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SEXUAL SELECTION AND SIGNALLING IN THE LIZARD *PLATYSAURUS MINOR*

Belinda Ann Lewis

A dissertation submitted to the Faculty of Science, University of the Witwatersrand, Johannesburg, in fulfilment of the requirements for the degree of Master of Science.

Johannesburg, 2006

I declare that this dissertation is my own unaided work. It is being submitted for the degree of Master of Science in the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination in any other University.

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Belinda A. Lewis

6th day of December 2006

ABSTRACT

Sexual selection may influence aspects of male morphology associated with territoriality, female choice, aggression and contest success. Attributes that are most commonly selected for include body size, condition, weaponry, endurance and bright coloration. I investigated the relationships between morphology, use of space and home range quality, and access to females. Specifically, I examined the relationships between colour, body size and condition, and whether morphology could predict aggression or contest success. Colour spectral data were analyzed using both traditional measures of colour (hue, chroma, brightness) and principal components. Males with darker, more saturated chests, and more saturated throats, had larger home ranges. Home range quality, as determined by refuge number and prey availability, was associated with blue chests and blue throats and chests, respectively. Males with larger home ranges had higher numbers of associated females and spent more time courting females. Larger males in better condition had darker, more saturated chests. Males in better body condition were also more aggressive. There was a consistent trend for larger males to win more contests, but this relationship was only significant in analyses using traditional measures of colour.

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1. CHAPTER ONE: GENERAL INTRODUCTION

Sexual selection influences the evolution of morphology, behaviour and mating systems in a variety of taxa (Andersson, 1994). Sexual selection arises owing to differences between individuals in the traits that affect reproductive success (Andersson, 1994; Panhuis et al., 2001), and may ultimately lead to speciation (Higashi et al., 1999; Panhuis et al., 2001). Due to anisogamy, the unequal contribution of gametes, and the different parental effort between the sexes, sexual selection is often due to competition between males for mates (Andersson, 1994; Clutton-Brock and Vincent, 1991). This often results in asymmetries in the behavioural and morphological attributes that are important in female mate choice or in male competitive ability or both (reviewed in Andersson, 1994; Kleene, 2005; Watson and Thornhill, 1994). Variation within the sexes can be particularly pronounced in polygynous species in which variance in mating success is high (Schuster and Wade, 2003).

The male morphological characteristics most often influenced by sexual selection include body size, condition, weaponry, endurance and threat signals including bright coloration (Andersson, 1994; Baird et al., 2003; Shuster and Wade, 2003). Behavioural attributes include territory defence, mate guarding and the evolution of alternative reproductive tactics (Andersson, 1994; Baird et al., 2003, Shuster and Wade, 2003). These different reproductive tactics may be genetically pre-determined (Zamudio and Sinervo, 2003), but more commonly arise from differences in the size, age, condition

and other morphological variation of individuals (Andersson, 1994; Shuster and Wade, 2003). If the different strategies have similar fitness benefits, a mixed evolutionary stable strategy will exist. Alternatively, they may arise from variation in environmental influences or other constraints on individuals (Andersson, 1994; Shuster and Wade, 2003). Genetically pre-determined strategies often result in fixed distinct morphs with discrete morphology and behaviour (Andersson, 1994; Kinsgston et al., 2003; Sinervo, 2000) while plastic strategies most often result in a range of phenotypes with associated behavioural differences (Baird et al., 2003; Shuster and Wade, 2003). These different behaviours and phenotypes are controlled to varying degrees by genetic, hormonal, social or other environmental cues and may change over time (Crews and Moore, 1986).

In territorial species, traits which influence space use or territory quality may be under sexual selection (Andersson, 1994). Females may choose either morphological attributes of the male and/or aspects of his territory (Bart and Earnst, 1999). The defence of resources important to females could therefore have fitness benefits for a male. In species that establish territories there is often a correlation between male morphology and territory size or quality, usually resulting from male-male competition for high quality territories or from lower quality males being unable to bear the associated costs of territoriality (Candolin and Voigt, 2001). The association between territory size and/or quality and colour is best understood in birds (Keyser and Hill, 2000; Marchetti, 1998; Pryke and Andersson, 2003; Siefferman and Hill, 2005; Wolfenbarger, 1999). In the tree lizard *Urosaurus ornatus* (Thompson and Moore,

1991), brighter males defend their territories more aggressively. Sand lizard (*Lacerta agilis*) males with more saturated green patches are more likely to initiate and win contests (Olsson, 1992). In the side-blotched lizard the different colour morphs all have associated reproductive behaviours and tactics (Sinervo et al., 2000). Orange males defend large territories and are highly aggressively, while blue throated males guard females on their territories (Zamudio and Sinervo, 2003). Yellow throated males are non-territorial and sneak copulations with females (Zamudio and Sinervo, 2003).

Sexual selection is the most important driving factor in the evolution of bright, sexually dimorphic body coloration and visual displays in males (Andersson, 1994). These visual signals can be used, amongst other things, to attract and court potential mates, to maintain territories and to hold social groups together (Endler, 1992). The diversity in types and function of visual communication is partially responsible for the diversification in morphology and colour amongst different species (Endler, 1992). Several groups of lizards rely on this coloration in combination with static or dynamic visual displays during both courtship and contests (Ord et al., 2002). An increase in the intensity of male-male competition is associated with more and more elaborate displays (Ord et al., 2002). Associations between colour and behaviour are common in a number of taxa including reptiles, crabs, fish and birds (Bart and Earnst, 1999; Candolin, 2000; Kingston et al., 2003; Olson, 1992; Takeda, in press; Thompson and Moore, 1991).

An efficient visual signal, including colour signals, must stimulate the visual system of the viewer within the visual background against which the signal is perceived (Fleishman and Persons, 2001). Current signal evolution models attempt to explain signal diversity with a variety of social, perceptual and environmental factors (Ord et al., 2002). The original terrestrial range of colour vision was probably tetrachromatic, consisting of four 'main' colours, their combinations and including the near ultra-violet part of the spectrum (Honkavaara et al., 2002). Over thirty-five species of birds, and a number of reptile and amphibian species have been found to possess tetrachromatic vision (Honkavaara et al., 2002). In some lizard species secondary sexual traits are reflected in both the visible and ultraviolet (UV) spectrum (Honkavaara et al., 2002). For this reason, studies investigating the effects of colour signals on behaviour must use objective techniques that eliminate human colour bias (Cuthill et al., 1999).

1.1. Study animal: *Platysaurus minor*

Platysaurus minor are cordylid lizards (Broadley, 1978) and members of a genus endemic to lower eastern and southern Africa (Scott et al., 2004). Like all flat lizards, *P. minor* are rupicolous (Broadley, 1978) and are characterised by extreme sexual dichromatism. Males are brightly coloured and females conservatively coloured (Scott et al., 2004). *Platysaurus minor* have a restricted distribution in South Africa from the Waterberg to the foothills of the Blouberg (Branch, 1998). The congeneric *P. broadleyi* is the most extensively studied member of this group. In this species, male colour has been linked to fighting ability and reproductive tactic (Whiting et al., 2006).

However, there is currently little published information on aspects of this species' life history and social behaviour. The determinants of territoriality, contest success and the presence or absence of alternative reproductive tactics within the species are unknown. Because males exhibit obvious intrapopulation variation in throat colour, they are suitable for investigating the link between aspects of colour and sexual selection and signalling.

While several studies have investigated the role of colour in signalling behaviour in discrete colour morphs (e.g. Sinervo et al., 2000) or males with different sized badges (Anderholm et al., 2003; Thompson and Moore, 1991), few have quantified the role of the spectral qualities of these colour patches, especially in wild reptilian populations. Specifically, I investigated the role of male morphology (including colour) on inter- and intra-sexual signalling in a natural population of *P. minor* lizards. Male morphological variables included body and head size, condition and the spectral reflectance of the throat, chest and flank. I quantified male spatial patterns and the resources found on these home ranges. In addition, I examined the determinants of access to potential mates including male morphology and home range size and quality, and I investigated whether these variables influenced the amount of time that males spent courting females. I determined whether or not trade-offs existed between time spent in contests and time available for foraging. Finally, I examined possible morphological predictors of contest success and aggression.

2. CHAPTER TWO: WHICH MALE TRAITS PREDICT SPACE USE AND ACCESS TO FEMALES IN THE LIZARD *PLATYSAURUS MINOR*?

2.1. Abstract

Individual males of many different species differ in their ability to acquire and defend territories. Space use is often associated with access to potential mates and thus, male fitness. I investigated the relationship between male morphology (body size and condition, head size, and aspects of body colour) and home range size and quality, and how these related to access to females, in the flat lizard *Platysaurus minor.* Spectral data were analyzed using both traditional measures of colour (hue, chroma and brightness) and principal components analysis (PCA). Males with darker chests had larger home ranges. The chroma or colour saturation of the throat and chest were also predictors of home range size, with high saturation being associated with larger home ranges. Males with more blue than green chests had more refuge sites. Prey availability was higher on areas defended by males with blue throats and chests. Larger home ranges consistently had more associated females, and the males on these large areas spent more time courting females. These results suggest a relationship between morphology and potential fitness in terms of access to large, high quality home ranges and thereby, access to potential mates.

2.2. Introduction

Intraspecific variation in territoriality and spatial patterns are controlled by a number of factors including the quantity, quality and distribution of food as well as distribution of mates, habitat features and availability of refuges (reviewed in Mahler and Lott, 2000). In territorial species, females may choose either morphological attributes of the male and/or aspects of his territory (Bart and Earnst, 1999). Securing a territory that may provide control of the resources important to females could therefore have fitness benefits for a male. The determinants of territory quality vary between species based on their reproductive and ecological needs (Reaney and Whiting, 2003). In species in which males establish breeding territories, male morphology often influences the quality of the territory a male is able to control, as territorial disputes may be settled by contests (Candolin and Voigt, 2001). Associations exist between male morphology and home range size, resource defence and access to females in some lizard species. In the tree agama, *Acanthocercus articollis articollis,* males that defended home ranges with higher prey availability overlapped more with females (Reaney and Whiting, 2003). In the striped plateau lizard, *Sceloporus virgatus,* larger males and males that overlapped the home ranges of more females were more likely to sire clutches (Abell, 1997). However, colour has not been objectively quantified in any of these systems with the aim of relating it to space use. We thus have a poor understanding of how colour may relate to resource defence.

Because parental investment differs between males and females, they adopt fundamentally different tactics to maximise reproductive success (Andersson, 1994).

Unlike females, whose reproductive success is normally limited by the cost of egg production (in birds and mammals add to this, parental care), male fitness may be increased by mating with multiple females (Andersson, 1994; Shuster and Wade, 2003). This polygynous form of social organisation, in which males may reproduce with more than one female (Shuster and Wade, 2003), combined with territory defence, is common in diurnal lizards (Baird et al., 2003). There is evidence from a range of taxa that male mating success in these polygynous systems may be skewed in favour of males with large or high quality territories, large body size, good body condition and bright coloration (Andersson, 1994; Baird et al., 2003; Shuster and Wade, 2003). These characteristics may have a dual role, affecting competitive ability in contests and territory acquisition, by signalling status, and playing an important role in female mate choice (reviewed in Andersson, 1994; Hews, 1993). Associations between colour and behaviour exist in a diverse range of taxa including crabs (Takeda, in press), fish (Candolin, 2000; Kingston et al., 2003) and birds (Bart and Earnst, 1999). Coloration in particular, likely plays an important role in female mate choice in a number of bird (Delhey et al., 2003; Hill, 1991; Siitari, et al., 2002),) fish (Bakker, 1993; Kingston, et al., 2003) and insect species (Krebs and West, 1988). The relative importance of male coloration in lizards for inter- or intra-sexual signalling remains under contention although evidence of female choice for bright males does exist in eastern collared lizards (Baird et al., 1997) and broad-headed skinks (Cooper and Vitt, 1993).

