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Beyond Abundance:

**The direct and indirect effects of predation
in a terrestrial trophic web**

Thesis submitted by

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BSc (Hons) University of Cape Town

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for the degree of Doctor of Philosophy

in the School of Marine and Tropical Biology

James Cook University



Clockwise from top: The study site at Ramsey Bay, Hinchinbrook Island, picture taken from Nina Peak towards north; juvenile *Carlia storri*; varanid access study plot in *Melaleuca* woodland; spider *Argiope aethera* wrapping a march fly; mating pair of *Carlia rubrigularis*; male *Carlia rostralis* eating huntsman spider (Family Sparassidae). © C. Manicom

Abstract

We need to understand the mechanism by which species interact in food webs to predict how natural ecosystems will respond to disturbances that affect species abundance, such as the loss of top predators. The study of predator-prey interactions and trophic cascades has a long tradition in ecology, and classical views have focused on the importance of lethal predator effects on prey populations (direct effects on density), and the indirect transmission of effects that may cascade through the system (density-mediated indirect interactions). However, trophic cascades can also occur without changes in the density of interacting species, due to non-lethal predator effects on prey traits, such as behaviour (trait-mediated indirect interactions). Studies of direct and indirect predation effects have traditionally considered predator control of herbivore populations; however, top predators may also control smaller predators. Due to their versatility and high predation rates, intermediate-level predators (mesopredators) may have disproportionably larger effects on lower trophic levels than top predators. Despite knowledge of the importance of indirect predation effects, and the effects of mesopredators, there is little evidence of the relative importance of density- and trait-mediated effects of predation in complex terrestrial trophic systems.

My study consisted of a manipulative field experiment where the effects of top predators and mesopredators were both simultaneously and individually isolated. I manipulated the access of varanids (top predators) and skinks (mesopredators) to areas at my study site using large (200 m²) fenced study plots, and determined the effects of these predators on spiders (lower-order mesopredators), other arthropods and primary producers. To appreciate the impact that predation had on fauna, a detailed understanding of the ecology of the prey species was needed. Small skinks dominated the faunal community at my study site and thus were likely to make a large contribution to energy flow in the system, both as prey to higher trophic levels and as predators of lower trophic levels. Current knowledge of the demography, ecology and life history strategies of small, tropical skinks was inadequate. I described the population structure, survival rates, reproductive seasons and recruitment patterns of the dominant skink species at my study site, and I defined their growth patterns, age at maturity,

sexual dimorphism and relationship with ectoparasites. I found that these closely-related, sympatric skinks shared similarities in many aspects of their life history, but that different mechanisms acted on juvenile skinks to cause various amounts of sexual dimorphism of adult body size. Observations of skink activity, use of microhabitat and behaviour revealed that skinks were highly active; suggesting that they were efficient and effective foragers, but also conspicuous and highly vulnerable to predators. From diet analysis, I determined that skinks were selective in their prey choice, consuming certain prey types and sizes that were in short supply in the environment.

The species varied in the prey they consumed, but spiders and orthopterans were consistent prey types for all skinks. Skinks were found to have a strong direct effect on spider abundance in study plots; they reduced the density of cursorial spiders and of web-building spiders close to the ground. The number of web-building spiders was, in turn, negatively correlated with the abundance of aerial arthropods. Herbivore damage to leaves was reduced in skink access plots. The selective removal by skinks of other predators (spiders) and herbivores (orthopterans) from the trophic system was thus shown to have far-reaching indirect effects that cascaded through the system to alter the composition of the arthropod community, and the amount of damage to local vegetation.

Varanids did not directly alter the abundance of skinks or arthropods, but did have strong indirect effects. Skinks significantly reduced their activity in the presence of varanids, likely leading to lower energetic requirements and less foraging. The cascading effects of predation on skink activity were evident when comparing arthropod community composition among study plots: skinks directly altered the structure of the arthropod community by consumption and in the presence of varanids, skink foraging was restricted. In the absence of varanids, however, skinks were 'released' from predation threat, and only those arthropod taxa rarely consumed by skinks were abundant. Varanids thus indirectly altered arthropod community composition by altering skink behaviour, clear evidence of a trait-mediated indirect effect of predation. This is the first study, to my knowledge, to experimentally show the effect of behaviourally mediated mesopredator release on lower trophic levels, and such behavioural predator effects may be very influential in community ecology. The results of my study reveal

the strength and importance of indirect predation effects, and show that measuring more than just the abundance of individuals is vital to determine the full effects of predator removal.

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Declaration on Ethics

The research presented and reported in this thesis was conducted within the guidelines for research ethics outlined in the *National Statement on Ethics Conduct in Research Involving Humans* (1999), the *Joint NHMRC/AVCC Statement and Guidelines on Research Practice* (1997), the *James Cook University Policy on Experimentation Ethics. Standard Practices and Guidelines* (2001), and the *James Cook University Statement and Guidelines on Research Practice* (2001). The proposed research methodology received clearance from the James Cook University Experimentation Ethics Review Committee (approval number A677).

(Signature)

(Date)

Preface

The only data used in this thesis that I did not collect myself were spider counts collected by Joanne Bussey (Honours student, James Cook University, 2005) in April – May 2005, and July – August 2005 (Chapter 9).

I collected data from April 2003 to December 2004 during seven field trips to my study site on Hinchinbrook Island as part of my job as a research officer for the School of Tropical Biology, James Cook University.

Chapter 7 (Diet and prey selection of sympatric tropical skinks) is currently in press (*Austral Ecology*), myself and Lin Schwarzkopf are authors. The manuscript presented as Appendix B (Self-made shelters protect spiders from predation) was written by myself, with co-authors Lin Schwarzkopf, Ross Alford and Thomas Schoener, and was published in 2008 (*Proceedings of the National Academy of Sciences* 105 [39]: 14903–14907). The manuscript presented as Appendix C (The cost of failing to thermoregulate is higher in the tropics: A conceptual model and empirical test) was written by Mathew Vickers, with myself and Lin Schwarzkopf as co-authors. It is currently under review (*The American Naturalist*).

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Thank you so much to Nicola Peterson, who introduced me to Hinchinbrook Island, and taught me how to catch, handle and measure lizards. And to Joanne Bussey, who got the ball rolling on spider counts and has generously allowed me to use her data. My sincere thanks to Rick Mayfield, who constructed the enclosures at my study site in 1997, and to Ashley Frisch, who repaired them in 2003.

This project would not have been at all possible without the help of many volunteers who very generously braved the heat, sandflies, and cheap cask wine to join me on Hinchinbrook Island. I am extremely grateful for every lizard captured, every spider counted and every insect sampled, but also for the company, ideas and energy – thank you to Ainslie Langdon, Alex Howard, Alycia Nolan, Angie Shuetrim, Ashley Curran, Ashley Pearcy, Bene Eftevand, Bec Adams, Brad Evans, Brendan Meale, Buck Buckley, Chris Ryen, Danene Jones, Deb Bower, Don Miles, Eric Russell, Erin Albin, Heather Mlynarski, Hunter Petersen, Jacqui Herbert, John Llewelyn, Kathryn Markey, Kathryn Rose, Malin Gustafsson, Manue Botte, Margit Wilhelm, Marie Magnusson, Matt Barbour, Megan Barnes, Øyvind Syrrist, Rach Viney, Rich Duffy, Scott Pollock, Seb Adams, Stephanie Vucko, Steve Mastromonaco, Stewart Lee, Tara Burrows and Tim Atwood.

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Table of contents

Abstract.....	i
Statements of access and sources	iv
Declaration on Ethics	v
Preface	vi
Acknowledgements	vii
List of figures.....	xvi
List of tables.....	xix

Chapter 1

Introduction and overview	1
Loss of top predators and the implications for trophic web ecology.....	1
Measuring density- and trait-mediated interactions in trophic webs: importance, current limitations and ways forward	2
Lizards as model organisms.....	3
Thesis overview.....	4

Chapter 2

Description of the study site and general field methods.....	7
Study site, climate, vegetation and fauna	7
Study system and experiment design	9
Habitat available within study plots.....	14
Skink sampling	16
Stomach contents and reproductive condition	17
Activity observation surveys.....	18
Spider census.....	18
Arthropod sampling.....	19
Herbivory.....	20

Chapter 3

The population ecology of tropical sympatric skinks	21
Abstract.....	21
Introduction	22
Methods	23
Skink population estimates	23
Skink survival and recapture probability	25
Skink longevity.....	26
Juvenile recruitment and survival	26
Timing of reproduction, age and sex ratios.....	27
Skink body condition.....	27
Habitat, microhabitat, habits and behaviour of skinks	28
Space use	28
Analyses.....	28
Results.....	29
Skink species at the study site	30
Description of <i>Carlia</i>	31
Population estimates.....	33
Survival and recapture rates	34
Reproduction, sex ratios, longevity and body condition of <i>Carlia</i> at the study site	36
Juvenile recruitment, survival and age ratios	40
Habitat, microhabitat, habits and behaviour of <i>Carlia</i> species	44
Space use by <i>Carlia</i> species.....	48
Discussion.....	49
Population structure and reproduction of <i>Carlia</i> at the study site.....	49
Habitat and behaviour of <i>Carlia</i>	52

Chapter 4

Juvenile growth and sexual size dimorphism in sympatric tropical lizards: proximate and ultimate causes	54
Abstract.....	54

Introduction	55
Methods	58
Sexual dimorphism	58
Growth.....	58
Size and age at maturity	59
Survival	59
Prey size dimorphism.....	61
Analyses.....	61
Results.....	61
Sexual dimorphism	61
Age-size growth curves.....	64
Growth rate.....	67
Survival	69
Prey size dimorphism.....	70
Discussion.....	71
Shape dimorphism	72
How do observed patterns in dimorphism develop? Size dimorphism due to growth rate and age at maturity	74
 Chapter 5	
No fitness costs in the relationship of <i>Carlia</i> with trombiculid mite larvae	80
Abstract.....	80
Introduction	81
Methods	83
Study species	83
Measurement of fitness related variables	84
Statistical analysis of fitness-related variables	85
Modelling survival probabilities.....	86
Results.....	89
Discussion.....	95

Chapter 6

Differences in the physical structure of <i>Carlia</i> limb axillae: the relationship with mite infestation.....	100
Abstract.....	100
Introduction	101
Methods	103
Results.....	104
Discussion.....	106

Chapter 7

Diet and prey selection of sympatric tropical skinks	108
Abstract.....	108
Introduction	109
Methods	110
Diet composition	110
Available prey	111
Analyses.....	111
Results.....	113
Dietary composition	113
Prey size.....	117
Comparison of diet with available prey	118
Selectivity for sizes	123
Discussion.....	126
Foraging mode	126
Prey size differences among the species	127
Prey selectivity by <i>Carlia</i>	128
Consequences of selectivity.....	130

Chapter 8

The relative importance of density- and trait-mediated predator effects in a terrestrial system: varanid effect on skink abundance and behaviour.....	132
Abstract.....	132

Introduction	134
Methods.....	137
Skink population density estimates.....	137
Skink survival and recapture probability	138
Skink activity.....	138
Skink growth rate, body size, body condition and parasite load	139
Statistical analysis	140
Results.....	140
Skink density	140
Survival and recapture rates	144
Skink activity.....	145
Juvenile growth rate, adult body size and body condition, and ectoparasite load ...	146
Discussion.....	151

Chapter 9

Direct and indirect effects of predators in a multi-level trophic web	156
Abstract.....	156
Introduction	158
Study system	160
Methods.....	161
Experimental design and manipulated species.....	161
Arthropod abundance and proportion of herbivory	161
Habitat.....	162
Analyses.....	162
Results.....	165
Exclusion of skinks	165
Cursorial spiders.....	166
Web-building spiders	166
Other arthropods.....	169
Herbivory	172
Habitat.....	173

Discussion.....	175
-----------------	-----

Chapter 10

Concluding remarks and future directions	181
---	------------

Beyond abundance	184
------------------------	-----

Future directions	184
-------------------------	-----

References.....	186
------------------------	------------

Appendix A

The threat from aerial predators to skinks at the study site.....	215
---	-----

Appendix B

Self-made shelters protect spiders from predation.....	224
--	-----

Appendix C

The cost of failing to thermoregulate is higher in the tropics: A conceptual model and empirical test.....	230
--	-----

List of figures

Figure 2.1. Location of the study site at Ramsay Bay on Hinchinbrook Island, north-eastern Queensland, Australia.....	7
Figure 2.2. Mean monthly minimum and maximum temperature (°C) and rainfall (mm) for the study period, showing 99-year average temperatures (°C) and 135-year average precipitation (mm).	8
Figure 2.3. Timeline of the experiment, showing months and seasons when sampling took place.....	9
Figure 2.4. The trophic web at the study site, arrows show direct predation and indicate direction of energy flow.	11
Figure 2.5. Layout of the study plots at the study site.....	13
Figure 2.6. Study plots: (a) tall fenced plot to exclude varanids, (b) hole in fence at ground level to allow access to small lizards, (c) sealed fence to exclude small lizards, (d) low fenced plot to allow access to varanids, (e) unfenced control plot.....	13
Figure 2.7. Schematic diagram of a single study plot, showing grid design and location of sampling points.....	15
Figure 3.1. Total skinks captured in study plots on each sampling occasion.....	29
Figure 3.2. The three most abundant species at the study site on Hinchinbrook Island: (a) <i>Carlia rostralis</i> , (b) <i>C. rubrigularis</i> , and (c) <i>C. storri</i>	32
Figure 3.3. Distribution of body sizes for the three <i>Carlia</i> species from the study site.	32
Figure 3.4. Population estimate for each species of <i>Carlia</i>	34
Figure 3.5. Survival probability between each sampling occasion, from mark-recapture models of the three <i>Carlia</i> species.	35
Figure 3.6. Ratio of males to females in the population in each month of the year sampled, for the three <i>Carlia</i> species.	37
Figure 3.7. Ratio of gravid females to non-gravid females in the population in each month of the year sampled, for the three <i>Carlia</i> species.....	38

Figure 3.8. Residual values for males and females of the three <i>Carlia</i> species in the late wet, early dry, late dry and early wet seasons.....	40
Figure 3.9. Recruitment of juveniles of each <i>Carlia</i> species between sampling occasions. ...	41
Figure 3.10. Ratio of adults to juveniles for each month of the year sampled, for the three <i>Carlia</i> species.	42
Figure 3.11. Proportion of juvenile skinks, marked first as hatchlings, surviving to three, six and 12 months, for the three <i>Carlia</i> species.	43
Figure 3.12. The proportion of each species of <i>Carlia</i> captured within each habitat type.....	44
Figure 3.13. Number of skinks observed (logarithmic scale) at four categories of height above ground, for each of the <i>Carlia</i> species.	45
Figure 3.14. Daily activity patterns of the three <i>Carlia</i> species at the study site.	46
Figure 3.15. Skink behaviour observed during activity surveys, for the three <i>Carlia</i> species.	47
Figure 3.16. Area of space used by <i>Carlia</i> species calculated from individuals captured on more than five occasions.	48
Figure 4.1. Mean snout-vent length (SVL) and 95% confidence intervals of male and female <i>Carlia rostralis</i> , <i>C. rubrigularis</i> and <i>C. storri</i>	62
Figure 4.2. Growth trajectories of male and female <i>Carlia</i> lizards: <i>C. rostralis</i> , <i>C. rubrigularis</i> and <i>C. storri</i> from the von Bertalanffy model, with minimum size and age at maturity for each sex.....	66
Figure 4.3. Mean snout-vent length (SVL) between captures versus growth rate, with lines of best fit from regression equations for male and female for the three species.	68
Figure 6.1. Three <i>Carlia</i> species from the study site on Hinchinbrook Island with detail of limb axillae below, (a) <i>C. rostralis</i> , (b) <i>C. rubrigularis</i> and (c) <i>C. storri</i>	103
Figure 6.2. Scanning electron micrographs of species (a) <i>C. rostralis</i> , (b) <i>C. rubrigularis</i> and (c) <i>C. storri</i>	105
Figure 6.3. SEM of attached chigger mite <i>Eutrombicula</i> sp. <i>in situ</i> within limb axilla of <i>Carlia rostralis</i>	106
Figure 7.1. Relative abundance of prey types in the traps (available prey), and in the stomachs of <i>C. rostralis</i> , <i>C. rubrigularis</i> and <i>C. storri</i> in the wet season and dry season.....	120

Figure 7.2. Multidimensional scaling plot of species' diet (<i>C. rostralis</i> , <i>C. rubrigularis</i> , <i>C. storri</i> and trap samples based on Bray-Curtis similarities, for wet and dry season.	121
Figure 7.3. Relative abundance of three size categories of major prey types in the traps (available prey) and in the stomachs of <i>C. rostralis</i> , <i>C. rubrigularis</i> and <i>C. storri</i>	125
Figure 8.1. Mean density estimates from POPAN models of skinks in the three treatments at each sampling occasion.....	143
Figure 8.2. Survival and recapture probability of skinks in the three treatments.	145
Figure 8.3. Active skinks in the three treatments at each sampling occasion.	146
Figure 8.4. Juvenile growth rate of the three <i>Carlia</i> species, in the three treatments.....	147
Figure 8.5. Adult body size of males and females of the three <i>Carlia</i> species in the three treatments.	148
Figure 8.6. Mean residual body condition value for males and females of each <i>Carlia</i> species in the three treatments.	149
Figure 8.7. Mean mites per skink of skinks with mites, for the three <i>Carlia</i> species in the three treatments.	150
Figure 9.1. Mean number of new skinks captured per hour in each treatment.	165
Figure 9.2. Mean number of cursorial spiders in the five treatment types.....	166
Figure 9.3. Mean number of web-building spiders at four height-above-ground categories in the five treatment types.....	168
Figure 9.4 (a) Canonical discriminant function analysis of arthropod orders in the five different treatment types. Points represent centroids for each study plot, (b) Taxon eigenvectors (standardized canonical discriminant function coefficients) based on log-transformed data, (c) plots [a] and [b] with explanatory groupings superimposed...	170
Figure 9.5. Negative linear relationship between aerial arthropod density and web-building spider abundance	171
Figure 9.6. Mean proportion of leaf damage for each treatment type.	172
Figure 9.7. Principal component analysis (PCA) biplot showing habitat variables explaining most of the variation in habitat among treatment types.....	173
Figure 9.8. The trophic web at the study site, showing the links and relative interaction strength for each trophic level.	179

List of tables

Table 2.1. List of fauna recorded at the study site at Ramsey Bay, Hinchinbrook Island	10
Table 2.2. Description of treatment types and number of replicates.....	12
Table 2.3. The start and end dates of the various types of sampling activity, with the number of sampling occasions on which each activity was performed.	14
Table 3.1. The skink species captured at the Hinchinbrook Island study site.	31
Table 3.2. Truncated results from the POPAN formulation in Program MARK showing the best eight models describing the survival (ϕ) and recapture (p) probability, probability of entry into the population ($PENT$) and population size (N) of all <i>Carlia</i> at the study site.	33
Table 3.3. Summary of Cormack-Jolly-Seber mark-recapture models describing survival (ϕ) and recapture (p) rates of <i>Carlia rostralis</i> , <i>C. rubrigularis</i> and <i>C. storri</i>	35
Table 3.4. Longevity of <i>Carlia</i> species, estimated from longest recaptured individual of each sex.	39
Table 3.5. Summary of Pradel mark-recapture models describing survival (ϕ), recapture (p) and recruitment (f) rates of <i>Carlia rostralis</i> , <i>C. rubrigularis</i> and <i>C. storri</i>	41
Table 4.1. Regression analyses of morphological traits (log-transformed) on $\log_{10}SVL$ between sexes for adult <i>Carlia</i> lizards	63
Table 4.2. Residual error mean-square (sum of squares divided by the sample size, N) for the non-linear regression of SVL increment (mm) on time interval (days) using two growth models, for the three <i>Carlia</i> species. The von Bertalanffy growth model had the lowest mean-square error for all species and was used for further analyses.	64
Table 4.3. Growth parameters ($\pm$ 95% support plane confidence intervals): a (asymptotic SVL in mm), k (characteristic growth rate) and b for the von Bertalanffy model for the three <i>Carlia</i> species.	65
Table 4.4. Body size at sexual maturity of the three <i>Carlia</i> species.	66
Table 4.6. Summary of mean maximum length (mm) and mean maximum width (mm) of arthropod prey from diet analysis of male and female <i>Carlia</i> species with ANCOVA	

results for difference in slope (interaction sex x SVL) and intercept (sex) between sexes.....	71
Table 5.1. Models used to assess survival (ϕ) and recapture (p) probability of <i>Carlia</i> , as a function of mite load and time.	87
Table 5.2. Relationship between ectoparasite load at initial and subsequent capture, and between the change in ectoparasite load and the time interval between captures (days) for three <i>Carlia</i> species.....	90
Table 5.3. Multiple regression results for the effect of mite load on relative growth rate for the three <i>Carlia</i> species.	90
Table 5.4. The effect of individual mite load on fitness-related variables for three <i>Carlia</i> species.	91
Table 5.5. Logistic regression results for effect of mites on reproductive status of females and predator avoidance of all skinks for the three <i>Carlia</i> species.....	92
Table 5.6. Summary of the most suitable mark-recapture models used to assess the variation in survival (ϕ) and recapture (p) probability as a function of mite load (mites), time and constancy ($\bullet$) of the three <i>Carlia</i> species.	94
Table 6.1. Area available for mite attachment (mm ²) and proportion of bare skin in limb axillae of the three <i>Carlia</i> species.	105
Table 7.1. Number of stomachs from which contents were identified, with mean number of prey taxa, and mean number of prey items per stomach for the three <i>Carlia</i> species. Results of Mann-Whitney U-tests to test differences in prey taxa and prey items between the wet and dry seasons are shown here (z and P values).	114
Table 7.2. Relative abundance (% rel), relative volume (% vol), frequency of occurrence (% freq) and index of relative importance (IRI) of various prey types for <i>Carlia rostralis</i> , <i>C. rubrigularis</i> and <i>C. storri</i> , with dietary niche breadth (B).....	116
Table 7.3. Overlap in diet composition by frequency of occurrence (Pianka's index) of the three <i>Carlia</i> species.	117
Table 7.4. Mean and range of prey length, and morphological characteristics of the three <i>Carlia</i> species.	118

Table 7.5. PERMANOVA results comparing sample type (trap samples [available prey], <i>C. rostralis</i> diet, <i>C. rubrigularis</i> diet and <i>C. storri</i> diet), season (wet and dry) and their interaction.....	122
Table 7.6. Electivities for prey types by the three <i>Carlia</i> species in the wet and dry seasons.	123
Table 7.7. Relative abundance (% rel) of three different prey size classes in traps and in stomachs of <i>Carlia</i> , and electivity (E) by skinks.	124
Table 8.1. Best fitting POPAN models ($\Delta QAIC_c = 0$) for each study plot, estimating survival (ϕ) and recapture (p) probability, probability of entry into the population ($PENT$) and total population size (N).....	142
Table 8.2. Estimate of adult population size, from mean population per study plot under best-fitting POPAN model from Program MARK.....	143
Table 9.1. Repeated measures ANOVA of number of exposed web spiders at different heights above ground in varanid access and exclusion, and skink access and exclusion study plots.....	167
Table 9.2. Summary of principal component axis loadings	174

Chapter 1

Introduction and overview

Species in ecosystems are linked in a highly interconnected network of interaction pathways to form an ecological community. Trophic webs, defined by interactions between predators and their prey, are the structure into which these communities are assembled.

Loss of top predators and the implications for trophic web ecology

Predators that occur at high trophic levels in ecological systems (top predators) have been rapidly declining worldwide, following environmental degradation, habitat loss, and direct persecution by humans (Berger et al. 2001; Friedlander and De Martini 2002; Baum et al. 2003). Top predators often exert a strong influence on their prey populations, and their decline can have far-reaching consequences for the structure and functioning of ecosystems (Ritchie and Johnson 2009). In particular, top predators can control the population of lower-order predators (mesopredators) so that loss of top predators from a system causes previously suppressed mesopredators to be 'released' (Soulé et al. 1992). The release of mesopredators has important implications for the ecology of trophic webs (Crooks and Soulé 1999); mesopredators generally occur at higher density than top predators, have a smaller range and higher predation rates and may therefore exert a disproportionately larger effect on lower trophic levels than top predators (Crooks and Soulé 1999; Ritchie and Johnson 2009). The control of community organisation through the effects of top predators on mesopredators is important in many systems (reviewed in Ritchie and Johnson 2009).

Predators can have both direct and indirect effects on prey communities, and can influence lower trophic levels via multiple pathways (Abrams 1995). Predators can remove prey individuals from the system by consuming them, and thereby alter the abundance of their prey (direct effects, Menge 1995). In this way, top predators can indirectly have effects on lower trophic levels (density-mediated indirect effects, Abrams et al. 1996) resulting in a trophic cascade (Polis and Strong 1996; Shurin et al. 2002). However, trophic cascades can

also occur without changes in the density of interacting species. Predators can induce costly anti-predator behaviour in their prey (trait-mediated interactions; Lima and Dill 1990; Schmitz et al. 2004), which can increase starvation mortality, and reduce the number of prey feeding on lower trophic levels. Or, predator effects on prey behaviour can occur without altering prey abundance. Anti-predation behaviour can reduce prey demand on resources so that predators can indirectly influence lower trophic levels, similar to density effects, but without consuming prey (trait-mediated indirect effects, Schmitz et al. 1997). Predicting the ecological consequences of top predator declines, and mesopredator release, requires an understanding of how predators influence communities, and how trophic cascades are initiated.

Measuring density- and trait-mediated interactions in trophic webs: importance, current limitations and new directions

Trait-mediated effects of predation may be as important as predator-induced changes in prey abundance (Trussell et al. 2003; Werner and Peacor 2003), and simply measuring the density response of prey is not sufficient to determine predator effects. Prey behavioural changes in response to predation should also be considered, and yet measures of the relative importance of density-mediated and trait-mediated interactions are very few (reviewed in Bolker et al. 2003; Luttbeg et al. 2003; Werner and Peacor 2003; but see Preisser et al. 2005 for meta-analysis). Understanding the relative importance of these effects in trophic cascades is crucial to predicting changes in trophic webs following large environmental disturbances, such as losing a top predator from a system.

Trophic web studies that consider both density- and trait-mediated effects of predation are limited; they are often carried out on a small spatial scale (e.g., Kunert and Weisser 2003), in unnatural environments (e.g., Peacor and Werner 2001; Trussell et al. 2006), or in simple systems (e.g., Schmitz 1998; Nelson et al. 2004). Large-scale studies of top predator removal and the subsequent indirect effects are generally correlative (e.g., Berger et al. 2001; Ripple and Beschta 2004, 2006, 2007), which is not surprising given the difficulty in manipulating top predator access while allowing natural movement of prey. There

is a need for experimental studies in complex natural systems, examining a wide range of taxa, to determine the relative importance of density- and trait-mediated predation effects in trophic cascades.

Experimental manipulation of predator access, such as predator exclosures, can provide insight into the mechanisms that influence ecological communities, and their direct and indirect responses to predator decline (Krebs et al. 1995). However, the effects of the removal of top predators on mesopredator feeding ecology and the cascading effects to lower trophic levels have rarely been explored using manipulative field experiments (Peacor and Werner 2001). My study, presented in this thesis, consisted of a manipulative field experiment where the effects of top predators and mesopredators were both simultaneously and individually isolated. Using large field enclosures, situated in an island National Park study site, I manipulated the access of large lizards (varanids) and small lizards (skinks) to areas and measured the effects on lower trophic levels (spiders, other arthropods and the vegetation).

Lizards as model organisms

Due to their relatively low energetic requirements, high densities, low dispersal distances and small spatial requirements lizards may have an incomparable potential to respond rapidly to experimental predator removal (Pough 1980; Huey et al. 1983). Lizards have been used in many studies to successfully demonstrate trophic cascades, filling the role of both top predator (Spiller and Schoener 1994; Dial and Roughgarden 1995) and intermediate predator (Schoener et al. 2002). Lizards can be easy to catch, mark and recapture, making measuring their population densities tractable. Also, they can be easy to observe in nature, making assessments of behavioural responses to predator removal possible.

Large lizards (varanids, genus *Varanus*) were the top predators at my study site. Varanids are generalist predators that opportunistically consume skinks (Shine 1986a; Weavers 1989; Lloyd et al. *unpublished data*). They were abundant at my study site (16 individuals.km⁻²) and exhibited high overlap with skinks in activity time and habitat used (Lloyd

2007). Small lizards (skinks, from the genus *Carlia*) were the dominant vertebrate species at my study site. *Carlia* are insectivores (Greer 1989) and thus are mesopredators in my study system. These skinks exhibit features that make them an ideal subject for the study of trophic interactions: they are diurnal and ground-dwelling, making them not only amenable for live capture and behavioural observations, but also frequently exposed to predators. They appear to have a strongly predator-influenced set of ecological and behavioural traits, such as restricted habitat use and activity times (*pers. obs.*).

To appreciate the impact that predation has on fauna, a detailed understanding of the ecology of individual species and whole assemblages is needed. Previous studies of *Carlia* have determined the diet (James 1983), reproduction (James and Shine 1985; Goodman 2006) and niche separation (Goodman 2007) of some species from this genus and have documented aspects of their behaviour (Whittier and Martin 1992; Langkilde and Schwarzkopf 2003; Langkilde et al. 2003). Despite these studies, large gaps remained in our knowledge, particularly in regard to the life history strategy and foraging ecology of this genus. Prior to my study, no life history data were available for any *Carlia*, and, correspondingly, there was no information about population structure, growth and survival rates, and sexual differences within species. Most importantly for a trophic web study, no previous study had determined prey selection by *Carlia*. Knowledge of the population ecology of these skinks was necessary to place them in context of the larger trophic web system. My study thus had two aims: (1) to establish the demography, ecology and life history strategies of *Carlia*, including diet, prey selection and their relationship with parasites, and (2) to determine the ecological consequences of top predator and mesopredator removal, by establishing the direct and indirect effects of predation on *Carlia*, the direct and indirect effects of predation by *Carlia*, and the cascading effects to lower trophic levels in a complex natural system.

Thesis overview

This thesis is organised as follows: Chapter 2 presents a description of my study site and the experimental study plots, and describes the methods used that are common to most

chapters. Chapter 3 introduces the skink study species (genus *Carlia*) and presents data on the basic ecology of the population, including population density and structure, reproductive patterns and the habitat use and habits of the species.

Chapter 4 compares the sexes in more detail, and describes the growth rate, maturation and sexual dimorphism in size and body shape among the study *Carlia*. In this chapter I demonstrate that the direction of sexual dimorphism differs among the species, due either to differences in the duration or rate of growth between sexes, but not to differential survival or niche partitioning of the sexes.

Chapters 5 and 6 examine the relationship between skinks and their ectoparasites: trombiculid mites. Knowledge of the host-parasite interactions of *Carlia* constitute part of the understanding of trophic web dynamics; the threat of predation may result in behavioural changes by skinks which can reduce growth rate and body condition, and this may have consequences in their relationship with parasites. Loss of body condition reduces immune response to infection and can decrease the ability of skinks to defend against parasites. In Chapter 5 I show that the *Carlia* species are differentially infested by mites, but that mites have no apparent detrimental effect on any measurable skink components of fitness. Chapter 6 presents a study of the mite attachment sites on *Carlia* and demonstrates that the structure and area available for mite attachment has no bearing on the level of mite infestation.

Chapter 7 presents a detailed study of the diet and selection of prey by *Carlia*, and shows that skinks generally focus their foraging efforts on prey types and prey sizes that are not abundant in the environment, and thus are more selective in their foraging and diet than previously assumed.

Chapters 8 and 9 investigate the trophic web at the study site. Chapter 8 demonstrates that varanids can have a significant effect on skink behaviour without an effect on skink abundance, but that these effects do not translate to changes in skink fitness, at least for the traits I measured. Chapter 9 builds on this work, and describes how skinks directly alter the abundance of spiders and the community composition of other arthropods, and indirectly affect primary production. In this chapter I show how top predator-induced

changes to mesopredator behaviour can cascade through the system. Finally, Chapter 10 discusses the significance of my findings and outlines areas for future research.

Appendix A presents a study that demonstrates that avian predators have very little influence on skinks at my study site, and that the study plots are not likely to differ in the protection they offer from avian predation. Appendix B is a published manuscript which describes the use of shelters by some web-building spiders and how these shelters provide protection from predation by skinks. Appendix C is a manuscript (currently in review) that examines the thermoregulatory efficiency of the skink species at the study site, by examining their preferred body temperatures and available environmental temperatures, and defines a new cost-benefit model of thermoregulation for tropical reptiles.

Chapter 2

Description of the study site and general field methods

Study site, climate, vegetation and fauna

My study was carried out at a site in Hinchinbrook Island National Park, Queensland, Australia ($18^{\circ}18'41''\text{S}$, $146^{\circ}16'24''\text{E}$). Hinchinbrook Island is a large continental island (37.4 km long, 10 km wide) separated from the mainland by a narrow channel (Figure 2.1). The whole island is a National Park and is located within the Wet Tropics World Heritage Area (Queensland Department of Environment and Resource Management 2009). The study site is a 5-ha, approximately level, corridor of land between the beach and an extensive fringing mangrove system at Ramsay Bay, on the island's north-east (Figure 2.1).

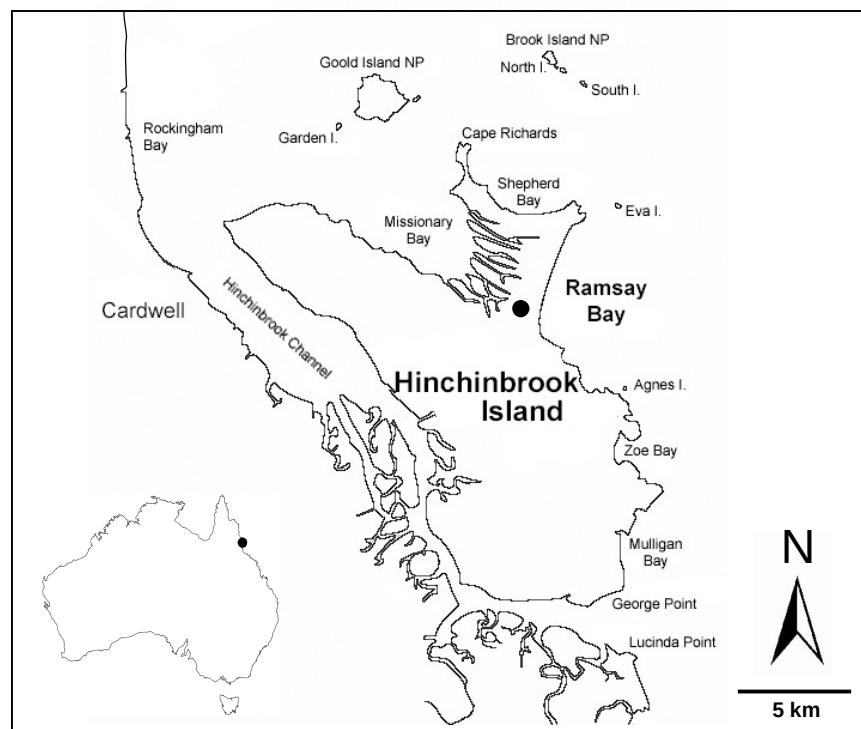


Figure 2.1. Location of the study site at Ramsay Bay on Hinchinbrook Island, north-eastern Queensland, Australia.

The Australian tropics are characterised by relatively little variation in temperature during the year, but highly variable, typically seasonal precipitation that produces discrete wet and dry seasons. The location encompassing my study site experiences a seasonally monsoonal climate; the dry season (May to September) is mild, with less than 60-mm rainfall per month and temperatures between 13 and 25 °C, the wet season (October to April) is hot and humid, with 470 mm average monthly rainfall and temperatures between 23 and 31.5° C (Australian Bureau of Meteorology 2008; Figure 2.2). In March 2006, a category-five tropical cyclone crossed the coast less than 100 km north of the study site, causing higher-than-average rainfall during March and April 2006, and localised flooding at the study site. The year (2006) was also characterised by relatively high rainfall in the dry season (336 mm precipitation in September 2006, Figure 2.2) and very high rainfall over the 2006 – 2007 wet season (Figure 2.2).

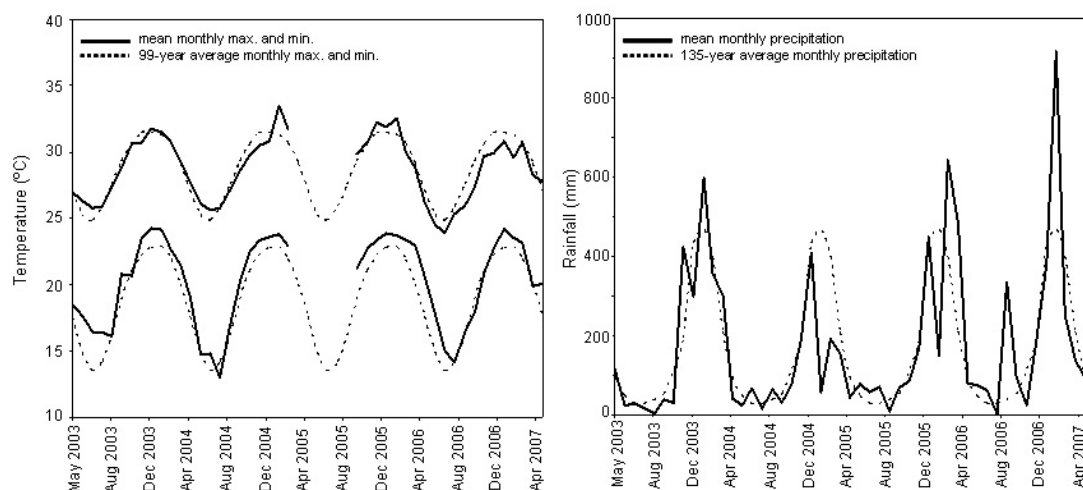


Figure 2.2. Mean monthly minimum and maximum temperature (°C) and rainfall (mm) for the study period, showing 99-year average temperatures (°C) and 135-year average precipitation (mm).

From Australian Bureau of Meteorology records for Cardwell Marine Parade weather station [site 032004], January 2008. No temperature data were available for April – September 2005.

Vegetation at the site is typically open woodland interspersed with areas of closed vine forest. The woodland consists of large paperbark trees *Melaleuca leucadendron*, *M. viridiflora* and *M. quinquenervia* with a *Terminalia* spp. shrub layer. The vine forest contains large trees *Eucalyptus crebra* and *Corymbia* spp., with a shrub and grass understorey

including *Xanthorrhoea* spp., *Rhodomyrtus trineural* and *Leptospermum polygalifolium*. *Pandanus* spp. features prominently in both woodland and forest habitat. The vertebrate fauna at the site is typical to northern Australian open forest (Table 2.1). Hinchinbrook Island lacks large predators common on the mainland, such as dingoes (*Canis lupis dingo*), feral cats (*Felis catus*) and quolls (*Dasyurus hallucatus*). The study site itself is effectively free from anthropogenic disturbance; there is one resort on the island located at the northern tip (at Cape Richards, ~15 km north of the study site, Figure 2.1), and a hiking trail traversing the east coast of the island directs walkers along the beach, rather than through the study area.

I visited the study site at approximately four-month intervals, from April 2003 to May 2007. These visits sampled the seasons: early dry season (April - May), late dry season (August – September) and early wet season (November – December). I visited the site twice in January, in 2004 and 2006 (Figure 2.3). Access to the island is restricted in February and March (late wet season) due to heavy rainfall and the threat of cyclones. Each sampling period was four to five weeks.

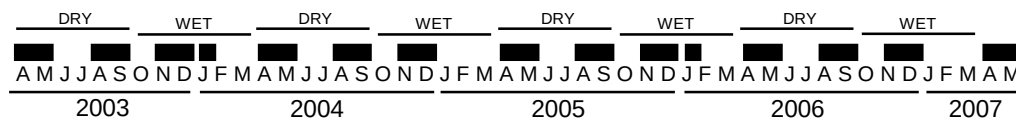


Figure 2.3. Timeline of the experiment, showing months and seasons when sampling took place.

Study system and experimental design

Small skinks were the most abundant vertebrate species, and varanids the dominant predators at the study site (*pers. obs.*). Varanids opportunistically feed on a range of prey, including skinks, and a variety of arthropod prey (Shine 1986a; Weavers 1989). Skinks feed on invertebrates, including spiders and various herbivorous insects (Brown 1991). The study system at Ramsay Bay, therefore, provided a multi-level trophic web (Figure 2.4) including: top-level predators (varanids), intermediate-level predators (skinks and spiders) and their prey (invertebrates), some of which are herbivorous insects that feed on primary producers.

Table 2.1. List of fauna recorded at the study site at Ramsey Bay, Hinchinbrook Island. This list is not exhaustive, and is intended to provide a general description of the study site.

Taxon	Common name (species or family name)		
Mammals		Melomys (<i>Melomys cervinipes</i>)	
		White-tailed rat (<i>Uromys caudimaculatus</i>)	
		Bandicoot (<i>Isoodon macrourus</i> ; <i>Perameles nasuta</i>)	
		Wallaby (<i>Wallabia bicolour</i>)	
		Wallaroo (<i>Macropus robustus</i>)	
		Flying fox (<i>Pteropus</i> spp.)	
Birds		Honeyeater (family Meliphagidae)	
		Shrike-thrush (family Pachycephalidae)	
		Sunbird (family Nectariniidae)	
		Gerygone (family Pardalotidae)	
		Dove (family Columbidae)	
		Cockatoo (family Cacatuidae)	
		Butcherbird (family Artamidae)	
		Corvid (family Corvidae)	
		Goshawk (family Accipitridae)	
		Nightjar (family Caprimulgidae)	
Amphibians		Tree frogs (<i>Litoria</i> spp.)	
		Cane toads (<i>Rhinella marina</i>)	
Reptiles	snakes	Scrub python (<i>Morelia amethistina</i>)	
		Slatey grey snake (<i>Stegonotus cucullatus</i>)	
		Brown tree snake (<i>Boiga irregularis</i>)	
		Common tree snake (<i>Dendrelaphis punctulata</i>)	
		Whip snake (<i>Demansia psammophis</i>)	
		Death adder (<i>Acanthophis praelongus</i>)	
	lizards	Varanids (<i>Varanus</i> spp.)	
		Skinks (including <i>Carlia</i> spp.; <i>Glaphyromorphis</i> spp.; <i>Saproscincis</i> spp.; <i>Ctenotus</i> spp.; <i>Cryptoblepharis</i> spp.; <i>Menetia timlowi</i> ; <i>Egernia frerei</i>)	
		Geckos (<i>Heteronotia binoei</i> ; <i>Gehyra dubia</i>)	

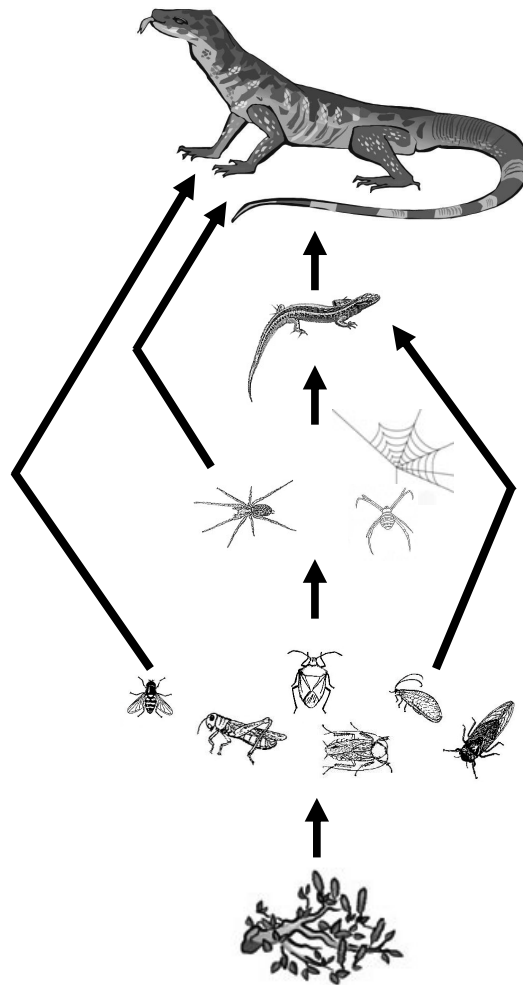


Figure 2.4. The trophic web at the study site, arrows show direct predation and indicate direction of energy flow.

To determine the effect of removing top- and intermediate-level predators from this system, I excluded varanids and / or skinks from areas at the study site using a manipulative experiment. The experiment included 21 study plots, each 14.1 x 14.1 m (200 m²), allocated in a randomized block design to five treatments (Figure 2.5). There were five unfenced control plots and 16 plots surrounded by fences (Table 2.2). Fences surrounding eight plots were 1.2 m high and excluded varanid lizards (Figure 2.6 a). Four of these tall, fenced plots had 28 holes (30 mm x 30 mm) cut through the fence at ground level at 2-m intervals, to provide access to skinks (Figure 2.6 b), and the other four tall plots had no holes cut and any openings sealed with silicone sealant to prevent access by skinks (Figure 2.6 c). Fences surrounding an additional eight plots were 30 cm high, allowing access by varanids (Figure

2.6 d); four of these prevented access by skinks while four permitted access via holes.

Fences were metal-framed with 3-mm plastic mesh attached to the sides, extending 30 cm underground. A continuous strip of 30-cm wide aluminium sheeting attached to the top of each fence overhung the outside of the fence, preventing lizards from entering by climbing. A corridor of cleared vegetation surrounded each exclusion enclosure, and large trees were collared with aluminium sheeting to prevent climbing varanids gaining access. Corner posts and rope alone marked unfenced plots, which controlled for fence effects (Figure 2.6 e). The site was established and the study plots initially constructed in 1997, and the plots were maintained continuously as skink access or exclusion from May 2003 to the end of my study (May 2007).

Table 2.2. Description of treatment types and number of replicates.

Treatment		Number of plots	Description
Varanid	Skink		
exclusion	exclusion	4	Tall (1.2 m), fenced plots with all openings sealed.
exclusion	access	4	Tall (1.2 m), fenced plots with small holes cut into the fence at ground level.
access	exclusion	4	Low (30 cm), fenced plots with all openings sealed.
access	access	4	Low (30 cm), fenced plots with small holes cut into the fence at ground level.
(fenced control plots)			
access	access	5	Four corner posts joined with rope.
(unfenced control plots)			

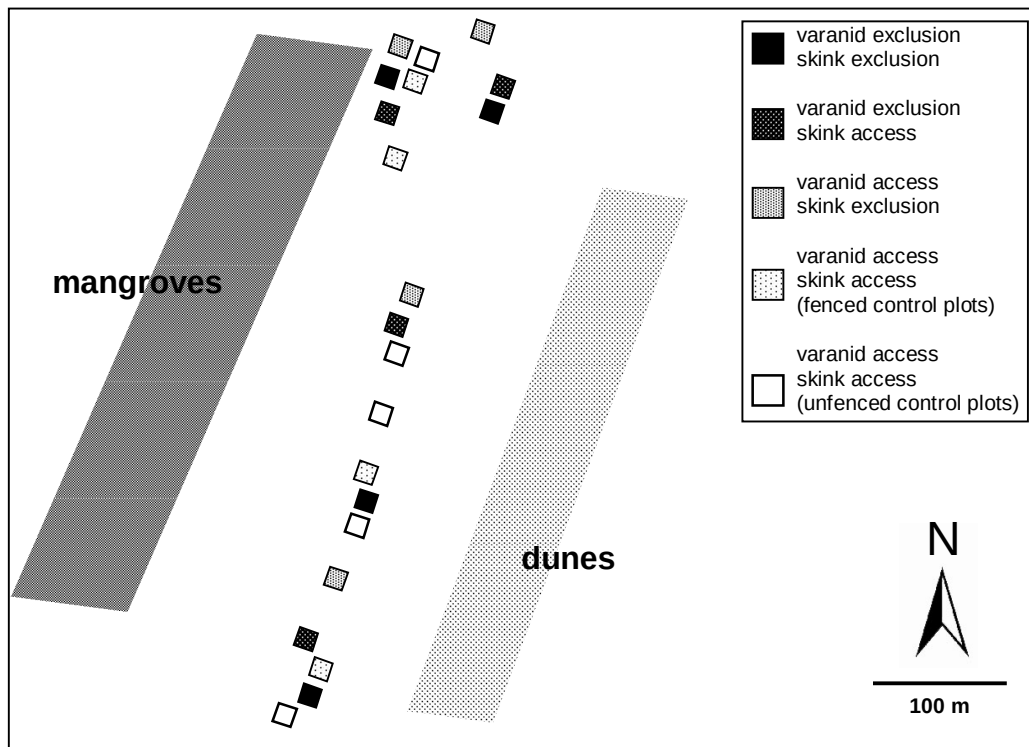


Figure 2.5. Layout of the study plots at the study site.



Figure 2.6. Study plots: (a) tall fenced plot to exclude varanids, (b) hole in fence at ground level to allow access to small lizards, (c) sealed fence to exclude small lizards, (d) low fenced plot to allow access to varanids, (e) unfenced control plot.

Table 2.3. The start and end dates of the various types of sampling activity, with the number of sampling occasions on which each activity was performed.

Sampling activity	Start and end of sampling dates	Number of occasions
Hand capture of skinks	August 2003 to May 2007	12
Pitfall trap capture of skinks	August 2003 to December 2005	8
Funnel trap capture of skinks	November 2005 to May 2007	5
Activity observation surveys	August 2005 to May 2007	6
Spider census	April 2005 to November 2006	6
Arthropod sampling	April 2005 to November 2006	6
Artificial spider webs	May 2007	1
Measure of herbivory	May 2007	1

Habitat available within study plots

The complexity of the habitat available in the study plots was surveyed in August 2005. Habitat was surveyed in 21 quadrats in each study plot by recording vegetation and habitat complexity in 1 x 1 m quadrats at alternate meters, along three evenly spaced transects across each plot (Figure 2.7). I recorded the following habitat variables in each quadrat: composition of ground cover (percentage of leaf litter, bare ground, trees, grass, shrubs, logs, etc.), and number, estimated height (m) and diameter at chest height (± 1 cm) of trees. Canopy cover (as a percentage) to 0.5 m, between 0.5 and 2 m and above 2 m was also recorded in each quadrat.

Light availability, amount of solar radiation and canopy cover in the study plots was quantified by hemispherical canopy photography (Roxburgh and Kelly 1995). I took four photographs in each study plot (Figure 2.7), in August 2005 (dry season) and at the same locations in January 2006 (wet season). The photographs were taken at ground level using a horizontally-levelled digital camera (CoolPix 995, Nikon, Tokyo, Japan), aimed at the zenith using a fish-eye lens of 180° field of view (FC-E8, Nikon). The camera was mounted on a wooden platform and adjusted for magnetic north. All photographs were taken in uniformly

overcast sky conditions to minimise variation in exposure and contrast. Photographs were analysed for canopy openness using Hemiview canopy analysis software v2.1 (1999, Delta-T Devices Ltd, United Kingdom), ensuring the same protocol for threshold settings. The hemispherical photographs were analysed for direct site factor (DSF), and indirect site factor (ISF). DSF and ISF refer to the photographic estimations of the proportion of direct and diffuse light levels at a given location relative to the levels at a location without any sky obstructions, respectively (Becker et al. 1989).

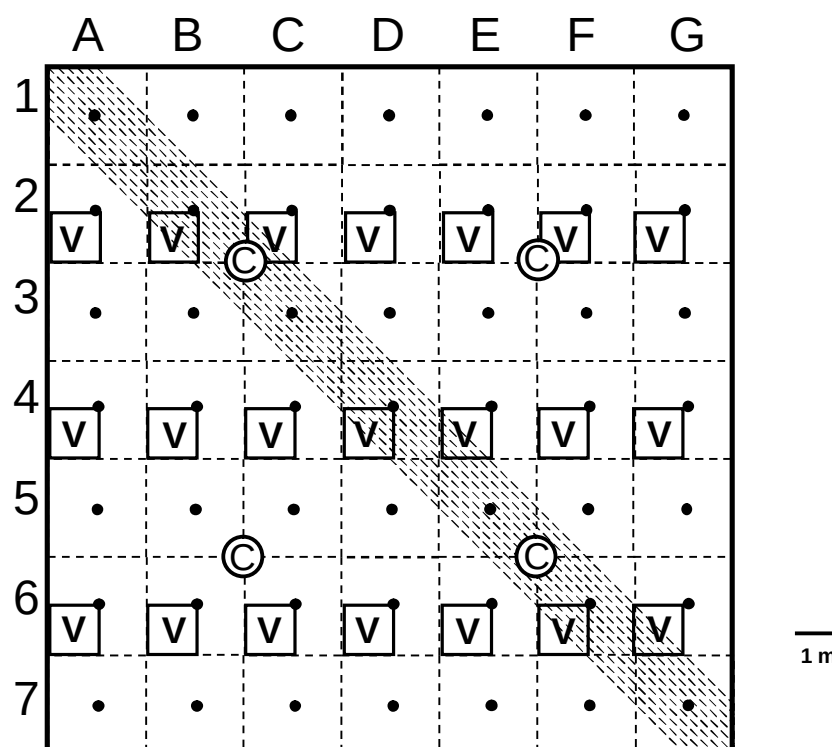


Figure 2.7. Schematic diagram of a single study plot, showing grid design and location of sampling points. Habitat and vegetation complexity recorded at $\boxed{V}$, hemispherical canopy photographs taken at $\odot$, and leaf litter depth measured at $\bullet$. Hatched diagonal transect shows spider census location.

I measured the depth of leaf litter in each study plot by pushing a 3-mm diameter graduated rod (± 5 mm) into the leaf litter to ground level. Litter depth was measured in the dry (June 2006) and wet (November 2006) seasons, in every 2 x 2 m of each plot ($n = 49$ per plot, Figure 2.7).

I measured available environmental temperature using digital temperature recorders (Thermochron iButtons™, Dallas Semiconductor Corporation, Dallas, TX). Four iButtons sampled environmental temperatures hourly in each study plot for the duration of each sampling period; they were placed in areas used by skinks: (1) on the leaf litter in the open, (2) on the leaf litter under vegetation, (3) under the leaf litter in the open, and (4) under the leaf litter in the shade ($N = 84$). The operative temperature obtained with a self-contained temperature recording device (such as an iButton) is similar to the rate of heating and cooling of a lizard model (Vitt and Sartorius 1999), and the effects of physical model attributes on operative temperatures are shown to be minor (Shine and Kearney 2001).

Skink sampling

Skinks were captured in all study plots at every sampling occasion, from August 2003 to May 2007. The day was divided into three capture periods: morning (0600 to 1000), midday (1000 to 1400), and afternoon (1400 to 1800). Every effort was made to ensure an equal number of catcher-hours were spent in each skink access plot, in each time period, on every sampling occasion. Skink exclusion plots were visited less frequently, but also for an equal number of catcher-hours in each time period. Skinks were captured by hand, 'fishing', pitfall trap and funnel trap (Table 2.3). To 'fish' for lizards, *Tenebrio* larvae were tied to a rod with thread and skinks were lifted out of vegetation and captured by hand as they bit the bait. Pitfall traps were 100-mm diameter PVC tubes of 200-mm depth, buried up to their top edge in the soil, and are designed to capture cryptic, litter-dwelling skinks. Two pitfall traps were buried in each study plot, and were checked for trapped animals twice a day. Funnel traps were shade-cloth mesh, 70-cm long with 20 x 20-cm openings at each end funnelling to a 5-cm diameter opening into an interior chamber. Between four and six funnel traps were deployed in each study plot, each trap was covered with shade cloth and leaf litter to avoid overheating. Funnel traps were checked for trapped animals once a day.

The area of each study plot was divided into 49 2-m squares (i.e., a grid of 7 x 7 2-m squares, using the evenly spaced metal fence posts, or markings on the rope of control plots; see Figure 2.7). At capture, the original location of each skink was recorded as a grid

reference. For hand-captured skinks, behaviour (basking, crawling, foraging, stationary, display, see Martin and Bateson 1989), microhabitat (leaf litter, log, in vegetation) and amount of solar radiation (sunlit, shaded, dappled) at the point of first sighting were recorded, along with time of day and weather conditions (cloud cover, wind, ground moisture). Skinks were individually held in marked, transparent, plastic ziplock bags until they were measured. Skinks were identified to species using a hand lens and identification key (Cogger 2000; Wilson 2005). I measured snout-vent length (SVL) and tail length using a ruler (± 0.5 mm), mass using a Pesola spring balance (± 0.1 g), and measured, using digital callipers (± 0.1 mm): head length (HL) from the tip of the snout to the anterior edge of the ear opening, head width (HW) across the widest part of the jaw (across ear opening), head depth (at the deepest part of the jaw) and interlimb length (ILL) from axilla to groin (i.e., the posterior point of insertion of the forelimb to the anterior point of insertion of the hindlimb). Head length and interlimb length were measured on the right side of the body. The presence of an intact or broken tail was recorded. The sex of each skink was determined by manual eversion of hemipenes, and adult females were palpated for the presence of eggs. Lizards were checked for the presence of ectoparasites, and the intensity of ectoparasite infestation was measured using a hand lens by counting the number of individual mites present on each lizard (Sorci et al. 1997). Ectoparasites were not removed. Each skink was then individually marked with a unique toe-clip by removing the distal one-third of a toe from each foot with sharp scissors (Dunham et al. 1988b). Skinks from skink access plots were returned to their point of capture within 24 hours, skinks captured in skink exclusion plots were released in similar habitat away from the study site. In this way, access plots maintained a natural population of skinks and exclusion plots remained relatively skink-free. At each recapture, skinks were identified by toe-clip and at the first capture for each sampling occasion, individuals were again measured, weighed, sexed, and mites counted.

