ECOLOGY AND SEXUAL SELECTION OF THE COMMON BARKING GECKO (*PTENOPUS GARRULUS*)

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A thesis submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirement for the degree of Doctor of Philosophy.

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This work is dedicated to my wife, Rachel Gallagher, who has endured many days alone in a foreign country while I was away doing field work, and also supported me tremendously financially and emotionally. I also dedicate this work to my parents, Terry and Diana Hibbitts, for nurturing my adventurous spirit and always encouraging my interest in biology.

ABSTRACT

I investigated three mechanisms (endurance rivalry, contest competition, and mate choice) of sexual selection and the influence of multiple signals on intrasexual and intersexual encounters in the common barking gecko (*Ptenopus garrulus*). Aspects of the ecology of barking geckos were also studied to facilitate the investigation of sexual selection. Barking geckos exhibited sexual size dimorphism in relation to head size, with males having wider heads. No differences in diet or size of prey ingested were observed between the sexes, indicating that niche divergence was not occurring. Therefore, the difference in head width was best explained by sexual selection (male contest competition). Barking gecko diet was dominated by termites by number and volume. The peak reproductive season was in October for both sexes.

I used activity patterns to determine if males emerged before females from winter dormancy, a key assumption of the protandry-based mating system model. Activity patterns were significantly different between males and females. Males were active in higher numbers early in the breeding season. Male and female activity patterns along with evidence that male territories were established before female emergence, testicular recrudescence likely coincides with male emergence, and larger males have larger territories and better reproductive success, suggest that barking geckos have a protandry-based polygynous mating system. I also tested for clustering of geckos on the landscape to determine if barking geckos lek. Clustering was found to occur in some instances, but barking geckos did not meet the criteria for a ‘classical’ lek species because males use calling sites containing resources (a burrow) that are also used by females.

Lizards frequently rely on chemical cues to detect the presence of a conspecific. Male lizards in particular, may chemically sample potential refuges to avoid rivals. Barking geckos were equally likely to use an artificial refuge scented by another male compared to a control, indicating that males do not use scent when selecting refuges.

I assessed the role of two signals, one acoustic (dominant call frequency) and one visual (yellow throat patch), in advertising residency and aggressive behavior in barking geckos. Larger males defended the largest home ranges and home ranges were maintained through calling, which is negatively correlated with body size. Body size also predicted some behavioural responses to field-playback trials. Small males retreated from the playback and large males were found to be aggressive towards the playback. Small relative throat patch size was also correlated with aggression and charging the playback. Finally, call frequency was correlated with the behaviour of charging the playback. I suggest that the frequencies of barking gecko calls constitute a long-range signal of body size, used by males for remote rival assessment and to advertise home range boundaries.

I also assessed the role of multiple signals (acoustic and visual) in reproductive success and I studied the effect of one mechanism of sexual selection, endurance rivalry, on reproductive success. Activity levels were similar for males which bred compared to those that did not breed, suggesting that endurance rivalry is not a significant mechanism of sexual selection in this population. Body size was the best predictor of reproductive success, suggesting that call frequency functions as a long range signal of body size used by females to assess potential mates.

PREFACE

This thesis has been written with each chapter as a stand-alone scientific manuscript, therefore there is some repetition of the materials and methods of some chapters and the description of the study system. Each chapter also contains an abstract, introduction and discussion.

Chapters that have been published are indicated at the beginning of each chapter. Chapter 2 and 4 are co-authoured with my PhD supervisor, Prof. Martin Whiting. Prof. Whiting gave advice on experimental design, analysis and writing.

Chapter 2 is also co-authoured with Prof. Eric Pianka and Prof. Raymond Huey. They contributed data on gut contents and gonadal measurements for 490 barking geckos and offered some writing advice.

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I thank the Northwest Parks Board for permission to conduct the research in their reserve and especially Steven Gore of Molopo Nature Reserve. Gerald and Ina Botha were also very supportive during my time at Molopo Nature Reserve.

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I thank the National Research Foundation for funding and the University of the Witwatersrand for a post-graduate merit award that provided financial support throughout my time as a student.

This work was cleared by the Animal Ethics Screening Committee of the University of the Witwatersrand (2003/29/2A).

DECLARATION

I declare that this thesis is my own, unaided work unless specifically acknowledged in the text. It has not been submitted before for any degree or examination at any other university, nor has it been prepared under the aegis or the assistance of any other body or organisation or person outside the University of the Witwatersrand, Johannesburg.

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16th day of May 2006

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CHAPTER ONE

INTRODUCTION

Signals are traits (behavioural or structural) which alter the behaviour of other animals (Maynard Smith and Harper, 2003). Most species use multiple signals in intraspecific communication, which may incorporate different sensory modalities. Multiple signals are either redundant, each conveying similar information (Møller and Pomiankowski, 1993; Johnstone, 1996); or may convey different information on individual quality (multiple messages hypothesis; Møller and Pomiankowski, 1993; Johnstone, 1996). Some sensory modalities may be better suited to different environmental conditions. For example, acoustic signals may be more likely to evolve in complex environments or in low light conditions, whereas visual signals may be more likely to evolve in open, simple environments, with more lighting. Signals are an integral part of sexual selection and are used to advertise traits such as body size, physiological state, foraging ability, fighting ability, and more.

In nature, species with sexual dimorphism are very common. Some of the most extreme examples are the common peafowl (*Pavo cristatus*), the golden toad (*Bufo periglenes*), the Augrabies flat lizard (*Platysaurus broadleyi*), and the white-tailed deer (*Odocoileus virginianus*). In each of these species males have extravagant characteristics that are not possessed by females. These traits could not be explained by natural selection, because if a trait benefited the survival of one sex it should also benefit the other sex (unless males and females inhabit different ecological niches). Therefore, Darwin (1871) proposed 'sexual selection' to explain extravagant traits in one sex. Darwin recognized two mechanisms of sexual selection: male contest competition and female choice. Since Darwin, three other mechanisms of sexual selection have been described (scrambles, endurance rivalry and sperm competition). For the purposes of this thesis, I will only discuss endurance rivalry, contest competition, and mate choice.

Endurance rivalry is a mechanism whereby males that spend the most time in breeding activity acquire the most mates. Endurance rivalry assumes that male breeding behaviour is energetically costly. Therefore, traits that increase a male's persistence of breeding behaviour will be favoured. Traits such as body condition and rate of body condition change have been found to be important in species that exhibit endurance rivalry (Judge and Brooks, 2001). Chorus tenure in several species of frogs has been shown to correlate with male reproductive success (Halliday and Tejedo, 1995). Also male persistence at breeding sites has been linked to reproductive success in insects (Banks and Thompson, 1985; Snedden, 1996), birds (Gibson and Bradbury, 1985; Höglund and Robertson, 1990), and mammals (Campagna and Le Boeuf, 1988; Apollonio et al., 1989). Systems in which males are involved in costly reproductive behaviours (such as calling) and have relatively long reproductive seasons (greater than one month) make good candidates for investigations into endurance rivalry.

Male contest competition (or intrasexual selection) occurs when males compete against each other for access to mates or territories. Secondary sexual characteristics associated with contest competition are generally referred to as 'armaments' (Berglund et al., 1986). Basically, armaments are any traits that will aid a male in a contest, for example, body size, head width, antlers, and horns. Males may also use signals in contest competition, to avoid the energetic and potential survival costs of a conflict (Rowher, 1982; Enquist and Leimar, 1983). Males may use different sensory modalities when signaling to other males: including auditory (Davies and Halliday, 1978), olfactory (Gosling and McKay, 1990; López and Martín, 2002), and visual signals (Rowher, 1982; Huhta and Alatalo, 1993; Whiting et al., 2003).

In most species, females are the choosy sex because females usually invest more in reproduction and the raising of offspring. In some species where males invest more in reproduction than females (e.g. pipefish), males are the choosy sex and females may be more ornamented (Berglund et al., 1986). By definition, mate choice is the process leading to the tendency of members of one sex to mate non-randomly with respect to one or more varying traits in members of the other sex (Heisler et al., 1987). Males also use different sensory modalities when attempting to attract mates (Breed et al., 1980; Ryan, 1985; Møller, 1988; Basolo, 1990; Jennions et al., 1995) and mates may be attracted to a male by his resources (Balmford et al., 1992; Hews, 1990; Backwell and Passmore, 1996). A female's mate choice response may be active or passive (Parker, 1983). Females may choose males emitting the greatest stimuli (passive) or they may reject males with the greatest stimuli in favour of another male (active).

I studied barking geckos because they potentially use auditory, olfactory, and visual signals when communicating with conspecific males and females. Geckos are one of the few lizard groups to vocalise and barking geckos are renowned for their vocal ability. Also it has been suggested that geckos are olfactory specialists (Schwenk, 1993). Vocalisations, vision, and olfaction in barking geckos provide an opportunity to explore how multiple signals function together in a single species and how signals using different sensory modalities are used in the environment.

In order to conduct in depth studies into topics such as sexual selection, knowledge of the basic natural history of the organism in question is imperative. Knowing reproductive season, diet, foraging behaviour, and other aspects of life history all facilitate successful studies of sexual selection. Ecological information is also important when determining the function of sexual size dimorphism (SSD), common to animals with male contest competition. For example, if there is no difference in the size of prey eaten by males and females then SSD in head size is not due to niche divergence and is more likely associated with sexual selection. Also, species with large geographic distributions may, for example, have populations that reproduce in different time periods at higher than at lower, latitudes. Therefore, basic natural history studies can greatly facilitate other studies, such as sexual selection.

Another important aspect of a species' ecology is its mating system. Mating system has a direct relationship to how individuals behave during intraspecific encounters. For example, in polygynous mating systems conflicts are expected to occur in male-male interactions causing the evolution of sexual selection for male armaments (Shuster and Wade, 2003). Four broad categories of mating systems have been identified: monogamy, polygyny, polyandry, and promiscuity (Krebs and Davies, 1993). However, all mating systems do not fit neatly into these categories and more discrete mating system categories have been proposed by Shuster and Wade (2003). Mating system categories, such as polygyny, can also be classified as resource based or non-resource based. In many circumstances resources are very important for acquiring a mate or mates. In birds, for example, males may return to breeding grounds earlier than females (protandry) to procure the best territory, and females choose a mate based on the quality of the territory (Searcy and Yasukawa, 1989). Protandry benefits males that arrive earlier than other males because they can occupy the best territories. Males that arrive earliest also have higher reproductive success (Olsson and Madsen, 1996, Olsson et al., 1999). However, early arriving males risk death because of adverse environmental conditions (Holzapfel and Bradshaw, 2002). Non-resource based mating systems such as dominance hierarchies and leks often develop through differences in population density (Davies 1991). When population densities are at high or low levels, energetic costs of territory defence should outweigh the advantages of territoriality (Emlen and Oring, 1977).

1.1 Study organism

I chose the common barking gecko (*Ptenopus garrulus garrulus*) for my studies of sexual selection and natural history. The barking gecko is a fossorial species found in southern Africa from the Namibia/Angola border south to the Northern Cape Province of South Africa and east to Limpopo Province of South Africa (Branch, 1998). In the eastern half of its range it is mainly associated with areas of Kalahari sand (Haacke, 1975). The barking gecko is a small species with adults reaching up to 60 mm SVL (Snout-vent length). The dorsal pattern has a background colour similar to that of the substrate from where it lives and small, scattered light coloured spots. The ventral surface is an immaculate white in females; however the males have a heart-shaped yellow throat patch (Branch, 1998).

The most interesting aspects of barking gecko natural history are its use of a burrow and its ability to vocalise. Barking geckos live in self constructed burrows. These burrows are dug into loose soils up to 38 cm in depth. Each burrow usually consists of an active tunnel that opens to the surface and one or more tunnels that end just below the surface that can be used as escape routes (Haacke, 1975). The entrance to the burrow is closed when the resident barking gecko is not active, presumably to maintain the burrow temperature and to avoid detection from predators. Barking gecko males also call from the entrance of their burrow. The call normally consists of five clicks which are emitted over about one second (Haacke, 1969). During peak calling (from sunset to an hour after sunset) barking geckos will call about every 30 seconds. Calling also occurs throughout the night when there is a bright moon and at dawn, but not with the same intensity as at sunset. Occasional barking gecko calls may also be heard on overcast days.

1.2 Objectives

My project had five major objectives. First, I described the ecology of the barking gecko in relation to sexual size dimorphism, diet, reproduction, and foraging mode. Second, I used activity and space-use patterns to test for protandry and lekking. Third, I used an experimental approach to test whether scent is important for barking gecko males when choosing refuges. Fourth, I determined male home range size and tested for correlations with male gecko traits. I then use playback trials to investigate the response of resident male barking geckos when presented with an intruder of known call frequency. I used logistic regression to determine which male traits predict behavioural responses and then used a multiple regression to determine which male traits best predict aggressiveness. I also analyzed male weight loss throughout the breeding season to determine cost of male vocalization. And lastly, I described the breeding behaviour and examined the traits of male barking geckos that were reproductively successful using a multiple regression analysis. Also I determined whether the reproductive success of males relates to endurance rivalry.

CHAPTER TWO

ECOLOGY OF THE COMMON BARKING GECKO (*PTENOPUS GARRULUS*) IN SOUTHERN AFRICA[1]

2.1 Abstract

I examined museum specimens of the Common Barking Gecko (*Ptenopus garrulus*) from the Kalahari and Namib Deserts to assess sexual size dimorphism, reproductive status, and diet. Males had significantly wider heads than females of the same body size; however, *P. garrulus* showed no sexual dimorphism in any other morphological character. The smallest mature male was 36 mm snout-vent length while the smallest female was 31 mm. Peak reproductive activity for both sexes was in September and October. Clutch size was fixed at one large egg (average size = 5.9 x 4.4 mm); all eggs were in the right ovary, but more than one clutch may be laid in a single breeding season. *Ptenopus garrulus*, when compared with other geckos, produces very large offspring and thereby invest heavily in a single offspring. I recorded 15 arthropod orders in the diet of *P. garrulus*. Termites dominated their diet both numerically and volumetrically. Males and females ate prey of similar taxa and sizes, suggesting that trophic partitioning is absent. Therefore, the evidence suggests that the evolution of head width differences is driven by male contest competition.

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[1] Published in the Journal of Herpetology: Hibbitts TJ, Pianka ER, Huey RB, and Whiting MJ. 2005. Ecology of the common barking gecko (*Ptenopus garrulus*) in southern Africa. J Herpetol 39:509-515.

2.2 Introduction

Basic natural history data are fundamental to understanding and developing life history theory. In this regard, squamate reptiles have been the focus of relatively intensive ecological study because unlike many other vertebrates, they are often easily sampled and identifiable prey items are readily recovered (e.g., Pianka, 1986; Huey et al., 2001; Vitt et al., 2003). Recently, Vitt et al. (2003) synthesized the global ecology of squamates to test the influence of phylogenetic history on current patterns of community assemblages. This analysis depended in part on life history data. Future analyses will benefit from more extensive data sets that include more taxa from geographically disparate areas and possibly, more detailed natural history data.

