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

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Ecology and Life History of Chameleons

G. JOHN MEASEY, ACHILLE RASELIMANANA, and ANTHONY HERREL

Chameleons have been relatively neglected in terms of their ecology, perhaps in part, because of their cryptic nature. As detailed in this review, the majority of studies on chameleons *in situ* have been conducted relatively recently (during the past 15 years), and most of these center on the extremely diverse island of Madagascar. Although there are some data on chameleon ecology in southern Africa and Europe, mainland African chameleons represent a relatively overlooked group of lizards.

Chameleons display a unique set of morphological characteristics that set them apart from all other lizards, including gripping feet, independently moving eyes, a ballistic tongue and prehensile tail (Chapter 2), and it may be expected that these unique traits would also set them apart ecologically. While ecological data on some chameleons suggests that they adhere to many lizard generalities, the exceptions show that there is far more to learn about the ecology of chameleons.

Although some arboreal lizards are arranged into many specialist guilds (e.g., *Anolis* lizards), only two morphologically and taxonomically distinct guilds are recognized for chameleons: arboreal and ground-dwelling forms. Their cryptic behavior and camouflage continues to complicate their study, but new information on life-history traits is opening up insights into niche partitioning. Chameleon life-history traits exhibit many of their most unusual features. Like other lizards, chameleons lay eggs with late stage embryos and have viviparity in extremes of altitude and latitude. Unlike any other lizards, some chameleons lay eggs with early gastrula, which develop slowly and can undergo diapause in order for hatchlings to emerge during optimal seasons. Unlike any other tetrapod, one chameleon species (*Furcifer labordi*) is known to have an extreme annual life cycle, in which the population exists as developing eggs for 8 to 9 months of the year. However, like other lizards, many chameleons survive less favorable seasons by seeking out dry and stable conditions in which to aestivate.

Chameleons are lizards that do not conform to either sit-and-wait or active foraging strategies. Instead, it has been proposed that they have an unusual intermediary behavior, termed “cruise foraging.” Most chameleons studied appear to be generalist opportunists, increasing their range of food sizes as they get larger, so that the largest include both vertebrate and invertebrate food items in their diet. Like other lizards, chameleons (especially xeric-adapted species) regularly ingest plant matter, presumably in order to supplement their water intake.

5.1 HABITAT

Existing data suggest that chameleon assemblages are divided according to habitat (Fig. 5.1 in the color insert), with the major division falling between open-canopy habitats (savanna, heathland, grassland, and woodland and closed-canopy habitats (forest). Species that frequent open habitats appear to be most tolerant of disturbance, while forest species are most often reported as being habitat specialists and thus restricted. Forest-dwelling chameleons appear to make up the majority of taxa. Around 132 species (ca. 67%) of chameleons are forest dwelling (Tilbury [2010] estimates that 70% of mainland African taxa are restricted to forest habitats). It appears most likely that the ancestor of all chameleons was a forest leaf-litter specialist from mainland Africa (Tolley et al., 2013; Chapter 7). Some chameleon taxa appear to be typically forest dwelling: *Brookesia, Kinyongia, Rhampholeon,* and *Calumma*. One genus is typically open habitat: *Chamaeleo,* with a last group that appears to have members occupying both forest and open habitats: *Bradypodion, Trioceros, Furcifer,* and *Rieppeleon*. A recent phylogenetic analysis of habitat use in chameleons concludes that nonforest taxa are ecologically derived (Tolley et al., 2013).

Forest Chameleons

Chameleon communities appear to reach peaks of species diversity within forested habitats (Fig. 5.1A,C). For example, up to eight species have been found at a single site in northern Madagascar (Brady and Griffiths, 2003); four species from Mount Manengouba and Mbulu Hills, Cameroon (Gonwouo et al., 2006), and eight species in the East Usambaras, Tanzania (Patrick et al., 2011). Note that these numbers for species that occur in sympatry are much lower than those reported from relatively small areas such as 20 species in a 1-degree square in northern Madagascar (Chapter 7). Diverse sympatric assemblages have given rise to the hypothesis that chameleons are arranged into the sorts of specialist guilds observed in *Anolis* lizards. Caribbean *Anolis* lizards have radiated repeatedly into different arboreal niches (twig, trunk, crown) and show associated morphological specializations. While the convergence of these ecomorphs in the different islands of the Greater Antilles has become a textbook case for adaptive radiations, we are still largely ignorant of how forest chameleons may partition their niches beyond the division (both taxonomic and functional) of leaf-litter and arboreal guilds (but see Townsend et al., 2011 b). In addition, much of the data collected is based on sleeping (roosting) animals, as chameleons are cryptic and difficult to observe during the day. Consequently, detailed investigations exploring the relationship between daytime and nighttime substrate use are required in order to properly interpret these data.

Density

Chameleon densities have been measured in a number of studies and often involve a comparison of sympatric species within and between habitats based on roosting data. Densities of some species get particularly high, exceeding 100 chameleons ha^{-1}, but other, sympatric species (recorded in the same surveys and therefore with presumably the same accuracy) can have particularly low densities, with <1 chameleon ha^{-1}. For example, Karsten and colleagues (2009b) found *Furcifer verrucosus* at high densities (97.7 ha^{-1}; 95% confidence interval [CI], 60.2 to 158.6) in the arid southwest of Madagascar, but *F. antimena* in the same surveys reached only a fifth of this density (17.0 ha^{-1}; 95% CI, 9.3 to 30.9). In the central high plateau of Madagascar, Randrianantoandro et al. (2009) estimated a density of 39.7 ha^{-1} for *Calumma crypticum,* 27.3 ha^{-1} for *F. lateralis,* and 16.4 ha^{-1} for *F. minor* at the same site. Differences in density within a community of *Brookesia* have been observed in the western region of Madagascar, where ubiquitous species most tolerant to habitat disturbance are the most abundant (Randrianantoandro et al., 2007b). Raxworthy (1991) searched forests at mid and low altitudes in northwest Madagascar during the day, finding *Brookesia stumpffi* to be more than 10 times more abundant than three other *Brookesia* species. In dry deciduous forests of northern Madagascar, *B. stumpffi* can reach exceptionally high densities of nearly 150 ha^{-1}, more than twice as high as sympatric *F. petteri* and *F. oustaleti* (Lowin, 2012). In summer surveys in southern Madagascar, *B. nasus* was found at 37 ha^{-1} but *C. malthe* in the same area reached only 10 ha^{-1} while *C. oshaughnessyi* was at <1 ha^{-1} (Brady and Griffiths, 2003). By winter, the same authors had found clear changes in the densities of many species, and this change appeared to relate to body size groups. It would, however, be interesting to test this hypothesis at other sites and with other species assemblages.

Some changes in densities between seasons are directly attributable to the life history of the species concerned, especially where seasonal influences are strong. In such cases, chameleons may aestivate or even die (see below and Box 5.1). However, the degree to which densities vary between seasons, as well as between years, in the same habitat (e.g. Brady and Griffiths, 1999, 2003; and see below) is likely to depend on a host of biotic (e.g. predation) and abiotic (e.g. precipitation, fire) factors, none of which have been investigated using sufficiently extensive time scales.

Vertical Distribution

Most information on vertical distributions of chameleons in forests consists of data from roosting sites when chameleons are found at night using torchlight searches. Roosting sites may be selected for their size (e.g., branch diameter) and proximity to other chameleons (e.g., Randrianantoandro et al., 2007a). Anecdotal observations suggest that chameleons

BOX 5.1 Life History of *Furcifer Labordi*: An Annual Chameleon

Chameleons that inhabit highly seasonal climates are likely to synchronize their life histories with the most productive seasons. One extreme example of this is *Furcifer labordi,* which inhabits the arid southwest of Madagascar; a region that has a distinct biphasic annual climate of low temperatures and low rainfall (April to October) and high temperatures and high rainfall (November to March). During their study in the cold dry season, Karsten et al. (2008) did not find chameleons (*F. labordi, F. verrucosus*), although adult *F. labordi* have been seen in the field from October until early April (A. Raselimanana, personal observation). At the onset of the warm, rainy season, there is synchronous hatching of eggs of both species. During this relatively short (5 months) active season one of these species (*F. labordi*) undergoes juvenile growth, maturation, courtship, and death, leaving only eggs to continue through the next generation (Karsten et al., 2008). However, a captive male overwintered without taking food from June until October (A. Raselimanana, personal observation), and it may be that future studies will reveal survival of a small number of adults.

In their study of *F. labordi*, Karsten et al. (2008) documented synchronous hatching and rapid daily growth rates of juveniles wof nearly 2% snout–vent length (mass: 4% for males, 2% for females) for fewer than 60 days (November to January). At this time, growth ceased, and snout–vent length even reduced in some individuals after this time. During the next 30 days, most females in the population became gravid and laid eggs (February). Once egg-laying ceased, adults quickly disappeared from the area in as little as 2 weeks such that by early March, no adults could be found. Over the next 3 months (April to July) the eggs were thought to be in torpor, as temperatures in this region plummet, with embryonic development occurring only from August through November. The onset of rains and the concurrent rise in temperature signal the synchronous hatching of the next cohort, with few to no adults remaining in the environment. While no other chameleon is currently known to have such an extreme life history as that of *F. labordi,* very few data exist on the majority of species.

change roost sites, as well as the position on a perch, depending on weather conditions; for example, rain, high winds, and cold temperatures result in roosting sites that involve inner branches or areas under leaf cover (Raselimanana and Rakotomalala, 2003; Raholdina, 2012). Some authors suggest that roost sites are a limited resource and as such are vigorously defended (cf. Burrage, 1973). Concordantly, most chameleons are found roosting alone, although in some leaf species, males and females have been found to roost in pairs during the mating season (Wild, 1994; A. Raselimanana, personal observation). Some leaf chameleons roost vertically on stems with their head orientated upward, and some stay in mate-guarding position overnight during the breeding season (*Brookesia exarmata, B. minima, B. nasus,* and *B. ramanantsoai;* Glaw and Vences, 2007; A. Raselimanana, personal observation). Mate guarding, using roosts in close proximity, appears to be relatively common in chameleons (Toxopeus et al., 1988; Cuadrado, 2001; Chapter 6). Most authors agree that roost sites are selected to minimize nocturnal predation, especially from snakes (see below). Newly hatched or newborn chameleons also roost close to each other at the extremity of leaves, vines, or small branches. Perch diameters are not random with respect to available perches (e.g. Razafimahatratra et al., 2008), and their selection is likely related to hand and foot size because of the relationship between the latter and gripping performance (cf. Herrel et al., 2011; Chapter 4). This implies that maintaining a good grip on a perch during the night is an important roosting requirement. Perch sites for arboreal species are typically on isolated branches or leaves (often at the distal tip), presumably as the smallest branches are less likely to support the weight of many predators, and/or so that potential predators that do approach provide vibrations that give the chameleon advance warning. While there are no empirical observations to back up these inferences, some chameleons readily drop from perches if disturbed (see below). The importance of the selection of nocturnal roosting sites may have played a fundamental role in the evolution of arboreality in chameleons. Roosting most likely evolved in the chameleon ancestor to reduce predation by nocturnal ground-dwelling predators.

