	CC2	0.577	0.333	0.111	6.17	4	0.187
	CC3	0.292	0.086	0.029	1.12	1	0.291
Microhabitat openness vs. morphology	CC1	0.745	0.555	0.185	15.14	6	0.019
	CC2	0.547	0.300	0.100	4.63	2	0.099
Refuge use vs. morphology	CC1	0.709	0.502	0.167	11.52	9	0.242
	CC2	0.448	0.200	0.067	2.80	4	0.592
	CC3	0.008	0.001	0.001	0.01	1	0.978

* Indicates significant values following table-wise sequential Bonferroni correction.

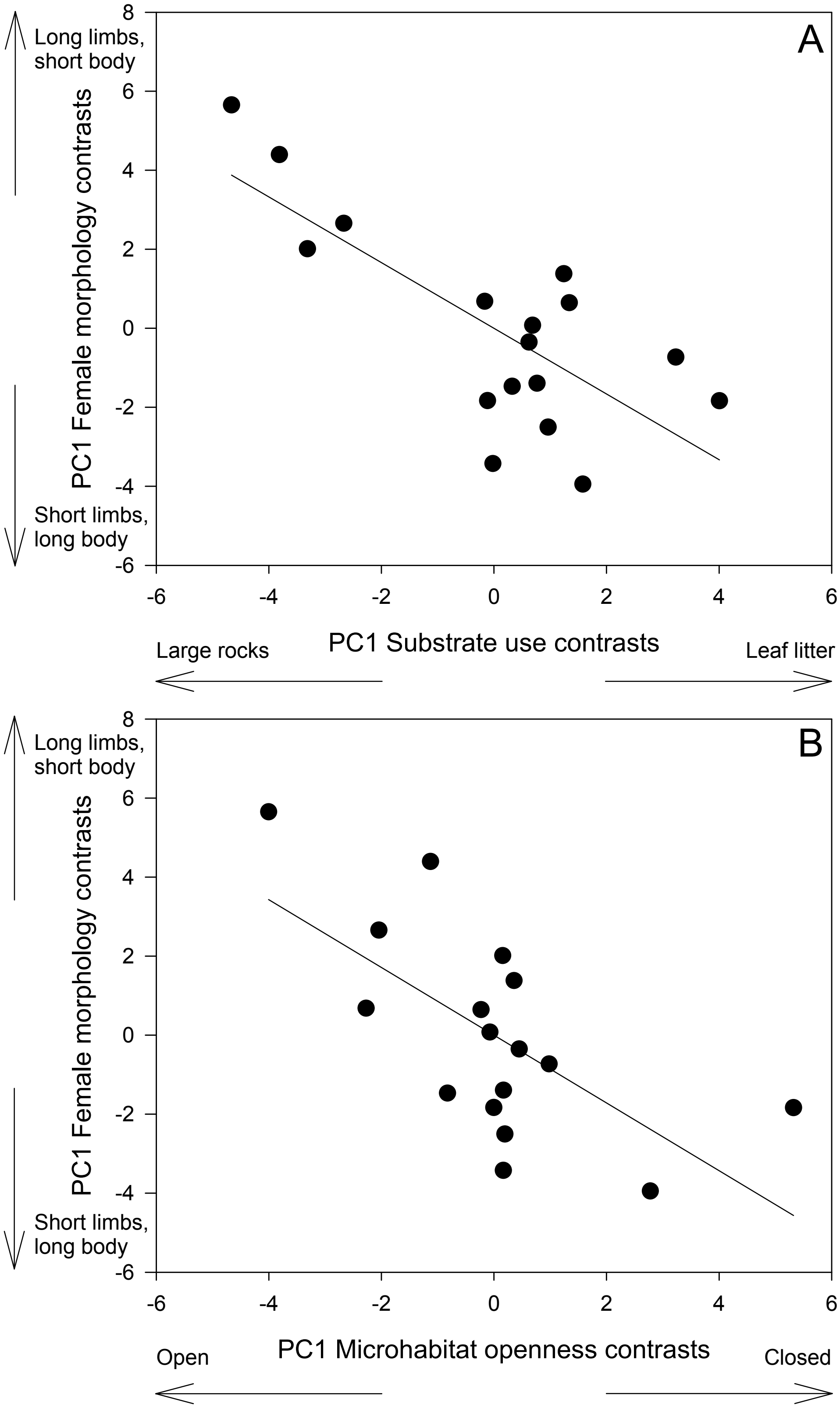

Figure 4.4. The relationship between PC1 substrate contrasts and PC1 morphology contrasts (A), and PC1 microhabitat openness contrasts and PC1 morphology contrasts (B) for females of 18 species of Lygosomine lizards. Relationships are based on canonical correlations of principal components analyses performed separately on the morphological and substrate use and microhabitat openness data.

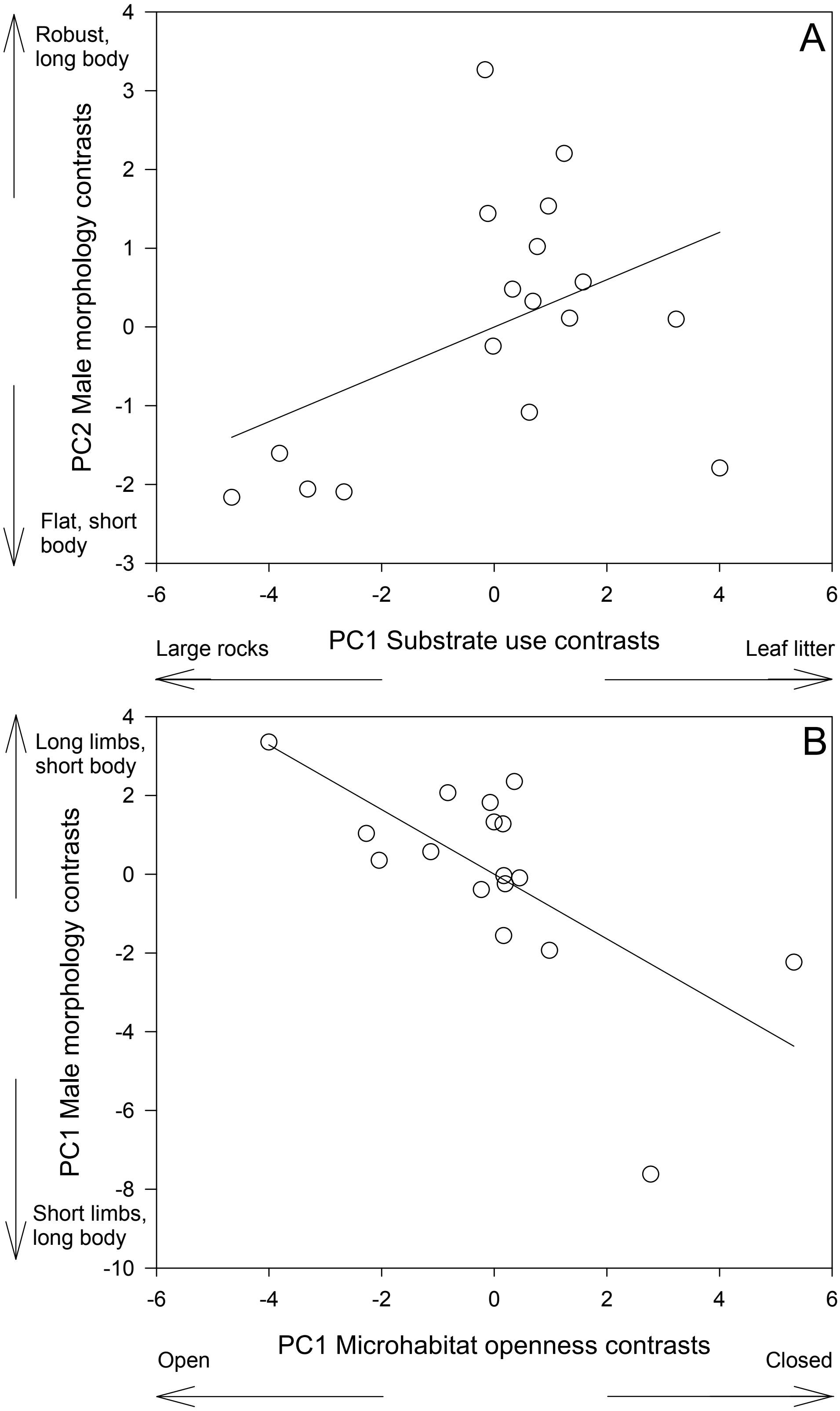

Figure 4.5. The relationship between PC1 substrate contrasts and PC2 morphology contrasts (A), and PC1 microhabitat openness contrasts and PC1 morphology contrasts (B) for males of 18 species of Lygosomine lizards. Relationships are based on canonical correlations of principal components analyses performed separately on the morphological and substrate use and microhabitat openness data.

Limb length and microhabitat use

In addition to flattened bodies, other studies of lizards have found that climbing species have short limbs (Zaaf et al., 1999; Zaaf and Van Damme, 2001). I found that females of species from rocky habitats had longer limbs (Table 4.6; Figure 4.4A). For lizards in general, it appears that for species from open, terrestrial habitats there is likely to be one of two alternative behavioural strategies that can lead to two forms of evolutionary morphological divergence. Firstly, at the approach of a threat, individuals can run at high speed, and reduce the time required to reach shelter, or they can remain motionless, and flatten their body against the substrate. If lizards run from predators they typically evolve long hind limbs and short forelimbs to enhance speed and cover long distances quickly (Snyder, 1954; Cartmill, 1985; Melville and Swain, 2000). Indeed, numerous studies have identified a trend for species from more open habitats, or from wider perches in less cluttered habitats, to evolve longer hind limbs and greater sprint speeds (Losos, 1990a; Miles, 1994; Melville and Swain, 2000). However, in cases where lizards rely on crypsis to avoid detection, they should have short, flat bodies and heads, and colours that match the background, with reduced selection on increased limb length and sprint speed (Losos, 1990a; Schulte et al., 2004). An analogous antipredator syndrome occurs in cordylid lizards that have evolved varying amounts of body armour. In cordylid lizards, more heavily armoured species have shorter limbs, run more slowly and remain closer to refuges than less armoured species (Losos et al., 2002).

This study suggests that whereas species have adapted in a convergent manner to similar habitats, not all species are have adapted morphologically to the habitat occupied to the same extent. Of the rock-dwelling *Carlia* species, *C. mundivensis* occupies open, rocky boulder habitats, but unlike other rock-using *Carlia* has short limbs, a robust body and slow sprinting and climbing speeds (Appendix 1). These differences suggest that other factors (e.g., proximity to refugia, increased wariness, the possession of body armature; see above) may mitigate against, or reduce the degree of morphological differentiation required despite the occupation of similar habitats (see also Losos et al., 2002; Schulte et al., 2004; Appendix 1).

My phylogenetic analyses of species from three habitats found no difference in limb lengths. Grouping habitats into categories may have hampered my ability to detect between-habitat differences in limb length. Categorizing species into the most frequently used habitat may be too crude, as it may neglect important information on habitat use (e.g., Zaaf and Van Damme, 2001; Van Damme et al., 2003). For example, in my study *C. rococo* was classified as a rock-user, but was also frequently found among leaf litter, where it often takes cover (Greer, 1989). Such species may exhibit intermediate traits, such as medium-length limbs or semi-flattened bodies, or

experience increased selective pressure in the less-frequently used habitat. Alternatively, assuming that the most frequently used habitat is responsible for most of the selection on morphology may be incorrect (Zaaf and Van Damme, 2001; Van Damme et al., 2003). Instead, selection may be imposed by the most difficult-to-use habitat, or the habitat containing the most predators, even if used infrequently (see also Hertz et al., 1988; Irschick et al., 2005c). Moreover, this study used each species' mean habitat use, which may have reduced the ability to detect subtle sexual differences in habitat use.

Intersexual differences and evidence for fecundity and sexual selection

Males were more dorsoventrally flattened than females of the same species. In addition, occupying large rocks was associated with short inter-limb lengths in both sexes. Females had long limbs whereas males had shortened tails. One potential cause of these differences is the agent and magnitude of divergent ecological roles operating on each sex. For example, the need to accommodate offspring when gravid may select against body flattening, and the resultant reduction in abdominal volume in females. The fact that males were flatter than females suggests that without the advantage of increased fecundity, the taller body morph of females may place them at a disadvantage in terms of their ability to access crevice refuges. Indeed, it would be instructive to know whether sexual differences in body shape affect crevice and refuge use (e.g., Schlesinger and Shine, 1994; Webb and Shine, 2000) in rock-using lizards from this group. It is possible however, that the benefits of flattening may be that it increases the range of available rock-crevices, or may assist in reducing energetic requirements of locomotion on angled surfaces.

In males, male combat success is an important selective force associated with intrasexual differentiation (Darwin, 1871; Andersson, 1994). Traits correlated with increased performance may provide males with a selective advantage in situations of male-male combat or territory maintenenace (Husak et al., 2006). For instance, increased head size provides a selective advantage in lizards that use bite force in male-male combat (Huyghe *et al.,* 2005; Lappin and Husak, 2005), and functional relationships have been identified between increased head size and bite force in lizards (Herrel et al., 1999; Lappin et al., 2006). Similarly, there may be strong selection for body flattening, or traits associated with body flattening, if such traits are correlated with combat success or mate choice (e.g., body size and shape; Andersson 1994, Shine 1994). Similar arguments could be made for interlimb lengths and tail length, but it is, at present, unknown whether any of these traits relate to male reproductive success.

Because there was only one arboreal species (*Cy. virgatus*) in my study, it was impossible to test predictions on evolutionary shifts in morphology between arboreal and rock-using species. Indeed, the degree of body flattening in each group may be determined not by the substrate *per se*, but instead by how much time species in each group spend vertical rather than horizontal. The similarity in morphology of arboreal and rock-using skinks has been noted previously (Melville and Swain, 2000), however, comparisons of morphology and performance of additional skink genera (e.g., *Emoia*, *Mabuya*) are required to conclusively test putative adaptive differences between arboreal and rock-using species.

This study demonstrates substantial sexual differences in body shape and morphology among habitats in Lygosomine lizards. These habitat-specific differences suggest sexual and fecundity selection affects sexes differently across habitats and provides evidence that fecundity selection on abdominal space for eggs and offspring, selects against morphological traits (i.e., body height) presumed to be related to performance (e.g., locomotion on inclined surfaces, fitting into rock crevices) in rock-using lizards. Natural selection on locomotor ability and sexual selection for male-male combat, or mate choice for males with flatter bodies (or other correlated traits) are responsible for the flatter morphology of male lizards from rocky habitats.

Chapter 5

Master of them all: performance specialisation does not cause trade-offs in tropical lizards

(in press [*Evolutionary Ecology Research*])

Introduction

Natural selection acts on morphological traits, in theory shaping them to optimise habitat use (Futuyma, 1998; Schluter, 2000). Thus, based on the premise that form follows function, studying performance in the context of habitat variability provides a powerful test of adaptive traits (Arnold, 1983, Ricklefs and Miles, 1994; Lauder, 1996). It seems intuitive that some adaptations promoting excellent performance in a single habitat might reduce performance in other habitats, so that “jack-of-all-trades is master of none” (Huey and Hertz, 1984b). For example, limb lengths of arboreal lizards provide a clear example of an adaptation that causes a trade-off between performance ability in one habitat compared to others: *Anolis* with long limbs that occupy wide perches are quick and agile (Losos, 1990a, b; Losos et al., 1994; Irschick and Losos, 1998; Irschick, 2000), but have reduced speed and agility on narrow perches (Losos and Sinervo, 1989; Sinervo and Losos, 1991; Macrini and Irschick, 1998). Similarly, Chameleons trade-off sprint speed against clinging ability as leg length increases (Losos et al., 1993). However, in lacertid lizards, a group that uses wide, flat substrates such as rock, there appears to be no trade-off between sprinting and climbing ability for species with longer limbs (Vanhooydonck and Van Damme, 2001). Thus, whereas the link between limb-length and performance has been well explored (Garland, 1985; Losos 1990a; Garland and Losos, 1994), the extent to which morphology may constrain performance, causing trade-offs in performance in different habitats remains an open question (Losos and Sinervo, 1989; Sinervo and Losos, 1991; Vanhooydonck and Van Damme, 2001). Many trade-offs appear to depend on the substrate used. Examining the evolution of morphology (body shape and limb length) and performance in a group using a variety of substrates may clarify whether tradeoffs are substrate-dependent.

Skinks occupy a wide array of habitats and exhibit a diverse range of morphologies, with different body shapes and limb-lengths (Greer, 1989; Cogger and Heatwole, 1984; Melville and Swain, 2000; Pianka and Vitt, 2003). Long limbs and dorsoventral flattening associated with rock-using has evolved independently several times in Australian skinks (Ingram and Rawlinson, 1978; Covacevich, 1984;

Greer, 1989; Chapter 4). Biomechanical theory predicts that long hind-limbs are beneficial for locomotion of ground-dwelling species in open habitats, where they enable longer strides and faster locomotion (Cartmill, 1985; Pounds, 1988; Vanhooydonck and Van Damme, 2001). Climbing species should have equal-length fore- and hind limbs, in order to grip securely (Cartmill, 1985; Zaaf et al., 1999; Losos et al., 1993) and to stride similar distances with both limbs (Arnold, 1998; Vanhooydonck and Van Damme, 2001). Some climbing species have dorsoventrally flattened bodies, possibly to lower the centre of gravity and prevent toppling, and rigid bodies with reduced lateral bending perhaps to increase stability (Van Damme et al., 1997). Despite the putative benefits of a flattened morphology for climbing, there has been no test of the influence of flattening on performance (Herrel et al., 2002). Moreover, Lacertid lizards show little evidence body flattening, or morphological differentiation among habitats (Vanhooydonck and Van Damme, 1999). Thus, an investigation of performance trade-offs using a group of morphologically divergent, rock- and leaf-litter dwelling species should determine whether performance trade-offs due to limb length are generally present.

I measured four performance traits (sprinting, climbing, clinging and jumping) in related scincid lizards that use a range of different habitats (trees, rocks, ground and leaf litter), to examine how morphology and performance were related in lizards that use a variety of substrates, have different body morphology and are not specialised solely for arboreal climbing. Specifically, I examined i) the relationship between specific morphological traits and performance, and, ii) whether there was evidence for trade-offs among sprinting, climbing, clinging and jumping of lizards with different morphological traits.