Platysaurus minor are rupicolous cordylid lizards restricted to northern South Africa from the Waterberg mountain range to the foothills of the Blouberg (Broadley, 1978; Branch, 1998). *Platysaurus* species are characterised by extreme sexual dichromatism, with brightly coloured males and conservatively coloured females (Broadley, 1978). *Platysaurus minor* males exhibit extensive intrapopulation polymorphism in throat, chest and flank coloration. Their throat coloration ranges from blue, to green to yellow, including combinations of these colours (this chapter). Their chest colour ranges from black to blue and their flank colour from yellow to orange-brown (this chapter). Both territorial and floater/satellite males exist within the population (this chapter and chapter 3). *Platysaurus minor* males court females using a push-up display while circling the female, which emphasises the colour of the throat and chest region. During male-male interactions, a ventral side display maximises the impact of these regions as well as their ventral stripes. During these displays a male will raise one side of its body to an angle greater than 60º so that the rival has a clear view of their ventral surface. This behaviour may be performed from a stationary position or while approaching the rival male.

I examined the relationship between male morphology, use of space, and access to potential mates in a natural population of *Platysaurus minor*. I first measured spectral qualities of the throat, chest and flank colour patches, as well as head dimensions, body size and condition. In lizards, colour (Hamilton and Sullivan, 2005; Thompson and Moore, 1991), body size (Calsbeek and Sinervo, 2002; Whiting et al., 2006), condition (Lopez et al., 2002) and head dimensions (Lopez et al., 2002; Reaney and

Whiting, 2003) have all been found to predict competitive ability or male mating success, although this does not hold true for all species (Lappin and Husak, 2005). I investigated the usefulness of these measurements as predictors of space use and space quality, as judged by prey availability and number of available shelters. I then examined the extent to which these morphological measurements were associated with the number of females living on a particular home range, and whether they influenced the amount of time males spent courting these females. Home range size and quality variables were included in these analyses. In a resource defence polygynous system, where males defend resources important to females, we would expect a correlation between space use or quality and male access to potential mates. If no correlation exists, presuming that all important mating success variables within this species have been taken into account, females most likely select males based on male quality, and not the resources defended by these males.

2.3. Methods and materials

2.3.1. Study area

I conducted field work during September - October 2004 at the Madikela Private Nature Reserve (24° 0 S′, 28° 26′ E) in the foothills of the Waterberg mountain range, Limpopo Province, South Africa. I captured each lizard by noosing and permanently marked them with a unique pattern of toe-clipping (Fisher and Muth, 1989). In addition, I painted temporary numbers on their backs using non-toxic xylene-free paint pens to facilitate individual recognition in the field. One hundred-nine males and 98 females were caught and marked during the study period. The study area was

approximately 160 x 40 m on a limestone outcrop with a granite base. The majority of the area was composed of a single outcrop, although stand-alone rocks within the study area were also sampled. The Waterberg mountain range is a savanna biome, characterised by a mix of grass and trees (Cowling et al., 1997), the most common of which are *Acacia* spp., the african beachwood (*Faurea saligna*), common hookthorn (*Acacia caffra*) and red seringa (*Burkea africana*).

2.3.2. Male traits

I recorded the floolowing morphological measurements for each male: mass (nearest 0.1g using a digital scale), snout-vent length (SVL; nearest mm), head width (widest point at occiput) and length (from the tip of the snout to tympanum) (both to the nearest 0.01 mm using digital callipers). Head measurements were transformed to a dimension-free variable using residuals from linear regression on body size (Miles, 1994). A standard body condition index was similarly determined using SVL and mass (Jakob et al., 1996). All morphological measurements were taken in the early evening and lizards returned to their point of capture the following day.

The reflectance of each male's throat, chest and flanks was measured using an Ocean Optics USB2000 optic spectrometer and deuterium-tungsten DT-1000 mini light source connected to a fibre-optic probe. These readings were taken from the same position on each lizard. The probe was mounted in a probe-holder to ensure that all readings were taken from 5 mm diameter areas at a constant distance from the surface, at an angle of 45°. Measurements were taken relative to a 99% WS-1 white reflectance

standard and each measurement consisted of the average of three consecutive readings. Spectral reflectance between 320 - 700 nm was used in analyses as this represents the broadest range of known lizard vision (Loew et al., 2002). All experimental procedures were approved by the University of the Witwatersrand Animal Ethics Committee (certificate number 2004 72 2a).

Variation in reflectance spectra were analyzed using principal components analysis (PCA), which makes no assumptions about the receiver's visual system (Cuthill et al., 1999). I also used traditional measures of hue (spectral location), brightness (spectral intensity) and chroma (spectral purity) (Endler, 1990; Pryke et al., 2001). Principal components were biologically interpreted by correlating principle component eignenvectors with wavelength at each 5 nm interval (Cuthill et al., 1999). Hue was calculated as the peak wavelength corresponding to maximum reflectance. Brightness was calculated as the sum of the mean reflectance. Chroma was calculated using the formula $[R_{320-\lambda(50)} - R_{\lambda(50)-700}]/R_{320-700}$ (e.g. Pryke et al., 2001; Andersson et al., 2002) using λ(R50) as the segment divider where λ(R50) is the wavelength half way between minimum and maximum reflectance. This quantifies variation in chroma which is a function of slope height and steepness. Traditional segment colour analysis is simpler to interpret and comparable between studies but is likely to less accurately capture variation in the shape of reflectance curves than PCA (Grill and Rush, 2000). Both methods were thus used in analyses.

2.3.3. Use of space and home range quality

The position of each marked lizard was determined by scan sampling. Each day I walked the same transect three times: early morning, noon and again in the late afternoon. I regressed home range area on the number of lizard sightings to determine the minimum number of sightings required to adequately measure home range size. The area of each lizard's home range was determined using the minimum convex polygon method (Rose, 1982). Home range area reached an asymptote at nineteen sightings. Therefore, nineteen or more sightings was determined sufficient to gauge home range size, resulting in 24 male lizard home ranges to use in analysis (sightings≥18: R^2=0.35, N=32, P=0.021; sightings≥19: R^2=0.43, N=24, P=0.158). Six lizards were sighted more than 18 times in totally different areas and were judged to be floater males. This sample size was however deemed too small to use in statistical analysis.

The relationship between space use and male morphology was assessed using multiple stepwise regression. I also assessed percentage overlap; which is the percentage of an individual's home range that is shared by other individuals (Abell, 1998). To determine the extent to which rival males overlap in space, I determined overlap pressure, which is the amount of home range shared by each individual divided by the home range size of the focal individual (Abell, 1998). Overlap pressure, which takes into account home range size, and gives more weight to space shared by more than two individuals (Abell, 1998), was used in multiple regression analysis to determine the relationship between spatial overlap and male traits.

I assessed two aspects of area quality: prey abundance and the number of suitable refuge sites. To determine the prey abundance of individual lizard home ranges three sticky traps were placed at random in each home range between 0800 - 1200 h for six consecutive days during the study. Aerial prey availability was determined using a single sweep net, sampling the lizard's home range for 15 min per day. As large a random proportion of the lizard's home range as possible was sampled during this time. Numerical abundance was determined at the level of insect order. All insects judged small enough for flat lizards to eat were regarded as prey items as no experimental data on prey size was available. The number of suitable refuge sites was subjectively determined within each area as crevices deep enough, and with entrances narrow enough, to provide refuge. The relationship between both measures of quality (prey abundance and number of refuges) and male traits was assessed using multiple regression.

2.3.4. Access to females and Courtship

I recorded females sighted within known male home ranges. Females sighted in multiple males' home ranges were scored in all those areas. The relationship between the number of associated females and male characteristics, including space use and quality, was assessed using multiple regression. I also determined the time spent in courtship by each male, using focal animal sampling. Time spent performing behaviours was recorded using a stop watch and a dictaphone. Courtship behaviour included approaching females, push-up displays and physical nudging. Focal sampling

lasted thirty minutes each and were conducted between 0900 - 1100 h, during peak lizard activity. I conducted 104 focal samples on 43 male lizards. The number of focal samples per male ranged from 1 to 4. When more than one focal sample was obtained from an individual lizard, the average duration of different behaviours was used in analysis. The relationship between time spent in courtship and male traits including space use and quality was assessed using multiple regression. All data were normally distributed except for home range size, which was log transformed to obtain normality. All regression analyses used stepwise model selection with a criterion for remaining within the final model of $P<0.1$. In each case, two models were assessed, one incorporating principal components of reflectance spectra and the other incorporating the traditional summary measures of hue, chroma and brightness. All analyses were done in SAS v9.1.

2.4. Results

2.4.1. Colorimetry

Individual lizards showed large amounts of variation in spectral reflectance of all the measured regions. Individual throat coloration ranged from blue, to green to yellow, including combinations of these colours while chest colour ranged from black to blue. Individual flank colour varied from yellow to orange-brown. Figures 2.1.a, b and c show examples of this variation in of the throat, chest and flank respectively.