Morphology is tightly linked to an organisms' ecology (Miles, 1994). Sexual size dimorphism (SSD) is of special interest because the size difference between males and females potentially affects many aspects of their ecology (Andersson, 1994). The three most common explanations for SSD are: (1) intersexual resource partitioning (Schoener, 1967); (2) sexual selection (usually male contest competition—Trivers, 1976); and (3) fecundity selection (Hedrick and Temeles, 1989; Shine, 1989; Stamps, 1995). When SSD has an ecological basis, one sex usually has an alternative feeding strategy in which different sized prey are selected due to size-related functional constraints (Houston and Shine, 1993). This phenomenon may arise either due to competition for resources or as a by-product of sex-related selective pressures, such as sexual selection. Sexual selection is most commonly associated with situations where the male is larger than the female. Larger male size results from male-male interactions associated with competition for territories and/or access to mates (Vitt and Cooper, 1985; Olsson et al., 2002). Males may also be smaller than females in situations where the males have to search for widely scattered females and where a small-male advantage exists (e.g., horned lizards—Zamudio, 1998). Fecundity selection is the idea that larger females are capable of producing more (or larger) eggs or offspring (Fitch, 1981; Olsson et al., 2002). Basic ecological data such as diet and reproduction are necessary to explain the evolution of SSD.

I studied the ecology of the Common Barking Gecko, *P. garrulus*, a small sized (max 60 mm SVL) lizard of the Kalahari and Namib Deserts of southern Africa. This species constructs burrows that are up to 38 cm deep in loose soils and usually have several branches (Haacke, 1975). Males have yellow throats and emit calls from the entrance of their burrows at dusk and dawn (Haacke, 1969). Pianka and Huey (1978) studied aspects of the ecology of several species of geckos in the southern Kalahari. They reported that *P. garrulus* had an invariant clutch size of one and that termites dominated their diet by volume. My study had three main objectives: (1) to determine the extent of sexual size dimorphism; (2) to examine seasonal and sexual differences in diet; and (3) to examine the reproductive ecology of males and females and especially to examine offspring size relative to female size.

2.3 Materials and Methods

I examined 150 specimens (Transvaal Museum) that had been collected in the following regions of Southern Africa: Northern Namibia, Southern Namibia, Central Botswana, Namaqualand, Kgalagadi Transfrontier Park, and Limpopo Province of South Africa. I examined an additional 490 specimens of *P. garrulus* collected in 1969 and 1970 in the Kalahari region of Botswana, Namibia, and South Africa by ERP and RBH. Diet and reproductive status from all specimens were analyzed. Methods used for these specimens are discussed in Pianka and Pianka (1976) and Pianka and Huey (1978).

2.3.1 Sexual size dimorphism

I measured the SVL (snout-vent length), tail length, head width, head depth, head length, torso length (axilla to groin), arm length (head of humerus to the end of the claw on the longest finger), humerus length, leg length (head of femur to the end of the claw on the longest toe), femur length, pes length, and fourth toe length of 150 preserved specimens (Transvaal Museum). All measurements were made to the nearest 0.01 mm using digital callipers. Characters were chosen based on studies of sexual selection and sexual dimorphism (head characters and torso length) and observations of *P. garrulus* breeding behavior (arm and leg characters). Sex of juveniles was verified by dissection. Prior to testing for sexual dimorphism, I log transformed all variables and subjected each to an ANCOVA with log SVL as the covariate. A *t*-test for unequal variances was used on the raw SVL data. I used a reduced major axis (RMA) regression (Fairbairn, 1997) to investigate growth patterns of those characters, which were significantly different between the sexes.

2.3.2 Reproduction

Growth patterns of characters were determined via dissection. Females were determined to be sexually mature when they contained oviductal eggs or enlarged vitellogenic follicles. For gravid females, length and width of the egg was measured to the nearest 0.01 mm with digital callipers. Egg volume was estimated for each egg using the formula for a prolate spheroid (Vitt, 1991). Sexual maturity in males was determined by finding enlarged testes and convoluted epididymides. I measured the length and width of the left testis to the nearest 0.01 mm and estimated testes volume (formula for prolate spheroid). I used a Kruskal-Wallis test to determine differences in testes volume and egg length by month. Hatchlings were obtained during a field study of *P. garrulus* in 2003 and 2004 at Molopo Nature Reserve (25º50'S, 22º55'E) located in the eastern Kalahari, Northwest Province, South Africa, focusing on other aspects of their life history.

2.3.3 Diet

Stomach contents were identified to order. Number and types of prey items were recorded for each individual. Measurements of length and width were made for complete prey items (to nearest 0.01 mm) and used to estimate volume (formula for prolate spheroid). I conducted correlations of prey size to SVL and head width, and prey size to head width with the effects of SVL removed. I tested for differences in diet between the sexes using chi-square tests. I also tested for differences in prey size consumed between the sexes using ANCOVA with head width as a covariate and with a t-test assuming unequal variances. I use a chi-square test to examine variation in diet by month. Dietary niche breadth was determined using Simpson's (1949) diversity index.

2.3.4 Foraging mode

A population of *P. garrulus* at Molopo Nature Reserve was studied to determine foraging mode. The substrate was sand throughout, and the vegetation was dominated by *Acacia mellifera* and *A. erioloba*, with very little ground cover. All focal observations were made between 1900 and 2200 h in November 2004.

Foraging mode is often determined from measurements of movements per minute (MPM) and percent time spent moving (PTM). A criterion of PTM = 10 was used by Perry (1995) to distinguish between ambush and active foraging, with ambush foragers falling below 10. I quantified foraging mode using 10-minute focal observations of 11 individual adult *P. garrulus.* The observer sat about 4 m from the burrow using an artificial light source to view the activity. Geckos appeared to act normally under these conditions. All observations were carried out on individuals that were visible at the entrance to their burrows. Any movement and prey capture attempts were recorded. Adult *P. garrulus* are solitary inhabitants of a burrow. The individuals observed were of known size and sex from an ongoing population study at the same site.

2.4 Results

2.4.1 Sexual size dimorphism

Males (mean ± 1 SE: 44.9 ± 0.4) and females (mean ± 1 SE: 45.2 ± 0.4) did not differ significantly in SVL ($t_{628} = 0.519$, $P = 0.60$). However, males had significantly wider heads than females when controlling for SVL ($F_{133} = 8.5$, $P = 0.004$; Fig. 2.1). The sexes did not differ in any other morphological characters ($P > 0.05$). Head width of males grew isometrically with SVL ($r^2 = 0.89$, slope = 0.997, 95% CI = 0.807-1.071), whereas female head width grew less quickly than SVL ($r^2 = 0.87$, slope = 0.888, 95% CI = 0.807-0.970; Fig. 2.1).

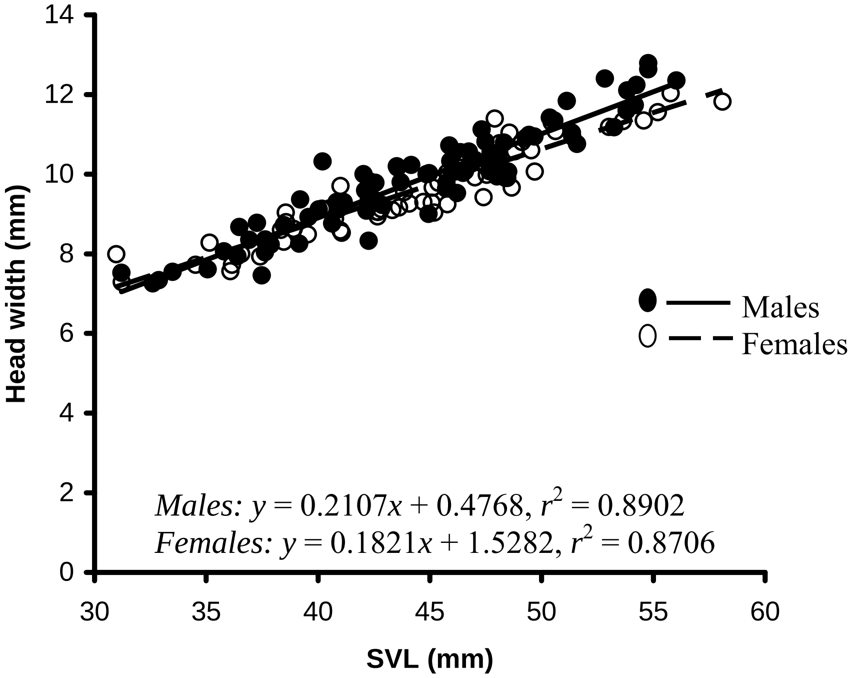

Figure 2.1. Relationship between head width and snout-vent length of male and of female *P. garrulus.*

2.4.2 Reproduction

Minimum size at sexual maturity for males was 36 mm SVL. Testicular volume peaked in September and October (Fig. 2.2) and these two months were significantly different than testicular volume in all other months ($H_{7,257} = 114.2$, $P < 0.001$). Minimum size at sexual maturity for females was 31 mm SVL. Egg volume was highest in September and October ($H_{7,56} = 17.6$, $P = 0.014$) and a similar statistical pattern to testicular volume existed, although not as strong. Eggs were present from August through April (Fig. 2.3). Clutch size was fixed at one; however, eight percent of all females ($N = 4$) had two eggs at different stages of development suggesting that they lay a second clutch. All eggs were in the right oviduct, even when a second egg was developing.

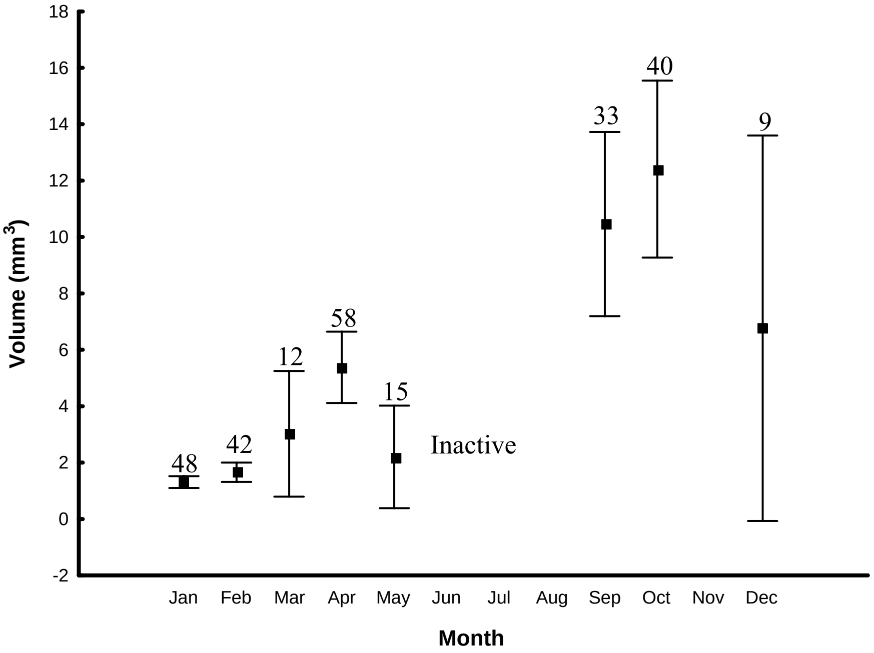

Figure 2.2. Estimated testis volume by month. Mean (± 1 SE) is displayed for each month. Sample size is listed above each error bar. Months with fewer than five males are excluded.

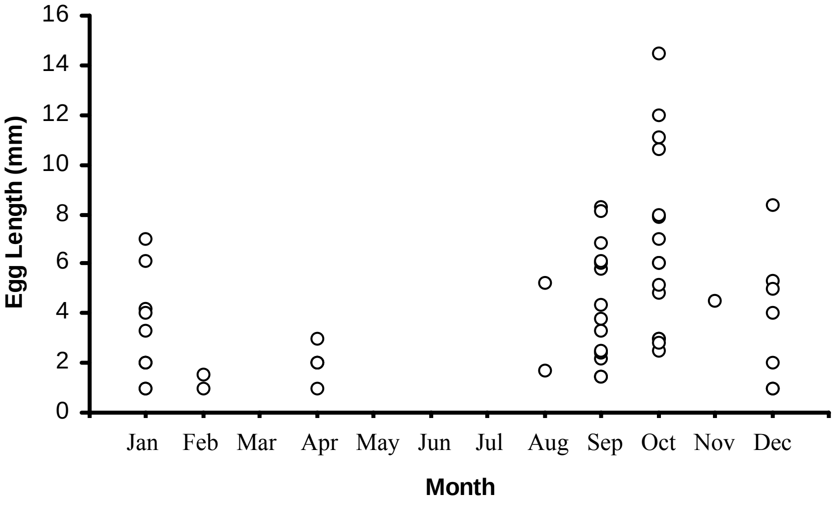

Figure 2.3. Length of individual eggs in relation to month.

Fifty-five *P. garrulus* less than 30 mm SVL were collected during field work, with the two smallest individuals measuring 22 mm SVL. This size is also smaller than that reported for hatchlings by Haacke (1975). Minimum hatchling size was large relative to size at sexual maturity. Hatchling *P. garrulus* were also large relative to adult female size when compared to hatchling/female size in other gekkonids (Fig. 2.4). The regression line explained most of the variation ($r^2 = 0.95$), and *P. garrulus* was the only outlier.

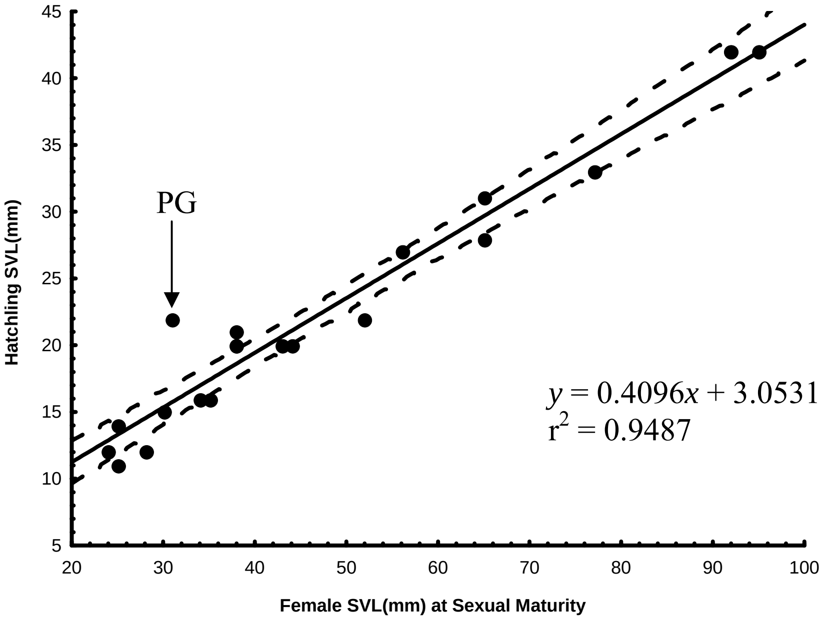

Figure 2.4. Comparison of minimum hatchling size to female SVL at sexual maturity in 19 gekkonid species (Inger and Greenburg, 1966, *Cyrtodactylus malayanus*; Vitt, 1986; and references therein, *Phyllopezus pollicaris, Hemidactylus mabouia, Lygodactylus klugei, Gymnodactylus geckoides, Pseudogonatodes guianensis, Lygodactylus somalicus, Lygodactylus picturatus, Gonatodes concinnatus, Lepidodactylus lugubris, Hemidactylus frenatus, Gehyra mutilata*; Marquet et al., 1990, *Garthia gaudichaudi*; Doughty and Shine, 1995, *Phyllurus platurus*; Vitt and Zani, 1997, *Thecadactylus rapicauda*; Okada et al., 2002, *Gekko hokouensis*; Colli et al., 2003, *Gymnodactylus amarali*). Arrow marks *P. garrulus*.