We do know that roosting site is disassociated from foraging habitat in leaf chameleons, which hunt in the leaf litter during the day and perch in low vegetation at night. Moreover, arboreal species move from their nighttime perches during the day, but there are few data on daytime foraging areas. One study in which arboreal forest chameleons (*Trioceros oweni, Calumma gracilis,* and *T. cristatus*) were followed moving from their roost to foraging areas suggested that all species moved up from roost sites toward the highest branches by midday and returned to lower roosts in the evening (Akani et al., 2001). In this study, the majority of feeding took place midmorning (from 9 to 11 AM) and in the evening (from 3 to 5 PM) for all species (Akani et al., 2001). These authors attribute the inactive period during the middle of the day to a time when chameleons escape from the heat (although this contradicts data on forest temperatures, see Gehring et al., 2008) and avoid predation by hiding behind large leaves. In a study of captive chameleons in a large tropical house, Gehring et al. (2008) found that radio-tracked *Furcifer pardalis* spent most of their time in the top third and on the periphery of available trees (see below), descending only to make longer lateral movements. Although it has been asserted that roost sites are good indicators of foraging locations (Carpenter and Robson, 2005), there appear to be no data on the majority of species to back up this claim.

Leaf chameleons (e.g., Fig. 5.1D) are known to forage on the forest floor, but also catch insects from low vegetation (e.g., Raxworthy, 1991; see below). Moreover, these chameleons spend the night roosting in low vegetation. In the East Usambara Mountains, leaf chameleons (*Rhampholeon temporalis*) roost close to the ground (mean ± SD, 0.60 ± 0.45 m), while larger (typically arboreal) species roosted from 2.0 to 4.5 m high (Patrick et al., 2011). In Cameroon, most *R. spectrum* were found roosting below 1 m, but some individuals were found as high as 2 m (Wild, 1994). Broadley and Blake (1979) report roosting sites up to 4.5 m for *R. marshalli,* and they suggested that this may be indicative of a difference in predators in the eastern highlands of Zimbabwe. Sympatric species may differ in the precise choice of roost site, both by vegetation type, substrate diameter, and roost height (Carpenter and Robson, 2005; Randrianantoandro et al., 2007a; Herrel et al., 2011; Patrick et al., 2011). In Madagascar, sympatric leaf chameleons show different roosting heights, with hatchlings and juveniles being found lower than adults (see Razafimahatratra et al., 2008). However, even species such as *Brookesia stumpffi,* which has relatively high roosts for a leaf chameleon (mean height, 0.43 m), still roost 2 m lower than sympatric *Furcifer angeli* (Carpenter and Robson, 2005). In two studies of leaf chameleons, no significant differences between sexes were found for roost height (Randrianantoandro et al., 2007a; Razafimahatratra et al., 2008). However, male *F. pardalis* were found to roost higher than females (Andreone et al., 2005). As we now know that gripping strength is related to perch choice (Herrel et al., 2011), future studies will need to disentangle observed perch differences in ontogeny, sex, and species from morphological constraints.

Only one member of the genus *Brookesia* (*B. ebenaui*) is always found in trees during the day, roosting between 2 to 3 m high (Glaw and Vences, 2007). Conversely, one of the large forest species from the arboreal genus *Trioceros* (*T. cristatus*) appears to inhabit the leaf litter on the forest floor or low-lying shrubs (Akani et al., 2001). Data on diet suggest that this species may rely on large prey not available to smaller sympatric leaf chameleons (*Rhampholeon spectrum*), and others have commented that stomach contents contained mainly terrestrial insects (Klaver and Böhme, 1992). *Trioceros cristatus* also has a relatively short tail, which is typically associated with ground dwelling (Klaver and Böhme, 1992; Boistel et al., 2010).

Few searches have been made specifically in forest canopies, and suggestions of partitioned use of this habitat type are based mostly on anecdotal observations and thus remain speculative. For example, large species have been suggested to be canopy specialists (Raxworthy, 1988; Nečas, 2004), yet quantitative data are lacking. Large species were rarely observed in the forest canopy of Nosy Be, Madagascar, and only a single *Furcifer pardalis* was found in a 10-day canopy search, but otherwise it appeared to be absent from the forest (Andreone et al., 2005). Parcher (1974) reported that *F. willsii* inhabits only the upper canopy, as few animals were found roosting with sympatric species but five adults were found in the upper canopy. Similarly, in the Anjozorobe Forest in the central high plateau of Madagascar, *F. willsii* was the only species recorded from the upper canopy area (A. Raselimanana, personal observation).

The available data are not sufficient to confirm or reject the existence of more than a single partition of forest chameleons into arboreal and leaf-litter guilds. Whether or not more complex partitioning exists, and existence of specializations toward the use of the forest canopy or understory niches, remains a challenge for future studies of these lizards.

Horizontal Distribution

Within forests, chameleons have been said to favor tree falls or ecotones between forest and adjacent habitat (e.g., Metcalf et al., 2005; Reisinger et al., 2006). While it is certainly true that forest chameleons can be found in gaps and on edges, this may be because the forest canopy is mostly unavailable to human observation. Therefore, the important caveat for observations made from ground surveys for chameleons (which make up the majority of studies) is that chameleons may remain unobserved in the canopy and understories.

Several authors have investigated edge effects on the abundance of chameleons in forests. The periphery of the forest appears to be an environment where both forests and nonforest species co-occur (e.g., Patrick et al., 2011). These (often unnatural) ecotones might be attractive to chameleons for a number of reasons, including increases in prey diversity and abundance, basking opportunities, visibility for intraspecific communication, and vegetation structure. Natural edge effects, such as those produced by tree falls or along streams and rivers, are present in many forests, and there is evidence to suggest that these areas also have an increased abundance of chameleons. Gaps from tree falls seem to be important, with more *Bradypodion caeruleogula* roosting in them than on forest edges or in the forest interior (Reisinger et al., 2006). *Furcifer pardalis,* which normally does not enter forest, has been found within forest along river transects (Andreone et al., 2005; Raselimanana, 2008), and *Calumma* were more abundant in riparian vegetation while for *Brookesia,* the converse was true (Andreone et al., 2005). However, riparian habitat had equal or higher densities of all of chameleon species (including *Brookesia* species) in other surveys (Jenkins et al., 2003; Rabearivony, 2012). Yet, it is not clear that it is the river or the canopy opening around which chameleons cluster. For example, *Rhampholeon spectrum* was particularly abundant in riparian forest vegetation, independent of whether streams were running or dry (Wild, 1994). Metcalf et al. (2005) investigated the edge effect from forest paths, which represent a relatively small canopy opening. They found a significant decrease in abundance away from paths for two species of *Furcifer* (*F. oustaleti* and *F. rhinoceratus*). In addition, there is a suggestion that some chameleons may migrate to riparian vegetation during the dry season (Brady and Griffiths, 1999; Rabearivony et al., 2007).

Because many forest species are restricted to forest patches, discontinuation of habitat does not allow migration between populations. This appears to be the most common cause of disjunct distributions in East Africa (e.g., Measey and Tolley, 2011), and it may also contribute to speciation (Tolley et al., 2011; Chapter 7). Exceptions also occur; for example species like *Furcifer lateralis* and *F. oustaleti* are regularly found walking across open ground from one forest patch to another (A. Raselimanana, personal observation). Where habitat is continuous, there appears to be a distinct altitudinal turnover of some species, while others inhabit a wide range of altitudes. In West Africa, *Rhampholeon spectrum* is found from 500 to 1900 m, passing through discontinuous distributions of 10 species of *Chamaeleo* and *Trioceros* (Wild, 1994; Akani et al., 2001), while in East Africa, altitudinal partitioning is reported between *R. temporalis* and *R. brevicaudatus* (Emmett, 2004). Luiselli (2006) conducted simulations based on survey data in West Africa, which suggested that chameleons in lowland forests are distributed according to food niche resources rather than spatial niche resources, while the opposite was true for montane species. In Madagascar, *Calumma* and *Furcifer* exhibit a distribution structure along altitudinal gradients (Nussbaum et al., 1999; Raselimanana et al., 2000), but this seems particularly pronounced in species of the genus *Brookesia* (Raxworthy and Nussbaum, 1995; see Andrews, 2008). Species assemblages in general can change in structure even within contiguous blocks of undisturbed forest (Brady et al., 1996; Brady and Griffiths, 1999; Jenkins et al., 1999; Rabearivony, 1999). Landscape features (e.g., rivers) are often suggested to be barriers (see Chapter 7), but as Raselimanana and Rakotomalala (2003) point out, chameleons are likely to be able to traverse even large rivers when these are bridged by fallen trees. Further research is required to help define the ecological niches of most chameleons, especially in relation to species turnover in continuous habitat.

Disturbance

Disturbed forests lack certain chameleon species while other species appear more tolerant or apparently even thrive after disturbance (e.g., Rabearivony et al., 2007; Irwin et al., 2010). Regardless, leaf chameleons generally seem to be negatively affected by habitat disturbance, which results in a reduced abundance of their leaf-litter habitat. *Brookesia minima,* for example, was absent from highly disturbed habitats (Jenkins et al., 2003). In another study on *Brookesia* distributions, abundance was generally higher at undisturbed sites (*B. thieli*, 58 ha^{-1}; *B. minima*, 7 ha^{-1}) as compared with burnt sites (*B. thieli*, 20 ha^{-1}; *B. minima*, 0.0 ha^{-1}) (Rabearivony, 1999). Small patches of forest appear to be able to maintain individuals (e.g., Wild, 1994), although it is not known whether such populations are sustainable in the long term. Nevertheless, it is also worth noting that some species, like *B. stumpffi,* reach high densities in plantations (e.g., of coffee and cacao; F. Glaw, personal communication).

A significant interaction between habitat type (high-disturbance, low-disturbance, and riparian) and the presence of *Calumma* spp. was found in eastern Madagascar (Jenkins et al., 2003). High-disturbance habitats were found to have a negative effect on all species in that study. However, at least some species, such as *C. brevicorne* and *C. nasutum,* appear to increase in density whenever the habitat is disturbed (Brady and Griffiths, 1999, 2003). Densities of *Furcifer pardalis* are much higher along roads or transformed habitats, and this species is absent from pristine or closed forest (Andreone et al., 2005; Rabearivony et al., 2007). Brady and Griffiths (2003) found low densities of *C. brevicorne* in undisturbed forest at several sites, but high densities along the forest edge. At a high-altitude site in central Madagascar, *Furcifer* species dominated in open heathland and agricultural lands, while *Calumma* dominated in humid forest (Randrianantoandro et al., 2010). While exceptions do occur, these mostly consist of individuals of *Furcifer* species being found at the forest periphery. It has been speculated that highly disturbed habitats represent a sink for some chameleon populations, being maintained by dispersing individuals or newly hatched juveniles from adjoining forest (Jenkins et al., 2003).