Stomach contents and reproductive condition

Adult skinks were sacrificed each season (during 2006 – 2007) to determine diet and reproductive condition. Skinks were captured by hand after 1200 on sunny days, so that they would have had the opportunity to feed before capture. Each skink was measured, sexed and

mites counted as detailed above. Skinks were euthanased shortly after capture, and preserved immediately in 70% ethanol. Dissection took place in the laboratory. Reproductive condition was assessed by recording, for females, the number of follicles in each ovary, or the presence of enlarged follicles, vitellogenic follicles or oviductal eggs, and for males the presence of enlarged testes. The length and width (at longest and widest point) of eggs (or largest follicle in each ovary) and testes were measured with digital callipers (± 0.1 mm). Entire intestinal tracts of preserved skinks were removed and the total volume of stomach contents was determined by displacement of water in a graduated 1000 or 3000 mm³ syringe barrel (accurate to 10 mm³). I identified the contents of each stomach to ordinal level for insects, class or ordinal level for other invertebrates, and species level for vertebrates, using a dissecting microscope (Hadlington and Johnston 1998). The length (from head to abdomen (cephalothorax to abdomen in spiders)) and width (at the widest point) of each prey item were measured with digital callipers (± 0.1 mm). Number and location of internal parasites (nematodes) was recorded.

Activity observation surveys

To observe skink behaviour and activity, I slowly walked zig-zag transects through skink access plots and recorded all skinks encountered, without disturbing skinks. Transects were timed (and took 7 min). Skinks were not captured. I identified skinks to species and to sex where possible. Behaviour (using the protocols of Martin and Bateson 1989), microhabitat and amount of solar radiation were recorded as detailed above, without disturbing the skink. I visited each skink access plot on at least six occasions in each daily time period (see above) on each sampling occasion. I did not record skinks flushed from hiding places, only active skinks were considered for these observations and these surveys therefore differ from skink capture sessions.

Spider census

Spiders were censused by complete counts in a 1-m wide transect diagonally across each study plot (Figure 2.7). Spiders were identified to family, and species or morphospecies.

The height above ground of each individual was recorded. Each individual web-building spider censused was categorised as either exposed or sheltered based on its exposure to lizards in its resting position: exposed in the web, or sheltered in a retreat such as a curled leaf, web-funnel, or cocoon. To minimize possible effects of disturbance on web spiders, the plots were not entered by researchers for a minimum of 60 days before each spider survey (i.e., spider census was the first task on each sampling occasion). Spiders on fences were excluded from analyses.

Arthropod sampling

Arthropods were sampled by extracting invertebrates from samples of the leaf litter and using pitfall and pan traps in each study plot on six sampling occasions (Table 2.2). To sample sedentary invertebrates, two cores of leaf litter of 300-mm diameter were taken from each study plot on each sampling occasion, from locations separated by 10 m. Leaf litter cores were transferred to modified Berlese funnels within 24 hours, and air-dried for a minimum of 60 hours (Bestelmeyer et al. 2000). Invertebrates in the leaf litter were funnelled into a solution of water and detergent. Weight of dry leaf litter was measured with a Pesola spring balance (± 5 g). Invertebrates were extracted from a total of 252 leaf-litter cores. Pitfall traps were 35-mm diameter PVC tubes buried up to their top edge in the soil to sample surface-active invertebrates, and pan traps were 150-mm diameter yellow plastic bowls, designed to sample aerial insects. Eight pitfall and eight pan traps were installed in a grid design 4 m apart in each study plot. All traps were half filled with a solution of water and detergent, and sampled available prey for five days on each sampling occasion.

All invertebrate samples were transferred to 70% ethanol in the field and returned to the laboratory for sorting. Insects were identified to ordinal level (but Formicidae were identified separately from other Hymenoptera), and other arthropods to class or ordinal level, using a dissecting microscope (Hadlington and Johnston 1998). Arthropod body length was measured with an ocular micrometer and each individual was assigned to one of three length classes: <3 , 3 – 6, and >6 mm.

To sample prey available to web-building spiders, 84 arthropod sticky traps (four in each study plot) were erected for three consecutive days in May 2007. Sticky traps were made of a strip of clear plastic (1 m x 0.2 m), painted with transparent, adhesive Tanglefoot™ (The Tanglefoot Company, Grand Rapids, Michigan). The bottom edge of each sticky trap was pegged to the ground and the top edge suspended in the vegetation to sample arthropods from ground level to 1 m above the ground. Traps were designed to work like spider webs: flying and jumping arthropods were caught in the transparent adhesive, identified to order in the laboratory and body length category and height above ground recorded.

Herbivory

A static measure of the amount of herbivory on vegetation in the study plots was assessed at the end of the study. One leaf was cut from each shrub or tree with leaves growing within 1 m of the ground, from each study plot. Leaves were selected by choosing only full grown terminal leaves, and if there were many, from the branch pointing closest to north. Between eight and 290 leaves were sampled from each study plot, depending on availability. I recorded the height above ground of each leaf, plant species and type of leaf damage (no damage, holes [entirely missing areas] and scars [necrotic areas]; Spiller and Schoener 1997), and dried the leaves in a plant press. Leaves were scanned and saved as digital images using a flatbed scanner. Missing areas of each individual leaf were filled using the paint function in Adobe Photoshop v7.0 (Adobe Systems Inc. 2002), and the leaf area (number of pixels) of each original and filled leaf was determined using UTHSCSA ImageTool v3.0 imaging software (Wilcox et al. 2002). The difference in leaf area between original and filled leaves, divided by total leaf area, was recorded as the proportion of herbivory.

Chapter 3

The population ecology of tropical sympatric skinks

Abstract

Lizards may occur in dense assemblages of high species diversity, often forming the most prominent vertebrate faunal component of an ecosystem, this is particularly apparent at Hinchinbrook Island, where small skinks, particularly three species from the genus *Carlia*, dominate the faunal community. The large skink population is likely to make a large contribution to energy flow in the community, both as prey to higher trophic levels and as predators of lower trophic levels. The demography, ecology and life history strategies of *Carlia* are largely unknown. I found that adult skink survival rate was high in the wet season (October to March), and declined in the early dry season (April to June), corresponding with the end of the reproductive season and poor body condition. Reproductive activity began in the dry season (August) for some species and peaked during the wet months. Peak recruitment of juveniles into the population occurred in the early dry season. Juvenile skinks comprise a large proportion of the population in April and May each year, but only ~10% of juveniles survive to 12 months. Female *Carlia* are longer-lived than males and have a lifespan of approximately three years. *Carlia* at the study site occupy all available terrestrial habitats, and are active at all times of day, and all year. The species share a similar niche and yet do not appear to substantially partition the available resources, suggesting abundant food and space at the study site.

Introduction

Skinks are a highly diverse and speciose group of lizards that vary so greatly in size and morphology, habitat and microhabitat use, that they cannot be stereotyped (Cogger 2000; Pianka and Vitt 2003). Lizards, in general, including skinks, are more abundant in tropical areas than in temperate ones, both in species richness and in abundance of individuals (Bennett and Gorman 1979). Lizards are also more abundant on islands than on adjacent areas of the mainland of comparable habitat (Case 1975). Where tropical and island effects coincide, lizards may occur in dense assemblages of high species diversity, often forming the most prominent vertebrate faunal component of the ecosystem (Bennett and Gorman 1979). This is particularly apparent at my study site on Hinchinbrook Island, where small skinks dominate the faunal community. The large skink population is likely to make a significant contribution to energy flow in the community, both as prey to higher trophic levels and as predators of lower trophic levels.

Despite the abundance and high species richness of skinks in tropical Australia, detailed descriptions of habitat use, behaviour and population ecology of assemblages of tropical skinks are very few in comparison with other regions. The majority of ecological studies on Australian skink assemblages have been conducted on desert species (Pianka 1986; Henle 1989; James 1991a; Vitt 1991; Twigg et al. 1996), and in temperate zones (Wapstra and Swain 1996; Rohr 1997; Wapstra and Swain 2001; Melville 2002). The consistent high temperatures and food availability of the tropics mean that skinks living in these areas may remain active for all of the year, resulting in considerable differences in life history compared to their temperate area counterparts (James and Shine 1985). Extended activity leads to a faster growth, earlier maturity and a longer breeding season for tropical species (James and Shine 1985). However, it also increases exposure to predators so that tropical skinks may have shorter life spans (James and Shine 1988).

The large skink population on Hinchinbrook Island is dominated by three species from the genus *Carlia*, referred to commonly as rainbow skinks because of the spectacular colouration of mature males, particularly during the breeding season (Wilson 2005). Australian *Carlia* are almost all found in the tropical and subtropical part of the continent

(Cogger 2000). They are found in diverse habitats, from tropical rainforest to open woodland, spinifex grassland and suburban gardens, and on various substrates, including sandy soils, leaf litter and bare granite (Greer 1989). While previous studies have considered the reproduction (James and Shine 1985; Goodman 2006), niche separation (Goodman 2007), phylogeny (Stuart-Fox et al. 2002; Dolman et al. 2006; Dolman and Hugall 2008) and behaviour (Whittier and Martin 1992; Langkilde and Schwarzkopf 2003; Langkilde et al. 2003) of some species from this genus, no previous study has described the demography, population ecology and life history strategies of *Carlia*. My long-term mark-recapture study of the skinks on Hinchinbrook Island provided an opportunity to describe the population ecology of three tropical, sympatric species of *Carlia*, knowledge of which is particularly important in this system since it underlies the interactions the skinks have with higher and lower trophic levels. This chapter serves as an introduction to the population ecology of the three dominant skink species on Hinchinbrook Island; *Carlia rostralis*, *C. rubrigularis* and *C. storri*, which are the focus of my thesis, and describes the density, survival rate and demography of this skink community, along with their behaviour, habitat and space use.

Methods

Lizards were captured at the study site according to the methods described in Chapter 2. Upon capture, each individual was measured and marked with a unique toe-clip (see Chapter 2) so that a capture history of each individual was recorded for the duration of the study. Three species of skink from the genus *Carlia* made up the majority of the lizard population at the study site (see Results), therefore, besides a brief description of the skink species at the site, all other measures of skink population ecology refer to the three *Carlia* species.

Skink population estimates

I used the Jolly-Seber (JS) method (Jolly 1965; Seber 1965) to estimate the size of the *Carlia* population at the study site. The JS method estimates the probability of survival, the probability of recapture and the population size from multi-sample capture-recapture data. The population from which the sample is drawn is assumed to be 'open', as the method

allows additions (births and immigration) and losses (deaths and emigration) between each of the sampling occasions. I used the POPAN formulation in Program MARK (Arnason and Schwarz 1995; White and Burnham 1999) to estimate the population size of the three *Carlia* species at the study site, based on the JS estimation. Population size was estimated from recaptures of marked skinks, captured at approximately four-month intervals between August 2003 and May 2007 (12 occasions). The following parameters were estimated from POPAN models: ϕ (apparent survival), p (recapture probability), $PENT$ (probability of entry into the population at each occasion) and N (size of super-population, i.e., the total number of individuals present within the population during the entire study period). A set of candidate models were tested for the dataset of all species combined, incorporating (1) species, (2) time variation (sampling occasion, time) or (3) time invariance ($\bullet$) for survival and recapture estimates. $PENT$ always varies with sampling occasion (time), and N is a single estimate for each species for all sampling occasions (Schwarz and Arnason 1996). For the full time variation model (x sampling occasions), POPAN generates $x - 1$ estimates of ϕ , x estimates of p , $x - 1$ estimates of $PENT$ (corresponding to the probability of entry into the population for occasions 2, 3, etc.) and one estimate of N . I used the multinomial logit-link function to estimate $PENT$, log-link to estimate N and sin-link to estimate ϕ and p . JS models assume that survival rates and catchability are the same for all animals in the population (marked and unmarked) at each sampling occasion (Schwarz and Arnason 1996). To test the validity of this assumption, I tested the goodness-of-fit of the most parameterised model (the fully species and time-dependent model: ϕ [species x time] p [species x time] $PENT$ [species x time] N [species]) using the program RELEASE in MARK (Pollock et al. 1990). There was no indication of a significant deviation from the assumption for skinks of any of the three species (χ^2 test from RELEASE test3: $P = 0.41$).

I used the corrected Akaike Information Criterion (AIC_c) as an objective means of model selection. The AIC_c identifies the most parsimonious model from the set of candidate models, that is, the model supported most strongly by the data, given the bias-corrected, maximum log-likelihood of the fitted model, with a penalty for the number of parameters used (Burnham and Anderson 1998). The AIC_c values and standard errors of parameter estimates were adjusted for overdispersion by calculating a dispersion factor from the goodness-of-fit

statistics (pooled χ^2 goodness-of-fit statistics divided by the total degrees of freedom). The AIC_c adjusted for dispersion is called the corrected quasi-likelihood AIC_c ($QAIC_c$). For each model, $\Delta QAIC_c$ was calculated, which is the difference between the $QAIC_c$ for that model and the smallest $QAIC_c$ among the set of models fitted. Models with $\Delta QAIC_c \leq 2$ were given the greatest support (Burnham and Anderson 2002). The Akaike weight of each model is also used as a measure of the relative likelihood of the best model compared with the other candidate models. Once I had identified the most likely POPAN model describing the population, I estimated the population size of each species of skink (*C. rostralis*, *C. rubrigularis* and *C. storri*) at each sampling occasion.

Skink survival and recapture probability

I used standard capture-mark-recapture methods to estimate monthly survival of recaptured adult skinks (Lebreton et al. 1992). These methods separate survival from recapture rates, where recapture rate is the probability of capturing an individual, given that it is alive and catchable at that time. I used the Cormack-Jolly-Seber (CJS) method (Cormack 1989) in Program MARK to (1) compare survival and recapture probabilities among the three *Carlia* species, and (2) to estimate survival and recapture rates of each species, from mark-recapture data. The CJS method assumes that every marked animal in the population at a certain time has the same probability of recapture and survival (Lebreton et al. 1992).

To test for heterogeneity in survival and recapture probabilities among the three species, I incorporated species-dependent models into the set of candidate models describing the observed capture histories, along with time-dependent models (time, and species x time) and a time-invariant model ($\bullet$). I tested the goodness-of-fit of the data to CJS model assumptions using the bootstrap procedure in MARK (1000 iterations). This method simulated data using the parameter estimates under the most general model, ϕ (species x time) p (species x time), and computed the deviance for this model based on each simulated data set. There was no indication of lack of fit of the general model ($P = 0.32$). I then calculated the variance inflation factor as the ratio of the observed deviance from the actual data to the mean of the simulated deviances (White et al. 2001), and this factor was used to adjust AIC_c .

values and estimates of sample variance. ΔQAIC_c values and Akaike weights were calculated as for POPAN models. Using this method, if there was heterogeneity in survival and recapture probability among the species, species-dependent models would be well supported by the data (i.e., $\Delta\text{QAIC}_c \leq 2$).

To estimate survival and recapture rates for each species, I tested a set of four candidate models on the capture history dataset of each species. The candidate model set used the time-dependent CJS model ($\phi[\text{time}] p[\text{time}]$, Lebreton et al. 1992) along with simplifications of this model constraining survival and/or recapture probabilities to be constant ($\phi[\text{time}] p[\bullet]$, $\phi[\bullet] p[\text{time}]$, or $\phi[\bullet] p[\bullet]$). Models were analysed using sin-link formulation, with parameters estimated through numerical maximum likelihood techniques. Again, I tested the CJS model assumptions for the most general model (in this case $\phi[\text{time}] p[\text{time}]$, for each species). There was no indication of lack of fit of the general model for any species of skink (from bootstrap goodness-of-fit statistics: *C. rostralis* $P = 0.62$; *C. rubrigularis* $P = 0.31$; *C. storri* $P = 0.44$).

Skink longevity

The lifespan of each *Carlia* species was conservatively estimated using the greatest number of days between the first capture and last recapture of a male and a female individual of each species.

Juvenile recruitment and survival

I used the Pradel method (Pradel 1996) to estimate recruitment of juveniles into the population, and population rate of increase. Measuring recruitment into a population is essentially equivalent to measuring survival in reverse, and can be carried out by inverting individual capture histories (Pradel 1996). I used the Pradel model in Program MARK, which models survival (ϕ), recapture (p) and recruitment (f) probabilities, to estimate recruitment into the population at each sampling occasion for the *Carlia* species. I grouped skink capture histories according to age (juvenile or adult) and assessed the effect of age, and sampling occasion (time) on recruitment into the population (models for f were: species; age; time; age

x time; species x time; species x age; species x age x time), keeping survival and recapture probabilities time-dependent for all models. There is no known goodness-of-fit test for Pradel models.

Individual capture histories of skinks caught first as hatchlings were used to determine the proportion of individuals surviving to three, six and 12 months and compare juvenile survival among the species. Difference in the number of months of juvenile survival among the species was determined by analysis of variance (ANOVA).

Timing of reproduction, age and sex ratios

Skinks were sexed and females palpated for the presence of eggs at each capture (Chapter 2). Age ratios (adults: juveniles) and sex ratios (adult males: adult females) were determined for each species at each sampling occasion, and compared among the species using ANOVA. Differences in sex and age ratios among the seasons were analysed with Kruskal-Wallis tests for non-parametric data, for each species.

Skink body condition

The relationship between body mass and body size was established for each species of *Carlia* using linear regression. Size corrected body weight, or body condition, was then calculated for each individual using the residuals from reduced major axis regression of the relationship between $\log_{10}$ -transformed body mass and $\log_{10}$ -SVL (Green 2001). I calculated residual values for each species to determine if sex differences in body condition occurred, and then for each sex for the three species, to determine the effect of season on body condition. Residual deviations from the general regression line indicated changes in body condition of the lizards. Positive mean residual values for a season indicated that most of the values were above the general regression line, showing that most individuals had a higher than average body condition at that time. I used only measurements collected from the first capture of each lizard. Any factor influencing body mass may bias an index of condition, for this reason I considered all adult males captured, but only non-gravid adult females for body condition analysis. Tail loss can also significantly influence the mass of small lizards (Dial and Fitzpatrick 1981); therefore only lizards with complete tails were used for this analysis. I

analysed differences in residual values between male and female lizards among the seasons for each species using ANOVA.

Habitat, microhabitat, habits and behaviour of skinks

The habitat at the study site consisted of a mosaic of open woodland and vine forest (Chapter 2). The habitat available in each study plot can be loosely categorised as: (1) open *Melaleuca* woodland consisting of large trees and sparse understorey vegetation, (2) *Melaleuca* woodland with a dense *Terminalia* shrub understorey, (3) closed vine thicket consisting of large trees with a shrub and grass understorey, or (4) *Pandanus* forest with sparse understorey vegetation, but complex habitat from fallen *Pandanus* fronds. The habitat types used by the skink species (based on captures of new lizards) were compared among species using log-linear models. I used the microhabitat and behaviour of skinks recorded during activity observations surveys (Chapter 2) to compare the behaviour and microhabitat of the species, as well as daily activity patterns of the species based on the number of observations at different times of day. The height above ground at which individuals of each species were observed was compared using a log-linear model.

Space use

Space use was determined from the grid locations of capture and recapture (within and between sampling trips) for individual skinks that were caught on multiple occasions (see Chapter 2). Area of space used by skinks was calculated using the minimum convex polygon (MCP) method in ArcView v9.1 geographic information system software (Environmental Systems Research Institute Inc., Redlands, CA, USA). This measure of space use cannot be interpreted as skink home range as I could not control the date of capture of individual skink and some skinks were caught over multiple seasons. The MCP data provided a measure of relative space use by skinks, this was compared among the species with Kruskal-Wallis tests.

Analyses

Analyses of mark-recapture data (for population estimates, survival and recapture probability and recruitment) were performed with Program MARK v5.1 (White and Burnham

1999). I used RMA for Java v1.21 (Bohonak and van der Linde 2004) for reduced major axis (RMA) regression analyses. Body mass and body length measurements were log-transformed before regression, and 1000 bootstraps of the data were used. All other statistical analyses were performed with the statistical package SPSS v16.0 (SPSS Inc., Chicago, IL, USA, 2007). Significance level was set at $P = 0.05$.

Results

Lizards were active year-round at the study site (Figure 3.1), there was no inactivity period. The highest rate of lizards captured per hour occurred in the early dry season (April – May) in all three years (Figure 3.1). A total of 2090 new individual lizards were captured in the study plots. Geckos were rarely captured within the study plots (< 20 individuals). The majority of lizards observed and captured at the study site were skinks (> 99.9%), and most skinks observed and captured were from the genus *Carlia* (> 86%).

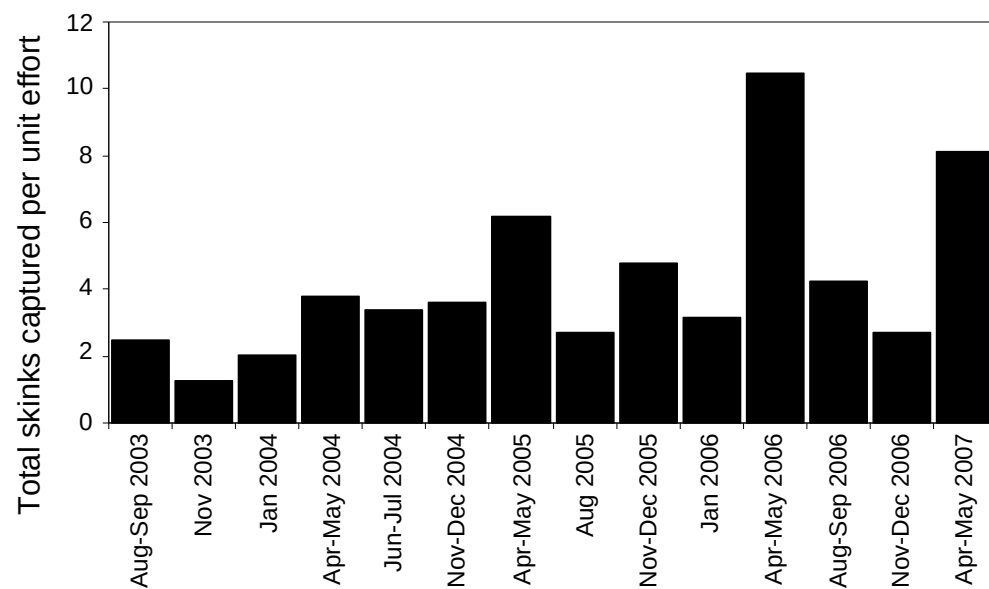


Figure 3.1. Total skinks captured in study plots per catcher-hour on each sampling occasion.

Skink species at the study site

Twelve species from the family Scincidae were captured at the study site on Hinchinbrook Island (Table 3.1). The majority of these species are small (< 60 mm SVL, < 5 g body mass), and all, except arboreal *Cryptoblepharus virgatus*, are ground dwelling (Greer 1989). Most species were captured on very few occasions, either because they occurred at low densities, or because they were highly secretive or cryptic, or not resident at the study site. For example, *Glaphyromorphus* sp. are fossorial (Greer 1989), thus individuals were only seen on the rare occasions when they surfaced above the leaf litter and were more often trapped in pitfall traps and funnel traps than captured by hand. *Menetia* are some of Australia's smallest reptiles (Wilson 2005) and individuals seldom venture far from cover. *Menetia timlowi* were seen at the study site, but infrequently captured due to their very small size and ability to rapidly retreat beneath the leaf litter. *Saproscincus* are shade-loving, heat-sensitive skinks (Greer 1989). *Saproscincus basiliscus* at the study site occupied heavily shaded habitats and were observed in low light conditions in the early morning and late afternoon, and on overcast days. *Egernia* live in complex burrows with multiple openings (Greer 1989). Major's skinks *Egernia frerei*, the largest skinks at the study site, were most commonly observed basking at the entrance to a burrow, into which they retreated when alarmed. For this reason *Egernia* were very rarely captured by hand and caught instead in funnel traps.

Three species from the genus *Carlia* were captured considerably more frequently at the site than any other species (Table 3.1). *Carlia rostralis*, *C. rubrigularis* and *C. storri* are diurnally surface active and heliothermic skinks (Wilson 2005), and were therefore easy to observe at the study site. The habits and life history patterns of these three species, and the demographics of their populations at the study site, are described in this chapter.

Table 3.1. The skink species captured within study plots at the Hinchinbrook Island study site.

Species	No. of new individuals ^a	Density (per 100 m ²) ^b	Mean adult body size (mm) ^c	Mean adult body mass (g)
<i>Carlia rostralis</i>	820	14.2	57.8 (112)	4.6
<i>Carlia rubrigularis</i>	548	7.1	46.7 (98)	2.4
<i>Carlia storri</i>	438	5.8	42.6 (69)	1.8
<i>Saproscincus basiliscus</i>	114	1.1	43.6 (23)	1.5
<i>Cryptoblepharus virgatus</i>	26	0.9	35.5 (12)	0.7
<i>Egernia frerei</i>	28	0.5	174.0 (5)	159.0
<i>Glaphyromorphus punctulatus</i>	57	0.5	53.8 (15)	2.1
<i>Menetia timlowi</i>	35	0.35	27.3 (6)	0.2
<i>Glaphyromorphus pumilus</i>	14	0.15	51.3 (11)	1.3
<i>Lampropholis coggeri</i>	6	0.12	35.8 (3)	0.9
<i>Ctenotus robustus</i>	3	0.04	94 (1)	17.0
<i>Ctenotus terrareginae</i> ^d	1	0.04	-	-

^a Number of new individuals captured during entire study (May 2003 to May 2007).

^b Density = new individuals captured during 2006 = crude estimate of density of each lizard species at the site for a representative year.

^c Mean size of sexually mature individuals (number of individuals measured)

^d *C. terrareginae* – only one juvenile captured.

Description of *Carlia*

Carlia are strongly visually-cued skinks and males often feature spectacular breeding hues (Wilson 2005). Of the three species at the study site, adult *C. rostralis* and *C. rubrigularis* are sexually dichromatic, males exhibit striking throat colouration, which is exaggerated during the breeding season (red in *C. rubrigularis* and black in *C. rostralis*, Figure 3.2), whereas females of these two species have pale orange (*C. rubrigularis*) or white (*C. rostralis*) throats. *Carlia rostralis* individuals also have orange flanks, brighter in males particularly during the breeding season. Both sexes of *C. storri* are non-dichromatic light brown (Figure 3.2). There is considerable body size variation among the three species (Figure 3.3). *Carlia rostralis* adults are largest, but *C. rostralis* juveniles overlap in body length with the other two species (Figure 3.3). The bimodal distribution of *C. rostralis* body size may be due to the large number of juveniles in the population.



Figure 3.2. The three most abundant species at the study site on Hinchinbrook Island: (a) *Carlia rostralis*, (b) *C. rubrigularis*, and (c) *C. storri*. Adult male skins are pictured.

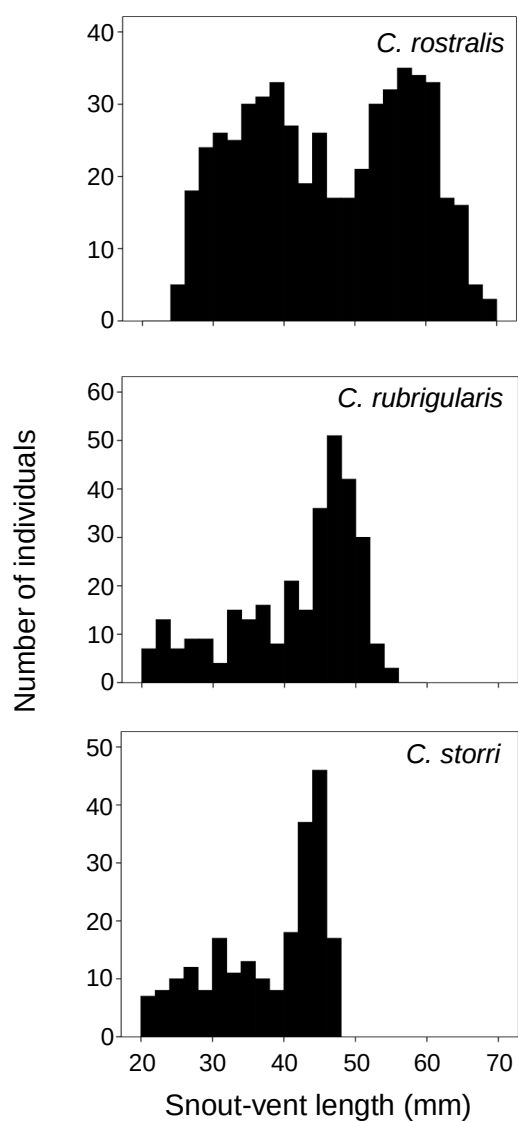


Figure 3.3. Distribution of body sizes for the three *Carlia* species from the study site.

Population estimates

The POPAN model: ϕ (time) p ($\bullet$) $PENT$ (time) N (species) (i.e., where survival was time-dependent, recapture rate was constant across all sampling occasions and the probability of entry into the population differed among time intervals and the size of the population differed among the species), was identified by AIC as the only suitable fit to the capture data of all species (Table 3.2). Models including species differences in survival or recapture probability received very little support from the data (Table 3.2; $\Delta QAIC_c > 77.0$). Thus, while the three species differed in their overall population size (Figure 3.4), they did not differ significantly in survival or recapture probability.

Table 3.2. Truncated results from the POPAN formulation in Program MARK showing the best eight models describing the survival (ϕ) and recapture (p) probability, probability of entry into the population ($PENT$) and population size (N) of all *Carlia* at the study site.

Model	$\Delta QAIC_c$	Model likelihood	Number of parameters
ϕ (time) p ($\bullet$) $PENT$ (time) N (species)	0.000	1.000	26
ϕ (time) p (time) $PENT$ (time) N (species)	8.740	0.013	37
ϕ (time) p ($\bullet$) $PENT$ (time) N ($\bullet$)	12.724	0.002	24
ϕ (time) p (time) $PENT$ (time) N ($\bullet$)	17.171	0.0002	35
ϕ ($\bullet$) p (time) $PENT$ (time) N (species)	50.021	0.000	26
ϕ ($\bullet$) p (time) $PENT$ (time) N (species)	62.422	0.000	24
ϕ (species) p (species) $PENT$ (time) N (species)	77.802	0.000	20
ϕ (species) p ($\bullet$) $PENT$ (time) N (species)	77.846	0.000	18

$\Delta QAIC_c$ = difference in dispersion-corrected Akaike Information Criterion calculated by subtracting the model $QAIC_c$ from the 'best' (i.e., lowest $QAIC_c$) model. Model likelihood = calculated as the AIC_c weight of each model divided by the AIC_c weight for the 'best' model.

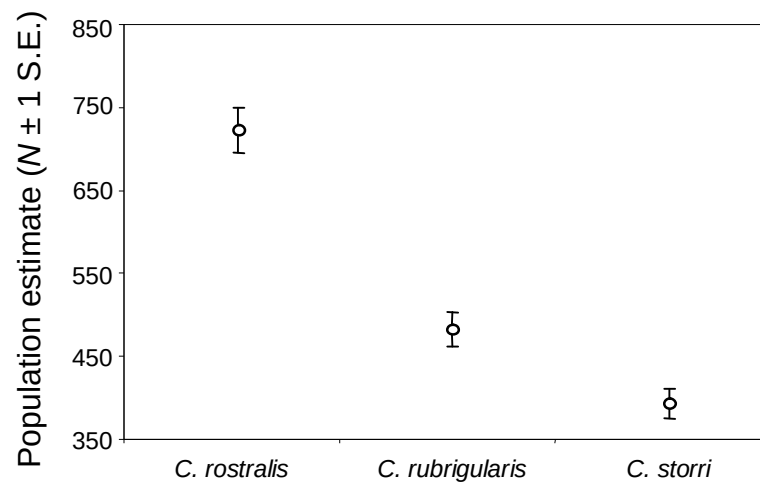


Figure 3.4. Population estimate (number of individuals, $\pm$ standard error) for each species of *Carlia*.

Survival and recapture rates

As for POPAN models (Table 3.2), CJS models revealed little difference in survival probability among the species (Table 3.3, survival models incorporating species have very little support: $\Delta\text{QAIC}_c = 14.6$). Survival of all three species differed strongly among the sampling occasions (i.e., among seasons, since sampling took place in early dry, late dry and early wet seasons over three years, see Chapter 2). Examination of the time-dependent survival, constant recapture model from each species showed consistently high survival probability (mean > 0.8) of skinks at the start of the wet season (September – October) and lower survival probability (mean < 0.4) during the early dry season (April, Figure 3.5).

There was some indication of species differences in recapture probability (Table 3.3: model 2, $\Delta\text{QAIC}_c = 3.33$), probability of recapture was slightly greater for *C. storri* (0.54 ± 0.05 S.E.) than *C. rostralis* (0.50 ± 0.03 S.E.) and *C. rubrigularis* (0.50 ± 0.04 S.E.).

Table 3.3. Summary of Cormack-Jolly-Seber mark-recapture models describing survival (ϕ) and recapture (p) rates of *Carlia rostralis*, *C. rubrigularis* and *C. storri*. See Table 3.2 for notation.

Model	ΔQAIC_c	Model likelihood	Number of parameters	Deviance
ϕ (time) p ($\bullet$)	0.000	1.000	12	619.462
ϕ (time) p (species)	3.338	0.188	14	618.724
ϕ (time) p (time)	4.834	0.089	21	605.863
ϕ (time x species) p ($\bullet$)	14.619	0.001	34	588.606
ϕ (time) p (species x time)	29.097	0.000	43	584.068
ϕ (species x time) p (species x time)	52.203	0.000	64	561.837
ϕ (species) p ($\bullet$)	80.478	0.000	4	716.130
ϕ (species) p (species)	80.592	0.000	6	712.213

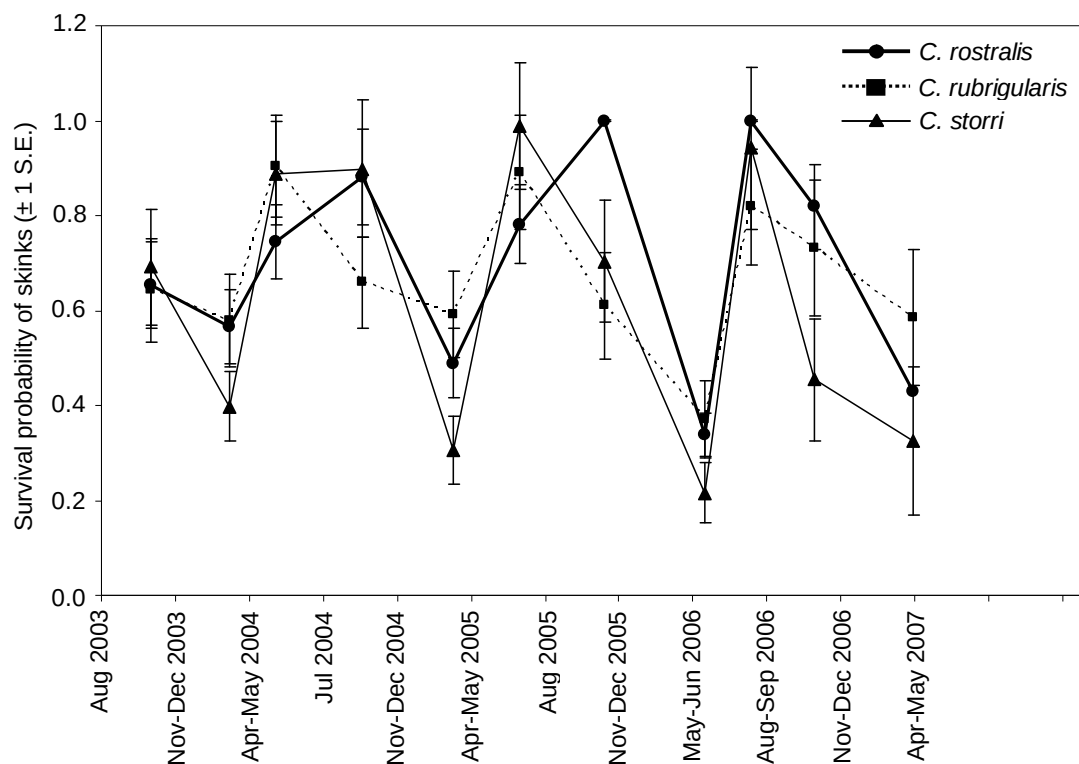


Figure 3.5. Survival probability ($\pm$ standard error) between each sampling occasion, from mark-recapture models of the three *Carlia* species.

Reproduction, sex ratios, longevity and body condition of Carlia at the study site

Overall adult sex ratios (across all years and seasons) did not vary among the three species (ANOVA: $F_{2,35} = 0.86$, $P = 0.43$). The ratio of *C. rostralis* males to females, however, varied among the seasons: the *C. rostralis* population was significantly female-biased in the early dry season (April to June) and the early wet season (October to December; Kruskal-Wallis test of seasonal difference in proportion of males across all years of sampling: $\chi^2 = 9.95$, d.f. = 3, $P = 0.02$; Figure 3.6). Similarly, female *C. storri* were somewhat (but not significantly) more frequently captured in the early dry and early wet seasons compared to conspecific males (*C. storri*: $\chi^2 = 2.53$, d.f. = 3, $P = 0.47$; and *C. rubrigularis*: $\chi^2 = 4.18$, d.f. = 3, $P = 0.24$; Figure 3.6).

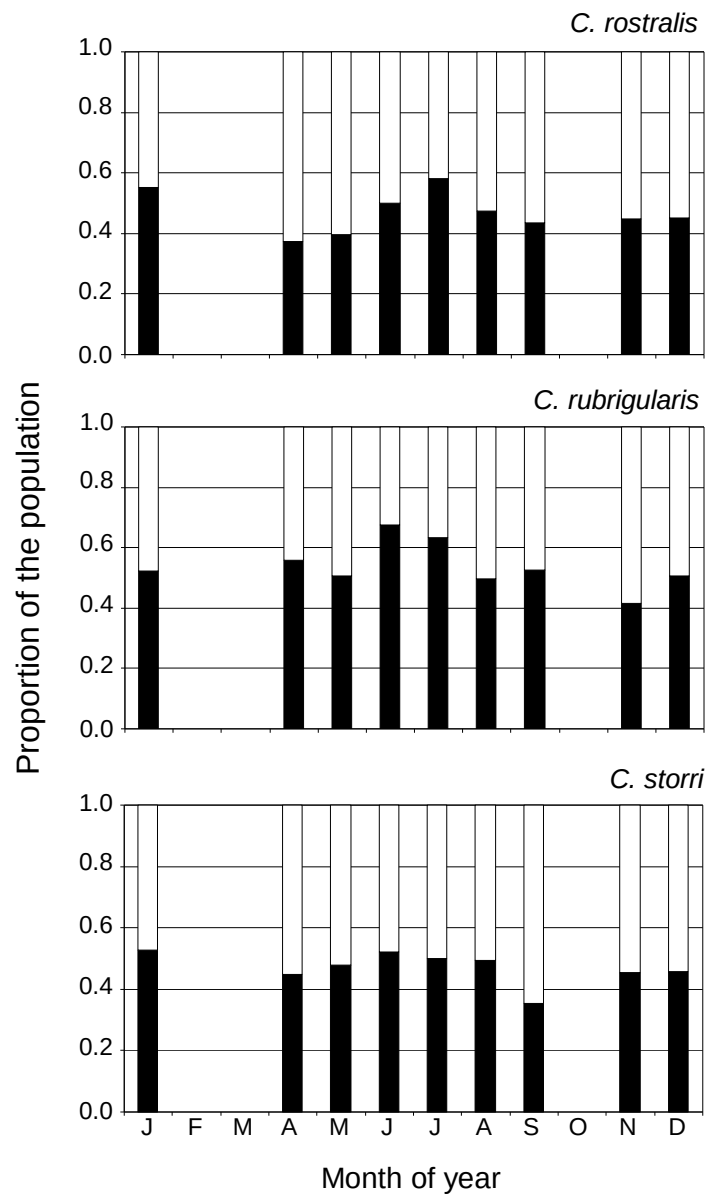


Figure 3.6. Ratio of males (black) to females (white) in the population in each month of the year sampled, for the three *Carlia* species.

From palpation of female *Carlia*, the ratio of gravid females to non-gravid females peaked in the wet season (December and January) for all species. The three species varied in length of breeding season: *C. rostralis* and *C. rubrigularis* started breeding in August (late dry season) and *C. storri* in November (start of wet season, Figure 3.7).

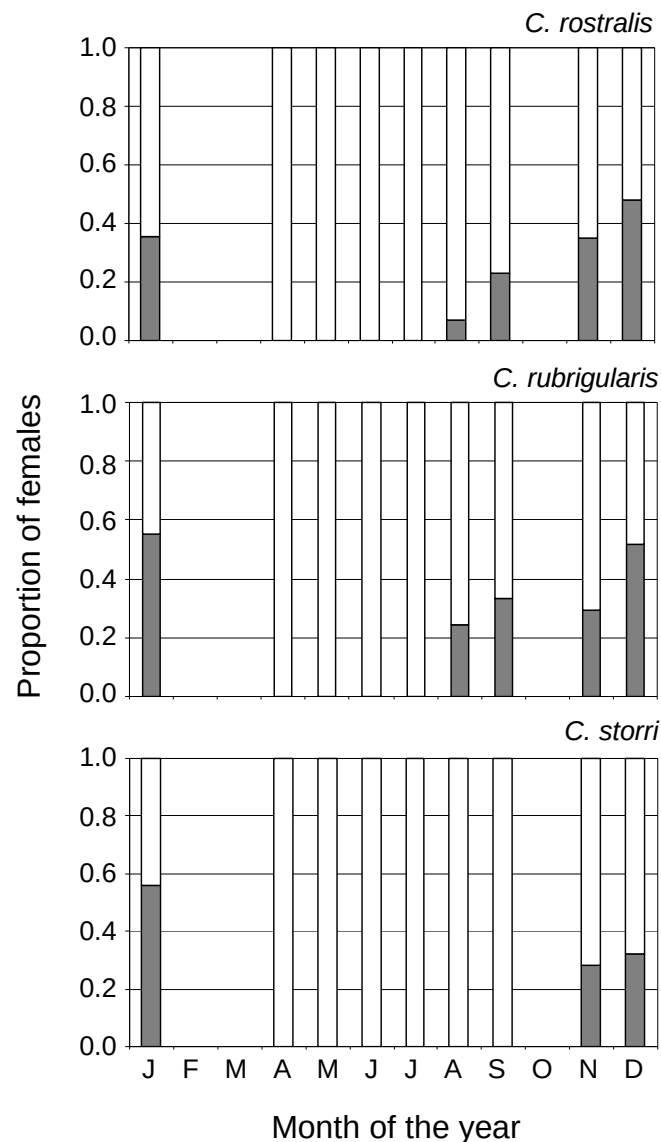


Figure 3.7. Ratio of gravid females (grey) to non-gravid females (white) in the population in each month of the year sampled, for the three *Carlia* species.

There was a significant relationship between body mass and snout-vent length for all three species (linear regression: *C. rostralis* $r^2 = 0.85$; *C. rubrigularis* $r^2 = 0.55$; *C. storri* $r^2 = 0.52$; all $P < 0.001$). Body condition, the residuals of reduced major axis regression of mass on snout-vent length, varied between the sexes of *C. rostralis* and *C. storri* (t-tests to compare residual values between males and females: *C. rostralis* $t = 2.9$, d.f. = 150, $P = 0.004$; *C. rubrigularis* $t = 0.81$, d.f. = 111, $P = 0.42$; *C. storri* $t = 2.34$, d.f. = 85, $P = 0.02$), the sexes were thus included as a factor in tests of seasonal differences in body condition. The body condition of males and females responded in similar ways to seasonal changes (ANOVA sex

x season: *C. rostralis* $F_{3,151} = 0.82$, $P = 0.48$; *C. rubrigularis* $F_{3,112} = 1.68$, $P = 0.18$; *C. storri* $F_{3,86} = 1.91$, $P = 0.14$; Figure 3.8). *Carlia rostralis* individuals were thinner in the wet season (lower than average body condition, as indicated by negative residual values), and fatter in the dry season (ANOVA season: $F_{3,151} = 3.26$, $P = 0.02$; Figure 3.8). Body condition of *C. rubrigularis* and *C. storri* individuals did not differ significantly among the seasons (ANOVA season: *C. rubrigularis* $F_{3,112} = 0.67$, $P = 0.57$; *C. storri* $F_{3,151} = 0.14$, $P = 0.93$; Figure 3.8), but in both species females were thinnest (i.e., lowest body condition compared to average) in the early dry season.

Longevity of skinks, estimated from the longest recaptured male and female of each species, was approximately three years for females of all species (Table 3.4). Male skinks appear to have a shorter lifespan than females. The skinks for this estimation were captured first as adults, so these estimates may be at least six months short of an accurate indication of lifespan.

Table 3.4. Longevity of *Carlia* species, estimated from longest recaptured individual of each sex.

Species	Sex	Age (months)
<i>C. rostralis</i>	♀	39.9 (3.3 years)
	♂	23.0 (1.9 years)
<i>C. rubrigularis</i>	♀	36.9 (3.1 years)
	♂	15.8 (1.3 years)
<i>C. storri</i>	♀	34.5 (2.8 years)
	♂	24.2 (2.1 years)

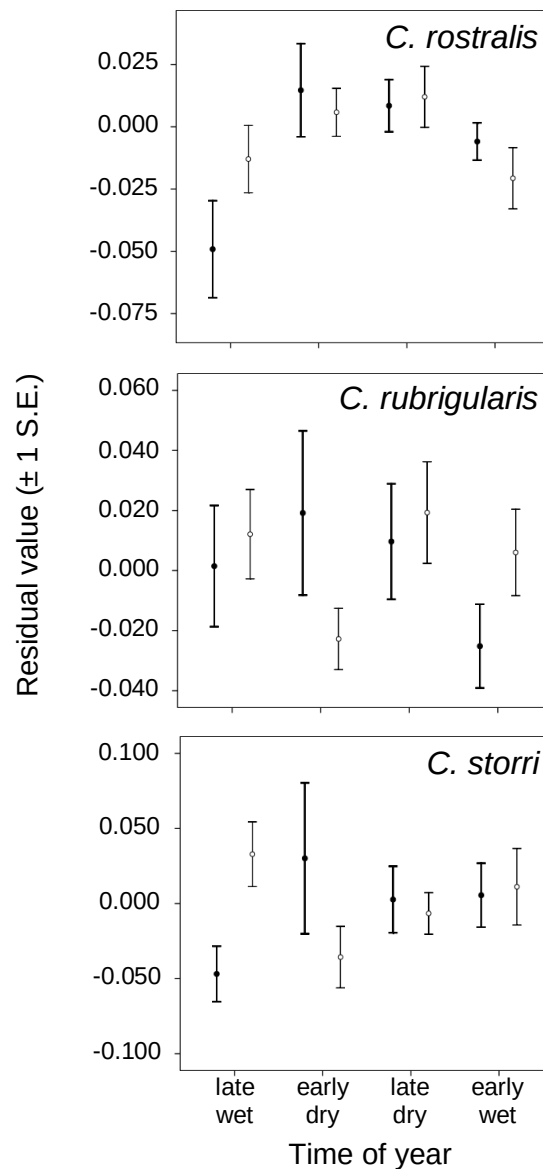


Figure 3.8. Residual values (from RMA regression of $\log_{10}$ -body mass on $\log_{10}$ -body size, $\pm$ standard error) for males (filled symbol) and females (open symbol) of the three *Carlia* species in the late wet (January to March), early dry (April to June), late dry (July to September) and early wet (October to December) seasons.

Juvenile recruitment, survival and age ratios

Pradel models incorporating 'species', 'age' and 'time' to define population recruitment rate were best supported by the data (Table 3.5). In other words, recruitment of juveniles and adults occurred at different times of year, and recruitment rates differed among the species. Parameter estimates of juvenile recruitment at each sampling occasion showed that recruitment into the population started in the late wet (January), peaked in the early dry

season (April – May) and was low (or zero) in the late dry and early wet seasons (July to December, Figure 3.9).

Table 3.5. Summary of Pradel mark-recapture models describing survival (ϕ), recapture (p) and recruitment (f) rates of *Carlia rostralis*, *C. rubrigularis* and *C. storri*. See Table 3.2 for notation.

Model	ΔAIC_c	Model likelihood	Number of parameters	Deviance
ϕ (time) p (time) f (species x age x time)	0.000	1.000	86	1247.837
ϕ (time) p (time) f (age x time)	34.391	0.000	46	1367.642
ϕ (time) p (time) f (species x time)	326.462	0.000	59	1632.326
ϕ (time) p (time) f (species x age)	328.111	0.000	33	1688.398
ϕ (time) p (time) f (age)	341.606	0.000	29	1710.142
ϕ (time) p (time) f (time)	344.123	0.000	37	1696.128
ϕ (time) p (time) f (species)	375.620	0.000	30	1742.097

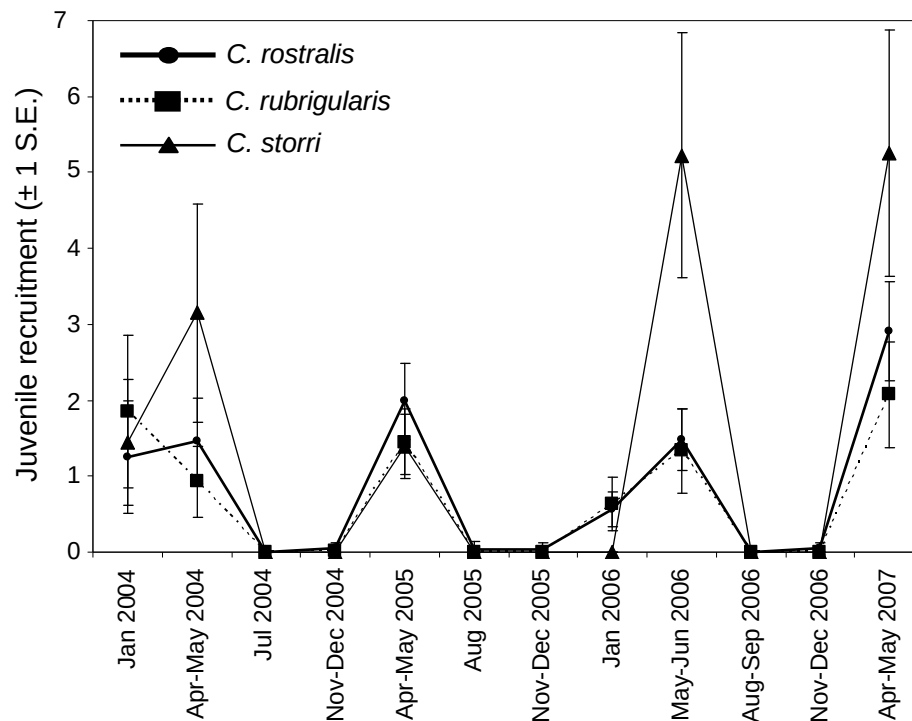


Figure 3.9. Recruitment of juveniles of each *Carlia* species between sampling occasions.

The species did not differ in the overall proportion of juveniles in their populations (ANOVA $F_{2,35} = 0.72$; $P = 0.22$), however the population of each species was composed of a significantly greater proportion of juveniles in the early dry season (April to June) than at other times of year (Kruskal-Wallis test of seasonal differences: *C. rostralis* $\chi^2 = 9.74$, d.f. = 3, $P = 0.02$; *C. rubrigularis* $\chi^2 = 9.05$, d.f. = 3, $P = 0.03$; *C. storri* $\chi^2 = 9.90$, d.f. = 3, $P = 0.02$; Figure 3.10).

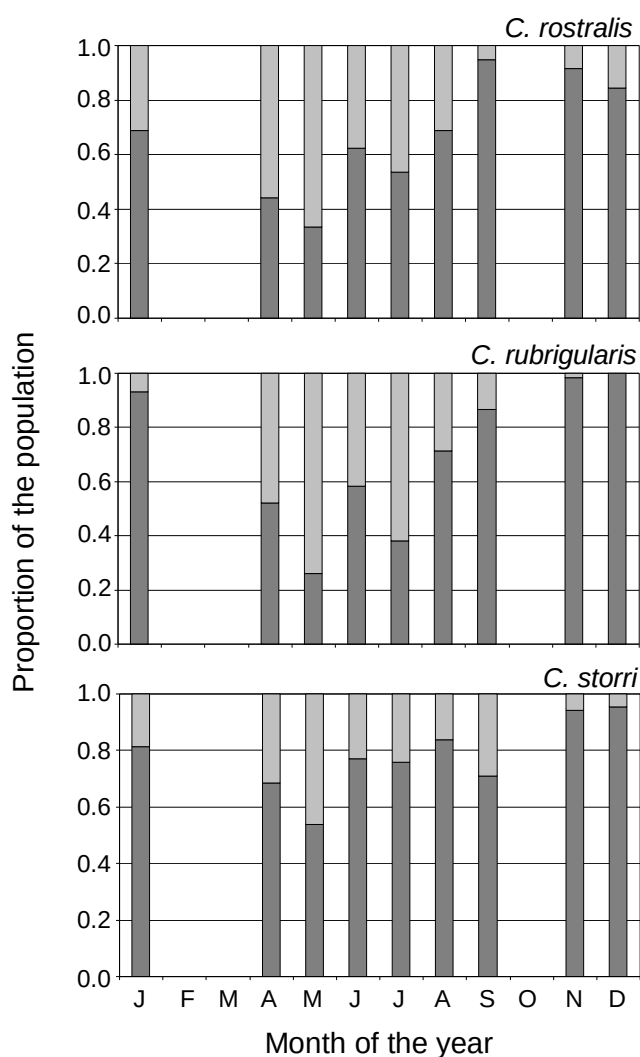


Figure 3.10. Ratio of adults (dark grey) to juveniles (light grey) for each month of the year sampled, for the three *Carlia* species.

Survival of juveniles to three, six and 12 months was determined from recaptures of marked hatchlings of each species each year. A high proportion of juveniles survived for at least three months (Figure 3.11), but significantly fewer survived to six months, and fewer still to 12 months (ANOVA of arcsin-transformed proportion of juveniles surviving, months survival: $F_{2,35} = 49.44$, $P < 0.001$). There was no significant difference among the species in the proportion of juveniles surviving (ANOVA species x months survival: $F_{4,35} = 0.95$, $P = 0.45$).

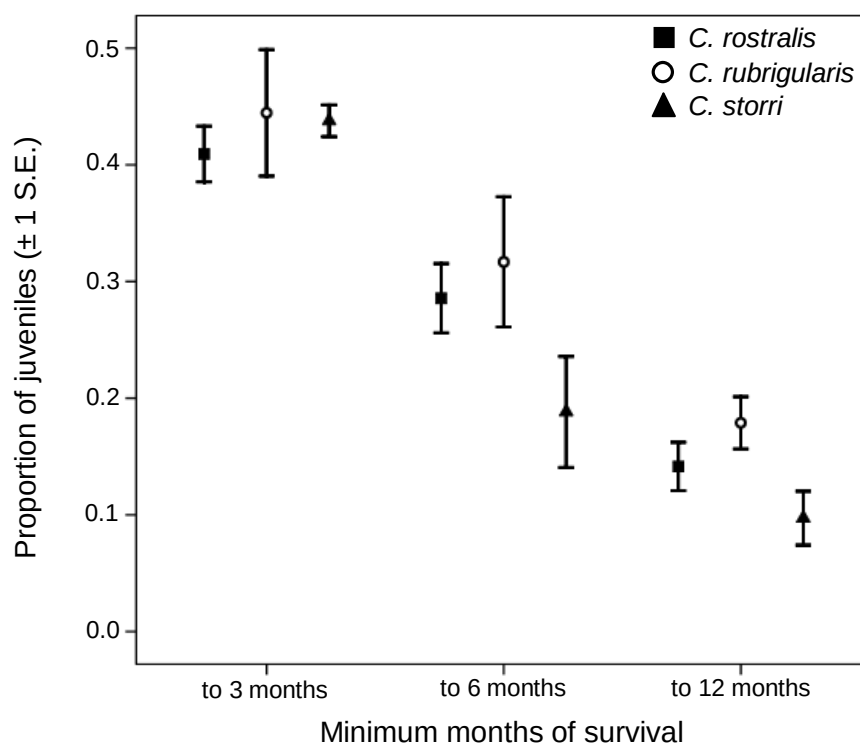


Figure 3.11. Proportion of juvenile skinks ($\pm$ standard error), marked first as hatchlings, surviving to three, six and 12 months, for the three *Carlia* species.

Habitat, microhabitat, habits and behaviour of Carlia species

- Habitat and microhabitat differences

The three species were randomly distributed among the available habitat types (log-linear analysis, habitat x species: $G = 0.71$, d.f. = 6, $P = 0.994$; Figure 3.12). All three species were highly terrestrial (Figure 3.13), they were observed most frequently on the leaf litter at ground level and only rarely above this, within 20 cm of the ground (log-linear analysis partial association, height: $G = 1938.9$, d.f. = 3, $P < 0.001$; but interaction species x height: $G = 8.21$, d.f. = 6, $P = 0.22$). *Carlia storri* was observed above ground level more often than the other two species (partial association, species: $G = 112.2$, d.f. = 2, $P < 0.001$, Figure 3.13).

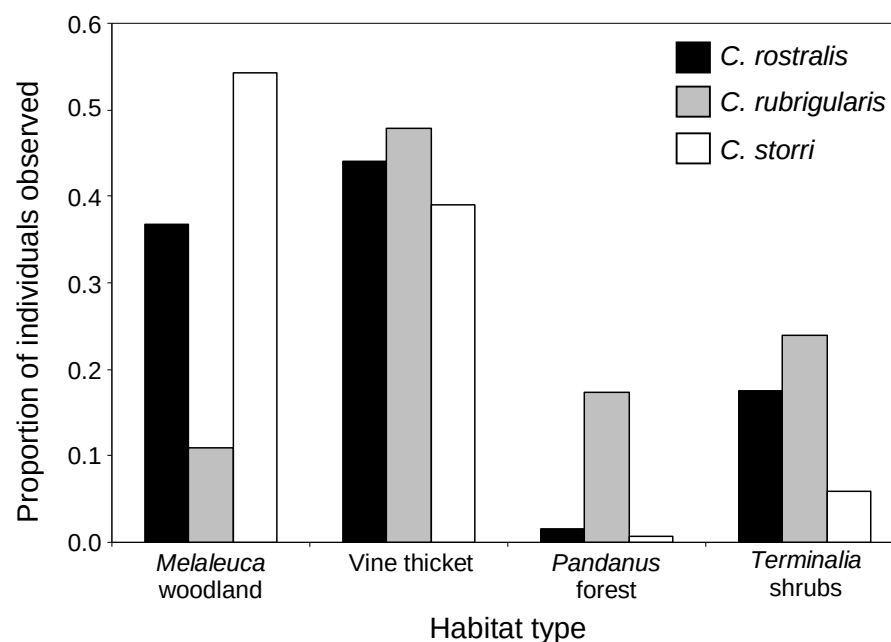


Figure 3.12. The proportion of each species of *Carlia* captured within each habitat type.