2.4.3 Diet

I identified 17 categories of prey (Table 2.1). Numerically, termites (51.1%) and ants (35.6%) dominated the diet. Volumetrically, termites were again the most important prey type (60%) followed by ants (8.9%) and beetles (8%). More gecko stomachs contained ants (46%) than any other food item, followed by termites (39%) and beetles (19%) (Table 2.1). Eighteen percent (*N* = 115 out of 640) of all stomachs were empty and 17 geckos had eaten sloughed skins. The four most common prey types comprised at least 90% of the diet in all months. Termites were most prevalent in December, comprising 70% of the diet by number. Ants were eaten more commonly than termites in March and September and were most prevalent in September, making up 47% of the diet (by number) in that month. During all other months, termites were the most commonly eaten prey (Fig. 2.5). However, there were no significant differences between months ($\chi^2_7 = 0.15$; $P < 0.9$). *Ptenopus garrulus* are inactive in the winter months of June and July.

Table 2.1. Summary of the diet of *Ptenopus garrulus*. Total number and percent number categories include 640 specimens. Volume and percent volume categories are from 150 specimens dissected by TJH. Volumetric data for the other 490 stomachs are presented in Pianka and Huey (1978). Volumes for the 490 specimens were not combined with the other 150 specimens because different methods of volume estimation were used. Frequency is the number of stomachs containing the particular food item.

Prey Type	N	N%	Freq.	V(mm^3)	V%
Myriopoda					
Centipedes	2	0.06	2	-	-
Arachnida					
Acarina	2	0.06	2	-	-
Aranea	67	2.2	54	82.6	0.8
Solpugidae	6	0.2	6	-	-
Pseudoscorpiones	2	0.06	2	4.7	<0.1
Hexapoda					
Blattoidea	7	0.2	5	421.1	4.3
Coleoptera	191	6.2	120	788.4	8.0
Diptera	10	0.3	9	10.3	0.1
Hemiptera	60	1.9	35	709.3	7.2
Hymenoptera					
Formicinae	1100	35.6	294	875.9	8.9
Other	14	0.5	12	346.4	3.5
Isoptera	1578	51.1	247	5883.3	60.0
Neuroptera	4	0.1	2	50	0.5
Lepidoptera	8	0.3	7	316.9	3.2
Orthoptera	16	0.6	16	303.2	3.1
Thysanoptera	7	0.2	6	13	0.1
Larvae	12	0.4	12	17	0.2
Total	3086	100.0		9822.1	100.0
Niche Breadth		2.5		2.6	

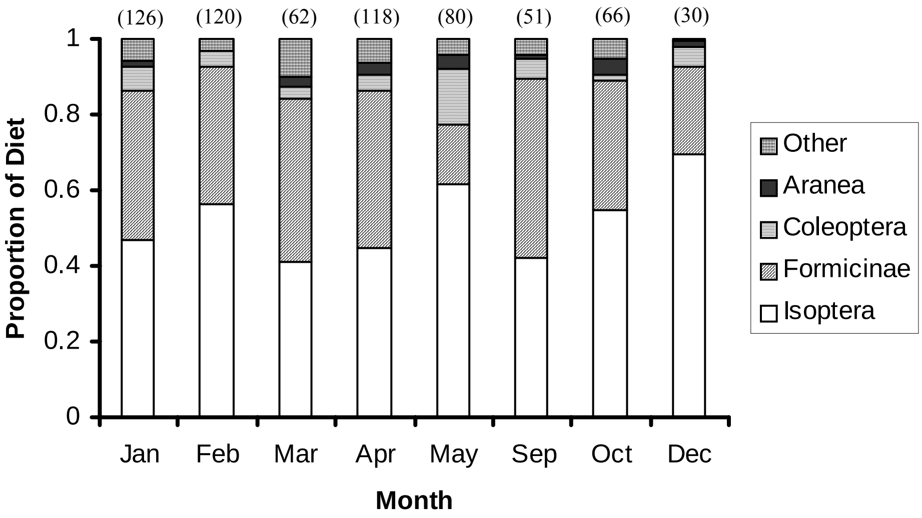

Figure 2.5. Seasonal representation of the four most abundant prey types by prey number found in gut contents of *P. garrulus*. Number of guts examined is listed in parentheses.

No differences existed between males and females in the numbers of the four most abundant prey groups and a group of all other prey items ($\chi^2_3 = 3.62$; $P < 0.5$). There is a significant correlation between prey size and SVL ($r = 0.39$, $P < 0.001$) and prey size and head width ($r = 0.4$, $P < 0.001$), but with the effects of SVL removed there is no difference between prey size and head width ($r = 0.099$, $P = 0.44$). No difference between the sexes in relation to size of prey eaten was found when accounting for head width ($F_{59} = 0.287$, $P = 0.59$) or when not accounting for head width ($t_{170} = 0.158$, $P = 0.87$).

2.4.4 Foraging mode

I determined MPM and PTM for six male and five female adult *P. garrulus*. All trials except one (8.6 min) were for the full 10 min. *P. garrulus* were classic ambush foragers. With the sexes pooled, adults moved infrequently (MPM = 0.4 ± 1.9, 0 - 2.1) and spent little time moving (PTM = 4.6 ± 1.9 s, 0 - 16.7).

2.5 Discussion

Males and females were sexually dimorphic only in relation to head width, with males having wider heads. Two major functions have been attributed to wider head width in one sex: ecological segregation in diet (Schoener, 1971; Camilleri and Shine, 1990; Shine, 1991) and sexual selection (male contest competition) (Vitt and Cooper, 1985; Saenz and Conner, 1996; Kratochivíl and Frynta, 2002; Reaney and Whiting, 2002). To determine if head shape dimorphism is related to sexual selection, experiments must be conducted that deal with either mate choice or male-male interactions (Tokarz, 1995). However, ecological segregation in diet can be addressed by analyzing the diet of each sex. Increased head width should increase gape size allowing the sex with the wider head to eat larger prey items (Schoener, 1971; Camilleri and Shine, 1990). I found no difference in the diet of males and females. Termites and ants were the dominant prey of both sexes and the size of prey items eaten by males and females did not differ significantly. Thus, the dimorphism in head size seems unrelated to food niche segregation. The other explanation for SSD in head size in *P. garrulus* is sexual selection. Males have two traits that are likely "ornaments" for sexual selection. They vocalize from the mouth of their burrow and will defend an area within a radius of one meter (pers. obs.); and males also have yellow throat patches, which are absent in females. I also observed frequent bite mark scars on males in the field (pers. obs.). Larger male head width is therefore best explained by male contest competition, though fights between males have not been witnessed.

Males attained sexual maturity at 36 mm and females at 31 mm. Normally in gekkonids, males attain sexual maturity at smaller or similar sizes to females (Inger and Greenburg, 1966; Vitt and Zani, 1997; Vitt et al., 1997; Okada et al., 2002). These sizes can be reached in less than a year. The greater size of maturity for male *Ptenopus* may be due to some form of reproductive suppression by rival males. Male *P. garrulus* have an advertisement call, and the pitch of that call is negatively correlated with body size (pers. obs.). If a small male calls too close to a larger resident male, the smaller male might be physically challenged by the larger male and could suffer an injury. Males observed in the field frequently bore bite mark scars (pers. obs.). Small males are unlikely to secure matings in this scenario, and sexual maturity may be delayed to reduce conflict with larger males. Alternatively, males may grow at a more rapid rate than females and mature at the same age or females may choose larger males for copulations causing the evolution of later maturation.

Breeding is restricted to early summer months with peak testicular volume and largest egg size in October. Rainfall in the Kalahari can be quite erratic but hatchlings of eggs laid in October will likely emerge after significant summer rains when insect prey is expected to peak (late December to early January).

Females have an invariant clutch size of one, but four individuals had a second egg at an earlier developmental stage. Not enough individuals with two eggs were found to search for a correlation between female size and number of clutches. All gekkonids have an invariant clutch size; however most produce two eggs with one egg produced in each ovary (Fitch, 1970). A growing number of species have been reported to have a clutch size of only one (see Werner, 1989, *Cyrtodactylus amictophilis*, *Tropiocolotes steudneri*, and *Gehyra variegata*; Marquet et al., 1990, *Garthia gaudichaudi*; Vitt and Zani, 1997, *Thecadactylus rapicauda*). Interestingly, all *P. garrulus* eggs (*N* = 56) were in the right ovary, suggesting that the left ovary may be non-functional. *Thecadactylus rapicauda* is a large gecko (up to 126 mm SVL) that also lays one egg, but produces eggs in both ovaries (Vitt and Zani, 1997). Most single-egg gekkonids are small (<35 mm SVL and weigh <1 g), which may explain why they have one egg clutches (Fitch, 1970). But adult *Ptenopus* can exceed 55 mm SVL and weigh more than 4 g, which is as large as many geckos that produce two-egg clutches. The reason for a single-egg clutch is unknown. A plausible adaptive explanation is that larger juveniles have a survival advantage; however, phylogenetic history may also be an explanation through similar juvenile size in close relatives. Hatchling *P. garrulus* are very large in relation to adult female size, and this ratio is much larger than for any other gecko reported (Fig. 2.4). One factor limiting egg size is the size of the pelvic aperture (Vitt, 1986; Sinervo and Licht, 1991). The hard-shelled eggs producing relatively large juveniles in *P. garrulus* suggest that an adaptation in the size of the pelvic aperture may have occurred, permitting a larger than expected egg to be laid.

Ptenopus garrulus diet consisted mainly of termites, both numerically and volumetrically. However, these lizards should not be considered termite specialists. In arid areas of southern Africa, termites are patchily distributed both spatially and temporally (Lepage and Darlington, 2000; Traniello and Leuthold, 2000). Some of the sampled geckos had eaten more than 30 *Hodotermes* termites, indicating that the resource is patchy.

Ptenopus are normally sit-and-wait foragers, waiting at the mouth of their burrow to ambush prey; confirmed by the observed low values for MPM and PTM. When termites swarm, however, *P. garrulus* come out of their burrows – even during the day – and become transient wide foragers (Huey and Pianka, 1981) and at these times they are often killed by shrikes (Huey and Pianka, 1981). *Ptenopus garrulus* may gain significant amounts of their nourishment while actively foraging during termite swarms and or termite foraging aggregations.

A broad survey of diets of many ($N \approx 200$) lizard species revealed differences among three major clades (Pianka and Vitt, 2003; Vitt et al., 2003). Iguanians tend to consume more ants than gekkotans or autarchoglossans. *Ptenopus garrulus* is unusual among gekkotans in consuming ants. Among the diets of desert geckos listed by Pianka (1986), only the diurnal Kalahari gecko *Lygodactylus capensis* consumes more ants than does *P. garrulus*.

In conclusion, I found that males become sexually mature at a larger size than females. *Ptenopus garrulus* have single egg clutches that are always produced in the right ovary. And, in relation to size, they have larger offspring than other geckos. Finally, *P. garrulus* are among a relatively small number of geckos to consume ants. These findings along with their use of a self-constructed burrow and calling behaviour make the ecology of *P. garrulus* unique among other known gekkonids.

CHAPTER THREE

PROTANDRY, BUT NOT LEKKING, IN THE COMMON BARKING GECKO (*PTENOPUS GARRULUS GARRULUS*)

3.1 Abstract

I studied clustering and activity patterns in the common barking gecko (*P. g. garrulus*) with two aims: to test whether they conform to a protandrous model (male first emergence) of mating system and to test whether they are a classic lek species. Several key hypotheses of the protandry model were supported: more males than females were active early in the breeding season, male territories were established before female emergence, testicular recrudescence likely coincides with male emergence, and larger males have larger territories and better reproductive success. Because barking geckos have been known to aggregate (based on burrow spatial distribution) and defend territories from which they advertise vocally, I also tested whether they form a classic lek. I found no evidence for barking geckos forming classic leks. Previous work has shown that females remain in the burrows of males following copulation, that males defend territories, and that both males and females may mate multiply. Therefore, male barking geckos conform to a mating system that is a protandrous, resource-defense polygyny, but which does not meet the criteria of a classical lek system.

3.2 Introduction

Mating systems fall into two broad categories: resource based and non-resource based. Resource based mating systems are often forms of polygyny in which a subset of individuals controlling resources tend to obtain the majority of matings. Resource defense polygyny is typically associated with species in which males actively defend territories with high-quality resources such as food or refuges (Hews, 1990; Hasselquist, 1998; Kwiatkowski and Sullivan, 2002). In polygynous systems individuals may become spatially clumped, especially when resources are patchily distributed. For example, in *Uta palmeri* lizard densities were greater in areas with higher densities of bird nests (Hews, 1990). Bird nesting sites had higher densities of arthropods, which are a major food source for *U. palmeri*. Also, tree lizards (*Urosaurus ornatus*) are in much higher densities along washes with large mesquite trees than in flatlands (Vitt et al., 1981, M'Closkey et al., 1990).

In some cases, it is advantageous for males to establish their territories before females are active in the area (protandry; Wirklund and Fagerström, 1977), with the earliest active males acquiring the best territories. Females then arrive and choose a mate based on his traits or on resources within his territory. Fitness benefits to protandry for females are that most breeding males are present and females have the opportunity of evaluating several males simultaneously (Crews, 1975). Males benefit by increasing their fitness when they emerge earlier (selection for early males; Olsson and Madsen, 1996, Olsson et al., 1999; Jenssen et al., 2001). Conversely, females that delay emergence may have a better choice among high quality males that have already established territories (selection for delayed females; Jenssen et al., 2001). Within each sex there is still likely to be variation in spring (breeding season) emergence time. Jennsen et al. (2001) list five key hypotheses and a series of assumptions (not listed here) that need to be met in order to satisfy protandry: (1) male first arrival to breeding area; (2) males establish territories before the arrival of females; (3) testicular recrudescence before female arrival; (4) testosterone increases as males first arrive and again as breeding begins; and (5) larger males develop protandry-based benefits before smaller males.

In some instances males may appear to be active earlier due to reasons other than protandry. Males may be clustered on the landscape and sampling in areas with clusters could falsely indicate activity by males before females, as is the case with breeding aggregations of frogs. Males form choruses under certain conditions and sampling in frog choruses will be biased towards males. However, females may be active in other habitats, in similar numbers as males. Therefore, accounting for potential spatial disparity in the sexes is key to determining their mating system.

Male breeding aggregations in which territories are clustered and which lack any form of resource, are referred to as leks (Emlen and Oring, 1977; Höglund and Alatalo, 1995). "Classical" leks meet four criteria: (1) the male provides no parental care; (2) mating occurs on an arena which females visit and on which males aggregate for the sole purpose of reproduction; (3) male display sites contain no significant resources required by females; (4) mates are selected at the arena through female choice (Bradbury, 1981). Lekking can be dynamic, depending on population density, such that lek formation is favoured under relatively high population density (Langbein and Thirgood, 1989; Clutton-Brock et al., 1993). Accordingly, as male density increases, territory size will decrease to a critical point where the costs of territory defense outweigh the benefits of controlling resources for female use (Emlen and Oring, 1977)

Barking geckos (*Ptenopus g. garrulus*) are small lizards (maximum snout-vent-length = 60 mm) found in the Namib and Kalahari deserts of southern Africa. Barking geckos live individually in burrows (Haacke, 1975), which are opened when active and remain closed when inactive. Also, individual geckos will use the same burrow from a week to several months (pers. obs.), facilitating individual identification. These features also allow both the measurement of daily activity of individual geckos and their spatial organization in the landscape.