Methods

Skinks in the sub-family Lygosominae occupy a range of microhabitat types (e.g., boulder-dominated mountains, rocky coastal inter-tidal zones, leaf litter, loose soil, and trees, Greer, 1989; Cogger, 2000) and exhibit a broad array of morphological variation in body shape and limb length (Greer, 1989; Cogger, 2000). To explore the effect of evolutionary changes in morphology on locomotion in skinks, species from five genera (*Cryptoblepharus*, *Carlia*, *Eulamprus*, *Lampropholis, Techmarscincus*) and a diverse range of microhabitat types, were examined (Ingram and Rawlinson, 1978; Ingram and Covacevich 1980, 1989; Cogger, 2000; Goodman, unpub. data; Chapter 3) (Table 2.1 and 2.2).

Table 5.1. Species names (N, sample sizes) and mean morphological traits (all in mm, except body mass in g) for 18 Scincid species examined in this study. All values are means (± standard error).

Species	N	Snout-vent length (mm)	Body mass (g)	Inter-limb Length (mm)	Body Height (mm)	Fore-limb length (mm)	Hind-limb length (mm)	Tibia length (mm)	Femur length (mm)
Carlia jarnoldae	12	41.16 ± 0.71	1.59 ± 0.09	19.97 ± 0.40	4.37 ± 0.15	14.75 ± 0.28	19.90 ± 0.30	4.88 ± 0.08	6.58 ± 0.12
Carlia laevis	5	35.21 ± 0.28	0.73 ± 0.05	18.14 ± 0.36	3.10 ± 0.12	9.31 ± 0.27	13.37 ± 0.34	3.17 ± 0.06	4.87 ± 0.08
Carlia longipes	14	61.57 ± 1.21	5.66 ± 0.47	29.95 ± 0.78	7.58 ± 0.23	23.08 ± 0.36	33.47 ± 0.50	7.94 ± 0.15	10.45 ± 0.21
Carlia mundivensis	8	55.53 ± 1.82	4.29 ± 0.46	26.86 ± 1.01	6.27 ± 0.25	21.26 ± 0.69	28.24 ± 0.84	7.32 ± 0.27	9.75 ± 0.29
Carlia pectoralis	10	44.45 ± 1.02	1.87 ± 0.14	21.81 ± 0.59	5.18 ± 0.14	15.85 ± 0.34	22.64 ± 0.36	5.30 ± 0.11	7.19 ± 0.16
Carlia rhomboidalis	15	47.20 ± 0.93	2.54 ± 0.25	23.09 ± 0.53	5.50 ± 0.17	16.73 ± 0.26	22.58 ± 0.34	5.48 ± 0.09	7.36 ± 0.10
Carlia rococo	9	39.77 ± 1.13	1.06 ± 0.08	19.72 ± 0.72	3.64 ± 0.13	12.63 ± 0.34	17.16 ± 0.39	4.15 ± 0.08	5.96 ± 0.10
Carlia rostralis	8	59.89 ± 2.01	5.48 ± 0.45	29.68 ± 1.05	7.62 ± 0.30	22.09 ± 0.19	30.69 ± 0.37	7.32 ± 0.14	9.70 ± 0.17
Carlia rubrigularis	13	51.79 ± 1.20	3.53 ± 0.14	25.96 ± 0.59	6.21 ± 0.16	19.18 ± 0.42	25.76 ± 0.50	6.12 ± 0.14	8.42 ± 0.16
Carlia scirtetis	16	65.08 ± 1.71	5.32 ± 0.37	30.47 ± 0.88	6.55 ± 0.17	29.19 ± 0.59	39.76 ± 0.88	10.88 ± 0.29	13.19 ± 0.30
Carlia storri	5	40.72 ± 0.95	1.59 ± 0.17	19.67 ± 0.31	5.02 ± 0.11	15.59 ± 0.51	21.64 ± 0.44	5.07 ± 0.16	6.82 ± 0.21
Cryptoblepharus litoralis	14	42.48 ± 0.74	1.14 ± 0.08	21.89 ± 0.52	3.27 ± 0.08	16.08 ± 0.33	20.10 ± 0.28	4.81 ± 0.09	6.69 ± 0.13
Cryptoblepharus virgatus	14	36.06 ± 0.63	0.55 ± 0.04	18.40 ± 0.34	2.40 ± 0.06	13.44 ± 0.27	15.94 ± 0.28	3.84 ± 0.06	5.21 ± 0.08
Eulamprus brachysoma	12	68.43 ± 1.59	6.79 ± 0.39	35.45 ± 0.99	7.35 ± 0.24	22.85 ± 0.39	31.94 ± 0.58	7.23 ± 0.14	10.60 ± 0.19
Eulamprus quoyii	5	103.39 ± 2.58	30.03 ± 2.80	52.88 ± 1.75	12.71 ± 0.51	31.16 ± 0.64	45.57 ± 0.51	10.02 ± 0.21	14.46 ± 0.51
Lampropholis mirabilis	13	47.24 ± 0.89	1.89 ± 0.12	23.00 ± 0.43	4.55 ± 0.10	16.66 ± 0.29	23.19 ± 0.43	5.75 ± 0.13	7.64 ± 0.15
Lampropholis robertsi	12	46.97 ± 0.75	2.06 ± 0.12	25.13 ± 0.38	5.16 ± 0.14	14.28 ± 0.15	18.60 ± 0.29	4.33 ± 0.06	6.44 ± 0.09
Techmarscincus jigurru	10	70.43 ± 1.34	5.51 ± 0.31	37.71 ± 0.81	6.26 ± 0.11	24.28 ± 0.44	33.36 ± 0.57	7.69 ± 0.16	10.74 ± 0.24

Table 5.2. Species names (N, sample sizes) and mean performance traits (in ms-1, except cling force * see below, and jump distance in mm) for each of the 18 Scincid species examined in this study. All values are means (± standard error). *Cling forces used in analyses were raw gram pull-force values, presented are values converted to Newtons (1 gram pull-force = 9.80665 mN; Losos, 1990a).

Species	Label	N	Climbing speed (ms^{-1})	Sprint speed (ms^{-1})	Cling Force (mN)*	Jump distance (mm)
Carlia jarnoldae	Cj	12	0.73 ± 0.05	0.52 ± 0.05	157.72 ± 12.41	268.50 ± 27.70
Carlia laevis	Cle	5	0.39 ± 0.03	0.57 ± 0.02	11.34 ± 03.36	237.60 ± 12.06
Carlia longipes	Cln	14	1.24 ± 0.05	1.20 ± 0.10	373.47 ± 20.43	351.25 ± 17.51
Carlia mundivensis	Cm	8	0.83 ± 0.07	0.83 ± 0.06	358.56 ± 26.48	257.88 ± 48.58
Carlia pectoralis	Cp	10	0.80 ± 0.06	0.86 ± 0.05	135.33 ± 08.75	316.60 ± 21.28
Carlia rhomboidalis	Crh	15	0.93 ± 0.04	0.77 ± 0.06	202.02 ± 10.34	323.07 ± 9.98
Carlia rococo	Crc	9	0.63 ± 0.03	0.90 ± 0.05	77.47 ± 20.82	194.11 ± 19.66
Carlia rostralis	Cro	8	1.07 ± 0.08	0.99 ± 0.11	343.23 ± 34.77	408.88 ± 31.64
Carlia rubrigularis	Crb	13	0.89 ± 0.04	1.02 ± 0.08	185.57 ± 19.93	304.85 ± 17.07
Carlia scirtetis	Csc	16	1.49 ± 0.08	2.06 ± 0.08	470.07 ± 25.22	330.20 ± 19.98
Carlia storri	Cst	5	0.82 ± 0.08	0.80 ± 0.09	125.53 ± 15.63	264.00 ± 46.24
Cryptoblepharus litoralis	Cyl	14	0.90 ± 0.08	1.48 ± 0.06	203.14 ± 08.20	229.00 ± 12.25
Cryptoblepharus virgatus	Cyv	14	0.86 ± 0.06	0.90 ± 0.06	119.43 ± 07.62	222.43 ± 9.92
Eulamprus brachysoma	Eb	12	1.28 ± 0.03	1.67 ± 0.07	809.05 ± 42.17	342.67 ± 13.24
Eulamprus quoyii	Eq	5	1.37 ± 0.09	2.33 ± 0.25	1398.43 ± 69.18	364.20 ± 30.50
Lampropholis mirabilis	Lm	13	0.92 ± 0.06	1.27 ± 0.07	196.51 ± 07.40	274.54 ± 24.11
Lampropholis robertsi	Lro	12	0.63 ± 0.05	0.58 ± 0.04	140.56 ± 13.19	242.67 ± 16.83
Techmarscincus jigurru	Tj	10	1.10 ± 0.05	1.22 ± 0.06	392.27 ± 17.30	280.00 ± 14.67

Lizard sampling and morphological measurements

Details on lizard sampling and morphological measurements are given in Chapter 2.

Performance measures

Details on the measurement of lizard sprinting, climbing, clinging and jumping performance are given in Chapter 2.

Analyses

NON-PHYLOGENETIC ANALYSES

Mean values for each morphological measure for each species was $\log_{10}$-transformed prior to analyses to improve normality (Sokal and Rohlf 1995). Each trait was regressed against $\log_{10}$-transformed snout-vent length and the residuals calculated and used in subsequent analyses as size-corrected performance and morphological measures. Body height was calculated as the mean of mid-body, pectoral and pelvis height. Biomechanical predictions posit that terrestrial lizards should have shorter fore-limbs than hind-limbs. I calculated the limb ratio using a regression of log hind-limb length regressed against log fore-limb-length (Vanhooydonck and Van Damme, 2001; Zaaf and Van Damme, 2001). Furthermore, the tibia should be long relative to the femur in the hind-limb of ground dwelling species, to assist rapid running on broad, level surfaces. However in climbers, both limbs should have a low intra-limb ratio, which should increase the ability to grip perches (Vanhooydonck and Van Damme, 2001). I calculated tibia:femur length from the regression of tibia length against femur length (Vanhooydonck and Van Damme, 2001). Species with a large tibia:femur length have a long tibia relatively to their femur.

PHYLOGENETIC ANALYSES

Details on phylogenetic independent contrasts analyses, including standardisation procedures are presented in Chapter 2. Limb ratio was calculated using an ordinary least-squares regression of the contrasts of hind-limb length against the contrasts of fore-limb-length (Vanhooydonck and Van Damme, 2001; Zaaf and Van Damme, 2001). Tibia:femur length was calculated from the regression of the contrasts of tibia length against the contrasts of femur length (Vanhooydonck and Van Damme, 2001).

Details on the phylogeny used for the phylogenetic independent contrasts analyses is given in Chapter 2 (Figure 2.9). To determine those morphological traits (body height, fore-limb length, hind-limb length and tibia:femur ratio) both non-phylogenetic and phylogenetic that accounted for most of the variation in performance, I used backward, stepwise, multiple regression (phylogenetic data through the origin, See Garland et al., 1992). This technique provides a partial regression coefficient (β) between the response variable (performance trait) and significant morphological traits with each of the other variables statistically held constant. As correlated predictors may introduce problems of (multi)collinearity in multiple regression analyses, I tested that tolerance among correlated variables was above 0.1 (Quinn and Keough, 2002). Initial data inspection revealed fore-limb and hind-limb length were highly correlated, with low tolerance (both < 0.09). Consequently, I used the measure of limb-length with the highest significant correlation with each performance measure. In the absence of a significant correlation, I used hind-limb length, due to its importance in most aspects of lizard locomotion (Garland, 1985; Garland and Losos, 1994; Bonine and Garland, 1999). The use of a single measure of limb-length in analyses considerably increased tolerance (all > 0.2). I report partial regression coefficients (β) ± standard error and model r^2 values for both non-phylogenetic and phylogenetic analyses.

Results

Non-phylogenetic analyses

There were considerable interspecific differences in size and morphology (Table 5.1), with a similar degree of interspecific variation in performance among the species examined (Table 5.2). There was a significant positive correlation between sprint and climb speed ($r = 0.55$, $P = 0.01$) and between climbing speed and cling force (Figure 4.2, $r = 0.76$, $P < 0.001$; Table 3). All other performance measures were not significantly correlated (Table 5.3).

A backwards, step-wise, multiple regression model with residual sprint speed as the dependent variable and residual body height, hind limb length and the ratio of tibia:femur length as independent variables resulted in a significant model ($r^2 = 0.54$, $F_{1,\ 17} = 5.44$, $P = 0.011$), with body height as the only contributing independent variable, indicating that lizards with flatter bodies sprint faster (partial regression coefficient β ± S.E. = -0.748 ± 0.199). The same model using climbing speed as the dependent variable identified fore-limb length as the only contributing variable ($r^2 = 0.72$, $F_{1,\ 17} = 11.98$, $P < 0.001$): species with longer fore-limbs climb faster (β = 0.780 ± 0.297). Cling force was determined by fore-limb length ($r^2 = 0.50$, $F_{1,\ 17} = 4.73$, $P = 0.018$), so that species with longer fore-limbs cling more strongly (β = 0.991 ± 0.395). There was no relationship between jump distance and any of the morphological variables I measured ($r^2 = 0.26$, $F_{1,17} = 1.63$, $P = 0.228$).

Phylogenetic analyses

Overall, the results from the phylogenetically corrected data were broadly congruent with those of the un-corrected data. The four measures of performance were all significantly and positively correlated with each other (Table 5.3). Sprint speed was positively correlated with climb speed (Figure 2, r = 0.71, P < 0.001). Climbing speed was strongly correlated with the ability to cling to a rock-like substrate (Figure 5.2, r = 0.67, P < 0.001). Climbing ability was also correlated with jump distance (Figure 5.2, r = 0.59, P < 0.05). There was a positive non-significant relationship between cling force and sprint speed.

In a backwards, step-wise multiple regression (through the origin) with sprint speed as the dependent variable and the residual contrasts of body height, hind-limb length and the ratio of tibia:femur length as independent variables, only hind-limb length contributed significantly (r^2 = 0.75, $F_{1, 16}$ = 40.56, P < 0.001), indicating that the evolution of longer hind-limbs has coincided with faster sprint speeds (partial regression coefficient β = 0.856 ± 0.135). A similar model, using jump distance as the dependent variable, was not significant (r^2 = 0.20, $\mathrm{F}_{1, 16}$ = 1.14, P > 0.36). The same model with climbing speed as the dependent variable indicated that residual contrasts of fore-limb length contributed significantly to variation in climbing speed (r^2 = 0.87, $F_{1, 16}$ = 62.51, P < 0.001). This suggests that increased fore-limb length has evolved in concert with an increase in climbing speed (β = 0.795 ± 0.101). A similar model with cling force as the dependent variable retained residual contrasts of fore-limb length as the only variable contributing significantly to the model (r^2 = 0.43, $F_{1, 16}$ = 6.11, P < 0.05), indicating that an increase in fore-limb length evolved in concert with cling ability (β = 0.515 ± 0.209).

Discussion

Specialisation for a given task is thought to preclude simultaneous specialisation for others, thus preventing specialized species from performing well at multiple tasks (Huey and Hertz, 1984b; Stearns, 1992; e.g., 'jack-of-all-trades is master of none'). However, in cases where selection for performance at one task enhances performance in other areas (e.g., sprinting, climbing and clinging) there may be no trade-off in ability. My study found no evidence of trade-offs in performance at sprinting, climbing and clinging in this group of skinks, instead, good performance in one of these tasks was positively correlated with good performance in the others. Differences in limb-length explained much of the variation in performance among species, with sprint speed correlated with hind-limb length, whereas climbing speed and clinging ability were correlated with fore-limb length.

Hind- and forelimb lengths were correlated as well. However, despite theoretical predictions there was no evidence that the evolution of a flatter body *per se* resulted in a direct performance benefit, as indicated by the phylogenetic analyses.

Absence of performance trade-offs

Biomechanical predictions suggest performance trade-offs should occur when morphological traits that enhance performance at one task negatively affect another. Using this reasoning, some studies have predicted a trade-off between sprinting and climbing, as morphological traits optimal for horizontal locomotion apparently oppose those required for optimal vertical locomotion (Cartmill, 1985; Zaaf et al., 1999; Zaaf and Van Damme, 2001). However, my study found no support for this, as all performance measures (including both horizontal and vertical locomotion) were positively associated. Recent evidence suggests that the expectation of trade-offs among performance abilities must be considered within the ecological context of the group examined (Vanhooydonck and Van Damme, 2001). There were no trade-offs among sprinting, clambering, and climbing in lacertid lizards (Vanhooydonck and Van Damme, 2001). Thus, the relationships between sprinting, climbing and clinging for scincids resemble those in lacertids. The strong positive correlation between sprinting and climbing, in both these groups, and between clinging and climbing in scincids implies that these traits require similar morphological features.

Positive correlations between sprinting and climbing are directly opposite to the findings for Anoles and chameleons, where trade-offs occur between sprinting speed and climbing speed. Characters enhancing sprinting and climbing apparently vary with substrate use. Anoles and chameleons use twigs and branches as perches (Schoener, 1968; Losos, 1990a; Irschick et al., 1997), whereas skinks and lacertids use broad, flat substrates such as rocks, bare earth and leaf litter (Pianka, 1969a; Vanhooydonck and Van Damme, 1999; Chapter 3). Surprisingly, the morphological features enhancing sprinting and climbing speed on broad surfaces do not enhance both performance traits on narrow perches.

The apparent absence of trade-offs among performance traits in skinks and lacertids does not mean that they do not occur in other areas. For example, body shape has a strong influence on reproductive output in lizards (Vitt and Congdon, 1978; Vitt, 1981; Vitt and Price, 1982), and the flat body of many fast, rock-using skinks may reduce fecundity. Alternatively, a trade-off may occur in other performance measures, such as endurance (Vanhooydonck et al., 2001). However, the clear message from this study is that morphologically more derived species were

Table 5.3. Pearson correlation coefficients of performance and morphological traits for 18 Scincid species of the sub-family Lygosominae. Non-phylogenetic correlations (n = 18, above) are for residual (size-corrected against SVL) values. Phylogenetic correlations (n = 17, in bold below) are for (size-corrected against SVL contrasts) standardised independent contrasts.