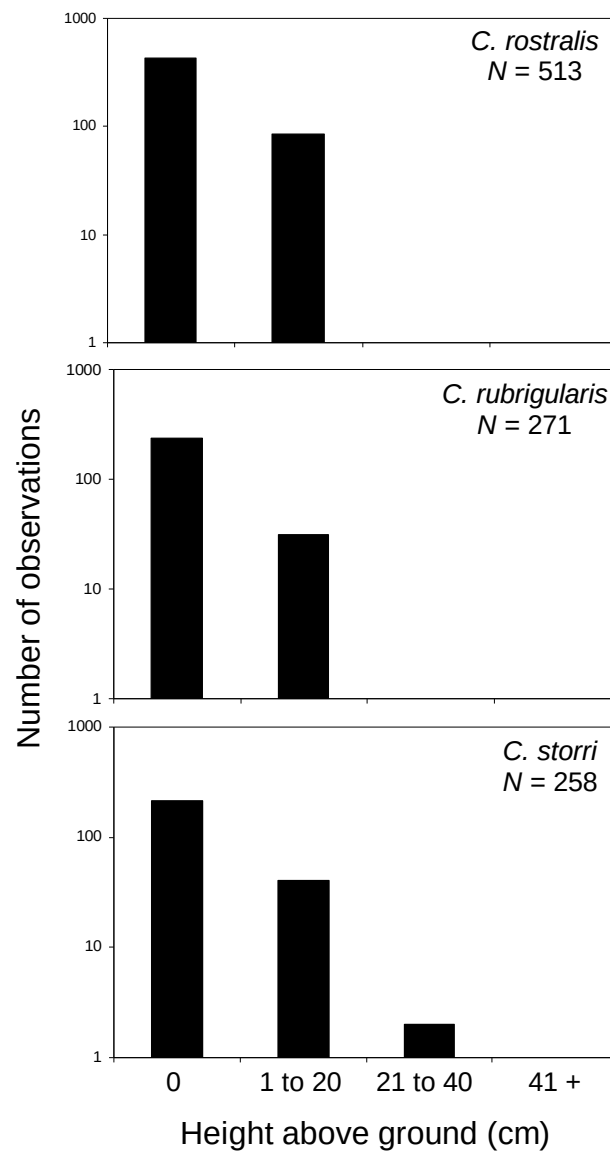


Figure 3.13. Number of skinks observed (logarithmic scale) at four categories of height above ground, for each of the *Carlia* species.

- Habits and behavioural differences

Skink activity observation surveys aimed to record only active skinks, to provide an indication of daily activity patterns of lizards at the study site (Chapter 2). All three species were observed at all times of day surveyed (Figure 3.14). There was generally a peak in activity (number of skinks observed) early in the day (0800), but *C. storri* individuals were more active in the late morning and afternoon (Figure 3.14).

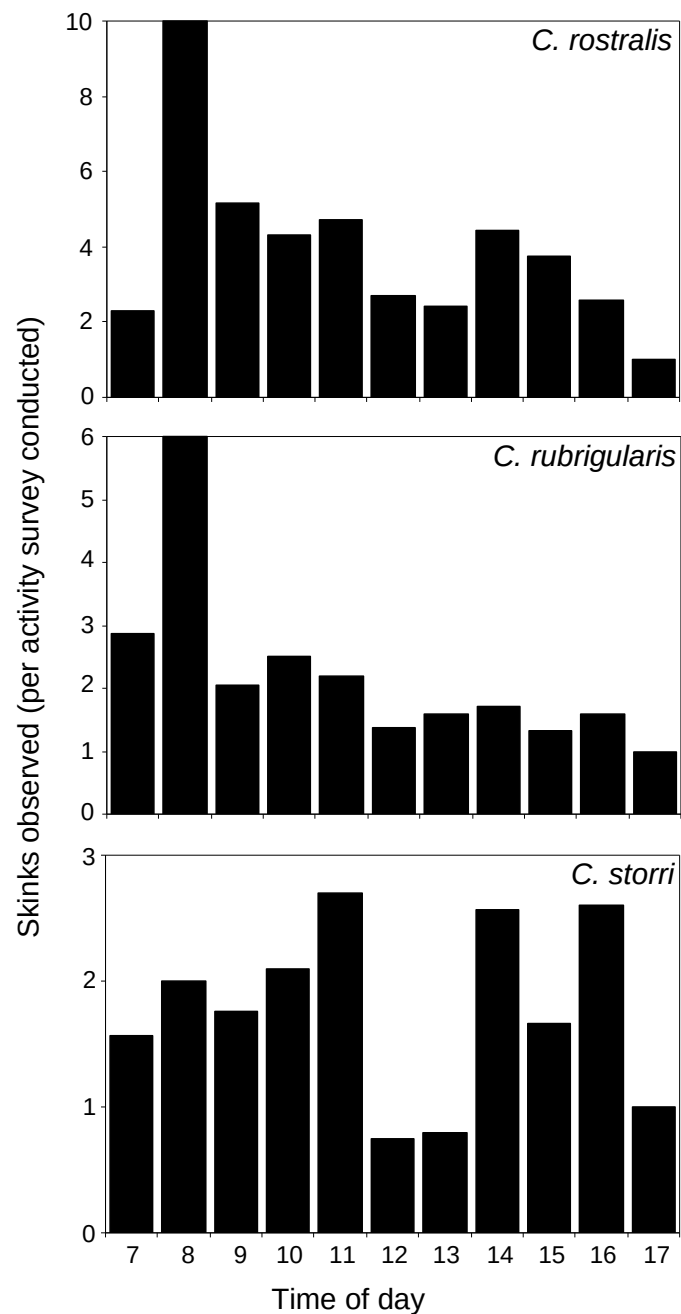


Figure 3.14. Daily activity patterns of the three *Carlia* species at the study site.

Note the difference in y-axis scale among the figures.

Skink behaviour was categorised as 'basking', 'immobile', 'moving', 'foraging' and 'display'. 'Basking' skinks were defined by their posture and sunny microhabitat. Motionless skinks in shaded microhabitat were defined as 'immobile', and could have been either resting and avoiding the high temperatures of sunny patches, or trying to avoid detection. Skinks that were actively searching for food (tongue flicking, searching the leaf litter, i.e., 'foraging') were differentiated from individuals that were moving to cover ground ('moving'). 'Display' included social interaction and courtship behaviour, and

comprised tail waving, head bobbing and body posturing during dominance and courtship interactions (see Whittier and Martin 1992 and Langkilde et al. 2003 for types and definitions of *Carlia* social behaviour). All species spent the majority of their time moving (Figure 3.15). *Carlia storri* were seldom observed basking or foraging. *Carlia rostralis* individuals were observed head bobbing at conspecifics, and *C. rubrigularis* use head bobbing and frequent tail waving to conspecifics, congeners and potential predators (researchers). No obvious display behaviour was ever observed in *C. storri* individuals.

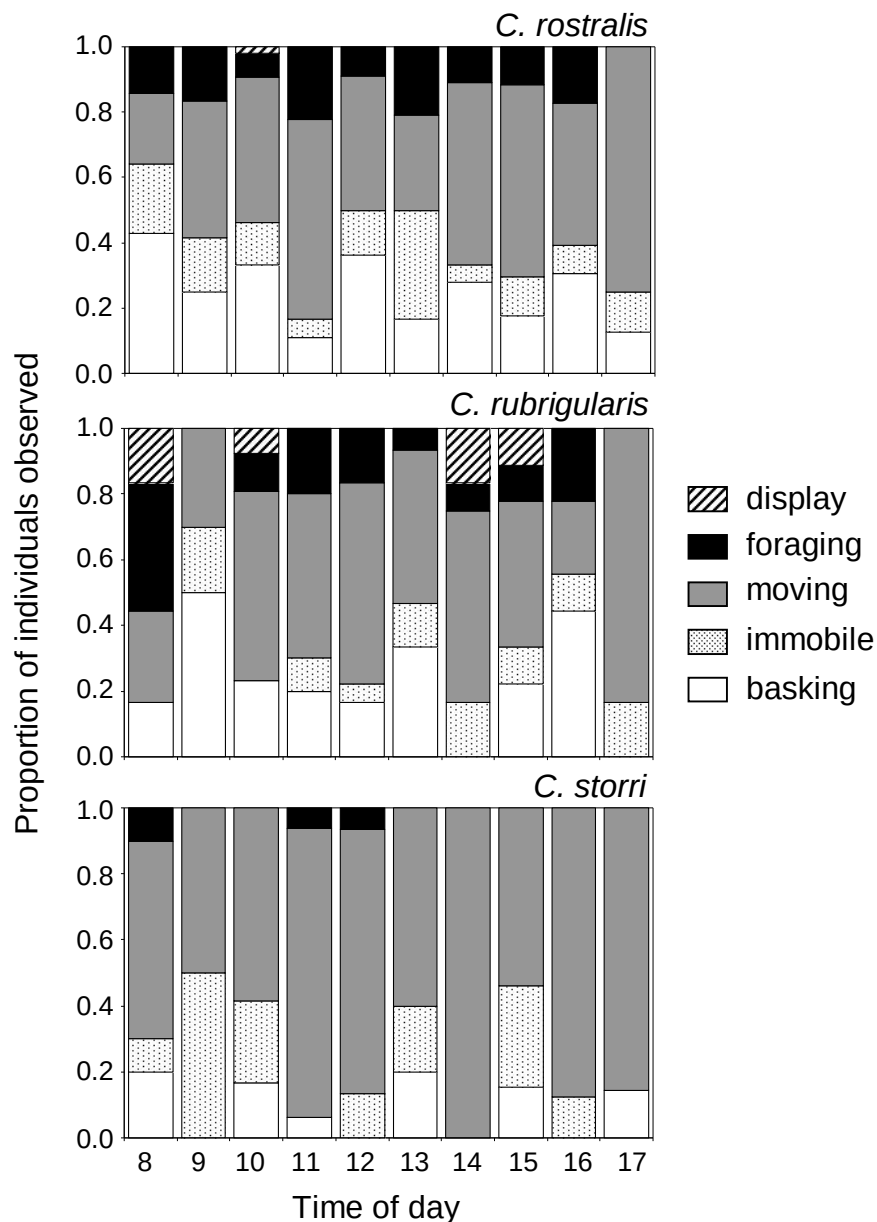


Figure 3.15. Skink behaviour observed during activity surveys, for the three *Carlia* species.

Space use by *Carlia* species

Space use data were obtained for 211 individual lizards. There was no relationship between MCP area and number of fixes when I used at least five fixes (*C. rostralis*, $r_{\text{spearman}} = 0.26$ [$P = 0.10$]; *C. rubrigularis*, $r = 0.16$ [$P = 0.60$]; *C. storri*, $r = 0.35$ [$P = 0.10$]). I removed individuals for which I did not have sufficient fixes from the dataset, leaving a sample of 94 space use areas for analysis. The species differed in space use (Kruskal-Wallis test: $\chi^2 = 7.84$, d.f. = 2, $P = 0.02$; Figure 3.16); *C. storri* individuals were captured over a significantly smaller area than the other two species (Figure 3.16).

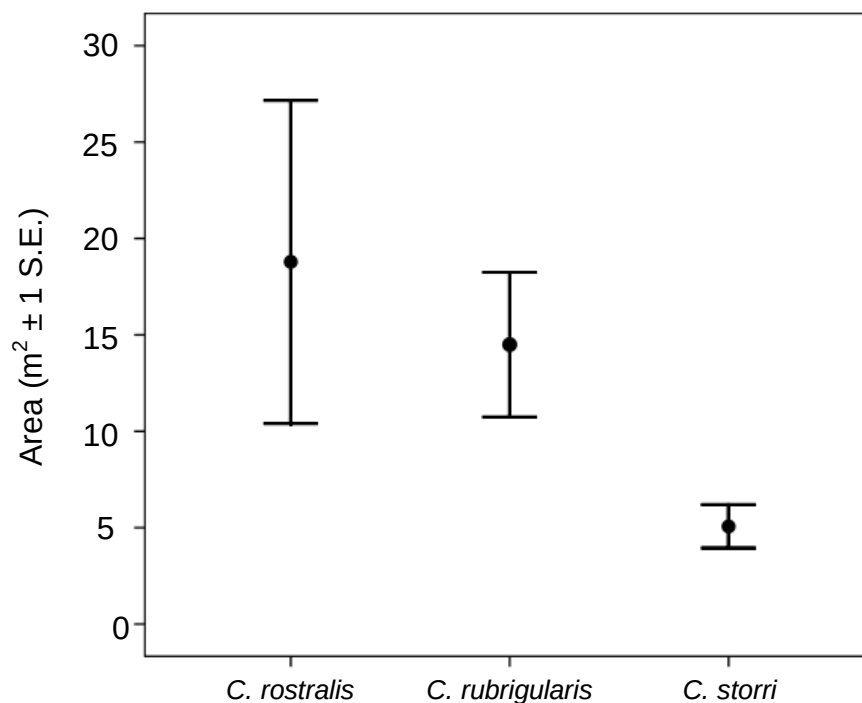


Figure 3.16. Area of space used by *Carlia* species (m^2 , $\pm$ standard error) calculated from individuals captured on more than five occasions.

Discussion

The lizard community at Hinchinbrook Island was composed almost entirely of skinks (see Table 2.1). The only other lizards frequently observed or captured within or near the study plots were varanids (three species: *Varanus varius*, *V. panoptes* and *V. scalaris*), and aspects of the ecology of the varanid population at the study site are described in another study (Lloyd 2007). Here, I describe the population ecology of the three most abundant skink species at the study site: *Carlia rostralis*, *C. rubrigularis* and *C. storri*. Skinks were active year-round at the study site, showed no period of inactivity, consistent with other tropical reptiles (James and Shine 1988). These skinks were small (<5 g), but occurred at high density at the study site (~25 individuals per 100m²) and, thus, were a conspicuous part of the ecosystem. *Carlia* are diurnal, surface active, heliothermic and insectivorous (Wilson 2005), and may be expected to be important in trophic interactions at the study site, both as predators of lower trophic levels and prey of higher trophic levels. The three *Carlia* species coexist sympatrically at the study site, and sympatric species usually need to partition available resources to reduce competition, and may exhibit very different reproductive timing, recruitment, activity and microhabitat use if resources are limited (Pianka 1973).

Population structure and reproduction of Carlia at the study site

Carlia rostralis was the largest of the three species, and maintained the largest population (Figure 3.4), however, *C. rostralis* did not have a significantly greater probability of survival than the other two species (Table 3.3). All three species had similarly fluctuating adult survival rates; consistently greater survival over the late dry season (> 80% probability of survival between July and September) and the wet season (October to March), and lowest survival over the early dry season (April to June; Figure 3.5). The survival probability of the *C. storri* population was particularly low (never greater than 40%) over the early dry season (Figure 3.5).

Longevity of skinks was similar among the three species; females are longer-lived than males in all species, and lived to approximately three years (Table 3.4). Sex ratios fluctuated slightly during the year, from a small female-bias in the population in the early dry

and early wet seasons (for *C. storri*, significantly for *C. rostralis*) to a male-dominated population in other months (Figure 3.6). Fluctuating sex ratios suggest variation in the activity of the sexes (Le Galliard et al. 2005a), or the seasonal female-bias may correspond with reduced female agility in the reproductive season making female skinks easier to capture.

Lizard reproduction is frequently timed to occur during the wettest months, although some tropical species reproduce all year round (James and Shine 1985; Clerke and Alford 1993). Male *C. rostralis* and *C. rubrigularis* display striking nuptial colouration in the wet season (*pers. obs.*); the throats of male *C. rostralis* turn from grey to black, and the throats of male *C. rubrigularis* from pale pink to orange. The number of gravid females in the population similarly peaked for all three species in the wet season, but both *C. rostralis* and *C. rubrigularis* had lengthy breeding seasons, with gravid females observed in the population as early as August (Figure 3.7). Reproductive activity in the cool, dry months suggests that reproduction in these species is not initiated by increasing temperature or precipitation, but may be related to increasing day length instead (Clerke and Alford 1993). *Carlia storri* females were not found with eggs before November, and thus had a comparatively contracted reproductive season, possibly activated by rainfall, temperature or humidity.

The low likelihood of adult survival in the early dry season, exhibited by all three species but particularly *C. storri*, may coincide with the end of the reproductive season, an hypothesis that would be verified by a decline in skink body condition in the early dry season. Reproduction is energetically expensive for lizards and is associated with reduced food intake, slower growth rates and increased susceptibility to predators and parasites (Schwarzkopf and Shine 1992; Schwarzkopf 1993, 1996; Sinervo and DeNardo 1996; Abell 2000). A measure of body condition (body mass relative to body size) was used as an indicator the lizard's stored energy and general health (Jakob et al. 1996), and for all three species reduced body condition corresponded with reproductive, or post-reproductive activity and reduced adult survival. Both male and female *C. rostralis* exhibited a decline in body condition in the wet season; *C. rostralis* individuals had significantly reduced body condition in the wet months compared to in the dry (Figure 3.8). For *C. rubrigularis* and *C. storri*, the seasonal period of reduced body condition differed between males and females, but not significantly; males had body reduced condition in the wet season (early in season for male *C.*

rubrigularis, later in season for male *C. storri*; Figure 3.8) and females of both species had reduced condition in the early dry season. I was not able to distinguish between reproducing and non-reproducing skinks for body condition analyses (except for gravid females, which were excluded from analysis), and this may account for the lack of a significant difference among the seasons for all species.

Variation in body condition among the seasons, sexes and species was possibly an indicator of differences in the seasonal timing of peak reproductive effort by males and females of each species. Generally, male condition was lowest during the wet (breeding) season, consistent with the expenditure of energy on display of nuptial colour, courtship behaviour and mating. Female condition was, generally, lowest at the end of the breeding season (early dry months), consistent with egg-bearing. Female *Carlia* are oviparous, produce invariant clutches of two eggs and may lay up to three clutches in a season (James and Shine 1988; Cogger 2000; Goodman 2006).

Inter-specific competition among juvenile skinks would be reduced if the timing of emergence of hatchling skinks was staggered (James and Shine 1985). If resources were scarce at the study site, sympatric species may reproduce at different times to reduce competition among hatchlings (James and Shine 1985). Juvenile recruitment into the *Carlia* population at the study site, however, was similar for the three species. Recruitment began late in the wet season (January) and peaked in the early dry season for all three species (Figure 3.9). The similarity in reproductive season and juvenile recruitment among the species suggests that competition for resources is not strong enough to drive differences in reproductive timing among the species, and that resources may not be limited at the study site.

Juvenile skinks constituted a substantial proportion of the population in April and May (Figure 3.10). Approximately 40% of all skink hatchlings captured at the study site survived to at least three months, but less than half of these survived to 12 months (Figure 3.11). The *C. storri* population consistently had the highest juvenile recruitment rates (Figure 3.9) and high survival to three months (Figure 3.11), but *C. storri* hatchlings were least likely to survive to six or 12 months of age compared to the other two species. Poor juvenile survival combined

with very low post-reproduction adult survival of *C. storri* likely account for the relatively small population size of this species at the study site.

Habitat and behaviour of Carlia

Other comparative studies of lizard communities have demonstrated that sympatric species partition available resources in three ways: space, time and food (Pianka 1973). The diet and prey selection of these skinks is described in detail in Chapter 4, and here I consider the division of habitat and activity times among the species. The landscape at the study site consisted of a mosaic of available habitat for skinks, from vine thicket with dense understorey cover, to open woodland with sparse understorey cover. *Carlia rubrigularis* was captured more often in habitat with dense cover and complex structure (vine thicket, *Pandanus* forest) than *C. rostralis* and *C. storri*, but the species did not differ significantly in their distribution. All three species were highly terrestrial (Figure 3.13) and, therefore, do not partition the available resources by their use of the habitat. *Carlia* were observed most frequently on the leaf litter at ground level and only very rarely on twigs, logs and low vegetation within 20 cm of the ground. *Carlia storri* was observed above ground level more often than the other two species (Figure 3.13). All three species are active throughout the day (Figure 3.14). Both *C. rostralis* and *C. rubrigularis* exhibit a peak in activity in the early morning, whereas for *C. storri* daily activity was more evenly distributed. The tropics are defined by very high daily maximum temperatures (see annual average temperatures for the study site in Chapter 2), with the temperature of the substrate at the study site frequently hotter than 50° C in the middle of the day (Appendix C). Small-bodied ectotherms need to actively avoid critically high temperatures (Herczeg et al. 2006), and it is not surprising that few skinks were observed in the middle of the day (Figure 3.14). The similarity in daily activity between *C. rostralis* and *C. rubrigularis*, and the lack of a peak in activity by *C. storri* suggests that the species do not temporally divide the available resources.

Space use by the three *Carlia* is consistent with body size (Figure 3.16); *C. storri* had a significantly smaller space use than the other two species. Large lizards usually have a large home range (or use of space) due to larger resource requirements (Schoener and Gorman 1968). Observation of specific behaviours displayed by the species at different times

of day did not reveal many differences among the three species (Figure 3.15). All three species spend most of their time moving, necessary for shuttling between the sun and shade, and searching for food, and consistent with the behaviour needed by small ectotherms to maintain energetic demands (Herczeg et al. 2006). *Carlia* use display behaviour, such as head bobbing, body posturing and tail waving, to signal dominance to conspecifics or congeners, receptiveness to mates and awareness of predators (Whittier and Martin 1992; Langkilde et al. 2003). Social behaviour was observed frequently in *C. rubrigularis* and sometimes in *C. rostralis*, but never by *C. storri* individuals (Figure 3.15; *pers. obs.*). The social system of *C. storri* may be relatively simple, and this behavioural difference among the species may correspond with the lack of breeding colouration in monochromatic *C. storri*, compared to the other two species (Figure 3.2).

The three sympatric *Carlia* species, while different in body size and appearance, show remarkable similarity in most other aspects of their ecology, even though they compete directly with each other for space and food at the study site. The environment provided by the study site may not be limited in resources, and skinks may not need to compete for access to abundant arthropod prey, suitable habitat and optimal activity and reproductive periods. I continue to examine differences among the three species in more detail when considering growth rate, maturity and sexual dimorphism (Chapter 4) and susceptibility to parasites (Chapter 5), their diet and prey selection (Chapter 7), but have considered the three species as one trophic unit in the study of the complex trophic web at the study site (Chapters 8 and 9), justified by the similarity in the ecology, demography and resource use among the species presented here.

Chapter 4

Juvenile growth and sexual size dimorphism in sympatric tropical lizards: proximate and ultimate causes

Abstract

Sexual differences in animal body size (sexual size dimorphism, or SSD) can ultimately be selected for by dominance, fecundity or competitive advantage of large adult size. But selection pressures during juvenile development can influence sexual dimorphism of adults, and selection pressures on adult body size and juvenile growth rates may differ. Studies that address the relative contributions of both selection on adult body size *and* sexually dimorphic patterns of growth and maturity are particularly informative with respect to understanding the evolution of size dimorphism, yet such studies are rare. I investigated growth rates and resulting patterns of SSD in three sympatric, congeneric lizard species, *Carlia rostralis*, *C. rubrigularis* and *C. storri*, by determining growth pattern, probability of survival, and trophic niche partitioning between the sexes of each species, and among the species. The direction of SSD differed among the species (*C. rostralis* had larger males, *C. storri* had smaller males and *C. rubrigularis* were not sexually dimorphic in size), due either to differences in the duration of growth or to the rate of growth between sexes, but not to differential survival or niche partitioning of the sexes. Sex-specific trade-offs in the allocation of energy to growth and reproduction, and differential timing of maturation caused sexual divergence in growth, leading to SSD. Various different mechanisms, even within closely-related, sympatric species, acted on juvenile lizards to cause various amounts of dimorphism of adult body size. Knowledge of the variation in the development of SSD was important for interpreting the differences, or the lack thereof, in adult body size in these three lizard species. Variation in the direction of SSD among these three species is consistent with their different social systems, suggesting that there is selection on adult body size to produce the specific outcomes of juvenile growth rates or maturational timing in each species.

Introduction

Differences in body size between adult males and females of a species (sexual size dimorphism, or SSD) most likely evolves in response to three processes: (1) sexual selection for large male size, (2) fecundity selection for large female size, and (3) natural selection for resource partitioning (Darwin 1871; Andersson 1994; Fairbairn 1997). Sexual selection is defined as selection for characters (such as large body size, large antlers or tusks, attractive plumage) that give some males an advantage, in terms of mating success, over others (Carothers 1984; Anderson and Vitt 1990). Sexually selected characters have evolved either by female choice for high quality mates, or by successful competition with other males to monopolise access to females, or both (Darwin 1871; Andersson 1994). Selection for increased female size arises when large females can produce more or better offspring, or reproduce more frequently (Berglund et al. 1986; Schulte-Hostedde and Millar 2000). Alternatively, when body size is related to resource use, natural selection for competition avoidance between the sexes can lead to dimorphism in body size or shape of trophic structures (Schoener 1967; Shine 1989).

To determine the ultimate causes of SSD, studies traditionally observe sexual size differences of adults, and determine the functional significance of the large size in the larger sex (e.g., Clutton-Brock et al. 1985; Schulte-Hostedde and Millar 2000; Karubian and Swaddle 2001; Badyaev et al. 2001a; Olsson et al. 2002). However, knowledge of adult size differences may provide little insight into the mechanisms underlying the evolution of sexual dimorphism within taxa. For instance, survival may be sex-biased, so that one sex lives longer than the other and grows to a larger size, or variation in adult sexual dimorphism can be influenced by evolutionary forces acting on juvenile development, which may be very different from those acting on adults (Clutton-Brock et al. 1985; Badyaev et al. 2001a). Sexes share most of the genes that control basic aspects of growth, and sex-biased expression of these genes during development is required to achieve adult sexual size dimorphism (Fairbairn 1997; Badyaev 2002). The sexes can differ markedly in their growth patterns, in rate of growth, duration of growth, age at maturity and survival rate; factors that can themselves be the subject of selection (Clutton-Brock et al. 1985; Stamps 1993; Stamps and Krishnan 1997; Badyaev et al. 2001b). Species that exhibit similar adult SSD may have markedly different developmental processes (Leigh 1992), or sexes may have similar ontogeny, but may differ in their probability of survival and therefore differ in adult body size (Clutton-Brock et al. 1985;

Watkins 1996). Sexual differences in growth patterns can evolve rapidly and knowledge of sex-specific growth trajectories, patterns of maturation and the probability of survival of animals in natural systems is crucial to understanding and interpreting the development of sexual dimorphism in animals and the evolutionary and functional significance of differences between taxa (Shine 1990; Stamps 1993; Badyaev 2002; Cox and John-Alder 2007).

Lizards are frequently used as models for the study of SSD; there are widespread examples of dimorphism among lizards, and much variation in the direction and magnitude of SSD in this group. There is evidence that both sexual selection and avoidance of competition have influenced patterns in lizard SSD, but often the possible causes of variation in body size are numerous, and distinguishing their relative importance is difficult (Cooper and Vitt 1989; Wikelski and Trillmich 1997). For instance, sexual selection for large males has been linked to female choice (Cooper and Vitt 1993), male aggression and contest behaviour (Carothers 1984; Anderson and Vitt 1990; Cox et al. 2003) and territory acquisition success (Stamps and Krishnan 1994) in lizards. However, selection for small males can occur when females are less readily encountered and male mating success is increased by diverting energy to mate searching rather than growth (Zamudio 1998). Large-bodied females can maximise clutch size, and thus fecundity can select for female-larger size dimorphism in lizards (Tinkle et al. 1970; Olsson et al. 2002). But females may alternatively opt to use resources for reproduction rather than growth as a strategy to maximise fecundity (Schwarzkopf 1993). Sexual size differences may also be caused by partitioning trophic resources between sexes to reduce competition (Schoener 1967; Powell and Russell 1984; Vitt and Cooper 1985; Watkins 1996).

Selection may act differentially on various morphological traits of each sex, causing dimorphism in morphological trait size (Butler and Losos 2002). Additionally, selection can mould sexual dimorphism in shape independent of size. Since male lizards often fight using their jaws, there is selection for large head size for competition with other males, maintaining territories, and thereby increasing access to females (Vitt and Cooper 1985; Anderson and Vitt 1990; Schwarzkopf 2005). Difference in head size may also cause partitioning of trophic resources, with large-headed lizards able to exploit larger-bodied prey (Herrel et al. 1999). Females with longer or broader abdomens have increased space to accommodate developing young, and so selection for increased fecundity increases interlimb distance in female lizards (Brana 1996; Olsson et al. 2002).

Most studies of lizard SSD look at the functional significance of a larger sex (Anderson and Vitt 1990; Olsson et al. 2002; Stuart-Smith et al. 2007). However, although size differences between the sexes may transpire due to sexual selection on adults, it is also possible that such differences could emerge as proximate outcomes of different growth trajectories, maturation patterns and survival rates between the sexes. Lizards may experience sexual differences in periods of peak growth (Cox and John-Alder 2007), duration of growth (Watkins 1996) or in survival (James 1991b). Understanding and identifying stages at which body size differences occur is important for determining how sexual size dimorphism has evolved, and long-term mark-recapture studies are useful in providing this information. Similarly, comparing the evolution of SSD in related species can be useful to reveal ecological differences causing differences in patterns of sexual dimorphism. However, comparing related species can be confounded if these species use different habitats, because selection pressures vary in different environments (Goodman et al. 2008). Variation in the local environment leads to variations in age at maturity and asymptotic size (Madsen and Shine 1993; Wikelski and Trillmich 1997; Ferguson and Fairbairn 2000), and the direction and magnitude of sexual size dimorphism can vary among different populations of the same species, due to geography (Angilletta et al. 2004), latitude (Blanckenhorn et al. 2006), and altitude (Roitberg and Smirina 2006).

To compare the evolution of dimorphism in body size and shape among species, and to determine the effect of patterns of growth, maturation and survival on sexual dimorphism among species, it is important to compare closely-related, sympatric species that share the same ecological niche. In this study I examine morphological variation in three species of scincid lizards (genus *Carlia*). Males are larger than females in the majority of lizard families (Fitch 1981), but in the family Scincidae there is no consistent pattern of dimorphism (Vitt and Cooper 1985; James 1991b; Olsson et al. 2002; Schwarzkopf 2005). I examined sex-specific growth trajectories, age of maturation, and survival rates from multi-year monitoring of three sympatric *Carlia* species.

Methods

This study considers the three most abundant skink species at the study site: *Carlia rostralis*, *C. rubrigularis* and *C. storri* (Chapter 3). Skinks were captured, sexed and measured for snout to vent length (SVL), mass, head length (HL), head width (HW), and interlimb length (ILL) using the methods described in Chapter 2. Skinks were individually marked by toe-clip (Chapter 2).

Sexual dimorphism

Morphological characters from adult lizards were used to examine body shape dimorphism. I $\log_{10}$ -transformed all variables before analysis to meet the assumptions of least-squares regression. I compared shapes of males and females using analysis of covariance (ANCOVA) on each morphological character with sex as the factor and $\log_{10}$ SVL as the covariate. A significant interaction term indicated that there were differences between the slopes of the lines for males and females (Sokal and Rohlf 1981). If there was no significant interaction between sexes and mean SVL in the model, the interaction term was eliminated from the model, and the model used again, including only main effects. This process reveals differences in the intercepts of the regressions for males and females, given that there are no differences between slopes (Sokal and Rohlf 1981).

Growth

I estimated growth rates ($\text{mm} \cdot \text{day}^{-1}$) of toe-clipped lizards based on the difference in SVL between captures, divided by the number of days between captures. “Negative growth” was probably measurement error, but because negative measurement error could not be differentiated from positive error of a similar magnitude, I included negative increments in the analyses (apparent “negative growth” occurred in 2.5% of the records across all three species). I fitted mark-recapture data for each species to the von Bertalanffy and logistic-by-length models using standard methods (Fabens 1965; Schoener and Schoener 1978; Frazer and Ehrhart 1985). Data for each sex were analysed separately using non-linear, least squares regression to determine the parameters a (asymptotic body length), and k (intrinsic growth rate). Only lizards with intact tails were considered for this analysis. The model with the smallest residual mean square was considered the closest estimate to the growth characteristics of the species (Schoener and Schoener 1978).

I used the methods of Fabens (1965) and Schoener and Schoener (1978) to derive age-size curves for both sexes of each species, using the logistic-by-length model and the von Bertalanffy model. Length models were better indicators of lizard growth, since mass measurements varied more among repeated measures on the same individual (*pers. obs.*). I did not collect eggs of lizards from the study site to measure body size at hatching, and so estimated length zero (L_0) using the size of the smallest captured lizard of each species (25.0, 22.0, and 20.5 mm for *C. rostralis*, *C. rubrigularis*, and *C. storri*, respectively). These lizards had probably hatched just before capture, because their body sizes were similar to the mean body size of captive hatchlings (25.38 [n = 3], 23.12 [n = 35] and 20.04 [n = 23] mm for *C. rostralis*, *C. rubrigularis* and *C. storri* respectively, measured for another study, B.A. Goodman, *unpublished data*; Goodman 2006). Fitted growth curves, using the model that best fitted the data, were compared with actual sizes of lizards from recapture data of individual lizards to verify the accuracy of the growth curves.

Growth rates of males and females were compared using ANCOVA with sex as the factor, growth rate as the dependent variable and mean SVL (mid-point SVL between first capture and last capture) as the covariate. Species differences were examined using ANCOVA with species as the factor, growth rate as the dependent variable and mean SVL as the covariate.

Size and age at maturity

During the study, I dissected 49 *C. rostralis* (25 females, 24 males), 54 *C. rubrigularis* (27 females, 27 males) and 49 *C. storri* (24 females, 25 males) for analysis of diet and reproductive condition (Chapter 2). I determined the minimum size at sexual maturity for females as the SVL of the smallest female containing vitellogenic follicles or oviductal eggs, and for males as the SVL of the smallest male with enlarged testes. Ages at maturity were extrapolated from sizes at maturity using the growth model parameters.

Survival

I used standard mark-recapture methods to estimate monthly survival and related parameters from toe-clipped skinks (Lebreton et al. 1992). These methods separate survival from recapture rates, where recapture rate is the probability of capturing an individual, given that it is

alive and catchable at that time (Cooch and White 2009). I used the Cormack-Jolly-Seber (CJS) method (Cormack 1989) in Program MARK v5.1 (White and Burnham 1999) to compare survival and recapture probabilities of males and females of the three *Carlia* species, from mark-recapture data. Details of this method are described in Chapter 3. Briefly, to test differences in survival and recapture probability between sexes, I included sex as a factor in the mark-recapture data, using only the capture histories of lizards caught first as adults, because sex could be determined for these individuals. I compared four candidate models *a priori* for survival probability in MARK: sex dependent, time dependent, sex x time dependent (survival varies between the sexes with time), or constant survival probability. Using this approach, a best-supported survival model that included sex as a factor would provide strong evidence for sex-specific differences in survival rate (Burnham and Anderson 1998). Models were analysed using sin-link formulation, with parameters estimated through numerical maximum likelihood techniques. The CJS method assumes that all individuals have the same probability of survival and recapture. I tested these assumptions using the goodness-of-fit (GOF) bootstrap procedure in MARK to test the fit of the most highly parameterised CJS model.

From 1000 bootstrap replicates to test GOF, there was no indication of a significant deviation from assumptions for any species (*C. rostralis* $P = 0.57$; *C. rubrigularis* $P = 0.23$; *C. storri* $P = 0.24$). I used the corrected Akaike Information Criterion (AIC_c) as an objective means of model selection. The AIC_c identifies the most parsimonious model from the set of candidate models, which is the model supported most strongly by the data, given the bias corrected, maximum log-likelihood of the fitted model, with a penalty for the number of parameters used (Burnham and Anderson 1998). The AIC_c values and standard errors of parameter estimates were adjusted for overdispersion by calculating a variance inflation factor from the GOF statistics. The AIC_c adjusted for overdispersion is called the corrected quasi-likelihood AIC ($QAIC_c$).

For each model, I calculated $\Delta QAIC_c$, the difference between the $QAIC_c$ for that model and the smallest $QAIC_c$ among the set of models fitted. Models with $\Delta QAIC_c < 7$ are considered plausible, and models with $\Delta QAIC_c \leq 2$ given the greatest support (Buckland et al. 1997). Models were also weighted so that the likelihood of each model could be compared relative to the other models considered. Once the most parsimonious models had been identified, I estimated survival

and recapture rates for males and females of each species of skink and determined if survival and recapture probability differed between sexes based on overlap of 95% confidence intervals.

Prey size dimorphism

Size measurements (total length and width to the nearest 0.1mm using digital calipers) were made for every arthropod prey item in the stomach of adult lizards (see number of dissected lizards above; Chapter 2). The maximum prey dimensions of male and female lizards relative to lizard body length were compared for each species using ANCOVA with maximum prey length or width as the variable, sex as the factor and SVL as the covariate.

Analyses

Except where otherwise stated, all statistical analyses were performed using the statistical package SPSS v16.0 (SPSS Inc., Chicago, IL, USA, 2007). When multiple measurements existed for an individual, only the measurements made at the last capture were included in analyses. Significance level was set at $P = 0.05$.

Results

Sexual dimorphism

I found significant sexual dimorphism in two of the three species of skink. In *C. rostralis*, adult males were significantly larger (mean SVL = 57.7mm; range 43.0 – 69.0mm) than adult females (mean SVL = 53.2mm; range = 39.0 – 63.0mm; $t = 7.9$; d.f. = 366; $P < 0.001$; Figure 4.1). *Carlia storri* showed the reverse pattern, with adult females reaching a larger body size (mean SVL = 43.0mm; range = 34.0 – 48.0mm) than adult males (mean SVL = 41.5mm; range = 30.0 – 46.0mm; $t = -3.6$; d.f. = 183; $P < 0.001$; Figure 4.1). *Carlia rubrigularis* males and females did not differ significantly in body size (mean SVL: males = 46.2mm; range 34.0 – 53.0mm; females = 45.9mm; range 33.0 – 54.0mm; $t = 0.5$; d.f. = 272; $P = 0.6$; Figure 4.1).

Head length and head width increased more rapidly with body length for males than for females in *C. rostralis* (slope of regressions; Table 4.1). In *C. rubrigularis*, male head dimensions

were longer but narrower than female head dimensions at a given SVL (Table 4.1). In *C. storri*, head length of males increased faster and head width was broader at a given body length than that of females (Table 4.1). Within males, head length of all three species increased at a similar rate with increasing body length, but head width increased with body length at a different rate in the three species (fastest for *C. rostralis* males, slowest for *C. storri* males with increasing body length; ANCOVA, head length: $F_{2,416} = 1.93$; $P = 0.15$; head width: $F_{2,416} = 4.04$; $P = 0.02$).

At the same body length, female *C. rostralis* and *C. rubrigularis* have a longer interlimb length than males (difference in intercepts; Table 4.1), but there was no significant difference between the slopes of the relationship between interlimb length and SVL for the two sexes in either species. For *C. storri*, there was no significant difference between male and female interlimb length, or between the slopes of the relationship with body length for either sex (Table 4.1). Within females, interlimb length of all three species was similar at a given body length and increased at a similar rate with increasing body length (ANCOVA, species: $F_{2,406} = 0.39$; $P > 0.5$; slopes: $F_{2,406} = 2.1$; $P > 0.1$).

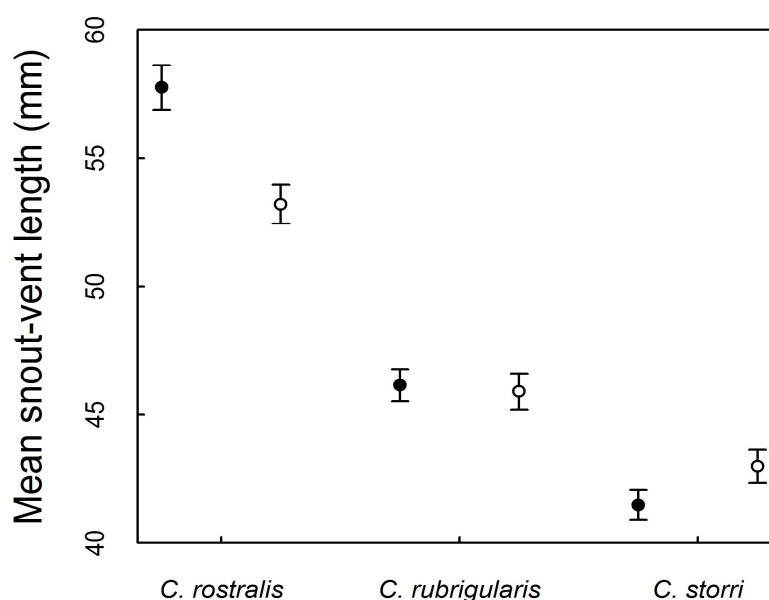


Figure 4.1. Mean snout-vent length (SVL) and 95% confidence intervals of male and female *Carlia rostralis*, *C. rubrigularis* and *C. storri*. Filled circles indicate males and open circles indicate females.

Table 4.1. Regression analyses of morphological traits (log-transformed) on $\log_{10}\text{SVL}$ between sexes for adult *Carlia* lizards. All values are $\pm$ standard error.

Species	sex	N	Character regressed with SVL								
			Head length			Head width			Interlimb length		
			b (slope)	a (intercept)	R ²	b (slope)	a (intercept)	R ²	b (slope)	a (intercept)	R ²
<i>C. rostralis</i>	♂	176	0.85 ($\pm$ 0.02)	- 0.39 ($\pm$ 0.04)	0.88	1.00 ($\pm$ 0.05)	- 0.83 ($\pm$ 0.09)	0.67	0.97 ($\pm$ 0.03)	- 0.20 ($\pm$ 0.06)	0.82
	♀	192	0.67 ($\pm$ 0.02)*	- 0.10 ($\pm$ 0.07)	0.80	0.80 ($\pm$ 0.05) *	- 0.50 ($\pm$ 0.09)	0.54	1.02 ($\pm$ 0.04)	- 0.28 ($\pm$ 0.07)*	0.76
<i>C. rubrigularis</i>	♂	147	0.76 ($\pm$ 0.04)	- 0.25 ($\pm$ 0.07)	0.71	0.78 ($\pm$ 0.08)	- 0.47 ($\pm$ 0.13)	0.41	0.98 ($\pm$ 0.06)	- 0.23 ($\pm$ 0.09)	0.69
	♀	127	0.68 ($\pm$ 0.04)	- 0.13 ($\pm$ 0.06)*	0.74	0.81 ($\pm$ 0.09)	- 0.52 ($\pm$ 0.14)*	0.41	0.99 ($\pm$ 0.06)	- 0.25 ($\pm$ 0.09)*	0.72
<i>C. storri</i>	♂	94	0.81 ($\pm$ 0.04)	- 0.34 ($\pm$ 0.07)	0.79	0.77 ($\pm$ 0.09)	- 0.46 ($\pm$ 0.14)	0.47	1.23 ($\pm$ 0.06)	- 0.63 ($\pm$ 0.11)	0.80
	♀	91	0.53 ($\pm$ 0.05) *	- 0.11 ($\pm$ 0.07)	0.61	0.60 ($\pm$ 0.08)	- 0.21 ($\pm$ 0.13)*	0.40	1.16 ($\pm$ 0.07)	- 0.51 ($\pm$ 0.11)	0.78

$P < 0.0001$ for all regression models.

* indicates significant differences between males and females in slopes or intercepts ($P < 0.05$) of the regressions based on ANCOVA, with $\log_{10}\text{SVL}$ as the covariate.

Age-size growth curves

Time intervals between capture and recapture of individual skinks ranged from 42 to 1196 days (mean = 271.9 days). I used 186 growth intervals from individual *C. rostralis*, 147 growth intervals from individual *C. rubrigularis* and 100 growth intervals from individual *C. storri* for analyses (mean intervals between captures were 273, 288 and 245 days, respectively). The von Bertalanffy model accounted for a larger percentage of variance in the data sets for all three species than did the logistic model (Table 4.2). All following analyses were, therefore, based on the von Bertalanffy growth model ($L = a [1 - be^{-kt}]$). Table 4.3 gives the parameter estimates for asymptotic size (a), characteristic growth rate (k) and the parameter for body size at known age (b , derived from hatchling size) for males and females of each species (Fabens 1965; Schoener and Schoener 1978). Asymptotic sizes expected by the von Bertalanffy model were similar to body sizes of the largest individuals sampled.

Table 4.2. Residual error mean-square (sum of squares divided by the sample size, N) for the non-linear regression of SVL increment (mm) on time interval (days) using two growth models, for the three *Carlia* species. The von Bertalanffy growth model had the lowest mean-square error for all species and was used for further analyses.

Species		N	von Bertalanffy model	Logistic-by-length model
<i>C. rostralis</i>	♂	87	7.01	7.83
	♀	99	4.39	4.87
<i>C. rubrigularis</i>	♂	71	4.70	5.10
	♀	76	4.27	4.73
<i>C. storri</i>	♂	49	5.45	5.72
	♀	51	2.86	2.91

Table 4.3. Growth parameters ($\pm$ 95% support plane confidence intervals): a (asymptotic SVL in mm), k (characteristic growth rate) and b for the von Bertalanffy model for the three *Carlia* species.

Species		N	a ($\pm$ 95% CI)	k ($\pm$ 95% CI)	b
<i>C. rostralis</i>	♂	99	64.23 ($\pm$ 1.3695)	0.004 ($\pm$ 0.0005)	0.611
	♀	87	60.388 ($\pm$ 0.9585)	0.005 ($\pm$ 0.001)	0.586
<i>C. rubrigularis</i>	♂	51	50.162 ($\pm$ 1.1965)	0.004 ($\pm$ 0.0005)	0.561
	♀	49	50.1 ($\pm$ 0.8625)	0.007 ($\pm$ 0.0015)	0.561
<i>C. storri</i>	♂	76	44.003 ($\pm$ 1.459)	0.005 ($\pm$ 0.002)	0.534
	♀	71	46.046 ($\pm$ 0.922)	0.005 ($\pm$ 0.001)	0.554

Males reach sexual maturity at a smaller body size than females for all three species (Table 4.4). Comparison of the body length growth curves for adult skinks of each species (Figure 4.2) show marked differences between sexes within each species. Based on the von Bertalanffy model, age at sexual maturity for *C. rostralis* was approximately 180d (6 months) for males and 266d (approximately 9 months) for females (Figure 4.2). Male and female *C. rostralis* increased in body length at a similar rate until reaching sexual maturity, after which female growth rate decreased earlier than that of males (Figure 4.2). In *C. rubrigularis*, male growth rate decreased at an earlier age than that of females (Figure 4.2), and females were fully grown at least 12 months before males. Therefore, although age at sexual maturity was similar for both sexes (210d for males and 218d for females [approx 7 months]), body size at maturity differed by 6.0mm. In contrast, *C. storri* males and females mature at markedly different ages. Sexual maturity is reached at age 216d (7 months) for males and 324d (11 months) for females of *C. storri* (Figure 4.2).

Table 4.4. Body size at sexual maturity of the three *Carlia* species.

Species		SVL (mm)
<i>C. rostralis</i>	♂	47.0
	♀	51.0
<i>C. rubrigularis</i>	♂	38.0
	♀	44.0
<i>C. storri</i>	♂	36.0
	♀	41.0

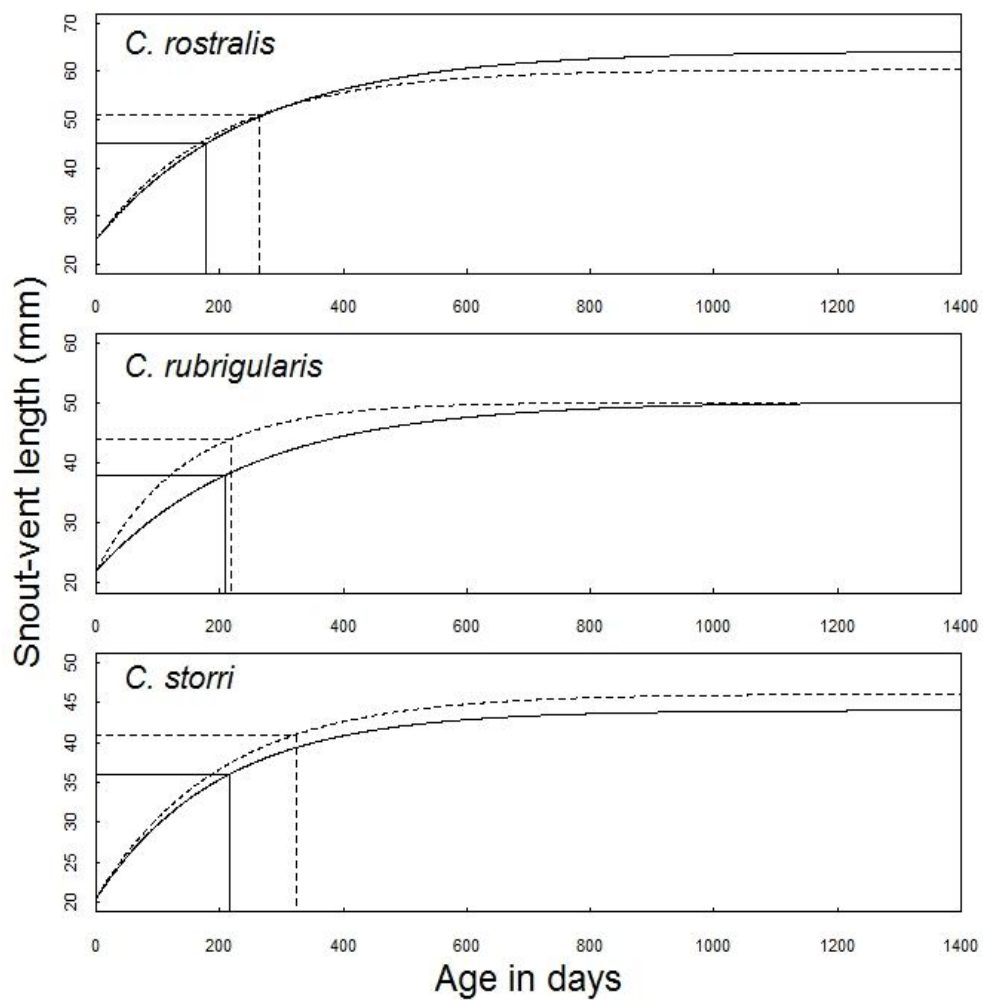


Figure 4.2. Growth trajectories of male and female *Carlia* lizards: *C. rostralis*, *C. rubrigularis* and *C. storri* from the von Bertalanffy model, with minimum size and age at maturity for each sex. Solid lines indicate males, dashed lines indicate females.

Growth rate

In the von Bertalanffy model, growth rate varies inversely with lizard SVL (Andrews 1982). In both sexes of all three species, the rate of growth in length was highest for juveniles and decreased linearly with increasing size (Figure 4.3). ANCOVA showed that for *C. rostralis*, males and females had similar growth curves and the same growth rate at a given body size (slope: $F_{1,182} = 2.66$; $P = 0.1$; sex: $F_{1,182} = 1.63$; $P = 0.2$; Figure 4.3). *Carlia storri* showed a similar pattern (Figure 4.3), with males and females growing at comparable rates (slope: $F_{1,96} = 2.1$; $P = 0.15$; sex: $F_{1,96} = 2.55$; $P = 0.11$). In *C. rubrigularis* however, female growth was fast at small body size but decreased more quickly with increasing SVL than did male growth ($F_{1,143} = 4.8$; $P = 0.03$; Figure 4.3). For a given SVL, *C. rostralis* grew fastest and *C. storri* slowest, but overall growth rate did not differ significantly among the species (ANCOVA, species: $F_{2,421} = 5.12$; $P < 0.01$; slopes: $F_{2,421} = 0.244$; $P = 0.78$). In other words, all three species experience the same growth pattern of rapid juvenile growth that slows with increasing body size.

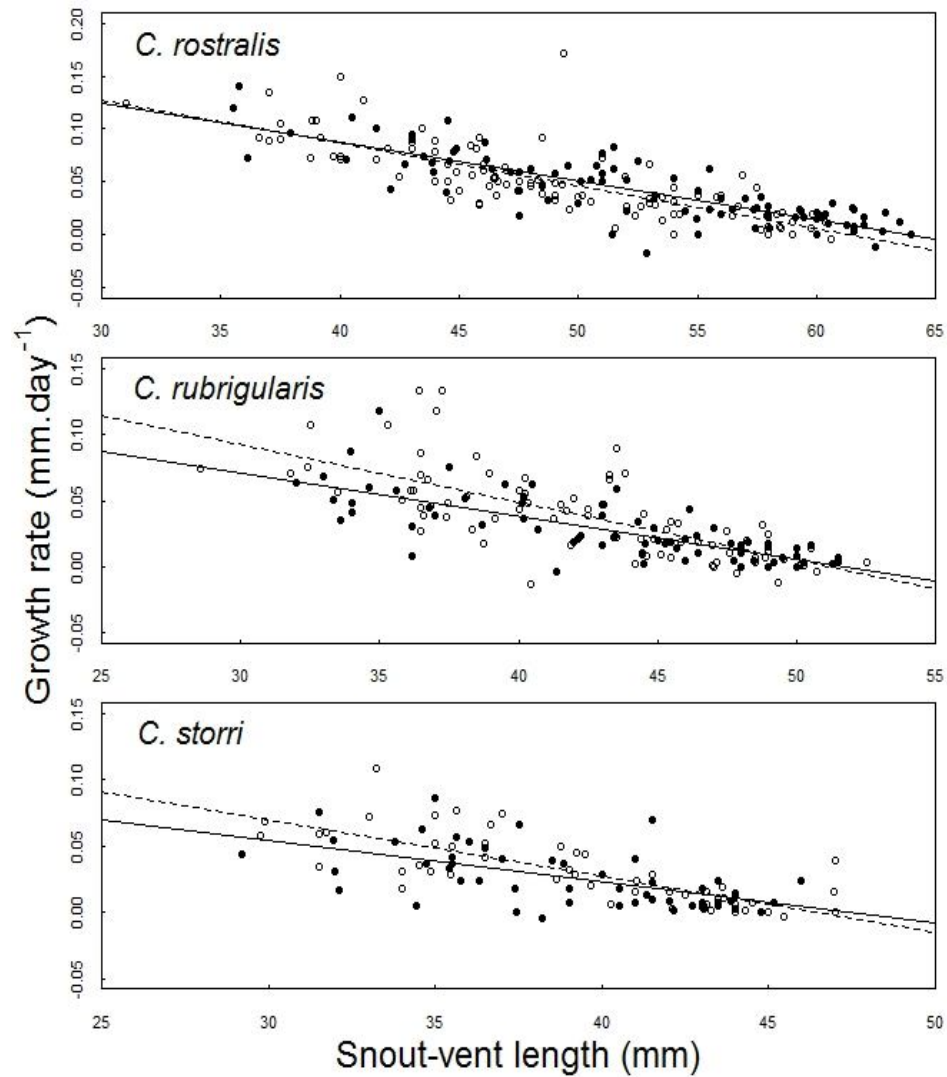


Figure 4.3. Mean snout-vent length (SVL) between captures versus growth rate, with lines of best fit from regression equations for male (filled circles, solid lines) and female (open circles, dashed lines) for the three species. Results of regressions of mid-point snout-vent length vs growth rate:

C. rostralis male d.f. = 1, 85, $r = -0.8$; *C. rostralis* female d.f. = 1, 97, $r = -0.8$;
C. rubrigularis male d.f. = 1, 69, $r = -0.75$; *C. rubrigularis* female d.f. = 1, 74, $r = -0.7$;
C. storri male d.f. = 1, 47, $r = -0.5$; *C. storri* female d.f. = 1, 49, $r = -0.8$;

all $P < 0.001$.

Sex-specific survival

Survival differed more among time intervals than it did between males and females of *C. rostralis*. The most parsimonious survival model using the CJS method for *C. rostralis* was time-dependent survival, constant recapture rate (QAIC_c weight = 0.73; Table 4.5). This models received three times the support in the data than the second-ranked model, which incorporated sex-dependent survival (ϕ [sex * time] p [•], Δ QAIC_c = 2.24; QAIC_c weight = 0.24; Table 4.5).

Carlia storri survival was similarly driven more by seasonal variation (time) than by sex differences, but recapture rate was strongly sex-dependent (best model: ϕ [time] p [sex], QAIC_c weight = 0.99; Table 4.5). Female *C. storri* ($p = 0.69$, 95% CI ± 0.12) were significantly more likely to be recaptured on any given occasion than male *C. storri* ($p = 0.35$, 95% CI ± 0.12). There was very little support for a model including survival differences between the sexes for *C. storri* (Table 4.5).

For *C. rubrigularis*, however, the most parsimonious model was the sex-dependent survival model (ϕ [sex] p [•], QAIC_c weight = 0.47; Table 4.5), where male survival = 0.57 (95% CI ± 0.07) and female survival = 0.67 (95% CI ± 0.06). Thus, female *C. rubrigularis* were 10% more likely to survive than males, but were not significantly different in survival probability (due to overlap of confidence intervals). The model including sex-dependent recapture rate (ϕ [sex] p [sex]) also received good support (Δ QAIC_c = 0.92, QAIC_c weight = 0.29; Table 4.5), where female *C. rubrigularis* were more likely (but not significantly) to be recaptured ($p = 0.56$, 95% CI ± 0.09) than male *C. rubrigularis* ($p = 0.48$, 95% CI ± 0.11).

Table 4.5. Summary of maximum likelihood comparison of mark-recapture models, estimating survival (ϕ) and recapture (p) probability as a function of sex, time, a combination of sex and time (sex*time) or constant ($\bullet$) for the three *Carlia* species. The Akaike weight of each model is used as a measure of the relative likelihood of the best model compared with the other candidate models. Models with the greatest support are shown in bold font.

