SEXUAL SELECTION, SOCIAL BEHAVIOR, AND CONSERVATION OF CHAMELEONS IN SOUTHWESTERN MADAGASCAR

By

KRISTOPHER BRETT KARSTEN

Bachelor of Science in Biology
Truman State University
Kirksville, Missouri
1997

Master of Science in Biology
Texas Christian University
Fort Worth, Texas
2000

Submitted to the Faculty of the
Graduate College of the
Oklahoma State University
in partial fulfillment of
the requirements for
the Degree of
DOCTOR OF PHILOSOPHY
May, 2008

SEXUAL SELECTION, SOCIAL BEHAVIOR, AND CONSERVATION OF CHAMELEONS IN SOUTHWESTERN MADAGASCAR

Dissertation Approved:

Stanley F. Fox
Dissertation Adviser

Christopher J. Raxworthy

Troy A. Baird

Matthew B. Lovern

Michael W. Palmer

A. Gordon Emslie
Dean of the Graduate College

ACKNOWLEDGMENTS

I owe many thanks to my dissertation advisers, Stan Fox and Chris Raxworthy, and to my committee members, Troy Baird, Matt Lovern, and Mike Palmer. All these individuals have substantially contributed to my development as a scientist either through intellectual conversation, courses they have taught, and/or through financial support. Their contributions to this dissertation greatly improved it. I am grateful to each for everything they have done to benefit me as a person, scientist, and future colleague.

This body of work is a collaboration in the truest sense. It is important to recognize that all chapters in this dissertation are the result of the incredible amount of work and input by each coauthor: Laza Andriamandimbiarisoa, Stan Fox, and Chris Raxworthy. I thank Laza, especially, for his input as a coworker in the field, his understanding and patience throughout the field study, his ability to quickly grasp new concepts and improve upon them, and his friendship and camaraderie. I wish him great success as he continues his career in biology and I hope to continue working with him as a colleague for future research.

Many people were responsible for improving the quality of this research in the field. Each is mentioned in the chapter-specific acknowledgment sections, but my colleagues at the University of Antananarivo were an integral part of the success of my dissertation, especially Daniel Rakotondravony and Olga Ramilijaona. Hannah Thomas and Daren Kidney of Frontier were extremely generous with their time and advice on logistical support in the field. Field studies in Madagascar were made possible due to the assistance of the Ministries des Eaux et Forêts, the Association Nationale pour la Gestion des Aires Protégées, and many other government and non-governmental organizations. I thank the many people of Madagascar who assisted me throughout my visits. Research was supported by a grant from the National Science Foundation (DEB 99-84496) to Chris Raxworthy.

I am thankful that I was able to work and associate with so many great graduate students. Day Ligon, Jerry Husak, and Aaron Place especially stood out; we shared many great intellectual conversations and some great not so intellectual social situations. I greatly value the friendships we formed during our time at Oklahoma State University. I look forward to continuing to work with them as we all move forward into the next stages of our careers.

One of the most positive influences on me as a researcher and person has been my interaction with my former adviser, Gary Ferguson. Without his knowledge, patience, and understanding with a novice—and often difficult—pupil, I would have given up my dream of pursuing this career path long ago. I continued to rely upon him for much advice for my dissertation even though I am no longer his student; I hope to continue to have him as my mentor for as long as he will allow as I continue my career.

Finally, I am indebted to the people who have helped me the most: my family. My parents, Connie and Eric Parsons and Larry and Jacque Karsten, have always encouraged me to pursue what I am passionate about, no matter how far-fetched those dreams may be. The person who has suffered the most during my doctoral degree, and deserves most of the credit for its success, is my wife, Melanie. Her unconditional support, positive

outlook, friendship, and infinite patience have made me a better person. And I thank my sons, Brady and Alex, who, although they presently have no idea how much they have helped me in completing my dissertation, brought balance to my life and ignited a new-found passion to be the best that I can be as both a researcher and role model.

TABLE OF CONTENTS

LIST OF TABLES

Table Page

CHAPTER I.

Table Page

CHAPTER II.

CHAPTER III.

CHAPTER IV.

LIST OF FIGURES

Figure Page

CHAPTER I.

CHAPTER II.

CHAPTER III.

Figure Page

CHAPTER IV.

I. Social behavior of two species of chameleons in Madagascar: insights into sexual selection

Abstract

Signalling plays a critical role in social behaviour, particularly in polygynous systems where males compete with rival males and use signals to attract mates. We quantified visual signals and social behaviour in two previously unstudied species of chameleons in Madagascar, *Furcifer labordi* and *F. verrucosus*. Females of both species displayed distinct colour patterns which signalled sexual receptivity. Non-receptive females rejected all male courtship. Potentially receptive *F. verrucosus* females mainly allowed males to attempt copulation whereas potentially receptive *F. labordi* females were selective. We found that the fleshy, paddle-like rostral appendage in *F. labordi* was used only during courtship, whereas other studies showed that hard, keratinized ones were used for male combat. During male-male contests, *F. labordi* had much more physically intense encounters, possibly to more accurately assess opponent quality since adult male *F. labordi* were significantly and naturally more size-matched than adult male *F. verrucosus*. Our study elucidated the role of social signals in these species, illustrated the atypical social behaviour of chameleons compared to other lizards, and provided testable hypotheses to further delineate sexual selection in this understudied group. Sexual selection, especially intersexual selection, appears more likely in *F. labordi*.

Introduction

An important aspect of social behaviour is its potential influence on mating success and fitness, especially in the context of intra- and intersexual selection. For many vertebrates, signals used during social behaviour are often those associated with sexually selected traits in polygynous mating systems: colourful displays, potential indicators of fighting ability, or acoustic signals (Andersson 1994; Berglund et al. 1996; Welch et al. 1998; Jenssen et al. 2000; Andersson et al. 2002; Endler et al. 2005; Vanhooydonck et al. 2005; Lappin et al. 2006; Meyers et al. 2006; Whiting et al. 2006). In these systems, rival males often employ signals to communicate aspects of fighting ability, but they can also direct these signals toward females during courtship (Berglund et al. 1996; McGlothlin et al. 2005). Thus, social behaviour—and its effects on sexual selection—plays an important role in the evolution of many animal social systems (Andersson 1994).

Many lizard species use physical displays, often coupled with colour as a visual signal, in male-male contests or to court females (Jenssen et al. 2000; Ord and Martins 2006). Presumably, many of these displays signal some aspect of male ‘quality’ (Brandt 2003; Lailvaux and Irschick 2006; Lappin et al. 2006). Although lizards use many forms of displays for social behavior, their roles can be complex (Baird et al. 2007; Sullivan and Kwiatkowski 2007; Fitze et al. 2008). For example, displays typically used for male combat have the potential to serve also as courtship displays, but not always. Lizard social signals are diverse, ranging from throat or ‘dewlap’ extensions with or without head bobs (Jenssen et al. 2000), potentially coupled with pushup displays (Meyers et al. 2006; Baird et al. 2007), to reflecting conspicuous colours or ultraviolet wavelengths

(Whiting et al. 2006). Despite the bias on male social signals in polygynous systems, female visual signals (e.g., signalling reproductive status) may also play an important role in social communication (Baird 2004).

During their typical diurnal activities, chameleons are cryptic. However, during bouts of intra- or intersexual communication, they can rapidly exhibit conspicuous visual displays (Ferguson et al. 2004; Stuart-Fox et al. 2006; Stuart-Fox and Moussalli 2008). Unlike most other lizards, chameleons are not known to use stereotyped pushup displays; however, chameleons do employ the use of extended lateral displays. Chameleons are also morphologically diverse, and males often possess exaggerated secondary sexual characters (Parcher 1974; Bickel and Losos 2002), which may potentially be correlated with some aspect of quality or performance, and in turn be subject to inter- or intrasexual selection, or both.

Establishing a composite understanding of complex social behaviour can be difficult in understudied groups without establishing a baseline framework. Therefore, an ethogram becomes an important tool in understanding behaviour and social communication in these understudied taxa (Martin et al. 2005; Norris and Hosie 2005; Kunz et al. 2006), such as is the case with most species of chameleons (for exceptions see Parcher 1974; Cuadrado 2001; Kelso and Verrell 2002; Stuart-Fox and Whiting 2005; Stuart-Fox et al. 2006). Lack of studies in this taxon is mostly due to an inability to conduct field observations due to the very cryptic nature of chameleons during periods of non-communication. Despite these studies on chameleon behaviour, we know virtually nothing about species in Madagascar, and no detailed behavioural studies have been published to date in scientific publications on our two focal species. Using the chameleons, *F. labordi* and *F. verrucosus*, the purposes of this paper are to 1) quantify and develop an ethogram of generalized courtship behaviour and intraspecific male-male agonism for each species, 2) determine if males of each species differently court females who signal reproductive status with condition-specific coloration, 3) determine if there are species-specific differences in female response to courting males depending upon female reproductive status, 4) compare the species with respect to agonistic behaviour of victorious and losing males in intraspecific male-male encounters, 5) develop a composite understanding of the social behaviour of these species, and 6) provide testable hypotheses to further elucidate the role of sexual selection in chameleons.

Materials and methods

Study site and species

Furcifer labordi is a medium-sized, sexually dimorphic, diurnal chameleon inhabiting the western and south-western regions of Madagascar. Males reach an average adult snout-to-vent length (SVL) of 87.25 mm (n = 99) and females 71.02 mm (n = 55) in our study populations. Males also possess large cranial casques and rostral appendages. *Furcifer verrucosus* is also a sexually dimorphic species, with males having an average SVL of 148.59 mm (n = 51) and females 113.28 mm (n = 30) in our study population. This species also possesses a cranial casque, but lacks a rostral appendage. Like most other species of lizards in Madagascar, both species are seasonally active and reproduce during the wet season, approximately from November to April, depending on region.

The study site was located approximately 30 km north of the provincial capital of Toliara (Tuléar), near the village of Ranobe (23°01’30” S, 43°36’36” E). This region is spiny forest with a sand substrate, and vegetation that usually does not exceed 3 m in height except for occasional trees that may reach to 10 m height. During the wet season, this region has a mean monthly precipitation of 89.9 mm (Vose et al. 1992).

We collected all data from 20 December 2003 – 06 February 2004, capturing most specimens at night when they were easiest to find. Upon capture, we marked locations and transported lizards to a field camp, where we held them overnight in plastic containers covered with plastic mesh. The following morning we measured body size (SVL), total length (TL), mass, and secondary sexual characters: rostral length, height, and width (in *F. labordi* only); casque depth, height, and width; jaw length; number of dorsal cones and height of tallest dorsal cone. All chameleons received a temporary identification mark consisting of three, small, painted, colour-coded dots on the hindlimb. We also gave all individuals a permanent identification by toe-clipping the most distal phalanx in a three-toe combination, with only one toe clipped per foot. We observed no adverse side-effects of this marking procedure on the behaviour and survival of individuals, nor did we observe any partial or full phalanx regrowth to confuse individual markings. We returned all lizards to their point of capture within 24 hours.

Arena trials

The day after capture, we conducted all trials in an outdoor, neutral arena (none of the lizards were caught in the vicinity of the arena). The arena was approximately 1x1 m square and 2 m in height. We built the rectangular frame from small, cut saplings and covered it with 1.25-cm square plastic mesh. Inside the arena was natural vegetation, which we trimmed back from the mesh. Two observers carefully recorded all behavioural data from behind a blind. Preliminary studies revealed that the presence of observers concealed by a blind did not affect the behaviour of either male or female chameleons alone or during social interactions (Karsten, unpublished data), and behaviour during arena trials was similar to that of free-ranging, radio-tagged individuals (Karsten and Andriamandimbiarisoa, personal observation).

We conducted 108 behavioural trials, each 30 minutes, resulting in 54 hours of observation. We recorded the frequencies of observed categories of social behaviour (Table 1) for 47 male-female trials with *F. labordi*, 28 male-female trials with *F. verrucosus*, 26 male-male trials with *F. labordi*, and 7 male-male trials with *F. verrucosus*. Additionally, we calculated a graded agonism score for each individual by ranking each class of behaviour in an individual's repertoire according to its intuitive 'cost.' Hyper-aggressive behaviour that carried substantial risk for physical injury received the highest values, whereas behaviour that minimized cost of injury was given negative values (Table 2, see also Baird et al. 1997). During male-male encounters, submissive colour carried the most negative value since it signalled absolute submission, effectively ending further social interaction. The losers of the interaction were those that fled the encounter, typically toward the ground, or became dislodged during a fight. This protocol yielded a clear winner and loser for all trials.

If copulation occurred during intersexual trials, we recorded male preparation time, duration of copulation, female-desired duration of copulation, and male ability to retain copulation after perceived female unwillingness. Once females exhibited a willingness to copulate (i.e., they did not show any aggressive displays, agonism, or physical confrontations), males began a rather predictable sequence of events. Once females raised their tails and presented the cloaca, the male superimposed the female, established a grasp, then prepared the hemipenes for intromission. Male *F. labordi* then continually grasped, released, and regrasped the female, which we defined as male preparation time. Once copulation began, both lizards remained relatively motionless. After a period of time, it was usually the female who began movement, attempting to end copulation. We recorded this time between the beginning of copulation and the beginning of female movement as the female's desired duration of copulation. After this, the male retained his grasp for as long as he was physically able, which we describe as male ability to retain copulation. Total duration of copulation was from the beginning of intromission until the end of the male's ability to retain copulation.

Results

Casque sexual dimorphism

Both species were sexually dimorphic in casque height, measured from the top of the casque to the angle of the jaw. Male *F. labordi* casques grew at significantly faster rates than did females (ANCOVA test of difference of slopes, $F = 128.21$, df = 1,150, $p < 0.001$; Figure 1). In *F. verrucosus*, the rates at which the casques grew were different, but not significantly so (ANCOVA test for slopes, $F = 3.36$, df = 1,77, $p = 0.07$, *ns*). Casque height (corrected for SVL) was sexually dimorphic, with males having significantly larger casques than females (ANCOVA test for difference of intercepts, $F = 55.49$, df = 1,78, $p < 0.001$). Using the slopes obtained from casque size regressed against SVL, we calculated a ratio of male to female casque growth dimorphism for each species. The degree of sexual dimorphism in casque height growth was greater in *F. labordi* (male:female = 1.81) than in *F. verrucosus* (male:female = 1.45). The rate of growth in casque height relative to body size was significantly greater in *F. labordi* males compared to *F. verrucosus* males (ANCOVA test for difference of slopes, $F = 6.41$, df = 1,146, $p = 0.01$).

Female colour patterns

Females of each species displayed two distinct colour patterns. In *F. labordi* early in the reproductive season, females exhibited a conspicuous yellow spot on the anterior flank (near the pectoral girdle) against emerald green background coloration with smaller faint yellow spots on the lateral sides of the body. When approached by a courting male, the faint yellow spots became conspicuously contrasted against a dark green to black background. This colour pattern was consistent among females who were sexually non-receptive (NR), rejecting all male courtship (100%, n = 26). The other colour morph exhibited by females, occurring only in the latter portion of the season, consisted of pastel violet spots on a light green background when passive, and the anterior flank spot was bright red. These females exhibited characteristics consistent with sexual receptivity and we hereafter refer to them as potentially receptive (PR). When approached by courting males, PR females either remained in this passive, receptive coloration or turned to a background colour of black with heavily contrasting purple spots, red flank spot, and orange spots along the dorsal crest, which signalled behavioural non-receptivity.

Furcifer verrucosus females also had two distinct colour patterns, but they were not tied to the phenology of the breeding season. Females that were almost a solid brick-red with a faint, broad, dull grey lateral band were sexually non-receptive (NR), and they universally rejected male courtship (100%, n = 21) whereas the other colour pattern was predominately a subtle grey with light green-yellow along the majority of the neck and flank. These females allowed nearly all courting males to attempt copulation; it signalled potential receptivity (PR).

Male colour patterns

Male *F. labordi* had a thin, white, lateral line and were mostly emerald green, with slightly darker green vertical banding along the flank. When aggressive, these males changed colour very little, but increased contrast between the two shades of green (with the bands becoming darker). We sometimes also observed this pattern when they courted females, but not always. When submissive, males reduced contrast and hue to appear almost a solid, pale green.

Male *F. verrucosus* also had a white lateral line, above which they were a mottled grey or brown with darker brown/black bands. Below the white lateral line, they were of similar mottled colour, but with flecks of green and/or blue intermixed among the grey/brown. When aggressive or in the presence of females, males increased the contrast of the banding above the lateral line, and developed bright green and blue below the lateral line, over the entire tail, and on the lower jaw. Submissive males reduced contrast and became a generally pale, drab grey/brown colour.

Intersexual encounters

Furcifer labordi

During trials with NR females (n = 26), males often used (i.e., used in highest percent of trials) head bob, approach, and retreat (Table 3). Non-receptive females typically responded to unwanted males with gular display, colour change to dark rejection colour, lateral display, and mouth gape (Table 4). In trials with PR females (n = 21), males often used approach, head bob, superimposition, mouth gape, and attack (Table 3), while females most frequently used lunge, mouth gape, gular display, bite-release, lateral display, attack, and bite-clamp (Table 4).

During the breeding season, the two distinct colour patterns of females (NR or PR, described above) appeared sequentially, with NR occurring first. Social behaviour and outcomes of intersexual interactions were dichotomous and predictable based on female colour signals (Figure 2). Non-receptive females displayed aggressive rejection behaviour (agonistic displays and dark coloration) toward males 100% of the time (n = 26) and male mating success was 0%. However, with PR females (n = 21), male mating success depended upon the female response. When females remained in passive coloration, male mating success was 100%. Conversely, when females changed from passive to rejection colour, males continued to court in all instances, but subsequent to persistent courtship, females either remained in rejection coloration or changed back to passive coloration and allowed males to copulate. In the 11 trials where females initially displayed rejection coloration, males responded with rostral nudges in 54.5% of them, which consisted of approaching the female (from any direction) and subsequently manoeuvring to a position slightly behind her despite her aggressive behaviour toward the male. From here, the male then applied lateral pressure against the female's flank at mid-body. In one instance, the female reverted back to receptive colouration, remained behaviourally passive, and the male copulated with her.

Males significantly altered their behaviour, depending upon female colour signalling (PR or NR) ($\chi^2 = 262.0$, df = 15, $p < 0.001$). Although the mean number of male head bobs remained relatively similar toward the two female colour patterns, aggressive courtship behaviour like colour change, mouth gape, gular display, lateral display, approach, attack, fight, lunge, bite-release, bite-clamp, superimposition, and chase all were higher toward PR than to NR females (Table 3). Since males successful in copulation with PR females may behave with differing levels of aggressive courtship (graded agonism scores) than males who were unsuccessful with PR females, we separated these categories for analysis. Behaviour of males presented to NR females, of successful males presented to PR females, and of unsuccessful males presented to PR females, was significantly different in the level of agonism (ANOVA, $F = 3.97$, df = 2,43, $p = 0.03$). Pairwise comparisons revealed that males who were successful in copulation with PR females had significantly higher graded agonism than both males presented to NR females and unsuccessful males presented to PR females (Holm-Sidak $t = 2.65$ and 2.23, $p = 0.01$ and 0.03, respectively; Figure 3). However, there was no significant difference in graded agonism between males presented to NR females and unsuccessful males presented to PR females (Holm-Sidak $t = 0.14$, $p = 0.89$, *ns*). Thus, aggressive behaviour was highest in those males that were successful in copulation with PR females.

Potentially receptive females behaved significantly different toward males than did NR females ($\chi^2 = 647.4$, df = 14, $p < 0.001$). The mean number of mouth gape, approach, attack, fight, lunge, bite-release, bite-clamp, chase, retreat, and flee increased, indicating heightened agonism in PR compared to NR females. Other behaviour that indicated willingness to mate was higher in PR compared to NR females (e.g., tail raise and cloacal presentation). Because of the greater variance in agonism of PR females compared to NR females, we analyzed female graded agonism using Kruskal-Wallis ANOVA. Female graded agonism scores were significantly different among NR females, PR females who allowed copulation, and PR females who did not allow copulation (H = 15.99, df = 2, $p < 0.001$; Figure 3). Post-hoc pairwise comparisons showed that PR females who did not allow copulation were significantly more agonistic than both NR females and PR females who allowed copulation (Dunn's Q = 3.40 and 3.86, $p < 0.05$). Agonism in NR females and PR females who allowed copulation were not significantly different (Dunn's Q = 1.07, $p > 0.05$, *ns*).

Furcifer verrucosus

Similar to *F. labordi*, female *F. verrucosus* displayed two distinct colour patterns during the breeding season. Unlike *F. labordi*, their colour patterns did not occur sequentially and were intermixed throughout the breeding season, although NR tended to be more common at the end of the breeding season. Males readily courted females of both colour patterns, but the intersexual sequence of behavioural responses to each colour differed in comparison to *F. labordi* (Figure 4). Non-receptive females were usually successful in rejected mating attempts (n = 10), and in only one instance was a male able to physically overpower a female and attain forced copulation. Potentially receptive females always remained in grey/green, passive coloration (n = 18). Despite the lack of colour change, some PR females responded with agonistic rejection behaviour (displays and physical confrontation), and male mating success was reduced to 0% in this scenario. The two males who were behaviourally rejected by receptively coloured females were significantly smaller than males who were not (t = 2.63, df = 16, $p = 0.02$).

In the presence of NR females, males most frequently used head bob, approach, retreat, and superimposition (Table 3). Non-receptive females most frequently used overt, aggressive acts such as mouth gape, gular display, lateral display, attack, lunge, bite-clamp, and changed to a darker, aggressive colour (Table 4). Male behaviour toward PR females was similar to that directed toward NR females, with head bob, approach, and superimposition most often used (n = 18; Table 3). Potentially receptive females clearly used behaviour indicative of willingness to mate, such as tail raise, cloacal presentation, and colour change to an exaggerated green colour, not rejection (Table 4). Another frequently observed behaviour of PR females was retreat, but this was used exclusively after copulation had already occurred.

Males were less agonistic toward PR females and exhibited significantly different behaviour toward PR than toward NR females ($\chi^2 = 40.7$, df = 13, $p < 0.001$; Table 3). Males who courted PR females used less attack, fight, bite-release, and bite-clamp compared to when they courted NR females. Low sample size and sufficient variation in male behaviour led to no significant differences in agonism among males who courted NR females, who were successful with PR females, and who were unsuccessful with PR females (ANOVA, $F = 1.15$, df = 2,25, $p = 0.33$, *ns*). However, there is a clear trend in which males who courted NR females tended to show more agonism (mean ± 1 SEM; 107.6 ± 33.4) than did males who were successful with PR females (68.2 ± 19.5) and males who were unsuccessful (57.0 ± 16.7).

Females altered behaviour toward males depending on reproductive status ($\chi^2 = 237.3$, df = 14, $p < 0.001$; Table 4); PR females used less mouth gape, approach, attack, fight, lunge, bite-release, bite-clamp, and chase, which indicated lower agonism and lower female resistance. Similarly, females had a strikingly different graded agonism behaviour depending on whether they were NR, PR with males who achieved copulation, and PR with males who were unable to achieve copulation (Kruskal-Wallis ANOVA, H = 15.91, df = 2, $p < 0.001$). Post-hoc pairwise comparisons showed that agonism was significantly greater in NR females compared to PR females who did and did not mate (Dunn's Q = 3.87 and 2.63, $p < 0.05$, respectively). There were no significant differences between PR females who mated and those that were willing but did not mate (Dunn's Q = 1.20, $p > 0.05$, *ns*). Thus, PR females showed similar aggression toward both successful and unsuccessful males. Potentially-receptive females were less agonistic than NR females, but strong female choice is unlikely in this species.

Interspecies comparisons

When courting NR females, *F. labordi* and *F. verrucosus* males significantly differed in their behaviour ($\chi^2 = 40.7$, df = 14, $p < 0.001$; Table 3) and graded agonism

(Mann-Whitney $U = 237.0$, $p = 0.04$). Despite overt female rejection, *F. verrucosus* males were more persistent and aggressive in their courtship, using more head bob, approach, attack, fight, lunge, bite-release, bite-clamp, and superimposition than *F. labordi* (Table 3). However, *F. verrucosus* males also retreated and fled more in response to the female's rejection. Male *F. labordi* frequently used lateral displays when courting NR females, whereas that behaviour was lacking in *F. verrucosus* (Table 3).

Males also showed significant differences between species for behaviour patterns ($\chi^2 = 325.3$, df = 15, $p < 0.001$) when courting PR females (Table 3). However, males who were successful may have exhibited different levels of agonism toward females than males who were not. When we compared male agonism toward PR females (with species and mating success as factors), there were no significant differences between species (2-way ANOVA, $F = 1.02$, df = 1,35, $p = 0.32$, *ns*). Thus, although the types of behaviour males of each species used were different, the level of overall graded agonism was not. *Furcifer verrucosus* males were persistently as aggressive in courtship toward PR females as they were with NR females (Table 3). *Furcifer labordi* males, who were generally non-aggressive with NR females, exhibited greater agonism toward PR females and used more mouth gape, gular and lateral display, attack, fight, lunge, bite-release, bite-clamp, and chase behaviour than *F. verrucosus* (Table 3)—a stark contrast to their courtship of NR females. The only occurrence of rostral nudging was in *F. labordi* during courtship of PR females. Similar to trials with NR females, male *F. labordi* frequently used lateral displays when courting PR females, whereas that behaviour was lacking in *F. verrucosus*.

Non-receptive female *F. labordi* utilized a different suite of behaviour than NR *F. verrucosus* ($\chi^2 = 203.6$, df = 12, $p < 0.001$) and had significantly lower graded agonism (Mann-Whitney $U = 259.5$, $p = 0.01$). Non-receptive *F. verrucosus* females were more overt in their rejection behaviour and showed much more mouth gape, attack, fight, lunge, bite-clamp, and chase than NR *F. labordi* females (Table 4).

On the other hand, PR *F. labordi* females used much more aggressive behaviour than the passive, PR *F. verrucosus* ($\chi^2 = 218.9$, df = 14, $p < 0.001$), as evident by more aggressive colour change, mouth gape, gular display, lateral display, approach, attack, fight, lunge, bite-clamp, and chase behaviour (Table 4). Because of potential differences among females paired with males that achieved copulation and males that did not, we analyzed female graded agonism using a 2-way ANOVA with species as one factor, and male mating success as the other. There were significant differences between PR females of each species (2-way ANOVA, $F = 32.42$, df = 1,35, $p < 0.001$), female agonism as a function of male mating success (2-way ANOVA, $F = 15.37$, df = 1,35, $p < 0.001$), and their interaction (2-way ANOVA, $F = 14.30$, df = 1,35, $p < 0.001$). Post-hoc analyses revealed that *F. labordi* females who mated with males had significantly lower agonism than *F. labordi* females who did not allow copulation (Holm-Sidak $t = 5.58$, $p < 0.001$), but there were no significant differences among PR *F. verrucosus* females who did and did not copulate (Holm-Sidak $t = 0.10$, $p = 0.92$, *ns*). There was no significant difference between species among females that copulated (Holm-Sidak $t = 1.44$, $p = 0.16$, *ns*). However, there was a significant difference between species among females that did not copulate (Holm-Sidak $t = 6.35$, $p < 0.001$), with *F. labordi* exhibiting much greater agonism toward males despite their potential receptivity. These data strongly suggest that *F. labordi* females have much stronger female choice than do *F. verrucosus*.

In *F. labordi*, males were able to achieve copulation 61.9% of the time when courting PR females (n = 21). Despite the apparent passivity of PR *F. verrucosus* females toward courting males, male mating success varied, with only 50% of trials ending with male success (n = 18; Figure 4). In the remaining trials where males were unsuccessful, this was due to the inability of the males to achieve a proper copulatory grasp. After several attempts to copulate with behaviourally receptive females (i.e., females who remained motionless and exhibited cloacal presentation), males turned aggressive toward the females (attacking, lunging, and biting), which resulted in female flight and no further behavioural interactions.

Copulation was significantly longer in *F. verrucosus* (389.9 ± 42.9 seconds) than *F. labordi* (211.7 ± 12.6 seconds; Mann-Whitney $U = 158.0$, $p < 0.001$). Male preparation time was absent in *F. verrucosus* except for one individual, who prepared for 5 seconds, while male *F. labordi* spent significantly longer in preparation (137.9 seconds ± 46.1; Mann-Whitney $U = 135.0$, $p < 0.001$; Table 5). Desired copulation duration of females was significantly greater in *F. verrucosus* (357.6 seconds ± 47.5) compared to *F. labordi* (168.5 seconds ± 10.2; Mann-Whitney $U = 169.0$, $p = 0.003$; Table 5), although the duration of male ability to retain copulation was similar between the two species (*F. labordi*: 43.2 seconds ± 11.4; *F. verrucosus*: 41.6 seconds ± 13.2; Mann-Whitney $U = 96.0$, $p = 0.59$, *ns*; Table 5).