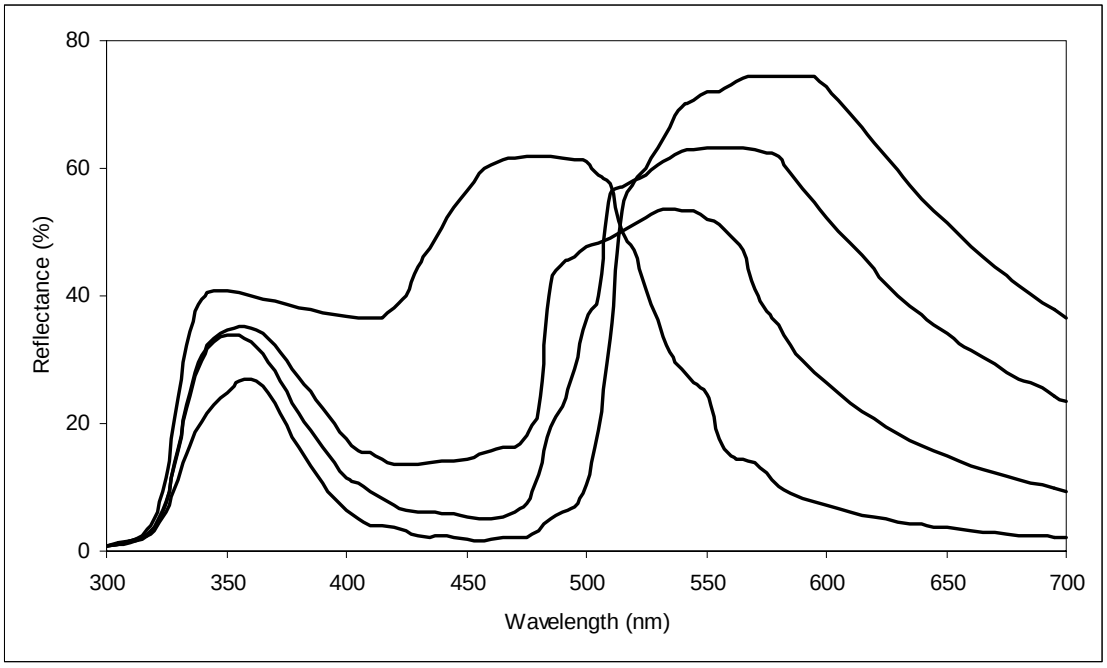

Figure 2.1.a: Variation in individual spectral reflectance in the throat region

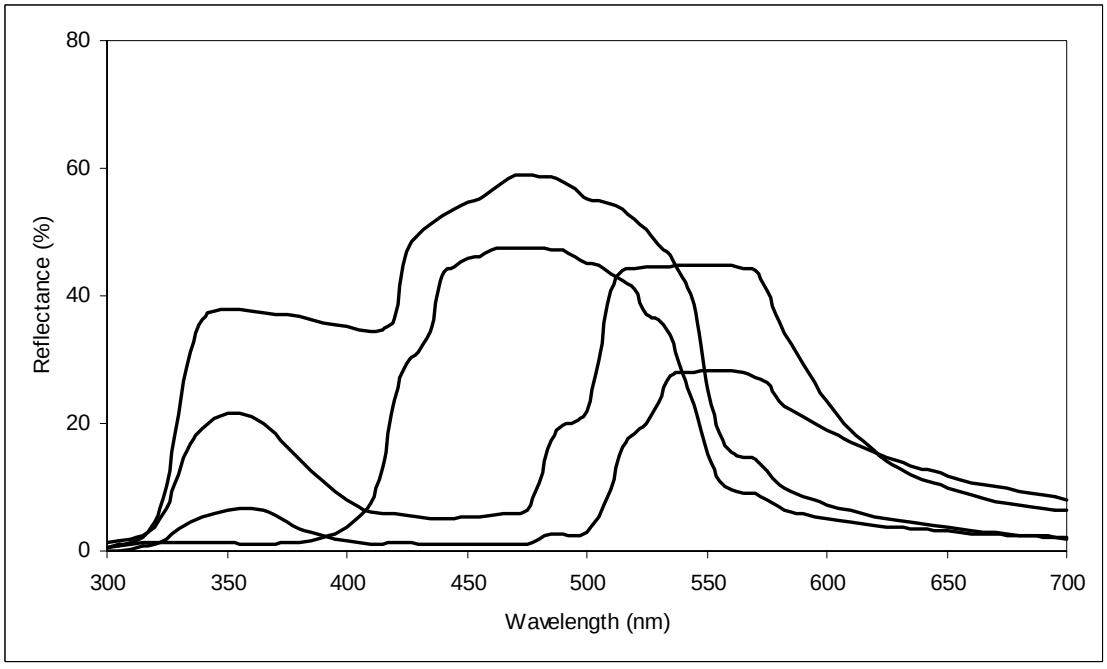

Figure 2.1.b: Variation in individual spectral reflectance in the chest region

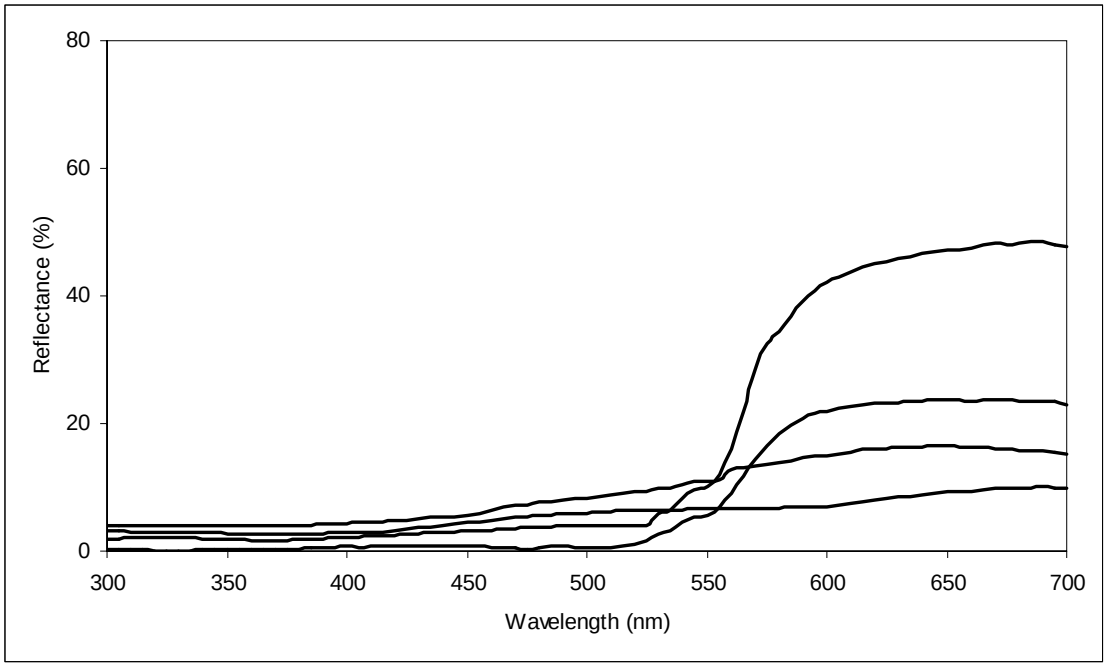

Figure 2.1.c: Variation in individual spectral reflectance in the flank region

The first two principal components explained over 80% of the variation for each body region (Table 2.1.). As the third PC explained only a small proportion of the variation in reflectance spectra, I used only the first two PCs in subsequent multiple regression analyses to minimize the number of variables and for ease of biological interpretation (Stuart-Fox et al., 2003).

Table 2.1. Proportion of variation explained by principal components 1 and 2.

Body Region	**PC1**	**PC2**	**Total**
Throat	0.50	0.31	0.81
Chest	0.55	0.28	0.82
Flank	0.78	0.18	0.95

Although PC1 was typically correlated with mean reflectance (brightness; Cuthill et al., 1999), in this case, most of the variation was in curve shape rather than mean reflectance. PC1 of the throat described variation in reflectance at short relative to long wavelengths (Figure 2.2.a) and primarily differentiated males with blue versus green throats. Accordingly, PC1 of the throat was strongly correlated with hue (r = 0.81*; P* <0.0001) and negatively correlated with chroma (r = -0.49*; P* = 0.0009). PC2 of the throat was highly correlated with brightness (r = 0.94*; P*<0.0001).

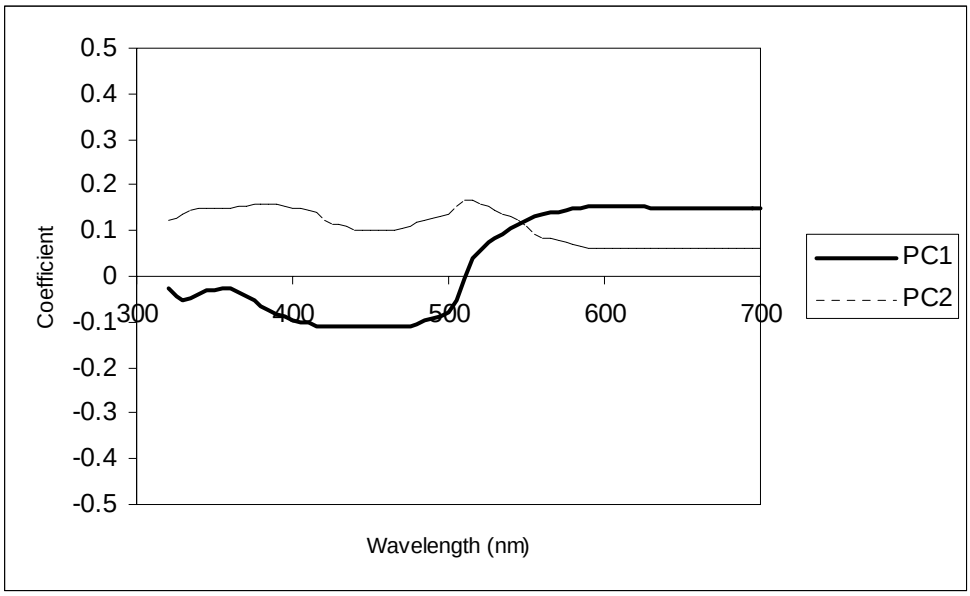

Figure 2.2.a: Wavelength and principal component eigen vector values of the first two principal components of the throat

In contrast to the throat, the chest reflectance varied most in brightness. Accordingly, PC1 of the chest indicated brightness and was highly positively correlated with the traditional measure of brightness (r = 0.93*; P*<0.0001). PC2 of the chest described

variation in curve shape and was correlated with both traditional measures of chroma (r = 0.63; P<0.0001) and hue (r = -0.51; P = 0.0005). Specifically, PC2 described variation in the ratio of reflectance at wavelengths above and below 550 nm (Fig. 2.2.b.) and primarily differentiated between males with blue and males with green chests.

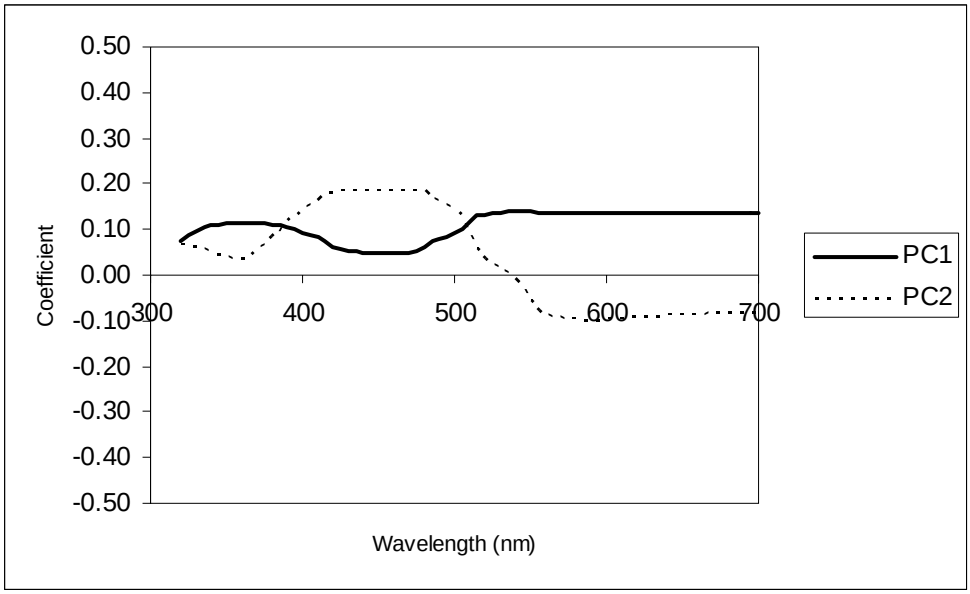

Figure 2.2.b: Wavelength and principal component eigen vector values of the first two principal components of the chest

PC1 of the flank correlated strongly with brightness (r = 0.92; P<0.0001). PC2 reflects variation in curve shape, specifically the ratio of reflectance at wavelengths above and below 550 nm (Fig. 2.2.c) and differentiated males with yellow-orange flanks from those with orange-brown flanks.

