

---

**SIZE DIMORPHISM IN THE AGAMID *RANKINIA DIEMENSIS*:**

**PATTERNS, ADAPTIVE SIGNIFICANCE**

 **& EVOLUTIONARY PATHWAYS**

**JEMINA FARIA STUART-SMITH (BSC. HONS)**

Submitted in fulfilment of the requirements for the Degree of Doctor of  
Philosophy

SCHOOL OF ZOOLOGY  
UNIVERSITY OF TASMANIA  
2007

---

---

## DECLARATION AND AUTHORITY ACCESS

This thesis contains no material which has been accepted for a degree or diploma by the University of Tasmania or any other institution, and to the best of my knowledge and belief, this thesis contains no material previously published or written by another person, except where due acknowledgement is made in the text of this thesis.

This thesis may be made available for loan and limited copying in accordance with the *Copyright Act*, 1968.

Signed: 

(Jemina Stuart-Smith)

Date: 29-11-07

---

## ABSTRACT

Body size is one of the most important life history traits of an organism, with links to, and influences on, almost all areas of an organism's ecology and evolution.

Size divergence between males and females of the same species, termed sexual size dimorphism (SSD), reflects three major processes acting on body size: sexual selection (intra- and inter-specific competition), natural selection (fecundity advantage), and selection related to niche divergence. Each of these selection pressures has the potential to magnify or reduce the degree of size difference between the sexes.

This thesis examines SSD in an agamid lizard, *Rankinia diemensis*, which exhibits female-biased dimorphism within a taxonomic group that is typically dominated by male-biased SSD. This investigation of size dimorphism addresses the above ultimate processes as well as determining the potential proximate mechanisms (the physical process producing the size difference) between males and females.

Assessment of overall size and other morphological traits (e.g. head, limb and tail sizes) revealed that although females have larger overall body size, other traits are proportionally longer in males, suggesting that several selection pressures are at work. Geographic comparison also revealed that these sizes are not static – larger individuals (overall size) were found in the northernmost population studied, and trait size also varied geographically, but the overall degree of size difference between sexes from each site did not vary. This suggests that the net selection pressures acting on geographically distinct populations are similar. It also

---

---

indicates that a combination of genetic and environmental factors may influence size, but there are constraints on the degree of size divergence that can occur between the sexes.

Analysis of size at hatching, growth trajectories and size asymptotes between the sexes revealed that males and females hatch at a similar size and grow at similar rates prior to maturity. Males and females begin to diverge in size (including overall size and trait sizes such as head, limb and tail measurements) at three to four years of age. Male growth rate asymptotically approaches zero at maturity, while females continue growing throughout life; however both sexes live to approximately the same age. It is therefore the combination of delayed maturity and post-maturity growth in females that allows them to attain larger size than males.

Size-specific reproductive output exists in *R. diemensis* with a strong positive relationship between female body size and fecundity, but no other aspect of reproductive output in females is dependent on size (e.g. average egg mass, relative clutch mass). This suggests that larger size does not permit females to put more energy into individual eggs, it only allows them to increase the number of eggs they can lay – suggesting that fecundity selection is a major driving force behind SSD in *R. diemensis*.

As males are the smaller sex, it suggests that there is no strong positive selection on male body size. This is despite such selection being common in other agamids, where size determines contest success with conspecifics. Competition

---

---

experiments revealed typical agamid male-male antagonistic interactions, with large size linked to aggressive/dominant behaviour. In males this could be a function of trait size (not overall size), since limb and head movements are the primary forms of communicative display in agamids. It could also suggest that there are opposing selection pressures acting on males to mature smaller. This is also reinforced by the field study component of this thesis, where the use of microhabitat differed between males and females, and is most likely linked to rival or courtship displays. Males used higher structural habitat, typical for male agamids, which engage in displays from these posts. Males also perched in more exposed areas than females. Mature females utilized sites with higher temperatures, analogous to previous research that has found that a female can have considerable influence on her offspring during egg development *in utero*. These sex-specific behaviours are likely to promote niche divergence between the sexes, potentially reducing intra-specific competition.

Overall this thesis reveals that a complex interplay of different selection pressures acting on size is responsible for the observed SSD in *R. diemensis*. My findings demonstrate the influence of morphological variation on key life history components - such as reproductive output, mating system and microhabitat use. Furthermore, this thesis emphasizes the importance of viewing SSD evolution in the context of not only why one sex is large, but also why the other is small, and further demonstrates the complexity of trait evolution.

---

## ACKNOWLEDGEMENTS

This thesis could not have been completed without the help of the following people, to whom I am forever grateful:

Rick Stuart-Smith: it might break tradition to acknowledge you before my supervisors, but no-one could possibly have helped me more throughout this project, or been more influential to its, or my, direction than you. I am not sure if I would have started a PhD without your belief and encouragement, and I certainly doubt I could have finished it without your support throughout.

Erik Wapstra: you came on to this project halfway through and provided an incredible amount of direction and depth to it. Your input greatly improved the framework and flow of this study, and I am particularly grateful for all of your help in manuscript preparation and submission. It took us a while to agree on the right way to tackle a paper together, but we worked it out in the end, and I have always valued your ideas and input.

Roy Swain: your encouragement and enthusiasm during my Honours project was incredibly influential in my decision to undertake this PhD. Your enthusiasm is inspirational, and I am forever grateful for how much interest you showed in my work and for always having time to stop and chat.

Sue Jones: you were a fantastic mediator, and I always felt that you were there if I needed you, whether it was someone to complain to, or a shoulder to cry on.

Natalia ‘Natski’ Atkins: I could not have completed this thesis and maintained my sanity without you. I appreciate all your help and for so much fun along the way. I’ve missed having you around since you handed your thesis in.

Ashley Edwards: thanks for so much help – for the dragons that you caught, those torturous days digging up eggs for incubating, and help in seminar preparation. I really love your enthusiasm, and appreciate the time you’ve spent helping me.

---

---

To all those people who contributed to the project somehow, or perhaps more importantly, made it so much fun along the way:

Natasha Wiggins – a great friend, thanks for all the honest footy tipping advice; Anthony Reid – without those constant coffee interruptions, I probably would have finished long ago, but I am especially grateful for your stats advice and for making me so many cuppas; Scotty Ling – always great to chat with, although with an uncanny ability to work urchins into absolutely any topic of conversation; Adam Stephens – always good fun, despite your intentional misinformation campaign regarding footy tipping; Fiona ‘stumps’ Spruzen – morning tea was never the same after you left; Geoffy While – always fun & a great office buddy; Heidi Auman – always great to chat with; Regina Magierowski – my gym buddy; Sue Baker; Anne Watson; Sarah Tassell; Erin FlynnE; Keisuke Itonaga; Amelia Hall; Paulo Duharte – for the Burnie 10; Marlies Jahn – for catching the only 3-legged dragon I’ve ever seen; Chloe Cadby and Lou Cromer.

Other zoology/UTAS staff who helped/provided support in some way: Sherrin Bowden (there is no better secretary), Barry Rumbold, Kate Hamilton, Wayne Kelly, Richard Holmes, Alastair Richardson, Simon Talbot, Randy Rose, Leon Barmuta & Kit Williams. Also, to the University Sports Centre staff – particularly Nadia & Helen – for all those classes and gym inspiration.

And finally, my family: Dean, Anita & Adam have always given me support and encouragement, although I don’t know if you ever quite understood why I love uni so much, and why I’ve spent so much time there. My mum, dad and Restu have always been there for me – hopefully you’ll read this thesis and finally understand what I’ve been doing for the past few years, and why it has taken so long. Trish, Pete, Sarah and Rob – your support and confidence in me throughout this PhD, and since we met, is greatly appreciated.

---

## CONTENTS

DECLARATIONS	I
ABSTRACT	II
ACKNOWLEDGEMENTS	V
CONTENTS	VII
CHAPTER 1: GENERAL INTRODUCTION	1
Sexual dimorphism	2
Sexual size dimorphism (SSD)	3
Studying SSD: Scales of analysis	6
SSD in agamid lizards	13
Study species	14
Research aims	15
Presentation of thesis	16
Thesis outline – summary of papers	17
References	22
CHAPTER 2: SIZE DIMORPHISM	27
Abstract	28
Introduction	29
Methods	33
Results	38
Discussion	43
References	50
CHAPTER 3: PROXIMATE MECHANISMS	55
Abstract	56
Introduction	57
Methods	61
Results	64
Discussion	68
References	72
CHAPTER 4: FECUNDITY	75
Abstract	76
Introduction	77
Methods	79
Results	82
Discussion	88
References	93

---

---

CHAPTER 5: COMPETITION	96
Abstract	97
Introduction	98
Methods	102
Results	107
Discussion	110
References	115
 CHAPTER 6: NICHE DIVERGENCE	 119
Abstract	120
Introduction	121
Methods	124
Results	127
Discussion	136
References	142
 CHAPTER 7: GENERAL DISCUSSION	 146
References	159

SUPPORTING DOCUMENT: SPECIES BIOLOGY & REPRODUCTIVE ECOLOGY

---

## CHAPTER 1

# GENERAL INTRODUCTION

---

## **CHAPTER 1**

### **GENERAL INTRODUCTION**

#### **SEXUAL DIMORPHISM**

In some taxa, morphological differentiation between males and females is so distinct that sexes of a single species may appear, and have been originally described, as completely different species (e.g. the mallard, *Anas platyrhynchos*; Andersson, 1994; Owens & Hartley, 1998). In other species, like the European swift (*Apus apus*) and the spotted hyena (*Crocuta crocuta*), the sexes are almost identical in appearance (Andersson, 1994; Owens and Hartley, 1998).

Morphological differentiation between sexes of mature adults is termed sexual dimorphism (SD; Fairbairn, 1997), and is a major focus for evolutionary biologists since understanding the evolutionary processes that influence body size allows identification of adaptation and avenues for evolutionary change (Sugg *et al.*, 1995).

Sexual dimorphism occurs in most taxa, but varies substantially among, and even within, species (Blanckenhorn, 2005; Fox & Czesak, 2006; Kaliontzopoulou *et al.*, 2007). The influence of sexual dimorphism spans numerous aspects of an animal's biology – including behaviour, ecology, physiology, demography and evolution (Cox *et al.*, 2003). Differences between the sexes can arise in the form of shape, size, colour, armaments and ornaments (Badyaev & Hill, 2003; Preest, 1994; Stuart-Fox & Ord, 2004; Storz *et al.*, 2001). Sexual dimorphism is expressed in vastly different forms, for example, canine size, cranium size and

---

coat colour in New World monkeys (Masterson & Hartwig, 1998); longevity in *Homo sapiens* (Teriokhin *et al.*, 2004); plumage colour and beak size in birds (Owens & Hartley, 1998; Price & Birch, 1996; Temeles *et al.*, 2000); and body size and shape in some mammals, reptiles, fish, seabirds and birds of prey (e.g. Bouteiller-Reuter & Perrin, 2004; Krüger, 2005; Lindenfors *et al.*, 2003; Olsson, *et al.*, 2002; Young, 2005).

#### SEXUAL SIZE DIMORPHISM

Sexual size dimorphism (SSD) is the difference in body size between mature males and females of the same species (Andersson, 1994; Fairbairn, 1997). Body size is a fundamentally important attribute, and one that is subject to strong and ongoing evolution (Blanckenhorn *et al.*, 2003). It is strongly correlated with many physiological and fitness related traits (Blanckenhorn, 2000; Blanckenhorn & Demet, 2004; Peters, 1983; Reis, 1989; Stearns, 1992), and is often one of the most conspicuous differences between males and females (Andersson, 1994).

Andersson's (1994) taxonomic review of sexual size dimorphism in the major animal taxa is detailed in Table 1. Here I summarise the most common direction of size-dominance, but there are species within each group that show the opposite trend for size dimorphism.

Female-biased SSD (females the larger sex) occurs in most taxa, particularly invertebrates, and the fecundity advantages associated with large size are thought to be the major reason for this form of dimorphism (Andersson, 1994). There are of course exceptions, including a number of birds, reptiles and mammal groups,

---

which often exhibit male-male contest for resource defence and mate gain, where large male size is clearly an advantage (Andersson, 1994).

Table 1. Andersson’s (1994) taxonomic review of sex-specific body size difference found throughout the animal kingdom. This shows the general trend found in these groups.

TAXONOMIC GROUP	LARGER SEX
Invertebrates	Females
Fishes	Females
Amphibians	Females
Reptiles	
Lizards	Males
Snakes	Females
Birds (excl birds of prey)	Males
Birds of prey	Females
Mammals	Males

Some extraordinary examples of size dimorphism exist. The female blanket octopus, *Tremoctopus violaceus* Chiaie, is approximately 200 cm in length, while the males are a mere 2-3 cm long; and weight ratios are likely to reach up to 40000:1 (Norman *et al.*, 2002). This size difference has enormous implications for all aspects of life history strategy, form and development in this species. Males have evolved proportionally large eyes, thought to aid in mate location, and their small size presumably reduces development time and the metabolic needs required for mate search.

Anglerfishes also exhibit extreme sexual dimorphism, with females reaching 60 times the length, and being half a million times heavier than the dwarf males (Pietsch, 2005). This group uses sexual parasitism as a reproductive mode to compensate for these phenomenal differences in body size. Males often attach to

the female, their circulatory systems mesh and the male becomes permanently dependent on the female for nutrition (Pietsch, 2005).

Equally as complex are the size dimorphism systems of clownfish. Clownfish such as *Amphiprion percula* exhibit female-biased size dimorphism with a twist. Individuals have both male and female gonads (Munday *et al.*, 2006; Dimijian, 2005) and are capable of sex change – so that the largest female is dominant in the group that she lives in, but if she dies or is displaced, the second-ranked fish, a male, takes her place – not only in terms of hierarchy, but also sex and body size, since an increase in rank is then associated with an increase in body size and a change in sex (Buston, 2003). This is the case for many fish, where the capacity for sex changing allows exploitation of dynamic resources (Munday *et al.*, 2006). This system benefits when there are differential reproductive advantages with size/age – such that fertility increases faster with size (or age) in one sex (Warner, 1988; Munday *et al.*, 2006). Sex change is not an option for most other vertebrate species because of the morphological specialisation required for reproduction and internal fertilisation.

There is, of course, a range of advantages and disadvantages associated with large and small size (Andersson, 1994; Rivas & Burghardt, 2001; see Table 2). Large size can have overall advantages associated with foraging opportunity and reduction in pressure from the number of potential predators, whereas small size can have advantages associated with early maturation or generation time. Disadvantages are associated with each; these include larger organisms incurring higher mobility costs and having greater energetic requirements for sustaining

---

larger size, whereas smaller size may mean higher (relative) energy costs for daily activity (Andersson, 1994; Rivas & Burghardt, 2001).

Table 2. Advantages and disadvantages of large body size. Those for small size can be inferred as the opposite (adapted from Andersson, 1994; Rivas & Burghardt, 2001).

	Advantages	Disadvantages
Males & females	Greater prey type/size available Prey subduing easier Lower feeding frequency Fewer predators Lower relative energetic cost Greater body temperature stability	More conspicuous to predators Greater absolute energetic requirements More conspicuous to prey Higher mobility costs Prolonged maturation
Females	Increased fecundity Potentially larger offspring	
Males	Increased matings if intra-specific competition	Higher mobility cost to increase mate encounter likelihood

STUDYING SSD: SCALES OF ANALYSIS

Tinbergen (1963) proposed four major ways of addressing questions in biology: in terms of trait morphology, which is how body size can be viewed, these questions can be illustrated as follows (adapted from Barnard, 2004):

FUNCTION: what is the trait for? This addresses the role of the trait  
in the life of the organism; how it is used and what it is used for.

MECHANISM: how is that trait achieved? What advantage does the trait  
allow which results in it to be selected for?

DEVELOPMENT: how does that trait develop? What are the physical or  
physiological causes of the trait development?

EVOLUTION: how has the trait evolved? This examines phylogenetic  
pathways that lead to the current state.

This approach to analysing trait development (or other questions in biology) can be further viewed as the examination of **ultimate** and **proximate** causal factors. It is through addressing these causal factors that many researchers have sought, and achieved, explanations for assessment of the value of SSD (Rutherford, 2004; Wainwright & Reilly, 1994; Watkins, 1996). These two causal mechanisms are now reviewed with specific reference to SSD:

**ULTIMATE CAUSES** seek to explain a trait in terms of its evolutionary history and functional significance (Tinbergen 1963; Watkins, 1996). This encompasses the three major selection hypotheses responsible for producing SSD: natural selection; sexual selection (Darwin, 1871; Hedrick & Temeles, 1989; Temeles *et al.*, 2000); and the niche divergence hypothesis (e.g. Hedrick & Temeles, 1989; Webster, 1997; Reeve & Fairbairn, 1999; Losos *et al.*, 2003; Serrano-Meneses & Székely, 2006). These three selection hypotheses describe those *evolutionary* pathways leading to SSD; they describe the *reason* why size differences evolved (Barnard, 2004). In view of this, the study of SSD provides a model for understanding how evolution works – either at the population or species level (Rutherford, 2004). These three ultimate causes are described in relation to SSD:

**Natural selection** explains the mechanisms whereby those individuals best adapted to their environment survive and reproduce, passing on their (favourable) genes. Darwin (1871) defined natural selection as ‘depending on the success of both sexes, at all ages, in relation to the general conditions of life’, differentiating this from sexual selection, which was defined as ‘depending on the success of

---

certain individuals over others of the same sex, in relation to the propagation of the species'. In relation to SSD, natural selection can act directly on body size when reproductive success or survival is correlated to size. The 'fecundity advantage' hypothesis is thought to be a major evolutionary pathway whereby natural selection acts on SSD (Darwin, 1871; Andersson, 1994). Large body size will be selected for if it carries a reproductive advantage such as the ability to produce more offspring. Aside from the costs associated with large size presented for males and females in Table 2, there are some severe detrimental costs associated with increasing reproductive output, and these constraints explain why there is not always selection for increasing body size. Trade-offs between reproduction and growth are central to life history theory, and longevity is often reduced by the number and timing of offspring produced (Westendorp & Kirkwood, 1998).

**Sexual selection** was first articulated by Darwin (1871), and has since traditionally been divided primarily into competition and mate choice. It occurs when differential reproductive success causes competition over mates and it produces traits that benefit mate acquisition (e.g. mate attraction) – e.g. body size, colour or markings, or ornamentation. Sexual selection has traditionally been viewed as acting principally on males, so females often seek these traits since they represent higher fitness (Andersson, 1994), and this is then likely to lead to exaggeration of that trait. This theory is usually based on an antagonistic relationship with natural selection, since sexual selection can produce traits that attract a mate or allow competitive advantage over a conspecific, resulting in successful mate acquisition, but this is often negated by detrimental influences on

---

the organism's survival (e.g. Doherty *et al.*, 2003). A common example of this is where large body size in males has evolved because of the intra-specific advantages that large size provides in male-male competitive interactions to secure a resource (i.e. a mate, a territory, a food resource etc) (Shine, 1989), so large body size is selected for, but this increase in body size may be associated with the cost of large size – for example, easier detection by predators and greater metabolic requirements (see Table 2).

The **niche divergence hypothesis** (or 'ecological niche' hypothesis) proposes that intersexual resource partitioning occurs and explains sex-based size differences (Arnold, 1983; Shine, 1989). Arnold (1983) first hypothesized that differences in phenotype (e.g. between sexes - morphology and physiology) result in differences in functional capabilities. Phenotypic variation allows differential adaptation for different habitat types (Schulte *et al.*, 2004). Sexes often use different aspects of their habitat, and in some cases the degree of spatial and temporal segregation in habitat use can be as great as that of two completely different species (Butler *et al.*, 2007). When the sexes are specialised to utilise different resources, there is less overall demand for a potentially scarce resource (i.e. reducing inter-specific competition). For example, the work of Temeles *et al.* (2000) on hummingbirds (*Eulampis jugularis*) exhibiting sexual dimorphism in bill length and curvature showed that males and females fed most efficiently at the flower species which corresponded to either bill type – thereby resulting in spatial separation of foraging. Moreover, their study showed that this also corresponded with the evolution of floral dimorphism, with male and female dimorphism in flower shape and size to match feeding strategy of male and female hummingbirds.

---

# LINKING THE ULTIMATE CAUSES

Blanckenhorn's (2000, 2005) figure (Figure 1) illustrates the links between the selection forces of sexual selection, natural selection and the niche divergence hypothesis in producing size differences between males and females (and others, including viability selection and genetic constraints, described below). It shows body size distributions for the most common pattern observed in vertebrates - when males are larger than females, but can also be used to understand SSD with female-biases. This figure encapsulates the major processes examined in this thesis.

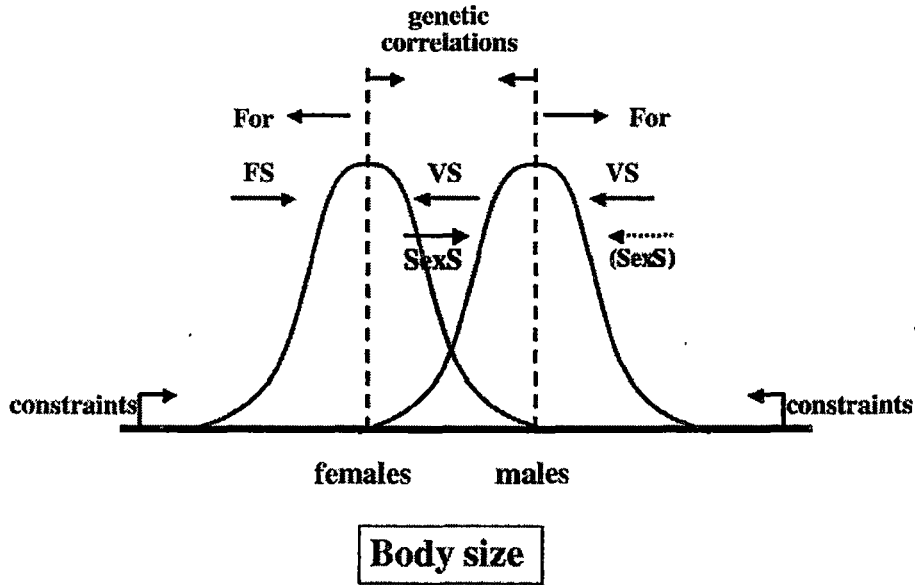


Figure 1. The evolution of SSD as shown by Blanckenhorn's (2000, 2005) differential equilibrium model.

In this figure, fecundity selection (FS) selects for increased body size in females, since large size is often positively correlated with fecundity (e.g. Reeve & Fairbairn, 1999; focus of Chapter 4); however, this is not as strong as the overall viability selection favouring small females, or the sexual selection promoting

large size in males. Sexual selection (SexS) typically selects for increased body size in males, through intra-specific competition and size-specific contest success (focus of Chapter 5). Adult and juvenile viability selection (VS) selects for reduced body size in both males and females, since large size often incurs greater costs (see Table 2 for summary of advantages and disadvantages associated with large body size). Foraging (For) specialization may select for divergent body sizes of males and females, encompassing the niche divergence hypothesis (e.g. Meiri *et al.*, 2005; Shine, 1986; Temeles *et al.*, 2000; the focus of Chapter 6). SSD results when these major selective pressures equilibrate differently in the sexes – when the costs and benefits of each produce different optimal sizes for males and females.

There is often some dispute as to how to view the selection processes acting on SSD, particularly with respect to the ecological niche divergence hypothesis. Some researchers view sexual selection as the only plausible explanation for SSD (e.g. Drovetski *et al.*, 2006), sometimes niche divergence is viewed under the veil of natural selection through reduced resource competition (e.g. Kaliontzopoulou *et al.*, 2007) and sometimes it is not perceived as a primary cause of SSD (e.g. Cox *et al.*, 2003). In this thesis, I view the ecological niche hypothesis as a separate selection pressure since, although it is often perhaps not as dominant a force as natural or sexual selection, it still holds the potential to exert selection on sex-specific body size, and therefore should still be examined in its own right. Recent work on this area is making it increasingly evident that niche partitioning can exert considerable influence on body size and should be viewed separately (e.g. Shine, 1986, Shine *et al.*, 2003; Temeles *et al.*, 2000).

---

**2. PROXIMATE CAUSES** are concerned with physical or physiological factors associated with Tinbergen's four questions. A proximate approach includes the 'mechanism' and 'development' questions, and covers those tangible explanations for body size differences (Blanckenhorn, 2005; Cox *et al.*, 2005). Proximate causes examine the underlying ontogenetic, physiological and behavioural mechanisms behind specific trait evolution and maintenance (Tinbergen 1963; Watkins, 1996). For example, Watkins (1996) found that in the iguanid lizard, *Microlophus occipitalis*, male-biased dimorphism resulted from continued post-maturity growth in males (combined with increased longevity), and lack of post-maturity growth in females, and these two proximate mechanisms produced the observed age-size distribution patterns. Similarly, Cox *et al.* (2005) examined the proximate behavioural, ecological and physiological mechanisms involved in growth regulation in *Sceloporus undulates*. They found that differences in testosterone levels between the sexes corresponded to sex-specific differences in growth, behaviour and colour (Cox *et al.*, 2005). Earlier work by Marler & Moore (1988) similarly linked aggression and testosterone levels with energy expenditure, both revealing the influence that endocrine mechanisms can have on growth regulation.

Proximate mechanisms often examine the ontogenetic stage at which SSD occurs (Shine, 1990). There are two primary stages when size can be determined during ontogeny: at maturity – through sex-specific differences in growth rate or age at maturity (i.e. processes operating on juveniles), or through sex-specific differences in growth rate or survival that occur post-maturity, i.e. processes operating on

---

adults (Shine, 1990). Recent work has emphasized the importance of including focus on sources of influence to growth rate at various life stages, such as physiological factors (e.g. endocrine control; Haenel & John-Alder, 2002; Cox *et al.*, 2005).

Although much work focuses on the ultimate causes of SSD, recent work suggests that proximate mechanisms should also be investigated thoroughly (e.g. Cox *et al.*, 2005). Proximate explanations provide the means through which ultimate causes are played out. An approach encompassing complimentary explanations of SSD – ultimate and proximate causality – is the most appropriate and thorough way to accurately assess explanations for sex-specific size differences.

#### SSD IN AGAMID LIZARDS

In lizards, females are often the larger sex (Andersson, 1994). This is typically associated with increased fecundity in larger females and a lack of territoriality in males. Male-male rivalry and size-dependent contest success is a common selective force leading to large body size in vertebrates (see Andersson, 1994). In lizards, however, there are also families that show distinct male-biases in body size.

The family Agamidae show strong territoriality and reliance on large male body size for contest success (Andersson, 1994; Shine, 1998). The Australian agamids are a conspicuous group; they are extremely visually oriented (Greer, 1989). Males are typically the larger sex, and aggression and other dominance displays between conspecifics are well studied (Greer, 1989; Olsson, 1995; Ord *et al.*,

---

2001). Male dragons are often conspicuous by size, colour and behaviour (Greer, 1989; Ord *et al.*, 2001) – they are often brightly coloured (LeBas & Marshall, 2000; Stuart-Fox & Ord, 2004) and highly aggressive (Peters & Ord, 2003; Radder *et al.*, 2006).

Shine *et al.* (1998) presented the direction of dimorphism in a number of agamids, illustrating just how common male-biased SSD is, with 19 out of 21 species examined showing large male size, and all but one also showing proportionally larger head size in males. In fact, Shine *et al.* (1998) presented the only published work of an agamid, *Draco melanopogon*, in which females are larger and also have proportionally larger heads and longer tails than males.

#### STUDY SPECIES – *RANKINIA [TYMPANOCRYPTIS] DIEMENSIS*

The mountain dragon, *Rankinia [Tympanocryptis] diemensis* is a relatively small dragon lizard found throughout Tasmania and in parts of southeastern mainland Australia (Cogger, 1992; Hutchinson *et al.*, 2001). It is the only representative of the family Agamidae in Tasmania, and it is the most southerly-distributed dragon in the world. It is one of only three oviparous reptiles in Tasmania (Hutchinson *et al.*, 2001). Although this thesis presents several key aspects of this species' ecology and behaviour, I have also included more detail on its ecology and reproductive biology in the Supporting Document (p 161-166; Stuart-Smith *et al.*, 2005), which was the first paper to thoroughly explore the ecology of this species.

*Rankinia diemensis* is unusual among agamid lizards in that it exhibits strong female-biased SSD, with a mean snout-vent length (SVL) of 66 mm ( $\pm 1.28$ ) in

---

females and 52 mm ( $\pm 0.639$ ) in males (from a single population, southeast Tasmania), although maximum sizes recorded are 84.5 mm SVL for females and 66 mm SVL for males (Stuart-Smith *et al.*, 2005). It is an ideal species for examining SSD for a number of reasons: it exhibits dimorphism unusual for its taxonomic group; the size difference between males and females is quite obvious and distinct – suggesting that a very strong set of selective pressures operate separately on the sexes; it is a cold-climate reptile – Tasmania’s temperate climate is characterised by lower temperatures than those experienced on mainland Australia (Heatwole and Taylor, 1987). This allows investigation of possible temperature-related influences on size. This species also has variable clutch size (see Stuart-Smith *et al.*, 2005; Supporting Document), which highlights the potential for size-related fecundity advantages to exist.

#### RESEARCH AIMS

The overall aim of this thesis is to examine the evolution, form and function of female-biased sexual size dimorphism within the framework of a system where large male size is typically expected (Australian agamid lizards). I examine the roles and implications of specific phenotypic variation in body size on behaviour, reproduction and development, and address some of the ecological and evolutionary implications that this can present for life history strategy. Selection intensity can vary between species, and between the sexes of a single species - it can target different aspects of size and structure, generating the same outcome from an entirely different suite of mechanisms. To account for this, I have taken a thorough approach to understanding trait function and evolution in order to emphasize the multifaceted nature of SSD, and, through this, stress the need to

---

integrate various major mechanisms when viewing trait evolution. Wainwright and Reilly (1994) stipulated that a complete appreciation of morphology necessitates information on functional, historical and ecological perspectives. I define and explain the size differences in *R. diemensis*, examine these in light of the three major ultimate causes, identify potential proximate mechanisms responsible, and elucidate the influence of environmental factors also shaping the degree of size differences. This not only provides a broad overview of body size in terms of the causes and consequences of sexual dimorphism, but also provides a more complete view of the niche that this species occupies. Although I primarily focus on ultimate approaches in this thesis, I address proximate mechanisms by looking at growth rates (Chapter 2), and also by including geographic comparison of sizes (Chapter 1), which hints at environmental influence on body size.

#### PRESENTATION OF THESIS

This thesis consists of 5 data chapters and 1 supporting document, each prepared and submitted for (or to be submitted for) publication in relevant scientific journals. Each paper can be viewed as a stand-alone piece of work; however, when fitted in the context of this thesis, they provide the flow and logic required to address the overall questions of this study. I am the primary author on all prepared and submitted manuscripts. I was responsible for literature searches, data collection, data entry and analyses, and manuscript preparation; however, I recognise the contribution of supervisors and co-workers by acknowledging them as co-authors. Due to the nature of this thesis, each chapter may incur some repetition, particularly in terms of animal collection and, of course, species

---

descriptions. Additionally, each chapter is formatted according to the journal it was submitted/accepted to, and so formatting may differ between chapters.

#### THESIS OUTLINE – SUMMARY OF PAPERS

CHAPTER 2: Size dimorphism in *Rankinia [Tympnocryptis] diemensis* (Family Agamidae): sex-specific patterns and geographic variation.

(Accepted, pending revision: *Biological Journal of the Linnean Society*)

Phenotypic variation between the sexes of a single species can influence a multitude of life history strategies and attributes. Precise knowledge of sex-related phenotypic variation is therefore vital for understanding ecology, biology and behavioural attributes of a species. The first step is clear: to identify the nature of that phenotypic variation, in this case, body size. However, despite much work in this area, many studies still over-simplify this phenomenon – by including one measurement of size to represent an individual's entire morphology – instead of incorporating several morphological features (e.g. Bonduriansky & Rowe, 2003). Studies often also fail to look for differences not only within a population, but also between populations of the same species (e.g. Pearson *et al.*, 2002). This is important, since environmental factors may vary with latitude and have the power to significantly influence growth and body size. Thermal latitudinal gradients are particularly important when dealing with reptile size (e.g. Sears & Angilletta, 2004), and the existence of geographic differences in SSD allows the opportunity to examine these other factors that can influence body size (Madsen & Shine,

---

1993). I include overall body size in examination of SSD in *R. diemensis* and also morphological trait sizes (e.g. head, limb and tail sizes) to examine sex-specific size differences on another level.

CHAPTER 3: A proximate approach to examining female-biased size dimorphism in the agamid lizard, *Rankinia [Tympnocryptis] diemensis*.

(Unsubmitted manuscript)

Identifying the nature of SSD in Chapter 2 is the first step of the story. We then need to understand how different morphology is achieved, i.e. potential physical processes that are responsible for observed SSD and allometries. There is a range of proximate mechanisms potentially responsible for the observed female-biased size difference ranging from females hatching at larger size than males to sexes having different growth trajectories or females having greater longevity than males (St Clair, 1998; Rutherford, 2004). This chapter presents and analyses growth patterns in *R. diemensis*. In particular I am interested in the size at which the sexes diverge in size, and what this means for growth trajectories, age and size at maturity and longevity.

CHAPTER 4: Is fecundity the ultimate cause of female-biased size dimorphism in the dragon lizard *Rankinia [Tympnocryptis] diemensis*?

(Stuart-Smith, Swain, Stuart-Smith & Wapstra. 2007. *Journal of Zoology* London

doi:10.1111/j.1469-7998.2007.00324.x)

---

Natural selection is one of the primary evolutionary driving forces behind sex-related size differences in most organisms through size-specific fecundity advantages. Large female size is typically attributed to the ability of large females to produce more offspring (Reeve & Fairbairn, 1999). Since Darwinian theory suggests that natural selection should favour any characteristic that maximizes reproductive output, if there are size-related fecundity advantages this may, in part, explain why female *R. diemensis* are larger than males. To explore this, I examined the relationship between female body size and a range of reproductive output parameters, including fecundity.

CHAPTER 5: The role of body size in competition and mate choice  
in an agamid with female-biased size dimorphism

(Stuart-Smith, Swain & Wapstra. 2007. *Behaviour* 144: 1087-1102)

Once the potential role of natural selection is examined via fecundity, the next important step is to investigate the influence of sexual selection pressures.

Investigation of the influence of sexual selection addresses whether SSD is shaped by factors such as competition. This chapter deals with specific behavioural links to body size, focusing on the two most influential forces of sexual selection: mate choice and intra-sexual competition. Male body size typically determines the outcomes of intra-specific competition in the majority of animals – whether it is through defence of a resource or by defeating an opponent to gain access to females (e.g. Stamps, 1983; Olsson, 1995). The armament-ornament model (Berglund *et al.*, 1996) predicts that females will benefit from choosing males that

---

win these outcomes, thus selecting for traits, such as body size, that promote intra-sexual competition success (e.g. Mateos & Carranza, 1999). Female choice is thus a major component of sexual selection, as females tend to choose males of higher perceived quality (Calsbeek & Sinervo, 2002), or when male mate choice occurs, size-fecundity relationships mean that larger females are the preferred choice (e.g. Herdman *et al.*, 2004; Wong & Jennions, 2003). This chapter focuses on the questions - what is the functional consequence of body size? and is there intra-specific competition based on size?

CHAPTER 6: Sex specific activity patterns and resource use in a dimorphic agamid lizard.

(In review: Stuart-Smith, Swain & Wapstra)

Morphological or phenotypic differences between the sexes may cause or result in niche segregation via differences in microhabitat utilisation between the sexes, which can lessen the impact of inter-sexual competition (Attum *et al.*, 2007). This paper addresses the ecological niche divergence theory to further explain size differences. Niche divergence can occur at spatial and temporal levels – through timing of reproductive events, diel habitat use, and differences in structural variables used by both sexes. It occurs when different sizes or traits adapt the sexes to different ecological roles (Shine, 1986; Temeles *et al.*, 2000). Specialised morphological traits can result from or allow this niche separation. For example, when prey types are segregated to certain areas of the habitat, specialisation of traits to access or capture the prey may occur.

---

SUPPORTING DOCUMENT: Reproductive ecology of the mountain dragon *Rankinia*

*[Tympnocryptis] diemensis* (Reptilia: Squamata: Agamidae) in Tasmania.

(Stuart-Smith, Swain & Welling. 2005. *Papers and Proceedings of the Royal Society of Tasmania* 139: 23-28)

This paper combines work from my Honours project (Duraj, 2002) and data gathered during my PhD. It provides an important framework for understanding the study species and its distinctive nature as a study system for understanding SSD. This paper provides a general overview of the ecology of *Rankinia diemensis* with data from egg incubations, observational studies and other work on this species. Its importance to this thesis lies in providing the reader with a first-off account of the species and its life history strategy – identifying it as an egg-layer in a cool-temperate climate, linking reproductive cycles to climatic factors, recognising the importance of crypsis and behaviour, and identifying body size differences as a major player in the life history, adaptation and evolution of this species.