One consistent feature of disturbed forest habitats is that species with a preference for open-canopy habitats are quick to move in. A difference in distribution of seven species was found during transect walks in the East Usambara Mountains (Patrick et al., 2011). Interestingly, the sample contained the typical savanna species *Calumma dilepis*, which was occasionally found on the forest edge, but absent from within the forest. Hebrard and Madsen (1984) also report the presence of *C. dilepis,* becoming sympatric with forest species in deforested areas. Other species such as *Kinyongia matschiei* and *Rhampholeon temporalis* were found only within the forest (Patrick et al., 2011). In West Africa, *C. gracilis* moved into disturbed forest patches that were previously inhabited by *Trioceros* spp. (Akani et al., 2001).

Nonforest Chameleons

While the majority of chameleon species occur in forested habitats, a smaller group has radiated into habitats that have been broadly classified as: (i) bushes and heathland scrub, grassland (Fig. 5.1E), (ii) open canopy dry forest and savanna, and (iii) desert (Fig. 5.1F). The movement out of forests to open-canopy habitats occurred in multiple lineages of *Chamaeleo* and *Furcifer* in the early Miocene, while the transition into grassland and heathlands in *Bradypodion* and *Trioceros* occurred much later, at the start of the Pliocene (Tolley et al., 2013). The unifying feature of all of these nonforested or open habitats is that the chameleons have increased exposure, as this environment is less buffered from solar radiation, with a notable decrease in humidity. These chameleons (together with those from the dry forests of southwest Madagascar) have had to undergo physiological adaptations to deal with water stress as well as behavioral and morphological adaptations to cope with new substrate types. Living in a more open habitat, these chameleons may be more visible to potential predators (Herrel et al., 2013; Chapter 3); consequently, the most brightly colored and highly ornamented species are typically forest dwellers (e.g., Fig. 5.1B) and are frequently missing from open habitats, although there are exceptions. Unlike forest chameleons, open-habitat species are typically allopatric, with occasional range overlaps and sympatry of arboreal and leaf forms (e.g., *Rieppeleon* and *Chamaeleo* in East African savannas). The vegetation types they inhabit are also vulnerable to fire, which is able to impose dramatic reductions in chameleon populations, but also results in a changed landscape for any individuals that survive the fire. A total of 47 chameleon species (26% of all chameleons, not including morphs or species for which habitat is not known) are recognized as inhabiting such open habitats.

Like chameleons in forests, open-habitat species are often bounded by the vegetation types that they inhabit. This implies that in continental Africa, where open habitats are now extensive, these species are characteristically wide ranging. However, some species inhabit a restricted range of vegetation; well-documented examples of this occur in southern Africa, with ecomorphs adapted to open habitats occurring in the genus *Bradypodion* (Measey et al., 2009; Herrel et al., 2011; Hopkins and Tolley, 2011). *Bradypodion* ecomorphs adapted to open habitats are generally smaller, have less bright coloration, and have smaller ornaments than their sister taxa living in forest or woodland (Tolley and Burger, 2007; Stuart-Fox and Moussalli, 2008) (Fig. 5.1F). The history of the radiation of certain lineages of this genus of dwarf chameleons out of forest can be found in Box 5.2.

Mountaintops often emerge out of the forest zone and are frequently dominated by heathland scrub. Some chameleons that enter this habitat appear to have speciated there. The genus *Calumma* is mostly forest dwelling, but three species *C. vatosoa*, *C. peyrierasi,* and *C. jejy* all occur in shrubland adjacent to forest. *C. peyrierasi* also seems to be in the high-altitude heathland above the forest belt. Raholdina (2012) found higher densities (42.7 ha^{-1}) of *Furcifer*

BOX 5.2 *Bradypodion* Radiation out of Forests

All chameleons of the genus *Bradypodion* were once considered to be a single species (*B. pumilum*), with a bewildering array of forms (Hillenius, 1959; Mertens, 1966), although now the genus is considered to be composed of 17 species. These chameleons are allopatrically distributed from the coast to roughly 300 km inland in southern Africa, an area that passes through seven vegetation biomes (Branch, 1988; Tolley et al., 2004; Tolley and Burger, 2007). Today, arid biomes dominate the interior of the subcontinent (savanna, grassland, and Nama Karoo) following a process of aridification that occurred in two pulses of substantial uplifting of the east coast: 250 m and 900 m at 20 Mya and 5 Mya, respectively (McCarthy and Rubidge, 2005). These geological processes saw the end to much of the dominant forested vegetation in the area with aridification of the interior and a concurrent diversification of the ancestors of the chameleons.

The presence of a relatively large number of fairly recent lineages of dwarf chameleons in southern Africa, their mixture of preferred habitats in a number of biomes, and the existence of a robust phylogeny (Tolley et al., 2004, 2006, 2013), has allowed workers to investigate the evolutionary consequences of movement of these species from ancestral forested areas to biomes with open habitat types. In order to interpret these studies, it has been critical to determine the direction of this evolutionary radiation, which has been done by optimizing habitat on a phylogeny of the genus, confirming that the historical habitat for the most recent common ancestor was forest (Tolley et al., 2008).

Moreover, repeated radiations out of the forests of southern Africa into savanna (*B. thamnobates, B. transvaalense*), grassland (*B. melanocephalum*), and fynbos (ecomorphs of *B. pumilum, B. damaranum, B. gutturale*) took place. Reconstruction of ancestral vegetation for these lineages shows radiations into open habitat, corresponding with most dramatic uplifting 5 Mya (Tolley et al., 2008), a period that also corresponds to rapid diversification of the fynbos biome (Fig.5.1e).

The movement from closed to open habitat carries with it an increased exposure to predators (e.g., Stuart-Fox et al., 2006a; Stuart-Fox and Moussalli, 2008). Consequently, *Bradypodion* show a clear shift from bright to dull colors corresponding to the radiation into more open habitats (Branch, 1988; Stuart-Fox and Moussalli, 2007; Measey et al., 2009; Hopkins and Tolley, 2011). However, a study that investigated whether this change in habitat related to a change in camouflage found no evidence for increased crypsis in open habitat species; instead, *Bradypodion* inhabiting forests were found to exhibit greater changes in color associated with increasing contrast against background for social signaling (Stuart-Fox and Moussalli, 2008).

Morphologically, forest lineages are typically larger-bodied species with long tails, high casques, and long hands and feet, while those in open habitats are smaller, have lower casques, and have shorter hands and feet (Branch, 1998; Stuart-Fox and Moussalli, 2007; Measey et al., 2009, Tolley and Hopkins, 2011). There are some data (for *B. pumilum*) to suggest that these changes are adaptive, such that long tails can be used to increase grip force on wider perches (Herrel et al., 2011). However, an increased bite-force performance in open-habitat *B. pumilum* could not be attributed to a change in diet (Measey et al., 2011), but was instead postulated to be due to a reduction in ability to settle disputes by signaling.

campani in the central plateau highland of Madagascar associated with ericoid vegetation, as compared with lower densities (28.6 ha^{-1}) in other areas. In mainland Africa, *Trioceros kinetensis, T. rudis, T. hoehnelii, T. affinis, T. bitaeniatus, T. goetzei, T. harennae, T. nyirit,* and *T. schubotzi* all inhabit similar shrubby habitats at high elevations. The species of the *bitaeniatus* group of *Trioceros* are also noteworthy, as they all exhibit viviparity in addition to inhabiting regions up to and above 3000 m. *Kinyongia* are usually strongly associated with forest, although there are a few notable exceptions which suggest some Kinyongia species have flexibility. For example, *K. gyrolepis* has been found in shrubby habitats at high altitudes (Greenbaum et al., 2012), and *K. boehmei* is sometimes found in ericaceous habitat above cloud forests, in low-intensity agricultural areas, and into the alien vegetated shrubland below the forest limits in the Taita Hills (G.J. Measey, personal observation). This suggests that even forest-dwelling species may occasionally move into adjacent non-forested habitats when conditions are favourable, although there to appear to be limits. For example, despite being able to use vegetation adjacent to primary forest, *K. boehmei* are separated into distinct populations associated with forests that are separated by only a few kilometers of savanna (Measey and Tolley, 2011).

Forest ecotones appear to be strongly associated with an increased diversity of chameleons (see above), and it appears that many species utilize disturbed habitat outside of forests. Such habitat types do arise naturally; for example, hurricanes or cyclones can remove large sections of forest. Forest can also be impacted by landslides and mudslides, so perhaps it is not surprising that some species appear to be specially adapted to the fringe areas and disturbed forest (see above for examples). Broad habitat distributions are considered to result in different life histories for chameleons in Madagasar, where large sexually dimorphic species (*Furcifer*) require more open habitat for basking and intraspecific communication (Andreone et al., 2005). Many of the species that inhabit the forest edge ecotone are some of the largest, brightest species (e.g., *F. pardalis, Trioceros jacksonii*). Temperature and humidity variation should increase at the forest-edge ecotone, and many species that can tolerate this also have wide distributions, suggesting that they are also capable of migrating over larger distances. Outside the forest, different species also appear to have different vegetation height preferences. Lin and Nelson (1980) found that sympatric *T. hoehnelii* and *T. jacksonii* inhabited different vegetation within their study area: *T. hoehnelii* were found predominantly in areas of open secondary scrub, rarely above 2 m, while *T. jacksonii* were mostly in trees above 2 m.

Savanna species have the largest distribution of all chameleons, in part because the savanna now covers large areas of continental Africa (see Chapter 7). The open nature of the habitat makes them more visible, and one of the few studies of chameleon behavior during the day comes from a common sub-Saharan species, *Chamaeleo dilepis*. Unlike other chameleons *C. dilepis* is usually found alone (Toxopeus et al., 1988; see below), and a behavioral study found divergent microhabitats between the sexes. Hebrard and Madsen (1984) investigated diel perches and observed sexual differences in perch height and perch type. During the dry season, males chose higher perches (2.8 m, vs. 1.5 m for females) without leaves (but no measures of roosting sites were made). Higher male perch heights have previously been associated with the sexual displays of male lizards (Andrews, 1971). However, in the rainy season no sexual differences in habitat use were found, and males were found to move significantly further than females (males, 4 to 17 m per day; females, 1 to 3 m) (Hebrard and Madsen 1984). It is also worth noting here that male *C. chamaeleon* are thought to spend more time on the ground and that females perch lower in trees during summer (Pleguezuelos et al., 1999). Savanna species appear to be tolerant of disturbance and regularly take up residence in gardens. The majority of species of the genus *Chamaeleo* are not forest dwelling (only two species seem to inhabit wet forest: *C. necasi* in the coastal forest of the Dahomey Gap, West Africa and *C. zeylanicus* in India and Sri Lanka).

In addition to the radiation of large arboreal chameleons into the savannas, some members of one genus of leaf chameleons—*Rieppeleon*—appear to have moved out of the rainforest into adjacent savanna (Matthee et al., 2004). These small chameleons live in low bushes and grasslands and can frequently be found walking on the ground. Savannas have large areas of grassland where all these chameleons can be found, frequently sitting in isolated bushes. Madagascar has relatively small natural savanna areas, but they are inhabited with chameleons such as *Furcifer lateralis* and *F. campani*.

Another well-studied chameleon inhabits scrubland areas of southern Europe; *Chamaeleo chamaeleon* were found to select habitats with south to southwesterly facing slopes in southern Spain to take advantage of the increased radiance (Hódar et al., 2000). Moreover, these chameleons were found to favor trees with increasing density above 1 m and to avoid shrubs and dead trees.