Intrasexual encounters

Within species comparisons

During agonistic intrasexual encounters, winning *F. labordi* males showed significantly different behaviour ($\chi^2 = 156.8$, df = 14, $p < 0.001$; Table 6) and greater graded agonism ($t = 4.09$, df = 50, $p < 0.001$) than their losing, conspecific counterparts. As expected, winning males used more frequent aggressive tactics while the subordinate males used less and resorted more frequently to fleeing and retreating (Table 6).

Winning and losing *F. verrucosus* males also showed significantly different behaviour ($\chi^2 = 26.7$, df = 12, $p = 0.01$) and winning males had significantly greater agonism than did losing males (Mann-Whitney $U = 68.5$, $p = 0.04$). Winning males had higher frequencies of more aggressive behaviour, whereas losing males, as expected, showed lower proportions of aggressive behaviour and higher proportions of submissive behaviour (Table 6).

Interspecies comparisons

In general, *F. labordi* males tended to be much more aggressive and had higher graded agonism scores per trial during male-male encounters than did *F. verrucosus*. This pattern is true for interspecies comparisons for both winners and losers. Winners of each species used statistically similar behaviour patterns ($\chi^2 = 17.6$, df = 11, $p = 0.09$, *ns*); however, *F. labordi* winners had significantly greater levels of mean graded agonism ($t = 2.73$, df = 31, $p = 0.01$) compared to winners of *F. verrucosus*. The losers of each species differed in their behavioural frequencies ($\chi^2 = 24.5$, df = 12, $p = 0.02$) and were nearly significantly different in graded agonism (*t* = 2.03, df = 31, *p* = 0.051, *ns*), with *F. labordi* losers using more aggressive types of behaviour than losing *F. verrucosus* (Table 6) and having higher average mean graded agonism scores. *Furcifer labordi* males escalated into longer and fiercer combat encounters, whereas *F. verrucosus* interactions were usually very brief and less confrontational.

Discussion

Visual signalling is often used in both an intra- and intersexual context in many vertebrate mating systems. The chameleons in this study utilized behavioural signalling in both contexts and exhibited markedly different social behaviour between species (Table 7). The theory of intersexual selection predicts that females may choose males, either directly or indirectly, based on qualities that presumably benefit the female. Mate choice in lizards has largely been considered uncommon (Olsson and Madsen 1995); however, some studies have recently demonstrated that it may play a more important role than once thought in lizards (Baird et al. 1997; Lopez et al. 2002; Hamilton and Sullivan 2005; Lopez et al. 2006; Martín and López 2006; Sullivan and Kwiatkowski 2007; Fitze et al. 2008). In *F. verrucosus*, it appears that mate choice plays little role: PR females mainly allowed males to attempt copulation by remaining motionless and presenting their cloacae. Despite this, male mating success was variable, indicating a potential for an indirect mode of intersexual selection (i.e., not female choice). By contrast, potentially receptive *F. labordi* females were selective. With respect to intrasexual selection, game theory predicts that more size-matched opponents should escalate into more intense physical encounters (Earley et al. 2002). Indeed, during male-male contests, the more naturally size-matched *F. labordi* had much more physically intense encounters than *F. verrucosus*.

In both species we studied, female colour pattern distinctly characterized sexual receptivity, a phenomenon present in other lizard taxa (Cooper and Greenberg 1992; Baird 2004) and other chameleon species (Cuadrado 1998; Kelso and Verrell 2002). Males have the potential to accurately assess probable female response from the onset. To reinforce this signal, females of both species increase aggressive displays toward courting males while adorned with NR coloration (Table 4). Despite strong sexual size dimorphism, females are quite adept at successfully defending themselves from unwanted males, which were much larger than females. Out of 57 trials in which females behaviourally rejected males (both species combined), only one time was a male successful at forced copulation (1.8% of trials).

Non-receptive female behaviour of both species was very predictable, but the behavioural repertoires of PR females were strikingly different between species. Potentially receptive *Furcifer verrucosus* females showed very little mate choice, and in most cases, they allowed any male to approach and attempt copulation. Very rarely did PR *F. verrucosus* females behaviourally reject males, and they did so without changing their colour signal. Rejected males were significantly smaller than those who were accepted. It appears there is a size threshold against which PR *F. verrucosus* females assess courting males: individuals greater than this threshold are allowed to attempt copulation without behavioural rejection and males below are not, nor are they large enough to forcibly coerce copulation. The *F. verrucosus* males allowed to approach and attempt copulation had varying reproductive success; male mating success mostly depended on the male’s ability to gain a superior copulatory grasp, not female choice. *Furcifer verrucosus* females became aggressive only when a male attempted copulation, did not achieve intromission, and then reattempted intromission. Males also became aggressive after a failed intromission attempt and attacked females until they retreated. Why these males exhibited such a peculiar, and apparently counter-productive fitness tactic is unknown.

While female *F. verrucosus* showed little mate choice, potentially receptive *F. labordi* females were discriminating. During courtship, *F. labordi* females either engaged in aggressive displays, behaviour, and colour change, or they became passive, allowing male copulation. Both scenarios were frequent. The proportion of PR female *F. labordi* that exhibited any type of rejection behaviour was greater than in *F. verrucosus*, which supports a stronger level of mate choice for this species. Thus, it seems that intersexual selection may potentially act upon male traits such as size and secondary sexual characters.

Since colour pattern is correlated with female sexual receptivity and females can successfully thwart male courtship advances, males should be able to clearly assess immediately whether females are likely to exhibit strong rejection behaviour. Males should adjust their courtship behaviour accordingly unless there is a fitness advantage in continuing this energetically costly behaviour. Despite this logical prediction, male *F. verrucosus* courted vigorously regardless of female receptivity colour, indicating there is a potential fitness advantage for doing so. On the other hand, male *F. labordi* expended very little energy courting NR females. Why one species adheres to these communicatory rules while the other does not is not clear; however, it may depend upon the species-specific mating system. For example, males that defend a territory with multiple females in it might continue courtship in hopes of retaining females in his territory. Radio-tagged *F. verrucosus* males do utilize relatively small spatial areas compared to radio-tagged *F. labordi*, which sometimes wander vast relative distances up to 50 m in a day (Karsten, unpublished data). Since male *F. labordi* wander over indefensible home ranges, encounter fewer potential mates, and expend more energy in locomotion, it may be too costly to court NR females when the probability of success is probably close to zero.

Kelso and Verrell (2002) suggest that there is a potential benefit for male chameleons to court NR females if females store sperm. Because *F. labordi* is annual and has a reproductive period less than 60 days (Karsten, unpublished data), females do not live to reproduce in more than one year and they are unlikely to produce multiple clutches per year. Thus, sperm storage is not likely in this species, either within the same season or from one year to the next. However, other *Furcifer* chameleons that have multiple clutches per season can lay a second clutch within ca. 45-60 days (Ferguson et al. 2004, and references therein). Because gravid *F. verrucosus* females were found as early as mid-December (Karsten, unpublished data), and the end of the active season is not until March, this species has the potential to produce multiple clutches per season and sperm storage would be adaptive. They are also perennial, introducing the possibility of sperm storage from one year to the next. This hypothesis to explain attempted copulation with NR females in *F. verrucosus* and not *F. labordi* is plausible, but sperm storage in either of these species is unknown. Further studies are required to address the ultimate underpinnings of why males of some chameleon species continue to court NR females while others do not.

The specific role of rostral appendages has been enigmatic in chameleons. Parcher (1974) demonstrated that some species use their rostral appendages during male-male combat, but never during courtship. While his data show this for three species he studied, there has been an underlying assumption that perhaps this is the case for all species with rostral appendages. We clearly show that *F. labordi*, a species with a distinct rostral appendage, did not use them during male-male combat. Instead, males used rostral appendages only during courtship encounters in which they attempted to persuade resistant females to allow copulation. Although this finding appears contrary to Parcher (1974), it may not be when one considers that there are two types of rostral appendages: those that are keratinized and pointed and others that are fleshy, flat, and paddle-like. The three species that Parcher found to use rostral appendages for male-male combat all had keratinized rostral appendages. *Furcifer labordi*, on the other hand, has flat, fleshy appendages. Coincidentally, the only species Parcher studied that did not use its rostral appendage for male-male combat (*Calumma nasuta*; formerly *Chamaeleo nasutus*) also has a flat, fleshy appendage similar to that of *F. labordi*. However, he never observed this species using its rostral appendage for female courtship, either. Instead, Parcher suggested that the rostral appendage serves as a species indicator. Based on our data and his, we present a new hypothesis to explain the evolution of chameleon rostral appendages: species with harder, keratinized appendages have evolved them for male-male combat via intrasexual selection, whereas flat, fleshy rostra are used in courtship behaviour and may be subject to intersexual selection.

In many lizard species, particularly territorial ones, head bobs are an integral part of male-male displays and agonism. Citing Jenssen et al. (2000), Lailvaux and Irschick (2006: p. 265) go so far as to state that head bobbing or pushup displays are considered "critical for male-male lizard contests." This assertion has merit since many lizard taxa do utilize head bobbing and/or pushup displays in species in which males aggressively interact with one another. However, in the two species of chameleons in the present study, there was no use of head bobs in male-male communication. Instead, these male chameleons used head bobs only during courtship and neither species used pushups in any context. Head bobs may actually be widespread in the courtship behaviour of some genera of chameleons as Parcher (1974) found results similar to ours in all six species he studied (genera *Furcifer* and *Calumma*; formerly *Chamaeleo*). Interestingly though, with chameleons of the genus *Brookesia*, a stem lineage of chameleons (Raxworthy et al. 2002; Townsend and Larson 2002), Parcher found no evidence of head bobs being used in either intra- or intersexual contexts.

We never observed male or PR female *F. verrucosus* using lateral displays during courtship. However, during male-male interactions, males used this behaviour frequently as also did females when behaviourally signalling their non-receptivity. Thus, in *F. verrucosus*, lateral displays are a signal employed only during times when the intention is to display the physical ability to combat another individual. *Furcifer labordi*, a species characterized by physical combat in all possible social interactions, frequently used lateral displays. It is plausible that chameleons use lateral displays as a generalized signal of physical ability in multiple social contexts. Indeed, this is the case in other lizards, as extended lateral displays significantly correlate with, and are honest signals of, male performance (Brandt 2003). Husak et al. (2006) clearly showed that male lizards with superior performance were more dominant than males with lesser performance. Accordingly, we hypothesize that chameleons utilize lateral displays as an honest signal of fighting ability and our data lend support, as both species use numerous lateral displays during periods of potential physical agonism.

Unlike the numerous empirical examples of a positive correlation between male performance and male fighting ability, there is little evidence of a link between female choice and male functional performance (Lailvaux and Irschick 2006; Husak and Fox 2008). If male chameleons use lateral displays as a signal of fighting ability, males could conceivably use these same traits to signal quality to females (Berglund et al. 1996). In many taxa, there is evidence that females can prefer superior males with ‘good genes’, and these offspring have better physiological performance and survival (Petrie 1994; Welch et al. 1998; Møller and Alatalo 1999; Drickamer et al. 2000; Bluhm and Gowaty 2004; Evans et al. 2004; Byers and Waits 2006). In the chameleon most likely to exhibit intersexual selection (*F. labordi*), males used lateral displays in both male-male and male-female social contexts. Contrary to previously proposed hypotheses, lateral displays in *F. labordi* may provide evidence of a link between female choice and male functional performance, whereas it is unlikely to have evolved as an honest dual-context signal in *F. verrucosus* since males do not utilize lateral displays in courtship.

It is clear that during male-male encounters, *F. labordi* escalated into more aggressive physical bouts than did *F. verrucosus*. Most encounters by the latter entail a brief display of visual signals from a distance followed shortly by colour change to signal dominant or subordinate status. The former, on the other hand, nearly always engaged in strong physical activity during male-male encounters. Do these data imply that *F. verrucosus* males are not physically aggressive toward each other? This is not likely since wild male *F. verrucosus* do engage in very fierce fights among rival males, resulting in deep, semi-permanent bite marks along appendages (Karsten and Andriamandimbiarisoa, personal observation) We have also found males with large portions of skin missing from around the jaw, exposing the underlying muscles and bone and accompanied by teeth imprints on the adjacent skin. We found one individual with a missing tail and traces of chameleon bite marks, a strong indication of extreme male combat considering these lizards do not exhibit tail autotomy. Thus, it is very clear that both species engage in fierce combat when necessary; however it is rarer in *F. verrucosus*.

Lailvaux & Irschick (2006) suggest that increased energetically costly behaviour provides male lizards increasingly accurate assessments of an opponent's performance. Often in lizards, fights between size-matched opponents do escalate to greater levels of agonism and aggression than do fights between more disparate body sizes (Jenssen et al. 2005). Because *F. labordi* is an annual species (Karsten, unpublished data), all adult males are of the same age-cohort and showed significantly less variation in SVL than did adult male *F. verrucosus* (F-test, $F = 4.089$, df = 98,50, $p < 0.0001$). Thus, it appears, as Lailvaux & Irschick (2006) suggest, that interactions between relatively closer size-matched *F. labordi* adult males require more accurate assessment of an opponent's physiological performance (i.e., greater escalation of energetically costly behaviour). In *F. verrucosus*, a species with more variation in adult male body sizes, many encounters can be resolved using less energetically costly behaviour, as predicted by game theory (Earley et al. 2002). We can therefore explain the injuries we observed in some *F.*

verrucosus males if these males encountered rivals of similar body size and then escalated their agonism to attain more accurate information of their rival's physiological performance.

In chameleons, there is a positive correlation between residual casque height and bite force (A. Herrel, unpublished data). Thus, casque height may signal male fighting ability to other males, but that does not prohibit its possible dual use as a signal of male quality to females (Berglund et al. 1996). Male *F. labordi* had casques that grew significantly larger relative to their body size, and exhibited a greater degree of sexual dimorphism in casque growth, than did the closely related *F. verrucosus*. *Furcifer labordi* not only engaged in intense male-male fights more frequently than *F. verrucosus*, but *F. labordi* females exhibited stronger female choice as well. An alternative—and very different—hypothesis to explain stronger dimorphism in casque height in *F. labordi* is that males and females might eat different prey that requires different bite forces. However, there are no observed qualitative or quantitative sexual differences in prey selection for radio-tracked individuals of either species (Karsten, personal observation).

The results of this study underscore the important role of social behaviour in vertebrate mating systems. Despite their close phylogenetic affinities, these species are markedly different in both courtship behaviour and male fighting tactics. Female receptivity, as indicated by coloration, influences male courtship behaviour in *F. labordi*, but not *F. verrucosus*. *Furcifer labordi* is a much more aggressive species in both male-female and male-male contexts and is more likely to exhibit intersexual selection. With such strikingly diverse and overt social behaviour, these species suggest that a broad comparative study within the *Furcifer* chameleons will provide exciting potential for exploring the evolutionary plasticity of social behaviour.

Acknowledgements

Field studies in Madagascar were made possible due to the assistance of the Ministries des Eaux et Forêts, the Association Nationale pour la Gestion des Aires Protégées, and the Université d'Antananarivo, Département de Biologie Animale. We thank D. Rakotondravony and O. Ramilijaona for their assistance with the project and H. Thomas and D. Kidney for offering valuable logistical advice. We would like to thank T. A. Baird, J. Husak, M. Lovern, and M. Palmer for review of earlier versions of the manuscript. We thank A. Herrel for data on chameleon bite force. Research support in Madagascar was provided by an award to Christopher J. Raxworthy from the National Science Foundation (DEB 99-84496). All field work was conducted using approved Animal Care guidelines and permits from the government of Madagascar.

References

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

Andersson, S., Pryke, S. R., Örnborg, J., Lawes, M. J. & Andersson, M. 2002. Multiple receivers, multiple ornament, and a trade-off between agonistic and epigamic signaling in a widowbird. *American Naturalist*, 160, 683-691.

Baird, T. A. 2004. Reproductive coloration in female collared lizards, *Crotaphytus collaris*, stimulates courtship by males. *Herpetologica*, 60, 337-348.

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

Baird, T. A., Hranitz, J. M., Timanus, D. K. & Schwartz, A. M. 2007. Behavioral attributes influence annual mating success more than morphological traits in male collared lizards. *Behavioral Ecology*, 18, 1146-1154.

Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58, 385-399.

Bickel, R. & Losos, J. B. 2002. Patterns of morphological variation and correlates of habitat use in chameleons. *Biological Journal of the Linnean Society*, 76, 91-103.

Bluhm, C. K. & Gowaty, P. A. 2004. Social constraints on female mate preferences in mallards, *Anas platyrhynchos*, decrease offspring viability and mother productivity. *Animal Behaviour*, 68, 977-983.

Brandt, Y. 2003. Lizard threat display handicaps endurance. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 270, 1061-1068.

Byers, J. A. & Waits, L. 2006. Good genes sexual selection in nature. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 16343-16345.

Cooper, W. E. & Greenberg, N. 1992. Reptilian coloration and behavior. In: *Biology of the Reptilia, Volume 18, Physiology E, Hormones, Brain, and Behavior* (Ed. by Gans, C. & Crews, D.), pp. 298-422. Chicago, Illinois: University of Chicago Press.

Cuadrado, M. 1998. The use of yellow spot colors as a sexual receptivity signal in females of *Chamaeleo chamaeleon*. *Herpetologica*, 54, 395-402.

Cuadrado, M. 2001. Mate guarding and social mating system in male common chameleons (*Chamaeleo chamaeleon*). *Journal of Zoology*, 255, 425-435.

Drickamer, L. C., Gowaty, P. A. & Holmes, C. M. 2000. Free female mate choice in house mice affects reproductive success and offspring viability and performance. *Animal Behaviour*, 59, 371-378.

Earley, R. L., Attum, O. & Eason, P. 2002. Varanid combat: perspectives from game theory. *Amphibia-Reptilia*, 23, 469-485.

Endler, J. A., Westcott, D. A., Madden, J. R. & Robson, T. 2005. Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution*, 59, 1795-1818.

Evans, J. P., Kelley, J. L., Bisazza, A., Finazzo, E. & Pilastro, A. 2004. Sire attractiveness influences offspring performance in guppies. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 2035-2042.

Ferguson, G. W., Murphy, J. B., Ramanamanjato, J. B. & Raselimanana, A. P. 2004. *The Panther Chameleon: Color Variation, Natural History, Conservation, and Captive Management*. Malabar, Florida: Krieger Publishing Company.

Fitze, P. S., Cote, J., Martinez-Rica, J. P. & Clobert, J. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. *Journal of Evolutionary Biology*, 21, 246-255.

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

Husak, J. F. & Fox, S. F. 2008. Sexual selection on locomotor performance. *Evolutionary Ecology Research*, in press.

Husak, J. F., Lappin, A. K., Fox, S. F. & Lemos-Espinal, J. A. 2006. Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia*, 301-306.

Jenssen, T. A., Decourcy, K. R. & Congdon, J. D. 2005. Assessment in contests of male lizards (*Anolis carolinensis*): how should smaller males respond when size matters? *Animal Behaviour*, 69, 1325-1336.

Jenssen, T. A., Orrell, K. S. & Lovern, M. B. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. *Copeia*, 140-149.

Kelso, E. C. & Verrell, P. A. 2002. Do male veiled chameleons, *Chamaeleo calyptratus*, adjust their courtship displays in response to female reproductive status? *Ethology*, 108, 495-512.

Kunz, A. K., Ford, M. & Pung, O. J. 2006. Behavior of the grass shrimp *Palaemonetes pugio* and its response to the presence of the predatory fish *Fundulus heteroclitus*. *American Midland Naturalist*, 155, 286-294.

Lailvaux, S. P. & Irschick, D. J. 2006. A functional perspective on sexual selection: insights and future prospects. *Animal Behaviour*, 72, 263-273.

Lappin, A. K., Brandt, Y., Husak, J. F., Macedonia, J. M. & Kemp, D. J. 2006. Gaping displays reveal and amplify a mechanically based index of weapon performance. *American Naturalist*, 168, 100-113.

Lopez, P., Amo, L. & Martin, J. 2006. Reliable signaling by chemical cues of male traits and health state in male lizards, *Lacerta monticola*. *Journal of Chemical Ecology*, 32, 473-488.

Lopez, P., Munoz, A. & Martin, J. 2002. Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. *Behavioral Ecology and Sociobiology*, 52, 342-347.

Martín, J. & López, P. 2006. Vitamin D supplementation increases the attractiveness of males' scent for female Iberian rock lizards. *Proceedings of the Royal Society B-Biological Sciences*, 273, 2619-2624.

Martin, R. A., Hammerschlag, N., Collier, R. S. & Fallows, C. 2005. Predatory behaviour of white sharks (*Carcharodon carcharias*) at Seal Island, South Africa. *Journal of the Marine Biological Association of the United Kingdom*, 85, 1121-1135.

McGlothlin, J. W., Parker, P. G., Nolan, V. & Ketterson, E. D. 2005. Correlational selection leads to genetic integration of body size and an attractive plumage trait in dark-eyed juncos. *Evolution*, 59, 658-671.

Meyers, J. J., Irschick, D. J., Vanhooydonck, B. & Herrel, A. 2006. Divergent roles for multiple sexual signals in a polygynous lizard. *Functional Ecology*, 20, 709-716.

Møller, A. P. & Alatalo, R. V. 1999. Good-genes effects in sexual selection. *Proceedings of the Royal Society of London Series B-Biological Sciences*, 266, 85-91.

Norris, K. M. & Hosie, C. A. 2005. A quantified ethogram for oviposition in *Triturus* newts: Description and comparison of *T. helveticus* and *T. vulgaris*. *Ethology*, 111, 357-366.

Olsson, M. & Madsen, T. 1995. Female choice on male quantitative traits in lizards - why is it so rare? *Behavioral Ecology and Sociobiology*, 36, 179-184.

Ord, T. J. & Martins, E. P. 2006. Tracing the origins of signal diversity in anole lizards: phylogenetic approaches to inferring the evolution of complex behaviour. *Animal Behaviour*, 71, 1411-1429.

Parcher, S. R. 1974. Observations on the natural histories of six Malagasy Chamaeleontidae. *Zeitschrift für Tierpsychologie*, 34, 500-523.

Petrie, M. 1994. Improved growth and survival of offspring of peacocks with more elaborate trains. *Nature*, 371, 598-599.

Raxworthy, C. J., Forstner, M. R. J. & Nussbaum, R. A. 2002. Chameleon radiation by oceanic dispersal. *Nature*, 415, 784-787.

Stuart-Fox, D. & Moussalli, A. 2008. Selection for social signalling drives the evolution of chameleon colour change. *Plos Biology*, 6, 22-29.

Stuart-Fox, D. M., Firth, D., Moussalli, A. & Whiting, M. J. 2006. Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. *Animal Behaviour*, 71, 1263-1271.

Stuart-Fox, D. M. & Whiting, M. J. 2005. Male dwarf chameleons assess risk of courting large, aggressive females. *Biology Letters*, 1, 231-234.

Sullivan, B. K. & Kwiatkowski, M. A. 2007. Courtship displays in anurans and lizards: theoretical and empirical contributions to our understanding of costs and selection on males due to female choice. *Functional Ecology*, 21, 666-675.

Townsend, T. & Larson, A. 2002. Molecular phylogenetics and mitochondrial genomic evolution in the Chamaeleonidae (Reptilia, Squamata). *Molecular Phylogenetics and Evolution*, 23, 22-36.

Vanhooydonck, B., Herrel, A. Y., Van Damme, R. & Irschick, D. J. 2005. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Functional Ecology*, 19, 38-42.

Vose, R. S., Schmoyer, R. L., Steurer, P. M., Peterson, T. C., Heim, R., Karl, T. R. & Eischeid, J. K. 1992. The Global Historical Climatology Network: Long-Term Monthly Temperature, Precipitation, Sea Level Pressure, and Station Pressure

Data. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee: ORNL/CDIAC-53, CDIAC NDP-041.

Welch, A. M., Semlitsch, R. D. & Gerhardt, H. C. 1998. Call duration as an indicator of genetic quality in male gray tree frogs. *Science*, 280, 1928-1930.

Whiting, M. J., Stuart-Fox, D. M., O'Connor, D., Firth, D., Bennett, N. C. & Blomberg, S. P. 2006. Ultraviolet signals ultra-aggression in a lizard. *Animal Behaviour*, 72, 353-363.

Table 1: Definitions for social behaviour used during male-male and male-female interactions.

Behaviour	**Description**
Intersexual colour change	Change of colour pattern during courtship
Head bob	Undulation of head in up and down motion
Mouth gape	Exposes teeth and colour contrast of the interior lining of the mouth
Gular display	Dorsoventral flattened extension of skin below the jaw
Lateral display	Perpendicular exposure of a laterally flattened body; tail curled; expansion of lungs to as large a size as possible
Approach	Motion toward another individual at higher rates than normal locomotion
Attack	Initiation of a physical confrontation
Fight	Both individuals participate in the encounter aggressively; involving pushing and biting
Lunge	Quick movement specifically directed toward another individual
Bite-release	Biting, followed by a quick release (within about 1 second)
Bite-clamp	Biting, followed by prolonged closure of the jaw
Superimposition	An individual contacts and gains a superior position on another
Chase	Continued pursuit of an individual
Retreat	Motion away from another individual who is either displaying or attempting physical contact; pace is similar to normal locomotion
Flee	Rapid attempt to separate from an individual; pace is much faster than normal locomotion; usually involves falling to ground
Tail raise	Female elevates tail from normal, resting position
Cloacal presentation	Passive female upwardly tilts pelvis, exposing cloaca
Rostral nudge	Placing the rostrum next to the flank of another individual with application of force in a lateral direction
Threat display	Expansion of lungs and curling the tail, but without using perpendicular lateral displays
Aggressive colour change	Change to bright colour display during a male-male encounter
Submissive colour change	Change of colour display during a male-male encounter; dull and drab colouration compared to typical cryptic colouration

Table 2: Weights to compute graded agonism during male-male and male-female social interactions. Behaviour that carries a higher cost of physical injury is weighted greater, whereas behaviour that minimizes the probability of physical injury is weighted negative. Dashes indicate that the specific behaviour pattern was not used in that particular social context.

	Social Interaction	
Behaviour	Male-female	Male-male
Fight	+4	+4
Attack	+3	+3
Bite-release	+3	+3
Bite-clamp	+3	+3
Superimposition	+3	--
Approach	+2	+2
Lunge	+2	+2
Chase	+2	+2
Mouth gape	+1	+1
Gular display	+1	+1
Lateral display	+1	+1
Colour change	+1	--
Head bob	+1	--
Threat display	--	+1
Aggressive colour	--	+1
Retreat	-1	-1
Flee	-1	-1
Tail raise	-1	--
Cloacal presentation	-2	--
Submissive colour	--	-2

Table 3: Behavioural frequencies for males of both species presented to both non-receptive and potentially receptive females. Data are mean values per 30-minute interaction. The percentage of total trials in which we observed each behaviour pattern is in parentheses. Dashes indicate the behaviour pattern was absent.

	With non-receptive females		With potentially receptive females	
	Furcifer labordi	*Furcifer verrucosus*	*Furcifer labordi*	*Furcifer verrucosus*
Colour change	0.08 (8%)	0.10 (10%)	0.29 (29%)	0.33 (33%)
Head bob	29.84 (88%)	92.60 (80%)	27.10 (67%)	53.39 (89%)
Mouth gape	0.20 (19%)	0.20 (20%)	1.91 (52%)	0.17 (11%)
Gular display	0.20 (15%)	0.10 (10%)	0.95 (48%)	0.33 (17%)
Lateral display	0.27 (19%)	--	0.95 (48%)	--
Approach	0.64 (50%)	1.40 (80%)	2.10 (91%)	1.83 (89%)
Attack	0.08 (8%)	0.70 (30%)	1.71 (52%)	0.17 (11%)
Fight	--	0.90 (30%)	0.25 (10%)	--
Lunge	0.12 (12%)	1.10 (30%)	2.52 (48%)	0.17 (11%)
Bite-release	0.04 (4%)	0.20 (20%)	0.67 (33%)	--
Bite-clamp	0.04 (4%)	0.30 (20%)	0.48 (24%)	0.06 (6%)
Superimposition	--	1.20 (60%)	0.71 (62%)	1.22 (72%)
Chase	0.08 (8%)	0.10 (10%)	0.57 (33%)	0.28 (11%)
Retreat	0.72 (46%)	1.20 (70%)	0.62 (43%)	0.50 (22%)
Flee	0.08 (8%)	0.20 (10%)	0.14 (14%)	--
Rostral nudge	--	--	3.05 (29%)	--

Table 4: Behavioural frequencies for non-receptive and potentially receptive females of both species. Data are mean values per 30-minute interaction. The percentage of total trials in which we observed each behaviour pattern is in parentheses. Dashes indicate the behaviour pattern was absent.

