

Ecology of Three Sympatric Species of the Genus *Chamaeleo* in a Tropical Upland Forest in Cameroon

ULRICH HOFER,^{1,2} HANNES BAUR,³ AND LOUIS-FÉLIX BERSIER¹

¹Department of Vertebrates, Natural History Museum, Bernastrasse 15, 3005 Berne, Switzerland;
E-mail: ulrich.hofer@nmbe.unibe.ch

²Department of Invertebrates, Natural History Museum, Bernastrasse 15, 3005 Berne, Switzerland

³Zoological Institute, University of Neuchâtel, rue Emile-Argand 11, 2007 Neuchâtel, Switzerland

ABSTRACT.—The three species of chameleons inhabiting the primary forest on the western slope of Mount Kupe, Cameroon, *Chamaeleo montium*, *Chamaeleo pfefferi*, and *Chamaeleo quadricornis*, are compared with respect to elevational distribution, diet, and body size. *Chamaeleo montium* is restricted to lower elevations and markedly separated in elevational distribution from its congeners, which are exclusively found in the submontane forest. The three species prey almost entirely on arthropods, mostly coleopterans, heteropterans, hymenopterans, dipterans, and spiders; niche breadth values that incorporate prey availability are high and suggest opportunistic feeding. Niche overlaps are high with respect to prey type, but the smallest species, *C. pfefferi*, differs significantly from its congeners in terms of prey volume. Body size difference is largest between the two syntopic species, *C. pfefferi* and *C. quadricornis*, and identically low to the allotopic *C. montium*. The results on dietary segregation and morphological similarity are in accordance with competition limiting elevational distributions of the chameleons on Mount Kupe.

The Chamaeleonidae are a clade of old-world diurnal lizards (Klaver and Böhme, 1986), with 94% of species living on continental Africa or Madagascar. Most species are characterized by a unique combination of morphological adaptations to arboreal life, namely a laterally compressed body, a prehensile tail, and toes that are fused to form grasping pads. The documented natural history of individual species, however, is very limited. Field studies on chameleons are remarkably few (Tilbury, 1997) and deal mostly with species from open habitats of the Mediterranean and Africa and from Madagascar (e.g., Burrage, 1973; Lin and Nelson, 1981; Hódar et al., 2000). The ecology of most of the 54 species inhabiting continental African forests remains poorly known, in particular those restricted to the relic forests of the afro-montane Archipelago.

The Cameroon Highlands are an extensive volcanic mountain range running from Bioko Island to Mount Cameroon in the southwest on to the Bamenda and Adamawa Highlands in the northeast, with the Obudu and Mambila Plateaus extending into Nigeria. They support a diverse amphibian and reptile fauna, including eight species in the genus *Chamaeleo* (subgenus *Trioceros*), most of them montane endemics with restricted distributions. The remnant primary forest of one such peak, Mount Kupe, is inhabited by three species: *Chamaeleo quadricornis quadricornis* and *Chamaeleo pfefferi* are probably endemic to submontane and montane forests of Mount Kupe, the Bakossi and Mwanenguba Mountains, whereas *Chamaeleo montium* is reported from hill forest and farmland of the entire Cameroon Highlands (Euskirchen et al., 2000). Until recently *C. pfefferi* was only known from the type specimen, collected on Kupe and described by Tornier in 1900. Nine decades later, the species was rediscovered. Wild (1993) reported two specimens from Mwa-

nguba and one from Kupe and gave a brief description of a female.

Preserving forest habitats is among the priorities in chameleon conservation (Tilbury, 1997; Euskirchen et al., 2000). Because of selective logging and exploitation for firewood and building material, forest degradation on the western slope of Mount Kupe reached an elevation of 1200 m during the fieldwork of this study. *C. pfefferi*, the rarest and smallest of the three chameleon species encountered on Mount Kupe, is likely to be particularly vulnerable to this disturbance. If degradation continues in a similar way on the surrounding mountains, *C. pfefferi* will be severely endangered over its entire range. An ecological study on the herpetofaunal assemblage from the western slope of Mt. Kupe (Hofer et al., 1999, 2000) resulted in more data on this little known species and its two congeners. In this paper, we compare the ecology of the three species with respect to elevational distribution, diet, and body size.