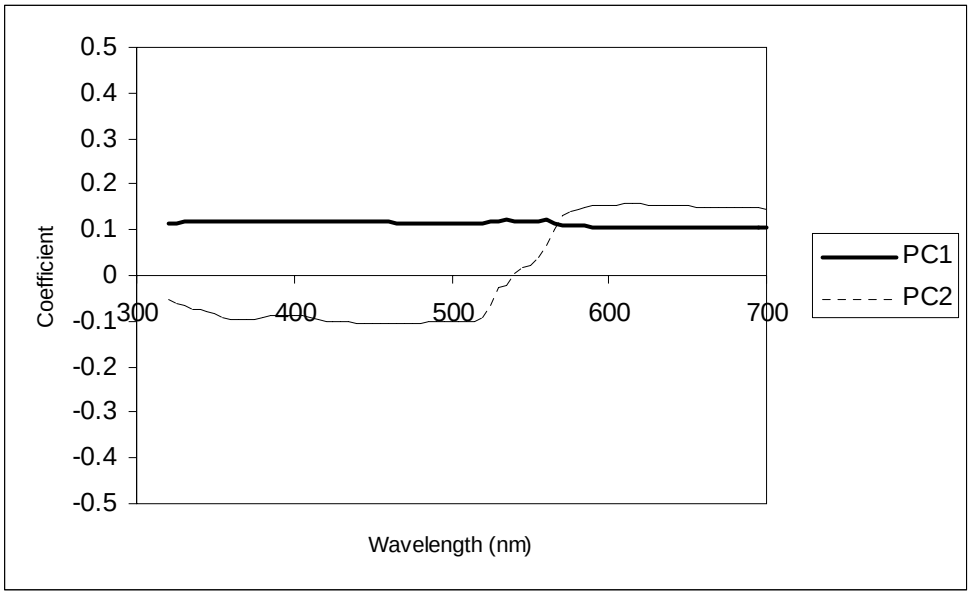

Figure 2.2.c: Wavelength and principal component eigen vector values of the first two principal components of the flank

2.4.2. Which male traits predict space use, overlap and home range quality?

Home range size was significantly associated with Principal Component (PC) 1 of the chest (Partial R^2 = 0.18*; SEO*=-0.14*; P*=0.0400). Where SEO is the standardised coeffieicent estimate calculated by multiplying the parameter estimate by the standard deviation of that variable. This makes parameter estimates comparable as a measure of effect size. Therefore, males with darker chests had larger home ranges. Similarly, for the model based on traditional measures, chest colour saturation (chest chroma - Partial R^2 = 0.21*; SEO*=-0.22*; P*=0.0227) and throat colour saturation (throat chroma - Partial R^2 = 0.17*; SEO*= -0.15*; P*=0.0238) were predictors of home range size, while there was a trend for males with darker chests to have larger home ranges (chest brightness - Partial R^2 = 0.10*; SEO*= -0.11*; P*=0.0639) (overall R^2=0.49).

No traits were significant predictors of number of refuges in the model based on principal components although PC1 of the chest (Partial R^2 =0.12*; SEO*=-1.02*; P*=0.0925) was retained in the final model. Therefore, there was a trend for males with darker chests to have more crevices. In the model based on traditional colour measures, however, the hue of the chest was a strong predictor of refuge availability (Partial R^2 =0.31*; SEO*=-1.94*; P*=0.0012). Males with blue chests had home ranges with more shelters than males with green chests. There was also a weak trend for males with more saturated chests (chest chroma: partial R^2 =0.13*; SEO*=2.84*; P*=0.0806) and green throats (throat hue: partial R^2 =0.12*; SEO*=2.71*; P*=0.0761) to have more crevices. PC1 of the throat and PC2 of the chest were significantly correlated with prey availability (Partial R^2=0.32*; SEO*= -3.78*; P*=0.015 and Partial R^2=0.17*; SEO*= -2.39*; P*=0.0387 respectively; Model R^2=0.49). Therefore, males with more blue than green throats and chests had more prey within their home ranges. Throat hue was also significantly correlated with prey availability in the traditional model (R^2=0.27*; SEO*=-2.07*; P*=0.0285), with males with blue throats having higher prey availability. Larger areas had significantly more refuge sites (R^2=0.62*; P*=0.0009) but there was no relationship between home range size and prey availability (R^2=0.05*; P*=0.386). Therefore, when refuge number was used in subsequent models it was corrected for home range size using a ratio of number of crevices per unit area.

Mean home range overlap was 16±27% (SD) and ranged from 0-87%. Fourteen of the 24 males had completely exclusive ranges, with no overlap at all. Neither model

produced morphological predictors of variation in male overlap in terms of overlap pressure.

2.4.3. What makes a ladies' man?

The number of females per male home range ranged from 0 – 4 (mean = 2±1.142 (SD)). In both models only home range size predicted the number of female associations, with a larger home ranges containing more females (Partial R^2 =0.34*; SEO*=1.06*; P*=0.0116).

Males with larger home ranges spent significantly more time courting females in both models (R^2=0.25*; SEO*=0.55*; P*=0.0307) and there was a trend for males defending areas with lower prey availability to spend more time courting (R^2=0.14*; SEO*=-0.00*; P*=0.0718, both models total R^2=0.39). When home range size and quality were removed from the models, no aspect of male morphology predicted time spent courting mates. I found no relationship between the number of associated females and time spent in courtship (R^2=0.02*; P*=0.5262) or between time spent in courtship relative to the number of associated females (*N*=9; R^2=0.05*; P*=0.1519). This is surprising given the prior positive correlations between home range size and time spent in courtship and home range size and number of females.

2.5. Discussion

Chest coloration was consistently associated with both home range size and quality in terms of refuge number. Throat colour also predicted home range size, prey availability and refuge number in the traditional colour measures model. Chest and throat coloration therefore may signal individual male quality. Males with darker chests tended to have larger and better quality home ranges. Dark chests are related to male status in the lizard *Ctenophorus ornatus* (Lebas and Marshall, 2000) and in a number of bird species (e.g. Veiga, 1993). In *Platysaurus minor* these dark patches may make the coloration of the throat more conspicuous, increasing its effectiveness as a colour signal. In addition, male quality may be signalled by the area of the dark chest patch. Individuals with larger patches are expected to have darker spectral reflectance further up their chests, while individuals with smaller patches would already be showing throat coloration at the position these readings were taken. Alternatively, this relationship may be the result of a negative association between chest brightness and other factors influencing status (Delhey, 2003), such as the trade-offs that occur between multiple ornaments in widow birds (Andersson et al., 2002) and blue tits (Gross, 1996).

Correlations between male morphology and resource quality often occur in species in which males establish breeding territories (Candolin and Voigt, 2001). This can result from male-male competition for high quality territories or from lower quality males being unable to bear the associated costs of territoriality (Candolin and Voigt, 2001). I found no relationship between body size and home range size and quality as only

colour variables were retained in the models. This result was unexpected because body size is a predictor of contest success in this species (see chapter 3) as well as in a number of other taxa (reviewed in Andersson, 1994) and may influence territory acquisition. However, exceptions do occur; in the eastern collared lizard (Baird et al., 2003) as well as some bird species (Hagelin, 2002; Hill et al., 1999) behavioral or other dynamic indicators of quality may override male body size in intra and inter-sexual signaling. There is no relationship between male body size and territory quality in the European beewolf (Strohm and Lechner, 2000) or the yellow-browed leaf warbler (Marchetti, 1998). In such situations, territory occupancy may override body size due to the home advantage of the resident male (Olsson, 1992). In addition, a prior relationship between territory ownership and fighting ability may exist, or there may be differences in motivation between contestants (Maynard Smith, 1982). A residency advantage has been reported for a number of lizard species (Olsson, 1992) including the congeneric *Platysaurus broadleyi* (Whiting, 1999).

Crevices are an important source of refuges from predators in a number of rock dwelling lizards (Cooper, 2003a; Martin and Lopez, 1999a). The minimum distance between a lizard and a refuge influences the risk of foraging and thus influences its behaviour (Cooper, 2003b). Lizards with home ranges with a higher number of suitable refuge sites may be at less risk of predation, are more easily able to regulate their body temperature (Stevenson, 1985), and they may lessen the cost of high-risk reproductive behaviours such as mate guarding (Cooper and Vitt, 2002) or the risk of bright coloration (Martin and Lopez, 1999b). Lizards that defend areas with high prey

abundance also have easier access to food resources. As both of these determinants of spatial quality have fitness benefits, it is likely that higher quality males will defend these resources. These benefits obviously hold true for females as well, and may attract them. Multiple refuges may also be important for gravid females due to their decreased speed and endurance (Cooper et al., 1990).

Home range overlap varied greatly from no overlap at all to 87% overlap. No aspect of male morphology predicted home range overlap in terms of overlap pressure. This may be because male-male overlap is not detrimental in this species and males whose ranges overlap lose no fitness benefits as they still may maintain exclusive territories. Males may also be allocating their resources more towards courting females over a larger less exclusive area rather than in a totally exclusive smaller area (Abell, 1997).

The number of females per home range was consistently positively correlated with home range size. Space use is positively correlated with the number of associated females in several lizard species including *Ctenophorus maculosus* (Olsson, 1995) and *Ctenophorus ornatus* (Lebas, 2001). Estimates of male mating success in lizards may be based on measures of male-female overlap as copulations are often not observed (Abell, 1997, Morrison et al., 2002). This is a reasonable measurement of mating success as overlap does correlate with paternity (Abell, 1997) at least in some lizard systems. Females had relatively small home ranges compared to males, suggesting a polygynous mating system (Stamps, 1983). While few copulations were observed, females appeared to stay in one place and simply mated with the male in that area. In

some lizard species, female lizards most commonly mate with the male whose home range overlaps their own (Stamps, 1983). Females were only observed copulating with more than one male when territories changed ownership, and did not appear co-operative towards either male. Changes in home range ownership were observed on two occasions. I found no evidence that females were selecting for either resources or the males themselves.

The time males spent courting females was significantly correlated with home range size in both models. There was also a trend for males with lower prey availability to spend more time courting mates. Males with larger ranges have increased access to females and may thus spend more time courting them. Males with lower prey availability may allocate more time to courting mates as less of their time is spent foraging.

My study shows that male coloration in *P. minor* plays an important role in the acquisition of large, high quality areas. Colour may thus be linked to male quality. My results also suggest that the spatial distribution of females has little to do with either male or home range quality. The higher number of associated females on larger home ranges is most likely the result of larger areas containing more female home ranges by default. This increased access to females, while not guaranteeing an increased reproductive output (Lebas, 2001), does suggest that individual male range size, as determined by male morphology, is likely to be associated with fitness.

3. CHAPTER THREE: WHICH MALE TRAITS PREDICT AGGRESSION AND CONTEST SUCCESS IN THE LIZARD *PLATYSAURUS MINOR*?

3.1. Abstract

Male contest competition (intrasexual selection) for mates can result in the defence of space and resources, the establishment of social hierarchies, and the evolution of exaggerated morphological traits. I examined the relationship between colour and body size and condition to determine whether colour signalled male quality. Specifically, I investigated whether male morphology (body size and condition, head width and length, and spectral reflectance of the throat, chest and flank) could predict aggression or contest success. I then investigated whether male flat lizards (*Platysaurus minor*) traded-off foraging time against time spent in contests during territory defence. Larger males in better condition had darker, more saturated chests. Males with better body condition were consistently more aggressive and thus more likely to escalate contests to physical contact. There was a consistent trend for larger males to win more contests, but this relationship was only significant in analyses using traditional measures of colour (hue, chroma, brightness). No relationship existed between time spent in contests and time foraging. These results suggest colour, body size and condition, reliably signal some aspects of male quality and play a role in the outcome and escalation of male-male contests, and are thus likely to influence fitness.

3.2. Introduction

Sexual selection theory states that morphological variables, like colour, may reliably signal male quality provided that these traits are condition dependent such that only high quality males may achieve maximum trait expression (Grafen, 1992).
A correlation between colour and other determinants of male quality have been reported in many species including side-botched lizards (Sinervo et al., 2000), blue grosbeaks (Keyser and Hill, 2000), and eastern bluebirds (Siefferman and Hill, 2005). As coloration is generally an energetically cheap signal, with few direct costs, the honesty of the colour signal is thought to be maintained predominantly by the associated hormonal compromises of the immune system, increased conspicuousness to predators, and socially during contests (reviewed in Whiting et al., 2003).

