The Biology of Chameleons

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Edited by KRYSTAL A. TOLLEY and ANTHONY HERREL

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Cover illustration: *Trioceros johnstoni* from the Rwenzori Mountains, Uganda. Photo by Michele Menegon.

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FOREWORD

In putting together this book, we stand on the shoulders of others. The extensive bibliography presented here spans centuries, and the resulting body of literature is based on the work of researchers who dedicated their minds to a deeper understanding of chameleons. We have taken pieces of this great puzzle and have made a start at constructing the whole picture, but there are many glaring gaps. In some respects, it seems there are too many pieces missing and the emerging picture is only a hazy nebula of unclear, scattered, and fragmented bits. But the excitement that comes with the challenge of scientific thought, of asking the questions "why" and "how," is what compels us to keep looking for the missing pieces. For chameleons, the many missing pieces are the why and how of their remarkable evolutionary radiation, and we must keep questioning, even if we never complete the puzzle.

Although this book is built on the works of others, putting together this volume has been a group effort of the authors, all of whom enthusiastically came to the party. Each author brought their own expertise, and together we have made something more than any one of us could have done alone. It has been an extraordinary experience working with this team. As editors, we expected to be herding cats, but on the contrary, the process was surprisingly smooth. Of course, each of the chapters was reviewed by our peers, all of whom invariably provided positive and constructive criticism on the content. It is surprising how many things we missed initially, and we owe much to our colleagues for taking time to review and comment on these chapters: Salvidor Bailon, Bill Branch, Angus Carpenter, Jack Conrad, Frank Glaw, Rob James, Charles Klaver, Lance McBrayer, John Poynton, Phil Stark, Andrew Turner, James Vonesh, Bieke Vanhooydonck, and Martin Whiting. We are grateful to several friends and colleagues who permitted complimentary use of their photos, including Bill Branch, Marius Burger, Tania Fouche, Adnan Moussalli, Devi Stuart-Fox, and Michele Menegon. We also owe much to Chuck Crumly for eagerly taking on the initial responsibility of producing this book, as well as the National Research Foundation of South Africa and Centre National de la Recherche Scientifique and Groupement de Recherche

International for providing the funds that allowed the editors of this volume to collaborate and to aspire. The follow-up production team at UC Press (Lynn Meinhardt, Ruth Weinberg, Kate Hoffman, Blake Edgar, and Deepti Agarwal) were excellent in providing advice and assistance throughout the process. In all, this has been a brilliant experience, despite initial reservations in taking on such a big project. It's clear that the ease of putting this together was due to an outstanding team of authors, all of whom are passionate about their subject and have not forgotten how to ask "why."

SIX

Chameleon Behavior and Color Change

DEVI STUART-FOX

Although in many respects chameleon behavior resembles that of other lizards, there are also unusual characteristics associated with their unique morphology (Chapter 2). Chameleons are perhaps most famous for their ability to change color, a characteristic that has seen the term *chameleon* adopted in popular language to mean someone changeable or who unconsciously mimics others. Color and color change are integral to all aspects of chameleon behavior, including social, thermoregulatory, antipredator and foraging behavior. Consequently, this chapter focuses on both coloration and behavior in chameleons and will outline the modes of communication in chameleons, highlighting the importance of vision to all aspects of chameleon behavior. Chameleon color change, including the mechanism, triggers, and general function and evolution of color change are covered, as well as a detailed review of coloration and social behavior associated with reproduction. Finally, this chapter synthesizes knowledge of antipredator behavior in chameleons, including camouflage and escape behaviors.

One aspect of social behavior that is of central importance for many taxa is parental care and parent–offspring interactions more generally; however, there is no evidence of direct parental care in chameleons. In terms of indirect parental care, the placement of offspring at parturition could conceivably influence their subsequent survival in live-bearing species. Another form of parent–offspring interaction is cannibalism, which is relatively common in *Chamaeleo chamaeleon*, and may account for differences in habitat preferences of juveniles and adults (Keren-Rotem et al., 2006). However, many other factors, such as body size, diet, thermal requirements, and predation risk could also account for age-specific habitat differences, which appear to be quite common in chameleons. Cannibalism may be relatively common, particularly among larger species. Apart from potential cannibalism, parent–offspring interactions are minimal or entirely absent, particularly for egg-laying species.

Although there are other general reviews of the biology of chameleons, which cover many aspects of behavior described here (Martin, 1992; Nečas, 2004; Pianka and Vitt, 2003; Tilbury, 2010), the goal of this chapter is to provide a relatively detailed synthesis of coloration and behavior. This is placed within a broader ecological and evolutionary context where possible, highlighting important gaps in our understanding. Hopefully, this review will stimulate additional research on coloration and behavior in these remarkable animals.

6.1 SENSORY SYSTEMS AND MODES OF COMMUNICATION

Given the central importance of color and color change to chameleons, it is not surprising that vision is their most important sense (see Chapter 2) and that communication is primarily via the use of visual signals. The optical system of chameleons is covered in greater depth in Chapters 2 and 4; however, it is worth emphasizing several features that give chameleons exceptional eyesight. First, chameleons have the highest density of visual cells (cones) in the retina recorded (756,000 per square millimeter) (Wall, 1942), giving them extreme visual sensitivity. Second, their independently moving, protruding eyes have at least 180-degree movement in all directions, providing an exceptional field of view (Mates, 1978). Third, chameleons have an apparently exclusive reliance on accommodation cues to judge distance (Harkness, 1977). Accommodation cues can be used by each eye independently, allowing chameleons to accurately judge distance with one eye (Ott et al., 1998) and to gain monocular parallax cues simply from eye rotation, without moving their head or body (Pettigrew et al., 1999). Lastly, the optical power of the eye is contributed exclusively by the cornea rather than the lens (Ott and Schaeffel, 1995). Because the cornea is further forward than the lens, the nodal (focal) point is separated from the axis of rotation of the eye (Pettigrew et al., 1999). This results in increased magnification of the retinal image (the largest known for vertebrates). In other words, chameleons have long-focus or telescopic vision (Pettigrew et al., 1999). The highly developed vision of chameleons is likely to influence the evolution of social communication using visual signals and also poses a challenge to understanding these signals from the point of view of chameleons.

In contrast to the highly developed visual system, the olfactory and auditory systems in chameleons are relatively insensitive. The Jacobson organ used for olfaction in squamate reptiles is vestigial or lacking (see Chapter 2). Although some species possess temporal glands at the corners of their mouths that produce strong-smelling secretions, these may be more likely to be used as a predator deterrent or prey attractant than for intraspecific communication. There are, however, reports of males following the path taken by a female through dense vegetation, despite not being able to see her (Tilbury, 2010), which suggests the possible use of olfactory signals. The auditory system in chameleons is similarly underdeveloped, being less sensitive than that of humans (Wever, 1968; Wever, 1969b). Vocalization is sometimes incorporated into threat displays, with some species exhibiting a hissing exhalation. According to Tilbury (2010, p. 83), *Trioceros goetzei* produces a "high-pitched exhalation squeaky wheeze" when first handled. However, there is no evidence that these auditory signals are used for intraspecific communication.

Chameleons may use tactile signals in the form of substrate (plant-borne) vibration, which is commonly used by insects but rare in vertebrates. Some chameleons vibrate in short bursts at a high frequency. This behavior has been documented in an antipredator context in several species of *Brookesia* (Raxworthy, 1991) and *Chamaeleo calyptratus* when disturbed by humans and also during courtship (Barnett et al., 1999). Barnett et al. (1999) quantified the vibrational signals in *C. calyptratus,* showing that there are two types with initial dominant frequency of around 150 Hz and 20 Hz. These are transmitted to the receiver either directly or via vegetation. Vibration has also been anecdotally reported in *Rhampholeon*, *Rieppeleon,* and several species of *Trioceros* and *Chamaeleo* (Lutzmann, 2004; Tilbury, 2010). This has led some authors to suggest that vibrational signaling is likely to be widespread among the Chamaeleonidae (Barnett et al., 1999; Tilbury, 2010).