There are three lines of evidence suggesting that the mating system of barking geckos is a polygyny. First, barking geckos are sexually dimorphic. Males have larger heads than females and this is unrelated to diet (Hibbitts et al., 2005); they vocalise (Haacke, 1969) and they have yellow throat patches. Second, males live in largely exclusive home ranges and defend their territory when under a perceived threat from a rival male (Chapter 5). Third, males may copulate with multiple females and vice versa, in the same breeding season (pers. obs.). Because females remain in the burrow of the male following copulation, it is likely that the mating system is a resource defense polygyny.

The breeding behaviour of barking geckos (described in Chapter 6) may also contribute to any observed clustering. Females approach calling males and breed with a male in his burrow. Afterwards the female remains in the male burrow and the male constructs a new burrow nearby. This behaviour would cause a clustering of females around successful males.

The closely related Koch's barking gecko (*Ptenopus kochi)* occurs in the Namib Desert and like *P. g. garrulus,* also lives in burrows and vocalizes (Haacke, 1975). A previous study of its social behaviour proposed that males vocally advertise to females from leks (Polakow, 1997). Based on this hypothesis, I tested whether *P. g. garrulus* aggregate to form leks. I also quantified activity patterns and used previously collected data to test whether barking geckos conform to a protandy-based model of mating system.

3.3 Methods

3.3.1 Study System

Barking geckos are crepuscular and construct burrows in loose soils that are up to 38 cm deep with at least one escape tunnel ending just below the surface (Haacke, 1975). Burrows are occupied by only one barking gecko. Males have wider heads than females of the same body size (Hibbitts et al., 2005) and unlike females, they have a yellow throat patch and they emit calls from the mouth of their burrow at dusk and dawn on warm nights between September and April

(Haacke, 1969). This vocalization consists of a loud clicking call (average five clicks) that signals body size and advertises territory ownership (Chapter 5). Larger males with lower frequency calls have higher reproductive success (Chapter 6).

3.3.2 Study Area

I studied barking geckos (*P. g. garrulus*) at the Molopo Nature Reserve (25º50'S, 22º55'E) in the Kalahari Desert, Northwest Province, South Africa. My main study area was a 1.11 ha plot. The vegetation of the plot was dominated by *Acacia mellifera* with *A. erioloba* and *Boscia albitrunca* interspersed. There was very little ground cover, which facilitated location of gecko burrows and making behavioural observations. The site was divided into 10 m^2 sections. I recorded the latitude and longitude of the corners of the site and every 10 m along each side using a Garmin GPS 76. Latitude and longitude points were entered into ArcMap 8.0 for visual representation of the plot.

3.3.3 Spatial patterns

In addition to my main study area (1.11 ha), I chose four plots to test for spatial aggregation in the landscape, a prerequisite for lekking. The plots were chosen mainly for accessibility; however, the sites were more than 1 km from each other. At each site I used a 60 m tape measure and compass to make a 50 m^2 plot which was divided into twenty-five, 10 m^2 sections. I searched for and flagged, gecko burrows, at each plot during the hour before sunset for three days. I used Sadieshell version 1.22 to determine the distance to regularity (*D*) for each plot

(Perry, 1995). *D* is the cumulative distance that burrows would have to be moved to make a regular (uniform) distribution of burrows on the landscape. *D* observed is then compared with corresponding values from random permutations (*D* random) of the counts amongst the sample units. A formal randomization test is performed by calculating what proportion of the random permutations are larger or as large as *D* observed to determine a *p*-value.

3.3.4 Temporal patterns

I monitored adult male spatial patterns on the main study plot at four different times (September 30, N = 44; October 10, N = 40; October 25, N = 42; November 10, N = 32; of 2004) to analyse clustering and if clustering changed through time. I only considered adult male barking geckos that were 36 mm snout-vent length or greater (Hibbitts et al., 2005). I used data from gecko activity monitoring (see “activity” below) to tease out male spatial patterns at each of the dates listed above. I used Sadieshell version 1.22 to determine if there was significant clustering on the different dates (see above).

3.3.5 Resources

I characterised vegetation by estimating ground cover and foliage projection cover (amount of the section with cover directly overhead) to the nearest 5% for each section on the main plot. I used the vegetation estimates to determine the extent to which barking geckos used 10 m quadrats that had a high percentage of ground cover or foliage projection cover. Regression analysis established the relationship between the number of burrows in a quadrat and the percentage of ground cover or foliage projection cover.

I also used a paired design to determine if barking geckos constructed burrows at sites with non-random vegetation characteristics. First, I chose a burrow and measured the distances to grass and woody vegetation as well as ground cover and foliage projection cover within a 1 m^2 quadrat centered on the burrow. Next, I walked 10 m in a random direction from the burrow location and measured the same vegetation characteristics (non-site 'burrow'). I then compared the burrow and random location using a paired *t*-test (two-tailed). I arc-sine transformed all percentage data.

I recorded temperature data at 30 systematically selected sites on the main study plot. Temperature was recorded every 30 mins, 10 cm below the surface, using DS1921 Thermochron iButtons (Dallas Semiconductor) from 16 October to 9 November 2004. A mean temperature from each site was used to test for a correlation with gecko abundance. I also placed 30 sticky traps at the same locations on three different nights 10 days apart during the field season, to quantify food availability. Prey abundance was calculated by simply summing all captured prey that geckos could eat from the three nights at each sampling location. I used regression analysis to compare temperature and prey abundance to gecko abundance in a 20 square m area centred on each iButton and sticky trap location respectively.

3.3.6 Activity

The main study plot was monitored daily from 9 September to 18 November 2004 to measure both male (N = 83) and female (N = 75) gecko activity during the breeding season. I marked each burrow with a labelled 30 cm dowel stick. Geckos closed their burrows during the day and opened them about one hour before sunset if they were active. The activity at each burrow was monitored every night. I specifically avoided finding geckos by their call to avoid biasing my data towards males. Geckos were caught while surface active near their burrow or by luring them out with small insects. Each gecko was toe-clipped for permanent identification and a number was drawn on the head for easy visual identification. The sex and age class (juvenile/adult) was determined for each gecko based on minimum size at sexual maturity (Hibbitts et al., 2005). Geckos were released the following day in the burrows from which they were captured. I used a two-factor ANOVA with sex and reproductive period (early, middle, late breeding season) as the factors testing for differences in activity between sex and period.

3.4 Results

3.4.1 Do barking geckos lek?

I observed clustering at only one of the four 50 m^2 plots (Table 3.1). Number of burrows compared to percent ground cover poorly explained the observed variation in the number of gecko burrows per 10 m^2 quadrat ($r^2 = 0.01$).

Similarly, percent foliage projection cover did not explain a large portion of the observed variation in the number of gecko burrows per 10 m^2 quadrat ($r^2 < 0.001$).

Clustering was observed at the main study plot on all four dates analyzed (Table 3.2); however, the locations of the male clusters did not change over time (Fig 3.1). I observed a maximum of three male barking geckos within a 10 m^2 quadrat. A similar number of male barking geckos were observed on September 30, October 10, and October 25 (0.40, 0.36, 0.38 per quadrat); however, fewer males were active on November 10 (0.23 per quadrat). In November many males simply became inactive,

remaining in their burrows with their entrances closed. I did not observe any adult males dispersing to new locations on the surface or at another burrow location within my study plot.

Table 3.1. Clustering statistic for four 50 m^2 sampling plots. Distance to regularity (*D* is the required distance to evenly distribute the observed number of burrows) observed for the four plots. *D* random is the average of all random permutations of the observed number of burrows. Significant clustering is in bold.

Plot number	*N* (geckos)	*D*	*D* random	*p*
1	34	18.6	22.35	0.95
2	39	19.12	21.57	0.78
3	31	31.51	18.84	**0.01**
4	62	25.9	26.9	0.51

Table 3.2. Clustering statistics for four days (September 30, October 10, October 25, and November 10, 2004) on the main study plot. Distance to regularity (*D* is the required distance to evenly distribute the observed number of burrows) observed on the four days. *D* random is the average of all random permutations of the observed number of burrows. All values were significant.

Date	*N* (geckos)	*D*	*D* random	*p*
September 30	44	114.35	55.94	0.013
October 10	40	88.69	50.46	0.013
October 25	42	109.89	54.73	0.013
November 10	32	81.50	51.04	0.013

Burrows were located significantly closer to grasses ($t_{49} = -2.74$, $p = 0.009$) and woody vegetation ($t_{49} = -3.66$, $p < 0.001$) than expected by chance; however, burrows were not located in areas that had higher percent ground cover ($t_{49} = 0.88$, $p = 0.38$) or foliage projection cover ($t_{49} = 1.77$, $p = 0.08$) than expected by chance. Barking geckos did not choose burrow locations based on temperature ($r^2 = 0.03$, $F_{29} = 0.78$, $P = 0.38$) or prey abundance ($r^2 = 0.009$ $F_{29} = 0.24$, $P = 0.63$).

(a)

						1.54			**1.72**	**2.29**	**2.46**	
			-1.89			**2.27**	**3.89**	**2.66**		**4.17**		
		-1.99	-1.55	**1.66**		-1.86	**3.18**		**3.14**	**1.55**		
-1.78	-1.80				-2.73	-1.61	-2.37	**4.31**	**3.29**			-1.87
-1.84			-2.73		-2.59	-2.90	**3.88**	**4.25**	**2.73**			-2.08
		-3.44		-2.35	-3.58	-1.97	-1.56					
		-2.69	-3.44	-3.20	-3.08	-2.10						
		-5.44	-4.02	-2.20								
	-2.65	-5.40	-4.11	-2.75								
	-6.74	-4.71	-4.25	-2.74								
-2.24	-6.94	-5.98	-5.26	-3.45								

(b)

			-1.99									
		-1.73			**1.77**	**2.08**		**1.66**	**3.55**	**2.07**		
-2.92	-3.70	-2.56		**1.75**	**2.29**		**2.83**		**2.33**	**3.33**		
-2.69	-2.61			-2.48	**2.00**	-1.78	-1.63		**3.69**			-1.71
		-2.31	-1.69	-1.93	-2.58	1.77	-1.74	**2.36**	**2.83**			
		-2.19	-3.56			-2.15						
		-3.82			-2.77	-2.02	-2.36					
				-3.54								
			-5.05	-2.96								
		-2.09	-4.11	-3.93								
	-2.49	-5.85	-5.18	-3.04								

(c)

					1.74	**1.93**					**1.76**	
		-1.59			**2.92**	**1.72**	**2.15**	**2.85**			**1.55**	
-1.85	-1.51	-2.68	-2.48				**1.86**		**2.28**	**3.17**		
-2.52	-3.44	-2.20	**1.95**		-1.59			**2.69**	**4.53**			-1.94
-3.85	-1.83	-2.83	-2.37		-2.31	-1.79	**2.02**	**3.03**			-1.75	-2.41
-2.31	-4.53	-3.42		-2.47	-1.88							-2.73
		-2.24	-3.37	-2.74	-3.46		-2.04					
		-4.86		-3.68								
			-5.67	-2.65								
	-2.58	-5.09	-3.40	-3.22								
-1.56	-7.69	-5.33	-4.94	-3.96								

(d)

						1.50						
		-2.00	-1.63			**1.83**				**1.74**		
		-2.32		**1.72**								
-3.33	-2.00		**1.57**		**2.14**		-1.50		**3.67**	**1.63**		
-2.25		-1.51	-2.19		-2.03	-1.73		**1.89**	**1.69**			
-1.79	-3.43	-3.14	-2.71		-1.52							
		-2.90	-1.76	-1.53								
		-2.38		-3.01								
	-3.08		-3.66	-3.21								
	-3.49	-3.95	-3.96	-3.35								
-1.83	-2.10	-4.72	-4.04	-3.20								

Figure 3.1. Representation of clustering at the main 1.11 ha study plot on four dates using 10 m grid squares. a) September 30, 2004, b) October 10, 2004, c) October 25, 2004, d) November 10, 2004

Numbers in the square represent *v* (deviation from the average number of burrows per grid square combined with the distance a burrow ‘moves’ to create evenness). Hypothetically, if two grid squares have two burrows each and one is surrounded by squares also with burrows, while the other is not, the first grid square will have a higher *v* because the ‘movement’ of its burrows to create the same number of burrows per grid square is greater. Only values of *v* greater than the absolute value of 1.5 are shown. Those grid squares with *v* values in bold are contributing burrows and areas with several bold numbers are clusters. Those areas with unbolded numbers are receiving burrows and clusters of unbolded numbers are gaps. Notice that the clusters of male gecko burrows are in similar locations throughout the breeding season.

3.4.2 Activity

Peak activity for 235 individual barking geckos was late October. The interaction between sex and 20-day period significantly affected activity patterns (Table 3.3, Fig. 3.2). Males were more active in the first two periods and male and female activity was similar in the last period (Table 3.4, Fig. 3.2). Higher male activity could occur if males become active and remain active for longer than females. In this scenario, by simply examining daily gecko activity more males may appear to be active earlier when as many females were active, but for shorter periods of time (making less females active on the same day). Therefore, I plotted accumulation curves of male and female captures to show that more individual males were active early in the breeding season than females (Fig. 3.3). The first seven days, which coincide with the steep part of the male accumulation curve, were excluded because I was adding significant numbers of active individuals to my sample (Fig. 3.3).

Table 3.3. A two-factor ANOVA of differences in male and female activity patterns between periods for barking geckos. Period one is from September 15 to October 6, period two from October 7 to October 26, and period three from October 27 to November 16.

Effect	SS	df	F	p
Intercept	185437.5	1	2889.1	< 0.0001
Sex	632.9	1	9.86	0.002
Period	2195.6	2	17.104	< 0.0001
Sex*Period	977.5	2	7.615	0.0008

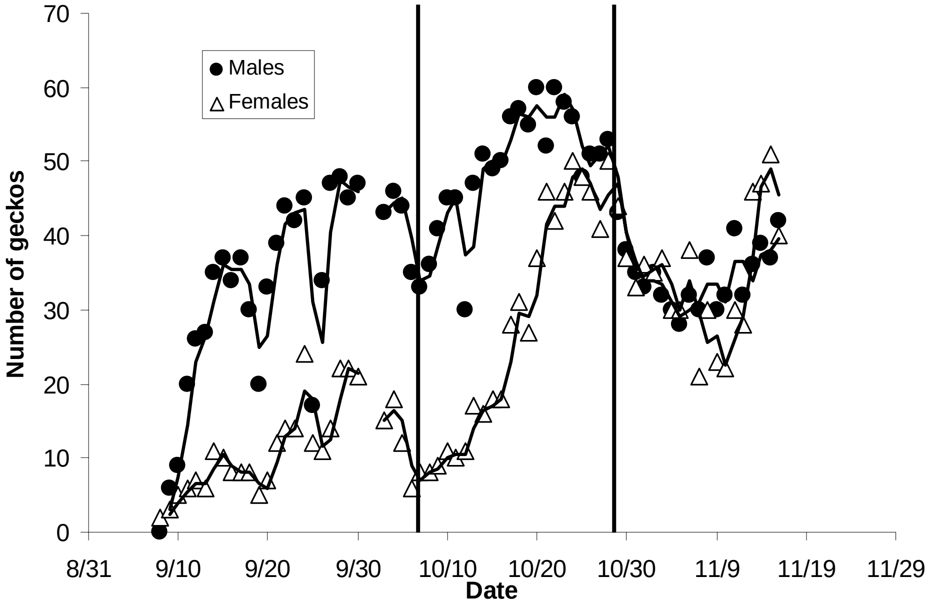

Figure 3.2. Number of male and female barking geckos active per day during the breeding season (2004). Vertical lines divide periods.