	Climbing speed	Cling force	Jump distance	Body height	Fore-limb length	Hind-limb length	Tibia : Femur ratio	FLL : HLL ratio
Sprint speed	0.55* __0.71**__	0.24 __0.21__	-0.09 __0.44__	-0.55* __-0.20__	0.35 __0.78**__	0.27 __0.85**__	0.24 __0.08__	-0.13 __0.41__
Climbing speed		0.76** __0.67**__	0.32 __0.59*__	-0.13 __-0.39__	0.83** __0.88**__	0.74** __0.82**__	0.73** __0.48*__	-0.07 __0.05__
Cling force			0.10 __0.19__	-0.04 __-0.10__	0.69** __0.56*__	0.50* __0.42__	0.52* __0.37__	-0.33 __-0.25__
Jump distance				0.46 __-0.20__	0.17 __0.50*__	0.33 __0.53*__	0.27 __0.20__	0.45 __0.21__
Body height					0.05 __0.89**__	0.29 __0.90**__	0.12 __-0.46__	0.64** __0.19__
Fore-limb length						0.92** __0.94**__	0.88** __0.21__	0.00 __0.07__
Hind-limb length							0.87** __0.14__	0.39 __0.41__
Tibia : Femur ratio								0.17 __-0.14__

* - 0.05 > p > 0.01; ** 0.01 > p > 0.001.

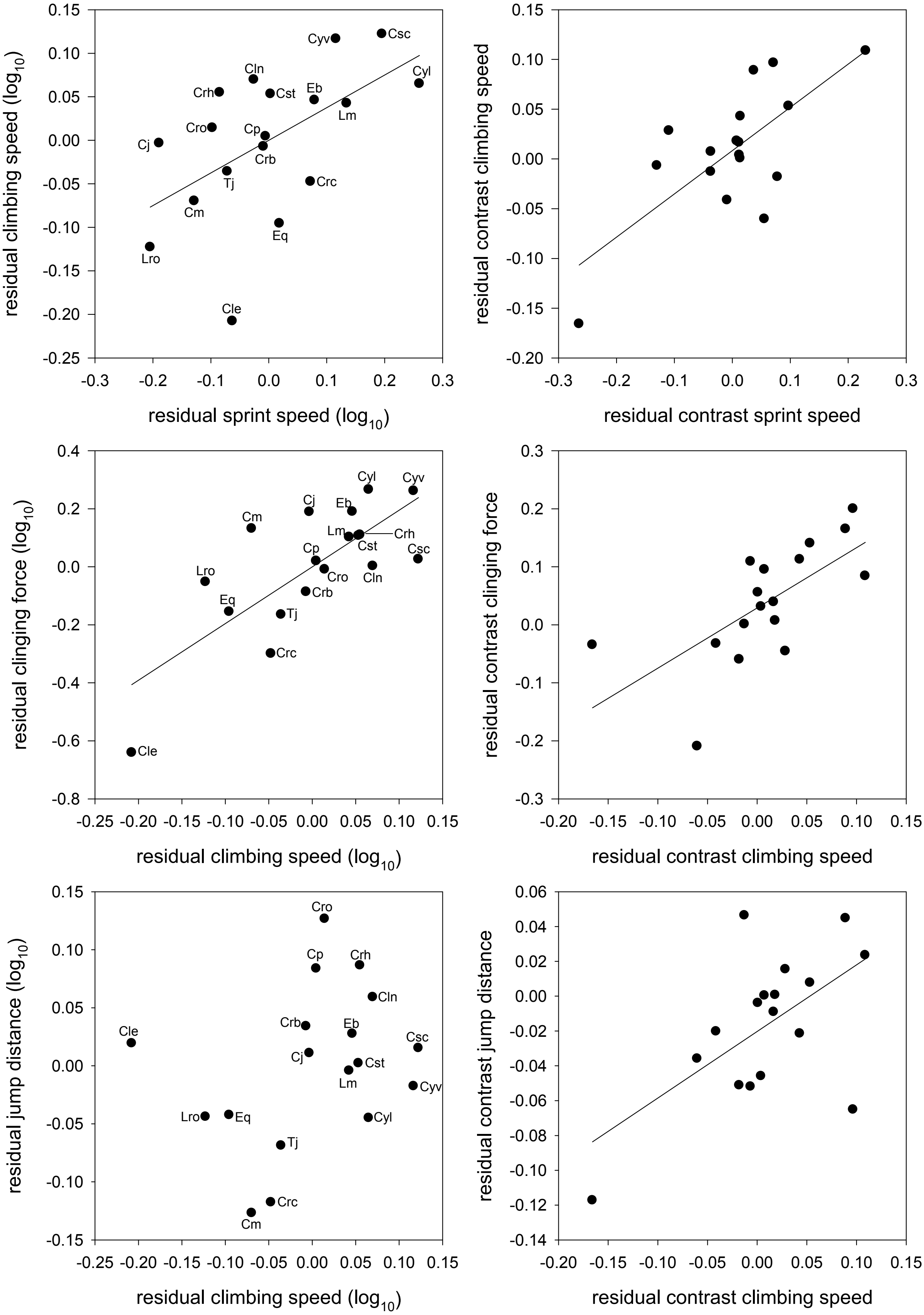

Figure 5.2 Relationships between four performance measures (sprinting, climbing, clinging force, jump distance). Left panels show non-phylogenetic residuals of performance means per species. Labels indicate species. Right panels show residual phylogenetic independent contrasts of performance means per species.

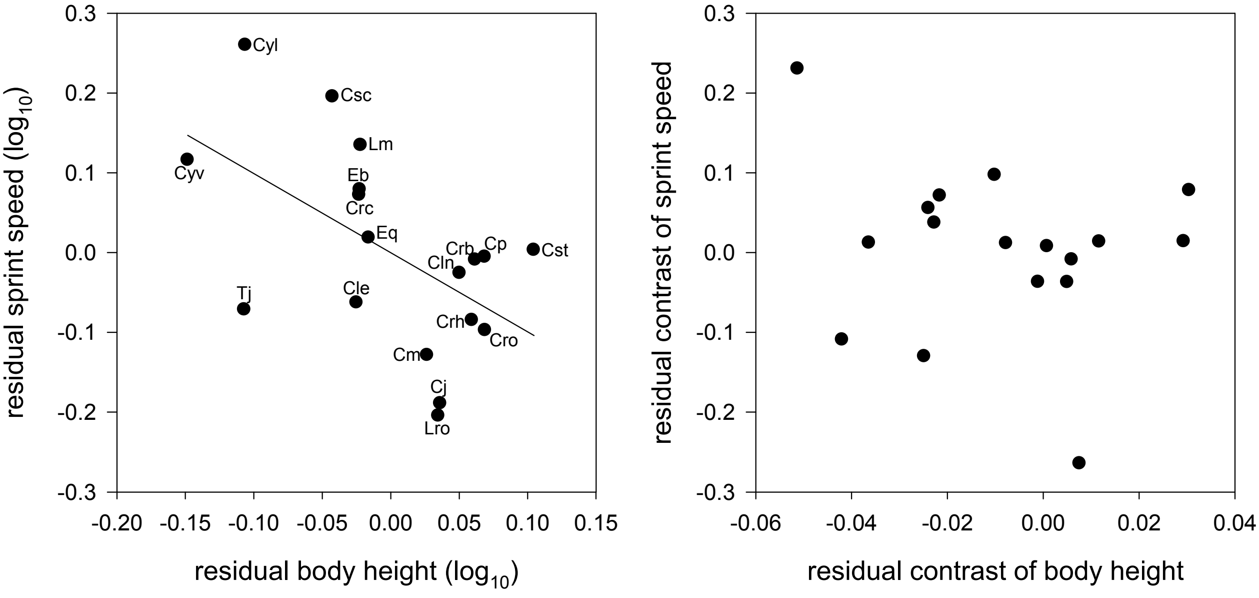

Figure 5.3 Relationship between body height and sprint speed. Left panel shows non-phylogenetic residuals of species means for sprint speed. Labels indicate species. Right panels show residual phylogenetic independent contrasts of species mean body height against species mean sprint speed.

simply better at a greater range of tasks that are sufficiently similar that no trade-offs among them occurs.

Limb length and performance

In this study, lizards with longer hind-limbs sprinted faster. This relationship has been noted for lizards and in other vertebrate groups (e.g., Losos, 1990a; Garland and Janis, 1993; Garland and Losos, 1994), and is caused by the increased stride length achieved with longer hind-limbs (Hildebrand, 1974; Cartmill, 1985; Losos, 1990a). Losos (1990b) identified an inverse relationship between fore-limb length and sprint speed in 14 species of Anolis. But for the group of scincids in my study, there was no indication that running was impeded by long forelimbs; longer forelimbs were either unrelated to running speed (uncorrected data) or were strongly positively correlated with running speed (phylogenetically corrected data). Climbing speed was also enhanced by long forelimbs, and by long fore-limbs and hind-limbs. Increased fore-limb length, or fore limbs and hind limbs of equal length, are beneficial for climbing species as it allows them to stride similar distances with each limb (Arnold, 1998; Vanhooydonck and Van Damme, 2001). Individuals climbing angled substrates should also benefit from increased tension provided by longer fore-limbs, which would prevent tumbling backwards (Cartmill, 1985; Alexander, 1992; Aerts et al., 2000). Relative to the width of their body, the species in this study generally occupy broad substrates, such as rocks (see Chapter 3). Thus, longer hind and fore limbs appear to combine to allow increased stride length, equal stride length and increased pulling forces to enhance locomotion when climbing.

A direct consequence of increased running speed in lizards is the tendency for the body to lift, leading to bipedal locomotion (Aerts et al., 2003). While increased stride length increases speed, the increased propensity for the fore-body to lift in a way that leads to bipedalism, presents an obvious problem of flipping backwards on inclined surfaces (Aerts et al., 2003). In climbing lizards, morphological traits that lower the centre-of-mass and bring it forward should reduce the possibility of fore-body lifting. In addition to body flattening (Van Damme et al., 1997), these traits include increased fore-limb length to widen the base of support, and a more sprawled form of locomotion (Aerts et al., 2003). My study found support for increased fore-limb length to increase performance in climbing and clinging, and while non-phylogenetic analyses revealed body flattening aided sprint performance, the phylogenetic analyses did not support this finding (See below – Hypotheses for the role of body flattening).

Lizards with longer fore-limbs had greater clinging ability. The basis of the increased cling ability observed in this study is not known, but may be related to an increased base-of-support (Aerts et al., 2003), or an increased number of sub-digital lamellae, which may increase frictional forces and improve contact on irregular surfaces (Cartmill, 1985; Losos, 1990a). Increased cling ability in species with longer fore-limbs should also assist climbing by improving traction on an inclined slope. In a comparative examination of lizard clinging ability, Zani (2000) found that an evolutionary increase in claw height and a reduction in toe length was correlated with an increased ability to cling to course substrates, but provided no information on how limb-length related to cling ability or toe length. My previous study (Chapter 4; Appendix I) indicated that limb-length and digit-length were strongly correlated in this group of scincids, suggesting that increased limb-length and toe length may act in concert to increase clinging ability in this group. For example, species with longer limbs may be able to produce greater tension, or may possess greater amounts of muscle mass or different muscle fiber types for clinging. Increased amounts of muscle mass in long-limbed species seems unlikely in this group, with most high performance species having thin, gracile limbs, however, muscle fibre types have not been examined.

Jumping ability was correlated with both fore-limb and hind-limb length in this study. There should be a tight correlation between relative hind-limb length and jump performance (Zug, 1972; Emerson, 1978, 1985; Losos et al., 1989; Losos, 1990a, b; Harris and Steudel, 2002), as a greater hind-limb length provides a greater distance over which it can extend and accelerate the body (Cartmill, 1985; Alexander, 1992). The correlation between fore-limb length and jump distance is presumably due to the tight correlation between fore-limb and hind-limb length (Table 5.3). That is, species with long hind-limbs jump the greatest distances, but also have long fore-limbs; it is unlikely that long fore-limbs would be directly related to increased jump distance (Emerson, 1985; Losos, 1990a).

Alternative hypotheses for the role of body flattening

While the non-phylogenetic analyses suggest there is a benefit of body flattening on sprint speed in scincid lizards, this relationship disappeared in the phylogenetic analyses, which suggests this relationship is relatively weak. Counter to predictions, there was no evidence that dorsoventral flattening aided climbing, despite a relatively strong (phylogenetic) correlation between body flattening and climbing speed. In this case, a comparison involving a larger number of species may prove worthwhile. However, dorsoventral flattening may have a more indirect benefit on climbing not identified in this study. One aspect of vertical locomotion that would likely benefit from a flatter body is energy efficiency. Efficiency of locomotion at low temperatures may have been an important factor in the evolution and ecology of arboreal lizards, such as geckos (Autumn et al., 1999; Zaaf et al., 2001). For example, a ground-dwelling skink used almost 200% more energy to perform one unit of vertical work than a climbing gecko (Farley and Emshwiller, 1996). Within a taxonomic group, more dorsoventrally flattened species should expend less energy on postural adjustments, and overcoming the forces of gravity, due to their lowered centre of mass and reduced propensity to topple backwards on inclined surfaces (i.e., *Plica plica*, Vitt, 1991b; Aerts et al., 2003). In this scenario, the degree of body flattening would be unrelated to climbing speed, but would allow species to perform such tasks more efficiently. The majority of species in this study, other than *E. quoyii*, are relatively light (< 6 g) and weigh considerably less than the threshold mass (40 g) at which climbing performance is notably reduced by a heavy body (Huey and Hertz, 1982, 1984a). However, it is unknown whether climbing species in this study had lowered energetic costs, relative to non-climbing congeners. Field observations of flattened, rock-using species (e.g., *Carlia scirtetis*) indicate that they are extremely swift-moving (Table 5.2), relative to less flattened congeners. Future research, including measurements of field metabolic rates, energetic costs of climbing, and food acquisition and assimilation efficiency are required to test this idea.

A further, alternative hypothesis for the function of a flat body is that it may increase the ease with which individuals can take refuge in crevices, as do iguanids (Vitt, 1981; Vitt et al., 1997; Pianka and Vitt, 2003). While plausible, field observations of many of the flattest rock-using species in this study suggest that flatness as an adaptation for crevice using is unlikely. The role of a flattened body for using crevices appears to be relatively minor for skinks (pers. obs.), as, when approached, most species pass narrow crevices, instead using large gaps (relative to the height of the lizard) between rocks or rock overhangs as refuges (Goodman, in press; Appendix I). In addition, when observed inside rock crevices, these species do not wedge themselves into the narrowest part of the cervices and lack the sharply keeled scales that aid this behaviour in other taxa (e.g., *Egernia cunninghami* group; Cogger, 2000; Chapple, 2003).

Chapter 6

Life on the rocks: microhabitat–performance correlates in a group of tropical lizards

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Introduction

The ability for organisms to effectively perform tasks, such as escaping predators or capturing prey, influences fitness by affecting survival, reproduction, and growth (Arnold, 1983; Garland and Losos 1994; Irschick and Garland, 2001). While many studies have examined and identified relationships between ecology and morphology (Miles and Ricklefs 1984; Losos, 1990a; Pounds, 1988; Reviewed in Garland and Losos, 1994) fewer have measured correlations between realized habitat use and performance (Losos, 1990a; Irschick and Losos, 1999; Melville and Swain, 2000; Vanhooydonck and Van Damme, 2003; Mattingly and Jayne, 2004).

If performance is adaptive one prediction is that we expect that species preferentially occupy habitats in which their performance traits are maximized, while avoiding habitats where performance may be compromised (Irschick and Losos, 1999; Irschick, 2002). Thus, an untested assumption, in the absence of interspecific and intersexual competition, is that the habitat(s) used by a species represent those habitats in which performance is optimal. However, relatively few studies have documented a link between performance and habitat use (c.f., Lauder, 1983; Wainwright et al., 1991; Irschick and Losos, 1999; Irschick, 2002; Mattingly and Jayne, 2004).

There is a predictable pattern of relationships between morphological evolution and performance in response to perch diameter in several groups of perch climbing lizards, including Anoloids and Polychrotids (Losos and Sinervo, 1989; Irschick and Losos 1999; Macrini and Irschick, 1998), and within populations of *Sceloporus occidentalis* (Sinervo and Losos, 1991). However, whereas trait evolution is predictable in response to perch diameter in these groups (Losos, 1990a; Irschick et al,. 1997), an obvious suite of predictable traits does not seem to occur in lizards from other groups occupying arboreal habitats or other substrates (Vanhooydonck and Van Damme 1999; Kohlsdorf et al., 2001; Bickel and Losos, 2002; Herrel et al., 2002), or with different escape strategies or armature (Losos et al., 2002; See review in Schulte et al., 2004). Thus, studies of the correlation between morphological evolution and performance in more non-iguanian lizards are required to clarify expected patterns of morphological evolution in response to habitat variation.

I compared microhabitat use of 18 species of scincid lizard from the Lygosomine sub-family including species from the genera *Carlia, Cryptoblepharus*, *Eulamprus*, *Lampropholis* and *Techmarscincus*. These species occupy a range of habitat-types (Ingram and Covacevich, 1989; Ingram, 1990; Cogger, 2000), and my earlier work described two important ecological gradients of habitat use for these species, leaf litter to rock, and closed to open habitat (Chapter 4). In addition, these species selected microhabitats non-randomly with respect to availability and showed considerable interspecific overlap in microhabitat use (Chapter 3), suggesting that microhabitat use is selected to optimise performance, given interspecific and intersexual competitive interactions. Thus, these lizards provide an excellent model group within which to examine patterns of morphological evolution in response to habitat use.

Studies relating habitat use and performance have typically used population means and combined morphological traits of both sexes (Miles, 1994; Melville and Swain, 2000), or only examined a single sex (Losos, 1990a; Kohlsdorf et al., 2001). Such studies fail to consider the role of sexual dimorphism and intersexual morphological differences and how they affect the relationship between microhabitat use and performance capabilities. Typically, lizards exhibit intersexual differences in morphology, for example, in skinks males of rock-using species are more dorsoventrally flattened than females (Chapter 4). There is also within-sex differences in morphology related to habitat use: females of species from rocky habitats have longer limbs and shorter bodies than females of species that use leaf litter. Males from rocky habitats have longer limbs, and shorter and flatter bodies than males that are generalists and use leaf litter. Intrasexual comparisons indicate that both sexes have evolved increased limb length in response to increased habitat openness (Chapter 4).