Male contest competition can result in the exaggeration and diversification of armaments, such as horns or lizard throat and body coloration (Andersson, 1994; Baird et al., 2003; Shuster and Wade, 2003; Whiting et al., 2006). A number of lizard families rely on coloration in combination with static or dynamic visual displays during courtship and contests (Ord et al., 2002). An increase in the intensity of competition has been associated with the evolution of increasingly elaborate displays (Ord et al., 2002). Colour badges signal dominance or fighting ability and can be used to prevent contests or reduce the cost of fighting, particularly between individuals with large differences in status (Olsson, 1994; Whiting et al., 2003). Badge size has been found to be a predictor of contest success in the tree lizard *Urosaurus ornatus* (Thompson and Moore, 1991) and the sand lizard *Lacerta agilis* (Olsson, 1992). An

experimental enlargement of badge size in sand lizards resulted in an increase in mate acquisition of almost 400% (Anderholm et al., 2003). Both residency (Olsson and Shine, 2000) and morphology (Olsson, 1992) have also been cited as important determinants of contest success in different lizard species. Contests are most often settled by the assessment of asymmetries in predictors of fighting ability between contestants (Andersson, 1994, Maynard Smith, 1982). In lizards these asymmetries may be body size (Andersson, 1994; Calsbeek and Sinervo, 2002), colour (Hamilton and Sullivan, 2005; Whiting et al., 2006), condition and/or head dimensions (Lopez et al., 2002). However, when differences in the value of the contested resource to the combatants are high, or when differences in morphological asymmetries are very small, the effect of residency may be more important (Olsson and Shine, 2000).

Competition between males for mates and territories almost always involves direct or indirect costs. Direct costs include the energy required to patrol territory borders (Marler and Moore, 1989) which may reduce body condition (Whiting et al., 2006), as well as increased predation risk (Marler and Moore, 1988) or physiological costs (Briffa and Elwood, 2005). Indirect opportunistic costs are usually those that detract from maintenance activities such as foraging (Wittenberger, 1981).

Platysaurus minor are colourful, rupicolous cordylid lizards (Broadley, 1978). They have a restricted distribution in north-eastern South Africa from the Waterberg to the foothills of the Blouberg (Branch, 1998). Currently, there is no published information on the link between condition and morphology, the morphological determinants of

aggression and contest success or the costs of fighting in *Platysaurus minor* although this relationship has been investigated in *Platysaurus broadleyi* (Whiting et al., 2006). All *Platysaurus* species are characterised by extreme sexual dichromatism with brightly coloured males and conservatively coloured females (Scott et al., 2004). *Platysaurus minor* males exhibit large amounts of intrapopulation polymorphism in coloration. Throat colour can be blue, green, or yellow, or any combination of the three (Chapter 2). Their chest colour ranges from black to blue and their ventral stripes from yellow to orange-brown (Chapter 2). Males signal to rivals with a ventral side display that maximises the visibility of throat, chest and flank coloration. During these displays a male raises one side of its body to an angle greater than 60º so that the rival has a clear view of their ventral surface. This behaviour may be performed from a static position or while approaching the rival male. These displays may be combined with other aggressive behaviours such as chasing, lunging or biting.

I examined the relationship between body size and condition and male coloration as both of these factors may influence colour expression (Baird et al., 2003). A positive correlation would suggest that colour reliably signals male traits that may be important for assessment by competitors. I then investigated the relationship between morphology and aggression and contest success. I examined these correlations with aggression and fighting ability separately, because although aggression levels are not always an indicator of fighting ability (Barlow et al., 1986) they can influence contest outcome or even reproductive strategy (Sinervo et al., 2000). I also investigated possible trade-offs between time spent in territory defence and time spent foraging. A

recent study showed that territoriality is costly, resulting in decreased body condition in another flat lizard species (Whiting, et al., in press). A negative relationship between territory defence and foraging effort would suggest that lower condition relates not just to differences in energy reserves, but also different allocation of energy resources. Males who expend more time in territory defence may allocate less time to foraging. While a few studies have quantified the energetic costs of contests (e.g. Cleveland, 1999; Hack, 1997; Whiting et al., 2006) few have quantified opportunity costs.

3.3. Methods and Materials

3.3.1. Study area

The Madikela Private Nature Reserve is situated in the foothills of the Waterberg, Limpopo Province, South Africa (24° 0 S´, 28° 26´ E). The Waterberg mountain region is a savanna, characterised by a mixture of grass and trees (Cowling et al., 1997). The most common trees include *Acacia* species, the african beachwood (*Faurea saligna*), common hookthorn (*Acacia caffra*) and red seringa (*Burkea africana*). My study area was approximately 160 x 40 m on a limestone outcrop with a granite base. During September and October 2004, I captured each lizard on the main outcrop and surrounding stand alone rocks by noosing, and permanently marked them with a unique pattern of toe-clipping (Fisher and Muth, 1989). I also painted temporary numbers on their backs using non-toxic xylene-free paint pens to facilitate easy recognition in the field. I captured 109 males during the study period.

3.3.2. Male traits

For each male I took the following morphological measurements: mass (nearest 0.1g using a digital scale), snout-vent length (SVL; body length from the tip of the snout to the ventral vent; measured to the nearest mm), head width (widest point at occiput) and length (from the tip of the snout to tympanum) (both to the nearest 0.01 mm using digital callipers). Head measurements were transformed to a dimension-free variable using residuals from linear regression on body size. I determined a standard body condition index similarly using SVL and mass (Jakob et al., 1996). All lizards were measured in the early evening and returned to their point of capture early on the following day. This should not interfere with their territorial behaviour as these lizards are diurnal and quickly resumed normal behavioural patterns upon release.

The reflectance of the throat, chest and flanks of each male was measured using an Ocean Optics USB2000 optic spectrometer and deuterium-tungsten DT-1000 mini light source connected to a fibre-optic probe. All readings were taken from the same position on each lizard. A probe-holder ensured that all readings are taken at an angle of 45° from a 5 mm diameter area and at a constant distance from the lizard. The average of three consecutive readings was used in analysis and all measurements were relative to a 99% WS-1 white reflectance standard. I used spectral reflectance between 320 - 700 nm in analyses as this represents the broadest range of known lizard vision (Loew et al., 2002). All experimental procedures were approved by the University of the Witwatersrand Animal Ethics Committee (certificate number 2004 72 2a).

Principal component analysis (PCA), which makes no assumptions about the visual system of the receiver (Cuthill et al., 1999), was used to analyse variation in reflectance spectra. In addition I used traditional measures of hue (spectral location), brightness (spectral intensity) and chroma (spectral purity) (Endler, 1990; Pryke et al., 2001). I biologically interpreted principal components by correlating them with their eignenvectors at each 5 nm interval (Cuthill et al., 1999). I calculated hue as the peak wavelength corresponding to maximum reflectance. Brightness was calculated as the sum of the mean reflectance. Chroma was calculated using the formula $[R_{320\text{-}\lambda(50)} - R_{\lambda(50)\text{-}700}]/R_{320\text{-}700}$ (e.g. Pryke et al., 2001; Andersson et al., 2002) using λ(R50) as the segment divider where λ(R50) is the wavelength half way between minimum and maximum reflectance. This quantifies variation in chroma which is a function of slope height and steepness. I used both methods as while traditional segment colour analysis is simpler to interpret and comparable between studies it is less likely to accurately capture variation in the shape of reflectance curves (Grill and Rush, 2000).

In order to test whether male colour expression was related to other aspects of male morphology, I regressed body condition and size against coloration of the three body regions (throat, chest and flank) for both principal components and hue, chroma and brightness colour measures (N=107).

3.3.3. Aggression, contest success and foraging trade-offs with territory defence

I conducted 104 behavioural focal observations on 43 male lizards. When multiple focals were conducted on a single male, the mean duration of behaviours were calculated. The number of focals per male ranged from 1 – 4. I investigated the relationship between time spent foraging and in contests by recording frequency and duration of individual behaviours and behaviour bouts, on a dictaphone. All time spent chasing, lunging after and eating prey, was scored as foraging. Focal observations lasted 30 min each and were conducted between 0900-1100 h, during peak lizard activity. All behaviours were calculated as proportions of the total time that the lizard was in sight. If the lizard was out of sight for longer than five minutes the focal sample was discarded. An aggression index (Table 3.1.) was determined from these behavioural observations. All observed aggressive behaviours were ranked and given a corresponding aggression score. This ranking system represents the observed escalation of aggressive encounters and presumably the escalation of energetic costs and increased risk of physical injury. This scheme is analogous to those used in other contest studies (e.g. Hack, 1997). In order to calculate the frequency of specific behaviours, I used only those behaviours recorded during focal animal sampling. Each aggression score was multiplied by the observed frequency of the different behaviours and the total aggression score determined by addition of these scores. If an individual was observed in multiple agonistic encounters, the average aggression score of these encounters was used in analysis. I investigated the relationship between aggression and male morphology with a logistic stepwise multiple regression (N = 43).

Table 3.1. Aggression index used in analysis

Behaviour	Aggression score
Runs away	0
Ventral Display	1
Lunge	2
Chase	3
Bite or grab	4

I recorded the duration (s), location (to determine if either individual was a resident) and the outcome of all male-male contests (win or lose). No ties were observed and it was possible to class all individuals as either resident or non-resident as no contests were observed on neutral ground. Only contests in which there was an obvious reaction to the initiator were used in analysis. One individual (winner or loser) was selected from each contest encounter at random and included in a logistic stepwise multiple regression used to determine the relationship between morphology and contest success (Hardy and Field, 1998). I used this method as the behaviour of individuals within a contest are not independent of each other and thus only the behaviour of one individual could be used in analysis. When more than one contest was observed between the same individuals, I used the outcome of the first observed encounter. This resulted in a total of 18 encounters used in analysis. As residency may already reflect fighting ability or resource holding potential (Maynard Smith, 1982), I analysed the data both with and without residency as a predictor separately, to investigate the effects of morphology and residency on contest success.

I regressed time spent in foraging and time spent in contests to determine if a trade-off existed. I also regressed time spent foraging with body condition to test if males who foraged more were in better condition.

3.4. Results

3.4.1. Colorimetry

Individual lizards showed large amounts of variation in spectral reflectance of all the measured regions. Individual throat coloration ranged from blue, to green to yellow, including combinations of these colours while chest colour ranged from black to blue. Individual flank colour varied from yellow to orange-brown. Figures 2.1.a, b and c show examples of this variation in of the throat, chest and flank respectively.

As the first two principal components explained over 80% of the variation for each body region (Table 2.1.), I used only the first two PCs in subsequent multiple regression to minimize the number of variables and for ease of biological interpretation (Stuart-Fox et al., 2003).

Principal component and traditional measures correlations are shown graphically in chapter 2. PC1 is typically correlated with mean reflectance (brightness) (Cuthill et al., 1999), but in this case, the majority of the variation was in curve shape rather than mean reflectance. Therefore, PC1 of the throat described variation in reflectance at short relative to long wavelengths (Figure 2.2.a) and primarily differentiated between males with blue, and males with green, throats. PC1 of the throat was strongly

correlated with hue (r = 0.81; P <0.0001) and negatively correlated with chroma (r = -0.49; P = 0.0009). PC2 of the throat was highly correlated with brightness (r = 0.94; P<0.0001).

Chest reflectance, however, varied most in brightness. Accordingly, PC1 of the chest indicated brightness and was highly correlated with the traditional measure of brightness (r = 0.93; P<0.0001). PC2 of the chest was correlated with both traditional measures of chroma (r = 0.63; P<0.0001) and hue (r = -0.51; P = 0.0005) and described variation in curve shape, specifically, variation in the ratio of reflectance at wavelengths above and below 550 nm (Fig. 2.2.b.). This differentiates between males with blue and males with green chests.

PC1 of the flank is strongly correlated with brightness (r = 0.92; P<0.0001), while PC2 reflects variation in curve shape. This variation is specifically in the ratio of reflectance at wavelengths above and below 550 nm (Fig. 2.2.c), and separates males with yellow-orange flanks from those with orange-brown flanks.