	Non-receptive females		Potentially receptive females	
	Furcifer labordi	*Furcifer verrucosus*	*Furcifer labordi*	*Furcifer verrucosus*
Colour change	0.96 (96%)	0.70 (70%)	0.57 (52%)	0.50 (50%)
Mouth gape	2.65 (73%)	6.60 (80%)	5.33 (81%)	0.61 (22%)
Tail raise	--	0.10 (10%)	0.10 (10%)	0.78 (72%)
Cloacal presentation	--	--	0.52 (52%)	0.61 (56%)
Gular display	7.85 (96%)	7.10 (80%)	1.29 (76%)	0.39 (22%)
Lateral display	6.58 (92%)	6.50 (80%)	1.00 (67%)	--
Approach	0.12 (12%)	0.30 (10%)	0.24 (14%)	--
Attack	0.54 (35%)	4.10 (80%)	6.43 (57%)	0.61 (22%)
Fight	--	0.90 (30%)	0.24 (10%)	--
Lunge	0.92 (50%)	10.40 (80%)	9.62 (91%)	0.72 (22%)
Bite-release	0.27 (15%)	0.20 (20%)	4.57 (71%)	0.17 (11%)
Bite-clamp	0.12 (8%)	1.70 (80%)	2.67 (57%)	0.06 (6%)
Chase	--	0.30 (10%)	0.05 (5%)	--
Retreat	0.69 (46%)	0.30 (20%)	1.33 (52%)	1.50 (67%)
Flee	0.15 (12%)	0.10 (10%)	0.86 (52%)	0.33 (11%)

Table 5: Mean duration ± 1 SEM and percentage of total copulation time for various temporal segments for both focal species.

Time (seconds)	*F. labordi* (n = 13)	*F. verrucosus* (n = 9)
Duration of copulation	211.7 ± 12.6	389.9 ± 42.9
Desired female duration	168.5 ± 10.2	357.6 ± 47.5
Male ability to retain copulation	43.2 ± 11.4	41.6 ± 13.2
Male preparation time	137.9 ± 46.1	0.6 ± 0.6
Percentage of copulation time		
Desired female duration	81.1%	91.2%
Male ability to retain copulation	19.0%	11.0%
Male preparation time	48.0%	0.2%

Table 6: Behavioural frequencies for winning and losing males of both species during male-male social interactions. Data are mean values per 30-minute interaction. The percentage of total trials in which we observed each behaviour pattern is in parentheses. Dashes indicate the behaviour pattern was absent.

	Furcifer labordi		*Furcifer verrucosus*	
	Winners	Losers	Winners	Losers
Mouth gape	3.04 (92%)	1.38 (85%)	0.86 (71%)	0.43 (29%)
Gular display	5.54 (100%)	4.08 (96%)	3.14 (86%)	1.57 (43%)
Threat display	5.27 (92%)	4.04 (96%)	2.57 (71%)	1.57 (43%)
Lateral display	4.81 (92%)	3.81 (92%)	2.00 (71%)	1.43 (43%)
Approach	1.23 (62%)	0.27 (23%)	0.29 (29%)	0.29 (29%)
Attack	0.96 (69%)	0.46 (46%)	0.43 (43%)	0.14 (14%)
Fight	0.42 (38%)	0.42 (38%)	--	--
Lunge	1.50 (81%)	0.62 (38%)	0.57 (43%)	0.29 (29%)
Bite-release	0.19 (19%)	--	0.14 (14%)	--
Bite-clamp	0.27 (27%)	0.23 (23%)	--	--
Chase	0.15 (15%)	--	0.14 (14%)	--
Retreat	0.12 (12%)	1.77 (92%)	--	1.14 (71%)
Flee	--	1.12 (65%)	--	0.57 (43%)
Aggressive colour	0.69 (65%)	0.04 (4%)	0.86 (86%)	0.43 (43%)
Submissive colour	--	0.85 (81%)	--	0.86 (86%)

Table 7: Comparative social behaviour of *Furcifer labordi* and *F. verrucosus*.

Social component	*Furcifer labordi*	*Furcifer verrucosus*
Males		
Fight escalation	Frequently	Rarely
Head bobs used for male-male signals	Never	Never
Head bobs used for courtship	Always	Always
Adjust courtship based on female colour	Yes	No
Male mating success when attempting copulation with behaviourally receptive females	High	Variable
Females		
Resistant females may shift to behavioural receptivity subsequent to persistent courtship	Often	Never
Colour signalling of reproductive status	Yes	Yes
Potential for direct mate choice by females	Strong	Weak

FIGURE LEGENDS

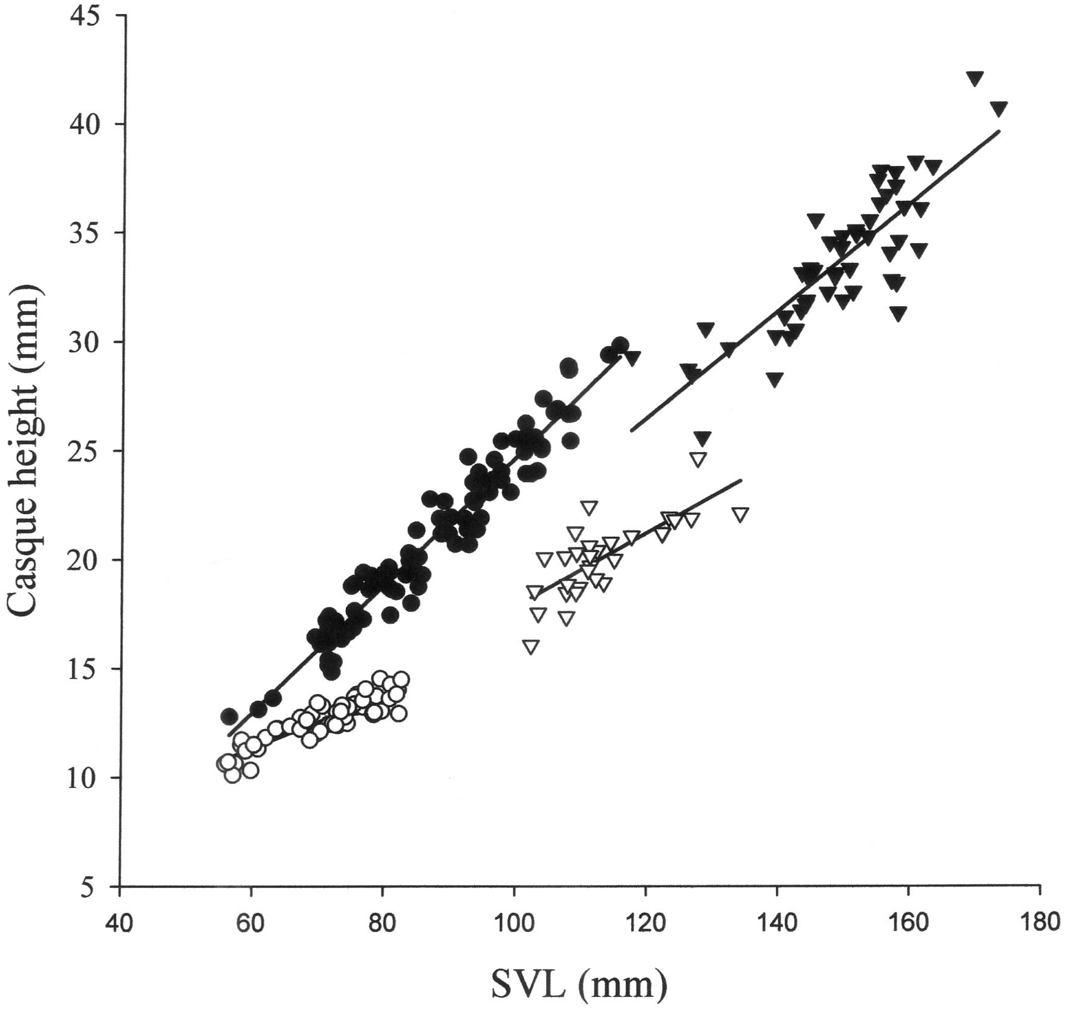
Figure 1: Casque height regressed on SVL for each species and sex. Circles indicate *F. labordi*, triangles *F. verrucosus*. Males are solid symbols and females are open. Both species are sexually dimorphic in casque characteristics, and *F. labordi* has a greater degree of sexual dimorphism in casque growth than does *F. verrucosus*.

Figure 2: Dichotomous courtship ethogram for male and female *Furcifer labordi*. Arrows direct toward an outcome. Percentages indicate the proportion of trials resulting in the following outcome. Number of trials in which the outcome occurred are in parentheses.

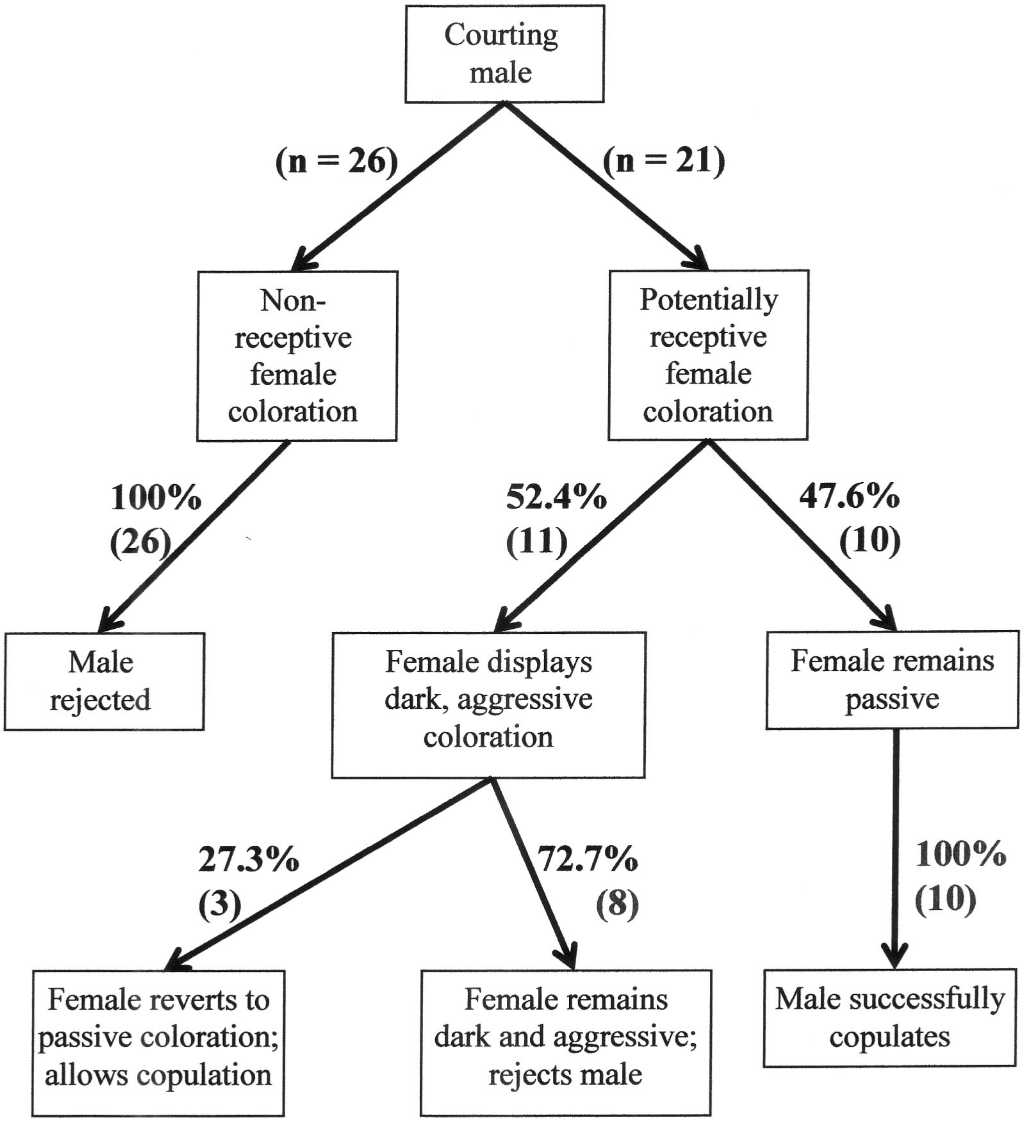
Figure 3: Mean graded agonism for *F. labordi* males (black bars) and females (white bars) during interactions between males and NR females, males and PR females who allowed copulation, and males and PR females who rejected male courtship. Error bars are +1 SEM. Males who were successful in achieving copulation had significantly higher graded scores than did males presented to NR females and males who were unsuccessful with PR females. Females who were PR but did not allow male copulation had significantly higher graded agonism than PR receptive females who did allow copulation and NR females.

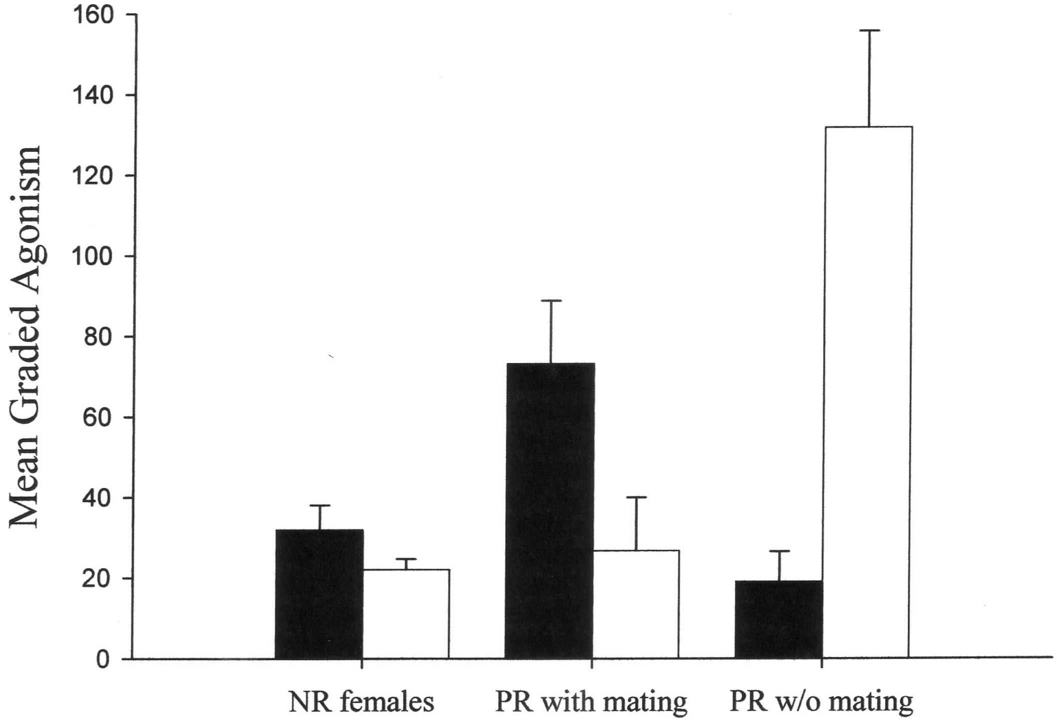
Figure 4: Dichotomous courtship ethogram for male and female *Furcifer verrucosus* chameleons. Arrows direct toward an outcome. Percentages indicate the proportion of

trials resulting in the following outcome. Number of trials in which the outcome occurred are in parentheses.

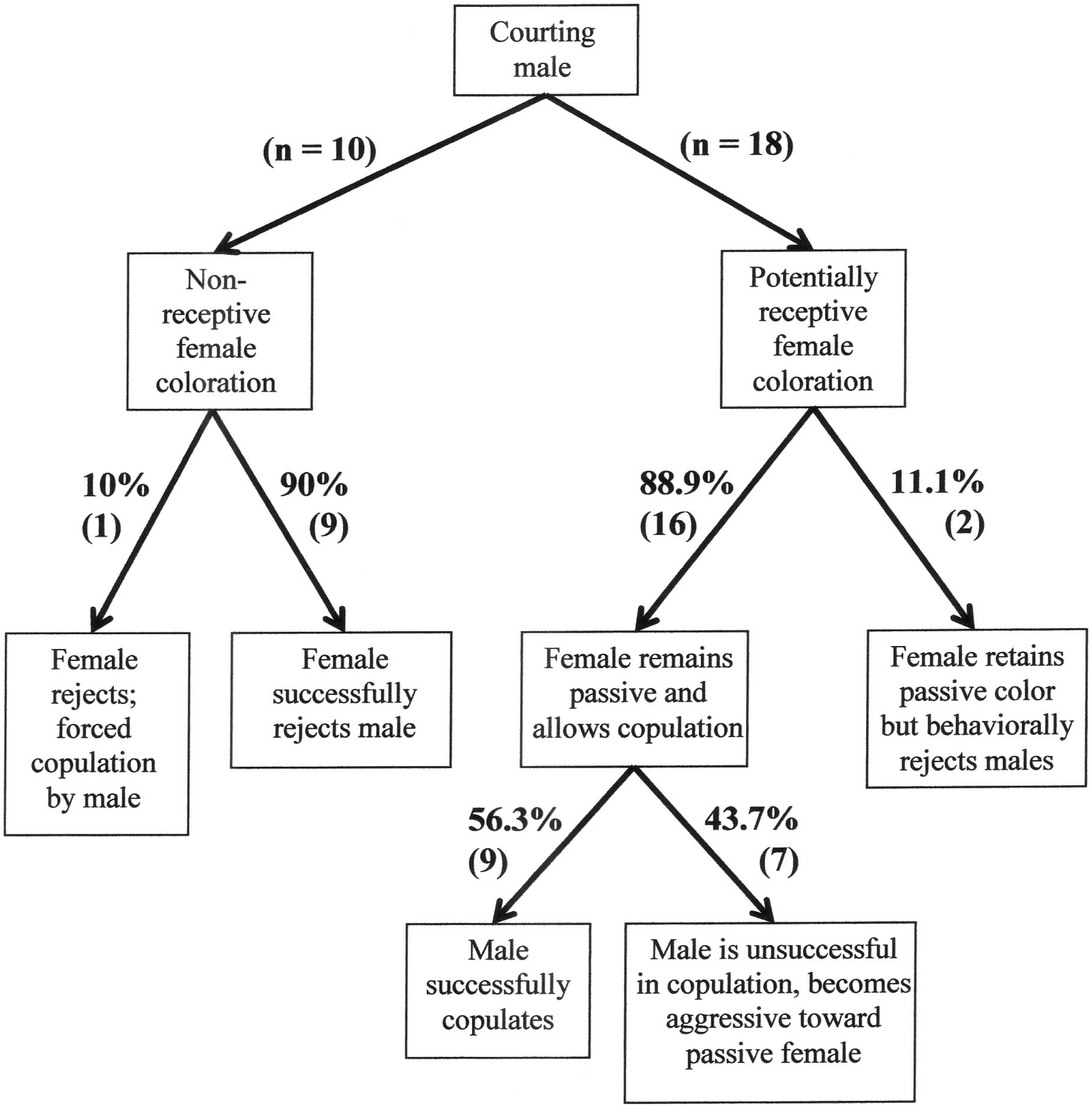

45
40
35
30
25
20
15
10
5
Casque height (mm)
40
60
80
100
120
140
160
180
SVL (mm)

Furcifer labordi




Mean Graded Agonism
0
20
40
60
80
100
120
140
160
NR females
PR with mating
PR w/o mating

Furcifer verrucosus



II. Sexual selection on body size and secondary sexual characters in two closely related, sympatric chameleon species in Madagascar

Abstract

In polygynous mating systems, sexual selection can drive the evolution of male characters beneficial to winning fights (intrasexual selection), for improving their mating success through mate choice (intersexual selection), or both. However, it may be difficult to disentangle the relative contributions of intra- and intersexual selection on multiple traits that may be of dual utility. We used field arena trials to determine which morphological traits best explained male fighting ability and male mating success in two species of chameleons in Madagascar, *Furcifer labordi* and *F. verrucosus*. In *F. labordi*, male fighting success was best predicted by body size and cranial casque height and male mating success was best predicted by body size and width of the rostral appendage. In *F. verrucosus*, we found strong intrasexual selection for increased male body size and fewer dorsal cones, a trait that may correspond to age and experience. Although there is no mate choice in this species, male mating success with receptive females is highly variable. Fewer dorsal cones and larger size-corrected casque height best explained male mating success; traits that may again indicate age or experience. Although difficult to determine the relative contributions of intra- and intersexual selection on traits with dual

benefits (both fighting and mate choice), we documented both types of selection on body size and secondary sexual characters in these two chameleon species.

Introduction

Sexual selection affects traits that enhance fitness by way of increased mating success (Endler 1983; Andersson 1994; Wikelski and Trillmich 1997; Weatherhead and Dufour 2005; Husak and Fox 2008). In polygynous mating systems, sexual selection may favour traits that are beneficial to males for fighting (intrasexual selection), for improving mating success through mate choice (intersexual selection), or both. Traits under intrasexual selection often are potential indicators of fighting ability (Berglund et al. 1996; Jenssen et al. 2000; Pratt et al. 2003; Emlen et al. 2005; Vanhooydonck et al. 2005b; Lappin et al. 2006; Meyers et al. 2006), but these may also serve a dual purpose of improving mating success during courtship, and be under concomitant intersexual selection (Berglund et al. 1996; McGlothlin et al. 2005). Conversely, traits that first evolved through intersexual selection may later evolve as adaptive during male-male contests (Benson and Basolo 2006; Morris et al. 2007). Thus, it may be difficult to disentangle the relative contributions of intra- and intersexual selection (Fitze et al. 2008), particularly in mating systems in which multiple traits may improve both fighting and mate choice. This can be especially difficult to determine in natural populations when it is not possible to isolate each type of selection.

Lizards have often provided model systems to elucidate the role of sexual selection (LeBas 2001; Vanhooydonck et al. 2005b; Husak et al. 2006a; Meyers et al.

2006; Whiting et al. 2006; Baird et al. 2007; Irschick et al. 2007a; Husak and Fox 2008). Despite the richness of sexual selection studies in lizards, only recently have studies demonstrated that it may play a more important role than once thought in lizards (Baird et al. 1997; Lopez et al. 2002; Hamilton and Sullivan 2005; Lopez et al. 2006; Martín and López 2006b, a; Sullivan and Kwiatkowski 2007; Fitze et al. 2008); intersexual selection in polygynous lizards has generally been considered rare (Olsson and Madsen 1995; Tokarz 1995). Consequently, most studies have almost exclusively focused on intrasexual selection. Although the many studies that have found no evidence of mate choice in lizards have greatly improved our understanding of sexual selection, a focus on only single traits (cf. multiple signals) may obscure the ability to detect intersexual selection (Hamilton and Sullivan 2005). A more narrowly-focused scope of intersexual selection studies—and the potential interpretation that it does not exist—has important evolutionary implications: the combined effects of intra- and intersexual selection on male traits together can be stronger than either is alone (Fitze et al. 2008).

Sexual selection on males can result in the evolution of exaggerated secondary sexual characters, which may be indicative of selection on the underlying mechanism: whole-animal performance (Lailvaux and Irschick 2006; Irschick et al. 2007a; Irschick et al. 2007b). For example, there is a positive correlation between male secondary sexual characters and bite force in some lizards (Vanhooydonck et al. 2005a; Vanhooydonck et al. 2005b; Irschick et al. 2006; Meyers et al. 2006). In chameleons, casque size may be such an indicator of bite force since individuals with larger casques should presumably have more jaw musculature, and in some chameleon species, casque height is correlated with male fighting success (Stuart-Fox et al. 2006). In the two species of chameleons we studied, *Furcifer labordi* and *F. verrucosus*, one of the most conspicuous secondary sexual characters is the large, cranial casques of males. Despite being well-suited for studies of sexual selection, the effects of sexual selection on the evolution of body size and secondary sexual characters in chameleons is largely unstudied (but see Parcher 1974; Stuart-Fox et al. 2006). The paucity of behavioural studies in this group is mostly a result of the difficulty associated with field research due to poor visibility in forest canopies, which is then compounded by the secretive and cryptic behaviour of chameleons (Raxworthy 1988).

The purpose of or study was to quantify and delineate the relative effects of both intra- and intersexual selection in two closely related, sympatric species of chameleons that exhibit a strong potential for sexual selection on male secondary sexual characters and body size (Karsten et al. in review-b). To elucidate the role of intra- and intersexual selection, we used a multi-model information-theoretic approach (Burnham and Anderson 2002) to evaluate several candidate models (hypotheses) that explained patterns in male mating success (intersexual selection) and male fighting ability (intrasexual selection). In addition, we specifically tested the hypothesis that male casque size significantly differed between males that won fights and males that lost. We predicted that males that won dyadic encounters should have larger casques than losers.

Methods

Study site and species

Furcifer labordi is a medium-sized, sexually dimorphic, diurnal chameleon inhabiting the western and south-western regions of Madagascar. In our study population, adult males had a mean snout-to-vent length (SVL) of 87.3 mm, whereas mean female SVL was 71.0 mm (Karsten et al. in review-b). Males also possess large cranial casques, have numerous (but generally small) cones along the dorsal crest, and also have notable rostral appendages. *Furcifer verrucosus* is also a sexually dimorphic species, and in our study population, adult males had a mean SVL of 148.6 mm and adult females 113.3 mm (Karsten et al. in review-b). This species also possesses a cranial casque, but has fewer (but generally large) dorsal cones and lacks a rostral appendage. Like most other species of lizards in Madagascar, both species are seasonally active and reproduce during the wet season.

The study site, Ranobe forest (23°01’30” S, 43°36’36” E), was located in south-western Madagascar, approximately 30 km north of Toliara. The forest of this region is spiny forest and vegetation is typically xerophyllous thickets that include the family Didiereaceae and the genus *Euphorbia* (Koechlin 1972). Vegetation usually does not exceed 3 m in height, but occasionally can be up to 10 m in larger tree species. The forest floor is sand. Toliara mean annual rainfall is 420 mm with the wet season typically from December to February (Jury 2003): mean monthly precipitation for these months is 89.9 mm (Vose et al. 1992). Mean annual temperature is 24.2 °C. Like most arid environments, daily (day vs. night) and seasonal (wet vs. dry) temperature differences are high. Daytime temperatures range from approximately 32 °C to 40 °C during the breeding season (K. B. Karsten, unpublished data).

All data were collected 20 December 2003–06 February 2004. We collected specimens at night when they were easiest to capture (Raxworthy 1988). Upon capture, we marked locations and transported lizards to a base camp. The following morning, we measured body size (SVL) and total length (TL) to the nearest 0.1 mm using calipers, and measured mass using spring balances to the nearest 0.1 g (≤ 10 g) or 1 g (> 10 g). In addition, we measured secondary sexual characters to the nearest 0.1 mm using calipers: rostral length, height, and width; cone height; jaw length; and casque height, depth, and width (Table 1). Rostral measurements were applicable only to *F. labordi*. Rostral length was the distance from the maxilla to the apex of the appendage, rostral height was the distance from top to bottom at the approximate midway point of the appendage, and rostral width was also taken at the approximate midway point. We measured cone height of the larger of the fourth or fifth cone along the dorsal crest, which was representative of the height of cones posterior to this. We measured jaw length from the angle of the jaw to the apex of the dentary bone. Casque height was the distance from the top of the cranium to the apex of the casque, casque width was width at the base of the casque, and casque depth was the distance from the anterior ridge of the casque to the posterior ridge, also measured at the base of the casque. We also counted cones in the dorsal crest of each species (Table 1). However, in *F. verrucosus*, smaller cones are often in between larger cones. To be included in our count, the cone had to be the same approximate height as the larger cones (i.e., we did not include these smaller cones). Thus, any increase in the heterogeneity of cone height as an organism grows would results in a reduced cone count. The cones of both species continue along the tail, becoming progressively smaller the more posterior they occur. Because these small, hard-to-distinguish cones were strikingly different than the majority of the dorsal crest, we chose our cutoff point to be the transition from the typical 'larger' cones and the 'smaller' cones that continued along the tail. The same two researchers (KBK and LNA) made all measurements and conferred for each count. To ensure consistency, they compared counts of random individuals and also compared multiple counts of a set of same individuals. Dorsal cone counts were consistent between the two persons and among repeated counts.

We gave all individuals a permanent identification by toe-clipping the most distal phalanx in a three-toe combination, with only one toe clipped per foot. We observed no adverse side-effects of this marking procedure on the behaviour and survivability of individuals, nor did we observe any partial or full phalanx regrowth to confuse individual markings. After arena trials (see below), we returned all lizards to their point of capture within 24 hours.