## REFERENCES

- ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press, New Jersey.
- ARNOLD, S.J. (1983). Morphology, performance and fitness. *American Zoologist*, 23: 347-361.
- ATTUM, O., EASON, P. & COBBS, G. (2007). Morphology, niche segregation, and escape tactics in a sand dune lizard community. *Journal of Arid Environments*, 68: 564-573.
- BADYAEV, A.V. & HILL, G.E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution and Systematics*, 34: 27-49.
- BARNARD, C.J. (2004). *Animal behaviour: mechanism, development, function and evolution*. Harlow; Pearson/Prentice Hall.
- BERGLUND, A., BISAZZA, A. & PILASTRO, A. (1996). Armaments and ornaments: an evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58: 385-399.
- BLANKENHORN, W.U. (2000). The evolution of body size: what keeps organisms small? *The Quarterly Review of Biology*, 75: 385-407.
- BLANKENHORN, W.U. (2005). Behavioural causes and consequences of sexual size dimorphism. *Ethology*, 111: 977-1016.
- BLANKENHORN, W.U., KRAUSHAAR, U. & REIM, C. (2003) Sexual selection on morphological and physiological traits and fluctuating asymmetry in the yellow dung fly. *Journal of Evolutionary Biology*, 16: 903-913.
- BLANKENHORN, W.U. & DEMET, M. (2004). Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology*, 44: 413-424.
- BONDURIANSKY, R. & ROWE, L. (2003). Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. *Evolution*, 57: 2046-2053.
- BOUTELLER-REUTER, C. & PERRIN, N. (2004). Sex-specific selective pressure on body mass in the white-toothed shrew, *Crocidura russula*. *Journal of Evolutionary Biology*, 18: 290-300.
- BUSTON, P. (2003). Size and growth modification in clownfish. *Nature*, 424: 145-146.
- BUTLER, M.A., SAWYER, S.A. & LOSOS, J.B. (2007). Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature*, 447: 202-205.
- CALSBECK, R. & SINERVO, B. (2002). Uncoupling direct and indirect components of female choice in the wild. *Proceedings of the National Academy of Sciences of the USA*, 99: 14897-14902.
- COGGER, H. (1992). *Reptiles and Amphibians of Australia*. Reed/Reed New Holland.
- COX, R.M., SKELLY, S.L. & JOHN-ALDER, H.B. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, 57: 1653-1669.
- COX, R.M., SKELLY, S.L., & JOHN-ALDER, H.B. (2005). Testosterone inhibits growth in juvenile male eastern fence lizards (*Sceloporus undulatus*): implications for energy allocation and sexual size dimorphism. *Physiological and Biochemical Zoology*, 78: 531-545.
- DARWIN, C. (1871). *The descent of man and selection in relation to sex*. Princeton

- University Press. New Jersey, USA.
- DIMIJIAN, G.G. (2005). Evolution of sexuality: biology and behaviour. *Baylor University Medical Proceedings*, 18: 244-258.
- DOHERTY, JR., P.F., SORCI, G., ROYLE, J.A., HINES, J.E., NICHOLS, J.D. & BOULINIER, T. (2003). Sexual selection affects local extinction and turnover in bird communities. *Proceedings of the National Academy of Sciences of the USA*, 100: 5858-5862.
- DROVETSKI, S.V., ROHWER, S. & MODE, N.A. (2006). Role of sexual and natural selection in evolution of body size and shape: a phylogenetic study of morphological radiation in grouse. *Journal of Evolutionary Biology*, 19: 1083-1091.
- DURAJ, J.F. (2002). Maternal and environmental influences on the early life stages of the mountain dragon, *Tympanocryptis diemensis*. Unpublished Honours Thesis, University of Tasmania.
- FAIRBAIRN, D.J. (1997). Allometry for sexual size dimorphism: patterns and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics*, 28: 659-687.
- FOX, C.W. & CZESAK, M.E. (2006). Selection on body size and sexual size dimorphism differs between host species in a seed-feeding beetle. *Journal of Evolutionary Biology*, 19: 1167-1174.
- GREER, A.E. (1989). *The Biology and Evolution of Australian Lizards*. Surrey Beatty & Sons Pty Ltd, Australia.
- HAENEL, G.J. & JOHN-ALDER, H.B. (2002). Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, *Sceloporus undulatus*. *Oikos*, 96: 70-81.
- HEATWOLE, H. & TAYLOR, J. (1987). *Ecology of Reptiles*. Surrey Beatty & Sons, Pty. Ltd. Sydney.
- HEDRICK, A.V. & TEMELES, E.J. (1989). The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution*, 4: 136-138.
- HERDMAN, E.J.E., KELLY, C.D. & GODIN, J-G. J. (2004). Male mate choice in the guppy (*Poecilia reticulata*): do males prefer larger females as mates? *Ethology*, 110: 97-111.
- HUTCHINSON, M., SWAIN, R. & DRIESSEN, M. (2001). *Snakes and Lizards of Tasmania. Fauna of Tasmania Handbook No. 9*, University of Tasmania.
- KALIONTZOPOULOU, A., CARRETERO, M.A. & LIORENTE, G.A. (2007). Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology*, 268: 152-165.
- KRATOCHVÍL, L. & FRYNTA, D. (2002). Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). *Biological Journal of the Linnean Society*, 76: 303-314.
- KRÜGER, O. (2005). The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. *Evolutionary Ecology*, 19: 467-486.
- LEBAS, N.R. & MARSHALL, N.J. (2000). The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus*. *Proceedings of the Royal Society of London*, B, 267: 445-452.
- LINDENFORS, P., SZÉKELY, T. & REYNOLDS, J.D. (2003). Directional changes in sexual size dimorphism in shorebirds, gulls and alcids. *Journal of*

- Evolutionary Biology*, 16: 930-938.
- LOSOS, J.B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution*, 44: 1189-1203.
- LOSOS, J.B., BUTLER, M. & SCHOENER, T.W. (2003). Sexual dimorphism in body size and shape in relation to habitat use among species of Caribbean *Anolis* lizards; in *Lizard Social Behaviour*, Fox, S.F., McCoy, J.K. & Baird, T.A. (eds), Ch 11 356-380. The John Hopkins University Press, US.
- MADSEN, T. & SHINE, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution*, 47: 321-325.
- MARLER, C.A. & MOORE, M.C. (1988). Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioural Ecology and Sociobiology*, 23: 21-26.
- MASTERSON, T.J. & HARTWIG, W.C. (1998). Degrees of sexual dimorphism in *Cebus* and other New World Monkeys. *American Journal of Physical Anthropology*, 107: 243-256.
- MATTEOS, C. & CARRANZA, J. (1999). Effects of male dominance and courtship display on female choice in the ring-necked pheasant. *Behavioural Ecology and Sociobiology*, 45: 235-244.
- MEIRI, S., DAYAN, T. & SIMBERLOFF, D. (2005). Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology*, 86: 1432-1440.
- MUNDAY P.L., BUSTON P.M. & WARNER, R.R. (2006). Diversity and flexibility of sex-change strategies in animals. *Trends in Ecology and Evolution*, 21: 89-95.
- NORMAN, M.D., PAUL, D., FINN, J. & TREGENZA, T. (2002). First encounter with a live male blanket octopus: the world's most sexually size-dimorphic animal. *New Zealand Journal of Marine and Freshwater Research*, 36: 733-736.
- OLSSON, M. (1995). Territoriality in Lake Eyre dragons *Ctenophorus maculosus*: are males 'superterritorial'? *Ethology*, 101: 222-227.
- OLSSON, M., SHINE, R., WAPSTRA, E., UJVARI, B. & MADSEN, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution*, 56: 1538-1542.
- ORD, T.J., BLUMSTEIN, D.T. & EVANS, C.S. (2001). Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings of the Royal Society of London, B*, 268: 737-744.
- OWENS, I.P.F. & HARTLEY, I.R. (1998). Sexual dimorphism in birds: why are there so many different forms of dimorphism? *Proceedings of the Royal Society of London B*, 265: 397-407.
- PEARSON, D., SHINE, R. & WILLIAMS, A. (2002). Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia*, 131: 418-426.
- PETERS, R.A. & ORD, T.J. (2003). Display response of the Jacky dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecology*, 28: 499-506.
- PETERS, R.H. (1983). *The ecological implications of body size*. Cambridge University Press, New York, USA.
- PIETSCH, T.W. (2005). Dimorphism, parasitism, and sex revisited: modes of

- reproduction among deep-sea ceratioid anglerfishes (Teleostei: Lophiiformes). *Ichthyological Research*, 52: 207-236.
- PREEST, M.P. (1994). Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *Journal of Herpetology*, 28: 292-298.
- PRICE, T. & BIRCH, G.L. (1996). Repeated evolution of sexual colour dimorphism in passerine birds. *The Auk*, 113: 842-848.
- RADDER, R.S., SAIDAPUR, S.K., SHINE, R. & SHANBHAG, B.A. (2006). The language of lizards: interpreting the function of visual displays of the Indian rock lizard, *Psammophilus dorsalis* (Agamidae). *Journal of Ethology*, 24: 275-283.
- REEVE, J.P. & FAIRBAIRN, D.J. (1999). Change in sexual size dimorphism as a correlated response to selection on fecundity. *Heredity*, 83: 697-706.
- REISS, M.J. (1989). *The allometry of growth and reproduction*. Cambridge University Press, Cambridge, UK.
- RIVAS, J.A. & BURGHARDT, G.M. (2001). Understanding sexual size dimorphism in snakes: wearing the snake's shoes. *Animal Behaviour*, 62: F1-F6.
- RUTHERFORD, P.L. (2004). Proximate mechanisms that contribute to female-biased sexual size dimorphism in an anguid lizard. *Canadian Journal of Zoology*, 82: 817-822.
- SCHULTE, J.A. II, LOSOS, J.B., CRUZ, F.B. & NUNEZ, H. (2004). The relationship between morphology, escape behaviour and microhabitat occupation in the lizard clade *Liolaemus* (Iguanidae: Tropidurinae\*: Liolaemini). *Journal of Evolutionary Biology*, 17: 408-420.
- SEARS, M.W. & ANGILLETTA JR., M.J. (2004). Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. *Integrative and Comparative Biology*, 44: 433-442.
- SERRANO-MENESES, M-A. & SZÉKELY, T. (2006). Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos*, 113: 385-394.
- SHINE, R. (1986). Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia*, 69: 260-267.
- SHINE, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology*, 64: 419-461.
- SHINE, R. (1990). Proximate determinants of sexual differences in adult body size. *The American Naturalist*, 135: 278-283.
- SHINE, R., KEOGH, S., DOUGHTY, P. & GIRAGOSSYAN, H. (1998). Costs of reproduction and the evolution of sexual dimorphism in a 'flying lizard' *Draco melanopogon* (Agamidae). *Journal of Zoology London*, 246: 203-213.
- SHINE, R., SHINE, T., & SHINE, B. (1998). Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and colour pattern. *Biological Journal of the Linnean Society*, 80: 1-10.
- STAMPS, J.A. (1983). The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). *Behavioural Ecology and Sociobiology*, 12: 19-33.
- ST CLAIR, R.C. (1998). Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. *Oecologia*,

- 115: 501-501.
- STEARNS, S.C. (1992). *The evolution of life histories*. Oxford University Press, New York, USA.
- STORZ, J.F., BALASINGH J., BHAT H.R., NATHAN P.T., DOSS D.P.S., PRAKASH A.A. & KUNZ, T.H. (2001). Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Biological Journal of the Linnean Society*, 72: 17-31.
- STUART-FOX, D.M. & ORD, T.J. (2004). Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society of London, B*, 271: 2249-2255.
- STUART-SMITH, J., SWAIN, R. & WELLING, A. (2005). Reproductive ecology of the mountain dragon, *Rankinia [Tympanocryptis] diemensis* (Reptilia: Squamata: Agamidae) in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*, 139: 23-28.
- SUGG, D.W., FITZGERALD, L.A. & SNELL, H.L. (1995). Growth-rate, timing of reproduction, and size dimorphism in the southwestern earless lizard (*Cophosaurus texanus scitulus*). *Southwestern Naturalist*, 40:193-202.
- TEMELES, E.J., PAN, I.L., BRENNAN, J.L. & HORWITT, J.N. (2000). Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science*, 289: 441-443.
- TERIOKHIN, A.T., BUDILOVA, E.V., THOMAS, F. & GUEGAN, J-F. (2004). Worldwide variation in life-span sexual dimorphism and sex-specific environmental mortality rates. *Human Biology*, 76: 623-641.
- TINBERGEN, N. (1963). On aims and methods of ethology. *Zeitschrift für Tierpsychologie*, 20: 410-433.
- WAINWRIGHT, P.C. & REILLY, S.M. (1994). Introduction. In: *Ecological Morphology: Integrative Organismal Biology*. Wainwright, P.C. & Reilly, S.M.(Eds). The University of Chicago Press, Chicago.
- WARNER, R.R. (1988). Sex change and the size-advantage model. *Trends in Ecology and Evolution*, 3: 133-136.
- WATKINS, G.G. (1996). Proximate causes of sexual size dimorphism in the iguanian lizard *Microlophus occipitalis*. *Ecology*, 77: 1473-1482.
- WEBSTER, M. S. (1997). Extreme sexual size dimorphism, sexual selection, and the foraging ecology of Montezuma *Orpendolas*. *Auk*, 114, 570-580.
- WESTENDORP, R.G.J. & KIRKWOOD, T.B.L. (1998). Human longevity at the cost of reproductive success. *Nature*, 396: 743-746.
- WONG, B.B.M. & JENNIONS, M.D. (2003). Costs influence male mate choice in a freshwater fish. *Proceedings of the Royal Society of London B*, 270: S36-S38.
- YOUNG, K.A. (2005). Life-history variation and allometry for sexual size dimorphism in Pacific salmon and trout. *Proceedings of the Royal Society B*, 272: 167-172.

---

## CHAPTER 2

# SIZE DIMORPHISM

## **CHAPTER 2**

### **Size dimorphism in *Rankinia [Tympnocryptis] diemensis* (Family Agamidae): sex-specific patterns and geographic variation**

Manuscript submitted as: Stuart-Smith, J., Stuart-Smith R.D., Swain, R., & Wapstra E. (accepted, pending final revision). Size dimorphism in *Rankinia [Tympnocryptis] diemensis* (Family Agamidae): sex-specific patterns and geographic variation. *Biological Journal of the Linnean Society*.

#### **ABSTRACT**

Sexual dimorphism has implications for a range of biological and ecological factors, and intersexual morphological differences within a species provide an ideal opportunity for investigating evolutionary influences on phenotypic variation. We investigated sexual size dimorphism in an agamid species, *Rankinia [Tympnocryptis] diemensis*, to determine whether overall size and/or relative trait size differences exist and whether geographic variation in size dimorphism occurs in this species. Relative trait proportions included a range of head, limb and inter-limb measurements. We found significant overall intersexual adult size differences; females were the larger sex across all sites but the degree of dimorphism between the sexes did not differ between sites. This female-biased size difference is atypical for agamid lizards, which are usually characterised by large male body size. In this species, large female-biased SSD appears to have evolved as a result of fecundity advantages. Relative morphological traits also differed significantly between the sexes, but in the opposite direction: relative head, tail and limb sizes were significantly larger in males than females. This

---

corresponds to patterns in trait size usually found in this taxonomic group, where males use head and limb size in contest success such as male-male rivalry. We found no significant intersexual difference in hatchlings in overall body size, indicating that ontogenetic processes produce the overall body size differences present in the adult form. There were, however, morphological differences in hatchlings, including tail, interlimb, thigh and hindlimb lengths that varied between sites, suggesting genetic or environmental influences on trait evolution.

## INTRODUCTION

Body size variation dictates a variety of life history components, has implications for the ecology, biology and evolution of a species, and is often the most prominent difference between the sexes (Andersson, 1994; Watkins, 1996; Stamps, Losos & Andrews, 1997; Blanckenhorn, Kraushaar & Reim, 2003). Body size bias between the sexes (sexual size dimorphism, SSD), is a widespread phenomenon occurring in a variety of taxa (e.g. Andrews & Stamps, 1994; Butler, Schoener & Losos, 2000; Schulte-Hostedde, Millar & Gibbs, 2002; Lindenfors, Székely & Reynolds, 2003; Fox & Czesak, 2006). The function and evolution of SSD can be explained by two major hypotheses: sexual selection typically acting to increase male size (intra-sexual selection hypothesis), and natural selection for increased female size (fecundity advantage hypothesis) (Blanckenhorn, 2000; Storz *et al.*, 2001; Cox, Skelly & John-Alder, 2003; Rutherford, 2004).

Interspecific variation in body size is common in lizards, with males the larger sex in most genera (Anderson & Vitt, 1990; Lappin & Swinney, 1999; Olsson *et al.*,

---

2002; Rutherford, 2004), and can be present on several levels, including not only dimorphism in overall body size, but also in specific morphological trait sizes, such as head or limb sizes. This dimorphism is typically associated with territoriality and aggressiveness towards conspecifics since large body size is often correlated to contest success and mate preference (Tokarz, 1985; Cooper & Vitt, 1993; Howard, Moorman & Whiteman, 1997; Calsbeek & Sinervo, 2002; Wong & Candolin, 2005).

Sexual size dimorphism in adults results from differential physiological, behavioural and ecological processes occurring during some stage of development (Badyaev, 2002; Rutherford, 2004; Le Galliard *et al.*, 2006). The potential proximate mechanisms responsible for observed size differences include differences between the sexes in size at birth, growth rate and duration, age at maturity, and longevity (St. Clair, 1998; Badyaev, Whittingham & Hill, 2001; Rutherford, 2004), therefore, understanding or identifying stages at which body size differences occur is crucial for elucidating how SSD has evolved (Le Galliard *et al.*, 2006).

Since body size variation is subject to a variety of selective pressures, it is likely that as well as potential differences between the sexes, there may also be spatial correlations that vary across the species' distribution (Storz *et al.*, 2001).

Environmental thermal regimes are the leading force driving geographic differences in body size within a species (Angilletta *et al.*, 2004; Sears & Angilletta, 2004; Angilletta, Steury & Sears, 2004). In mammals, larger body sizes in cooler habitats are typical (Bergmann's Rule); a pattern linked to the

---

surface area to volume ratio and associated reduction in heat loss rate of larger-sized organisms, or to a decrease in season length (Storz *et al.*, 2001; Blanckenhorn *et al.*, 2006). In ectotherms, large body size is either associated with warmer climates – likely to be related to the need to regulate body temperature via behavioural mechanisms (Adolph & Porter, 1993; Sears & Angilletta, 2004); or follows Bergmann’s trend of larger size in cooler climates when optimal resource allocation models exist (Angilletta *et al.*, 2004; Kozłowski, Czarnołęski & Dańko, 2004). Squamate reptiles (snakes and lizards) tend to show the converse of Bergmann’s rule, and may be explained by rapid heat advantages in cool climates or lower densities producing lax competition and less need for larger body size (Ashton & Feldman, 2003). Spatial variation in lizard body size is also known to result from differential habitat use, demographic factors (Stamps *et al.*, 1997; Cox *et al.*, 2003) and geographic differences in selection pressures – the stronger the selection pressures, the more one sex will be pushed to the limits of size variation (Drovetski, Rohwer & Mode, 2006).

Patterns in SSD can vary geographically in terms of the extent or magnitude of size difference, or even in the direction of SSD (see Spidle, Quinn & Bentzen, 1998; Young, 2005; Tamate & Maekawa, 2006). Examination of the strength and nature of geographical variation in body size is essential for assessing the significance of evolutionary pressures and constraints that lead to SSD (Blondel *et al.*, 2002). Evidence of latitudinal clines in life history traits such as development time in the yellow dung fly (Blanckenhorn & Demont, 2004), sexual dimorphism in sea-run masu salmon (Tamate & Maekawa, 2006), or growth and size at maturity in Eurasian perch (Heibo, Magnhagen & Vøllestad, 2005) indicate that

these traits can be influenced by environmental (e.g. temperature) or selective pressures which vary geographically. When differences in a particular biological trait, such as body size, arise across the range of a species, we can use this to understand the causes and consequences of that difference in trait evolution (Braña, 1996; Pearson, Shine & Williams, 2002; Mann, O’Riain & Hofmeyr, 2006). In Australian frogs, *Limnodynastes tasmaniensis* and *L. peronii*, latitudinal and climate related variation in body size appears also linked with geographical variation in sexual selection (Schäuble, 2004). Large male size is favoured when breeding seasons are long (in cool climates) and bigger size permits greater energy storage and allows extended reproductive periods (Schäuble, 2004), thus resulting in selective pressures for males to become larger.

This study provides a detailed analysis of morphological variation in the mountain dragon, *Rankinia [Tympanocryptis] diemensis* (Reptilia: Squamata: Agamidae) (Gray, 1841). This sexually dimorphic reptile exhibits dimorphism contrary to its taxonomic group: females are significantly larger than males (Stuart-Smith *et al.*, 2007 *a*). SSD is widespread amongst the agamid lizards of Australia, but male-biased SSD is a typical characteristic of this group (e.g. Shine *et al.*, 1998). In Tasmania, *R. diemensis* represents the only agamid lizard, and although the state’s cool-temperate climate has resulted in a limited reptile fauna, *R. diemensis* is relatively widespread. This species is also present in some areas of southeast Australia, including the Furneaux Group, Flinders Island, southern Victoria and in some higher-level elevations of Victoria and New South Wales (Hutchinson, Swain & Driessen, 2001). *Rankinia diemensis* also exhibits some typical male agamid competition and aggression displays, which in other agamids is associated

with resource acquisition and mate choice (Ord & Evans, 2003; Peters & Ord, 2003; Watt & Joss, 2003; Osborne, 2005), suggesting that body size differences may be more complex than expected. Thus, we will include not only a measure of overall body size, but also measurements of morphological trait sizes (relative to body size), since this will indicate more specific selection pressures (Kaliontzopoulou, Carretero & Liorente, 2007) and can provide insight into the more intricate details of a species life-history strategy. We include hatchling and adult measurements to test whether any observed differences are present at hatching or whether sex-specific differences are a consequence of ontogenetic or post-maturity processes. We also investigate whether geographic variation exists, which will allow insights into the geographic sex-specific selective pressures acting on body size.

## METHODS

### *Study species and lizard capture*

The study species, *Rankinia [Tymanocryptis] diemensis*, is a relatively small agamid lizard inhabiting temperate south-eastern Australia. One of the most striking features of this species is the sex-biased size difference, whereby females attain greater body size than males (Stuart-Smith, Swain & Welling, 2005, Supporting Document; Stuart-Smith *et al.*, 2007 *a*, Chapter 4). SSD is widespread amongst the agamid lizards of Australia, but male-biased SSD is a typical characteristic of this group (e.g. Shine *et al.*, 1998). In Tasmania, *R. diemensis* represents the only agamid lizard, and although the state's cool-temperate climate has resulted in a limited reptile fauna, *R. diemensis* is relatively widespread. This species is also present in some areas of southeast Australia, including the

Furneaux Group, Flinders Island, southern Victoria and in some higher-level elevations of Victoria and New South Wales (Hutchinson, Swain & Driessen, 2001).

In this study, adult lizards were caught and measured from Clifton Beach area and nearby Cape Deslacs Nature Reserve (CL) in south-eastern Tasmania (42°59'S, 147°32'E; elevation: 45-65 m; n = 69 females, 22 males); Blackman Dam (BD) area in central Tasmania (42°13'S, 147°14'E, elevation: 700-800 m; n = 61 females, 58 males), and Flinders Island (FI) (40°3'S, 147°55'E, elevation: 20-35m; n = 43 females, 5 males) (Figure 1). Size at maturity has previously been described in this species (see Stuart-Smith *et al.*, 2005, Supporting Document; 2007 *a*, Chapter 4) and we used this as well as our later observations of male and female reproductive behaviour and state (minimum size for adults in this study: males = 40 mm; females = 43 mm). All populations are geographically distinct and samples are believed to be representative of populations (at each site).

To obtain hatchling measurements, gravid females were captured by hand during the oviposition period (austral spring) in 2004 from two of the above geographically distinct sites: Clifton area (CL; n clutches = 18) and Blackman Dam area (BD; n clutches = 12). This allowed the opportunity to investigate whether intersexual size differences were apparent at hatching, with the advantage of allowing us to control incubation conditions (preserved specimens were not used for hatchling measurements). Females from each site were collected and allowed to oviposit in outdoor enclosures (see Stuart-Smith *et al.*, 2007 *a*, Chapter 4). Eggs were collected immediately (CL = 127, BD = 89), measured ( $\pm 0.01$  g)

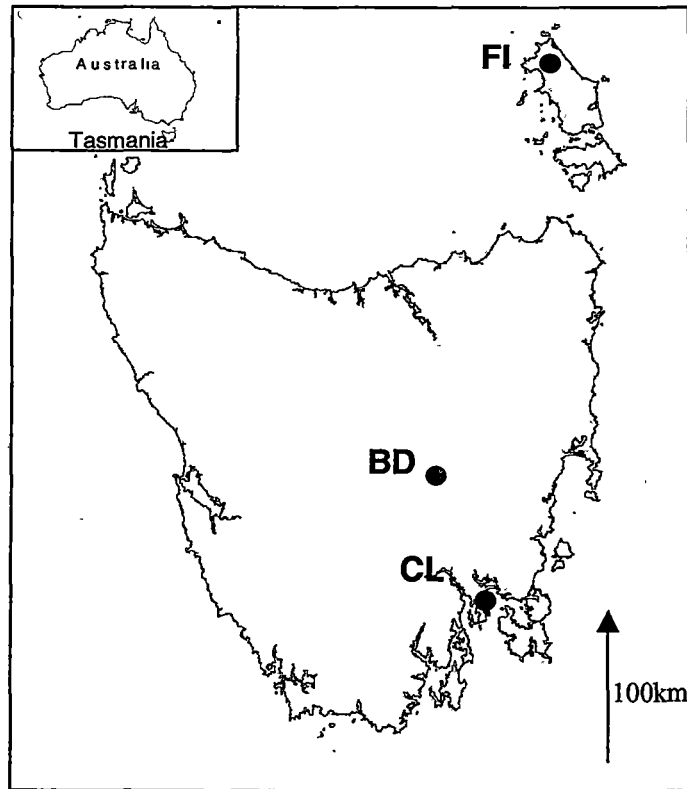


Figure 1. Spatial location of populations of *Rankinia diemensis* sampled in Tasmania, southern Australia; FI: Flinders Island; BD: Blackman Dam; and CL: Clifton area

and placed in individual 600 ml plastic containers that had been 1/3 filled with moist vermiculite (7 parts vermiculite: 1 part water). Containers were placed in a Contherm<sup>®</sup> Digital series incubator at a constant 28 °C. Eggs were monitored daily and rotated within the incubator weekly. At hatching, hatchlings were removed from containers and measured ( $\pm 0.01$  g and  $\pm 0.01$  mm; see below for morphological measurements), and sexed by hemipenes eversion (Harlow, 1996; Wapstra *et al.*, 2004).

#### *Morphological measurements*

Adult and hatchling *R. diemensis* were measured for the following morphological traits using electronic callipers ( $\pm 0.1$  mm): snout-vent length (SVL), tail length

(TL), head width (HW), head depth (HD), head length (HL), snout-parietal length (SP), inter- (IL) fore- (FLL) and hind-limb (HLL) lengths, thigh width (Th) and pes length (PES; i.e. a measure of foot length taken from the tip of the longest digit to the heel). Both live ( $n = 266$ ) and preserved specimens ( $n = 27$ ) were included. Preserved adult specimens were made available from the Queen Victoria Museum in Launceston ( $n = 11$ ; 7 from FI, 4 from CL), the University of Tasmania ( $n = 5$ ; from CL) and Melbourne Museum ( $n = 11$ ; all FI).

### *Statistical analyses*

We examined overall body size (SVL) differences between sexes and sites and the relative differences in morphometrics between sexes. Body size differences were examined using ANOVA of SVL with sex and site as fixed factors for adults and hatchlings separately (Table 1). To examine morphological differences between sexes and sites we first regressed morphometric measurements against snout-vent length (SVL) to determine whether transformations were required before calculating relative morphometric measurements. All relationships were linear and no transformations were required, therefore all measurements used were simply divided by SVL to provide a reliable measure controlling for SVL. Principal components analysis (PCA) was then used to identify variation in morphology between sexes and sites using relative morphometric measurements (excluding SVL). Subsequent analyses were based on those principal components that accounted for the greatest variation. We included the first five principal components (PCs) in multivariate analysis of variance (MANOVA) to test between sex differences in morphology across populations for adults and hatchlings separately, but will present only the first 3 principal components which

---

accounted for > 66 % of the variation (see Table 2). PCs 4 and 5 were included to ensure that we were conservative in our analyses, even though they only made up 9.5 % and 7.8 % of the total variation, however the MANOVA showed PCs 4 and 5 were non significant; we do not present these. Graphs presented are based on relative values, not PCs, for ease of (biological) interpretation.

Hatchlings (CL; n = 101, BD; n = 45) were measured for the same morphological variables as adults to determine if morphological variation was present at hatching. To account for any effects of clutch, we averaged all measurements of each sex in each clutch and used these in all analyses.

Table 1. Effect of site and sex on SVL of adult and hatchling *Rankinia diemensis* as identified by ANOVA.

	Effect	SS	df	<i>F</i>	P
Adult	Sex	4758.152	1	80.285	<0.0001
	Site	878.967	2	7.415	0.0010
	Sex × site	31.465	2	0.265	0.7670
	Error	13808.988	233		
Hatchling	Sex	0.010	1	0.008	0.930
	Site	4.167	2	3.359	0.073
	Sex × site	0.067	1	0.054	0.817
	Error	57.063	46		

Table 2. Factor loadings of morphological variables on the first three principal component axes (PC1, PC2 and PC3) calculated for adult *Rankinia diemensis*

Variable	PC1	PC2	PC3
Tail length	0.041	<b>0.617</b>	<b>-0.368</b>
Head width	<b>-0.414</b>	-0.285	-0.052
Head depth	<b>-0.371</b>	-0.247	0.041
Head length	<b>-0.347</b>	-0.170	<b>-0.354</b>
Snout-parietal length	<b>-0.406</b>	-0.138	-0.266
Inter-limb length	-0.122	-0.056	<b>0.528</b>
Thigh width	-0.287	<b>0.453</b>	-0.099
Pes length	<b>-0.374</b>	0.195	-0.149
Hind-limb length	-0.235	<b>0.381</b>	<b>0.358</b>
Fore-limb length	<b>-0.334</b>	0.194	<b>0.474</b>
Variance explained (%)	40.3	15.2	10.5
Cumulative variation (%)	40.3	55.5	66.1

## RESULTS

### *Overall body size (SVL) differences between sexes and age groups*

ANOVA revealed significant differences between site and sex for adult SVL

(Table 1), with Tukey's HSD post hoc test indicating that females are

significantly longer than males, and that males and females from FI are

significantly longer than their counterparts from both BD and CL populations

(Figure 2). Hatchling SVL was not significantly different between sites or sexes

(Table 1). There was no significant sex  $\times$  site interaction for adults or hatchlings

(Table 1).

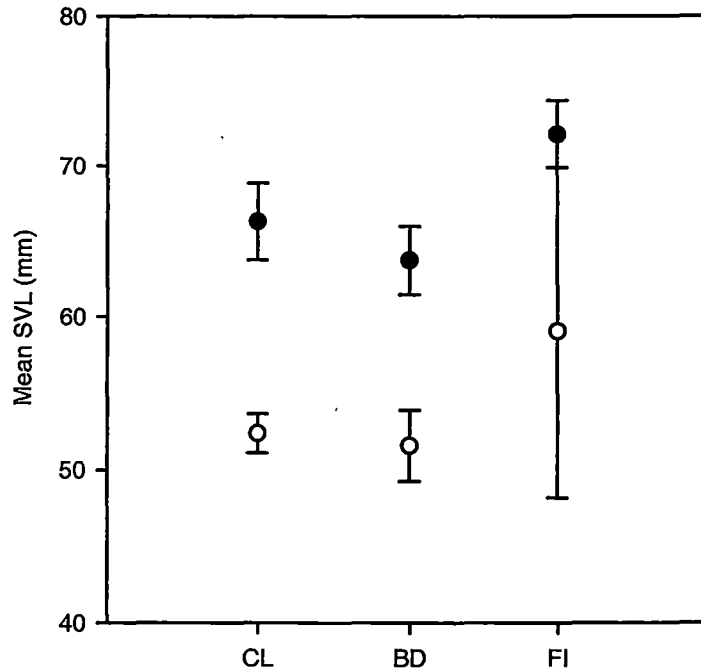


Figure 2. Mean snout-vent length (SVL) and 95% confidence intervals of adult *Rankinia diemensis* of sexes (male = black fill, female = clear fill) and sites within Tasmania (BD = Blackman Dam, CL = Clifton, FI = Flinders Island).

#### *Differences in morphological traits between sexes and age groups*

The first three axes of the PCA were identifiable as an overall relative body size vector between sexes for adults, explaining 66.1% of the total variation (Table 2). The first axis (PC1) had tail length as the only positive factor loading (Figure 3) and uniformly moderate negative factor loadings for head measurements (width, depth, length, snout-parietal) forelimb and pes measurements (Figure 4). The second axis (PC2) had high positive loadings for tail, thigh and hind limb length. The third axis had high negative loadings for inter-limb length and tail base, and high positive loadings for hind limb length. *A priori* contrasts revealed significant differences between sites based on all PCs at some level (Table 3).

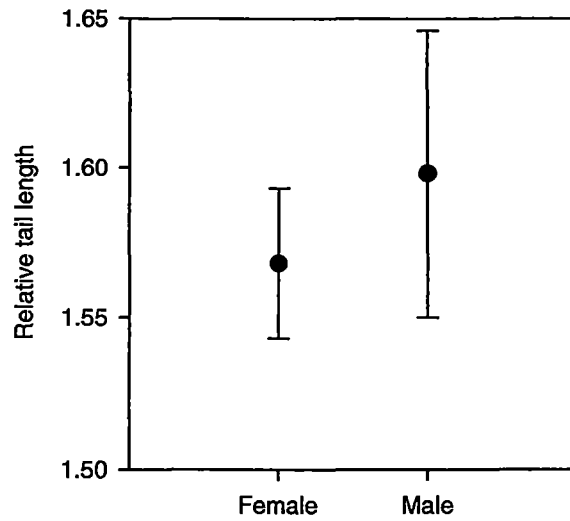


Figure 3. Mean and 95% confidence intervals for relative tail lengths of adult male and female *Rankinia diemensis* ( $\text{mm} \cdot \text{mm}^{-1}$ ).

Bonferroni adjustments were implemented due to multiple contrasts and non-orthogonal comparisons (with a recalculated  $P = 0.0125$ , based on each-way site comparisons). The 2-way MANOVA (Pillai's Trace) revealed a highly significant effect of sex and site on relative adult morphological measurements based on the first five PCs identified in PCA (Table 4). PC1 had significant differences between CL and the other two sites, with CL having smaller heads (HW, HD and SP) and limbs (HLL, FLL and Pes) than FI or BD. PC2 differed between all sites, with BD having shorter tails than the other 2 populations, and CL having smaller thigh widths (Th) than BD or CL. PC3 differed between BD and the other two sites, with BD having slightly longer inter-limb lengths than FI, but FI had longer tails and hind limbs than BD on this axis.

The first three axes of the PCA were identifiable as an overall relative body size vector for hatchlings, explaining 69.4 % of the total variation (Table 5). PC1 was characterised by moderate positive head measurements. PC2 was characterised by negative tail and interlimb measurement loadings, and positive hindlimb length. PC3 was characterised by high negative loadings for hindlimb, thigh, interlimb and tail measurements (Table 5). The 2-way MANOVA (Pillai's Trace) of hatchling relative morphological measurements revealed a significant effect of site, which occurred on PC2 and PC3 (Table 4). PC2 was weighted by high negative tail, interlimb and hindlimb lengths, while PC3 by high negative hindlimb, interlimb and thigh lengths. CL had longer tail and interlimb lengths (corresponding to greater SVL found at CL); and BD had slightly greater hindlimb and thigh lengths than CL.

Table 3. *A priori* contrast revealing site differences in first three PCs (PC1, PC2 and PC3) of relative adult morphological measurements across sites (BD = Blackman Dam, CL = Clifton, FI = Flinders Island).

	Contrast	df	Contrast SS	<i>F</i>	P
PC1	BD vs CL	1	1.401	6.67	0.0104
	BD vs FI	1	1.211	5.76	0.0171
	CL vs FI	1	5.023	23.90	<0.0001
PC2	BD vs CL	1	44.468	0.00	<0.0001
	BD vs FI	1	28.638	0.00	<0.0001
	CL vs FI	1	136.814	0.00	<0.0001
PC3	BD vs CL	1	215.679	70.95	<0.0001
	BD vs FI	1	138.131	45.44	<0.0001
	CL vs FI	1	0.001	0.00	0.9836

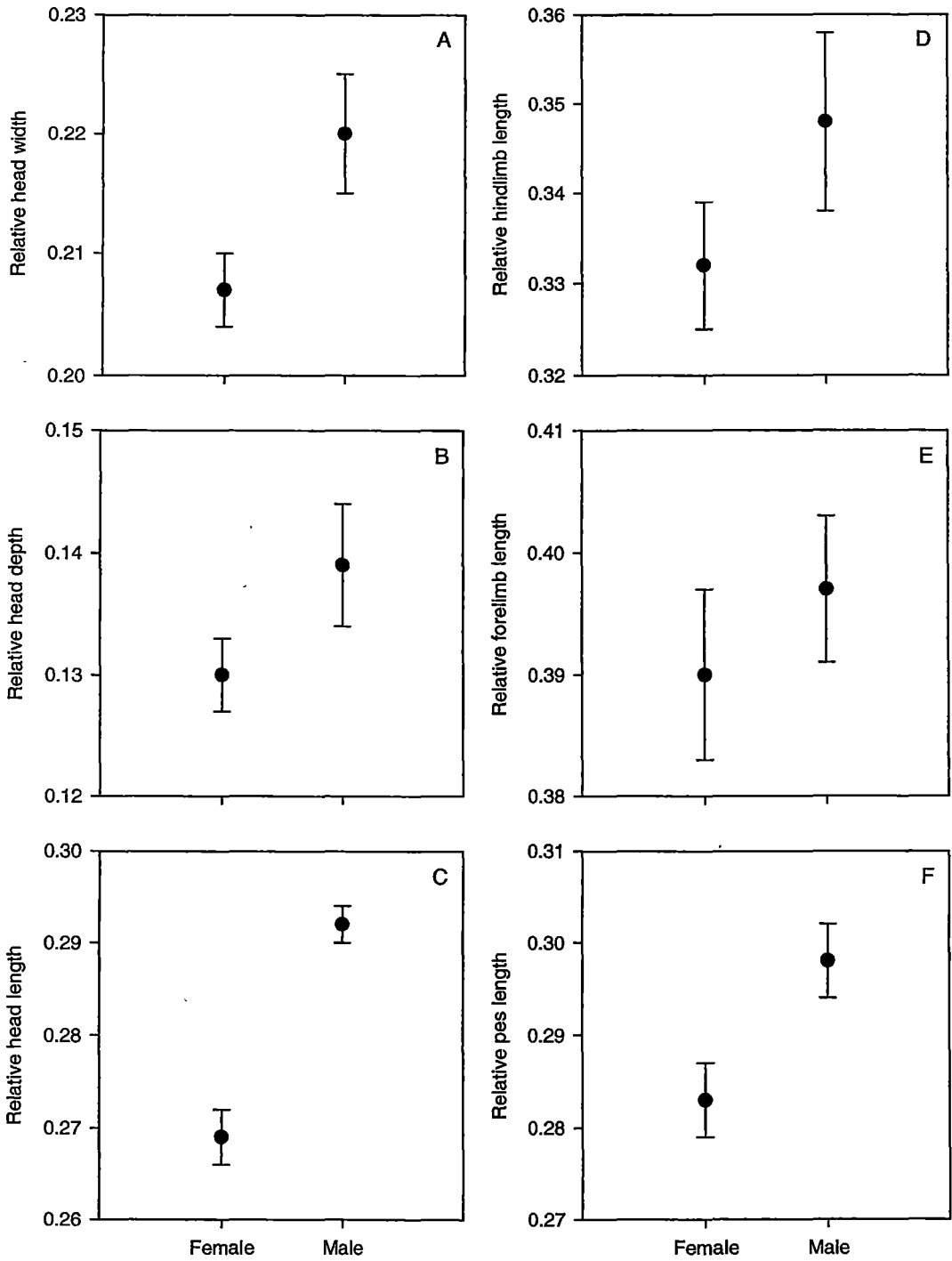


Figure 4. Mean and 95% confidence intervals for relative head and limb sizes of adult male and female *Rankinia diemensis* ( $\text{mm}.\text{mm}^{-1}$ ).

Table 4. Effects of sex and site on relative morphological measurements of adult and hatchling *Rankinia diemensis* as revealed by MANOVA. The analysis is based on the first five principal components identified in PCA.

	Effect	df	Pillai's Trace	<i>F</i>	<i>P</i>
Adult	Sex	5, 235	0.322	22	<0.0001
	Site	5, 235	0.475	14.46	<0.0001
	Sex × site	5, 235	0.577	1.33	0.2115
Hatchling	Sex	5, 46	0.056	0.50	0.7724
	Site	5, 46	0.330	5.0	0.0038
	Sex × site	5, 46	0.099	0.93	0.4714

Table 5. Factor loadings of morphological variables on the first three principal component axes (PC1, PC2 and PC3) calculated for hatchling *Rankinia diemensis*.