Because of their overriding importance, the remainder of this chapter will focus on visual signals.

6.2 COLOR CHANGE

Mechanism

Coloration and color change in chameleons is a function of specialized cells called "chromatophores." Chromatophores are cells in the dermis of ectotherms that are responsible for generating skin and eye color (Bagnara and Hadley, 1973; Fox, 1976). There are four main types of chromatophore, each containing different types of pigment. Xanthophores and erythrophores are very similar, distinguished primarily by their color (yellow-orange and red, respectively). They are located nearest the surface and contain carotenoid or pteridine pigments (generating reds, oranges, and yellows). Beneath the xanthophores are iridophores (also called "guanophores"), which contain colorless crystals of guanine pigment, arranged as stacks of platelets separated by cytoplasm. Their appearance is a function of the structural arrangement of platelets. For instance, depending on their spacing, the stacked guanine platelets may preferentially scatter shorter wavelengths of light and transmit longer wavelengths (Tyndall scattering), resulting in a blue appearance. Melanophores comprise the deepest layer and, as their name suggests, contain melanin pigment, generating black and brown coloration. The melanophores are large, stellate (star-like) cells with long dendrites ("arms") that extend between the iridophores and overlay the xanthophores.

Chameleon coloration is a function of the type, density, and arrangement of chromatophores. For example, green coloration may be generated by the combination of yellow xanthophores underlain by blue iridophores. The extent of color change and range of colors exhibited is species-specific, as it depends on the types and distribution of chromatophores characteristic of that species.

Color change occurs because of the movement of pigment-containing organelles within chromatophores. For example, the darkening of the skin is a result of the concentration or dispersions of motile vesicles ("packets") containing melanin pigment (the melanosomes) within the melanophores (Bagnara and Hadley, 1973). When the melanosomes are aggregated within the center of the cell, the skin appears very pale, whereas when they are dispersed throughout the dendrites to the skin's surface, the skin appears dark. Varying the degree of dispersion of the melanosomes blocks reflectance of the iridophores but not the xanthophores or erythrophores, so the skin appears yellow-red. Color change may also occur because of changes in the spacing of platelets within the iridophores, a phenomenon that has been demonstrated in fish (Clothier and Lythgoe, 1987), amphibians (Bagnara and Hadley, 1973), and the ornate tree lizard, *Urosaurus ornatus* (Morrison et al., 1996). However, it is currently not known whether movement of platelets in iridophores or pigments in xanthophores and erythrophores is involved in color change in chameleons specifically.

Color change may occur because of multiple "triggers" that fall into four main categories: (1) in response to temperature; (2) as a reflexive response to light (via photoreceptors in skin); (3) as a function of physiological state (e.g., receptivity); and (4) as a response to sensory input (surroundings, presence of prey, predators, or conspecifics). Most discussions of color change in chameleons state that it reflects their "mood"; however, the precise meaning of this phrase is unclear. Temperature-dependent color change is discussed briefly below, and the latter three triggers of color change are elaborated on in subsequent sections.

Color change in response to temperature is well known in iguanian lizards, including chameleons. However, temperature-associated color change in chameleons appears to be dependent on habitat. Specifically, among Kenyan populations of three species, *Trioceros jacksonii* and *T. ellioti,* which occur in low-latitude, midelevation evergreen forests, show limited or no change in reflectance with temperature, whereas *Chamaeleo dilepis*, which occupies a greater range of seasonally variable, subtropical savannah environments shows significant changes (Walton and Bennett, 1993). Chameleon species from higher latitudes or altitudes have been observed to perch on the top of a bush first thing in the morning, laterally compress their body and orient one flank toward the sun, and adopt a dark-brown to black coloration, often only on the flank oriented toward the sun (Burrage, 1973; Walton and Bennett, 1993). Walton and Bennett (1993) estimated that this behavior increased the rate of radiant heat gain in *C. dilepis* by 7%. This is likely to have advantages in terms of increasing activity time and locomotor performance. Chameleons may also become pale to increase reflectance during exposure to high levels of solar radiation, such as observed for *C. dilepis* on roads and in open areas at midday (Walton and Bennett, 1993).

Color change is controlled by neural and hormonal mechanisms in chameleons. Color change has been shown to occur not only in response to direct nervous stimulation (electrical stimulation of spinal nerves) in *Bradypodion pumilum* (Hogben and Mirvish, 1928) but also to hormones of pituitary origin in *Trioceros jacksonii* (Bagnara and Hadley, 1973). As in other reptiles, the primary hormone affecting aggregation or dispersion of melanosomes is likely to be melanophore-stimulating hormone (MSH) but adrenocorticotropic hormone (ACTH) has also been shown to induce darkening in *T. jacksonii* (Bagnara and Hadley, 1973). Control of color change in chameleons is poorly understood. It may be that a range of neurotransmitters and hormones of neural, adrenal, gonadal or thyroid origin (e.g., melatonin from the pineal gland or the catecholamines epinephrine and norepinephrine), and complex interactions between them, influence color change as in other reptiles (reviewed in Bagnara and Hadley, 1973; Cooper and Greenberg, 1992)

Function and Evolution

As for many other animals, coloration is strongly related to behavior and affects social communication, camouflage from predators and prey, and thermoregulation. Color change can be seen as a compromise between opposing selection resulting from these multiple, often conflicting functions. A widespread solution to the problem of needing to be conspicuous and cryptic at different times is to have bright display colors that can be revealed when needed but remain concealed at other times (Cooper and Greenberg, 1992). Display colors may be located on body regions that can be flashed (e.g., dewlap) or revealed through display postures (e.g., ventral or ventrolateral coloration). Color change is a special case of this strategy, allowing chameleons to exhibit conspicuous color patterns during social communication while remaining concealed from predators and prey at other times (Stuart-Fox and Moussalli, 2011).

Within the Chamaeleonidae, the ability to change color varies markedly—from limited changes in brightness (e.g., shades of brown) to remarkable changes in both color and pattern. Why is the ability to change color so much more developed in some species than in others? The answer to this question cannot be inferred from the function of coloration, as color has multiple purposes in chameleons. Although color change in chameleons is often associated with camouflage, it also functions in social communication and thermoregulation. Thus, the evolution of color change may be driven by selection for camouflage against different backgrounds, selection for signaling functions, or thermoregulatory requirements. These selective forces generate different, testable predictions, which are detailed elsewhere (Stuart-Fox and Moussalli, 2009, 2011).

The camouflage and social signaling hypotheses have been tested in dwarf chameleons (*Bradypodion* spp.). Stuart-Fox and Moussalli (2008) tested whether the capacity for color change is associated with particular habitat features or with higher variance in background color (relative to the animal's movement) as predicted by the camouflage hypothesis. They also tested a prediction of the social-signaling hypothesis that species showing the greatest color change should use sexual signals that are more conspicuous to conspecific receivers. To measure color change, color was measured in response to different stimuli, including another male or female and model predators (bird and snake). As the greatest color change occurred during male–male contests, color change was quantified as the difference between an individual's dominant coloration (submissive opponent) and his submissive coloration (dominant opponent). Color change was estimated for 21 lineages of dwarf chameleons (*Bradypodion* spp.). The phylogenetic comparative analysis showed that those with greatest capacity for color change had social signals that were more conspicuous to the chameleon visual system but did not occupy habitats with greater variance in background color. Although color change clearly serves a camouflage function in chameleons, results of this study suggest that the remarkable ability for chromatic change in dwarf chameleons may have evolved to facilitate social signaling rather than background matching. Ideally, this should be corroborated with additional comparative evidence for an association between degree of color change and other indicators of the strength of sexual selection, within and between species. Such indicators of strong sexual selection may include highly skewed reproductive success or mating systems that promote skewed reproductive success, and greater sexual dimorphism (Stuart-Fox and Moussalli, 2011).