MATERIALS AND METHODS

Mount Kupe (4°45'N, 9°42'E) in the Southwest Province of Cameroon, is a steep-sided, cone-shaped mountain 2064 m in height and covered by approximately 2100 ha of undisturbed closed canopy forest. Forest at elevations between 1000 and 1800 m is of the submontane type; below and above there are narrow transitional zones between submontane and lowland, and submontane and montane forest, respectively (Thomas, 1986). Primary forest below 900 m has largely been logged or is severely degraded. Mean annual rainfall on Mount Kupe is 4891 mm (Suchel, 1972). The rainy season lasts from April to October; of the remaining months, three receive less than 200 mm. Temperatures taken at the onset and completion of each sampling period ranged from 13.8°C (1900 m, night) to 23.8°C (900 m, day). A more detailed description of the study site is given in Hofer et al. (2000).

We acquired data on elevational distribution and

² Corresponding Author.

microhabitats between March and November 1994; dietary information and data on morphometry were collected during a five-week period in October and November 1995, at the end of the rainy season. We restricted fieldwork to primary forest on the western slope of the mountain, between 800 and 2064 m. Samples of the herpetofauna were taken along transects parallel to the contour line at night and in daytime, with equivalent sampling effort at 12 points between 900 and 2000 m, separated by 100 m in elevation (see Hofer et al., 1999). To estimate species' relative abundance at a given altitude, we marked individuals of *C. pfefferi* and *C. quadricornis* by clipping spines from their gular crests. In *C. montium*, because of a lack of comparably suitable appendages, we based individual recognition on morphometric data. This uncertainty could cause an overestimation of the species' abundance, but the recapture rates in the two other species (3.5 and 4%, respectively) suggest at most a small error.

Given the restricted range and potentially endangered status of *C. pfefferi* and *C. quadricornis*, we took all dietary and morphometric data from live animals, the former by keeping them in captivity for 1–4 days and collecting fecal pellets. These were removed from the cages, fixed in 3% formalin, stored in 75% ethanol and later examined under a stereomicroscope. Arthropod prey fragments usually consisted of the entire head, prothorax, legs, elytra, etc., and allowed for easy and unambiguous identification of major taxa (Table 1). Wings of soft bodied specimens such as flies and midges successfully resisted digestion.

We estimated prey volumes for all prey categories except minute prey types consumed by small numbers of chameleons (see Table 2). Volumes were obtained from the fecal pellets of 10 randomly selected individuals of each chameleon species. We randomly picked up to 10 fragments per prey category from the pellets, the number depending on the fragments available for volume estimates.

We investigated the invertebrate fauna by sweep net and Malaise trap samples at or near sites where chameleons were located, up to 5 m height in the vegetation (Table 1). These samples served as a reference collection, were helpful in identifying remnants in the pellets, and were used as rough estimates of prey availability, and of prey vertical stratification.

To assess whether a particular taxon is over- or underrepresented in a diet, we used a resampling method where 2000 "null" diets were generated for each *Chamaeleo* species. These theoretical diets had the same number of items as the observed diet and were built from the availabilities of the prey taxa for a particular *Chamaeleo* species. The null hypothesis that a prey taxon is consumed in proportion to its availability is tested by comparing its observed value in the diet with those from the resampling procedure. The two-tailed *P*-value is the proportion of resampled values smaller, or larger, than the observed one. Because multiple tests are performed for each diet, we applied a sequential Bonferroni correction (Rice, 1989).

Prey volumes were calculated with the formula for a prolate spheroid [$V = 4\pi/3 * (\text{length}/2) * (\text{width}/2)^2$]. Based on numbers, volumes (where estimated), and frequencies of occurrence for each prey type we computed dietary importance values I_i (Powell et al.,

TABLE 1. Density (number of individuals per hour of sampling) of invertebrates in the three major forest types on Mount Kupe. Taxa are ordered according to their overall abundance.