Variable	PC1	PC2	PC3
Tail length	0.092	<b>-0.586</b>	-0.219
Head width	<b>0.457</b>	0.079	0.248
Head depth	<b>0.461</b>	0.050	0.138
Head length	<b>0.473</b>	0.041	-0.100
Inter-limb length	-0.025	<b>-0.570</b>	<b>-0.381</b>
Thigh width	<b>0.338</b>	0.307	<b>-0.333</b>
Pes length	<b>0.307</b>	-0.292	-0.011
Hind-limb length	-0.111	<b>0.376</b>	<b>-0.739</b>
Fore-limb length	<b>0.353</b>	-0.033	-0.243
Variance explained (%)	39.3	18.7	11.4
Cumulative variation (%)	39.3	58	69.4

## DISCUSSION

This study confirmed significant body size and morphological trait size differences between adult male and female *Rankinia diemensis* and demonstrates that overall body size does not differ between the sexes at hatching, and there is

---

no sex-specific morphological trait variation at this early life stage that corresponds with that of adults. We have also confirmed significant geographic variation in body and morphological trait sizes within this species, but this does not lead to geographic variation in the degree of SSD. Although females achieve a greater overall body size than males, at hatching there is no difference between the sexes in snout-vent length.

It is atypical (but not unknown) for female agamids to be the larger sex; Shine *et al.*, (1998) illustrated this with 18 out of the 21 agamid species examined identified as having male-biased SSD. Greater overall size in females can be explained by the fecundity advantage hypothesis (see Stuart-Smith *et al.*, 2007 *a*, Chapter 4), and the small-male hypothesis complements this (Schneider *et al.*, 2000; Serrano-Meneses & Székely, 2006). Specifically, in this species, greater female size correlates with increased reproductive potential (Kent, 1987; Greer, 2002; Stuart-Smith *et al.*, 2007 *a*, Chapter 4). While we have limited information on male *R. diemensis*, in other species small male size can confer advantages such as early maturity, reduced energetic costs, greater agility, and potentially greater predator avoidance (Schneider *et al.*, 2000; Blanckenhorn, 2000). Given that there were no intersexual size differences at hatching, SSD in adults must reflect the presence of sex-specific growth patterns or differential selective pressures acting prior to or at maturity, and implies that selective pressures are not consistent throughout the life stages of this species (Badyaev *et al.*, 2001). Since there is no difference in body size (SVL) at hatching, sexes must diverge in body size at a later stage. Whether this stems from different pre- or post- maturity growth rates being greater for females, or greater longevity for females is not yet known.

---

Reptiles typically experience reduced growth post maturation, as energy is then proportioned into reproduction and its associated costs (Shine & Schwarzkopf, 1992; Wapstra, Swain & O'Reilly, 2001; Haenel & John-Alder, 2002), so females may either grow faster or mature later than males to achieve greater body size. Likewise, if females live longer or experience less size or sex-specific mortality (e.g. predation of large males since crypsis is further reduced in male-male visual displays when individuals are larger, since they are more obvious), they may reach greater sizes, however further work is needed to clarify this.

Intersexual differences exist on two levels in *R. diemensis*: overall body size and individual morphological trait size. In species with male-biased SSD, the primary selective force influencing this size difference is sexual selection, and for female-biased SSD, it is natural (fecundity) selection (Schulte-Hostedde *et al.*, 2002; Cox *et al.*, 2003). Despite clear female-biased SSD, we also found strong evidence for selection on male traits (head and limb and tail measurements), particularly those typically associated with male-male interactions in lizards, such as head size (e.g. Anderson & Vitt, 1990; Shine *et al.*, 1998; Kratochvíl & Frynta, 2002; Reaney & Whiting, 2002). Morphological trait variation did not differ between sexes at hatching, suggesting trait morphology must also diverge between the sexes at some later point, as well as the above-mentioned divergence in overall body size that occurs in this species. Large trait size in males is common in agamid lizards, and Shine *et al.* (1998) showed that in 18 out of the 21 agamid species examined, head size was larger in males (with 1 species unknown), in 19 species males had longer (or the same length) tails as females (2 species unknown). In contrast to our findings, 18 of these species exhibited male-biased SSD, and in only one

---

female-biased sexually dimorphic species, *Hypsilurus boydii*, males had relatively larger heads but tail length did not differ between the sexes. It is also possible that the sexes occupy different ecological niches or utilise different parts of their microhabitat – and have evolved independent adaptations to this (Shine, 1989; St. Clair, 1998; Badyaev *et al.*, 2001; Butler & Losos, 2002). For example, the proportionally longer limbs and tail in males may reflect increased use of arboreal structures, allowing better climbing ability and balance (e.g. Losos, 1990).

When we see differences in overall body size and individual morphological trait variation that occurs in an unusual manner, we are inclined to postulate that positive directional selection is operating at different levels. If females are large to increase egg production and males do not appear to require large body size, then why are their relative morphological traits larger than females? It is possible that head size in *R. diemensis* is related to competition or mate choice, despite there being seemingly little selection on overall size for large males. Although males are smaller than females, when referring to within-sex competition, it may be only those relative trait differences that are important for contest success (Stuart-Fox & Ord, 2004; Osbourne, 2005). Male dragons typically use limb and tail movement in male-male interactions (Radder *et al.* 2006; Stuart-Smith *et al.*, 2007 *b*, Chapter 5), and so longer limbs and tails may then promote greater display efficacy. If so, we then need to determine why this does not then create selection for increasing body size in males, with the most obvious reasoning being that an overall body size increase would constrain fitness more than it would benefit it. Increases in body size could be linked to greater mortality through increased potential for detection by predators by virtue of their size, greater metabolic costs and demands

---

of larger size, reduced agility and manoeuvrability and viability costs associated with an extended development time (Shine *et al.*, 1998; Blanckenhorn, 2000).

Population density can influence body size such that smaller males are likely to be selected for when populations are less dense – females are often sparsely distributed and smaller males mature earlier, are more agile (small male hypothesis, Schneider *et al.*, 2000) and require less energy for the distances they must travel to locate a mate (Stamps *et al.*, 1997).

As well as intra and inter sexual differences in dimorphism, we also confirmed significant geographic variation in body size of *R. diemensis*. This revealed that the Flinders Island and Clifton populations were comprised of larger lizards (per sex) than at Blackman Dam. The major differences between these populations include elevation, climate, and latitude. The larger lizards came from regions of low elevation, and warmer climate (FI and CL) – both appear similar in habitat type – coastal heath and sandy soil. These populations also presumably experience a reduced winter torpor period, since conditions are milder, due to their proximity to the coast and the subsequent maritime climate. It is possible then that larger size is attained through the ability to forage for greater time and being subject to less harsh conditions. However, despite geographic variation in body size being widespread in many animal taxa, it is often difficult to easily interpret the causal factors, since multiple processes may contribute (Madsen & Shine, 1993). In this instance, interpretation is also complicated since Flinders Island may be influenced by the ‘island rule’, where reduced predation and competition are common, and often result in larger body sizes in small-bodied species (Clegg & Owens, 2002; Lomolino, 2005; McClain, Boyer & Rosenberg, 2006). Although

---

we are not aware of similar studies on populations on mainland Australia, this information would provide a clearer picture of size trends, and possibly elucidate further climate-related size shifts, however we were unable to include these data in our study, and it is an area which will allow clearer understanding of geographic variation in SSD in this species.

Geographic variation in selective pressures may promote variation in more than one trait and potentially differentially between the sexes, which in turn leads to divergence between male and female body sizes and/or other traits. For example, in sea-run masu salmon (*Oncorhynchus masou*), relative male size increases with latitude, as a result of increasing operational sex ratios or sex-specific selection on males at these latitudes (Tamate & Maekawa, 2006). In *R. diemensis*, we found no difference in the degree of SSD between populations, suggesting that sex-specific selective pressures (fecundity and sexual selection) do not differ geographically despite the overall observed geographic differences in size. Such geographic variation in size is common and often attributed to differential natural and sexual selection pressures occurring throughout the species range (Pearson *et al.*, 2002; Schauble, 2004). It is likely that size differences between sites found in *R. diemensis* (i.e. the overall size differences that occur while the difference between sizes of the sexes remains fairly constant such that the FI population exhibits larger males and females than any other site) are the result of climatic or environmental factors which differ between sites, and that relative sex-specific selection pressures are static for this species.

Differences in morphological traits that occur between populations, such as the longer tail length of lizards at FI and CL than of those from BD may result from ecological or behavioural differences, or population demographics (Stamps *et al.*, 1997; Schulte-Hostedde *et al.*, 2002). Habitat use may account for differences in relative limb measurements in this species, although further work is needed to clarify this. If one population inhabits an area, for example, that requires more climbing or is comprised of less vegetative cover, longer limbs and tail may be selected for as a result of having to climb more, or require greater speeds to reach cover, and avoid predators in between, since limb and tail lengths in lizards are often correlated with speed and climbing ability (Losos, 1990; Van Damme, Aerts & Vanhooydonck, 1998; Herrel, Meyers & Vanhooydonck, 2001).

Although female-biased SSD in *R. diemensis* appears to have evolved as a consequence of fecundity advantages (Stuart-Smith *et al.*, 2007 *a*, Chapter 4), the knowledge that selection is also operating on males to produce differences in relative head and limb measurements between the sexes implies that aggression and dominance displays may still be important. This study has illustrated the importance of examining body size differences on several levels, and highlighted that geographic differences in size dimorphism should also not be overlooked since they provide valuable information on ecological and evolutionary influences to body size within a species.

## REFERENCES

- ADOLPH, S.C. & PORTER, W.P. (1993). Temperature, activity and lizard life histories. *The American Naturalist* 142: 273-295.
- ANDERSON, R.A. & VITT, L.J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* 84: 145-157.
- ANDERSSON M. (1994). *Sexual selection*. Princeton University Press, USA.
- ANDREWS, R.M. & STAMPS, J.A. (1994). Temporal variation in sexual size dimorphism of *Anolis limifrons* in Panama. *Copeia* 1994: 613-622.
- ANGILLETTA, M.J., NIEWIAROKSKI, P.H., DUNHAM, A.E., LEACHÉ, A.D. & PORTER, W.P. (2004). Bergmann's clines in ectotherms: illustrating a life-history perspective with sceloporine lizards. *The American Naturalist* 164: E168-E184.
- ANGILLETTA, M.J., STEURY, T.D. & SEARS, M.W. (2004). Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology* 44: 498-509.
- ASHTON, K.G. & FELDMAN, C.R. (2003). Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57: 1151-1163.
- BADYAEV, A.V. (2002). Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution* 17: 369-378.
- BADYAEV, A.V., WHITTINGHAM, L.A. & HILL, G.E. (2001). The evolution of size dimorphism in the house finch. III. Developmental basis. *Evolution* 55: 176-189.
- BLANCKENHORN, W.U. (2000). The evolution of body size: what keeps organisms small? *The Quarterly Review of Biology* 75: 385-407.
- BLANCKENHORN, W.U. & DEMONT, M. (2004). Bergmann and converse Bergmann latitudinal clines in arthropods: two ends of a continuum? *Integrative and Comparative Biology* 44: 413-424.
- BLANCKENHORN, W.U., KRAUSHAAR, U. & REIM, C. (2003). Sexual selection on morphological and physiological traits and fluctuating symmetry in the yellow dung fly. *Journal of Evolutionary Biology* 16: 903-913.
- BLANCKENHORN, W.U., STILLWELL, R.C., YOUNG, K.A., FOX, C.W. & ASHTON, K.G. (2006). When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution* 60: 2004-2011.
- BLONDEL, J., PERRET, P., ANSTETT M-C. & THÉBAUD, C. (2002). Evolution of sexual size dimorphism in birds: test of hypotheses using blue tits in contrasted Mediterranean habitats. *Journal of Evolutionary Biology* 15: 440-450.
- BRAÑA, F. (1996). Sexual dimorphism in lacertid lizards: male head increase vs female abdomen increase? *Oikos* 75: 511-523.
- BUTLER, M.A. & LOSOS, J.B. (2002). Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecological Monographs* 72: 541-559.
- BUTLER, M.A., SCHOENER, T.W. & LOSOS, J.B. (2000). The relationship between sexual size dimorphism and habitat use in the Greater Antillean *Anolis* lizards. *Evolution* 54: 259-272.
- CALSBECK, R. & SINERVO, B. (2002). Uncoupling direct and indirect components of female choice in the wild. *Evolution* 99: 14897-14902.
- CLEGG, S.M. & OWENS, I.P.F. (2002). The 'island rule' in birds: medium body

- size and its ecological explanation. *Proceedings of the Royal Society of London Series B, Biological Sciences* 269: 1359-1365.
- COOPER, JR W.E. & VITT, L.J. (1993). Female mate choice of large male broad-headed skinks. *Animal Behaviour* 45: 683-693.
- COX, R.M., SKELLY, S.L. & JOHN-ALDER, H.B. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution* 57: 1653-1669.
- DROVETSKI, S.V., ROHWER, S. & MODE, N.A. (2006). Role of sexual and natural selection in evolution of body size and shape: a phylogenetic study of morphological radiation in grouse. *Journal of Evolutionary Biology* 19: 1083-1091.
- FOX, C.W. & CZESAK, M.E. (2006). Selection on body size and sexual size dimorphism differs between host species in a seed-feeding beetle. *Journal of Evolutionary Biology* 19: 1167-1174.
- GREER, A.E. (2002). *The biology and evolution of Australian lizards*. Surrey Beatty & Sons Pty Ltd, Australia.
- HAENEL, G.J. & JOHN-ALDER, H.B. (2002). Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, *Sceloporus undulates*. *Oikos* 96: 70-81.
- HARLOW, P.S. (1996). A harmless technique for sexing hatchling lizards. *Herpetological Review* 27: 71-72.
- HEIBO, E., MAGNHAGEN, C. & VØLLESTAD, L.A. (2005). Latitudinal variation in life-history traits in Eurasian perch. *Ecology* 86: 3377-3386.
- HERREL, A., MEYERS, J.J. & VANHOODYDONCK, B. (2001). Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. *Biological Journal of the Linnean Society* 74: 305-314.
- HOWARD, R.D., MOORMAN, R.S. & WHITEMAN, H.H. (1997). Differential effects of mate competition and mate choice on eastern tiger salamanders. *Animal Behaviour* 53: 1345-1356.
- HUTCHINSON, M., SWAIN, R. & DRIESSEN, M. (2001). *Snakes and lizards of Tasmania*. Fauna of Tasmania Handbook No. 9. Department of Primary Industries, Water and Environment, Tasmania.
- KALIONTZOPOULOU, A., CARRETERO, M.A. & LIORENTE, G.A. (2007). Multivariate and geometric morphometrics in the analysis of sexual dimorphism variation in *Podarcis* lizards. *Journal of Morphology* 268: 152-165.
- KENT, D.S. (1987). Notes on the biology and osteology of *Amphibolurus diemensis* (Gray 1941), the mountain dragon. *Victorian Naturalist* 104:101-104.
- KOZŁOWSKI, J., CZARNOŁĘSKI, M. & DAŃKO, M. (2004). Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integrative and Comparative Biology* 44: 480-493.
- KRATOCHVÍL, L. & FRYNTA, D. (2002). Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). *Biological Journal of the Linnean Society* 76: 303-314.
- LAPPIN, A.K. & SWINNEY, E.J. (1999). Sexual dimorphism as it relates to natural history of leopard lizards (Crotaphytidae: *Gambelia*). *Copeia* 1999: 649-660.
- LE GALLIARD, J-F., MASSOT, M., LANDYS, M.M., MEYLAN, S. & CLOBERT J.

- (2006). Ontogenetic sources of variation in sexual size dimorphism in a viviparous lizard. *Journal of Evolutionary Biology* 19: 690-704.
- LINDENFORS, P., SZÉKELY, T. & REYNOLDS, J.D. (2003). Directional changes in sexual size dimorphism in shorebirds, gulls and alcids. *Journal of Evolutionary Biology* 16: 930-938.
- LOMOLINO, M.V. (2005). Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography* 32: 1683-1699.
- LOSOS, J. (1990). Ecomorphology, performance capability, and scaling of West Indian *Anolis* lizards: an evolutionary analysis. *Ecological Monographs* 60: 369-388.
- MADSEN, T. & SHINE, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* 47: 321-328.
- MANN, G.K.H., O'RIAIN, M.J.O. & HOFMEYER, M.D. (2006). Shaping up to fight: sexual selection influences body shape and size in the fighting tortoise (*Chersina angulata*). *Journal of Zoology* 269: 373-379.
- MCCLAINE, C.R., BOYER, A.G. & ROSENBERG, G. (2006). The island rule and the evolution of body size in the deep sea. *Journal of Biogeography* 33: 1578-1584.
- OLSSON, M., SHINE, R., WAPSTRA, E., UJVARI, B. & MADSEN, T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56: 1538-1542.
- ORD, T.J. & EVANS, C.S. (2003). Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): an experimental analysis. *Behaviour* 140: 1495-1508.
- OSBORNE, L. (2005). Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). *Journal of Ethology* 23: 189-197.
- PEARSON, D., SHINE, R. & WILLIAMS, A. (2002). Geographic variation in sexual size dimorphism within a single snake species (*Morelia spilota*, Pythonidae). *Oecologia* 131: 418-426.
- PETERS, R.A. & ORD, T.J. (2003). Display response of the Jacky dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecology* 28: 499-506.
- RADDER, R.S., SAIDAPUR, S.K., SHINE, R. & SHANBHAG, B.A. (2006). The language of lizards: interpreting the function of visual displays of the Indian rock lizard, *Psammophilus dorsalis* (Agamidae) *Journal of Ethology* 24: 275-283.
- REANEY, L.T. & WHITING, M.J. (2002). Life on a limb: ecology of the tree agama (*Acanthocercus a. atricollis*) in southern Africa. *Journal of Zoology* 257: 439-448.
- RUTHERFORD, P.L. (2004). Proximate mechanisms that contribute to female-biased sexual size dimorphism in an anguid lizard. *Canadian Journal of Zoology* 82: 817-822.
- SCHÄUBLE, C.S. (2004). Variation in body size and sexual dimorphism across geographical and environmental space in the frogs *Limnodynastes tasmaniensis* and *L. peronii*. *Biological Journal of the Linnean Society* 82: 39-56.
- SCHNEIDER, J.M., HERBERSTEIN, M.E., DE CRESPIGNY, F.C., RAMAMURTHY, S. & ELGAR, M.A. (2000). Sperm competition and small size advantage for males of the golden orb-web spider *Nephila edulis*. *Journal of*

- Evolutionary Biology* 13: 939-946.
- SCHULTE-HOSTEDDE, A.I., MILLAR, J.S. & GIBBS, H.L. (2002). Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution* 56: 2519-2529.
- SEARS, M.W. & ANGILLET, M.J. (2004). Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. *Integrative and Comparative Biology* 44: 433-442.
- SERRANO-MENESES, M.A. & SZÉKELY, T. (2006). Sexual size dimorphism in seabirds: sexual selection, fecundity selection and differential niche-utilisation. *Oikos* 113: 385-394.
- SHINE, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology* 64: 419-461.
- SHINE, R., KEOGH, S., DOUGHTY, P. & GIRAGOSSYAN, H. (1998). Costs of reproduction and the evolution of sexual dimorphism in a 'flying lizard' *Draco melanopogon* (Agamidae). *Journal of Zoology*, London 246: 203-213.
- SHINE, R. & SCHWARZKOPF, L. (1992). The evolution of reproductive effort in lizards and snakes. *Evolution* 46: 62-75.
- SPIDLE, A.P., QUINN, T.P. & BENTZEN, P. (1998). Sex-biased marine survival and growth in a population of coho salmon. *Journal of Fish Biology* 52: 907-915.
- STAMPS, J.A., LOSOS, J.B. & ANDREWS, R.M. (1997). A comparative study of population density and sexual size dimorphism in lizards. *The American Naturalist* 149: 64-90.
- ST. CLAIR, R.C. (1998). Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. *Oecologia* 115: 501-507.
- STORZ, J.F., BALASINGH, J., BHAT, H.R., NATHAN, P.T., DOSS, D.P.S., PRAKASH, A.A. & KUNZ, T.H. (2001). Clinal variation in body size and sexual dimorphism in an Indian fruit bat, *Cynopterus sphinx* (Chiroptera: Pteropodidae). *Biological Journal of the Linnean Society* 72: 17-31.
- STUART-FOX, D.M. & ORD, T.J. (2004). Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *The Royal Society* 271: 2249-2255.
- STUART-SMITH, J., SWAIN, R., STUART-SMITH, R.D. & WAPSTRA, E. (2007, a). Is fecundity the ultimate cause of female-biased size dimorphism in *Rankinia [Tymanocryptis] diemensis*? *Journal of Zoology* (London). doi:10.1111/j.1469-7998.2007.00324.x
- STUART-SMITH, J., SWAIN, R. & WAPSTRA, E. (2007 b). The role of body size in competition and mate choice in an agamid with female-biased size dimorphism. *Behaviour* 144: 1087-1102.
- STUART-SMITH, J., SWAIN, R. & WELLING, A. (2005). Reproductive ecology of the mountain dragon, *Rankinia (Tymanocryptis) diemensis* (Reptilia: Squamata: Agamidae) in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 139: 23-28. (Supporting Document).
- TAMATE, T. & MAEKAWA, K. (2006). Latitudinal variation in sexual size dimorphism of sea-run masu salmon, *Oncorhynchus masou*. *Evolution* 60: 196-201.
- TOKARZ, R.R. (1985). Body size as a factor determining dominance in staged

- agonistic encounters between male brown anoles (*Anolis sagrei*). *Animal Behaviour* 33: 746-753.
- VAN DAMME, R., AERTS, P. & VANHOODYDONCK, B. (1998). Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. *Biological Journal of the Linnean Society* 63: 409-427.
- WAPSTRA, E., SWAIN, R. & O'REILLY, J. (2001). Geographic variation in age and size at maturity in a small Australian viviparous skink. *Copeia* 2001: 646-655.
- WAPSTRA, E., OLSSON, M., SHINE, R., EDWARDS, A., SWAIN, R. & JOSS, J.M.P. (2004). Maternal basking behaviour determines offspring sex in a viviparous reptile. *Proceedings of the Royal Society London B (Suppl.)* 271: S230-S232
- WATKINS, G.G. (1996). Proximate causes of sexual size dimorphism in the Iguanid lizard *Microlophus occipitalis*. *Ecology* 77: 1473-1482.
- WATT, M.J. & JOSS, J.M.P. (2003). Structure and function of visual displays produced by male Jacky dragons, *Amphibolurus muricatus*, during social interactions. *Brain, Behaviour and Evolution* 61: 172-183.
- WONG, B.B.M. & CANDOLIN, U. (2005). How is female mate choice affected by male competition? *Biological Reviews* 80: 559-571.
- YOUNG, K.A. (2005). Life-history variation and allometry for sexual size dimorphism in Pacific salmon and trout. *Proceedings of the Royal Society B* 272: 167-172

---

CHAPTER 3

PROXIMATE MECHANISMS

---

### CHAPTER 3

A proximate approach for assessing female-biased size dimorphism in the agamid lizard, *Rankinia diemensis*.

(Unsubmitted manuscript)

#### ABSTRACT

The proximate causes for sexual size dimorphism (SSD) include the physical and physiological processes that act to produce the size difference often observed in adult males and females. Quantifying these processes allows determination of how and when size differences occur. I used skeletochronology to determine the relationship between size and age and assess the age at which sexes diverge in size in an agamid lizard with female-biased SSD. I explored whether age at hatching, differential growth rates, size at maturity, cessation of growth at maturity, or longevity, were responsible for producing the female-biased SSD patterns observed in *Rankinia diemensis*. I determined size at hatching by measurement of neonates and captured individuals of all size classes from a single population to determine age and growth parameters for both sexes. There were no inter-sexual differences in body size parameters at hatching (including overall body size, snout-vent length [SVL], and trait sizes such as head, limb and tail size), and growth trajectories were similar for both males and females for the first two years of life. Sex-specific size differences emerge at three to four years of age, where females reach a larger size. This indicates that the size differences

---

observed between adults are determined by processes acting during late juvenile development or at near maturity. Differences in the growth asymptote further contributed to SSD in *R. diemensis*, with male growth slowing at maturity (at approximately 3 years of age). Females continued to grow past the maximum size reached by males, potentially maturing later than males, thereby reaching greater body size. It is likely that this delay in maturity in females is linked to the benefits of larger size for reproductive-mediated advantages. Morphological traits (including head, limb and tail measurements) increase isometrically with body size in both sexes, following the same pattern of timing of size divergence as SVL.

## INTRODUCTION

Growth patterns and age at sexual maturity are important mechanisms in determining an individual's size (Adolph & Porter, 1996; Berrigan & Charnov, 1994; Brown *et al.*, 1999). They are therefore central to understanding the actual processes responsible for the size differences between adult males and females of the same species (sexual size dimorphism, SSD) that are observed in many taxa (St Clair *et al.*, 1994; Haenel & John-Alder, 2002). Sex-specific adult size differences may reflect differential initial sizes, growth trajectories or asymptotes between the sexes, or can reflect differential survival (Haenel & John-Alder, 2002; Stamps & Andrews, 1992). The primary physical avenues, the *proximate* mechanisms, through which sex-based size differences occur are therefore for the larger sex to be born/hatch larger, to grow for longer, to mature at a later age, or to live longer (Andrews & Stamps, 1994; St Clair, 1998; Badyaev *et al.* 2001; Haenel & John-Alder, 2002; Rutherford, 2004; Cox & John-Alder, 2007). Other

---

factors such as recruitment to, and migration from a population, behavioural exclusion, and size specific mortality, may further impact on the observed size structure of a population (Shine, 1990; Haenel & John-Alder, 2002; Rutherford, 2004).

Table 1 (modified from Stamps 1993 and Watkins, 1996) summarises the major proximate factors responsible for size differences between males and females, and identifies the mechanism behind each. For example, size dimorphism at maturity can be the result of different growth prior to maturity (the proximate cause), or it can be due to either a difference in growth rate or in the growth asymptote that occurs in either sex.

Table 1. Proximate gender-specific mechanisms leading to SSD (modified from Stamps 1993 and Watkins, 1996).

PROXIMATE FACTOR	SEX-SPECIFIC DIFFERENCE	MECHANISM
Growth	Trajectories	Asymptote/ rate
Neonate size	Size at birth/hatching	Sex-specific investment
Maturity	Age at maturity	Age- and sex- specific hormones
Age distribution	Age-specific mortality	Recruitment (adult) Mortality (adult)
	Age-specific migration	Behavioural exclusion Recruitment (juvenile) Migration (adult)

The growth rate of an individual can influence a number of fundamentally important life history traits – ranging from reproductive output, the age and size it

achieves at maturity, and its longevity (Andrews, 1982; Bronikowski, 2000).

Rapid growth in early life can reduce longevity, presumably through implications for future resource allocation (Olsson & Shine, 2002). High reproductive rates can also be detrimental to an individual's long-term survival, via the same mechanisms (e.g. Arnqvist & Nilsson, 2000; Westendorp & Kirkwood, 1998).

Although growth rate has a strong genetic component, it can also be influenced by a range of external factors (St Clair *et al.*, 1994). For example, temperature has a strong influence on growth rate, particularly in ectothermic animals (e.g.

Bronikowski, 2000; Sinervo, 1990; Sinervo & Adolph, 1994), as do other limiting factors such as food and water availability, which can also, in turn, be regulated by competition intensity (Andrews, 1982; Lorenzon *et al.*, 1999; Madsen & Shine, 2000).

When investigating growth patterns and trajectories, it is often logistically difficult to determine an individual's age because it often relies on long-term field studies including making repeated observations on individuals of known age (which presents a suite of logistical difficulties). Skeletochronology (histological cross sections of bones) is an accurate tool for assessing age and determining growth and longevity in reptiles from temperate climates, and provides a solution to many of the logistical difficulties otherwise required to attain this information (e.g. Castanet *et al.*, 1993; Castanet & Smirina, 1990; Smirina, 1994; Guarino *et al.*, 2003; Leclair *et al.* 2005; Wapstra *et al.*, 2001). It is important to assess age-specific size in reptiles, since growth is often discontinuous, is often staggered by periods of slow growth (e.g. after hatching or maturity, or season), and can be influenced by environmental factors (Andrews, 1982). The accuracy of

---

skeletochronology can be strengthened by employing several validation techniques, such as incorporating animals of known age, and is particularly advantageous when undertaken with the use of phalanges since it negates the need to sacrifice the animal (Guarino *et al.*, 2003).

Skeletochronology involves using histological cross sections of long bones (usually either phalangeal or femoral bones) to determine age. This technique uses osseous growth marks (cyclical growth marks that relate to seasonality) by identifying times of arrested development (LAGs, Lines of Arrested Growth), such as a period of hibernation or torpor (e.g. Ortega-Rubio *et al.*, 1993). I used skeletochronological methods to determine the age of individual *Rankinia [Tymanocryptis] diemensis*, a sexually dimorphic agamid lizard of south-eastern Australia in which females are the larger sex. This species undergoes a lengthy torpor period, particularly in Tasmania (Stuart-Smith *et al.*, 2005, Supporting Document), making it an ideal candidate for using skeletochronology to assess age. Female-biased sexual size dimorphism (SSD) is atypical of agamid lizards which usually express strong male-biased size dimorphism for combat and male-male rivalry (e.g. Shine *et al.*, 1998). Therefore, understanding growth patterns is important in revealing the mechanisms producing sex-specific size. We can also only fully understand SSD in agamids once we understand the exceptions to the rule - how selection and proximate mechanisms act in species like *R. diemensis* - which exhibit morphologies contradictory to the norm for this taxonomic group.

Here I assess whether female *R. diemensis* grow faster, mature later, or live longer than males in an attempt to identify the mechanism through which this size

---

difference is attained. By identifying how and when the divergence in body size occurs, we can then also begin to understand how external factors can impact on the size difference. Previous work has already identified that there is no size difference between the sexes at time of hatching (Stuart-Smith *et al.*, *in press*; Chapter 2), so they must diverge in size at some point during development. I also include investigation of morphological trait growth patterns to determine their relationship with body size. This is done by using the histological age estimates of individual lizards and comparing trait size (and growth patterns of traits) to body size and age.

## METHODS

### *Study species*

The study species, *Rankinia [Tymanocryptis] diemensis* (Squamata: Agamidae), is a relatively small, cryptic dragon lizard inhabiting areas of south-eastern Australia, including Tasmania (Stuart-Smith *et al.*, 2005, Supporting Document). This temperate lizard undergoes a relatively long torpor period, lasting up to 7 months (Stuart-Smith *et al.*, 2005, Supporting Document). It is highly dimorphic, with the average size of mature females in the study population 63.7 mm (SE  $\pm$  1.134), and 51.5 mm for males (SE  $\pm$  1.118). This study included lizards from one population in Central Tasmania (42°13'S, 147°14'E, elevation: 700-800 m). Lizards were captured throughout the activity season (October – April, 2003) as part of a mark-recapture study (see Chapter 6), where toe-clipping allowed identification of individuals and also provided the phalanges to be used in skeletochronology. The intensity of the field program means that the individuals included in this study comprise most of the population. Individuals across all age

---

groups were obtained ( $n = 91$ ). Individuals were measured using electronic callipers ( $\pm 0.1$  mm) for snout-vent length (SVL; mm) and head (width and length; mm), limb (fore and hind; mm) and tail (length; mm) measurements (see below). I also obtained femoral and phalangeal bones from 4 individuals preserved at the University of Tasmania for comparison with and to validate the use of phalanges for ageing.

#### *Age determination*

Age determination techniques were adapted from Castanet *et al.* (1993), Castanet & Smirina (1990), and Wapstra *et al.*, (2001). Toe-clips were stored in 70 % ethanol prior to skeletochronological sectioning. Each bone was decalcified in 5% nitric acid for 4-7 hours, and then rinsed with water for 10-12 hours. Bone preparation included dehydration to allow embedding in wax; this involved 60 minute periods spent in increasing increments of ethanol concentrations (to slow the rate of water loss from the cells, preventing damage to cells and tissues: 0 %, 50 %, 70%, 90%, 100%I, 100%II, 50:50 ethanol:xylene, 100% xylene; then in wax at 60 °C: wax I, wax II). Each bone was embedded in wax using a separate wax box mould, and cooled on ice, using a heated scalpel to slowly mix the wax while cooling (to ensure bone did not move while wax set and to ensure no bubbles formed and wax set at the same rate throughout the mould). Once cool, each block was trimmed and then sectioned at 8  $\mu$ m using a rotary microtome to transversely section each bone. Serial sections of almost the entire length of each digit were cut to ensure that the mid-diaphysis region was sectioned. Each serial section of ribbon was transferred to a glass slide. Slides were left on a warming plate (40 °C) until sections adhered to the slide. To stain with Erlich's

---

haematoxylin, I employed a series of re-hydration procedures, leaving each slide in increasing concentrations of distilled water for 30 mins each (i.e. the reverse procedure for the above-mentioned dehydration procedure: xylene; xylene:ethanol, 100% ethanol (II), 100% ethanol (I), 90% ethanol, 70 % ethanol, 50% ethanol, water). They were then placed in Erlich's haematoxylin stain for 15-20 minutes before being placed back in a mixture of distilled water and ammonia. To mount slides, I dehydrated at 15-minute intervals (using the above-mentioned procedure) before mounting with DPX, (Di-n-butyl Phthalate in xylene; a colourless, synthetic resin) and a cover slip. Lines of arrested growth (LAGs) were counted using a compound microscope, and verified using a second independent observer. Observers agreed on all but two of the sections and since this could not be resolved (due to poor sections), these two individuals were not included in any further analyses. Counting LAGs involved counting and measuring the diameter of each LAG, as well as the outer and inner diameters of the bone section using an eyepiece graticule. Endosteal reabsorption was estimated by using bone diameters of hatchlings and cross-validation of femur and toe-clip LAGs helped to validate the process. The age of individuals was established by the number of winters (including actual LAGs, and back-calculation of those that may have been lost in older individuals, see Wapstra *et al.*, 2001).

Age determination by counting LAGs was validated in a 3 ways:

1. LAG comparison between femur and toe-clips ( $n = 4$ ) to ensure that growth rings in toe-clips corresponded to growth rings in other bones;

2. Using initial LAGs in hatchlings ( $n = 9$ ) to assess size at hatching;
3. LAG comparison of individual lizards captured in successive years (i.e. toe-clip taken in two successive years;  $n = 3$ ).

#### *Size measurements*

The aim was to elucidate the proximate mechanisms responsible for SSD in *R. diemensis*, and linked to this is understanding whether morphological trait sizes, which also differ between the sexes, diverge concurrently with SVL. For this, I compared trait sizes with body sizes. The traits assessed represent those that were found to be significantly different between the sexes (see Chapter 2): head sizes (length and width), limb sizes (hind limb and forelimb) and tail length.

#### RESULTS

Age determination validation techniques showed that skeletochronology is an accurate measure of age in *R. diemensis*. I obtained a direct correlation between number of LAGs counted between femur and toe-clip individuals ( $n = 4$ ) and lizards captured in successive years ( $n = 3$ ) had all increased by 1 LAG in their phalange. Growth trajectories of *R. diemensis* were estimated using the Gompertz curve, which was the most suited to the sigmoidal growth apparent in this species. This model indicates that growth is slowest at the start and end of a time series, and has been shown to be an effective estimation of growth patterns in other lizard species (e.g. El Mouden *et al.*, 1999). The model and parameters were chosen based on minimising overall sums of squares (SS) using a randomised procedure.

The Gompertz equation for the line of curve is as follows:

$$SVL = A + Ce^{-e^{-B(X-M)}}$$

where  $A$  is the lower asymptote,  $C$  is the upper asymptote,  $e$  is an exponential,  $B$  is growth rate,  $X$  is age and  $M$  represents the time of maximum growth (units of time expressed in annual LAGs). Figure 1a shows the raw data without the Gompertz equation fitted, also indicating size and age at maturity. The growth trajectories for both sexes of *R. diemensis* are presented in Figure 1b. This shows initial similar sizes for males and females, and similar growth patterns until three to four years of age. At this point, male growth asymptotically approaches zero, and females continue to grow, at a slower rate. The divergence in size begins at age three, and at age 5 (when confidence intervals do not overlap) the sexes are separate). Figure 1b also shows slow initial and late growth for both sexes and an increase in growth rate between the ages of two and four years (see Andrews, 1982 for similar patterns). Both males and females reach similar maximum ages (females 8 years;  $n = 1$ ; males and females 7 years,  $n = 6$ ). The relationship between trait morphology and age was similar to that of SVL for all traits included, such that trait size diverged at similar age (Figure 2). This supports data from Chapter 5, where trait size is found to be directionally proportional to SVL.

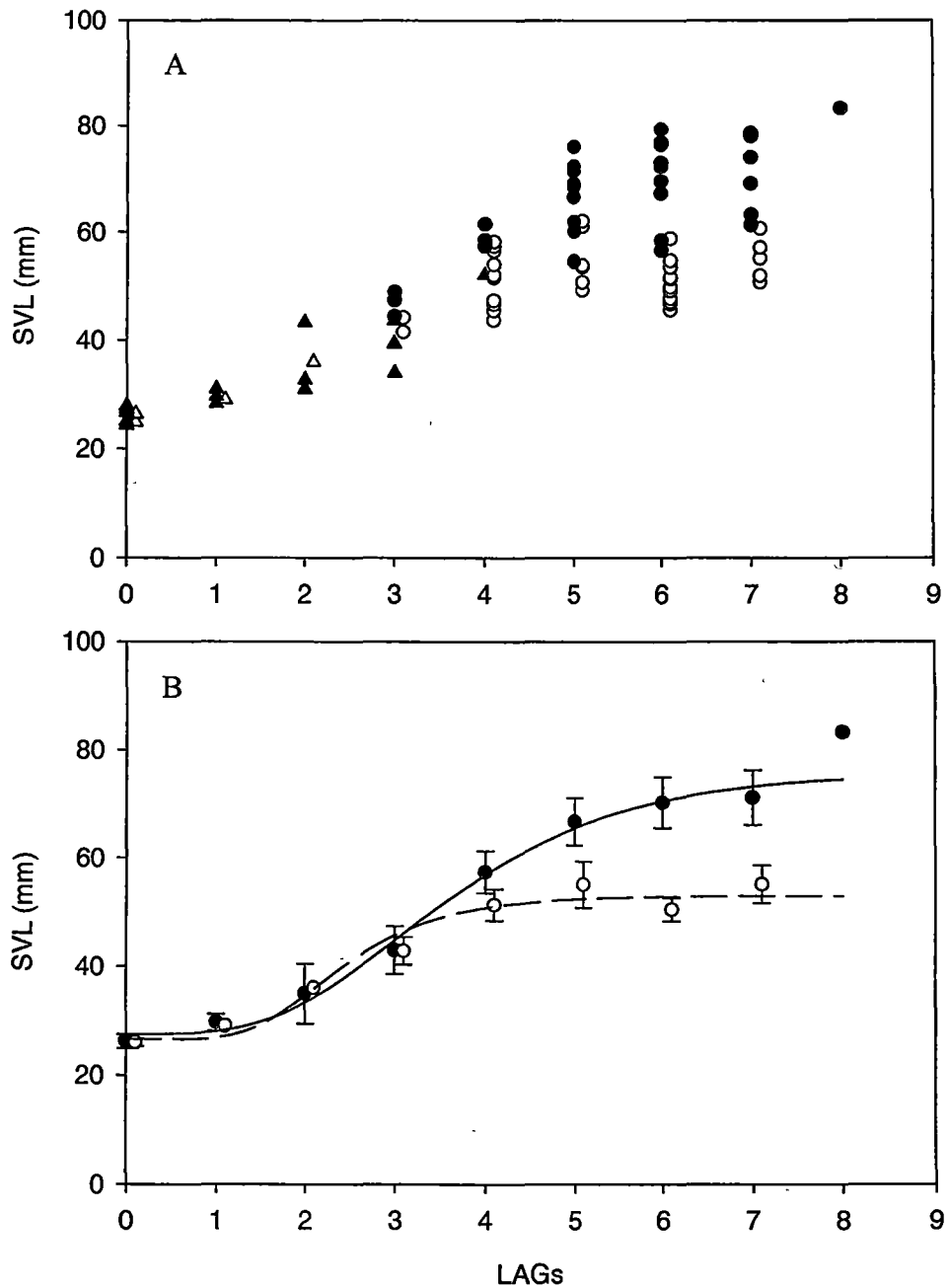


Figure 1a) Raw data of SVL and age in *R. diemensis*, (male = white fill; female = black fill; adults = circles, sub-adults = triangles). 1b). Relationship between SVL and age (means and 95 % confidence intervals) for male and female *Rankinia diemensis* (male = white fill; female = black fill) with the Gompertz function fitted (male = broken line, female = unbroken line).