6.3 SOCIAL AND REPRODUCTIVE BEHAVIOR

Mating System and Territoriality

Chameleons are polygamous. Males may mate with more than one female and females may mate with different males during the same or different ovarian cycles. Females are known to mate repeatedly with the same male during the relatively brief period of receptivity within an ovarian cycle (Tilbury, 2010). Whether a female will mate with more than one male within an ovarian cycle is likely to depend on male density (and therefore encounter rate) and the intensity of mate guarding or territoriality. If given the opportunity, however, females will mate with more than one male when receptive (Cuadrado and Loman, 1997).

The mating system has been studied in the most detail in the common chameleon, *Chamaeleo chamaeleon* (Cuadrado, 2001). In this species, males guard females, with the period of guarding ranging from 0 to 46 days (mean, 13.2 days). Males may sequentially guard up to eight females, although not all guarding episodes result in successful copulation or reproduction. Males cease guarding shortly after mating, when the female shows clear signs that she is no longer receptive. Spatial organization in this species is complex and varies depending on the nature of female home ranges. Some males defend stable nonoverlapping home ranges (i.e., territories) that incorporate the home range of one or more females when females have small, stable home ranges. Other males simply follow and defend an area around a guarded female if her movements are more erratic (Cuadrado, 2001).

Mate guarding appears to be common in chameleons. For example, male *Trioceros jacksonii* and *T. hoehnelii* actively defend an area around the female and stay with the female for up to several months (Toxopeus et al., 1988). However, the extent of mate guarding appears to vary among species, even within the same genus, with *Chamaeleo dilepis* appearing to be solitary, tolerating the presence of another individual only during mating (Brain, 1961; Toxopeus et al., 1988). In species of *Brookesia* and *Rhampholeon,* in which females are substantially larger than males, mate guarding may take the form of the male riding on the female's back. Tilbury (2010) has recorded male *Rhampholeon gorongosae* being carried by the female for up to 10 days.

The prevalence of territoriality, the consistent defense of area against conspecifics, is unclear in chameleons. Unambiguous territoriality has only been documented in *Chamaeleo namaquensis,* in which both sexes vigorously defend territories (Burrage, 1973). Male

Ch. chameleon may show defense of stable territories associated with mate guarding (Cuadrado, 2001; see above). *Calumma brevicorne* and *Ca. oshaughnessyi ambreensis* maintain small, discrete home ranges, often being faithful to a single roosting site on consecutive days, although the extent to which these species actively defend territories is unclear (Kauffmann et al., 1997). By contrast, *Ca. oshaughnessyi oshaughnessyi* have relatively large and overlapping home ranges and seldom return to the same roost site (Kauffmann et al., 1997). Absence of roost-site fidelity has been documented in several other species (Hebrard, 1980). However, roost-site fidelity provides little indication of territoriality. *Bradypodion pumilum,* for example, defend roosting sites from conspecifics (specific site defense; Stamps, 1977), but do not show defense of a consistent area surrounding them and, therefore, cannot be considered territorial (Burrage, 1973). *Ch. dilepis* show no indication of territoriality, often moving considerable distances and showing no indication of having a stable home range, although they vigorously repel any conspecifics that they encounter except potential mates (Brain, 1961). Studies of territoriality in arboreal species with three-dimensional home ranges are particularly challenging. Consequently, relatively little information is available on territoriality and its relationship to mating systems in chameleons.

Courtship, Copulation, and Sperm Storage

In most species studied to date, males persistently court both receptive and nonreceptive females (see following section on "Female Reproductive Status"). Males usually begin courtship from a distance with a lateral display, involving lateral compression, legs rigidly beneath the body and tail coiled (Cuadrado and Loman, 1999; Kelso and Verrell, 2002; Stuart-Fox and Whiting, 2005) (Fig. 6.1 in the color insert). This lateral display is similar to that used in aggressive encounters, and its primary purpose seems to be to maximize the signaler's apparent size, potentially allowing size assessment by the receiver. Courtship also includes approach with head movements, the precise nature of which varies among species. For instance, male *Chamaeleo calyptratus* exhibit both a slow head roll and rapid vibration (Kelso and Verrell, 2002). Courting male *Bradypodion* shake the head rapidly from side to side (personal observation). The speed, duration, and amplitude of the side-to-side head movements in chameleons may be analogous to the species-specific stereotyped head-bobs of iguanian lizards (Carpenter, 1977). As in iguanian lizards, the head movements are often displayed during both courtship and contests; although whether they differ consistently between these two contexts is unknown.

Following initial courtship displays, the male will attempt to approach the female and position himself behind her. He may then attempt to mount straight away, or, if the female does not accept mounting, the male may repeatedly nudge or rub her. For example, male *Chamaeleo calyptratus* courting nonreceptive females approached the female from behind, gave short bursts of vibrations and repeatedly nudged (head butted) and rubbed their chins on the female. This sequence of behaviors was primarily shown toward nonreceptive females and after unsuccessful attempts to mount (Kelso and Verrell, 2002). Similar persistent courtship and nudging behavior toward behaviorally rejecting females has been recorded in *Furcifer labordi* and in one case, the female changed back to passive coloration and allowed copulation (Karsten et al., 2009c). During copulation, receptive females generally remain relatively drably colored and passive when the male approaches, allowing him to mount, while nonreceptive females exhibit characteristic conspicuous coloration and courtship rejection behaviors (described in the section below on "Female Reproductive Status").

Successful mounting and copulation involves the male grasping the female's flank or dorsal keel with his front feet, coiling his tail around hers and inserting a hemipene into her cloaca (Fig. 6.2 in the color insert). Copulation lasts from less than a minute (*Chamaeleo chamaeleon;* Cuadrado and Loman, 1997) to up to an hour (*C. calyptratus;* Kelso and Verrell, 2002). Males and females adopt drab coloration during mating, the male visibly darkening from his previous bright courtship/display coloration. During mating, females of some species, such as *C. calyptratus,* exhibit short bursts of vibration (Kelso and Verrell, 2002) and males may repeatedly stroke the female's flank with his hindfoot (Brain, 1961; Tilbury, 2010). The female appears to initiate disengagement by moving (personal observation; Brain, 1961; Tilbury 2010).

Chameleons exhibit long-term sperm storage (weeks to months and across female ovarian cycles). The occurrence of sperm storage in chameleons is reviewed by Tilbury (2010). Multiple broods in the absence of mating between broods has been recorded in *Chamaeleo africanus, C. chameleon, Furcifer lateralis, Bradypodion pumilum,* and several species of *Trioceros* (Tilbury 2010, and references therein, and sperm storage is likely to be the rule rather than the exception in chameleons. However, the consequences of female sperm storage for male and female fitness have not been studied. The most obvious explanation for female sperm storage is to ensure fertilization when encounter rates with males are very low or uncertain. Alternatively, it may allow females with asynchronous/continuous breeding to progress rapidly from one ovarian cycle to the next without incurring the potentially high costs of copulation. A third possibility is that it facilitates sperm competition and cryptic female choice, whereby females may have some control over the use of ejaculates for fertilization when there are ejaculates from two or more males within her reproductive tract (Uller et al., 2010). Thus, sperm storage is likely to exert strong selection on both male and female mating behavior and the evolution of mating strategies in chameleons.