There appear to be several evolutionary radiations of chameleons into arid habitats, and specific adaptations are associated with these. The first radiation was into seasonal forests that undergo distinct arid periods during which some chameleons are active, while others aestivate (see below). Adaptations for survival in these areas of climatic extremes include reproductive diapause (see Box 5.3), aestivation and for at least one species, and a complete change of the life cycle (see Box 5.1). Movement into extremely seasonal forests appears to be gradual. Only three species from the genus *Furcifer* (*F. major, F. oustaleti,* and *F. verrucosus*) inhabit the most arid deciduous forests in the southwestern regions of Madagascar, where mean rainfall is around 420 mm, typically confined to only 3 months, from December to February. Others appear in transitional and deciduous forest in the southwest and western region of Madagascar; including *F. antimena, F. labordi, Brookesia bonsi, B. decaryi, B. brygooi, B. perarmata,* and *B. stumpffi* (Raxworthy and Nussbaum, 1995; A. Raselimanana, personal observation). During the dry season, adult *Brookesia* aestivate under debris, or dig into loose soil (Brady and Griffiths, 2003).

A second radiation into arid habitat involves several species from the genus *Chamaeleo* that have moved into arid regions and even true deserts. For example, Swakopmund, which is within the range of *C. namaquensis,* has annual rainfall of around 14 mm (although horizontal precipitation in the form of coastal fog may be much higher) (Fig. 5.1g,h). These chameleons experience extreme diel temperatures: from 8 to 56°C (Burrage, 1973). They appear to cope with these stressors by means of behavioral and physiological adaptations, including what Burrage (1973) referred to as "ploughing." This behavior involves digging groves into the substrate where the chameleon makes contact with warmer or cooler sand. Together, body compression, color (brightness) change, and ploughing allow daily behavioral thermoregulation when ambient temperatures are

BOX 5.3 Embryonic Diapause

Embryonic diapause in chameleons is a unique form of developmental arrest that is unknown in other squamates (Andrews and Karsten, 2010). Embryonic diapause occurs when eggs are in gastrulae at the time of laying, and gastrulation occurs so slowly that development is effectively arrested for periods of several months (Bons and Bons, 1960; Andrews and Donoghue, 2004; Ferguson et al., 2004). In addition to embryonic diapause, embryos of some chameleon species also undergo cold torpor. In *Chamaeleo chamaeleon,* eggs with embryos in diapause are laid prior to the onset of winter, with the onset of winter conditions causing a second suspension of embryonic development. Despite *C. chamaeleon* egg clutches being laid over the course of several weeks, hatching is synchronous over a number of days more than 10 months after being laid. Ferguson et al. (2004) suggested that high temperatures during diapause prolongs developmental resting, whereas low temperatures during diapause, followed by an elevation in temperature, ends the diapause and accelerates development to term.

In experiments and field-measured nests, Andrews et al. (2008) manipulated the temperature of nests of *C. chamaeleon* to determine how nest temperatures and embryonic development were synchronized. By maintaining egg clutches at prewinter temperatures, they were able to prevent embryos from entering the period of cold torpor and to show that development continues to hatching. In both the field and laboratory clutches held at field temperatures, Andrews and colleagues showed that embryonic development began as soon as temperatures began to rise after winter. This general warming of all nests synchronizes the development of embryos, giving rise to synchronous hatching and emergence of juveniles in late summer, which may be important in diluting predation pressure and optimizing hatching at the time of maximum food availability.

Synchronous hatching of juveniles is known in many chameleons that inhabit highly seasonal environments. The dry deciduous forests of southwestern Madagascar are a good example, and researchers there believed that that embryo development was inhibited during the winter (dry colder) season so that hatchlings from different clutches emerge synchronously (Brady and Griffiths, 1999). Documentation of this is provided by two species that inhabit this environment (see Box 5.1).

not favorable. Burrage also notes that these chameleons are known to burrow completely into the substrate. Similarly, at night *C. namaquensis* were reported to make use of burrows, presumably to escape the cold temperature typical of the desert. This is the only species of chameleon that does not necessarily roost at night; instead, animals lie on the ground, possibly to maximize the ventral area in contact with the substrate (G.J. Measey, personal observation).

Chamaeleo calcaricarens inhabits the dry savanna and semidesert of Ethiopia, but there appear to be far fewer ecological data on this species. Spawls (2000) notes that, like *C. namaquensis, C. calcaricarens* is capable of moving rapidly and that it may aestivate throughout the dry season.

5.2 LIFE-HISTORY TRAITS

Chameleons exhibit a diverse array of life-history traits, from annual species, that spend most of their year as an egg, to large and long-lived species. The body size of extant lizards in this family covers four orders of magnitude and includes candidates for the world's smallest vertebrate (*Brookesia tristis,* 0.2 g, and the even smaller *B. micra*) (Glaw et al., 2012) to one of the largest arboreal lizards (*Calumma parsonii,* 700 g) (Abate, 1998). Live young are known to have evolved 108 times in squamates (Blackburn, 1999, 2006), and at least twice in chameleons (Tinkle and Gibbons, 1977; Andrews and Karsten, 2010; Schulte and Moreno-Roark, 2010; see also Tolley et al. 2013). Egg retention is considered to be the first step to viviparity, but most squamates either lay eggs with embryos about one-third developed (stage 30) or retain eggs until development is complete (i.e., are viviparous) (Shine and Thompson, 2006). However, chameleons lay eggs that can have one of three distinct strategies: eggs with early gastrula, eggs with well-developed embryos, and completely formed embryos (viviparous). Laying eggs with an early-stage gastrula allows chameleons to remain in the egg for unfavorable periods, and it has emerged that in some species a period of diapause allows eggs to remain unhatched for up to a year (see Box 5.3). The presence of the early embryologic stage in chameleons is thought to have evolved from an ancestor with (conventional) late-stage oviposition (Shine and Thompson, 2006). In their phylogeny, Andrews and Karsten (2010) suggest exactly the opposite: from late-stage oviposition (*Brookesia* and *Rhampholeon*) to viviparity (*Bradypodion*) to late arrested development and late early-stage oviposition (*Chamaeleo* and *Furcifer*). A model wherein the majority of squamates are prevented from this early-stage oviparity by nest sites that are not sufficiently hydrically stable (Shine and Thompson, 2006) suggests that female chameleons would have highly selective nest choice to maintain stable soil moisture levels.

Oviparity and Viviparity

Viviparity is thought to have its origins in cold environments: high latitudes or altitudes (Shine, 1985), and this hypothesis appears to holds true for chameleons (Andrews and Karsten, 2010; Schulte and Moreno-Roark, 2010). Viviparity has evolved in southern African *Bradypodion,* which occur at relatively high latitudes (up to 34.7°S), and *Trioceros,* which inhabit the highest montane areas in central Africa (up to 4 000 m asl). It is worth noting that *Bradypodion* are not at the most extreme latitude, which is taken up by an oviparous species *Chamaeleo chamaeleon* (up to 37°N), which has an embryonic diapause and goes into a state of torpor to avoid the coldest period (see Box 5.3). However, our current climate is at an interglacial stage, and some chameleon distributions are likely to have shifted during glacial periods. There are also oviparous chameleons at high altitudes, such as the Malagasy species: *Calumma hilleniusi* and *Furcifer campani*. Both are adapted to high elevations and cold montane habitats (temperatures ≤0°C during winter), but incubation periods vary, about 90 days for the former and 140 to 265 days for the latter (Glaw and Vences, 2007).

Variation in reproductive traits is thought to be an adaptation to unpredictable variation in the environment, notably rainfall (Shine and Brown, 2008). Although the majority of chameleon species live in forests, where the hydric environment is relatively stable, many species have moved into totally arid environments and yet others have moved into environments where the rainy season is particularly short. A good example of this is the dry deciduous forests of southwestern Madagascar, where the chameleons exhibit some of the most extreme life-history traits. The population of *Furcifer labordi* spends the 9-month dry season as eggs, synchronously hatching at the onset of rains (Karsten et al., 2008) (Box 5.1). The sympatric

F. verrucosus can be found throughout the year, with juveniles reaching adult size during the rains and aestivating during the long, cold, dry season (Karsten et al., 2008).

Several species of chameleons have been documented to store sperm, and it has been suggested that storage in this family of lizards may be considerably longer than in other more mobile species (Birkhead and Møller, 1993). However, this suggestion was based on a study with a low sample size (four species) and there are few new data to indicate whether duration of sperm storage is related to low densities or slow movement. Detailed studies of the phenology of viviparous and oviparous chameleon species exist, and there are examples of both species with continuous reproduction as well as species with distinct annual cycles. The entire genus *Bradypodion,* which inhabits the subtropical and Mediterranean climatic zones of southern Africa (see Box 5.3) is bear live young (Branch, 1998; Tolley and Burger, 2007). Reproduction in *B. pumilum* females is aseasonal; they can give birth year round and are capable of bearing multiple generations within a year (Jackson, 2007). Males had distinct biannual testicular peaks before and after the dry summer. This species also seems capable of sperm storage (Atsatt, 1953), and it is possible that other *Bradypodion* spp. share these life-history traits (Jackson, 2007). Similarly, *Trioceros bitaeniatus* gives birth to live young throughout the year in Kenya and *T. montium* lays eggs in both wet and dry season in Cameroon (Bustard, 1966; Herrmann and Herrmann, 2005). Lin (1980) made a detailed study of the reproductive traits of live-bearing and oviparous species of *Trioceros: T. jacksonii* and *T. hoehnelii,* respectively. *T. jacksonii* exhibited a distinctly annual reproductive cycle. Males were found to have an annual testicular cycle, peaking just before the onset of the rains in March and prior to mating observed in May. Females began the production of yolked follicles at this time, with a peak of ovulation in August. Gestation began in August and continued until February, when females were observed giving birth until March. Toxopeus et al. (1988) found that *T. jacksonii* could regularly be found in male–female pairs throughout pregnancy, suggesting some form of mate guarding. Following parturition, females entered a period of postreproductive quiescence, as fat bodies accumulated to reach their peaks in May (Edgar, 1979).

In his examination of the sympatric oviparous, *Trioceros hoehnelii*, Lin (1980) noted that this species was mostly aseasonal, with high testicular activity year round and mating observed in nearly every month. Females had yolked follicles throughout the year, with eggs with advanced embryos being laid year round. Females were also able to store sperm. Toxopeus et al. (1988) also studied *T. hoehnelii,* finding that while animals were often found in male–female pairs, these partners were frequently changed, although duration in pairs increased when females were notably gravid. Lin (1980) speculated that *T. hoehnelii* and *T. jacksonii* had evolved in allopatry, although they are now sympatric in the anthropogenically altered habitat of the central Kenyan highlands. Based on the presence of juveniles throughout the year, Wild (1994) suggested that *Rhampholeon spectrum* probably breeds all year round. Dominancy of juvenile *Furcifer campani* (91% vs. 3% subadults and 9% adults) has been reported at the beginning of the warm and rainy season in Madagascar, while adults were abundant during the wet season (80% vs. 20% subadults and 0% juvenile) and in winter (85.4% vs. 4.1% juveniles and 10.5% subadults; Raholdina, 2012).