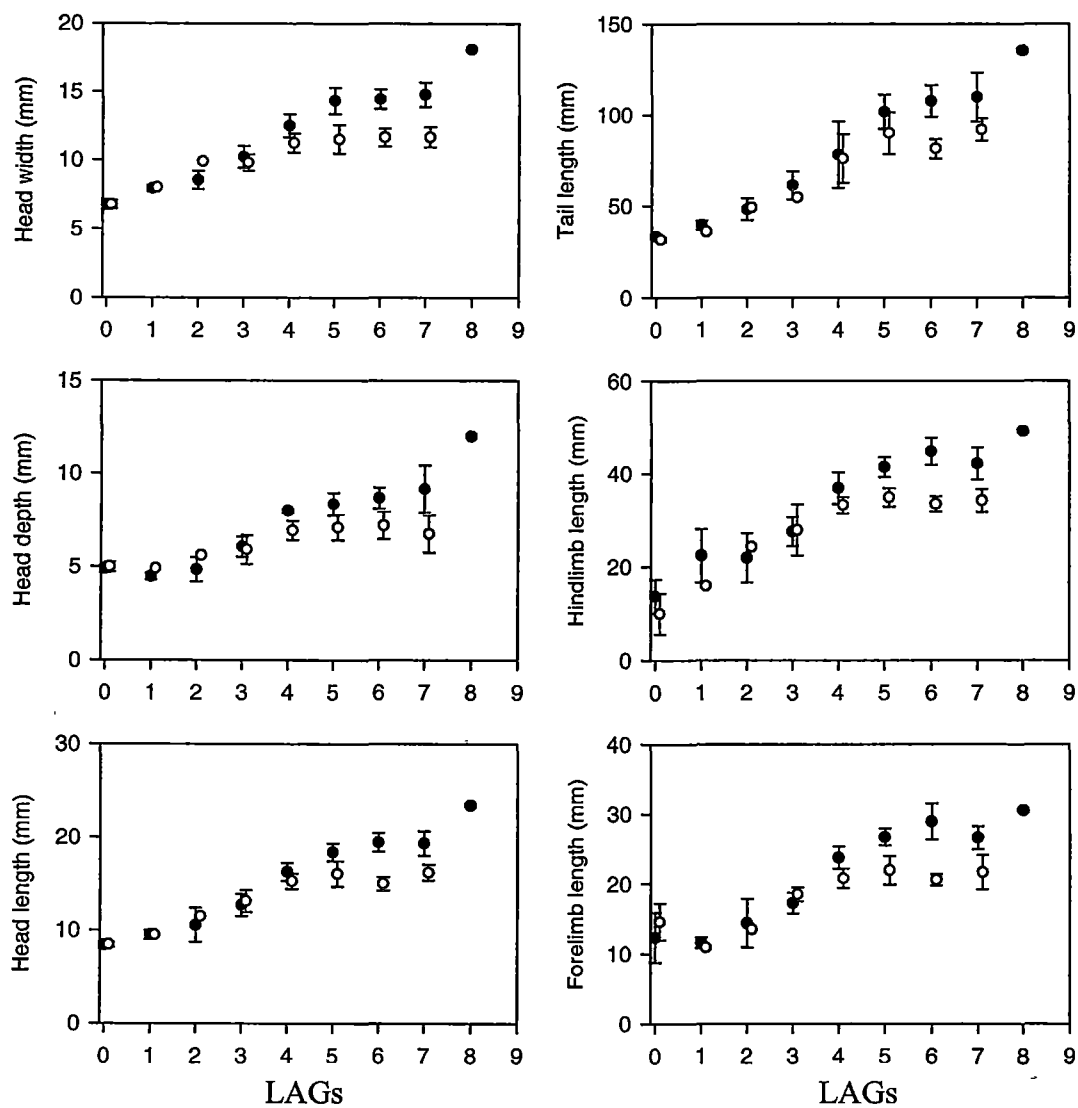


Figure 2. Relationship between trait size and age (means and 95 % confidence intervals) for male and female *Rankinia diemensis* (male = white fill; female = black fill).

## DISCUSSION

Skeletochronological analysis was used to quantify the growth patterns of male and female *R. diemensis* and revealed that growth cessation at an earlier age in males, combined with delayed maturity and potentially continued post-maturity growth in females, is responsible for the observed difference in adult body sizes. Since previous work (see Stuart-Smith *et al.*, *in press*; Chapter 2) has identified a similar degree of size difference between geographically isolated populations (despite different sizes of both sexes at different sites), I can further identify that there is an underlying commonality of proximate mechanisms and selective pressures that lead to the observed SSD in *R. diemensis*.

In many lizards, growth is the most rapid during the juvenile life stage (e.g. Haenel & John-Alder, 2002; Watkins, 1996; Wapstra *et al.*, 2001). In temperate-climate reptiles, when hatching occurs immediately prior to winter torpor, individuals must build energy stores required for torpor within a limited time. This climate limits the amount of time an individual can thermoregulate and spend foraging, and reduces the opportunity for growth on both a daily and seasonal basis (Adolph & Porter, 1996; Sinervo & Adolph, 1994; Uller & Olsson, 2003). Cool climates can often result in slower growth rates and maturation at a larger body size compared to tropical counterparts (Angilletta *et al.*, 2004). This pattern of slow initial growth found in *R. diemensis* corresponds to Andrew's (1982) early models of reptile growth patterns, which often show discontinuous growth that is linked to energy allocation limitations. Growth is particularly limited in the first season for *R. diemensis*, since hatching occurs in March, and torpor begins in April – May (with June the start of austral winter). Agamids typically inhabit hot

---

dry or tropical regions (see Cogger, 2000) and require higher preferred body temperatures than other lizard genera inhabiting the same region (see Greer, 1989 for comparison of preferred body temperatures of a range of lizard genera in Australia). Adolph and Porter (1996) compiled data to show that most temperate zone oviparous lizards reach maturity at one year of age, with a further peak (in the number of species that reach maturity) at two years (representing data from 10 families and 102 species). In this context, *R. diemensis* exhibits somewhat delayed maturity (~3-4 years) suggesting that it does not begin reproducing until relatively later in life. This may indicate that the climate experienced in Tasmania may be particularly restrictive for these reptiles in terms of activity time, growth energetics and reproductive seasonality (see Adolph & Porter, 1996; Sinervo & Adolph, 1994; for similar conclusions in *Sceloporus* lizards).

The sexes are similar in size at hatching and growth is slow for the first two years of life. Growth trajectories are similar between the sexes for the first three years of life. This follows the trend observed for most sexually dimorphic vertebrates – near identical morphology during early life stages and development, and then highly divergent growth patterns to achieve the size dimorphism expressed as adults (e.g. Badyaev, 2002 and references therein). At maturity, male growth rate decreases and asymptotically approaches zero, as is common in other lizards (Olsson & Shine, 1996; Shine & Charnov, 1992). Females appear to delay maturity (for a minimum of one season) and grow, at least to some extent, post maturity. These growth patterns also correspond to bimaturation theories. Where a relationship exists between SSD and sexual bimaturation, the larger sex often becomes reproductive at an older age than the smaller sex (Stamps & Krishnan,

---

1997). It is the delayed maturity that allows one sex to reach greater size, since reproduction requires resources which take away from that which is available for growth (e.g. Stearns & Crandall, 1981; Tinkle, 1969; Watkins, 1996; Wapstra *et al.*, 2001).

Recent work indicates strong positive selection on female body size due to fecundity related advantages of large size (Stuart-Smith *et al.*, 2007 *a*, Chapter 4). Delayed female maturity, and potentially ongoing post maturity growth, provide the mechanism for females to attain the larger sizes required to be able to increase fecundity. Delayed maturity often infers lower lifetime reproductive output since it means fewer reproductive seasons (Galán, 1996; James, 1991). However, there is a trade-off since there is also evidence to support the premise that rapid growth in early life comes with the disadvantage of reducing survivorship later in life (Olsson and Shine, 2002). Since previous work has outlined that relative clutch mass (RCM) is not proportional to size (Stuart-Smith *et al.*, 2007 *a*, Chapter 4), and that the only way for a female to increase her reproductive potential is to attain larger size, then delaying reproduction to reach larger size is an effective strategy for increasing reproductive output in this species. Slowed growth and delayed maturity can be advantageous if large size also conveys the advantage of larger clutch sizes (James, 1991; Tinkle *et al.*, 1970), as occurs in *R. diemensis*.

Longevity appeared relatively similar between male and female *R. diemensis* in this study. The maximum age reached was 8 seasons ( $n = 1$  female), with similar numbers of both sexes reaching 7 LAGs ( $n = 5$  males, 6 females). Other Australian agamids such as *Moloch horridus* and *Chlamydosaurus kingii* reach a

---

similar age (approximately 6 years) (Griffiths, 1999; Pianka & Pianka, 1970); however, they inhabit tropical regions and are thus able to reach larger size in the same time frame.

Trait morphology appeared to diverge at approximately the same time as SVL for males and females. Trait size is directly proportional to SVL in *R. diemensis* (see Chapter 6), and so it is then not surprising that growth of traits corresponds to the same pattern as SVL, with slow initial and late growth, and divergence beginning at three years. Figure 3 shows that growth rate of morphological traits is similar to SVL for males and females. These data identify that trait and size divergence patterns are similar, and that trait dimensions isometrically increase with body size for both males and females (see Bonduriansky & Rowe, 2003; Herrel & O'Reilly, 2006).

This study clearly allows us to rule out several potential proximate mechanisms of SSD in *R. diemensis*. This species does not show sex - specific differences in size at hatching, growth rate during early life stages, or longevity. Size at maturity and differences in post-maturity growth and size asymptote are therefore the proximate mechanisms responsible for the female-biased SSD in *R. diemensis*.

## REFERENCES

- ADOLPH, S.C. & PORTER, W.P. (1996). Growth, seasonality, and lizard life histories: age and size at maturity. *Oikos*, 77: 267-278.
- ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press, Princeton, NJ.
- ANDREWS, R.M. (1982). Patterns of Growth in Reptiles. In: Gans, C. & Pough, F.H. (eds). *Biology of the Reptilia, Vol 13, Physiology D. Physiological Ecology*. Academic Press, New York, pp 273-319.
- ANDREWS, R.M. & STAMPS, J.A. (1994). Temporal variation in sexual size dimorphism of *Anolis limifrons* in Panama. *Copeia*, 1994: 613-622.
- ANGILLETTA, M.J. JR., STEURY, T.D. & SEARS, M.W. (2004). Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44: 498-509.
- ARNQVIST, G. & NILSSON, T. (2000). The evolution of polyandry: multiple mating and female fitness in insects. *Animal Behaviour*, 60: 145-164.
- BADYAEV, A.V. (2002). Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution*, 17: 369-378.
- BADYAEV, A.V., WHITTINGHAM, L.A., & HILL, G. (2001). The evolution of sexual size dimorphism in the house finch. III. Developmental basis. *Evolution*, 55: 176-189.
- BERRIGAN, D. & CHARNOV, E.L. (1994). Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. *Oikos*, 70: 474-478.
- BONDURIANSKY, R. & ROWE, L. (2003). Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. *Evolution*, 57: 2046-2053.
- BRONIKOWSKI, A.M. (2000). Experimental evidence for the adaptive evolution of growth rate in the garter snake, *Thamnophis elegans*. *Evolution*, 54: 1760-1767.
- BROWN, R.P., ZNARI, M., EL MOUDEN, E., & HARRIS, P. (1999). Estimating asymptotic body size and testing geographic variation in *Agama impalearis*. *Ecography* 22, 277-283.
- CASTANET, J., FRANCILLON-VEILLOT, H., MEUNIER, F.J. & DE RECQLES, A. (1993). Bone and individual aging. In: *Bone*, volume 7. B.K. Hall (Ed). CRC Press, London pp 245-283.
- CASTANET, J. & SMIRINA, E. (1990). Introduction to the skeletochronological method in amphibians. *Annales des Sciences Naturelles, Zoologie*, 11: 191-196
- COX, R.M. & JOHN-ALDER, H.B. (2007). Growing apart together: the development of contrasting sexual size dimorphisms in sympatric *Sceloporus* lizards. *Herpetologica*, 63: 245-257.
- EL MOUDEN, E., ZNARI, M., & BROWN, R.P. (1999). Skeletochronology and mark-recapture assessments of growth in the North African agamid lizard (*Agama impalearis*). *Journal of Zoology London*, 249: 455-461.
- GALÁN, P. (1996). Sexual maturity in a population of the lacertid lizard *Podarcis bocagei*. *Herpetological Journal*, 6: 87-93.
- GREER, A.E. (1989). *The Biology and Evolution of Australian Lizards*. Surrey Beatty & Sons Pty Ltd, Australia.

- GRIFFITHS, A.D. (1999). Demography and Home Range of the Frillneck Lizard, *Chlamydosaurus kingii* (Agamidae), in Northern Australia. *Copeia*, 1999: 1089-1096.
- GUARINO, F.M., LUNARDI, S., CARLOMAGNO, M., & MAZZOTTI. (2003). A skeletochronological study of growth, longevity, and age at sexual maturity in a population of *Rana latastei* (Amphibia, Anura). *Journal of Bioscience*, 28: 775-782.
- HAENEL, G.J. & JOHN-ALDER, H.B. (2002). Experimental and demographic analyses of growth rate and sexual size dimorphism in a lizard, *Sceloporus undulates*. *Oikos*, 96: 70-81.
- HERREL, A. & O'REILLY, J.C. (2006). Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology*, 79: 31-42.
- JAMES, C.D. (1991). Growth rates and ages at maturity of sympatric scincid lizards (*Ctenotus*) in Central Australia. *Journal of Herpetology*, 25: 284-295.
- KOZŁOWSKI, J., CZARNOŁĘSKI, M. & DAŃKO, M. (2004). Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integrative and Comparative Biology*, 44: 480-493.
- LECLAIR, M.H., LECLAIR, JR., R., & GALLANT, J. (2005). Application of skeletochronology to a population of *Pelobates cultripes* (Anura: Pelobatidae) from Portugal. *Journal of Herpetology*, 39, 199-207.
- LORENZON, P., CLOBERT, J., OPPLIGER, A. & JOHN-ALDER, H. (1999). Effect of water constraint on growth rate, activity and body temperature of yearling common lizard (*Lacerta vivipara*). *Oecologia*, 118: 423-430.
- MADSEN, T. & SHINE, R. (2000). Silver spoons and snake body sizes: prey availability early in life influences long-term growth rates of free-ranging pythons. *Journal of Animal Ecology*, 69: 952-958.
- OLSSON, M. AND SHINE, R. (1996). Does reproductive success increase with age or with size in species with indeterminate growth? A case study using sand lizards (*Lacerta agilis*). *Oecologia*, 105: 175-178.
- OLSSON, M. AND SHINE, R. (2002). Growth to death in lizards. *Evolution*, 56: 1867-1870.
- ORTEGA-RUBIO, A., KHODADDOST, M., & SERVÍN, R. (1993). Skeletochronology in the Mezquite lizard, *Sceloporus grammicus*. *Proceedings of the Oklahoma Academy of Science*, 73: 31-34.
- PIANKA, E. R. & PIANKA, H. D. (1970). The Ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. *Copeia*, 1970: 90-103.
- RUTHERFORD, P. (2004). Proximate mechanisms that contribute to female-biased sexual size dimorphism in an anguid lizard. *Canadian Journal of Zoology*, 82: 817-822.
- SHINE, R. (1990). Proximate determinants of sexual differences in adult body size. *American Naturalist*, 135: 278-283.
- SHINE, R. & CHARNOV, E.L. (1992). Patterns of survival, growth and maturation in snakes and lizards. *The American Naturalist*, 139: 1257-1269.
- SHINE R, KEOGH S, DOUGHTY P, GIRAGOSSYAN H. (1998). Costs of reproduction and the evolution of sexual dimorphism in a 'flying lizard' *Draco melanopogon* (Agamidae). *Journal of Zoology*, London, 246: 203-213.
- SINERVO, B. (1990). Evolution of thermal physiology and growth rate between populations of the western fence lizard (*Sceloporus occidentalis*). *Oecologia*, 83: 228-237.

- SINERVO, B. AND ADOLPH, S.C. (1994). Growth plasticity and thermal opportunity in *Sceloporus* lizards. *Ecology*, 75: 776-790.
- SMIRINA, E.M. (1994). Age determination and longevity in amphibians. *Gerontology*, 40: 133-146.
- STAMPS, J.A. (1993). Sexual size dimorphism in species with asymptotic growth after maturity. *Biological Journal of the Linnean Society*, 50: 123-145.
- STAMPS, J.A. & ANDREWS, R.M. (1992). Estimating asymptotic size using the largest individuals per sample. *Oecologia*, 92: 503-512.
- STAMPS, J. & KRISHNAN, V.V. (1997). Sexual bimaturation and sexual size dimorphism in animals with asymptotic growth after maturity. *Evolutionary Ecology*, 11: 21-39.
- STEARNS, S.C. & CRANDALL, R.E. (1981). Quantitative predictions of delayed maturity *Evolution*, 35: 455-463.
- ST CLAIR, R. (1998). Patterns of growth and sexual size dimorphism in two species of box turtles with environmental sex determination. *Oecologia*, 115: 501-507.
- ST CLAIR, R. GREGORY, P.T., & MACARTNEY, J.M. (1994). How do sexual differences in growth and maturation interact to determine size in northern and southern painted turtles. *Canadian Journal of Zoology*, 72: 1436-1443.
- STUART-SMITH, J., STUART-SMITH, R. D., SWAIN, R. & WAPSTRA, E. (*in press*, pending final revision). Size dimorphism in *Rankinia* [*Tympanocryptis*] *diemensis* (Family Agamidae): sex-specific patterns and geographic variation. *Biological Journal of the Linnean Society*.
- STUART-SMITH, J., SWAIN, R., STUART-SMITH, R., AND WAPSTRA, E. (2007 a). Is fecundity the ultimate cause of female-biased size dimorphism in a dragon lizard? *Journal of Zoology* London, doi:10.1111/j.1469-7998.2007.00324.x
- STUART-SMITH, J., SWAIN, R., & WELLING, A. (2005). Reproductive ecology of the mountain dragon, *Rankinia* (*Tympanocryptis*) *diemensis* (Reptilia: Squamata: Agamidae) in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania*. 139: 23-28.
- TINKLE, D.W. (1969). The concept of reproductive effort and its relation to the evolution of life histories of lizards. *The American Naturalist*, 103: 501-516.
- TINKLE, D.W., WILBUR, H.M., AND DUNHAM, A.E. (1970). Evolutionary strategies in lizard reproduction. *Evolution*, 24: 55-74.
- ULLER, T. & OLSSON, M. (2003). Life in the land of the midnight sun: are northern lizards adapted to longer days? *Oikos*, 101: 317-322.
- WAPSTRA, E., SWAIN, R. & O'REILLY, J. (2001). Geographic variation in age and size at maturity in a small Australian viviparous skink. *Copeia*, 2001: 646-655.
- WATKINS, G.G. (1996). Proximate causes of sexual size dimorphism in the Iguanian lizard *Microlophus occipitalis*. *Ecology*, 77: 1473-1482.
- WESTENDROP R.G.J. AND KIRKWOOD T.B.L. (1998). Human longevity at the cost of reproductive success. *Nature*, 396: 373-376.

---

CHAPTER 4

FECUNDITY

---

## CHAPTER 4

### Is fecundity the ultimate cause of female-biased size dimorphism in the dragon lizard *Rankinia [Tympnocryptis] diemensis*?

Manuscript published as: Stuart-Smith, J., Swain, R., Stuart-Smith R.D., and Wapstra E. (2007). Is fecundity the ultimate cause of female-biased size dimorphism in the dragon lizard *Rankinia [Tympnocryptis] diemensis*? *Journal of Zoology* London, doi:10.1111/j.1469-7998.2007.00324.x

#### ABSTRACT

Fecundity selection is one of the most influential underlying driving forces responsible for body size differences between the sexes of a species. Reproductive output is one of the most important aspects of an animal's life history strategy, and any trait that acts to improve this will be under strong selection. Body size is one potential trait that can influence fecundity and when a species exhibits female-biased size dimorphism, fecundity provides an ideal starting point for understanding why dimorphism in body size exists. Female-biased sexual size dimorphism is uncommon in vertebrates, including lizards. To explore the relationship between female-biased size dimorphism and fecundity we examined maternal size and clutch data collected over four years from a temperate-zone agamid, *Rankinia [Tympnocryptis] diemensis*. We measured the following descriptors of reproductive output: clutch size and mass, relative clutch mass (RCM), average egg mass and offspring size. We found a positive relationship between maternal size and clutch size and mass, but no relationship between maternal size and RCM, average egg mass, or hatchling size, demonstrating that relative reproductive output is not influenced by female size, and that the only

---

way to increase reproductive output is for the female to attain greater body size.

There exists an overall strong relationship between maternal body size and fecundity, thereby providing a potential explanation as to why female size is under selection in this species.

## INTRODUCTION

Fecundity selection is one of the most fundamental evolutionary forces acting to increase an animal's body size (Blanckenhorn, 2000). Typically, fecundity is highly correlated with body size and condition (Radder and Saidapur, 2000; Radder and Shanbhag, 2004; Shine, 1988), is one of the most important life history traits of an organism (Shanbhag *et al.*, 2000) and, as well as being linked to body size, is also a primary ultimate cause of sexual size dimorphism (SSD) (Darwin, 1874; Reeve and Fairbairn, 1999; Shine, 1988). A positive correlation between maternal body size and reproductive output is termed the fecundity advantage hypothesis, and results from selection favouring large female body size (Andersson, 1994; Rutherford, 2004).

Fecundity is limited by various life history trade-offs and physiological restrictions. Clutch size can be constrained not only by female body size and volume, but also through restrictions in the finite quantity of energy that is available (Ford and Siegel, 1989; Forsman, 2001; In Den Bosch and Bout, 1998; Morita *et al.*, 1998; Nussbaum, 1981; Partridge and Harvey, 1985; Shanbhag, *et al.*, 2000), and egg size can be constrained by the size of the pelvic girdle (Congdon and Gibbons, 1987), by limited space within the body cavity, limits to developmental time or minimal viable egg size limitations (Kratochvíl and Frynta,

---

2006). These limitations also impose a trade-off between the number and size of offspring produced (Brockelman, 1975; Sinervo 1990; Smith and Fretwell, 1974), suggesting that a female cannot typically increase clutch size without decreasing the individual size of her offspring (Sinervo, 1990). The wide range of restrictions on reproductive output means that the forces selecting to increase fecundity are often powerful and easily observable, and can be used as explanatory factors for observing the direction of both evolution and adaptation (Blanckenhorn, 2000; Olsen and Cockburn, 1993).

In most invertebrate and ectothermic species exhibiting typical female-biased SSD, and some endotherms exhibiting this atypical form of dimorphism, fecundity is thought to be a key selective force driving the morphological differentiation of the sexes (Bondrup-Nielsen and Ims, 1990; Schulte-Hostedde, Millar and Gibbs, 2002; Shine, 1988). Identifying whether body size is linked to fecundity in animals exhibiting SSD therefore provides an ideal avenue for looking at how evolution operates (Blanckenhorn, 2000), and helps to isolate the principal selective pressures at work.

Our study investigated the premise that maternal size can influence reproductive output in a species exhibiting strong SSD, and thus be identified as a major driving force in body size differences between the sexes. *Rankinia*

[*Tympanocryptis*] *diemensis*, Family Agamidae, exhibits marked female-biased SSD (Stuart-Smith, Swain and Welling, 2005). The average snout-vent length (SVL) of females at the study population is 66.3 mm (SE  $\pm$  1.280), and 52.4 mm (SE  $\pm$  0.639) for males (Stuart-Smith *et al.*, unpubl. data). The Australian agamids

---

typically show distinct *male*-biased size dimorphism, and males exhibit aggressive social behaviours towards conspecifics associated with territoriality and mate choice (Ord and Evans, 2003; Osborne, 2005; Peters and Ord, 2003; Watt and Joss, 2003). Thus our species shows dimorphism atypical to not only its taxonomic group, but also to that seen in most lizards, squamates and vertebrates. Thus, to investigate if female size-dependent fecundity could explain this apparent size dimorphism we examined the link between female body size (and condition) and reproductive output in *Rankinia diemensis*.

## MATERIALS AND METHODS

### *Species and study area*

The mountain dragon, *Rankinia [Typanocryptis] diemensis* (Gray, 1841), is a relatively small, cryptic agamid lizard. It is endemic to south-eastern Australia, including Tasmania, where it is the only agamid lizard and one of only three oviparous reptiles on the island (Cogger, 1992; Greer, 1989; Hutchinson, Swain and Driessen, 2001), and it is also iteroparous. Tasmania's cool temperate climate and island status have resulted in a limited reptile fauna, but *R. diemensis*, is widespread, occupying cool to mild coastal heath regions, open forested dry sclerophyll forests, and even sub-alpine heathlands of the Central Plateau (approx 1200 m elevation). In this study, lizards were collected from a continuous population, the Clifton Beach area and Cape Deslacs Nature Reserve in south-eastern Tasmania (42°59'S, 147°32'E; elevation: 45-65 m).

Reproductive output in oviparous reptiles is estimated in various ways, including examination of clutch size, offspring body size and condition (Niewiarowski and

---

Dunham, 1994; Shanbhag *et al.*, 2000). Hatchling size is a reliable measure of offspring fitness, since larger hatchling size is typically highly correlated to future fitness (Bowden *et al.*, 2004; Civantos and Forsman, 2000). We therefore included all of these characteristics in order to encompass a thorough view of reproductive output and its links to maternal body size in this species.

#### *Field and laboratory techniques*

Gravid females were captured by hand (while digging nest burrows) during the oviposition period (austral spring: October/November) in 2001, 2002, 2003 and 2004. ( $n = 23, 26, 26$  and  $18$  respectively). Female mass ( $\pm 0.01$  g) and SVL ( $\pm 0.01$  mm) were recorded immediately following oviposition. Females were housed individually in outdoor enclosures containing soil substrate at the University of Tasmania. Females were monitored daily for signs of oviposition behaviours: primarily that of 'test' burrow digging, which indicates that oviposition is close (Stuart-Smith *et al.*, 2005). Immediately after oviposition females were removed from the enclosure, and eggs were uncovered. Date of oviposition, clutch size, and individual egg masses ( $\pm 0.01$  g) were recorded.

To examine offspring characteristics in relation to egg and female size we incubated eggs from one year (2004) and measured hatchling characteristics. Individual eggs were placed in 600 ml plastic containers that were 1/3 filled with moist vermiculite (at a ratio of 7 parts vermiculite: 1 part water). Containers were placed in a Contherm® Digital Series incubator set at a constant 28 °C. Containers were labelled, monitored daily and rotated randomly weekly. Upon

---

hatching, hatchlings were removed from containers, and mass ( $\pm 0.01$  g) and SVL ( $\pm 0.01$  mm) measured, with date of hatching recorded.

### *Analyses*

A combination of ANCOVA and regression analyses were used to examine the effects of female size on clutch and offspring characteristics. Tukey's post hoc test was used to test for differences between years. Two measures of female size (mass and SVL), as well as body condition, were used as independent variables. Female body condition values were calculated from the residuals of the regression of post-oviposition female mass and female SVL, as described by Sinervo (1990).

Clutch characteristics included in analyses were clutch size, clutch mass, average egg mass, and relative clutch mass (RCM). Relative clutch mass is a measure of reproductive output relative to (or controlling for differences in) maternal size, and, as the relationship between clutch mass and female mass is linear, it is simply calculated by dividing clutch mass by post oviposition female mass (Shine, 1980). As we had clutch characteristics from multiple years, but female sizes varied among these years (see results), an ANCOVA test for homogeneity of slopes (interaction term between female size and year) was used to determine whether relationships between female size and clutch characteristics were consistent across years (i.e. slopes were not significantly different between years). In cases where there were no yearly differences, the data from all years were pooled and regression analyses were conducted on pooled data. In cases where relationships between female size and clutch characteristics differed significantly across years (i.e. the ANCOVA assumption of homogeneity of slopes was violated), separate

---

analyses were conducted for years in which relationships differed. Pearson's correlation was calculated for clutch size versus mass to examine the trade-off between number and size of eggs produced.

Offspring characteristics (i.e. hatchling characteristics) analysed included clutch means of hatching success (measured as the proportion of each clutch that successfully hatched) and hatchling body size (mass and SVL). Separate regressions were performed with each measure of female size as the independent variable and each offspring characteristic as the dependent variable. All relationships evident between female size and clutch or offspring characteristics were linear, and no transformations were required.

## RESULTS

### *Female size and condition*

Female SVL distributions for gravid females differed across the four sample years (Figure 1 shows female mass, SVL and condition across years) - with females caught in 2001 and 2002 smaller than those caught in 2003 and 2004 ( $F_{3,86} = 20.971, P < 0.001$ ). Female post-oviposition mass differed significantly among years similar to SVL, with those caught in 2001 and 2002 smaller than those caught in 2003 and 2004 ( $F_{3,86} = 3.031, P = 0.034$ ), but body condition remained consistent ( $F_{3,86} = 1.758; P = 0.161$ ).

### *Clutch characteristics*

Numbers of eggs collected per year were as follows: 2001 = 143, 2002 = 185, 2003 = 203, and 2004 = 124. The relationship between clutch size and female size was consistent between years and thus data were pooled (ANCOVA: female mass

---

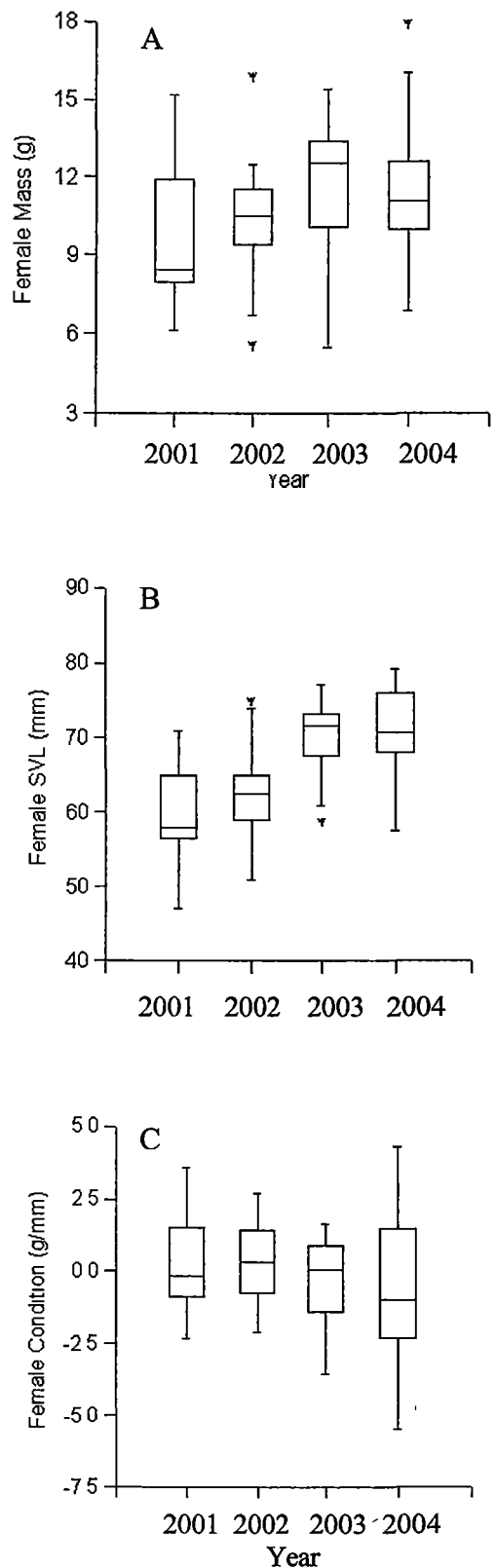


Figure 1. Box and whisker plots showing female size [(A) mass, (B) SVL and (C) condition] - for adult *Rankina diemensis* collected over four seasons (2001-2004). Plots show percent quartiles about the median with minimum and maximum values represented by lines, and outliers represented by Ψ.

× clutch size  $F_{3,85} = 0.286, P = 0.836$ ). Relationships between female size and clutch mass, average egg mass and RCM did differ between some years, so data were pooled for only those years that were the same. Longer, heavier and better-conditioned females produced more eggs. There was a significant positive relationship between female mass and clutch size that was consistent across all years (clutch size =  $2.136 + 0.417\text{female mass}$ ,  $r^2 = 0.455, P < 0.001, n = 90$ ; Figure 2). Based on these regression results, on average a female of 5 g (approx. size at maturity based on smallest known female to reproduce) lays 4.2 eggs, and each additional egg produced is associated with an increase of approximately 2.4 g of body mass. Female body condition and SVL also showed positive significant relationships with clutch size (clutch size =  $6.567 + 0.375\text{female condition}$ ,  $r^2 = 0.167, P < 0.001, n = 90$ ; clutch size =  $-0.725 + 0.112\text{female SVL}$ ,  $r^2 = 0.256, P < 0.001, n = 90$ ), but were not as good a predictor of this measure of fecundity as female mass.

Clutch mass significantly increased with increasing female mass in all years, but this increase was of a slightly lower magnitude in 2001 than in the other years (2001: clutch mass =  $1.405 + 0.333\text{female mass}$ ,  $r^2 = 0.618, P < 0.001, n = 23$ ; 2002-2004: clutch mass =  $2.286 + 0.398\text{female mass}$ ,  $r^2 = 0.364, P < 0.001, n = 67$ ).

There was no relationship between average egg mass and female mass or condition in any year ( $P > 0.05$  all years), but a very weak positive relationship existed with female SVL in 2002 and 2003 (average egg mass =  $0.134 + 0.009\text{female SVL}$  in 2002,  $r^2 = 0.156, P = 0.046$ ; average egg mass =  $-0.681 +$

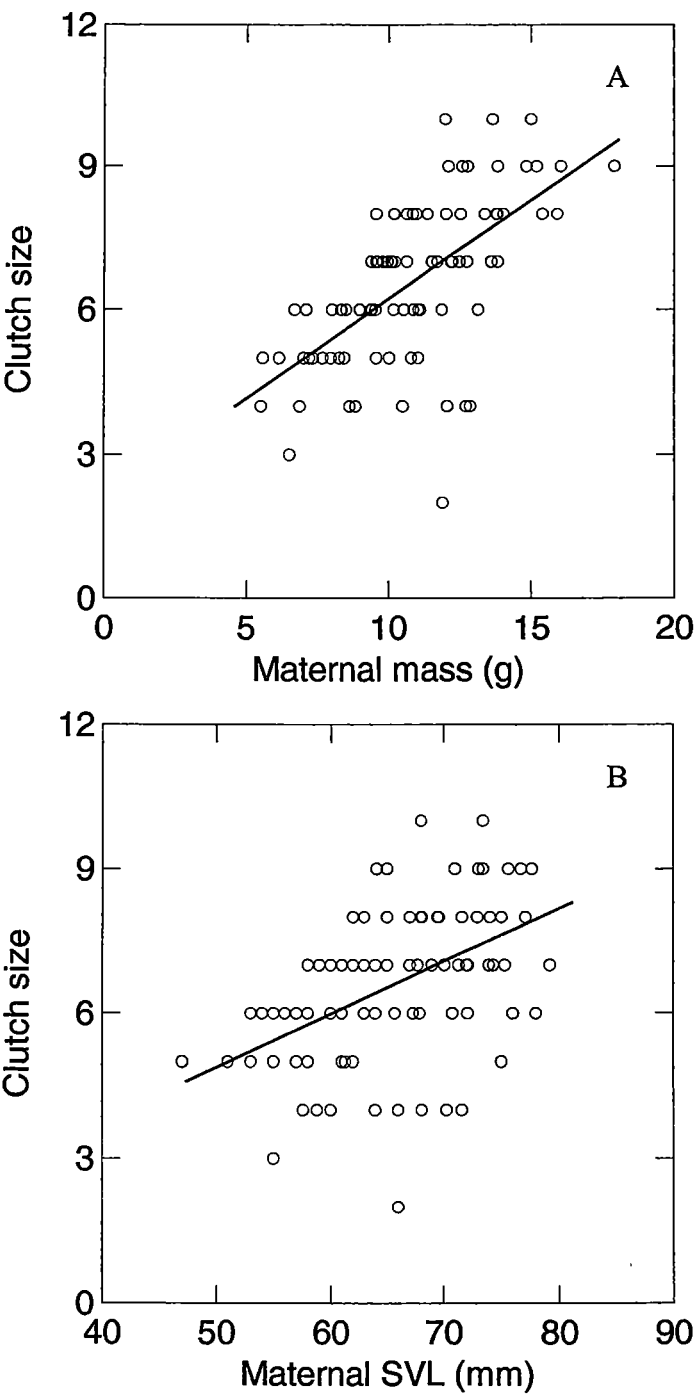


Figure 2. Relationship between maternal size (A. mass and B. SVL) and reproductive output in *Rankinia diemensis*, with clutch size (number of eggs per clutch) representing reproductive output.

0.020 female SVL in 2003,  $r^2 = 0.230$ ,  $P < 0.001$ ), and given the slope of the line, although statistically significant, we did not consider this relationship was strong enough to be biologically significant. RCM was not related to any measure of female size in any year (all  $P > 0.05$ ). No correlation was found between clutch size (number of eggs) and average egg mass (Pearson's Correlation Coefficient,  $r = 0.05$ ,  $n = 90$ ,  $P < 0.05$ ). This relationship was also explored while controlling for the variance in total reproductive investment, done by regressing clutch size and average egg mass on female size (mass and SVL) independently. Graphical analysis of residuals revealed no observable relationship.

#### *Offspring characteristics*

Egg mass was positively correlated to hatchling mass (Pearson's Correlation Coefficient,  $r = 0.551$ ,  $n = 105$ ,  $P < 0.05$ ) and hatchling SVL (Pearson's Correlation Coefficient,  $r = 0.431$ ,  $n = 105$ ,  $P < 0.05$ ) (Figure 3). The hatching success of clutches was not related to any of the measures of female size (all  $P > 0.05$ ), with a large amount of variability in hatching success observed overall (hatching success ranged from 33% to 100%). No relationships existed between average hatchling size (mass and SVL) and maternal size (SVL, mass and condition) (all  $P > 0.05$ ).