Female Reproductive Status

Female chameleons show characteristic colors and behavior to signal reproductive status, in particular to signal that they are gravid and nonreceptive. Although male courtship toward receptive females is often more frequent and intense (Cuadrado, 1998b; Kelso and Verrell, 2002), males also persistently court nonreceptive females (although this may not be the case in all species, e.g., *F. labordi*, Karsten et al., 2009c). In species in which males court nonreceptive females, they may presumably gain reproductive benefits due to female sperm storage. Females exhibit conspicuous color patterns and specific behaviors to signal nonreceptivity, presumably to reduce costs associated with male courtship and harassment (Cooper and Greenberg, 1992). Interestingly, in *Chamaeleo chamaeleon,* female movement rate (horizontal distance covered per observation period) was significantly higher once they had developed sexually receptive coloration, together with much higher rate of copulations and rejections. Cuadrado (1998b) hypothesized that the higher movement rate was perhaps as a response to the more intense courting.

Female coloration in relation to reproductive status has been studied in depth in a few species of *Chamaeleo*. In *C. calyptratus,* receptive females have faint blue spots, while nonreceptive females have bright orange markings that appear 24 hours after mating (Kelso and Verrell, 2002). Female common chameleons (*C. chamaeleon*) develop yellow spots when receptive, and shortly after copulation they exhibit dark body coloration with bluish and yellow spots, combined with aggressive rejection displays (Cuadrado, 1998b; and see below). Females that did not develop yellow spots during the breeding season skipped reproduction despite persistent courtship by males (Cuadrado, 1998b). In *Furcifer labordi,* female coloration appears to be associated with sexual maturity. Early in the breeding season, smaller, nonreceptive females exhibit a conspicuous yellow spot on the anterior flank and smaller faint yellow lateral spots on a green background. In larger, sexually mature females the anterior flank spot is bright red, the lateral spots are violet, and the background coloration is lighter green (Karsten et al., 2009c). These sexually mature females are potentially receptive but may either accept or reject male courtship and copulation. By contrast, coloration of *F. verrucosus* females appears to be associated with sexual receptivity rather than maturity. Females showing gray and light green-yellow allow nearly all courting males to attempt copulation, whereas brick-red females reject all male courtship attempts (Karsten et al., 2009c). Characteristic coloration of gravid females has also been documented for other species, such as yellow-red patches on the lower half of the body in *C. zeylanicus* (Singh et al., 1983) and black spots and yellow stripes in *C. africanus* (Bonetti, 1998, in Tilbury, 2010).

Nonreceptive females tend to be highly aggressive toward courting males, exhibiting an open mouth, often with hissing, swaying or vigorous rocking, and a laterally flattened body. These behaviors have been observed in a range of species, including dwarf chameleons (Stuart-Fox and Whiting, 2005), *Chamaeleo zeylanicus* (Singh et al., 1983), *C. chameleon* (Cuadrado, 1998b, 2000), *C. gracilis* (Bustard, 1967), and *C. calyptratus* (Kelso and Verrell, 2002). The aggressive rejection behavior is generally accompanied by characteristic color change involving dark or highly contrasting coloration (Fig. 6.3 in the color insert). However, this is not the case for all species, even those that are relatively closely related. For example, among potentially receptive females, behaviorally rejecting *Furcifer labordi* females show black background coloration with highly contrasting orange, purple, and red spots, whereas behaviorally rejecting *F. verrucosus* females do not change color (Karsten et al., 2009c). This difference may be related to differences in predation pressure on the two species. Alternatively, it may be associated with differences in the degree of male harassment, which may be greater in *F. labordi* because of more intense competition over mates as a result of more synchronous reproduction (Karsten et al., 2009c).

If the aggressive display is not a sufficient deterrent, females may chase and bite courting males. For instance, in *Bradypodion pumilum,* courting males were bitten by nonreceptive females in 28% of laboratory behavioral trials, and males that attempted mounting the female were more likely to be bitten (Stuart-Fox and Whiting, 2005). Female aggressive rejection appears to successfully deter males, as males reduced courtship with increasing intensity of female rejection and males were more likely to approach and court smaller females (Stuart-Fox and Whiting, 2005). Male *Chamaeleo calyptratus* adjust both the length and content of their courtship displays toward receptive versus nonreceptive females (Kelso and Verrell, 2002). Males courted nonreceptive females for significantly longer periods, even though they courted and mated with receptive females much more frequently than with nonreceptive females (Kelso and Verrell, 2002).

There is little evidence of active female mate choice in chameleons, with receptive females of many species appearing to accept all male advances. However, females of some species may exhibit mate choice by rejecting or accepting males when receptive, as appears to be the case in *Furcifer labordi* (Karsten et al., 2009c). In *Chamaeleo chameleon,* the female initiates long walks when courted by a male. During the walks, the pair is exposed to interference from other males and is more exposed to predation. Cuadrado and Loman (1997) hypothesized that given the presumed cost of this behavior, it may benefit females by allowing indirect female mate choice or at least mate assessment.

Male Aggressive Behavior

Male chameleons engage in ritualized aggressive displays, which may escalate to physical combat in some species and may sometimes result in injury. The prevalence and intensity of male aggressive behavior in chameleons suggests that male–male competition is likely to be important in gaining access to receptive females and preventing other males from doing so.

Ritualized aggressive displays involve characteristic color change. For example, on encountering another male, male *Chamaeleo gracilis* from Sierra Leone initially become paler and more uniform in coloration (blotches disappearing) but with intensified spots (Bustard, 1967). Courting male *Furcifer labordi* and *F. verrucosus* increase the contrast of their coloration, and in the latter species, males developed bright green and blue over the lower half of their bodies (Karsten et al., 2009c). In many species of dwarf chameleon (*Bradypodion* spp.), coloration intensifies dramatically, resulting in high-contrast color combinations (Stuart-Fox et al., 2007). For example, *Bradypodion transvaalense* males become orange and black. Among *Bradypodion* spp., species that have greater capacity for color change have male display colors that contrast more with the background vegetation and comprise more contrasting color combinations (to the chameleon visual system) as compared with species with less capacity for color change (Stuart-Fox and Moussalli, 2008). Some of these color combinations are likely to appear more conspicuous to the chameleon visual system than to humans. The display coloration of *B. damaranum* includes both green and ultraviolet-blue-green, which contrast highly in the chameleon visual system but appear similar to humans (Stuart-Fox et al., 2007). While display coloration varies substantially among species, submissive coloration generally comprises drab grays and browns, often darker and drabber than cryptic coloration.

Ritualized aggressive behavior in chameleons invariably involves lateral displays comprising lateral compression, extension of the legs vertically beneath the body, and extension of the gular region to appear as large as possible (Fig. 6.1 in the color insert). In some species, such as *Bradypodion,* this posture is accompanied by horizontal extension and/or coiling of the tail, which may add to the appearance of large size. Many species accompany this posture with head shaking. However, in *Furcifer labordi* and *F. verrucosus,* males used head movements only in a courtship context (Karsten et al., 2009c).

Following approach and display, one individual may assume submissive coloration. Alternatively, if the contestants are closely matched, the contest may escalate to lunging and biting. In extreme cases, chameleons may lock their jaws together and wrestle, each attempting to push its opponent along the branch in a contest of strength. Male *Trioceros jacksonii* lock their three horns together and push each other along the branch in an obvious contest of strength (personal observation) (Fig. 6.4 in the color insert). They also violently twist their horns into each other in a corkscrew fashion and the male with longer horns can inflict damage by piercing the tissue of his rival with the tips of his horns (M. Whiting, personal communication). Whether rostral appendages are used in male–male combat appears to vary among species. Species with keratinized appendages may be more likely to use them in combat rather than courtship, whereas species with flat, fleshy appendages, such as *Furcifer labordi,* may use them only during courtship (Karsten et al., 2009c). Keratinized rostral appendages and bites can cause surface wounds, but more serious injury from male contests is likely to be rare in most species. Escalated fights have been observed in the field in *Bradypodion pumilum,* with males locking jaws and falling from perches to the ground in prolonged wrestling matches (Burrage, 1973). The contest may continue for extended periods (many minutes and potentially up to an hour) until one male retreats and adopts submissive coloration. Escalated physical fights may be rare or absent in some species, with contests confined to ritualized displays.