In their study of another oviparous species, *Chamaeleo chamaeleon* in southwestern Spain, Andrews et al. (2008) again found a distinctly annual reproductive cycle. Males in this species were also found to practice mate guarding for a short period (around 2 weeks) during a distinct mating season when females were receptive to mating (Cuadrado, 2001) and leave once females show specific body coloration and behavior to indicate that they were gravid (Cuadrado, 2000). Chameleons are capable of continuous reproduction or annual cycles irrespective of whether the species is oviparous or viviparous. However, any species with diapause in eggs would be expected to exhibit an annual cycle.

Clutch size and hatchling size have both been shown to be strongly correlated with female body size. This has been shown intraspecifically for *Trioceros hoehnelii* and *T. jacksonii* (Lin, 1980), *T. montium* (Herrmann and Herrmann, 2005), *Chamaeleo chamaeleon* (Diaz-Paniagua et al., 2002) and over 33 other species (Andrews and Karsten, 2010). The largest recorded clutch sizes are from some of the largest egg-laying species, which may lay nearly 100 eggs (*C. calyptratus* and *T. melleri*), while those giving birth to live young reach approximately half this number (*T. jacksonii*). The smallest chameleons have clutches of 2 eggs (e.g., *Brookesia tristis*). Residuals of body size and hatching size indicated the existence of a trade-off between these traits as has been observed for most lizards: larger clutches result in smaller hatchlings and smaller clutches in larger hatchlings (Andrews and Karsten, 2010). Further, the strength of this relationship was found to increase when independent phylogenetic contrasts were included. Hence, like many other lizards, chameleons exhibit a continuum of reproductive strategies between large clutches with small hatchlings (<10 mm) and small clutches with large hatchlings (around 100 mm).

Egg-laying chameleons bury their eggs meticulously in the ground. Some ground-dwelling species deposit eggs singly within depressions under large leaves, while others dig holes of varying depths. Eggs of *Brookesia stumpffi* can be found in depressions under dead leaves on the forest floor (Raxworthy, 1991). Many people have observed female chameleons laying eggs, noting the vulnerability of the female during this long process. Hódar et al. (2000) and Brain (1961) both remarked on the search by females of *C. chamaeleon* and *C. dilepis* (respectively) for suitable ground conditions in which to dig holes. As many species may select different habitats for their offspring (see below), females move over considerable distances in order to oviposit. It is also the only time when chameleons have been seen to be active at night (*C. dilepis,* Brain, 1961). Egg chambers are dug obliquely into the soil, and eggs in small clutches are normally deposited singly, with soil separating each one, while large clutches are deposited together. Optimal nesting sites may be in high demand as precisely the same nesting site has been seen to be used multiple times by different individuals of *Kinyongia boehmei* (Measey, 2008).

Temperature changes with soil depth, decreasing and becoming more stable as depth increases. For example, temperature in areas inhabited by *Kinyongia boehmei* was constant by a depth of 30 cm (irrespective of whether the soil was in forest or cultivated areas). Yet, temperature changed by nearly 4°C over 700 m of altitude (Measey et al., 2009). *Chamaeleo calyptratus* was found to have consistent developmental rates between 28 and 30°C.

Development was significantly slower, yet hatchlings were significantly heavier at 25°C (Andrews, 2008). In southwestern Spain, nests of *C. chamaeleon* are laid up to 45 cm deep, where they undergo a seasonal change in temperature of nearly 20°C (Andrews et al., 2008). In contrast, nest temperature for *K. boehmei* eggs buried at 18 cm in a Kenyan forest underwent a change of only 4°C over a year (Measey, 2008). No temperature-dependent sex determination takes place in chameleons, as suggested by experiments with *C. calyptratus* (Andrews, 2005). *Archaius tigris* is notable in that females deposit their eggs in the leaf funnels of the introduced wild pineapple plants that are common in the Seychelles (Van Heygen and VanHeygen, 2004). Whether other plants (such as palms) would have been used before the arrival of the bromeliads is not known.

Once laid, chameleon eggs are susceptible to any number of vertebrate and invertebrate predators (see below). Likewise, hatchlings are likely to have high mortality between emergence from the nest and their first movement into surrounding vegetation. Chameleons are known to exhibit a diverse period of development, ranging from a few weeks to as long as a year. Andrews and Karsten (2010) proposed three groups with respect to other squamates for these highly divergent developmental rates: normal (50 to 70 days), slow (70 to 175 days), and arrested (175 to 365 days; see Box 5.3).

Ontogenetic Habitat Shift

Ontogenetic habitat shifts are hypothesized to occur widely within chameleons as they do in other arboreal lizards, as this prevents interactions between adults and juveniles (e.g., Irschick et al., 2000; Vanhooydonck et al., 2005). Ontogenetic habitat shifts may avoid cannibalism (see below) and competition and also aid in dispersal. Moreover, juveniles may inhabit areas with large numbers of small prey, which may not be suitable for adults (see below). In both experimental studies and observations on free-ranging *Chamaeleo chamaeleon,* juveniles were found to forage and sleep at lower heights than adults, which generally climbed to the top of available vegetation (Keren-Rotem et al., 2006). Juveniles were found to avoid adults (but not other juveniles), and when provided with an opportunity, most adults attempted to feed on juveniles.

Ontogenetic shifts in perch size may be facultative if, as observed in other arboreal reptiles, branch selection is dependent on animal size (Irschick and Losos, 1998). Keren-Rotem et al. (2006) found that adult *Chamaeleo chamaeleon* foraged and slept on thicker branches than juveniles. Specifically, most juveniles were found sleeping on grasses while adults slept on woody vegetation. Stratification of roosting level is well illustrated by *Brookesia decaryi,* whose hatchlings roost almost among the leaf-litter followed by juveniles, then by adults at the top (Razafimahatratra et al., 2008). Herrel et al. (2011) studied the perch selection of *Bradypodion pumilum* ecomorphs in heathland and wooded environments, concluding that perch and hand/foot size were well correlated. Moreover, larger hands were found to be stronger on larger perches (see Chapter 4). These authors excluded juveniles and subadults from their study, but observations suggest that juveniles of *B. pumilum* regularly occupy microhabitats distinctly different from those of adults, such as grasses at the periphery of wooded areas (G.J. Measey and A. Herrel, personal observation). Similarly, gravid *B. thamnobates* have been observed to deposit their young in grassland before returning to woodland type gardens (J. Herd, Howick, South Africa, personal communication). When eggs or juveniles are placed in a different environment by females, their migration becomes obligatory as they age.

Seasonality

Many of the studies that have been conducted on chameleons over time have suggested some degree of seasonality in density, reproduction, and other life-history traits. Lin and Nelson (1980) studied two Kenyan species, finding that *Trioceros hoehnelii* was aseasonal, while *T. jacksonii* showed distinct seasonal patterns of reproduction in both males and females. *T. jacksonii* gave birth in January, when insect abundance peaked. Despite the comparative aseasonality, the reproductive output of *T. hoehnelii* was found to be significantly reduced in the dry season (Lin and Nelson 1980), suggesting that reproduction is linked to climatic parameters.

Chameleon densities have been found to be lower in winter than in summer at one eastern Malagasy site for some species (*Brookesia nasus, B. superciliaris, Calumma brevicorne,* and *C. oshaughnessyi*) (Brady and Griffiths, 2003), while for others there was no change (*C. gastrotaenia*), or even an increase in winter densities (*C. nasutum* 51.7 ha^{-1} in winter as compared with 16.7 ha^{-1} in summer). Density fluctuations between seasons are suggested to correlate with body size (Brady and Griffiths, 2003). Similarly, at Ranomafana National Park, density estimates were greater in the summer (*B. superciliaris,* 39 ha^{-1}; *B. nasus,* 41 ha^{-1}; *B. thieli,* <0.1 ha^{-1}) as compared with the winter (*B. superciliaris,* 14 ha^{-1}; *B. nasus,* 6 ha^{-1}; *B. thieli,* <0.1 ha^{-1}) (Rabearivony, 1999). Smaller-bodied chameleon species at Andranomay (*C. glawi* and *C. nasutum*) displayed increases in population density between the summer and winter seasons, while the densities of larger-bodied species (*C. brevicorne* and *C. oshaughnessyi*) tended to decline over the same period (Brady and Griffiths, 1999).

Despite the considerable seasonal variation in densities of chameleons, there is little explanation of why some individuals are active and others inactive during unfavorable seasons. An unpublished study on *Bradypodion pumilum* suggests that reduced winter densities are not attributable to a reduction in population size, but rather to a reduction in the number of animals seen on exposed perches during winter. Different animals were found roosting on different nights, with the total number of observations related to weather conditions (K. Dicks, personal communication). Conversely, some species really do have a dramatic change in their seasonal abundance (Box 5.1), and it remains to be seen how widespread this phenomenon is.

Individual chameleons may disappear during winter in very cold or high-elevation areas, when they are thought to hibernate. Anecdotal reports suggest *C. calcaricarens* may aestivate during winter in Jijiga, Ethiopia (Spawls, 2000). *Bradypodion thamnobates* in the Drakensberg have been seen to move inside houses or under boxes in garages, remaining inactive for many months. *Rhampholeon marshalli* has diapause for around 6 months in the

Vumba Mountains of Zimbabwe (1730 m asl) (Broadley and Blake, 1979). Aestivation may also occur in extremely dry seasons (see Box 5.1). Like other lizards, chameleons appear to seek out dry and stable conditions in which to aestivate.

Growth and Longevity

Most reports of chameleon growth appear to come from animals bred in captivity, with relatively few studies conducted in natural populations. One notable exception compared the growth of caged juveniles (but not adults) with those from recaptures of *Trioceros hoehnelii* and *T. jacksonii,* finding that caged individuals had a significantly lower average growth rate (~0.05 $\text{mm} \cdot \text{d}^{-1}$) than recaptured animals (~0.1 $\text{mm} \cdot \text{d}^{-1}$) (Lin and Nelson, 1980). Burrage (1973) found a mean growth rate of 0.17 $\text{mm} \cdot \text{d}^{-1}$ for *Bradypodion pumilum* between birth and maturity, which he considered to be at 50 mm snout–vent length (SVL) (but see Jackson et al., in review, and below). He also found that growth rates changed during the year, reaching up to 0.29 $\text{mm} \cdot \text{d}^{-1}$ for animals born in November at the start of the austral summer. For *Chamaeleo namaquensis,* Burrage (1973) found sexually different growth rates with 0.25 $\text{mm} \cdot \text{d}^{-1}$ for males and 0.38 $\text{mm} \cdot \text{d}^{-1}$ for females. Burrage (1973) commented on a number of other studies (e.g., Brain, 1961) of growth rates of captive animals, noting that none compared with animals in the wild. It is likely that an advance in husbandry techniques has resulted in many captive chameleons able to grow at rates equivalent to or even faster than those in the wild (C. Anderson, personal communication). Yet, the information on natural growth rates is generally lacking (but see Box 5.1).