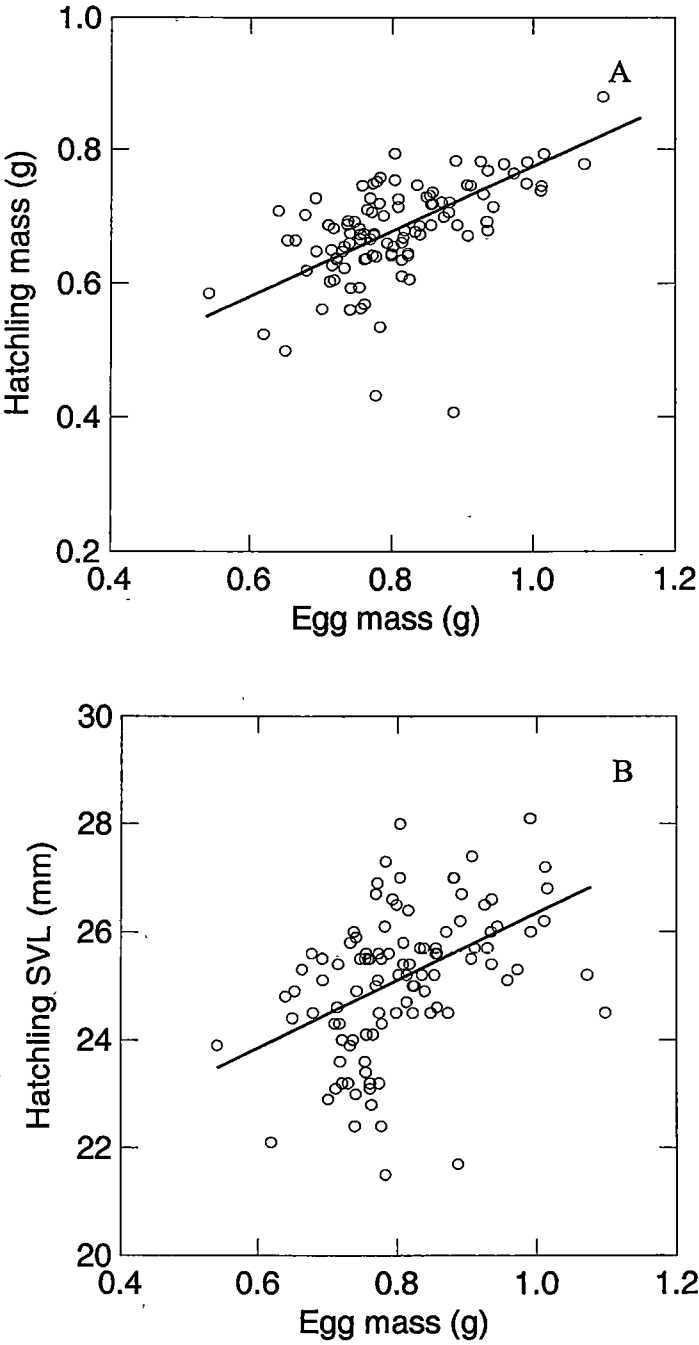


Figure 3. Relationship between egg and hatchling size (A. hatchling mass and B. hatchling SVL) in *Rankinia diemensis*.

## DISCUSSION

Oviparity in reptiles is fraught with complex interrelationships among maternal body size, clutch and egg sizes (Radder and Shanbhag, 2003). This study shows strong evidence for the functional basis of increased female size being highly correlated with fecundity. Female size (mass, SVL) and condition in *R. diemensis* significantly influenced the primary clutch parameter of size (and therefore total clutch mass) and through this supports the idea that fecundity is a major selective pressure acting to increase female body size in *R. diemensis*. Adaptive variation in clutch size is a fundamental aspect of life-history evolution because fecundity represents a direct indication of fitness (James and Whitford, 1994). These data also indicate that egg size may be optimised, since there is little variation in egg size, and it is not related to female size, or could be explained by the existence of minimal viable egg size (Kratochvíl and Kubička, 2006). When combined with variable clutch sizes, this implies that size-selective pressures acting on maternal body size are a major mechanism behind the ability to increase reproductive output in this species. From these data it is clear that large females have a fecundity advantage and selection should favour large female body size (Blanckenhorn, 2000).

There was no observable link between female size and relative clutch mass (RCM) or average egg mass, indicating that larger females do not produce *proportionally* greater reproductive output. This is fundamentally important in helping to explain SSD in this species. It means that females do not vary the size of their eggs, so they do not produce fewer large eggs, and that they do not invest in reproduction relative to their body size. The only way then for a female to

---

increase her reproductive output is to be larger, and produce a greater *number* of eggs. The data revealed that for a mature female who first averages approximately 4 eggs per clutch, for every additional egg she must first gain approximately 2.4 g in body mass. Since the average female mass in this study is approximately 10 g, this means that she must increase her body size by almost a quarter of her body mass in order to increase her reproductive output. This indicates that reproductive output is strongly linked to maternal body size in this species, and so selection should favour large females.

In other similarly-sized agamids, such as those in the genus *Ctenophorus*, sexual dimorphism usually favours large males; however, maternal size is often still highly correlated to clutch size, showing that relatively large female size is still selected for (Harlow, 2000). Large male size is typically attributed to contest success in male-male interactions and mate choice in agamids and many other animals (Censky, 1997; Harlow, 2000; Ord and Evans, 2003). We postulate then that size differences in *R. diemensis* are highly correlated with fecundity advantages, and that large male body size is not essential for resource gain.

Similar studies on other organisms exhibiting dimorphism contrary to the norm of their taxonomic group, such as in yellow-pine chipmunks (Schulte-Hostedde *et al.*, 2002), support similar theories. Yellow-pine chipmunks exhibit female-biased dimorphism, which is atypical of mammals (Bondrup-Nielsen and Ims, 1990).

Schulte-Hostedde *et al.* (2002) found no correlation between male size and reproductive success, along with stabilizing selection on survival for smaller body size, explaining why body size is smaller in males. In birds of prey and some seabirds, where female-biased SSD is common, size is often attributed to greater

---

reproductive output as a consequence of being able to hunt larger prey, and thereby increase their body size (Krüger, 2005). In these birds, the small-male hypothesis, where males are smaller allowing greater agility and foraging efficiency, is also widely accepted (Andersson and Wallander, 2004; Catry, Phillips and Furness, 1999; Krüger, 2005). In this study we were unable to ascertain a measure of male reproductive success, but have demonstrated a clear link between maternal size and reproductive output. Certainly this species is also atypical of agamids in not having obvious male-male interactions – males are typically quite cryptic and do not possess the striking colouration of some other agamids (LeBas and Marshall, 2001; Stuart-Fox and Ord, 2004). It is likely that the cryptic nature of *R. diemensis* (Cogger, 2000; Stuart-Smith *et al.*, 2005) plays a role in limiting the overall body size in this species, and potentially also helps to explain why males are smaller. If small body size and crypsis, including camouflage and cryptic behaviour, increases survival chances, but reproduction is highly linked to female size, then small body size overall is favourable for reproductive success and survival.

It is also likely that the temperate environment that this species inhabits places significant constraints on the size of both sexes, since the activity period is severely reduced (Stuart-Smith *et al.*, 2005). It is often postulated that species from temperate regions will have larger body size and a correlation between body size and reproductive output (James and Shine, 1988). But in this small temperate species the constraint in size may partially lie in environmental limitations, and in particular the high degree of seasonality and long torpor period which reduces the annual activity time, and therefore time during which growth occurs. It also places

---

strong constraints on hatchlings undergoing their first torpor, which they must enter as little as 6 weeks from hatching, implying that hatchling survival may be low, and that a female increases chances of offspring reaching maturity by producing more eggs. This species produced an average of 6.6 eggs per year in this study ( $SE = \pm 0.16$ ) (average female size 66.3 mm ( $SE \pm 1.280$ ), which appears slightly higher than in slightly larger sized agamids, *Ctenophorus decresii* (average female size 74.7 mm SVL) and *Amphibolurus muricatus* (average female size 89.5 mm SVL). *Ctenophorus decresii* averages 4.8 eggs per clutch (Harlow, 2000) and *Amphibolurus muricatus* averages 5.7 eggs per clutch (Harlow and Taylor, 2000). So then if overall body size is limited, and large male size is not essential for contest success, but reproductive output is benefited by large female size, then fecundity may be an important driving force behind body size differences between the sexes of this species.

There was no correlation between clutch size and average egg mass, implying no trade-off between these two traits. This is also suggested by there being no influence of female size on average egg mass, i.e. average egg mass does not vary significantly with female body size. Life history models predict a trade-off between the number and size of offspring produced (Bernardo, 1996; Brockelman, 1975; Smith and Fretwell, 1974), so that resources must be allocated to either a few large, or many small eggs. Natural selection favours an increase in reproductive output (Brockelman, 1975), which can be addressed by producing fewer large offspring – with greater chances of survival; or many smaller offspring, increasing the overall number produced, thereby increasing the chances of at least some being successful. This can also be addressed by maintaining egg

---

size and increasing body size. Selection also operates on individual offspring (egg size in this case) – such that fitness can require an optimal level of resources packaged into each egg (Bernardo, 1996). Given that egg size did not differ with female size, and that egg size is proportional to hatchling size, there is potentially selection on optimal egg/hatchling size, and females increase output by increasing clutch size.

This study provides evidence that fecundity-related selective pressures are operating to increase female body size in this species and therefore has implications for understanding the importance of SSD. Body size is a fundamentally important aspect of an animal's biology – with physiological, behavioural and ecological implications for life history strategy (Thompson and Pianka, 2001). Reproductive output is often correlated with body size in animals with varying clutch sizes (Ford and Siegel, 1989). In lizards, including many Australian agamids, clutch size is positively correlated with body size (Harlow, 2000; Harlow and Taylor, 2000), but in this instance, its significance lies in providing the basis for understanding selective pressures at work. Australian agamids typically show male-biased size dimorphism, but females of *R. diemensis* are considerably larger than males, indicating strong selective pressures acting to increase female size in this species. This then provides the first step in understanding the role of body size in the life history strategy of this species, and, it also offers insights into the functional basis of female-biased SSD in this species.

---

## REFERENCES

- ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press, Princeton, NJ.
- ANDERSSON, M. & WALLANDER, J. (2004). Relative size in the mating game. *Nature* 431, 139-141.
- BERNARDO, J. (1996). The particular maternal effect of propagule size, especially egg size: Patterns, models, quality of evidence and interpretations. *Am. Zool.* 36, 216-236.
- BLANCKENHORN, W.U. (2000). The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* 75, 385-407.
- BONDRUP-NIELSEN, S. & IMS, R.A. (1990). Reversed sexual size dimorphism in microtines: are females larger than males or are males smaller than females. *Evol. Ecol.* 4, 261-272.
- BOWDEN, R.M., HARMS, H.K., PAITZ, R.T., & JANZEN, F.J. (2004). Does optimal egg size vary with demographic stage because of a physiological constraint? *Funct. Ecol.* 18, 522-529.
- BROCKELMAN, W.Y. (1975). Competition, the fitness of offspring, and optimal clutch size. *Am. Nat.* 109, 677-697.
- CATRY, P., PHILLIPS, R.A., & FURNESS, R.W. (1999). Evolution of reversed sexual size dimorphism in skuas and jaegers. *Auk* 116, 158-168.
- CENSKY, E.J. (1997). Female mate choice in the non-territorial lizard *Ameiva plei* (Teiidae). *Behav. Ecol. Sociobiol.* 40, 221-225.
- CIVANTOS, E. & FORSMAN, A. (2000). Determinants of survival in juvenile *Psammodromus algiris* lizards. *Oecologia* 124, 64-72.
- CONGDON, J.D. & GIBBONS, J.W. (1987). Morphological constraint on egg size: A challenge to optimal egg size theory? *Proc. Nat. Acad. Sci.* 84, 4145-4147.
- COGGER, H. (1992). *Reptiles and Amphibians of Australia*. Reed/Reed New Holland.
- DARWIN, C. (1874). *The descent of man, and selection in relation to sex*. Murray, London.
- FORD, N.B. & SIEGEL, R.A. (1989). Relationships among body size, clutch size, and egg size in three species of oviparous snakes. *Herpetologica* 45, 75-83.
- FORSMAN, A. (2001). Clutch size versus clutch interval: life history strategies in the colour-polymorphic pygmy grasshopper *Tetrix subulata*. *Oecologia* 129, 357-366.
- GREER, A.E. (1989). *The Biology and Evolution of Australian Lizards*. Surrey Beatty & Sons Pty Ltd, Australia.
- HARLOW, P. (2000). Incubation temperature determines hatchling sex in Australian rock dragons (Agamidae: Genus *Ctenophorus*). *Copeia* 2000, 958-964.
- HARLOW, P.S. & TAYLOR, J.E. (2000). Reproductive ecology of the jacky dragon (*Amphibolurus muricatus*): an agamid lizard with temperature-dependent sex determination. *Austral Ecol.* 25, 640-652.
- HUTCHINSON, M., SWAIN, R. & DRIESSEN, M. (2001). *Snakes and Lizards of Tasmania. Fauna of Tasmania Handbook No. 9*. University of Tasmania.
- IN DEN BOSCH, H.A.J. & BOUT, R.G. (1998). Relationships between maternal

- size, egg size, clutch size and hatchling size in European lacertid lizards. *J. Herpetol.* 32, 410-417.
- JAMES, C. & SHINE, R. (1988). Life-history strategies of Australian lizards: a comparison between tropics and the temperate zone. *Oecologia* 75, 307-316.
- JAMES, C.D. (1991). Annual variation in reproductive cycles of scincid lizards (*Ctenotus*) in central Australia. *Copeia* 1991, 744-760.
- JAMES, C.D. & WHITFORD, W.G. (1994). An experimental study of phenotypic plasticity in the clutch size of a lizard. *Oikos* 70, 49-56.
- KRATOCHVÍL, L. & FRYNTA, D. (2002). Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). *Biol. J. Linn. Soc.* 76, 303-314.
- KRATOCHVÍL, L. & KUBIČKA, K. (2006). Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards. *Funct. Ecol.*, in press.
- KRÜGER, O. (2005). The evolution of reversed sexual size dimorphism in hawks, falcons and owls: a comparative study. *Evol. Ecol.* 19, 467-486.
- LEBAS, N.R. & MARSHALL, N.J. (2001). No evidence of female choice for a condition-dependent trait in the agamid lizard, *Ctenophorus ornatus*. *Behaviour* 138, 965-980.
- NIEMIAROWSKI, P.H. AND DUNHAM, A.E. (1994). The evolution of reproductive effort in squamate reptiles: costs, trade-offs, and assumptions reconsidered. *Evolution* 48, 137-145.
- NUSSBAUM, R.A. (1981). Seasonal shifts in clutch size and egg size in the side-blotched lizard, *Uta stansburiana* Baird and Girard. *Oecologia* 49, 14-20.
- MORITA, K., YAMAMOTO, S., TAKASHIMA, Y., MATSUISHI, T., KANNO, Y. & NISHIMURA, (1999). Effect of maternal growth history on egg number and size in wild white-spotted char (*Salvelinus leucomaenis*). *Can. J. Fish. Aquat. Sci.* 56, 1585-1589.
- OLSEN, P.D. & COCKBURN, A. (1993). Do large females lay small eggs? Sexual dimorphism and the allometry of egg and clutch volume. *Oikos* 66, 447-453.
- ORD, T.J. & EVANS, C.S. (2003). Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): an experimental analysis. *Behaviour* 140, 1495-1508.
- OSBORNE, L. (2005). Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). *J. Ethol.* 23, 189-197.
- PARTRIDGE, L. & HARVEY, PH. (1985). Evolutionary biology - costs of reproduction. *Nature* 316, 20-21.
- PETERS, R.A. & ORD, T.J. (2003). Display response of the Jacky Dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecol.* 28, 499-506.
- RADDER, R.S. & SHANBHAG, B.A. (2003). Interrelationships among reproductive traits of female lizard, *Sitana ponticeriana* (Cuvier). *Curr. Sci.* 85, 89-91.
- RADDER, R.S. & SHANBHAG, B.A. (2004). Factors influencing offspring traits in the oviparous multi-clutched lizard, *Calotes versicolor* (Agamidae). *J. Bioscience* 29, 105-110.
- REEVE, J.P. & FAIRBAIRN, D.J. (1999). Change in sexual size dimorphism as a correlated response to selection on fecundity. *Heredity* 83, 697-706.

- RUTHERFORD, P.L. (2004). Proximate mechanisms that contribute to female-biased sexual size dimorphism in an anigid lizard. *Can. J. Zool.* 82, 817-822.
- SCHULTE-HOSTEDDE, A.I. & MILLAR, J.S. (2002). 'Little chipmunk' syndrome? Male body size and dominance in captive yellow-pine chipmunks (*Tamias amoenus*). *Ethology* 108, 127-137.
- SCHULTE-HOSTEDDE, A.I., MILLAR, J.S. & GIBBS, H.L. (2002). Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution* 56, 2519-2529.
- SHANBHAG, B.A., RADDER, R.S. & SAIDAPUR, S.K. (2000). Maternal size determines clutch mass, whereas breeding timing influences clutch and egg sizes in the tropical lizard *Calotes versicolor* (Agamidae). *Copeia* 2000, 1062-1067.
- SHINE, R. (1980). 'Costs' of reproduction in reptiles. *Oecologia* 46, 92-100.
- SHINE, R. (1988). The evolution of large body size in females: a critique of Darwin's "Fecundity Advantage" model. *Am. Nat.* 131, 124-131.
- SINERVO, B. (1990). The evolution of maternal investment in lizards: An experimental and comparative analysis of egg size and its effects on offspring performance. *Evolution* 44, 279-294.
- SMITH, C.C. & FRETWELL, S.D. (1974). The optimal balance between size and number of offspring. *Am. Nat.* 108, 499-506.
- STUART-FOX, D.M. & ORD, T.J. (2004). Sexual selection, natural selection and the evolution of dimorphic colouration and ornamentation in agamid lizards. *Proc. R. Soc. Lond. B* 271, 2249-2255.
- STUART-SMITH, J., SWAIN, R. & WELLING, A. (2005). Reproductive ecology of the mountain dragon, *Rankinia [Tymppanocryptis] diemensis* (Reptilia: Squamata: Agamidae) in Tasmania. *Pap. Proc. Soc. Tas.* 139, 23-28.
- THOMPSON, G.G. & PIANKA, E.R. (2001). Allometry of clutch and neonate sizes in monitor lizards (Varanidae: Varanus). *Copeia* 2001, 443-458.
- WATT, M.J. & JOSS, J.M.P. (2003). Structure and function of visual displays produced by male Jacky Dragons, *Amphibolurus muricatus*, during social interactions. *Brain Behav. Evol.* 61, 172-185.
- ZNARI, M., EL MOUDEN, E., & FRANCILLON-VELLOT, H. (2002). Long-term variation in reproductive traits of Bibron's Agama, *Agama impalearis*, in western Morocco. *Afr. J. Herpetol.* 51, 1:57-58.

---

## CHAPTER 5

# COMPETITION

## **CHAPTER 5**

### **The role of body size in competition and mate choice in an agamid with female-biased size dimorphism**

Manuscript published as: Stuart-Smith, J., Swain, R., and Wapstra E. (2007). The role of body size in competition and mate choice in an agamid with female-biased size dimorphism. *Behaviour* 144:1087-1102.

#### **ABSTRACT**

Competition and mate choice are fundamentally important components of social systems. We investigated intra-sexual competition and inter-sexual competition (mate choice) in *Rankinia diemensis*: an agamid lizard with female-biased size dimorphism. We examined intra-sexual interactions during contests and mate choice in relation to body size for both males and females. In male-male competition trials, proportions of two display types differed depending on body size, with more tail flicks produced by bigger males, and more hand-waves displayed by smaller males. These behaviours hold particular biological significance for agamid lizards – tail-flicks convey aggressiveness and therefore dominance, while hand-waves often denote submissiveness. In female-female competition trials, a greater difference in body size between the two conspecifics resulted in the larger female directing more pushes towards the smaller female. This female competition may be important in the social system and could be involved in resource defence. We found no indication of size-based mate choice for males or females. This suggests mate preferences may not be based on body size in this species. This may be linked to female-biased size dimorphism in this

species, but it also supports previous studies that have failed to demonstrate female choice in reptiles.

## INTRODUCTION

Darwin (1871) first recognised competition and mate choice as the two principal components of sexual selection that account for differences in reproductive success of an individual (Andersson, 1994) and these components are still unequivocally regarded as the most influential driving forces behind sexual selection (Andersson, 1994, Olsson & Madsen, 1998; Wong & Candolin, 2005). Outcomes of these interactions influence fundamental components of any social system, including resource acquisition, reproductive success and offspring survival (e.g. Calsbeek & Sinervo, 2002; Wong & Candolin, 2005). Contest success and mate selection are often based on phenotypic traits which usually accurately reflect high quality and may permit an advantage over conspecifics (Bonduriansky, 2001; Ord & Evans, 2003). Further, sexual selection often promotes the evolution of characteristics such as exaggerated body size, colourful markings or extravagant traits essential for competition and mate attraction (Andersson 1994; Whiting *et al.*, 2003). These morphological traits serve to determine ranking, attract mates, gain access to resources and ultimately may be linked to offspring fitness. In species that do not show sex-specific colour or ornamental traits (that act in mate choice) or armament traits (weapons used in contests; Whiting *et al.*, 2003), but do express distinct sexual size dimorphism (SSD), body size may play a fundamental role in sexual selection.

In agamid lizards, there is opportunity for both components of sexual selection to occur (Olsson, 1993; Olsson *et al.*, 2003; Watt & Joss, 2003; Radder *et al.*, 2006).

Male agamids are typically the larger sex and often engage in aggressive territorial displays and combat with rivals (e.g. Olsson 1995; Peters and Ord, 2003; Radder *et al.*, 2006). Males defend females or their home ranges to ensure no other males have access, or to gain ‘mating rights’, to a large number of females via resource exclusion of other males (Stamps 1983; Olsson 1995). The armament-ornament model also suggests that females benefit from using traits that are selected for in male-male rivalry contests as determinants of mate choice (Matteo & Carranza, 1999). This intra-sexual competition also occurs in order to acquire additional resources –such as food, shelter, nesting site or home range (Howard *et al.*, 1998; Ord & Evans, 2003). In general, inter-sexual competition, specifically mate choice, is thought to promote inheritance of favourable traits such as mating success and viability of offspring (Andersson 1994). Typically, females exhibit greater parental investment than males, and are therefore expected to be more particular in their choice of mate (Darwin 1871; Olsson 1993; Calsbeek & Sinervo 2002). Conversely, males typically make relatively smaller parental investment and, hence, male choice should be under less selective pressure than female choice (Olsson, 1993). The exception to this is when males have high mating costs or when female fecundity is strongly linked to reproductive success, and then choice of a highly fecund female is an advantage (Olsson 1993; Kraak & Bakker, 1998; Dosen & Montgomerie, 2004; Olsson *et al.*, 2004). Numerous studies have provided a link between mate preference and body size (Kraak & Bakker, 1998; Jones *et al.*, 2001; Dosen & Montgomerie, 2004), since large body size often represents greater fecundity in females (Kraak & Bakker, 1998; Shanbhag *et al.*, 2000; Radder & Shanbhag, 2004; Stuart-Smith *et al.*, in press) or higher quality in males (Amundsen & Forsgren, 2003; Spence & Smith, 2006).

---

In species where males are the smaller sex, it is difficult to estimate and understand how important body size is for intra-sexual interactions and the choice of mates – since selective pressures typically lead to an increase in size to aid these interactions. This is made particularly interesting when the species of focus, *Rankinia diemensis*, belongs to a family (Agamidae) that characteristically shows marked male-biased SSD. In most agamids male-biased SSD is linked to the establishment and defence of territories for resource acquisition (Ord & Evans, 2003), and mate access is often based on aggressive and conspicuous defence of a territory (Shine, 1990; Ord & Evans, 2003; Watt & Joss, 2003; Olsson, 1995; Osborne, 2005), so the existence of female-biased sexual dimorphism and apparent lack of male territories in *R. diemensis* presumably has significant implications for sexual selection strategies in this species (Stuart-Smith *et al.*, submitted). Despite the lack of male-biased size dimorphism and lack of evidence of territorial activity in this species, males do possess proportionally greater head and limb sizes than females (Stuart-Smith *et al.*, in press), suggesting selection acting on these morphological traits, and indicating that opponent assessment may still be important despite small body size in males. As female body size is linked to fecundity (Stuart-Smith *et al.*, in press), it may be predicted that males should show preference for larger females. Although male interactions and behaviours are well documented in agamids (Peters & Ord, 2003; Watt & Joss, 2003; Osborne, 2005; Radder *et al.*, 2006), much less attention has been paid to female behaviour and interactions (Censky, 1997; LeBas & Marshall, 2001), which, particularly in a species where large female body size is selected for, may be just as important as male interactions.

---

In agamids, visual displays are used to mediate social behaviour (Ord *et al.*, 2002; Watt & Joss 2003), and most agonistic interactions between competitors are resolved through the use of behavioural displays for opponent assessment, without having to resort to physical combat, which may be energetically costly and risks physical injury (Ord & Evans 2003; Hurd 2004). Agamid lizards possess a diverse array of visual signals, with communication between individuals conducted through discrete and sequentially predictable motor patterns, with focus on a core display of push-ups and head-bobs (Ord & Blumstein 2002; Peters & Ord, 2003; Watt & Joss 2003, Radder *et al.*, 2006). These signals are used in territory acquisition, resource defence, and mate choice (Ord & Blumstein 2002; Peters & Ord, 2003), and denote aggressive or submissive gestures.

The primary objective of this paper is to investigate size-dependent outcomes in intra- and inter-sexual competitive interactions in an agamid lizard (*Rankinia diemensis*) where body size is obviously under strong selective pressure, albeit not in accordance with the norm for this taxonomic group. These two behavioural components are fundamental driving factors behind gender-related size differences in agamids, usually producing a bias towards large male size. We incorporate both male and female contest interactions in our study. In agamids, most previous work (e.g., Ord *et al.*, 2002; Ord and Evans, 2003; Watt & Joss, 2003) has focussed on male interactions since this group is typically driven by large male body size. Given that success in male-male interactions may be determined by body size in relation to other males, we hypothesise that male body size will still be an important predictor of male success in such competition in our system. We further hypothesise that body size in female *R. diemensis* will be an important predictor of male mate choice (because large females are the most

fecund) and contest success in female-female interactions if resources (such as perches or nest sites) are limited. We discuss our results in relation to these hypotheses and other selective pressures acting on body size in the two sexes – thus providing potential explanations for the observed female-biased size dimorphism in this species.

## METHODS

### *Study species, collection and housing*

The mountain dragon, *Rankinia diemensis*, is a small, typically ground-dwelling cryptic species that inhabits areas of southeastern Australia, including Tasmania (Cogger, 2000; Stuart-Smith *et al.*, 2005). This species exhibits strong female-biased SSD, with a maximum snout-vent length of 84 mm recorded for females, and 66 mm for males (Stuart-Smith *et al.*, in press). Like most agamids, this species possesses an array of behavioural displays, with head-bobs and hand-waving the two most prominent elements of its' agonistic repertoire, but which also includes tail-flicks and pushing.

Fifty-eight adult *R. diemensis* (20 females, 38 males) were collected from a single population near Oatlands in Central Tasmania (42°13'S, 147°14'E), Australia, in September/October (austral spring) 2004. Collection began as soon as lizards emerged from winter torpor to ensure they were captured prior to mating, and no females were gravid when captured. Males emerge from torpor in September, females in October, and eggs are usually oviposited in November/December (Stuart-Smith *et al.*, 2005). Each lizard was measured for snout-vent length (SVL) ( $\pm 0.01$  mm) and given a unique identification number and housed individually in the outdoor enclosures of the University of Tasmania Animal Yards. Enclosures

were approximately 100 cm in diameter, with sides approximately 80 cm high to prevent escape. Head and limb size are proportional to SVL in this species (Stuart-Smith *et al.*, submitted), which is why we used SVL as the standard measure of body size differentiation for the basis of this study. Male SVL ranged from 43 – 60 mm, with a mean of 53.1 mm ( $\pm 0.75$  SE). Female SVL ranged 60 – 83 mm, with a mean of 71.2 mm ( $\pm 1.45$  SE).

#### *Intra-sexual competition trials*

Individuals of both sexes were grouped into trials according to size. Each individual was ranked according to SVL. This ranked group was then divided in half (animals in the top half were larger than those in the bottom half). Pairs were chosen so that the overall size difference between each pair was maximised (i.e. the largest of the largest individuals, paired with the largest of the smaller individuals). If we had simply paired the biggest individual with the smallest, the degree of size difference for all intermediate lizards would have been quite small, and perhaps not have provoked any size-related interactions.

Pairs were randomly chosen for the trials. Trials were conducted in a test arena (Figure 1) which consisted of non-reflective Perspex sides and removable marine carpet flooring to allow washing between each trial to remove any scent left by individuals. The floor was also covered lightly with soil, which was discarded after each trial. A tripod was set up with a Sony® video camera to record each trial and an observer (hidden from view of the subjects) was present throughout to monitor behaviour. Trials were conducted between 1100 hrs and 1500 hrs on days when air temperatures were between 20 – 25 °C, there was limited cloud cover,

and minimal wind. Pairs were placed in the adjoining compartments at the beginning of each trial. Placement of big and small individuals in either side was randomised to negate any arena effects. A middle compartment held a single central basking perch which individuals could only access during the trial. Covers

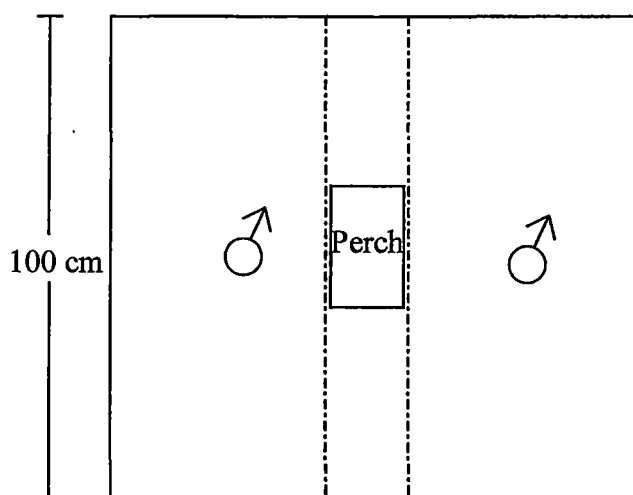


Figure 1. Diagram of the test arena used in competition trials of *Rankinia diemensis* (using male-male competition for diagram; however, female-female trials also included) (dashed line represents removable screen covering for transparent Perspex partition).

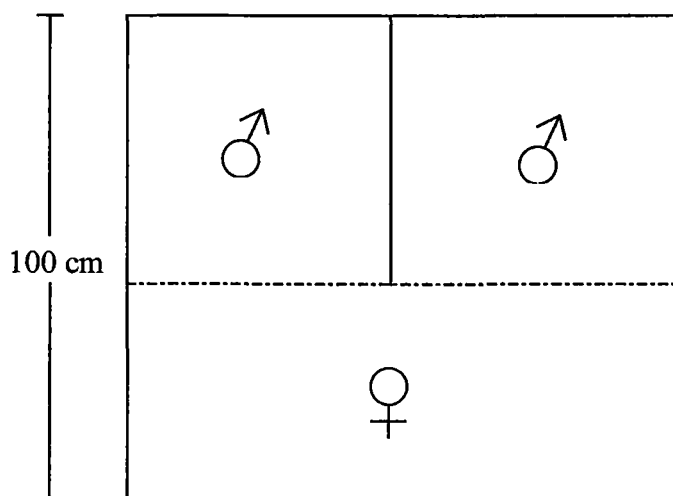


Figure 2. Diagram of the test arena used in mate choice trials of *Rankinia diemensis* (using female choice of male size for diagram; however male choice of female size also included in trials) (dashed line represents removable screen covering for transparent Perspex partition).

were inserted so that subjects were not visible to each other prior to testing, and subjects were left for 15 minutes prior to each trial to settle into the arena conditions. Covers were then removed and individuals could access each other and the central basking perch. Preliminary trials using additional animals showed that once individuals had encountered each other, the highest intensity of interactions occurred within the first 5-10 minutes. Based on this, trial time ran for 15 minutes from when individuals were first introduced to each other. Behaviours recorded from later video analysis were number of head-bobs (HB), hand-waves (HW), tail flicks (TA), flee responses (FL), direct approaches (AP), tongue-flicks at the opponent (TF), tongue-flicks on ground (TFG), times opponent was pushed (PU), number of exploratory moves (neither fleeing or approaching opponent) (EX). We also recorded number of individual bouts in each trial (a bout was considered to be any period of time spent within 30 cm of each other when displaying), total bout time, average number of displays per bout and total number of displays.

All statistical analyses were performed using SYSTAT® Version 9. Non-parametric procedures were used when underlying assumptions were not met for parametric analyses. We used Wilcoxon signed-ranks tests to investigate competition interactions using behavioural counts, including individual behaviours and trial statistics (total number of displays and display rate/bout). We include one-tailed probabilities (but also report two-tailed probabilities) when appropriate for male behaviours, where we assume display type is in accordance with previous work (Peters & Ord, 2003; Watt & Joss, 2003). We also used regression analyses to determine whether the size difference (SVL) between competitors influenced behaviour.

*Mate choice trials*

Both male and female mate choice trials were conducted. Test individuals were given a choice between two different sized individuals of the opposite sex. Individuals were paired as above, except females were tested weekly for receptivity, and so pairs were arranged according to those available for use. An arena (Figure 2) consisted of 2 compartments of equal size, each with a basking perch, but with a solid partition so that individuals (of the same sex) were not visible to each other. A third compartment adjoining the front of these contained the test individual (i.e. the one choosing) – with equal access to both compartments via a clear Perspex partition. Prior to the trial beginning, the clear partition was fitted with an opaque cover, which was removed when the trial started. Placement of individuals in either side of the arena was randomised as in competition trials, to avoid any biases due to arena effects. The trials were video-taped as described above. We also tested individuals weekly for receptivity to the opposite sex. This consisted of placing individuals in test conditions with individuals of the opposite sex and monitoring behaviour. If for example, a female did not respond, or showed non-receptive posturing ('rejection posturing' see Cogger, 1978; Olsson, 2001a), then this female was omitted from all further trials and returned to her place of capture.

We considered that proportionally greater time spent with one individual was indicative of mate preference. We used Wilcoxon matched-pairs signed-ranks tests with two-tailed probabilities that assumed a normal distribution to test subject association mate preferences (Howard *et al.*, 1998). This determined whether the test subject spent a greater proportion of time or performed a greater

number of displays with either big or small individual. Mate preferences could also be a function of own size relative to the choice individuals (Amundsen & Forsgren, 2003), so we also included regressions using SVL (of the chooser) and the time spent with either big or small individual.

## RESULTS

### *Competition trials*

Males exhibited some of the stereotypical display behaviours previously reported in other agamids (Watt & Joss, 2003; Radder *et al.*, 2006), including head-bobs, tail flicks and hand waves. In male competition trials, there was no relationship between proportion of behaviours exhibited by either big or small males in each trial when regressed against difference in SVL between the two ( $n = 19$ , all  $P > 0.2$ ). There was no relationship between the difference in male SVL and the mean bout times of each trial ( $n = 19$ ,  $r^2 = 0.130$ ,  $P = 0.130$ ). Two behaviour types differed in proportion displayed; bigger males produced more tail flicks (TA) ( $Z = 1.725$ ,  $n = 19$ ,  $P = 0.084$ ) (one-tailed  $P = 0.042$ ), while smaller males produced more hand-waves (HW) ( $Z = -1.853$ ,  $n = 19$ ,  $P = 0.064$ ) (one-tailed  $P = 0.032$ ); (Figure 3). The other seven behaviour types recorded (pushes, head-bobs, approaches, fleeing, tongue-flicks on opponent, tongue-flicks on ground, exploratory moves) did not significantly differ in display production between big or small males ( $n = 19$ ,  $P > 0.2$ ) (Figure 3). The total number of displays was not significantly different between big or small males ( $Z = 0.463$ ,  $n = 19$ ,  $P = 0.643$ ).

Females exhibited some typical agamid displays, including head-bobs and handwaves. In female competition trials, there was no relationship between the difference in SVL and bout time in any trial ( $n = 10$ ,  $r^2 = 0.100$ ,  $P = 0.783$ ) (Figure

4). There was no significant difference in the proportion of displays exhibited by either big or small females ( $n = 10$ , all  $P > 0.1$ ) (Figure 3b). The total number of displays produced was not significantly different between big or small females ( $Z = -1.245$ ,  $n = 10$ ,  $P = 0.213$ ), and the difference in SVL between big and small females in each trial was regressed against each behaviour to determine whether the size disparity between competitors had any influence on proportion of display type exhibited. There was a significant positive relationship between the difference in female SVL and the proportion of pushes directed at the opponent (Log proportion of pushes =  $3.182(\log \text{ difference in SVL} + 0.518)$ ;  $r^2 = 0.601$ ;  $P = 0.014$ ), with bigger females eliciting more pushing actions towards smaller females when the size difference between the two was maximal. There was no significant difference between proportion of displays exhibited by either big or small females for any other display type ( $n = 10$ , all  $P > 0.3$ ).

#### *Mate choice trials*

In the male choice trials, there was no difference in the proportion of time spent with either sized female ( $Z = -0.154$ ,  $n = 10$ ,  $P = 0.878$ ). There was also no significant difference in the proportion of direct movements towards either a big or small female ( $Z = 0.141$ ,  $n = 10$ ,  $P = 0.888$ ). There was no relationship between the size of the male (SVL) choosing and time spent with either the big or small female ( $n = 10$ ,  $r^2 = 0.326$   $P = 0.358$ ).