3.4.2. Body condition, size and male colour

Larger males had significantly darker chests when using principal components or traditional colour measures (PC1 of the chest and chest brightness both: R^2=0.05; P=0.0207) and there was a trend for these males to have more blue than green throats when using traditional measures (throat hue: R^2=0.03; P=0.0591). There was also a trend for males in better body condition to have darker chests (PC1 of the chest:

R^2=0.03*; P*=0.0598) when using principal components. Brightness, chroma and hue measurements significantly associated better body condition with high chest saturation (chest chroma: R_2=0.07*; P*=0.0044) and there was a trend for these males to have more blue than green throats (throat hue: R^2=0.03*; P*= 0.0617).

3.4.3. Aggression, contest success and foraging trade-offs with territory defence

Body condition was the strongest predictor of aggression in both models based on PCs and traditional measures of colour (both: R^2 = 0.19*; SEO* = 0.39*; P* = 0.0036). Males in better condition were more aggressive (Figure 3.1.).

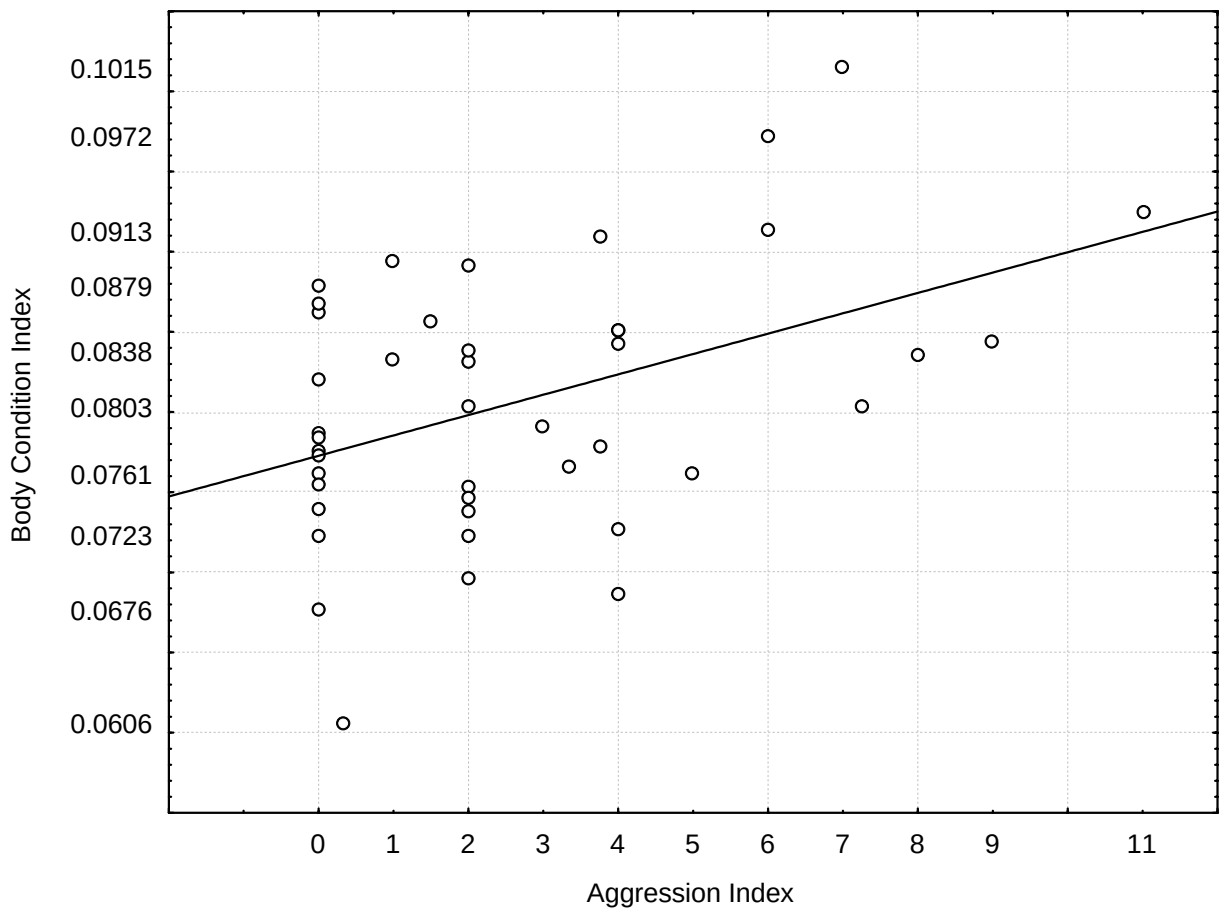

Figure 3.1: Relationship between aggression and body condition

There was a trend for larger males to win more contests ($\chi_{2;1}$= 6.92*; SEO* = 3.31*; P* = 0.0696) when using principal component analysis whether residency was included in the model or not. For the model based on traditional measures, when residency was excluded from the model, SVL was significantly associated with contest outcome ($\chi_{2;2}$= 1.98*; SEO* = 2.76*; P* = 0.044) and there was a trend for individuals with yellow-orange flanks to win over individuals with orange-brown flanks ($\chi_{2;2}$= 0.13*; SEO* = 1.11*; P* = 0.087). When residency was included, body size was still significantly

positively associated with contest success ($\chi_{2;1}$= 1.98*; SEO* = 2.76*; P* = 0.044), while there was a trend for residents ($\chi_{2;1}$= 3.53*; SEO* = 2.40*; P*= 0.06) and lizards with more saturated flanks (flank chroma: $\chi_{2;1}$= 3.01*; SEO* = 1.70*; P* = 0.083) to win contests.

Mean time spent foraging was proportionately 0.0035±0.0045 (SD) of the total time individuals were observed while mean time spent in contests was proportionately 0.0019 ±0.00489 (SD) of the total observed time. No relationship existed between the time spent foraging and the time spent in territory defence (Figure 3.2.; R^2 = 0.005*; P* = 0.653) or between body condition and time spent foraging (R^2=0.05*; P*=0.1519). A more robust measure of contest and foraging behaviour may have involved frequency measures of these behaviours. Unfortunately they were not recorded as such.

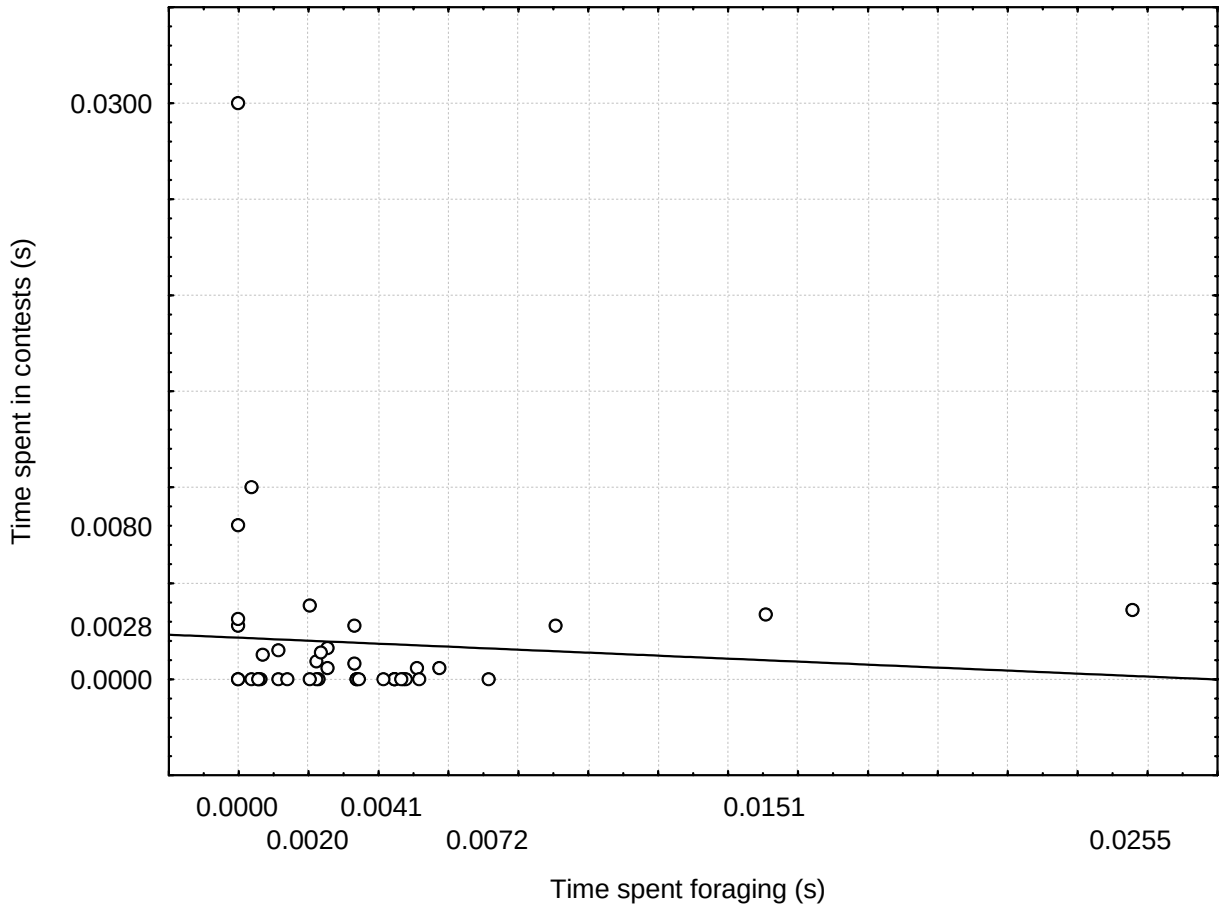

Figure 3.2: Relationship between time (s) spent in contests and time spent foraging. All data points represent fraction of time spent in each activity out of entire time each individual was observed

3.5. Discussion

Condition was a strong predictor of aggression, with males in better condition exhibiting higher levels of aggression, consistent with the view that fighting imposes strong direct costs. Increased energy reserves and/or the ability to recover expended energy quickly allow individuals to indulge in costly tactics (Andersson, 1994). Ritualized aggression is used to avoid or reduce the costs of contests by signalling the

most likely outcome of an encounter (Maynard Smith, 1982). Contests only escalated to physical contact in five (11.6%) of the observed interactions. Males with higher body condition were more likely to escalate these aggressive encounters as they are more likely to be able to withstand the energetic costs of physical fighting as well as the risks of injury. Males were captured with bite marks on the neck and missing phalanges, most likely gained during contests, highlighting the risk of these escalated encounters.

Body size was the only consistent predictor of contest success. In species with intense male competition, a larger body size frequently predicts contest success (reviewed in Andersson, 1994) and this relationship holds true for a number of lizard species (e.g. Olsson, 1992; Lopez et al., 2002; Whiting et al., 2006) as well as some fish (Draud and Lynch, 2002), birds (Hagelin, 2002) and insects (Hack, 1997). The widespread use of size deceptive postural modifiers during contests emphasizes the historic and present importance of body size in these encounters (Jenssen et al., in press).

The colour and saturation levels of a male's flank were found to be correlated with contest success, but not significantly or consistently. The ventral side display of these lizards during contests increases the conspicuousness of this body region. Throat and chest coloration have been found to be predictors of territory size and quality in this species (Chapter2) and thus must play some role in male-male interactions or signal individual male quality. Both body condition and size were correlated with throat and chest coloration. This suggests that colour honestly signals certain aspects of male

quality that predict fighting ability and aggression levels. Throat coloration is a predictor of contest success in the congeneric lizard *Platysaurus broadleyi* (Whiting et al., 2006). The failure to detect a direct relationship between male coloration and aggression or contest success in this study could be due to low statistical power associated with small sample size.

