Diet of the Invasive Lizard *Chamaeleo jacksonii* (Squamata: Chamaeleonidae) at a Wet-Forest Site in Hawai'i[1]

Fred Kraus[2,3] and David Preston[2]

Abstract: We assessed diet from a sample of Jackson's chameleons inhabiting wet forest in Volcano Village, Hawai'i Island, Hawai'i. Most lizards contained food in their gastrointestinal tract, diet was broad, and large numbers of invertebrates, mostly insects, were consumed. Native insects composed the largest component of dietary items, and these spanned most of the body-size range found in the native invertebrate community. Taxonomic composition of diets does not conform to expectations for iguanian lizards inasmuch as hymenopterans form only a small portion of consumed items. Insect chemical or stinging defenses did not preclude consumption by lizards. The study site is a mixture of native and alien vegetation. Chameleons collected from alien plants contained larger numbers of native prey items than did those lizards removed from native plants, suggesting that lizard residency on non-native plants will not reduce their predation impact on native invertebrates in mixed forest. Our results confirm the finding of a similar study in dry-forest habitat on Maui that Jackson's chameleons are likely to pose a substantial threat to a broad range of native invertebrate biodiversity in Hawai'i.

Chamaeleo jacksonii Boulenger, 1896, is a medium-sized (snout–vent length up to ~160 mm) lizard native to humid and wet forests of Kenya and Tanzania. It was introduced into Hawai'i via the pet trade in the early 1970s and, with considerable assistance from chameleon fanciers, has spread widely throughout the state in wet, mesic, and dry forests. Two different modelling approaches have shown that this species is physiologically capable of colonizing most nonalpine habitats within Hawai'i (Rödder et al. 2011; Kraus et al. 2012); hence, it seems poised to invade most native habitats in the state. These chameleons also occur at high population densities and occupy a novel predatory niche, so

they seem capable of posing a severe conservation threat to many native arthropods (Kraus et al. 2012). An earlier study of animals from native dry forest on Maui demonstrated that *C. jacksonii* feeds on a wide diversity of invertebrates, with endemic Hawaiian invertebrates composing 35% of all prey items (Kraus et al. 2012). It has also been shown on O'ahu that these chameleons consume some species of endangered land snails as well as native insects (Holland et al. 2010). The impression gained from that earlier dietary information is that these chameleons are generalist opportunistic predators that will consume any small animal that comes within reach and attracts their notice. So as to further explore the dietary range of this species we conducted a follow-up study of the diet of *C. jacksonii* under different habitat conditions: a largely native wet forest on Hawai'i Island. The intent of this study was threefold: to further assess how catholic the diet of this lizard is, to determine whether similarly large numbers of native invertebrates are consumed across these differing (wet- versus dry-forest) habitats, and to investigate whether more native prey are consumed by lizards found occupying native versus alien plants.

[2] Bishop Museum, 1525 Bernice Street, Honolulu, Hawai'i 96817.

[3] Corresponding author (fkraus@hawaii.edu).

MATERIALS AND METHODS

We obtained a sample of 34 *Chamaeleo jacksonii* from Volcano Village and immediate vicinity, 1,100–1,200 m elevation, Hawai'i Island. Habitat in this area comprises a mix of largely native overstory species with several invasive trees (primarily *Morella faya*) and understory shrubs (primarily *Tibouchina urvilleana*). We collected most lizards ($n = 28$) at night while they were sleeping on vegetation, but one was collected in daytime while active. For all these animals the plant species on which they were perched was recorded so as to ascertain whether animals perched on native vegetation were more likely to have native prey items in their digestive tracts. Five additional animals were collected by others living in or near Volcano and given to us; some of these were obtained while they were crossing roads. Consequently, there is no perch information for any of those animals.

We fixed animals in formalin or froze them within a few hours of collection to terminate digestion; we later fixed frozen animals in formalin. We then stored all animals in 70% ethanol at Bishop Museum (BPBM 21741, 21743, 35305–35327, 35409–35415, 35418–35419) and measured snout–vent length (SV) of all lizards. We removed digestive tracts from specimens, opened them, and removed their contents. Using a binocular dissecting scope, we then sorted these contents by taxon, identified them to the lowest taxonomic level possible, and counted their numbers. We determined identifications of dietary items (whole specimens [when present] or diagnostic fragments) by comparison with authoritatively identified specimens in the Bishop Museum entomology collections. The bulk of removed contents comprised partially digested and disarticulated arthropods mixed with unidentifiable debris. Because a single individual prey item was partially or wholly disarticulated during consumption, we counted these arthropod parts separately and determined the total number of prey items per taxon by choosing the identifiable part with the highest count. For example, if there were 20 pairs of elytra from species A but only

five legs, the total count of prey items for species A was 20.