Arena trials

The day after capture, we conducted all trials in an outdoor, neutral arena (none of the lizards were caught in the vicinity of the arena). The arena was approximately 1x1 m square and 2 m in height. We built the rectangular frame from small, cut saplings and covered it with 1.25-cm square plastic mesh. Inside the arena was natural vegetation, which we trimmed back from the mesh. Two observers (KBK and LNA) carefully recorded all behavioural data from behind a blind. Preliminary studies revealed that the presence of observers concealed by a blind did not affect the behaviour of either male or female chameleons alone or during social interactions (K. B. Karsten, unpublished data).

We conducted 108 behavioural trials, each 30 minutes, resulting in 54 hours of observation. We recorded the social behaviour of each individual (described in detail in Karsten et al. in review-b) for 47 male-female trials and 26 male-male trials with *F. labordi*, and 28 male-female trials and 7 male-male trials with *F. verrucosus*. In some of the male-female trials in both species, females displayed sexually unreceptive coloration and rejected males in 100% of the 36 trials (Karsten et al. in review-b). For the present analyses, we excluded these trials, leaving 21 male-female trials with receptively coloured *F. labordi* and 18 with receptively coloured *F. verrucosus*. During these trials, the male was classified as either ‘successful’ if copulation occurred, or ‘unsuccessful’ if no copulation occurred. The losers of the male-male interactions were those that fled the encounter, typically toward the ground, or became dislodged during a fight and did not return to interact. This protocol yielded a clear winner and loser for all trials.

After the arena trials, radio transmitters weighing less than 10% of the animal’s body mass were affixed to the dorsal ridge of 11 lizards using liquid adhesive (7 *F. labordi* and 4 *F. verrucosus*). We located each lizard daily and made brief focal observations (< 30 minutes), 3-4 times per day. Although these data were not sufficient to test hypotheses of sexual selection, they did allow us to qualitatively compare social interactions among free-ranging individuals to those that took place in the arena. The social interactions of free-ranging, radio-tagged individuals were similar to those of arena interactions.

Statistical analyses

In chameleons, casque size is hypothesized to be correlated with bite force (Karsten et al. in review-b, A. Herrel unpublished data), which is important in determining winners of fights in other lizards (Huyghe et al. 2005; Lappin and Husak 2005; Husak et al. 2006b; Lailvaux and Irschick 2007). Therefore, we made an a priori decision to test for significant differences in casque height between winning and losing males of both species using paired t-tests. Additionally, we always included this variable in the paired logistic regression models (see below) applied to male-male trials of both species.

We measured or counted 11 morphological variables for *F. labordi* and 8 for *F. verrucosus* (the same 11 for *F. labordi* minus the 3 rostral variables). We first used Principal Components Analysis (PCA) to reduce the number of variables for both intra- and intersexual selection trials. For each of the first few PCA axes, we determined which of our measured variables loaded the highest with the synthetic PCA variable, and retained it as a candidate variable. If two variables loaded highly with a PCA axis, but in opposite directions, we retained both as candidate variables. We determined how many axes to use from the PCA by assessing when only minimal explanatory power was gained by adding another axis. Although our choice of how many PCA axes to include was arbitrary, its purpose was as a data reduction technique, and even the inclusion of up to 4 axes reduced the number of candidate variables substantially. Although PCA chooses axes orthogonal to each other, we recognized there may be some correlation between the remaining candidate variables. We determined if any candidate variables were correlated, and if so, we regressed each one against the variable chosen from PC1 (in all cases, SVL) to calculate residuals. We then used these residuals for subsequent model testing.

From the a priori data reduction using PCA, we built models (a set of alternative hypotheses) using combinations of the remaining variables. Each model was then subsequently tested using logistic regression, where the dependent variable was binary: either ‘winner’ or ‘loser’ for male-male trials, or ‘successful’ or ‘unsuccessful’ at copulation in male-female trials. To determine which model(s) best explained the binary outcome, we used an information-theoretic approach that focuses on the strength of evidence provided by a set of a priori alternative hypotheses rather than a statistical test of null hypotheses (Anderson et al. 2000; Burnham and Anderson 2002). The Akaike Information Criterion (AIC), based on Kullback-Leibler information (Kullback and Leibler 1951; Anderson et al. 2000; Anderson and Burnham 2002; Burnham and Anderson 2002), is an information-theoretic derivative of the log-likelihood function that provides the best measure of model fit in the case of observational data (Burnham and Anderson 2002): the model with the lowest AIC is the most informative hypothesis. Due to a lower than preferred ratio of sample size (n) to model parameters (K), we used the second-order criterion (AIC_c), which uses a bias-corrected term for smaller sample sizes (Burnham and Anderson 2002). Like the AIC, the lowest AIC_c reflects the best-fitting model, and all supported hypotheses were considered within 2 units of the smallest AIC_c (Weller and Zabel 2001; Burnham and Anderson 2002; Compton et al. 2002). For each model, we also defined the number of estimable parameters (K), the difference in AIC_c between the model of interest and the AIC_c of the best model (ΔAIC_c), and the model’s Akaike weight (ω). The ΔAIC_c allows for direct comparison of models relative to the best-fitting, and the Akaike weight gives the relative weight each hypothesis carries in the overall explanation of the dependent variable.

For male-male trials, it would be inappropriate to use standard logistic regression since contest outcome is determined from trait values relative to the opponent, and not absolute trait values. For example, if body size is important, then large males may be classified as losers simply because they were paired with an even larger male, not because their overall body size is ‘small’ compared to the rest of the sample population. Because the binary dependent variable (winner vs. loser) was paired, we used a paired (or matched-case or conditional) logistic regression (no intercept model) instead of standard logistic regression for these data (Hosmer and Lemeshow 2000; Keating and Cherry 2004). To perform paired logistic regression, we calculated the differences for each variable by subtracting the loser’s value from the winner’s, then performed a standard logistic regression on the differences with the constant term excluded (Rocke and Samuel 1999; Hosmer and Lemeshow 2000; Compton et al. 2002; Row and Blouin-Demers 2006). Rather than evaluating the absolute measure of the traits, the results are interpreted as relative differences in morphology (Hosmer and Lemeshow 2000). We used the same information-theoretic approach as we did for the male-female trials, employing AIC_c for smaller sample sizes.

Odds ratios provide an additional interpretation of logistic regression models (Keating and Cherry 2004), and we made use of them. In logistic regression, the odds of an event happening (the positive binary outcome in this example) increase by e^{β} for every one unit change in x (Agresti 2002; Compton et al. 2002); where β is the estimated coefficient and, in our data, x is the value state of the morphological variable included in the model. An odds ratio greater than one increases the odds of the event and an odds ratio less than one decreases the odds. For example, if the odds ratio for a given morphological variable is 1.50 for event *A*, then an increase of one unit along the axis of the morphological variable increases the odds of event *A* happening by 50%. An odds ratio of 0.75 indicates that an advance of one unit along the morphological axis decreases the odds of event *A* by 25%.

Although an information-theoretic approach is powerful in explaining model fit, it makes no distinction of model ‘quality’ (Anderson and Burnham 2002; Burnham and Anderson 2002). In some instances, possible candidate models may produce biologically unrealistic estimates (Compton et al. 2002) and therefore not achieve the goal of being a useful predictor of reliable parameter estimates. Worse yet, unstable parameter estimates indicate that the maximum of the log-likelihood is not found and the resultant information criteria (models) will be incorrect (Anderson and Burnham 2002). Accordingly, we assessed the results of each model analysis and selected only the most robust (i.e., stable) models for interpretation. We assessed model stability three ways. First, the statistical software explicitly identifies unstable parameters. Second, the 95% confidence interval of the odds ratios should not include 1.0 (Compton et al. 2002). Third, we determined if the predictions of the odds ratios produced realistic magnitudes (i.e., not zero or infinity). Unstable models violated all of these criteria and were not included in the final interpretation of results.

Although multiple models with multiple variables may be the best-fitting explanations as a whole, it is also possible to determine the relative influence that each individual variable has in explaining the dependent variable. To determine which variables were under the strongest intra- and intersexual selection pressures, we calculated the relative importance weight for each, $\omega_+(i)$ (Burnham and Anderson 2002).

These weights were calculated by summing the Akaike weights, ω, of each model in which the variable occurs, thus allowing direct comparison of relative influence.

We performed all statistical analyses using the software, JMP, version 7.0.1 (SAS Institute, Inc., Cary, North Carolina, USA).

Results

Furcifer labordi

The PCA for the male-male data set (n = 52) revealed 3 PC axes that accounted for 91.8% of the variation in male morphology (Table 2). The variables most associated with PC1 were indicative of body size and traits highly correlated with body size (eigenvectors in parentheses, here and throughout): the highest 3 eigenvectors were SVL (0.35), casque depth (0.35), and mass (0.34). Most variables (8 of the 11) were highly associated with PC1 (eigenvectors > 0.30); however, we chose only one variable that was indicative of body size, SVL. Rostral width (0.83) contributed the most to PC2. The number of dorsal cones counted (0.82) explained the most variation in PC3. We then used SVL, rostral width, and number of cones counted, in addition to our planned inclusion of casque height, to build models analyzed by paired logistic regression. Number of cones counted and casque height were significantly correlated with SVL. Therefore, we used residuals of these two variables (from regressions of each vs. SVL) for logistic regression analyses.

Using pre-selected variables, we tested 15 models using paired logistic regression, all of which were stable and considered in the final interpretation of results. Body size

(SVL) and the combination of SVL and residual casque height were the best supported hypotheses in explaining male fighting success (AIC_c = 55.84 and 56.82, ω = 0.35 and 0.21, respectively; Table 3). Four variables were represented among 15 models: differences in SVL, residual casque height, rostral width, and residual number of dorsal cones counted. The difference in SVL had the largest $\omega_+(i)$ and was the variable likely to be under the strongest intrasexual selection ($\omega_+(i) = 1.00$; Table 4). Although body size (and likely all traits correlated with it) was the most important variable in determining the winner of male-male agonistic encounters, differences in size-corrected casque height also contributed to male fighting success (Figure 1A). Snout-vent length was greater in winning males (mean ± 1 SEM; 82.0 ± 2.6 mm; n = 26) than losing males (77.3 ± 2.7 mm; n = 26) and casque height was also greater in winning males (10.1 ± 0.5 mm; residual mean = 0.05 ± 0.15; n = 26) than losing males (9.2 ± 0.5 mm; residual mean = -0.05 ± 0.15; n = 26). However, the planned comparison for differences in residual casque height between winners and losers failed to find significant difference (t = -0.48, df = 25, p = 0.64; *ns*). The best-fitting model of SVL alone resulted in an odds ratio of 1.27 (95% CI = 1.11-1.53). Thus, for every 1 mm increase in SVL relative to an opponent, the odds of winning the fight increased 27%.

The PCA for the male-female data set (n = 21) revealed 4 PC axes that accounted for 93.5% of the variation in male morphology (Table 2). The variables most associated with PC1 were indicative of body size and all traits highly correlated with it: the highest 3 eigenvectors were SVL (0.34), mass (0.34), and jaw length (0.34). Similar to the male-male data set, most variables (8 of the 11) were highly associated with body size (eigenvectors > 0.30). We again chose only SVL to represent the body size axis. Number of dorsal cones counted (0.84) was most associated with PC2 and rostral width (0.61) explained the most variation in PC3. The remaining variable added, from PC4, was rostral height (-0.85). We used these four variables to construct all possible models for logistic regression analysis. In this data set, rostral height and rostral width were significantly correlated with SVL, but number of cones was not. We used residuals of rostral width and height (from regressions of each vs. SVL) for logistic regression.

Using the a priori variables for male-female trials, we developed 15 models for standard logistic regression, 2 of which were unstable. Of the remaining 13, the best supported hypothesis that explained male mating success was that which included SVL and size-corrected rostral width ($AIC_c = 17.9$, $\omega = 0.50$; Table 5). However, a second hypothesis that included SVL, size-corrected rostral width, and size-corrected rostral height was also supported ($AIC_c = 18.3$, $\omega = 0.41$). Among the 13 models, 4 variables were considered (Table 4): SVL, residual rostral width, residual rostral height, and number of cones counted. Residual rostral width and SVL were most influential in determining whether or not males achieved copulation ($\omega_+(i) = 0.99$ and 0.92, respectively; Figure 1B). Successful males had wider rostral appendages (1.06 ± 0.03 mm; residual mean = 0.05 ± 0.03; n = 13) than unsuccessful males (0.87 ± 0.02 mm; residual mean = -0.08 ± 0.02; n = 8). Successful males had larger measured rostral heights, but smaller residuals (5.3 ± 0.2 mm; residual mean = -0.02 ± 0.13; n = 13) than unsuccessful males (4.8 ± 0.3 mm; residual mean = 0.03 ± 0.19; n = 8). Successful males had larger SVL (100.2 ± 2.9 mm, n = 13) than unsuccessful males (89.9 ± 4.4 mm, n = 8). For the best-fitting model of SVL and residual rostral width, the odds ratio for SVL was 1.22 (1.04-1.68), meaning that an increase of 1 mm in SVL increased the odds of copulation by 22%. The odds ratio for residual rostral width becomes difficult to interpret biologically since it is based on size-corrected data and not actual widths and the fact that mean widths were less than 1 measurable unit (1 mm). The odds ratio for residual rostral width was an astonishing 1.66×10^{15} (9.66×10^{4}-4.29×10^{38}). Although it is not likely possible to increase the residual rostral width by a full millimetre, this odds ratio clearly indicates that any increase in rostral width relative to body size dramatically improves the odds of mating success.

Furcifer verrucosus

We analyzed the male-male data set in *F. verrucosus* (n = 14) and found 3 PC axes that accounted for 88.9% of the variation in male morphology (Table 2). The variable most positively associated with PC1 (greatest eigenvector) was casque width (0.44), but PC1 was also strongly negatively associated with SVL (-0.41). Because these variables were opposing, we included both for future analyses. Variables most associated with PC2 were dorsal cone height (0.68) and number of dorsal cones (0.67). Because these may play different roles in social signalling, we included both for the paired logistic regression. For PC3, casque height was positively associated (0.54) and number of cones counted (-0.60) negatively associated. We used differences in SVL, casque width, number of cones counted, cone height, and casque height to build models analyzed by logistic regression. Casque height and casque width were the only variables significantly correlated with SVL, so we used residuals of these two variables (from regressions of each vs. SVL) for logistic analyses.

We constructed and tested 30 models based on our a priori variables; however, 14 of the models failed our criteria for suitability (see methods). Three hypotheses were considered supported in the final analysis: SVL alone, SVL and number of cones counted, and SVL and size-corrected casque width (AIC_c = 13.4, 14.0, and 15.3, ω = 0.33, 0.25, and 0.13, respectively; Table 6). The odds ratio for the only variable included in the best-fitting model, SVL, was 1.18 (1.03-1.57). Thus, an increase in SVL by 1 mm greater than an opponent increased the odds of winning the fight by 18%. In the 16 models used for interpretation, 5 variables were represented: SVL, number of cones counted, residual casque height, residual casque width, and cone height. The number of dorsal cones counted was fewer in successful males (21.1 ± 1.0; n = 7) than unsuccessful males (22.7 ± 1.2; n = 7), but body size (SVL) was the most important variable in determining the winner of male-male agonistic encounters ($\omega_+(i)$ = 0.85; Table 4; Figure 2A): winning males had larger SVL (154.7 ± 2.6 mm; n = 7) than losing males (142.6 ± 4.6 mm; n = 7). Winning males had narrower casque widths, but larger residuals (15.9 ± 0.8 mm; residual mean = 0.48 ± 0.57; n = 7) than losing males (17.3 ± 1.1 mm; residual mean = -0.48 ± 0.48; n = 7). The reversed pattern in the mean residual width may be due to one winning male that had a much larger residual casque width than all the others. Casque height was greater in successful males (16.6 ± 0.9 mm; residual mean = 0.83 ± 0.66; n = 7) than unsuccessful males (16.3 ± 0.8 mm; residual mean = -0.83 ± 0.54; n = 7), but residuals were not significantly different between winners and losers (t = -1.66, df = 6, p = 0.15; *ns*). However, small sample size precludes a strong elimination of this hypothesis. Nine of the 14 models not included in the final interpretation contained the variable for residual casque height, indicating it may have had some influence that we were not able to detect with our sample size.

The PCA for the male-female data set (n = 18) revealed 4 PC axes that accounted for 97.0% of the variation in male morphology (Table 2). The variables most associated with PC1 were indicative of body size and all traits highly correlated with it: the 4 highest eigenvectors were mass (0.41), jaw length (0.40), casque width (0.39), and SVL (0.38). In total, 7 of 8 variables were highly associated with PC1 (eigenvectors > 0.30). Because SVL is a standard measure of body size in lizards, and all other variables were indicative of body size, we designated SVL as our indicator variable even though mass had a larger eigenvector. The number of dorsal cones counted (0.97), the only variable not significantly correlated with SVL, was most associated with PC2 and dorsal cone height (0.84) explained the most variation in PC3. The remaining variable added, from PC4, was casque height (0.87). We used these four variables to construct the models for logistic regression analysis. In this data set, cone height and casque height were significantly correlated with SVL, but number of cones counted was not. We used residuals of cone height and casque height (from regressions of each vs. SVL) for logistic regression analyses.

We developed 15 models for standard logistic regression using the a priori variables for male-female trials but discarded 1 due to its instability. Three hypotheses were supported as the ones that explained male mating success the best: number of cones counted, size-corrected cone height, size-corrected casque height; number of cones counted alone; and number of cones counted and residual casque height (AIC_c = 18.1, 19.3, and 19.8, ω = 0.38, 0.21, and 0.16, respectively; Table 7). Analysis of the 14 stable models yielded 4 variables: SVL, number of cones counted, residual cone height, and residual casque height. Successful males tended to have greater casque heights (16.5 ± 0.9 mm; residual mean = 0.49 ± 0.62; n = 9) than losing males (15.0 ± 0.6 mm; residual mean = -0.49 ± 0.33; n = 9), but the number of dorsal cones we counted had the greatest weight ($\omega_+(i) = 0.99$; Table 4; Figure 2B). Successful males tended to have similar-sized dorsal cones, but smaller residuals (3.2 ± 0.2 mm; residual mean = -0.09 ± 0.17; n = 9), than losing males (3.3 ± 0.3 mm; residual mean = 0.09 ± 0.23; n = 9). We calculated odds ratios for each variable from the best-fitting model (cones, residual cone height, and residual casque height). The odds ratio for number of cones counted was 0.27 (0.02-0.66); an increase of 1 cone counted decreased the odds of successful copulation by 73%. The odds ratios for residual cone height and residual casque height are difficult to interpret for the same reasons provided previously (see intersexual selection results for *F. labordi*), but they were $1.67\mathrm{x}10^{-4}$ ($3.33\mathrm{x}10^{-16}$-0.52) for residual cone height and 20.92 (1.57-$1.01\mathrm{x}10^{5}$) for residual casque height.

Discussion

In vertebrate mating systems, sexual selection can strongly influence the evolution of morphological traits, producing substantial differences between the sexes in body size (Schütz and Taborsky 2005; Raihani et al. 2006) and/or exaggerated secondary sexual characters (Berglund et al. 1996; Benson and Basolo 2006; Møller et al. 2006). However, it has been unclear what role sexual selection plays in the evolution of sexual dimorphism in chameleons. Previously, we found that the social system of *F. labordi* exhibited a strong potential for both intra- and intersexual selection: fights between males escalated to fierce, long physical combat and females were highly selective (Karsten et al. in review-b). In the present study, we found that in *F. labordi* there was intrasexual selection for body size and size-corrected casque height (Table 3; Figure 1A) and intersexual selection for body size and size-corrected rostral width (Table 5; Figure 1B). We also previously described the social system of *F. verrucosus* and found that it was likely to have intrasexual selection (Karsten et al. in review-b). If present, intersexual selection appeared to either be very subtle, or at least not in the form of overt behavioural mate choice: sexually receptive females allowed nearly all males to attempt copulation, although male mating success with these passive females was highly variable (Karsten et al. in review-b). In the present study, we found intrasexual selection for body size in *F. verrucosus* (Table 6; Figure 2A) and intersexual selection for males that had both fewer counted dorsal cones and increased size-corrected casque height (Table 7; Figure 2B).

Because *F. verrucosus* does not exhibit strong mate choice, and cones do not appear to possess any functional advantage to achieving copulation, it is unclear why this trait varies with reproductive success in males attempting copulation with behaviourally receptive females. One hypothesis may be that the fewer dorsal cones that we counted may correlate with age or experience. In juvenile males, all dorsal cones are the same relative height, and by our counting criterion (see methods), juveniles would have higher dorsal cone counts. However, in adult males, only some of the cones grow to be tall (and were counted), while shorter, underdeveloped (uncounted) cones are inter-dispersed. Thus, even though the actual number of cones an individual possesses does not change throughout its life span, our method of counting dorsal cones in *F. verrucosus* may result in a ‘decrease’ of counted cones with age, even among adults (e.g., first year adult males compared to second year adults). An alternative hypothesis to explain the advantage of having fewer dorsal cones counted is that increased heterogeneity of dorsal cone height (i.e., fewer cones counted by our criterion) may be correlated with some other advantageous trait not readily apparent, such as immune status for example. Females may therefore be using dorsal cone heterogeneity as an alternative visual cue if they are exhibiting a subtle form of mate choice. While the role of dorsal cones may have multiple explanations, it clearly is an important trait corresponding to both male fighting and mating success in *F. verrucosus* (Tables 4, 6, & 7; Figure 2).

We found that in *F. labordi*, both intra- and intersexual selection were strong, particularly for body size, which was expected since this species’ social system exhibited strong potential for both (Karsten et al. in review-b). Sexual size dimorphism in this species is considerable. We also found evidence of sexual selection on the rostral appendage in males (Table 4; Figure 1B). In most animals, rostral appendages are typically viewed as weapons for male combat likely to be under intrasexual selection (Andersson 1994; Emlen et al. 2005), and in chameleons, the rostral appendages found in some species are used exclusively for male combat (Parcher 1974). What was surprising in our results was that we found strong intersexual selection for the rostral appendage, especially its width. When males encounter a receptively coloured female who is behaviourally resistant, males will often manoeuvre adjacent to the female and apply lateral pressure with the rostral appendage, which in some instances results in the female switching from behavioural rejection to behavioural receptivity (Karsten et al. in review-b). Wider rostral appendages may be advantageous if females use the amount of pressure applied by the male as a possible cue for male physical performance, condition, or 'quality' in their assessment of suitable mates.

An optimal male fitness strategy should be to invest his limited energetic resources most heavily in the traits that maximize fitness, even at the expense of other traits (Maklakov et al. 2006; Simmons and Emlen 2006). For example, in a mating system with predominately intrasexual selection, males should invest most heavily in the traits that favour fighting ability, whereas in a system with strong female choice, they should invest most in the traits preferred by females. Indeed, *F. verrucosus* has a mating system with predominately intrasexual selection and males do exhibit striking growth rates (K. B. Karsten, unpublished data). Large body size is extremely important for winning fights with other males (Table 4). However, in a mating system subject to both types of sexual selection, one could envision a competing trade-off between resources allocated toward either intra- or intersexually selected traits. An apparent resolution to this trade-off would be if a trait served the dual purpose of increased fighting ability and mating success. In *F. labordi*, a species with strong intra- and intersexual selection, we found that body size was important in both contexts (Table 4). Therefore, *F. labordi* males should invest heavily in growth. Growth rates in *F. labordi* are extreme: males can potentially increase body size from hatchling to adult by 300-400% in under two months (Karsten et al. in review-a). The trade-off for *F. labordi* then becomes how to allocate resources for body size compared to the rostral appendage. Examining patterns of allometric growth in body size and secondary sexual characters may reveal patterns of how males manage this trade-off of resources.

In other polygynous lizards, head size positively correlates with bite force in males (Herrel et al. 1999; Herrel et al. 2001) and bite force can predict social dominance (Lailvaux et al. 2004; Huyghe et al. 2005; Husak et al. 2006b). Therefore, stronger bite force may aid males in potentially acquiring better, high-quality territories than those males with weaker bite forces (Lappin and Husak 2005). Contrary to our predictions, we found no evidence that winning males had larger size-corrected casques than losers in *F. verrucosus*. However, that does not preclude its importance in determining the outcome of male-male trials. Of the 14 models of male fighting success that were unstable (and removed from consideration) in *F. verrucosus*, 9 of them included residual casque height. Although unstable models do not provide reliable estimates of parameters, their direction is probably still important (Compton et al. 2002). This suggests that casque height may be a biologically important variable in *F. verrucosus*, but that our models were unable to make biologically realistic predictions with it, possibly as a result of the small sample size associated with our male-male trials in this species. In contrast to *F. verrucosus*, we did find that residual casque height played an important role in male fighting success in *F. labordi* (Tables 3 & 4), although not as important as SVL (Figure 1A). However, for both species, it is also possible that casque size is not the best indicator of male fighting ability, but instead it is the performance associated with it (bite force) that may be the underlying target of sexual selection (Lailvaux and Irschick 2006; Irschick et al. 2007a; Irschick et al. 2007b). Future studies that measure bite force may better elucidate the role of the casque in chameleon social systems.

As others have demonstrated, mate choice in lizards may play a more important role than once thought (Baird et al. 1997; Lopez et al. 2002; Hamilton and Sullivan 2005;

Lopez et al. 2006; Martín and López 2006b, a; Sullivan and Kwiatkowski 2007; Fitze et al. 2008). Our present study confirms the presence of strong female choice in *F. labordi*, which contributes to the growing body of literature that mate choice in lizards may not be as uncommon as once thought. Additionally, we showed that direct female choice in *F. labordi* and male mating success in *F. verrucosus* was not predicted the best by a single individual trait, but rather there was selection for multiple male traits. Intersexual selection for multiple traits together may be of greater relative importance than for individual traits alone (Marchetti 1998; Calkins and Burley 2003; Hamilton and Sullivan 2005; McGlothlin et al. 2005; Taylor et al. 2007). Intuitively, multiple traits provide multiple forms of information to females regarding male quality or the most suitable mates (Candolin 2003). In these chameleons, both intra- and intersexual selection are likely to be acting upon suites of morphological variables since we found that nearly all the best supported hypotheses were multivariate, even when accounting for the correlation of these variables with body size.

Chameleons are morphologically diverse, highly visual with elaborate and conspicuous displays, and males often possess exaggerated secondary sexual characters (Parcher 1974; Bickel and Losos 2002; Stuart-Fox et al. 2006; Karsten et al. in review-b). Our results explain how these traits may have evolved in these two sexually dimorphic species adorned with secondary sexual characters. In *F. labordi*, large body size was important for both mating and fighting success in males, and to a lesser extent, so was size-corrected casque height. We also found strong support for the evolution of their rostral appendage, which was of slightly greater relative importance in explaining male mating success than SVL, even when corrected for body size. Body size was also important for male fighting success in *F. verrucosus*, and although females of this species exhibit little mate choice, there may be a cryptic mode of intersexual selection for increased age/experience (fewer dorsal cones counted). Our results may shed light on the evolution of sexually selected traits in other chameleons with similar morphological combinations. Although generally difficult to disentangle the relative contributions of intra- and intersexual selection on multiple traits, we determined the influence of both forms of sexual selection on body size and secondary sexual characters in these two chameleon species.

Acknowledgments

Field studies in Madagascar were made possible due to the assistance of the Ministries des Eaux et Forêts, the Association Nationale pour la Gestion des Aires Protégées, and the Université d'Antananarivo, Département de Biologie Animale. We thank D. Rakotondravony and O. Ramilijaona for their assistance with the project and H. Thomas and D. Kidney for valuable logistical advice. We thank T.A. Baird, M. Lovern, and M. Palmer for comments on an earlier version of the manuscript and A. Herrel for unpublished data on bite force. We also thank A. Roberts and M. Palmer for statistical advice. Research was supported by a grant from the National Science Foundation (DEB 99-84496) to CJR.

Literature cited

Agresti, A. 2002. *Categorical Data Analysis*, Second edn. Hoboken, New Jersey: John Wiley & Sons, Inc.

Anderson, D. R., Burnham, K. P. & Thompson, W. L. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management*, 64, 912-923.

Anderson, D. R. & Burnham, K. R. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management*, 66, 912-918.

Andersson, M. 1994. *Sexual Selection*. Princeton, New Jersey: Princeton University Press.

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

Baird, T. A., Hranitz, J. M., Timanus, D. K. & Schwartz, A. M. 2007. Behavioral attributes influence annual mating success more than morphological traits in male collared lizards. *Behavioral Ecology*, 18, 1146-1154.