Taxon	Forest type		
	Lower transitional 900 m	Sub-montane 1000–1800 m	Upper transitional 1900–2000 m
Diptera	5.18	28.33	66.40
Coleoptera	11.88	22.36	8.53
Heteroptera	8.65	9.62	4.00
Arachnida	6.82	9.30	5.60
Orthoptera	4.57	7.08	8.00
Hymenoptera	0.12	5.92	5.87
Blattoptera	1.58	2.11	1.07
Isopoda	0.61	0.79	4.00
Collembola	0.06	1.59	2.13
Lepidoptera	0.55	1.27	0.80
Progoneata	1.34	0.63	0.27
Lepidoptera Larvae	0.37	1.00	0.27
Psocoptera	0.12	0.85	1.33
Trichoptera	0.06	0.48	0
Archaeognatha	0.18	0.32	0.27
Plecoptera	0.06	0.21	0.53
Dermoptera	0	0.32	0
Chilopoda	0	0.21	0
Gastropoda	0.12	0.11	0
Coleoptera Larvae	0.06	0.11	0
Thysanoptera	0	0.11	0
Annelida	0.12	0	0
Mantodea	0.12	0	0
Neuroptera	0.06	0	0
Odonata	0.06	0	0
Puppa	0.06	0	0
# of sampling periods	9	10	2
sample hours	17	19	4
# of individuals	702	1754	409

1990). As a measure of opportunistic feeding by the chameleons we used Smith's (1982) index of niche breadth FT , relating the proportions of prey taxa consumed to their abundance in the environment (Table 1). Interspecific differences in prey volumes were compared by Mann-Whitney tests.

The similarity in diet composition between two species was estimated with the symmetric niche overlap coefficient (Pianka, 1973). Because availability of food resources is not the same for all three species of chameleons, we computed dietary similarity using g -based values (Winemiller and Pianka, 1990). For food type i , the g_i -value is the geometric mean of its proportion p_i in the diet and of its electivity, which is the ratio of p_i to the relative availability of i . A permutation test used by Solow (1993) for the comparison of diversity indices was applied on the dietary raw data matrix to see whether observed overlaps between syntopic species differed from what would be expected if they select prey items indiscriminately (i.e., when no niche segregation in terms of prey category is involved). We performed a two-tailed test with 2000 per-

TABLE 2. Prey types and dietary niche breadths of three species of *Chamaeleo* on Mount Kupe, Cameroon. n_c : Total number of chameleons in each sample; n_i : Total number of invertebrates in the faeces; p_d : Proportion of each prey category in the diet. p_d values significantly smaller than their corresponding availability are marked by (-), those significantly larger by (+); $no.$: Number of individuals whose pellets contain items of the respective prey category. I : Dietary importance values (Powell et al. 1990). Prey volumes were estimated for categories marked by an asterisk (*). Standardized Smith's FT index of niche breadth: a value of 1 corresponds to a use proportional to resource availability; 95% confidence intervals are given in parentheses.

Prey category	<i>C. montium</i> $n_c = 35; n_i = 395$			<i>C. pfefferi</i> $n_c = 29; n_i = 488$			<i>C. quadricornis</i> $n_c = 43; n_i = 591$		
	p_d	$no.$	I	p_d	$no.$	I	p_d	$no.$	I
Arachnida*	0.142	28	0.114	0.041 ⁽⁻⁾	16	0.065	0.113	34	0.130
Progoneata	0.010	3	0.013				0.008	5	0.015
Plecoptera	0.003	1	0.004						
Orthoptera*	0.051 ⁽⁻⁾	15	0.098	0.006	3	0.013	0.007 ⁽⁻⁾	4	0.028
Blattoptera*	0.020	8	0.190				0.005 ⁽⁻⁾	3	0.082
Psocoptera				0.006	3	0.013			
Heteroptera*	0.243 ⁽⁺⁾	33	0.149	0.135	24	0.129	0.154 ⁽⁺⁾	36	0.159
Psylloidea*	0.008 ⁽⁺⁾			0.033	7	0.027			
Neuroptera	0.028	3	0.012						
Lepidoptera*	0.061 ⁽⁺⁾	10	0.077	0.016	8	0.111	0.025	14	0.046
Lepidoptera larvae*	0.028 ⁽⁻⁾	13	0.060	0.074 ⁽⁺⁾	17	0.078	0.046 ⁽⁺⁾	18	0.047
Diptera*	0.104 ⁽⁺⁾	9	0.043	0.172 ⁽⁻⁾	26	0.182	0.284	40	0.161
Hymenoptera*		23	0.079	0.182 ⁽⁺⁾	22	0.112	0.117 ⁽⁺⁾	30	0.088
Hymenoptera larvae*				0.012	3	0.099	0.017	7	0.033
Coleoptera*	0.281	32	0.157	0.322 ⁽⁺⁾	29	0.179	0.222	40	0.211
Coleoptera larvae	0.003	1	0.004						
Gastropoda							0.002	1	0.003
Arthropod eggs	0.020	1	0.009						
Smith's FT	0.939 (0.912-0.962)			0.880 (0.848-0.909)			0.868 (0.826-0.905)		

