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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 Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given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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I thank the people of Gungardes, especially Ronnie Harrigan and the traditional owners and custodians of Black Mountain for allowing me access to this site, so I could work on some amazing lizards. I thank Beck, Jon Spencer, E. D. Metal, Q. Otsa and P. J. Harvey for their unwavering support and inspiration over the past several years. A final mention must go to my own personal supervisor, Joanne Isaac for her love, help (in all areas) and encouragement over the past three years. Finally, the past four months have placed the rest in perspective thanks to the 'little man', Kai (aka 'The Little').

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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