Similarly, in the female choice trials there was no difference in the proportion of time spent with either sized male ( $Z = -0.879$ ,  $n = 19$ ,  $P = 0.379$ ). There was also no significant difference in the proportion of direct movements towards either a big or small female ( $Z = 0.057$ ,  $n = 19$ ,  $P = 0.955$ ), and no relationship between

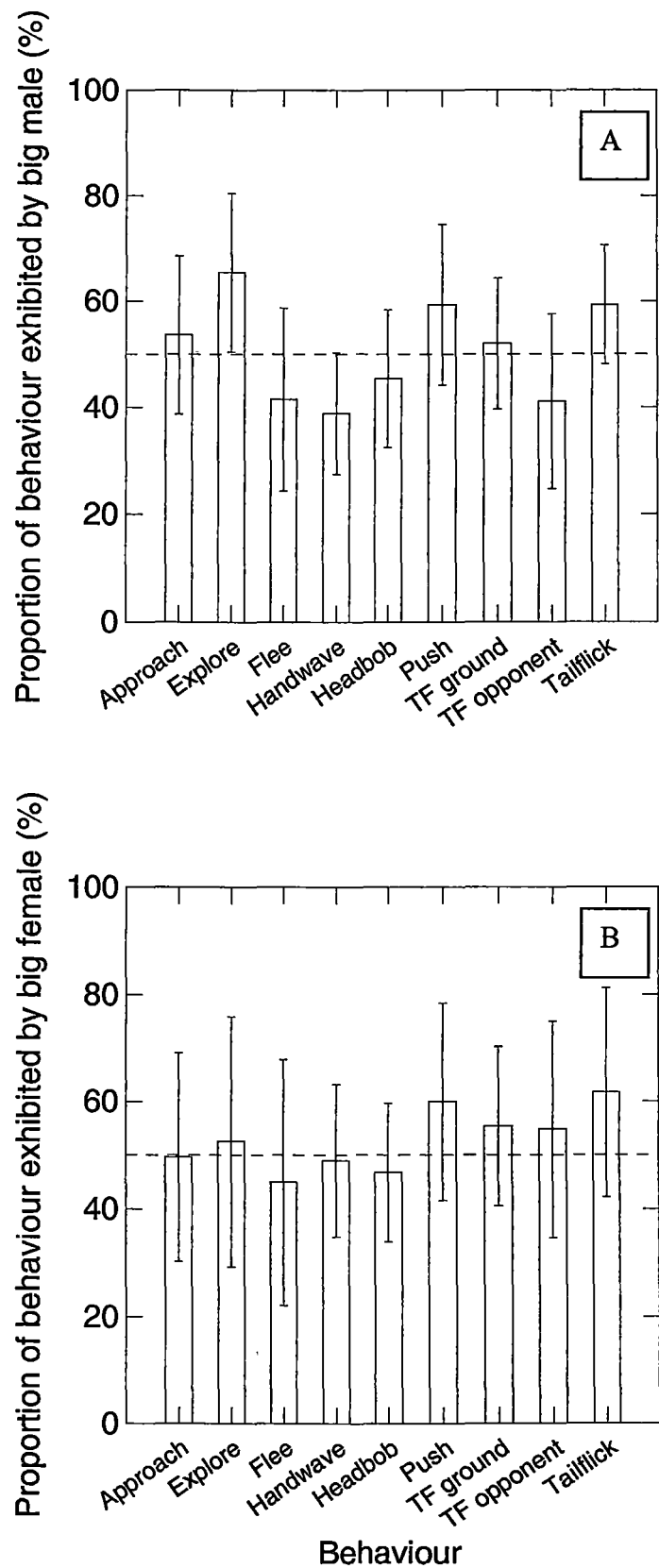


Figure 3. Proportion of behaviour exhibited by the larger individual *Rankinia diemensis* in (a) male-male competition trials and (b) female-female competition trials (TF = tongue-flick; graph using means and 95% confidence intervals; dotted line representing 50% mark, where behaviour equal between lizards).

the size of the female (SVL) choosing and time spent with either the big or small male potential choice ( $n = 19$ ,  $r^2 = 0.103$   $P = 0.694$ ).

## DISCUSSION

Our intra-sexual competition data suggest that body size may play a role in contest success and interactions for both adult male and female *R. diemensis*. Male-male contest interactions reveal differences in display type used by big and small individuals, with two specific displays differing in usage. These displays, hand-waves and tail flicks, have important biological significance for agamids (Ord & Evans, 2003; Peters & Ord, 2003; Hurd, 2004). Bigger males produced proportionally more tail flicks than smaller males, but small males displayed more hand-waves. Hand-waves are typical of agamid non-assertive displays when challenged by a more aggressive male, conveying submission and non-aggressive intent (Watt & Joss, 2003). Tail flicks typically represent aggression or intent to challenge a rival male (Peters & Evans, 2003; Watt & Joss, 2003; Langkilde, *et al.*, 2005). These data suggest that male size may still play a role in social situations and contest success, despite this being a species where males are the smaller sex; however, further work is needed to clarify this result. In particular, a field-based assessment of competitive interactions would provide better understanding of display context and use.

Body size can influence a suite of behavioural and social interactions, and in sexually dimorphic taxa (where males are the larger sex), it is generally assumed that larger males are more dominant and represent a better quality mate (Blanckenhorn 2000; Hingle *et al.*, 2001; Shackleton *et al.*, 2005). Conversely

when females are the larger sex, greater size often permits increased fecundity, and therefore a better quality mate (Darwin 1871; Shine 1988; Olsson 1993).

There are opposing advantages that select for small body size since there are viability costs associated with being large (Blanckenhorn, 2000). For example – the small-male hypothesis (Andersson & Wallander, 2004) – correlates mating potential to the agility associated with small size (Andersson, 1994). Male-male competition still appears important in this system, suggesting perhaps it is not absolute size that is important, but relative size compared to other male conspecifics. This species exhibits several levels of dimorphism complexity with head and limb size proportionally larger in males than females, but these sizes still increase proportional to own body size (Stuart-Smith *et al.*, submitted), which, when viewed in the context of our data, may then be important for competitive interactions.

In terms of female-female competition, our data revealed no difference in the type of behaviour employed in confrontations between big or small lizards, with the exception that bigger females exhibited proportionally more opponent-directed pushing movements than smaller individuals when the size difference between the two was greater. Previous work has already established fecundity selection as the primary driving force behind large female size in *R. diemensis* (Stuart-Smith *et al.*, in press); however, large size may also be important in competitive interactions for females. The aggressiveness identified in this study (i.e. pushes against smaller females) may suggest a system where hierarchical posturing occurs and may be important for nest site choice, where larger females are able to out-compete the smaller individuals and thus secure superior nesting locations or mates. Although evidence for female-female competition is rare in reptiles,

numerous studies have documented a correlation between nest site choice and offspring phenotype (e.g. Shine and Harlow, 1996; Shine *et al.*, 1997; Doody, 1999).

We found no evidence to suggest that mate choice (male or female) is based on body size in *R. diemensis*. This raises important questions of mate preference and trait selection in this species. Although agamids are usually visually oriented (Cooper, 1989), lack of choice based on visual cues such as body size does occur in this genus (e.g. Olsson, 2001a). Additionally, the ability to differentiate between the effects of competition and mate choice on reproductive success is often fraught with difficulties (Horne & Ylönen, 1996; Matteo & Carranza, 1999); since there can be a plethora of traits that determine this success. In reptiles, body size often determines male success in acquiring a mate. This can be the direct result of out-competing rivals for females, or indirectly through defence of a resource that will attract a mate (reviewed in Olsson & Madsen, 1998). This is consistent for many non-reptilian species as well (e.g. Andersson & Wallander, 2004; Herdman *et al.*, 2004).

Mating success tends to be greater for dominant males, although this does not always mean that females prefer dominant males (Spence & Smith, 2006). Since males are relatively smaller in *R. diemensis*, it suggests limited selection for body size and thus, not surprisingly, large body size was not a determinant of mate acquisition. Female choice has also rarely been documented in reptiles (Olsson & Madsen, 1995; Tokarz, 1995; Olsson & Madsen, 1998, LeBas & Marshall, 2001), so our data are not unusual in this respect. This is thought to be either because females may be more particular in their choice of mate, and so attempts to classify

traits on which their choice is based may be incorrect, or that female choice does not exist in some species, since the risks associated with choice may be too high for females (reviewed in Olsson and Madsen, 1995). On the other hand, male mate choice of larger females is quite common, since large body size is often correlated with higher fecundity (Olsson, 1993; Kraak & Bakker, 1998; Shine *et al.*, 2001; Herdman *et al.*, 2004).

In *R. diemensis* large female body size is correlated with greater fecundity (Stuart-Smith *et al.*, in press); however, the lack of male mate selection based on size in this species may then be related to relative body size differences. Size-assortative mating strategies may exist in this *R. diemensis*, especially given the large size difference between males and females, or mate choice may be based on some trait we have not accounted for in this study. In guppies males prefer smaller females when the size difference between the sexes is greater (Dosen & Montgomerie, 2004), suggesting that more complex choice mechanisms can exist, which may have been overlooked in this study. The fact that we still identified aggression differences in males (linked to body size) is important as indicates that size may play a role in mate choice – and that it could be complicated by factors such as age, mating displays, previous matings, size-assortative mating (Olsson, 1993; Olsson, 2001b; Shine *et al.*, 2001) or aggression levels. We cannot discount male or female mate choice in the wild – since a host of other variables must also be taken into account – such as non-uniform mate preferences or single-sex choice systems (Bergstrom & Real, 2000; Amundsen & Forsgren 2003). Shackleton *et al.* (2005) found that, in black field crickets, although larger males won more fights than smaller males, females did not prefer to mate with these dominant males – adding to a growing list of papers that have discarded a relationship between male

dominance and attractiveness (Bonduriansky & Rowe, 2003; Wong, 2004; Shackleton *et al.*, 2005).

## REFERENCES

- AMUNDSEN, T. & FORSGREN, E. (2003). Male preference for colourful females affected by male size in marine fish. *Behav. Ecol. Sociobiol.* 54: 55-64.
- ANDERSSON, M. (1994). *Sexual Selection*. Princeton University Press, Princeton, NJ.
- ANDERSON RA, VITT LJ. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. *Oecologia* 84: 145-157.
- ANDERSSON, M. & WALLANDER, J. (2004). Relative size in the mating game. *Nature*. 431: 139-141.
- BLANCKENHORN, W.U. (2000). The evolution of body size: what keeps organisms small? *Q. Rev. Biol.* 75: 385-407.
- BONDURIANSKY, R. (2001). The evolution of male mate choice in insects: a synthesis of ideas and evidence. *Biol. Rev.* 76: 305-339.
- BONDURIANSKY, R. & ROWE, L. (2003). Interactions among mechanisms of sexual selection on male body size and head shape in a sexually dimorphic fly. *Evolution*. 57: 2046-2053.
- CALSBECK, R. & SINERVO, B. (2002). Uncoupling direct and indirect components of female choice in the wild. *Proc. Natl. Acad. Sci. USA*. 99: 14897-14902.
- CENSKY, E.J. (1997). Female mate choice in the non-territorial lizard *Ameiva plei* (Teiidae). *Behav. Ecol. Sociobiol.* 40: 221-225.
- COGGER, H.G. (1978). Reproductive cycles, fat body cycles and socio-sexual behaviour in the Mallee dragon, *Amphibolurus fordi* (Lacertilia: Agamidae). *Aust. J. Zool.* 26: 653-672.
- COGGER, H. (2000). *Reptiles and Amphibians of Australia*. Reed New Holland, Sydney, Australia.
- COOPER, W.E. JR. (1989). Absence of prey odor discrimination in agamid and iguanid lizards in applicator tests. *Copeia*. 1989: 472-478.
- DARWIN, C. (1871). *The descent of man and selection in relation to sex*. D. Appleton & Co., New York.
- DOODY, J.S. (1999). A test of the comparative influences of constant and fluctuating incubation temperatures on phenotypes of hatchling turtles. *Chelonian Conserv. Bi.* 3: 529-531.
- DOSEN, L.D. & MONTGOMERIE, R. (2004). Female size influences mate preferences of male guppies. *Ethology*. 110: 245-255.
- HERDMAN, E.J.E., KELLY, C.D. & GODIN, J-G. J. (2004). Male mate choice in the guppy (*Poecilia reticulata*): do males prefer larger females as mates? *Ethology*. 110: 97 – 111.
- HINGLE, A., FOWLER, K., & POMIANKOWSKI, A. (2001). Size-dependent mate preference in the stalk-eyed fly *Cyrtodiposis dalmanni*. *Anim. Behav.* 61: 589-595.
- HORNE T.J. & YLÖNEN, H. (1996). Female bank voles (*Clethrionomys glareolus*) prefer dominant males: but what if there is no choice? *Behav. Ecol. Sociobiol.* 38: 401-405.
- HOWARD, R.D., MARTENS, R.S., INNIS, S.A., DRNEVICH, J.M. & HALE, J. (1998). Mate choice and mate competition influence male body size in Japanese medaka. *Anim. Behav.* 55: 1151-1163.
- HURD, P.L. (2004). Conventional displays: Evidence for socially mediated costs of threat displays in a lizard. *Aggressive Behav.* 30: 326-341.
- JONES, K.M., MONAGHAN, P. & NAGER, R.G. (2001). Male mate choice and female fecundity in zebra finches. *Anim. Behav.* 62: 1021-1026.

- 
- KRAAK, S.B.M. & BAKKER, T.C.M. (1998). Mutual mate choice in sticklebacks: attractive males choose big females, which lay big eggs. *Anim. Behav.* 56: 859-866.
- LANGKILDE, T., SCHWARZKOPF, L. & ALFORD, R.A. (2005). The function of tail displays in male rainbow skinks (*Carlia jarnoldae*). *J. Herpetol.* 37: 325-328.
- LEBAS, N.R. & MARSHALL, N.J. (2001). No evidence of female choice for a condition-dependent trait in the agamid lizard, *Ctenophorus ornatus*. *Behaviour*. 138: 965-980.
- MATTEO, C. & CARRANZA, J. (1999). Effects of male dominance and courtship display on female choice in the ring-necked pheasant. *Behav. Ecol. Sociobiol.* 45: 235-244.
- OLSSON, M. (1993). Male preference for large females and assortative mating for body size in the sand lizard (*Lacerta agilis*). *Behav. Ecol. Sociobiol.* 32: 337-341.
- OLSSON, M. (1995). Territoriality in Lake Eyre dragons *Ctenophorus maculosus*: are males 'superterritorial'? *Ethology*. 101: 222-227.
- OLSSON, M. (2001a). No female mate choice in Mallee dragon lizards, *Ctenophorus fordi*. *Evol. Ecol.* 12: 129-141.
- OLSSON, M. (2001b). 'Voyeurism' prolongs copulation in the dragon lizard *Ctenophorus fordi*. *Behav. Ecol. Sociobiol.* 50: 378-381.
- OLSSON, M., & MADSEN, T. (1995). Female choice on male quantitative traits in lizards – why is it so rare? *Behav. Ecol. Sociobiol.* 36: 179-184.
- OLSSON, M. & MADSEN, T. (1998). Sexual selection and sperm competition in reptiles. In: *Sperm competition and sexual selection* (Birkhead, T.R., & Moller, A.-P., eds.). Academic Press, London.
- OLSSON, M., MADSEN, T., UJVARI, B. & WAPSTRA, E. (2004). Fecundity and MHC affects ejaculation tactics and paternity bias in sand lizards. *Evolution*. 58: 906-909.
- OLSSON M, SHINE R, WAPSTRA E, UJVARI B, MADSEN T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56: 1538-1542.
- ORD, T.J. & BLUMSTEIN, D. T. (2002). Size constraints and the evolution of display complexity: why do large lizards have simple displays? *Biol. J. Linn. Soc.* 76: 145-161.
- ORD, T.J. & EVANS, C.S. (2003). Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): An experimental analysis. *Behaviour*. 140: 1495-1508.
- ORD, T.J., PETERS, R.A., EVANS, C.S. & TAYLOR, A.J. (2002). Digital video playback and visual communication in lizards. *Anim. Behav.* 63: 879-890.
- OSBORNE, L. (2005). Information content of male agonistic displays in the territorial tawny dragon (*Ctenophorus decresii*). *J. Ethol.* 23: 189-197.
- PETERS, R.A. & EVANS, C.S. (2003). Introductory tail-flick of the Jacky dragon visual display: signal efficacy depends upon duration. *J. Exp. Biol.* 206: 4293-4307.
- PETERS, R.A. & ORD, T.J. (2003). Display response of the Jacky dragon, *Amphibolurus muricatus* (Lacertilia: Agamidae), to intruders: a semi-Markovian process. *Austral Ecol.* 28: 499-506.
- RADDER, R.S., SAIDAPUR, S.K., SHINE, R. & SHANBHAG, B.A. (2006). The language of lizards: interpreting the function of visual displays of the
-

- Indian rock lizard, *Psammophilus dorsalis* (Agamidae). J. Ethol. 24: 275-283.
- RADDER, R.S. & SHANBHAG, B.A. (2004). Factors influencing offspring traits in the oviparous multi-clutched lizard, *Calotes versicolor* (Agamidae). J. Bioscience. 29: 105-110.
- SHACKLETON, M.A., JENNIONS, M.D., & HUNT, J. (2005). Fighting success and attractiveness as predictors of male mating success in the black field cricket, *Teleogryllus commodus*: the effectiveness of no-choice tests. Behav. Ecol. Sociobiol. 58: 1-8.
- SHANBHAG, B.A., RADDER, R.S. & SAIDAPUR, S.K. (2000). Maternal size determines clutch mass, whereas breeding timing influences clutch and egg sizes in the tropical lizard *Calotes versicolor* (Agamidae). Copeia. 2000: 1062-1067.
- SHINE, R. (1988). The evolution of large body size in females: a critique of Darwin's fecundity advantage model. Am. Nat. 131: 124-131.
- SHINE, R. (1990). Function and evolution of the frill of the frillneck lizard, *Chlamydosaurus kingii* (Sauria: Agamidae). Biol. J. Linn. Soc. 40: 11-20.
- SHINE, R., ELPHICK, M.J. & HARLOW, P.S. (1997). The influence of natural incubation environments on the phenotypic traits of hatchling lizards. Ecology. 78: 2559-2568.
- SHINE, R. & HARLOW, P.S. (1996). Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. Ecology. 77: 1808-1817.
- SHINE, R., MADSEN, T.R.L., ELPHICK, M.J. & HARLOW, P.S. (1997). The influence of nest temperatures and maternal brooding on hatchling phenotypes in water pythons. Ecology. 78: 1713-1721.
- SHINE, R., O'CONNOR, D., LEMASTER, M.P. & MASON, R.T. (2001). Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. Anim. Behav. 61: 1133-1141.
- SPENCE, R. & SMITH, C. (2006). Mating preference of female zebrafish, *Danio rerio*, in relation to male dominance. Behav. Ecol. 17: 779-783.
- STAMPS, J.A. (1983). The relationship between ontogenetic habitat shifts, competition and predator avoidance in a juvenile lizard (*Anolis aeneus*). Behav. Ecol. Sociobiol. 12: 19-33.
- STUART-SMITH, J., SWAIN, R. & WELLING, A. (2005). Reproductive ecology of the mountain dragon, *Rankinia [Tymanocryptis] diemensis* (Reptilia: Squamata: Agamidae) in Tasmania. Pap. Proc. Soc. Tas. 139: 1-6.
- STUART-SMITH, J., STUART-SMITH, R.D., SWAIN, R., & WAPSTRA, E. (submitted). Size dimorphism in *Rankinia [Tymanocryptis] diemensis* (Family Agamidae): sex-specific patterns and geographic variation.
- STUART-SMITH, J., SWAIN, R., STUART-SMITH, R.D. & WAPSTRA, E. (in press). Is fecundity the ultimate cause of female-biased size dimorphism in the dragon lizard *Rankinia [Tymanocryptis] diemensis*? J. Zool.(Lond.).
- TOKARZ, R.R. (1995). Mate choice in lizards: a review. Herpetol. Monogr. 9: 17-40.
- WATT, M.J. & JOSS, J. (2003). Structure and function of visual displays produced by male Jacky dragons, *Amphibolurus muricatus*, during social interactions. Brain Behav. Evolut. 61: 172-184.
- WHITING, M.J., NAGY, K.A. & BATEMAN, P.W. (2003). Evolution and

- Maintenance of Social Status-Signaling Badges. In: Lizard Social Behaviour (Fox, S.F., McCoy, J.K. and Baird, T.A., eds.). The John Hopkins University Press, p. 47-82.
- WONG, B.B.M. (2004). Superior fighters make mediocre fathers in the Pacific blue-eye fish. *Anim. Behav.* 67: 583-590.
- WONG, B.B.M. & CANDOLIN, U. (2005). How is female choice affected by male competition? *Biol. Rev.* 80: 559-571.

# NICHE DIVERGENCE

## CHAPTER 6

### Sex-specific activity patterns and microhabitat use in a size-dimorphic agamid lizard.

Manuscript submitted as: Stuart-Smith, J., Swain, R., & Wapstra E. Sex-specific activity patterns and microhabitat use in a size-dimorphic agamid lizard. (in review)

#### ABSTRACT

Spatial patterning, activity patterns and microhabitat use are important components of a species' behaviour and ecology. In systems where differences in body size between the sexes are distinct, this habitat use information can reveal resource partitioning, niche specialisation and temporal activity differences according to sex and size. I recorded movement, activity patterns and structural and thermal habitat use of mountain dragons (*Rankinia diemensis*) in central Tasmania, Australia, using mark-recapture methods. This species exhibits unusual size dimorphism for agamids, with females the larger sex. The temporal patterns observed between sexes and age groups conform to that of general reptilian activity – where adult males emerge from winter torpor prior to adult females (typical of a protandrous system) or sub-adults of both sexes. Adult females emerge soon after for mating and reproduction, beyond which time adult activity is much reduced. Adults moved greater distances than juveniles, suggesting that foraging or reproductive-related needs require more movement. Although non-significant, the data also suggest that adult females move greater distances than adult males or sub-adults. This is potentially in search of suitable nest sites or

---

reflecting the need to thermoregulate at a higher temperature when eggs are developing *in utero*, and so acquiring better basking sites. Microhabitat use differed between adult males and females – with thermal variables more important in determining female habitat use (higher perch and air temperatures) and structural variables more important for male habitat use (greater perch height and distance to cover). This may reflect the habitat use of males being dictated by behavioural associations in male-male competition typical of agamids and the need for females to bask during egg development.

## INTRODUCTION

Spatial and temporal partitioning of habitat is one mechanism that allows the coexistence of species in highly competitive populations (Tessier and Leibold 1997), and it can also occur between the sexes of a single species (e.g. Butler *et al.* 2000; Verwajen *et al.* 2002). Morphological, physiological and behavioural adaptations are often linked to specific microhabitat use (Vanhooydonck *et al.* 2000; Bickel and Losos 2002; Chuang *et al.* 2006), and as a consequence, understanding microhabitat use and spatial patterning provides valuable information on social systems, behaviour, and ecology (e.g. Perry and Garland 2002; Stone and Baird 2002; Haenel *et al.* 2003; Wone and Beauchamp 2003). Additionally, physical habitat structure and its use can elucidate interactions such as competition intensity, resource partitioning, and predator avoidance capabilities (Petren and Case 1998; Melville and Schulte 2001; Stuart-Smith *et al.* 2007*c, d*). Investigation of habitat use in relation to phenotypic variation within a species is critical for understanding the habitat-specific functional limits on morphology (Losos *et al.* 2003). Understanding the link between phenotype and ecology thus

---

---

allows elucidation of trait evolution pathways, function, performance, and adaptation (Koehl 1996; Melville and Swain 2000), and, moreover, reveals information on specific habitat use and niche specialisation.

Body size differences between the sexes of a single species can arise from, and have consequences for, the behavioural strategies of both sexes (Blanckenhorn 2000, 2005). In sexually dimorphic organisms, body size may play a critical role in behaviour, activity, and social status (Rivas and Burghardt 2001; Meiri *et al.* 2005; Mann *et al.* 2006). Body size can influence such behavioural attributes as home range size of an animal (Rocha 1999), prey size and type consumed (Shine *et al.* 1996; Butler *et al.* 2000), and use of structural habitat (Butler *et al.* 2000). For example, larger animals typically occupy a larger home range (Perry and Garland 2002), and males usually have larger home ranges than females (Rose 1982). One of the foremost theories on the evolution of sexual size dimorphism (SSD) is the niche divergence hypothesis, which suggests that differential habitat use between the sexes acts to reduce intersexual competition in resource-limited situations (Shine 1986; Shine, 1989). For example, work on hummingbirds (Temeles *et al.* 2000) has shown that bill length and curvature of males and females is specific to different flower types in which each sex feeds. Each sex is highly specialised for feeding at flowers from two different plant species – and since the plant species are the major food source for the birds, this allows resource separation between the sexes, therefore reducing competition for limited food resources (Temeles *et al.* 2000).

---

---

When we have species with SSD, we are often interested in whether this reflects a difference in resource use and associated specialist behaviour which can then result in further niche separation. When species exhibit SSD contrary to the norm (i.e. for their taxonomic group), it becomes even more important to see how these size differences are correlated to niche use and sex-specific segregation. *Rankinia diemensis* (Squamata: Agamidae) is a small, cryptic dragon lizard endemic to southeastern Australia. It exhibits unusual dimorphism for agamids – females are the larger sex (Stuart-Smith *et al. in press*), in a group that generally exhibits strong male-biased size dimorphism. Male-biased SSD in agamids is often strongly linked to sexual selection on male-male combat and territory defence (see Shine *et al.* 1998; Peters and Ord 2003; Radder *et al.* 2006a). Thus, this species provides a novel system for investigating the effect of sex and size on habitat use since it is dimorphic in both body size and limb proportions (Stuart-Smith *et al. in press*), with females being the larger sex and having overall larger limbs related to body size (due to fecundity selection; Stuart-Smith *et al.* 2007a, Chapter 4), but males exhibiting *proportionally* larger head and limb sizes for their body size. I do not, however, know how this phenotypic variation translates to habitat use, seasonal activity or ecology in this species. There is virtually no field data on *R. diemensis*, and one of the reasons for this is its camouflaged colouration and cryptic behaviour (Stuart-Smith *et al.* 2005, Supporting Document). Recent data (from behavioural test arenas, see Stuart-Smith *et al.* 2007b, Chapter 5) suggests that size-specific behavioural interactions occur in *R. diemensis*, with larger males displaying more aggressive postures towards smaller males than the converse. Male agamid behaviour often includes perching and displaying, involved in social hierarchy, competition, mate detection and courtship display, and territorial

---

---

displays (e.g. Shine 1990; Ord *et al.* 2001; Radder *et al.* 2006a,b). This size-based male-male hierarchy is perhaps not expected in *R. diemensis* since net selection on male body size is clearly not strong; however, the existence of these behaviours may suggest a complex system with different consequences for, and selection pressures on, body size. If selection pressures operate differently on body size between the sexes in *R. diemensis*, this may translate to differing size-specific behaviour which may promote sex-specific microhabitat use.

I employed mark-recapture (MR) methods on a natural population of *R. diemensis* in Central Tasmania to investigate sex- and size- specific microhabitat use and activity patterns. I specifically aimed to understand spatial and temporal activity patterns of the sexes, which may not conform to patterns usually associated with this taxonomic group given the unusual direction of SSD. I included perch height and distance to cover as structural variables of microhabitat use (i.e. capture site), and, as thermal properties are important for ectothermic organisms (Melville and Schulte 2001), I included perch and air temperature as our microclimate thermal variables. I hypothesize that males will be more conspicuous (perch higher and in more open/exposed areas) than females despite being smaller in size because they still engage in typical agamid male-male antagonistic behaviour (Stuart-Smith *et al.* 2007d). Similarly, since maternal basking environments are known to influence offspring fitness (e.g. Shine and Harlow 1996; Wapstra 2000), I hypothesize that mature females will spend more time in areas of higher temperature. Potentially, any observed difference in behaviour between the sexes could result in microhabitat difference and niche divergence, and the distinct body

---

---

size/proportions between adult males and females could further promote this differential habitat use.

## METHODS

*Rankinia diemensis* is an oviparous agamid lizard with annual reproduction and highly seasonal activity (Stuart-Smith *et al.* 2005, Supporting Document). The species is primarily ground dwelling, although there is no comprehensive information on its specific microhabitat use to date. Females emerge in late spring, and lay eggs late spring/early summer (Stuart-Smith *et al.* 2005, Supporting Document).

I used a MR study on a population of *R. diemensis* located between Oatlands and Interlaken in the Tasmanian Central Highlands (42°13'S, 147°14'E, elevation: 700-800 m). The study was conducted from (austral) spring (October) 2003 to autumn (April) 2004, i.e. throughout their entire active season. The study site was approximately 150 m x 220 m and was subject to little disturbance. It was also bordered by “buffer” zones – which helped to define the study area, on one side by an old quarry, on two sides by an unused road and cleared land on another side, and an open rocky scree on the other, where no individuals were found. A 2-person field team visited the site 3-7 times per week (weather-dependent) and conducted random searches of the entire area between 9am and 6pm. I frequented the area less later in the season when recaptures became low as lizards began to submerge into torpor and weather became unfavourable more frequently. Researchers had prior experience spotting and capturing this species (e.g. Stuart-Smith *et al.* 2005; 2007a,b), and the same 2 people conducted the entire survey to

---

---

limit observer biases. Lizards were captured by hand, measured (by a single observer) for snout-vent length (SVL), tail (TL), head width (HW) and hindlimb length (HLL). I include these trait measures so that I can compare size differences between males and females and investigate the potential for niche differentiation based on different trait and body sizes. Lizards were toe-clipped to allow future identification, and also marked dorsally with a permanent, non-toxic marker. I sexed individuals by eversion of hemipenes (including subadults; see Harlow, 1996). All observations were independent – i.e. the same lizard was only captured once per day. Date of capture was recorded, as was ground, air and perch temperature ( $\pm 0.1$  °C; using a handheld digital Omega<sup>®</sup> thermometer), location (measured using a hand-held GPS), perch height (cm from ground), and distance to nearest cover ( $\pm 1$  cm to nearest potential refuge). Our original intention was to elucidate home ranges; however, I was not able to recapture individual animals on enough occasions to do this, despite being at the field site most suitable days during the season. Our data allowed assessment of movement patterns and comparison of male and female microhabitat use during the breeding season. Other research has shown that ecological niches are often only divergent during the breeding season (e.g. Radder *et al.* 2006a), so I incorporate data from this important period to compare male and female microhabitat use.

### *Statistical analyses*

#### *Movement*

For each individual recaptured during the peak breeding period (November), I randomly selected two recapture dates and calculated distance moved (m) per day between these dates. Distance was estimated as the straight-line distance between

---

---

the two GPS points. I tested for differences in movement between sexes and age groups by 2-way ANCOVAs, (with sex and age group as fixed factors, and SVL as a covariate) and using log distance moved per day.

### *Habitat characteristics*

One capture date was randomly selected for each individual to be used as a measure of microhabitat use. I used Principal Components Analysis (PCA) on 4 habitat variables (perch height, distance to cover, perch temperature and air temperature) (using Primer 5) to provide uncorrelated PCs that I could then analyse using ANCOVA. The PCA included sex and age group (adult and sub-adult) as factors. I used the first 2 PCs in separate ANCOVAs with sex and age group as fixed factors and SVL as a covariate (using SYSTAT V10). I also considered perch type (rock, ground or log separately) for each sex across all age groups (adult, juvenile and hatchling) using a random capture for each individual, as I was interested in overall habitat use differences.

## RESULTS

### *Activity patterns*

I captured 92 lizards through systematic searches of the study area; this consisted of 30 adult males, 26 adult females, 9 juvenile males, 11 juvenile females, 10 hatchling males and 6 hatchling females (total = 56 adults, 36 sub-adults). I obtained 283 observations of individuals from the population used in this study. The mean number of recaptures per individual was 3.14 ( $\pm 0.19$  SE) and ranged between 0 and 13 recaptures. Figure 1 shows a size frequency distribution in SVL for mature *R. diemensis* from the study population in 2003, depicting the size

---

---

overlap of mature males and females. Maturity is based on previous estimates and obtaining reproductively active individuals from this study (See Stuart-Smith *et al.* 2005). Figure 2 shows the percentage of each age group captured per month throughout the activity season, clearly showing that adult males were the first demographic to emerge from winter torpor, being the most commonly observed group in October and November. Adult females were then recorded more in November and December than any other demographic, but then numbers were fairly low for both sexes throughout the remainder of the season. Juvenile males still appeared before juvenile females, but then numbers were consistent between the sexes for the remainder of the season. Hatchlings were not recorded until March, when they began hatching from nests (see also Stuart-Smith *et al.* 2005).

#### *Trait sizes*

Figure 3 shows the relationship between SVL and other morphological traits for males and females. This shows the area at which trait sizes do not overlap (i.e. those points to the top right of the dotted line, which are all females since they attain larger SVL and therefore have larger traits). In all three traits, tail, head width and hind limb length, females attain larger trait size (as a result of their larger body size).

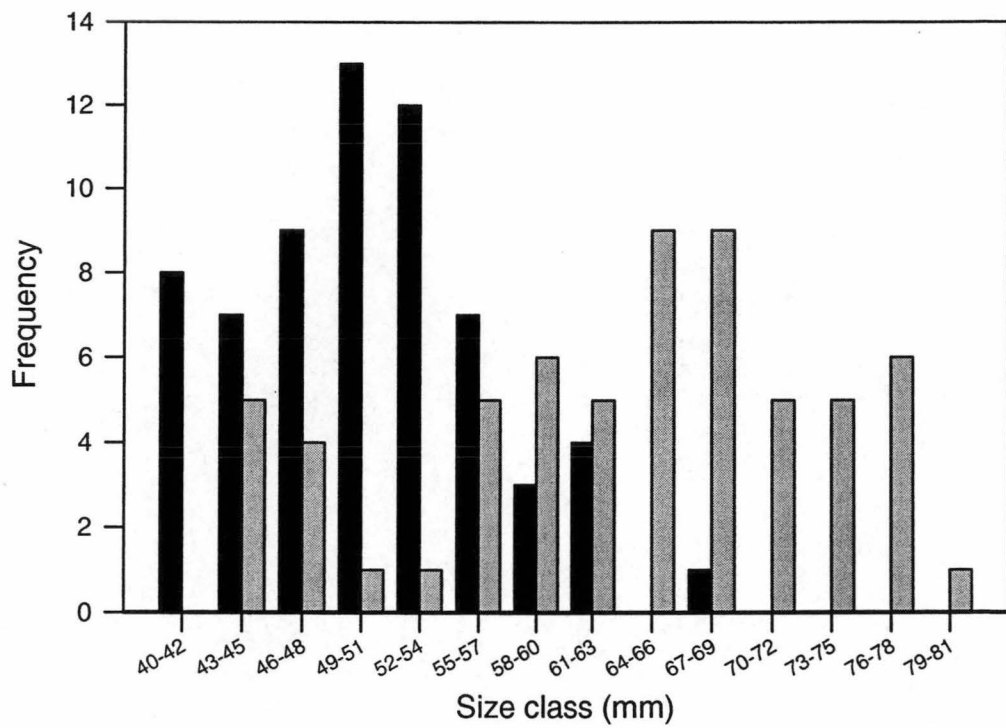


Figure 1. Size frequency distribution in SVL for mature male and female *Rankinia diemensis* at the study site in Central Tasmania during 2003 (males = black, females = grey).

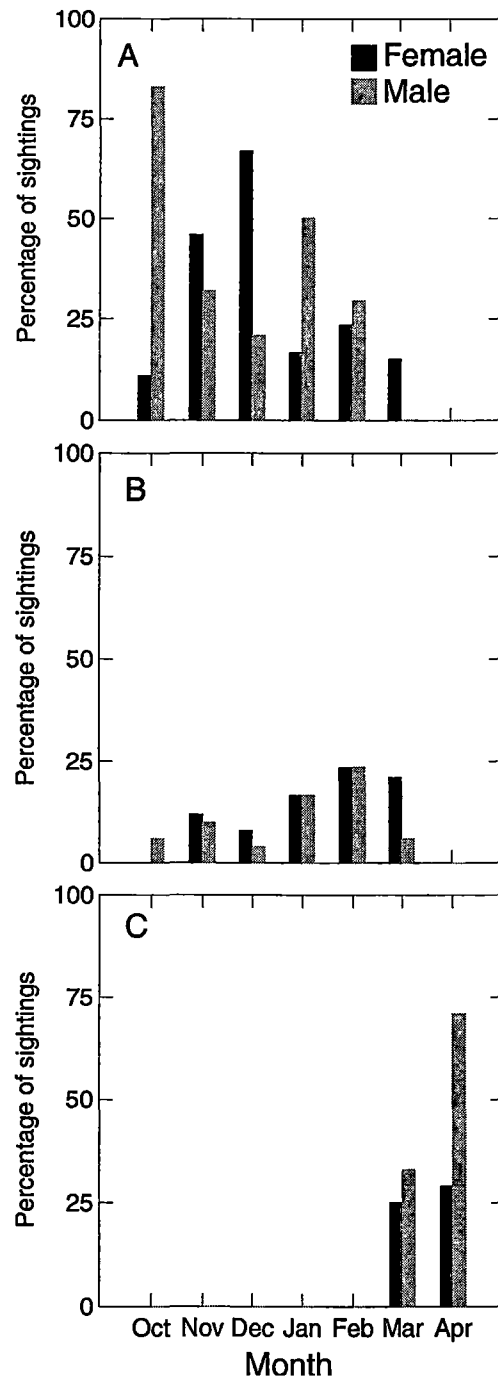


Figure 2. Percentage of sightings per month for each sex and age group of *Rankinia diemensis* from a single population in central Tasmania, 2003 (A = adults, B = juveniles, C = hatchlings).

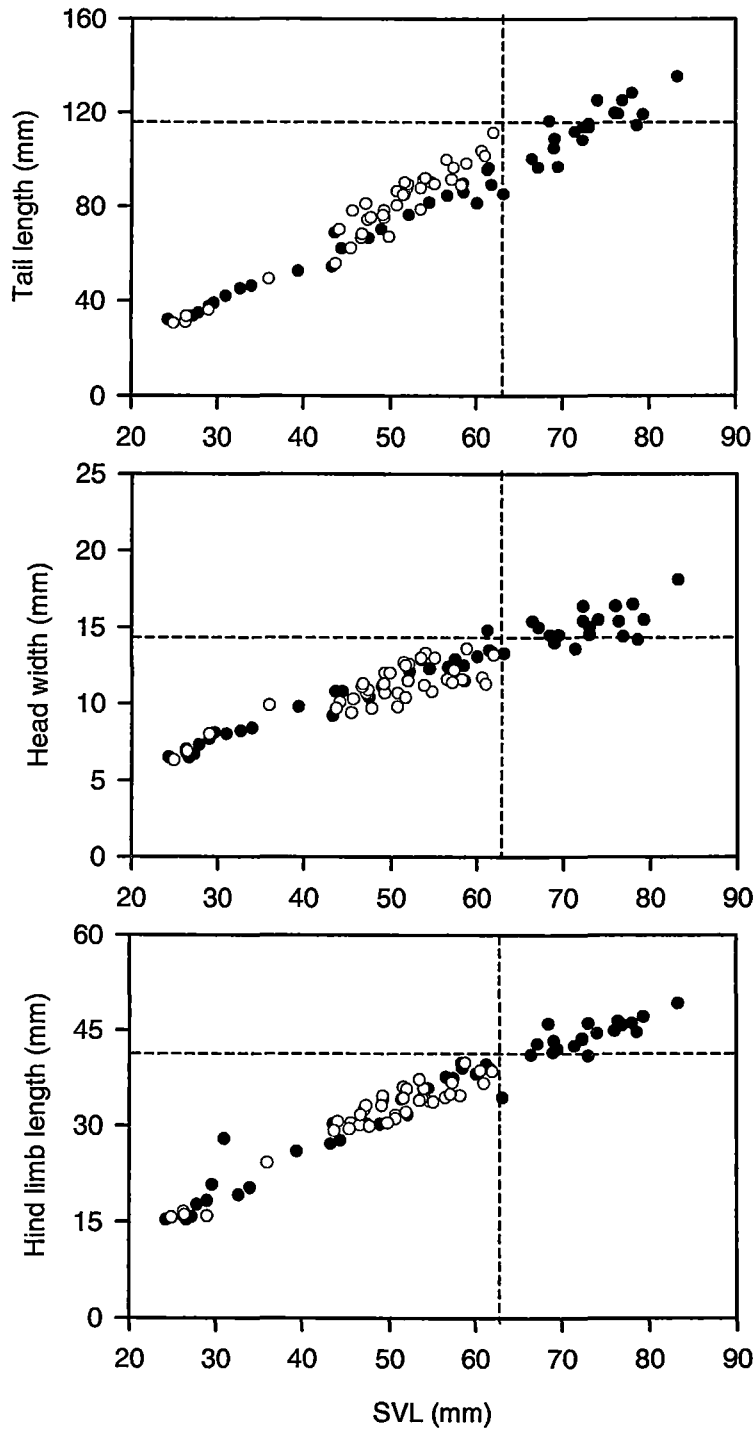


Figure 3. Relationship between trait morphology (mm) and SVL in *Rankinia diemensis* (male = white fill; female = black fill) (A: tail length; B: head width; C: hindlimb length). Dashed vertical line represents SVL where trait size does not overlap in males and females.