mutations, whereby within each prey category all individuals found to consume the respective category (the number values of Table 2) were randomly assigned to each of the two species tested. The same procedure was repeated with the importance values I , instead of g -values.

Morphometric comparisons were based on snout-vent lengths (SVL) and mouth-lengths (ML, measured with a caliper from tip of snout to angle of mouth) of the 10 largest individuals of each sex (Duellman, 1978), except for *C. pfefferi*, where only seven males were available. Means are given with ± 1 SD, and size ratios were computed using these means. We tested for significant differences in body size using Mann-Whitney U -Tests and applied Holm correction (Rice, 1989) for multiple comparisons.

RESULTS

In 1994, we observed 85 individuals of *C. quadricornis*, 49 *C. pfefferi*, and 55 *C. montium*. Each species occurred in a limited range of the altitudinal gradient (Fig. 1). *Chamaeleo montium* was found from the lowest elevations up to 1200 m. *Chamaeleo quadricornis* and *C. pfefferi* were confined to the submontane forest, covering an elevational range of 800 m and 900 m, respectively. *Chamaeleo montium* and *quadricornis* exhibited an "ecological contiguity" in elevational distribution (Dale, 1984), in that the upslope boundary of the former coincided exactly with the downslope boundary of the latter.

The largest species was *C. quadricornis* (males: SVL = 106 ± 23.2 mm, ML = 19 ± 3.2 mm, $N = 10$; females: SVL = 106 ± 18.9 mm, ML = 19 ± 2.9 mm, $N = 10$), followed by *C. montium* (males: SVL = 99 ± 8.7 mm, ML = 17 ± 1.8 mm, $N = 10$; females: SVL = 89 ± 9.3 mm, ML = 15 ± 0.8 mm, $N = 10$) and *C. pfefferi* (males: SVL = 76 ± 8 mm, ML = 14 ± 0.8 mm, $N = 7$; females: SVL = 70 ± 3 mm, ML = $13 \pm$

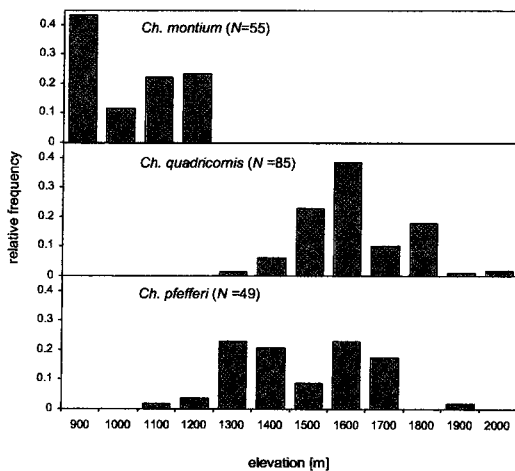


FIG. 1. Relative abundance of the three species of the genus *Chamaeleo* inhabiting the primary forest along the elevational gradient on the western slope of Mount Kupe, Cameroon.