This study assessed predictions of five conceptual models of locomotion as applied to lizard species in a single clade that occupy a broad range of habitats. The first model was generated using performance relationships and tradeoffs identified in studies of arboreal *Anolis,* and a species in the family *Phrynosomatidae* (e.g., Losos and Sinervo, 1989; Sinervo and Losos, 1991). This model (Figure 6.1a) also predicts that species from increasingly rock-dominated habitats should have good jumping ability or jumping response (Irschick and Losos, 1998) to allow rapid movement to cover, and to assist with crossing gaps within the habitat. This model (Figure 6.1a) predicts that species have good climbing ability to scale inclined surfaces, and good clinging ability to assist with climbing. However, due to the trade-off between climbing ability and sprinting identified in studies of *Anolis* and Phrynosomatids, species from rocky environments should be poor sprinters because they are good climbers (Figure 6.1a). The second model was generated using predictions from biomechanical studies. This model (Fig. 6.1b i) suggests that species from open habitats should evolve rapid running speed, reducing the time required to cover long distances to reach refuges (Snyder, 1954; Pianka, 1969a; Thompson, 1985; Snell et al., 1988; Jayne and Irschick, 2000). Numerous studies have identified a trend for species from more open habitats to evolve greater sprint speeds (Snell et al., 1988; Melville and Swain, 2000). From these studies, we expect that species from open habitats would be poorer at climbing and clinging, because these skills are not required in open habitats (Figure 6.1b i), whereas their congeners in cluttered habitats would be better at clambering over and through obstacles. Another version of this model (Fig. 6.1 b ii) is generated if limb length is the independent axis. Species with long hind limbs usually have rapid sprint speeds (Snyder, 1954; Losos, 1990a; Miles, 1994). In this version, the longer hind-limbs associated with high sprint speed should reduce climbing and clinging performance (Figure 6.1b ii). However, while early studies involving *Anolis* indicate that species with greater sprint speeds also have enhanced jump performance (Losos, 1990a, b), more recent studies indicate that long limbs are not necessary correlated with enhanced jump performance (Toro et al., 2004). Thus, the biomechanical / arboreal model (Figure 6.1 b ii) offers two potential predictions for jump performance.

In contrast to these previous predictions, models that integrate biophysical predictions, natural history information, and data from species other than perch climbing lizards (Figure 6.1c i & ii), predict that sprinting, climbing and clinging performance (not jumping) should be high in one environment, and low in the other environment, i.e., sprint speed and the other performance traits do not trade off in these models (see Vanhooydonck and Van Damme, 2001; Chapter 5). In the first integrated model (Fig. 6.1c ii) the independent axis is the gradient from leaf litter to rocky habitats. This model predicts that running speed will be enhanced in rocky environments because bare rocks must be crossed quickly to avoid predators. Likewise, cling ability should be greater to assist with climbing inclined surfaces. The converse should occur in cluttered, leaf litter dominated habitats, where slow running speeds, and/or frequent stopping, are optimal for an escape strategy based on crypsis, particularly if individuals are frequently obscured by leaf litter and vegetation. Climbing, clinging and jumping are likely to be irrelevant to optimal performance in this habitat. In the second integrated model, the predictions are similar to the first (i.e., there is no trade off among performance traits), but the independent axis ranges from open to closed habitat. This model posits that species from open, terrestrial habitats need to run quickly to avoid predators and therefore should evolve long hind limbs, and have enhanced sprint speed and climbing ability to enhance speed on inclined surfaces and good clinging ability to assist with climbing (Figure 6.1c ii.). As suggested above, jumping performance may not be related to habitat type. In this model, closed habitats do not select for fast running, climbing, clinging or jumping, but may select for crypsis and cryptic behaviours. Because rocky habitats are frequently very open (e.g., boulder fields), these two models are similar, but because rocky habitats can be covered by complex vegetation (and be closed; Goodman, in press), and leaf litter habitats can be open, I consider these distinct habitat gradients in this paper.

This study examines the relationship between two habitat gradients (leaf litter to rock, and closed to open), and one morphological gradient (limb length) and performance in tropical scincid lizards, testing the conceptual models outlined above for males and females separately. My results suggest that trade-offs in the morphology performance relationship in females is due to fecundity selection. In this case, natural selection for improved locomotor function in particular habitats, evident in males, is weakened in females by selection for increased fecundity. My results support the proposed integrated models, with species that use mostly rocky and/or open habitats performing well at three of the four performance tasks, compared to species from leaf litter and/or closed habitats. Despite theoretical biomechanical predictions, increased limb length was unrelated to jumping ability in this study. Thus, rapid speed, and good climbing and clinging ability was selected in rocky and open habitats, whereas the reverse was favoured in leaf litter and closed habitats. Tradeoffs, predicted by some other conceptual models (6.1 a, b) of lizard performance, were not supported.

Methods

Habitat use and performance

Each species of skink was allocated to one of three microhabitat types based on the most commonly used microhabitat type for each species (see below, and Chapter 3). I used the principal component axes of substrate use and microhabitat openness calculated in Chapter 4 as a quantification of the gradients of substrate use and habitat openness. Methodology used to obtain performance measures used here is given in Chapter 2.

Analyses

NON-PHYLOGENETIC ANALYSES

The relationships between body size (SVL) and each performance trait were examined using Pearson product-moment correlations. Relative size-corrected measures of performance were analysed using snout-vent length as a covariate and ecotype category as a factor in ANCOVA, following testing for homogeneity of slopes.

PHYLOGENETIC ANALYSES

Details on phylogenetic methodology are given in Chapter 2. A previous study examined the relationship between substrate use, microhabitat openness, refuge use and morphology (Chapter 4) and the relationship between morphology and performance in males (Chapter 5) for this group of Lygosomine skinks. Analyses in the present study used the scores of the principal component axes (henceforth PCs) of independent contrasts from each data set (substrate use and microhabitat openness; Losos, 1990a; Schulte et al., 2004) after checking that all PC axes were multivariate normal, I tested for outliers using Mahalanobis distances. In the PC analyses of substrate use and habitat openness the first PC axis explained more than 50% of the data and was used in correlation analyses. To establish relationships between each performance trait with the dominant ecological (substrate use, microhabitat openness) axis, I used the standardised (size-corrected) contrast of each performance measure and PC1 of each ecological principal component axis in Pearson product-moment correlations. Canonical correlations were used to assess the relationship between all of the PC axes of microhabitat openness and substrate use with each of the performance measures for each species (Miles and Ricklefs, 1984; Losos, 1990a).

Results

Non-phylogenetic analyses of ecotypes and performance

There was considerable spread in the size of individuals from the three ecotypes (Figure 6.2a and 6.2b). Traditional non-phylogenetic ANOVAs identified no significant size differences between sexes for any species from the three ecotypes (Table 6.1), and all performance traits were significantly and positively correlated with snout-vent length (All $r > 0.68$; $P < 0.002$; Figure 6.2a and 6.2b). A MANCOVA with snout-vent length as covariate and ecotype as factor revealed a significant difference among species from the three ecotypes (Pillai's trace: $F_{6, 46} = 3.19$, $P < 0.05$), but no difference among sexes in the four performance tasks (Pillai's trace: $F_{3, 22} = 0.53$, $P > 0.66$) and a non-significant interaction (Habitat X Sex; Pillai's trace: $F_{6, 42} = 0.53$, $P > 0.78$). This indicates that individual of both sexes from the same ecotype display similar performance at the four performance tasks examined.

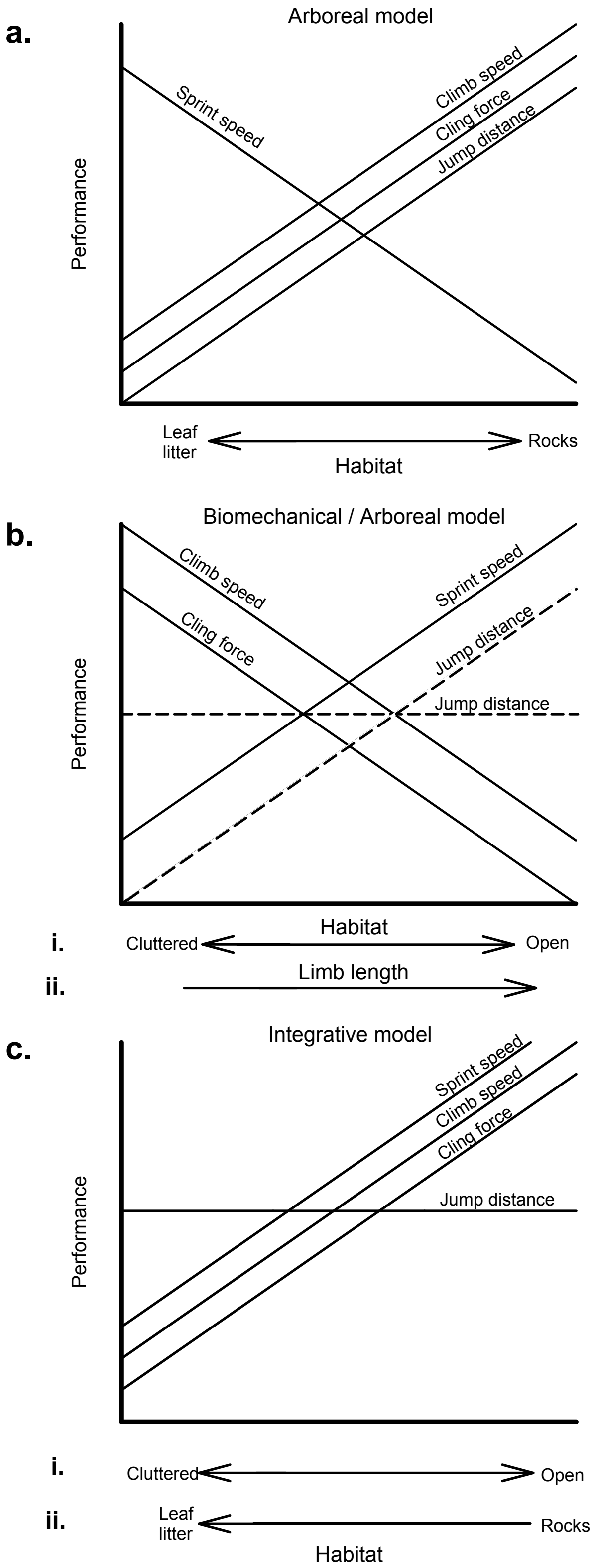

Figure 6.1 Predictive models showing expected relationships between; a. a gradient of habitat use from leaf litter to rocks and four measures of performance, b. i. a gradient of habitat use from cluttered/closed habitats to open habitats and four measures of performance, and ii. increased limb length and four measures of performance, c. i. a gradient of habitat use from cluttered/closed habitats to open habitats and four measures of performance, and ii. a gradient of habitat use from leaf litter to rocks and four measures of performance. Note: the shape of the relationships described may vary as lines represent predictive performance relationships. See text for descriptions.

Phylogenetic performance correlations with substrate use, habitat openness and refuge use

The use of phylogenetic comparative methods was justified based on the large number of significant *K*-values for morphological traits (Chapter 2; Table 2.3). Phylogenetic simulation ANCOVAs revealed there was no difference in the performance of either sex of species from different ecotypes. Of the eight comparisons, no fewer than 139 out of the 1000 simulated *F*-values exceeded the traditional non-phylogenetic ANCOVA *F*-value (Table 6.1). Comparisons of PC1 from each of substrate use and microhabitat openness described the majority of the variation in the principal components (Chapter 4) and were used in correlations with the residual contrasts of each performance trait.

Correlations between ecological gradients and performance

FEMALES

The first substrate use PC axis was positively correlated with residual contrasts of sprinting and climbing speed and described a gradient where high positive values were species that perched high above the substrate and occupied habitats with large rocks (rocks > 0.5 m^3), to species that used the ground and habitats with a lot of leaf litter ground cover (Table 6.2). The relationship between PC1 of substrate use and clinging ability, and the relationship between PC1 of microhabitat openness and climbing speed where positive and non-significant (Table 6.2). Thus there was an evolutionary trend for species that typically occupied habitats dominated by large rocks to have increased sprinting and climbing performance (Figure 6.3a). The residual contrasts of sprinting speed were positively correlated with the contrasts of PC1 for microhabitat openness (Figure 6.3a). That is, there was an evolutionary trend for species that occupied habitats close to nearby vegetation or habitats with a high percentage of undergrowth and canopy cover to be slower sprinters (Table 6.2).

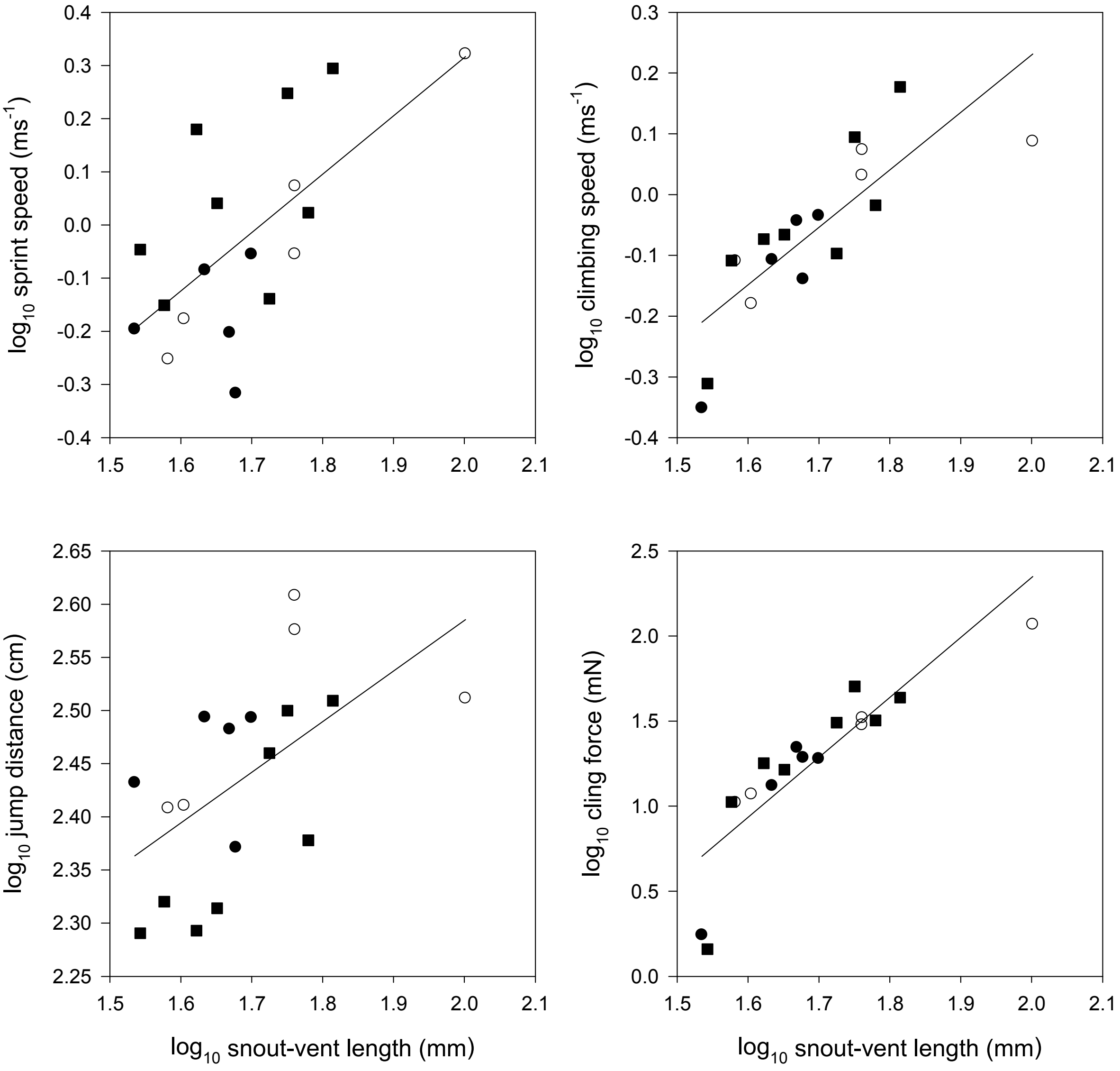

Figure 6.2a. The relationship between snout-vent length and four measures of performance of females examined in this study. Note the homogeneous spread of ecotypes with body size indicating the independence of size, ecotype and performance. Symbols represent: squares, rock-using species; open circles, generalist species; closed circles, leaf-litter dwelling species.

MALES

Males and females had similar patterns of correlations between substrate and microhabitat use and performance; however, males also exhibited a significant positive correlation between substrate use PC1 and clinging ability, and between the microhabitat openness PC1 and climbing speed (Table 6.2). Thus, in males, using rocky habitats has lead to the evolution of increased clinging performance (Figure 6.3b), whereas the occupation of more open habitats has caused an increase in climbing performance (Figure 6.3b).