### *Movement*

Movement analyses were based on 29 adults (11 males; 18 females) and 10 sub adults (4 males; 6 females) that were recaptured more than once during November (excluding hatchlings, which were not present at this time). The 2-way ANCOVA showed no interaction between sex and age group or an effect of sex. There was, however, a significant effect of age group on movement despite SVL not being significant (Table 1, Figure 4). This indicates that movement, although not related to SVL, differs between age groups; adults moved greater distances than sub-adults. Females tended to move greater distances than males but this was not statistically significant (Figure 4, untransformed data).

Table 1. Effect of sex and age group on movement per day (m) during breeding season for adult and sub-adult *Rankinia diemensis* as detected by 2-way ANOVA.

Effect	SS	df	<i>F</i>	P value
Sex	0.552	1	1.534	0.224
Age group	1.905	1	5.297	<b>0.028</b>
SVL	0.000	1	0.001	0.973
Sex × Age group	0.800	1	2.224	0.145
Error	12.225	34		

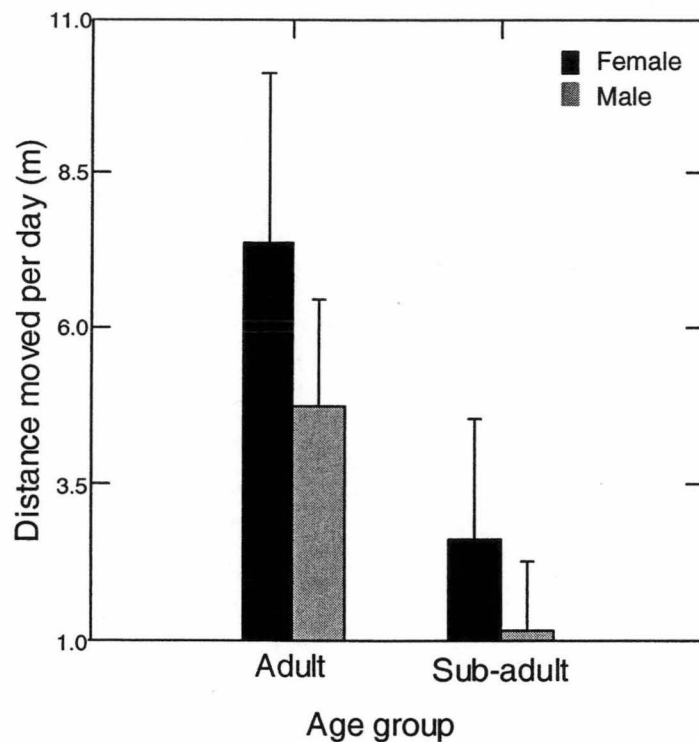


Figure 4. Mean distance (+ SE) moved per day during a single month in the reproductive season (austral spring, 2003) for adult and sub-adult individuals from a single Tasmanian population of *Rankinia diemensis*.

#### *Microhabitat use*

Using all individuals ( $n = 92$ ), the first 2 PCs explained 67.3 % of the total variation in microhabitat use. The first PC was heavily weighted by thermal components (perch and air temperature), and the second PC was heavily weighted by the structural components of perch height and distance to cover (Table 2). The ANCOVAs for PCs 1 and 2 met the assumption of homogeneity of slopes, as indicated by non-significant covariate interaction terms. As a result, I ran unsaturated models with covariate interaction terms omitted for both PCs. These

showed a significant effect of sex, but no effect of age group for both thermal variables (Table 3, Figure 5) and structural variables (Table 4, Figure 6). Adult females used areas of higher air and perch temperature, while males used higher perches and areas further from refuge sites. Females were found in areas where air temperature was on average 22 °C, while males were in areas of on average 19 °C. Female perch temperatures averaged 33 °C, while males were on perches averaging 29 °C. Males perched in areas on average 35 cm distance from cover, while females perched in areas on average 29 cm from cover. Males perched at heights averaging 22 cm from the ground, whereas females typically perched at heights averaging 12 cm from the ground. The type of perch used by the two sexes and age groups (Figure 7 reflects this), with more observations of adult males on logs and more adult females observed on the ground. Juvenile males and females spent more time on logs and rocks than the ground, and hatchlings were only observed on the ground.

Table 2. Factor loadings of the four microhabitat variables on the first and second principal component axes (PC1 and PC2) computed for male and female adult and sub-adult *Rankinia diemensis* (higher positive loadings indicated in bold).

Variable	PC1	PC2
Air temperature	<b>0.684</b>	-0.194
Perch temperature	<b>0.700</b>	-0.010
Perch height	0.008	<b>0.730</b>
Distance to cover	0.205	<b>0.655</b>
Variance explained (%)	38.7	28.6
Cumulative variance (%)	38.7	67.3

Table 3. Effect of sex and age on microhabitat use during breeding season for adult and sub-adult *Rankinia diemensis* as detected by 1-way ANCOVA for thermal variables (PC1) (non-significant covariate interactions omitted for this analysis, and significant *P* values in bold).

Effect	MS	df	<i>F</i>	P value
Sex	12.113	1	9.196	<b>0.003</b>
Age group	0.021	1	0.016	0.899
SVL	0.241	1	0.183	0.670
Sex × Age group	1.643	1	1.248	0.267
Error	1.317	92		

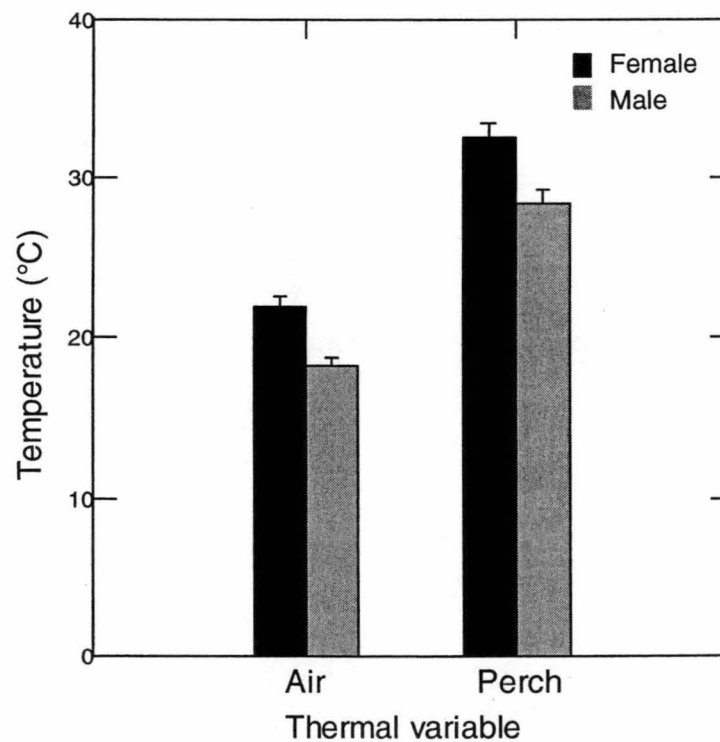


Figure 5. Comparison of mean air and perch temperature (°C) (+ SE) of microhabitat occupied by male and female *Rankinia diemensis* from a single Tasmanian population studied during the breeding season, austral spring, 2003.

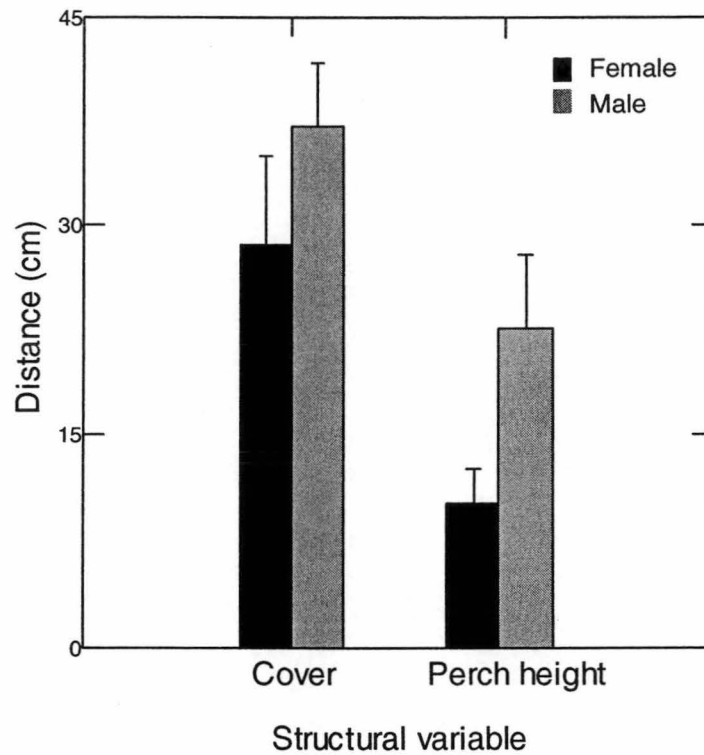


Figure 6. Comparison of mean perch distance to cover and perch height use (cm) (+ SE) by male and female *Rankinia diemensis* from a single Tasmanian population studied during the breeding season, austral spring, 2003.

Table 4. Effect of sex and age on microhabitat use during breeding season for adult and sub-adult *Rankinia diemensis* as detected by 1-way ANCOVA for structural variables (PC2) (non-significant covariate interactions omitted for this analysis, and significant *P* values in bold).

Effect	MS	df	<i>F</i>	P value
Sex	1.466	1	9.384	<b>0.003</b>
Age group	0.389	1	2.492	0.118
SVL	0.062	1	0.397	0.530
Sex × Age group	0.277	1	1.771	0.187
Error	0.156	92		

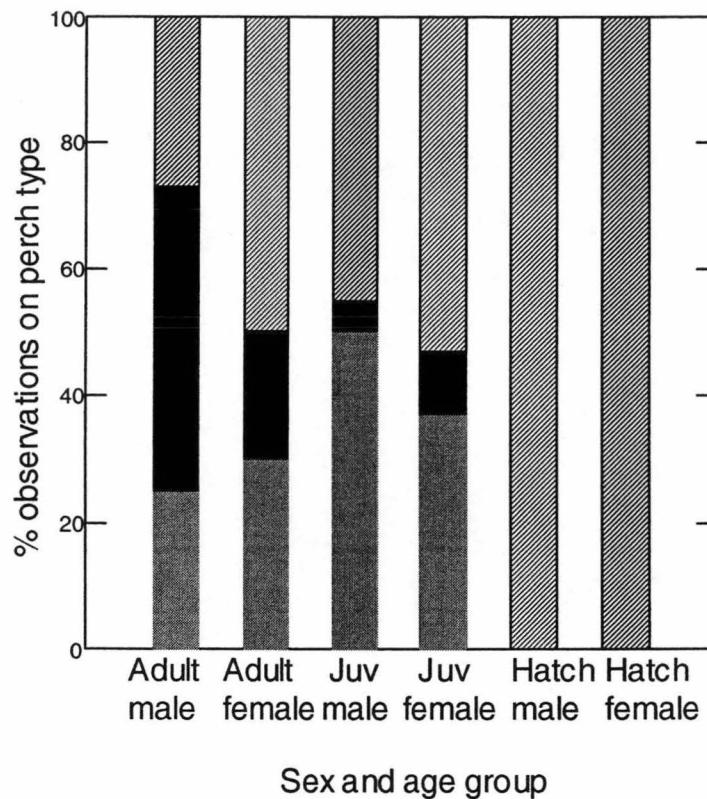


Figure 7. Percentage of perch types used throughout the activity season for adult, juvenile and hatchling male and female *Rankinia diemensis*, 2003 (grey = rock, black = log, striped = ground).

## DISCUSSION

The activity of males and females of all age groups (adults, juveniles and hatchlings) of *R. diemensis* varied temporally through the active season.

Following winter torpor, adult males comprised 75 % of the total number of lizards sighted during October. This is consistent with emergent patterns in other species, where adult male lizards emerge sooner than adult females to initiate spermatogenesis and to allow contest and establishment of dominance hierarchies

and territories (Baird *et al.* 2001; Jenssen *et al.* 2001; Rutherford and Gregory 2003). Adult female *R. diemensis* emerged soon after, and comprised close to, or over, 50 % of all lizards sighted during November and December – when egg development and oviposition occurs. This also allows egg incubation (in nests) to occur early and allow time for incubation. It is also the start of summer, which is important for offspring survival since the environment experienced in the nest not only affects development time, but can also influence body size and growth rate in hatchlings of other species (e.g. Shine and Harlow 1996; Alberts *et al.* 1997; Olsson and Shine 1997; Shine *et al.* 1997). Reduction of incubation duration is particularly beneficial for oviparous species in temperate climates, not only because it reduces the time spent in the nest, where temperature extremes can make eggs unviable, but also because it allows the hatchlings more time to forage and bask prior to the first winter torpor (e.g. Olsson and Shine 1997).

Juvenile *R. diemensis* appear to exhibit a more consistent activity pattern than adults. Juvenile males again emerged earlier than juvenile females, but were then consistently sighted along with females throughout the season. Hatchlings emerged from nests in March, and were active during March-April. This suggests that rapid embryonic development has not evolved in this species, most likely as a result of the cold climate it inhabits (Andrews *et al.* 1999; Shine 1999), since incubation periods of first clutches are over 3 months (also see Stuart-Smith *et al.* 2007a). It is expected that second clutches will undergo shorter incubation periods, since temperatures are on average warmer later in the season. However, since the Central Tasmanian climate can be unpredictable and a delay in hatching could expose eggs to lethally low temperatures (for e.g., see Shine 1999), it is not

expected that second clutching is either particularly effective, or employed frequently. Male hatchlings made up almost 75 % of the total hatchling sightings in April, suggesting that female hatchlings may either enter winter torpor before males or that more males hatched later in the season. This sex bias often occurs when factors such as temperature affect offspring sex (e.g. Bull 1985; Harlow and Taylor 2000; Warner and Shine, 2005). Sex-specific differences in hatchling mortality often also occur in reptiles (e.g. Olsson *et al.* 2004); however, I do not have the data required to address these possibilities.

Differences in structural and thermal properties used by males and females (discussed in detail below) may suggest some level of niche divergence between the sexes. Niche divergence often acts to reduce competition for resources between the sexes; typically occurring when resources are limited or populations are dense (Tessier and Leibold 1997; Verwaijen *et al.* 2002; Attum *et al.* 2007). Male and female *R. diemensis* separate along two microhabitat axes: structural and thermal variables. Males use higher perches and more exposed areas than females, and females were found in areas of higher temperature than males. The most likely explanation for these observations is that males and females use microhabitat differently because they have different behavioural requirements. This divergence in microhabitat use could potentially benefit the species by reducing competition (e.g. for food, resources etc, Temeles *et al.*, 2000). Males use higher perches presumably to increase conspicuousness and for male-male rivalry, and females probably use warmer sites to aid in reproduction. Although niche divergence ideas are usually based on the premise that a limiting resource produces the need to segregate (e.g. Temeles *et al.* 2000), other mechanisms, such

---

as behavioural or physiological differences, can also further reinforce the degree of niche divergence.

Males perched higher and at greater distance from refuge sites than females. Male lizards often perch high and engage in competitive interactions with other males (e.g. Olsson 1995; Baird *et al.* 2001; Calsbeek and Marnocha 2006) including in agamids (e.g. Radder *et al.* 2006 *a*; Stuart-Smith *et al.* 2007*b*, Chapter 5). This may allow a vantage point for detection of competitors, assist in attracting a mate through courtship display, or be part of social hierarchy or dominance-determination interactions with competitors (Radder *et al.* 2006*a*), and occurs mainly in the breeding season. Females were observed more often on the ground. Perching high presumably puts an individual at greater risk of being detected by predators. Since females rarely take part in hierarchical posturing (e.g. Radder *et al.* 2006*b*), staying on the ground and close to cover may reduce the risk of predation associated with increased conspicuousness (see also Radder *et al.* 2006*a*). I found no difference in perch height between sub-adult males and sub-adult females (height was similar to that of adult females) supporting the idea that perching differences are related to adult male dominance behaviour.

The microhabitat thermal variables recorded (perch and air temperature) were higher for adult females than males, but there was no difference in thermal microhabitat use between sub-adult males and females. Differences between adult male and female thermal microhabitat use is a common pattern, especially during the breeding season when females need to develop eggs at a higher, more consistent temperature, because extremes can result in death of the embryo (Shine

---

1999). Active thermoregulation is particularly important in reptiles, and it has been shown that the basking temperatures experienced by the mother while offspring are developing can affect offspring development and phenotype (in both oviparous and viviparous species; Rummery *et al.* 1994; Shine 1995; Andrews *et al.* 1997; Shine *et al.*, 1997; Shine and Downes 1999; Wapstra 2000).

Reproductive females tend to maintain higher body temperature than males (Brown and Weatherhead 2000) during vitellogenesis and, even in oviparous squamates, some embryo development occurs *in utero* prior to oviposition (Shine 1995; Mathies and Andrews 1999), suggesting that the thermal requirements of the mother are important for offspring development, as is nest temperature.

Differences in habitat use between sexes and age groups (spatially and temporally) can correspond to differences in prey type availability (e.g. Shine 1986). Studies by Herrel *et al.* (2006) and Macrini and Irschick (1998) found that males, females and sub adults used different perch heights and types, and that they also consumed different prey types as a result. In *R. diemensis*, not only do males and females use different perch heights, but they have different body sizes and head sizes, which could further promote differences in diet. Head size can potentially influence capture time, subduing and swallowing different prey types, which may then further reinforce the niche divergence in the sexes (Preest 1994; Shine 1999; Verwaijen *et al.* 2002). Thus, different use of perches and other microhabitat variables (and differences in head sizes; Figure 3) could lead to adults targeting prey of different sizes in this way, thereby reducing potential for inter-sexual resource competition. Despite proportionally larger head (and limb and tail) sizes in males, adult females still express overall larger sizes (see Figure

---

3, dashed lines for point where sexes do not overlap in trait size; also Stuart-Smith *et al. in press*), suggesting that females may potentially take larger prey items (for example), which may result in niche separation. This may also be influenced by seasonal variability such as prey type that differs temporally, and can further influence behaviour patterns.

Typically, lizards with longer limbs have greater locomotory ability and occupy open or exposed areas (Attum *et al.* 2007); however, although male *Rankinia diemensis* have proportionally longer limbs than females (Stuart-Smith *et al. in press*), females have larger overall limb sizes, yet do not use more open habitats (i.e. further from cover). Males perch on objects (e.g. rocks, logs) more than females, which is probably attributable more to behavioural differences than to habitat segregation due to resource limitation. Overall, different behavioural and physiological requirements compel either sex to use their thermal and structural habitat differently, which may then reinforce the level of niche divergence that occurs, potentially reducing competition.

## REFERENCES

- ALBERTS, A. C., PERRY, A. M., LEMM, J. M. & PHILLIPS, J. A. (1997). Effects of incubation temperature and water potential on growth and thermoregulatory behaviour of hatchling Cuban rock iguanas (*Cyclura nubila*). *Copeia* 1997, 766-776.
- ANDREWS, R. M., MATHIES, T., QUALLS, C. P. & QUALLS, F. (1999). Rates of embryonic development of *Sceloporus* lizards: do cold climates favour the evolution of rapid development? *Copeia* 1999, 692-700.
- ANDREWS, R. M., QUALLS, C. P. & ROSE, B. R. (1997). Effects of low temperature on embryonic development of *Sceloporus* development. *Copeia* 1997, 827-833.
- ATTUM, O., EASON, P. & COBBS, G. (2007). Morphology, niche segregation, and escape tactics in a sand dune lizard community. *Journal of Arid Environments* 68, 564-573.
- BAIRD, T. A., SLOAN, C. L. & TIMANUS, D. K. (2001). Intra- and inter-seasonal variation in the socio-spatial behaviour of adult male collared lizards, *Crotaphytus collaris* (Reptilia, Crotaphytidae). *Ethology* 107, 15-32.
- BICKEL, R. & LOSOS, J. (2002). Patterns of morphological variation and correlates of habitat use in Chameleons. *Biological Journal of the Linnean Society* 76, 91-103.
- BLANCKENHORN, W. U. (2000). The evolution of body size: what keeps organisms small? *The Quarterly Review of Biology* 75, 385-407.
- BLANCKENHORN, W. U. (2005). Behavioural causes and consequences of sexual size dimorphism. *Ethology* 111, 977-1016.
- BROWN, G. P. & WEATHERHEAD, P. J. (2000). Thermal ecology and sexual size dimorphism in northern water snakes, *Nerodia sipedon*. *Ecological Monographs* 70, 311-330.
- BUTLER, M. A., SCHOENER, T. W. & LOSOS, J. B. (2000). The relationship between sexual size dimorphism and habitat use in greater Antillean *Anolis* lizards. *Evolution* 54, 259-272.
- CALSBECK, R. & MARNOCHA, E. (2006). Context dependent territory defense: the importance of habitat structure in *Anolis sagrei*. *Ethology* 112, 537-543.
- CHUANG, L.-C., LIN, Y.-S. & LIANG, S.-H. (2006). Ecomorphological comparison and habitat preference of 2 cyprinid fishes, *Varicorhinus barbatulus* and *Candida barbatus*, in Happen Creek of Northern Taiwan. *Zoological Studies* 45, 114-123.
- HAENEL, G. J., SMITH, L. C. & JOHN-ALDER, H. B. (2003). Home-range analysis in *Sceloporus undulates*. II A test of spatial relationships and reproductive success. *Copeia* 2003, 113-123.
- HARLOW P. S. (1996). A harmless technique for sexing hatchling lizards. *Herpetological Review* 27, 71-72.
- HERREL, A., JOACHIM, R., VANHOODYDONCK, B. & IRSCHICK, D. J. (2006). Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal of the Linnean Society* 89, 443-454.
- JENSSEN, T. A., LOVERN, M. B. & CONGDON, J. D. (2001). Field-testing the protandry-based mating system for the lizard, *Anolis carolinensis*: does the model organism have the right model? *Behavioural Ecology and Sociobiology* 50, 162-172.

- KOEHL, M. A. R. (1996). When does morphology matter? *Annual Reviews in Ecology and Systematics* 27, 501-542.
- LOSOS, J. B., BUTLER, M. & SCHOENER, T. W. (2003). Sexual dimorphism in body size and shape in relation to habitat use among species of Caribbean *Anolis* lizards; in *Lizard Social Behaviour*, Fox, S. F., McCoy, J. K. and Baird, T. A. (eds), Ch 11 356-380. The John Hopkins University Press, US.
- MACRINI, T. E. & IRSCHICK, D. J. (1998). An intraspecific analysis of trade-offs in sprinting performance in a West Indian lizard species (*Anolis lineatopus*). *Biological Journal of the Linnean Society* 63, 579-591.
- MANN, G. K. H., O'RIAIN, M. J. & HOFMEYER, M. D. (2006). Shaping up to the fight: sexual selection influences body shape and size in the fighting tortoise (*Chersina angulata*). *Journal of Zoology*, London 269, 373-379.
- MEIRI, S., DAYAN, T. & SIMBERLOFF, D. (2005). Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology* 86, 1432-1440.
- MELVILLE, J. & SWAIN, R. (2000). Evolutionary relationships between morphology, performance and habitat openness in the lizard genus *Niveoscincus* (Scincidae: Lygosominae). *Biological Journal of the Linnean Society* 70, 667-683.
- MELVILLE, J. & SCHULTE II, J. A. (2001). Correlates of active body temperature and microhabitat occupation in nine species of central Australian agamid lizards. *Austral Ecology* 26, 660-669.
- OLSSON, M. (1995). Territoriality in Lake Eyre dragons *Ctenophorus maculosus*: are males 'superterritorial'? *Ethology* 101, 222-227.
- OLSSON, M. & SHINE, R. (1997). The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *Journal of Evolutionary Biology* 10, 369-381.
- ORD, T. J., BLUMSTEIN, D. T. & EVANS, C. S. (2001). Intrasexual selection predicts the evolution of signal complexity in lizards. *Proceedings for the Royal Society of London B* 268, 737-744.
- PERRY, G. & GARLAND JR., T. (2002). Lizard home ranges revisited: effects of sex, body size, diet, habitat, and phylogeny. *Ecology* 83, 1870-1885.
- PETREN, K. & CASE, T. J. (1998). Habitat structure determines competition intensity and invasion success in gecko lizards. *Proceedings of the National Academy of Sciences, USA* 95, 11739-11744.
- PREEST, M. R. (1994). Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *Journal of Herpetology* 28, 292-298.
- RADDER, R. S., SAIDAPUR, S. K. & SHANBHAG, B. A. (2006 a). Big boys on top: effects of body size, sex and reproductive state on perching behaviour in the tropical rock dragon, *Psammophilus dorsalis*. *Animal Biology* 56, 311-321.
- RADDER, R. S., SAIDAPUR, S. K., SHINE, R. & SHANBHAG, B. A. (2006 b). The language of lizards: interpreting the function of visual displays of the Indian rock lizard, *Psammophilus dorsalis* (Agamidae). *Journal of Ethology* 24, 275-283.
- RIVAS, J. A. & BURGHARDT, G. M. (2001). Understanding sexual size dimorphism in snakes: wearing the snake's shoes. *Animal Behaviour* 62, F1-F6.

- 
- ROCHA, C. F. D. (1999). Home range of the tropidurid lizard *Liolaemus lutzae*: sexual and body size differences. *Review of Brazilian Biology* 59, 125-130.
- ROSE, B. (1982). Lizard home ranges: methodology and functions. *Journal of Herpetology* 16, 253-269.
- RUMMERY, C., SHINE, R., HOUSTON, D. L. & THOMPSON, M. B. (1994). Thermal biology of the Australian forest dragon, *Hypsilurus spinipes* (Agamidae). *Copeia*, 1994, 818-827.
- RUTHERFORD, P. L. & GREGORY, P. T. (2003). How age, sex, and reproductive condition affect retreat-site selection and emergence patterns in a temperate-zone lizard, *Elgaria coerulea*. *Ecoscience* 10, 24-32.
- SHINE, R. (1986). Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* 69, 260-267.
- SHINE, R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* 64, 419-464.
- SHINE, R. (1990). Function and evolution of the frill of the frillneck lizard, *Chlamydosaurus kingii* (Sauria: Agamidae). *Biological Journal of the Linnean Society* 40, 11-20.
- SHINE, R. (1995). A new hypothesis for the evolution of viviparity in reptiles. *The American Naturalist* 145, 809-823.
- SHINE, R. (1999). Egg-laying reptiles in cold climates: determinants and consequences of nest temperatures in montane lizards. *Journal of Evolutionary Biology* 12, 918-926.
- SHINE, R. & DOWNES, S. J. (1999). Can pregnant lizards adjust their offspring phenotypes to environmental conditions? *Oecologia* 119, 1-8.
- SHINE, R., ELPHICK, M. & HARLOW, P. S. (1997). The influence of natural incubation environments on the phenotypic traits of hatchling lizards. *Ecology* 78, 2559-2568.
- SHINE, R. & HARLOW, P. S. (1996). Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology* 77, 1808-1817.
- SHINE, R., HARLOW, P. S., BRANCH, W. R. & WEBB, J. K. (1996). Life on the lowest branch: sexual dimorphism, diet and reproductive biology of an African twig snake, *Thelotornis capensis* (Serpentes, Colubridae). *Copeia* 1996, 290-299.
- SHINE, R., KEOGH, J. S., DOUGHTY, P. & GIRAGOSSYAN, H. (1998). Costs of reproduction and the evolution of sexual dimorphism in a "flying lizard" (*Draco melanopogon*, Agamidae). *Journal of Zoology* (London) 246, 203-213.
- STONE, P. A. & BAIRD, T. A. (2002). Estimating lizard home range: The Rose model revisited. *Journal of Herpetology* 36, 427-436.
- STUART-SMITH, J., STUART-SMITH, R. D., SWAIN, R. & WAPSTRA, E. (in review). Size dimorphism in *Rankinia [Tympanocryptis] diemensis* (Family Agamidae): sex-specific patterns and geographic variation.
- STUART-SMITH, R. D., STUART-SMITH, J. F., WHITE, R. W. G., & BARMUTA, L. A. (2007 a). The impact of an introduced predator on a threatened galaxiid fish is reduced by the availability of complex habitat. *Freshwater Biology*, doi: 1-1111/j.1365-2427.2007.01787.x
- STUART-SMITH, R. D., STUART-SMITH, J. F., WHITE, R. W. G., & BARMUTA, L. A. (2007 b). The effects of turbidity and complex habitats on the feeding
-

- of a galaxiid fish are clear and simple. *Marine and Freshwater Research* 58, 429-435.
- STUART-SMITH, J., SWAIN, R., STUART-SMITH, R. D., & WAPSTRA, E. (2007 *a*). Is fecundity the ultimate cause of female-biased dimorphism in the dragon lizard, *Rankinia [Tympanocryptis] diemensis*? *Journal of Zoology* London. doi:10.1111/j.1469-7998.2007.00324.x
- STUART-SMITH, J., SWAIN, R., & WAPSTRA, E. (2007 *b*). The role of body size in competition and mate choice in an agamid with female-biased size dimorphism. *Behaviour* 144, 1087-1102.
- STUART-SMITH, J., SWAIN, R., & WELLING, A. (2005). Reproductive ecology of the mountain dragon, *Rankinia (Tympanocryptis) diemensis* (Reptilia: Squamata: Agamidae) in Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 139, 23-28.
- TEMELES, E.J., PAN, I.L., BRENNAN, J.L. & HORWITT, J.N. (2000). Evidence for ecological causation of sexual dimorphism in a hummingbird. *Science*, 289: 441-443.
- TESSIER, A. J. & LEIBOLD, M. A. (1997). Habitat use and ecological specialization within lake *Daphnia* populations. *Oecologia* 109, 561-570.
- VANHOODYDONCK, B., VAN DAMME, R. & AERTS, P. (2000). Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards. *Functional Ecology* 14, 358-368.
- VERWAJEN, D., VAN DAMME, R. & HERREL, A. (2002). Relationship between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* 16, 842-850.
- WAPSTRA, E. (2000). Maternal basking opportunity affects juvenile phenotype in a viviparous lizard. *Functional Ecology* 14, 345-352.
- WONE, B. & BEAUCHAMP, B. (2003). Movement, home range, and activity patterns of the Horned Lizard, *Phrynosoma mcallii*. *Journal of Herpetology* 37, 679-686.

---

## CHAPTER 7

# GENERAL DISCUSSION

## **CHAPTER 7**

### **GENERAL DISCUSSION**

Body size is one of the most important life history traits of an organism, with links to, and influences on, almost all areas of an organism's ecology and evolution (John-Alder *et al.*, 2007). The entire life cycle of an organism can often be broadly scaled to body size (Han & Straškraba, 1998). Size is a major determinant of what an individual needs and how long it must devote to achieving those needs (Han & Straškraba, 1998). Growth patterns and adult body size result from the culmination of a multitude of physiological and ecological factors, acting on various components and stages of an organism, and reflect the diversifying power of selection (Lailvaux & Vincent, 2007).

Schmidt-Nielsen (1985) highlighted the acute consequences that body size can have on body structure and form, identifying knowledge of an organism's size as being absolutely essential to an understanding of how that animal performs and, indeed, how it survives. How big an animal is dictates its metabolic rate, nutritional needs, and the strength required for structural support; it affects heart rate and blood circulation, gas exchange constraints, and the form and arrangement of limbs and muscles necessary to move efficiently (see Schmidt-Nielsen, 1985). These requirements all influence the adaptation and evolution of body form – they place constraints on inter-sexual size extremes, on the types of habitats suitable for occupation and on the prey type that can be consumed. If we can begin to understand the relationship between body size and an animal's

---

requirements – whether it be the need to attract a mate, to forage efficiently, or to achieve optimal thermal temperatures, then we can begin to understand how an organism functions in a specific area: we can define its niche, and assess the evolutionary pathways that have led to its present form.

Understanding body size variation, or other forms of phenotypic variation within a species, is central to understanding adaptation and evolution of particular traits (e.g. Koehl, 1996; Losos, 1990; West-Eberhard, 2003). From this we can predict how and why that trait is advantageous in a particular circumstance, then theorize (and ultimately test) which selective pressures have led to its evolution (Losos, 1990). Body size differences between the sexes can influence intra- and inter-sexual relationships, can affect habitat use and provide avenues for competition reduction within a species (Meiri *et al.*, 2005). The processes responsible for sex-based differences are highly complex and involve interactions between genetic and environmental influences (Shine, 1990).

This thesis provides a comprehensive analysis of sexual size dimorphism (SSD) in the agamid lizard, *Rankinia diemensis*. It provides insight into not only the size difference at present, but also how and why size differences between the sexes of a single species can occur. Studies of SSD are often complicated by the influence of different factors simultaneously affecting the size distributions of adult males and females (Hedrick & Temeles, 1989; Stamps *et al.*, 1994). Recognizing this, I have taken the holistic approach of investigating major sources of influence, to collectively demonstrate the full extent of the causes and consequences of body size and how these can amplify or constrain the size difference (e.g. Shine, 1989).

---

---

My data confirm that SVL and trait sizes are the direct target of selection, and reveal that these traits are the product of not only female fecundity selection, but also signal the cumulative effects of selection acting in opposing directions in males and females. Similar work by Olsson *et al.* (2002) on the snow skink, *Niveoscincus microlepidotus*, showed comparable cumulative effects of fecundity and sexual selection – with large trunk size in females the product of positive selection on females, yet under negative selection in males. This was thought to have links to male-male rivalry and sexual selection pressures when trunk size is less important in males.

This thesis was initially framed around Blanckenhorn's differential equilibration model (Blanckenhorn 2000, 2005; General Introduction, page 10). Now I can summarise the factors that lead to female-biased SSD in *Rankinia diemensis* and fit my data for this species into Blanckenhorn's schematic representation (Figure 1). This summarises both how selection pressures are reflected in this species, and also how this type of model can be modified once specific causal factors have been investigated.

The first step in evaluating the evolutionary pressures that have led to, and the adaptive significance of, any sexually dimorphic trait is to quantify the sex-specific patterns. This is somewhat simplified in Figure 1 – which depicts only one measure of size difference. In reality, size differences (morphology) should be examined at more than one level, as quantifying sex-specific differences based on one measure of size is simplistic, and, as this thesis reveals, can lead to

---

overlooking the combination of different selection pressures acting on different areas of morphology.

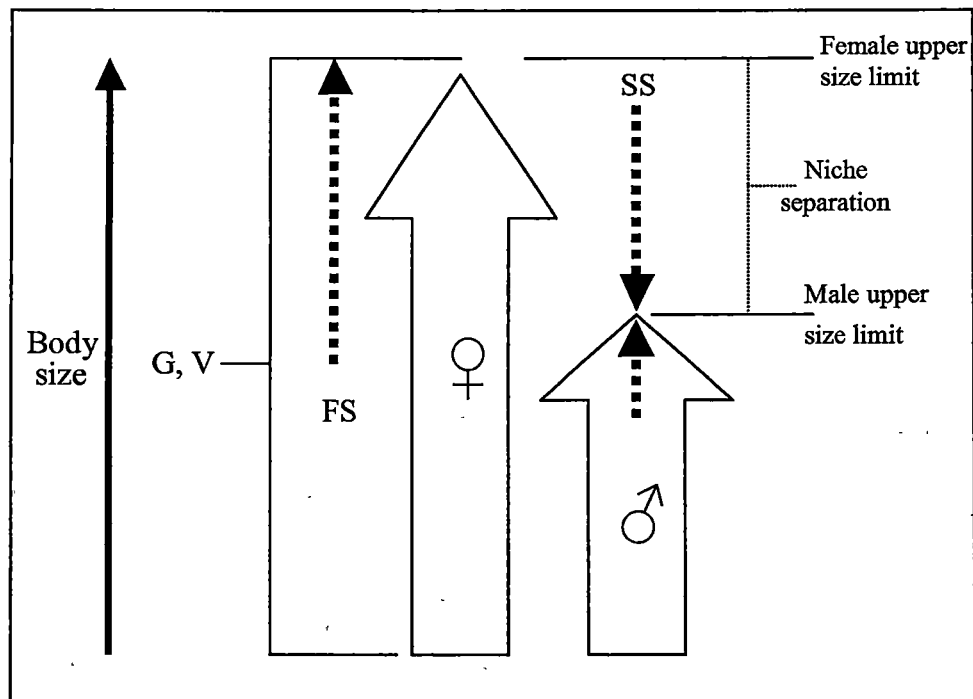


Figure 1. Diagrammatic representation of major causes and consequences of SSD in adult female (♀) and male (♂) *Rankinia diemensis*. Dotted arrows represent selection: FS = fecundity selection, SS = sexual selection. G = genetic constraints, V = viability constraints on size. Niche separation represents that period of adult size where the sexes do not overlap, promoting the separation of resource use between the sexes. Diagram adapted from Blanckenhorn (2000), and modified for *R. diemensis*.

Figure 1 now shows larger body size in (adult) females than males, but still indicates the level of size overlap that exists. Just as importantly, the area of adult size that does not overlap indicates the potential for niche divergence at those sizes. Genetic (G) and viability (V) factors constrain size differences, regulating the degree of differentiation that can occur between the sexes as well as the overall size reached for each sex (Reeve & Fairbairn, 2001; Weatherhead &

Dufour, 2005). Any trait that is influenced by sexual selection will also be influenced by natural selection, which means that there are limitations on its evolution (Oufiero & Garland, 2007). Fecundity (FS) selection is a major driving force producing large female size, and must be stronger than sexual selection on male body size (SS) to produce the female-biased dimorphism that exists.

Although selection may operate to increase male size, since large males are more aggressive (using more aggressive posturing) than smaller males (possibly to allow the establishment of successful dominance hierarchies), either the selection for small size must outweigh this (e.g. selection on early maturity), or genetic and viability constraints acting on size in this species are only outweighed by the benefit of increased reproductive output. Each selection pressure may amplify or constrain the size of each sex (Shine, 1989).

The array of selection pressures and causal factors that operate means that identifying the major cause of evolution of one particular trait is relatively straightforward and achievable. However, being able to understand and separate the multitude of forces that can act simultaneously on SSD is a complex and difficult process, but one which will tell us more about trait adaptation and morphological differentiation in a species.

Chapter 2 identifies the sex-specific differences in size – body size and morphological trait size in *R. diemensis*. Small male size, particularly in agamids, would seem to confer the lack of the well-studied intra-sexual male competition that relies heavily on large male size in determining contest success (e.g. Radder *et al.*, 2006, Watt & Joss, 2003). However, in *R. diemensis* there is evidence that

---

male-male rivalry does exist - with larger males more aggressive towards smaller males (see Chapter 5). This suggests that size, albeit not necessarily overall body size in males, may still be under selection. Head, limb and tail size are proportionally larger in males than in females, again suggesting that trait size is under strong selection in males.