For dietary items that we could identify to species or to a set of very similar species, we estimated prey-volume by (1) measuring from the entomology collection at the Bishop Museum the maximum body length, width, and height (to the nearest 0.05 mm) of 10 specimens of the consumed species; (2) averaging these sample body measurements; (3) using these averages to calculate an average volume for each prey species using the equation for a scalene ellipsoid ($V = 4/3 \pi abc$, where a, b, and c are the three body axes); and (4) multiplying those species-averaged volumes by the relevant number of dietary items identified within each stomach to estimate total food volume for each lizard. For dietary items that we could not identify to species, we measured the dimensions of the consumed items directly. The benefit of measuring whole specimens of identified species from the entomology collection is that it provides a more accurate measure of prey volume than estimating the same from partially digested fragments of prey. Of 795 dietary items, all could be identified to family, 703 to genus, and 344 to species; only four were so fragmented by digestion that we could not identify them or estimate their volume. Taxonomy and provenance for all identified arthropod dietary items followed Nishida (2002). We labeled, stored in vials with 95% ethanol, and maintained in the collections of the Bishop Museum all recovered and sorted material. We assessed statistical differences with *G* tests and Mann-Whitney *U* tests implemented in Minitab 14. We used means for comparisons of prey numbers, and we used medians for comparisons of prey volume because of the additional order of magnitude observed in the range of those numbers. We assessed prey diversity using the Shannon-Wiener index.

RESULTS

We retrieved from our sample of lizards a total of 795 dietary items from 48 taxa. We identified 26 of these dietary taxa to species, 17 to genus, and five to family. This comprised 43.3% of dietary items identified

to species, 45.2% to genus, and 11.6% to family.

All chameleons but one had food items in their digestive tract (97.1%); all but four food items were arthropods. Nonarthropods included two land snails (*Oxychilus alliarius*) and two lizards (*Lampropholis delicata*). Numbers of food items per chameleon ranged from 0 to 77 (mean = 23.4, SD = 3.18). For stomachs containing food, numbers of prey species per chameleon ranged from 1 to 12 (mean = 5.6, SD = 0.45), and prey volumes per lizard ranged from 0.009 to 5.10 ml (mean = 0.76 ml, SD = 0.17). For stomachs containing food, numbers of prey did not differ between sexes (Mann-Whitney $U = 168.5$, $n_F = 11$, $n_M = 21$, $P = .62$), nor did prey volume (Mann-Whitney $U = 163.0$, $n_F = 11$, $n_M = 21$, $P = .47$). Median numbers of prey for males were 22 and median numbers for females 16; median volumes for males were 0.38 ml and for females 0.45 ml. The largest prey items (*Elimaea punctifera*) were 48 mm long; however, most prey were of small size (Figure 1). Male and female lizards did not differ significantly in body size (male median = 98 mm, median female = 105 mm, Mann-Whitney $U = 191.5$, $n_F = 11$, $n_M = 21$, $P = .71$).

Endemic Hawaiian taxa composed 46.9% of dietary items, adventive aliens composed 31.7%, intentionally introduced aliens composed 9.8%, and taxa whose provenance could not clearly be identified composed 11.6%. For animals with food in their stomach, numbers of prey per lizard varied from 1 to 77 (mean = 24.1, SD = 3.20), and volume varied from 0.009 to 5.104 ml (mean = 0.758 ml, SD = 0.169). Numbers of endemic prey items per lizard varied from 0 to 58 (mean = 11.3, SD = 1.99), and volumes of endemic prey items per lizard varied from 0 to 0.405 ml (mean = 0.094 ml, SD = 0.019). Numbers of endemic prey did not differ between sexes (Mann-Whitney $U = 186.0$, $n_F = 11$, $n_M = 21$, $P = .87$), nor did volumes of endemic prey (Mann-Whitney $U = 198.5$, $n_F = 11$, $n_M = 21$, $P = .51$): median numbers of endemic prey for males were nine and median numbers for
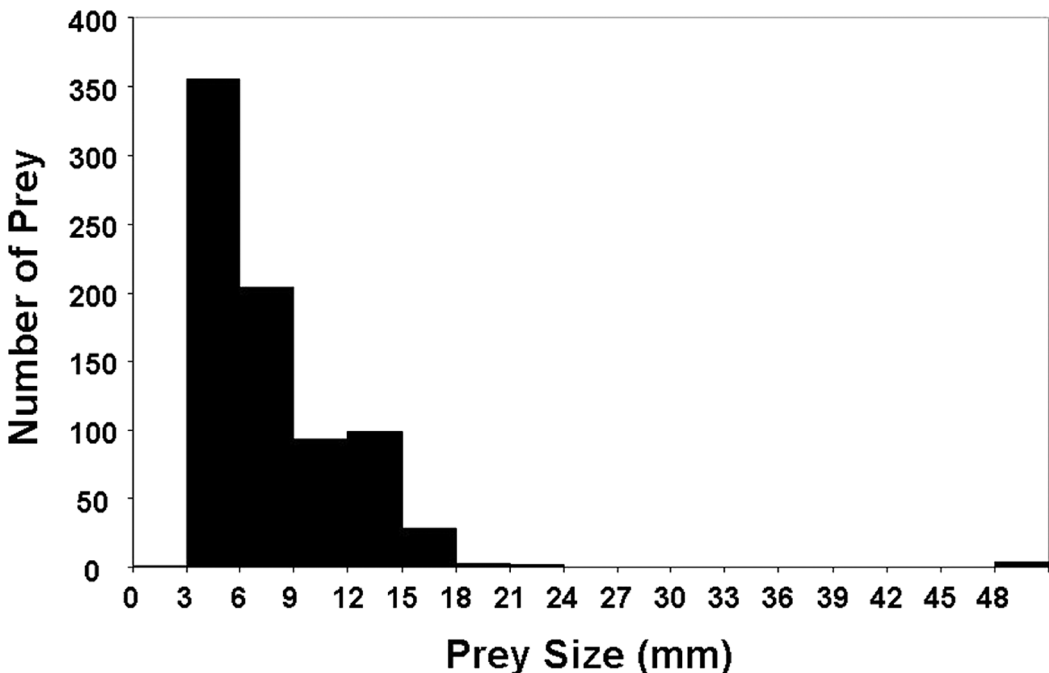