Table 3.4. Tukey's HSD post hoc test showing significant differences between periods and sexes. Average number of geckos active per sex/period in parenthesis. Significantly different relationships are in bold.

	Female 1 (30.1)	Female 2 (40.2)	Female 3 (39.9)	Male 1 (38.4)	Male 2 (49.0)	Male 3 (36.5)
F 1		**0.002**	**0.002**	**0.018**	**0.0001**	0.119
F 2	**0.002**		0.999	0.978	**0.009**	0.673
F 3	**0.002**	0.999		0.991	**0.005**	0.746
M 1	**0.018**	0.978	0.991		**0.0008**	0.975
M 2	**0.0001**	**0.009**	**0.005**	**0.0008**		**0.0001**
M 3	0.119	0.673	0.746	0.975	**0.0001**	

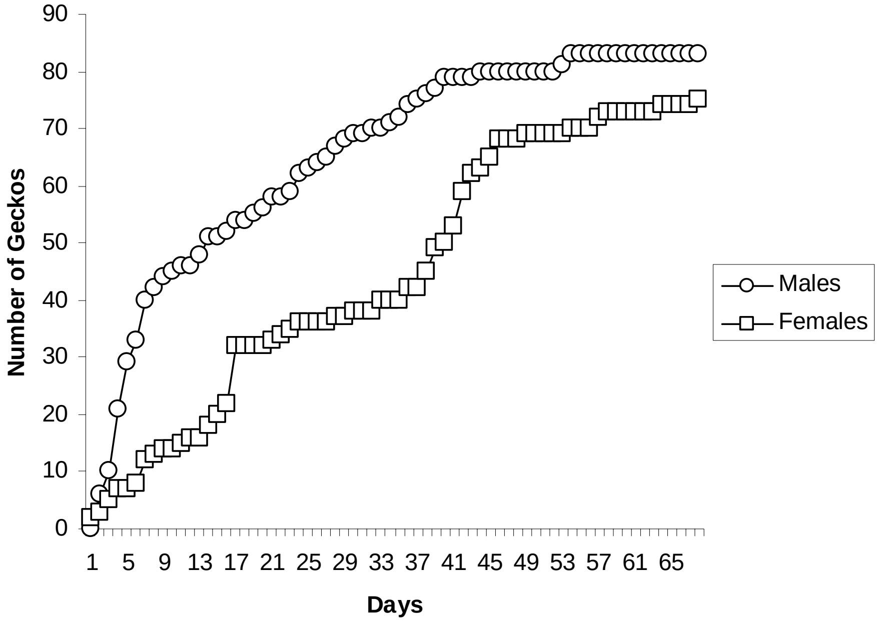

Figure 3.3. Accumulation of new male and female barking gecko captures in the study population. This shows that more males were captured than females earlier in the breeding season confirming greater male activity.

3.5 Discussion

Barking geckos met some, but not all, of the criteria of a classic lek species. First, males do not exhibit parental care, however, this criterion is not meaningful with respect to reptiles because there is little or no parental care in reptiles. Second, males that form leks typically cluster in a display arena that is not an area normally used for feeding or refuge. On the main plot male barking geckos remained in the same area throughout the study, whether or not they were calling (a male remained underground when not calling and was observed in the same burrow as last seen when activity resumed), and in some cases were captured in the same area on consecutive years (pers. obs.). This indicates that males reside in long-term home ranges and likely only move when forced out by other males. While males do not move to arenas, clustering was found in one of the four plots and at the main study site, suggesting that clustering may be density dependent; however, the only 50 m^2 plot showing clustering had the fewest individuals. Third, male display sites contain no significant resources required by females. I assume that barking geckos did not choose burrow locations based on temperature or prey availability because I could not detect any significant variation in these variables on my main study site. Barking geckos chose burrow locations that were closer to both grasses and woody vegetation than expected. This may afford the burrow some protection from disturbance, particularly in areas where ungulates are active. The Kalahari typically supports a variety of ungulates, all of which could inflict damage on gecko burrows through trampling. Burrows in the open may also be more susceptible to disturbance from strong winds. Also, males leave their burrows, which are a structural resource, to the female after copulation

(Chapter 6). It is unknown whether the burrow is constructed specifically for the female but the female in many cases uses the burrow for oviposition and refuge until she is sexually receptive again. Lastly, in classical leks mates are selected at the arena through female choice. The call of barking geckos is used as a signal of body size and is possibly used by females to choose mates and large males have greater reproductive success than small males (Chapter 6). Therefore, barking geckos only meet the first and possibly last criteria of a 'classical' lek. I propose that barking geckos do not form leks and that any clustering on the landscape is related to other factors such as vegetation or chance.

Although the criteria for a classical lek were not met, some clustering in barking geckos may still be explained by breeding behaviour. As in most things in ecology, the degree of lekking forms a continuum from classical lekking species such as a sage grouse (*Centrocercus urophasianus*—Wiley, 1973) to species that meet only one or a few criteria of lekking. Barking geckos fall somewhere on this continuum. When they do aggregate, females have the opportunity to choose from multiple males. But unlike lekking birds that display elaborate plumage in concert with courtship dances and vocalization, geckos remain largely hidden, but call from the mouth of their burrow. This 'chorus' may act as a stimulus, priming the female. Furthermore, clustering may increase the opportunity for reproduction for some individuals. Small barking gecko males are more reproductively successful when their territories are located near large males (unpubl. data). This suggests that smaller males may be acting as 'satellites' establishing territories near large males to intercept females moving towards the large male. This is different, however, than the typical satellite male scenario seen in marine iguanas (*Amblyrhynchus cristatus*), in which small males mimic female coloration and patrol the edges of large male territories trying to sneak copulations (Wikelski et al. 1996). Small male barking geckos do not attempt to sneak or force copulations with females, instead they rely on calling to attract mates.

Barking geckos show characteristics consistent with a protandry-based mating system (Crews, 1975; Wirklund and Fagerström, 1977; Jensson et al., 2001). The key feature of protandry is male first emergence. Males were more active than females in the early and middle of the breeding season, with most males active before most females. Another key assumption of protandry is that males should establish territories before female emergence. I found most males were calling from their burrows (which serve as the core of their territory) when the females emerged from winter dormancy. Under protandry, testicular recrudescence is expected to be complete before female emergence. Male peak testicular size is in September and October (Hibbitts et al., 2005) and likely coincides with male emergence from winter dormancy. Therefore, males are likely primed and ready to breed when females emerge. Finally, larger males develop protandry-based benefits before smaller males (sensu Jenssen et al., 2001). Large male barking geckos have higher fitness than small males and also have larger home ranges (Chapter 5). This suggests that large males have established better territories due to early emergence, large males out-compete smaller males, or females prefer to breed with large males (or some combination of the three).

Males of other lizard species typically defend females (Cooper and Vitt, 1993; Censky, 1995; Salvador and Veiga, 2001) or defend territories with resources for female use (Hews, 1990; Olsson and Shine, 2000) to increase reproductive success. Barking geckos are unique in that they establish territories before female emergence and attract females with their call (Chapter 6) relying on their traits for mate attraction. Additional studies of lizards and other taxa with features similar to barking geckos are needed to establish how widespread protandry is and under what evolutionary scenario protandry is likely to evolve.

CHAPTER FOUR

DO MALE BARKING GECKOS (*PTENOPUS GARRULUS GARRULUS*) AVOID REFUGES SCENTED BY OTHER MALES?[2]

4.1 Abstract

Lizards frequently rely on chemical cues to detect the presence of a conspecific or a predator, or to sample and detect potential prey. Male lizards in particular, may chemically sample potential refuges to avoid rivals. I tested whether male common barking geckos (*Ptenopus g. garrulus*) that normally refuge in burrows, avoid refuges scented with a rival male. Geckos were equally likely to use an artificial refuge scented by another male compared to a control. I conclude that scent is an unimportant cue for rival male recognition in *P. g. garrulus* based on 1) the result of this experiment; 2) during 510 man hours of field work I did not observe a single gecko tongue-flick; and 3) males respond aggressively to recordings of rival males and this appears to be the primary mechanism maintaining male spatial patterns.

4.2 Introduction

Lizards commonly use chemical cues in a variety of contexts. Lizards are known to detect the scent of prey (Cooper, 1995a), predators (Dial et al., 1989; Cooper, 1990; Downes and Shine, 1998; Downes, 2002), and conspecifics (Cooper and

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[2] Published in African Journal of Herpetology. Hibbitts TJ and Whiting MJ. 2005. Do male barking geckos (*Ptenopus g. garrulus*) avoid refuges scented by other males? Afr J Herpetol 54:191-194.

Vitt, 1984a, b; Alberts and Werner, 1993; Regalado, 2003). The evolution of chemosensory specialisation is likely under a scenario where vision is limited by darkness (but see Roth and Kelber, 2004), and most gecko species are nocturnal (Pianka and Vitt, 2003). It has also been argued that geckos are olfactory specialists (Mason, 1992; Schwenk, 1993). Geckos have been split into two major families: the Eublepharidae and the Gekkonidae (Pianka and Vitt, 2003), the latter includes the barking gecko, *P. g. garrulus*. Several studies have demonstrated the role of olfaction in the behaviour of eublepharid geckos. These include conspecific, predator, and prey recognition in *Coleonyx variegatus* (Greenburg, 1943; Dial et al., 1989; Cooper, 1998), predator recognition in *C. brevis* (Dial and Schwenk, 1996), and conspecific and prey recognition in *Eublepharis macularius* (Mason, 1992; Cooper, 1995b). In the Gekkonidae, chemical cues are used for sex recognition in *Hemidactylus flaviviridus* (Mahendra, 1953) and *H. mabouia* (Regalado, 2003), and predator recognition in *Oedura lesueurii* (Downes and Shine, 1998). Furthermore, male *H. mabouia* showed aggressive behaviour in the presence of male rival chemical cues in an experimental laboratory setup and make use of visual, chemical and vocal signals to communicate with conspecifics (Regalado, 2003).

In male lizards where contest competition occurs, territories may be maintained using visual signals (Whiting, 1999), chemical cues (Lopéz and Martín, 2002) and/or vocalisation (Chapter 5). In addition, the costs of fighting (injury, energetic expenditure, and increased risk of predation) are ameliorated through the use of status signals and rival recognition whereby individual recognition allows knowledge of a rival’s fighting ability (reviewed in Whiting et al., 2003). Such rival recognition may be of a chemical (Lopéz and Martín, 2002) or visual (Whiting, 1999) nature.

I tested whether male *Ptenopus g. garrulus* are capable of detecting a male rival’s scent using refuge selection trials. *Ptenopus g. garrulus* is a small sized (max 60 mm SVL) gecko of the Kalahari and Namib Deserts of southern Africa. They construct burrows up to 380 mm deep with one active entrance and one or more tunnels ending just below the surface (Haacke, 1975). Each gecko is usually the sole inhabitant of its burrow, although a burrow may be shared with a juvenile for short periods of time (pers. obs.). The burrow entrance is used as a sit-and-wait foraging lookout from which prey (mainly termites and ants) are ambushed (Hibbitts et al., 2005). Males also call from the entrance of their burrow, which signals territory occupancy (Chapter 5) and may also act as a signal to females. Apart from foraging, males rarely leave their burrows. However, males will leave and enter or construct a new burrow under two scenarios: (1) when males become mature they may disperse to another area (especially when they are within the home range of a larger male); and (2) after breeding, the female remains in the male’s burrow and the male moves to a new location nearby (pers. obs.). The ability to detect chemical signals could aid in selection of a new burrow or burrow location and avoid a costly conflict with a resident male. My objective was to determine if male *P. g. garrulus* avoided a refuge that had been scented by other males.

4.3 Methods

My study took place at the Molopo Nature Reserve research station, Northwest Province, South Africa (25º 50’ S, 22º 55’ E). I collected 32 adult male *P. g. garrulus*; 12 were used as scent donors and 20 were tested for chemical recognition of rival males. All geckos were housed individually in 340 × 220 ×135 mm plastic tubs. The bottom of each tub was covered with sand and each tub had a 95 × 95 mm ceramic tile as a refuge. The geckos were fed termites weekly and the sand was misted with water every second week. For each experiment two male geckos were used to create a composite scent on a single 95 × 95 mm tile. The scent of the two geckos was extracted by wiping each down with a hexane soaked paper towel. The cloacal region is a source of glandular and faecal material that has been shown to be important chemical cues in some species of lizard (Cooper and Vitt, 1984a; b). As a result, I obtained scent from both the cloacal and body regions of geckos. The soaked paper towel was wiped onto a clean tile and the hexane was allowed to evaporate, leaving the composite scent of the two geckos (Shine et al., 2003). Donor geckos were given at least five days to recover their scent before being used again.

The experiment took place in a 340 × 220 × 135 mm plastic tub. The bottom of the tub was covered with sand and the scented tile was placed at one end of the tub. A clean tile (control; wiped with water) was placed at the opposite end of the tub. A male gecko was then placed into the centre of the tub and left alone for 24 h. Trials were conducted only when ambient temperature was sufficiently warm to allow gecko activity (night temperature > 15 ºC). The experiment was ended during daylight after at least 24 h, ensuring that the gecko would be under a refuge. The location of the gecko was recorded and the gecko was released after only being used once. I examined the sand substrate for any disturbance, to determine if the gecko had been under the other refuge during the trial. Although the geckos did not leave detectable tracks, they would dig out a depression under the tile.

4.4 Results

In all experiments ($N = 20$) the gecko used only one of the refuges and was under the refuge at the termination of the experiment. An equal number of geckos selected the control ($N = 10$) and male-scented ($N = 10$) refuges.

4.5 Discussion

Male *P. g. garrulus* showed no evidence of discriminating refuges based on scent, suggesting that scent is unlikely to be important for male rival recognition in this gecko species. An alternative explanation is that geckos simply ran for the first refuge and did not leave because of the stress and perceived predation risk associated with the experimental setup. This scenario could over-ride any normal behaviour associated with recognition of a rival male's scent. However, the close proximity (about 150 mm) of the two refuges suggests that if male chemical cues act as signals of status, then the gecko should move to the neighbouring (control) refuge sometime during the duration of the experiment (24 h). I also made sure that at the beginning of the experiment that the gecko did not seem to be stressed. The gecko was not running around the plastic tub, but was positioned in the centre of the tub and not moving when the lid was set in place. I found no evidence to suggest that any male abandoned a male-scented refuge.