Species	ϕ	p	n	$\Delta QAIC_c$	Akaike weight	QDeviance
<i>C. rostralis</i>	time	$\bullet$	12	0.00	0.73	357.82
	sex * time	$\bullet$	23	2.24	0.24	336.70
	time	sex	13	7.67	0.02	367.56
	sex * time	sex	23	8.57	0.01	345.19
	time	time	21	16.10	0.00	356.99
<i>C. rubrigularis</i>	sex	$\bullet$	3	0.00	0.47	289.52
	sex	sex	4	0.92	0.29	288.40
	c	$\bullet$	2	2.59	0.13	294.14
	time	sex	13	3.91	0.07	272.63
	time	$\bullet$	12	5.55	0.03	276.40
<i>C. storri</i>	time	sex	13	0.00	0.99	175.29
	time	$\bullet$	12	16.36	0.00	193.81
	sex * time	sex	24	17.54	0.00	168.26
	sex * time	$\bullet$	23	26.15	0.00	179.17
	$\bullet$	sex	3	30.06	0.00	226.36

Number of model parameters (n), Akaike's Information Criterion ($QAIC_c$), differences in AIC_c ($\Delta QAIC_c$), and Akaike weights for candidate models describing survival (ϕ) and recapture (p) of skinks at monthly intervals.

Prey size dimorphism

Male and female lizards consumed similar-sized prey in all three species. Prey size did not increase with increasing body size significantly faster in either sex and there was no significant difference in size of the largest prey in the stomachs of either sex for any species (Table 4.6).

Table 4.6. Summary of mean maximum length (mm) and mean maximum width (mm) of arthropod prey from diet analysis of male and female *Carlia* species with ANCOVA results for difference in slope (interaction sex x SVL) and intercept (sex) between sexes.

Species	sex	N	Mean maximum prey length (mm, $\pm$ S.E)	Mean maximum prey width (mm, $\pm$ S.E)	a (slope)		b (intercept)	
					F, d.f	P	F, d.f	P
<i>C. rostralis</i>	♂	23	13.5 ($\pm$ 1.8)	4.2 ($\pm$ 0.5)				
	♀	26	12.7 ($\pm$ 1.4)	4.2 ($\pm$ 0.5)	0.055, 1	0.8	0.025, 1	0.9
<i>C. rubrigularis</i>	♂	26	7.5 ($\pm$ 0.9)	2.9 ($\pm$ 0.7)				
	♀	22	8.9 ($\pm$ 1.1)	2.9 ($\pm$ 0.4)	0.008, 1	0.9	1.763, 1	0.2
<i>C. storri</i>	♂	21	7.0 ($\pm$ 0.9)	2.1 ($\pm$ 0.3)				
	♀	19	6.6 ($\pm$ 0.8)	2.0 ($\pm$ 0.2)	0.05, 1	0.8	0.067, 1	0.8

N = number of skinks measured, S.E. = standard error

Discussion

In this study, sympatric skinks in the genus *Carlia* had strongly contrasting patterns of sexual size dimorphism (SSD). *Carlia rostralis* was the largest species and had the fastest growth and male-biased size dimorphism. *Carlia rubrigularis* females grew more rapidly, but for a shorter period than males, resulting in similar adult body size for the two sexes. *Carlia storri*, the smallest species, grew slowly relative to the others and had female-biased dimorphism. Regardless of variation in sexual body size dimorphism, all three species were broadly similar in terms of sexual shape dimorphism: males usually had larger head dimensions, and females had longer interlimb lengths, consistent with sexual and fecundity selection for reptiles. If survival probability is sex-biased, then one sex may live longer than the other and grow to a larger size so that body size dimorphism may reflect differential survival rate between sexes (James 1991b; Watkins 1996). For these *Carlia* species, SSD was not due to higher mortality of one sex; I found no significant sex difference in survival of any of the three species. Size of prey items did not differ between the sexes for any species and therefore natural selection due to trophic partitioning is an unlikely force driving sexual

dimorphism in these species. Size differences between males and females must, therefore, be due to other mechanisms.

Shape dimorphism

- Head Size Dimorphism

Sexual dimorphism in lizards can be caused by selection for large males to outcompete rivals or to attract the attention of females (Shine 1989; Olsson and Madsen 1995), or lizards may be dimorphic due to selection for resource partitioning, so that intersexual competition is reduced (Schoener 1967; Shine 1986b). Regardless of variation in body length dimorphism, males of all three species had larger head dimensions. Lizards with longer and wider heads, like most male *Carlia*, have larger gape, compared to individuals with smaller head dimensions (Herrel et al. 1999). Trophic resource partitioning can select for head size differences observed between the sexes, or may also result secondarily from sexually selected dimorphism, with the larger sex able to capture and consume larger and harder-bodied prey (Vitt and Cooper 1985; Herrel et al. 1996; Cox et al. 2003). Estimates of the intensity of trophic competition between males and females are lacking, but in all three species in this study, the size and type (taxonomic groups) of prey consumed did not differ between male and female lizards. Thus, it is unlikely that avoidance of dietary overlap selects for larger head size in males and, even though male lizards in our study had relatively larger heads, they did not use this size difference to exploit larger prey and reduce competition.

Lizards fight using their jaws (Carpenter and Ferguson 1977) and male aggression by biting has been documented in both *C. rostralis* and *C. rubrigularis* (Whittier and Martin 1992; Torr 1994). A large and robust head increases the strength of jaws and bite performance (Herrel et al. 1999), which should increase fighting ability and give males an advantage over other males in contests for territory and access to females, and therefore increase mating success (Trivers 1976; Vitt and Cooper 1985; Gvozdik and van Damme 2003). Many lizards use their jaws during copulation (Carpenter and Ferguson 1977) and large-headed male lizards have greater mating success (Vitt and Cooper 1985; Gvozdik and van Damme 2003). Male *Carlia* initiate copulation by grasping the female with a bite to her flank, often needing to

subdue struggling females with a firm grip, which may need to be readjusted and maintained for 2 to 3 minutes for insemination to take place (*pers. obs.*, Langkilde and Schwarzkopf 2003). Greater bite strength would probably increase insemination success, increasing reproductive success. It is likely that selection for larger head size in male *Carlia* is related to increased copulation success.

Gular nuptial colouration is an important sexual signal in contest competition and for determining mate preference (Andersson 1994), and for lizards with gular nuptial colouration, larger heads provide a greater area of colour to display (Vitt and Cooper 1985), greater access to females, and therefore increased mating success (Anderholm et al. 2004). Both *C. rostralis* and *C. rubrigularis* males exhibit striking gular colouration (black and red, respectively) during the breeding season, and there could be selection for relatively larger heads of males of these two species due to increased contest and mating success of males with larger advertisement area. However, *C. storri* males also have relatively larger head dimensions than female conspecifics, and yet these males do not display colour. Comparison of the three species showed that *C. storri* males had narrower heads than the other two species at the same body size. Taken together, these pieces of evidence suggest that there may be selection for larger colour patches in species with colour, giving them wider heads, in addition to selection on males of all three species for larger heads and stronger bite force.

- Interlimb length dimorphism

Female *C. rostralis* and *C. rubrigularis* have longer interlimb length than males of the same body length, and adult *C. storri* females have a longer absolute interlimb length, due to their larger asymptotic size. This body shape dimorphism often occurs in lizards, because there is selection for increased clutch size in females, and females with longer bodies can carry more offspring (Anderson 1994; Olsson et al. 2002; Schwarzkopf 2005). Larger-bodied females typically produce larger clutches (Stuart-Smith et al. 2007), but *Carlia* produce fixed clutch sizes (James and Shine 1988; Goodman 2006). Instead of acting on clutch size, selection for increased egg size may influence female abdomen size in *Carlia*. Abdomen volume can limit egg size (Shine and Greer 1991), and if females produce eggs of maximal

size, then egg size should correlate with maternal abdomen size in invariant clutch producers. Egg size and maternal body size are correlated in *C. rubrigularis* (Goodman 2006), but not in the other two species (B. A. Goodman, *unpublished data*) or in five other species of *Carlia* (James and Shine 1988). Greater interlimb length as a mechanism for increasing fitness via increased egg size may only be selected in some *Carlia*. However, comparison of the three species in our study showed that female *C. rubrigularis* do not have a faster rate of increase in interlimb length, or longer interlimb length at a given size than the other two species. This indicates that, while larger interlimb length increases available space in the body cavity for eggs relative to males, it is unlikely that there is strong fecundity selection for specific abdomen lengths directly related to egg size, at least in these three species.

How do observed patterns in dimorphism develop? Size dimorphism due to growth rate and age at maturity

Body size dimorphism occurred mainly as a consequence of different growth trajectories in males and females. The von Bertalanffy growth model provided the best fit to the growth data of *Carlia* skinks (Table 4.1). In this model, growth rate varies inversely with lizard body length, with the rate of growth in length greatest for young lizards and decreasing as body size increases. In all three *Carlia* species, female growth rate slowed after reaching sexual maturity. For example, selection did not favour differential growth of young male and female *C. rostralis*, instead size dimorphism occurred because the sexes differed in the duration of growth: females reached asymptotic body length soon after sexual maturity whereas males continued to grow (Figure 4.2). In *C. rubrigularis*, female growth was initially considerably faster than that of males. *Carlia rubrigularis* females reached sexual maturity relatively early (Figure 4.2) by growing rapidly as juveniles, and differed significantly from males in that their growth rate decreased faster with increasing body length until females and males were monomorphic at their asymptotic size (Figure 4.2). Growth rates of *C. storri* males and females did not differ significantly, but female *C. storri* grew somewhat faster than males throughout life (Figure 4.2). In *C. storri*, female body size relative to that of conspecific males was determined by the timing of maturation. Female *C. storri* delayed sexual maturity to approximately 11 months, thereby having a longer growth period than females of the other

two species, and maintained a larger size than *C. storri* males. Female *C. storri* had a shorter interval between recaptures than males, suggesting that females of this species spent more time active, possibly because they needed to spend more time foraging to meet metabolic requirements than did smaller males, and were therefore more readily recaptured.

The sexes often differ in body growth because they differ in the amount of time, resources and energy allocated to reproduction (Dunham et al. 1989; Anderson and Vitt 1990). In all three *Carlia* species, female growth rate slowed after reaching sexual maturity, most likely because more energy was allocated to reproduction at the expense of body growth in females (e.g., Schwarzkopf 1993). Reproduction can consume resources in many ways: to support maturation, i.e., changes in morphology or physiology related to reproduction, to support mating behaviour, to compete for resources needed for reproduction, and to provision eggs, before and after fertilisation (Schwarzkopf and Shine 1992; Stamps et al. 1998). Reproductive females may also reduce activity and food intake to reduce their vulnerability to predators (Schwarzkopf 1996). Since *Carlia* produce invariant-sized clutches of two eggs, and the relationship between maternal body size and clutch volume is weak, selection for increased fecundity may instead act on the frequency of reproduction. The growth of females of all three species is affected similarly by energy allocation to reproduction (i.e., growth slows equally after maturation), and so it is unlikely that it is selection on female size that drives differences in SSD among the species.

Without strong selection on female body size, and with little influence of natural selection to reduce competition for resources, it is likely that sexual selection on male body size is strong, and that sexual selection drives differences in the sexual dimorphism among these three species. Similarly, SSD in sympatric *Sceloporus* lizards developed due to differences in energy allocation to reproduction between the sexes, but this allocation had different effects on the sexes compared to my study; there was reduced growth due to reproduction in males of one species and in females of another (Cox and John-Alder 2007). In *Carlia*, there was no evidence that the energetic costs of male reproduction (such as increased aggressive interactions and greater movement; Abell 2000) affected male growth rate, since achieving sexual maturity did not slow the growth of males of any species (Figure 4.2).

Large males may be selected as mates because of their large size (Cooper and Vitt 1993), but female preference for large males has rarely been documented in lizards (Olsson and Madsen 1995; LeBas and Marshall 2001). Thus, selective pressures giving large males the ability to repel competitors and defend high quality resources are believed to be a more important determinate of male size than is female choice (reviewed in Olsson and Madsen 1998). These interactions ensure that large, dominant males have increased access to females, and therefore greater reproductive success (Vitt and Cooper 1985; Anderson and Vitt 1990). *Carlia rostralis* males are highly aggressive: lunging, chasing and biting in fights for dominance (Whittier and Martin 1992). Male-biased SSD is generally more pronounced in lizards with male aggression and territoriality than in species lacking these behaviours (Carothers 1984; Cox et al. 2003) and in *C. rostralis*, males have head dimensions that become increasingly larger proportional to their own body size, suggesting strong selection on this trait. Male dominance of *C. rostralis* was positively correlated with male body length in laboratory trials (Whittier and Martin 1992) and in a natural system it is likely that large-bodied *C. rostralis* males dominate smaller conspecifics in combat. *Carlia rostralis* occur at high densities at the study site relative to *C. rubrigularis* and *C. storri* (14 *C. rostralis* individuals per 100m²; Chapter 3). This would lead to a high encounter rate with conspecifics, so that male *C. rostralis* may need to compete for access to females by attacking other males and defending good quality territory. In this system, selection should favour large males with large heads because they have advantages in male-male competition, territory defence, display of breeding colour, copulation success, and, therefore, reproductive success.

Sexual selection can also select for small males, for instance in populations where densities are low and females are widely dispersed, so that male mating success depends on the number of females encountered rather than competitive advantages over other males (Zamudio 1998). In this type of system, selection favours small males that reach sexual maturity at an early age, are highly mobile, and that can spend time and energy searching for mates instead of food (Trivers 1976). Population densities of *C. storri* are low relative to the other two *Carlia* species at the study site (6 individuals per 100 m²; Chapter 3) and it is likely that individual male *C. storri* that can spend a large proportion of time and energy finding a mate when females are highly dispersed, will achieve greater reproductive success. In this

case, selection should favour males that mature early and grow to a relatively small asymptotic size, and can therefore devote energy to actively searching for mates rather than food acquisition and growth. Male and female *C. storri* grow relatively slowly, and this, along with their low densities at the study site, suggests that *C. storri* are not strong competitors for resources. *Carlia storri* females delay sexual maturity relative to the other two species, and their comparatively slower growth rate combined with a restricted breeding season for this species (November to January; Chapter 3) means that most *C. storri* females only reach sexual maturity after one breeding season has passed. Thus, females of this species are larger when breeding for the first time, the following year, compared to faster-maturing species. Slower growth and delayed sexual maturity may be the strategy used by *C. storri* females to increase survival and ensure high reproductive potential (Stearns 1992). *Carlia storri* males do not appear to require large body size, yet their relative head proportions are larger than those of females. Since *C. storri* are widely dispersed I expect encounter rates between individuals to be low, and male territory defence and combat to therefore be unnecessary. Additionally, *C. storri* do not display breeding colouration. This suggests that there is strong selection for large head dimensions for successful copulation and increased mating success in these lizards.

If *C. rostralis*, the largest of the sympatric species, has male-biased dimorphism due to high density and the need for male competition, and *C. storri*, the smallest species, has female-biased dimorphism due to low density and the need for males to be small and mobile to find mates, why then is *C. rubrigularis*, with intermediate size and density, sexually monomorphic for overall body size? If adult body size alone were considered, I would assume that selection pressures on body size were similar for male and female *C. rubrigularis*. Instead, young female *C. rubrigularis* grow rapidly and mature early to achieve the same adult body size as male conspecifics. Male *C. rubrigularis* are aggressive (Torr 1994) and display gular nuptial colour, and therefore probably compete for females and resources. Male *C. rubrigularis* have relatively longer heads than females, which would assist in mating, competition with conspecific males and the area of breeding colour on display, yet in this species this selection does not result in larger overall body size of males. While very little is known about the use and benefit of nuptial colouration in *Carlia* lizards, it is likely that the area

of bright colour on display is important in dominance interactions, and that a larger colour patch leads to increased mating success, as in other lizard species (Anderholm et al. 2004). It is possible that, in *C. rubrigularis*, size of colour patch on display is more important than overall body size in competitive interactions and subsequent mating success (as in side-blotched lizards, *Uta stansburiana*; Calsbeek and Sinervo 2002). Alternatively, *C. rubrigularis* may be the only study species in which females also experience selection for large body size. I predict that female *C. rubrigularis* may also need to compete for and defend resources, or compete with other females for reproductive opportunities, and large size may be an advantage driving selection of fast growing young females. The relatively broader heads of female *C. rubrigularis*, assuming that jaws are also used for combat in female lizards, supports a female competitive advantage. Female *C. rubrigularis* have a slightly greater probability of survival than males, perhaps indicating that they are better competitors and able to exploit resources more efficiently. Competitive interactions of female lizards are rarely documented (Woodley and Moore 1999; Rubenstein and Wikelski 2005), but not unlikely since females have a large energetic investment in gametes and parental care, and need to ensure access to resources.

Sexual differences in animal body size can ultimately be selected for by dominance, fecundity or competitive advantages of large adult size. But selection pressures during juvenile development can influence sexual dimorphism of adults, and these selection pressures may differ between adults and juveniles (Stamps and Krishnan 1997; Le Galliard et al. 2006). Studies that address the contribution of selection on adult body size *and* sexually dimorphic patterns of growth and maturity are particularly informative to understanding the evolution of size dimorphism, yet such studies are rare (Stamps 1993; Badyaev 2002). Environmental conditions can influence the degree of dimorphism exhibited by taxa (Post et al. 1999), thus comparison of sympatric species can provide valuable insight into the mechanisms driving the evolution of SSD. Based on my results, future studies on the ecological and evolutionary determinants of life history and sexual dimorphism variation in this group should focus on the different social systems of each species and their use of space and resources. The use of nuptial colouration by some male *Carlia*, and its influence on *Carlia* social systems, and benefit to territory acquisition and male mating success, need further

consideration. The molecular phylogeny of *Carlia* shows rapid differentiation of 30 species early in the evolution of the genus (Stuart-Fox et al. 2002; Dolman and Hugall 2008). If the evolution of sexual dimorphism in this genus was driven by the evolution of social systems and the use of nuptial colouration, these factors may have lead to the rapid speciation of this genus (as in the extreme case of cichlid fish, Seehausen and van Alphen 1999 and see Hochberg et al. 2003).

Sympatric *Carlia* exhibit trade-offs between growth and reproduction, delayed maturation or differential juvenile growth to achieve various degrees and directions of adult SSD. Studying variation in the development of SSD is important because it can reveal sexual differences in selection pressures, such as those on juvenile growth and timing of maturation, not evident from observations of adult body size alone.

Chapter 5

No fitness costs in the relationship of *Carlia* with trombiculid mite larvae

Abstract

Hosts are expected to suffer damaging consequences from an association with an ectoparasite, leading to a reduction in host body condition, growth and survival. Evolutionary association with hosts can, however, reduce the virulence of parasites. Once this has occurred, even a slight variation in a parasitic relationship might change a detrimental association into a commensal or mutually beneficial one. *Carlia* lizards are frequently hosts to large numbers of conspicuous larval trombiculid mites, and yet appear to be in excellent health. In this study relationships between mite load and components of fitness of *Carlia* hosts were analysed (including growth rate, survival, body condition, predator vulnerability, reproduction and feeding) to test two alternate hypotheses: mites behave as parasites (lizard fitness is negatively affected by mites), or mites behave as commensals or mutualists (lizard fitness is unaffected or positively correlated with mites, i.e., mites counteract their own detrimental effects by providing some advantage to lizards). There was no evidence that ectoparasites had consistently negative effects on *Carlia* fitness; the intensity of ectoparasite infestation had no significant effect on growth rate, body condition or feeding success, regardless of species, season or lizard body size. Mite load did not affect reproductive success or predator avoidance. The presence of mites did not negatively affect lizard survival, and, for one species, survival probability increased with greater mite load. Trombiculid mite larvae may counteract their damaging effects by providing a benefit to *Carlia*, and the lizard-mite relationship may be commensal or mutually beneficial, rather than purely parasitic.

Introduction

Species do not exist in isolation; symbioses, or different species living together in a mutual, commensal or parasitic relationship, are among the most widespread interactions between species. Consequently, the fitness outcomes for the species involved in a symbiotic interaction can have major ecological and evolutionary consequences (Campbell 1993). Symbioses comprise a continuum that is often not easily partitioned into mutualism, commensalism, or parasitism. For example, commensalism is the middle range in the spectrum of these relationships, but commensals can be very similar to parasites that only extract a small cost from their host, whereas some mutualists demand high resources for their service that is barely compensated by the benefits of the association (Leung and Poulin 2008). The balance between costs and benefits in a symbiosis depends on a range of factors and often only slight variations are required to shift that balance. When we consider ectoparasites, such as mites, ticks, fleas or lice living on a host animal, we think immediately of irritation, removal of host resources, and potential disease. Ectoparasites consume host resources from outside the host's body and are, by definition, costly to host fitness (Price 1980). But what if the interaction between a host and its ectoparasite was not detrimental to host fitness? How much variation in cost or benefit is needed to shift a parasitic relationship to a commensal, or even mutually beneficial one?

Hosts are expected to suffer damaging consequences from association with ectoparasites. Ectoparasites typically attach to the skin of their host and consume blood or nutrients. They can induce anaemia (Lehmann 1992), transmit pathogens and blood parasites (Schall and Smith 2006; Holmstad et al. 2008) and cause lesions of the skin (Goldberg and Holshuh 1992). Ectoparasites are also capable of altering host body functioning by obstructing movement, feeding, and even breathing (Salvador et al. 1999; Walter and Proctor 1999). Ectoparasites compete for nutritional resources that would otherwise be used by the host for growth, maintenance, reproduction, activity, and fortification of the immune system against infection, and thereby change the energy budget of their hosts, either by draining energy reserves, or by stimulating an immune response. Reduced energy can alter the metabolic rate of the host, and this can lead to poor body condition (Møller et al. 1994;

Klukowski and Nelson 2001) and mortality (Booth et al. 1993). Reduced energy can also lead to decreased foraging efficiency (Barber et al. 2000) and therefore reduced body condition and growth rate, causing higher mortality of hosts (Sorci et al. 1994; Brown et al. 1995; Clobert et al. 2000; Finley and Forrester 2003; Hawlena et al. 2006). Reduced reproductive success from ectoparasitism can be caused either by an adjustment of reproductive effort that helps hosts to reduce the effects of parasitism (Fitze et al. 2004), or a reduction in effort as a consequence of the negative effects of parasitism (Møller 1990, 1993; McKilligan 1996; Neuhaus 2003). Ectoparasites also frequently attach to areas of the body where they may impair movement (Salvador et al. 1999), potentially making the host more conspicuous and reducing their ability to escape predators. Behavioural changes associated with ectoparasites, such as grooming (Forbes and Baker 1990; Cotgreave and Clayton 1994; Hawlena et al. 2007), can also lead to increased susceptibility to predation (Baker and Smith 1997; Main and Bull 2000). Alternatively, the concept that well-adapted parasites evolve reduced virulence because their fitness depends on that of their host challenges the assumption that ectoparasites reduce host fitness. Parasites that have a detrimental effect on the fitness of their hosts are clearly parasites. But the effect of parasites can sometimes be far less pathogenic, resulting in a benign association that is almost commensal (Ewald 1983; Schall 1986). If parasites have very little or no detrimental impact on host life history or fitness, are they still parasites?

While parasite-induced changes to host metabolism and energy requirements are difficult to measure in natural populations (Booth et al. 1993), these metabolic changes transfer to measurable effects on host body condition, growth and survival. However, very few field studies have measured the effect of ectoparasitism on the fitness of host animals (Booth et al. 1993; Hudson and Dobson 1995; Fitze et al. 2004; and see review by Lehmann 1993) and indeed, of the few field studies of the consequences of ectoparasite infection, some have found very little effect of ectoparasites on host fitness (Vaughan and Coble 1975; Bull and Burzacott 1993; Johnson and Albrecht 1993; Christian and Bedford 1995; Pacejka et al. 1998; Abell 2000; Schlaepfer 2006). Field studies that fail to demonstrate an impact of ectoparasites may have the flaw that they have insufficient data to document potentially subtle effects of parasites, or deal with a parasite that kills heavily infested hosts before they are sampled,

thus allowing only low infestation rates, with low host impact, to be sampled (Wharton and Fuller 1952; Lehmann 1993). Ectoparasites on the bodies of vertebrate adult hosts can be difficult to quantify and monitor regularly, especially in the case of mammals and birds where counts of ectoparasite load are hampered by hair and feathers. Additionally, manipulation of parasite numbers, or of host behaviour to increase parasite numbers, can contribute to stress in host populations, which can often magnify the apparent effects of parasites (Arnold 1986; Eisen 2001). For these reasons, we know very little about how ectoparasites affect the fitness and survival of vertebrate adult hosts. Host-parasite studies are needed in natural systems of unmanipulated hosts that include frequent sampling, large numbers of both infested and uninfested hosts, and a range of ectoparasite infestation levels (Scott and Dobson 1989). My long-term study of rainbow skinks in north-eastern Australia provided an opportunity to examine the presumed link between ectoparasite infestation and host fitness. Rainbow skinks are frequently hosts to high loads of trombiculid mites (Arnold 1986), and yet appear to be in good condition and excellent health (*pers. obs.*).

In the present study, I examined the prevalence and intensity of trombiculid mite larvae living on three species of skinks from the genus *Carlia*. I analysed relationships between mite load and components of fitness of skinks to test two alternative hypotheses about the functional nature of the interaction. I predicted that if mites were behaving as parasites, skink growth rate, survival, body condition, and reproductive and feeding success should be negatively affected by the abundance of mites. Alternatively, I expected that if mites were commensal, or mutualistic, skink fitness would be unaffected, or positively correlated with mite abundance, respectively. Positive effects of mites could be achieved if mites counteracted their own detrimental effects by providing some benefit to skinks.

Methods

Study species

The three most abundant skink species at my study site (Chapter 3) were used for this study: *Carlia rostralis*, *C. rubrigularis* and *C. storri*. *Carlia* are hosts to larval trombiculid mites belonging to the genus *Eutrombicula* (Acari: Trombiculidae) (Arnold 1986; B. Halliday

pers. comm.). These larvae hatch from eggs in the leaf litter and attach themselves to vertebrate hosts where they feed on blood and liquefied tissues and may remain attached for several weeks (Goldberg and Bursey 1991; Walter and Proctor 1999). After feeding, the engorged larvae return to the leaf litter and transform into non-parasitic, litter-dwelling nymphs before becoming free-living adult mites (Sasa 1961). Larval mites attach where the skin is thin (Wharton and Fuller 1952), and on *Carlia* they are frequently found in the limb axillae (Arnold 1986). Trombiculid mites are often red (Arnold 1986), and *Eutrombicula* sp. at my study site were a bright orange. Because *Eutrombicula* sp. mites are parasitic only during their larval stage and feed only for a maximum of a few weeks, they are only dependent on their skink hosts for a relatively short period. For this reason we might expect the long-term welfare of the host to be of little concern to mites and the negative effect of mites to be particularly severe on skinks, in contrast to other ectoparasites with a longer feeding period (Ewald 1983).

Measurement of fitness related variables

I captured, measured and marked skinks using the methods described in Chapter 2. Skinks were checked for the presence of mites on all sampling occasions between April 2005 and May 2007, and the intensity of mite infestation was measured using a hand lens by counting the number of individual mites present on each skink (Chapter 2). I estimated growth rates ($\text{mm} \cdot \text{day}^{-1}$) of skinks as described in Chapter 4. Body condition is a measure of the size of an individual's energy reserves relative to its body size (Jakob et al. 1996) and is used as an indicator of the amount of stored energy and general health of an individual. Body condition was calculated from the residuals from reduced major axis (RMA) regression between $\log_{10}$ -transformed body mass and $\log_{10}$ -SVL (Green 2001). Only skinks with intact tails were used in analyses of body condition and growth rate. Feeding success was determined from the volume of stomach contents of sacrificed skinks (methods described in Chapter 2). Reproductive status of female skinks was determined by palpating the abdomen for follicles or oviductal eggs (Chapter 2). I recorded the reproductive status of adult females caught during the breeding season (August to March for *C. rostralis* and *C. rubrigularis*, November to March for *C. storri*, see Chapter 3). Tail loss by skinks was used as an indication of a close encounter with a predator or with a competitive conspecific (Pafilis et al. 2009), and

skinks that lost their tails during capture or measurement were excluded from tail loss analysis. Skinks without a full tail, or with tail regrowth, were noted at capture.

Statistical analysis of fitness-related variables

The prevalence of mite infestation of each species, and the mite load of lizards with mites were compared among species using non-parametric tests (χ^2 and Kruskal-Wallis tests, respectively). Mite load (number of mites on each skink) was $\log_{10}(n + 1)$ -transformed before analyses. For analyses of body condition, reproductive success and vulnerability to predators, only measurements taken at the first capture of individual skinks was used. I used simple correlation to evaluate the relationship between body size and mite load, and between mite loads of skinks at capture and recapture, and between the change in mite load and the time interval between captures. For multiple-capture analyses (growth rate), mite load was calculated as the mean number of mites at capture and recapture. Linear regression was used to determine the relationship between mite load and growth rate. Growth rate was negatively correlated with skink body length (SVL, for males and females of all three species $r > 0.7$, $P < 0.001$). To correct for SVL effects, log-transformed SVL was used as an independent variable along with mite load in a multiple regression model.

The cost of carrying ectoparasites may vary depending on host breeding condition and access to resources (de Lope et al. 1993), and I expected season to have an effect on size-corrected body mass, or body condition, and on volume of stomach contents, since both food availability and breeding are seasonal (James and Shine 1985; Chapter 3). The effect of mite load on body condition and feeding success (volume of stomach contents) in the wet and dry seasons was determined using analysis of covariance (ANCOVA), with $\log_{10}$ -transformed body mass as the dependent variable, SVL and mite load as covariates and season as the factor. However, there was no relationship between SVL and the volume of adult skink stomach contents; therefore the effect of mite load on feeding success was determined using ANCOVA with volume of stomach contents as the dependent variable, season as the factor and only mite load as the covariate. Binary logistic regression was used to determine the effect of mite load on female reproductive status and on tail loss. For reduced major axis

regression I used RMA for Java v1.21 (Bohonak and van der Linde 2004). All other analyses were performed using JMP v4.0.2 (SAS Institute Inc. 2000) and significance was accepted at $P = 0.05$. Tests generated many non-significant results, and so the power of these analyses was calculated to increase the strength of the inferences made from the results. The power of a statistical test is the probability that it will yield statistically significant results given that there is a biologically real effect in the population being studied (Thomas and Krebs 1997).

Modelling survival probabilities

Many variables may affect the survival of skinks (Dunham et al. 1988a). In the present study, my goal was to determine how mite load affected the survival of *Carlia*. I estimated survival probabilities using the general methods of Lebreton et al. (1992) and Burnham and Anderson (2002). Program MARK v5.1 (White and Burnham 1999) was used to assess the fit of different models to each species' data set of capture histories and to generate maximum-likelihood estimates of survival and recapture probability, modelled as linear-logistic functions of individual mite load (Nichols 2005). To do this I considered the median mite load of each skink over all captures and recaptures as a covariate, and modelled survival based on mite load, time, and the interaction of ectoparasite load and time on survival probability (i.e., the effect of mites on survival varied with time). The explanatory power of these models was compared with that of a model assuming constant survival. Recapture probability, the probability that a marked skink alive in the study area during the sampling period was captured, was modelled as a function of mite load, time variation and constancy (see model notation in Table 5.1).

Table 5.1. Models used to assess survival (ϕ) and recapture (p) probability of *Carlia*, as a function of mite load and time.

Model	Description
ϕ (mites)	Survival varies monotonically with mite load, nature of relationship explained by slope β_1
ϕ (mites x time)	Interaction between mite load and time interval - survival affected by mite load (as above) but this varies among time intervals (seasons)
ϕ (time)	Survival varies with time, or among seasons. No effect of mite load.
ϕ (•)	Survival is constant, no effect of mite load or time.
p (mites)	Recapture probability varies monotonically with mite load, nature of relationship explained by slope β_3
p (time)	Recapture probability varies with time, or among seasons. No effect of mite load.
p (•)	Recapture probability is constant, no effect of mite load or time.

Survival (ϕ) and recapture (p) rates were modelled as a function of the covariate $mites_j$ (where j corresponded to an individual skink) as follows:

$$\phi_j = \frac{e^{\beta_0 + \beta_1 mites_j}}{1 + e^{\beta_0 + \beta_1 mites_j}} \dots\dots\dots \text{Eq. 5.1}$$

$$p_j = \frac{e^{\beta_2 + \beta_3 mites_j}}{1 + e^{\beta_2 + \beta_3 mites_j}} \dots\dots\dots \text{Eq. 5.2}$$

Equation 5.1 represents a linear-logistic model of survival as a function of an intercept parameter, β_0 , and a slope parameter (β_1) for the covariate $mites_j$, and, similarly, Equation 5.2 represents a linear-logistic model of recapture rate as a function of an intercept parameter, β_2 , and a slope parameter β_3 . I tested the likelihood that survival and recapture probability corresponded to one of two models: (1) mite load was not relevant to skink survival probability (only β_0 used in Eq 5.1, only β_2 used in Eq 5.2 respectively), or (2) survival or recapture rate

varied monotonically with mite load (both β_0 and β_1 in Eq 5.1, both β_2 and β_3 in Eq 5.2 respectively). If the effect of mite load on survival varied with time, parameters β_0 and β_1 were used in an equation for each time interval. Hypotheses were tested by comparing predictions (negative, neutral or positive effect of mites) with the signs of the estimated β parameters (negative or positive intercept and slope) under well-supported models.

The utility of median mite load as a predictor of survival and recapture rate of skinks was assessed using Akaike's Information Criterion (AIC_c) as a model selector (Burnham and Anderson 2002), which allows multiple hypotheses to be evaluated simultaneously. The AIC_c identifies the most parsimonious model from the set of candidate models, that is, the model best supported by the data, given the bias-corrected, maximum log-likelihood of the fitted model, with a penalty for the number of parameters used (Burnham and Anderson 1998). Models were analysed using logit-link formulation, with parameters estimated through numerical maximum likelihood techniques. I assumed that all individuals had the same probability of survival and recapture. The goodness-of-fit (GOF) of the models was tested by assessing the fit of the most general model without covariates (ϕ [time] p [time]) using the bootstrap procedure in MARK. From 1000 iterations, there was no indication of a significant deviation from assumptions for any species (all $P > 0.3$). A variance inflation factor was then computed for each species' model set (the ratio of the observed deviance from the actual data set to the mean of the simulated deviances; Anderson et al. 1994), and this factor was used to adjust model selection criteria and estimates of sampling variance. The adjusted AIC is termed the corrected quasi-likelihood AIC_c ($QAIC_c$). For each model, $\Delta QAIC_c$ was calculated (the difference between the $QAIC_c$ for that model and the smallest $QAIC_c$ among the set of models fitted). Models with $\Delta QAIC_c \leq 2.00$ were considered statistically similar (Burnham and Anderson 2002). In preliminary analyses I explored the potential for a quadratic relationship between survival and mite load for each species (by using mite load and its square as covariates). In all cases these models would either not reach convergence, or had $\Delta QAIC_c$ values greater than 2.00 from that of the best-fitting model, and so were not considered further.

Results

Two hundred and seventy five of 554 *C. rostralis* (49.6%), 212 of 343 (61.8%) of *C. rubrigularis* and 54 of 239 (22.5%) of *C. storri* were infested with trombiculid mites ($\chi^2 = 17.31$, d.f. = 2, $P < 0.001$). No other ectoparasites (such as ticks) occurred on *Carlia* at the study site. Of the skinks infested, the number of individual mites on each skink ranged from 1 to 235 (mean of 15.37 mites per *C. rostralis* [± 1.57 S.E.], *C. rubrigularis*: 18.19 [± 1.78 S.E.] and *C. storri*: 4.67 [± 0.65 S.E.]). The species differed significantly in mite load (mean of 15.37 mites per individual *C. rostralis* [± 1.57 S.E.], *C. rubrigularis*: 18.19 [± 1.78 S.E.] and *C. storri*: 4.67 [± 0.65 S.E.]; Kruskal-Wallis test of difference in mites per individual across species: $\chi^2 = 20.31$, d.f. = 2, $P < 0.001$). Mites were found in the limb axillae and inside the ears of *Carlia*. Mean intensity of infestation was weakly correlated with body size; negatively for *C. rostralis* (mite load = $0.73 - 0.006 \times \text{body size}$; $r = 0.11$, $P = 0.01$, $N = 554$) and positively for *C. rubrigularis* (mite load = $0.18 + 0.01 \times \text{body size}$; $r = 0.13$, $P = 0.01$, $N = 343$), but no relationship was evident for *C. storri* ($r = 0.015$, $P = 0.82$, $N = 239$). But there was no significant relationship between body size and median number of mites for any species (*C. rostralis*: $r = 0.201$, $N = 44$, $P = 0.186$; *C. rubrigularis*: $r = 0.137$, $N = 33$, $P = 0.44$; *C. storri*: $r = 0.084$, $N = 27$, $P = 0.67$).

The mite load of individuals at recapture was related to the intensity of infestation at initial capture for *C. rostralis* and *C. rubrigularis*, but not for *C. storri* (Table 5.2). *C. rostralis* and *C. rubrigularis* individuals that suffered from a high ectoparasite load at first capture still had a high ectoparasite infestation at subsequent captures (mean time interval between captures was $182.0 \text{ days} \pm 9.1$ S.E.). The average mite load did not differ between years (Table 5.2, Wilcoxon paired test for mean mite load at first and subsequent capture for each species: *C. rostralis* $z = -0.82$, $P = 0.41$, $N = 81$; *C. rubrigularis* $z = -1.21$, $P = 0.23$, $N = 61$; *C. storri* $z = -1.07$, $P = 0.29$, $N = 40$). Most skinks had a greater mite load when recaptured compared with their initial capture, but this was not significant for any species (*C. rostralis* $\chi^2 = 1.0$, d.f. = 1, $P = 0.32$; *C. rubrigularis* $\chi^2 = 2.3$, d.f. = 1, $P = 0.13$; *C. storri* $\chi^2 = 0.25$, d.f. = 1, $P = 0.62$; Table 5.2). The relationship between the change in ectoparasite load and the length of time between successive captures of individual skinks was not significant (Table 5.2).

Table 5.2. Relationship between ectoparasite load at initial and subsequent capture, and between the change in ectoparasite load and the time interval between captures (days) for three *Carlia* species.

Significant relationships ($P < 0.05$) are shown in bold.

Species	N	Mean mite load at first capture ($\pm$ S.E)	Mean mite load at second capture ($\pm$ S.E)	Relationship: mite load at first and second capture <i>r</i> value, (<i>P</i> value)	Relationship: change in mite load and time interval between captures <i>r</i> value, (<i>P</i> value)
<i>C. rostralis</i>	81	5.7 ($\pm$ 1.9)	6.0 ($\pm$ 1.9)	0.317 (0.004)	0.036 (0.747)
<i>C. rubrigularis</i>	61	11.0 ($\pm$ 3.04)	14.3 ($\pm$ 3.5)	0.499 (< 0.001)	0.139 (0.286)
<i>C. storri</i>	40	0.5 ($\pm$ 0.2)	0.8 ($\pm$ 0.4)	0.048 (0.767)	0.121 (0.457)

S.E. = standard error

There was no significant effect of mite load on relative growth rate for any species (Table 5.3, all $P > 0.2$). Relative body mass (or body condition) was not affected by mite load for any species (ANOVA on body mass-size residuals, Table 5.4). There was no effect of ectoparasites on body condition when accounting for season in the variation, however, power analysis suggested that a larger sample size was needed to detect a significant effect for *C. rostralis*. Mite load also had no effect on feeding success for any species (stomach contents volume ANCOVA, Table 5.4) during any season.

Table 5.3. Multiple regression results for the effect of mite load on relative growth rate ($\text{mm}\cdot\text{day}^{-1}$, with the effects of skink body size removed) for the three *Carlia* species.

Species	N	estimate	F	d.f.	<i>P</i>	Power
<i>C. rostralis</i>	140	0.004	1.57	1, 137	0.21	0.11
<i>C. rubrigularis</i>	82	0.004	0.62	1, 79	0.43	0.05
<i>C. storri</i>	62	0.001	0.002	1, 59	0.97	0.05

N = number of skinks measured, d.f.= degrees of freedom

Table 5.4. The effect of individual mite load on body condition and feeding success (volume of stomach contents) for three *Carlia* species.

Species	N	Dependent variable	Interaction	F	d.f.	P	Power
<i>C. rostralis</i>	321	Body condition	Mite load	0.3	1, 315	0.872	0.050
			Mite load x season	2.05	1, 315	0.153	0.174
	49	Volume of stomach contents	Mite load	0.982	1, 45	0.329	0.050
			Mite load x season	0.014	1, 45	0.910	0.050
<i>C. rubrigularis</i>	252	Body condition	Mite load	0.48	1, 246	0.489	0.050
			Mite load x season	0.70	1, 246	0.403	0.050
	52	Volume of stomach contents	Mite load	1.19	1, 48	0.281	0.065
			Mite load x season	0.09	1, 48	0.770	0.050
<i>C. storri</i>	159	Body condition	Mite load	0.002	1, 153	0.967	0.050
			Mite load x season	0.13	3, 153	0.720	0.050
	47	Volume of stomach contents	Mite load	0.06	1, 43	0.804	0.050
			Mite load x season	0.878	1, 43	0.354	0.050

Effect of mite load on body condition was determined by analysis of variance of reduced major axis regression residuals of body mass ($\log_{10}$ -transformed) and body size ($\log_{10}$ -SVL). Effect of mite load on volume of stomach contents (feeding success) was determined by analysis of covariance, with body size as the covariate. The interaction of mite load and season was tested as a model.

There was no significant effect of mite load on tail loss (vulnerability to predators or conspecifics) or female reproductive status (Table 5.5); however the direction of the relationship for all species suggested a beneficial effect of mites. Mean number of mites was greater in skinks that avoided predators or conspecifics, or won competitive interactions (i.e., had intact tails) and in reproductively successful females in all species.

Table 5.5. Logistic regression results for effect of mites on reproductive status of females and predator avoidance of all skinks for the three *Carlia* species.

Species	Dependent variable	Category	N	Mean mites ($\pm$ S.E.)	χ^2	P
<i>C. rostralis</i>	♀ Reproductive status	Reproductive	50	6.84 ($\pm$ 2.71)	0.798	0.372
		Nonreproductive	69	4.44 ($\pm$ 1.18)		
	Predator avoidance	Tail loss	76	5.10 ($\pm$ 1.03)	2.895	0.089
		No tail loss	446	8.20 ($\pm$ 0.87)		
<i>C. rubrigularis</i>	♀ Reproductive status	Reproductive	42	13.2 ($\pm$ 4.3)	1.909	0.167
		Nonreproductive	32	6.84 ($\pm$ 2.07)		
	Predator avoidance	Tail loss	76	9.38 ($\pm$ 2.59)	1.076	0.299
		No tail loss	256	12.03 ($\pm$ 1.25)		
<i>C. storri</i>	♀ Reproductive status	Reproductive	24	1.07 ($\pm$ 0.61)	2.002	0.157
		Nonreproductive	19	0.24 ($\pm$ 0.16)		
	Predator avoidance	Tail loss	24	0.62 ($\pm$ 0.32)	0.924	0.336
		No tail loss	204	1.17 ($\pm$ 0.22)		

The capture histories of 661 individual adult *Carlia* (300 *C. rostralis*, 225 *C. rubrigularis* and 136 *C. storri*) were used to evaluate the effect of mite load on survival and recapture probability at the study site. Mite load was calculated as the median number of mites carried by each individual skink using mite counts from every capture or recapture, and was included as a covariate for each individual skink. The most parsimonious models for *C. rostralis* included individual mite load as a factor influencing recapture rate but not survival. Survival probability varied among the seasons (time) but not with varying mite load. Models with survival modelled as a function of mite load were poorly supported ($\Delta\text{QAIC}_c > 5.3$; Table 5.6). The second best model ($\Delta\text{QAIC}_c = 1.63$; Table 5.6) suggested a positive relationship between recapture rate and median mite load ($\beta_3 = 0.65$, SE [β_3] = 0.98, 95%CI = -1.27 to 2.57). Only one model suitably described survival of *C. rubrigularis* (Table 5.6) and this included median mite load as a covariate. When mite load was removed from survival, the

model performance was poor ($\Delta\text{QAIC}_c > 6.0$; Table 5.6). The top model indicated a strong positive relationship between survival and individual mite load ($\beta_1 = 3.17$, SE $[\beta_1] = 2.70$, 95%CI = -2.13 to 8.47), *C. rubrigularis* individuals with a larger median mite load had a greater probability of survival. Recapture probability of individuals varied among seasons (time), but was not dependent on mite load. The most parsimonious model describing *C. storri* survival included time only; probability of survival for *C. storri* individuals was seasonally dependent and recapture probability was constant regardless of time or mite load. Models of survival including median mite load for *C. storri* were poorly supported by the data ($\Delta\text{QAIC}_c > 5.3$; Table 5.6).

Table 5.6. Summary of the most suitable mark-recapture models used to assess the variation in survival (ϕ) and recapture (p) probability as a function of mite load (mites), time and constancy ($\bullet$) of the three *Carlia* species. Table shows best six models (determined by AIC) for each species (not necessarily the same), the most parsimonious models ($\Delta\text{QAIC}_c < 2.00$) are bold.

Species	Model	Np	QAIC _c	ΔQAIC_c	QDeviance	Model Likelihood
<i>C. rostralis</i>	ϕ (time) p ($\bullet$)	7	623.69	0.00	609.39	1.00
	ϕ (time) p (mites)	8	625.32	1.63	608.93	0.44
	ϕ (time) p (time)	11	626.92	3.23	604.20	0.20
	ϕ (time) p (mites x time)	16	628.03	4.34	594.54	0.11
	ϕ (mites + time) p (time)	14	629.02	5.34	597.45	0.08
	ϕ (mites x time) p ($\bullet$)	13	629.49	5.81	602.51	0.05
<i>C. rubrigularis</i>	ϕ (mites) p (time)	6	496.91	0.00	484.59	1.00
	ϕ (mites) p ($\bullet$)	1	499.47	2.56	497.45	0.28
	ϕ ($\bullet$) p (time)	7	502.96	6.05	488.52	0.05
	ϕ (mites) p (mites)	4	503.93	7.02	495.77	0.03
	ϕ ($\bullet$) p ($\bullet$)	2	505.69	8.78	501.64	0.01
	ϕ (mites x time) p ($\bullet$)	14	506.91	10.00	477.23	0.01
<i>C. storri</i>	ϕ (time) p ($\bullet$)	7	306.34	0.00	285.16	1.00
	ϕ (mites x time) p ($\bullet$)	10	311.67	5.33	297.08	0.07
	ϕ (mites x time) p (mites)	13	312.35	6.01	284.37	0.05
	ϕ (mites x time) p (time)	14	312.99	6.66	282.70	0.04
	ϕ (time) p (mites)	8	313.15	6.81	296.38	0.03
	ϕ (time) p (time)	11	319.48	13.14	296.06	0.001

Variance inflation factors used to adjust for overdispersion: *C. rostralis* (= 1.059), *C. rubrigularis* (= 0.896), *C. storri* (= 1.016). Shown are number of model parameters (Np), Akaike's Information Criterion corrected for overdispersion (QAIC_c), the difference between the QAIC_c for each model and the smallest QAIC_c among the set of models fitted (ΔQAIC_c) and the model weight for candidate models describing survival (ϕ) and recapture (p) probability of skinks.

Discussion

I found no evidence that trombiculid mite larvae living on *Carlia* had consistently negative effects on fitness. The incidence of ectoparasites on lizards at the study site was high, almost half the *Carlia* population hosted larval mites. Lizards also had a range of infestation levels (from no mites, to more than 200 mites per lizard) and mean infestation intensity was high, particularly in relation to lizard body size, compared with other studies of lizard-ectoparasite interactions (Bull and Burzacott 1993; Salvador et al. 1999; Main and Bull 2000; Kerr and Bull 2006; Schlaepfer 2006). This population therefore provided a good opportunity to test the effects of the association between skinks and mites. The intensity of ectoparasite infestation had no significant effect on growth rate, body condition or feeding success for any species, regardless of season or skink body size. Mite load did not affect reproductive success or the ability to avoid predators, and the presence of mites did not negatively affect skink survival. This study contrasts with research (see citations in Introduction) where ectoparasite load was associated with increased mortality, reduced reproductive success and loss of body mass of hosts, but is supported by other studies on lizards that have reported no effect of ectoparasites: Bauwens et al. (1983) found no effect of ticks on sand lizard (*Lacerta agilis* and *L. vivipara*) survival, and Bull and Burzacott (1993) found that tick loads on sleepy lizards (*Tiliqua rugosa*) did not affect host survival or growth. Mite load was not significantly related to any measure of fitness or body condition in male plateau lizards *Sceloporus virgatus* (Abell 2000), nor in anoline lizards *Norops polylepis* (Schlaepfer 2006). We may also expect that fewer studies with negative results are published than those with positive results, so it is difficult to gauge how widespread low mite effects might be.

The nature of my study was correlational, rather than experimental, and therefore I have not isolated the effects of parasitism (Scott and Dobson 1989). However, the ability to track individual skinks of known infestation status, and compare growth rate and survival of infested and uninfested skinks in a natural system, provides important information on the effects of mites on infected individuals in nature. The range of parameters measured in this study, along with the large number of individuals and the interesting comparison of ectoparasite infestation among three sympatric species, makes this study unique among

studies of ectoparasite effects and robust in its results.

Trombiculid mites can transmit blood parasites, cause anaemia and lesions of the skin, and can induce a metabolic cost to skinks (Goldberg and Holshuh 1992; Bull and Burzacott 1993; Klukowski and Nelson 2001; Schall and Smith 2006). Ectoparasite infestations can cause skinks to move less and bask more (Main and Bull 2000). The large infestations of mites seen in the limb axillae and ears of skinks in this study may make skinks more susceptible to predation due to reduced movement and hearing (Salvador et al. 1999). This documented ectoparasite-induced change in the physiology, metabolism and behaviour of skink hosts leads to an expectation that trombiculid mites will have a detrimental effect on *Carlia* fitness and survival. Ectoparasite load was constant over time for most skinks (Table 5.2) and since trombiculid mites only stay attached for a few weeks (Goldberg and Bursey 1991), this suggests that certain skinks were particularly susceptible to ectoparasites and became reinfested.

Contrary to expectation however, I found that constant infestation of *Carlia* by trombiculid mites did not hinder growth of host skinks, did not impact on general skink health and energy reserves, and did not affect skink feeding or reproductive success (Tables 5.3, 5.4 and 5.5). For one species (*C. rubrigularis*) skinks with large mite loads had greater (rather than reduced) survival probability. Trombiculid mites therefore appear to be benign, or beneficial, in their association with *Carlia*, and do not behave as parasites. Mites do, however, attach to and feed on their skink hosts and are, by definition, parasitic (Walter and Proctor 1999). The lack of detrimental effect of mites on skinks in any of the components of fitness measured suggests that mites may provide some beneficial service to skinks that counteracts the negative effects induced by consuming host resources.

How does this population of skinks, which are continuously reinfested with ectoparasites that attach to the skin and use skink resources, not suffer obvious adverse effects from this association? While my data suggested that carrying mites did not negatively affect, or may have even directly benefited skinks, it is possible that the patterns I observed reflected a correlation of mite load with some other attribute of the skinks, such as body size, access to resources, breeding season, or behavioural changes, that in turn affected fitness and survival. Another possibility is that high parasite loads are only detrimental to the weaker

individuals in the population, so that only healthy skinks with high mite loads remain. I have considered the potential for correlation between skink mite load and these attributes, and it is unlikely. First, mite infestation was not strongly correlated with skink body size in this study. Larger, older skinks, while having more available space to hold a large number of attached ectoparasites and more exposure opportunities for infestation by mites, were not consistently more susceptible to infestation than small skinks. Since trombiculid mites attach to their host for a short time period, it is unlikely that exposure is a function of time at the time scales I examined. Second, mite load was not correlated with body condition. Skink body mass, relative to body size, had no bearing on mite infestation of *Carlia*. And third, in this study skink components of fitness were monitored in natural conditions over multiple years and seasons. Seasonally high prey abundance at my study site (in the wet season, see Chapter 7), coincides with the breeding season during which courtship, mating activity and egg production exert a cost on skink energy reserves (James and Shine 1985; Schwarzkopf 1993; Abell 2000). While hosts may completely compensate for the negative fitness effects of parasites if food is readily available, parasites may be costly to the fitness of their host under stressful environmental conditions (de Lope et al. 1993). The deleterious effects of parasites may be exacerbated during these periods of food or reproductive stress and I therefore accounted for the effect of season in analyses. And third, behavioural changes of skinks, measured by encounter rate, did not translate to reduced survival or increased predator attacks. Infestation by ectoparasites could have caused skinks to behave differently, for instance have reduced sprint speed or agility, and made them easier to capture, thereby increasing my chance of encountering them and causing an impression that skinks that were hosts to large numbers of ectoparasites survived longer. Alternately, greater encounter rate of researchers with mite-infested skinks would suggest greater vulnerability of these individuals to other visual predators (such as larger skinks, snakes and birds), which would have caused reduced survival or increased tail loss. For *C. rostralis*, skinks carrying greater numbers of mites were more likely to be recaptured than skinks with few or no mites (Table 5.6) but this high recapture rate of infested skinks was not coincident with elevated survival rates: survival was not significantly affected by mite load in *C. rostralis*. And I found no significant effect of mite load on tail loss for any species; in fact, skinks that lost their tails had smaller mite loads than

skinks with intact tails (Table 5.5). For *C. rubrigularis*, mite load had no effect on recapture rate, but positively influenced survival; skinks infested with a large number of mites were more likely to survive than skinks with few or no mites. A possible explanation for high survival and recapture probability of parasitised skinks might be that successful, long-lived skinks have small, well-established home ranges and may therefore frequently use the same favourable refuges; cool, moist locations where mite populations may be high. Kerr and Bull (2006) found tick load was influenced by refuge use in radio-tracked sleepy skinks (*Tiliqua rugosa*), and a relationship between ectoparasites and refuge use has also been documented for birds (e.g., Brown and Brown 1986), and mammals (e.g., Butler and Roper 1996). Survival and recapture rates of *C. storri* were unrelated to mite load.

Alternatively, susceptibility to parasites, as a behavioural or physiological trait, may be positively genetically correlated with individual components of fitness (Sorci and Clobert 1995), so that individuals susceptible to parasite infestation also grow faster, survive longer and reproduce more. Parasites prefer healthy hosts (e.g., Bize et al. 2008). It is also possible that the relationship between *Carlia* and trombiculid mites is historically well established, and these ectoparasites have co-evolved with skinks so that their effects have become benign. If mites benefit from their association with *Carlia*, and skinks have developed a resistance to the effects of mites so that they do not cause harm, the relationship is commensal rather than parasitic.

In my study system, it is also possible that mites are not just 'hitching a ride' but actually provide a service to skinks, enhancing the breeding colouration of males in *C. rostralis*, and of both males and females of *C. rubrigularis*. There is remarkable similarity between the lateral colouration of breeding *Carlia* and the colour of *Eutrombicula* mites (*pers. obs.*). In many species that display orange colour as a secondary sexual trait, females prefer brighter males (Houde and Endler 1990; Hill 1991; Bakker and Milinski 1993). Thus, possibly, skinks provide shelter and a blood meal to developing mite larvae, and may, in turn, benefit from enhanced intensity and larger area of orange colour on display. Consistent with this hypothesis, *C. storri* has comparatively low mite infestation levels and does not display orange colour. Increased area and intensity of breeding colour may ensure larger or better quality territory and increased reproductive success, as it does in other skinks and in

vertebrates more generally (Olsson 1994; Evans and Norris 1996; Godin and Dugatkin 1996; Anderholm et al. 2004). A large area of orange colouration was correlated with success in male-male contests of another *Carlia* species (*C. jarnoldae*; S. Maclagan, *unpublished data*). Thus, the relationship between *Carlia* and orange mite larvae may have shifted from parasitism to something more like commensalism, despite the energetic resources that mites extract from skinks.

Bright colour displayed by males is often correlated with parasite resistance, and females choose bright males based on this honest signal of genetic value (Hamilton and Zuk 1982; Milinski and Bakker 1990; Houde and Torio 1992; Thompson et al. 1997; Faivre et al. 2003; Mougeot et al. 2007). In *Carlia*, bright colour is enhanced by parasites, so that the signal would not be an honest indicator of parasite resistance. Manipulative experiments to test the 'benefits' of increased mite load on individual skinks in terms of mating success and territory size are needed to explore this idea. This study highlights the necessity to confirm, rather than assume, that a symbiont is parasitic.

Chapter 6

Differences in the physical structure of *Carlia* limb axillae: the relationship with mite infestation

Abstract

Many lizards have folds or pockets of skin that contain ectoparasites. The skin within these pockets has few or no scales and is highly vascularised allowing ectoparasites access to the skin, improved feeding conditions and safety from host grooming. Lizards with mite pockets are more likely to be infested with ectoparasites than closely related lizards without pockets. In Chapter 5 I showed that three closely related, sympatric *Carlia* skinks were hosts to larval trombiculid mites that infested the axillae. The skink species differed in their degree of larval mite infestation: *C. rostralis* and *C. rubrigularis* were highly infested and carried large numbers of mites, while *C. storri* was considerably less susceptible to mite infestation and carried fewer mites when infested. In this study, I used scanning electron microscopy (SEM) of molds of skink axillae to determine whether mite pockets were present in the limb axillae of some *Carlia* species, and to describe the difference in physical structure of the axillae among the species to see if differences in physical structure might explain the different susceptibility of the 3 species to infestation. SEM images revealed areas of irregular scales in the limb axillae of all three *Carlia* species, but no specialised folds or pockets of skin. Therefore, the presence of many more mites in two species was not explained by the presence of mite pockets. Also, the area of irregular scales in *C. storri* was smaller than the area observed in the axillae of *C. rostralis* and *C. rubrigularis*, but not small enough to explain the considerably reduced mite load carried by *C. storri* individuals. Mite loads on *C. storri* individuals were, therefore, not limited by area available for attachment; relative susceptibility to mite infestation among species was likely due other factors unrelated to axilla structure.