While there was a trend for residents to win contests, this result was not significant or consistent across models. The resident advantage may be because of a prior relationship between territory ownership and fighting ability (Maynard Smith, 1982), particularly when interactions are between a satellite and resident male, or due to different motivation levels between contestants (Maynard Smith, 1982). While a resident advantage, combined with other physical predictors of contest success, has been described for crickets (Hack, 1997), cichlids (Draud and Lynch. 2002), and lizards (Olsson, 1992), including the congeneric *Platysaurus broadleyi* (Whiting, 1999), my study fails to highlight the role of residency as a determinant of contest success in this species. This may be associated with low statistical power due to sample size.

I found no relationship between time spent in territory defence and time spent foraging. However, the lack of correlation between time spent foraging and body condition suggests that time spent foraging may not be as important as type or size of consumed prey or the frequency of foraging events in determining energy consumption. In addition, in this study I investigated the correlation between these

behaviours in males that were all territorial. A comparison of these variables between territorial and floater males might yield different results. While six floater males were identified (chapter 2), this number was not sufficient to use in analyses. However, while this study does not show any opportunity costs of fighting in this species, territory defence is indeed costly (Andersson, 1994) and in another flat lizard species, *Platysaurus broadleyi,* territorial males had significantly lower body condition than floater males (Whiting et al., 2006). It is thus likely that the higher energetic costs of territory defence would be reflected in some other variable. This may include an accelerated loss of body condition during the reproductive season due to increased territorial patrolling, or may be associated with higher levels of testosterone and the resulting compromise of the immune system (Peters, 2000).

I show that larger males are more likely to win contests and that males in better condition are more likely to escalate them. However, certain aspects of throat and chest colour are associated with male body size and condition. In addition, throat and chest colour influence territory acquisition in this species (chapter 2) and must play a role in male-male interactions. As fighting ability and aggression levels may both be important determinants of reproductive tactic, and colour is associated, albeit indirectly, with both of these variables, my study shows an association between male morphology, colour, behaviour and potential fitness.

4. DISCUSSION AND CONCLUSIONS

My study is novel in the way that it investigates the role of an objective measurement of male body colour in space use, resource defence and access to mates in a wild population of lizards. Currently, the role of colour in space use and resource defence is poorly understood in lizard species. In summary, I found that *Platysaurus minor* males with darker and more saturated chests had significantly larger home ranges. Males with more blue than green chests had more refuges available on these home ranges. Prey availability was higher on areas defended by *P. minor* males with blue throats and chests. Larger home ranges had higher numbers of associated females and the males on these areas spent more time courting females. My study shows no evidence for female choice for either males or the resources they defend.

My study also investigates the less extensively studied opportunistic costs of fighting, that is the indirect costs associated with territory defence. I also examined the importance of these measurements of colour as predictors of levels of aggression and likely contest success. I found that males with darker and more saturated chests to be larger and in better condition. More aggressive males, those more likely to escalate contests to physical contact, had better body condition than less aggressive males. Larger *P. minor* males consistently won more contests. I found no opportunistic costs of territory defence in the species. My results reflect and contribute to current sexual selection theory as body size, condition and bright coloration are the male morphological characteristics most often influenced by sexual selection (Andersson,

1994; Baird et al., 2003; Shuster and Wade, 2003). My study highlights the role of these attributes in male-male competition within this species.

Aspects of chest and throat coloration predicted space use and access to resources while body condition and size predicted aggression levels and contest success. This is unexpected as males with the greatest competitive ability are able to defend larger areas containing the better resources (Eckert and Weatherhead, 1987). A link between home range size and quality and fighting ability or other determinants of reproductive tactic has been found in a number of other systems (e.g. Siefferman and Hill, 2005, Sinervo et al., 2000). However, both body size and condition were already correlated with aspects of throat and chest colour. This prior correlation between these variables may explain the lack of significant associations between colour and aggression and contest success in the models.

A number of discrepancies existed between models analyzed using principal components and those using measures of hue, brightness and chroma. These discrepancies are common as neither of these techniques is superior to the other under all conditions and appropriate use of these techniques is highly system specific (Grill and Rush, 2000). Hue, brightness and chroma measurements are more common as these variables are easier to interpret biologically and comparable across studies. Both of these techniques produce more detailed and less biased data than subjective observational techniques (Grill and Rush, 2000). Principal component analysis is more sensitive to variation in colour hue, while both techniques provide good information on

variation in brightness (Grill and Rush, 2000). Since information on the visual system of *P. minor*, including cone pigments and spectral sensitivities of is not available; I used both techniques in my analysis to quantify as much information on colour variation as possible.

This study opens a number of interesting avenues for further research. A more detailed investigation, with a larger sample size, into the factors influencing contest success would highlight the relative importance of residency, morphology and coloration in this species. Laboratory lizard rearing experiments could determine whether colour is genetically or environmentally determined. Paternity tests could test the usefulness of home range size as a predictor of reproductive success in *Platysaurus minor.* As alternative reproductive tactics are now known to exist within this species, this opens for further research into the male morphological variables associated with these strategies.

My study used objective measures of colour to determine correlations between male morphology and other variables that may be influenced by sexual selection. I found a clear link between morphology, including coloration, and a number of attributes that may increase male fitness. Colour thus plays an important role in intra-sexual signalling in *Platysarus minor.*

5. REFERENCES

Abell, A. J. (1997) Estimating paternity with spatial behaviour and DNA fingerprinting in the striped plateau lizard, *Sceloporus virgatus* (Phrynosomatidae), Behav. Ecol. Sociobiol., 41: 217—226

Abell, A.J. (1998) Male-female spacing patterns in the lizard, *Sceloperus virgatus,* Amphibia-Reptilia, 20:185-194

Anderholm, S. Olsson, M. Wapstra, E. and Ryberg, K. (2003) Fit and fat from enlarged badges: a field experiment on male sand lizards, Proceedings of the Royal Society B: Biological Sciences , 271: S142 - S144

Andersson, M. (1994) Sexual Selection. Princeton University Press, Princeton

Andersson, S., Pryke, S. R., Ornborg, J., Lawes, M. J. & Andersson, M. (2002) Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signalling in a widowbird, American Naturalist, 160: 683-691

Baird, T.A., Fox, S.F. and McCoy, J.K. (1997) Population differences in the roles of size and coloration in intra- and intersexual selection in the collared lizard, C*rotaphytus collaris*: influence of habitat and social organization, Behavioral Ecology, 8(5): 506-517

Baird, T.A., Timanus, D.K. and Sloan, C.L. (2003) Intra- and Intersexual Variation in Social Behaviour: Effects of Ontogeny, Phenotype, Resources and Season, in Lizard Social Behaviour, eds Fox, S.F., McCoy, J.K. and Baird, T.A., John Hopkins University Press

Bakker, T.C.M. (1993) Positive genetic correlation between female preference and preferred male ornament in sticklebacks, Nature, 363: 255-257

Barlow, G. W., Rogers, W. and Fraley, N. (1986) Do Midas Cichlids win through prowess or daring? It depends, Behav. Ecol. Sociobiol., 19: 1-8.

Bart, J. and Earnst, S.L. (1999) The relative importance of male and territory quality in paring success of male rock ptarmigan (*Lagopus mutus*), Behav. Ecol. Sociobiol., 45(5): 355-359

Branch, W.R. (1998) Field guide to the Snakes and other Reptiles of Southern Africa, 3rd Ed. Struik Publishers, Cape Town

Briffa, M. and Elwood, R.W. (2005) Rapid change in energy status in fighting animals: Causes and effects of strategic decisions, Animal behaviour, 70: 119-124

Broadley, D.G. (1978) A Revision of Genus *Platysaurus* (Sauria: Cordylidae). Occ. Pap. Natn. Mus. Rhodesia. Ser. B, 6(4): 131-185

Calsbeek, R. and Sinervo, B. (2002) The ontogeny of territoriality during maturation, Oecologia, 132 (3): 468-477

Candolin, U. (2000) Increased signaling effort when survival prospects decrease: male–male competition ensures honesty, Animal Behaviour, 60: 417–422

Candolin, U. and Voigt, H. (2001) Correlation between male size and territory quality: consequence of male competition or predation susceptibility? OIKOS 95: 225-230

Cleveland, A. (1999) Energetic costs of agonistic behaviour in two herbivorous damselfishes (*Stegastes*), Copeia, 4: 857-867

Clutton-Brock, T.H. and Vincent, A.C.J. (1991) Sexual selection and the potential reproductive rates of males and females, Nature, 351: 58-60

Cooper, W.E. Jr. (2003a) Shifted balance of risk and cost after autotomy affects use of cover, escape, activity, and foraging in the keeled earless lizard (*Holbrookia propinqua*), Bahav. Ecol. Sociobiol., 54: 179-187

Cooper, W.E. Jr. (2003b) Effect of Risk on of Escape Behaviour by a Lizard, *Holbrookia propinqua,* in Relation to Optimal Escape Theory, Ethology, 109(8): 617-626

Cooper, W.E. Jr. and Vitt, L.J. (1993) Female mate choice of large male broad-headed skinks. Animal Behaviour, 45: 683-693

Cooper, W.E. Jr. and Vitt, L.J. (2002) Increased predation risk while mate guarding as a cost of reproduction for male broad-headed skinks (*Eumeces laticeps*), Acta. Ethol., 5: 19-23

Cooper, W.E. Jr., Vitt, L.J., Hedges, R. and Huey, R.B. (1990) Locomotor impairment and defense in gravid lizards (*Eumeces laticeps*): behavioral shift in activity may offset costs of reproduction in an active forager, Behav. Ecol. Sociobiol., 27(3): 153-157

Cowling, R.M., Richardson, D.M. and Pierce, S.M. (1997) Vegetation of Southern Africa. Cambridge University Press, Cambridge, UK

Crews, D. and Moore, M.C. (1986) Evolution of mechanisms controlling mating behaviour, Science, 231:121-125

Cuthill, I. C., Bennett, A. T. D., Partridge, J. C. & Maier, E. J. (1999) Plumage reflectance and the objective assessment of avian sexual dichromatism, American Naturalist, 160: 183-200

Delhey, K., Johnsen, A., Peters, A., Andersson, S. and Kempenaers, B. (2003) Paternity analysis reveals opposing selection pressures on crown coloration in the blue tit (*Parus caeruleus*), Proc. R. Soc. Lond. B, 270: 2057–2063

Draud, M. and Lynch, P.A.E. (2002) Asymmetric contests for breeding sites between monogamous pairs of convict cichlids (*Archocentrusnigrofasciatum, Cichlidae*): Pair experience pays, Behaviour, 139: 861-873

Eckert and Weatherhead, (1987) Competition for territories in red-winged blackbirds: Is resource holding potential realized? Behav. Ecol. Sociobiol., 20(5): 369-375

Endler, J. A. (1990) On the measurement and classification of colour in studies of animal colour patterns, Biological Journal of the Linnean Society, 41: 315-352

Endler, J.A. (1992) Signals, Signal Conditions, and the direction of Evolution, The American Naturalist, 139: s125-153

Fisher, M. and Muth, A. (1989) A technique for permanently marking lizards, Herpetological Reveiw 20: 45–46

Fleishman, L.J. and Persons, M. (2001) The Influence of stimulus and background colour on signal visibility in the lizard *Anolis Cristatellus,* J. of Experimental Biology, 204: 1559-1575

Grafen, A. (1992) Sexual selection unhandicapped by the Fisher process, J. of Theoretical Biology, 144: 473-516

Grill, C. P. & Rush, V. N. 2000. Analysing spectral data: comparison and application of two techniques, Biological Journal of the Linnean Society, 69: 121-138

Gross, M. R. (1996) Alternative reproductive strategies and tactics: diversity within sexes, Trends in Ecology and Evolution, 11: 92–98

Hack, M.A. (1997) Assessment strategies in the contests of male crickets, *Acheta domesticus* (L.), Animal Behaviour, 53: 733-747