0.9 mm, $N = 10$). Differences in SVL and ML were highly significant for the pairs *quadricornis-pfefferi*, *montium-pfefferi*, and female *quadricornis-montium*; nonsignificant body size differences concern male *C. quadricornis-C. montium*.

Remains in fecal pellets were grouped into 18 prey categories (Table 2). We found two to nine different prey categories in the feces of the specimens (mean 5.2 ± 1.4). The single nonarthropod prey item identified was a gastropod. Coleopterans, heteropterans, hymenopterans, dipterans, and spiders dominated, both in terms of proportional representation in the species' diets (up to 32% for a single category) and in the numbers of individuals that consumed them (Table 2). The reference samples (Table 1) contained all but two of the prey categories identified in the fecal pellets. Orthopterans, dipterans, and Blattoptera members were underrepresented in some diets when compared to their proportional representation in the reference collection, whereas heteropterans, hymenopterans, and caterpillars were over represented (Table 2). Although our reference samples hardly represent perfectly the availability of prey categories for each chameleon species, the use of the conservative Bonferroni correction makes it likely that significant differences (indicated by + and - signs in Table 2) reflect a selectivity of the chameleons. Observed selections, however, are not highly indicated: Niche breadth values for the three species ranged from 0.880 to 0.939 (Table 2), indicating similar proportions of all prey categories in diets and reference samples. The reference samples revealed that chameleons also prey on arthropods that live near the ground or are terrestrial (i.e., Tetrigoidea).

Niche overlaps computed from g -values, which account for prey availability, reveal no segregation in terms of prey categories. For the syntopic pair *C. pfefferi-C. quadricornis*, the g -based overlap was 0.91 ($P = 0.672$); for the two allopatric species pairs *C. pfefferi-C. montium* and *C. montium-C. quadricornis* values were 0.89 ($P = 0.309$) and 0.88 ($P = 0.464$), respectively. Overlaps using I -values, which incorporate prey volumes but omit availability, were high but significantly smaller than expected under a random assignment of prey categories to chameleons species; overlaps are 0.91 ($P = 0.026$) for *C. pfefferi-C. quadricornis*, 0.68 ($P = 0.001$) for *C. pfefferi-C. montium*, and 0.86 ($P = 0.001$) for *C. montium-C. quadricornis*. Considering prey volume only, niche segregation was conspicuous (Fig. 2): *Chamaeleo pfefferi* selected smaller prey than its congeners (Mann-Whitney U -Test: $P < 0.001$ in both cases), whereas there was no difference in prey volume between *C. quadricornis* and *C. montium* (Mann-Whitney U -Test: $P = 0.281$).

DISCUSSION

The three chameleon species from Mount Kupe prey almost exclusively on arthropods. High niche breadth values (Smith's FT) indicate opportunistic feeding with respect to prey taxa. Comparable data on the feeding habits of free-ranging chameleons are rare and concern essentially species from open or desert habitats. Two studies of the common chameleon (*Chamaeleo chamaeleon*) from southeastern Spain and Malta Island that provide dietary information using fecal pellets, revealed 88 and 100% arthropods in the diets,

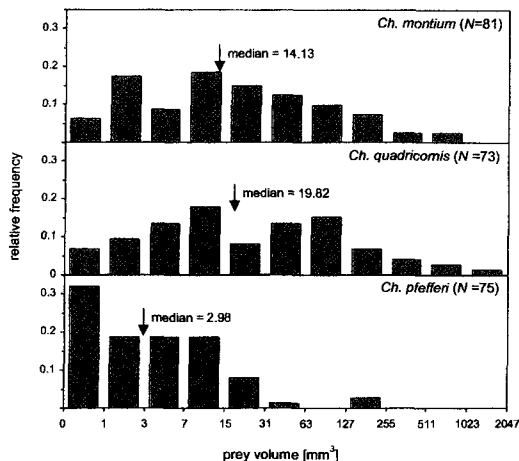


FIG. 2. Frequency distribution of prey volumes of the dominant categories in the diets of the three species of the genus *Chamaeleo* inhabiting the primary forest on the western slope of Mount Kupe, Cameroon.

respectively (Luiselli and Rugiero, 1996; Pleguezuelos et al., 1999), the single exception being juvenile lizards (Luiselli and Rugiero, 1996). As in the diets of the three tropical species, Diptera, Hymenoptera, and Heteroptera were among the numerically dominant groups. Orthoptera were also among the dominant groups in *C. chamaeleon* diets and consumed in approximate proportion to their availability. They are underrepresented in the diets of the species from Mount Kupe, both in numbers and with respect to their availability in the environment, a result likely to reflect the marked difference in habitat complexity.