The intensity of male aggression is likely to vary within and among species. Within species, the intensity of male–male competition is likely to be more intense during the breeding season, particularly in seasonally reproducing species (Singh et al., 1983). Intrasexual selection may also vary among populations depending on density and/or habitat, with important consequences for the evolution of male ornamentation and behavior. For example, closed-habitat ecomorphs of *Bradypodion pumilum* have a central pink flank patch and rugose casques, and the size of these traits predict fighting ability (Stuart-Fox et al., 2006b). By contrast, the open-habitat ecomorph is smaller and less ornamented but has a stronger bite force for its size (Measey et al., 2009). The intensity of male–male aggression can also differ among closely related species. For example, *F. labordi* exhibits much more male–male aggression than *F. verrucosus,* which may be related to competition over mates, as reproduction in the former is much more synchronous (Karsten et al., 2009c). Variation in the intensity of intrasexual selection associated with ecology and life history is likely to be important in explaining the morphological diversity—particularly in coloration and ornamentation—apparent in chameleons.

6.4 SEXUAL DIMORPHISM: BODY SIZE AND ORNAMENTATION

Sexual dimorphism in body size (SSD) varies from female-biased to male-biased. In *Rhampholeon* and *Brookesia* for example, females are larger than males, whereas in *Chamaeleo, Calumma,* and *Furcifer,* males tend to be larger than females (Nečas, 2004). In some genera, such as *Bradypodion,* both forms of dimorphism are found, although female-biased SSD predominates (Stuart-Fox, 2009). SSD is likely to reflect a complex combination of selective forces, including sexual and natural selection on both male and female body size. Natural selection is likely to act directly on both male and female body size. For example, both male and female *Bradypodion* spp. are smaller in habitats with a higher density of perches, such as grasslands and heaths with short dense shrubs. Males, but not females, are also relatively larger in forested habitats (Stuart-Fox and Moussalli, 2007). Sexual selection on male body size appears to vary among species, with larger size not necessarily being advantageous. For example, in *Bradypodion pumilum,* larger males are not necessarily likely to win contests (Stuart-Fox et al., 2006b). In *Ch. chamaeleon,* success rate per courtship attempt was no greater for larger males, although larger males put more effort into courting and had higher overall reproductive success (Cuadrado and Loman, 1997; Cuadrado, 2001). Selection for fecundity is likely to favor larger female body size, since larger females tend to bear more offspring (Burrage, 1973; Lin and Nelson, 1981; Cuadrado, 1998a), although reproductive effort also decreases with size and age in several species (Lin and Nelson, 1981; Cuadrado, 2001). The variation in natural and sexual selection on male and female body size is likely to account for the great diversity of sexual dimorphism apparent in the Chamaeleonidae. In this regard, chameleons are similar to most other lizard families (e.g., Iguanidae, Agamidae, Lacertidae, Teiidae, Scindidae, Gekkonidae), in which sexual size dimorphism varies from female-biased to male-biased, depending on demographic and ecological factors (reviewed in Fitch, 1981).

In contrast to body size, which shows various forms of sexual dimorphism across the chameleons, males are either similar to females or more ornamented. Ornaments include rugose cranial casques, occipital lobes, a wide range of keratinized or fleshy rostral appendages, a range of gular ornamentation (lobes, flaps, and spines) and enlarged scales on the flank (detailed in Nečas, 2001; Tilbury, 2010). Even in species or populations with little ornamentation, males tend to have relatively larger heads, which is likely to result from intrasexual selection, as males engage in physical combat (described above) and head size is related to bite force (Measey et al., 2009). Male ornaments are used in male–male contests both directly (e.g., the rostral horns of *Trioceros jacksonii*) and indirectly via emphasis during lateral displays and head movements.

6.5 ANTIPREDATOR BEHAVIOR

Chameleons' primary defense against predators is camouflage. Chameleons can change both their colors and their patterns to varying extents (depending on the species) in order to match their backgrounds or perhaps disrupt the body outline. Many arboreal chameleons are able to exhibit uniform or mottled green hues to match moss or leaves as well as brown and gray hues to match twigs and vines. Chameleons that are mostly terrestrial or adapted to environments with little vegetation (e.g., *Chamaeleo namaquensis*) may have a more restricted color repertoire, mostly consisting of changes in brightness from cream, gray, brown, and black. Many chameleons also adopt a light and dark botched color pattern, associated with antipredator behaviors. For example, *Brookesia superciliaris,* adopting the freeze and roll behavior (see below), show blotched coloration on the exposed upper flank, which according to Raxworthy (1991, p. 22), "disrupts the body profile against the dead leaves." However, there have been no experimental demonstrations that blotched coloration in chameleons is a form of disruptive camouflage, which hinders recognition of the body outline by creating the appearance of false edges and boundaries (Stevens and Merilaita, 2009), rather than background matching. Some species may exhibit specific patterns that aid camouflage. For instance, grassland species often show horizontal stripes on the flank and underside, resembling the vertical stripe pattern of grass when the chameleon is holding onto a vertical grass stalk (Tilbury, 2010).

As chameleons have exceptional vision, they may often detect a threat before they are themselves detected. In addition to camouflage, many arboreal chameleons flatten themselves laterally and flip to the other side of the branch or twig to which they are clinging. During experiments in which a model snake (boomslang [*Dispholidus typus*]) and a stuffed fiscal shrike (*Lanias collaris*) were presented to chameleons (Stuart-Fox et al., 2006a, 2008), my colleagues and I were struck by their ability to accurately maneuver so that the twig remained between themselves and the line of sight of the predators. This behavior is widespread among cryptic, arboreal iguanian lizards and geckos.

The primary predators of chameleons are arboreal snakes and birds. However, chameleons are also preyed upon by mammals, particularly mongooses, larger reptiles and amphibians, and some invertebrates such as large mantids and spiders (see Nečas, 2001; Tilbury 2010, and Chapter 5 for a more detailed list of chameleon predators). These predators differ in their foraging tactics and sensory capabilities. For example, birds rely exclusively on visual cues for prey detection (Kassarov, 2003), whereas most snakes use olfactory cues in addition to visual cues (Schwenk, 1995). Birds have greater visual acuity (the spatial frequency resolvable at maximum contrast), which is due to greater cone density in the retina than that of snakes (Osorio et al., 1999). Birds also have superior color vision, as they are tetrachromats, having four types of visual pigment (Hart, 2001), rather than the three types of visual pigments of most snakes studied to date (Sillman et al., 1997, 1999, 2001).

Stuart-Fox and Moussalli (2009) showed that among 21 populations of dwarf chameleon (*Bradypodion* spp.), including all currently recognized species and several morphologically and genetically distinct lineages (Stuart-Fox et al., 2007; Stuart-Fox and Moussalli, 2008), 13 differed in the camouflage response to model bird and snake predators. Chameleons showed consistent behavioral responses to the two predators, consisting of lateral compression, flipping to the opposite side of the branch and occasionally dropping from the perch (see below). The frequency of these behaviors did not differ toward the two predators (Stuart-Fox et al., 2006a), but in all cases in which chameleons showed different color responses to the two predators, they showed greater background matching (lower contrast against the background) in response to the bird than the snake. Although they showed closer background matching in response to birds, they appear more camouflaged (i.e., less chromatically contrasting against the background) to snakes because snakes have poorer color discrimination. These results raise the possibility that chameleons fine-tune their color response to maximize camouflage in response to different predators (see Stuart-Fox et al., 2006a, 2008; Stuart-Fox and Moussalli, 2009, for discussion of this phenomenon).