Hagelin, J.C. (2002) The kinds of traits involved in male–male competition: a comparison of plumage, behavior, and body size in quail, Behavioral Ecology, 13(1): 32-41

Hamilton, P.S. and Sullivan, B.K. (2005) Female mate attraction in ornate tree lizards, *Urosaurus ornatus*: a multivariate analysis, Animal Behaviour, 69: 219-224

Hardy, I.C.W. and Field, S.A. (1998) Logistic analysis of animal contests, Animal Behaviour, 56: 787-792

Hews, D.K. (1993) Food resources affect female distribution and male mating opportunities in the iguanian lizard, *Uta palmeri,* Animal Behaviour, 46(993): 279-291

Hill, G.E. (1991) Plumage coloration is a sexually selected indicator of male quality, Nature, 350: 337-339

Higashi, M., Takimoto, G. and Yamamura, N. (1999) Sympatric speciation by sexual selection, Nature, 402(2): 523-526

Honkavaara, J., Koivula, M., Korpima¨ki, E., Siitari, H. and Viitala, J. (2002) Ultraviolet vision and foraging in terrestrial vertebrates, OIKOS, 98:505-511

Jakob, E., Marshall, S. and Uetz, G. (1996) Estimating fitness: a comparison of body condition indices, OIKOS, 77: 61-67

Keyser, A.J. and Hill, G.E. (2000) Structurally based plumage colour is an honest indicator of quality in male blue grosbeaks, Behavioural Ecology 11: 202 – 209

Kingston, J.J., Rosenthal, G.G. and Ryan, M.J. (2003) The role of sexual selection in maintaining a colour polymorphism in the pygmy swordtail, *Xiphophorus pygmaeus,* Animal Behaviour, 65: 735-743

Kleene, K.C. (2005) Sexual selection, genetic conflict, selfish genes, and the atypical patterns of gene expression in spermatogenic cells, Developmental Biology, 277: 16-26

Krebs, R.A. and West, D.A. (1988) Female mate preference and the evolution of female3-limited batesian mimicry, Evolution, 42: 1101-1104

Lappin, A.K. and Husak, J.F. (2005) Weapon Performance, Not Size, Determines Mating Success and Potential Reproductive Output in the Collared Lizard (*Crotaphytus collaris*), American Natrualist, 166: 426-436

LeBas, N.R. (2001) Microsattelite determination of male reproductive success in a natural population of the territorial ornate dragon, *Ctenophorus ornatus*, Molecular Ecology 10: 193 - 203

LeBas, N.R. and Marshall, N.J. (2000) No evidence of female choice for a condition dependant trait in the agamid lizard, *Ctenophorus ornatus*, Behaviour, 138(8): 965-980

LeBas, N.R. and Marshall, N.J. (2000) The role of colour in signalling and male choice in the agamid lizard *Ctenophorus ornatus,* Proceedings of the Royal Society of London, 267: 445-452

Loew, E. R., Fleishman, L. J., Foster, R. G. & Provencio, I. (2002) Visual pigments and oil droplets in diurnal lizards: a comparative study of Caribbean anoles, Journal of Experimental Biology, 205: 927-938

Lopez, P., Munoz, A. and Martin, J. (2002) Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta Monticola*, Behavioural Ecology and Sociobiology, 52 (4): 342-347

Maher, C.R. and Lott, D.F. (2000) A review of ecological determinants of territoriality within vertebrate species, The American Midland Naturalist, 143(1): 1-29

Marchetti, K. (1998) The evolution of multiple male traits in the yellow-browed leaf warbler, Animal Behaviour, 55(2): 361-76

Marler, C.A. and Moore, M.C. (1988) Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards, Behavioural Ecology and Sociobiolgy, 23(1): 21-26

Marler, C.A. and Moore, M.C. (1989) Time and energy costs of aggression in testosterone-implanted free-living male spiny lizards (*Sceloporus jarrovi*), Physiological Zoology, 62: 1334-1350

Martin, J. and Lopez, P. (1999a) When to come out from a refuge: risk sensitive and state-dependent decisions in an alpine lizard, Behav. Ecol., 10: 487–492

Martin, J. And Lopez, P. (1999b) Nuptial Coloration and Mate Guarding Affect Escape Decisions of Male Lizards *Psammodromus algirus,* Ethology, 105: 439-447

Maynard Smith, J. (1982) Evolution and the theory of games. Cambridge University Press, Cambridge

Miles, D.B. 1994. Covariation between morphology and locomotor performance in sceloporine lizards. In: Lizard Ecology: Historical and Experimental Perspectives (eds L. J. Vitt & E. R. Pianka), pp. 207–235. Princeton University Press, Princeton, NJ.

Morrison, S.F., Keogh, S.J. and Scott, I.A.W. (2002) Molecular determination of paternity in a natural population of the multiply mating polygynous lizard *Eulamprus heatwolei*, Molecular Ecology, 11 (3): 535-540

Olssen, M. and Shine, R. (2000) Ownership influences outcome of male-male contests in the scincid lizard, Behavioural Ecology, 11: 587-590

Olsson, M. (1992) Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*, Animal behaviour, 44: 386-388

Ord, T.J., Blumstein, D.T., Evans, C.S. (2002) Ecology and signal evolution in lizards, Biological Journal of the Linnean society, 77: 127-148

Panhuis, T.M., Butlin, R., Zuk, M. and Tregenza, T. (2001) Sexual selection and speciation, Trends in Ecology and Evolution, 16(7): 364-371

Peters, A. (2000) Testosterone treatment is immunosuppressive in superb fairy-wrens, yet free-living males with high testosterone are more immunocompetent, Proceedings of the Royal Society of London B, 267: 883-889

Pryke, S. R., Andersson, S. & Lawes, M. J. (2001) Sexual selection of multiple handicaps in the red-collared widowbird: Female choice of tail length but not carotenoid display, Evolution, 55: 1452-1463

Pryke, S.R. and Andersson, S. (2003) Carotenoid-based status signalling in red-shoulder widowbirds (*Euplectes axillaris*): epaulet size and redness affect captive and territorial competition, Behavioural Ecology and Sociobiology, 53(6): 393-401

Reaney, L.T. and Whiting, M.J. (2003) Are female tree agamas (*Acanthocercus atricollis atricollis*) turned on by males or resources? Ethology, Ecology and Evolution, 15:19-30

Rose, B. (1982) Lizard home ranges: Methodology and Functions, Journal of Herpetology, 16: 253-269

Scott, I.A.W., Keogh, J.S. and Whiting, M.J. (2004) Shifting sands and shifty lizards: molecular phylogeny and biogeography of African flat lizards (*Platysaurus*), Molecular Phylogenetics and Evolution, 31: 618-629

Siefferman, L. and Hill, G.E. (2005) UV blue structural coloration and competition for nest boxes in male eastern bluebirds, Animal behaviour, 69: 67-72

Shuster, S.M. and Wade, M.J. (2003) Mating Systems and Strategies, Princeton University Press, Princeton

Sinervo, B., Miles, D. B., Frankino, W. A., Klukowski, M. and DeNardo, D. F. (2000) Testosterone, endurance, and darwinian fitness: Natural and sexual selection on the physiological bases of alternative male behaviors in side-blotched lizards, Hormones and Behavior, 38: 222-233

Stamps, J.A. (1983) Sexual selection, sexual dimorphism and territoriality in lizards, in Lizard Ecology: Studies of a Model Organism eds Huey, R. B., Pianka, E. R. and Schoener, T. W., Harvard University Press, Cambridge

Stevenson, R.D. (1985) Body size and limits to the daily range of body temperature in terrestrial ectotherms, The American Naturalist, 125: 102-117

Strohm, E. and Lechner, K. (2000) Male size does not affect territorial behaviour and life history in a Sphecid wasp, Animal Behaviour, 59: 183-191

Stuart-Fox, D.M., Moussalli, A., Marshall, J. and Owens, I.P.F. (2003) Conspicuous males suffer higher predation risk: visual modeling and experimental evidence from lizards, Animal Behaviour, 66: 541-550

Takeda, S. (In press) Behavioral evidence for body colour signalling in the fiddler crab *Uca perplexa* (Brachyura: Ocypodidae) Journal of Experimental Biology and Marine Ecology

Thompson, C.W. and Moore, M.C. (1991) Throat colour reliably signals status in male tree lizards, *Urosaurus ornatus,* Animal behaviour, 42: 745-753

Thompson, C.W., Moore, I.T. and Moore, M.C. (1993) Social, environmental and genetic factor in the ontogeny of phenotypic differentiation in a lizard with alternative male reproductive strategies, Behavioural Ecology and Sociobiology, 33: 137-146

Veiga, J.P. (1993) Badge size, phenotypic quality, and reproductive success in the house sparrow, Evolution, 49:570-572

Watson, P.J. and Thornhill, R. (1994) Fluctuating asymmetry and sexual selection, Trends in Ecology and Evolution 9(1): 21-25

Whiting, M.J. (1999) When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi,* Behavioural Ecology and Sociobiology, 46(3): 210-214

Whiting, M.J., Nagy, K.A. and Bateman, P.W. (2003) Evolution and Maintenance of Social Status-Signalling Badges: Experimental Manipulations in Lizards, in Lizard Social Behaviour, eds Fox, S.F., McCoy, J.K. and Baird, T.A., John Hopkins University Press

Whiting, M.J., Stuart-Fox, D.M., O'Connor, D., Firth, D., Bennet, N.C. and Blomberg, S. (2006) Ultraviolet signals ultra-aggression in a lizard, Animal Behaviour, Animal Behaviour 72:353-363.

Wittenburger, J.F. (1981) Animal Social Behaviour, Duxbury press, Boston

Wolfenbarger, L. (1999) Red coloration of male northern cardinals correlates with mate quality and territory quality, Behavioural Ecology, 10(1): 80-90

Zamudio, K.R. and Sinervo, B. (2003) Ecological and Social Contexts for the Evolution of Alternative Mating Strategies, in Lizard Social Behaviour, eds Fox, S.F., McCoy, J.K. and Baird, T.A., John Hopkins University Press

Table A.1: Male Morphological Attributes

Attribute	Mean	Max	Min	Std Dev
Mass (g)	5.558	7.2	4.5	0.595
SVL (mm)	66.93	74	63	2.529
BCI (dimension free)	0.0829	0.101	0.068	0.007
Head Length (dimension free)	-0.392	5.679	-11.082	3.7042
Head Width (dimension free)	-0.531	5.256	-11.364	3.7486
Throat Hue (nm)	521.162	580	360	44.143
Throat Chroma	0.694	0.92	-0.284	0.188
Throat Brightness	1966.617	2847.013	867.005	467.441
Chest Hue (nm)	503.953	575	350	47.416
Chest Chroma	0.815	0.958	0.485	0.107
Chest Brightness	928.29	2229.878	136.561	475.274
Side Hue (nm)	683.372	700	640	17.068
Side Chroma	0.154	0.548	0.002	0.134
Side Brightness	689.315	1639.812	53.175	455.309

Table A.2: Home Range and Behavioural Attributes

Attribute	Mean	Max	Min	Std Dev
Home Range Size (log)	0.702	1.582	-0.04	0.337
Number females	2	4	0	1.142
Number Refuges	6.916	15	2	2.903
Prey Availability (item/home range)	10.294	27	0	5.524
Percentage Overlap Competitors (%)	15.753	87.374	0	27.244
Overlap Pressure Competitors (dimension free)	0.157	0.874	0	0.272
Percentage Overlap Mates (%)	37.13	76.719	0	21.855
Overlap Pressure Mates (dimension free)	0.371	0.767	0	0.219
Proportion of time spent in Courtship	0.006	0.027	0	0.007
Proportion of time spent in Prey Capture	0.0035	0.0255	0	0.005
Proportion of time spent in Contests and Defense	0.002	0.03	0	0.005