FIGURE 1. Size distribution of prey retrieved from 33 *Chamaeleo jacksonii* on Maui. $n = 795$ measurable prey items.

females eight; median volumes for males were 0.053 ml and for females 0.082 ml. The Shannon-Wiener index for identified prey items was 3.01, suggesting a considerable degree of prey diversity among food items analyzed at the lower taxonomic levels (species or genus) at which most of our prey items were identified. Food items per lizard that could not have their provenance (endemic versus alien) determined because of identification uncertainty varied from 0 to 18. These numbers were sufficiently small that overall assessment of lizard impact on endemic prey is unlikely.

Analyzed taxonomically, homopterans composed the greatest numbers of prey, followed by dipterans and coleopterans (Table 1). Together, these three taxa formed 74.8% of all dietary items. The large majority of endemic insects consumed at Volcano Village were homopterans of the genera *Oliarus* and *Nesophrosyne*, composing 27.9% of all prey items, but several other native species across a diversity of orders were taken as well (Table 2).

When analyzed by volume, however, the results are somewhat different. In that case, dipterans and coleopterans were still important (35.2% and 17.7% of prey volume, respectively), but hymenopterans and orthopterans composed significant volumes as well (16.9% and 13.7% of prey volume, respectively). Adventive aliens composed 59.4% of food items by volume, endemic species composed 12.5%, intentionally introduced aliens composed 13.0%, and taxa whose provenance could not clearly be identified composed 15.1%.

The one lizard without food items in its digestive tract was collected in daytime from a lime tree (*Citrus aurantifolia*). Of the remaining 27 specimens for which perch species was identified, 21 were collected on native plant species (12 on *Metrosideros polymorpha*, 4 on *Acacia koa*, 2 on *Coprosma ochracea*, 2 on *Dicranopteris linearis*, 1 on *Vaccinium calycinum*) and 6 were found in alien species (4 on *Tibouchina urvilleana*, 2 on *Morella faya*). Unexpectedly, lizards found on alien plants had a higher percentage of endemic prey items in their digestive tract than did animals collected on native plants (57.6% versus 45.5%, $G = 4.4877$, df = 1, $P = .034$).

DISCUSSION

Few studies have been done on chameleon diets, with much of this information involving alien *Chamaeleo chamaeleon* in Spain (Blasco et al. 1985, Pleguezuelos et al. 1999) and Malta (Luiselli and Rugiero 1996) and *C. africanus* in Greece (Dimaki et al. 2001). Relatively few species have been studied in their native range (Burrage 1973, Wild 1994, Hofer et al. 2003, Keren-Rotem et al. 2006). None of these studies identified dietary items below the level of insect order. A prior study of *C. jacksonii* from a native dry forest on southern Maui (Kraus et al. 2012), however, identified most dietary items to the level of species or genus, and several interesting features about the diets of these lizards were discovered. First, these dry-forest chameleons consumed a large number of small prey items, with a mean of 41.8 dietary items per stomach and a range of 0–352. Second, dietary breadth was wide, with a Shannon-Wiener index of diversity at the genus/species level of 2.56. Dipterans, heteropterans, and homopterans composed the predominant prey items. Third, ants, other hymenopterans, and beetles composed small proportions of the chameleons' diets; this is unusual for iguanian lizards, which are largely ambush predators reliant on visual cues for prey detection and prey preferentially on those taxa. It was, however, consistent with other evidence suggesting that, among iguanians, chameleons are unusual in being cruise foragers (Hagey et al. 2010). Should this foraging strategy prove applicable to chameleons as a whole, it would suggest that chameleon diets may have shifted as their foraging strategy changed. Directly relevant to conservation concerns are that (1) a large number of native insects (35.2% of total) was consumed, and (2) cropping rates seem likely to be high because of the large numbers of prey items in the lizards' digestive tract and because chameleons have been reported to take 3–15 meals per day and to have high digestion rates that quickly clear their digestive tracts (Burrage 1973).