Despite a lack of adequate quantitative data on canopy invertebrates from Mount Kupe, we consider the strong correspondence of dietary and reference sample composition unlikely to have arisen by chance. The remains of arthropods that live near the ground or are terrestrial in the diets show that the chameleons must occasionally forage from the lowest branches just above the herb layer or even on the forest floor. Data on common chameleons from open habitats showed that they regularly walk on the ground to move between plants and for oviposition (e.g., Hódar et al., 2000) but that they forage essentially in shrubs and trees with a mean height of < 4 m (Pleguezuelos et al., 1999).

Null model tests on the elevational distribution pattern of the entire herpetofaunal assemblage of Mount Kupe suggest that the three chameleon species are not distributed according to individual physiological tolerance limits along the gradient, and that their distributions are probably not independent of each other (Hofer et al., 1999). An ecotonal boundary is unlikely to limit the distributions because the elevational range at around 1200 m that separates the two submontane species from *C. montium* is situated 300 m above the transitional zone between lowland and submontane forest. If interspecific competition had a substantial impact on the local elevational distributions, we would expect it to be reflected in some form of niche segregation between the syntopic *C. pfefferi* and *C. quadri-*

cornis and a lack of it between these species and the allotopic *C. montium*. Although all three species showed a high overlap in taxonomic composition of their diets, our results indicate a clear niche segregation with respect to prey size between *C. pfefferi* and its congeners but no difference in prey size between the allotopic *C. quadricornis* and *C. montium*. Consistent with the findings on dietary segregation and mean prey size are the body size differences, largest between *C. pfefferi* and *C. quadricornis*, and identically low to *C. montium*, that is, the syntopic species are the most distant in terms of size ratio (1.33 : 1.51). Following Hutchinson's "1.3 rule" (1959) for size-adjacent close competitors found in sympatry, the observed ratios were the minimum needed to allow the two submontane species to coexist, whereas the conspicuous elevational separation of *C. montium* would result from a size difference that prevents coexistence with at least *C. quadricornis*. Moreover, the two syntopic species have slightly but significantly narrower niche breadths (FT values) than *C. montium* (Table 2). The results on dietary segregation, morphological similarity, and distributional limits of the three chameleon species on Mount Kupe are suggestive of competition. Unfortunately, the restricted range and critical status of the two submontane species limit our ability to confirm the role of competition experimentally.

Acknowledgments.—Fieldwork was supported by grants from the Swiss Development Corporation and the Swiss Academy of Sciences, and by the Natural History Museum of Berne. L-FB was supported by the Swiss National Science Foundation grant 31-52566.97 and the Novartis Foundation. The Mount Kupe Forest Project provided logistic help and housing in Nyasoso. E. J. Ebung, E. H. Njume, and N. S. Epie assisted the whole, A. Witschi, C. Wild, and I. C. Ojiawum parts of the fieldwork. D. Borcard, G. R. Smith, M. Cuadrado, and an anonymous reviewer made valuable comments on earlier drafts of the manuscript.