Chameleons may also employ a form of movement-based camouflage, which may reduce the probability of detection by either predators or prey. Chameleons often rhythmically rock backward and forward as they walk—the characteristic "jerky walk." A common explanation is that they are imitating a swaying leaf or vegetation moving in the breeze; however, this has never been demonstrated experimentally. The behavior is widespread in highly cryptic, generally slow-moving, ambush predators, notably chameleons and some snakes (Fleishman, 1985) and mantids (stick insects). An alternative potential explanation is that chameleons rock back and forth while they walk to create parallax, enabling depth perception in both eyes simultaneously. This explanation, however, is unlikely because rocking behavior is not seen in the pygmy genera but is restricted to the arboreal genera (Tilbury, personal communication). Furthermore, chameleons use accommodation cues (changes in optical power of the eye to maintain focus with varying distance) to judge distance (Harkness, 1977). This allows them to accurately judge distance with one eye, without the use of parallax.

At night, chameleons become pale (cream to almost white) and very easily visible in flashlight. This reflects the resting state of the melanophores with melanosomes concentrated rather than dispersed. Photoreceptors in the skin of chameleons respond to light, triggering dispersion of melanosomes. Thus, chameleons darken rapidly in response to light, even when remaining with their eyes closed. Many chameleon biologists have observed that when a chameleon is captured at night, the side on which the flashlight was shone becomes dark, while the opposite side of the chameleon remains pale. *Brookesia* and *Rhampholeon* appear to be exceptions to this generalization, retaining their brown coloration to some degree at night. Raxworthy (1991) has proposed that this may have a cryptic function even when the chameleons roost among green leaves, since most nocturnal predators are color-blind and the brown and green may match in luminance rather than color. However, *Brookesia* also have much more limited capacity for color change, which may equally explain their relatively lesser degree of pallor when roosting.

Because of their pallor, chameleons stand out against the background at night and may therefore be vulnerable to predators. Perhaps as a result, chameleons perch in places that may be difficult for predators to reach, such as on the ends of vines and at the tips of thin twigs and grass stems. These perches may be just strong enough to support the weight of a chameleon but not a nocturnal snake or mammal predator. If the twig or vine moves excessively, disturbing the chameleon, it may let go of the perch and drop to the ground, where it either remains perfectly still or writhes until is it buried out of site among dead leaves (Tilbury, 2010). Many arboreal species accompany this "dropping" behavior with a "hopping" motion as they initiate their fall, perhaps to aid the probability of escape (Tilbury, personal communication).

The behavior of dropping from perches may vary depending on species and degree of threat. In *B. transvaalense,* my colleagues and I observed it in less than 10% of trials in which we presented chameleons with model predators (10 of 116 trials = 8.6%; Stuart-Fox et al., 2006a). However, falling from perches is common in *Chamaeleo chamaeleon,* having been observed in the majority (>60%) of simulated predator attacks (approach by humans), when they were perched in open bushes in which they had a higher probability of detection. When perched in denser bushes, "free falling" was observed less frequently overall and more commonly in hatchlings than in juveniles or adults (Cuadrado et al., 2001). Such dropping or death-feigning behavior may also be shown by juveniles or subadults in response to a threat from a much larger conspecific (Brain, 1961). Thus, chameleons appear to alter their antipredator behaviors based on probability of detection and age class, which may reflect vulnerability to predators or threat from a conspecific.

Chameleons sometimes also appear to show death-feigning behavior, remaining curled up and perfectly still and appearing to be dead when handled. Raxworthy (1991) described seven types of antipredator behavior, including what appears to be death-feigning, in which the chameleon would freeze in an upright stiff posture when handled. Raxworthy (1991) also described behaviors that appear to be leaf mimicry. These were freezing and rolling, in which the chameleon would fold the legs under the belly, roll to one side, and remain motionless and dorsal flattening, which gave the chameleon "a very flattened leaf-like appearance."

When chameleons have been detected by a predator or are cornered or stressed, they may exhibit a range of secondary defenses against potential predators. These include threat displays, vibration, and "spine-thrusting" in *Brookesia*. Spine-thrusting entails vigorous thrusting out of dorsolateral spines during lateral convulsions and is observed only in species with dorsolateral spines (Raxworthy, 1991). The threat displays include lateral compression, swaying, open mouth, and distended throat. Open-mouthed threat displays may be accompanied by a hissing sound (Cuadrado et al., 2001). These displays often reveal brightly colored gular interstitial skin, the color of which varies greatly among species and even within species. For instance, among the dwarf chameleons (*Bradypodion* spp.), interstitial gular skin may be white, red, orange, purple or black, and bright orange or black within *B. occidentale* (personal observation). Although the behavioral postures are similar to threat displays during male contests, males do not show the same conspicuous display colors during contests and under threat-induced stress (personal observation). The latter tend to be highly contrasting light and dark blotches rather than the bright hues often seen during male courtship displays and contests.

Chameleon coloration and behavior is diverse, with exceptions to almost every generalization that can be made. This is despite the fact that coloration and behavior in most contexts has been studied in very few species. Color lability in chameleons is associated with complex social and antipredator behaviors. Coloration, ornamentation, and associated social behaviors are likely to vary in relation to ecology and life history, which are diverse in the Chamaeleonidae. In particular, factors such as seasonality and synchrony of reproduction, spatial organization and density, and habitat-associated predation pressure are all likely to influence the intensity of both intersexual and intrasexual selection, with important consequences for morphological and behavioral adaptations.

Another factor that may influence the evolution of coloration, ornamentation, and behavior in chameleons is the number of sympatric chameleon species. Discussion of the function of coloration and behavior in this chapter has been limited to intraspecific interactions, because experiments specifically testing a species-recognition role for visual signals in chameleons are lacking. However, interspecific competition could also potentially drive the evolution of signal diversity, as appears to be case for the dewlaps of *Anolis* lizards (Ord and Stamps, 2009, and references therein). It would be interesting to test whether the degree of difference in visual signals (coloration, ornamentation, and behavior) among closely related species is positively related to the number of sympatric species (discussed in Chapter 5). Experiments testing whether individuals respond more strongly to conspecific or heterospecific signals would also be informative.

Observational field studies of chameleon behavior are particularly challenging because of the difficulty of locating these exceptionally well-camouflaged animals. Telemetry can be used for larger species but has so far not been possible for smaller species. This makes it difficult to study the ecological context of behavior, which is important for understanding its diversity and evolution. However, chameleons are well suited to laboratory and field manipulative behavioral experiments, as evidenced by many of the studies cited in this chapter and extensive laboratory research on reproduction and thermoregulation in some species (e.g., *Chamaeleo calyptratus*) (Andrews, 2007, 2008; Andrews et al., 2008; Andrews and Karsten, 2010). Consequently, there is much scope for studying the functional significance of visual signals, particularly in relation to sexual selection. Specifically, given the substantial life-history variation among chameleons (e.g., Karsten et al., 2008), they may be excellent models for studying life-history effects on the strength of sexual selection. As chameleons have the most developed capacity for color change among terrestrial vertebrates, they are also ideally suited to understanding adaptive, dynamic camouflage and the visual features important for effective camouflage (see Stuart-Fox and Moussalli, 2011).