The intra - and inter - sexual geographic differences in SVL and trait size identified in Chapter 2 also suggest that other factors can limit body size in this species. Geographic differences may be due to local adaptation (i.e. genetic modification) or ecological-based modifications (Madsen & Shine, 1993). However, to ascertain whether this observation is consistent with latitude (and thus climatic factors), or associated with the island rule, future work would need to include not only data from additional island populations (i.e. throughout the Furneaux Group), but also from mainland Australia.

There has been an increasing focus on the role of external factors on the magnitude and even the existence of SSD (e.g. John-Alder *et al.*, 2007). Their work showed that external factors, such as environment, could potentially influence the magnitude of SSD. Using growth rate experiments of lizards known to exhibit SSD, John-Alder *et al.* (2007) reared lizards in ideal laboratory conditions (i.e. without food/resource limitations that may occur in the wild), and found that the sex-specific size difference that occurred in the wild did not eventuate in lizards reared under ideal conditions. This work suggests that environmental factors strongly influence energy acquisition and/or resource allocation in natural populations, and that there are sex-specific differences in

---

---

these resource limitations that are responsible for SSD. In *R. diemensis*, although I have not directly addressed the genetic versus non-genetic factors responsible for SSD using empirical methods, differences between geographically distinct populations strongly suggest the capacity for environmental influence.

The degree (or extent) of SSD did not differ geographically. This suggests that, despite factors acting to change overall sizes, these do not lead to differing degrees of SSD, and that genetic constraints operate to limit the size difference that can occur between males and females. This means that, even if we viewed Figure 1 under different populations of *R. diemensis*, although the upper size limits reached for each sex would differ, the difference between the two would not. This finding further promotes the idea that, although niche divergence may occur, it is not the driving factor, but a consequence of male-female size differences. If it were a primary causal factor, I would not expect the males and females to be consistently different among sites. In gape-limited animals, like snakes, the degree of male-female size difference is often determined by prey size (Pearson *et al.*, 2002). I would assume that the potential for prey type and size should differ among sites, but the absence of geographical variation in SSD in *R. diemensis* suggests that underlying genetic factors are constraining the difference in size that can occur between the sexes or that the same pressures are operating across different populations.

Typically, in dimorphic species, sexes are almost identical in morphology during early life stages, and highly divergent growth patterns result in size differences at adulthood (Badyaev, 2002). Sexes were similar sizes at hatching and growth

---

patterns (Chapter 3) revealed an initially slow period of growth in *R. diemensis*. This is likely linked to the temperate climate and its impact on the activity duration of a species (e.g. Adolph & Porter, 1993; Angilletta *et al.*, 2004). The temperate climate severely reduces the annual and diurnal activity periods of reptiles, which rely on environmental sources of thermal energy to create their own energy (Adolph & Porter, 1993). These restricted activity periods may impart particularly high constraints upon neonates. The mark-recapture study (Chapter 6) showed that hatchlings emerge from nests as late as April, which leaves very little time prior to the onset of winter to forage and build the reserves required to enter torpor.

In terms of addressing the difference in size reached by either sex (i.e. in Figure 1, the upper size limits reached for each and potentially when they diverge in size), although I found no size differences present at hatching (and found none, even among geographically distinct populations; Chapter 2), I identified the 3-5 year age cohort as being the point where sexes diverge in body size. Trait and body size comparisons also revealed that trait growth is proportional to SVL growth, so both body size and trait size diverge at the same age. Males reach maturity earlier and cease growth, but females continue to grow post maturity (see also Rutherford, 1994; Shine, 1990), thus allowing size to asymptote later, and thereby identifying the major proximate (causal) mechanism responsible for sex-specific size differences in *R. diemensis*. Although I do not have age-size data for other populations, I can hypothesize that body size of both sexes on Flinders Island (for example) reflect either later attainment of sexual maturity or faster growth prior to maturity. From this, I can conclude that it is not size at hatching, early life growth

---

patterns or longevity differences between the sexes that result in SSD in adulthood. Age and size at maturity and post-maturity growth are the proximate factors responsible for SSD in *R. diemensis*.

Once the nature of the body size differences and proximate mechanism causing them were identified, the next step was to tease apart the often-interactive effects of differential selection pressures. These were examined by three major ideas that I addressed separately in Chapter 4 (natural selection: fecundity, Figure 1: FS), Chapter 5 (sexual selection: competition, Figure 1: SS) and Chapter 6 (niche divergence hypothesis, Figure 1: niche separation; or the areas where the sexes do not overlap in size).

Fecundity is often a major selective influence on female body size (Blanckenhorn, 2000). My data supported this theory – indicating that larger females do produce a greater number of eggs (i.e. large size = increased fecundity), and more importantly, that egg production is not proportional to body size. This implies that fecundity selection has a major influence on female size in this species, but reflects little on small male size. There is comparatively lower selective pressure on male size through, for example, size-dependent male reproductive success. With female size greater than males and reproductive output in females being so highly dependent on body size, it can then be argued that fecundity selection is the major driving force producing large female size in *R. diemensis*. From this, I conclude that the female bias in *R. diemensis* is ultimately a consequence of the benefit of increase reproductive output conferred by large body size.

---

---

Sexual selection is still likely, however, to impact on male size. Figure 1 shows both positive and negative selection pressures acting on this trait. Male intra-specific competition is present, and male trait size is proportionally larger than in females – suggesting positive selection. The mark-recapture study (Chapter 6) indicated that males move less distance than females in the mating season, but there were differences in structural habitat use, which may reflect the need for small male size. Males perched higher and at greater distances from refuge sites than females. Smaller size allows males to perch higher and in more exposed (and thus obvious) positions to attract mates or ward off competitors, without increasing the likelihood of detection by predators. In this respect, small size, particularly for males, despite often being regarded as a limitation, is also advantageous to survival, so selection may be acting to decrease size. Small size advantages in males in other animals have benefits in development time, sperm competition, and agility (Huber, 2005; Brandt & Andrade, 2007). More data would be needed to quantify specific size-dependent advantages in male *R. diemensis*, including perhaps investigation of size-specific male reproductive success and performance. If large male size was associated with high energetic costs (due to territory defence, mate attraction and aggression), then selection would also act to favour small males (Schulte-Hostedde *et al.*, 2002).

The mark-recapture chapter (6) identified two thermal microhabitat characteristics that also differed in use by adult males and females. Females were more likely to be found in areas of higher temperatures than males. This most likely reflects the above male-male competition, and the necessity for reproductively active females to seek warmer sites for egg development and incubation (Shine & Harlow, 1996).

---

One of the most common niche segregating mechanisms comes from consumption of different prey sizes related to larger head size (Pearson *et al.*, 2002; Shine *et al.*, 1998). Although males have proportionally larger heads, head size is still bigger in females because of their larger body size (Chapters 3, 5). This may allow adult females to subdue and consume larger prey items, thus potentially lowering inter-specific food competition. To further quantify this, data are also needed on population dynamics and resource availability (since niche divergence often occurs in the face of increased population density), as well as a comparison of stomach contents analysis with available prey types, for males and females.

Overall, this thesis emphasizes the importance of encompassing major relevant factors when examining even just one component of life history strategy, such as morphological trait form and function. It highlights the complexity of trait size evolution and adaptation. Although fecundity selection is a key element contributing to large female size, it is likely that sexual selection, viability selection or genetic constraints act to keep size small in males. A thorough study of SSD needs to understand not only why one sex is larger, but also why the other sex is smaller (Fokidis *et al.*, 2007). Although small male size would normally lead us to predict a lack of male-male rivalry, further analysis revealed that perhaps it is trait size and not overall size that determines contest success. Niche divergence also plays a subsidiary role – since the evolution of proportionally larger head and limb sizes may be linked to male-male rivalry, but the overall greater size in female trait measurements may allow different food types to be consumed – the separation of niches may be a consequence, not a cause of size differences. In *R. diemensis*, although natural selection plays a pivotal role in sex

---

divergence, both sexual selection and niche divergence may play subsidiary roles in the evolution and continuance of this size difference. It is also the divergent growth in later life, brought on by early maturation of males and post-maturity growth of females that provides the mechanism allowing this size difference to occur. It is this specific culmination of ultimate and proximate mechanisms acting on body and trait size in both sexes that produces the somewhat intriguing female-biased SSD found in *R. diemensis*.

## REFERENCES

- ADOLPH, S.C. & PORTER, W.P. (1993). Temperature, activity, and lizard life histories. *The American Naturalist*, 142, 273-295.
- ANGILLETTA, M.J. JR., STEURY, T.D. & SEARS, M.W. (2004). Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. *Integrative and Comparative Biology*, 44, 498-509.
- BADYAEV, A.V. (2002). Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. *Trends in Ecology and Evolution*, 17, 369-378.
- BADYAEV, A.V. & HILL, G.E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution and Systematics*, 34, 27-49.
- BLANCKENHORN, W.U. (2000). The evolution of body size: what keeps organisms small? *Quarterly Review of Biology*, 75, 385-407.
- BLANCKENHORN, W.U. (2005). Behavioural causes and consequences of sexual size dimorphism. *Ethology*, 111, 977-1016.
- BRANDT, Y. & ANDRADE, M.C.B. (2007). Testing the gravity hypothesis of sexual size dimorphism: are small males faster climbers? *Functional Ecology*, 21, 379-385.
- FOKIDIS, H.B., RISCH, T.S. & GLENN, T.C. (2007). Reproductive and resource benefits to large female body size in a mammal with female-biased sexual size dimorphism. *Animal Behaviour*, 73, 479-488.
- HAN, B.-P. & STRAŠKRABA, M. (1998). Size dependence of biomass spectra and population density I. The effects of size scales and size intervals. *Journal of Theoretical Biology*, 191, 259-265.
- HEDRICK, A.V. & TEMELES, E.J. (1989). The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution*, 4, 136-138.
- HUBER, B.A. (2005). Sexual selection research on spiders: progress and biases. *Biological Reviews*, 80, 363-385.
- JOHN-ALDER, H.B., COX, R.M. & TAYLOR, E.N. (2007). Proximate developmental mediators of sexual dimorphism in size: case studies from squamate reptiles. *Integrative and Comparative Biology*, 47, 258-271.
- KOEHL, M. A. R. (1996). When does morphology matter? *Annual Reviews in Ecology and Systematics* 27, 501-542.
- LAILVAUX, S.P. & VINCENT, S.E. (2007). Ecological dimorphisms: an introduction to the symposium. Symposium: *Ecological dimorphisms in vertebrates: proximate and ultimate causes*. *Integrative and Comparative Biology*, 1-3.
- LOSOS, J. B., BUTLER, M. & SCHOENER, T. W. (2003). Sexual dimorphism in body size and shape in relation to habitat use among species of Caribbean Anolis lizards; in *Lizard Social Behaviour*, Fox, S. F., McCoy, J. K. and Baird, T. A. (eds), Ch 11 356-380. The John Hopkins University Press, US.
- MADSEN, T. & SHINE, R. (1993). Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution*, 47, 1-4.
- MEIRI, S., DAYAN, T. & SIMBERLOFF, D. (2005). Variability and sexual size dimorphism in carnivores: testing the niche variation hypothesis. *Ecology*, 86, 1432-1440.

- 
- OLSSON M, SHINE R, WAPSTRA E, UJVARI B, MADSEN T. (2002). Sexual dimorphism in lizard body shape: the roles of sexual selection and fecundity selection. *Evolution* 56: 1538-1542.
- OUFIERO, C.E. & GARLAND, T., JR., (2007). Evaluating performance costs of sexually selected traits. *Functional Ecology*, doi 10.1111/j.1365-2435.2007.01259.x
- PEARSON, D., SHINE, R. & HOW, R. (2002). Sex-specific niche partitioning and sexual size dimorphism in Australian pythons (*Morelia spilota imbricata*). *Biological Journal of the Linnean Society*, 77, 113-125.
- RADDER, R. S., SAIDAPUR, S. K. & SHANBHAG, B. A. (2006). Big boys on top: effects of body size, sex and reproductive state on perching behaviour in the tropical rock dragon, *Psammophilus dorsalis*. *Animal Biology* 56, 311-321.
- REEVE, J.P. & FAIRBAIRN, D.J. (2001). Predicting the evolution of sexual size dimorphism. *Journal of Evolutionary Biology*, 14, 244-254.
- RUTHERFORD, P. (2004). Proximate mechanisms that contribute to female-biased sexual size dimorphism in an anguid lizard. *Canadian Journal of Zoology*, 82, 817-822.
- SCHMIDT-NIELSEN, K. (1985). *Scaling: Why is animal size so important?* Cambridge University Press, Cambridge.
- SCHULTE-HOSTEDDE, A.I., MILLAR, J.S. & GIBBS, H.L. (2002). Female-biased sexual size dimorphism in the yellow-pine chipmunk (*Tamias amoenus*): sex-specific patterns of annual reproductive success and survival. *Evolution*, 56, 2519-2529.
- SHINE R. (1989). Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *The Quarterly Review of Biology*, 64, 419-461.
- SHINE, R. (1990). proximate determinants of sexual differences in adult body size. *The American Naturalist*, 135, 278-283.
- SHINE, R. & HARLOW, P.S. (1996). Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology*, 77, 1808-1817.
- SHINE, R., HARLOW, P.S., KEOGH, J.S. & BOEADI. (1998). The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology*, 12, 248-258.
- STAMPS, J.A., KRISHNAN, V.V. & ANDREWS, R.M. (1994). Analyses of sexual size dimorphism using null growth-based models. *Copeia*, 1994, 598-613.
- WATT, M.J. & JOSS, J.M.P. (2003). Structure and function of visual displays produced by male Jacky dragons, *Amphibolurus muricatus*, during social interactions. *Brain, Behaviour and Evolution*, 61, 172-183.
- WEATHERHEAD, P.J. & DUFOUR, K.W. (2005). Limits to sexual size dimorphism in red-winged blackbirds: the cost of getting big? *Biological Journal of the Linnean Society*, 85, 353-361.
-

---

# SUPPORTING DOCUMENT

---

## REPRODUCTIVE ECOLOGY OF THE MOUNTAIN DRAGON, *RANKINIA (TYMPANOCRYPTIS) DIEMENSIS* (REPTILIA: SQUAMATA: AGAMIDAE) IN TASMANIA

by Jemina Stuart-Smith, Roy Swain and Andrew Welling

(with three tables and two text-figures)

Stuart-Smith, J., Swain, R. & Welling, A. 2005 (16xii): Reproductive ecology of the Mountain Dragon, *Rankinia (Tympanocryptis) diemensis* (Reptilia: Squamata: Agamidae) from Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* 139: 00–00. ISSN 0080-4703. School of Zoology, University of Tasmania, Private Bag 5, Tasmania, 7001 Australia (J.S.S., R.S., A.W.). \*Author for correspondence.

The mountain dragon, *Rankinia (Tympanocryptis) diemensis* (Gray, 1841), is the only member of the Agamidae in Tasmania. It occurs in some of the coldest regions occupied by any dragon in Australia, and is found in a variety of habitats ranging from coastal heath to alpine scrub. This paper examined the reproductive ecology of *R. diemensis* in the most southerly range of its distribution, providing baseline data on timing of reproductive events, reproductive cycles, nesting behaviour and ovipositioning, clutch characteristics and incubation conditions. Winter torpor lasts approximately seven months with males emerging in early September and spermatogenesis occurring from September–November. Females emerge later, with vitellogenesis occurring from September–December. Gravid females may be found between October and January, but females are non-vitellogenic from late December until the following season. The first clutch is typically laid from October–December, with a variable clutch size (~11 eggs). Females store sperm and a second clutch may be laid five weeks after the first. Eggs incubated in artificial enclosures at low altitude hatched after 72–106 days, after experiencing an average daily temperature of 19°–22°C, and a range of 5°–39°C.

**Key Words:** Agamidae, dragon lizard, reproductive ecology, *Rankinia*, Tasmania

### INTRODUCTION

*Rankinia diemensis* (Gray, 1841) is the only lizard species representative of the Family Agamidae, commonly known as dragon lizards, found in Tasmania; the remaining 17 species comprising Tasmania's lizard fauna are all skinks in the Family Scincidae (Hutchinson *et al.* 2001). It is distinctive among Australian dragons as it is the southernmost agamid in the world and occurs in arguably the coldest habitats occupied by any agamid in Australia (Kent 1987, Hutchinson *et al.* 2001). It is one of only three oviparous reptiles in the State — a strategy in itself that is atypical of cold-climate reptiles (Shine 1985).

*Rankinia diemensis* is a small cryptic species that exhibits strong female-biased size dimorphism (Cogger 1992). It is widespread throughout all of Tasmania east of Tyler's Line (a faunal divide defined by Shield *et al.* 1989) and occurs also in the Furneaux Group, Flinders Island and nearby islands in Bass Strait, as well as in Victoria and southern New South Wales. On the Australian mainland it is mostly restricted to higher altitudes, giving rise to its common name, the 'mountain dragon' (Kent 1987). This species has frequently been re-classified, but we use genus *Rankinia* because most recent phylogenetic analyses by Melville *et al.* (2001) places the current status of this species in this monotypic group, rather than including it in the genus *Tympanocryptis*.

Agamids are typically distributed through hot, arid or tropical regions (Greer 1989, Witten 1993) and the cool-cold temperate climates found in Tasmania represent extreme conditions and result in a greatly reduced activity season compared to that of the island's skink fauna. Winter torpor in adult *R. diemensis* lasts for seven months (J.S.S. unpubl. data), significantly longer than that occurring in viviparous alpine skinks (e.g., *Niveoscincus microlepidotus* (O'Shaughnessy, 1874): 5–6 months). This paper provides

preliminary data on the reproductive ecology of *R. diemensis*. Our aim is to provide baseline information on a species that has not been studied anywhere in its distribution and that represents an important element of the herpetological fauna of Tasmania.

### MATERIALS AND METHODS

This study presents previously unpublished data collected over three breeding seasons (Welling 1999, Duraj 2002); animals were observed *in situ* or collected and held for study in individual outdoor enclosures at the University of Tasmania. The information presented relates predominantly to reproductive ecology but relevant data on morphology and behaviour are also provided.

#### Lizard collection

Gravid females were caught (while digging nesting burrows) by hand from areas of southeastern Tasmania in October/November 1998 and 2001 for investigation of reproductive output and strategy. Collections were made from similar habitat (coastal heathland and dry sclerophyll forest) in and around the Cape Deslacs Reserve, Clifton Beach, Kingston township and the University grounds. Individual enclosures were circular (made of sheet metal: diameter 1 m; walls 40 cm high), located on a easterly-facing slope and filled with brown road gravel to a depth ranging from 15–30 cm. Rocks and litter provided cover and vantage points, while a wire netting lid provided protection from predators. The entire set of enclosures was protected under bird netting. Water was provided *ad libitum* and food (ants or mealworms) was provided three times per week.

## Nesting Behaviour and Egg Collection

Females preparing to oviposit undertake a period of test burrow-digging that lasts for several days. Once this behaviour was observed captive females were monitored twice daily. Date of test burrows was recorded, as were behaviours associated with actual nest-digging and laying. After oviposition, females were removed, weighed ( $\pm 0.1$  g) and a range of morphometric characteristics (snout-vent and tail lengths; head width, depth, length; and interlimb and limb measurements) recorded using electronic calipers accurate to  $\pm 0.01$  mm. Most eggs were carefully uncovered, transferred to the laboratory, weighed using a Sartorius electronic balance ( $\pm 0.01$  g) and used in a series of incubation experiments not reported here.

## Natural Egg Incubation

A total of five nests (two in 1999, three in 2002) were randomly selected to remain *in situ* in outdoor enclosure nests. The nests were carefully uncovered so that a temperature logger could be placed adjacent to eggs to automatically record nest temperature every 15 minutes for the duration of the incubation period.

## Reproductive Cycles

Gonad development and reproductive status were assessed by dissection of preserved material held in the collections of the Queen Victoria Museum, Launceston, and the Tasmanian Museum and Art Gallery, Hobart ( $n = 62$ : 14 adult males, 26 adult females and 22 juveniles). The animals had been collected from areas across Tasmania between 1936 and 1998, and were collected during all months of the activity season.

In males, the testes were measured using electronic digital calipers accurate to  $\pm 0.01$  mm and testicular volume was calculated from the volume of an ovoid, and the epididymides were inspected for the presence of spermatozoa in the lumen. Subsequently, males were subjectively categorised as active (enlarged testes and milky epididymides), regressed (small testes and dark epididymides), or recrudescing (moderate enlargement of testes, but dark epididymides). Females were dissected ( $n = 26$ ) and classified based on the size and appearance of the follicles and the presence of oviductal eggs. The number of ovarian follicles and their diameter was recorded (using electronic calipers). Animals were categorised as: non-vitellogenic (follicle diameter  $< 1$  mm), vitellogenic (follicle diameter 1–2 mm), gravid (oviductal eggs present) or recrudescing (vitellogenic follicles  $> 1$  mm).

## RESULTS AND DISCUSSION

## Morphology

*Rankinia diemensis* is a relatively small, cryptic, dragon lizard exhibiting strong female-biased size dimorphism. In Tasmania the largest snout-vent length (SVL) we have recorded for females is 84 mm and for males is 66 mm. Table 1 allows comparison of mass and size of adults of both sexes (also see fig. 1). Sexual size dimorphism is common in Australian agamids; however, in most species males are the larger sex, a characteristic linked to the establishment and defence of territories (Brattstrom 1971). In most agamids, males are aggressive and conspicuous defenders of territories and this forms the basis of mate selection. The existence of female-biased sexual dimorphism and apparent lack of male territories in *R. diemensis* may have significant implications for sexual selection strategies in this species.

Colouration varies from pale beige, through to light and dark greys, bright orange or red-brown (J.S.S. unpubl. data, Hutchinson *et al.* 2001, fig. 1), with mixes of all colours seen in individuals. There does not appear to be sexual dichromatism in this species, which relies heavily on camouflage for avoidance of predators. The colouring reflects this – usually varying according to habitat; it also has modified epidermal scales characteristic of all agamids (Witten 1993), in the form of rough or spiny scales (Hutchinson *et al.* 2001). A distinctive line of dark diamond-shaped marks runs dorsally along the spine from head to tail base – with patches of lighter colour between the 'diamonds' (fig. 1). When the animal is cold, it becomes dark and patterning is obscured (Hutchinson *et al.* 2001). Colour changes also occur in the base colour of individuals (i.e., between the diamonds). These changes can occur relatively quickly (within minutes), and are common among agamids, probably pertaining to social interactions (Greer 2003).

## Behaviour

## Crypsis

Although *R. diemensis* relies heavily on camouflage to avoid predator detection, it also employs cryptic behaviour, spending most of its time motionless, even to the extent of appearing to regulate breathing. When approached it will typically run a short distance, before stopping abruptly (Hutchinson *et al.* 2001). The sudden stop is unexpected by the observer, and, even though it does not always occur when cover has been reached, it is still an effective form of predator escape because the observer's eye typically follows the direction of

TABLE 1  
Comparison of snout-vent length, mass and tail length  
for adult male and female *Rankinia diemensis*

	Snout-vent length (mm)			Mass (g)			Tail length (mm)		
	Range	Mean	N	Range	Mean	N	Range	Mean	N
Male	49–66	57	24	2.8–6.8	4.6	24	82–113	97	24
Female	56–82	72	34	5.6–13.4	10.3	33	82–137	117	33

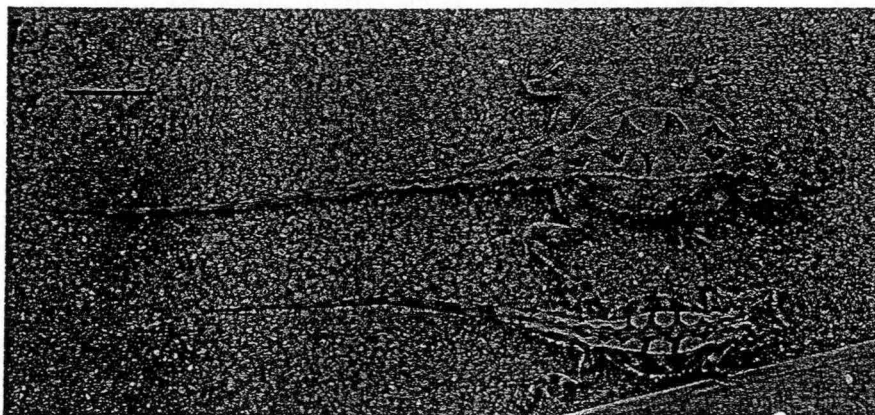


FIG. 1 — Dorsal patterning and sexual size dimorphism in *Rankinia diemensis* (gravid female top, male below).

movement beyond the lizard. The camouflage provided by the lizard's outline, colouration and patterning makes the motionless animal very difficult to detect.

#### Timing of events

Adults may undergo a torpor lasting up to seven months, but hatchlings appear to spend significantly less time in torpor — presumably since they do not have the ability to build sufficient reserves to support such an extended period without food. Field observations reveal that hatchlings remain active well into the autumn months (late April), while adults are rarely seen by late summer (mid-February). Adults have been maintained in laboratory torpor conditions for six months at 5°C — indicating that arousal from torpor to forage is not necessary, but during this time they have been observed drinking water occasionally.

Field observations reveal that males emerge in early spring (early September) at least two weeks before females. They spend considerable time perched on logs or rocks (at heights up to 1 m), which is atypical of their normal cryptic behaviour. It is unclear whether either sex maintains a territory, but there is certainly no obvious territorial behaviour. Females emerge later in spring, and are able to lay a clutch by early-mid summer (November to mid-December). Females prefer relatively open sites to lay their eggs — disturbed soil is often favoured and the sides of quarries and edges of dirt roads are often used as nest sites.

Early in summer, and once the breeding season has finished, both males and females moult. Activity then undergoes one further peak of reduced intensity (late December to mid-January) when second clutching may occur. From this point on, adults are rarely seen. Immature lizards (including hatchlings from the previous year) are active throughout the season. Hatchlings emerge in March/April, and are active as long as the warmer weather lasts. Although hatchlings are commonly sighted, older juveniles are rarely seen at any time. This may be due to high mortality over the first winter season, consequent on the long incubation period and emergence close to the onset of winter, but it may also

reflect the extremely cryptic behaviour typical of adults outside the breeding season.

#### Displays and communication

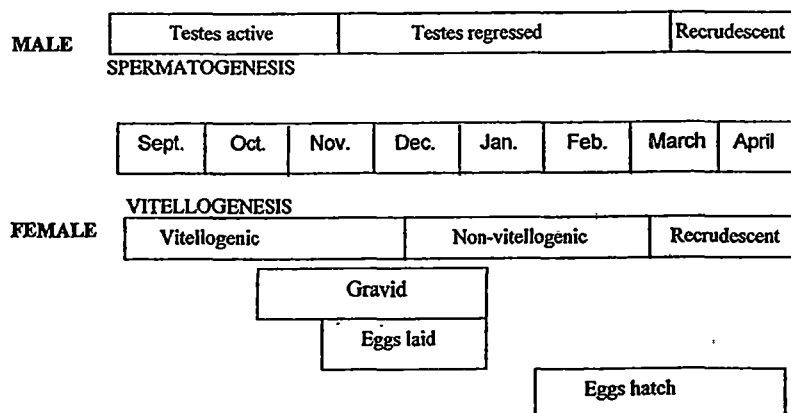
Communication is visual among *R. diemensis*, as in agamids generally (Greer 1989, Witten 1993, Ord & Evans 2003), but hissing has been heard at capture (J.S.-S. unpubl. data.). This behaviour is not unheard of in dragons, although it is rare (Greer 1989). Agamids typically produce discrete visual displays to mediate social behaviour (Watt & Joss 2003), and some of these are utilised by *R. diemensis*, including arm-waving, head-bobbing, and tail lashing. Typically these displays denote aggressive or submissive behaviour. The structure or function of these displays has not been determined for *R. diemensis* and are the subject of a current study (J. S.-S.).

### Reproduction

#### Reproductive cycles

Environmental conditions, particularly climatic, can have a strong influence on reproductive cycles. Oviparous lizards are not common in areas of cold, variable conditions because they do not have control over the conditions experienced during egg incubation (Heatwole & Taylor 1987). When seasonal temperatures are highly variable, as in Tasmania's climate, there is only a short summer period for reproduction, embryonic development and offspring dispersal to occur. Examination of museum specimens indicated that spermatogenesis occurs from early September to early November ( $n=15$ ) with testes size reaching a maximum in late September. Testes have regressed to one quarter of their maximum volume by late October, and remained regressed thereafter until late February. Recrudescence begins in March (fig. 2). Late October to early November appears to be the main mating period, during which time males store sperm in their epididymides.

Females emerge from winter torpor later than males (late September), with vitellogenesis occurring from September–December, and gravid females recorded from late October

FIG. 2 — Calendar of major reproductive events in males (top) and females (below) of *Rankinia diemensis*.

to January. Females are non-vitellogenic from late December to March, when recrudescent begins (fig. 2).

#### Nesting behaviour and ovipositioning

Females produce first clutches between October and December in Tasmania. Gravid females usually excavate a series of 'test' burrows prior to digging the final nest; these are more shallow than the final nest, and remain uncovered. Females maintained in artificial outdoor enclosures ( $n=23$ ) averaged two test burrows prior to oviposition, and the average time between the first test burrow and oviposition was five days. Test burrows surrounding natural nests (verified by uncovering nests) have also been observed in the wild, and on three occasions burrows have been filled in on a different day to which they were excavated. Test burrows are often quite close to the final nest site, and females have been observed digging burrows within 1.5 m of each other, at the same time, and in full view of each other. Observations of extensive 'tongue-flicking' (in enclosures) prior to oviposition suggest that chemical cues may be an important determinant in nest site selection. Nests are usually located in relatively open areas — with no direct shading, but still in close proximity to some form of cover.

Final burrow excavation and ovipositing takes most of a day and, if started late, may spill over to a second day. Before starting females exhibit heightened alertness for as long as two hours, usually perched on a vantage point about 30 cm above ground at the edge of an open patch. Digging involves excavating soil with the forelimbs and flicking it backwards with the larger hind limbs. Digging takes place at an angle, creating a burrow 60–85 mm deep ( $n=23$ ). During laying, the female reverses her position so that her head and forelimbs protrude from the nest, as does her tail (bent around to one side). When laying is finished she exits from the burrow, and may turn and move the eggs about with her snout before covering them. Digging and oviposition takes several hours. When finished the female covers the eggs by flicking soil back into the nest with her fore- and hind- limbs, with intermittent bouts of rapid fore-

limb stamping and snout-pushing of the soil covering the eggs, presumably to compact it. She may spend as much as two hours on this activity; once completed it is impossible to locate the nest visually.

#### Clutch characteristics

Clutch size varies from 2–11 eggs, with female size being positively correlated with clutch size. Egg mass at oviposition is between 0.4 and 1.0 g (for eggs that hatch successfully), with dimensions averaging 11.0 x 7.0 mm (see table 2 for egg measurements). A second clutch can be produced five weeks after the first, but almost invariably this will contain fewer eggs than the first. Reduced clutch size later in the season is typical of lizards that produce multiple clutches in a single breeding season (Nussbaum 1981, Forsman 2001). James & Whitford (1994) concluded that progressively smaller clutches in the side-blotched iguanid *Uta stansburiana* (Baird & Girard, 1852) was an adaptive response to poor environmental conditions that occur late in the season; they argued that smaller clutches lower the risk of reproductive failure for the

TABLE 2  
Reproductive investment and egg dimensions  
at oviposition

	Mean ( $\pm$ s.e. <sup>1</sup> )	Range
Relative clutch mass <sup>2</sup> (%)	45 (2)	0.16–0.71
Clutch size	6.0	2–11
Clutch mass (g)	4.52 (0.23)	1.82–7.01
Egg mass (g)	0.69 (0.01)	0.43–1.01
Egg length (mm)	11.0 (0.07)	7.0–14.5
Egg width (mm)	7.0 (0.05)	5.0–8.0

<sup>1</sup> s.e. = standard error)

<sup>2</sup> Relative clutch mass = (mass of eggs)/(mass of female – mass of eggs)\*100

female. Similarly for *R. diemensis*, environmental conditions deteriorate later in the season, with cooler temperatures, reduced photoperiod, and often increases in rainfall. In *R. diemensis*, however, individual eggs in the second clutch are larger, indicating that, although fewer eggs are being produced, more energy is being allocated to each egg. Presumably this provides more energy for development if this is prolonged by poor incubation conditions and/or larger hatchlings with a greater chance of survival when emergence occurs very late in the season. Size at emergence has significant consequences for a hatchling's subsequent growth, survival (Sinervo 1993), and ability to forage effectively and escape predators (Phillips *et al.* 1990).

Females held in captivity from early spring, without access to males, are able to lay a second clutch, clearly demonstrating their ability to store sperm. Among Australian agamids this has only been demonstrated for one other species: the bearded dragon, *Pogona barbata* (Cuvier, 1829) (Amey & Whittier 2000), though it may be quite common. The advantages associated with sperm storage include improving opportunities for sperm competition between sperm from different males (Parker 1970) (assuming that females mate with more than one male). It may also reduce competition between the sexes for resources, thus facilitating production of a second clutch, and it also ensures that reproduction is still possible if the potential of encountering males is low (Kumari 1990) or if male activity decreases later in the season.

#### Incubation

Incubation duration ranged from 72–106 days in these nests with a hatching success of ≥80%; duration strongly depended on the temperatures experienced during incubation. Warmer nest temperatures have strong implications for hatchling survival as they result in shorter incubation times, meaning longer foraging and basking times prior to the first winter torpor (Gutzke & Packard 1987, Packard & Packard 1988).

Data from temperature loggers in the five nests located in our outdoor enclosures revealed that eggs experienced average daily temperatures of between 19° and 22°C, although the range was from 5°–39.5°C. As expected, clutches that spent a greater amount of time at lower temperatures, had longer incubation durations. Since the period available to hatchlings for foraging prior to winter is limited, earlier emergence, from nests located in warmer incubation sites will provide more time for basking and foraging. Maternal nest site choice may therefore be a key determinant of a female's reproductive success. Unlike many other agamids, temperature-related sex determination does not occur in *R. diemensis* (J.S.S. unpubl. data).

#### CONCLUSIONS

*Rankinia diemensis* is a relatively small cryptic dragon lizard, although Tasmanian specimens reach a larger size than their mainland counterparts (Copper 1992). In Tasmania, and probably elsewhere, its life history strategy is constrained by climate, which necessitates spending much of its time in torpor, severely reducing the time available for reproduction and growth. Egg incubation periods are long, due to cool nest temperatures, and hatchling survival is endangered by the short period of time prior to winter in which fat reserves are built.

TABLE 3  
Duration of incubation and nest temperatures in five nests located in artificial enclosures

Duration of incubation (days)	Nest temperature	
	Mean (±s.e.)	Range
72	19.7 (0.09)	5.6–38.1
78	20.3 (0.09)	8–39
99	21.1 (0.10)	10.3–38.1
106	17.3 (0.06)	8–37.5
106	17.7 (0.12)	6–39.5

The species presents an ideal opportunity for examining the evolution and adaptation of life history in oviparous lizards to cool climates. Although we have provided the first extensive data on the reproductive ecology of the mountain dragon in Tasmania, many questions remain. Regarding reproduction, the existence of pronounced female-biased size dimorphism, very unusual for agamid lizards, raises intriguing questions about sexual selection strategies and their responses to climatic constraints. Likewise, an understanding of how conditions during and immediately following torpor influence survival and reproductive investment would yield valuable insight into how this unusual dragon maintains successful populations even on the exposed Central Plateau of Tasmania.

#### ACKNOWLEDGEMENTS

We wish to thank Rick Stuart-Smith for his assistance in both field and laboratory work. This work was approved by the Animal Ethics Committee, University of Tasmania, permit numbers 98075 and A0006070; collecting of animals was authorised by collecting permits (FA98189; FA01238) issued by the Department of Primary Industries, Water and the Environment, Tasmania.

#### REFERENCES

- Amey, A.P. & Whittier, J.M. 2000: The annual reproductive cycle and sperm storage in the bearded dragon, *Pogona barbata*. *Australian Journal of Zoology* 48: 411–419.
- Copper, H.G. 1992: *Reptiles and Amphibians of Australia*, Fourth Edition. Reed Books, Australia.
- Duraj, J.F. 2002: Maternal and environmental influences on the early life stages of the mountain dragon, *Tymanocryptus diemensis*. Unpublished Honours thesis, University of Tasmania.
- Greer, A.E. 1989: *The biology and evolution of Australian lizards*. Surrey Beatty & Sons Pty Ltd, Australia.
- Gutzke, W.H.N. & Packard, G.C. 1987: Influence of the hydric and thermal environments on eggs and hatchlings of bull snakes *Pituophis melanoleucus*. *Physiological Zoology* 60: 9–17.
- Heatwole, H. & Taylor, J. 1987: *Ecology of Reptiles*. NSW, Australia, Surrey Beatty and Sons Pty Ltd.
- Hutchinson, M., Swain, R. & Driessen, M. 2001: *Snakes and Lizards of Tasmania*. Fauna of Tasmania Handbook No. 9. University of Tasmania.
- James, C.D. & Whitford, W.G. 1994: An experimental study of phenotypic plasticity in the clutch size of a lizard. *Oikos* 70: 49–56.

- Kent, D.S. 1987: Notes on the biology and osteology of *Amphibolurus diemensis* (Gray, 1841), the mountain dragon. *Victorian Naturalist* 104: 101–104.
- Melville, J., Schute II, J.A. & Larson, A. 2001: A molecular phylogenetic study of ecological diversification in the Australian lizard genus *Ctenophorus*. *Journal of Experimental Zoology (Molecular and Developmental Evolution)* 291: 339–353.
- Ord, T.J. & Evans C.S. 2003: Display rate and opponent assessment in the Jacky dragon (*Amphibolurus muricatus*): An experimental analysis. *Behaviour* 140: 1495–1508.
- Packard, G.C. & Packard, M.J. 1988: The physiological ecology of reptilian eggs and embryos. In Gans, C. & Huey, R.B. (Eds): *Biology of the Reptilia*, Volume 16. Alan Liss, USA: 525–605.
- Phillips, J.A., Garel, A., & Packard, G.C. 1990: Influence of moisture and temperature on eggs and embryos of green iguanas (*Iguana iguana*). *Herpetologica* 46: 238–245.
- Shield, R.J., Koste, W. & Tan, L.W. 1989: Tasmania revisited: ro- tifer communities and habitat heterogeneity. *Hydrobiologia* 186/187: 239–245.
- Shine, R. 1985: The evolution of viviparity in reptiles: An ecological analysis. In Gans, C. & Biller, F. (Eds): *Biology of the Reptilia*, Volume 15., John Wiley, USA: 605–694.
- Sinervo, B. 1993: The effect of offspring size on physiology and life history: Manipulation of size using allometric engineering. *Bioscience* 43: 210–218.
- Watt, M.J. & Joss, J.M.P. 2003: Structure and function of visual displays produced by male Jacky Dragons, *Amphibolurus muricatus*, during social interactions. *Brain, Behaviour and Evolution* 61, 4: 172–183.
- Welling, A. 1999: A study of the ecology of the mountain dragon, *Tympanocryptis diemensis*. Unpublished Honours thesis, University of Tasmania.
- Witten, G.J. 1993: Chapter 29: Agamidae. In Glasby, C.J., Ross, G.J.B. & Beesley, P.L. (Eds) *Fauna of Australia Volume 2A Amphibia and Reptilia*, Australian Government Publishing Service, Canberra: 255–260.

(accepted 27 June 2005)