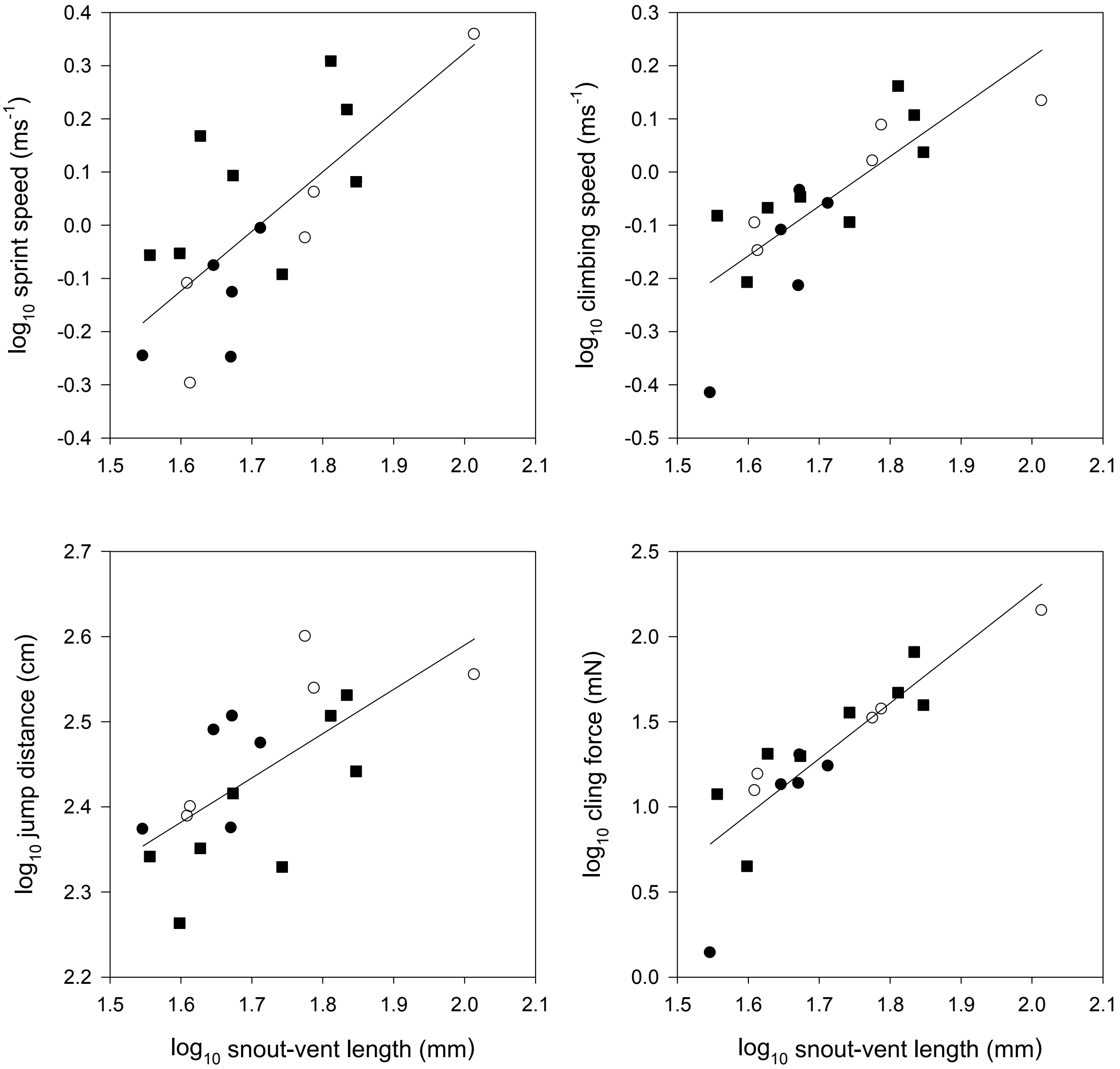

Figure 6.2b. The relationship between snout-vent length and four measures of performance for males examined in this study. The homogeneous spread of ecotypes with body size indicates the independence of ecotype and performance. Symbols represent: squares, rock-using species; open circles, generalist species; closed circles, leaf-litter dwelling species.

Relationships between ecology, morphology and performance

FEMALES

Canonical correlation analyses revealed there was a significant correlation between the first two canonical axes for substrate use – performance, and the first canonical axis of the microhabitat openness – performance and the morphology – performance canonical axes (Table 6.3). The substrate use – performance analysis revealed a significant positive relationship between species that perch high above

Table 6.1. Phylogenetic simulation and conventional one-way ANOVA results of $\log_{10}$-transformed measures of body size (snout-vent length) and phylogenetic simulation and conventional ANCOVA of performance traits for 18 Lygosomine skink species from three habitat types (rock-using, litter-using and generalist habitat categories). Table *F* and *P*-values are for conventional ANCOVA, except snout-vent length, which is non-phylogenetic ANOVA. Among-group differences are considered significant when the traditional *F*-value exceeds the simulated *F*-value (F_{phylo}).

Trait	df	Female			Male		
		F	F_{phylo}	*P*	*F*	F_{phylo}	*P*
Snout-vent length	2, 15	0.95	4.872	0.411	1.06	4.957	0.370
Sprint speed	2, 14	2.66	5.356	0.103	2.74	5.036	0.097
Climbing speed	2, 14	1.02	5.290	0.384	2.52	5.770	0.114
Clinging force	2, 14	0.81	4.833	0.463	2.08	5.004	0.159
Jump distance	2, 14	3.29	5.010	0.066	2.00	5.180	0.169

Table 6.2. Pearson correlation coefficients of phlogentic independent contrasts (n = 17) and TIPs (n = 18) values for substrate use and microhabitat openness versus performance of males and females in 18 Scincid species of the sub-family Lygosominae. Both sets of correlations are size-corrected against SVL.

Performance trait	Substrate use PC1	Microhabitat openness PC1
Females		
Sprint	**0.801** (0.585)****	**0.787**** **(0.660)****
Climb	**0.571*** (0.326)	0.347 (0.393)
Cling	0.195 (0.256)	0.147 (0.311)
Jump	–0.143 (–0.284)	–0.332 (–0.363)
Males		
Sprint	**0.599* (0.574)****	**0.724**(0.713)****
Climb	**0.599*** (0.358)	**0.506*** (0.514)*
Cling	**0.509*** (0.380)	0.423 (0.470)
Jump	0.083 (–0.491)*	0.135 (–0.213)

* - 0.05 > p > 0.01; ** 0.01 > p > 0.001. Bold correlations are significant following Bonferroni correction.

the substrate and occupy large rock microhabitats (Substrate use PC1 described 59.6 % of the variance in CC1) and sprinting performance (Sprint performance described 58.6 % of the variance in CC1). This indicates an evolutionary trend for species from habitats composed of rocks to have increased sprinting performance. The second substrate use – performance canonical axis was also significant, and revealed a relationship between species that occupy habitats with rocks to habitats dominated by bare earth (Substrate PC2 described 45.8 % of the variance in CC2) and climbing performance (Climbing performance described 90.2 % of the variance in CC2). Thus, rocks appear to promote the evolution of increased climbing ability.

The microhabitat openness – performance analysis revealed an inverse relationship among species from closed to open habitats (Microhabitat openness PC1 described 100 % of the variance in CC1) and sprinting performance (Sprinting performance described 79 % of the variance in CC1), and indicates that species from more open habitats have greater sprint performance. The morphology – performance analysis (Table 6.3), revealed a relationship between longer limbs and limb elements (morphology PC1 described 61 % of the variance in CC1) and increased climbing performance (Climbing performance described 74.5 % of the variance in CC1), highlighting the importance of limb length for climbing.

MALES

Correlations among substrate use, microhabitat openness and performance were similar in males and females (Table 6.3). Using large rocks and perch angles (Substrate use PC3 described 85 % of the variance in CC1) increased climbing performance (Climb performance described 13 % of the variance in CC1). The second canonical axis (Substrate use PC3 described 82 % of the variance in CC2) related substrate use to climbing performance (Climbing performance described 62 % of the variance in CC2), and highlights the importance of rock use in the evolution of climbing performance in this group of tropical lizards.

Microhabitat openness (Microhabitat openness PC1 described 100 % of the variance in CC1) was positively related to sprinting performance (Sprinting performance described 76 % of the variance in CC1), indicating an evolutionary trend for species from habitats with little vegetation to evolve increased sprint performance. Finally, morphology – performance (Table 6.3) identified a relationship between longer limbs and limb elements (morphology PC1 described 86 % of the variance in CC1) and increased sprint speed (Sprinting performance described 92 % of the variance in CC1).

Discussion

This study clearly supports the integrated models of performance evolution outlined in the introduction. I found no evidence of tradeoffs between performance traits, predicted by the arboreal, biophysical and limb length models. Instead, species with increased use of rocky and open habitats were faster at sprinting and climbing, and better at clinging compared to species from leaf-litter and cluttered/closed habitats (Figure 6.1c). In addition, there were differences among ecotypes and sexes in performance. In males, cling-ability was related to substrate type, and climbing ability was related to habitat openness; these habitat-performance relationships were weaker or did not hold for females. In my study, jump ability was not correlated with any of the variables postulated as independent axes in the conceptual models, in males or females (Figure 6.1c).

Table 6.3. Canonical correlations comparing the relationship between the substrate use and microhabitat openness relationships and each of four performance measures in females and males of 18 species of Scincids.

Canonical Variable	Canonical Correlation	Canonical R^2	Canonical Redundancy	Statistical test		
				χ^2	d.f.	P
Females						
Substrate use-performance	0.897	0.805	0.268	34.942	12	0.001*
	0.778	0.605	0.202	15.321	6	0.018
	0.543	0.294	0.098	4.184	2	0.123
Microhabitat openness-performance	0.895	0.802	0.401	23.146	8	0.003*
	0.457	0.209	0.104	2.928	3	0.403
Morphology-Performance	0.915	0.838	0.279	29.944	12	0.003*
	0.688	0.473	0.157	8.111	6	0.230
	0.184	0.034	0.011	0.413	2	0.813
Males						
Substrate use-performance	0.848	0.720	0.240	29.90	12	0.003*
	0.818	0.670	0.223	14.63	6	0.023
	0.324	0.105	0.035	1.33	2	0.515
Microhabitat openness-performance	0.855	0.731	0.365	23.81	8	0.002*
	0.669	0.447	0.224	7.40	3	0.060
Morphology-Performance	0.937	0.879	0.500	30.804	12	0.002*
	0.511	0.261	0.048	5.497	6	0.482
	0.380	0.144	0.009	1.866	2	0.393

*values significant following table-wide sequential Bonferroni correction.

Rockiness-to-Leaf-Litter and Open-to-Closed habitat gradients

In *Anolis*, perch diameter provides a primary axis of interspecific separation (Irschick et al., 1997; Losos, 1990a, 1995), with most species separating along a gradient of perch width, in which wider perches have lead to the evolution of increased limb length and faster running performance (Losos and Sinervo, 1989; Losos and Irschick, 1996, Macrini and Irschick, 1998). My study identified an analogous relationship between performance and limb-length (Chapter 4) over a gradient of leaf-litter to rock use in this group of skinks. Further, the differences defined by this gradient of microhabitat use and performance is ecologically relevant, and as with the relationships between perch width and limb length in *Anolis* (e.g., Losos and Sinervo, 1989; Irschick and Losos, 1999) an increased use of rocks was accompanied by a significant increase in limb length (Chapter 4) and increased sprinting, climbing and clinging performance. Such changes in limb length have clear implications for performance ability (Losos, 1990a; Garland and Losos, 1994; Chapter 5). However, contrary to the predictive model based on anoles (Figure 6.1a), lizards from rocky habitats also had increased sprint speed, highlighting a fundamental difference in performance traits between lizards that use perches compared to species that use broad substrates. It appears that Lygosomine skinks experience more intense selection for these three performance traits when associated with varying levels of rock use.

Interestingly, there was no relationship between either of the ecological gradients and jump performance, despite its importance for lizards from other groups (e.g., *Anolis*; Losos, 1990a; Irschick et al., 2005b; Toro et al., 2004). Jumping may be less important in this group of skinks than in Anoles, and it may be that in habitats with broad substrates (e.g., rocks rather than narrow branches), where sprinting and climbing / clambering is of greater importance the benefit of jumping is much reduced. Alternatively, jump performance may be less related to limb length than to muscle physiology in these skinks, whereby species with different relative limb lengths from different habitats can jump similar distances (see Toro et al., 2004).

An implicit assumption of studies relating morphology to performance is that behaviour is not a confounding factor (Garland and Losos, 1994; Irschick, 2002; see Huey et al., 2003). An example of this behaviour may alter the way species perform under natural conditions, such that attempts to link field measures of performance to laboratory measures of performance are not straight forward (e.g., Irschick, 2002; Huey et al., 2003; Mattingly and Jayne, 2004; Irschick et al., 2005c). A behaviour that may circumvent selection on increased jump distance is if individuals jump while running at high speed. In such cases, individuals may be more reliant on achieving adequate speed to bridge gaps in the habitat than on the ability to jump greater distances from a standing start. Species from rocky habitats, where selection on jumping is probably most intense, are faster sprinters, and field observations of several of the rock-using species indicate this form of saltatory locomotion is frequently used (pers. obs). Thus, it seems plausible that selection may operate first to increase sprint speed in rocky habitats, which in turn, enabled individuals to bridge gaps in the habitat more effectively, without a selective

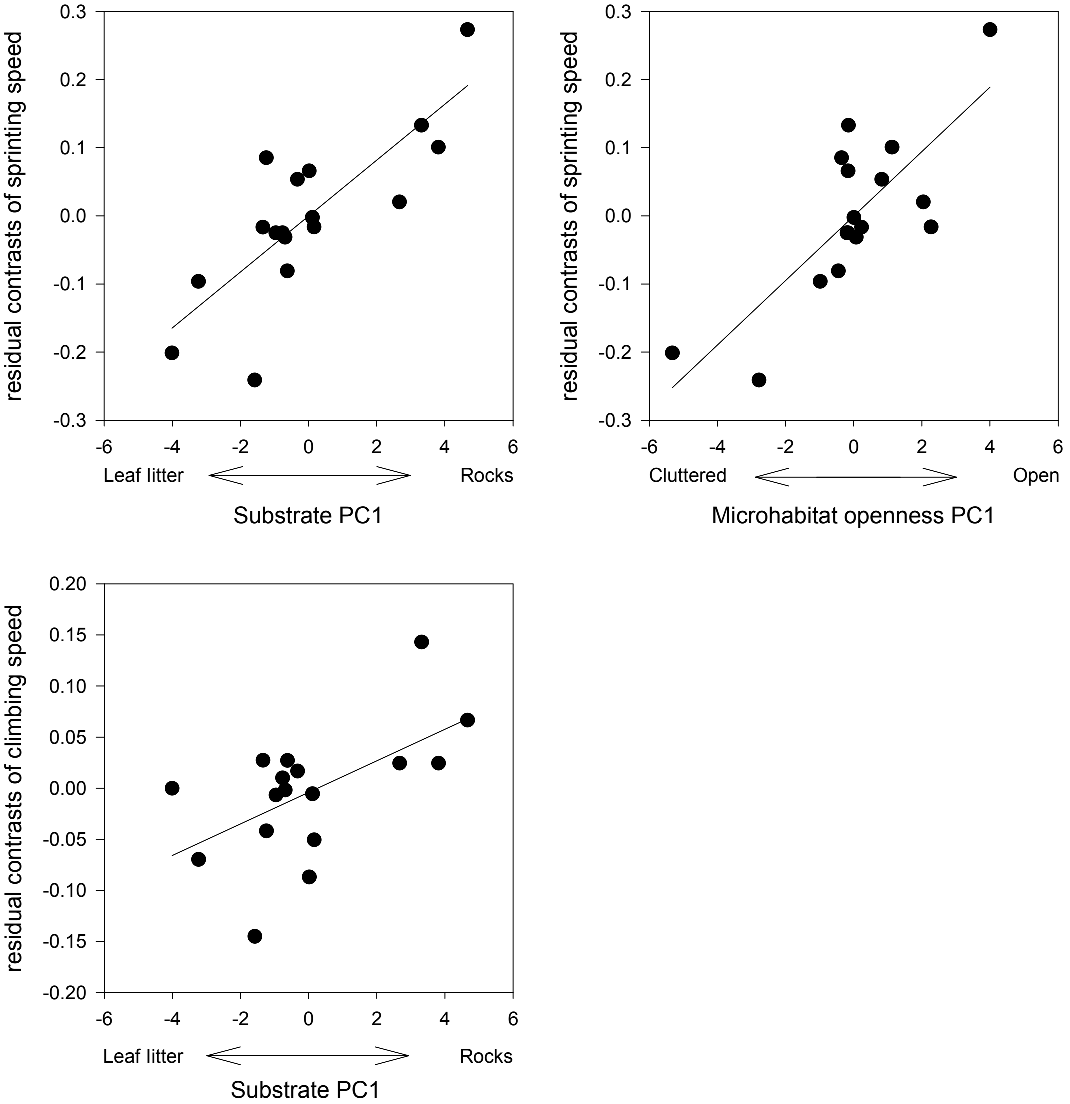

Figure 6.3A. Correlations between two performance measures and a gradient of habitat use from rocks to leaf litter and a gradient of habitat use from open to cluttered/closed habitats for females of the 18 Scincid species examined in this study.

increase in jump performance.