Introduction

Lizards are often hosts to ectoparasites such as mites and ticks (Frye 1991). Ectoparasites not only drain the host's energy reserves and potentially transmit disease, but also cause lesions of the skin and can obstruct host movement, hearing, feeding, and even breathing (Goldberg and Holshuh 1992; Salvador et al. 1999; Walter and Proctor 1999). Many lizard species have folds or pockets of skin that frequently contain ectoparasites (Arnold 1986). The skin within these pockets has few or no scales and is highly vascularized allowing ectoparasites access to the easily punctured host integument (Benton 1987). It also allows improved grip on the host and safety from host grooming, allowing ectoparasites to benefit from an association with these structures (Arnold 1986; Reardon and Norbury 2004). Pockets occur in many taxa that are not closely related, and lizards with pockets are more likely to be infested with ectoparasites than are closely related lizards without pockets (Arnold 1986). Containing an infestation of ectoparasites in a fold or pocket of skin would provide some damage limitation for lizards, reducing disturbance of the skin and superficial organs (Benton 1987). Arnold (1986) proposed the arguable theory that these pockets of skin have evolved by natural selection to limit and contain the damage caused by ectoparasites by restricting them to an area of the body that can be modified to cope with the detrimental effects. The skin in these pockets is resilient to damage and recovers rapidly after the ectoparasites cease feeding and drop out (Arnold 1986). Generally, pockets are deep skin invaginations and are located in areas near the legs and ears of the lizard (laterally on the neck and chest, and proximal end of the tail, and in the armpit and groin regions), and, in experiments, these pockets reduced ectoparasite attachment in areas where they may impair locomotion and hearing (Salvador et al. 1999). However, severe tissue damage can be caused by ectoparasites feeding within pockets, disputing the theory that pockets are specialised adaptive sites (Bauer et al. 1990; Goldberg and Holshuh 1992).

The prevalence of infection by larval trombiculid mites (genus *Eutrombicula*, Acari: Trombiculidae) differs among *Carlia* species (Arnold 1986), including three closely related, sympatric *Carlia* species (Chapter 5). These three species of sympatric *Carlia* (*Carlia rostralis*, *C. rubrigularis*, and *C. storri*; Figure 6.1) are small, active and terrestrial skinks, which forage and take refuge amongst the leaf litter (Chapter 3). Thus, all three have equal

opportunity to encounter larval trombiculid mites, which live in leaf litter and soil (Walter and Proctor 1999). However, these *Carlia* skinks each differ in their degree of larval mite infestation: *C. rostralis* and *C. rubrigularis* are highly infested (49.6% and 61.8% of the population, respectively) while *C. storri* is significantly less susceptible to mite infestation (22.5% of the population; Chapter 5). The species also differ in the average trombiculid mite loads carried; considering only lizards with mites, *C. rostralis* had 17.6 ± 2.7 (mean $\pm$ standard error) mites per individual, *C. rubrigularis* had 21.4 ± 2.8 mites per individual, and *C. storri* had only 3.3 ± 0.8 mites per individual (Chapter 5). Further, while the axillae of *C. rostralis* and *C. rubrigularis* were the sites most frequently infested, mites were commonly found in the ear region of *C. storri* (*unpublished results*). From these observations, I inferred that *C. storri* may have a markedly different structure of the axillae, lacking pockets. Knowledge of the proximate factors that influence parasite loads, such as the physical ability to host parasites, may help to understand the selective pressures faced by hosts and host-parasite evolution. In the present study I examine the axillae of the three *Carlia* species using scanning electron microscopy (SEM) to (1) establish that mite pockets are present in the limb axillae of some *Carlia* species and (2) to determine the difference in physical structure of the axillae among the species to attempt to explain their different susceptibility to infestation.

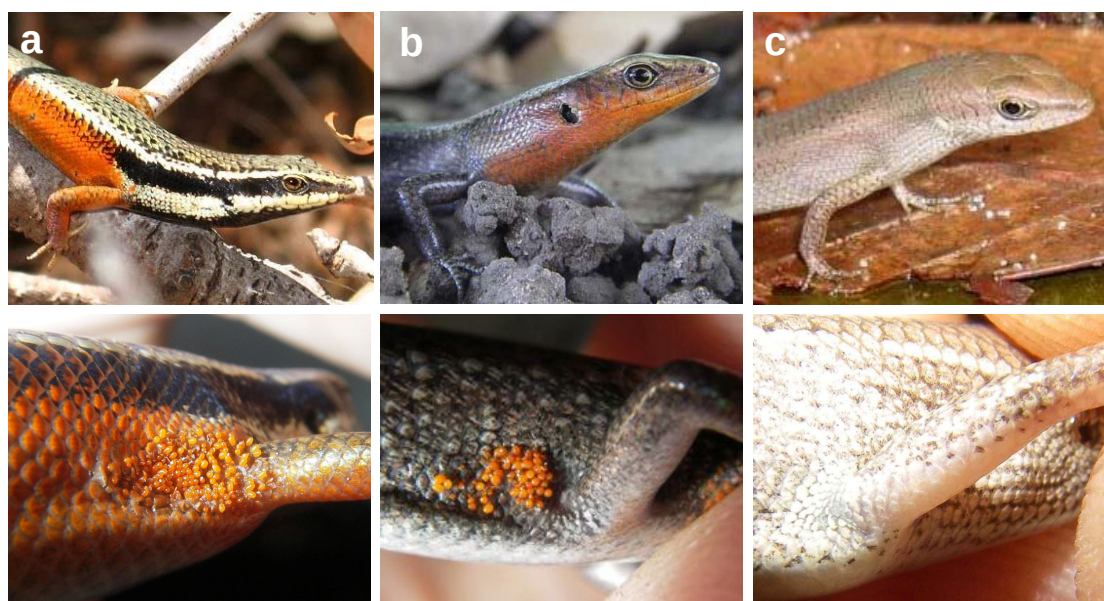


Figure 6.1. Three *Carlia* species from the study site on Hinchinbrook Island with detail of limb axillae below, (a) *C. rostralis*, (b) *C. rubrigularis* and (c) *C. storri*. Adult male individuals pictured.

Methods

In April 2008, 18 individual *Carlia* lizards were captured (six individuals each of *C. rostralis*, *C. rubrigularis*, and *C. storri*) at the study site on Hinchinbrook Island and returned to the laboratory. Skinks were measured for snout-vent length (SVL) and individually housed in a constant temperature room, and provided with food and water *ad libitum*. Within 10 days of capture, a high-resolution mold of the right-side limb axilla epidermis was made of each skink using polyvinylsiloxane impression material and epoxy resin (Vucko et al. 2008). This method allows high-quality reproduction of the epidermis of live skinks. The epoxy relief molds were sputter-coated with gold and examined using a JEOL JSM – 5410V scanning electron microscope (SEM). The shape and structure of the scales in the limb axilla region were compared among the three species. The area of irregular scales in this region and the proportion of bare skin available for the attachment of ectoparasites in the axillae was determined from the SEM images by calculating the proportion of scales and bare skin in each axilla using Image J (v1.36b) processing and analysis software (Abramoff et al. 2004). The area of irregular scales in the limb axilla was calculated relative to SVL of each lizard to give a mean area for each species, and compared among the species using analysis of

variance (ANOVA). Proportion of bare skin (relative to skin covered by scales) was compared among the species using analysis of covariance (ANCOVA), with proportion of bare skin as the dependent variable, species as the factor, and body length (SVL) as the covariate. Statistical analyses were performed using SPSS v16.0 (SPSS, Inc., Chicago, IL, USA, 2007) and significance level was set at $P = 0.05$.

Results

Visual examination of SEM images revealed that scales in the limb axillae were distinctly different from the surrounding flank scales. Flank and dorsal scales were smooth, flat, regularly shaped, and tightly overlapping in all species (Figure 6.2 a). Scales in and around the axilla region were irregularly shaped (conical or three-dimensional), loosely overlapping or spaced with relatively large interscale regions. I considered this area available for the attachment of mites due to the high proportion of exposed skin in the region compared with surrounding areas (Figure 6.2 b). The species differed in the area available for the attachment of mites when taking body size into account (Table 6.1, area available for mite attachment relative to SVL; ANOVA $F_{2,17} = 14.87$, $P = 0.01$; Figure 6.2 b). The area available for the attachment of mites was smaller for *C. storri* individuals than for the other two species (Table 6.1). There was no difference among the species in the proportion of bare skin exposed in the limb axillae (Table 6.1; ANCOVA: $F_{2,17} = 0.91$, $P > 0.4$; Figure 6.2 c). *Eutrombicula* sp. mites were observed *in situ* within limb axillae of *Carlia* skinks (Figure 6.3).

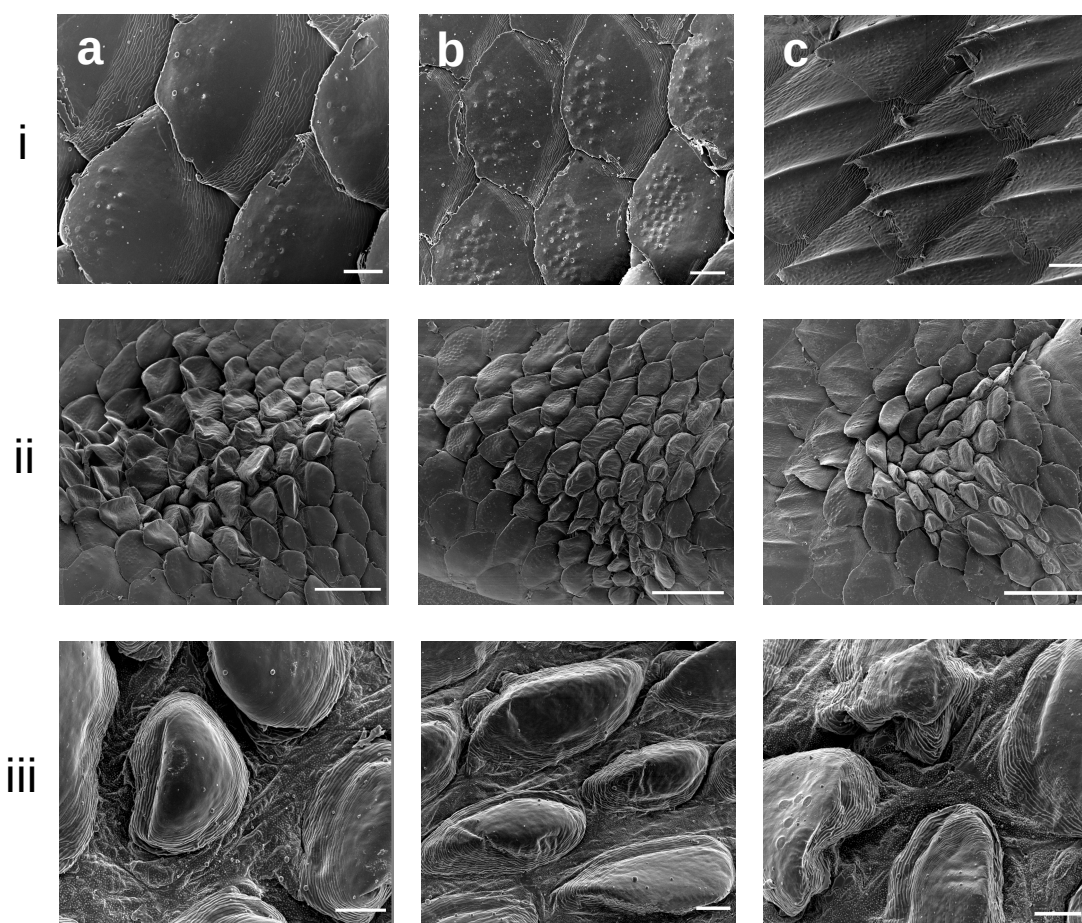


Figure 6.2. Scanning electron micrographs of species (a) *C. rostralis*, (b) *C. rubrigularis* and (c) *C. storri* showing (i) flank scales (scale bars = 100 μm), (ii) limb axilla (scale bars = 500 μm) and (iii) scales within limb axillae (scale bars = 50 μm).

Table 6.1. Area available for mite attachment (mm^2) and proportion of bare skin in limb axillae of the three *Carlia* species.

Species	N	Total area available for mite attachment (mean relative to SVL $\pm$ S.E mm^2)	Mean proportion of bare skin relative to total area in limb axilla ($\pm$ S.E)
<i>C. rostralis</i>	6	78.82 $\pm$ 7.64	0.31 $\pm$ 0.02
<i>C. rubrigularis</i>	6	61.31 $\pm$ 6.81	0.33 $\pm$ 0.02
<i>C. storri</i>	6	38.00 $\pm$ 4.82	0.32 $\pm$ 0.01

N = number of skinks measured, S.E. = standard error

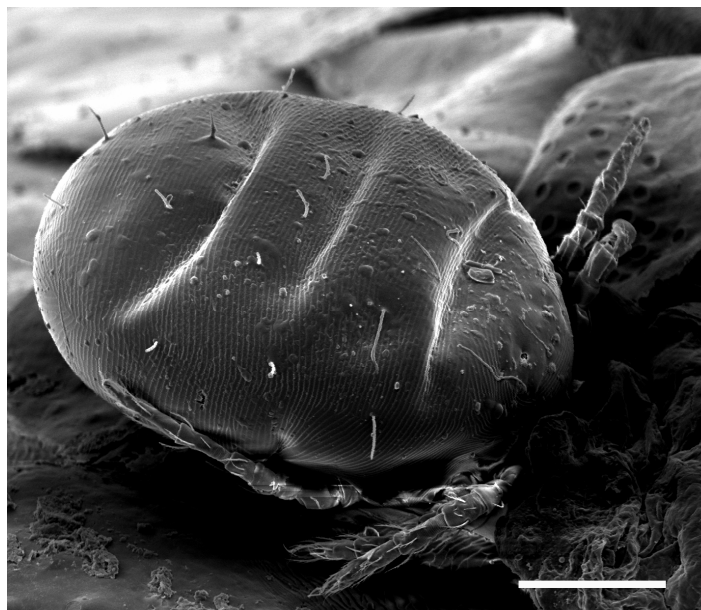


Figure 6.3. SEM of attached chigger mite *Eutrombicula* sp. *in situ* within limb axilla of *Carlia rostralis* (scale bar = 100 μ m).

Discussion

There is strong site specificity of trombiculid mites for *Carlia* axillae (Arnold 1986; Chapter 5) and examination of the SEM images reveals an area of irregular scales in the axillae region. Trombiculid mites have short mouthparts and need to attach beneath the scales of their reptile hosts to feed (Bertrand and Modry 2004; Figure 6.3) and all three *Carlia* species possessed an area of conical or loosely overlapping scales in the axillae that appeared suitable for mite attachment. The area of irregular scales in the axillae of *C. storri* individuals was considerably smaller than for the other two species (Table 6.1), approximately half that in the axillae of *C. rostralis* individuals and two thirds that of *C. rubrigularis* individuals (Table 6.1). However, *C. storri* individuals with mite infestations had only approximately one sixth the mite load of the other two species (Chapter 5). Thus, area available for the attachment of mites was apparently not the factor restricting the mite load of *C. storri*.

Although scales in the axillae were distinctly different from the surrounding flank and dorsal scales of all three *Carlia* skinks examined, the patch of irregular scales seen in the limb axillae of *Carlia* skinks was very different from the deep invaginations and folds of skin termed

'mite pockets' in other lizard families (see images in Arnold 1986; Bauer et al. 1990; Bertrand and Modry 2004; Torres-Carvajal 2007). Pockets where ectoparasites aggregate may have originated as skin appendages used in crypsis, display behaviour, or intraspecific identification (Arnold 1986; Bauer et al. 1990). Skink scales are characterised by dermal ossicles, a mosaic of small bones underlying each scale (Greer 1989), and skinks are less likely to have the loose skin that in many other taxa forms folds, crevices, and pockets. Bauer et al. (1990, 1993) have argued that ectoparasites opportunistically occupy skin folds and pockets, and the origin and maintenance of pockets is not explained by their benefit in containing infestations of ectoparasites on the lizard host. Examination of the axillae of *Carlia* supports this argument. The presence of irregular scales in the axillae of all three species of *Carlia* skink suggests that scales in this region are arranged to allow ease of movement of the forelimb. The small, conical, or loosely overlapped scales in the axillae region of *Carlia* skinks create a distinct patch, necessary for limb articulation, which, incidentally also provides exposed skin for the opportunistic attachment of mites.

It is possible that, in *C. rostralis* and *C. rubrigularis*, these patches of scales are characterised by resilient skin with a high concentration of lymphoid cells and these species encourage the clustering of feeding ectoparasites in these areas to ameliorate damage. However, if pockets have evolved to limit damage to lizards, they should, in theory, function to keep ectoparasites out of areas where they may impede locomotion. In other lizard species, deep pockets function to cluster mites in sites that do not restrict movement (eg. neck pockets of *Sceloporus variabilis* [Arnold 1986], *Sceloporus jarrovi* [Golberg and Holshuh 1992], *Psammmodromus algirus* [Salvador et al. 1999] and *Agama caudospinosa* [Bertrand and Modry 2004]). Trombiculid mites on *Carlia* skinks aggregate in an area where they may hinder articulation of the forelimb, further evidence that it is unlikely that scale patches in the axillae of *Carlia* skinks have evolved to host mites. Different susceptibility to mite infestation among the three *Carlia* species at my study site (Chapter 5) was likely due other factors unrelated to the presence or area of mite pockets, or limb axilla structure.

Chapter 7

Diet and prey selection of sympatric tropical skinks

Abstract

Skinks are generally opportunistic predators; taking available prey from the environment as it is encountered. Variation in their diet composition is thought to reflect differences in prey abundance in the environment. I studied diet composition and prey selection in the three sympatric skink species (genus *Carlia*) at my study site on Hinchinbrook Island by comparing contents of skink stomachs with arthropod prey available in their habitat. *Carlia* were entirely carnivorous and fed on a range of arthropod prey. I found high overlap in diet and prey size among the three species and between the wet and dry seasons, but found that skinks generally focused their foraging efforts on prey types and prey sizes that were not abundant in the environment. Spiders (Aranea), orthopterans, blattarians, isopods and termites (Isoptera) were important prey of skinks, but these arthropods were rarely trapped in the environment. Skinks also frequently consumed large-bodied prey, despite the higher relative abundance of small prey in the environment. Thus, my results show that skinks were more selective in their foraging and diet than previously assumed. Selection of prey by consumers is a fundamental ecological process, important to consumers for maintaining energy requirements to grow and reproduce, but equally important to the community dynamics of the prey consumed.

Introduction

Feeding and food selection are fundamental ecological processes, important to consumers for maintaining energy requirements to grow and reproduce, but equally important to the community dynamics of the prey consumed (Stephens and Krebs 1986; Sih et al. 1998). Small insectivorous lizards are an interesting study organism in which to measure food selection, because they have low metabolic rates, and, therefore, very low energy requirements compared with similar-sized endotherms (Pough 1980). At the same time, small arthropod prey are generally highly abundant in the environment (Schoener and Janzen 1968; Stamps and Tanaka 1981) so insectivorous lizards are not often restricted by food shortages, and, presumably, can afford to be selective. Studying diet composition is useful to predict how a species forages, but determining food selection requires knowledge of the prey available (Diaz and Carrascal 1990). Few studies, however, have sampled the prey available to lizards extensively enough to determine whether they select prey (but see Perez-Mellado et al. 1991).

Small skinks are a diverse and dominant component of the reptile community in Australia. Small scincids are typically classified as widely foraging, opportunistic predators which do not exhibit distinct patterns of prey selection, apart from those imposed by body size restrictions (Pianka 1969; Taylor 1986; Lunney et al. 1989; Brown 1991; Wapstra and Swain 1996). Variation in diet composition among different populations of skinks is thought to reflect differences in prey abundance in the environment, but few previous studies have considered prey availability in relation to prey selection by skinks (James 1991c; Perez-Mellado et al. 1991). Three species of *Carlia* dominate the reptile community at my study site (Chapter 3). Superficially, these species share similar microhabitat, activity times and behaviour, and have access to the same range of arthropod prey (Chapter 3). *Carlia* are believed to be generalist predators, consuming a variety of arthropod prey in proportions relative to availability in the environment (James 1983). However, I found that the stomach contents of these small lizards seldom contained prey items that were abundant in the lizards' habitat (*pers. obs.*). My aim was to thoroughly sample the community of arthropod prey available to lizards to determine diet composition and prey selection in a community of sympatric *Carlia* skinks. I examined (1) diet composition and prey size in three species, (2) dietary overlap between seasons and

among species and the degree of trophic partitioning in this community, and (3) the extent of prey selection by the three species, by comparing types and sizes of prey consumed with prey available in the environment.

Methods

This study considers the three most abundant skink species at my study site: *Carlia rostralis*, *C. rubrigularis* and *C. storri* (Chapter 3).

Diet composition

I collected stomach samples from adult *Carlia* captured during the wet season (October - April) and dry season (May - September) of 2006 and 2007, as described in Chapter 2. Briefly, I captured lizards by hand after 1200 on sunny days, and measured snout-to-vent length (SVL), body mass, head length, head width and head depth of each individual. Lizards were euthanased shortly after capture and preserved immediately in 70% ethanol. I removed the entire intestinal tracts of preserved lizards in the laboratory and determined the total volume of stomach contents by displacement of water in a graduated 1000 or 3000 mm³ syringe barrel. I identified the contents of each stomach to ordinal level for insects, class or ordinal level for other invertebrates, and species level for vertebrates, using a dissecting microscope. The length (from head to abdomen [cephalothorax to abdomen in spiders]) and width (at the widest point) of each prey item were measured.

The content of lizard stomachs was measured by (1) the numbers of each taxon of prey, (2) the total volume of food, measured by estimating the amount of water (ml) displaced by the stomach and food, and then subtracting the volume displaced by the stomach alone, and (3) the volume of each prey item, estimated from length and width measurements, using the formula for a prolate spheroid (volume = $4/3\pi$ [prey length/2] • [prey width/2]²).

Available prey

I obtained estimates of the abundance and diversity of available potential prey for *Carlia* by extracting invertebrates from samples of the leaf litter, pitfall traps, and pan traps at five locations (the unfenced control study plots) within the study site during the wet and dry seasons of 2006 and 2007 (methods, and number of traps detailed in Chapter 2). Invertebrate samples were transferred to 70% ethanol and returned to the laboratory for sorting. I identified the invertebrates in the trap samples as for stomach contents samples, and assigned each to one of three length classes: <3, 3 – 6, and >6 mm. There are problems inherent to any method of measuring prey availability (Wiens 1984). I assumed that the relative abundances of the different prey types in the traps reflected their availability to lizards at the study site, however there was no way to test the accuracy of this assumption as prey availability depends not only on abundance but also on behaviour (Freed 1980). I reduced this sampling bias by pooling the prey trapped by the three techniques and dividing by the number of days of trapping, to give overall estimates of sedentary, surface-active and aerial prey available to lizards per day.

Analyses

I compared the volume of stomach contents, number of prey types and prey items per individual and mean length of prey between males and females of each *Carlia* species using t-tests. To test for differences between the seasons I compared number of prey types and number of prey items per stomach (using Mann-Whitney U-tests for each species), and volume of stomach contents (using t-test for each species) between the wet and dry seasons. I compared the mean volume of stomach contents among the species by analysis of covariance (ANCOVA) with body size (SVL) as the covariate.

I summarised diets as the proportion of the total number of prey items in the stomach (numerical percentage), the proportion of the total volume of prey items in the stomach (volumetric percentage) and the proportion of lizards eating each prey taxon (frequency percentage). Any of these methods used alone is subject to bias. The index of relative importance ($IRI = [N + V] \cdot F$) of prey types is a single estimate which takes into account the

numerical percentage (N), volumetric percentage (V) and frequency percentage (F) of each prey type, and thereby reduces bias towards large-sized or sporadically abundant prey (Pinkas et al. 1971). Dietary niche breadth ($B = 1/\sum p_i^2$), where p_i is the proportion of prey type i in the diet, was calculated from frequency data using the inverse of Simpson's diversity index (Simpson 1949; Pianka 1973). Values of niche breadth can vary from 1 (use of a single prey category) to n (equal use of all prey categories; Costa et al. 2008). I evaluated diet similarity between the sexes, between pairs of species and between seasons by using Pianka's index of dietary overlap ($O_{jk} = \sum p_{ij} p_{ik} / [\sum p_{ij}^2 \sum p_{ik}^2]^{1/2}$), where p_i is the frequency of occurrence of prey item i in the diet of species j and k (Pianka 1973). Values of overlap vary between 0 (total separation) and 1 (total overlap). I compared prey size differences (log-transformed) among the three species. I tested the difference in mean length of individual prey items consumed between the wet and dry seasons using t-tests for each species, and compared the differences among the species by analysis of variance (ANOVA). I used linear regression to test the relationship between lizard body size (SVL) and prey length, and ANCOVA with SVL as the covariate to test differences in prey size consumed by the three species, once lizard body size effects were removed.

I compared the difference in body size (SVL) among the species with ANOVA. Correlations between prey size and lizard morphological variables were estimated by Spearman rank correlation (r_s). Selection for prey taxa by lizards was compared with the availability of prey types in the environment per day in the wet and dry season using Ivlev's electivity index ($E = [r_i + p_i]/[r_i - p_i]$), based on the proportion of prey type i in the diet (r) and in the environment (p) (Ivlev 1961; Jacobs 1974). Values of electivity between -1 and 0 indicate negative selectivity (meaning that the prey type is available in the environment but not selected by lizards), and values between 0 and +1 indicate positive selectivity (meaning that the prey type is relatively more common in lizard diet than would be expected from availability in the environment, i.e., lizards select prey types). The electivity index was also used to compare prey sizes available in the environment with prey sizes consumed by lizards.

I analysed statistical differences between the diet of each species and the prey available in the environment in both the wet and dry seasons using a permutational multivariate analysis of variance (PERMANOVA) of Bray-Curtis similarities among the

replicate samples (Anderson 2001). I compared the diet of each species with available prey using planned contrasts, and tested the interaction with season (wet and dry). PERMANOVA assumes that dispersion is similar across the groups measured; I tested for homogeneity of dispersions within the sample groups with PERMDISP (Anderson 2004). PERMDISP tests for multivariate dispersion using various distance and dissimilarity measures and results are reported as the average within-group distance of each group from its centroid. A multi-dimensional scaled (MDS) plot of the Bray-Curtis similarities among the species' diet and trapped available prey in the wet and dry seasons (data not transformed) was compiled to provide a visual representation of the relative similarities among samples. PERMANOVA, PERMDISP and MDS were performed with the software package PRIMER v6.1.11 (Plymouth Routines in Multivariate Ecological Research, Clarke and Gorley 2006), PERMANOVA and PERMDISP include permutation tests for significance; 9999 permutations were used in all tests. All other variances and regressions were analysed using the statistical package SPSS v16.0 (SPSS Inc., Chicago, IL, USA, 2007). Significance level was set at $P = 0.05$.

Results

Dietary composition

I collected stomach samples from a total of 152 adult *Carlia* during 2006 and 2007 (Table 7.1). Preliminary analyses (and see Chapter 4) showed no significant differences between the sexes of any species in the volume of stomach contents, number of prey types, number of prey items or the size of prey consumed, and therefore the results presented are for both sexes combined. Stomachs contained similar numbers of prey items and prey types in the wet and dry seasons (Table 7.1). Volume of stomach contents did not differ between the wet and dry seasons for any species (*C. rostralis*: $t = 0.31$, d.f. = 46; *C. rubrigularis*: $t = -0.11$, d.f. = 39; *C. storri*: $t = -1.35$, d.f. = 37; all $P > 0.1$). I combined the seasons to display taxonomic composition of the stomach contents of the three species.

Table 7.1. Number of stomachs from which contents were identified, with mean number of prey taxa, and mean number of prey items per stomach for the three *Carlia* species. Results of Mann-Whitney U-tests to test differences in prey taxa and prey items between the wet and dry seasons are shown here (z and P values).

species	season	N	Mean number of prey taxa (per stomach $\pm$ S.E.), difference between seasons		Mean number of prey items (per stomach $\pm$ S.E.), difference between seasons	
				$z; P$		$z; P$
<i>C. rostralis</i>	wet	26	2.83 ($\pm$ 0.33)	-0.09; 0.93	5.13 ($\pm$ 1.20)	-0.5; 0.62
	dry	24	2.82 ($\pm$ 0.39)		4.36 ($\pm$ 0.94)	
<i>C. rubrigularis</i>	wet	27	2.84 ($\pm$ 0.35)	-1.67; 0.10	4.08 ($\pm$ 0.59)	-1.46; 0.14
	dry	27	2.04 ($\pm$ 0.32)		4.04 ($\pm$ 1.36)	
<i>C. storri</i>	wet	21	2.79 ($\pm$ 0.39)	-0.09; 0.75	3.26 ($\pm$ 0.56)	-1.07; 0.28
	dry	27	2.73 ($\pm$ 0.38)		4.09 ($\pm$ 0.57)	

N = number of skinks measured, S.E. = standard error

The majority of arthropod prey consumed by *Carlia* was restricted to eight orders of insects, along with spiders (Aranea), isopods, centipedes (Chilopoda) and gastropods (Table 7.2). Psocopterans, dermapterans and collembolans were encountered in stomach samples on only one or two occasions, and were excluded from further analysis. Unidentifiable prey items were all arthropods. Vertebrates occurred only in *C. rostralis* stomach samples. In all three cases these vertebrate diet items were skinks, and consisted of only the tips of tails of *C. rubrigularis* (two) and *C. storri* (one). I found large amounts of sloughed skin in a few stomachs, consistent with other studies of skink diet (Bustard and Maderson 1965; Taylor 1986). In all cases it appeared that the lizard had eaten its own integument. Interpretation of the importance of various prey taxa to *Carlia* lizards varied depending on whether the abundance, volume or frequency of occurrence of prey type was considered. Numerically, termites (Isoptera) dominated the diet of *C. rostralis* and *C. rubrigularis*, and flies (Diptera) the diet of *C. storri* (Table 7.2). However, larger bodied invertebrates such as cockroaches (Blattaria), grasshoppers and crickets (Orthoptera), and lepidopteran larvae (caterpillars), were volumetrically important prey taxa (Table 7.2). For this reason, I found it useful to consider the relative importance of prey taxa from all measures: abundance, volume and

frequency of each prey type in the diet, and determine taxon importance based on IRI (Hart et al. 2002).

Spiders, particularly active hunters (such as salticids, lycosids, zodariids) and orthopterans were relatively important components of the diets of all three species (Table 7.2). The species differed in their consumption of certain taxa: cockroaches and adult beetles (Coleoptera) featured strongly in *C. rostralis* diet, isopods and lepidopteran larvae in *C. rubrigularis* diet, and flies in *C. storri* diet (Table 7.2). Termites comprised only a small volume of lizard stomach contents, and were considered a less important prey taxon by this method, but were eaten by at least 10% of *Carlia* from all species.

Mean volume of stomach contents was greatest for *C. rostralis* ($183.7 \text{ mm}^3 \pm 31.06$), followed by *C. rubrigularis* ($75.6 \text{ mm}^3 \pm 21.04$) and *C. storri* ($45.0 \text{ mm}^3 \pm 7.70$). Mean contents volume did not differ among species once body size effects were removed (ANCOVA; SVL: $F_{1, 125} = 0.01$, $P > 0.9$; interaction of species x SVL for stomach contents volume: $F_{2, 125} = 1.29$, $P > 0.3$).

Table 7.2. Relative abundance (% rel), relative volume (% vol), frequency of occurrence (% freq) and index of relative importance (IRI) of various prey types for *Carlia rostralis*, *C. rubrigularis* and *C. storri*, with dietary niche breadth (B).

Prey type		<i>C. rostralis</i>				<i>C. rubrigularis</i>				<i>C. storri</i>			
		% rel	% vol	% freq	IRI	% rel	% vol	% freq	IRI	% rel	% vol	% freq	IRI
Blattaria		10.38	29.47	38.00	515.04	4.76	13.14	18.50	136.08	3.45	6.90	16.67	62.26
Orthoptera		8.49	16.89	30.00	258.98	6.93	11.70	25.93	197.29	8.05	6.75	20.83	111.23
Coleoptera	adults	11.32	5.69	36.00	208.32	3.03	2.52	11.11	25.01	5.17	4.23	25.00	84.81
	larvae	0.47	0.20	2.00	0.45	2.60	2.71	9.26	19.96	1.15	2.90	4.17	6.09
Hymenoptera	ants	6.13	0.52	12.00	27.14	3.03	0.29	7.41	9.80	8.05	2.02	18.75	68.09
	others	4.72	2.07	16.00	36.93	3.03	4.15	11.11	32.51	8.62	3.26	20.83	89.33
Diptera	adults	2.36	1.56	10.00	13.32	6.06	9.45	18.50	117.28	13.79	5.84	27.08	191.86
	larvae	0.94	2.12	4.00	4.16	—	—	—	—	1.15	0.11	4.17	1.90
Lepidoptera	adults	2.83	2.36	10.00	17.65	3.46	6.40	14.82	59.76	4.02	10.54	12.50	65.72
	larvae	3.77	2.27	14.00	28.76	11.26	9.81	20.40	174.05	6.90	11.74	12.50	84.09
Hemiptera		5.66	3.34	18.00	55.13	4.76	4.92	18.52	72.84	4.60	4.40	14.58	47.38
Isoptera		21.70	0.68	10.00	76.13	21.21	1.65	12.96	118.04	3.45	0.60	10.42	15.24
Psocoptera		—	—	—	—	—	—	—	—	1.15	0.39	4.17	2.31
Dermaptera		—	—	—	—	0.43	0.06	1.85	0.37	—	—	—	—
Collembola		—	—	—	—	—	—	—	—	0.57	0.01	2.08	0.44
Aranea	web	2.83	0.40	10.00	10.98	5.63	2.32	14.82	47.39	8.05	3.50	20.83	86.79
	hunters	8.49	13.32	30.00	222.52	11.26	16.72	33.33	380.41	12.64	11.67	31.25	274.20
Chilopoda		1.42	6.04	6.00	15.21	0.43	0.72	1.85	0.87	—	—	—	—
Isopoda		5.66	5.60	18.00	68.92	12.12	12.22	27.78	274.63	6.90	3.83	6.25	24.20
Gastropoda		1.42	0.56	6.00	4.04	0.00	0.00	—	—	—	—	—	—
Unidentified arthropods		—	1.00	12.00	4.08	—	1.22	3.7	—	—	14.41	16.67	86.70
Vertebrates	Scincidae	1.42	1.35	6.00	5.64	—	0.00	—	—	—	—	—	—
Slough		—	4.58	6.00	9.36	—	0.00	—	—	2.30	6.89	8.33	27.64
Totals		n = 212	2499.9 mm³	n = 147		n = 231	989.4 mm³	n = 136		n = 174	833.3 mm³	n = 133	
B		9.83	6.71	13.69		9.45	8.87	12.65		12.33	11.69	15.37	

Trophic diversity was highest for *C. storri* for the relative abundance, volume and frequency of occurrence of prey types, because individual *C. storri* consistently consumed a high variety of prey types (Table 7.2). Despite differences among the species in the relative importance of some taxa consumed, overlap in diet between each pair of species was high ($O > 0.72$, Table 7.3). *C. storri* diet was most different from the other two species (dietary overlap was higher between *C. rostralis* and *C. rubrigularis* in both the wet and dry seasons). Dietary overlap between pairs of species was consistent across the seasons. Very high dietary overlap also existed between males and females within species ($O > 0.87$, Table 7.3) and within species between the wet and dry seasons ($O > 0.8$, Table 7.3).

Table 7.3. Overlap in diet composition by frequency of occurrence (Pianka's index) of the three *Carlia* species.

Niche overlap	<i>C. rostralis</i>	<i>C. rubrigularis</i>	<i>C. storri</i>
between male and female	0.87	0.88	0.87
between wet and dry season	0.94	0.93	0.80
between pairs of species – wet season	—— 0.81 ——	—— 0.75 ——	
	—— 0.76 ——		
between pairs of species – dry season	—— 0.82 ——	—— 0.72 ——	
	—— 0.76 ——		

Prey size

The mean length of prey consumed did not differ significantly between the wet and dry seasons for any species (Table 4; t-tests of prey length: *C. rostralis* [d.f. = 47]: $t = -0.29$; *C. rubrigularis* [d.f. = 44]: $t = -0.42$; *C. storri* [d.f. = 37]: $t = -0.37$; all $P > 0.6$), but did differ among the three *Carlia* species (Table 7.4; ANOVA of prey length: $F_{2,133} = 15.49$, $P < 0.001$). The mean body size of the three *Carlia* differed significantly (Table 7.4; ANOVA: $F_{2,138} = 151.93$, $P < 0.001$). Mean prey length consumed by each species coincided with skink body size; *C. rostralis* individuals ate the largest prey and *C. storri* the smallest (Table 7.4). A linear relationship of the form $L = -4.48 + 0.21 \text{ SVL}$, where L was the mean length of prey individuals in each stomach (mm) and SVL the snout-vent length of the lizard (mm), had a

slope significantly greater than 0 ($r = 0.41$, $P < 0.001$), confirming that larger lizards generally eat larger prey. Once body size effects were accounted for, there were no further differences in the size of prey consumed by the three species (ANCOVA with SVL as the covariate; SVL: $F_{1, 123} = 0.77$, $P > 0.3$; interaction of species x SVL for prey length: $F_{2, 123} = 2.23$, $P > 0.1$).

The length of the largest prey item eaten by each skink was positively correlated with all the measured head size variables (Table 7.4; SVL: $r_s = 0.41$; head length: $r_s = 0.38$; head width: $r_s = 0.32$; head depth: $r_s = 0.29$; all $P < 0.001$, one-tailed t-test). The range of prey lengths consumed included the smallest sizes of prey for all species; i.e., skinks that ate large prey did not exclude smaller prey from their diet (Table 7.4), so prey size overlap existed among species.

Table 7.4. Mean and range of prey length, and morphological characteristics ($\pm$ standard error) of the three *Carlia* species.

	<i>C. rostralis</i>	<i>C. rubrigularis</i>	<i>C. storri</i>
<i>N</i> (prey items measured)	163	159	133
Mean prey length (mm)	7.75 ($\pm$ 0.5)	5.20 ($\pm$ 0.3)	4.49 ($\pm$ 0.3)
Range of prey length (mm)	0.5 - 40.0	0.5 - 88.0	0.5 - 15.0
<i>N</i> (skinks measured)	46	45	39
Mean SVL (mm)	58.22 ($\pm$ 0.65)	46.53 ($\pm$ 0.48)	43.64 ($\pm$ 0.40)
Mean head length (mm)	12.37 ($\pm$ 0.17)	10.22 ($\pm$ 0.09)	9.54 ($\pm$ 0.10)
Mean head width (mm)	8.20 ($\pm$ 0.12)	6.67 ($\pm$ 0.09)	5.90 ($\pm$ 0.09)
Mean head depth (mm)	5.65 ($\pm$ 0.08)	4.56 ($\pm$ 0.08)	4.33 ($\pm$ 0.08)

Comparison of diet with available prey

I considered only the arthropod orders recorded in the stomachs of lizards as available prey. For instance, taxa such as thrips (Thysanoptera), mites (Acarina), millipedes (Diplopoda) and scorpions were frequently caught in traps but never found in lizard stomachs and I therefore excluded these taxa from available prey analyses. Even though dietary overlap between the seasons was high for all species (Table 7.3), the abundance of available

prey fluctuated seasonally (2083.0 arthropods trapped per day in the wet season, and 1529.7 arthropods trapped per day in the dry season). For this reason I compared *Carlia* diet with available prey in the wet and dry seasons separately.

Available prey were abundant in the wet season and the composition of the wet season trap samples was dominated by a relatively large proportion of Hymenoptera (ants) and flies compared to the dry season (Figure 7.1). However, there was a greater variety of prey types available to lizards in the dry season; there were relatively (relative to total numbers of prey items) more non-ant hymenopterans (bees and wasps), hemipterans (true bugs), spiders, beetles and lepidopterans trapped in the dry season compared to the wet (Figure 7.1). Compared to prey availability, lizard diet was generally consistent across seasons, and was independent of the availability of various prey types in the environment (Figure 7.1). The MDS plot showed little difference between samples from the wet and dry seasons, but skink diet samples were clearly dissimilar to the available prey samples in both seasons (Figure 7.2). The prey consumed by each species differed significantly from the prey available in the environment (PERMANOVA, Table 7.5). This difference was due at least partly to the high variability among the samples of available prey, compared with skink diet samples (PERMDISP: significant heterogeneity in dispersion from the group centroid among the samples; $F_{3,222} = 16.36$; $P = 0.001$). Skink diet and available prey did not differ between the wet and dry seasons, and the difference in skink diet and available prey did not change with the interaction of season (Table 7.5).

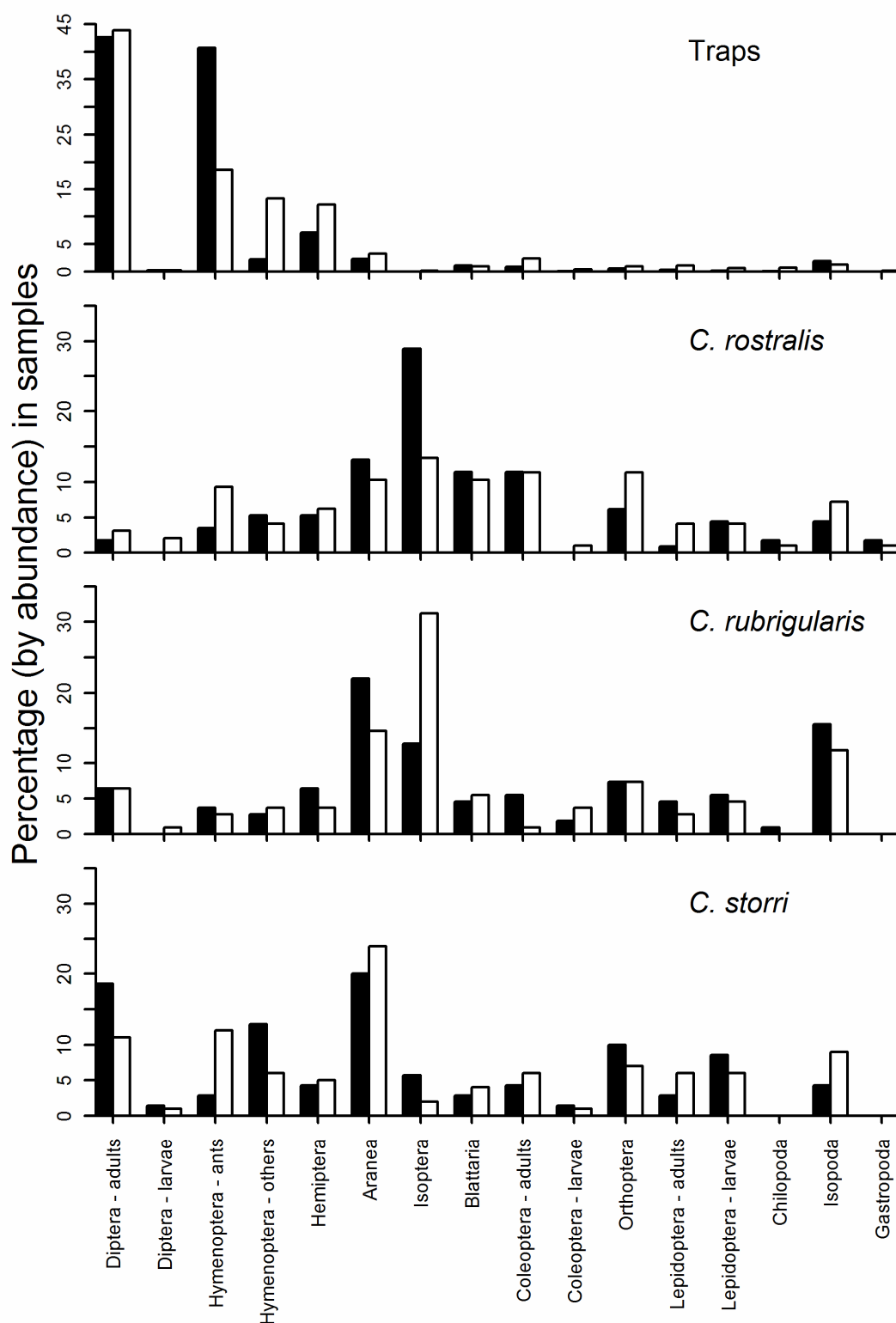


Figure 7.1. Relative abundance of prey types in the traps (available prey), and in the stomachs of *C. rostralis*, *C. rubrigularis* and *C. storri* in the wet season (filled bars) and dry season (open bars). Note the difference in y-axis scale for trap samples.

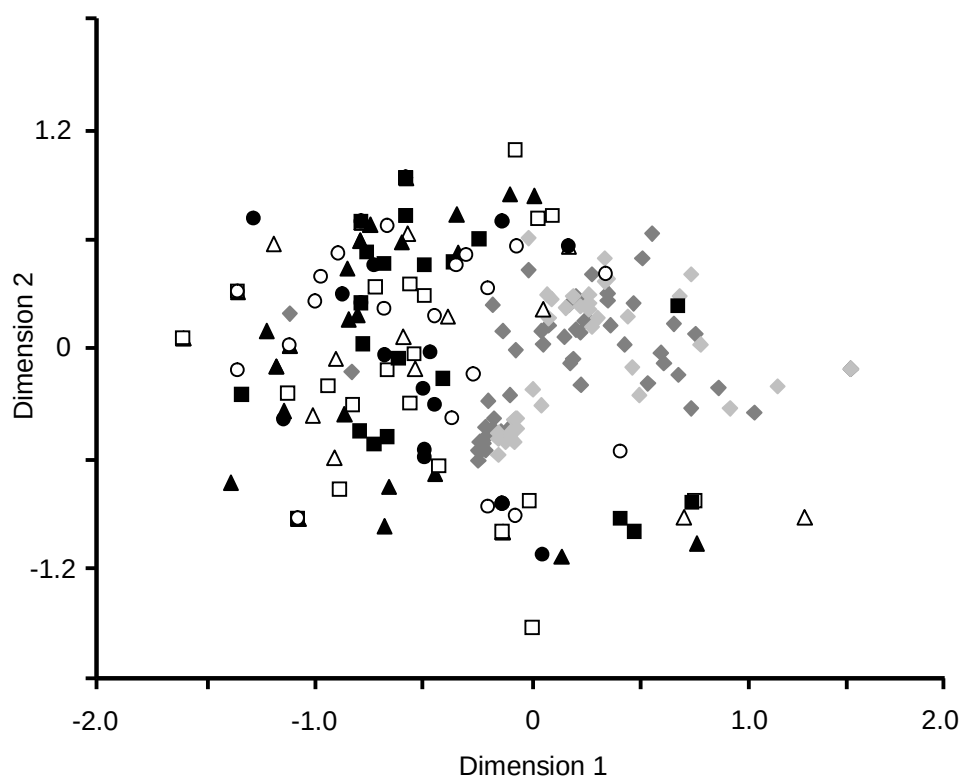


Figure 7.2. Multidimensional scaling plot of species' diet (*C. rostralis* [triangles], *C. rubrigularis* [squares], *C. storri* [circles] and trap (diamonds) samples based on Bray-Curtis similarities, for wet season (filled, or light grey symbols) and dry season (open, or dark grey symbols). Stress = 0.22. Stress is a measure of the degree of distortion of distances when forced to plot (in two dimensions, in this case). This value is considered high (Kruskal and Wish 1978), and is due to high dispersion in trap (available prey) samples.

Table 7.5. PERMANOVA results comparing sample type (trap samples [available prey], *C. rostralis* diet, *C. rubrigularis* diet and *C. storri* diet), season (wet and dry) and their interaction. Significant results are shown in bold font.

Factor	F value	d.f.	P value
Sample type	12.15	3	0.001
<i>C. rostralis</i> x available prey	23.11	1	0.001
<i>C. rubrigularis</i> x available prey	22.04	1	0.001
<i>C. storri</i> x available prey	17.31	1	0.001
Season	0.10	1	0.996
Season x sample type	1.17	3	0.269
<i>C. rostralis</i> x available prey x season	1.84	1	0.076
<i>C. rubrigularis</i> x available prey x season	1.34	1	0.22
<i>C. storri</i> x available prey x season	1.34	1	0.236

d.f. = degrees of freedom

Electivity scores for the various prey types in the wet and dry indicated that lizards were highly selective for most prey types (Table 7.6). Lizards did not consume ants or flies in proportions relative to their availability in the environment in either season (Table 7.6). Spiders, adult beetles and adult and larval lepidopterans were relatively less abundant in the environment, but were frequently consumed by lizards in the wet season (Figure 7.1), and therefore showed high electivity scores (Table 7.6). Isopods were relatively scarce in the environment, yet eaten by lizards in the dry season (Table 7.6). Cockroaches and orthopterans were important prey taxa that were relatively uncommon in the environment in both seasons. Non-ant hymenopterans formed a greater proportion of the available prey in the dry season (Figure 7.1), electivity scores were, therefore, higher in the wet season since consumption of non-ant hymenopterans by lizards was similar across seasons or greater in the wet season (*C. storri*). Hemipterans were the only prey type consumed by lizards in accordance with their availability, particularly in the wet season (Table 7.6). Despite the use of three trap types and many trap days to sample all available prey, termites and gastropods were very infrequently caught in traps (they constituted 0.17 and 0.14% of the available prey

trapped, respectively). Gastropods were only consumed by three *C. rostralis*, but termites were consumed by 11% (17 / 152) of *Carlia* in very large numbers.

Table 7.6. Electivities for prey types by the three *Carlia* species in the wet and dry seasons. Positive electivities (i.e., prey type is relatively more common in lizard diet than expected from availability in the environment) are in bold.

Species		<i>C. rostralis</i>		<i>C. rubrigularis</i>		<i>C. storri</i>	
Season		wet	dry	wet	dry	wet	dry
Blattaria		0.83	0.85	0.63	0.73	0.46	0.65
Orthoptera		0.85	0.86	0.87	0.79	0.90	0.78
Coleoptera	adults	0.87	0.68	0.74	-0.40	0.68	0.47
	larvae	—	0.49	0.91	0.82	0.89	0.48
Hymenoptera	ants	-0.83	-0.29	-0.83	-0.72	-0.86	-0.17
	others	0.43	-0.49	0.13	-0.54	0.71	-0.34
Diptera	adults	-0.92	-0.86	-0.73	-0.72	-0.38	-0.57
	larvae	—	0.84	—	0.67	0.77	0.70
Lepidoptera	adults	0.50	0.62	0.88	0.48	0.81	0.72
	larvae	0.95	0.76	0.96	0.78	0.97	0.83
Hemiptera		-0.12	-0.28	-0.02	-0.50	-0.23	-0.38
Isoptera		1.00	0.98	1.00	0.99	1.00	0.86
Aranea		0.71	0.55	0.82	0.66	0.80	0.78
Chilopoda		0.94	0.24	0.88	—	—	—
Isopoda		0.41	0.72	0.79	0.82	0.39	0.77
Gastropoda		0.99	0.80	—	—	—	—

Selectivity for sizes

Small prey (< 3 mm) were considerably more abundant in traps than larger prey (Table 7.7). *Carlia* lizards, however, consumed prey from the three size categories in almost equal proportions, so that they showed higher selectivity for larger prey (Table 7.7).

Considering the size available and the size consumed of some prey types (those taxa from which more than 10 individuals were measured from stomach contents and trap samples) showed that lizards generally consumed prey sizes relative to their body size rather than in relation to its availability (Figure 7.3). In general, *C. rostralis* consumed prey from the largest size category, *C. rubrigularis* from the mid- and large-size categories. Exceptions for these two species are the large proportion of small (< 3 mm) ants and flies, which are very rarely consumed. *C. storri* consumed most prey from the mid- and small-size categories, frequently consuming prey according to its availability.

Table 7.7. Relative abundance (% rel) of three different prey size classes in traps and in stomachs of *Carlia*, and electivity (E) by skinks.

Prey size		<i>C. rostralis</i>		<i>C. rubrigularis</i>		<i>C. storri</i>	
class	% rel in traps	% rel	E	% rel	E	% rel	E
< 3 mm	75.91	29.67	-0.44	38.03	-0.33	38.13	-0.33
3 - 6 mm	17.06	26.79	0.22	37.09	0.37	38.75	0.39
> 6 mm	7.03	43.54	0.72	24.88	0.56	23.13	0.53
Number of prey items measured	14709	209		213		160	

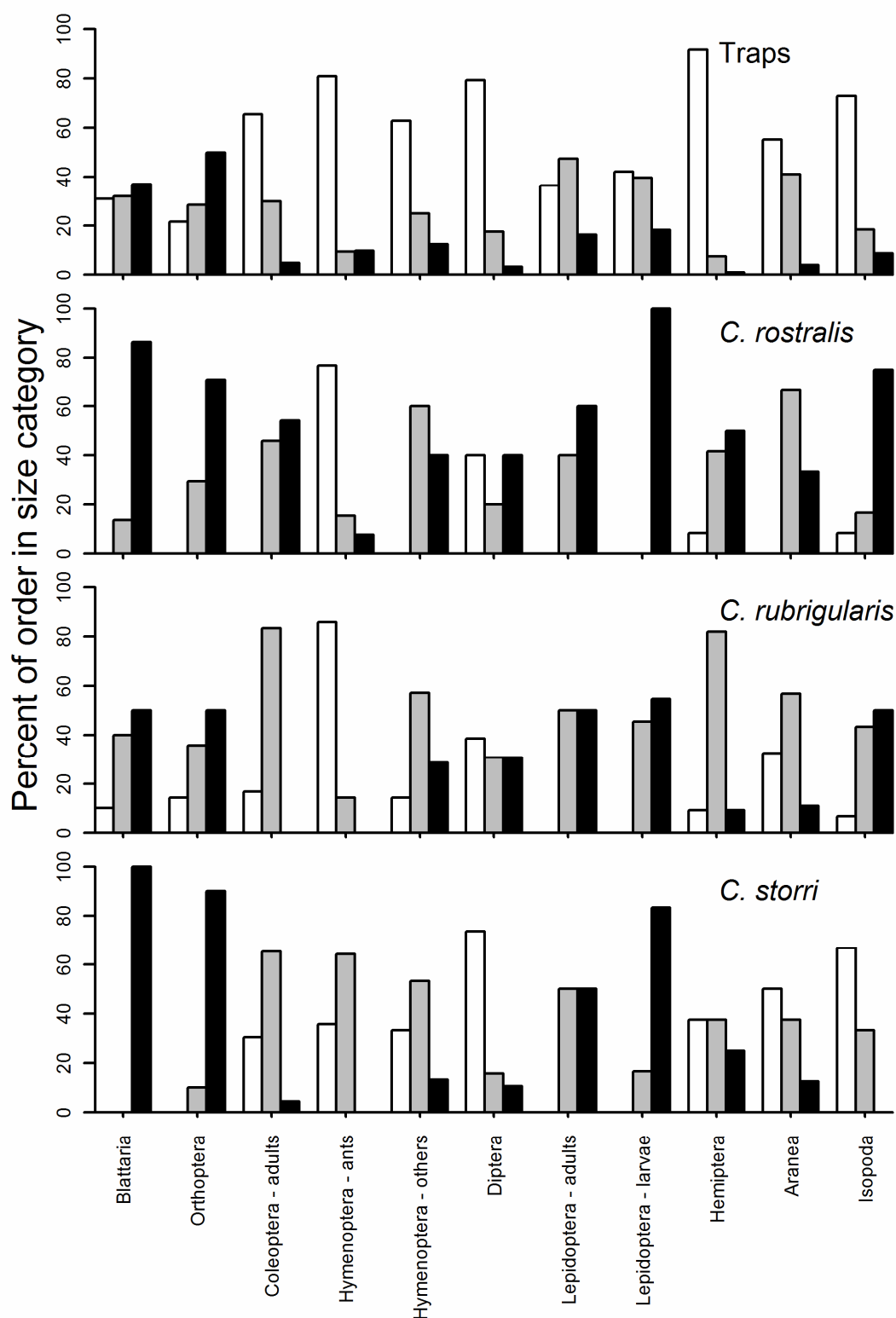


Figure 7.3. Relative abundance of three size categories of major prey types in the traps (available prey) and in the stomachs of *C. rostralis*, *C. rubrigularis* and *C. storri*. Prey size categories are <3 mm (open bars), 3 to 6 mm (grey bars) and >6 mm (filled bars).

Discussion

Skinks are often portrayed in the literature as generalist predators, taking available prey from the environment as it is encountered. However, my study clearly demonstrates that these skinks were selective, they consumed certain prey types and sizes that were in short supply in the environment. *Carlia* were entirely carnivorous and fed on a variety of arthropod prey. The species varied in the prey they consumed, but spiders and orthopterans (crickets and grasshoppers) were consistent prey types for all three *Carlia* examined. Diet was similarly diverse for all three species, and there was high overlap in dietary niche between males and females, and between pairs of species. High dietary overlap indicated that these species consumed an equally variable range of prey types, but the relative importance of each prey type in the diet differed among the three species.

Foraging mode

Small skinks are generally considered to be widely foraging, actively searching their habitat for sedentary or patchily distributed prey (Huey and Pianka 1981; Brown 1991). Some diurnally active prey types consumed by the three species suggest that *Carlia* may also employ ambush foraging techniques, and that small diet differences among the species may be explained by differences in foraging mode. Spiders identified from *Carlia* stomach contents were more often active hunters than web builders. Spiders such as lycosids and zodarids are nocturnal, as are crickets, and would be encountered by *Carlia* during active searches of the leaf litter during the day, when these prey are sedentary. But jumping spiders (salticids) and grasshoppers are also consumed by *Carlia*. These prey types are highly mobile, and more suited to less active foragers (Huey and Pianka 1981; Toft 1985; Anderson and Karasov 1988). Of the three species, the diet of *C. storri* was most different: it had the smallest overlap with other species and highest diversity. *Carlia storri* is small, agile, and cryptic compared to *C. rostralis* and *C. rubrigularis*, and although all three species are terrestrial (Chapter 3; Manicom et al. 2008), *C. storri* is the species most often seen climbing in grass and low vegetation (Chapter 3). *Carlia rostralis* frequently consume cockroaches and adult beetles, relatively sedentary prey types commonly encountered at ground level. Similarly, the diet of

C. rubrigularis includes a number of relatively sedentary isopods and lepidopteran larvae. *Carlia rostralis* and *C. rubrigularis* also consume large numbers of termites, patchily distributed, hidden prey that are available only to active searching predators (Huey and Pianka 1981; Vitt and Cooper 1986). *Carlia storri*, however, eat large numbers of dipterans and a relatively large number of non-ant hymenopterans (such as wasps and bees), active, mobile prey that would most likely be captured by ambush foraging, and it is possible that *C. storri* employs this foraging mode more regularly than the other two species. That all three species consume both active and sedentary prey supports the hypothesis that active and ambush foraging are not discreet modes of prey capture (Magnusson et al. 1985). It is likely that the foraging modes of *Carlia* species fall between the extremes of the 'active' and 'ambush' continuum, and observations of the foraging behaviour of these three species, in particular measuring numbers of movements over time, are required to confirm the mode of prey capture employed.