An important life-history variable is the time to maturity, which in lizards is generally longer with increasing body size. Chameleons appear to conform to this rule, with one of the largest species, *Chamaeleo parsonii*, taking 3 to 5 years to reach maturity (Brady and Griffiths, 1999). Lin and Nelson (1980) calculated growth rate and size of smallest mature female or male based on birth size. Their results suggested that *Trioceros hoehnelii* males and females reached maturity within a year, while *T. jacksonii* took just under 2 years. In both cases, females matured up to 20% more quickly than males. Burrage (1973) calculated that male *C. namaquensis* matured in 210 days, while females took only 150 days to achieve a slightly larger size at maturity. Jackson (2007) found the opposite for *B. pumilum,* in which males mature at a smaller size (41 mm) than females (53 mm); yet, both were mature in 18 months. Wager (1958; in Schaefer, 1971) states that *C. dilepis* can mature within a year. However, many Malagasy chameleons appear to reach maturity at large sizes within a single season, such as *Furcifer labordi* (see Box 5.1) and *F. campani,* which reach maturity in 3 months (Raselimanana and Rakotomalala, 2003). In captivity, other species are similarly reported to reach maturity relatively quickly: *F. willsii,* 4 months; *F. minor,* 5 months; *C. brevicorne,* 8 months (Le Berre, 1995).

The life span of most tetrapods has generally been found to correlate with body size (Blanco and Sherman, 2005), and there are some data to suggest that the largest chameleons are long-lived: *Trioceros melleri* may live as long as 12 years in captivity (Le Berre, 1995), while *T. montium* often lives beyond 9 years (Klaver and Böhme, 1992).

Longevity of wild chameleons is very poorly documented, with the majority of studies coming from animals bred in captivity. As chameleons are notoriously hard to keep in captivity, it is hard to estimate the bias these kind of data may introduce.

Longevity has been calculated from maximum sizes observed in the field, and growth rate of mature individuals (Lin and Nelson, 1980). Male and female *Trioceros hoehnelii* were found to have a similar longevity of around 4.5 years, while for *T. jacksonii,* smaller males have a shorter life span by as much as a third of the 6.6-year expected life span of females. *Furcifer pardalis* was studied using skeletochronology and showed that although adults were large, most individuals had a single line of arrested growth (LAG). Andreone et al. (2005) interpreted this as evidence that animals were around 1 year old (the largest individual in their sample was the only animal with 2 LAGs). There is some suggestion, that chameleons that grow fast may also die young (see Box 5.1), although exactly how widespread this phenomenon is within chameleons remains unknown.

Survival rates for smaller *B. pumilum* were found to be lower (from 0.49 for 45 mm SVL) than larger animals (0.98 for 80 mm SVL) over a single season (9 weeks) within the Cape Town metropolitan area (Tolley et al., 2010). While there have been no other formal studies of survival, Burrage (1973) estimated that 40% of his marked *B. pumilum* survived the 3-year duration of his study, and Bourgat (1968) recorded survival of 43% of *F. pardalis* after a single year.

5.3 FORAGING AND DIET

Diet has been poorly documented for chameleons, but they are known to eat, at least occasionally, relatively large prey (e.g., Broadley, 1973; Luiselli and Rugiero, 1996; Herrel et al., 2000; Keren-Rotem et al., 2006). Yet, most studies of fecal remains suggest they are opportunistic predators of invertebrates (Burrage, 1973; Pleguezuelos et al., 1999; Akani et al., 2001; Hofer et al., 2003). Chameleons have excellent visual acuity, which allows the assessment of prey from a distance (Ott and Schaeffel, 1995; Chapter 2). They have large heads and exhibit strong tongue retractors with supercontractile properties that can relay large items into the mouth (Herrel et al., 2001b; Chapter 4). Chameleons are also known to have a relatively high bite force (Vanhooydonck et al., 2007), which may be related to a diet of hard or oversized prey items, and/or to intrasexual and intersexual combat involving fighting and the biting of opponents (Bustard, 1967; Stuart-Fox and Whiting, 2005; Tolley and Burger, 2007; Measey et al., 2009; Chapter 6). Like other lizards, many chameleons are known to drink free-standing water by lingual protrusion.

Cruise Foraging

Chameleons are lizards that do not conform to either sit-and-wait or active foraging strategies. Instead, it has been proposed that they have an unusual intermediary behavior, termed “cruise foraging” (Butler, 2005; see also, Williams and McBrayer, 2011 for an alternative explanation). A cruise forager examines its environment, moves a short distance, and then conducts more scans (Regal, 1978). As a cruise forager makes these short movements within its environment, it would be expected to encounter sedentary prey in addition to active prey. Increases in movement would logically result in more encounters with sedentary prey and a commensurate reduction of active prey in the diet. Based on behavioral observations, the South African Cape Dwarf Chameleon, *Bradypodion pumilum,* conformed to this intermediary foraging mode (Butler, 2005), and more recently the same behavior was found in an invasive population of *Trioceros jacksonii* in Hawaii (Hagey et al., 2010). Cruise foraging suggests a similar proportion of active and passive prey types as compared with those in the environment, and Measey et al. (2011) found exactly this for *B. pumilum* from heathland habitats. However, ecomorphs from wooded habitats were found to have more active prey, suggesting that the degree of cruising may change in proportion to the availability of active and passive prey types. There is also a suggestion of ontogenic adjustment as Keren-Rotem et al. (2006) found that prey of adults were more sedentary than those of juvenile *C. chamaeleon*.

Although lingual capture appears to be the dominant method of chameleon feeding, there are also anecdotal reports that chameleons pursue and capture prey in their jaws, although these need to be confirmed (see Takashi, 2008, and below). *Chamaeleo namaquensis* is notable in that it inhabits an area with very low abundance of prey and appears to have moderated its behavior. Burrage (1973) described *C. namaquensis* running parallel with prey and then taking the prey in their jaws; however, other observations record these chameleons running after prey and simultaneously using lingual capture (M. Burger, personal communication). It was also noted that *C. namaquensis* are capable of searching for or ambushing prey that hides during pursuit (Burrage, 1973). Neither of these behaviors appears to fit into the cruise-foraging mode described by Butler (2005), and it may be that the Chamaeleonidae exhibit a range of foraging strategies.

Chameleon Diet

In their study of the diet of three sympatric chameleons in a Nigerian forest, Akani et al. (2001) suggested that some were more generalist (*Chamaeleo gracilis*) than others (*Trioceros cristatus*), based on relative niche overlap estimates (see Pianka, 1986). However, this method presumes good sample sizes for all taxa compared, and it is notable that the most specialized species had the smallest sample size (only 15 fecal pellets). Only two studies have attempted to compare potential prey to those ingested by chameleons. In the first, three montane chameleons from Cameroon (*Trioceros montium, T. pfefferi,* and *T. quadricornis*) had a niche breadth almost equal to the resources available (Hofer et al., 2003). Measey et al. (2011) analyzed prey in terms of hardness and evasiveness for two ectomorphs of *B. pumilum,* finding that the ecomorph in open habitat was neutral with respect to both measures, while those from woodland appeared to select more soft items (avoiding hard ones) and consume less sedentary prey. They interpreted these differences to differing availability of prey abundance and suggested that this may change in different seasons.

Seasonal changes in the diet of *Bradypodion pumilum* (woodland ecomorph) were most prominent in the change in the proportion of dipterans, which peaked at 80% in autumn and winter and sunk to 13% in spring (figures calculated from Burrage, 1973). Similarly, a peak in ground-dwelling carabids (up to 15%) also occurred in the winter months (Burrage, 1973). Marked seasonal changes in diet have also been observed in a population of *Chamaeleo chamaeleon* in southeastern Spain (Pleguezuelos et al., 1999), where hard hymenopteran taxa (mostly bees and wasps) made up the greatest part of *C. chamaeleon* diet in spring. By summer through to autumn, the major dietary component was orthopterans, the largest of prey in their study. Pleguezuelos et al. (1999) suggest that this shift represents a change in orthopteran availability and the more terrestrial nature of animals in summer, when males spend more time on the ground and females are found lower in the trees (see above). The other surprising finding in their study is the small size of some prey in relation to that of the chameleon, to which they conclude that chameleons typically rely on many small items (from 1.1 mm or 0.7% of SVL), rather than taking larger more infrequent meals. A study of invasive *Trioceros jacksonii* in Hawaii similarly remarked on the large number of small prey eaten by even the largest animals (Kraus et al., 2012). Similarly, small-volume prey were found in all sizes of *C. dilepis* dissected from museum specimens (Reaney et al., 2012). Bringsøe (2007) observed a subadult *Archaius tigris* predating on worker ants (*Technomyrmex* cf. *albipes,* 2 to 2.5 mm) at the start of the dry season on Praslin in the Seychelles Islands, and Keren-Rotem et al. (2006) observed adult *C. chamaeleon* eating a fruit fly. Although not analyzed by Hofer et al. (2003), their data suggest neutral selection on prey hardness across all species but with some selection toward prey evasiveness for *Trioceros montium*. Although there is little evidence for specialization in the chameleon diet, future studies may find that in optimal conditions chameleons may select particular prey types.

Dietary differences are expected where chameleons inhabit different habitats, partition microhabitats, and/or vary greatly in body size. The most obvious dietary divergence might be expected between small, ground-dwelling genera (*Rhampholeon* and *Brookesia*), and large arboreal species within the same forest (i.e., *Trioceros, Kinyongia, Furcifer,* and *Calumma*). Akani et al. (2001) found that *R. spectrum* had the least food niche overlap with three other sympatric arboreal species (*C. gracilis, T. cristatus,* and *T. owenii*). Perhaps unsurprisingly, this significant dietary difference extended to prey size, which was significantly smaller for *R. spectrum* (most items <3 mm). Indeed, leaf chameleons are able to make use of abundant social insects, such as termites (Wild, 1994). The shift to smaller foods in smaller chameleons is expected, as large lizards tend to have a wider range of food sizes available (Vitt, 2000). Hofer et al. (2003) examined fecal pellets of several different chameleon species in Cameroon, finding that prey size was significantly smaller in the smaller species studied. This indicates that most small chameleons are size-restricted in their feeding. This could be considered surprising, as chameleons are known for their high bite force (Vanhooydonck et al., 2007), which may help to reduce large prey items to an ingestible size (Measey et al., 2009). However, a more recent study of diet and bite force in two ecomorphs of *Bradypodion pumilum* suggested that diet is not dependent on the use of high bite forces (Measey et al., 2011).

There is some evidence that chameleons may position themselves in places where prey is abundant. Animals are often found in tree clearings and forest-edge ecotones, where invertebrate activity is also increased. Forest streams and ponds may be frequented for the same reason (Bringsøe, 2007; Jenkins et al., 2003; G.J. Measey, personal observation—see above), although there may be other reasons that these areas are selected (Jenkins et al., 2003). In urban Madagascar, *Furcifer pardalis* is well known to use flowering plants (e.g., *Lantana camara*) or trees (e.g., Jacaranda or fruit trees). Gardeners often remark that chameleons will favor particular plants in bloom (see also, Parcher, 1974), and this has been borne out in surveys (e.g., Tolley and Measey, 2007). *Bradypodion pumilum* and *B. occidentale* have both been observed moving to the supratidal zone to feed on abundant flies and tenebrionids there (Burrage, 1973). *Chamaeleo namaquensis* has been observed moving into the intratidal zone to feed on the abundant arthropods present (Burrage, 1973). Loveridge (1953) remarked that *Rieppeleon brachyurus* was noted to gather around fruit (Mikwambi) eating the small fruit flies that are attracted to it. Similarly, *R. kerstenii* were found gathered around fresh goat feces in Kenya, eating the flies that were attracted to it (J. Measey, personal observation).