Both male and female skinks using open habitats sprinted faster than those using closed habitats. This fits well with the predictive model (Figure 6.1c i.), as species from open habitats must cover long distances unprotected to reach shelter or to outrun predators. Consequently, the requirement for increased speed selects for longer limbs (Snyder, 1954; Cartmill, 1985; Losos, 1990a). Males in open habitats also had faster climbing speeds, and better clinging ability than species from closed habitats, suggesting selection on performance in females is less intense, or morphological adaptation in

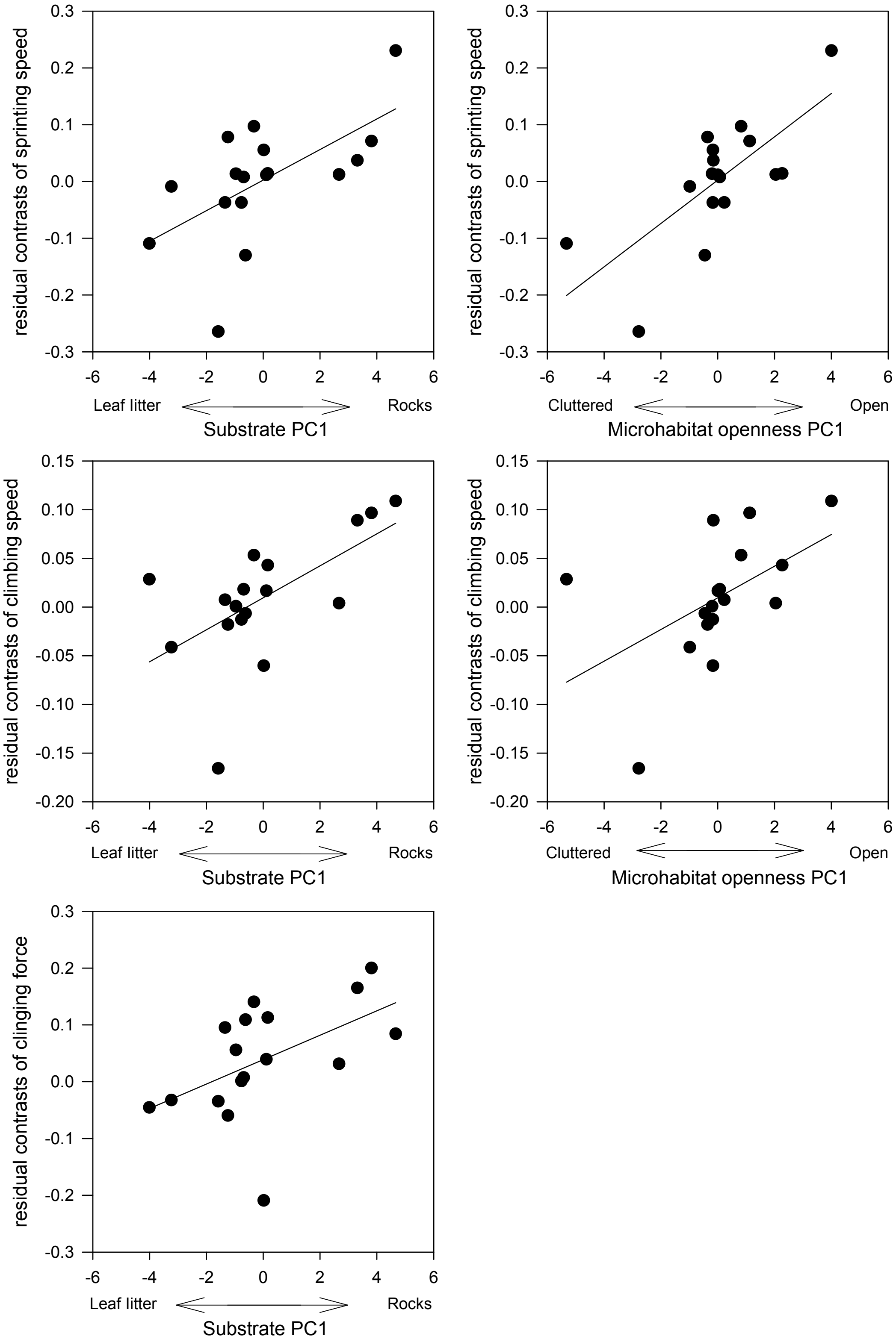

Figure 6.3B. Correlations between three performance measures and a gradient of habitat use from rocks to leaf litter and a gradient of habitat use from open to cluttered/closed habitats for females of the 18 Scincid species examined in this study.

females is constrained (see below). Whereas selection often differs, even among proximate habitats (Schneider et al., 1999), it seems unlikely that selection would be similar in both rocky and open microhabitats due to different predators. It is, however, plausible that these environmental gradients are sufficiently similar that good performance in one leads to good performance on the other.

The slower sprinting, climbing and poorer clinging performance of species from closed and leaf-litter dominated habitats, suggests that alternative traits are unimportant in predator avoidance or feeding success in these habitats. In the context of closed habitats, or among leaf litter accumulated on the forest floor, stealth for hunting prey or crypsis for avoiding predators are likely of utmost importance. As such, selection for increased performance may break down, particularly if predation is mostly by ambush predators (Huey and Pianka, 1981; Vitt, 1983), or when individuals are under cover or in retreats (Schlesinger and Shine, 1994; Downes and Shine, 1998). Moreover, while laboratory measures of climbing, sprinting and clinging likely provide a good measure of important performance criteria for species which use broad substrates, there is no equivalent data on the performance of species from leaf-litter habitats (e.g., sinusoidal locomotion, ability to remain motionless, crypsis). In such cases, the greater limb length of rock-using species may interfere with locomotion though leaf-litter or dense vegetation. However, it is currently unknown whether rock-using species would experience reduced locomotor performance if forced to use such habitats. Species of the scincid genus *Ctenotus* from open habitats have longer limbs than species from densely vegetated habitats (Pianka, 1969a; Garland and Losos, 1994). However, some long-limbed *Ctenotus* species circumvent this problem by folding their legs back and using sinusoidal locomotion in dense habitats (James, 1989), indicating that longer limbs may not handicap performance as predicted. Casual observations of the rock-using species *C. rococo* and the generalist species *C. longipes* indicate that both these species often run rapidly through small areas of leaf litter when pursued by a predator (pers. obs.). However, whether these species are effective at using leaf-litter over reasonable distances or experience a negative effect on speed or manoeuvrability when escaping is unknown (Vanhooydonck and Van Damme, 2003).

Intersexual differences in performance

While this study identified no differences among sexes in performance ability, there were differences in the relationships between performance and microhabitat use among the sexes. There was a significant correlation between clinging performance and substrate use for males, but not females. Similarly, while there was a significant, positive relationship between climb speed and microhabitat openness in males, this relationship was not significant in females, suggesting that selection on increased climbing performance in open habitats may operate less intensely in females, or may be related to bahvioural differences among sexes, such as remaining near refugia (Snell et al., 1988; Miles et al., 2001). Intersexual differences in performance may arise due to sexual selection (Darwin, 1871; Andersson, 1994), presumably due to fecundity selection for increased abdominal volume (Chapter 4). Thus, it appears male combat or mate searching selects for increased climbing and clinging ability. Enhanced cling ability is likely to lead to increased climbing speed, due to the need to cling well when climbing (Losos et al., 1993). In females, which typically move less and have smaller home ranges (Ferner, 1974; Lewis and Saliva, 1987; Melville and Swain, 1999; Perry and Garland, 2002), there may be less of a selective advantage of climbing and clinging. Alternatively, other factors imposing selection on morphology may constrain female morphology and prevent refining of adaptive changes leading to increased clinging and climbing ability. It is possible that climbing and clinging are related to male reproductive success. For example, several species of *Carlia* display male combat, including *Carlia jarnoldae, C.rubrigularis* and *C. rostralis,* that typically involves chasing and biting an opponent (Whittier and Martin, 1992; Whittier, 1993; Torr, 1994; Langkilde and Schwarzkopf, 2003). Individuals of *C. scirtetis* often chase and overpower and force other conspecifics from specific boulders, presumably within defined territories (pers obs.). Thus, cling ability may be an important performance trait linked to mating opportunities in rocky habitats. In males, increased climbing speed may increase reproductive success by allowing males to catch females for mating or for defending or patrolling territories (Hews, 1990; Molina-Borja et al., 1998; Lappin and Husak, 2005; Husak et al., 2006), if they are territorial. Clinging and climbing may be co-evolved or tightly correlated in males, as increased clinging ability is likely to be an important performance benefit for increased climbing speed.

Alternatively, constraints on female body morphology imposed by the requirement of carrying eggs may counter selection for high performance in climbing and clinging (see above). Thus, perhaps females experience similar selection for enhanced climbing and clinging ability as males, but are unable to respond to it, due to antagonistic selection between natural selection for survival and fecundity selection for reproductive output (Wikelski and Trillmich, 1997; Olsson and Shine, 2002; see also Lappin et al., 2006). In this case, male reproductive success could be unrelated to climbing and clinging ability, but males would still be better than females at these tasks.

The patterns displayed here suggest habitat has a dominant affect on the morphology and performance in this group of tropical lizards. However, despite a tighter correlation between the PC axes of habitat and performance in males compared with females, this study identified no intersexual differences in performance. This result suggests females display more variation in performance, which may be the result of intersexual differences in the antagonistic role of natural and sexual slection in this group of tropical lizards.

Chapter 7

Consequences of being ‘flat-out’: microhabitat selection constrains reproductive output in lizards

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Introduction

Reproductive output varies considerably among organisms and is determined by trade-offs between current and future reproductive expenditure, and shaped by historical, physiological and physical constraints (Darwin, 1959; Williams, 1966a; Hirshfield and Tinkle, 1975; Stearns, 1992; Roff, 2002). The amount of resources allocated to reproduction is a fundamental component of an organisms’ life history, and natural selection favours traits that maximise lifetime reproductive output (Williams, 1966b; Stearns, 1992; Roff, 2002).

One factor that influences reproductive output in vertebrates is abdominal volume (Pianka and Parker, 1975; Vitt and Congdon, 1978; Kaplan and Salthe, 1979). Interspecific comparisons in lizards indicate that lizard species with stout, robust bodies that are ‘sit-and-wait’ predators have larger relative clutch mass (RCM = clutch mass / maternal post-oviposition mass; Shine, 1980) than more streamlined ‘widely-foraging’ species (Vitt and Congdon, 1978). The volume constraint hypothesis posits that females are ‘full’ of eggs (Shine, 1992; Qualls and Shine, 1995). Therefore, for a given amount of abdominal space there is some maximal upper level of reproductive output (RCM: relative clutch mass) that is dictated by volume and not energy when females are completely full of eggs. There is some evidence to support this hypothesis: an experimental reduction in abdominal volume in lizards caused a reduction in clutch size and clutch mass (Du et al., 2005a), suggesting that volume acts as a proximate mechanism in lizards. However, females may not always fill their bodies completely with eggs, because it may not be the fittest strategy to do so. Costs of reproduction can be correlated with the mass of the clutch (i.e., with clutch mass relative to body mass RCM), so a reduced reproductive effort (i.e., clutch mass) can be favoured by selection if individuals with smaller clutch burdens experience a lower costs of reproduction have greater survivorship and higher fitness (Stearns, 1976; Vitt, 1981). Indeed, life history theory posits that current reproduction may be constrained by expectation of future reproductive opportunities (Williams 1966b; Stearns, 1992; Roff, 2002). In such cases, completely filling the abdominal cavity with eggs may lead to cost of reproduction via reduced locomotor speed, or inability to access refugia. Thus, reproductive output may not be constrained by volume, but future (expected) gains in reproduction, as well as survival differences across forthcoming years. In marine snakes, clutch masses were smaller than in terrestrial snakes, presumably because a reduced reproductive burden improves swimming performance (Shine, 1988). Although there are numerous studies of variation in reproductive output, there are few tests of how adaptations to particular lifestyles constrain reproductive output.

Changes in morphology may influence fitness (Williams, 1966b; Arnold, 1983; Irschick and Garland, 2001). Many rock-dwelling lizards have highly flattened body morphology, presumably because it assists locomotion among rocky habitats (Vitt et al., 1997; Goodman, in press, Appendix I; Chapter 5). Moreover, body flattening may also enhance predator escape ability by allowing lizards access to narrow crevices (Vitt, 1981; Deban et al., 1994). Flattening may, however, cause a reduction in body cavity volume, which may, in turn, reduce clutch mass (Vitt, 1981). This reduction in body volume would have more impact on fitness if females were usually full of eggs (i.e., they are subject to volume constraints). If however, females do not usually fill themselves with eggs, a reduction in body volume due to flattening may not have an important influence on reproductive output.

In a comparison of 18 species of skinks, I found that species from rocky habitats had flatter, shorter bodies than their congeners from other habitats (Chapter 4). Thus, rock-using skinks may have reduced abdominal volume compared to their leaf-litter dwelling relatives, which may, in turn, reduce reproductive output. However, the evolutionary connection between flatter bodies, lower abdominal volume and reduced reproductive output has not been established for any species. In this study I compared 18 species of Lygosomine skink to determine whether; i) dorsoventral flattening causes a reduction in abdominal volume, and ii) species with reduced abdominal volumes exhibit a concordant reduction in reproductive output.

Methods

Gravid lizards, close to parturition, were removed from a range of habitats from five sites in north-east Queensland and transported to the laboratory where they were allowed to give birth (Chapter 2). In captivity, each female was weighed and palpated weekly to assess the closeness of oviposition, with most females (87%) producing clutches within three weeks of arriving in the laboratory.

Measurement of clutch traits

Gravid females were checked at least four times per day for recently oviposited eggs or offspring. All eggs and offspring were weighed <3 hours after ovipositon (± 0.01 g) and each post-oviposition female was weighed (± 0.01 g) and the following measures recorded; snout-vent length, inter-limb length, mid-body width, pectoral height and pelvic height (± 0.01 mm). Clutch mass (CM) was calculated as the total mass of the wet clutch or the total mass of offspring produced at a single reproductive episode. However, abdominal volume may influence the water uptake of eggs *in utero* (Qualls and Andrews, 1999), such that eggs may vary in moisture content between oviposition and measurement. Therefore, I also measured reproductive burden (Sinervo et al., 1991; Miles et al., 2000; or also called Effective Clutch Mass, ECM; pre-oviposition mass–post-oviposition mass), which is the total mass loss at oviposition, and includes the combined mass of eggs, tissues and fluid. Effective Clutch Mass differs from absolute clutch mass as it is unaffected by differential post-oviposition water uptake of eggs. When abdominal volume influences water uptake, there should be a negative relationship between abdominal volume and clutch mass, while controlling for maternal size. I examined the relationships between abdominal volume and both measures of CM while removing the influence of maternal body size (post-oviposition mass). To test whether the two clutch mass measures differed in their relationship with post-oviposition mass, I used separate-slopes ANCOVA, with snout-vent length as the covariate and the clutch mass measure (effective or actual) as the factor.

Measurement of morphological traits

For details on measurement of most morphological traits see Chapter 2. Because of the difficulty associated with obtaining a reliable measure of mid-body height during pregnancy, I used a measure of abdominal volume determined by both the height of the pectoral and pelvic girdle and lizard body width at mid-body. In addition to these measurements, I measured the width (the widest part) at the mid-body region, and the width of the pectoral and pelvic girdles of each female. Each female was radiographed within one week of oviposition and measurements (± 0.01 mm) of the pectoral and pelvic girdles were taken directly from radiographs.

Calculation of abdominal volume

Maternal abdominal volume was calculated using the formula for a cylinder: $V = \pi r^2 h$, where h = inter-limb length (the distance between axilla and groin) and r is body radius. To account for inter-specific differences in the degree of lateral and vertical distension on abdominal volume, I included pelvic and pectoral height and width, and mid-body width in the measure of r. This measure of r is the product of one sixth of pectoral and pelvic height and width and one third of mid-body width all multiplied by one half. This measure was chosen so as to incorporate the influence of body flattening on abdominal volume, and to account for inter-specific differences in abdominal distension. Moreover, this measure should be more realistic than those based on a single measure of abdominal shape, such as height, or measures that assume mid-body shape remains cylindrical (e.g., Shine, 1992).

Analyses

NON-PHYLOGENETIC ANALYSES

To investigate the relationship between abdominal volume and reproductive investment (e.g., RCM), and to avoid comparing ratios, such as RCM (Shine, 1980), I calculated RCM as the residuals from the regression of $\log_{10}$-transformed mean clutch mass against of $\log_{10}$-transformed mean post-oviposition mass (Dunham et al., 1988; Shine, 1992). Interspecific differences in abdominal space available for eggs were estimated from residuals of a regression of $\log_{10}$-transformed mean clutch mass against maternal abdominal volume (Shine, 1992).

PHYLOGENETIC ANALYSES

Phylogenetic analyses were explained in Chapter 2, except that the standardized independent contrasts for clutch mass, post-oviposition mass and abdominal volume, were calculated using PDTREE (Garland et al., 1992). All phylogenetic regressions were calculated through the origin (Garland et al., 1992). I calculated evolutionary changes in RCM as the residuals from the regression of the standardised independent contrasts of mean clutch mass against the standardised independent contrasts of mean post-oviposition mass. Evolutionary change in the amount of space available for eggs was calculated using a regression of the standardised independent contrasts of mean clutch mass against the standardised independent contrasts of maternal abdominal volume (Shine, 1992). Relationships were investigated using correlation analyses. Backwards step-wise multiple-regression was used to assess which of the morphological measures of abdomen size was the best predictor of abdominal volume. For all analyses the level of significance was set with alpha at <0.05.

Results

Non-phylogenetic analyses

BODY SHAPE AND REPRODUCTIVE OUTPUT

There was considerable interspecific variation in body size and shape, and in the reproductive traits for the 18 skink species examined in this study (Table 7.1). Holding maternal body mass constant revealed no relationship between abdominal volume and absolute clutch mass ($r_p = 0.19$, $P = 0.49$) or between abdominal volume and effective clutch mass ($r_p = 0.21$, $P = 0.31$). A separate slopes ANCOVA comparing the relationships between the two measures of clutch mass and post-oviposition mass revealed a difference in the intercepts ($t = -28.99$, $P < 0.0001$), but no difference between the slopes of the two measures of clutch mass ($F_{1,16} = 2.45$, $P = 0.13$), indicating that there is no difference between the two measures of clutch mass in their relationship with post-oviposition mass. This suggests that differences in abdominal volume are not related to amounts of water uptake by clutches. Clutch mass was significant and positively related to inter-limb length ($r = 0.92$, $P < 0.0001$), suggesting that species with longer bodies produce clutches of greater mass. More importantly, clutch mass was positively correlated with abdominal volume ($r = 0.93$, $P < 0.0001$; Figure 7.1A). Thus, species with greater abdominal volume produced heavier clutches, and the relationship between abdominal volume and clutch mass was strongly determined by lizard size. RCM was significant and positively correlated with interspecific differences in abdominal space (N = 18, $r = 0.72$, $P < 0.001$; Figure 7.1B). An outlier analysis (Mahalanobis) revealed that *Eulamprus brachysoma* was an outlier. Excluding this species did not change the significant positive relationship between abdominal volume and reproductive output. Similarly, residuals from the regression of reproductive burden against snout-vent length versus relative abdominal volume revealed a positive significant relationship (N = 18, $r = 0.70$, $P = 0.0013$). This indicates that in this group of species, variation in body shape accounted for much of the variation in RCM, regardless of the measure of reproductive effort used.

Residual maternal abdominal volume was significantly positively related to residual maternal body flatness (N = 18, $r = 0.85$, $P < 0.0001$; Figure 7.1C), indicating that species with robust (less flat) bodies had greater abdominal volume. A backwards stepwise multiple regression with abdominal volume as the dependent variable, and the six morphological measures of abdominal shape used to determine abdominal volume as independent variables, revealed that body width and pelvic width were the two variables responsible for most of the variation in body shape (Table 7.2). Thus, abdominal volume is determined mainly by body and pelvic width.

Table 7.2. Results of the backward stepwise multiple regression comparing the six measures of abdominal shape used to calculate abdominal volume of 18 species of Lygosomine lizards. Significant variables are indicated in bold type. The model's R^2 was 0.74.