Prey size differences among the species

The high variety of prey types that *Carlia* exploit likely promotes the co-existence of these sympatric species, and the size of prey consumed further contributes to division of the trophic niche by these species. Considering the proportion of size categories of the major prey taxa in the stomachs of the three species shows that, for each prey type, the species generally focus their foraging efforts on different sizes of prey. The three species are distinctly different in body size, and larger lizards consumed larger prey (Table 7.4). This is consistent with other studies noting that the larger head dimensions of large-bodied lizards allow exploitation of large and hard-bodied prey not available to smaller individuals (Arnold 1983; Verwajen et al. 2002; Brecko et al. 2008). *Carlia rostralis*, the largest species, consumed considerably more hard-bodied prey (cockroaches and beetles) than smaller *C. rubrigularis* and *C. storri* and with some exceptions, *C. rostralis* consumed a large proportion of prey > 6 mm in length (see Figure 7.3). Only *C. rostralis* showed evidence of vertebrate predation, three stomachs contained a tip of the tail of another *Carlia* species. It is not unusual for skinks to eat other skinks (Brown 1991), in particular tails, which are readily autotomised by individuals in this family, but this evidence of intraguild attack suggests that in competition for

food and space, *C. rostralis* is likely the dominant species. Thus, while the three species had considerable similarity in diet, dietary niche breadth and overlap in the range of size of prey consumed, differences in lizard body size and foraging mode allowed some variation in the type and size of prey consumed. However, it is unlikely that competition for food is a central factor organising this community of sympatric lizards. Arthropod prey are seldom a limiting resource in a tropical system (Gaston 2000), and tropical insectivorous lizard species that feed on a variety of prey would not need to compete for abundant resources. Small dietary differences among the species may just as likely be a result, rather than a determinant, of small differences in behaviour or microhabitat used.

Prey selectivity by Carlia

The most interesting aspect of this study is the fact that these lizards, previously assumed to be non-selective, opportunistic predators, do not consume prey in the same relative abundances that they occurred in the traps. Assuming that the relative abundances of prey types in the traps reflects the relative abundance of prey available to lizards in the environment; my results show that *Carlia* diet is not simply determined by food availability and these lizards may be more discerning in their diet preferences than originally thought. If *Carlia* were generalist, opportunistic predators, their diet would consist largely of flies, ants and hemipterans, the most abundant prey types available at the study site (Figure 7.1). If they were generalist predators, the composition of *Carlia* diet would reflect seasonal availability of abundant prey types (Brown 1991). While *Carlia* eat a wide variety of arthropod prey, and could not be described as dietary specialists, the preferred prey of these lizards: spiders, orthopterans, isopods, beetles, cockroaches and termites, were relatively scarce in the environment. Additionally, the diet of *Carlia* remains relatively invariant across the seasons, despite the variation in the relative abundance of some prey taxa between the seasons. This suggests that *Carlia* actively select certain prey types and avoid others that are abundantly available. The exception is *C. storri*, for which flies are an important part of the diet. It could be argued that the arthropods abundant in the environment are unpalatable to lizards, or have defensive mechanisms, which cause them to be avoided as prey, but all three species do eat at least small quantities of flies, ants and hemipterans, and these taxa are frequently

important prey for other skinks (Taylor 1986; Lunney et al. 1989; James 1991c; Twigg et al. 1996; Wapstra and Swain 1996; Greenville and Dickman 2005). Broad-scale arthropod trapping at the study site ensured that the abundance of prey measured was a good representation of available prey for lizards. This is an improvement on other studies which include abundance of available prey, which only use one or two sampling methods (e.g., Stamps et al. 1981; Diaz and Carrascal 1990; James 1991c; Perez-Mellado et al. 1991; Griffiths and Christian 1996). However, some arthropods sampled in the environment were infrequently or never recorded in lizard stomachs and vice versa, suggesting that arthropod traps are potentially biased towards or against sampling certain invertebrate taxa. For instance, mites (Acari: Acariformes) were very abundant in the traps (*unpublished data*) but never recorded in *Carlia* stomachs, even though they have been reported in the diet of other Australian skinks (Brown 1991). And termites were recorded in lizard stomachs in very high numbers relatively frequently, but very rarely sampled in the environment. The termites recorded in *Carlia* stomach contents, arboreal *Nasutitermes* (Isoptera: Termitidae) and subterranean *Coptotermes* (Isoptera: Rhinotermitidae), are abundant and both nest types are a distinctive feature of the habitat at the study site. Termites are rarely surface-active during the day (James 1991c) and diurnally foraging lizards would need to actively break open *Nasutitermes* sp. galleries, or dig into *Coptotermes* sp. tunnels in order to gain access to this prey source. The fact that 11% of *Carlia* individuals had consumed termites before they were captured, in both the wet and dry seasons, suggests that lizards actively seek out termite nests as a prey source, at least sometimes.

Further evidence for selectivity in diet is shown in the size of prey consumed by lizards. Small prey (< 3 mm in length) were the most abundant in the environment, and prey abundance decreased with increasing size (Table 7.7; and see Schoener and Janzen 1968). The size of arthropods is a rough, but reliable, estimate of their energy content (Schoener 1971; Stamps et al. 1981), so that energy intake should be highest for larger prey. Scarce, large prey items, however, require more time to locate, capture, subdue and swallow than smaller prey (Pough and Andrews 1985), so that there is a trade-off between energy value and ease of consumption. Prey size is an important factor guiding prey choice in *Carlia*, particularly for *C. rostralis* and *C. rubrigularis*; lizards consume larger size classes from taxa

that have smaller individuals (Figure 7.3). However prey size does not appear to be a predictor of diet preference, *Carlia* select large prey but they do not consume only large-bodied taxa. *Carlia storri* generally consume prey from the smallest, most abundant size category (< 3 mm), and are therefore the least selective of the three species examined. *Carlia* ensure consistent energy intake by either the high abundance, or the high energetic value, of their prey.

In conclusion, *Carlia* generally focused their foraging efforts on prey types and prey sizes that were not abundant in the environment and were more selective in their foraging and diet than previously assumed. Studies of the growth, development and survival of insectivores fed experimentally on certain prey types have determined that arthropod prey items are not nutritionally equivalent and different prey types, even within an order of prey, can have markedly different effects on the development of predators of arthropods (Vogel et al. 1986; Toft and Wise 1999). Thus, small lizards may select certain prey based on its nutritional value, rather than its availability or size (Stamps et al. 1981; Perez-Mellado et al. 1991). Consumption of scarce prey by *Carlia* suggests that they may select for certain nutrients in their diets.

Consequences of selectivity

An important consequence of the relatively selective diet of *Carlia* is the potential for cascading effects through the food web. The arthropod prey types consumed by insectivorous lizards are herbivores, omnivores, detritivores, or predators themselves, and their removal from the food web by predatory lizards can have large impacts on ecosystem functioning (Spiller and Schoener 1990). Spiders dominate the diet of *Carlia*, and spiders are also predators of arthropods (Foelix 1996). The effect of spiders on the rest of the arthropod community has the potential to be considerably larger than that of lizards for three reasons: (1) spiders occur in larger numbers than lizards at the study site (*unpublished data*); (2) spiders employ a wide range of prey-capture techniques and have access to a variety of arboreal and aerial habitats (Uetz 1992) that are relatively inaccessible to terrestrial *Carlia* lizards; and (3) unlike small lizards, spiders are not gape-limited and have the potential to

consume a relatively greater size range of prey types due to the use of webs and venom in prey capture (Enders 1975). By selectively consuming spiders, and not opportunistically consuming all available prey, *Carlia* may indirectly have far-reaching effects on the composition of the arthropod community, and, so, my results build on other recent evidence for the importance of selective foraging in ecosystems (Beckerman et al. 2006).

Chapter 8

The relative importance of density- and trait-mediated predator effects in a terrestrial system: varanid effect on skink abundance and behaviour

Abstract

Prey can be affected by predators in two ways: directly, by being removed from the population by consumption (a density-mediated interaction), or indirectly, by a costly response to the threat of predation (a non-consumptive, or trait-mediated interaction). Few studies have been conducted in natural systems where direct and indirect effects of predators may co-occur and interact; my study examined the direct and indirect effects of top predator (varanid lizard) removal on a mesopredator (skink) population. Varanids had little direct effect, but a considerable trait-mediated effect on the skink population. The removal of varanids from study plots had no significant effect on the abundance of skinks, and survival rate of skinks was equivalent regardless of varanid access. However, the probability of recapturing individual skinks was greater where varanids were excluded and skinks were significantly more active in study plots where varanids were excluded, compared to where varanids had access. Skinks therefore avoided direct predation by varanids by altering their behaviour. This behavioural change did not, however, lead to an increase in growth rate, body size or body condition, or to a reduction in parasite load, for individuals free from the threat of predation. The benefit of increased activity for skinks in the absence of top predators did not translate to a fitness advantage for the characters I measured, but increased activity may allow more opportunity for fitness-related behaviours, such as territorial defence or reproductive behaviours, such as courtship and mating. The lack of a measurable effect may have occurred because skinks in varanid access plots, with low energy needs due to inactivity and abundant available resources due to low demand, benefit from high energy income during the limited time available for foraging. This high energy income may compensate for the fitness costs of fear, so that skinks in varanid access areas may be able to maintain their fitness and condition at

similar levels to that of conspecifics living in predator-free areas. Varanids have the potential to alter the dynamics of the whole ecosystem by initiating a trait change in skinks, and consideration of both direct and indirect effects are, therefore, important in examining predator influence on prey populations.

Introduction

Anti-predator behaviour, such as increased vigilance (Elgar 1989), reduced movement (Sih and McCarthy 2002) and the use of refuge sites (Sih 1997), reduces consumption of individuals by predators (Van Buskirk and McCollum 2000; Manicom et al. 2008), but comes at a cost. There is a trade-off for prey between avoiding predators and gaining resources (Lima and Dill 1990; Lima 1998b; Anholt et al. 2000; Brown and Kotler 2004). For instance, prey individuals that avoid consumption by predators by reducing their activity may have reduced energy income and a greater risk of starvation (Preisser and Bolnick 2008b). These costs can lead to reduced survival, growth and body condition of prey and so can influence prey population dynamics (Hodges et al. 1999; Krebs et al. 2001). Prey are thus potentially affected by predators in two ways: directly, by being removed from the population by consumption (a density-mediated interaction), or indirectly, by a costly response to the threat of predation (a non-consumptive, or trait-mediated interaction; Preisser et al. 2005).

The non-consumptive effects of predation can be just as important to prey population dynamics as consumption (Bolker et al. 2003; Werner and Peacor 2003; Nelson et al. 2004; Schmitz et al. 2004; Preisser et al. 2005; Creel and Christianson 2008; Preisser and Bolnick 2008a). Yet, these indirect effects of predation are largely ignored in ecology, or assumed to be positively correlated with the direct rate of predation, and therefore not measured (Creel and Christianson 2008). There is also no consensus on the mechanism of trait-mediated interactions, especially in terrestrial vertebrate ecosystems (Verdolin 2006; Cresswell 2008) because the direct effects of predators on prey density may arise simultaneously through various means. Ecological studies typically only examine how changes in prey densities, rather than their traits, affect prey population dynamics. Few studies have been conducted in natural systems where direct and indirect effects of predators may co-occur and interact. With the exception of a few terrestrial studies by Schmitz and colleagues (Beckerman et al. 1997; Schmitz et al. 1997; Schmitz 1998; Schmitz and Suttle 2001; Krivan and Schmitz 2004; Nelson et al. 2004) most studies that consider both density-mediated and trait-mediated predation effects have been conducted in low-diversity, aquatic systems.

My study examined the direct and indirect effects of predator exclusion on a prey population, by excluding predatory varanid lizards and measuring the density- and trait-mediated effects of a predator-free environment on resident skinks. Varanids forage opportunistically using both visual and auditory cues, they consume skinks when encountered, and thus have the potential to reduce skink density (Shine 1986a; *pers. obs.*). At the study site, more than 10% of varanid diet samples (from faecal analysis) contained skink remains (Lloyd 2007; Lloyd et al. *unpublished data*). When skinks detect potential danger, they cease activity and become motionless or move to safer microhabitats, hidden from predator view (Downes 2001; *pers. obs.*). Varanids, therefore, also have the potential to influence skink behaviour.

Skinks that reduce conspicuous activity to avoid varanids are likely to suffer from reduced food intake, either because their time available for foraging is limited, or because they are forced to move to less profitable habitat to avoid predation (Sih 1987; Lima and Dill 1990). Further, skinks that hide in retreats or move to safer habitats may do so at the expense of efficient thermoregulation (Martin and Lopez 1999b). For reptiles, particularly small-bodied skinks with low thermal inertia, careful behavioural thermoregulation is necessary to maintain optimal body temperature, which, in turn, is essential to effective physiological functioning (Bauwens et al. 1996; Appendix C). Food digestion, sprint speed and foraging efficiency rely on lizards maintaining favourable body temperatures (Avery 1982; Huey 1982). Anti-predator behaviour can thus have important energetic costs: there is evidence from both field and laboratory studies that a lizard's growth rate and body condition are limited by reduced food intake and reduced thermoregulatory opportunities (Andrews 1982; reviewed in Adolph and Porter 1993; Martin and Lopez 1999a). Reduced growth rate and poor body condition may have further fitness consequences; loss of body condition reduces immune response to infection (Møller et al. 1998) and can decrease the ability of skinks to defend against parasites.

Alternatively, predator-induced reduction in prey density or activity may have the opposite effect on prey, increasing growth and improving body condition (Van Buskirk and Yurewicz 1998; Peacor 2002; Abrams 2003). Reduction in either prey density or prey foraging activity should cause an increase in available resources (Buckley and Jetz 2007), so that

increased predation threat may actually improve conditions for surviving prey. Additionally, decreased foraging rates under the threat of predation may reduce the ability of prey to overexploit resources. Reduced foraging by intimidated prey can lead to an increase in prey growth rate and condition (Peacor 2002), since prey have more resources available to them at times when they can safely search for food. For instance, if varanids reduced the density of the skink population, they may release surviving skinks from competition for resources, and thereby enhance individual growth rate and body condition, and reduce parasite loads.

These benefits of predator-induced changes in prey density or behaviour may serve to improve the fitness of intimidated prey, but it is also possible, if they occur, that they only provide intimidated prey with the ability to maintain their fitness at similar levels to that of predator-free conspecifics. The costs (intimidation) and benefits (release from competition) of predation to surviving prey may thus balance so that there is little evidence of predator effect on prey.

Successfully avoiding predation by varanids may have important fitness and life history costs or benefits for skinks, but it is not clear from past studies whether skink fitness would suffer, benefit, or remain uninfluenced by the altered behaviour induced by the presence of varanids. By manipulating the access of varanids to study plots, I could measure the effect of predators on skinks. I measured the direct effect of varanids on skink density and survival, the indirect effect of varanids on skink traits (activity, or foraging behaviour), and the consequences of these effects on skink fitness: skink growth rate, body condition and parasite load. The relative importance of the direct and trait-mediated effects of predation, and the mechanism by which these effects alter the prey community have very rarely been shown in natural, terrestrial vertebrate systems (Schmitz and Suttle 2001; Nelson et al. 2004). Here I show that skinks avoid direct predation by varanids by altering their behaviour, but that this behavioural change does not translate to increased survival, growth rates or reduced parasite loads. However, skink behavioural change does allow more time for other activities, which may provide a fitness benefit not measured in my study.

Methods

This section of my study considers the effect of top predator removal on skink density, behaviour and fitness, and therefore I used only the study plots allowing skink access in this chapter (see Chapter 2, Table 2.1). The treatments used to test hypotheses for this section of the study were therefore: varanid exclusion (tall, fenced study plots), varanid access (low, fenced study plots) and control plots (unfenced study plots, which control for fence effects). Skinks in study plots were captured, measured, marked and released at the point of capture (as described in Chapter 2).

Skink population density estimates

I used the Jolly-Seber (JS) method (Jolly 1965; Seber 1965) to estimate adult skink density in each study plot, using the POPAN formulation in Program MARK v5.1 (Arnason and Schwarz 1995; White and Burnham 1999). The method for estimating skink population size is described in detail in Chapter 3. Briefly, density was estimated from recaptures of marked skinks, captured at approximately four-month intervals (12 occasions) between August 2003 and May 2007. The following parameters were estimated from POPAN models: ϕ (apparent survival), p (recapture probability), $PENT$ (probability of entry into the population at each occasion) and N (size of super-population, i.e., the total number of individuals present within the population during the entire study period). A set of candidate models were tested for each study plot, incorporating (1) time variation (sampling occasion, time) or (2) time invariance ($\bullet$) for survival and recapture estimates. To test the validity of the assumptions of the JS model, I tested the goodness-of-fit of the most parameterised model (the fully time-dependent model: ϕ [time] p [time] $PENT$ [time] N [$\bullet$]) using the program RELEASE in MARK (Pollock et al. 1990). There was no indication of a significant deviation from assumptions for skinks in any study plot (χ^2 tests from RELEASE test3, all $P > 0.4$). I used the corrected Akaike Information Criterion adjusted for overdispersion ($QAIC_c$) as an objective means of model selection. Models with $\Delta QAIC_c \leq 2$ were given the greatest support (Burnham and Anderson 2002). The Akaike weight of each model is also used as a measure of the relative likelihood of the best model compared with the other candidate models. Once I had identified

the best POPAN model for each study plot, I estimated the population size (n) of skinks in each study plot at each sampling occasion. I then analysed differences in skink density among varanid access, varanid exclusion and control plots using repeated measures analysis of variance (ANOVA) with sampling occasion as the repeated measure.

Skink survival and recapture probability

The Cormack-Jolly-Seber (CJS) method (Cormack 1989) in Program MARK v5.1 was used to estimate survival and recapture rates of recaptured adult skinks in each study plot. Details of this method are described in Chapter 3. Briefly, I tested a set of four candidate models for each study plot that incorporated time variation (time) or time invariance ($\bullet$) for survival and recapture estimates. I tested the assumption of the CJS model (every marked animal in the population at a certain time has the same probability of recapture and survival) for each study plot using the goodness-of-fit bootstrap procedure in MARK (1000 iterations). This method simulated data using the parameter estimates under the most general model (ϕ [time] p [time]) and computed the deviance for this model based on each simulated data set. There was no indication of lack of fit of the general model for skinks in any study plot (from bootstrap goodness-of-fit, all $P > 0.1$). ΔQAIC_c values and Akaike weights were calculated as for POPAN models. The time invariant model, where survival rate and capture probability are constant over the whole capture period (ϕ [$\bullet$] p [$\bullet$]) was considered plausible for describing survival and encounter rates of skinks in all study plots (model ϕ [$\bullet$] p [$\bullet$] had $\Delta\text{QAIC}_c < 2$ for all study plots). I used the estimates of survival and recapture probability derived from this model for each study plot to compare survival and catchability of skinks among the treatments, using Kruskal-Wallis tests. I used t-tests to determine differences in recapture probability between fenced and unfenced plots, and then between varanid access and exclusion plots.

Skink activity

Skinks active in study plots were counted during activity observation surveys, conducted on six occasions between August 2005 and May 2007 (see Chapter 2). I analysed differences in the mean number of active skinks among varanid access, varanid exclusion

and control study plots using multivariate approach to repeated measures ANOVA, with sampling occasion as the repeated measure, to determine the effect of treatment on skink activity.

Skink growth rate, body size, body condition and parasite load

Growth rates of the three most abundant species at the study site (*Carlia rostralis*, *C. rubrigularis* and *C. storri*) were described in detail in Chapter 4. Briefly, I estimated growth rates ($\text{mm}\cdot\text{day}^{-1}$) of marked lizards based on the difference in body length (snout to vent length, SVL) between captures, divided by the number of days between captures. I considered only skinks caught first as juveniles, so that comparisons among individuals were made at a similar stage of their growth curves (Chapter 4). Overall growth rate did not differ significantly among the species (Chapter 4); all three species experience the same growth pattern of rapid juvenile growth that slows with increasing body size. I analysed the effect of top predators on skink growth with analysis of covariance (ANCOVA) to test the effect of treatment, and the interaction species x treatment, on the growth rate ($\text{mm}\cdot\text{day}^{-1}$) of individual skinks, corrected for mid-point SVL (mm).

The body length (SVL) of adult skinks of the three most abundant species at the study site differed between sexes (for *C. rostralis* and *C. storri*) and among the species (Chapter 4). The mean body size of the largest one-third of adult skinks was determined for each sex and species in each study plot, and the effect of treatment on sex differences in log-transformed body size compared with ANOVA, for each species separately. Treatment differences in adult body size of each species were compared using Kruskal-Wallis tests.

Body condition (body mass adjusted for length) may be used as an indicator of previous food intake rate, amount of stored energy and general health (Jakob et al. 1996). Residuals describing body condition, calculated from reduced major axis regression of the relationship between body mass and SVL (both log-transformed, Green 2001), were calculated for each sex and species in each study plot and compared among sexes, species and treatments with ANOVA. Only the measurements taken at the first capture of each individual lizard were used, and gravid females were excluded from body condition analyses.

Certain skinks at the study site were susceptible to infestation by trombiculid mites that attached in the axillae and ears, and prevalence of mite infestation varied among the species (Chapters 5 and 6). Considering only the first capture of those individual skinks infested with mites, I calculated mean mite load (log-transformed) for each species in each study plot and compared mite load among treatments with ANOVA.

Statistical analysis

Except where otherwise mentioned, I used the package SPSS v16.0 (SPSS Inc., Chicago, IL, USA, 2007) for all statistical analyses, with significance level set at $P = 0.05$. Only measurements of body mass, size and ectoparasite load taken from resident skinks (i.e., skinks caught on two or more sampling occasions in a study plot) were used, and only for a single capture (except for growth rate, where measurements from the first and last capture were used). For ANCOVA I first tested for significant interaction terms before proceeding to test for main effects (Quinn and Keough 2002). If there was no significant interaction between factors, I eliminated the interaction terms from the model and used only main effects. For reduced major axis (RMA) regression I used RMA for Java v1.21 (Bohonak and van der Linde 2004). Body mass and body length measurements were log-transformed before regression.

Results

Skink density

The model best describing population size of skinks varied among the study plots; models allowing survival and capture probabilities to vary over sampling periods were most plausible in three study plots, models assuming constant survival rate and capture probability over the whole sampling period were likely in two study plots, and either survival or capture probability varied with sampling period in the remaining eight study plots (Table 8.1). From the best fitting model for each study plot ($\Delta\text{QAIC}_c = 0$; Table 8.1), I derived an estimate of skink population size for each study plot (skink density per 200 m²) at each sampling occasion. There was confounding at the start and the end of the sampling period in the fully time-

dependent model (ϕ [time] p [time] $PENT$ [time] N [•]) because the model, of necessity, makes assumptions about the relative catchability of animals on the first and last sampling occasions (Schwarz and Arnason 1996). To avoid spurious density estimates in some study plots, I excluded from further analysis the skink population size estimate from the first (August – September 2003) and last (April – May 2007) sampling occasion for all study plots. Estimates of skink population size in each study plot were similar among varanid treatments (Table 8.2). The abundance of skinks at the study site fluctuated with time, but with no consistent seasonal trend (Figure 8.1; Wilk's $\lambda = 0.09$, $F_{9,2} = 2.29$, $P = 0.341$). The presence of varanids had no significant effect on the density of skinks in the study plots (Figure 8.1; ANOVA MS = 293.35, $F_{2,10} = 2.32$, $P = 0.149$).

Table 8.1. Best fitting POPAN models ($\Delta\text{QAIC}_c = 0$) for each study plot, estimating survival (ϕ) and recapture (p) probability, probability of entry into the population ($PENT$) and total population size (N). These parameters vary with time or are constant over time ($\bullet$), depending on the model. The Akaike weight (QAIC_c weight) of each model is used as a measure of the relative likelihood of the best model compared with the other candidate models.

Study plot	Treatment	Best model ($\Delta\text{QAIC}_c = 0$)	QAIC_c weight
2	Varanid exclusion	ϕ (time) p ($\bullet$) $PENT$ (time) N ($\bullet$)	0.999
7		ϕ (time) p (time) $PENT$ (time) N ($\bullet$)	0.916
10		ϕ ($\bullet$) p ($\bullet$) $PENT$ (time) N ($\bullet$)	0.989
14		ϕ (time) p (time) $PENT$ (time) N ($\bullet$)	0.998
6	Varanid access	ϕ (time) p ($\bullet$) $PENT$ (time) N ($\bullet$)	0.961
8		ϕ ($\bullet$) p (time) $PENT$ (time) N ($\bullet$)	0.856
11		ϕ (time) p (time) $PENT$ (time) N ($\bullet$)	0.932
15		ϕ (time) p ($\bullet$) $PENT$ (time) N ($\bullet$)	0.99
17	Control plot	ϕ ($\bullet$) p ($\bullet$) $PENT$ (time) N ($\bullet$)	0.997
18	(varanid access)	ϕ ($\bullet$) p (time) $PENT$ (time) N ($\bullet$)	0.527
19		ϕ ($\bullet$) p (time) $PENT$ (time) N ($\bullet$)	0.982
20		ϕ (time) p ($\bullet$) $PENT$ (time) N ($\bullet$)	0.852
21		ϕ (time) p ($\bullet$) $PENT$ (time) N ($\bullet$)	0.945

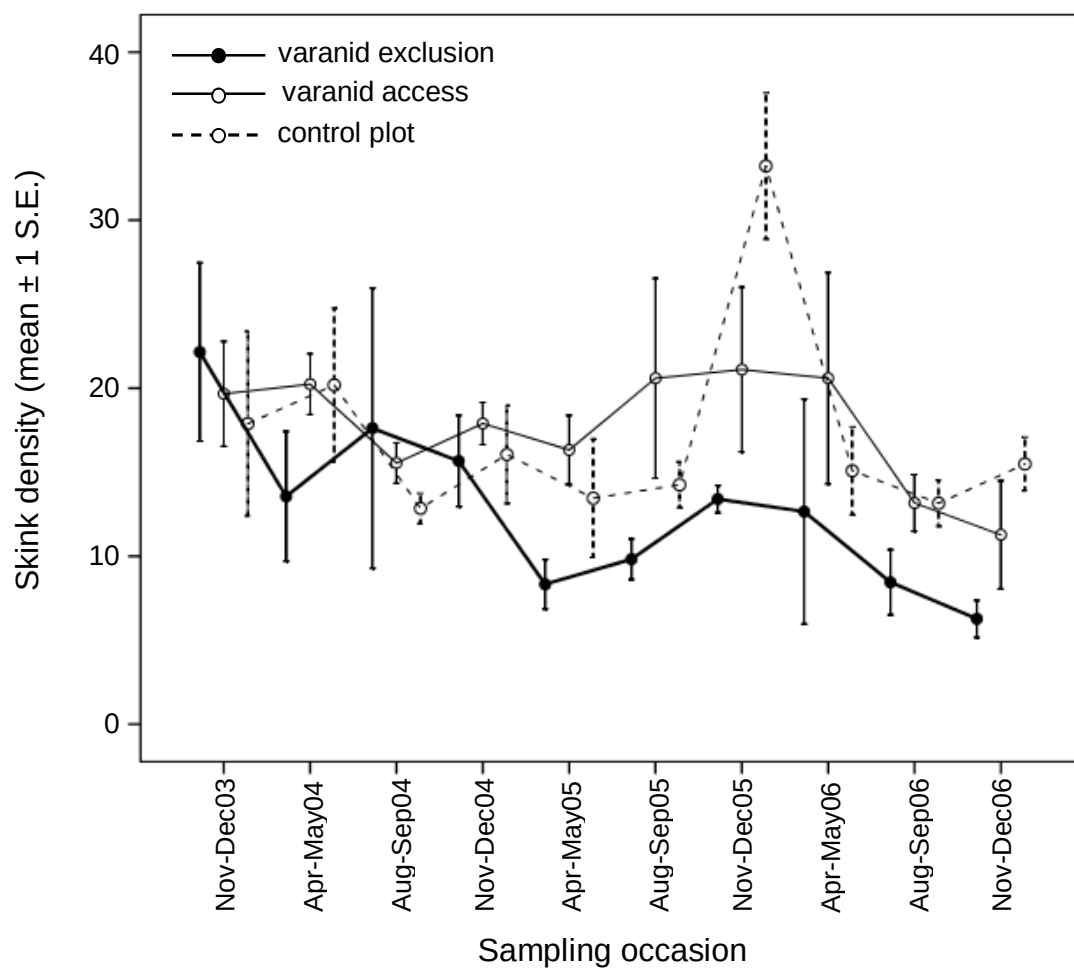


Figure 8.1. Mean density estimates ($\pm$ standard error) from POPAN models of skinks in the three treatments at each sampling occasion

Table 8.2. Estimate of adult population size, from mean population per study plot under best-fitting POPAN model from Program MARK.

Treatment (n plots)	Mean <i>n</i>	Variance	S.E.
Varanid exclusion plots (4)	15.23	35.95	2.99
Fenced varanid access plots (4)	15.49	19.46	2.21
Unfenced control plots (5)	16.98	4.61	0.96

n = population size estimate per study plot, S.E. = standard error.

Survival and recapture rates

Survival rates of skinks were consistently high in varanid exclusion plots and control plots (Figure 8.2), and were highly variable in fenced varanid access plots. Survival rate of skinks did not differ significantly among the treatments (Kruskal-Wallis $\chi^2 = 1.02$, d.f. = 2, $P = 0.601$; Figure 8.2).

Skinks in varanid exclusion plots had a higher probability of recapture than skinks in plots with access to varanids (Figure 8.2). Mean recapture rate did not differ significantly between fenced varanid access plots and unfenced control plots (two-tailed t-test: $t = 0.52$, d.f. = 7, $P = 0.62$). These two treatments were therefore combined to test the hypothesis that recapture rate of skinks was higher in varanid exclusion plots than varanid access plots, as was indeed the case (one-tailed t-test: $t = -2.09$, d.f. = 11, $P = 0.044$).

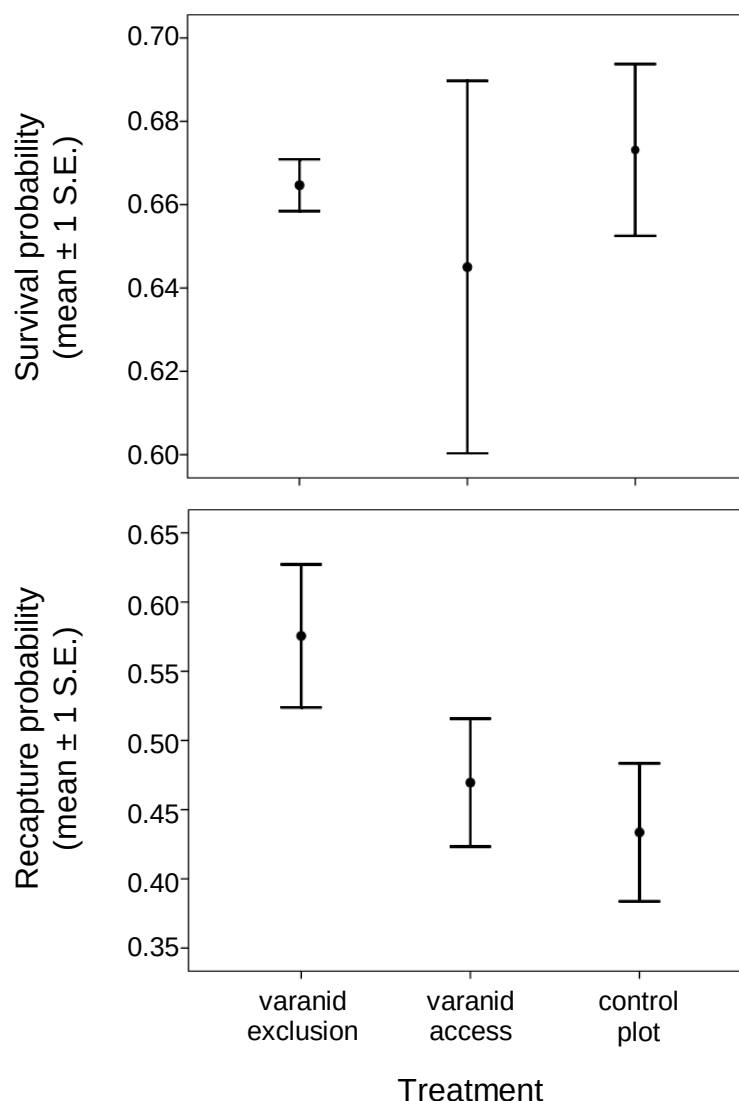


Figure 8.2. Survival (top) and recapture (bottom) probability ($\pm$ standard error) of skinks in the three treatments.

Skink activity

I adjusted the number of active skinks seen in each study plot by the number of surveys conducted per sampling occasion, and the density of skinks in the study plot at each sampling occasion. Since the last estimate of skink density from POPAN is likely to be inaccurate (see above), I could not adjust the number of active skinks by skink density for this occasion and the measure of activity for this sampling occasion was thus excluded from further analysis. Skink activity was, therefore, compared for five sampling occasions only. The number of skinks active in study plots differed among sampling occasions (Wilk's $\lambda = 0.15$,

$F_{4,7} = 9.77$, $P = 0.005$; Figure 8.3), but there was no clear seasonal trend in activity. There were consistently more active skinks observed in varanid exclusion plots (Figure 8.3) than in varanid access or control plots ($MS = 0.09$, $F_{2,10} = 8.19$, $P = 0.008$).

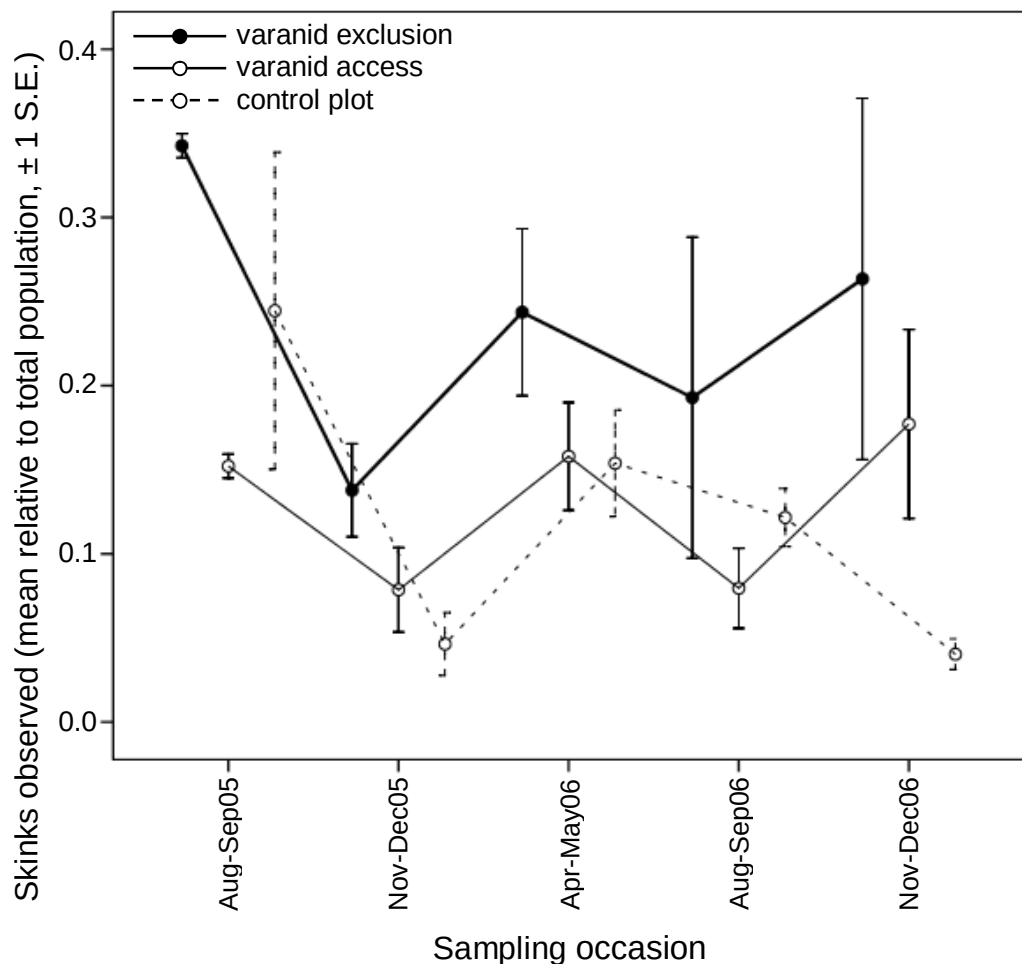


Figure 8.3. Active skinks (number of skinks observed during activity surveys relative to total population in study plots, $\pm$ standard error) in the three treatments at each sampling occasion.

Juvenile growth rate, adult body size and body condition, and ectoparasite load

There was no consistent effect of varanids on juvenile growth rate in the three species (Figure 8.4), mean growth rate of juvenile skinks was higher (*C. rubrigularis*), lower (*C. rostralis*) or similar (*C. storri*) when varanids were excluded from plots, compared to when varanids were allowed access. There was no significant difference in rate of growth of juveniles of the three species in response to the presence of varanids, at any body size

(ANCOVA species x treatment x mid-point SVL: $F_{4,142} = 0.158$, $P = 0.959$), and removal of the interaction term revealed no significant effect of treatment alone (ANCOVA treatment: $F_{2,142} = 0.385$, $P = 0.681$).

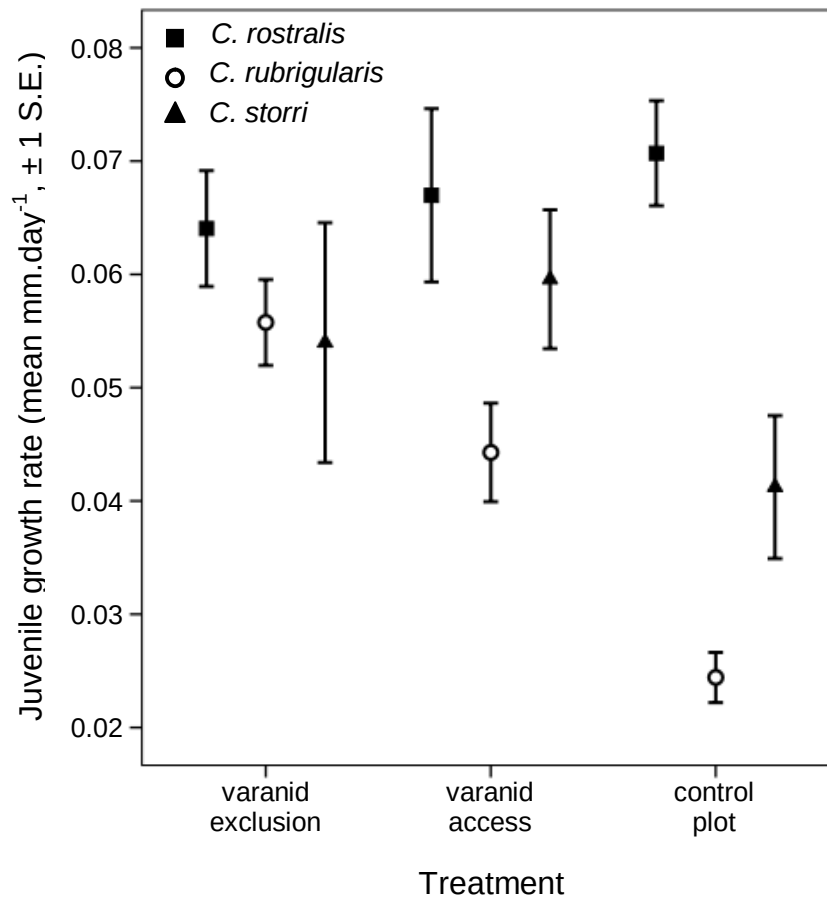


Figure 8.4. Juvenile growth rate (growth in body length [mm] per day, $\pm$ standard error) of the three *Carlia* species, in the three treatments.

The body size of male and female adult skinks did not differ significantly among the treatments, for any of the species (ANOVA sex x treatment: *C. rostralis*; $F_{2,25} = 0.21$, $P = 0.812$; *C. rubrigularis*; $F_{2,24} = 0.39$, $P = 0.681$; *C. storri*; $F_{2,24} = 0.19$, $P = 0.825$, Figure 8.5). The presence of varanids had no significant effect on the body size of adult lizards of any species (Kruskal-Wallis tests of difference among treatments: *C. rostralis*; $\chi^2 = 3.38$, d.f. = 2, $P =$

0.184; *C. rubrigularis*; $\chi^2 = 3.33$, d.f. = 2, $P = 0.189$; *C. storri*; $\chi^2 = 0.34$, d.f. = 2, $P = 0.845$,

Figure 8.5).

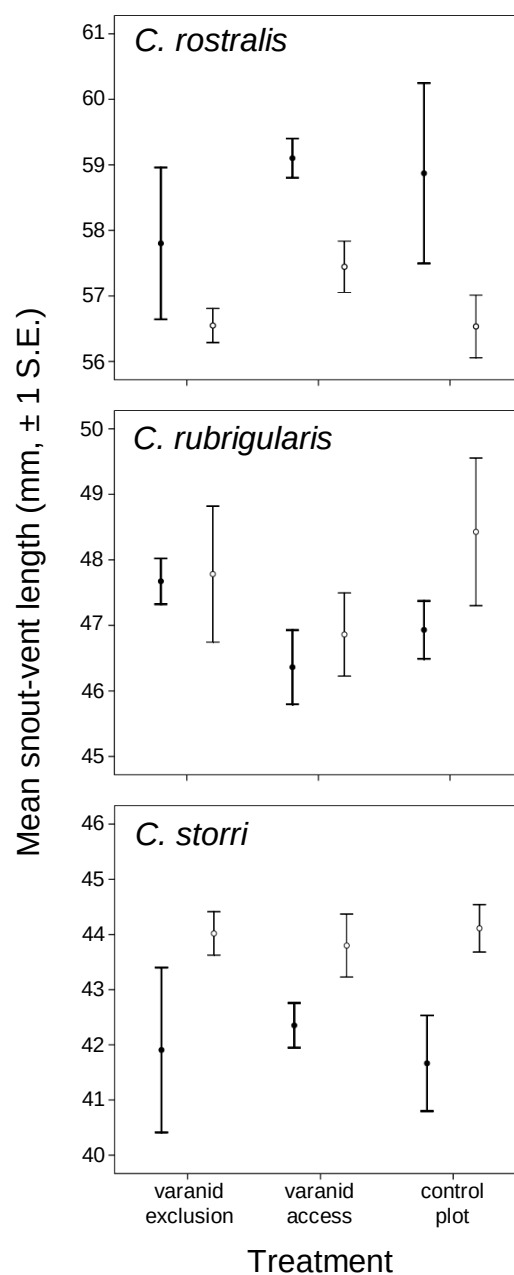


Figure 8.5. Adult body size (snout-vent length [mm], $\pm$ standard error) of males (solid symbol) and females (open symbol) of the three *Carlia* species in the three treatments.

Body condition of males and females of all three species did not vary significantly among the three varanid treatments (ANOVA sex $\times$ species $\times$ treatment: $F_{4,65} = 0.323$, $P = 0.861$, Figure 8.6), and the presence of varanids did not affect the body condition of the three

species significantly (ANOVA species x treatment: $F_{2,33} = 0.55$, $P = 0.702$). Removal of the interaction terms revealed no significant effect of treatment alone (ANOVA treatment: $F_{2,33} = 0.24$, $P = 0.789$).

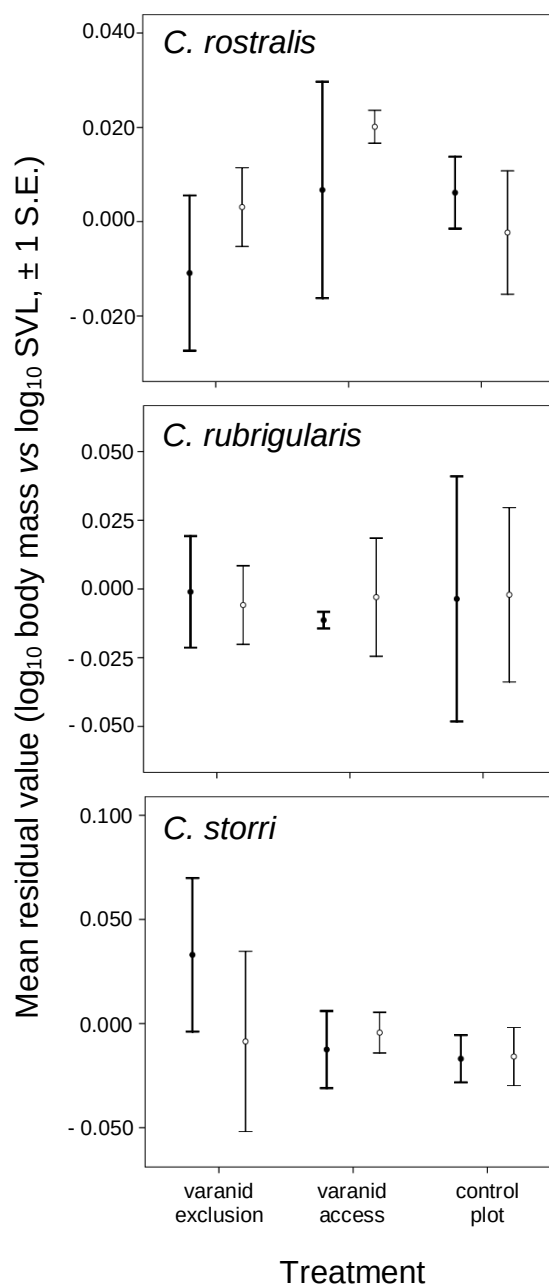


Figure 8.6. Mean residual body condition value (from reduced major axis regression of log₁₀ body mass against log₁₀ snout-vent length) for males (solid symbol) and females (open symbol) of each *Carlia* species in the three treatments. Positive mean residual values mean that most of the values for that group of individuals were above the general regression line, showing that most individuals had a higher than average body condition in that treatment.

The effect of varanid treatment on the ectoparasite load of skinks did not differ significantly among the species (ANOVA species $\times$ treatment: $F_{4,27} = 0.24$, $P = 0.914$). Of the infested skinks, mite loads were both greater and more variable on skinks living in varanid exclusion plots, and mite loads were consistently lower on *C. storri* individuals in all treatments (Figure 8.7). Removal of the interaction term from the analysis of variance revealed significant differences among treatments, i.e., skinks in varanid exclusion plots had more mites ($F_{2,27} = 3.81$, $P = 0.037$), and among species, i.e., *C. storri* had fewer mites than the other two species ($F_{2,27} = 6.38$, $P = 0.006$).

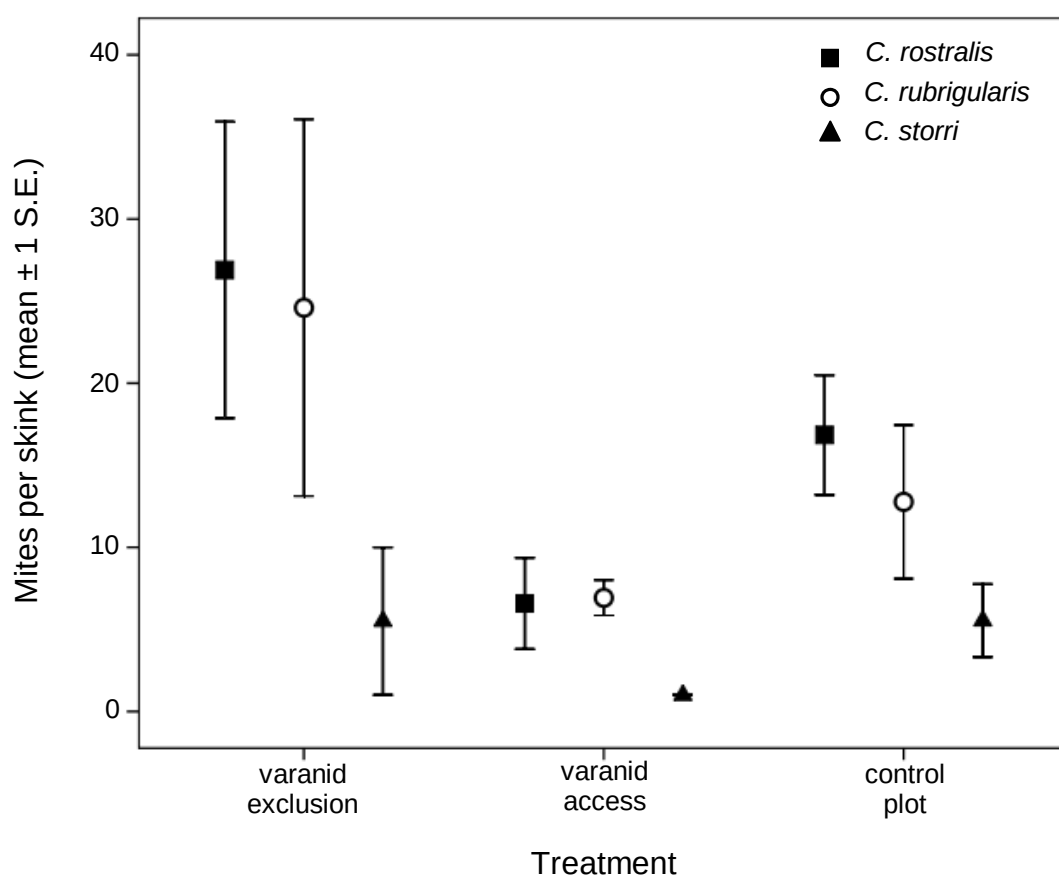


Figure 8.7. Mean mites per skink ($\pm$ standard error) of skinks with mites, for the three *Carlia* species in the three treatments.

Discussion

The effect of top predators on lower-order predators was assessed by preventing access of predatory varanids to areas where small skinks were resident. The removal of varanids from study plots had no significant effect on the abundance of skinks. Survival rate of skinks was equivalent regardless of varanid access, but the probability of recapturing individual skinks was greater where varanids were excluded. Also, skinks were significantly more active in study plots where varanids were excluded, compared to where varanids had access. This increase in activity did not, however, lead to an increase in growth rate or body condition, or to a reduction in parasite load, for individuals free from the threat of predation. Indeed, parasite load was higher in skinks in varanid exclusion plots. In other words, the benefit of increased activity for skinks in the absence of top predators did not translate to a measurable fitness advantage, at least for fitness characters assessed here.

Predators are frequently prey to higher levels of the food chain, and the same behaviour that makes an animal an efficient predator can also make it more vulnerable to predation (Lima and Dill 1990). For a *Carlia* skink, to be an efficient predator and to meet energy demands requires constant, active searching of the leaf litter for arthropod prey (Chapter 3; Chapter 7), and behavioural thermoregulation (Kearney et al. 2009; Appendix C). Active skinks are conspicuous, and therefore highly vulnerable, to hunting predators (Greene 1988). To avoid consumption by predators, skinks become motionless, or flee to a retreat (*pers. obs.*; Downes 2001). Predator avoidance therefore reduces activity, foraging, and thermoregulation time for skinks.

The study plots allowed freedom of access to small skinks. Skinks could move into and out of the study plots, from or into similar habitat available outside of plots, or into or out of another study plot that offered more or less protection from predators. Skinks living in varanid access plots were not only frequently exposed to the presence of foraging varanids, but also to the scent of varanids that had moved through the area. Therefore, both immediate, visual stimuli, as well as residual, non-visual stimuli contributed to perceived predation threat for skinks in this experiment (Lloyd et al. 2009).

I found that the presence of varanids had no significant effect on skink density in study plots, when compared with varanid removal plots (Figure 8.1). The study plots each supported a population of approximately 16 skinks, regardless of whether varanids had access to the area or not. This apparent lack of predator effect could occur because the large skink population living outside the study plots acted as a source, so that as skinks within varanid access plots were consumed, the vacant niches were filled by immigrating individuals and skink density remained constant (Stamps 1991; Le Galliard et al. 2005b). However, estimates of skink survival probability were not lower in varanid access plots (Figure 8.2), indicating that the same marked individuals were recaptured over time. Survival probability of skinks did not differ significantly among treatments, and, therefore, it is unlikely that predatory varanids significantly impacted skink population dynamics by direct consumption. Survival rate is a function of both an individual's survival probability and the probability that, conditional on surviving, the surviving individual is detected (i.e., the individual's recapture probability, Pollock et al. 1990). Estimates of recapture probability were significantly higher in varanid exclusion plots compared with plots where varanids had access (Figure 8.2). Assuming that skinks moved into and out of the study plots to meet their daily foraging and thermoregulatory needs, the high recapture rates of skinks in varanid exclusion plots suggested that skinks used these predator-free areas frequently and exhibited high site fidelity, so that skinks were more likely to be active and available for capture within varanid exclusion plots, compared to neighbouring varanid access plots. This was confirmed by observations of skink activity in the study plots. Skink activity surveys were intended to be unobtrusive to skinks, and to record only the number of active skinks in study plots. These surveys differed from skink capture-recapture sessions, in that inactive skinks were not disturbed from retreats. During skink surveys, there were significantly more active skinks observed in plots excluding varanids, than in plots to which varanids had access (Figure 8.3).

Since varanids had no significant effect on skink density or survival, fewer skinks were active in varanid access plots not because their numbers were reduced by consumption, but because the threat of predation caused them reduce their activity. Lizards alter their activity and basking rates and shift their microhabitat use when faced with increased predation risk (reviewed in Greene 1988; Martin and Lopez 1999a; Downes 2001). In areas to

which predatory varanids had access, skinks reduced conspicuous behaviour and either moved to safer areas, or remained inactive within retreats. The lack of effect of predators on the survival and density of skinks also suggests that skink anti-predator behaviour was highly effective at preventing capture and consumption of skinks by varanids. Thus, the strong effect of varanids on skink activity was likely due to predator cues alone. To my knowledge, no other study has provided an experimental demonstration of the success of anti-predator behaviour.

Due to the trade-off between effectively avoiding predation and gaining resources (see Introduction), anti-predator behaviour often occurs at a cost to prey fitness. Because inactivity in the presence of predators reduces foraging and thermoregulatory opportunities for skinks (Downes 2001), skinks in varanid access plots may experience reduced energy intake and altered physiological functioning (Skelly 1992; Martin et al. 2003; Cooper and Perez-Mellado 2004). Skinks may, therefore, exhibit reduced growth rates, poor body condition and high parasite load in areas to which varanids have access. Skinks resident in plots that excluded varanids should, therefore, have experienced a fitness advantage, i.e., they could forage, bask and interact with conspecifics with no threat of predation. In this study, however, skinks in varanid exclusion plots did not appear to benefit from predator-free activity. Juvenile growth rate (Figure 8.4), and adult body size (Figure 8.5) and body condition (Figure 8.6) of skinks living in varanid exclusion plots did not differ significantly from those of the less active skinks living in predator access areas. In an ectotherm, freedom from predation allows more activity, but more activity may mean higher body temperature and therefore higher cost of body maintenance (Spotila and Standora 1985). Thus, the advantage of increased activity may have been balanced, in my treatments, by the increased cost of activity, causing no obvious fitness benefit in terms of growth or body condition. It is conceivable that benefits of increased activity included increased opportunities to mate, defend territories, and reproduce (i.e., produce eggs), but these benefits were difficult to measure in my experiments.

The behavioural requirements for effective thermoregulation by tropical skinks may differ from those of temperate reptiles (Appendix C). Studies that document the thermoregulatory cost of inactivity, such as hiding in a retreat, generally study reptiles from temperate regions (Martin and Lopez 1999b; Downes 2001; Polo et al. 2005), which need to bask to attain optimal body temperatures. Tropical reptiles frequently need to actively avoid

high temperatures (Kearney et al. 2009; Appendix C), so that escaping to a cool retreat site may not be a thermal disadvantage to tropical skinks. For tropical *Carlia*, the temperature of retreat sites frequently reach, and remain within, preferred temperatures (Andersson et al. 2010) so that skinks can continue to thermoregulate while hidden in a retreat (Huey et al. 1989). However, although inactive tropical skinks may not face the same thermoregulatory costs of predator avoidance suffered by temperate reptiles, they do still experience a reduction in foraging and social behaviour opportunities when they have reduced activity.

Skinks need abundant or high-quality resources to maintain an energy budget for high activity (Spotila and Standora 1985). Active skinks living in predator-free areas, with more time available to forage, have the potential to overexploit their resources to maintain the high energy levels needed for foraging, thermoregulation and interacting with conspecifics. By consuming a large quantity of arthropod prey and limiting the available resources, skinks that are free from the threat of predation may only maintain fitness, rather than improving growth rate and body condition in the absence of predators.

Further to this, skinks living in varanid access plots may adopt behaviour that compensates for the fitness disadvantages of reduced activity, such as taking greater risks when foraging (e.g., Amo et al. 2007), or becoming more efficient at capturing and consuming prey. The combined effect of reduced foraging in the presence of predators by the whole prey community could cause an increase in available resources (Peacor 2002). Furthermore, prey that spend the majority of their time inactive may have low energy requirements (Johansson and Andersson 2009). Skinks in varanid access plots, with low energy needs due to inactivity, may benefit from high energy income in the limited time available for foraging, resulting from efficient capture of abundant arthropod prey. This high energy income may compensate for the fitness costs of fear, so that skinks in varanid access areas are able to maintain growth and body condition at similar levels to that of conspecifics living in predator-free areas.

Ectoparasite loads of skinks, however, were not similar among the predator treatments (Figure 8.7). Skinks with mites living in varanid exclusion plots had greater mite loads than those living in varanid access plots (Figure 8.7). Mite loads on *Carlia* skinks may be indicative of their residence time in areas, rather than poor condition (Bull and Burzacott

1993; and see Chapter 5). Ectoparasite loads on lizards are associated with frequent use of the same sites (Kerr and Bull 2006) and lizards suffer high parasite loads as a cost of living in favourable, good quality habitat (Main and Bull 2000). Greater ectoparasite loads may be a cost of living in a predator-free area for *Carlia*.