A final line of evidence further supports my result that *P. g. garrulus* do not use chemical cues to signal male presence: during approximately 510 man hours of field work I never observed *P. g. garrulus* tongue-flick in any context (including courtship, pers. obs.). Tongue-flicking (via vomerolfaction) is the primary means that most lizards use to detect chemical cues (Cooper, 1995a; Schwenk, 1995). Tongue-flicking has been observed in two species of *Hemidactlyus* geckos during courtship (Mahendra, 1953; Regalado, 2003) and is frequently used by eublipharid geckos such as *Coleonyx variegatus* (Cooper, 1998).

Ptenopus g. garrulus are unusual among lizards in that they use vocal signals and given that males have a yellow throat, they likely also use visual signals. Males emit calls from the mouth of their burrows (Haacke, 1969) and these calls can be heard from well over 200 m by the human ear. One possible function of the call is to signal body size of the territory holder in lieu of the potentially risky activity of patrolling the territory. Other male geckos will avoid areas already occupied by a calling male to avoid a costly conflict. Furthermore, during playback experiments resident males will rapidly approach a speaker broadcasting the call of a rival male (Chapter 5). Therefore, the long-range signal of the call may preclude the need for a short-range chemical cue. Another plausible explanation for the lack of scent discrimination in *P. g. garrulus* is the environment in which they live. The loose sandy soils on the surface are blown by frequent winds, presumably removing any scent left around the mouth of another male's burrow. When investigating a new burrow an intruder would have to enter the burrow to detect the scent of a resident, which would increase the chance of a conflict. Therefore, it may be that in this system, prevailing environmental conditions preclude the effective use of scent as a social cue.

I therefore conclude that *P. g. garrulus* likely do not use chemical cues to select refuges. My refuge selection results, observations of calling behaviour, environmental conditions that make chemical communication difficult, and the absence of tongue-flicking behaviour all suggest that male *P. g. garrulus* do not use scent discrimination to detect rivals.

CHAPTER FIVE

SETTLING CONFLICT IN BARKING GECKOS: A ROLE FOR VOCAL ADVERTISING

5.1 Abstract

Multiple signals that exploit different sensory modalities (e.g. acoustic, olfactory and visual signals) are often used in intraspecific communication, although their relative roles in male-male interactions are still poorly understood for most taxa. I assessed the role of two signals, one acoustic (dominant call frequency) and one visual (yellow throat patch), in advertising residency and aggressive behavior in the common barking gecko (*Ptenopus garrulus garrulus*). I show that male barking geckos maintain largely exclusive home ranges, with larger males maintaining larger home ranges. Larger males also have a lower dominant calling frequency. Field play-back experiments showed that when presented with a call of average frequency, resident males with low frequency calls were more likely to respond aggressively and charge the speaker compared to males with high frequency calls. However, body size and small relative throat patch size, rather than call frequency, were the best predictors of overall aggressiveness. I suggest that the frequencies of barking gecko calls constitute a long-range signal of body size, used by males for remote rival assessment and to advertise home range boundaries.

5.2 Introduction

Many species communicate with conspecifics using multiple signals, which may incorporate different sensory modalities (e.g. acoustic, olfactory and visual signals). Each type of signal may encode different information on individual quality (multiple messages hypothesis; Møller and Pomiankowski, 1993; Johnstone, 1996). Alternatively, some signals may be redundant, each signal conveying similar information with some error (Møller and Pomiankowski, 1993; Johnstone, 1996). This is particularly true of signals that incorporate different modalities as each signal may be suited to different environmental conditions. For example, in complex environments, acoustic signals may be more effective over long ranges whereas at short distances, visual and/or olfactory cues may be more important. While multiple signals have received recent attention in studies of sexual selection, few studies have examined the relative role of signals that exploit different sensory modalities, especially in the context of male-male competition.

Signals used in male contest competition commonly convey information on body size because size is often a reliable indicator of fighting ability or resource holding potential (RHP; Parker, 1974). Such signals facilitate accurate opponent assessment, potentially allowing contests to be settled more quickly through conventional displays rather than through more costly physical combat (Maynard Smith and Parker, 1976; Huntingford et al., 2000). Signals of body size include lateral displays in lizards (Olsson and Shine, 2000; Ord et al., 2001; Husak, 2004) and call frequency in anurans (Davies and Halliday, 1978; Arak, 1983; Ramer et al., 1983; Robertson, 1986; Bee and Perrill, 1996). Some signals may be honest indicators of size or RHP because there is a direct physical relationship between the signal and the quality being signalled (Maynard Smith and Harper, 1995; Taylor et al., 2000). Such signals, termed indices (Maynard Smith and Harper, 1995; Taylor et al., 2000), include fundamental frequency of some acoustic signals, which honestly signal body size because only large males can produce deep calls or roars (Arak, 1983; Wiley, 1983; Krebs and Dawkins, 1984). Signals may also be honest because of associated costs, such as increased predation risk (Ryan et al., 1981), reduced foraging opportunities (Woolbright and Stewart, 1987), and energetic costs of repeated signalling (Prestwich et al., 1989). For instance, fatigue in side-blotched lizards decreases the rate of their ritualised push-up display (Brandt and Allen, 2004). Calling is one of the most energetically costly activities for anurans (Pough et al., 1992). Therefore, there is likely an energetic cost to calling throughout the breeding season if males call regularly over a substantial period of time (Chappel et al., 1995).

In addition to functioning directly in male-male contests, signals may advertise home range or territorial boundaries to rivals. The space that individuals use during daily activity is their home range (Rose, 1982), while the area individuals defend is their territory (Stamps and Krishnan, 1998). Both home range and territory size may be linked to mating success or at least access to mates (Stamps, 1983; Hews, 1993; Smith, 1995). In complex environments or in environments with low-light conditions, rather than visual signals, long-range signals such as acoustic signals may be more likely to evolve to effectively signal residency (Ord et al., 2002). Such long-range signals prevent costly contests with predictable outcomes, where there is an obvious asymmetry in fighting ability.

Here, I assess the role of two potential signals, one acoustic and one visual, in male defence of space, and aggressive behavior, in the common barking gecko (*Ptenopus garrulus garrulus*). Barking geckos are small sized (max 60 mm snout-vent length; SVL) lizards of the Kalahari and Namib Deserts of southern Africa. Male barking geckos potentially have both an acoustic (loud clicking call) and a visual (yellow throat patch) signal, but the function of these traits is not known. Only males have yellow throats and vocalize; furthermore, males have wider heads, but are similar to females in body length (Hibbitts et al., 2005). Barking geckos construct burrows that are up to 38 cm deep in loose soils and these usually have several branches (Haacke, 1975). Males call from the entrance of their burrows at dusk and dawn (Haacke, 1969). Sexual dimorphism and their calling behavior have traditionally been used as evidence of their territoriality. However, territorial behavior of males has never been quantified. I quantified male spatial patterns and examined the relationships between male home range size, body size and two sexually dimorphic traits that exploit different sensory modalities: call frequency and throat patch area. I then used playback trials to test whether recorded vocalizations influence male aggressive behaviour. Finally, I examined male weight loss over the peak breeding period to determine whether regular calling activity is energetically costly.

5.3 Methods

5.3.1 Study Area

I studied barking geckos at the Molopo Nature Reserve (25º50'S, 22º55'E) in the Kalahari Desert, Northwest Province, South Africa. My study area was a 1.11 ha plot. The vegetation of the plot was dominated by *Acacia mellifera* with a few *A. erioloba* and *Boscia albitrunca* present. There was very little ground cover, which facilitated location of gecko burrows and making behavioral observations. The site was divided into 10 m square sections. I recorded the latitude and longitude of the corners of the site and every 10 m along each side using a Garmin GPS 76. Latitude and longitude points were entered into ArcMap 8.0 for visual representation of the plot.

5.3.2 Gecko morphology and male spacing patterns

The study area was monitored daily from 9 September to 18 November 2004 with the help of three field assistants. I marked each burrow with a labelled 30 cm dowel stick. Geckos closed their burrows during the day and opened them about one hour before sunset if they were active. The activity at each burrow was monitored every night. Geckos were caught while surface active near their burrows or by luring them out with small insects. Each gecko was toe clipped for permanent identification and a number was drawn on the head with an ultra fine point Sharpie® permanent marker for easy temporary identification. The following data were recorded for each gecko: snout-vent length (SVL), mass, throat patch size (if male), and burrow number. I measured SVL (hereafter referred to as body size) to the nearest mm using a plastic ruler and mass to the nearest 0.01 g with a digital balance. I used the software Simple PCI® to calculate throat patch size and total throat area from a scanned image of the venter of male geckos (Fig 5.1). Scans were obtained using a Canon canoscan N1220U flat bed scanner. From this I determined the proportion of the entire throat that each patch assumed. Proportions were arc-sine transformed in all analyses.

Geckos were released the following day in the burrow from which they were captured. I also recaptured male geckos during the last two weeks of the field season in order to reweigh them. The new mass measurement of each male was compared to its original mass to determine an average daily weight change. I compared the average daily weight change between groups of geckos that had high and low calling endurance. Geckos with high calling endurance were heard calling on at least 80% of the days between their initial and final capture. I noticed a discontinuity in calling between the groups with many individuals in the high endurance group calling on all days between captures and most individuals in the low endurance group calling on about 50% of the days between captures. These data were used to determine if there was an energetic cost to calling in barking geckos.

Figure 5.1. Example of scanned image of male throat patch

I determined burrow location by estimating the distance from the nearest corner stake in the 10 m square. The estimated burrow locations were entered onto the site base map in ArcMap 8.0. I printed the study area map and estimated home range size manually on graph paper, using the minimum convex polygon method (Rose, 1982). I modified this method to account for a one-meter radius around each burrow location, which is the approximate size of the territory that barking geckos will actively defend around their burrows (Polakow, 1997; pers. obs.). A one-meter radius circle was drawn around each burrow occupied and a tangential line was drawn connecting the circles into a polygon with rounded vertices. Barking geckos may use the same burrow for over a year or for shorter than one week (pers. obs.). Burrows are also used as a sit-and-wait foraging lookout (Hibbitts et al., 2005); therefore home range estimations are not based on sightings, but on burrow locations occupied. I only included males observed on at least 10 days. I tested whether body size, call frequency, and/or throat patch size are associated with home range size using Pearson correlations. I also calculated the number of other male home ranges overlapped by each male and percent overlap of each male's home range by other male home ranges (Abell, 1998).

5.3.3 Recordings of calling behavior and playback experiment

I recorded 74 calling male barking geckos using a Nagra IV-s analogue tape recorder and a Nakamichi CP-4 super directional shotgun microphone. The microphone was mounted on a tripod and directed at the gecko at a distance of one meter. Six calls (avg. 5 clicks per call; Fig 5.2) were recorded for each gecko. The recordings were digitized at a sampling rate of 48 kHz (16 bits) and analysed using Cool Edit Pro version 1.2a (Syntrillium Software Corporation, Phoenix, Arizona). An average dominant call frequency was determined for each gecko, for the six calls, and these were related to male traits including body size and relative throat patch area. I recorded 20 geckos prior to the study to obtain an average call for playback experiments. The call used for all playback experiments was 4366 Hz.

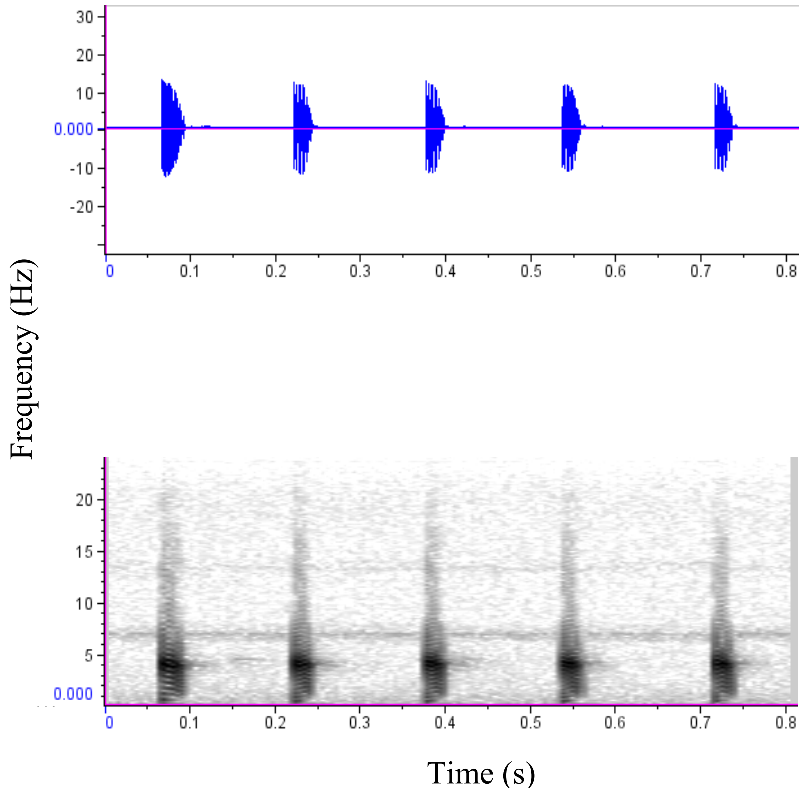

Figure 5.2 Oscillogram (top) and sonogram (bottom) displaying a typical 5-click call of a barking gecko (darker shading in the sonogram corresponds to the dominant frequency of each click)

For each actively calling barking gecko located, I recorded their call and conducted a playback experiment to test for an aggressive response. Playback experiments (*n* =

58) were conducted on the same or following day I located them, between 30 and 90 min after sunset. I played recordings on a Diamond DX121 CD player with the display lights covered. The CD player was positioned one meter from the gecko burrow and set to continuously play the playback call at 70 decibels at the burrow (Polakow, 1997). The trial was recorded from a distance of about 2.5 m with a Sony DCR TRV27E digital video camera with the super nightshot function. Trials were terminated when the gecko approached the speaker to within 10 cm, or after 10 minutes. I then captured the gecko either by hand or by digging it out of

its burrow, and took the same measurements listed above. None of the geckos dug out of their burrows were from the main study plot. The geckos were released the following evening at the point of capture.

The videos were viewed and the following behaviors were recorded for each gecko: orientation to playback call, call back, charge CD player, tail wag, and retreat into burrow. I tested for a relationship between the three most commonly observed behavioral responses (retreat, call back, charge) and body size, dominant call frequency, and relative throat patch size, using a multiple logistic regression. I also ranked aggressiveness of different behavioral responses on a scale of 0 to 5 (Table 5.1). I viewed “charge” as the most aggressive behavior, as an immediate charge without associated calling or tail wagging indicated no attempt to avoid physical combat with the intruder through signalling. Tail wagging was movement of the tail from side to side at a slow rate. Geckos would tail wag after a partial charge therefore I ranked charge and tail wag at a lower rank than charge. I used a multiple regression with stepwise model selection to examine what variables best explained aggressiveness. The criterion for retaining a variable in the model was $P<0.1$. Aggressiveness rank was treated as a continuous dependent variable and body size, body condition, dominant call frequency and relative throat patch size as independent variables. All means are reported ±1SE.

Table 5.1 Aggressiveness ranks of male geckos in relation to their response to a playback call.