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List of 196 Described Chameleon Species as of 2012, with the Broad Region in Which They Occur

Species	Region
Archaius tigris (Kuhl, 1820)	Seychelles
Bradypodion atromontanum Branch, Tolley, and Tilbury, 2006	Southern Africa
Bradypodion caeruleogula Raw and Brothers, 2008	Southern Africa
Bradypodion caffer (Boettger, 1889)	Southern Africa
Bradypodion damaranum (Boulenger, 1887)	Southern Africa
Bradypodion dracomontanum Raw, 1976	Southern Africa
Bradypodion gutturale (Smith, 1849)	Southern Africa
Bradypodion kentanicum (Hewitt, 1935)	Southern Africa
Bradypodion melanocephalum (Gray, 1865)	Southern Africa
Bradypodion nemorale Raw, 1978	Southern Africa
Bradypodion ngomeense Tilbury and Tolley, 2009	Southern Africa
Bradypodion occidentale (Hewitt, 1935)	Southern Africa
Bradypodion pumilum (Gmelin, 1789)	Southern Africa
Bradypodion setaroi Raw, 1976	Southern Africa
Bradypodion taeniabronchum (Smith, 1831)	Southern Africa
Bradypodion thamnobates Raw, 1976	Southern Africa
Bradypodion transvaalense (Fitzsimons, 1930)	Southern Africa
Bradypodion ventrale (Gray, 1845)	Southern Africa
Brookesia ambreensis Raxworthy and Nussbaum, 1995	Madagascar
Brookesia antakarana Raxworthy and Nussbaum, 1995	Madagascar
Brookesia bekolosy Raxworthy and Nussbaum, 1995	Madagascar
Brookesia betschi Brygoo, Blanc, and Domergue, 1974	Madagascar
Brookesia bonsi Ramanantsoa, 1980	Madagascar
Brookesia brygooi Raxworthy and Nussbaum, 1995	Madagascar
Brookesia brunoi Crottini, Miralles, Glaw, Harris, Lima, and Vences, 2012	Madagascar
Brookesia confidens Glaw, Köhler, Townsend, and Vences, 2012	Madagascar
Brookesia decaryi Angel, 1939	Madagascar
Brookesia dentata Mocquard, 1900	Madagascar
Brookesia desperata Glaw, Köhler, Townsend, and Vences, 2012	Madagascar

(Continued)

Species	Region
Brookesia ebenaui (Boettger, 1880)	Madagascar
Brookesia exarmata Schimmenti and Jesu, 1996	Madagascar
Brookesia griveaudi Brygoo, Blanc, and Domergue, 1974	Madagascar
Brookesia karchei Brygoo, Blanc, and Domergue, 1970	Madagascar
Brookesia lambertoni Brygoo and Domergue, 1970	Madagascar
Brookesia lineata Raxworthy and Nussbaum, 1995	Madagascar
Brookesia lolontany Raxworthy and Nussbaum, 1995	Madagascar
Brookesia micra , 2012	Madagascar
Brookesia minima Boettger, 1893	Madagascar
Brookesia nasus Boulenger, 1887	Madagascar
Brookesia perarmata (Angel, 1933)	Madagascar
Brookesia peyrierasi Brygoo and Domergue, 1974	Madagascar
Brookesia ramanantsoai Brygoo and Domergue, 1975	Madagascar
Brookesia stumpffi Boettger, 1894	Madagascar
Brookesia superciliaris (Kuhl, 1820)	Madagascar
Brookesia therezieni Brygoo and Domergue, 1970	Madagascar
Brookesia thieli Brygoo and Domergue, 1969	Madagascar
Brookesia tristis Glaw, Köhler, Townsend, and Vences, 2012	Madagascar
Brookesia tuberculata Mocquard, 1894	Madagascar
Brookesia vadoni Brygoo and Domergue, 1968	Madagascar
Brookesia valerieae Raxworthy, 1991	Madagascar
Calumma amber Raxworthy and Nussbaum, 2006	Madagascar
Calumma ambreense (Ramanantsoa, 1974)	Madagascar
Calumma andringitraense (Brygoo, Blanc, and Domergue, 1972)	Madagascar
Calumma boettgeri (Boulenger, 1888)	Madagascar
Calumma brevicorne (Günther, 1879)	Madagascar
Calumma capuroni (Brygoo, Blanc, and Domergue, 1972)	Madagascar
Calumma crypticum Raxworthy and Nussbaum, 2006	Madagascar
Calumma cucullatum (Gray, 1831)	Madagascar
Calumma fallax (Mocquard, 1900)	Madagascar
Calumma furcifer (Vaillant and Grandidier, 1880)	Madagascar
Calumma gallus (Günther, 1877)	Madagascar
Calumma gastrotaenia (Boulenger, 1888)	Madagascar
Calumma glawi Böhme, 1997	Madagascar
Calumma globifer (Günther, 1879)	Madagascar
Calumma guibei (Hillenius, 1959)	Madagascar
Calumma guillaumeti (Brygoo, Blanc, and Domergue, 1974)	Madagascar
Calumma hafahafa Raxworthy and Nussbaum, 2006	Madagascar
Calumma hilleniusi (Brygoo, Blanc, and Domergue, 1973)	Madagascar
Calumma jejy Raxworthy and Nussbaum, 2006	Madagascar
Calumma linota (Müller, 1924)	Madagascar
Calumma malthe (Günther, 1879)	Madagascar
Calumma marojezense (Brygoo, Blanc, and Domergue, 1970)	Madagascar
Calumma nasutum (Duméril and Bibron, 1836)	Madagascar
Calumma oshaughnessyi (Günther, 1881)	Madagascar
Calumma parsonii (Cuvier, 1824)	Madagascar
Calumma peltierorum Raxworthy and Nussbaum, 2006	Madagascar
Calumma peyrierasi (Brygoo, Blanc, and Domergue, 1974)	Madagascar

Species	Region
Calumma tarzan Gehring, Pabijan, Ratsoavina, Köhler, Vences, and Glaw, 2010	Madagascar
Calumma tsaratananense (Brygoo and Domergue, 1967)	Madagascar
Calumma tsycorne Raxworthy and Nussbaum, 2006	Madagascar
Calumma vatosoa Andreone, Mattioli, Jesu, and Randrianirina, 2001	Madagascar
Calumma vencesi Andreone, Mattioli, Jesu, and Randrianirina, 2001	Madagascar
Calumma vohibola Gehring, Ratsoavina, Vences, and Glaw, 2011	Madagascar
Chamaeleo africanus Laurenti, 1768	West-central Africa, North Africa
Chamaeleo anchietae Bocage, 1872	West-central Africa
Chamaeleo arabicus (Matschie, 1893)	Arabia
Chamaeleo calcaricarens Böhme, 1985	North Africa
Chamaeleo calyptratus Duméril & Duméril, 1851	Arabia
Chamaeleo chamaeleon (Linnaeus, 1758)	Europe, North Africa, Arabia
Chamaeleo dilepis Leach, 1819	Pan Africa
Chamaeleo gracilis Hallowell, 1842	East Africa, West-central Africa
Chamaeleo laevigatus (Gray, 1863)	East Africa
Chamaeleo monachus (Gray, 1865)	Socotra Island
Chamaeleo namaquensis Smith, 1831	Southern Africa
Chamaeleo necasi Ullenbruch, Krause, Böhme, 2007	West-central Africa
Chamaeleo senegalensis Daudin, 1802	West-central Africa
Chamaeleo zeylanicus Laurenti, 1768	Asia
Furcifer angeli (Brygoo and Domergue, 1968)	Madagascar
Furcifer antimena (Grandidier, 1872)	Madagascar
Furcifer balteatus (Duméril and Bibron, 1851)	Madagascar
Furcifer belalandaensis (Brygoo and Domergue, 1970)	Madagascar
Furcifer bifidus (Brongniart, 1800)	Madagascar
Furcifer campani (Grandidier, 1872)	Madagascar
Furcifer cephalolepis (Günther, 1880)	Comoros
Furcifer labordi (Grandidier, 1872)	Madagascar
Furcifer lateralis (Gray, 1831)	Madagascar
Furcifer major (Brygoo, 1971)	Madagascar
Furcifer minor (Günther, 1879)	Madagascar
Furcifer nicosiai Jesu, Mattioli, and Schimmenti, 1999	Madagascar
Furcifer oustaleti (Mocquard, 1894)	Madagascar
Furcifer pardalis (Cuvier, 1829)	Madagascar
Furcifer petteri (Brygoo and Domergue, 1966)	Madagascar
Furcifer polleni (Peters, 1874)	Comoros
Furcifer rhinoceratus (Boettger, 1893)	Madagascar
Furcifer timoni Glaw, Köhler, and Vences, 2009	Madagascar
Furcifer tuzetae (Brygoo, Bourgat, and Domergue, 1972)	Madagascar
Furcifer verrucosus (Cuvier, 1829)	Madagascar
Furcifer viridis Florio, Ingram, Rakotondravony, Louis, and Raxworthy, 2012	Madagascar