Benson, K. E. & Basolo, A. L. 2006. Male-male competition and the sword in male swordtails, *Xiphophorus helleri*. *Animal Behaviour*, 71, 129-134.

Berglund, A., Bisazza, A. & Pilastro, A. 1996. Armaments and ornaments: An evolutionary explanation of traits of dual utility. *Biological Journal of the Linnean Society*, 58, 385-399.

Bickel, R. & Losos, J. B. 2002. Patterns of morphological variation and correlates of habitat use in chameleons. *Biological Journal of the Linnean Society*, 76, 91-103.

Burnham, K. P. & Anderson, D. R. 2002. *Model selection and multimodel inference: a practical information-theoretic approach*. New York, New York: Springer.

Calkins, J. D. & Burley, N. T. 2003. Mate choice for multiple ornaments in the California quail, *Callipepla californica*. *Animal Behaviour*, 65, 69-81.

Candolin, U. 2003. The use of multiple cues in mate choice. *Biological Reviews*, 78, 575-595.

Compton, B. W., Rhymer, J. M. & McCollough, M. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): An application of paired logistic regression. *Ecology*, 83, 833-843.

Emlen, D. J., Marangelo, J., Ball, B. & Cunningham, C. W. 2005. Diversity in the weapons of sexual selection: Horn evolution in the beetle genus *Onthophagus* (Coleoptera : Scarabaeidae). *Evolution*, 59, 1060-1084.

Endler, J. A. 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes*, 9, 173-190.

Fitze, P. S., Cote, J., Martinez-Rica, J. P. & Clobert, J. 2008. Determinants of male fitness: disentangling intra- and inter-sexual selection. *Journal of Evolutionary Biology*, 21, 246-255.

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

Herrel, A., De Grauw, E. & Lemos-Espinal, J. A. 2001. Head shape and bite performance in xenosaurid lizards. *Journal of Experimental Zoology*, 290, 101-107.

Herrel, A., Spithoven, L., Van Damme, R. & De Vree, F. 1999. Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology*, 13, 289-297.

Hosmer, D. W. & Lemeshow, W. 2000. *Applied Logistic Regression*. New York, New York: John Wiley & Sons.

Husak, J. F. & Fox, S. F. 2008. Sexual selection on locomotor performance. *Evolutionary Ecology Research*, in press.

Husak, J. F., Fox, S. F., Lovern, M. B. & Van Den Bussche, R. A. 2006a. Faster lizards sire more offspring: Sexual selection on whole-animal performance. *Evolution*, 60, 2122-2130.

Husak, J. F., Lappin, A. K., Fox, S. F. & Lemos-Espinal, J. A. 2006b. Bite-force performance predicts dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia*, 301-306.

Huyghe, K., Vanhooydonck, B., Scheers, H., Molina-Borja, M. & Van Damme, R. 2005. Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology*, 19, 800-807.

Irschick, D., Bailey, J. K., Schweitzer, J. A., Husak, J. F. & Meyers, J. J. 2007a. New directions for studying selection in nature: studies of performance and communities. *Physiological and Biochemical Zoology*, 80, 557-567.

Irschick, D. J., Herrel, A., Vanhooydonck, B. & Van Damme, R. 2007b. A functional approach to sexual selection. *Functional Ecology*, 21, 621-626.

Irschick, D. J., Ramos, M., Buckley, C., Elstrott, J., Carlisle, E., Lailvaux, S. P., Bloch, N., Herrel, A. & Vanhooydonck, B. 2006. Are morphology-performance relationships invariant across different seasons? A test with the green anole lizard (*Anolis carolinensis*). *Oikos*, 114, 49-59.

Jenssen, T. A., Orrell, K. S. & Lovern, M. B. 2000. Sexual dimorphisms in aggressive signal structure and use by a polygynous lizard, *Anolis carolinensis*. *Copeia*, 140-149.

Jury, M. R. 2003. The climate of Madagascar. In: *The Natural History of Madagascar* (Ed. by Goodman, S. M. & Benstead, J. P.), pp. 75-87. Chicago, Illinois: University of Chicago Press.

Karsten, K. B., Andriamandimbiarisoa, L. N., Fox, S. F. & Raxworthy, C. J. in review-a. Discovery of a novel tetrapod life history: an annual chameleon living mostly as an egg. *Proceedings of the National Academy of Sciences of the United States of America*.

Karsten, K. B., Andriamandimbiarisoa, L. N., Fox, S. F. & Raxworthy, C. J. in review-b. Social behavior of two species of chameleons in Madagascar: insights into sexual selection. *Herpetologica*.

Keating, K. A. & Cherry, S. 2004. Use and interpretation of logistic regression in habitat selection studies. *Journal of Wildlife Management*, 68, 774-789.

Koechlin, J. 1972. Flora and vegetation of Madagascar. In: *Biogeography and Ecology in Madagascar* (Ed. by Battistini, R. & Richard-Vindard, G.), pp. 145-190. The Hague: Dr. W. Junk B. V.

Kullback, S. & Leibler, R. A. 1951. On information and sufficiency. *Annals of Mathematical Statistics*, 22, 79-86.

Lailvaux, S. P., Herrel, A., Vanhooydonck, B., Meyers, J. J. & Irschick, D. J. 2004. Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London Series B-Biological Sciences*, 271, 2501-2508.

Lailvaux, S. P. & Irschick, D. J. 2006. A functional perspective on sexual selection: insights and future prospects. *Animal Behaviour*, 72, 263-273.

Lailvaux, S. P. & Irschick, D. J. 2007. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *American Naturalist*, 170, 573-586.

Lappin, A. K., Brandt, Y., Husak, J. F., Macedonia, J. M. & Kemp, D. J. 2006. Gaping displays reveal and amplify a mechanically based index of weapon performance. *American Naturalist*, 168, 100-113.

Lappin, A. K. & Husak, J. F. 2005. Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard (*Crotaphytus collaris*). *American Naturalist*, 166, 426-436.

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

Lopez, P., Amo, L. & Martin, J. 2006. Reliable signaling by chemical cues of male traits and health state in male lizards, *Lacerta monticola*. *Journal of Chemical Ecology*, 32, 473-488.

Lopez, P., Munoz, A. & Martin, J. 2002. Symmetry, male dominance and female mate preferences in the Iberian rock lizard, *Lacerta monticola*. *Behavioral Ecology and Sociobiology*, 52, 342-347.

Maklakov, A. A., Bilde, T. & Lubin, Y. 2006. Inter-sexual combat and resource allocation into body parts in the spider, *Stegodyphus lineatus*. *Ecological Entomology*, 31, 564-567.

Marchetti, K. 1998. The evolution of multiple male traits in the yellow-browed leaf warbler. *Animal Behaviour*, 55, 361-376.

Martín, J. & López, P. 2006a. Links between male quality, male chemical signals, and female mate choice in Iberian Rock Lizards. *Functional Ecology*, 20, 1087-1096.

Martín, J. & López, P. 2006b. Vitamin D supplementation increases the attractiveness of males' scent for female Iberian rock lizards. *Proceedings of the Royal Society B-Biological Sciences*, 273, 2619-2624.

McGlothlin, J. W., Parker, P. G., Nolan, V. & Ketterson, E. D. 2005. Correlational selection leads to genetic integration of body size and an attractive plumage trait in dark-eyed juncos. *Evolution*, 59, 658-671.

Meyers, J. J., Irschick, D. J., Vanhooydonck, B. & Herrel, A. 2006. Divergent roles for multiple sexual signals in a polygynous lizard. *Functional Ecology*, 20, 709-716.

Møller, A. P., Chabi, Y., Cuervo, J. J., Lope, F., Kilpimaa, J., Kose, M., Matyjasiak, P., Pap, P. L., Saino, N., Sakraoui, R., Schifferli, L. & Hirschheydt, J. 2006. An analysis of continent-wide patterns of sexual selection in a Passerine bird. *Evolution*, 60, 856-868.

Morris, M. R., Tudor, M. S. & Dubois, N. S. 2007. Sexually selected signal attracted females before deterring aggression in rival males. *Animal Behaviour*, 74, 1189-1197.

Olsson, M. & Madsen, T. 1995. Female choice on male quantitative traits in lizards - why is it so rare? *Behavioral Ecology and Sociobiology*, 36, 179-184.

Parcher, S. R. 1974. Observations on the natural histories of six Malagasy Chamaeleontidae. *Zeitschrift für Tierpsychologie*, 34, 500-523.

Pratt, A. E., McLain, D. K. & Lathrop, G. R. 2003. The assessment game in sand fiddler crab contests for breeding burrows. *Animal Behaviour*, 65, 945-955.

Raihani, G., Szekely, T., Serrano-Meneses, M. A., Pitra, C. & Goriup, P. 2006. The influence of sexual selection and male agility on sexual size dimorphism in bustards (Otididae). *Animal Behaviour*, 71, 833-838.

Raxworthy, C. J. 1988. Reptiles, rainforest and conservation in Madagascar. *Biological Conservation*, 43, 181-211.

Rocke, T. E. & Samuel, M. D. 1999. Water and sediment characteristics associated with avian botulism outbreaks in wetlands. *Journal of Wildlife Management*, 63, 1249-1260.

Row, J. R. & Blouin-Demers, G. 2006. Thermal quality influences habitat selection at multiple spatial scales in milksnakes. *Ecoscience*, 13, 443-450.

Schütz, D. & Taborsky, M. 2005. The influence of sexual selection and ecological constraints on an extreme sexual size dimorphism in a cichlid. *Animal Behaviour*, 70, 539-549.

Simmons, L. W. & Emlen, D. J. 2006. Evolutionary trade-off between weapons and testes. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 16346-16351.

Stuart-Fox, D. M., Firth, D., Moussalli, A. & Whiting, M. J. 2006. Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. *Animal Behaviour*, 71, 1263-1271.

Sullivan, B. K. & Kwiatkowski, M. A. 2007. Courtship displays in anurans and lizards: theoretical and empirical contributions to our understanding of costs and selection on males due to female choice. *Functional Ecology*, 21, 666-675.

Taylor, R. C., Buchanan, B. W. & Doherty, J. L. 2007. Sexual selection in the squirrel treefrog *Hyla squirella*: the role of multimodal cue assessment in female choice. *Animal Behaviour*, 74, 1753-1763.

Tokarz, R. R. 1995. Mate choice in lizards: a review. *Herpetological Monographs*, 9, 17-40.

Vanhooydonck, B., Herrel, A., Van Damme, R., Meyers, J. & Irschick, D. 2005a. The relationship between dewlap size and performance changes with age and sex in a Green Anole (*Anolis carolinensis*) lizard population. *Behavioral Ecology and Sociobiology*, 59, 157-165.

Vanhooydonck, B., Herrel, A. Y., Van Damme, R. & Irschick, D. J. 2005b. Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Functional Ecology*, 19, 38-42.

Vose, R. S., Schmoyer, R. L., Steurer, P. M., Peterson, T. C., Heim, R., Karl, T. R. & Eischeid, J. K. 1992. The Global Historical Climatology Network: Long-Term Monthly Temperature, Precipitation, Sea Level Pressure, and Station Pressure Data. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee: ORNL/CDIAC-53, CDIAC NDP-041.

Weatherhead, P. J. & Dufour, K. W. 2005. Limits to sexual size dimorphism in red-winged blackbirds: the cost of getting big? *Biological Journal of the Linnean Society*, 85, 353-361.

Weller, T. J. & Zabel, C. J. 2001. Characteristics of fringed myotis day roosts in northern California. *Journal of Wildlife Management*, 65, 489-497.

Whiting, M. J., Stuart-Fox, D. M., O'Connor, D., Firth, D., Bennett, N. C. & Blomberg, S. P. 2006. Ultraviolet signals ultra-aggression in a lizard. *Animal Behaviour*, 72, 353-363.

Wikelski, M. & Trillmich, F. 1997. Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: An island comparison. *Evolution*, 51, 922-936.

Table 1: Phenotypic traits used to explain winners of male-male contests and successful males (those who copulated) in male-female interactions. Because *F. verrucosus* lacks a rostral appendage, RSTLEN, RSTHT, and RSTWID were used only for *F. labordi* analyses.

Variable	Description
SVL	Body size, measured as snout-vent length in mm
MASS	Mass, measured in g
RSTLEN	Length of the rostral appendage from base to tip in mm
RSTHT	Height of the rostral appendage in mm
RSTWID	Width of the rostral appendage in mm
CONES	Number of cones we counted (see methods) in the dorsal crest
CONEHT	Height of the largest of the 4th or 5th dorsal cone, in mm
JAW	Length from the angle of jaw to apex of dentary bone, in mm
CSQHT	Height of the cranial casque from base of skull to its apex, in mm
CSQWID	Width of the cranial casque at the base of the skull, in mm
CSQDEP	Depth of the cranial casque from anterior to posterior at base of skull, in mm

Table 2: Percent of variance in male morphology explained by Principal Components (PC) axes for both intra- and intersexual selection datasets in each species. Dashes indicate the axis was not included in analysis.

	PC1	PC2	PC3	PC4	Cumulative variance explained
F. labordi					
Male-male	73.3	10.9	7.6	--	91.8
Male-female	75.1	9.4	5.4	3.6	93.5
F. verrucosus					
Male-male	59.9	17.9	11.1	--	88.9
Male-female	74.0	13.0	5.8	4.2	97.0

Table 3: Model selection results for paired logistic regression models used to determine which variables best explain whether a male wins a male-male encounter in *F. labordi* (n = 26). Results show the Log-Likelihood function (Log L), number of estimated parameters (K), the selection criterion (AIC_c), simple differences (ΔAIC_c), and Akaike weights (ω). We found that body size alone (SVL) and body size accompanied with size-corrected casque height (SVL + CSQHT) best explained male fighting success. See Table 2 for descriptions of variables used to build the models. Supported hypotheses are in bold.

Model	Log L	K	AICc	ΔAICc	ω
SVL	**-26.88**	**1**	**55.84**	**0.00**	**0.347**
SVL + CSQHT	**-26.29**	**2**	**56.82**	**0.98**	**0.213**
SVL + RSTWID	-26.87	2	57.98	2.14	0.119
SVL + CONES	-26.87	2	57.99	2.14	0.119
SVL + CONES + CSQHT	-26.26	3	59.03	3.18	0.071
SVL + RSTWID + CSQHT	-26.29	3	59.07	3.23	0.069
SVL + RSTWID + CONES	-26.84	3	60.18	4.34	0.040
SVL + RSTWID + CONES + CSQHT	-26.25	4	61.35	5.51	0.022
RSTWID	-35.18	1	72.44	16.59	0.000
CSQHT	-35.81	1	73.69	17.85	0.000
CONES	-36.02	1	74.11	18.27	0.000
RSTWID + CSQHT	-35.06	2	74.36	18.52	0.000
RSTWID + CONES	-35.17	2	74.59	18.74	0.000
CONES + CSQHT	-35.72	2	75.69	19.85	0.000
RSTWID + CONES + CSQHT	-35.06	3	76.62	20.78	0.000

Table 4: Relative importance weights, $\omega_+(i)$, for each variable in both male-female and male-male contests for each species. Dashes indicate the variable was not included in any of the respective models. Variables with higher $\omega_+(i)$ are considered to be under stronger sexual selection relative to the other variables.

	Intrasexual selection		Intersexual selection	
Variable	*F. labordi*	*F. verrucosus*	*F. labordi*	*F. verrucosus*
SVL	1.00	0.85	0.92	0.17
RSTWID	0.25	--	0.99	--
CONES	0.25	0.27	0.02	0.99
CSQHT	0.37	0.10	--	0.60
CONEHT	--	0.17	--	0.49
RSTHT	--	--	0.43	--
CSQWID	--	0.27	--	--

Table 5: Model selection results for logistic regression models used to determine which variables best explain male mating success in *F. labordi* (n = 21). Results show the Log-Likelihood function (Log L), number of estimated parameters (K), the selection criterion (AIC_c), simple differences (ΔAIC_c), and Akaike weights (ω). We found that body size, size-corrected rostral width, and size-corrected rostral height best explained male mating success. See Table 2 for descriptions of variables used to build the models. Supported hypotheses are in bold.

Model	Log L	K	AIC_c	ΔAIC_c	ω
SVL + RSTWID	**-5.25**	**3**	**17.91**	**0.00**	**0.502**
SVL + RSTHT + RSTWID	**-3.91**	**4**	**18.33**	**0.42**	**0.407**
RSTWID	-8.88	2	22.43	4.52	0.052
RSTHT + RSTWID	-8.87	3	25.15	7.25	0.013
RSTWID + CONES	-8.88	3	25.16	7.26	0.013
SVL + CONES	-10.22	3	27.85	9.94	0.003
RSTHT + RSTWID + CONES	-8.87	4	28.24	10.33	0.003
SVL	-11.95	2	28.57	10.67	0.002
SVL + RSTHT + CONES	-10.15	4	30.80	12.90	0.001
SVL + RSTHT	-11.93	3	31.28	13.37	0.001
CONES	-13.72	2	32.10	14.19	0.000
RSTHT	-13.93	2	32.53	14.62	0.000
RSTHT + CONES	-13.69	3	34.80	16.89	0.000

Table 6: Model selection results for paired logistic regression models used to determine which variables best explain whether a male wins a male-male encounter in *F. verrucosus* (n = 7). Results show the Log-Likelihood function (Log L), number of estimated parameters (K), the selection criterion (AIC_c), simple differences (ΔAIC_c), and Akaike weights (ω). We found that body size, body size and number of dorsal cones counted, and body size and size-corrected casque width best explained male fighting success. See Table 2 for descriptions of variables used to build the models. Supported hypotheses are in bold.

Model	Log L	K	AICc	ΔAICc	ω
SVL	**-5.55**	**1**	**13.43**	**0.00**	**0.334**
SVL + CONES	**-4.47**	**2**	**14.04**	**0.61**	**0.246**
SVL + CSQWID	**-5.08**	**2**	**15.25**	**1.82**	**0.134**
SVL + CONEHT	-5.29	2	15.68	2.25	0.109
CSQHT + CSQWID	-5.63	2	16.35	2.92	0.078
SVL + CONEHT + CSQWID	-5.06	3	18.51	5.08	0.026
CONEHT + CSQHT + CSQWID	-5.60	3	19.59	6.16	0.015
CONES	-8.72	1	19.76	6.33	0.014
CSQWID	-8.78	1	19.88	6.45	0.013
CONEHT + CSQWID	-8.17	2	21.44	8.01	0.006
CONES + CONEHT	-8.20	2	21.49	8.06	0.006
CONEHT	-9.65	1	21.64	8.21	0.006
CSQHT	-9.66	1	21.65	8.21	0.005
CONES + CSQHT	-8.66	2	22.41	8.98	0.004
CONEHT + CSQHT	-9.64	2	24.37	10.94	0.001
CONES + CONEHT + CSQHT	-8.13	3	24.66	11.23	0.001

Table 7: Model selection results for logistic regression models used to determine which variables best explain male mating success in *F. verrucosus* (n = 18). Results show the Log-Likelihood function (Log L), number of estimated parameters (K), the selection criterion (AIC_c), simple differences (ΔAIC_c), and Akaike weights (ω). We found that body size, number of dorsal cones counted, size-corrected cone height, and size-corrected casque height best explained male mating success. See Table 2 for descriptions of variables used to build the models. Supported hypotheses are in bold.

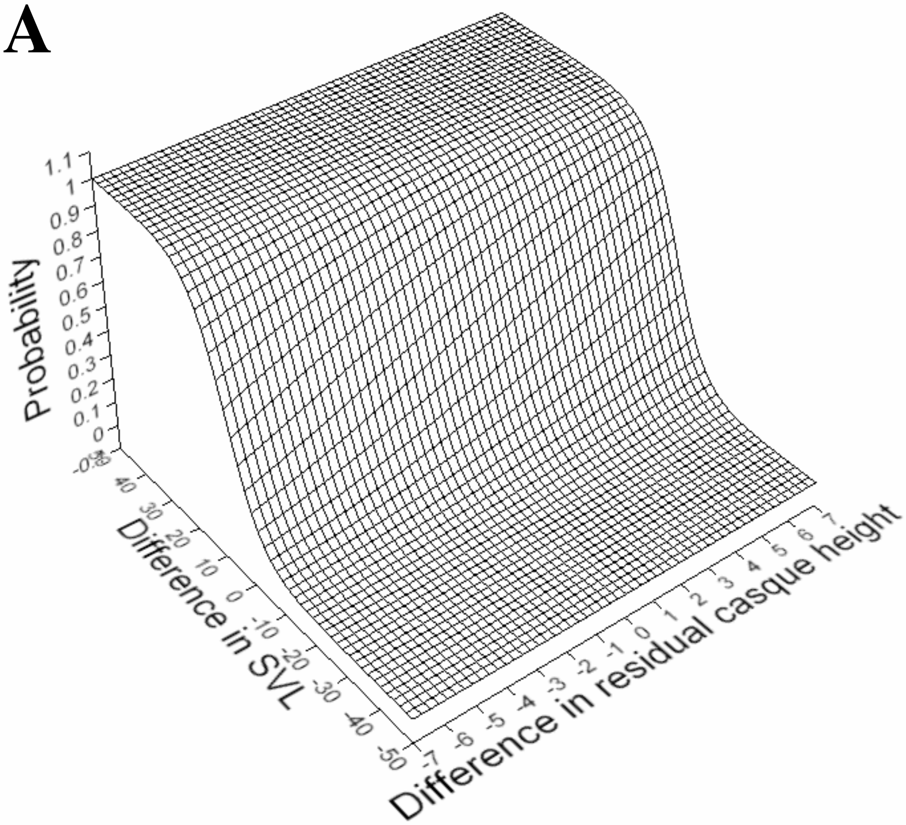
Model	Log L	K	AIC_c	ΔAIC_c	ω
CONES + CONEHT + CSQHT	**-3.51**	**4**	**18.10**	**0.00**	**0.383**
CONES	**-7.27**	**2**	**19.34**	**1.24**	**0.206**
CONES + CSQHT	**-6.06**	**3**	**19.84**	**1.74**	**0.160**
SVL + CONES	-6.71	3	21.13	3.03	0.084
CONES + CONEHT	-6.78	3	21.28	3.17	0.078
SVL + CONES + CSQHT	-5.50	4	22.08	3.98	0.052
SVL + CONES + CONEHT	-6.19	4	23.45	5.35	0.026
CSQHT	-11.45	2	27.70	9.60	0.003
CONEHT + CSQHT	-10.32	3	28.35	10.25	0.002
CONEHT	-12.24	2	29.28	11.18	0.001
SVL	-12.27	2	29.33	11.23	0.001
SVL + CSQHT	-11.23	3	30.18	12.08	0.001
SVL + CONEHT + CSQHT	-10.12	4	31.32	13.22	0.001
SVL + CONEHT	-12.03	3	31.77	13.67	0.000

FIGURE LEGENDS

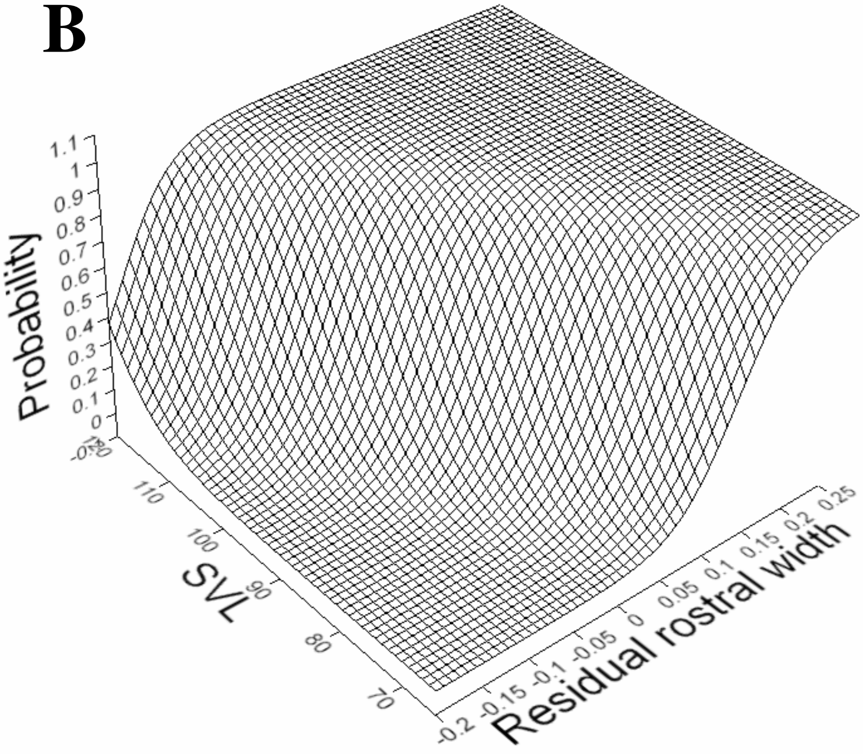
Figure 1: Models that show the probability of either fighting (A) or mating (B) success in *F. labordi*. **A.** Although an increase in difference between residual casque height slightly improves the probability of winning the fight, there is a strong increase in success probability for even slight differences in SVL. **B.** Male mating success depends strongly on residual rostral width: although body size is an important predictor of mating success, smaller males have higher probability of copulation if they have larger residual rostral widths whereas the larger males have a lower probability of success if they possess smaller residual rostral widths.

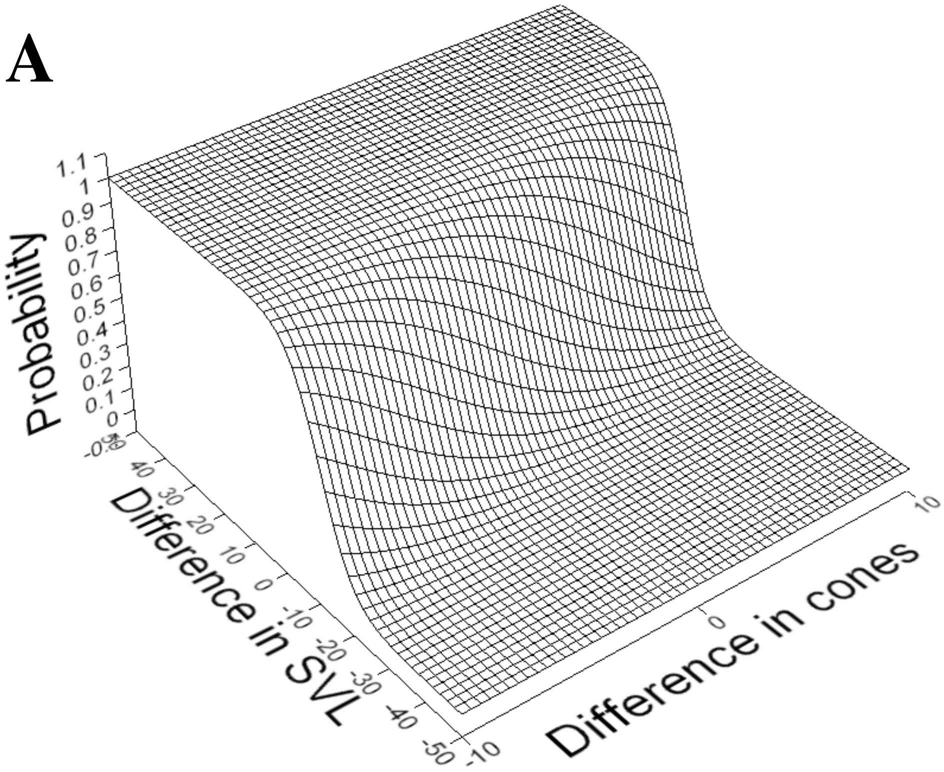
Figure 2: Models that show the probability of either fighting (A) or mating (B) success in *F. verrucosus*. **A.** The probability of winning a fight improves slightly for males with fewer cones, but there is a strong increase in fighting success for even slight differences in SVL. **B.** Male mating success depends strongly on the number of dorsal cones we counted (left side of axis is fewer); males in which fewer cones were counted have greater probability of mating success. An increase in residual casque height slightly increases the probability of mating success.