LITERATURE CITED

- BURRAGE, B. R. 1973. Comparative ecology and behaviour of *Chamaeleo pumilus pumilus* (Gmelin) and *C. namaquensis* A. Smith (Sauria: Chamaeleonidae). *Annals of the South African Museum* 61:1–158.
- DALE, M. R. T. 1984. The contiguity of upslope and downslope boundaries of species in a zoned community. *Oikos* 42:92–96.
- DUELLMAN, W. E. 1978. The biology of an equatorial herpetofauna in amazonian Ecuador. *Miscellaneous Publications of the Museum of Natural History, Univ. of Kansas* 65:1–352.
- EUSKIRCHEN, O., A. SCHMITZ, AND W. BÖHME. 2000. Zur Herpetofauna einer montanen Regenwaldregion in SW-Kamerun (Mt. Kupe und Bakossi-Bergland). IV. Chamaeleonidae, biogeographische Diskussion und Schutzmassnahmen. *Herpetofauna* 22: 21–34.
- HÓDAR, J. A., J. M. PLEGUEZUELOS, AND J. C. POVEDA. 2000. Habitat selection of the common chameleon (*Chamaeleo chamaeleon*) in an area under development in southern Spain: implications for conservation. *Biological Conservation* 94:63–68.
- HOFER, U., L.-F. BERSIER, AND D. BORCARD. 1999. Spatial organization of a herpetofauna on an elevational gradient revealed by null model tests. *Ecology* 80:976–988.
- . 2000. Ecotones and gradient as determinants of herpetofaunal community structure in the primary forest of Mount Kupe, Cameroon. *Journal of Tropical Ecology* 16:517–533.
- HUTCHINSON, G. E. 1959. Homage to Santa Rosalia or Why are there so many kinds of animals? *American Naturalist* 93:145–159.
- KLAVER, C., AND W. BÖHME. 1986. Phylogeny and classification of the Chamaeleonidae (Sauria) with special reference to hemipenis morphology. *Bonner Zoologische Monographien* 22:5–64.
- LIN, J.-Y., AND C. E. NELSON. 1981. Comparative reproductive biology of two sympatric tropical lizards *Chamaeleo jacksoni* Boulenger and *Chamaeleo hoehnelii* Steindachner (Sauria: Chamaeleonidae). *Amphibia-Reptilia* 3/4:287–311.
- LUISELLI, L., AND L. RUGIERO. 1996. *Chamaeleo chamaeleon* diet. *Herpetological Review* 27:78–79.
- PIANKA, E. R. 1973. The structure of lizard communities. *Annual Review of Ecology and Systematics* 4:53–74.
- PLEGUEZUELOS, J. M., J. C. POVEDA, R. MONTEERRUBIO, AND D. ONTIVEROS. 1999. Feeding habits of the common chameleon *Chamaeleo chamaeleon* (Linnaeus, 1758) in the southeastern Iberian Peninsula. *Israel Journal of Zoology* 45:267–276.
- POWELL, R., J. S. PARMERLEE JR., M. A. RICE, AND D. D. SMITH. 1990. Ecological observations of *Hemidactylus brookii haitianus* Meerwarth (Sauria: Gekkonidae) from Hispaniola. *Caribbean Journal of Science* 26:67–70.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- SMITH, E. P. 1982. Niche breadth, resource availability, and inference. *Ecology* 63:1675–1681.
- SOLOW, A. R. 1993. A simple test for change in community structure. *Journal of Animal Ecology* 62: 191–193.
- SUCHEL, J. B. 1972. La répartition des pluies et les régimes pluviométriques du Cameroun. *Travaux et Documents de Géographie Tropicale, Centre d'Etude de Géographie Tropicale-Centre National de la Recherche Scientifique* 5:1–287.
- THOMAS, D. W. 1986. Vegetation in the montane forest of Cameroon. In S. N. Stuart (ed.), *Conservation of Cameroon Montane Forests*, pp. 20–27. International Council for Bird Preservation, Cambridge.
- TILBURY, C. R. 1997. African chameleons: an overview of systematics and biology. In Z. Roček and S. Hart (eds.), *Herpetology '97*, pp. 208. Abstracts of the Third World Congress of Herpetology, Prague, Czech Republic.
- WILD, C. 1993. Notes on the rediscovery and congeneric associations of the Pfeffer's Chameleon *Chamaeleo pfefferi* (Tornier 1900) (Sauria: Chamaeleonidae) with a brief description of the hitherto unknown female of the species. *British Herpetological Society Bulletin* 45:25–32.
- WINEMILLER, K.O., AND E.R. PIANKA. 1990. Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60:27–55.

Accepted: 21 May 2002.