Aggressiveness rank	Response criteria
0	retreat into burrow or no response
1	orient to playback call
2	call back to playback call
3	call back then charge CD player
4	tail wag then charge CD player
5	charge CD player

5.4 Results

5.4.1 Male traits and home range

Mean male home range size of 51 individuals sighted on at least 10 days was 10.4 ± 1.5 m^2 (range = 3.1 – 53.0). Home range size was significantly positively associated

with body size ($r = 0.31$, $P = 0.02$, $n = 51$), but was not associated with relative throat patch area ($r = 0.15$, $P = 0.32$, $n = 49$) or dominant call frequency ($r = -0.24$, $P = 0.20$, $n = 31$). Males rarely overlapped spatially with other males (mean number overlapped = 0.12 ± 0.04, $n = 51$) and this overlap constituted a small total area per individual (mean percent overlap = 3.8 ± 1.7, $n = 51$).

5.4.2 Male body size and signal characteristics

Call frequency for 74 different males ranged between 3708 and 5207 Hz (mean = 4284 ± 31.8 Hz; Fig 5.3). Body size was negatively correlated with dominant call

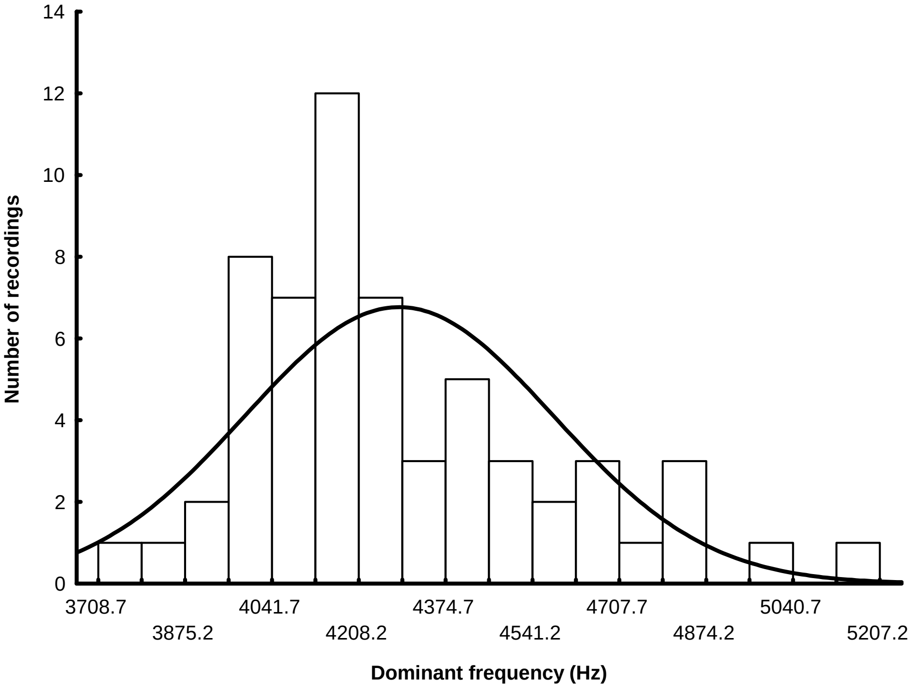

Figure 5.3 Distribution of dominant frequencies of 74 barking gecko calls

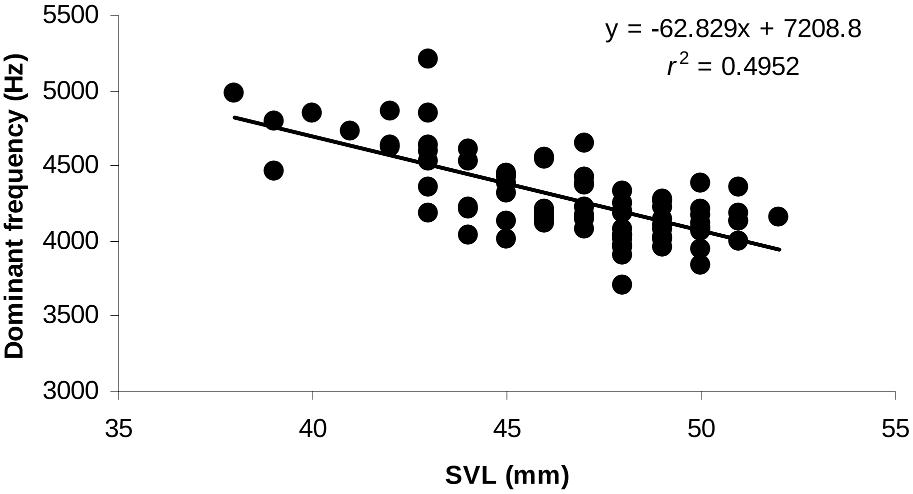

Figure 5.4 Significant relationship between body size (SVL) and dominant call frequency in barking geckos

frequency and explained a significant amount of variation in dominant call frequency ($r^2 = 0.50$, $F_{1,72} = 69.8$, $P < 0.001$; Fig 5.4). Body size and relative throat patch size were positively correlated, but body size explained very little of the variation in relative throat patch size ($r^2 = 0.06$, $F_{1,120} = 7.13$, $P < 0.009$).

5.4.3 Playback experiments

Geckos which retreated into their burrows were smaller than those which did not retreat (Table 5.2). No traits related to calling back were significant; however, males in poorer body condition tended to call back more than males in good body condition (Table 5.2). Finally, geckos which charged the speaker (playback) had significantly lower dominant call frequencies and smaller relative throat patches than those that did not charge (Table 5.2). Overall aggressiveness rank was positively associated with body size and negatively associated with relative throat patch area, suggesting that more aggressive geckos are larger with relatively smaller yellow throat patches (Table 5.3).

5.4.4 Cost of calling

Males that called more frequently were significantly larger than males in the group of less frequent callers ($t_{2,27} = 2.05$, $P = 0.007$) and lost more weight/day than males that did not call regularly (mean: 0.008 ± 0.001 g vs. 0.003 ± 0.001 g). However, daily change in weight was not significantly different between the groups after accounting for size ($t_{2,27} = 0.386$, $P = 0.35$). Only five of 31 recaptured adult male barking geckos gained weight between September and November of 2004. The six males recaptured after more than 50 days averaged weight loss of 16% (range 9 – 24%) of their body weight.

Table 5.2 Multiple logistic regressions comparing the three most frequently observed behavioral responses to play back calls (retreat, call back, charge) with male traits: body size (SVL), body condition, call frequency and relative throat patch size (TPS). Only factors retained in the final model (P<0.1) are shown.

Trait	Coefficient	SE	Wald	*P*
Retreat				
SVL	-0.2831	0.126	5.094	0.024
Call back				
Body condition	-3.0744	1.613	3.633	0.057
Charge				
Call frequency	-0.0115	0.004	7.688	0.006
TPS	-0.4602	0.197	5.442	0.020

Table 5.3 Multiple regression model in which aggressiveness rank, measured in response to playback calls, was explained by variance in body size (SVL), body condition, call frequency and relative throat patch size (TPS). Only factors retained in the final model (P<0.1) are shown. The R^2 of this model is 0.43.

	Coefficient	SE	F	*P*
Call frequency	-0.00147	0.00087	2.86	0.098
SVL	0.20211	0.07852	6.63	0.014
TPS	-0.10682	0.05032	4.51	0.040

5.5 Discussion

Male barking geckos are territorial. The almost complete lack of overlap in space among males strongly supports this. The call of male barking geckos influences male aggressive behaviours. Given that males are nocturnal and live in an open environment, vocal signals are likely to be particularly effective at a distance. Dominant call frequency was negatively correlated with body size. Larger males had calls of lower dominant frequency and larger home ranges, strongly suggesting that the vocalisation is an honest signal whose production is constrained by size. Variation in relative throat patch size was not well explained by body size although the most aggressive males that rushed the speaker during playback trials had smaller relative throat patch size. Dominant call frequency and relative throat patch size were therefore both indicators of gecko aggressiveness.

Barking geckos make decisions on whether to challenge an intruder based on the frequency of his call. Resident males that retreated into their burrows when presented with a recording of a calling intruder were significantly smaller than the expected size of the 'playback' male. Body size was also the most important indicator of overall aggressiveness. Larger geckos with small relative throat patches displayed more aggressive behaviors when presented with a calling intruder. Together, these results suggest that in barking geckos, call frequency signals body size, which is an important indicator of fighting ability in many lizard species (Trivers, 1976; Stamps, 1977; Tokarz, 1985; Vitt and Cooper, 1985; Olsson, 1992).

If relative throat patch size is important in male-male interactions, I would predict that males that are more aggressive would also have relatively larger throat patches (Olsson, 1994; Whiting et al., 2003). Assuming that the throat patch does act as a visual signal then either the relationship I found is an artefact of only eliciting aggressive responses through playback trials, or males perceive the throat patch in a different way. For example, either the efficacy or information content of the throat signal could be a function of the amount of yellow relative to white, rather than simply the amount of yellow. That is, yellow patches surrounded by a wider white margin may be more conspicuous or signal greater aggressiveness than patches surrounded by a thin white margin. Alternatively, relative throat patch area could be correlated with other signal properties such as the spectral qualities of the yellow patch. Also, properties of the throat patch may be indicators of factors such as testosterone, which is documented to increase aggression in male lizards (Civantos, 2002). A final possibility is that throat patch size is not used in male-male interactions and may instead be used in female choice. As males generally sit at the entrance to their burrows with only their head visible, the throat patch may facilitate assessment of male quality by females. In this scenario the throat patch could act as a visual signal at close proximity while the vocalisation could have the dual role of warning potential rivals and advertising to females.

My results provide confirmation that barking geckos are territorial because males generally occupied exclusive home ranges and reacted aggressively to the call of a rival during playback experiments. In the three instances of male spatial overlap a male shifted its area of activity in response to the presence of a new rival male. As male barking geckos spend the majority of their time within their burrows, which are used for both shelter and foraging activity (Haacke, 1975; Hibbitts et al., 2005), calling likely functions as a mechanism for maintaining exclusive space without the predation risk associated with territorial patrolling or flashing of conspicuous visual signals (Candolin and Voigt, 2001; Díaz-Uriarte, 2001).

The mechanism explaining how large individuals produce lower frequency calls in barking geckos is unknown. In most amphibians, the body and vocal sac act as a resonating chamber. Therefore, larger individuals produce lower frequency calls (Gehardt and Huber, 2002). If the vocal apparatus grows allometrically in barking geckos, the same principle is likely to apply. Protracted calling over the breeding season is energetically demanding in other acoustically signalling species (Pough et al., 1992; McCauley et al., 2000; Gehardt and Huber, 2002). In barking geckos, males that called regularly were larger and lost more weight, but the difference was not significant after accounting for body size. That most males lost weight over the peak breeding period suggests that there are energetic demands of reproduction, which may include calling. Larger males may have more energy reserves, allowing an increase in calling endurance.

Overall, my results suggest that barking geckos use calls as a long range signal of body size and aggressiveness in an environment in which visibility is reduced due to poor light conditions. Gecko calls were audible to the human ear at distances greater than 200 m whereas the throat patch is likely to only be visible to geckos over very short distances and only under certain light conditions (but see Roth and Kelber, 2004). To my knowledge, there have been no published reports of a lizard using an auditory cue to advertise territory ownership and aggressiveness. Many other gecko species produce calls (e.g. Marcellini, 1974, 1978; Werner et al., 1978; Frankenberg, 1982; Manley, 1990; Tang et al., 2001; Regalado, 2003), although the functions of their calls are not known. However, an increase in calling behavior in *Gekko gecko* has been shown to coincide with an increase in androgen levels and gonadal mass (Tang et al., 2001). A likely adaptive hypothesis is that calling behavior has evolved in nocturnal geckos to advertise territories over a long distance to take the place of visual displays in diurnal lizard species. In crepuscular barking geckos, however, males possess both a long-range auditory signal used to advertise home range boundaries and assess potential rivals and possibly a visual signal that may be important in close encounters.

CHAPTER SIX

LARGER MALES, NOT THOSE THAT CALL THE LONGEST, HAVE BETTER BREEDING SUCCESS IN BARKING GECKOS

6.1 Abstract

Multiple signals that exploit different sensory modalities are often used in intraspecific communication. I assessed the role of two potential signals, one acoustic (dominant call frequency) and one visual (yellow throat patch size), in breeding success of male common barking geckos (*Ptenopus g. garrulus*). I also studied the effect of one mechanism of sexual selection, endurance rivalry, on breeding success. Typically, female barking geckos seek out and locate males by their call. Following copulation, males abandon their burrows, now occupied by the female, and construct a new burrow nearby. Of 49 male geckos that I monitored, 20 (41%) bred a total of 31 times (1.55 copulations each), consistent with a classical sexual selection scenario in which only a subset of males breed each season. I measured male activity based on whether males opened their burrows (inactive males keep their burrows closed). Male activity levels were similar for males which bred compared to those that did not breed, suggesting that endurance rivalry is not a significant mechanism of sexual selection in this population. The best predictor of breeding success was body size, which was negatively correlated with dominant call frequency. I suggest that the frequencies of barking gecko calls constitute a long-range signal of body size, used by females to assess potential mates.

6.2 Introduction

Most species use multiple signals in intraspecific communication. These signals commonly incorporate different sensory modalities. However, few studies have investigated how signals using different sensory modalities affect the behaviour of signal receivers (reviewed by Partan and Marler, 2005). Multiple signals can be redundant, each conveying similar information (Møller and Pomiankowski, 1993; Johnstone, 1996); however, the signals may be enhanced when received together (Rybak et al., 2002). Multiple signals also may convey different information on individual quality (multiple messages hypothesis; Møller and Pomiankowski, 1993; Johnstone, 1996). Nonredundant signals may be received independently or the signals may be received together, eliciting a novel response (multimodal signal scenarios are classified in Partan and Marler, 1999). Some sensory modalities may be better suited to different environmental conditions (Maynard Smith and Harper, 2003). For example, acoustic signals may be more likely to evolve in complex environments or under low light conditions, whereas visual signals may be more likely to evolve in open, simple environments, with more ambient light.

Male reproductive success in lizards has historically been attributed to body size through male-male competition and/or mate guarding (Cooper and Vitt, 1993; Censky, 1995; Salvador and Veiga, 2001). However, more recent studies on female choice have shown that male symmetry (Martín and López, 2000; López et al., 2002), male colour (Kwiatkowski and Sullivan, 2002; but see LeBas and Marshall, 2001; Olsson, 2001), and major histocompatibility complex genotype (Olsson et al., 2003) are characters which females use to choose mates. The evolution of male traits due to female choice requires that a number of conditions be met (Andersson, 1994). In some cases, large males maintain higher quality territories attracting more females by virtue of the resources they control (Hews, 1990). Large males may also protect females from harassment by other males through mate guarding (Censky, 1995) or through territorial behaviour (Trillmich and Trillmich, 1984; McKinney, 1986; Wrangham, 1986; Clutton-Brock et al., 1992). Females may also prefer to breed with large males if there is a genetic benefit to her offspring. Large males are generally older and survival ability is likely correlated with heritable genetic traits such as locomotor performance (Jayne and Bennett, 1990). Traits such as badge size, colour, or vocalisation presumably signal some characteristic of the male such as immunocompetence/parasite resistance, body size, or genetic quality to a female (Andersson and Iwasa, 1996).

Large males may also be more successful because of endurance rivalry. Large males in good body condition should be able to perform courtship and defend territories longer (Judge and Brooks, 2001), assuming that there is an energetic cost to breeding behaviour. In frogs, there is a positive correlation between chorus tenure and reproductive success (Halliday and Tejedo, 1995). Males with the best body condition can remain in calling choruses longer than males in poor condition (Murphy, 1994).