Variable	*F*	*P*
Inter-limb length	2.827	0.115
Body width	9.742	**0.007**
Pectoral height	0.413	0.521
Pelvic height	0.068	0.798
Pectoral Width	0.041	0.842
Pelvic Width	4.760	**0.046**

Phylogenetic analyses

EVOLUTIONARY CHANGES IN BODY SHAPE AND REPRODUCTIVE OUTPUT

Phylogenetic analyses revealed patterns similar to the non-phylogenetic analyses. Clutch mass was positively correlated with abdominal volume (N = 17, r = 0.87, $P < 0.0001$). This indicates that evolutionary change in abdominal volume led to an increase in clutch mass, and abdominal volume and clutch mass are both strongly determined by lizard size. The comparison of residual contrasts of RCM and residual contrasts of abdominal volume were significant and positively correlated (N = 17, r = 0.69, $P = 0.0022$). This indicates that, in this group of species, evolutionary changes in body shape were the major cause of variation in RCM. Species that have evolved greater abdominal volumes have greater reproductive output.

Table 7.1. Mean maternal reproductive traits for 18 species of Lygosomine Scincid examined in this study. For details on the calculation of RCM and abdominal volume refer to materials and methods. Shown are means ± 1 standard error. Letter abbreviations for ecotype: G – Generalist, L – leaf litter-dwelling, R – Rock-using. Reproductive mode: O – Oviparous, V – viviparous.

Species (N)		Snout-vent length	Inter-limb length	Clutch Size	Post-oviposition mass	Clutch Mass	RCM	Clutch Volume	Abdominal Volume (mm^3)
Carlia jarnoldae (57)	G,O	42.74 ± 0.27	19.41 ± 0.56	1.88 ± 0.04	1.66 ± 0.04	0.32 ± 0.01	0.20 ± 0.01	313.30 ± 9.5	467.86 ± 37.3
Carlia laevis (13)	L,O	33.90 ± 0.43	18.20 ± 0.74	1.92 ± 0.08	0.68 ± 0.04	0.19 ± 0.01	0.29 ± 0.02	171.85 ± 10.8	285.41 ± 20.4
Carlia longipes (70)	G,O	58.49 ± 0.33	28.52 ± 0.46	2.00 ± 0.00	4.16 ± 0.08	0.99 ± 0.02	0.24 ± 0.00	913.79 ± 19.3	1817.77 ± 98.3
Carlia mundivensis (4)	R,O	58.52 ± 1.54	25.66 ± 0.97	2.00 ± 0.00	4.25 ± 0.53	1.17 ± 0.11	0.28 ± 0.01	929.24 ± 148.8	1416.29 ± 127.2
Carlia pectoralis (26)	L,O	43.73 ± 0.39	21.89 ± 1.07	1.96 ± 0.04	1.60 ± 0.04	0.37 ± 0.02	0.24 ± 0.01	371.79 ± 13.3	715.02 ± 87.4
Carlia rhomboidalis (12)	L,O	48.51 ± 1.12	23.81 ± 0.47	2.00 ± 0.00	2.30 ± 0.21	0.61 ± 0.03	0.28 ± 0.02	562.37 ± 46.4	897.38 ± 58.5
Carlia rococo (2)	R,O	39.05 ± 1.28	17.42 ± 0.80	2.00 ± 0.00	0.89 ± 0.06	0.25 ± 0.05	0.27 ± 0.04	258.54 ± 3.8	332.90 ± 32.6
Carlia rostralis (14)	G,O	59.05 ± 0.72	30.00 ± 0.62	1.71 ± 0.13	4.15 ± 0.18	0.69 ± 0.07	0.17 ± 0.02	628.31 ± 66.9	1805.29 ± 98.79
Carlia rubrigularis (91)	L,O	52.83 ± 0.35	25.44 ± 0.57	2.00 ± 0.00	2.99 ± 0.07	0.69 ± 0.01	0.24 ± 0.01	616.12 ± 11.0	1272.77 ± 100.5

Table 7.1 continued.

Carlia scirtetis (33)	R,O	67.23 ± 0.32	30.87 ± 0.69	1.91± 0.05	5.38 ± 0.12	0.98 ± 0.03	0.18 ± 0.01	859.37 ± 32.3	2347.92 ± 134.9
Carlia storri (23)	G,O	43.10 ± 0.34	19.82 ± 1.45	1.91± 0.06	1.71 ± 0.05	0.37 ± 0.02	0.22 ± 0.01	334.04 ± 20.3	565.54 ± 118.1
Cryptoblepharus litoralis (27)	R,O	44.50 ± 0.42	22.64 ± 0.72	1.78± 0.08	1.07 ± 0.04	0.32 ± 0.02	0.31 ± 0.02	291.80 ± 14.4	400.07 ± 27.0
Cryptoblepharus virgatus (28)	R,O	38.49 ± 0.35	19.72 ± 0.81	2.00± 0.05	0.58 ± 0.02	0.22 ± 0.01	0.38 ± 0.02	206.43 ± 8.1	278.92 ± 29.71
Eulamprus brachysoma (4)	R,V	76.19 ± 1.84	29.86 ± 1.08	5.25± 0.59	6.94 ± 0.45	2.69 ± 0.23	0.39 ± 0.02	—	1587.99 ± 240.9
Eulamprus quoyii (21)	G,V	104.10 ± 2.00	54.45 ± 2.82	6.12 ± 0.54	23.92 ± 0.15	5.66 ± 0.49	0.24 ± 0.02	—	10601.16 ± 1319.6
Lampropholis mirabilis (36)	R,O	47.80 ± 0.33	22.36 ± 0.58	2.81 ± 0.12	1.58 ± 0.04	0.44 ± 0.02	0.28 ± 0.02	414.10 ± 21.2	690.05 ± 43.8
Lampropholis robertsi (19)	L,O	42.41 ± 1.42	26.06 ± 0.63	2.26 ± 0.20	1.38 ± 0.13	0.45 ± 0.06	0.33 ± 0.03	398.18 ± 50.9	871.77 ± 58.6
Techmarscincus jigurru (8)	R, O	74.32 ± 1.62	32.77 ± 2.32	3.00 ± 0.33	5.58 ± 0.55	1.29 ± 0.16	0.24 ± 0.03	1151.21 ± 150.1	1407.29 ± 236.3

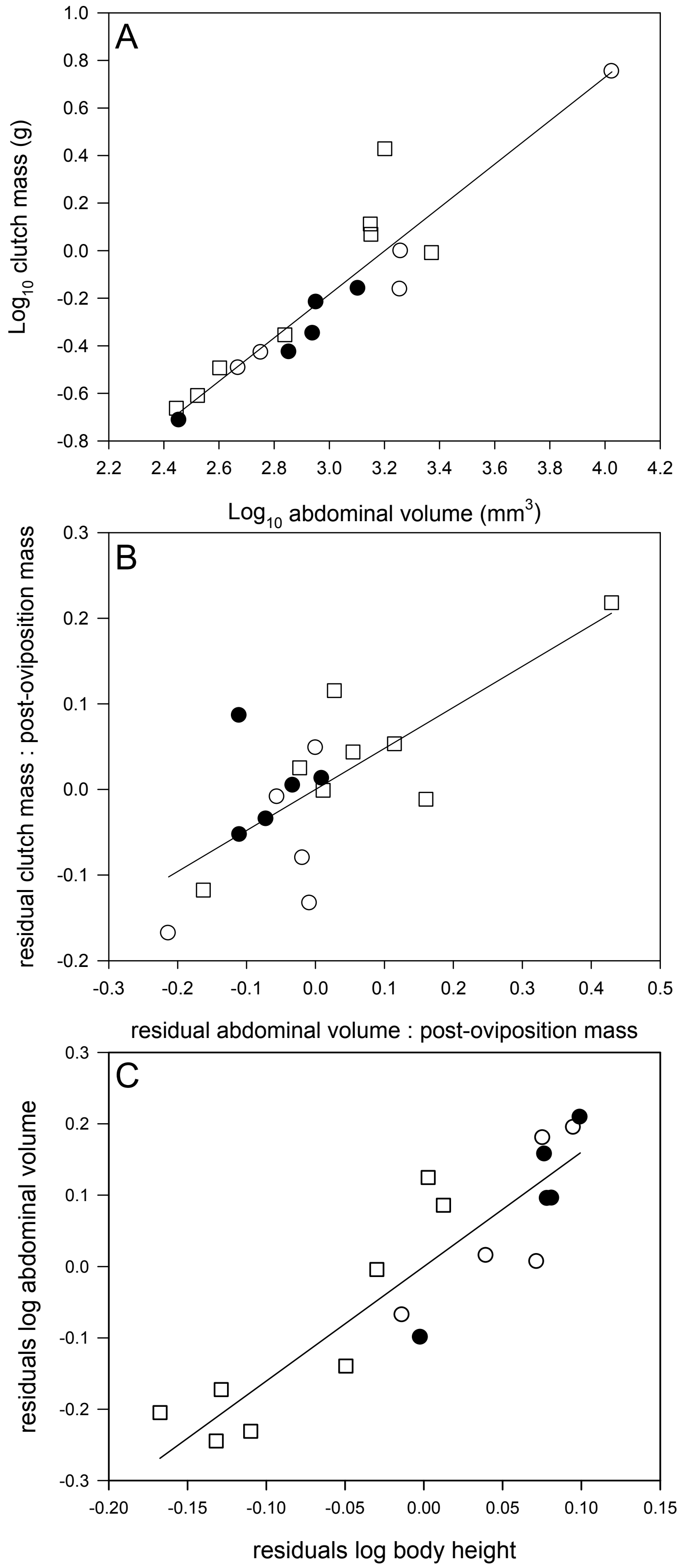

Figure 7.1. The relationship between A. abdominal volume and clutch mass B. residual abdominal volume and RCM and C. residual body height and abdominal volume of 18 species of scincid lizards. Refer to Chapter 6 for symbol legend.

Finally, residual contrasts of body flatness were significantly and positively related to residual contrasts of abdominal volume (N = 17, r = 0.64, P = 0.0056); that is, more robust (less flat) species had greater abdominal volumes. This indicates that the evolution of a flatter body does cause a reduction in abdominal volume.

Discussion

In this group of tropical skinks, body flattening was negatively correlated with abdominal volume, so that flatter species had lower abdominal volumes. Abdominal volume was strongly correlated with reproductive output (RCM), and flatter species had lower instantaneous reproductive output. These results provide strong evidence that an adaptive change in morphology towards a more flattened body does lead to a reduction in instantaneous reproductive output by a direct reduction in abdominal volume, lending support to the body constraint hypothesis.

Body shape and the evolution of RCM

The tight correlation between abdominal volume and RCM in both phylogenetic and non-phylogenetic analyses indicates that overall differences in body shape and volume are strong determinants of the evolution of among-species differences in RCM. Body size and shape have often been cited as the primary determinants of differences in reproductive output among a broad array of squamate reptiles, both among species (Vitt and Congdon, 1978; Dunham et al., 1988; Shine, 1992) and among populations within species (Forsman and Shine, 1995; Du et al., 2005b). Furthermore, the high phylogenetic correlation was similar to that identified in another study (r = 0.59; P < 0.001) that compared a taxonomically and ecologically diverse range of squamates (Shine, 1992). Previous interspecific comparisons of body-volume and RCM have typically involved taxa from a broad array of taxonomic groups (Vitt and Congdon, 1978; Miles and Dunham, 1992; Shine, 1992). My study focussed on a group of lygosomine scincids with close phylogenetic relationships, a group that display both oviparous and viviparous modes of reproduction and which have wide variation in abdominal volume and reproductive output (Table 7.1). Interspecific changes in relative clutch mass and subtle differences in body shape and volume have been detected among closely related skinks of the genus *Brachymeles* (Griffiths, 1994) and among populations of the skink *Lampropholis delicata* (Forsman and Shine, 1995) and the lacertid *Takydromus septentrionalis* (Du et al., 2005b). However, no study has examined the influence of body flattening in response to the occupation of rocky habitat on changes in abdominal volume, and whether this could influence reproductive output.

Relationships between body shape and RCM may occur because reproductive output is constrained below some upper limit, due to space limitations in the abdominal cavity or food processing or acquisition rates (Vitt and Congdon, 1978; Vitt, 1981). Body shape may determine reproductive output by way of the constraint it imposes on clutch mass, whereby body shape is the focus of natural selection on optimal reproductive effort (Shine, 1992). The high correlation between abdominal shape and both RCM and habitat (Chapter 4), suggests that changes in body shape are adaptive and have some functional role (e.g., assists in fitting into rock-crevices). Individuals with flatter bodies may gain a selective advantage as they have a wider range of rock crevices available to use, or may have lower energetic demands associated with locomotion on angled, or in structurally complex habitats (Chapter 5). An alternative hypothesis is that the habitats occupied by species with flatter bodies (i.e., rocky habitats) select for smaller egg size (Smith and Fretwell, 1974; Stearns, 1992), whereby the reduction in abdominal volume has evolved in response to a reduction in eggs size. Thus, natural selection has modified female size and shape, and therefore RCM, in accordance with selection operating on optimal egg size.

Differences in abdominal volume may influence water uptake by eggs before and after laying (Qualls and Andrews, 1999). Consequently, differences in wet clutch mass may lead to unreliable measures of reproductive output (RCM). Based on these predictions, flatter species could produce lighter eggs containing only less water, but just as much lipid and protein as species with more robust body morphology. Therefore, species with flatter boodies would have relatively lower RCMs than species with greater abdominal volumes, but still have equal investment in reproduction. In this study, of the relationship between RCM and maternal body size created from measures of wet egg mass, and effective clutch mass, had the same slope in relation to body size as measures of mass loss during reproduction, suggesting that conclusions about investment based on conventional (i.e., wet clutch mass) measures of RCM are reliable, and that uptake of water by eggs after laying is not a method used by females to allow a high reproductive investment to be stored in a small egg.

Does a flat body reduce reproductive output?

Flatter lizards should have less space within their abdomens to accommodate a clutch or brood (Vitt and Congdon, 1978; Vitt, 1981) and this study found that a flatter body was indeed correlated with a reduction in relative clutch mass. In the past, there has been considerable emphasis placed on the importance of space in defining RCM (e.g., Pianka and Vitt, 1975; Vitt and Congdon, 1978) and the ‘body-volume’ constraint hypothesis posits that all female’s will be equally and maximally full of eggs (Shine, 1992; Qualls and Shine, 1995). Thus, for the species examined in this study, all females appear to be maximally full of eggs. However, although there is a tight relationship between available space and RCM, variation exists. For example, viviparous individuals of the bimodally reproducing lizard *Lerista bougainvilli* have greater RCMs than oviparous individuals, indicating that some females of similar size are ‘more full’ of eggs (Qualls and Shine, 1995). Moreover, an experimental reduction in abdominal volume in the lacertid *Takydromous septentrionalis*, resulted in only partial reduction in clutch volume, with experimental lizards more distended by eggs than control or sham-operated groups (Du et al., 2005a). In my study, body width and pelvic width were the two variables responsible for most of the variation in body shape (Table 7.2). These studies suggest that while abdominal volume imposes an approximate limit to clutch volume, further distension and subtle differences in body shape may enable some females to be ‘more full’.

Studies of ecomorphology seek to show how adaptive changes in morphology, usually in response to changes in a specific environmental variable (e.g., perch width, predation pressure), can have a direct affect on performance or behaviour (Arnold, 1983; Garland and Losos, 1994; Irschick and Garland, 2001). This presumes that the direct pathway between morphological change and fitness occurs via performance (Arnold 1983; Garland and Losos, 1994). However, hypothetical cases may exist where changes in morphology may affect fitness without having an affect on performance (Garland and Losos, 1994). For example, albinism in snakes is not correlated with other changes in morphology or performance, but is still likely to reduce fitness because it increases the risk of predation: albino snakes are more visible than snakes with normal pigmentation (Garland and Losos, 1994). Moreover, while a pathway between morphological change and an affect on fitness may exist without passing through performance, no study has shown it (Garland and Losos, 1994). This study shows that this pathway can occur, as the changes in morphology examined (body flattening) in this study directly affected fitness (reproductive output) in a manner uncorrelated with whole-organism performance. This illustrates that a direct pathway can exist between morphological change and fitness (Arnold, 1983; Garland and Losos, 1994). That is, it suggests that in this group of lizards, the evolution of a flatter body as an adaptation for specific habitats does lead to a reduction in fitness (i.e., fecundity).

We expect that flatter species with reduced instantaneous reproductive output would have a commensurate increase in survival and longevity in the habitat occupied due to other factors, such as enhanced predator escape ability. But there is currently no data to test this hypothesis. In a non-phylogenetic comparison, species with flatter bodies had greater sprint speeds (Chapter 5), however, a phylogenetic analyses suggested there was no evolutionary relationship between these two variables. Studies of other species have shown that increased sprint speed is correlated with increased survivorship (Jayne and Bennett, 1990; Warner and Andrews, 2002; Miles, 2004), whether this is the case for this group of species is unknown. Clearly, while it is inappropriate to make direct fitness comparisons among species (Fisher, 1958; Endler, 1986; Irschick, 2001) the approach adopted in this study provides insight on the way morphological change may not always have the predicted effect on whole-organism performance. This study shows that for this group of Lygosomine lizards there is a clear evolutionary pathway between clutch mass and body shape, with body shape acting as a constraint on clutch mass and therefore, reproductive output.

CHAPTER 8

General Discussion

Aims of the thesis

My study sought to investigate the ecomorphology, performance relationships and reproductive output of a group of tropical skinks in northern Australia. The primary aim of interspecific studies of ecomorphology is to examine patterns of morphology and habitat use among species, incorporating a historical perspective into examinations of morphology and revealing factors responsible for differences among these traits (Losos, 1994; Wainwright and Reilly, 1994; Larson and Losos, 1996). This approach provides insight into the evolutionary consequences of morphological changes. Thus, the aim of this thesis has been to integrate available phylogenetic relationships with information on the ecology (microhabitat use, Chapters 3, 4 and 5), morphology (Chapters 4, 5 and 6), performance (Chapters 5 and 6), and reproductive output (Chapter 7), of a group of tropical skinks in order to gain a more thorough understanding of the processes that lead to the evolution of specific morphological and performance traits. The purpose of this chapter is to summarise the main findings of this thesis and discuss their relevance to current theory in ecomorphology, evolution and adaptation.