Vertebrates in the Diet

While chameleon prey can generally be described in terms of opportunistic selection of invertebrates of appropriate size, there are many examples noted in the literature of chameleons ingesting vertebrate prey. The largest chameleons, such as *Trioceros melleri,* have been kept in captivity and are widely reported to consume small birds and mice (Broadley, 1966; Nečas, 2004). Nigerian *T. cristatus* held in captivity are known to readily eat frogs and newly metamorphosed toads (Reid, 1986). However, documented examples of natural predation of vertebrates are more unusual. Capture of a bird (presumably an adult *Foudia madagascariensis*) by one of the largest chameleons (*Furcifer oustaleti*) went unseen, although the chameleon was seen with the bird in its mouth, which was then swallowed whole (García and Vences, 2002). Widespread reports of *T. melleri* eating red-billed firefinch (*Lagonosticta senegala*) and a Cordon Bleu (*Uraeginthus bengalus*) (e.g., Pitman, 1958; Broadley, 1973; Hockey et al., 2005), all stem from reports in Loveridge (1953). Although not in the original report, Pitman (1958) asserts that that these small birds were captured through lingual projection. There are assertions that other large chameleons, such as *F. parsonii,* also eat small birds and day geckos (*Phelsuma* spp.: Le Berre, 1995; Brady and Griffiths, 1999; Abate, 1998; Raselimanana and Rakotomalala, 2003). Although there are no reports of chameleons predating on nestlings, this does not seem unreasonable, and support for this hypothesis comes from reports of nesting adult birds mobbing chameleons (Paxton, 1991; Masterson, 1994, 1999). *Chamaeleo namaquensis* is documented to consume lizards, including day geckos (*Rhoptropus afer*) and lacertids (presumably, *Meroles* spp.). Moreover, small feathers and hairs have been found in fecal pellets (Burrage, 1973). Indeed Burrage (1973) reported that this chameleon has been observed to capture a Namib dwarf sand-adder (a 200-mm *Bitis peringueyi*). These records are all unsurprisingly from large chameleons (the mean snout–vent length of these species is 255 mm, as compared with 94 mm for other chameleons, or 110 mm, excluding leaf chameleon species), as large lizards often tend to include both vertebrate and invertebrate food items in their diet (Meiri, 2008).

Vertebrates may not be unusual dietary items of chameleons when they are abundant in the environment, and this is borne out by several of the relatively few dietary studies finding small vertebrate prey: frogs and lizards (Luiselli and Rugiero, 1996; Akani et al., 2001; Measey et al., 2011; Reaney et al., 2012).

Cannibalism

Chameleons are also widely reported to be cannibalistic (e.g., Broadley, 1966), although most instances of this are known from captivity, where animals are kept in confined conditions (but see Parcher, 1974). Similarly, large chameleons may eat smaller chameleons of different species, although again, the only records are from captive individuals (e.g., Ionides, 1948, in Loveridge, 1953). Keren-Rotem et al. (2006) observed an adult *Chamaeleo chamaeleon* predate a juvenile in the wild, and suggested that the risk of cannibalism in may be avoided by shifts in habitat use (see above).

Herbivory

Insectivorous lizards are also known to be, at least occasionally, herbivorous (Cooper and Vitt, 2002; Herrel, 2007). Chameleons are not widely recognized to deliberately ingest plant matter, with most instances attributed to accidental ingestion with prey (Burmeister, 1989; Schwenk, 2000; Cooper and Vitt, 2002). However, both *Chamaeleo calyptratus* and *C. chamaeleon* are regularly observed to eat plants and fruit in captivity (A. Herrel, personal observation), and reports of this can also be found in the literature (Lutzman, 2000). It may be expected that xeric-adapted chameleons may regularly ingest plant matter in order to supplement their water intake, as is generally true of other lizards in these conditions (Herrel et al., 2007b). Support for this view comes from the data of Burmeister (1989), who consistently found vegetal matter (seeds, leaves, flowers, leaf buds) in the diet of *C. chamaeleon* in arid Libya, and Keren-Rotem et al. (2006) who found fruit in the diet of most adults (but not juveniles) of *C. chamaeleon* in Israel. However, a detailed dietary study in less arid southeastern Spain did not report any plant matter (Pleguezuelos et al., 1999). Interestingly, *C. namaquensis* caught in the coastal areas of the Namib ate a higher proportion of plant matter than those caught inland (Burrage, 1973). Moreover, Burrage (1973) noted that of the plant matter ingested, principle items were the fleshy leaves of the dollar bush (*Zygophyllum stapffi*). It is possible that, like other lizards, chameleons in xeric habitats (e.g., *Chamaeleo calcaricarens*) will be found to regularly utilize plant matter in their diet.

Takahashi (2008) made a remarkable study of frugivory in *Furcifer oustaleti*. He observed an adult approaching a bunch of fruit (red fruit, 20 by 15 mm, of *Grangeria porosa*) and pulling them toward the mouth with a foot, whereupon half a fruit was bitten off and ingested. Burrage (1973) also notes that *C. namaquensis* often used its front feet to assist manipulation of oversized prey items. Takahashi (2008) saw a juvenile *F. oustaleti* deliberately take and ingest three small round black fruits of *Chassalia prince*. While both of these observations involved jaw prehension of the fruit, a further observation was made of an adult using lingual projection on a red fruit of *Malleastrum gracile*. One attempt was successful, but when the tongue failed to loosen another fruit, the chameleon walked up and used jaw prehension to take it. In an experiment with the same species, Takahashi (2008) found that jaw prehension was the norm for fruit, while tongue projection was generally used for flies, but he found exceptions to each. Not only is the observation that tongue projection was used on a fruit of interest, but the whole study took place during the wet season, when food was relatively abundant, suggesting that this large chameleon from an arid region of Madagascar regularly ingests fruit.

5.4 PREDATORS

A comprehensive review of predation on chameleons has not been undertaken. Here, the principle types of predators that consume chameleons are considered, with more attention to those that specialize in this prey type. Accounts of birds predating on chameleons may well be disproportionate in the literature because of observational bias. Similarly, there are many reports of the gut contents of snakes, and these may inflate their importance as predators as compared with some other groups, especially the invertebrates.

Chameleons are not likely to be able to flee from predators (although several authors remark at how fast chameleons are able to move: Spawls, 2000; Cuadrado et al., 2001; cf. Herrel et al., 2011) and instead need to rely on crypsis or active defense involving threatening behavior. As many are arboreal lizards, their chief predators are considered to be climbing mammals, birds, and snakes (Branch, 1998; Spawls, 2000). In addition, many authors comment on the increased vulnerability of female chameleons to predators while in the process of laying eggs (see above). In their review of predation of chameleons in Madagascar, Jenkins et al. (2009) found that birds outnumbered all other taxa recorded as chameleon predators. Yet, as noted earlier, this may reflect an investigatory/reporting bias. In addition to 19 species of birds, they found records for 5 snakes, 2 frogs, 1 primate, and 1 carnivore.

Invertebrates

Of all chameleon predators, the invertebrates probably exert the highest of all predatory pressures. Chameleon eggs are very vulnerable to many subterranean invertebrate predators, especially army ants (*Dorylus* spp.)m which predate upon most of what they encounter both above and below the ground. Ants are easily capable of overwhelming juveniles and possibly even adults if they do not flee their swarming raids (Lin, 1980). Viviparous chameleons are likely to avoid a large portion of predation risk from ants, but even their offspring are vulnerable, especially immediately after parturition (e.g., Bustard, 1966). Juvenile chameleons and small adults are also known to fall prey to large spiders and mantises (Parcher, 1974).

Amphibians

Medium-sized and large anurans occasionally predate upon small chameleons (Wild, 1994, Jenkins et al., 2009). *Amietophrynus camerunensis* is known to predate upon *Rhampholeon spectrum,* and there is an inverse relationship in the abundance of these toads and the chameleons (Wild, 1994), although Wild did not suggest predation as the cause, but rather competition. In Madagascar, one chameleon hatchling (genus *Furcifer* or *Calumma,* measuring 40 mm in total length) was found in a stomach of a *Mantidactylus femoralis* (42 mm SVL: Vences et al., 1999) and a *Ptychadena mascareniensis* preyed upon a juvenile *Furcifer lateralis* (D'Cruze and Sabel, 2005).

Snakes

Snakes probably have the largest predatory impact on adult chameleons, given that they do not solely rely on visual stimuli to find prey, thus allowing them to find cryptic, stationary prey, including chameleons. Many colubrid snakes are arboreal hunters that may rely on chameleon prey, although only few instances have been reported (Jenkins et al., 2009). In addition, terrestrial snakes (like the Malagasy *Pseudoxyrhopus ambreensis*) are known to prey upon chameleon eggs (Knoll et al., 2009).

In sub-Saharan Africa, the arboreal boomslang (*Dispholidus typus*) is a venomous colubrid snake that is known to take considerable numbers of chameleons (Haagner and Branch, 1993; Branch, 1998) and that in some situations may rely solely on chameleon prey (Loveridge, 1953). Vine snakes (*Thelotornis kirtlandii, T. capensis, T. mossambicanus,* and *T. usambaricus*) are all known to predate on chameleons, including terrestrial species (Loveridge, 1923; Menegon et al., 2009). Around half of all prey of *T. capensis* were found to be arboreal, including chameleons and day geckos (Shine et al., 1996), and Broadley (1983) suggested that these snakes are lizard specialists. Arboreal snakes from the genus *Philothamnus* (including *P. irregularis, P. semivariegatus,* and *P. angolensis*) are also widely reported to predate on chameleons (Lin and Nelson, 1980; Broadley, 1983). *Rhamnophis aethiopissa* and *Hapsidophrys lineatus* were both reported to be predators of *Rhampholeon* in West Africa (cf. Luiselli et al., 2000, 2001; Akani et al., 2001). Juveniles of large species, such as the green mamba (*Dendroaspis angusticeps*), also rely on small prey such as birds, their eggs, chameleons, and geckos (Broadley, 1983; Lloyd, 1974). These and other arboreal snakes are likely to be predators of most chameleons; for example, adult *Furcifer oustaleti* have been ingested by both terrestrial and arboreal snakes (*Madagascarophis colubrinus* and *Ithycyphus oursi*) (A. Raselimanana, personal observation; Crottini et al., 2010). A nighttime observation of predation of a *Brookesia superciliaris* by a *Parastenophis betsileanus* (Kaloloha et al., 2011) shows that roosting behavior is not always successful to escape from predation by snakes.