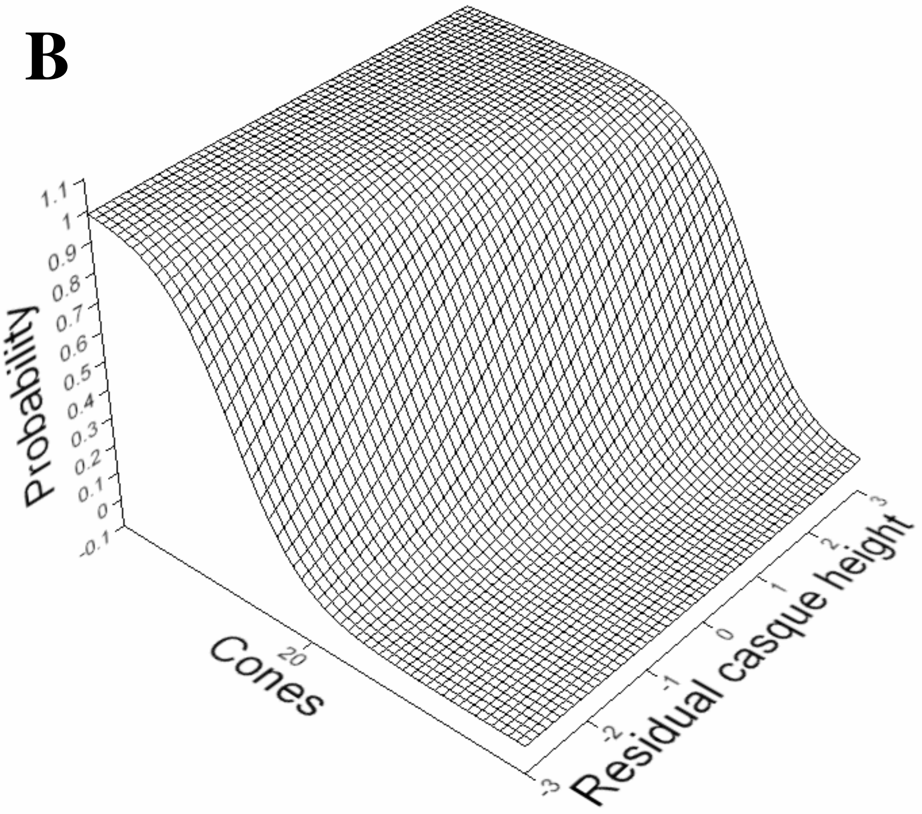
A


Probability
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
40
30
20
10
0
-10
-20
-30
-40
-50
Difference in SVL
-7
-6
-5
-4
-3
-2
-1
0
1
2
3
4
5
6
7
Difference in residual casque height

B


Probability
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
120
110
100
90
80
70
SVL
-0.2
-0.15
-0.1
-0.05
0
0.05
0.1
0.15
0.2
0.25
Residual rostral width


A
Probability
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
Difference in SVL
50
40
30
20
10
0
-10
-20
-30
-40
-50
Difference in cones
-10
0
10


B
Probability
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
-0.1
Cones
20
Residual casque height
3
2
1
0
-1
-2
-3

III. Discovery of a novel tetrapod life history: an annual chameleon living mostly as an egg

Abstract

The approximately 28,300 species of tetrapods (four-limbed vertebrates) almost exclusively have perennial life spans. Here, we report the discovery of a remarkable annual tetrapod from the arid southwest of Madagascar: the chameleon *Furcifer labordi*, with a post-hatching life span of just 4-5 months. At the start of the active season (November), an age cohort of hatchlings emerges; larger juveniles or adults are not present. These hatchlings grow rapidly, reach sexual maturity in less than two months, and reproduce in January-February. After reproduction, senescence appears and the active season concludes with population-wide adult death. Consequently, during the dry season, the entire population is represented by developing eggs that incubate for 8-9 months before synchronously hatching at the onset of the following rainy season. Remarkably, this chameleon spends more of its short annual life cycle inside the egg than outside of it. Our review of tetrapod longevity (>1,700 species) finds no others with such a short life span. These findings suggest that the notorious rapid death of chameleons in captivity may, for some species, actually represent the natural adult life span. Consequently, a new appraisal may be warranted concerning the viability of chameleon breeding programs, which could have special significance for species of conservation

concern. Additionally, because *F. labordi* is closely-related to other perennial species, this chameleon group may prove also to be especially well-suited for comparative studies that focus on life history evolution and the ecological, genetic, and/or hormonal determinants of aging, longevity, and senescence.

Introduction

Although there are almost limitless theoretical combinations of life history traits, they are remarkably constrained to a continuum of high reproductive rates, rapid growth, and short life spans on one end and the opposite set of traits on the other (Ricklefs and Wikelski 2002). Because of this, life history theory makes predictions of how traits should evolve for a given set of parameters. For example, organisms experiencing increased adult mortality rates should evolve shorter life spans and those experiencing increased juvenile mortality rates should evolve longer life spans (Austad and Fischer 1991; Stearns 1992; Holmes and Austad 1994; Ricklefs 1998; Roff 2002; Hughes and Reynolds 2005; Ricklefs 2006). Any change in fecundity, age at maturity, or age-specific mortality that reduces the value of adults and increases the value of juveniles will cause an evolutionary shift from the end of the continuum with slower growth, iteroparity, and longer life span toward the other end with faster growth, semelparity, and shorter life span (Young 1990; Stearns 1992).

Almost all the nearly 30,000 species of tetrapods (four-limbed vertebrates) have perennial life spans. Within tetrapods, some species with slow growth and delayed maturity exhibit exceptionally long life spans of up to 100+ years (Kirkwood 1985). At the other extreme, rapid sexual maturity and annual life spans are surprisingly rare. Among endotherms (mammals and birds), near-annual longevity is known only in 9 species of marsupials in the families Didelphidae and Dasyuridae, where it is restricted to males, and may also be facultative (Bradley et al. 1980; Cockburn et al. 1985; Karr et al. 1990; Dickman and Braithwaite 1992; Cockburn 1997; de Magalhaes and Toussaint 2002; Kraaijeveld et al. 2003). There are no examples of annual amphibians (Blanco and Sherman 2005). Among reptiles, lizards exhibit the shortest life spans (Shine and Charnov 1992), although the shortest-lived are capable of longevity > 1 year with multiple clutches per lifetime (Tinkle 1969; Tinkle et al. 1970). However, we know very little about taxa such as chameleons, which have proved difficult to study in the field due to poor visibility in forest canopies, compounded by their secretive and cryptic behavior (Raxworthy 1988).

Here, based on five seasons of field data, we report the surprising discovery of an annual tetrapod from the arid southwest of Madagascar: the chameleon *Furcifer labordi*, which has a post-hatching life span of just 4-5 months that concludes with synchronous adult population-wide death (Fig. 1). Consequently, *F. labordi* spends the majority of its lifetime as a developing embryo, and, except for the brief period when adults and their recently laid eggs are both present, the entire population is a single age cohort. This life history is more reminiscent of ephemeral insects than that of a typical tetrapod. We also compare this life history to a sympatric but perennial chameleon, *F. verrucosus*.

Materials and methods

The study site, Ranobe forest (23°01’30” S, 43°36’36” E), was located in southwestern Madagascar, approximately 30 km north of Toliara. The forests of the southwest are spiny forest and vegetation was typically xerophyllous thickets that included the family Didiereaceae and the genus *Euphorbia* (Koechlin 1972). The region is classified as a ‘desert and xeric shrubland’ ecoregion (Olson et al. 2001) and is the driest region in Madagascar, including during the wet, active season. Most rainfall is attributed to the brief and sporadic passage of tropical storms over the Indian Ocean (Jury 2003). The mean annual rainfall of Toliara is 420 mm, with the wet season typically from December to February (Jury 2003): mean monthly precipitation for these months is 89.9 mm (Vose et al. 1992). Mean annual temperature is 24.2 °C. Like most arid environments, daily (day vs. night) and seasonal (wet vs. dry) temperature differences are high. Data were collected over four field seasons: 22 February–5 March 2003, 20 December 2003–30 January 2004, 5 December–16 December 2005, and 4 November–12 December 2006. We reviewed historical precipitation data for Toliara (1951-2005) and found that the available data from the same periods as our study were within expected rainfall amounts in this dry region (i.e., the years we collected life history data were not characteristic of excessive drought compared to normal).

Furcifer labordi and *F. verrucosus* are sexually dimorphic chameleons, inhabit arid regions of Madagascar (Brygoo 1971), and are seasonally active only during the wet season. Both species have secondary sexual characters, but they are more exaggerated in *F. labordi*. *Furcifer verrucosus* males possess large cranial casques, whereas females do not. Male *F. labordi* have proportionately larger cranial casques than that of *F. verrucosus* (Karsten et al. In preparation-b) and also large rostral appendages; these typically ‘male’ traits are also present in females, but to a lesser degree.

All specimens were collected by hand at night; they often sleep within 2 m of the ground. Upon capture, we marked locations, placed lizards individually in cloth, mesh bags, and transported them to a base camp where they experienced the same environmental conditions as they would in the forest. We suspended the mesh bags from narrow cord to prevent predation from arboreal, nocturnal snakes. The following morning, we measured body size (SVL) and total length (TL) by holding each chameleon so that maximal extension was apparent (i.e., no observable curvature to the body or tail). These measurements were made to the nearest 0.1 mm using calipers. We measured mass using spring scales to the nearest 0.1 g (≤ 10 g) or 1 g (> 10 g). We returned all lizards to their point of capture within 24 hours and observed no adverse signs of social or handling stress in any individuals. Because of the brief period in which we possessed these individuals and because these chameleons do not ‘drink’ except during sporadic periods of rain, we did not provide any supplemental food or water.

We gave all individuals a permanent identification by toe-clipping the most distal phalanx in a three-toe combination, with only one toe clipped per foot. We observed no adverse side-effects of this marking procedure on the behavior and survivability of individuals, nor did we observe any partial or full phalanx regrowth to confuse individual markings. Radio transmitters weighing less than 10% of the animal’s body mass were affixed to the dorsal ridge of 7 *F. labordi* using liquid adhesive. We located each lizard daily and made brief (< 30 minutes) focal observations, 3-4 times per day.

For both species, we classified each individual as hatchling, juvenile, or adult. However, because *F. labordi* is unique in being comprised of a single cohort that transitions from juveniles to adults that are not sexually active initially, we also classified adults in this species as either pre-reproductive or sexually reproductive. Pre-reproductive adults were those exhibiting fully developed secondary sexual characters and noticeably larger body size relative to the rest of the population, but were present before courtship started in the population (10 January). After 10 January, adult females exhibited sexually receptive coloration and were sexually reproductive. All adult males exhibited hemipenal bulges. Hatchlings lacked secondary sexual characters (casque and dorsal crest, plus rostral appendage in *F. labordi*), and juveniles represented all other individuals.

We queried additional museum collections for localities and collecting dates of *F. labordi*. Our search yielded 8 specimens at the University of Michigan Museum of Zoology (UMMZ) collected by CJR 18-28 March 1995 at Ranobe, and 34 others at UMMZ collected from throughout the species' range. No other specimens with usable locality and/or collection date data were found in other collections.

Results

Following the cool, dry, inactive season, we observed no *F. labordi* until the first emergence of hatchlings on 11 November, with the onset of the wet season. Over the following 38 days, all *F. labordi* were a single age cohort of hatchlings and hatchlings-turned-juveniles, with no adults present until 20 December (Table 1). An annual species with synchronous hatching of a single cohort should show a strong, positive correlation between size and date during the growth phase for the entire population; and we found this pattern for *F. labordi*. Between 11 November and 3 January, SVL (snout-vent length) was positively correlated with date in both males ($n = 163$, $r = 0.745$, $P < 0.001$) and females ($n = 112$, $r = 0.759$, $P < 0.001$; Fig. 2A). *Furcifer verrucosus* differed from *F. labordi* in that SVL was not significantly correlated with date for either males or females ($n = 119$, $r = -0.024$, $P = 0.793$; $n = 96$, $r = 0.170$, $P = 0.097$, respectively; Fig. 2B). Juvenile *F. labordi* growth was exceptionally high: marked-recaptured males increased mean body mass by 4.1% daily ($n = 24$, mean ± 1 SE = 0.32 ± 0.07 g/day) and mean SVL by 1.86% daily ($n = 24$, 1.36 ± 0.11 mm/day). Female *F. labordi* also exhibited impressive growth rates during the same portion of the active season: marked-recaptured females increased mean body mass by 2.0% daily ($n = 3$, 0.09 ± 0.10 g/day) and mean SVL by 1.86% daily ($n = 3$, 1.26 ± 0.65 mm/day). The maximum growth rate observed in this species was as high as 2.6 mm/day. All post-hatching growth was restricted to a period of less than 60 days.

We first observed reproductive behavior on 10 January, and after this date all individuals exhibited adult morphology (Table 1), growth ceased (Fig. 2A), and was even negative within individuals. Although growth is largely considered irreversible in vertebrates, negative reptile growth has been previously reported for marine iguanas during periods of poor food availability and stress (Wikelski and Thom 2000). When reproduction in *F. labordi* began, we observed negative growth in a small set of marked-recaptured males ($n = 6$, -0.26 ± 0.30 mm/day). Within the population, growth ceased for both adult males ($n = 61$, $r = -0.085$, $P = 0.517$) and females ($n = 55$, $r = -0.654$, $P < 0.001$; Fig. 2A).

We observed no aestivation behavior by adults of *F. labordi*: none emerging at the beginning of the active season and none entering aestivation at the end of the active season. In contrast, we have observed both emerging and aestivation behavior multiple times in *F. verrucosus* and other arid-adapted chameleons. Additional museum specimens with known collecting dates and field records (see methods) support these conclusions. Adult *F. labordi* have never been found in the field between May and November, whereas *F. verrucosus* have been collected in all months except July and August. In the perennial *F. verrucosus*, we observed adults, juveniles, and hatchlings frequently throughout the beginning of the active season (Fig. 2B, Table 1). Based on size classes, *F. verrucosus* is comprised of at least three age cohorts once hatchlings emerge: 1) hatchlings, 2) sub-adults and adults from the previous year's hatch, and 3) older adults (Fig. 2B).

The frequency of gravid *F. labordi* females peaked from late January to late February. We observed a radio-tracked female excavating a nest and depositing a clutch of 11 eggs on 3 February: mean egg length was 11.7 mm (15.2% of her SVL) and total clutch mass was 4.4 g (36.7% of her pre-oviposition mass) (Karsten and Andriamandimbiarisoa 2008). We did not observe any gravid females after 2 March. We estimate that egg laying in *F. labordi* occurs mostly in February and incubation spans 8-9 months with hatching in November, similar to the 10-month incubation period observed in captivity (Nečas 1999; Kohler 2005). No species in the genus *Furcifer* are known to have incubation periods less than 8 months. These long incubation periods that are common among chameleons are the result of embryos being in diapause at the time of oviposition. Diapause terminates after several months but development remains arrested by cold torpor until nest temperature increases as the wet season approaches (Blanc 1974; Díaz-Paniagua et al. 2002; Díaz-Paniagua and Cuadrado 2003; Andrews and Donoghue 2004; Ferguson et al. 2004). Consequently, the eggs resume development and hatchlings synchronously emerge at the onset of the wet season in November (Fig. 1). Some other reptile species may hatch before emergence and overwinter inside the nest as hatchlings (Ultsch 2006). However, in chameleons, this scenario appears unlikely since the group is mostly characterized by long incubation periods; delayed nest emergence, after hatching, has never been observed for any captive chameleon (Blanc 1974; Nečas 1999).

In 2004, the last active adults (both species) were found on 11 February, but in 1995 active adults were collected as late as 28 March (see methods). Thus, the termination of the active season likely varies among years, falling approximately between February-April. After egg laying, the active season for *F. labordi* concludes with senescence and population-wide adult death. Developing eggs (incubating for 8-9 months) represent the entire population during the prolonged dry season, which is considerably longer than the post-hatching life span of 4-5 months (Fig. 1). On the other hand, adult and sub-adult *F. verrucosus* aestivate over the dry season.

Discussion

No other tetrapod species, including short-lived marsupials (Bradley et al. 1980; Bradley 1997; Cockburn 1997; Kraaijeveld et al. 2003) and lizards, are known to have a similar life-history as *F. labordi*. Previous reviews of other lizards (Tinkle 1969; Tinkle et al. 1970; Clobert et al. 1998) report 11 species as putatively annual. However, in all species in which survivorship was quantified by the original authors (*cf.* extrapolated from anecdotal literature), maximal post-embryonic longevity was actually greater than one year, and none exhibited obligate annual population turnover. Our review of longevity in tetrapods, which included > 1,700 species and 194 publications (available on request from the corresponding author), did not find obligate annual population turnover for any other tetrapod species, nor did we find any other tetrapod with a post-embryonic life span of only 4-5 months. *Furcifer labordi* is also unique among tetrapods in that it spends the majority of its life cycle inside the egg; a life history more reminiscent of ephemeral insects or aquatic vertebrates than that of other terrestrial tetrapods.

At the end of the active season, radio-tracked and marked-recaptured *F. labordi* exhibited worsening body condition, including physical characteristics typical of senescence such as reduced mass, slower locomotion, and reduced strength when gripping branches. For example, males lost an average of 0.30 ± 0.16 g/day at the end of the breeding season ($n = 6$) and we also observed multiple instances of radio-tracked chameleons falling from trees, for unknown reasons, during normal locomotor activity. Additionally, from 20 January-10 February, 2 of 7 radio-tracked individuals were found dead of unknown causes, but with no signs of mutilation. We also found several non-radio-tracked and unmarked dead *F. labordi* in a similar unmutilated condition toward the end of the active season. Conversely, for *F. verrucosus*, individuals continued to appear robust and healthy at the end of the breeding season, and none were found dead unmutilated.

Presently, it is unclear why *F. labordi* exhibits such a bizarre—and extreme—life history compared to other tetrapods. One hypothesis is that the harsh environment with extreme seasonality contributes to life history extremes. For example, short-lived, annual killifish deposit eggs in the mud that survive the harsh, dry season by entering a diapause; an adaptation to the highly fluctuating environment. Annualism is likely the ancestral character state; however, it has been evolutionarily lost by lineages found in more stable environments (Murphy and Collier 1997). Madagascar's climate is highly variable (Dewar and Richard 2007): environmental unpredictability is much greater than other tropical areas, especially in the southwest which exhibits unusually high interannual variability in rainfall. In response to stochastic climate fluctuations, many mammals of Madagascar differ from closely-related relatives in more stable environments in that the Malagasy species exhibit more extreme versions of either 'short-lived' or 'long-lived' life histories (Dewar and Richard 2007). Dewar and Richard (Dewar and Richard 2007) suggested both responses are possible 'solutions' to the same evolutionary 'problem.' Concordant with life history theory, the 'best solution' depends upon how environmental instability affects age-specific mortality (Stearns 1992; Roff 2002). Among several Malagasy mammals (carnivores, primates, tenrecs, and rodents), reduced juvenile survivorship due to environmental variability resulted in the evolution of longer life spans (Richard et al. 2002), whereas stochastic climatic variables that reduced adult survivorship resulted in the evolution of shorter life spans (Gould et al. 2003; Dewar and Richard 2007). If environmental unpredictability differentially affected age-specific survivorship in chameleons, this may help explain why *F. labordi* is annual while other sympatric chameleons are perennial.

An alternative, and not mutually exclusive, explanation may emerge at the interface between life history theory and hormone-behavior relationships. High adult mortality rates can drive the evolution of rapid growth and earlier age of reproduction (Austad and Fischer 1991; Stearns 1992; Holmes and Austad 1994; Ricklefs 1998; Hughes and Reynolds 2005; Ricklefs 2006), with the cost being decreased longevity, often as a result of a trade-off between resources allocated to somatic cell maintenance compared to reproduction (Kirkwood 1985; Stearns 1992; Sgro and Partridge 1999; Kirkwood 2002; Ricklefs 2006; Parsons 2007). Hormones can control these trade-offs (Zera and Harshman 2001). For example, increased androgens in both natural populations and by experimental manipulation can be correlated with mating success (Borgia and Wingfield 1991; Denardo and Sinervo 1994), but are also known to contribute to traits typically associated with increased adult mortality rates (e.g., reduced survival, increased parasite loads, increased energetic expenditure) (Marler and Moore 1988; Marler et al. 1995; Wikelski et al. 1999; Klukowski and Nelson 2001; Wingfield et al. 2001; Wikelski et al. 2005). It seems possible that a change in the social structure in ancestral *F. labordi*—to a social system characterized by increased androgen levels or sensitivity—could contribute to increased intrinsic and/or extrinsic adult mortality. Indeed, *F. labordi* is characterized by physically intense combat and agonistic courtship (Karsten et al. In preparation-a, b). A similar mode of evolutionary selection appears to have played a role in the evolution of semelparity in at least one other tetrapod, the marsupial *Phascogale calura* (Bradley 1997). Accounting for hormonal regulation of physiology and behavior is critical to a comprehensive understanding of life history evolution (Zera and Harshman 2001; Ricklefs and Wikelski 2002). Although our hypothesis is plausible, the role of hormones, and even behavior to a lesser extent (but see ref. Karsten et al. In preparation-b), is unexplored in chameleons. Our hypothesis can be tested by quantifying seasonal hormone profiles, social systems, and sexual selection within a phylogenetic comparative framework.

Mortality is high during the brief mating phase of the active season: 4 of 7 radio-tracked individuals died from predation or unknown causes from 20 January-10 February. The physically-intense social system of this species, the harsh and unpredictable environment it inhabits, with a brief active season and where adult mortality is already high, may exacerbate the compression of life into such a brief period. In accordance with life history theory, the result would be evolutionary selection for reduced life span, smaller body size, and earlier age of reproduction (Austad and Fischer 1991; Stearns 1992; Holmes and Austad 1994; Ricklefs 1998; Roff 2002; Hughes and Reynolds 2005; Ricklefs 2006). This may be advantageous for two reasons. First, since *F. labordi* is sympatric with other larger, but closely-related (Raxworthy et al. 2002; Townsend and Larson 2002), perennial chameleons, a shift in body size and age of reproduction may alleviate some dimensions of niche overlap. Second, the metabolic theory of ecology states that smaller organisms have more resources to allocate to reproduction than their larger-bodied counterparts, relative to body mass, producing new individuals and genes at faster rates (Brown and Sibly 2006).

Furcifer labordi has a life history like no other tetrapod, but yet it still conforms to predictions of life history theory: it experiences high adult mortality, is the smallest chameleon within a closely-related group, exhibits rapid growth, and has an early age of reproduction. What makes this species unique among tetrapods is how extreme it has compressed its suite of life history traits into a single, brief season and that it spends the majority of its life cycle in a more benign and predictable environment: the egg. In fact, its entire life span is shorter than the age of sexual maturity in many other chameleons (Nečas 1999). Our findings suggest that the notorious rapid death of chameleons in captivity may, for some species, actually represent the natural adult life span. Consequently, a new appraisal may be warranted concerning the viability of chameleon breeding programs, which could have special significance for species of conservation concern. Additionally, if chameleons become a better studied group, it will also be possible to construct life history tables to empirically test the evolution of semelparity in some species and why iteroparity is present in others. Because *F. labordi* is closely-related to other perennial species, this chameleon group may prove also to be especially well-suited for comparative studies that focus on life history evolution and the ecological, genetic, and/or hormonal determinants of aging, longevity, and senescence.

Acknowledgements

Field studies in Madagascar were made possible due to the assistance of the Ministries des Eaux et Forêts, the Association Nationale pour la Gestion des Aires Protégées, and the Université d'Antananarivo, Département de Biologie Animale. We thank D. Rakotondravony and O. Ramilijaona for their assistance with the project and H. Thomas and D. Kidney for valuable logistical advice. We thank M. Lovern, T.A. Baird, M. Palmer, R. Voss, R. Lehtinen, R.A. Nussbaum, and G. Schneider for their contributions. Research was supported by a grant from the National Science Foundation (DEB 99-84496) to CJR.

References

Andrews, R. M. & Donoghue, S. 2004. Effects of temperature and moisture on embryonic diapause of the veiled chameleon (*Chamaeleo calyptratus*). *Journal of Experimental Zoology Part a-Comparative Experimental Biology*, 301A, 629-635.

Austad, S. N. & Fischer, K. E. 1991. Mammalian aging, metabolism, and ecology: evidence from the bats and marsupials. *Journals of Gerontology*, 46, B47-B53.

Blanc, F. 1974. Table de développement de *Chamaeleo lateralis* Gray, 1831. *Annales des Embryologie et Morphologie*, 7, 99-115.

Blanco, M. A. & Sherman, P. W. 2005. Maximum longevities of chemically protected and non-protected fishes, reptiles, and amphibians support evolutionary hypotheses of aging. *Mechanisms of Ageing and Development*, 126, 794-803.

Borgia, G. & Wingfield, J. C. 1991. Hormonal correlates of bower decoration and sexual display in the satin bowerbird (*Ptilonorhynchus violaceus*). *Condor*, 93, 935-942.

Bradley, A. J. 1997. Reproduction and life history in the red-tailed phascogale, *Phascogale calura* (Marsupialia: Dasyuridae): the adaptive-stress senescence hypothesis. *Journal of Zoology*, 241, 739-755.

Bradley, A. J., McDonald, I. R. & Lee, A. K. 1980. Stress and mortality in a small marsupial (*Antechinus stuartii*, Macleay). *General and Comparative Endocrinology*, 40, 188-200.

Brown, J. H. & Sibly, R. M. 2006. Life-history evolution under a production constraint. *Proceedings of the National Academy of Sciences of the United States of America*, 103, 17595-17599.

Clobert, J., Garland, T. & Barbault, R. 1998. The evolution of demographic tactics in lizards: a test of some hypotheses concerning life history evolution. *Journal of Evolutionary Biology*, 11, 329-364.

Cockburn, A. 1997. Living slow and dying young: senescence in marsupials. In: *Marsupial biology: recent research new perspectives* (Ed. by Saunders, N. & Hinds, L.), pp. 28-40. Berlin: Springer.

Cockburn, A., Scott, M. P. & Scotts, D. J. 1985. Inbreeding avoidance and male-biased natal dispersal in *Antechinus spp* (Marsupialia, Dasyuridae). *Animal Behaviour*, 33, 908-915.

de Magalhaes, J. P. & Toussaint, O. 2002. The evolution of mammalian aging. *Experimental Gerontology*, 37, 769-775.

Denardo, D. F. & Sinervo, B. 1994. Effects of steroid hormone interaction on activity and home-range size of male lizards. *Hormones and Behavior*, 28, 273-287.

Dewar, R. E. & Richard, A. F. 2007. Evolution in the hypervariable environment of Madagascar. *Proceedings of the National Academy of Sciences of the United States of America*, 104, 13723-13727.

Díaz-Paniagua, C. & Cuadrado, M. 2003. Influence of incubation conditions on hatching success, embryo development and hatchling phenotype of common chameleon (*Chamaeleo chamaeleon*) eggs. *Amphibia-Reptilia*, 24, 429-440.

Díaz-Paniagua, C., Cuadrado, M., Blázquez, M. C. & Mateo, J. A. 2002. Reproduction of *Chamaeleo chamaeleon* under contrasting environmental conditions. *Herpetological Journal*, 12, 99-104.

Dickman, C. R. & Braithwaite, R. W. 1992. Postmating mortality of males in the dasyurid marsupials, *Dasyurus* and *Parantechinus*. *Journal of Mammalogy*, 73, 143-147.

Ferguson, G. W., Murphy, J. B., Ramanamanjato, J. B. & Raselimanana, A. P. 2004. *The Panther Chameleon: Color Variation, Natural History, Conservation, and Captive Management*. Malabar, Florida: Krieger Publishing Company.

Gould, L., Sussman, R. W. & Sauther, M. L. 2003. Demographic and life-history patterns in a population of ring-tailed lemurs (*Lemur catta*) at Beza Mahafaly Reserve, Madagascar: a 15-year perspective. *American Journal of Physical Anthropology*, 120, 182-194.

Holmes, D. J. & Austad, S. N. 1994. Fly now, die later: life-history correlates of gliding and flying in mammals. *Journal of Mammalogy*, 75, 224-226.

Hughes, K. A. & Reynolds, R. M. 2005. Evolutionary and mechanistic theories of aging. *Annual Review of Entomology*, 50, 421-445.

Karr, J. R., Nichols, J. D., Klimkiewicz, M. K. & Brawn, J. D. 1990. Survival rates of birds of tropical and temperate forests: will the dogma survive? *American Naturalist*, 136, 277-291.

Karsten, K. B. & Andriamandimbiarisoa, L. N. 2008. *Furcifer labordi* (Labord's chameleon), reproduction. *Herpetological Review*, *In press*.

Karsten, K. B., Andriamandimbiarisoa, L. N., Fox, S. F. & Raxworthy, C. J. In preparation-a. Sexual selection on body size and secondary sexual characters in two closely related, sympatric chameleon species in Madagascar.

Karsten, K. B., Andriamandimbiarisoa, L. N., Fox, S. F. & Raxworthy, C. J. In preparation-b. Social behavior of two species of chameleons in Madagascar: insights into sexual selection.