Patterns of microhabitat use

This group of tropical skinks used available microhabitats non-randomly, with species separating according to the substrate type, amount of leaf litter, ground cover, undergrowth, proximity to vegetation and the amount of canopy cover. More specifically, most of the separation in structural microhabitat was attributed to a gradient ranging from large rocks through to leaf litter. Substrate has been identified as an important feature separating several other lizard groups (Paulissen, 1988; Howard and Hailey, 1999; Melville and Swain, 2000; Melville and Schulte, 2001). Interestingly, published species descriptions of some of the species examined in this study (*L. mirabilis, C. rococo, C. scirtetis, T. jigurru*) suggest that they are specialized rock users (Ingram and Rawlinson, 1978; Ingram and Covacevich, 1988, 1989; Covacevich, 1984). This study supports this suggestion, and highlights the importance of the substrate in defining the positions of species in structural microhabitat space (Chapter 3). Overall, while all species tended to be active at the same times of day, there were cases where species from the same ecotype did not overlap in size, suggesting that separation may sometimes occur along axes other than substrate type (e.g., size). Further, assemblages consisting of more species showed evidence of species packing, and were less evenly packed than assemblages with only few species. In these skink assemblages, it appears additional species are accommodated by the occupation of more diverse niches.

The non-random microhabitat use and microhabitat separation suggests that these species assort and occupy microhabitats (presumably as determined from morphological adaptations) for which they are most well suited. However, while a key component of any concept of adaptation is the assumption that species will use habitats in which their morphology is most well suited (Lauder, 1996), assessing this idea requires a test of the relationship between habitat use and morphology (Arnold, 1983; Garland and Losos, 1994).

Relationships between morphology and microhabitat use

Examining the link between an organisms' functional morphology and its environment can provide much insight into adaptation (Arnold, 1983; Garland and Losos, 1994; Wainwright and Reilly, 1994). However, sexual selection may cause morphological differences between sexes, independent of ecologically mediated natural selection. In both sexes, species evolved increased limb length in response to increased habitat openness and the increased use of rocky habitats. In addition, there was evolutionary change in the degree of body flattening (body height and head height) in response to the occupation of rocky habitats. Thus, the evolution of a dorsoventrally flattened morphology appears to be an adaptive response to the occupation of rocky habitats in this group of lizards. Biomechanical models predict that climbing species should have flat heads and bodies to assist in keeping the body close to the climbing surface, to reduce the influence of gravity from pulling the body away from the substrate (Vitt, 1991b; Vanhooydonck and Van Damme, 1999; 2001; Zaaf and Van Damme, 2001). These models also predict that climbing species should have short limbs (Zaaf et al., 1999; Vanhooydonck and Van Damme, 2001; Zaaf and Van Damme, 2001), but I found that species adapted for rocky habitats (that require climbing) had longer limbs than non-climbing species (Chapter 4). In general, lizard species from open, terrestrial habitats, which lack armature (See Losos et al., 2002), may conform to one of two alternative behavioural strategies leading to divergence in morphological traits. Species can run at high speed at the approach of a threat, to reduce the time required to reach shelter, or they can remain motionless, and flatten their body against the substrate. Species adopting the former strategy should evolve longer hind limbs and short forelimbs to enhance speed to cover long distances quickly (Snyder 1954; Cartmill, 1985; Losos, 1990b; Appendix I). Indeed, numerous studies confirm that species evolve longer hind limbs and greater sprint speeds (Miles, 1994; Melville and Swain, 2000), when associated with more open habitats, or wide perches. In lizard species adopting the alternative strategy, which relies on motionless crypsis to avoid detection, species typically have short, flat bodies and heads, and colours that match the background, in this situation, selection on limb length for increased speed should be reduced (Losos, 1990a; Schulte et al., 2004). My study suggests that many rock or open habitat using species have evolved long limbs and rapid running speed, and that species from identical habitats show similar traits. However, while this may be the overall conclusion, other factors (e.g., proximity to refugia, increased wariness, possession of armature) may alter the general significance of these observations in particular cases. For example, *C. mundivensis* uses enclosed, rocky habitats, but has short limbs, a robust body and poorer performance than another rock-using species (Appendix 1). As such, *C. mundivensis* relies more on large approach distances to avoid predation (Goodman, in press; Appendix I), suggesting behavioural mechanisms may preclude or delay morphological adaptation under such circumstances (Huey et al., 2003; Schulte et al., 2004).

In this group of Lygosomine lizards, intersexual differences in morphology appear to be the result of sexual selection or selection for different locomotor or reproductive function in different habitats between the sexes. Species using rocky habitats had flatter bodies than species using leaf litter, and males were more dorsoventrally flattened than females. In both sexes, species evolve increased limb length in response to increased habitat openness. One potential cause of this intersexual difference is the type and magnitude of selection which operates independently on each sex. In this case, the need to accommodate eggs or offspring when gravid appears to select against body flattening and the resulting reduction in abdominal volume, in females to the same degree as in males (Shine, 1992; Stearns, 1992; Olsson et al., 2002).

The fact that males are flatter than females suggests that without the advantage of increased fecundity, the taller body morph of females would only have performance disadvantages, such as a reduction in the range of crevices that could be used for refuges. However, in Chapter 5 I found there was no relationship between the degree of body flattening and four measures of performance. Instead, it may be that male combat success is an important selective force associated with intrasexual differentiation (Darwin, 1871; Andersson, 1994). Traits correlated with increased performance may provide males with a selective advantage in situations of male-male combat. For example, increased head size provides a selective advantage in lizards that bite each other as part of male-male combat (Huyghe et al., 2005; Lappin and Husak, 2005), due to the functional relationship between increased head size and bite force (Herrel et al., 1999). In a similar way, there may be strong selection for body flattening, or traits associated with body flattening, if such traits correlate with increased male combat success or mate choice (e.g., body size; Andersson, 1994, Shine, 1994; Lappin et al., 2006).

Interestingly, phylogenetic analyses revealed no direct performance benefit of a flattened body plan (Chapter 5). Studies on other lizard groups have highlighted the importance of a flat body and head for fitting into rock crevices to take refuge from predators (Vitt, 1981; Lappin et al., 2006). Indeed, often such traits occur in conjunction with other mechanisms, such as lung inflation (Deban et al., 1994) and sharply keeled scales (Chapple, 2003) that reduce the possibility of predators extracting them directly from a crevice. However, other than a flat morphology, the species examined in this study lack other traits that may assist with remaining within a crevice. Thus, it appears that the flat body of the species examined may simply act to increase the relative availability of crevices that can be used as refuges (Chapter 5).

Morphology – performance relationships and locomotor trade-offs

This study found no support for the ‘jack of all trades master of none’ model, with no trade-offs observed between sprinting, climbing and clinging. The strong positive correlation between sprinting and climbing, in both skinks and lacertid lizards (Vanhooydonck and Van Damme, 2001), and between clinging and climbing in scincids implies that these traits require similar morphological features in those groups. Moreover, the positive relationship between sprinting and climbing was opposite to the negative relationship observed between those two variables in lizards that climb on narrow perches, indicating that the morphological traits that enhance sprinting and climbing ability on broad surfaces do not appear to enhance both performance traits on narrow perches.

Lizards with longer hind-limbs sprinted faster, which is probably due to the increased stride length achieved with longer hind-limbs (e.g., Hildebrand, 1974; Cartmill, 1985; Losos, 1990a). Further, although suggested in the literature, there was no indication that long fore-limbs impede running in my study (Losos, 1990b). Increased fore-limb length was strongly, positively correlated with running speed; climbing speed was enhanced by both increased fore- and hind-limb length. Increased fore-limb length, and equal length fore- and hind-limbs may be beneficial to speedy movement because they allow similar length strides to be taken with each limb (Arnold, 1998; Vanhooydonck and Van Damme, 2001). Longer fore-limbs probably benefit climbing by increasing tension, which should reduce the possibility of tumbling backwards when climbing an angled surface (Cartmill, 1985; Alexander, 1992; Aerts et al., 2000). Because increased locomotor speed may increase the tendency for the body to lift, resulting in bipedal locomotion (Aerts et al., 2003), morphological traits that lower the centre-of-mass and bring it forward should reduce the possibility of fore-body lifting. In addition to body flattening (Van Damme et al., 1997), these traits include increased fore-limb length to widen the base of support, and a more sprawled form of locomotion (Aerts et al., 2003). While my study found support for increased fore-limb length to increase performance in climbing and clinging, I found no evidence that a flatter body aided performance (Chapter 5).

Lizards with longer fore-limbs had greater clinging ability, which may be related to an increased base-of-support (Aerts et al., 2003), or number of sub-digital lamellae, which increase frictional forces and improve contact on surface irregularities (Cartmill, 1985; Losos, 1990a). Increased cling ability in species with longer fore-limbs should also assist climbing by improving traction on an inclined slope. Chapter 4 (and Appendix I) also indicate that species with long limbs also have long digits, which suggests that increased limb-length and toe length may combine to increase clinging ability in this group.

This study identified no relationship between morphology and jumping performance. However, while numerous other studies have highlighted the positive biomechanical advantage of increased limb length for increased jump distance (Emerson, 1978; Losos, 1990a), other work has shown that jump performance may be unrelated to limb length (Toro et al., 2004). As such, other morphological, and/or physiological (e.g., muscle mass, muscle physiology), and behavioural mechanisms (e.g., jumping while running) may play a prominent role in aiding jump performance in the absence of changes in limb length (Chapter 6).

However, the absence of trade-offs among the performance traits measured here in skinks and lacertids does not mean that trade-offs do not exist in other areas. Body shape has a strong influence on reproductive output in lizards (Vitt and Congdon, 1978; Vitt, 1981; Vitt and Price, 1982), and the flat body of many rock-using species reduced fecundity (see below). Alternatively, a trade-off may occur in other performance measures, such as endurance (Vanhooydonck et al., 2001). However, the clear message from this study is that morphologically specialized species were simply better at a greater range of tasks that are sufficiently similar that no trade-offs among them were required.

Microhabitat use – performance relationships

There was a strong positive relationship between limb-length and a gradient of rock to leaf-litter use in this group of skinks (Chapter 4). Further, the differences defined by this gradient of microhabitat use and performance are ecologically relevant, and an increased use of rocks was accompanied by a significant increase in limb length (Chapter 4) and increases in sprinting and climbing performance (Chapter 6). These relationships between limb length and performance have clear implications for adaptation (Losos, 1990a; Garland and Losos, 1994; Chapter 5; See above), and are analogous to the relationship between perch diameter and speed identified in *Anolis* (e.g., Losos and Sinervo, 1989; Irschick and Losos, 1999).

In addition to microhabitat type, both male and female skinks that occupied open habitats sprinted faster than those using closed habitats (See above). Males in open habitats also had faster climbing speeds, and better clinging ability than those from closed habitats, whereas these relationships were not significant for females. Possibly, male combat or mate searching selects for good climbing and clinging ability. Enhanced cling ability is likely to lead to increased climbing speed, because of the need to cling well when climbing (Losos et al., 1993). In females, which typically move less and have smaller home ranges, perhaps there is less of a selective advantage for climbing and clinging. Alternatively, other factors that impose selection on morphology, such as behaviour (Huey et al., 2003; Schulte et al., 2004) may constrain female morphology and prevent adaptation of clinging and climbing ability. For instance, gravid females with reduced speed and mobility are often also more wary (Bauwens and Thoen, 1981; Brodie, 1989; Schwarzkopf and Shine, 1992).

Intersexual differences in performance

Clinging performance was significantly correlated with substrate use for males, but not females. Similarly, while there was a significant, positive relationship between climb speed and microhabitat openness in males, this relationship was not significant in females, suggesting that selection on increased climbing performance in open habitats may operate less intensely in females. Intersexual differences in performance may arise due to sexual selection (Darwin, 1871; Andersson, 1994), and it is possible that climbing and clinging are related to male reproductive success. For example, the ability to cling well may be important for male-male combat. Both clinging and climbing ability may be important performance traits linked to reproductive success in rocky habitats in males, as increased climbing speed may increase reproductive success by allowing males to catch females for mating or to defend territories (Hews, 1990; Molina-Borja et al., 1998; Lappin and Husak, 2005), if they are territorial. Clinging and climbing may be co-evolved in males, as increased clinging ability is likely to be an important performance benefit for increased climbing speed. While females may experience similar selection for enhanced climbing and clinging ability as males, antagonistic selection between natural selection for survival (on performance) and fecundity selection (on body shape) for reproductive output (Wikelski and Trillmich, 1997; Olsson et al., 2002; See also Lappin et al., 2006), may restrict how they respond (see above Microhabitat use–performance relationships).

Specialist or generalist?

Differences in niche breadth are central to trade-offs between performing well in a few habitats, but poorly in a wider range of habitats (Futuyma and Moreno, 1988; Caley and Munday, 2003). Despite theoretical predictions for habitat restricted species, I found only partial evidence that habitat specialisation leads to increased performance. That is, the specialized use of few habitats was unrelated to the measures of performance examined (Chapter 6). Correlating the two gradients of habitat use (rock use and openness) with morphological and performance adaptation, revealed that for species specialised for using non-rock microhabitats performance was poorer than for species that frequently used rocks. Similarly, species specialised for closed habitats were poorer performers than species specialised for open habitats (Chapter 6).

Species specialised for closed and leaf litter habitats had slower sprinting, climbing and poorer clinging performance, suggesting that the performance traits of species from these habitats experience a reduced selective benefit for these performance traits. It appears that selection for stealth and/or frequent stopping while hunting prey, or as a form of crypsis for avoiding predators is likely of utmost importance. Under this scenario selection for increased performance is likely to be weakened. Nonetheless, the laboratory measures of climbing, sprinting and clinging likely provide a good measure of an important performance for species from broad substrates. A more robust test of this idea would require data on the performance of species from leaf-litter habitats (e.g., sinusoidal locomotion), as the greater limb length of rock-using species may interfere with locomotion though leaf-litter or dense vegetation. However, whether these species are effective at using leaf-litter over reasonable distances or experience a negative effect on speed or manoeuvrability when escaping is unknown (Vanhooydonck and Van Damme, 2003). Nonetheless, while my study did not investigate the decrement in performance along a habitat gradient relative to the proportion the habitat is used by a species, it does offer insight into the habitats species are likely to avoid (Irschick and Losos, 1999; Irschick, 2002).

Previous ecomorphology studies have established that perch diameter has been important in the evolution of *Anolis* morphology and performance (Losos and Sinervo, 1989; Irschick and Losos, 1999), and habitat openness in the evolution of morphology and performance of skinks in the genus *Niveoscincus* (Melville and Swain, 2000). My study established that gradients from rock to leaf litter and from closed to open habitats are important influences on performance in this group of tropical skinks (Chapter 6). Open habitat and rocky habitat (which is usually open) may be sufficiently similar that good performance in one leads to good performance in the other. The intersexual differences in the scincid group I studied suggests that selection for some performance tasks may affect sexes differently, either in the form of increased selection pressure on males for high performance, or by way of a constraint on female morphology and performance.

Does a flat body reduce reproductive output?

Body flattening was negatively correlated with abdominal volume, with flatter species having lower abdominal volumes. Abdominal volume was strongly correlated with reproductive output (RCM), such that flatter species had lower reproductive output. Body shape determines reproductive output by way of the constraint imposed on clutch mass (Vitt and Congdon, 1978; Shine, 1992). The high correlation between abdominal shape and both RCM and habitat (Chapter 4), suggests changes in body shape are adaptive and have some functional role (e.g., using rock-crevices). However, unlike previous suggestions of rock crevice use (e.g., Vitt, 1981), it appears that body flattening in this group of skinks allows the use of a wider range of retreat cervices, and may also be related to reducing the energetic demands of locomotion on angled surfaces and in structurally complex habitats (Chapter 5).

This study tested an unexplored pathway of Arnold's paradigm: whether adaptive changes in morphology affect fitness without passing through the intermediate stages of performance or behaviour (Garland and Losos, 1994). That is, an adaptive change in morphology (body flattening) as an adaptation for specific habitats was unrelated to enhanced performance, but lead to a reduction in fitness (i.e., fecundity). While the observed reduction in fecundity may be offset by increased survivorship or enhanced performance within the context of the habitat occupied, there is currently no data to test this idea. Moreover, flat, rock-using species with reduced instantaneous reproductive output should experience increased survival and longevity. Assuming all-things-are-equal, however, while reduced reproductive output is a consequence of a flat morphology, it may be inappropriate to compare fitness among species and relate such differences to interspecific differences in performance (Fisher, 1958; Endler, 1986; Irschick, 2002).

Directions for future research

This study of tropical skinks has laid the foundation for research that could address several areas of evolution, performance, life history and adaptive change. For example, future work could examine patterns of intraspecific variation in habitat use and whether populations from different habitats display both morphological and performance adaptation. While this study identified no trade-off between climbing and sprinting, or between climbing and clinging, it is not possible to reject the hypothesis that a trade-off does not exist in another area. Thus, it may prove beneficial to investigate another aspect of performance in this group (e.g., endurance; Vanhooydonck and Van Damme, 2001). Future work could examine intraspecifc variation in habitat use to test whether the interspecific patterns of morphology, performance and reproductive output, observed in this study, occurs within a species. Moreover, there was considerable variation in maximum performance among species (Chapters 5 and 6). Work on species from other groups (Anolis and Lacertids), suggests species with high performance use a lower proportion of their maximum performance ability on average in nature (Irschick and Losos, 1998; Irschick et al., 2005). This has never been examined in the Scincidae. Finally, an examination of the consequence of a reduced abdominal volume on other life history traits (e.g., increased longevity, delayed maturation, offspring size), such as whether the trade-off in volume is ameliorated in some other way, perhaps by way of a capture-mark-recapture study.

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APPENDIX I

Divergent morphologies, performance and escape behaviour in two tropical rock-using lizards (*Reptilia: Scincidae*)

(In press [*Biological Journal of the Linnean Society*])

APPENDIX II

Costs of reproduction in a tropical invariant-clutch producing lizard (Carlia rubrigularis). [Journal of Zoology 270 (2006) 235-243]

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