Chameleons often respond to the presence of snakes by dropping off their perch, both during the day and at night. The meticulous selection of perch sites, on isolated or distal branches or leaves, may be to avoid snakes by receiving advance warning of their presence, and/or because the perch cannot support the weight of the snake (or other predators). Stuart-Fox et al. (2006a) also found that chameleons become brighter when threatened by model snake predators (see Chapter 6). Lloyd (1974) made some interesting observations of two different arboreal snakes presented with *Chamaeleo dilepis.* Snakes were presented with a lateral view, heightened compression, extended gular region, and straightened legs, giving the impression of larger size (see also Stuart-Fox et al., 2006a). Moreover, the chameleon swayed and became very pale. Close inspection by the snake resulted in rapid jerking movements by the chameleon. Although this behavior allowed the chameleon to avoid predation by a green mamba, a boomslang quickly approached and ate the chameleon (Lloyd, 1974). These observations suggest that antipredator responses may be effective only against nonspecialist predators.

In addition to arboreal snakes, most snakes that eat lizards or frogs and that come across a chameleon of appropriate size are likely to eat it. For example, *Bradypodion ventrale* was found in the gut of *Crotophopeltis hotamboeia* and *B. dracomontanum* was regurgitated by *Psammophis crucifer* (Haagner and Branch 1993). The Namaqua dwarf adder (*Bitis schneideri*) was found predating on *B. occidentale* (Wessels and Maritz, 2009). In Israel, chameleons are predated by several snake species (e.g., *Malpolon monspessulanus, Hemorrhois ravergieri;* Keren-Rotem et al., 2006).

Mammals

Many small mammals may opportunistically take chameleons. For example, in Namibia *Chamaeleo namaquensis* is predated by the jackal *Canis mesomelas* (Burrage, 1973). Small arboreal carnivores, such as *Martes foina,* take *Chamaeleo chamaeleon* in Israel (Keren-Rotem et al., 2006). In addition, arboreal carnivorous mammals, such as civets and genets are likely to predate chameleons. Andriatsimietry et al. (2009) reported the presence of chameleon in the feces of the mongoose, *Galidictis grandidieri*, in southwestern Madagascar. *Calumma brevicorne* eggs have been reported to be vulnerable to predation by invasive *Rattus rattus* (Parcher, 1974). Broadley and Blake (1979) report that likely predators of *Rhampholeon marshalli* include civets and genets. Jenkins et al. (2009) report predation on chameleons by the Malagasy civet (*Cryptoprocta ferox*) and a lemur (*Lemur catta*). It is possible that many other primates would eat chameleons, but there are few reports of this in the literature.

A Malagasy mongoose *Galidia elegans* was observed attacking a large male *Calumma ambreense* in Montagne d'Ambre (A. Raselimanana, personal observation). The chameleon stayed in a vertical position along a small tree at 1.30 m from the forest floor. This terrestrial carnivore attempted to catch the chameleon by jumping several times before climbing onto a fallen log to get close. The mongoose was observed to attack the eyes first, and then tried to remove the hands of his victim from the support.

Birds

Although there are a large number of bird species that occasionally eat chameleons (e.g., *Larus hartlaubii;* see Hockey et al., 2005), there are considerably fewer that regularly have chameleons as part of their diet. Birds that regularly take chameleon prey include various raptor species, shrikes (Laniidae), helmetshrikes (Prionopidae), puffback shrikes, bush shrikes, tchagras and boubous (Malaconotidae), cuckoo-shrikes (Campephagidae), cuckoos (Cuculidae), rollers (Brachypteraciidae and Coraciidae), hornbills (Bucerotidae), and barbets (Lybiidae). Jenkins et al. (2009) reported a taxonomic division between avian predators and chameleon prey corresponding to the main division within terrestrial and arboreal chameleons. In the canopy, both specialists (e.g., *Eutriorchis astur* and *Falco zoniventris*) and generalists (e.g., *Buteo brachypterus*) predate on arboreal chameleons (*Furcifer* and *Calumma*). While on the ground, generalists (e.g., *Brachypteracias leptosomus*) forage in the leaf litter consuming terrestrial species (*Brookesia*). Interestingly, nocturnal birds were rarely found to predate on Malagasy chameleons.

Shrikes are predators of southern African *Bradypodion* chameleons, and are famed for hanging their prey on thorns (e.g. Wager, 1986; Branch, 1998; Tolley and Burger, 2007). The common fiscal (*Lanius collaris*) was used as a model predator by Stuart-Fox et al. (2006a), who found that *Bradypodion transvaalense* readily avoided these predators (see Chapter 6), and these authors considered that common fiscals are likely to exert a strong selection on chameleon antipredator responses. However, the substantial grip of some individual chameleons (see Herrel et al. 2011; Chapter 4) may help them to escape predation from at least some shrikes. In Cape Town, an adult common fiscal was seen trying to remove an adult *Bradypodion pumilum* from its perch on a reed by using its weight to hang from a single limb (G.A. Millar, personal communication). Despite this predation attempt going on for over 10 minutes, the bird finally flew away leaving the chameleon apparently unscathed. Most shrikes inhabit open habitats and are therefore likely to predate on savanna, grassland, and heathland chameleons (see above), but there are a few species that also inhabit forests. Other predatory birds inhabit dense forests, where chameleons may also be vulnerable to these predators. Broadley and Blake (1979) suggested that shrikes were important predators of *Rhampholeon marshalli,* and Hockey et al. (2005) record chameleons as prey items for the grey-headed bushshrike (*Malaconotus blanchoti*). Similarly, hornbills mostly inhabit more open habitats such as woodland and savanna, where they are regularly seen taking chameleons as prey (see Tolley and Burger, 2007). Hockey et al. (2005) report five species of hornbills to have chameleons in their diets (*Tockus damarensis, T. alboterminatus, T. leucomelas, T. monteiri,* and *Bucorvus leadbeateri*). Other generalists likely to be significant predators of chameleons are the barbets and boubous, of which Hockey et al. (2005) report chameleon prey for *Centropus burchellii* and *Laniarius aethiopicus*.

Jenkins et al. (2009) list several raptors as the principle avian predators of chameleons on Madagascar. In mainland Africa, three raptors stand out as likely to exert substantial predation pressure on chameleons. The African cuckoo-hawk (*Aviceda cuculoides*) has been found to specialize on chameleons in southern Africa. *Chamaeleo* and *Bradypodion* made up 6 of 25 prey items in South Africa, *C. dilepis* 20 of 39 prey items in Zimbabwe and 32 of 51 prey items in Kenya (Hockey et al., 2005; W. Tarburton, personal communication). Lin and Nelson (1980) suggest that the main chameleon predators in Kenyan highlands include lizard buzzards (*Kaupifalco monogrammicus*), which have a large distribution over much of sub-Saharan Africa. Lastly, the forest buzzard (*Buteo trizonatus*) is probably a substantial predator of chameleons. As chameleons range into more specialized terrain, the predatory avifauna will also change. Indeed, Burrage (1973) stated that the arid zone *Chamaeleo namaquensis* is predated upon by several opportunistic raptors (*Falco rupicolis, F. terinunculus,* and *Melierax musicus*).

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APPENDIX

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.

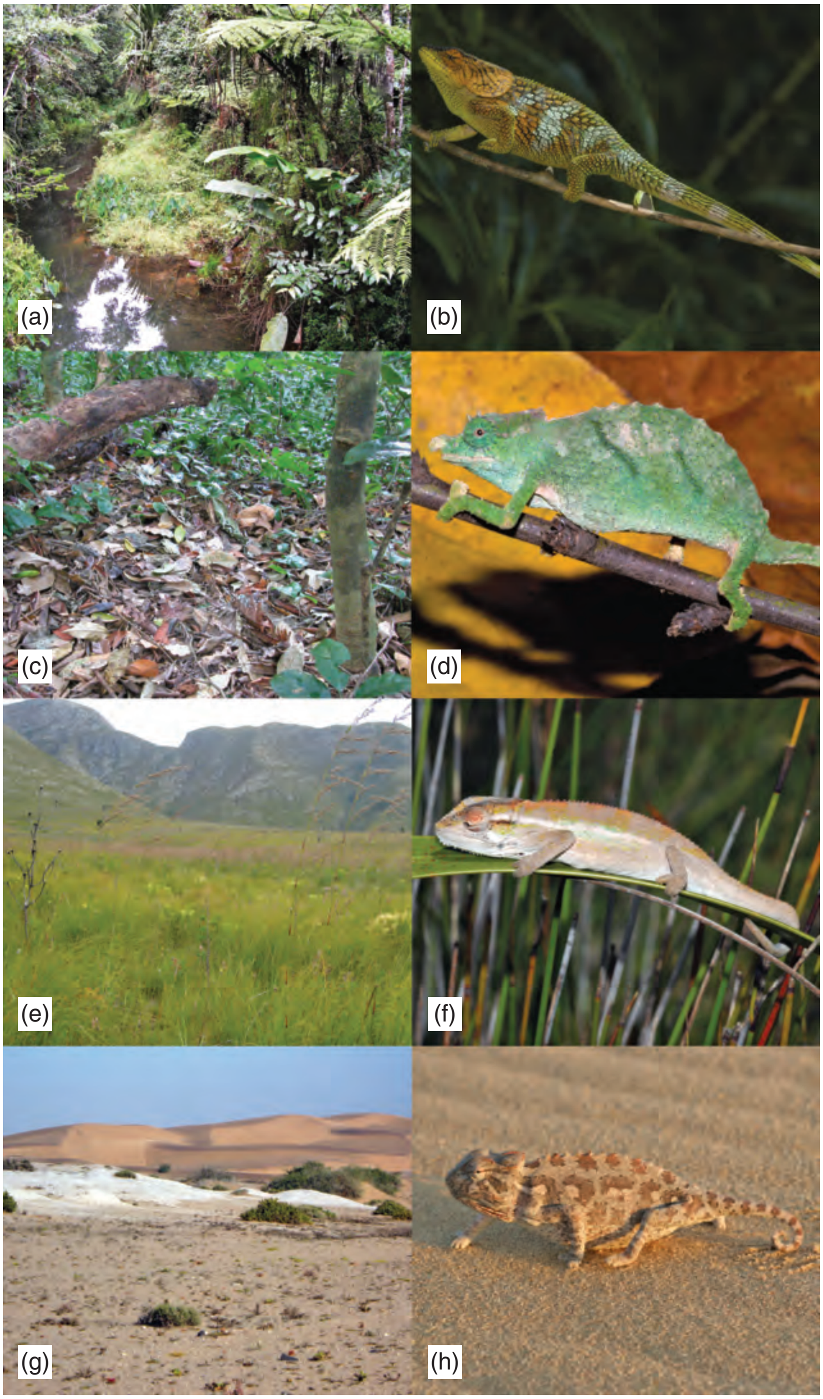

FIGURE 5.1. Diverse body forms and habitats of chameleons from forest, heathland, and desert habitats. A typical forested habitat (a), inhabited by *Calumma amber,* in northern Madagascar (b). The leaf-litter and associated low vegetation of forests (c), provides the habitat for leaf chameleons such as *Rhampholeon acuminatus* in East Africa (d). Some members of the genus *Bradypodion* inhabit fynbos, a southern African heathland habitat (e), like *B. taeniabronchum* from South Africa (f). Chameleons also inhabit desert environments (g) such as this area in western Namibia where *Chamaeleo namaquensis* lives (h).

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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