Kirkwood, T. B. L. 1985. Comparative and evolutionary aspects of longevity. In: *Handbook of the Biology of Aging* (Ed. by Finch, C. E. & Schneider, E. L.). New York, New York: Van Nostrand Reinhold.

Kirkwood, T. B. L. 2002. Evolution of ageing. *Mechanisms of Ageing and Development*, 123, 737-745.

Klukowski, M. & Nelson, C. E. 2001. Ectoparasite loads in free-ranging northern fence lizards, *Sceloporus undulatus hyacinthinus*: effects of testosterone and sex. *Behavioral Ecology and Sociobiology*, 49, 289-295.

Kohler, G. 2005. *Incubation of reptile eggs*. Malabar, Florida: Krieger Publishing Co.

Kraaijeveld, K., Kraaijeveld-Smit, F. J. L. & Adcock, G. J. 2003. Does female mortality drive male semelparity in dasyurid marsupials? *Proceedings of the Royal Society B-Biological Sciences*, 270, S251-S253.

Marler, C. A. & Moore, M. C. 1988. Evolutionary costs of aggression revealed by testosterone manipulations in free-living male lizards. *Behavioral Ecology and Sociobiology*, 23, 21-26.

Marler, C. A., Walsberg, G., White, M. L. & Moore, M. 1995. Increased energy expenditure due to increased territorial defense in male lizards after phenotypic manipulation. *Behavioral Ecology and Sociobiology*, 37, 225-231.

Murphy, W. J. & Collier, G. E. 1997. A molecular phylogeny for aplocheiloid fishes (Atherinomorpha, Cyprinodontiformes): the role of vicariance and the origins of annualism. *Molecular Biology and Evolution*, 14, 790-799.

Nečas, P. 1999. *Chameleons: Nature's hidden jewels*. Frankfurt am Main: Chimaira Buchhandelsgesellschaft.

Parsons, P. A. 2007. The ecological stress theory of aging and hormesis: an energetic evolutionary model. *Biogerontology*, 8, 233-242.

Raxworthy, C. J. 1988. Reptiles, rainforest and conservation in Madagascar. *Biological Conservation*, 43, 181-211.

Raxworthy, C. J., Forstner, M. R. J. & Nussbaum, R. A. 2002. Chameleon radiation by oceanic dispersal. *Nature*, 415, 784-787.

Richard, A. F., Dewar, R. E., Schwartz, M. & Ratsirarson, J. 2002. Life in the slow lane? Demography and life histories of male and female sifaka (*Propithecus verreauxi verreauxi*). *Journal of Zoology*, 256, 421-436.

Ricklefs, R. E. 1998. Evolutionary theories of aging: confirmation of a fundamental prediction, with implications for the genetic basis and evolution of life span. *American Naturalist*, 152, 24-44.

Ricklefs, R. E. 2006. Embryo development and ageing in birds and mammals. *Proceedings of the Royal Society B-Biological Sciences*, 273, 2077-2082.

Ricklefs, R. E. & Wikelski, M. 2002. The physiology/life-history nexus. *Trends in Ecology & Evolution*, 17, 462-468.

Roff, D. A. 2002. *Life History Evolution*. Sunderland, Massachusetts: Sinauer Associates, Inc.

Sgro, C. M. & Partridge, L. 1999. A delayed wave of death from reproduction in *Drosophila*. *Science*, 286, 2521-2524.

Shine, R. & Charnov, E. L. 1992. Patterns of survival, growth, and maturation in snakes and lizards. *American Naturalist*, 139, 1257-1269.

Stearns, S. C. 1992. *The Evolution of Life Histories*. Oxford: Oxford University Press.

Tinkle, D. W. 1969. Concept of reproductive effort and its relation to evolution of life histories of lizards. *American Naturalist*, 103, 501-516.

Tinkle, D. W., Wilbur, H. M. & Tilley, S. G. 1970. Evolutionary strategies in lizard reproduction. *Evolution*, 24, 55-74.

Townsend, T. & Larson, A. 2002. Molecular phylogenetics and mitochondrial genomic evolution in the Chamaeleonidae (Reptilia, Squamata). *Molecular Phylogenetics and Evolution*, 23, 22-36.

Ultsch, G. R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. *Biological Reviews*, 81, 339-367.

Vose, R. S., Schmoyer, R. L., Steurer, P. M., Peterson, T. C., Heim, R., Karl, T. R. & Eischeid, J. K. 1992. The Global Historical Climatology Network: Long-Term Monthly Temperature, Precipitation, Sea Level Pressure, and Station Pressure Data. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee: ORNL/CDIAC-53, CDIAC NDP-041.

Wikelski, M., Lynn, S., Breuner, C., Wingfield, J. C. & Kenagy, G. J. 1999. Energy metabolism, testosterone and corticosterone in white-crowned sparrows. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology*, 185, 463-470.

Wikelski, M., Steiger, S. S., Gall, B. & Nelson, K. N. 2005. Sex, drugs and mating role: testosterone-induced phenotype-switching in Galapagos marine iguanas. *Behavioral Ecology*, 16, 260-268.

Wikelski, M. & Thom, C. 2000. Marine iguanas shrink to survive El Niño - Changes in bone metabolism enable these adult lizards to reversibly alter their length. *Nature*, 403, 37-38.

Wingfield, J. C., Lynn, S. E. & Soma, K. K. 2001. Avoiding the 'costs' of testosterone: ecological bases of hormone-behavior interactions. *Brain Behavior and Evolution*, 57, 239-251.

Young, T. P. 1990. Evolution of semelparity in Mount Kenya lobelias. *Evolutionary Ecology*, 4, 157-171.

Zera, A. J. & Harshman, L. G. 2001. The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics*, 32, 95-126.

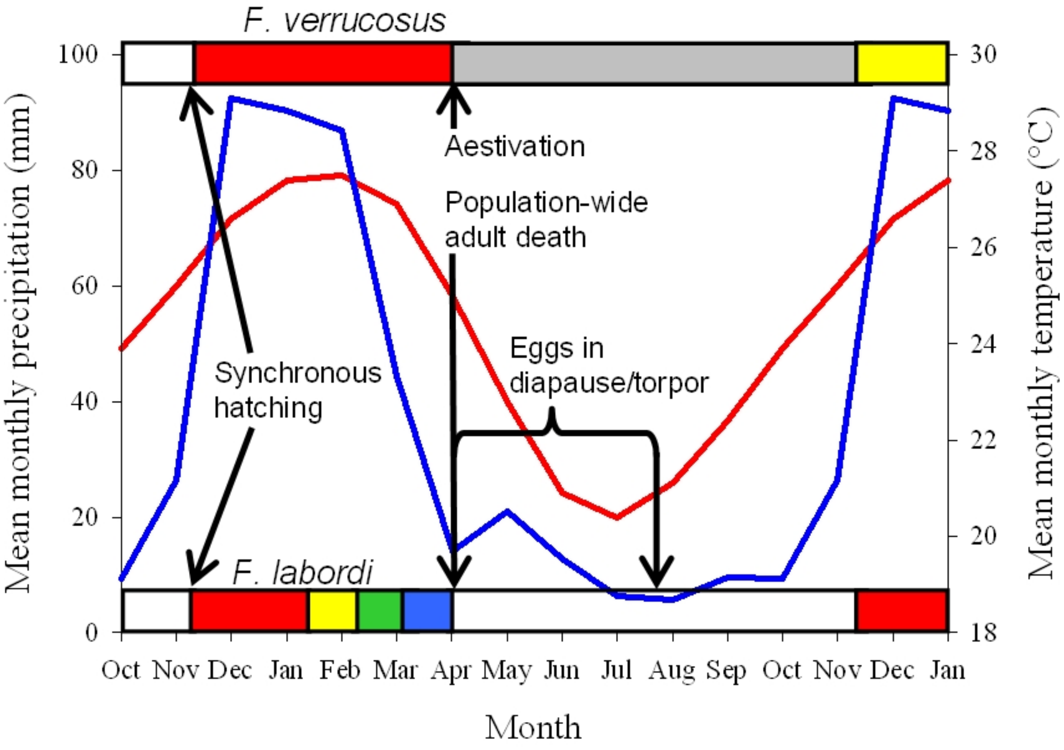
Table 1. Population demography of two chameleon species at Ranobe, Madagascar. Composite dates for data collected 2003-2006 for the annual species *Furcifer labordi* and the perennial species *F. verrucosus*. We were unable to use data for *F. verrucosus* from 17 December – 12 February due to non-random sampling of adults only; however, juveniles were present throughout the population for the entire active season. *Furcifer labordi* adults were either pre-reproductive (before 10 January) or sexually reproductive (after 10 January; see methods).

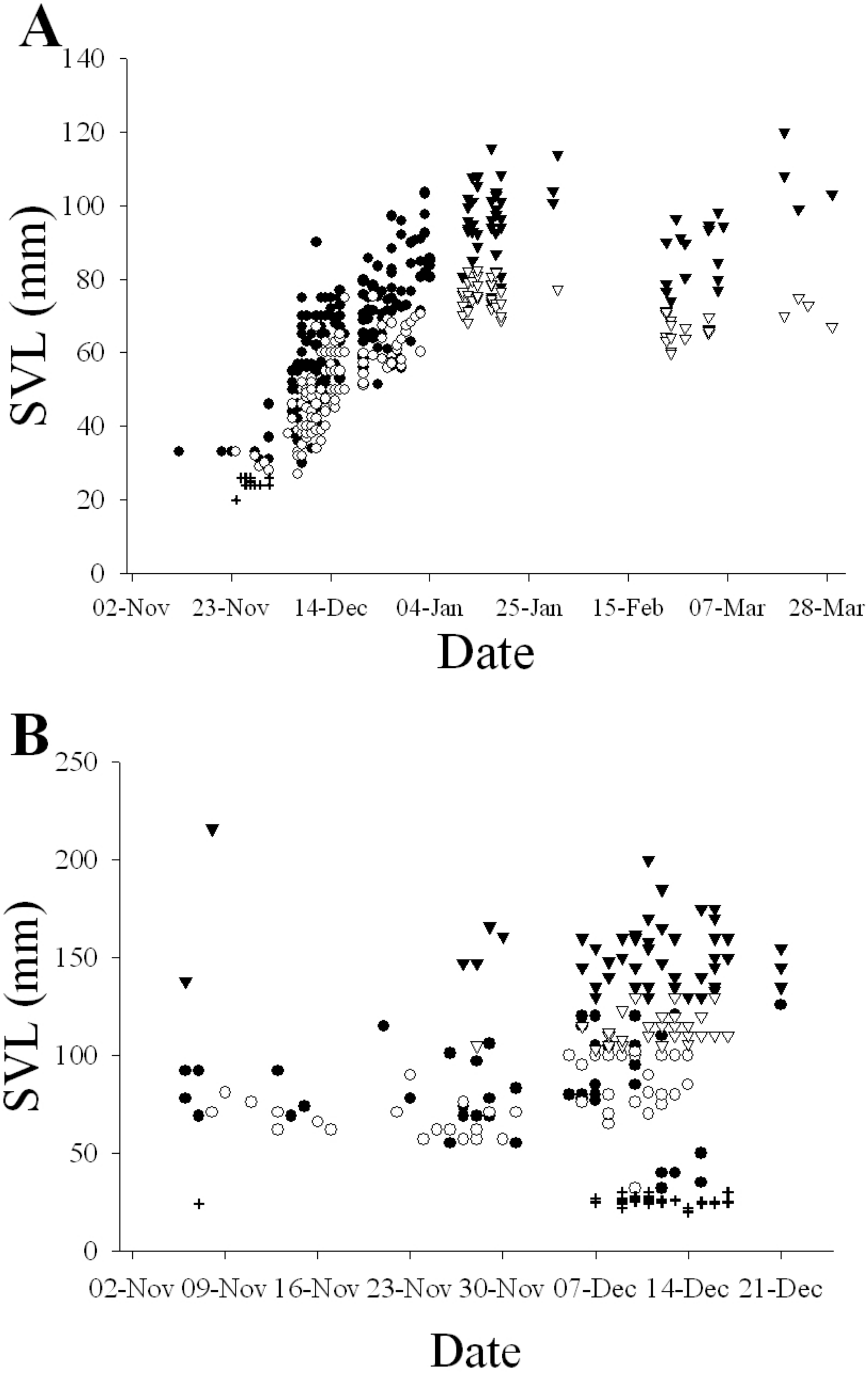
		Percentage of population		
Period of active season	n	Hatchling	Juvenile	Adult
Furcifer labordi				
11 Nov - 29 Nov	23	100	0	0
30 Nov - 06 Dec	28	32	68	0
07 Dec - 16 Dec	146	1	99	0
17 Dec - 29 Dec	83	0	24	76
29 Dec - 05 Mar	138	0	0	100
Furcifer verrucosus				
05 Nov - 30 Nov	48	2	79	19
01 Dec - 16 Dec	174	29	42	29
13 Feb - 05 Mar	104	0	88	13

FIGURE LEGENDS

Figure 1. The life histories of annual and perennial chameleon species. Study region climate and life history of two chameleons: the annual *Furcifer labordi* (lower bar) and a hatchling cohort of the perennial *F. verrucosus* (upper bar) over 15 months in southwest Madagascar. Toliara rainfall (blue line) and temperature (red line) (Vose et al. 1992). Life history phases: incubating eggs (open); juvenile growth (red); courtship (yellow); period of courtship and egg laying overlap (green); egg-laying and senescence (blue); juvenile aestivation (grey). The life span of *F. labordi* is a single year, with most of this time spent as a developing egg.

Figure 2. Cohorts of annual and perennial chameleon species. A. Composite data (1995, 2003-2006) for snout-vent length (SVL) and date in the annual *Furcifer labordi* cohort: unsexed hatchlings < 26 mm SVL (plusses); males (closed symbols); females (open symbols); sexed hatchlings, juveniles, and pre-reproductive adults (circles) and sexually reproductive adults (triangles). **B.** Composite data (2005-2006) for SVL and date for multiple cohorts of the perennial *F. verrucosus*: hatchlings < 30 mm SVL (plusses); pre-reproductive (circles) and sexually reproductive (triangles) individuals; males (closed symbols); females (open symbols). Data beyond 21 December are truncated to exclude biased sampling efforts. However, juveniles were present throughout the entire active season (see Table 1).


F. verrucosus
Aestivation
Population-wide adult death
Synchronous hatching
Eggs in diapause/torpor
F. labordi
Mean monthly precipitation (mm)
0
20
40
60
80
100
Mean monthly temperature (°C)
18
20
22
24
26
28
30
Oct
Nov
Dec
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Jan
Month


A
SVL (mm)
0
20
40
60
80
100
120
140
02-Nov
23-Nov
14-Dec
04-Jan
25-Jan
15-Feb
07-Mar
28-Mar
Date
B
SVL (mm)
0
50
100
150
200
250
02-Nov
09-Nov
16-Nov
23-Nov
30-Nov
07-Dec
14-Dec
21-Dec
Date

IV. Population densities and conservation priorities for chameleons of the spiny forests in the Toliara region of southwestern Madagascar

Abstract

Madagascar is a high conservation priority. Rainforests receive most of the focus, but the dry deciduous and spiny forests of south-western Madagascar house many endemics, are under high deforestation pressure, and remain largely unprotected. Charismatic vertebrates, like chameleons, face a secondary threat: harvesting for the commercial pet trade. Six chameleons inhabit the arid southwest near Toliara: *Furcifer antimena*, *F. belalandaensis*, *F. labordi*, *F. lateralis*, *F. oustaleti*, and *F. verrucosus*. We measured population densities of three of those species. *Furcifer verrucosus* has a large distribution, was dense (97.7 ha^{-1}; 95% CI = 60.2-158.6), and inhabited forests and anthropogenic habitats. *Furcifer labordi* was moderately dense (30.8 ha^{-1}; 13.4-70.9), but has a restricted range and a unique life history that makes it susceptible to perturbations from deforestation or illegal harvesting. *Furcifer antimena* was the least dense (17.0 ha^{-1}; 9.3-30.9) and has an even smaller distribution range. We lack density data for *F. lateralis*, but this species was abundant in anthropogenic habitats. In contrast, despite intensive sampling within its distribution, we found almost no *F. belalandaensis*. Within their respective ranges, there are no protected areas for *F. antimena* and *F.*

belalandaensis, and only one for *F. labordi* (but for northern populations). We recommend that high conservation priority be focused on *F. antimena*, *F. belalandaensis*, these southern populations of *F. labordi*, and their respective habitats. We suggest the establishment of a new protected area of ca. 50,000 ha that not only benefits these chameleons, but also the other rare endemic plants and animals of the southwest.

Introduction

Madagascar is widely recognized as a biodiversity ‘hotspot’ with high conservation priority and is well known for its highly endemic fauna (Myers et al. 2000; Ganzhorn et al. 2001; Lamoreux et al. 2006). Islands high in endemic species are particularly vulnerable to extinctions and are of high priority for preservation of species richness and phylogenetic diversity (Pimm et al. 1995; Lamoreux et al. 2006; Forest et al. 2007). It is estimated that Madagascar has more genetic diversity per unit area than anywhere else, and therefore, forest loss in Madagascar may have a greater impact on global biodiversity loss than other hotspots (Hannah et al. 1998).

There are several key areas of high endemism in Madagascar, and within the existing system of protected areas on the island, many of these centres for endemism are underrepresented (Wilmé et al. 2006). One such area identified by Wilmé et al. was the southwest, where our study took place. This region has the highest level of plant endemism in Madagascar (Rabesandratana 1984) and is listed as one of the 200 most important ecological regions in the world (Elmqvist et al. 2007). These forests have also been included in a list of at least 16 sites of “imminent extinction” (Ricketts et al. 2005).

Virtually all of the remaining primary and secondary forests in the southwest lack formal protection (Seddon et al. 2000; Du Puy and Moat 2003). The leading culprits of deforestation in the region are cattle grazing, harvesting of wood, and charcoal production (Fenn 2003, personal observation). These forests should be vital areas to focus conservation efforts to minimize the loss of endemic biodiversity, especially since spiny forests exhibit high endemism for plants, birds, mammals, and reptiles (Scott et al. 2006) with many species vulnerable or threatened (Seddon et al. 2000). There is an urgent need for more research focus in the southwest (Hannah et al. 1998), including research on chameleons (Brady and Griffiths 1999). Targeting chameleons for conservation may also indirectly benefit other endemic, threatened plants and animals.

There are 346 species of reptiles in Madagascar, with greater than 90% of those being endemic (Raxworthy 2003). Only two other biodiversity hotspots in the world rank higher in reptile endemism (Myers et al. 2000). The primary culprits for the rapid loss of endemic herpetofauna are habitat degradation and harvesting for the commercial pet trade (Raxworthy 1988; Brady and Griffiths 1999; Glaw and Vences 2003; Raselimanana and Rakotomalala 2003; Carpenter and Robson 2005). Deforestation rates, driven by high poverty rates and population growth (Goodman and Patterson 1997), are high (Consiglio et al. 2006; Banks et al. 2007): an estimated 110,000 ha per year between 1950 and 1985 with little sign of slowing down (Green and Sussman 1990). During the 1980s, 400,000 ha of seasonal forest (e.g., dry deciduous and spiny forests) were lost due to habitat degradation; a greater proportion of forest loss than in either tropical or montane regions (Whitmore 2000).

Historically, Madagascar was one of the most vigorous exporters of chameleons: nearly 200,000 between 1977 and 2001 (Carpenter et al. 2004). These numbers are probably gross underestimates of the true number since many likely went unreported or unrecorded. Little is known about the impacts of such removal on wild populations, even for the most commonly exported species. The purpose of this study was to determine population densities of three chameleon species inhabiting the lowland spiny forests of south-western Madagascar so as to identify conservation priorities for this underrepresented region of high plant and animal endemism. Six chameleon species inhabit these unprotected forests: *Furcifer antimena*, *F. belalandaensis*, *F. labordi*, *F. lateralis*, *F. oustaleti*, and *F. verrucosus*. All these species are broadly sympatric in a small region of the southwest, north of Toliara, making this group particularly amenable to applied conservation strategies. All chameleons in Madagascar are endemic (except for species introduced to Kenya, and probably Mauritius and Réunion) and highly threatened: all are listed in CITES Appendix I or II and *F. labordi* has been placed on the IUCN Redlist as a species of special concern (Carpenter et al. 2004). Despite being highly diverse, highly endemic, and highly threatened, there is little known about the present population status of many of Madagascar's chameleons, making responsible conservation decisions difficult, if not impossible. To effectively implement conservation priorities, areas of specific interest must be specified and reduced to a scale that is manageable by local authorities (Harris et al. 2005).

Methods

We collected population density data for three species (*F. antimena*, *F. labordi*, and *F. verrucosus*; Figure 1) which are all sexually dimorphic, medium to large-sized, diurnal chameleons with males being larger than females (Brygoo 1971; Karsten et al. in review-a, b). *Furcifer labordi* inhabits the western and south-western regions of Madagascar, whereas *F. verrucosus* has a larger distribution, occurring throughout most of the west, southwest, and south. *Furcifer antimena* has a much more restricted range, confined almost exclusively to the arid spiny forests near the provincial capital of Toliara (Brygoo 1971; Glaw and Vences 1994). All three species, like most other lizards in Madagascar, are seasonally active and reproduce during the wet season, which spans approximately November to as late as April, depending on region (Karsten et al. in review-a).

The climate of Madagascar varies such that the more northerly latitudes are tropical and sub-tropical with relatively stable conditions throughout the year. More southerly latitudes, where our study took place, are typically considered harsher environments with more pronounced differentiation between wet and dry season and greater variation in year-round climate (Vose et al. 1992; Jury 2003). Our northernmost study site was located ca. 30 km north of Toliara, near the village of Ranobe (23°02’20” S, 43°36’37” E; Figure 2). Ranobe is toward the extreme southern boundary of the distribution for *F. labordi* (Glaw and Vences 1994). The other site was approximately 10 km north of Toliara near the village of Belalanda (23°15’26” S, 43°38’05” E). The forests of the southwest were spiny forest and vegetation was typically xerophyllous thickets that included the family Didiereaceae and the genus *Euphorbia* (Koechlin 1972). Vegetation usually did not exceed 3 m in height except for occasional emergent trees that reached up to 10 m. The low forest canopy facilitated the detection of chameleons perched high; poor detection of chameleons in high forest canopies has hampered similar surveys in rainforests (Jenkins et al. 1999; Jenkins et al. 2003).

We estimated population density by recording chameleon encounter rates along a transect. Each 150-m transect consisted of 3 parallel lines spaced 20 m apart, with each line 50 m in length. We determined transect locations randomly along an east-west axis (footpath) within a known distribution range and forest type of each species, and randomly assigned the transect to be either north or south of the east-west axis. The compass direction of the 3 parallel lines of each transect was randomly determined. We established all transects at least 24 h prior to data collection and placed them at least 5 m away from the nearest footpath since habitat may vary between forest interior and edge, thereby influencing density estimates (Jenkins et al. 1999).

An increasingly popular method of estimating population densities of animals, including chameleons, is distance sampling (Buckland et al. 1993; Buckland et al. 2001). Distance sampling uses a probability detection curve determined by a set of perpendicular distances of each individual from a transect line. The program applies a series of functions to the data and selects the best-fitting model using the Akaike Information Criterion (AIC), which provides the best measure of model fit for observational data (Burnham and Anderson 2002). There are four underlying assumptions of the distance sampling model (Buckland et al. 1993; Buckland et al. 2001): 1) survey transects are placed randomly with respect to a species' distribution (i.e., they do not favour convenient patches of forests, such as footpaths), 2) the detection rate for organisms that are zero distance from the transect line is 100%, 3) organisms are detected prior to any movement or disturbance caused by the observer, 4) perpendicular distances to the transect can be measured accurately. Our methods met these assumptions. First, we randomly determined transect locations as described above (assumption 1). Second, chameleons are pale and highly reflective, making them easily identifiable, and we are confident that we detected all chameleons right on the transect (assumption 2). Third, because all sampling was conducted at night, all individual locations were recorded without any fleeing or movement (assumption 3), allowing for precise, accurate, perpendicular measurements from the transect line (assumption 4).

During data collection at Ranobe, we observed a distinct reduction in chameleon abundance at the end of the wet season. We have also observed this phenomenon in other years at Ranobe. The onset of the dry season varies from year to year due to stochastic climatic variables, but it generally occurs in February or March. We provide density estimates for the ‘late active season’ and the ‘early dry season.’ We have included *F. antimena* density estimates as ‘early dry season’ simply due to chronological conformity with the Ranobe data. However, it is possible that *F. antimena* may not show the same clear seasonal shift in abundance as the species at Ranobe since they are two separate, albeit similar, regions of spiny forest.

We collected all data from 16 February–18 March 2003. We surveyed the late active season transects at Ranobe between 16 February–26 February, and the early dry season transects between 4 March–8 March. We surveyed the Belalanda transects (*F. antimena* only) from 11 March–18 March. Upon encountering a chameleon, we identified the species, sex, and age (adult, juvenile, or hatchling). Adult females exhibited sexually receptive coloration, adult males exhibited hemipenal bulges, hatchlings lacked secondary sexual characters (casque and dorsal crest, and rostral appendage in *F. antimena* and *F. labordi*), and juveniles represented all other individuals. We measured the perpendicular distance of each chameleon to the transect line to centimetre accuracy using a 50-m tape measure and estimated population density using DISTANCE software (Thomas et al. 2004). The same two researchers performed all data collection.

Results

We found 149 chameleons along 22 transects (sites pooled). Only two species were present in Ranobe: *F. labordi* and *F. verrucosus*. Only one species was present at the Belalanda study site: *F. antimena*. However, another species occurs south of Belalanda village, but north of Toliara, in anthropogenic habitats: the widespread chameleon *F. lateralis* (personal observations). *Furcifer belalandaensis* is known from only a few individuals collected near the Fiherenana River and we found none in any of our transects. We also intensively searched (2003-2006) localities of museum-collected specimens along the Fiherenana River during 2003-2006, but found none. However, we have relocated a population of *F. belalandaensis* during a recent visit in 2008.

Late active season density estimates

Of the two sympatric species at Ranobe, *F. verrucosus* had the greatest density of 97.7 ha^{-1} (95% CI = 60.2-158.6, n = 67, transects = 6). The majority of individuals we surveyed were juveniles. Juvenile density was 80.2 ha^{-1} (42.8-150.1, n = 57, transects = 6). We were unable to select a robust model to estimate adult *F. verrucosus* densities due to low sample size. However, we developed a biologically relevant estimate of ca. 17.5 ha^{-1} for adults by subtracting the model for juvenile densities from the overall population density model. Clearly, adults were a much smaller component of the overall population at this period of the active season. *Furcifer labordi* is an annual species (Karsten et al. in review-a) and thus all *F. labordi* we encountered were adults during this time of the active season. The population density estimates during the late breeding season for this species was 30.8 ha^{-1} (13.4-70.9, n = 20, transects = 6).

Early dry season density estimates

During the early dry season, densities of both species were lower, but *F. verrucosus* was still far more abundant than *F. labordi*. *Furcifer verrucosus* decreased to an estimated 36.7 ha^{-1} (25.4-50.3, n = 37, transects = 6) and *F. labordi* to 4.0 ha^{-1} (0.5-33.4, n = 3, transects = 6). Due to low sample size, one should exercise caution when interpreting this density estimate for *F. labordi*. Regardless, it is clear that *F. labordi* abundance dramatically decreased. The 6 dry season transects yielded only 3 individuals compared to 20 found during the late active season, despite the same unit effort for each period (Table 1). The *F. verrucosus* population again was mostly juveniles, whose density we estimated as 29.2 ha^{-1} (18.3-46.4, n = 30, transects = 6). The only adult *F. verrucosus* found during this portion of the dry season were yearlings that had just reached adult size; no second year adults were present this late in the season.

We were unable to compare estimates of late active season and early dry season for *F. antimena*. Since we conducted the surveys at Belalanda after those at Ranobe, we have included them as early dry season estimates; however, it is unclear whether species at Belalanda enter aestivation as early as species at Ranobe. *Furcifer antimena* had an estimated density of 17.0 ha^{-1} (9.3-30.9, n = 22, transects = 11).

Discussion

Of the four legally exported species of chameleons in Madagascar (*F. lateralis*, *F. oustaleti*, *F. pardalis*, and *F. verrucosus*), population density estimates are known for only the latter two (Andreone et al. 2005, this study). Although there are no density data for *F. lateralis*, we found them to be abundant in anthropogenic habitat near the city of Toliara (and in other regions of Madagascar). We also found *F. verrucosus* in anthropogenic habitats. Carpenter et al. (2005) suggested that most *F. verrucosus* collected for the pet trade are from the Toliara region, indicating that populations in this region may be susceptible to overexploitation. Despite this, we found that the population at Ranobe was denser than that of *F. pardalis* at Nosy Be (Table 2), which Andreone et al. (2005) concluded were not under immediate threat from over-collection. Our results suggest that when limited to the current harvesting quota, *F. verrucosus* is not currently under immediate threat in this region.