In this chapter I demonstrated that skinks showed no significant density reduction in response to predators, but instead reduced their activity in the presence of varanids. Reduction of prey abundance occurs gradually over time, and the effect of predators on the density of prey is transmitted only in proportion to the individuals removed and not the entire prey population (Peacor and Werner 2001). In contrast, the nonconsumptive effects of predation can be very large. An activity reduction due to the presence of a predator is immediate, and it affects the whole prey population rather than only those individuals consumed (Peacor and Werner 2001). The cumulative effect of the predator over the lifetime of the prey can thus be highly significant. I have shown here that skinks effectively avoid direct predation by varanids by adjusting their behaviour, and that alteration in activity does not necessarily affect skink fitness in a measurable way. The arthropods eaten by *Carlia* skinks include herbivores, detritivores, and predators (Chapter 7). In this system, removal of top predators allows a behavioural release of mesopredators so that although neither the abundance nor fitness of skinks was altered by predation, varanids have the potential to change whole ecosystem dynamics by initiating this trait modification in their prey. Skinks may transmit the indirect effects of varanids to lower trophic levels when they shift their foraging and space use patterns in response to danger, so that the effect of the mere presence of top predators has the potential to cascade through the system (Beckerman et al. 1997; Schmitz et al. 1997).

Chapter 9

Direct and indirect effects of predators in a multi-level trophic web

Abstract

The dynamics of species within trophic webs are often closely linked to the dynamics of other species higher or lower on the trophic order, so that alterations to species abundance at one level of the food web has the potential to impact both directly and indirectly on interacting species. Predators consume prey, reducing prey density, and indirectly affect resource levels (a density-mediated indirect effect), or predators alter the behaviour of prey without reducing prey density, but similarly affect resource levels (a trait-mediated indirect effect). Due to their versatility and high predation rates, intermediate-level predators (mesopredators) may have disproportionably larger effects on lower trophic levels than top predators, and yet there is little evidence of the relative importance of density- and trait-mediated effects of predation in complex terrestrial trophic systems. My study consisted of a manipulative field experiment where the effects of top predators and mesopredators were both simultaneously and individually isolated. Varanids (top predators) and skinks (mesopredators) were allowed access or excluded from areas and the effect on spiders, other arthropods and primary producers determined. I found that skinks directly reduced the abundance of cursorial spiders, and the abundance of web-building spiders within the foraging range of skinks. Skinks directly altered the composition of the arthropod community by selectively consuming certain taxa from areas to which they had access, and thus indirectly reduced damage to primary producers in those areas. Skinks also increased aerial arthropod abundance via their reduction of spiders. Varanids indirectly changed the composition of the arthropod community by influencing skink behaviour; in the absence of varanids only those arthropod taxa rarely consumed by skinks were abundant. Here I show that top predator-induced changes in mesopredator activity, rather than mesopredator mortality due to predation, flowed through the system to alter the community composition of

lower trophic levels. This study demonstrates a trait-mediated indirect effect of experimental top predator removal in a complex terrestrial system.

Introduction

There is a need to develop predictive theory for the dynamics of food webs; understanding the mechanism by which species interact in food webs is important to develop knowledge of how natural ecosystems will respond to disturbances that affect species abundance (Yodzis 1996; Sinclair et al. 2000). The dynamics of species within trophic webs are often closely linked to the dynamics of other species higher or lower on the trophic order, so that alterations to species abundance at one level of the food web has the potential to impact both directly and indirectly on interacting species (Wootton 1994; Abrams 1995). Classical views of trophic cascades focus on the importance of lethal predator effects on prey populations, and the transmission of indirect effects (density-mediated indirect interactions), for example, the indirect, mutual relationship between predators and resources caused by direct consumption of prey by predators (Schoener 1993; Menge 1995). However, trophic cascades can also occur without changes in the density of interacting species, because of non-lethal predator effects on prey traits (trait-mediated indirect interactions; Abrams et al. 1996). For example, the risk of predation can change prey behaviour, such as foraging, so prey demand on resources is reduced and a trophic cascade occurs (Kerfoot and Sih 1987; Abrams 1995; Schmitz et al. 2000; Peacor and Werner 2001; Werner and Peacor 2003).

In the ecology of predator-prey interactions, very little is known about the interaction of lethal and non-lethal predator effects (Lima 1998a; Cresswell 2008). Most food web studies have focussed on the consequences of predator control of herbivore populations, and the associated trophic cascades (Hairston et al. 1960; reviewed in Pace et al. 1999). But top predators may also affect smaller predators (mesopredators) so that removal of top predators can lead to outbreaks of mesopredators (called 'mesopredator release', Crooks and Soulé 1999), resulting in increased predation on smaller prey. Top predators are usually relatively large-bodied, with a large foraging range and low density, and therefore low predation rate. Mesopredators are comparatively small-bodied, versatile predators and have the capacity to reach high densities, and can exert heavy predation pressure on prey communities (Johnson 2006; Ritchie and Johnson 2009). Mesopredators may, thus, have disproportionately large effects on lower trophic levels compared to top predators (Crooks and Soulé 1999; Ritchie and Johnson 2009). Top predators can control mesopredators either by killing and consuming

them, or by changing their behaviour (Preisser et al. 2005; Ritchie and Johnson 2009) and these effects can flow on to lower trophic levels as density- or trait-mediated indirect effects, respectively.

Although evidence suggests that both density- and trait-mediated indirect effects may be important causes of trophic cascades (Turner and Mittelbach 1990; Huang and Sih 1991; Abrams et al. 1996; Schmitz 1998; Bernot and Turner 2001; Trussel et al. 2006), measurements of the relative importance of each type of indirect predator effect are rare, particularly when taking mesopredator effects into account. Although the existence of prey behavioural responses to predators is well established, especially in aquatic systems, there is still little evidence of their importance, and cascading effects, in terrestrial food web dynamics (reviewed by Schmitz et al. 2000). Trophic cascades are often apparent in simple systems, however, terrestrial food webs frequently consist of multiple species that are highly interconnected (i.e., predators often feed on more than one trophic level), and this complexity makes trophic cascades appear weak in terrestrial systems (Halaj and Wise 2001; Shurin et al. 2002). Terrestrial studies that consider the effect of both density- and trait-mediated predation effects are, thus, often carried out on a small spatial scale, such as in small enclosures, or on a single plant (Lima 1998b; and see Schmitz 1998; Dyer and Letourneau 1999; Kunert and Weisser 2003), or are correlative rather than experimental (Berger et al. 2001; Ripple and Beschta 2006, 2007). These studies show that trait-mediated effects can occur in trophic cascades, but there is a need for manipulative field studies in complex systems, examining a wider range of taxa, to determine if these cascading effects occur in natural systems, and to determine how important they are, particularly in terrestrial systems.

The effect of the removal of top predators on mesopredator feeding ecology and the cascading effects to lower trophic levels has rarely been studied in manipulative field experiments (Peacor and Werner 2001; but see Hawlena and Perez-Mellado 2009). This is not surprising given the difficulty in manipulating top predator access while allowing natural movement by prey. My study consisted of a manipulative field experiment where the effects of top predators and mesopredators were both simultaneously and individually isolated. Varanids (top predators) and skinks (mesopredators) were allowed access or excluded from areas and the effect on spiders (lower-order mesopredators), other arthropods and primary

producers determined. One of the challenges in quantifying a behaviourally-mediated trophic cascade is separating predator effects on prey abundance from predator effects on prey behaviour. In my study, top predators did not significantly alter the abundance of their prey, but did affect prey behaviour; the presence of predatory varanids caused skinks to reduce activity (Chapter 8). In the current chapter, I examined how lethal and non-lethal predator effects influenced trophic interactions in a multi-level food chain, and I report on evidence that a trophic cascade in a terrestrial food chain can be driven by behaviour-mediated mesopredator population responses to predation. I discovered that top predator-induced changes in mesopredator activity, rather than mesopredator mortality due to predation, flowed through the system to alter the community composition of lower trophic levels.

Study system

Varanids are generalist predators that consume reptiles, including skinks (Shine 1986a; Weavers 1989). Skinks present at my study site were dominated by three species of *Carlia* (Chapter 3). In Chapter 8, I demonstrated that varanids did not reduce skink density, but did alter skink behaviour; skinks had reduced activity in study plots where varanids had access, relative to study plots where varanids were excluded.

Skinks at the study site forage at ground level, or on logs and in low vegetation within 20 cm of the ground (Chapter 3). Spiders constitute a large proportion of skink diet, as do cockroaches (Blattaria), grasshoppers and crickets (Orthoptera), butterfly and moth adults and larvae (Lepidoptera) and isopods (Chapter 7). Spiders at the study site can be broadly categorised into two functional groups: exposed, and sheltered. Skinks have a strong effect on web-building spiders that are exposed in their webs when at rest, but little effect on spiders that construct a shelter into which to retreat (Manicom et al. 2008; see Appendix B).

Methods

Experimental design and manipulated species

The experiment consisted of 16 fenced study plots designed to manipulate access to varanids and skinks, and five unfenced plots, which controlled for fence effects. Detail of the construction and design of the study plots was given in Chapter 2. Briefly, fenced study plots were surrounded by either tall (1.2 m) or short (30 cm) fences to exclude or allow access to varanids, respectively. These plots either had holes cut through the fence at ground level to allow access to small skinks, or were sealed to prevent access and exclude small skinks. The experiment thus used a 2 x 2 factorial design with the following four treatments: (1) both varanids and skinks removed and excluded ($N = 4$), (2) varanids excluded, skinks allowed access ($N = 4$), (3) skinks excluded, varanids allowed access ($N = 4$), and (4) both varanids and skinks allowed access (present at natural densities, $N = 4$). Open plots (unfenced control plots, $N = 5$) were compared with treatment 4 (both varanids and skinks allowed access) to test for the effect of fences.

Skinks were captured in the study plots by active searching and hand capture, or traps, on 15 occasions between May 2003 and May 2007 (Chapter 2). Skinks that were captured or trapped in skink access plots were released at their point of capture, but skinks in skink exclusion plots were released in similar habitat outside of the study plots. Study plots were revisited multiple times on each sampling occasion, and at different times of day, so that within each sampling occasion almost every skink resident at the study site was captured and skink exclusion plots were emptied of newly immigrated skinks.

Arthropod abundance and proportion of herbivory

Spiders at the study site were separated into two functional groups: web-building and cursorial (non-web building) species. Web-building spiders were further classified as exposed or sheltered, depending on their exposure to predators when at rest in the web (Chapter 2; Appendix B). Spiders in study plots were counted, and their height above ground measured, on six sampling occasions over two years, according to methods detailed in Chapter 2.

Arthropods were sampled in the study plots with pitfall traps and yellow pan traps, designed to capture ground-dwelling and aerial arthropods respectively (see details in Chapter 2). Arthropods were sampled on six occasions over two years, and were identified to class (order for insects) using a dissecting microscope.

At the end of the study (May 2007) I obtained a static measure of damage to leaves by herbivorous arthropods by collecting one terminal leaf from each shrub or tree in each study plot and measuring missing leaf area (see details in Chapter 2). The mean number of leaves sampled per study plot was 62.2 (SD = 64.1). I differentiated among different vegetation species and types of damage (Chapter 2). To reduce error due to differing herbivory on different leaf types, only leaves from *Terminalia* sp. shrubs and trees (74.4 % of all leaves sampled) were used. These leaves were considered the best representative of vegetation at the study site, but unfortunately were not available in all study plots (17 out of 21). Only holes (entirely missing areas) in leaves were considered in this study, holes accounted for 94.8 % of all damage to leaves.

Habitat

Treatment differences in habitat could confound measures of skink and arthropod abundance. I measured type and amount of vegetative cover, light penetrating the canopy, leaf litter depth and ground temperature above and under the leaf litter in each study plot (see Chapter 2) and used these variables to test for habitat differences among the treatments.

Analyses

The effectiveness of skink exclusion by the study plots was determined by comparing the mean number of new adult skink individuals caught in each treatment on each sampling occasion using analysis of variance (ANOVA) with sampling occasion ($N = 15$) as a repeated measure.

The effect of study plot fences on arthropod abundance was determined by comparing the numbers of arthropods in varanid and skink access plots (fenced control plots, $N = 4$) with numbers in open plots (unfenced control plots, $N = 5$). Control plots were

compared using ANOVA. If numbers did not differ significantly between fenced and unfenced control plots, these plots were combined to give nine replicate plots with both varanid and skink access. Cursorial spider numbers were analysed by two-way ANOVA, including varanids (access or exclusion) and skinks (access or exclusion) as factors and accounting for an interaction term in the model. For exposed web spiders, I analysed the difference in height above ground of exposed web spiders in the different treatments using an ANOVA model with repeated measures. The model had three main factors (height above ground, varanids, skinks) and one repeated factor (sampling occasion). Spider height x varanids (access or exclusion), and spider height x skinks (access or exclusion) were included as main effects to test the overall effects of varanids and skinks on exposed spider numbers at different heights above ground. Spiders on fences were not included in analyses.

Ground-dwelling arthropods (from pitfall traps) and aerial arthropods (from pan traps) trapped on all sampling occasions were combined for each trap type and divided by the number of days of trapping. Orders of ground-dwelling arthropods (as individuals per day) were $\log(n+1)$ -transformed, and the treatments were compared by canonical discriminant function analysis on these log-transformed variables. The variance within each variable and the correlation among variables was similar among the groups, meeting the assumptions of discriminant function analysis. The response of aerial arthropods to web-building spiders was determined by linear regression (aerial arthropods per day in each study plot on mean number of web-building spiders counted in each study plot per sampling occasion).

The proportion of herbivory on leaves within study plots was determined by dividing total damaged area by total leaf area for all leaves sampled in each study plot. I compared leaf damage in varanid and skink access plots (fenced control plots) with leaf damage in unfenced control plots using a t-test, and compared varanid access and exclusion with skink access and exclusion treatments using two-way ANOVA. I first tested for a significant interaction term before proceeding to test for main effects (Quinn and Keough 2002), and eliminated the interaction term from the model if there was no significant interaction between factors.

I used principal components analysis (PCA) to determine whether the treatments could be distinguished from each other on the basis of the habitat available. The hypothesis

that the multivariate set of habitat variables for each study plot differed significantly among treatment types was tested with permutational multivariate analysis of variance (PERMANOVA). PERMANOVA uses a permutation procedure to assess significance of non-parametric data, using the same logic as ANOVA (Anderson 2001). Habitat variables were normalised for comparison, and the correlation matrix was used to estimate the PCA. Euclidean distance was used as the measure of dissimilarity in PCA and PERMANOVA analyses.

PCA and PERMANOVA analyses were undertaken with PRIMER v6.1.11 software (Plymouth Routines in Multivariate Ecological Research, Clarke and Gorley 2006), all other statistical analysis was performed using SPSS v16.0 (SPSS, Inc., Chicago, IL, USA, 2007). Significance level was set at $P = 0.05$.

Results

Exclusion of skinks

Skink exclusion methods were successful and skink exclusion plots were consistently effective at reducing skink numbers; very few individuals were captured in skink exclusion plots compared to access plots (Figure 9.1). Numbers of skinks differed significantly among the treatments, but not among the different sampling occasions (between subjects: $F_{4,16} = 12.54$, $P < 0.001$; within subjects [sampling occasion]: $F_{14, 56} = 1.15$, $P = 0.405$).

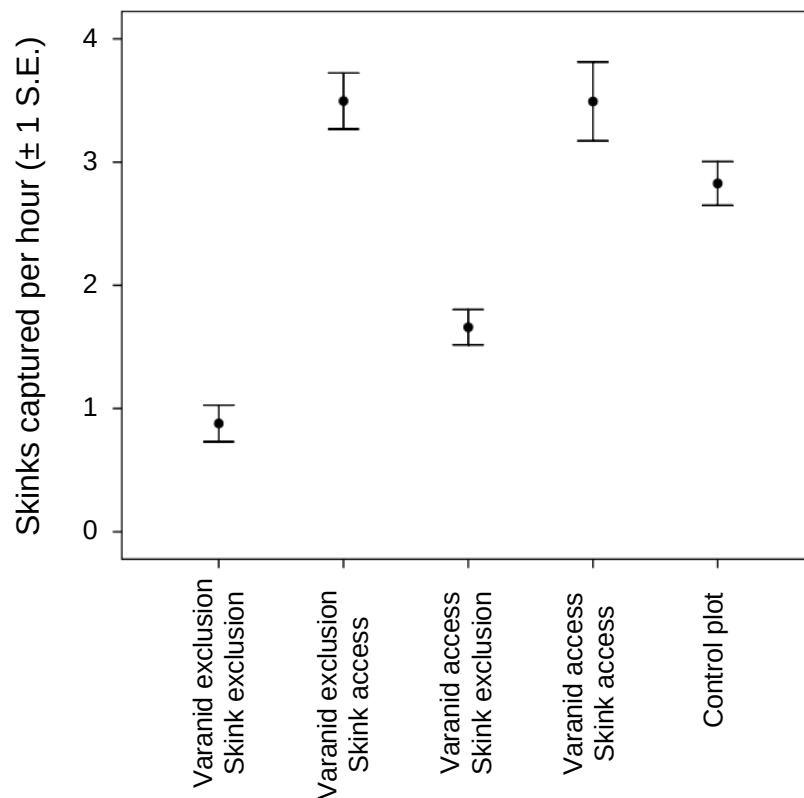


Figure 9.1. Mean number of new skinks ($\pm$ standard error) captured per hour in each treatment.

Cursorial spiders

Study plot fences had no significant effect on numbers of cursorial spiders (fenced and unfenced control plots ANOVA: $F_{1,8} < 0.001$, $P = 0.991$), thus control plots were combined for analysis of varanid and skink effects. There was no significant interaction between varanid and skink accessibility of plots in terms of cursorial spider numbers (ANOVA varanid x skink: $F_{1,20} = 0.76$, $P = 0.394$) and the presence of varanids had no significant effect on cursorial spiders (ANOVA varanid access/exclusion: $F_{1,20} = 0.22$, $P = 0.645$, Figure 9.2). Cursorial spider numbers were significantly reduced in plots where skinks had access, compared to those where skinks were excluded (ANOVA skink access/exclusion: $F_{1,20} = 11.89$, $P = 0.003$, Figure 9.2).

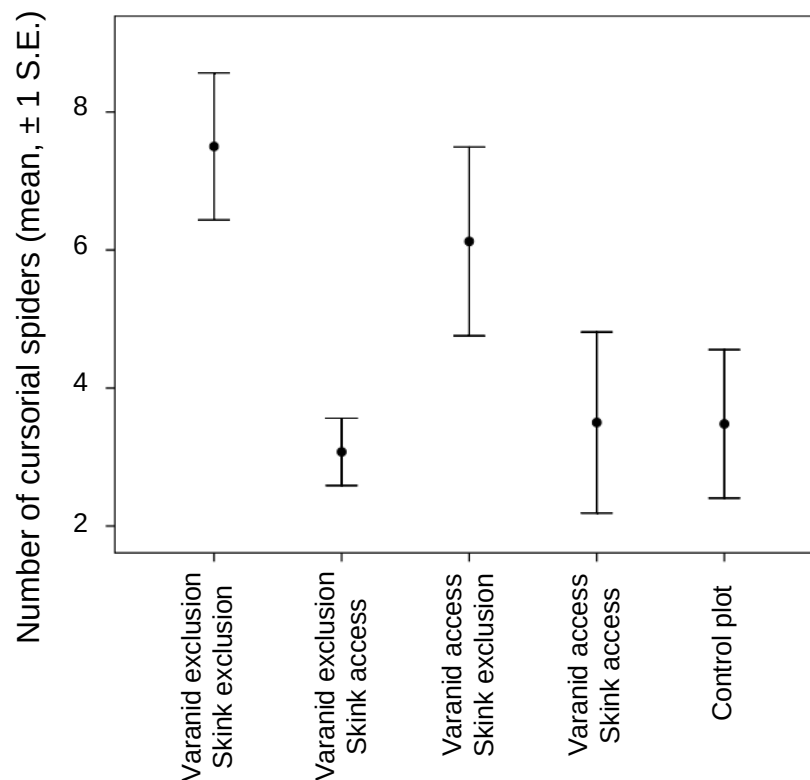


Figure 9.2. Mean number of cursorial spiders ($\pm$ standard error) in the five treatment types.

Web-building spiders

There was no significant difference in exposed web-building spider abundance at any height above ground between fenced and unfenced control plots (between subjects: $F_{1,7} = 0.03$, $P = 0.869$; within subjects [spider height]: $F_{3,5} = 1.82$, $P = 0.261$), thus there was no significant effect of fences on web spider numbers. Fenced and unfenced control plots were combined as the 'varanid access, skink access treatment' for analysis of treatment effects. Varanids had little effect on exposed web spider numbers, regardless of spider height above ground (Figure 9.3; Table 9.1). Skinks, however, had a strong effect on exposed web spider numbers (Table 9.1), in particular on spiders that built webs within 20 cm of the ground (Figure 9.3; Table 9.1). Exposed web spiders close to the ground were significantly more abundant in study plots where skinks were excluded compared to those where skinks had access. There was no significant interaction of varanids and skinks on exposed web spider numbers, at any height above ground.

Table 9.1. Repeated measures ANOVA of number of exposed web spiders at different heights above ground in varanid access and exclusion, and skink access and exclusion study plots. Significant terms are indicated in bold.

Effect	<i>F</i>	d.f.	<i>P</i>
<i>Between subjects</i>			
Varanids	0.36	1, 17	0.556
Skinks	8.06	1, 17	0.011
Varanids x skinks	0.04	1, 17	0.837
<i>Within subjects (spider height)</i>			
Varanids	1.19	3, 15	0.345
Skinks	4.08	3, 15	0.026
Varanids x skinks	0.16	3, 15	0.924

d.f. = degrees of freedom

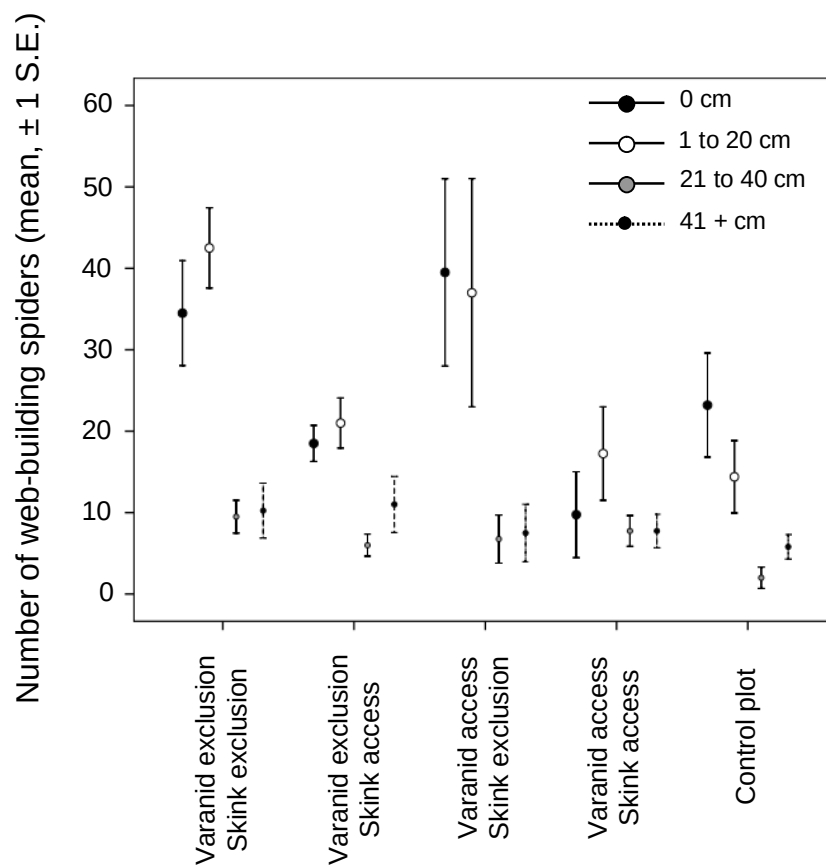


Figure 9.3. Mean number of web-building spiders ($\pm$ standard error) at four height-above-ground categories (ground level, between 1 and 20 cm from the ground, between 21 and 40 cm from the ground, above 41 cm from the ground) in the five treatment types.

Other arthropods

A canonical discriminant function analysis of log-transformed abundance of ground-dwelling arthropod orders revealed significant heterogeneity among treatments (Wilk's $\lambda = 0.001$, d.f. = 52, $P = 0.009$). The first canonical discriminant function, accounting for 93.1% of variance, showed significant separation of the treatments based on exclusion or access to skinks (Figure 9.4 a). First canonical axis scores were negative for skink access plots and positive for skink exclusion plots, with unfenced control plots centred on this axis (Figure 9.4 a). Discrimination among plots reflected a gradient strongly defined by spiders (Aranea), adult lepidopterans, flies (Diptera), springtails (Collembola) and isopods on the positive scale, and to a lesser extent by larval lepidopterans and orthopterans (grasshoppers and crickets; Figure 9.4 b). These taxa were abundant in skink exclusion plots and scarce in skink access plots (Figure 9.4 c). Skink access treatments were associated with high numbers of beetles (Coleoptera), ants (Formicidae) and true bugs (Hemiptera), with a smaller contribution from cockroaches (Blattaria) and mites (Acarina, Figure 9.4 c).

The second canonical discriminant function, accounting for 5.4% of variance, showed some separation of the treatments according to varanid access or exclusion (Figure 9.4 a). Plots where both varanids and skinks had access were characterised by higher abundance of beetles, true bugs and cockroaches (Figure 9.4 c). Plots from which varanids were excluded and skinks had access were associated with high numbers of ants and other Hymenoptera (Figure 9.4 c).

Aerial arthropod abundance was negatively correlated with mean web-building spider abundance ($r^2 = 0.27$, $P = 0.017$, Figure 9.5).

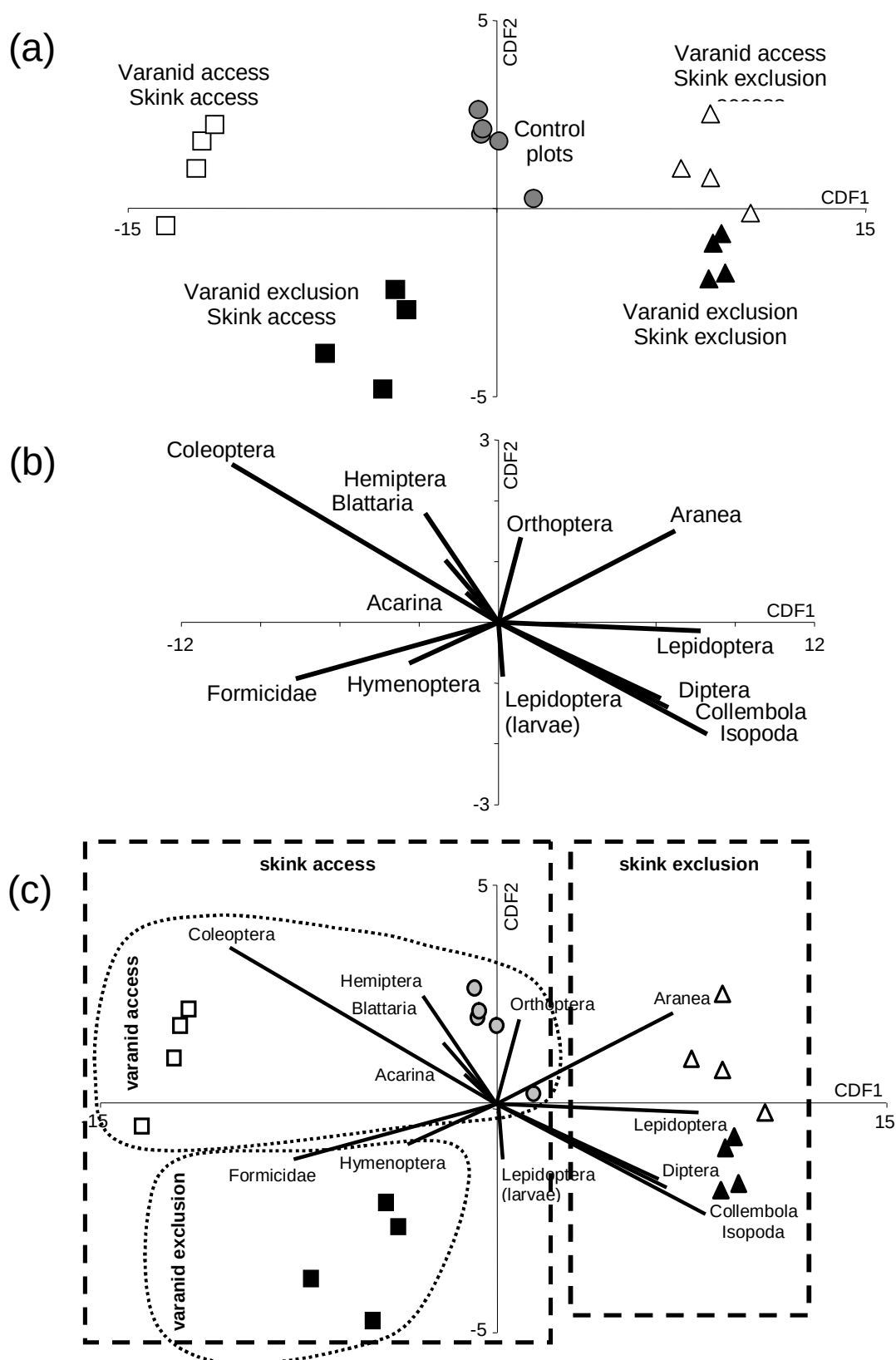


Figure 9.4 (a) Canonical discriminant function analysis of arthropod orders in the five different treatment types. Points represent centroids for each study plot, (b) Taxon eigenvectors (standardized canonical discriminant function coefficients) based on log-transformed data, (c) plots [a] and [b] with explanatory groupings superimposed, see text for details.

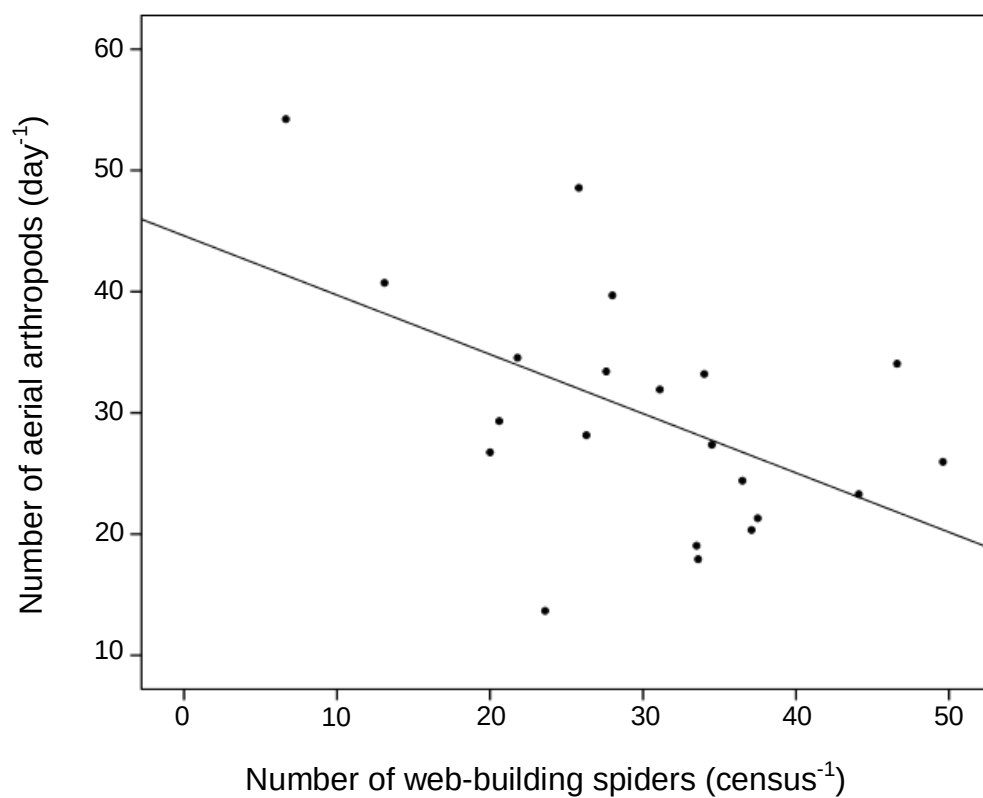


Figure 9.5. Negative linear relationship between aerial arthropod density and web-building spider abundance. Aerial arthropods = $-0.52 * (\text{spiders}) - 0.49$; $r^2 = 0.27$; $P < 0.05$.

Herbivory

There was no significant effect of fences on the proportion of damage to leaves from *Terminalia* sp. shrubs in study plots (t-test of difference between fenced and unfenced control plots: $t = 0.43$, d.f. = 6, $P = 0.679$). Control plots were thus combined into a single varanid and skink access treatment. The interaction of varanids and skinks (allowed access or excluded) was not significant (two-way ANOVA: $F_{1,16} = 1.07$, $P = 0.319$), I therefore removed this term from the model and analysed the variance in the data without the interaction term. Exclusion or access of varanids had no significant effect on leaf damage in the study plots (ANOVA: $F_{1,16} = 0.25$, $P = 0.626$). Exclusion of skinks, however, had a significant effect on leaf damage ($F_{1,16} = 5.74$, $P = 0.031$). There was more herbivory (i.e., a greater proportion of leaf damage) in study plots where skinks were excluded compared to plots where skinks had access (Figure 9.6).

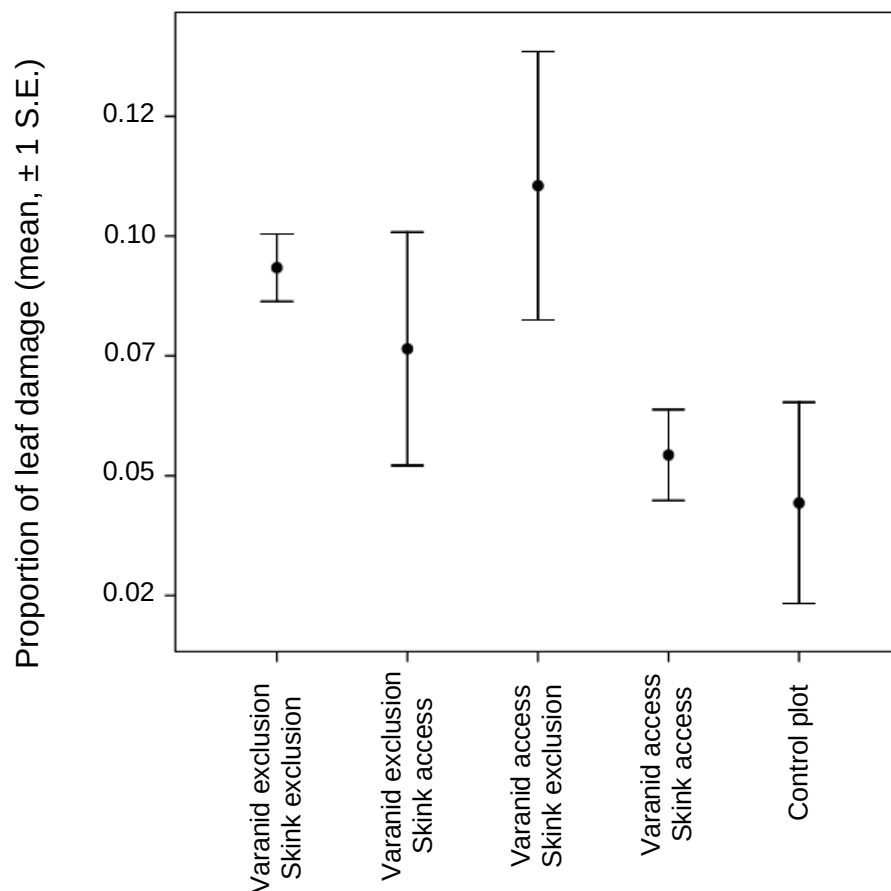


Figure 9.6. Mean proportion of leaf damage ($\pm$ standard error) for each treatment type.

Habitat

The PCA biplot indicates that the multivariate set of habitat variables, including canopy cover, light available and leaf litter depth, did not differ substantially among the treatment types (Figure 9.7). The PC1 axis represents a gradient of increasing direct light penetrating the canopy, and the PC2 axis represents a gradient of decreasing canopy cover above 2 m (Table 9.2). The variation in habitat within each treatment type was within the range of variation of all treatment types, as shown by the scatter of the replicate study plots on the PCA biplot (Figure 9.7). PERMANOVA confirmed that habitat variables did not differ significantly among treatments (4999 permutations: pseudo- $F_{4,20} = 0.94$, $P = 0.561$).

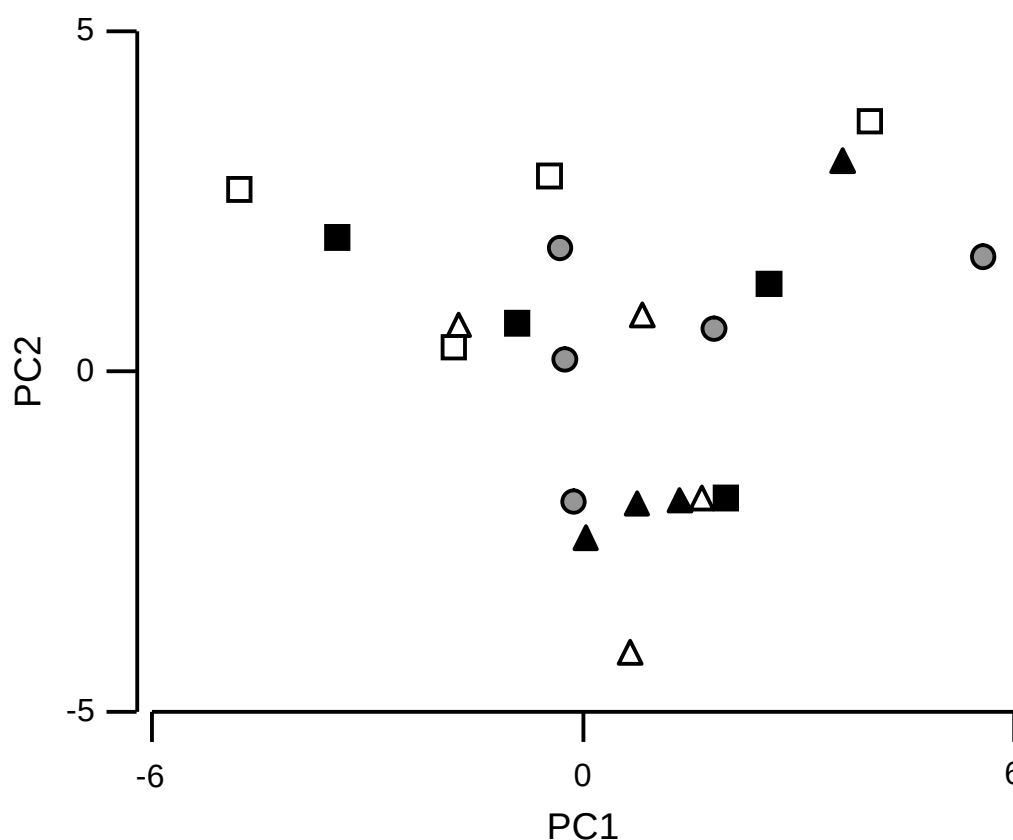


Figure 9.7. Principal component analysis (PCA) biplot showing habitat variables explaining most of the variation in habitat among treatment types (varanid access = open symbols, varanid exclusion = filled symbols, skink access = squares, skink exclusion = triangles, unfenced control plots = grey circles). The PC1 axis represents a gradient of increasing direct light penetrating the canopy, and the PC2 axis represents a gradient of decreasing canopy cover above 2 m.

Table 9.2. Summary of principal component axis loadings (only the first two principal components are shown).

Variable	PC1	PC2
% leaf litter ground cover	0.225	-0.295
% grass ground cover	0.144	-0.112
% bare ground	-0.237	0.295
% canopy cover: 0 to 50 cm	0.239	-0.359
% canopy cover: 50 to 200 cm	0.320	-0.149
% canopy cover: above 200 cm	0.240	-0.370
number of trees	-0.088	0.033
direct light level (DSF)	0.342	0.273
diffuse light level (ISF)	0.337	0.287
visible sky	0.339	0.276
leaf area index of canopy	-0.316	-0.253
leaf litter depth	0.006	0.055
maximum temperature of sun patch	0.110	0.193
maximum temperature of shade patch	0.130	0.003

Discussion

Skinks, as mesopredators in this system, had both direct and indirect effects on arthropod density. Skinks directly reduced the abundance of cursorial spiders and web-building spiders close to the ground, and directly altered the composition of the ground-dwelling arthropod community, leading to a greater proportion of damage to the vegetation in skink exclusion study plots. Skinks also indirectly increased the abundance of aerial arthropods via their reduction of web spider density. Varanids, as top predators, had no direct effect on skink (Chapter 8) or arthropod density. However, varanids indirectly altered the composition of the arthropod community by changing the behaviour of skinks. This study therefore demonstrates an indirect effect of trait-mediated mesopredator release on lower trophic levels, a predator effect that is very rarely shown in natural systems (Schmitz et al. 2000).

Varanids occurred at high densities at the study site ($\sim 16 \text{ km}^{-2}$; Lloyd 2007). The tall fences and collars around surrounding trees prevented varanids from entering varanid exclusion plots. Skinks occurred at very high densities at the study site ($\sim 30 \text{ m}^{-2}$; Chapter 3) but skink exclusion plots (sealed fenced plots) were effective at reducing skink numbers to significantly lower levels than skink access plots (Figure 9.1). The majority of skinks at the study site were ground-dwelling (Chapter 3) and foraged in the leaf litter and in vegetation within 20 cm of the ground (Chapter 3). Spiders form a significant component of skink diet (Chapter 7). Cursorial spiders hunt for their prey by prowling around in the leaf litter or jumping amongst the vegetation (Uetz 1977), behaviour that frequently places them within the foraging range of skinks. I found that the abundance of cursorial spiders was significantly reduced by skinks (Figure 9.2).

In a previous study, using the same experimental manipulation of skink numbers, I demonstrated that web-building spiders, which build a physical shelter in their webs in which to retreat when at rest, were protected from predation by skinks (Manicom et al. 2008; see Appendix B). With this knowledge, I considered only skink effects on exposed web-building spiders in this chapter. Spiders that build their webs low in the vegetation benefit from a greater abundance of prey and a greater availability of web construction sites (Manicom et al. 2008). However, locating a web within $\sim 20 \text{ cm}$ of the ground places spiders within the

foraging range of skinks. The density of exposed web-building spiders at ground level and within 20 cm of the ground was significantly reduced in skink access plots (Figure 9.3). Skinks reduced web-building spiders within their foraging range, but had little effect on spiders that built their webs higher up (Figure 9.3). From spider census, varanids had no significant effect on web-building or cursorial spider density, neither directly or indirectly via their interaction with skinks.

Due to the terrestrial lifestyle of the skinks at the study site, aerial arthropods occurred less frequently in their diet compared with ground-dwelling prey (Chapter 7). Spiders design and locate their webs to maximise their access to aerial prey, and the density of web-building spiders was negatively correlated with the abundance of aerial arthropods in study plots (Figure 9.5). Skinks, therefore, have an indirect positive effect on aerial arthropods, via their negative effect on the abundance of web-building spiders (Figure 9.8).

A canonical discriminant function analysis of the arthropod orders trapped at ground level in the study plots revealed significant heterogeneity among the study plots; the presence of skinks clearly separated the study plots on the first canonical axis and explained the majority of the variation in arthropod taxa among the plots. And the presence of varanids clearly separated the study plots on the second canonical axis. From analyses of the stomach contents of a sample of skinks at the study site, I found that skinks were selective in their foraging and chose specific types of arthropod prey items, regardless of their abundance in the environment (Chapter 7). Spiders (Aranea), cockroaches (Blattaria), grasshoppers and crickets (Orthoptera), butterfly and moth adults and larvae (Lepidoptera), isopods and termites (Isoptera) were important prey of skinks. Considering the arthropod taxa which contributed to the discrimination of study plots by skink access or exclusion (the first discriminant function), the arthropod taxa associated with skink exclusion plots (positive for the first discriminant function, i.e., clustered to the right on the CDF1 axis) constituted 56% of skink diet by volume, whereas the taxa associated with skink access plots (negative for the first discriminant function, i.e., clustered to the left on the CDF1 axis) constituted only 30% of skink diet by volume (Figure 9.4 c). Skinks consumed their preferred prey types in the plots to which they had access, so that these taxa were scarce in skink access plots and abundant in

skink exclusion plots (Figure 9.4 c). Skinks, therefore, significantly altered the composition of the arthropod community.

Varanids additionally altered arthropod community composition via their effect on skinks. Considering only the skink access plots; in the presence of varanids, the arthropod taxa that contributed to the discrimination of study plots on the second discriminant function (higher on second discriminant axis) constituted 26% of skink diet by volume, whereas in the absence of varanids (lower on second discriminant axis) the contributing arthropod taxa (ants, bees and wasps) made up only 4% of skink diet (Figure 9.4 c). In the absence of varanids, skinks were more active (Chapter 8) which lead not only to less restriction on foraging time for skinks, but also to greater energy demands and therefore increased consumption of arthropods. This caused a further alteration of the arthropod community; in the absence of varanids, skinks consumed most available arthropods and only those arthropod taxa rarely consumed by skinks remained (i.e., ants and other hymenoptera, see Chapter 7; Figure 9.4 c). The indirect effect of varanids on arthropods via their effect on skinks was not caused by skink mortality, since predation by varanids had no significant effect on skink densities relative to control plots (Chapter 8). The reduction in skink activity in the presence of varanids (Chapter 8), a trait-mediated effect of predation, allowed some arthropod taxa to escape predation by skinks, and the 'release' of skinks from the threat of varanid predation, as occurred in varanid exclusion plots, meant that skinks consumed more arthropods. This result is evidence that the behavioural response by skinks to the threat of predation from varanids was the mechanism driving the observed change in dynamics of the arthropod community.

The behavioural release of skink mesopredators by top predator removal may cause cascading trophic effects to the level of primary production. Skink removal from study plots had a significant effect on primary producers in this study; skinks remove some herbivorous arthropods from the system (such as orthopterans and lepidopteran larvae, Figure 9.4) and thereby reduce herbivore damage to leaves in the study plots to which skinks have access (Figure 9.6). Plant damage is a short-term response to herbivore activity, and is a direct reflection of herbivore density (Schmitz et al. 2000). Skinks, therefore, had an indirect positive effect on primary producers, via their negative effect on herbivorous arthropods (Figure 9.8). This result implies two mechanisms at work in this system, and highlights the importance of

skinks. First, the significant skink effect on plant damage suggests that, in this system, skinks had a greater effect on certain herbivorous arthropods than did spiders. If spiders consumed a larger number of herbivorous arthropods than skinks, skink access plots would be characterised by high levels of plant damage due to their reduction of spider abundance. And second, it suggests that the herbivorous arthropods frequently eaten by skinks (orthopterans and lepidopteran larvae; see Chapter 7) are more important consumers of primary production at the study site, compared with other herbivores rarely eaten by skinks, such as hemipterans. Thus, selective foraging by skinks (described in Chapter 7) may have important consequences for trophic dynamics. An effect of varanids on primary production was not evident from this static measure of herbivory, however, the long-term effects of herbivory, such as plant biomass growth and reproduction, were not measured here and may not be directly related to immediate tissue damage (Letourneau and Dyer 1998; Schmitz et al. 2000). Caution should be taken when using only short-term measures of plant damage (Schmitz et al. 2000); however other studies have found a strong association between short-term measures of plant damage and long-term measures of plant biomass (Bock et al. 1992; Marquis and Whelan 1994).

Systematic differences in habitat structure could have caused differences among the treatments in skink density, spider density, arthropod assemblage or herbivory levels. However, in my study the habitat and physical properties of the study plots did not differ significantly among the treatment types (Figure 9.7). Similarly, other predators, such as birds, could have had differential effects on skinks among the treatments. Birds have equal access to all study plots, and I have evidence (Appendix A) that avian predation attempts were very low at my study site and did not differ among treatments. The trophic interactions presented here, and their cascading effects, were therefore due to interactions among the manipulated species and their resources rather than physical differences among the treatment types.

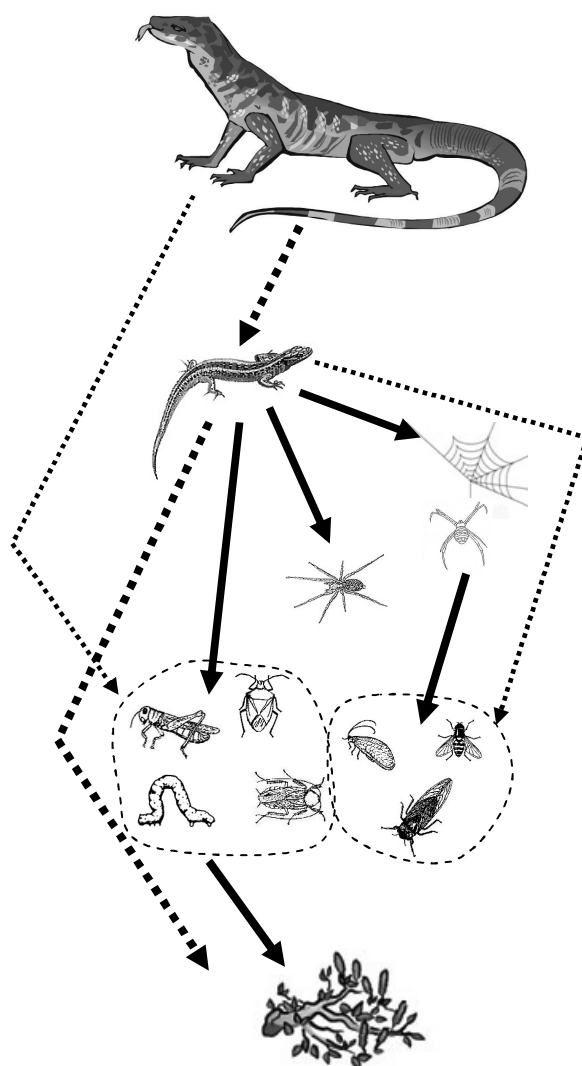


Figure 9.8. The trophic web at the study site, showing the links and relative interaction strength for each trophic level. Direct effects are indicated by solid arrows, indirect effects are indicated by dashed arrows, and the strength of the interaction (as revealed by predator exclusion experiments) is indicated by the weight of arrows.

In this chapter I have demonstrated the combination of direct and indirect influences of top- and intermediate-level predators on the structure of an ecological community. Skinks, as intermediate-level, or mesopredators, have a strong direct effect on the density of spiders and ground-dwelling arthropods, and an indirect effect on the abundance of aerial arthropods, via their effect on web-building spiders (Figure 9.8). Top predatory varanids influence the composition of the arthropod community via their effect on the behaviour of skinks (Figure 9.8). The density-mediated effect of skinks on herbivorous arthropods is stronger than the trait-mediated indirect effect of varanids on the arthropod community since it flows through the

system to the level of primary production as a trophic cascade, rarely observed in terrestrial systems (Shurin et al. 2002). The indirect effect of varanids on arthropods, via their reduction of the activity of skinks, however, is an important demonstration of the impact of trait-mediated indirect effects of predation. Such behavioural predator effects may be very influential in community ecology because they are immediate; they do not cause a gradual change in density, and do not require multiple generations for morphological or physiological predator-response changes to occur. Prey behavioural change in response to the presence or absence of predators can be instantaneous and, thus, the cascading effects to lower trophic levels may occur within the lifetime of a prey cohort (Peacor and Werner 2001). A quick response to predator removal may be particularly important when the prey are predators themselves, since the release of mesopredators from predation can have disproportionate effects on lower trophic levels (Ritchie and Johnson 2009). In this study I have experimentally shown that behavioural mesopredator release by the exclusion of top predators cascaded to lower trophic levels, and that this effect was evident over a relatively short time period. Thus, a trait-mediated indirect effect of top predator removal has been demonstrated in a complex terrestrial system.

Chapter 10

Concluding remarks and future directions

My study identifies the responses of prey to the direct and indirect effects of predators in a complex, terrestrial, multi-predator trophic system. Studies of multi-predator trophic webs are an important contribution to ecology; the activities that make an animal an effective predator also make the animal more vulnerable to predation, and the response of prey to predator removal is particularly important when the prey are predators themselves, as the release of mesopredators from predation can have disproportionately large effects on lower trophic levels.

To appreciate the impact that predation had on fauna, a detailed understanding of the ecology of the prey species was needed, and in gaining this understanding, I have made a substantial contribution to our knowledge of the ecology of tropical skinks. Three species of congeneric skinks (*Carlia* sp.) live in sympatry at my study site, and prior to my study very little was known about their life-history strategies. My long-term (2003 – 2007) mark-recapture study of the *Carlia* population on Hinchinbrook Island allowed me the opportunity to fill some of the gaps in our knowledge of this important group of skinks, which constitute a substantial component of the vertebrate fauna in the Australian tropics (Wilson 2005). Specifically, I have described the population structure, survival rates, reproductive seasons and recruitment patterns of three *Carlia* species (Chapter 3) and I have defined their growth patterns, age at maturity and sexual dimorphism (Chapter 4). I have shown that while the species' exhibit many similarities in life history and population demography, they contrast in the sex-bias of their dimorphism which suggests that the social systems of these skinks differ among species. I have also demonstrated the relationship between these skinks and their ectoparasites, trombiculid mite larvae (Chapter 5), which also differs among the species; two of the species are highly susceptible to ectoparasite infestation while the other is not. Differences in ectoparasite load among the species were not explained by species'

differences in the available area of attachment site of mites (Chapter 6), and so are likely explained by differences in their ecology.

My study has redefined knowledge of the foraging ecology of *Carlia*, which were previously assumed to be non-selective, opportunistic predators, and has shown instead that skinks were selective in their prey choice, consuming certain prey types and sizes that were in short supply in the environment (Chapter 7). An important consequence of the relatively selective diet of *Carlia* is the potential for cascading effects through the trophic web. The species varied in the prey they consumed, but spiders and orthopterans were consistent prey types for all skinks. The selective removal by skinks of other predators (spiders) and herbivores (orthopterans) from the trophic system was then shown to have far-reaching effects that cascaded through the system to alter the composition of the arthropod community, and the amount of damage to local vegetation (Chapter 9). In complex terrestrial trophic systems, the high interconnectedness of species often makes trophic cascades appear weak (Halaj and Wise 2001; Shurin et al. 2002). In my study system, where multiple predators (varanids, skinks, spiders) feed on more than one trophic level, it was exciting to reveal effects of skinks on plant damage (via herbivorous arthropods), and of varanids on arthropod composition (via skinks and spiders). Most interesting here, however, was that the indirect effect of the removal of the top predator (varanids) on the composition of arthropods occurred without an impact on the abundance of skinks (Chapter 8). The presence of varanids instead restricted only the activity of skinks, without impacting on skink density, which indicates that the further alteration of arthropod community composition by highly active skinks in the absence of varanids documented a behaviourally-mediated indirect predation effect by varanids on skinks; the arthropods most frequently consumed by skinks were depleted in plots where skinks were free from predation. Such trait-mediated effects are hypothesised to be as strong as density-mediated effects (Werner and Peacor 2003; Schmitz et al. 2004; Preisser et al. 2005) but rarely have behaviourally-mediated indirect interactions been shown in terrestrial environments (Preisser et al. 2005; Preisser et al. 2007), in particular in a complex vertebrate system. The mechanisms of trait change can be interesting in their own right as they have potential implications for behavioural and evolutionary biology (Endler 1980; Van Buskirk and McCollum 2000).

This is the first study, to my knowledge, to experimentally reveal the effect of behaviourally mediated mesopredator release (Crooks and Soulé 1999) on lower trophic levels. Understanding the mechanism of behaviourally mediated mesopredator release, and the knowledge that such effects do occur in terrestrial, vertebrate systems is critical to predicting the likely responses of terrestrial ecological communities to the loss of top predators, and is important for two reasons. First, prey behavioural change in response to the presence or absence of predators can be immediate and the cascading effects to lower trophic levels may, therefore, occur very rapidly. The speed with which behavioural effects may manifest and flow to lower trophic levels, compared to gradual population density changes or multi-generational prey morphological or physiological changes, is an important consideration when predicting the effects of the loss of top predators. Second, the impact of mesopredators on lower trophic levels can be considerably larger than that of top predator effects due to the comparatively greater density and versatility of mesopredators; the loss of top predators from systems and subsequent outbreaks of mesopredators has been implicated as a threat to vulnerable prey species (Courchamp et al. 1999; Le Corre 2008), a cause of species extinctions (Johnson et al. 2007) and a problem for commercial industries such as fisheries (Baum and Worm 2009).

Furthermore, to my knowledge, no previous study has experimentally shown that predator-avoidance behaviour actually causes reduced mortality of prey. Many studies have shown that animals alter their behaviour in the presence of predators, and that predator-avoidance behaviour is costly to prey in terms of fitness (e.g., Peacor and Werner 2000; Downes 2001). However, I have not yet found a study that documents the consistent success of predator-avoidance behaviour. I have demonstrated this in two instances in my study. Skinks reduce their activity in the presence of varanids, apparently to avoid detection. This reduction in activity was successful at avoiding predation; skinks in predator-access plots maintained similar densities and had similar probabilities of survival as skinks living in predator-free areas (Chapter 8), convincing evidence that a reduction in conspicuous activity is effective in predator avoidance. Additionally, in another part of this study (Manicom et al. 2008; see Appendix B), I experimentally demonstrated that spiders that built a physical

shelter in their webs into which to retreat when at rest were able to avoid predation and share space with their lizard predators, compared to exposed spiders which were consumed.