(Continued)

Species	Region
Furcifer willsii (Günther, 1890)	Madagascar
Kinyongia adolfifriderici (Sternfeld, 1912)	East Africa
Kinyongia asheorum Necas, Sindaco, Korený, Kopecná, Malonza, and Modrý, 2009	East Africa
Kinyongia boehmei (Lutzmann and Necas, 2002)	East Africa
Kinyongia carpenteri (Parker, 1929)	East Africa
Kinyongia excubitor (Barbour, 1911)	East Africa
Kinyongia fischeri (Reichenow, 1887)	East Africa
Kinyongia gyrolepis Greenbaum, Tolley, Joma, and Kusamba, 2012	East Africa
Kinyongia magomberae Menegon, Tolley, Jones, Rovero, Marshall, and Tilbury, 2009	East Africa
Kinyongia matschiei (Werner, 1895)	East Africa
Kinyongia multituberculata (Nieden, 1913)	East Africa
Kinyongia oxyrhina (Klaver and Böhme, 1988)	East Africa
Kinyongia tavetana (Steindachner, 1891)	East Africa
Kinyongia tenuis (Matschie, 1892)	East Africa
Kinyongia uluguruensis (Loveridge, 1957)	East Africa
Kinyongia uthmoelleri (Müller, 1938)	East Africa
Kinyongia vanheygeni Necas, 2009	East Africa
Kinyongia vosseleri (Nieden, 1913)	East Africa
Kinyongia xenorhina (Boulenger, 1901)	East Africa
Nadzikambia baylissi Branch and Tolley, 2010	East Africa
Nadzikambia mlanjensis (Broadley, 1965)	East Africa
Rhampholeon acuminatus Mariaux and Tilbury, 2006	East Africa
Rhampholeon beraduccii Mariaux and Tilbury, 2006	East Africa
Rhampholeon boulengeri Steindachner, 1911	East Africa
Rhampholeon chapmanorum Tilbury, 1992	East Africa
Rhampholeon gorongosae Broadley, 1971	Southern Africa
Rhampholeon marshalli Boulenger, 1906	Southern Africa
Rhampholeon moyeri Menegon, Salvidio, and Tilbury, 2002	East Africa
Rhampholeon nchisiensis (Loveridge, 1953)	East Africa
Rhampholeon platyceps Günther, 1893	East Africa
Rhampholeon spectrum (Buchholz, 1874)	West-central Africa
Rhampholeon spinosus (Matschie, 1892)	East Africa
Rhampholeon temporalis (Matschie, 1892)	East Africa
Rhampholeon uluguruensis Tilbury and Emmrich, 1996	East Africa
Rhampholeon viridis Mariaux and Tilbury, 2006	East Africa
Rieppeleon brachyurus (Günther, 1893)	East Africa
Rieppeleon brevicaudatus (Matschie, 1892)	East Africa
Rieppeleon kerstenii (Peters, 1868)	East Africa, North Africa
Trioceros affinis (Rüppel, 1845)	North Africa
Trioceros balebicornutus (Tilbury, 1998)	North Africa
Trioceros bitaeniatus (Fischer, 1884)	East Africa
Trioceros camerunensis (Müller, 1909)	West-central Africa
Trioceros chapini (De Witte, 1964)	West-central Africa
Trioceros conirostratus (Tilbury, 1998)	East Africa

Species	Region
Trioceros cristatus (Stutchbury, 1837)	West-central Africa
Trioceros deremensis (Matschie, 1892)	East Africa
Trioceros ellioti (Günther, 1895)	East Africa
Trioceros feae (Boulenger, 1906)	West-central Africa
Trioceros fuelleborni (Tornier, 1900)	East Africa
Trioceros goetzei (Tornier, 1899)	East Africa
Trioceros hanangensis Krause & Böhme, 2010	East Africa
Trioceros harennae (Largen, 1995)	North Africa
Trioceros hoehnelii (Steindachner, 1891)	East Africa
Trioceros incornutus (Loveridge, 1932)	East Africa
Trioceros ituriensis (Schmidt, 1919)	East Africa, Central Africa
Trioceros jacksonii (Boulenger, 1896)	East Africa
Trioceros johnstoni (Boulenger, 1901)	East Africa, Central Africa
Trioceros kinangopensis Stipala, Lutzmann, Malonza, Wilkinson, Godley, Nyamache, and Evans, 2012	East Africa
Trioceros kinetensis (Schmidt, 1943)	East Africa
Trioceros laterispinis (Loveridge, 1932)	East Africa
Trioceros marsabitensis (Tilbury, 1991)	East Africa
Trioceros melleri (Gray, 1865)	East Africa
Trioceros montium (Buchholz, 1874)	West-central Africa
Trioceros narraioca (Necas, Modry, and Slapeta, 2003)	East Africa
Trioceros ntunte (Necas, Modry, and Slapeta, 2005)	East Africa
Trioceros nyirit Stipala, Lutzmann, Malonza, Wilkinson, Godley, Nyamache, and Evans, 2011	East Africa
Trioceros oweni (Gray, 1831)	West-central Africa
Trioceros perreti (Klaver and Böhme, 1992)	West-central Africa
Trioceros pfefferi (Tornier, 1900)	West-central Africa
Trioceros quadricornis (Tornier, 1899)	West-central Africa
Trioceros rudis (Boulenger, 1906)	East Africa
Trioceros schoutedeni (Laurent, 1952)	East Africa
Trioceros schubotzi (Sternfeld, 1912)	East Africa
Trioceros serratus (Mertens, 1922)	West-central Africa
Trioceros sternfeldi (Rand, 1963)	East Africa
Trioceros tempeli (Tornier, 1900)	East Africa
Trioceros werneri (tornier, 1899)	East Africa
Trioceros wiedersheimi (Nieden, 1910)	West-central Africa

SOURCE: Glaw and Vences, 2007; Tolley and Burger, 2007; Tilbury, 2010; Uetz, 2012.

FIGURE 6.1. Male *Bradypodion transvaalense* in typical display posture with throat extended, body laterally compressed, one arm held rigidly with elbow bent at right angles, and tail coiled.

FIGURE 6.2. Copulation in *Trioceros jacksonii,* showing sexual dimorphism in ornamentation.

FIGURE 6.3. Female aggressive coloration and posture in *Bradypodion melanocephalum*. Females reject unwanted male courtship attempts by displaying highly contrasting coloration, gaping, and rocking rapidly from side to side. Unreceptive females will also chase and bite males that approach.

FIGURE 6.4. Male–male combat in *Trioceros jacksonii* involves locking together of the three rostral horns. Males often lock horns and push each other along a branch in a contest of strength. They may also violently twist their horns in corkscrew fashion, and the male with longer horns can inflict damage by piercing the tissue of his rival with the tips of his horns.

ABBREVIATIONS

asl	above sea level
cf.	compare
cm	centimeters
e.g.	for example
i.e.	that is
km	kilometers
m	meters
mm	millimeters
Mya	million years ago
Myr	million years
Ri.	Rieppeleon
Rh.	Rhampholeon
sp.	species (singular)
spp.	species (plural)

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