Knowledge of population density may facilitate identification of high priority species and habitats (Jenkins et al. 1999; Brady and Griffiths 2003; Jenkins et al. 2003; Andreone et al. 2005, Table 2). Species of relatively low density may warrant the highest conservation priority: *C. brevicornis*, *C. glawi*, *C. globifer*, *C. nasuta*, *C. oshaughnessyi*, and *F. antimena*. Population data also help identify the most appropriate areas to target conservation efforts for chameleons. For example, the preservation and management of *B. thieli* and *C. nasuta* would be far more effective at Andranomay instead of Vatoharanana, where they are scarce (Table 2). The area of greatest priority in south-western Madagascar is the spiny forest north of the Fiherenana River where *F. antimena* and *F. belalandaensis* occur. *Furcifer antimena* had low density, and *F. belalandaensis* was absent in this area during surveys from 2003-2006. We found *F. belalandaensis* in 2008, although its present population density is unknown. Our recent sampling, along with museum collection localities, indicate it is sympatric with *F. antimena*, albeit from a much smaller distribution (Brygoo 1971). It is estimated that only 44% of suitable deciduous dry southern forest and scrubland habitat and only 0.2% of deciduous seasonally dry western forest remains in the distribution of *F. antimena* (Brady and Griffiths 1999). With a restricted distribution void of any formal protection, low population density, paucity of remaining suitable habitat, and forest disturbance in the region (Figure 3), *F. antimena* and *F. belalandaensis* should be of high conservation priority in future protected area plans. Our results add to this growing database and represent the first data set for nonrainforest chameleon species.

Life history traits also should be taken into account when making conservation decisions (e.g., Andreone et al. 2005). Although *F. labordi* is moderately dense compared to other chameleons (Table 2), it may be especially susceptible to disturbance and illegal over-collection due to its unique, annual life history (Karsten et al. in review-a). After hatching, the entire population is nonreproductive individuals in November and

December. Sexual maturity is reached in January, and egg-laying begins in February. The end of the active season signals population-wide death for the adult cohort. The entire population is represented during the dry season by a single egg-only cohort. Substantial population reduction—especially before reproduction—could lead to catastrophic population crashes in a single generation. This species' habitat is largely unprotected and under high deforestation pressure (Figure 4), and because of its life history, *F. labordi* appears especially vulnerable to any degree of perturbation.

Recent modelling techniques provide useful insight in determining potential distributions of species (Raxworthy et al. 2003), including species with restricted samples and location data (Pearson et al. 2007). Although our data provide a baseline from which to begin determination of potential protected areas, these methods may improve the ability to target specific conservation priorities for species with restricted distributions such as *F. antimena*, *F. belalandaensis*, and *F. labordi*. Applied conservation strategies for these three species will likely also benefit other endemic plants and animals of the southwest. Currently, there are no protected areas within the range of *F. antimena* or *F. belalandaensis* and only one protected area for northern populations of *F. labordi* (Raselimanana and Rakotomalala 2003), which underscores the need to establish conservation priorities in the southwest.

Based on the composite data, the current legislation for collection and trade of chameleons, and the present allocation of protected areas within their ranges (or lack thereof), we offer the following recommendations. It appears that current disturbance and collection rates do not adversely affect *F. verrucosus*. *Furcifer labordi* is not presently available for legal exportation; therefore, deforestation is the main threat if illegal collection is minimized. With a potentially delicate life history strategy, being a species of special concern, and lacking any formal protection for southern populations, high conservation priority should be placed on these populations in the southwest. *Furcifer antimena* appears to be very susceptible to extirpation from disturbance. The distribution of this species is small and restricted. Additionally, the rare *F. belalandaensis* was sympatric with *F. antimena* near the Fiherenana River in 1995 and 2008 (CJR, unpublished data); conservation of *F. antimena* north of the Fiherenana River would also benefit this even rarer species. Thus, *F. antimena* should also be of high priority when making conservation decisions about this region.

Conclusions

Madagascar seeks to expand its protected forests from 1.7 million to 6 million ha (Norris 2006) with all protected areas belonging to a single national system (Système d'Aires Protégées de Madagascar, or SAPM) collectively managed by the government, funding agencies, non-governmental organizations, and the private sector. Much of the southwest has been identified as being in need of formal protection. However, current objectives place emphasis on spiny forests south of Toliara where protected areas are already established; the forests north of the Fiherenana River are distinct from these already protected forests (Seddon et al. 2000). Thus, a void of protection exists for the unique forests north of Toliara that are "severely degraded and as such deserves close monitoring" (Seddon et al. 2000, pg. 294); these forests house more species of conservation concern than any of the 5 protected areas south of Toliara (Seddon et al. 2000).

We suggest the addition of at least one new protected area in the southwest of ca. 50,000 ha that encompasses the distributions of *F. antimena*, *F. belalandaensis*, and southern populations of *F. labordi*. We recommend it extend from the Fiherenana River northward to the Manombo River (ca. 40 km) and extend at least 10-15 km inland to incorporate coastal and inland geography and the wetlands of Lac Andranobe and Lac Ranobe. As per the International Union for Conservation of Nature (IUCN) protected area categories, we recommend these forests be classified as a Category 4 protected area (managed areas that maintain species and habitats). Harvesting for the pet trade continues near Belalanda (personal observation) and needs better regulation. The low population densities and lack of protected areas warrant that CITES quotas remain unchanged, and collection and exportation of *F. antimena*, *F. belalandaensis*, and *F. labordi* remain illegal. We recommend that chameleon densities within the proposed preserve be monitored annually to assess the impacts of deforestation, which may be used as an indirect assessment for other endemic flora and fauna. To effectively and successfully implement protection of this new protected area, it is imperative that local economics be considered by SAPM (Tucker 2007).

Acknowledgements

Research was supported by funding from the National Science Foundation, Washington (DEB 99-84496) to CJR. We thank the authorities in Madagascar for permission to conduct fieldwork, D. Rakotondravony and O. Ramilijaona for their assistance, and T.A. Baird, M. Lovern, and M. Palmer for review of the manuscript. We extend gratitude to H. Thomas and D. Kidney for logistical advice in the field.

Literature Cited

Andreone, F., Guarino, F.M., Randrianirina, J.E., 2005. Life history traits, age profile, and conservation of the panther chameleon, *Furcifer pardalis* (Cuvier 1829), at Nosy Be, NW Madagascar. Tropical Zoology 18, 209-225.

Banks, M.A., Ellis, E.R., Antonio, Wright, P.C., 2007. Global population size of a critically endangered lemur, Perrier's sifaka. Animal Conservation 10, 254-262.

Brady, L.D., Griffiths, R.A., 1999. Status Assessment of Chameleons in Madagascar. IUCN, Gland, Switzerland and Cambridge, UK.

Brady, L.D., Griffiths, R.A., 2003. Chameleon population density estimates, In The Natural History of Madagascar. eds S.M. Goodman, J.P. Benstead, pp. 970-972. University of Chicago Press, Chicago, Illinois.

Brygoo, E.R., 1971. Reptiles Sauriens Chamaeleonidae: Genre *Chamaeleo*. Faune de Madagascar 33, 1-318.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., 1993. Distance Sampling: Estimating Abundance of Biological Populations. Chapman and Hall, London.

Buckland, S.T., Anderson, D.R., Burnham, K.P., Laake, J.L., Borchers, D.L., Thomas, L., 2001. Introduction to Distance Sampling: Estimating Abundance of Biological Populations. Oxford University Press, New York, New York.

Burnham, K.P., Anderson, D.R., 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer, New York, New York.

Carpenter, A.I., Robson, O., 2005. A review of the endemic chameleon genus *Brookesia* from Madagascar, and the rationale for its listing on CITES Appendix II. Oryx 39, 1-6.

Carpenter, A.I., Robson, O., Rowcliffe, J.M., Watkinson, A.R., 2005. The impacts of international and national governance changes on a traded resource: a case study of Madagascar and its chameleon trade. Biological Conservation 123, 279-287.

Carpenter, A.I., Rowciffe, J.M., Watkinson, A.R., 2004. The dynamics of the global trade in chameleons. Biological Conservation 120, 291-301.

Consiglio, T., Schatz, G.E., McPherson, G., Lowry, P.P., Rabenantoandro, J., Rogers, Z.S., Rabevohitra, R., Rabehevitra, D., 2006. Deforestation and plant diversity of Madagascar's littoral forests. Conservation Biology 20, 1799-1803.

Du Puy, D.J., Moat, J., 2003. Using geological substrate to identify and map primary vegetation types in Madagascar and the implications for planning biodiversity conservation, In The Natural History of Madagascar. eds S.M. Goodman, J.P. Bensted, pp. 51-74. University of Chicago Press, Chicago and London.

Elmqvist, T., Pyykönen, M., Tengö, M., Rakotondrasoa, F., Rabakonandrianina, E., Radimilahy, C., 2007. Patterns of loss and regeneration of tropical dry forest in Madagascar: the social institutional context. PLoS One 2, e402. doi: 410.1371/journal.pone.0000402.

Fenn, M., 2003. Learning conservation strategies: a case study of the Parc National d'Andohahela, In The Natural History of Madagascar. eds S.M. Goodman, J.P. Benstead, pp. 1494-1501. University of Chicago Press, Chicago, Illinois.

Forest, F., Grenyer, R., Rouget, M., Davies, T.J., Cowling, R.M., Faith, D.P., Balmford, A., Manning, J.C., Proches, S., van der Bank, M., Reeves, G., Hedderson, T.A.J., Savolainen, V., 2007. Preserving the evolutionary potential of floras in biodiversity hotspots. Nature 445, 757-760.

Ganzhorn, J.U., Lowry, P.P., Schatz, G.E., Sommer, S., 2001. The biodiversity of Madagascar: one of the world's hottest hotspots on its way out. Oryx 35, 346-348.

Glaw, F., Vences, M., 1994. A Fieldguide to the Reptiles and Amphibians of Madagascar, second edn. Moos Druck, Leverkusen, Germany.

Glaw, F., Vences, M., 2003. Introduction to amphibians, In The Natural History of Madagascar. eds S.M. Goodman, J.P. Benstead. University of Chicago Press, Chicago, Illinois.

Goodman, S.M., Patterson, B.D., 1997. Natural Change and Human Impact in Madagascar. Smithsonian Institution Press, Washington, D. C.

Green, G.M., Sussman, R.W., 1990. Deforestation History of the Eastern Rain Forests of Madagascar from Satellite Images. Science 248, 212-215.

Hannah, L., Rakotosamimanana, B., Ganzhorn, J.U., Mittermeier, R.A., Olivieri, S., Iyer, L., Rajaobelina, S., Hough, J., Andriamialisoa, F., Bowles, I., Tilkin, G., 1998. Participatory planning, scientific priorities, and landscape conservation in Madagascar. Environmental Conservation 25, 30-36.

Harris, G.M., Jenkins, C.N., Pimm, S.L., 2005. Refining biodiversity conservation priorities. Conservation Biology 19, 1957-1968.

Jenkins, R.K.B., Brady, L.D., Bisoa, M., Rabearivony, J., Griffiths, R.A., 2003. Forest disturbance and river proximity influence chameleon abundance in Madagascar. Biological Conservation 109, 407-415.

Jenkins, R.K.B., Brady, L.D., Huston, K., Kauffmann, J.L.D., Rabearivony, J., Raveloson, G., Rowcliffe, J.M., 1999. The population status of chameleons within

Ranomafana National Park, Madagascar, and recommendations for future monitoring. Oryx 33, 38-46.

Jury, M.R., 2003. The climate of Madagascar, In The Natural History of Madagascar. eds S.M. Goodman, J.P. Benstead, pp. 75-87. University of Chicago Press, Chicago, Illinois.

Karsten, K.B., Andriamandimbiarisoa, L.N., Fox, S.F., Raxworthy, C.J., in review-a. Discovery of a novel tetrapod life history: an annual chameleon living mostly as an egg. Proceedings of the National Academy of Sciences of the United States of America.

Karsten, K.B., Andriamandimbiarisoa, L.N., Fox, S.F., Raxworthy, C.J., in review-b. Social behavior of two species of chameleons in Madagascar: insights into sexual selection. Herpetologica.

Koechlin, J., 1972. Flora and vegetation of Madagascar, In Biogeography and Ecology in Madagascar. eds R. Battistini, G. Richard-Vindard, pp. 145-190. Dr. W. Junk B. V., The Hague.

Lamoreux, J.F., Morrison, J.C., Ricketts, T.H., Olson, D.M., Dinerstein, E., McKnight, M.W., Shugart, H.H., 2006. Global tests of biodiversity concordance and the importance of endemism. Nature 440, 212-214.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B., Kent, J., 2000. Biodiversity hotspots for conservation priorities. Nature 403, 853-858.

Norris, S., 2006. Madagascar defiant, In Bioscience. pp. 960-965.

Pearson, R.G., Raxworthy, C.J., Nakamura, M., Peterson, A.T., 2007. Predicting species distributions from small numbers of occurrence records: a test case using cryptic geckos in Madagascar. Journal of Biogeography 34, 102-117.

Pimm, S.L., Russell, G.J., Gittleman, J.L., Brooks, T.M., 1995. The future of biodiversity. Science 269, 347-350.

Rabesandratana, R., 1984. Flora of the Malagasy southwest, In Madagascar. eds A. Jolly, P. Oberlé, R. Albignac, pp. 55-74. Pergamon Press, Oxford.

Raselimanana, A.P., Rakotomalala, D., 2003. Chamaeleonidae, Chameleons, In The Natural History of Madagascar. eds S.M. Goodman, J.P. Benstead, pp. 960-969. University of Chicago Press, Chicago, Illinois.

Raxworthy, C.J., 1988. Reptiles, rainforest and conservation in Madagascar. Biological Conservation 43, 181-211.

Raxworthy, C.J., 2003. Introduction to the reptiles, In The Natural History of Madagascar. eds S.M. Goodman, J.P. Benstead, pp. 934-949. University of Chicago Press, Chicago, Illinois.

Raxworthy, C.J., Martinez-Meyer, E., Horning, N., Nussbaum, R.A., Schneider, G.E., Ortega-Huerta, M.A., Peterson, A.T., 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426, 837-841.

Ricketts, T.H., Dinerstein, E., Boucher, T., Brooks, T.M., Butchart, S.H.M., Hoffmann, M., Lamoreux, J.F., Morrison, J., Parr, M., Pilgrim, J.D., Rodrigues, A.S.L., Sechrest, W., Wallace, G.E., Berlin, K., Bielby, J., Burgess, N.D., Church, D.R., Cox, N., Knox, D., Loucks, C., Luck, G.W., Master, L.L., Moore, R., Naidoo, R., Ridgely, R., Schatz, G.E., Shire, G., Strand, H., Wettengel, W., Wikramanayake, E., 2005. Pinpointing and preventing imminent extinctions. Proceedings of the National Academy of Sciences of the United States of America 102, 18497-18501.

Scott, D.M., Brown, D., Mahood, S., Denton, B., Silburn, A., Rakotondraparany, F., 2006. The impacts of forest clearance on lizard, small mammal and bird communities in the arid spiny forest, southern Madagascar. Biological Conservation 127, 72-87.

Seddon, N., Tobias, J., Yount, J.W., Ramanampamonjy, J.R.M., Butchart, S., Randrianizahana, H., 2000. Conservation issues and priorities in the Mikea Forest of south-west Madagascar. Oryx 34, 287-304.

Thomas, L., Laake, J.L., Strindberg, S., Marques, F.F.C., Buckland, S.T., Borchers, D.L., Anderson, D.R., Burnham, K.P., Hedley, S.L., Pollard, J.H., Bishop, J.R.B., 2004. Distance 4.1, Release 2. Research Unit for Wildlife Population Assessment, University of St. Andrews, UK. http://www.ruwpa.st-and.ac.uk/distance/.

Tucker, B., 2007. Applying behavioral ecology and behavioral economics to conservation and development planning: an example from the Mikea forest, Madagascar. Human Nature-an Interdisciplinary Biosocial Perspective 18, 190-208.

Vose, R.S., Schmoyer, R.L., Steurer, P.M., Peterson, T.C., Heim, R., Karl, T.R., Eischeid, J.K., 1992. The Global Historical Climatology Network: Long-Term Monthly Temperature, Precipitation, Sea Level Pressure, and Station Pressure Data. ORNL/CDIAC-53, CDIAC NDP-041, Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, Oak Ridge, Tennessee.

Whitmore, T., 2000. Madagascan deforestation rate during the 1980s, In Diversité et Endémisme à Madagascar. eds W.R. Lourenço, S.M. Goodman, p. 125. Mémoires de la Société de Biogéographie, Paris, France.

Wilmé, L., Goodman, S.M., Ganzhorn, J.U., 2006. Biogeographic evolution of Madagascar's microendemic biota. Science 312, 1063-1065.

Table 1: Population density estimates for three species of chameleons in the Toliara region, south-western Madagascar, at the end of the active season and beginning of the dry season. Timing of the surveys had substantial impact on population densities of *Furcifer labordi* and *F. verrucosus*. Dashes indicate no available data.

	Late active season					Early dry season				
Species	D (ha^{-1})	n	95% CI	No. of transects	Total transect length (m)	D (ha^{-1})	n	95% CI	No. of transects	Total transect length (m)
F. antimena	--	--	--	--	--	17.0	22	9.3-30.9	11	1650
F. labordi	30.8	20	13.4-70.9	6	900	4.0	3	0.5-33.4	6	900
F. verrucosus	97.7	67	60.2-158.6	6	900	36.7	37	25.4-50.3	6	900

Table 2: Comparative frequency and population density estimates for *Brookesia*, *Calumma*, and *Furcifer* chameleons in Madagascar. Dashes indicate no data available from that study.

Species	D (ha^{-1})	n	Transect length (m)	Location	Reference
B. nasus	26.8	63	3920	Vatoharanana; forest	Jenkins et al. 1999
B. nasus	37.8	109	6575	Vatoharanana; footpath	Jenkins et al. 1999
B. minima	20.7	--	1500	Andranomay; riparian	Jenkins et al. 2003
B. minima	4.9	--	4500	Andranomay; low-disturbance	Jenkins et al. 2003
B. thieli	88.5	--	1500	Andranomay; riparian	Jenkins et al. 2003
B. thieli	51.7	--	4500	Andranomay; low-disturbance	Jenkins et al. 2003
B. thieli	--	1	3920	Vatoharanana; forest	Jenkins et al. 1999
B. thieli	--	0	6575	Vatoharanana; footpath	Jenkins et al. 1999
C. brevicornis	4.9	--	1500	Andranomay; riparian	Jenkins et al. 2003
C. brevicornis	12.9	--	4500	Andranomay; low-disturbance	Jenkins et al. 2003
C. brevicornis	--	1	3920	Vatoharanana; forest	Jenkins et al. 1999
C. brevicornis	6.7	23	6575	Vatoharanana; footpath	Jenkins et al. 1999
C. gastrotaenia	89.7	--	1500	Andranomay; riparian	Jenkins et al. 2003
C. gastrotaenia	33.1	--	4500	Andranomay; low-disturbance	Jenkins et al. 2003
C. glawi	12.7	40	3920	Vatoharanana; forest	Jenkins et al. 1999
C. glawi	15.2	72	6575	Vatoharanana; footpath	Jenkins et al. 1999

Table 2: Continued.

Species	D (ha^{-1})	n	Transect length (m)	Location	Reference
C. globifer	10.1	--	1500	Andranomay; riparian	Jenkins et al. 2003
C. globifer	3.9	--	4500	Andranomay; low-disturbance	Jenkins et al. 2003
C. nasuta	7.6		1500	Andranomay; riparian	Jenkins et al. 2003
C. nasuta	5.4	--	4500	Andranomay; low-disturbance	Jenkins et al. 2003
C. nasuta	--	1	3920	Vatoharanana; forest	Jenkins et al. 1999
C. nasuta	--	6	6575	Vatoharanana; footpath	Jenkins et al. 1999
C. oshaughnessyi	8.3	26	3920	Vatoharanana; forest	Jenkins et al. 1999
C. oshaughnessyi	10.8	52	6575	Vatoharanana; footpath	Jenkins et al. 1999
F. antimena	17.0	22	1650	Belalanda	This study
F. labordi	30.8	20	900	Ranobe; wet season	This study
F. labordi	4.0	3	900	Ranobe; dry season	This study
F. pardalis	42.2	193	4400	Nosy Be; roadside	Andreone et al. 2005
F. pardalis	17.4	69	4850	Nosy Be; agriculture/secondary	Andreone et al. 2005
F. verrucosus	97.7	67	900	Ranobe; wet season	This study
F. verrucosus	36.7	37	900	Ranobe; dry season	This study

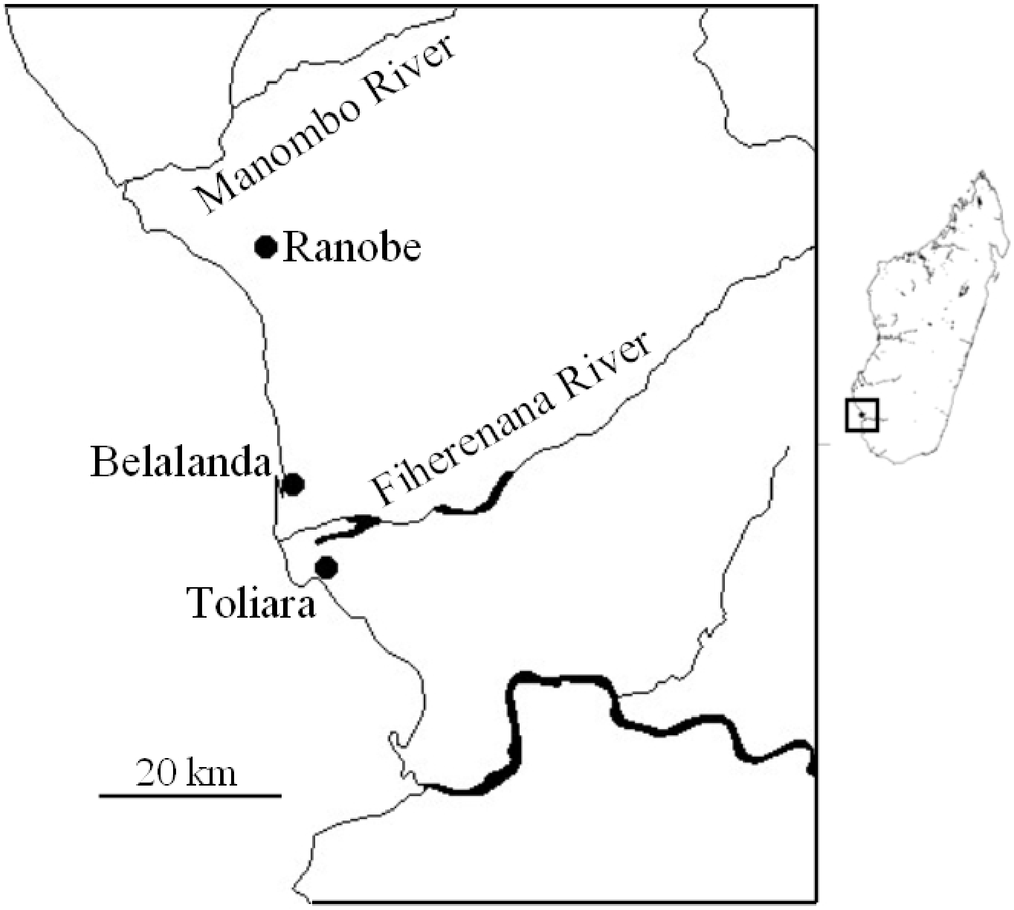
FIGURE LEGENDS

Figure 1: The three species of this study for which we calculated population density estimates: *Furcifer antimena* (top), *F. labordi* (middle), and *F. verrucosus* (bottom). Males on the left, females on the right.

Figure 2: Deciduous dry and spiny forests of south-western Madagascar. Density estimates for *Furcifer labordi* and *F. verrucosus* from near the village of Ranobe, ca. 35 km north of the provincial capital of Toliara. Density estimates for *F. antimena* from north of the village of Belalanda, ca. 10 km north of Toliara.

Figure 3: Intact spiny forest north of the village of Belalanda (upper); habitat of the restricted species *F. antimena* and *F. belalandaensis*. Highly disturbed forest (lower), mostly from harvesting of vegetation for charcoal.

Figure 4: Deciduous dry forest at Ranobe in 1995 (upper; CJR), inhabited by two locally abundant chameleon species: *Furcifer labordi* and *F. verrucosus*. The same study site in 2004 (lower; KBK), virtually void of vegetation and chameleons.


Manombo River
Ranobe
Fiherenana River
Belalanda
Toliara
20 km

VITA

Kristopher Brett Karsten

Candidate for the Degree of

Doctor of Philosophy

Thesis: SEXUAL SELECTION, SOCIAL BEHAVIOR, AND CONSERVATION OF CHAMELEONS IN SOUTHWESTERN MADAGASCAR

Major Field: Zoology

Biographical:

Personal Data: Born in Smithville, Missouri on 30 October, 1974, the son of Larry R. Karsten and Connie L. Parsons.

Education: Received a Bachelor of Science in Biology from Truman State University in Kirksville, Missouri in December, 1997; received a Master of Science in Biology from Texas Christian University in Fort Worth, Texas in May, 2000; completed the requirements for the Doctor of Philosophy in Zoology at Oklahoma State University, Stillwater, Oklahoma in May, 2008.

Experience: Adjunct Faculty, University of Central Oklahoma, 2004-2006: Animal Biology, General Biology. Instructor, Oklahoma State University, 2003-2005: Animal Biology. Graduate Teaching Assistant, Oklahoma State University, 2000-2008: Human Anatomy, Evolutionary Ecology, Comparative Vertebrate Morphology, Biology of Fish, Amphibians and Reptiles, Animal Biology, Introductory Biology. Graduate Teaching Assistant, Department of Biology, Texas Christian University, 1998 to 2000: Introductory Biology.

Professional Memberships: American Society of Ichthyologists and Herpetologists, Animal Behavior Society, Herpetologists' League, Sigma Xi, Society for Integrative and Comparative Biology, Society for the Study of Amphibians and Reptiles, Society for the Study of Evolution

Name: Kristopher Brett Karsten Date of Degree: May, 2008

Institution: Oklahoma State University Location: Stillwater, Oklahoma

Title of Study: SEXUAL SELECTION, SOCIAL BEHAVIOR, AND CONSERVATION OF CHAMELEONS IN SOUTHWESTERN MADAGASCAR

Pages in Study: 147 Candidate for the Degree of Doctor of Philosophy

Major Field: Zoology

Scope and Method of Study: Many extreme secondary sexual characters of animals are the result of sexual selection, or competitive acquisition of mates to sire offspring. These traits may aid males in winning fights (intrasexual selection), improve their mating success through mate choice (intersexual selection), or both. The purpose of my dissertation was to 1) determine social behavior in two species of chameleons in southwestern Madagascar, 2) determine how sexual selection may have resulted in the evolution of traits that may be advantageous to males during combat and courtship (i.e., large body size and exaggerated secondary sexual characters), and 3) use my opportunity in the field to address species of high conservation priority by measuring chameleon population densities.

Findings and Conclusions: Females of both species signaled sexual receptivity with distinct color patterns. *Furcifer labordi* was characterized by strong sexual size dimorphism and exaggerated secondary sexual characters. Body size and cranial casque height (which may indicate bite force during male fights) best predicted male fighting success and male mating success was best predicted by body size and the width of the rostral appendage in this species. In *F. verrucosus*, I found strong intrasexual selection for increased male body size and fewer dorsal cones, a trait that may correspond to age and experience. I found *F. verrucosus* to be dense and it inhabited forests and anthropogenic habitats. *Furcifer antimena* was the least dense of the three species and had a small, restricted distribution. *Furcifer labordi* was moderately dense, but also had a restricted distribution. There are no protected areas in Madagascar for *F. antimena* and only one for *F. labordi*. I recommended high conservation priority for the habitats of *F. antimena* and *F. labordi*. I proposed the establishment of a new protected area of ca. 50,000 ha which would not only benefit these chameleons, but also the other rare sympatric, endemic plants and animals of the southwest. An additional finding of my dissertation was that *F. labordi* has a unique life history: a post-hatching life span of just 4-5 months. Remarkably, this chameleon spends more of its short annual life cycle inside the egg than outside of it.

ADVISER'S APPROVAL: Stanley F. Fox