Beyond abundance

Most studies of trophic webs determine the effects of predators on lower trophic levels by measuring the abundance of organisms. In my study system, the strongest effects of top predator removal on the trophic web arise through trait-mediated indirect effects on skinks, rather than direct effects on their density. In order to detect these effects it was necessary to measure more than just the abundance of skinks, and look instead at skink behaviour. And, indeed, to detect the effect of skinks on their arthropod prey required measuring not just numbers of arthropod individuals, but instead identifying arthropod groups and establishing the effects of predation on community composition, and considering the niche occupied by prey, such as the height above ground of web-building spiders. Thus, it was only by establishing skink diet composition and foraging range that the real effects of predator removal could be determined. Ecological systems comprise enormous complexity, and it is necessary to pay careful attention to detail within systems in order to unravel the connections among organisms, practice that would be useful not only in the study of trophic webs but in any ecological system.

Future directions

Consistent with much ecological research, the answering of specific questions during my study has lead to the asking of many more. There are three major future directions that could be taken to continue this study. First, the study itself could continue for longer. The importance of long-term monitoring of ecological systems is well known (Carpenter et al. 1995; Menge 1997) and continuing to maintain the study plots at my study site and observe the effects of predator removal over multiple years would be invaluable towards determining whether predator effects attenuate or intensify over time. Switching the treatment type of study plots (i.e., removing and excluding varanids or skinks from previously accessible plots, and vice versa) and monitoring the resultant cascading effects to lower trophic levels would provide a compelling test of the potential speed of trait-mediated predator effects, and would

provide insight for the management of systems where predator reintroductions, or removal of invasive predators, are planned.

Second, a logical next step for a trophic web experiment would be to manipulate resources. In the case of my experiment, the abundance and composition of arthropods, or the amount of vegetation, could be manipulated within study plots (provided that new resource treatments could be replicated). The release from top predator exposure did not appear to provide skinks with any fitness benefits in my study (they did not experience significantly faster growth rate, better body condition or increased survival probability, see Chapter 8). Inactivity, due to the risk of predation, requires few resources to maintain body functioning (Adolph and Porter 1993), and I proposed that the release from inactivity in the absence of predators would mean more resources were required to maintain the high energy levels needed for foraging, thermoregulation and interacting with conspecifics. When resources are limiting, there may be no fitness advantage to being free from predators. Manipulating the resources available to skinks and their prey within study plots would demonstrate the extent of resource limitation in this system and would indicate the conditions under which top predator removal may impact on prey lifetime fitness and life history. It would also assist in understanding the relative strengths of top down and bottom up forces on the flow of energy, a theme not yet fully understood in terrestrial systems (Hunter and Price 1992).

Third, aspects of the ecology of the skinks themselves warrant further research, in particular the importance of the striking sexual dichromatism of some of species of *Carlia*. This phenomenon is rare amongst Australian terrestrial skinks (Stuart-Fox et al. 2002). In my study, species' differences in both sexual size dimorphism (Chapter 4) and ectoparasite load (Chapter 5) may be related to the display of breeding colouration, and this indicates significant differences in the social systems employed by species that are remarkably similar in many other aspects (Chapter 3). The skink species at my study site are ideal candidates for studying the importance of colour, because species that exhibit conspicuous breeding colouration coexist with species that do not. Understanding species differences with regard to colour use would provide insight into the social systems of these skinks, the selection pressures faced and the resultant community organisation.

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Appendix A

The threat from aerial predators to skinks at the study site

Abstract

Predation by birds is an important consideration for skinks. Although my experimental study plots allow equal access to birds and only manipulate access to varanids, the tall fences of varanid exclusion plots may disrupt the line of sight of aerial predators, and resident skinks in varanid exclusion plots may benefit from reduced predation from birds. To assess the frequency of avian predation attempts on skinks, and to compare predation attempts among the treatment plots, I exposed 174 life-like lizard models, designed to record predation attempts, to free-ranging predatory birds in the study plots, and along transects outside of the study plots, at my study site for 12 days. To test the efficacy of the lizard models, I exposed 50 of the same models to predatory birds at another site (test site) for the same length of time. At the study site, only one lizard model showed evidence of a predation attempt by a bird. Thus, there was no difference between the number of avian predation attempts on models exposed in the study plots and models exposed in transects at the study site (Fisher's exact test, $P = 1.00$), and no difference in bird predation among the treatment types (log-linear analysis, $P = 0.07$). At the test site, 13 lizard models showed evidence of a bird predation attempt, significantly more than at the study site (Fisher's exact test, $P < 0.001$), showing that the models were suitably realistic skink replicas. It appears that there is very little predation on skinks from predatory birds at my study site and thus there was no evidence that avian predation attempts on skinks differed among the study treatments. The influence of birds on skinks resident in the study plots can be assumed to be similar across the site.

Introduction

Predation by birds is an important consideration for lizards (Schoener and Schoener 1978; Barker and Vestjens 1989; Schwarzkopf and Shine 1992; Blomberg and Shine 2000; Stapley 2004). In an experimental study to test the effect of predators, such as my own study, predation by birds cannot be discounted. Predatory bird species at the study site on Hinchinbrook Island include the Black Butcherbird *Cracticus quoyi*, Australian Raven *Corvus coronoides*, Laughing Kookaburra *Dacelo novaeguineae*, Brown Goshawk *Accipiter fasciatus* and Peregrine Falcon *Falco peregrinus* (*pers. obs.*; Simpson et al. 1999). Orange footed scrub fowl *Megapodius reinwardt*, Varied Trillers *Lalage leucomela* and Spangled Drongos *Dicrurus bracteatus* are common insectivores at the study site (*pers. obs.*) and may consume small skinks occasionally (Jones et al. 1995; Simpson et al. 1999). Brahminy kites *Haliastur indus* and white-bellied sea eagles *Haliaeetus leucogaster* frequently hunt along the coastline adjacent to the study site (*pers. obs.*) and may occasionally prey on skinks at the site (Simpson et al. 1999).

Although all study plots in my experiment allowed equal access to birds (they were open at the top) and the effect of predation by birds on skinks should therefore be equivalent among all study plots, I aimed to quantify the amount of avian predation at the study site, and determine if tall plots (varanid exclusion) differed in amount of avian predation compared to low plots (varanid access) and unfenced plots. Predation studies are difficult to conduct because predation events are rarely observed in the wild. Life-like reptile models which record a predation attempt have been used successfully in numerous studies (Brodie 1993; Olsson 1993; Castilla and Labra 1998; Stuart-Fox et al. 2003; Shepard 2007) including one on *Carlia* (Schneider et al. 1999). To assess the relative frequency of bird attacks on skinks in treatment plots at my study site, I exposed life-like models of lizards to free-ranging avian predators at my study site on Hinchinbrook Island. I compared the total number of avian predation attempts on model lizards at my study site with those at another site to ensure the effectiveness of lizard models.

Methods

I constructed lizard models from adhesive putty (BluTack™) and attached them to rigid plastic bases (transparent acetate). The plastic bases were produced from the same template, based on the size and shape of a mid-sized *Carlia* skink (mature *C. rubrigularis*, 46.0 mm SVL). Models were painted with brown acrylic paint matched as closely as possible to skink dorsal colour. I compared the colour of the dorsal surface of real lizards with a range of brown paint swatches using a reflectance probe (Ocean Optics USB4000 spectrometer), with illumination provided by a pulsed xenon light source (Ocean Optics PX-2) at 50 strobes per second, held at a 45° angle approximately 5 mm from the surface (Endler 1990). Measurements were expressed relative to a Labsphere 99% certified reflectance standard. The dorsal colour of six individual skinks of each species (three males and three females) was measured, and the mean reflectance for each species established. I matched colours by measuring the spectral reflectance of various shades of brown paint and selecting the colour that matched the reflectance spectra of the dorsal surface of skinks as closely as possible. This way I also ensured that the paint used on models had similar reflectance as skink dorsal surfaces in the full range of light spectra, so that the models looked natural to birds as well as humans. Two colours were selected to match the three *Carlia* species at the study site: light brown (to match *C. rostralis* and *C. storri*, Figure A1) and dark brown (to match *C. rubrigularis*, Figure A1). A total of 174 model lizards were made, half of the total number ($n = 87$) were painted light brown, and half were painted dark brown ($n = 87$).

Models lizards were exposed to predators at the study site for 12 days in May 2005. Models were placed on the ground in likely basking positions in the study plots and along five transects at the study site. Basking positions were chosen, rather than retreat sites, because lizards are more vulnerable to visual predators, such as birds, when basking (Schwarzkopf and Shine 1992). Models were anchored to the leaf litter with wire (hidden between the putty and plastic base) to prevent them being carried away. Six model lizards (three light brown models and three dark brown) were placed in each study plot a minimum of 3 m from each other and from the edges of the plot. Five transects were established outside of study plots, in similar habitat. Ten model lizards were placed in each transect, at approximately 3-m intervals, with light and dark models alternating.

Models were collected at the end of the experiment and checked for predation attempts. The type of predator was determined by inspection of marks in the model putty using a dissecting microscope. Marks made by birds are V-shaped and lack tooth imprints (Brodie 1993; Husak et al. 2006). They are distinguished from those made by reptiles (U-shaped with distinct tooth imprints), rodents (incisors) and insects (mandibles, Shepard 2007). Only attacks made to the head or torso of the model were considered predation attempts (Shepard 2007).

To test the effectiveness of my model lizards as a measure of bird predation, I conducted a second study in woodland to the east of James Cook University campus (19°19'40" S, 146°45'43" E). *Carlia* are the dominant skink fauna in this habitat, specifically *C. jarnoldae* and *C. pectoralis* (*pers. obs.*). These skinks are similar in body size and dorsal colouration to *Carlia* at the Hinchinbrook Island study site (Wilson 2005; Figure A1), and model lizards were therefore a suitable match. The test site consisted of a dry creek bed (~5 m wide) with adjacent riparian vegetation. The microhabitat available to lizards at this site differed from the Hinchinbrook Island study site in that cover for retreating lizards is provided by rocks, roots and woody debris, rather than leaf litter and shrubs, but is similar in amount of canopy cover: trees provide a mosaic of open and closed canopy (*pers. obs.*). Avian predators at this site include corvids, kookaburras, goshawks, Black Kite *Milvus migrans* and Pacific Baza *Aviceda subcristata* (*pers. obs.*; Simpson et al. 1999). Fifty model lizards from the previous study (25 light brown and 25 dark brown) were repaired and repainted, and exposed to avian predators at the test site for 12 days in May 2008. Ten models were placed at 3-m intervals, on five transects across the creek bed and into adjacent vegetation, with light and dark models alternating. Models were again placed at ground level in likely basking positions, and anchored to the leaf litter or sand with wire, or glued to rocks. Models were examined at the end of the experiment and bird predation attempts were recorded.

I used a loglinear model and Fisher's exact tests to determine whether bird predation on model lizards differed among the treatments at the study site, and between sites (within study plots vs transects; study site vs test site), and that bird predation attempts did not differ between dark and light brown models (Sokal and Rohlf 1995). I used SPSS v16.0 (SPSS,

Inc., Chicago, IL, USA SPSS Inc. 2007) for statistical analyses, with significance level set at $P = 0.05$.

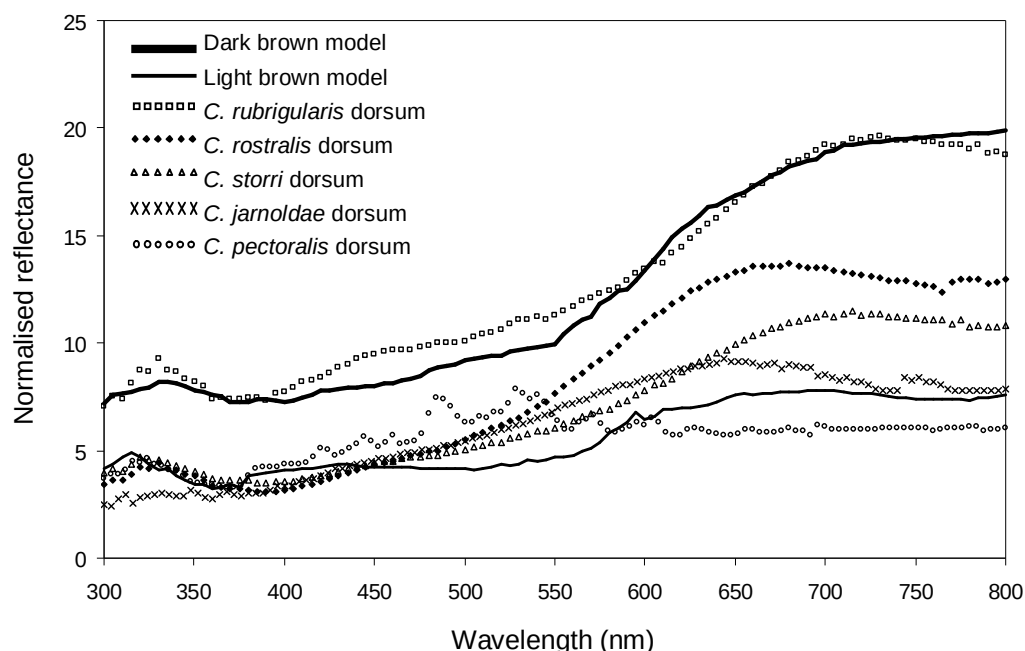


Figure A1. The reflectance spectra of *Carlia* and model lizard dorsal surfaces.

Results

Of the 174 models exposed to predators at my study site on Hinchinbrook Island, 45 were attacked by predators. Examination of the marks left in the model putty showed predation attempts by rodents ($N = 11$), insects ($N = 28$) and reptiles (large lizards or snakes, $N = 5$). Only one lizard model showed unambiguous bird bill marks, evidence of a predation attempt by a bird. This model was dark brown and from a varanid exclusion, skink access plot (see Chapter 2 for description of plots). There was therefore no difference in avian predation attempts among the treatment types (high vs low vs control plots, loglinear model partial association: $G = 5.45$, $d.f = 2$, $P > 0.06$). There was also no difference between the number of avian predation attempts on models exposed in the study plots (1 of 124) and models exposed in the transects (0 of 50, $N = 174$; Fisher's exact test, $P = 1.00$).

The very low frequency of bird attacks on models prompted a test of the effectiveness of lizard models at another site (test site). Bird predation attempts on model lizards were significantly more frequent at the test site (13 of 50) than at the study site (1 of 176, $N = 224$; Fisher's exact test, $P < 0.001$, Figure A2). There was no difference in predation attempts between light and dark models at either site (Fisher's exact test, $P = 0.44$, Figure A2).

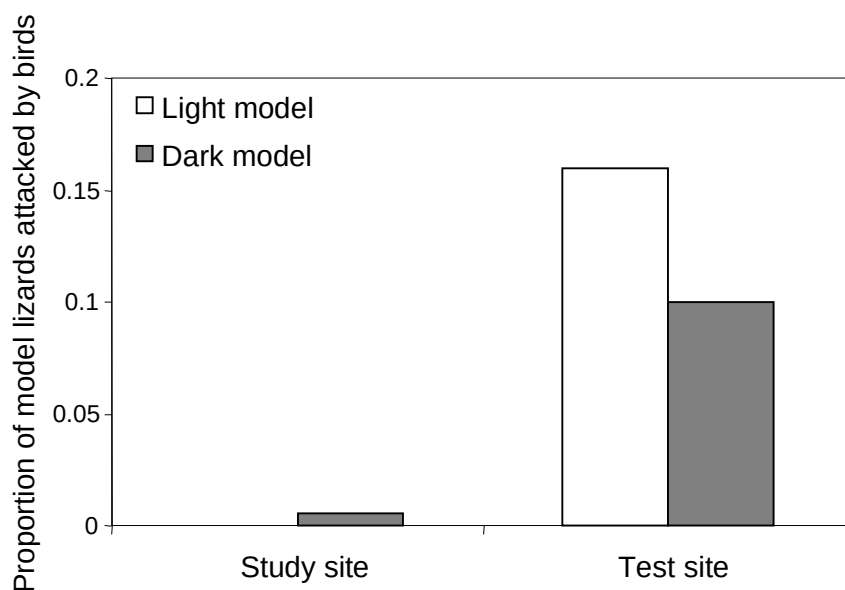


Figure A2. Proportion of the exposed model lizards attacked by birds at the study site on Hinchinbrook Island, and the test site at James Cook University campus.

Discussion

In this study I aimed to determine the difference in avian predation frequency in the different treatment types of my experiment. Although the study plots were all equally accessible to birds, it may be argued that the varanid exclusion plots offer some protection from avian predators. The tall fences of varanid exclusion study plots may disrupt the line of sight of aerial hunting predators, and therefore assist skinks in avoiding predation from birds (Denno et al. 2005). The use of life-like lizard models, the method frequently used to assess avian predation (see citations in Introduction), did not establish whether differences in bird

attack attempts on skinks existed among treatments in this study because only one lizard model recorded evidence of bird predation.

The use of lizard models to measure rate of predation has an obvious drawback: models do not move, and therefore may not be convincing prey for predatory birds (Curio 1976). However similar stationary lizard models have been used to measure differences in avian predation on lizards in other studies, between different lizard colour morphs (Olsson 1993; Stuart-Fox et al. 2003; Husak et al. 2006) and between different habitat types (Schneider et al. 1999; Shepard 2007). Birds attacked between five (Schneider et al. 1999) and 27% (Shepard 2007) of lizard models in previous studies, considerably more than occurred at my own study site (0.6%). I deployed the same models used at my study site at another site (a test site), for the same number of days at the same time of year. The test site was also host to *Carlia* skinks, of a similar body size (Langkilde et al. 2003) and colouration (Figure A1) to *Carlia* at my study site, and to similar predatory bird species (*pers. obs.*; Simpson et al. 1999). The test site comprised different habitat to the study site, and habitat is an important determinant of predator foraging efficiency (Denno et al. 2005). The test site was chosen not to compare the number of avian predatory attempts on skinks, but instead to test the effectiveness of lizard models as *Carlia* replicas. Lizard models at the test site suffered a high proportion (26%) of bird predation attempts, showing that the models were suitably realistic skink replicas.

It appears that there was very little predation on skinks from birds at my study site on Hinchinbrook Island; model lizards that recorded avian predation attempts elsewhere did not show evidence of bird predation when deployed at my study site. There was therefore no evidence that avian predation attempts on skinks differed among the study treatments and the influence of birds on skinks resident in the study plots can be assumed to be similar across the site.

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Appendix B

Self-made shelters protect spiders from predation

Carryn Manicom, Lin Schwarzkopf, Ross A. Alford and Thomas W. Schoener

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30 September 2008.

Appendix C

The cost of failing to thermoregulate is higher in the tropics: A conceptual model and empirical test

Mathew J. Vickers, Carryn Manicom and Lin Schwarzkopf

In review: *The American Naturalist*

Abstract

Thermoregulation is a critical aspect of the ecology of ectotherms, which make up the majority of species. In tropical environments, where most ectothermic vertebrates occur, average temperatures are often similar to preferred temperatures of tropical vertebrates. The close correspondence between average temperatures of tropical environments and preferred temperatures of many reptiles has led to a suggestion in the literature that tropical reptiles do not need to thermoregulate. While some tropical reptiles are thermoconformers, theory suggests that small diurnal ectothermic vertebrates, with low thermal inertia, that live in tropical environments with high thermal heterogeneity, such as savanna (i.e., the vast majority of tropical ectotherms), may need to thermoregulate to keep body temperatures below lethal temperatures. We empirically examine the preferred temperatures, body temperatures, available operative environmental temperatures, environmental thermal quality, and thermoregulatory precision of three species of small (~3 g) tropical scincid lizards living in woodlands (*Carlia rubrigularis*, *C. rostralis*, *C. storri*). In summer, thermal quality of the environment was low, because a high proportion of available temperatures were above lethal temperatures for these skinks. In winter, thermal quality of the environment was higher, as more available temperatures approached preferred temperatures. Contrary to predictions of the Cost-Benefit Model of thermoregulation, these skinks thermoregulated with high precision ($E > 0.8$) in summer, when thermal quality was lowest, and

thermoregulated with significantly less precision ($E < 0.6$) in winter, when thermal quality was higher. The response of these lizards to environmental temperatures was consistent with a new interpretation of the Cost-Benefit Model of thermoregulation, which takes into account the high cost of thermoconforming when environmental temperatures are lethally high.

Introduction

The tropical environment is diverse, ranging from dense canopy forest to desert, and reptiles can be found across this entire gradient. One ubiquitous feature of the tropics is high temperatures, with mean temperatures often around 30° C, near ideal for reptiles (Shine and Madsen 1996; Kearney et al. 2009), and large, nocturnal species, or inhabitants of thermally homogenous habitats such as dense forest, can behave as thermoconformers under these conditions (Acala and Brown 1966; Rand and Humphrey 1968; Hertz 1974; Huey 1974; Hertz 1992). However, the vast majority of the tropics consists of open woodland, such as savannah (Woinarski et al. 2007), providing highly thermally heterogeneous habitat that can facilitate thermoregulation, and tropical reptile species may have intermediate (Navarro-Garcia et al. 2008) or high (Wilhoft 1961; Porter and James 1979; Berkum 1988; Hertz 1992; Christian and Bedford 1995; Christian and Weavers 1996; Vitt et al. 1998) precision and efficiency of thermoregulation in these environments. Studies reporting low variability of body temperature in the tropics, may, however, be misleading about the precision of thermoregulation. For example, if tropical species are large-bodied and have high thermal inertia in areas where mean environmental temperature is similar to preferred body temperature, then their body temperature will remain close to preferred, yielding the observed high precision and apparent high efficiency of thermoregulation (Seebacher and Shine 2004). In other words, tropical reptiles may not need overt behavioural methods to maintain preferred body temperatures (Shine and Madsen 1996; Luiselli and Akani 2002). However, most reptiles are, for at least some portion of their lives, small bodied, and small diurnal reptiles with low thermal inertia (Stevenson 1985) may need careful, deliberate thermoregulatory behaviour to avoid dangerously high temperatures found in more thermally heterogeneous tropical habitats like savannah and open woodland (modeled by Kearney et al. 2009), though there is a paucity of studies testing this theory.

Whether thermoregulation occurs, what body temperature is maintained, and how precisely body temperature is controlled, is governed by costs and benefits (Huey and Slatkin 1976) that are independent of the environment. Maintaining body temperature (T_b) lower than the preferred or selected body temperature range (T_{sel}) brings a reduction in energy

requirements (Porter and James 1979), and in turn reduced foraging time and exposure to predators (e.g., Huey and Pianka 1981). However, this is accompanied by reduced locomotory performance (reviewed by Bennett 1990), with concomitant increased risks of predation (e.g., Christian and Tracy 1981) and reduced prey capture (e.g., Greenwald 1974). Over long periods, these low energy requirements may still exceed energy availability and foraging rate, leading to death (Tinkle 1967). On the other hand, higher T_b is accompanied by increased performance and in turn increased foraging and mating success (Bennett 1990; Dunham et al. 1989); the costs include increased metabolic expenditure and high food requirements (e.g., Huey and Dunham 1987; Waldschmidt and Porter 1987), with attendant increases in foraging requirements and exposure to predators (Schwarzkopf and Shine 1992). Additionally, increasing body temperature only slightly beyond thermal optima quickly leads to loss of coordination, righting ability, and ultimately death (Cowles and Bogert 1944). Accordingly, we expect to observe high effort and precision of lizard thermoregulation at high environmental temperatures, such as in open tropical habitat, risking the costs of high T_b s to gain performance benefits or maximize activity time and space (e.g., Grant and Dunham 1990), while carefully and deliberately avoiding extreme T_b s that impose unacceptably high costs such as death (Huey and Stevenson 1979; Gilchrist 1995).

This expectation contrasts with the Cost-Benefit Model of thermoregulation (Huey and Slatkin 1976), which predicts that as thermal quality (i.e., suitability of the thermal environment for an individual) of the environment decreases, the cost of thermoregulation increases (Figure C1), and therefore thermoregulatory effort should decrease (Hertz et al. 1993). This decrease in thermoregulatory effort manifests as less precise thermoregulation (Blouin-Demers and Nadeau 2005), and, eventually, thermoconformation as the thermal quality of the environment moves farther from a species' selected temperature range (T_{sel}), and there are examples of thermal conformation as thermal quality declines (Sartorius et al. 2002; Herczeg et al. 2006). Studies in which thermal conformation occurs in response to low thermal quality, and indeed, most studies of reptile thermoregulation are set in the temperate zone, and when thermal quality of the environment is not at or near the T_{sel} , the environment is typically cooler than T_{sel} (Figure C1, shaded portion). As the cost of thermoregulation increases, the cost of thermoconforming increases quite slowly because it is mainly defined

by the loss of thermoregulatory benefits, and mortality occurs only if exposure is very lengthy, or if thermal quality is very low (Figure C1, shaded portion). If, however, the decrease in thermal quality of the environment is due to environmental temperature exceeding T_{sel} (Figure C1, unshaded portion), the cost of thermoconforming increases rapidly and mortality can occur after even brief exposures to high temperatures (Figure C1, unshaded portion). The cost of not thermoregulating (death) becomes higher than the cost of thermoregulating (energetically expensive), and hence in high temperature environments, small reptiles should thermoregulate very carefully. Recent modeling suggests that, because most lizards occur in tropical environments, most lizards have to avoid high temperatures rather than low temperatures (Kearney et al. 2009), and that as climate warming continues, this situation will be exacerbated. Thus exposure of ectotherms to temperatures higher than preferred (Figure C1, unshaded portion), is a critical aspect of thermoregulation, but it is not accounted for in the Cost-Benefit Model (Huey and Slatkin 1976), and empirical data are lacking. Here we examine the claim that tropical ectotherms do not need to thermoregulate (e.g., Shine and Madsen 1996), with particular reference to the typical tropical situation: small reptiles in highly thermally heterogeneous environments that regularly exceed preferred temperatures. For three species of small sympatric skinks in the genus *Carlia* that occur in savanna woodland of tropical Australia, we measured body temperatures during activity (T_b), available thermal microclimates (T_e) in the habitat they used, and selected temperatures in a thermal gradient (T_{sel}) in summer and winter. We use these data to determine (1) whether thermal quality was sufficiently similar to T_{sel} to provide a 'salubrious' environment in which thermoregulatory behaviour was not necessary, (2) whether these species showed thermoregulatory behaviour, and (3) the precision of thermoregulation of these three species with respect to the costs and benefits of thermoregulation in different thermal environments (i.e., at different times of year).

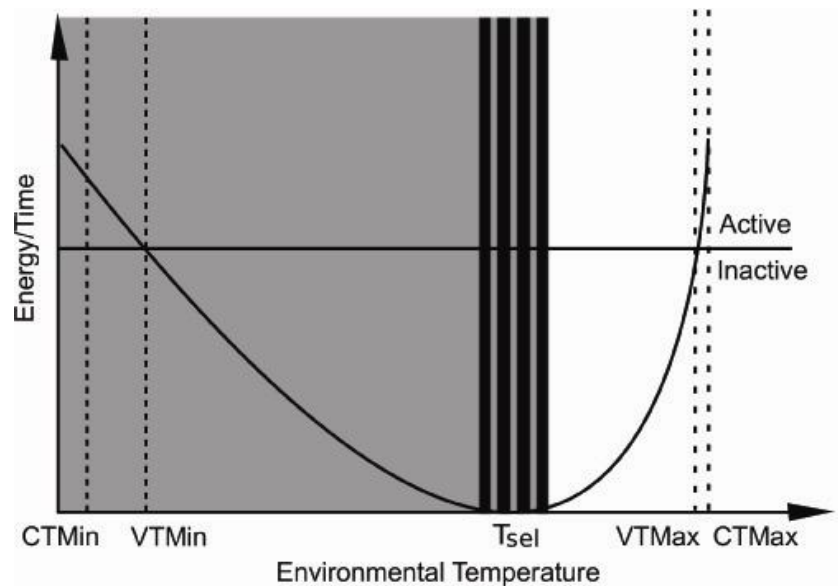


Figure C1. Cost and benefit of attaining preferred body temperature at a given environmental temperature. The solid curve indicates the cost of attaining preferred body temperature relative to available temperatures; the dashed horizontal line is the benefit (which we assume is constant). Nett gain is determined by subtracting cost from benefit, and is maximized when T_{sel} equals environmental temperature (cost = 0). Where the cost and benefit lines intersect, nett gain is zero, this point represents the Voluntary Thermal minimum or maximum (VT_{min} or max), and the animal seeks refuge to avoid more extreme environmental temperatures such as the Critical Thermal minimum or maximum (CT_{min} or max).

The distance from T_{sel} to VT_{max} and CT_{max} is much less than to VT_{min} and CT_{min} , which reflects the asymmetrical performance curve, where lizards perform better close to VT_{max} . The cost of thermoregulation increases much faster when $T_e > T_{sel}$ (unshaded portion) than for $T_e < T_{sel}$. The left, shaded side, exists for cases where $T_e < T_{sel}$, and is the typical case discussed in the literature; the right, unshaded side, is for the case where $T_e > T_{sel}$, a situation more common than once thought.

Methods

Species and study site

This study was conducted between August 2003 and August 2005, at a 5-ha site at Ramsay Bay (Hinchinbrook Island National Park, Queensland, Australia, 18° 24'S, 146° 17'E). Vegetation at the site was open woodland of paperbarks *Melaleuca leucadendron* and *M. quinquenervia* with a *Terminalia* sp. shrub layer, and vine forest containing *Eucalyptus crebra* and *Corymbia* spp. with a shrub and grass understorey including *Xanthorrhoea* spp.,

Rhodomirtus trineural and *Leptospermum polygalifolium*. The canopy provides a thermally heterogeneous environment, with about 50% of the substrate shaded. Sun and shade spots were similar in size, and were in the order of tens of centimetres to metres in area. The habitat is typified by leaf litter-covered ground, usually with moderately dense understorey of vines and low shrubs, providing a mosaic of sun and shade. Hinchinbrook Island experiences a seasonally monsoonal climate with mild, relatively dry conditions in April - September (winter), and hot, humid and wet weather from October - March, (summer).

Our study focused on the three most abundant diurnal lizard species, which represented more than 85% of the lizards observed (Chapter 3), *Carlia rostralis* ($n = 1032$, mean adult SVL = $54 \text{ mm} \pm 7.3 \text{ SD}$, mean adult mass = $4.8 \text{ g} \pm 2.4 \text{ SD}$), *C. rubrigularis* ($n = 856$, mean adult SVL = $45.5 \text{ mm} \pm 5.1 \text{ SD}$, mean adult mass = $2.7 \text{ g} \pm 1.6 \text{ SD}$), *C. storri* ($n = 566$, mean adult SVL = $41.4 \text{ mm} \pm 3.8 \text{ SD}$, mean adult mass = $2.0 \text{ g} \pm 1.4 \text{ SD}$). These skinks are ground-dwelling, cursorial predators, with overlapping habitat and activity times, and competed directly for food and space (Chapter 3).

Thermal indices

We used thermal indices developed by Hertz et al. (1993) and reviewed by Seebacher and Shine (2004, Table C1). Indices include preferred or selected temperature range for a species (T_{sel}), the distribution of available operative temperatures in that species' environment (T_e), the mean of the absolute deviation of T_e from T_{sel} (thermal quality or d_e), and the mean of the absolute deviation of field body temperatures (T_b) from T_{sel} (thermoregulatory precision, or d_b , Table C1). Thermal quality (d_e) of the habitat is typically regarded as high when $d_e < 3$, and a low when $d_e > 5$ (Hertz et al. 1993; Diaz and Cabezas-Dias 2004), and correspondingly, thermoregulation is expected to require less effort (or to be more precise) when thermal quality is highest (i.e., < 3). High precision of thermoregulation (low d_b) can be a side effect of living in a thermally congenial habitat, or can indicate that thermoregulation is a high priority to the animal (Blouin-Demers and Nadeau 2005). Conversely, high d_b can be caused by inattention to thermoregulation, or to poor habitat thermal quality impeding precise thermoregulation. The index E, calculated as $1 - d_b/d_e$, is the efficiency of thermoregulation (Table C1). A thermoconformer scores $E = 0$, a perfect

thermoregulator scores $E = 1$, and $E < 0$ implies that the animal's body temperature is farther from T_{sel} than the available environmental temperature.

Available environmental temperatures (T_e s) were not normally distributed, so measurements of the mean were not indicative of central tendency (Zar 1974). Median temperature provided a better measure the temperature of the average location, therefore we present median rather than mean environmental temperatures in our figures. Calculations of standard indices (d_e , d_b , E) were based on mean values for consistency with other published works.

Analysis of thermoregulatory effort was completed using linear regression of d_b and d_e (Blouin-Demers and Nadeau 2005). The model tested was that the slope of the regression was equal to zero ($m = 0$), though confidence intervals were constructed around m to determine whether $m = 1$. A slope of 1 ($m = 1$) implies that as thermal quality decreases (d_e increases), the effort of thermoregulating remains constant. A slope of $m > 1$ shows that effort declines as thermal quality declines (as predicted by the Cost-Benefit Model), and $m < 1$ is the opposite: thermoregulatory effort increases as thermal quality decreases.

Table C1. Definitions of the indices of thermoregulation from Hertz et al. 1993.

Index	Definition
T_{sel}	Selected body temperature. Central 50% of body temperatures measured in thermal gradient
T_e	Operative environmental temperature
d_e	Thermal quality of habitat, measured as mean unsigned deviation of T_e from T_{sel}
T_b	Field active cloacal temperature
d_b	Accuracy of thermoregulation, measured as mean unsigned deviation of T_b from T_{sel}
E	Efficiency of thermoregulation, $E = 1 - d_b/d_e$

Estimates of body or active temperature (T_b)

Field sampling took place over 64 summer days and 94 winter days, over three years (2003 - 2005). The study area was searched actively, and adult lizards were captured by

hand between 0700 and 1800 on sunny days. We recorded cloacal temperature (T_b) within 30 s of capture (to the nearest 0.1° C using a digital thermocouple thermometer [Type T, Model 90000]) of active lizards, not disturbed from retreat sites under cover, and chased for less than 30 s.

Estimates of operative environmental temperatures (T_e)

Available environmental operative temperatures (T_e) were measured hourly using digital temperature recorders (Thermocron iButtons™, $n = 42$), while lizards were being sampled. iButtons provide a suitable model of operative environmental temperatures available to small (<10 g) skinks (Vitt and Sartorius 1999). iButtons were placed on the substrate in the open at regular intervals over the entire site. We targeted areas used by skinks, avoiding very large areas (>20 m across) that received full sunlight for the entire day. iButtons were moved every two months to new locations, while maintaining similar distribution of iButtons across the site.

Table C2. Thermoregulation indices recorded for summer and winter for three *Carlia* species, T_{sel} (°C) was higher in summer than winter to better exploit higher environmental temperatures encountered in summer. Mean d_e was similar in summer and winter, though summer d_e SD was greater than winter, and summer had significantly more variable T_e than winter (see text). Precision of thermoregulation (d_b) was higher in summer than winter, a reflection of the high cost of thermoregulating under extreme conditions.

Species	Season	T_{sel}	d_e	d_b
<i>C. rostralis</i>	winter	26.4 - 29.3	3.62 (3.09)	1.40 (1.43)
	summer	28.0 - 32.0	3.37 (5.04)	0.65 (1.18)
<i>C. rubrigularis</i>	winter	25.4 - 28.3	2.95 (3.01)	1.67 (0.99)
	summer	28.2 - 31.4	3.66 (5.17)	0.71 (0.99)
<i>C. storri</i>	winter	25.5 - 29.0	2.94 (2.92)	1.66 (1.74)
	summer	29.4 - 32.3	3.93 (4.89)	0.62 (1.96)

Available Environmental Temperatures (T_e)

In both seasons d_e was around 3° C, indicative of high thermal quality (Table C2), though fluctuations in T_e were not the same in summer and winter. The different thermal regimes in summer and winter produced habitats of very different thermal quality. Variability in

T_e was significantly different between summer and winter (Bartlett's K-squared = 12666.44, d.f = 1, $P < 0.01$, winter (median $\pm$ MAD) $23.5^\circ \text{C} \pm 2.97$, summer $29^\circ \text{C} \pm 5.19$; Figure C2). The higher variability of T_e in summer was due to a high proportion of temperatures high enough to be dangerous to skinks (Figure C3).

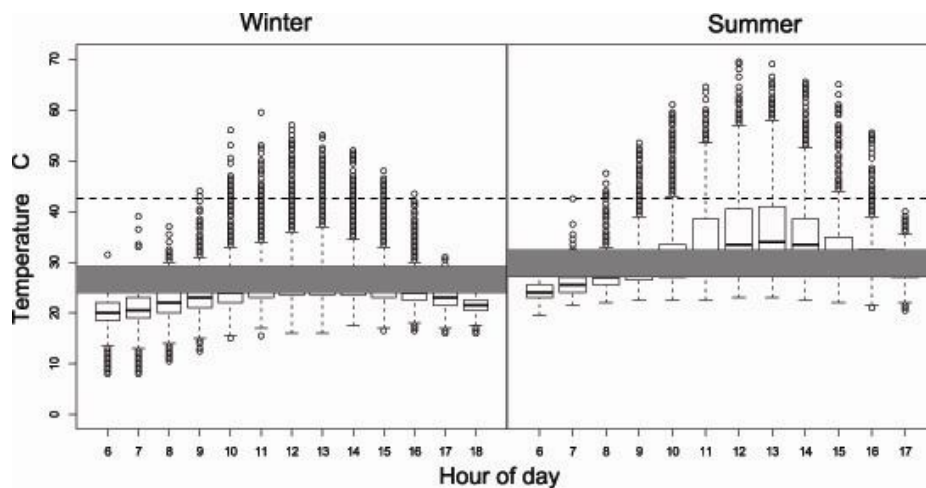


Figure C2. Hourly available operative environmental temperatures (T_e) at Hinchinbrook Island in winter and summer. Open circles are outliers estimated as $1.5 \times \text{IQR}$ outside 1st and 3rd quartile. The dashed line illustrates $VT_{\max}$, the shaded zone represents the maximum T_{sel} range for three species of *Carlia* skinks. (Winter T_e $n = 54,678$, summer T_e $n = 14,638$). Median T_e is typically within T_{sel} in winter, and below T_{sel} in the early morning and afternoon. Compared to this, summer has very hot days with early and late median T_e within T_{sel} , but through the middle of the day median T_e is above T_{sel} .

During winter, environmental thermal quality was quite high. From 1000 to 1600, median T_e was within the bounds of T_{sel} for all species (Figure C2). Typically, T_e was less than T_{sel} (Figure C3), though there were many sites where T_e was greater than T_{sel} , and even some greater than $VT_{\max}$ (Figure C3). Summer had similar morning temperatures to winter, where most T_e were less than T_{sel} (Figure C3), however from 1000 to 1500, median T_e was above T_{sel} for all species (Figure C2), and up to 40% of T_e were above $VT_{\max}$ (Figure C3). Thus, although mean de was around 3°C , a putative 'average location' throughout summer was too hot. This, combined with the prevalence of dangerously high T_e s indicated that in summer the environment was of low thermal quality.

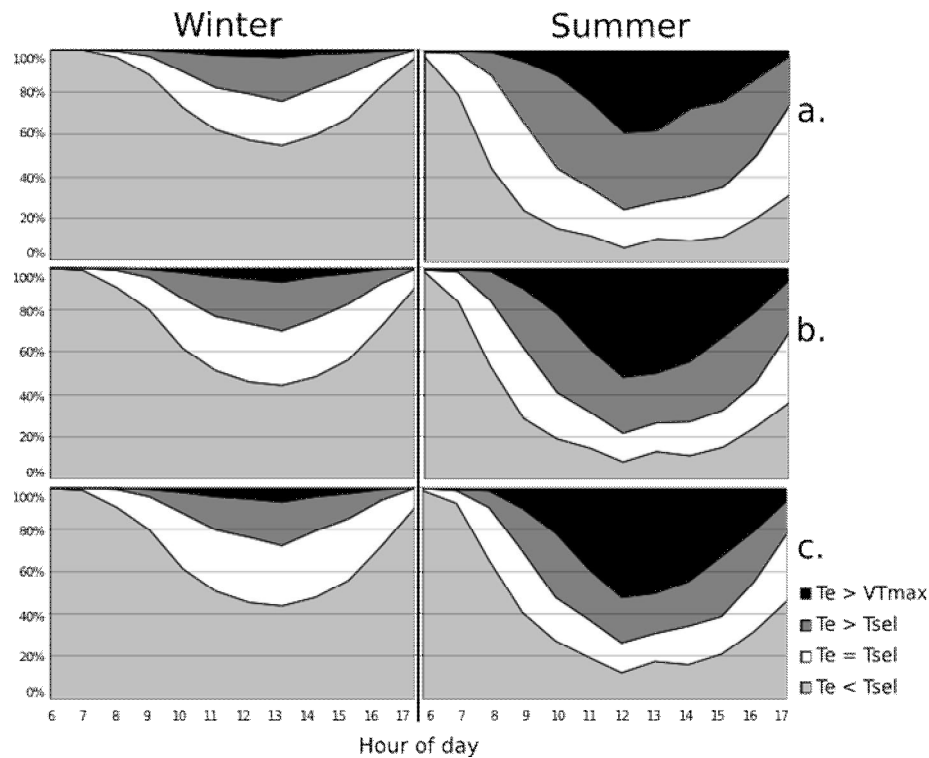


Figure C3. Proportion of T_e measurements that were less (light grey), equal (white), or greater than T_{sel} , as well as the proportion of T_e measurements less than (dark grey), and greater than (black) VT_{max} for three *Carlia* species in winter (left panels) and summer (right panels) throughout the day (winter $n = 163$ days, summer $n = 70$ days). Although d_e is similar in both seasons, the thermal profile was quite different. T_e was mostly less than T_{sel} during winter, though up to 5% of T_e was above VT_{max} . At least 50% of T_e in winter were high enough to raise T_b to at least T_{sel} . In summer, T_e was typically above T_{sel} , and up to 40% of T_e was above VT_{max} . For most of the day in summer, T_e cold enough to cool a lizard in the case of overheating was scarce, as little as 15% of the day.

Thermoregulatory Precision (d_b and E)

We collected body temperatures from 289 *C. rostralis* (88 summer, 201 winter), 259 *C. rubrigularis* (71 summer, 188 winter), and 192 *C. storri* (97 summer, 95 winter). In winter, the three species thermoregulated with intermediate efficiency, around 0.5, though in summer, all species thermoregulated with significantly high efficiency (0.8, Figure C4) despite the lower thermal quality of the habitat. The efficiency of thermoregulation was mostly driven by the precision of thermoregulation (d_b). In winter, all species were within the top 30% of all reported d_b values ($d_b < 1.7^\circ \text{C}$, Table C2; Blouin-Demers and Nadeau 2005). In summer, they were within the top 10% of reported values ($d_b < 0.8^\circ \text{C}$, Table C2). Thermoregulatory effort increased as thermal quality of the environment decreased (d_e increased) for all species

(Figure C5) across both seasons (*C. rostralis* [$d_b = 0.3173 \cdot d_e + 0.3477$, $R^2 = 0.31$, $P < 0.01$, $0.19 < m < 0.44$]; *C. rubrigularis* [$d_b = 0.2301 \cdot d_e + 0.9158$, $R^2 = 0.08$, $P = 0.03$, $0.02 < m < 0.44$]; *C. storri* [$d_b = 0.5305 \cdot d_e - 0.0919$, $R^2 = 0.25$, $P < 0.01$, $0.27 < m < 0.79$]).

In winter, T_b was often above T_{sel} (Figure C6), despite the distribution of T_e , where median T_e was often within T_{sel} (Figure C2), and most T_e were below T_{sel} (Figure C3). By comparison, in summer, median T_e was less often within, and often above, T_{sel} (Figure C2), and most T_e were above T_{sel} (Figure C3), yet T_b were distributed similarly to winter T_b , with similar proportions of T_b within and above T_{sel} , though in winter, there were more T_b below T_{sel} than summer (Figure C6). Maintaining T_b above T_{sel} in summer may be an uncontrollable side effect of high T_e , with the result that lizards sought refuge at midday rather than risk still higher T_b . Though in winter, the lizards had greater access to low T_e , and the lower variation in winter meant more T_e was available near T_{sel} than in summer (Figure C2, C3), implying a deliberate choice to maintain high T_b , or that precise thermoregulation in winter was relatively less important than another activity.

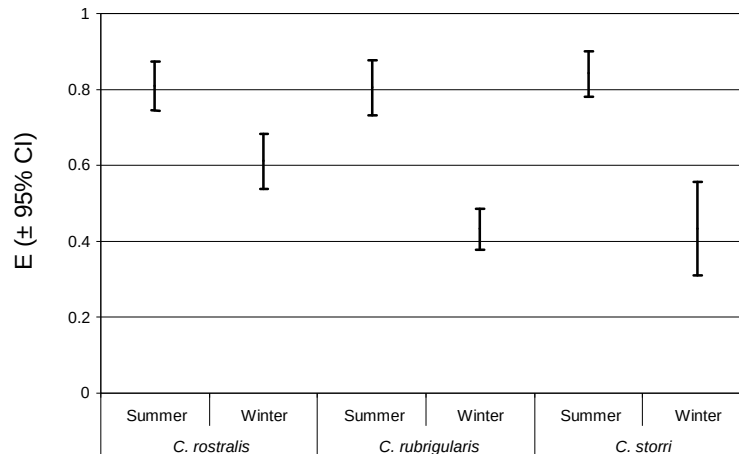


Figure C4. Efficiency of thermoregulation ($E \pm 95\%CI$) in summer and winter. E was significantly higher in summer than winter for all species.

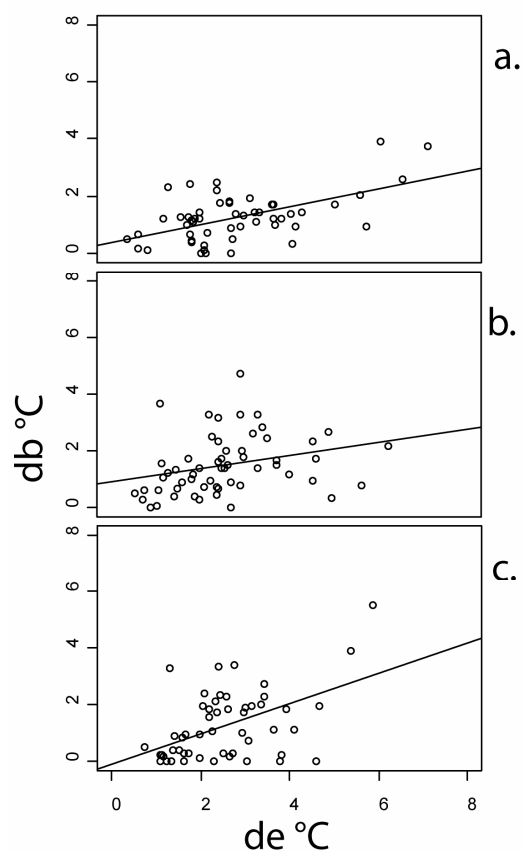


Figure C5. Values of mean d_b and d_e measured per hour across the study period for (a) *C. rostralis*, (b) *C. rubrigularis*, and (c) *C. storri*. Solid line is regression line, broken line is a reference line for $m = 1$.

Hypothesis tested: $m = 0$. In all cases, $m < 1$ (see text), hence as thermal quality decreases (d_e increases), thermoregulatory effort increases. This is contrary to the Cost-Benefit Model of thermoregulation that predicts thermoregulatory effort will decrease as thermoregulatory cost increases (thermal quality decreases).

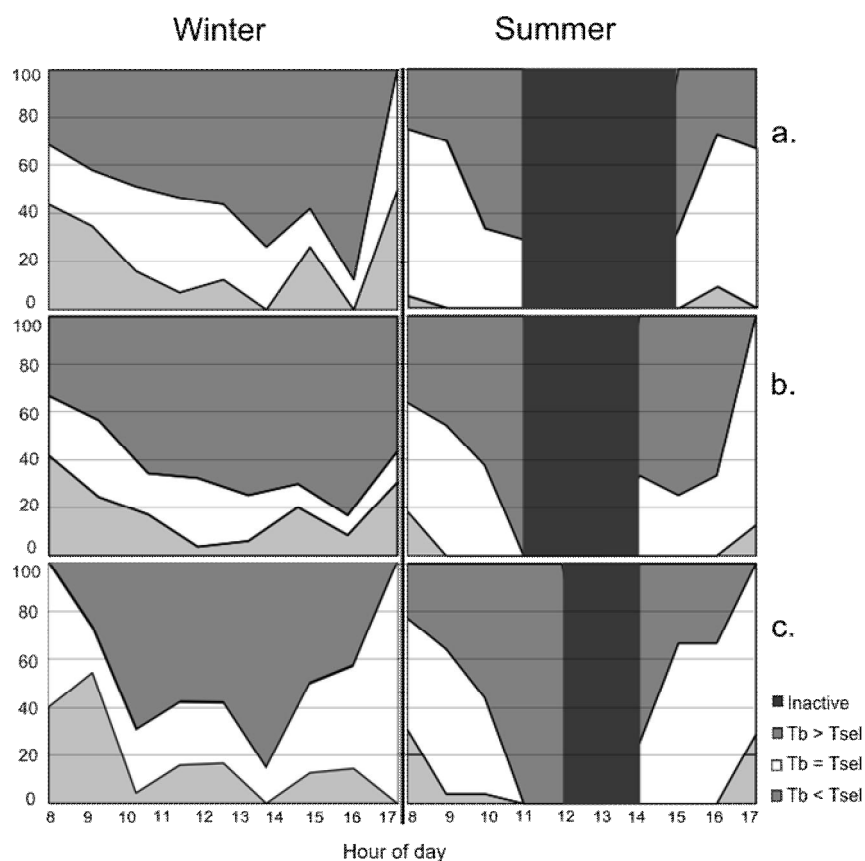


Figure C6. Proportion of T_b measurements that were less (grey), equal (white), or greater (dark grey) than T_{sel} for three *Carlia* spp. in winter (left) and summer (right) throughout the day. Dark shaded areas in the middle of the summer day is when lizards were inactive, and unavailable for T_b measurement.

Lizards maintained T_b above T_{sel} for most of the day in both seasons even though thermal profile through the day was quite different. In winter, encounters with high enough T_e to maintain T_b above T_{sel} .

Discussion

The Cost-Benefit Model and Precision of Thermoregulation in Tropical Lizards

The Cost-Benefit Model of thermoregulation predicts that when thermal quality is low, the cost of thermoregulation should eventually exceed the benefit, and individuals should reduce the precision of thermoregulation until they abandon it (Hertz et al. 1993; Blouin-Demers and Nadeau 2005). However, contrary to these predictions, our skinks thermoregulated more precisely (Figure C5), and significantly more efficiently (Figure C6), when thermal quality was lower than when thermal quality was higher.

Winter had lower precision (higher d_b , Table C2), and lower efficiency (lower E , Figure C4) of thermoregulation than summer. Further, less effort was invested in thermoregulation while thermal quality was low (Figure C6). Simple thermoconformation in winter would result in T_b having a similar distribution to T_e , which is not the case (Figure C3, C4): low precision in winter was due to body temperatures (T_b) higher than preferred temperatures (T_{sel} ; Figure C4) despite the relative abundance of sites with high thermal quality, and the bias for T_e to be below T_{sel} (Figure C3). The implication is that skinks actively maintained body temperatures (T_b) above preferred temperatures (T_{sel}). The skinks may have been deliberately increasing T_b to take advantage of increased performance or activity time and space, or, alternatively, increased body temperatures may have been a side effect of engaging in an activity other than thermoregulation. For example, foraging may have been best in areas, or at times, warmer than preferred body temperatures, with the associated effect of high T_b . A recent model suggests that predators of ectothermic prey should spend more time in hotter areas, which would increase T_b (Mitchell and Angilletta 2009). We have evidence that invertebrate diet item availability, and therefore foraging success, is indeed increased at warmer times of day for these skinks (*unpublished data*). Grant and Dunham (1990) also observed lizards in hot environments active at T_b s much higher than T_{sel} , and attributed this to the lizards' lack of time to complete daily activities (foraging) without spending some time at high T_b .

In summer, thermal quality was lower, yet contrary to the predictions of the Cost-Benefit Model of thermoregulation, the skinks invested more effort into thermoregulation (Figure C5), resulting in increased precision (Table C2) and efficiency of thermoregulation (Figure C6). Preferred temperature (T_{sel}) was higher in summer, and therefore closer to critical thermal maxima (CT_{max}). A higher preferred temperature increased the likelihood that T_{sel} would be available in the hotter, summer environment, but also meant that skinks had a reduced margin of error for imprecise thermoregulation. The distribution of environmental temperature in summer (T_e) was skewed positively, and most T_e was above T_{sel} throughout the day in summer. Few T_e were available below T_{sel} , and accordingly, T_b was often above T_{sel} . Combined with the reduced margin of error of thermoregulation, the poor thermal quality and highly skewed summer T_e necessarily resulted in more precise thermoregulation, the alternative being to risk exposure to lethal temperature. The high cost of failing to

thermoregulate (death) in summer lead to significantly higher thermoregulatory precision, rather than the decrease in thermoregulatory precision predicted by the Cost-Benefit Model. If the cost of thermoregulation increased but did not become lethal, as prevails in cool climates, thermoregulatory precision might have decreased as predicted (Hertz et al. 1993; Sartorius et al. 2002; Herczeg et al. 2006). Our data suggest that the present Cost-Benefit Model for thermoregulation needs to be extended to include the case where T_e exceeds T_{sel} , and an emphasis needs to be placed on the high cost of thermoconformity (Blouin-Demers and Nadeau 2005) rather than just the cost of thermoregulating, especially in extreme environments.

Although skinks thermoregulated more precisely in summer than winter, T_b was still often above T_{sel} in summer, just as it was in winter. As with winter, T_b above T_{sel} may have been a deliberate action on the part of the skinks, and possibly for similar reasons (i.e., improved performance and foraging success, *unpublished data*). On the other hand, the distribution of d_b and T_e were more similar in summer than winter (Figure C3, C4), suggesting that skinks may not have been able to lower T_b to T_{sel} while satisfying the need for enough time and space to complete required activities (Grant and Dunham 1990).

An increase in T_b may have improved performance enough to offset the costs of high metabolism at our study site, but extreme care was required when maintaining T_b above T_{sel} in summer. At the moderately high temperature of 50° C, small (< 12g) reptiles heat up at 4° C per minute (Herczeg et al. 2007) and at our study site T_e reached temperatures higher than 50° C on a regular basis. While increasing T_b may improve performance, the skinks had to ensure they would not to increase T_b beyond the point of 'no return' (i.e., loss of righting ability or CT_{max}). Thus, in summer, skinks retreated from the extreme temperatures prevailing in the middle of the day (Figure C4). Retreating into shelter sites could be interpreted as abandoning thermoregulation, but in this warm environment, shelter sites reach, and remain well within, preferred temperatures for *Carlia* throughout the day (Andersson et al. *in press*). Continuing thermoregulation in shelter sites is common in many reptiles (e.g., Huey et al. 1989), including *Carlia* (Andersson et al. *in press*).

Lizards Thermoregulating in Tropical Environments

Activity at temperatures higher than T_{sel} could have been due to unusually low T_{sel} in these lizards, but selected temperature ranges of these skinks was typical of small, ground-dwelling species, around 28-32° C (reviewed by (Blouin-Demers and Nadeau 2005). Preferred temperatures of these species were lower in winter than in summer, which also occurs in many lizard species (e.g., van Damme et al. 1987).

Median environmental temperature (T_e) at Hinchinbrook Island was often within the preferred temperature for these skinks, an observation common to many studies of reptile thermoregulation in the tropics (e.g., Shine and Madsen 1996; Luiselli and Akani 2002). Accordingly, d_e for the whole season was around 3° C (Table C2) for the three *Carlia* spp. across both seasons, implying that the environment was of high thermal quality, or a congenial thermoregulatory habitat (Hertz et al. 1993). However, in both summer and winter, midday T_e reached over 60° C, and median summer T_e at midday reached 35° C (Figure C2). Thus, the lizards at our study site, like many other, even temperate species, must avoid midday heat in both seasons, especially in summer. In winter, the lizards needed to bask in the morning to increase T_b , whereas from 1100 until almost 1600, T_e was such that lizards could apparently thermoconform. However, thermoconforming in winter would have exposed these skinks to temperatures greater than their voluntary maximum up to 5% of the time, which could cause mortality. Further to this, the distribution of T_b was different enough from T_e to imply deliberate thermoregulation (Figure C3, C4). In summer, median T_e was within T_{sel} in the morning and evening, but in the middle of the day in summer, only 30% of available environmental temperatures (T_e) were within T_{sel} , and accordingly, the skinks sought refuge and were unavailable for capture (Figure C3, C4). Even before 1200 and after 1500, when skinks were active, only a low percentage (20%) of habitats had ideal T_e , and up to 50% of locations had T_e above VT_{max} (Figure C3). Thus, in the middle of the day, all species reached the threshold where costs outweighed the benefits of remaining active, and the lizards retreated to refuge sites (Figure C4). In both winter and summer, behavioural thermoregulation was required, both to increase T_b and, more importantly, to avoid death through exposure to T_e exceeding critical thermal maximum temperatures. Our results

indicate that the high cost of low thermal quality, even when it only occurred relatively rarely, could drive the behaviour of these skinks.

Most tropical reptiles are small-bodied (or at least as juveniles), and are, therefore, highly susceptible to small-scale perturbations in T_e (Seebacher and Shine 2004). Also, many tropical reptiles live in environments with high thermal heterogeneity. Future models of thermoregulation must consider the well-known phenomenon that high temperatures disproportionately affect ectotherms (Huey and Kingsolver 1993), and that small-bodied ectotherms are highly affected by even moderate temperatures (50° C, Herczeg et al. 2007). Far from not needing to thermoregulate, small tropical ectotherms faced a complex thermal environment that differed widely between seasons, and required different, but precise, thermoregulatory behaviour.

The Cost-Benefit Model of thermoregulation (Huey and Slatkin 1976) focuses on the costs and benefits of thermoregulating and while overlooking the costs and benefits of failing to do so (Blouin-Demers and Nadeau 2005). Further, the Cost-Benefit Model does not examine the case where environmental temperature exceeds selected temperature (Huey and Stevenson 1979), which is apparently the rule, rather than an exception (Kearney et al. 2009). Increasing temperatures, as predicted by various climate change models (Deutsch et al. 2008), will likely increase exposure of lizards to lethally high temperatures, and thus further consideration of the effect of lethally high temperatures on thermoregulatory behaviour is warranted.

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