Here, I assess the role of two potential signals, one acoustic and one visual, in the breeding success of male common barking geckos (*Ptenopus g. garrulus*).

Barking geckos are small (max 60 mm SVL) lizards of the Kalahari and Namib Deserts of southern Africa. Male barking geckos potentially have both an acoustic signal (loud clicking call) that is negatively correlated with body size and a visual signal (yellow throat patch), which is not explained by body size (Chapter 5). These traits play a role in advertising male status. Large males with low frequency calls are more aggressive when presented with a playback call; however throat patch size relative to total throat area is smaller in more aggressive males (Chapter 5). It is unknown whether the call, the throat patch, or neither, functions in female choice. In addition to these traits being possessed exclusively by males, males also have wider heads, but not larger body size (Hibbitts et al., 2005). Barking geckos construct burrows that are up to 38 cm deep in loose soils and these usually have several branches (Haacke, 1975). Males call from the entrance of their burrows at dusk and dawn (Haacke, 1969). Here I describe breeding behaviour in wild barking geckos. Then, I use multiple logistic regression to investigate the role of two potential signals, morphology, and male activity (endurance rivalry) in male breeding success.

6.3 Methods

6.3.1 Study Area

I studied barking geckos in the Kalahari Desert at the Molopo Nature Reserve (25º50’S, 22º55’E), Northwest Province, South Africa. My study area was a 1.11 ha plot. The vegetation of the plot was dominated by *Acacia mellifera*, interspersed with *A. erioloba* and *Boscia albitrunca*. There was very little ground cover, which facilitated locating gecko burrows and making behavioural observations. The site was divided into 10 m square sections for easy location of geckos.

6.3.2 Breeding behaviour

I observed two instances actual copulation in barking geckos. I recorded the date, time, gecko movements, calling, duration and location of copulation during instances of breeding. Male behaviour observed during the observations of breeding events allowed me to determine number of copulations per male and the percentage of males who bred in the study population during the field season.

6.3.3 Endurance rivalry

The study area was monitored daily from 9 September to 18 November 2004. I marked each burrow with a labelled 30 cm dowel stick. Geckos closed their burrows during the day and opened them about one hour before sunset if they were active. The activity at each burrow was monitored every night by three observers and males were scored as active if their burrows were open. Male barking geckos always called on all nights that they were active during the breeding season (pers. obs.). Therefore, I used activity of males as an indicator of reproductive effort. I am assuming that all geckos are exerting equal effort into calling; however I am aware that this is not true and some variation in calling occurs.

6.3.4 Male traits

Geckos were caught while active on the surface near their burrows or by luring them out with small insects. Each gecko was toe-clipped for permanent identification and a number was drawn on the head for easy visual identification. The following data were recorded for each gecko: snout-vent length (body size), head width (HW), head depth (HD), throat patch size (if male), and burrow number. I measured body size to the nearest mm using a plastic ruler. HW and HD were measured to the nearest 0.01 mm with digital callipers. To determine throat patch area I used the software Simple PCI® to calculate throat patch size and total throat area from a scanned image of the venter of male geckos. Scans were obtained using a Canon canoscan N1220U flat bed scanner. These data were used to determine proportional patch coverage of the entire throat, which was arc-sine transformed for statistical analysis.

6.3.5 Vocal signals

Recordings of male barking geckos were made with a Nagra IV-s analogue tape recorder and a Nakamichi CP-4 super directional shotgun microphone. The microphone was mounted on a tripod and directed at the gecko at a distance of one meter. Six gecko calls (avg. 5 clicks per call) were recorded for each gecko. The recordings were digitized at a sampling rate of 48 kHz (16 bits). The calls were analysed using Cool Edit Pro version 1.2a (Syntrillium Software Corporation, Phoenix, Arizona). An average dominant call frequency was determined for each gecko.

6.3.6 Statistics

Simple linear regression was used to determine the relationships between call frequency and SVL, and relative throat patch size and SVL. HW and HD were corrected for body size by taking the residuals from regressions performed with HW and HD versus body size. I performed a multiple logistic regression using bred as the dependent variable and body size, HW, HD, call frequency, and relative throat patch size as the independent variables. I used a stepwise model selection with a criterion of $P < 0.1$ for inclusion in the model.

6.4 Results

6.4.1 Breeding behaviour

I observed two instances of breeding, one on September 11, 2003 at 1852 h and the other on September 12, 2004 at 1945 h. On both occasions the female oriented to, and approached, the burrow of a calling male. The male began calling more frequently after it saw the female. The female entered the male's burrow and the male copulated with the female within 5 cm of the opening of the burrow (they were still visible to the observer). The copulations lasted approximately 13 min and 10 min respectively. After copulation, both male and female geckos remained in the burrow for about 30 min. During this time the male could be heard calling from within the burrow and also from the mouth of the burrow. The male then left and moved about one meter away and began construction of a new burrow. The male was seen and heard calling from its new burrow the following day.

Forty-nine adult males were observed in the study area in 2004. Using the construction of a new burrow and the concurrent occupation of the males' former burrow by a female, as the criterion for breeding success, 20 (41%) males bred a total of 31 times (1.55 copulations per adult who bred). Only six of the 20 males bred multiple times. Additionally, 12 males did not copulate during the same time period because they were observed in the same burrow for the entire field season. I found inconclusive evidence for breeding in the other 18 males. In most of the 18 inconclusive cases the male moved burrow locations but a female was not observed in its former burrow.

6.4.2 Successful male traits

The only variable retained in the logistic regression model was body size (Table 6.1), which was significantly correlated with breeding success. All other variables did not meet the criterion of $P < 0.1$, including activity which was the first variable removed from the model during the backward elimination procedure.

Table 6.1 The logistic regression model with 'bred' as a dependent variable and body size (SVL), head width, head depth, dominant call frequency, relative throat patch size, and activity as independent variables. Only factors retained in the final model (P<0.1) are shown.

	Coefficient	SE	Wald	P
SVL	0.778	0.318	5.955	0.015

6.5 Discussion

Body size has also been reported to correlate with breeding success in other lizard species (Trivers, 1976; Ruby, 1981; Anderson and Vitt, 1990; Cooper and Vitt, 1993; Censky, 1995; Salvador and Veiga, 2001). However, in many of the previous cases male reproductive success has been inferred from success in male-male competition. Large male barking geckos are more aggressive than their smaller counterparts and consequently, small males are more likely to retreat when presented with a playback call (Chapter 5). Also, male barking geckos live in largely exclusive home ranges which are maintained through their calling behaviour (Chapter 5). Nevertheless, female choice may function as a mechanism for sexual selection in barking geckos. Females approached males from distances of greater than 3 m (likely much greater) under low light conditions, and probably out of sight of the calling male. This suggests that females assessed males based on their advertisement calls. Also, in the peak breeding season, up to 50 males call from within one hectare (pers. obs.), providing an opportunity for females to simultaneously evaluate multiple males.

The call of male barking geckos is negatively correlated with body size (Chapter 5) and therefore is likely an honest signal of body size that functions over long distances. The call influences male-male interactions and perhaps female mate choice. It is not uncommon for signals to serve dual functions, and this is the case for the majority of secondary sexual traits studied to date (Berglund et al., 1996). One major explanation for dual functioning traits being so prevalent is that ‘armaments’ evolve through male-male competition for territories or access to mates. The armaments become honest status signals which are then used by females to assess male quality (Berglund et al., 1996).

Male and female barking geckos do not differ in body size although males have larger heads (Hibbitts et al., 2005). If females prefer larger males, then it might be expected that males would be larger than females. Larger males are expected to win more male-male contests and have higher fitness. Similarity in body size between males and females may be explained by several nonmutually exclusive scenarios. In general, gekkonid females are larger than males (Fitch, 1981). Therefore, similarity in body size may be explained by phylogeny if ancestral females were large and females preferred larger males. Alternatively, larger females may be favoured by fecundity selection, canceling out body size differences between the sexes through different selection pressures. Hatchling survival is likely important for barking geckos since females lay one-egg clutches (Hibbitts et al., 2005). Larger females can produce a larger egg (Vitt and Congdon, 1978). Therefore, offspring from larger eggs likely have a survival advantage over offspring from small eggs. Natural selection (large offspring size) and sexual selection (larger males winning more contests) pressures probably balance each other in maintaining similar male and female body sizes in barking geckos.

In many frogs, male calling endurance predicts breeding success whereby males that were able to remain calling in a frog chorus the longest, were more likely to breed (Halliday and Tejedo, 1995). I found that activity, which positively correlates with calling in male barking geckos (pers. obs.), was not a factor that predicted breeding success in male barking geckos. Logically, calling activity will likely affect breeding success. However, other factors such as female choice and proximity to females are probably more important for breeding success in barking geckos.

The breeding behaviour of barking geckos is reminiscent of frog breeding systems in which males call to attract females, which then approach prospective mates. Barking gecko males also give up their burrows to the female after mating and dig a new burrow nearby. Females lay their eggs in their burrows; however there is no indication that males excavate burrows specifically for egg laying. Females also breed with males before they investigate the male’s burrow. Therefore, a male abandoning his old burrow to the recently bred female and his excavation of a new burrow, may have evolved to reduce predation risk on the recently bred female and not as a specific resource for egg laying. Also, burrow excavation is presumably a costly exercise and gravid females would need to conserve their energy for egg development and laying.

In summary, large males had greater breeding success than small males, and breeding success was not explained by endurance rivalry. Large males are also more successful in male contest competition (Chapter 5), suggesting that the call has the dual function of signaling size to rival males and quality to potential mates.

CHAPTER SEVEN

CONCLUSIONS AND FUTURE DIRECTIONS

I studied the ecology and sexual selection of barking geckos. Barking geckos consumed mostly ants and termites by number; however, termites were the most important prey item by volume. No differences were observed between the diets of males and females, although males had wider heads than females. Dietary similarity indicates that there is an absence of niche partitioning between the sexes which means head size differences are probably best explained by contest competition (see below). Males and females have synchronized reproductive seasons with peak testis volume and peak egg length occurring in October. Females lay one-egg clutches. Females in good body condition may lay up to two and possibly three clutches in one reproductive season. The hatchling size of barking geckos is large in comparison to female size at sexual maturity when compared to other gecko species. Therefore, barking geckos invest heavily into the production of large offspring, which likely have a survival advantage.

The mating system is best described as a resource defence polygyny. Males defend a home range with one (or more) structural resources (burrows). However, temperature and prey abundance did not predict gecko spatial patterns but vegetation had some influence on burrow locations. Compared to females, males become active earlier in the breeding season and remain more active than females for about the first two months. This is consistent with the male-first mating system termed protandry (Wirklund and Fagerström, 1977). Additionally, males live in largely exclusive home ranges and larger males lived in larger home ranges. This suggests that the male call might advertise territory ownership to other males in lieu of the potentially costly behaviour of patrolling territory boundaries.

It has been suggested that geckos are olfactory specialists (Schwenk, 1993), and in many lizard species scents are deposited to advertise territory possession and male quality (López & Martín, 2002, López et al., 2003). Male barking geckos did not discriminate between refuges scented with other males and unscented refuges.

Sexual selection best explains why male barking geckos have larger heads than females and why males vocalise. The mechanisms at play are most likely a combination of contest competition and mate choice. Since barking gecko calls are negatively correlated with body size and body size is an indicator of behaviour in response to playbacks it can be inferred that male barking geckos use their calls to advertise body size over relatively long distances under low-light conditions. When a male is confronted with a calling intruder (playback), he responds aggressively or hides. Large barking geckos were more likely to charge the hypothetical intruder, whereas small males would simply retreat into their burrow.

The male throat patch also was correlated with aggressiveness. Males with smaller throat patches relative to total throat area were more aggressive than males with large relative throat patches. The relationship between throat patch size and aggressiveness was contrary to my expectations. One explanation is that the amount of white to yellow on the throat may be more important than the overall yellow throat area. Another explanation is that testosterone may inhibit growth of the throat patch. Most of the spread of yellow on the throat occurs before maturity and maybe the increase of testosterone at sexual maturity inhibits further spread of the yellow patch. Unlike some other lizard species which head and throat coloration increases during the breeding season (Cooper et al., 1987), barking gecko's throat colour stays constant throughout the year (Haacke, 1975; pers. obs.); however, observations have not been made during the winter dormancy. This suggests that throat colour in barking geckos is not controlled by increased testosterone during the breeding season and therefore may be inhibited by testosterone during maturation like body growth in other lizards (Civantos, 2002). Alternatively, the throat patch may not be used as a signal in male-male interactions.

Male body size was also an important indicator of reproductive success. Large males probably were able to procure more copulations than small males (which usually did not breed). Males only advertised their presence to females by calling and females appeared to approach males on the basis of their call. This aspect of female behaviour suggests the likelihood of female choice and should be investigated in more detail. Many males call simultaneously, akin to a frog chorus, allowing a female to assess multiple males. Whether the female 'chooses' (active choice) a mate based on his call or simply approaches the nearest large male (passive choice) is unknown.

Barking gecko breeding behaviour is similar to that of many species of frogs in that male barking geckos produce calls and females move to a male's calling location. In frogs, calling tenure and reproductive success is highly correlated (Halliday and Tejedo, 1995). Surprisingly, I found no evidence that endurance rivalry is a mechanism of sexual selection in barking geckos. Several males called daily for the entire peak breeding season without any reproductive success, suggesting that call frequency and possibly territory location, are more important for reproductive success than endurance.

Barking geckos potentially use two types of sensory modalities when signalling to rivals (auditory and visual). Auditory signals were the only sensory modality that I confirmed that barking geckos use. In barking gecko habitat the auditory signal was especially important for signalling over long ranges. Visual signals were not confirmed to be used by barking geckos; however, there were some interesting correlations found between throat patch size and aggressiveness. Experimental studies manipulating the size of the throat patch in the field could lead to a better understanding of how the throat patch is involved in contest competition and mate choice.

In lizards, studies of sexual selection are dominated by male contest competition, mainly because it is relatively easily studied (e.g. Cooper and Vitt, 1988; Olsson, 1992; Olsson and Shine, 2000; Whiting et al., 2003; Stuart-Fox et al., 2005). Mate choice by females, however, still remains an enigma and is considered rare (but see Martín and López, 2000; Kwiatkowski and Sullivan, 2002; López et al., 2002; Olsson et al., 2003). One reason for the difficulty in studying mate choice is the inability to detect female receptivity. I found evidence of mate choice in barking geckos based on my field observations. Further experiments eliciting female responses to male calls of different frequencies could be informative; however, the trick is finding a method that females will respond to. Also, the throat patch was shown to indicate aggressiveness, but I am unsure what causes variation in throat patch size. Testosterone manipulations may be a first step to uncovering hormonal constraints to phenotypic expression.

Theoretical work on multiple signals appears to be outpacing empirical work. Lizards are good candidates for further studies on multiple signals because they use visual and olfactory signals, and often lizards are relatively abundant (Pianka and Vitt, 2003), allowing reasonable statistical power. Among lizards, geckos are especially good study organisms because some species also vocalize. We are only beginning to understand how multiple signals interact during intrasexual and intersexual encounters and how the use of different sensory modalities affects signal receivers. Future work using geckos may help elucidate how multiple signals interact to help a signal receiver make decisions during contest and mate choice situations.

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