TABLE 1

Composition of Dietary Items in Gastrointestinal Tract of 33 *Chamaeleo jacksonii* from Volcano Village, Hawai'i Island

Order	Family	No. Prey Items	% Prey Items	% Prey Volume
Squamata		2	0.25	3.00
	Scincidae	2	0.25	3.00
Araneae		11	1.38	0.52
	Tetragnathidae	9	1.13	0.44
	Thomicidae	2	0.25	0.08
Blattodea		3	0.38	0.87
	Blattelidae	3	0.38	0.87
Coleoptera		128	16.10	17.66
	Cerambicidae	3	0.38	0.81
	Chrysomelidae	1	0.13	0.00
	Coccinellidae	38	4.78	5.72
	Curculionidae	71	8.93	8.00
	Elateridae	15	1.89	3.13
Dermaptera		1	0.13	0.03
	Forficulidae	1	0.13	0.03
Diptera		185	23.27	35.24
	Calliphoridae	99	12.45	26.86
	Drosophilidae	1	0.13	0.00
	Stratiomyidae	37	4.65	5.49
	Syrphidae	48	6.04	2.89
Heteroptera		35	4.40	3.15
	Lygaeidae	2	0.25	0.01
	Miridae	14	1.76	0.24
	Nabidae	17	2.14	0.36
	Pentatomidae	2	0.25	2.53
Homoptera		182	35.47	4.02
	Cicadellidae	103	12.96	1.81
	Cixiidae	130	16.35	1.70
	Psylidae	49	6.16	0.51
Hymenoptera		32	4.03	16.94
	Apidae	2	0.25	1.41
	Ichneumonidae	5	0.63	0.28
	Sphaecidae	1	0.13	0.40
	Vespidae	24	3.02	14.85
Lepidoptera		38	4.79	3.96
	Crambidae	8	1.01	0.92
	Cosmopterygidae	13	1.64	0.27
	Geometridae	17	2.14	2.76
Orthoptera		29	3.64	13.74
	Gryllidae	25	3.14	2.04
	Tettigoniidae	4	0.50	11.70
Julida		40	5.03	0.27
	Julidae	40	5.03	0.27
Polydesmidae		2	0.25	0.17
	Paradoxosomatidae	2	0.25	0.17
Isopoda		5	0.63	0.38
	Porcellionidae	5	0.63	0.38
Gastropoda		2	0.25	0.04
	Zonitidae	2	0.25	0.04
Total		795	100.00	100.00

TABLE 2

Endemic Hawaiian Insects Composing Dietary Items in the Sample of 33 *Chamaeleo jacksonii* from Wet-Forest Habitat on Hawai'i Island Having Gastrointestinal Contents

Order	Family	Species	No. Prey Items	% Prey Items	% Prey Volume
Araneae	Tetragnathidae	*Tetragnatha* sp. 1	6	0.75	0.26
Araneae	Tetragnathidae	*Tetragnatha* sp. 2	3	0.38	0.18
Araneae	Thomicidae	*Mecaphesa* sp.	2	0.25	0.08
Coleoptera	Cerambicidae	*Plagithmysus* sp. 1	2	0.25	0.72
Coleoptera	Cerambicidae	*Plagithmysus* sp. 2	1	0.13	0.09
Diptera	Drosophilidae	*Drosophila* sp.	1	0.13	0.00
Heteroptera	Lygaeidae	*Nysius* sp.	2	0.25	0.01
Heteroptera	Miridae	*Sarona* sp.	6	0.75	0.06
Heteroptera	Miridae	*Hyalopeplus pellucidus*	5	0.63	0.18
Heteroptera	Nabidae	*Nabis blackburni*	6	0.75	0.13
Heteroptera	Nabidae	*Nabis lusciosus*	1	0.13	0.04
Heteroptera	Nabidae	*Nabis* sp. nr. *blackburni*	10	1.26	0.20
Heteroptera	Pentatomidae	*Coleoticus blackburniae*	2	0.25	2.53
Homoptera	Cicadellidae	*Nesophrosyne* sp.	92	11.57	1.60
Homoptera	Cixiidae	*Oliarus* sp.	130	16.35	1.70
Homoptera	Psylidae	*Megatrioza* sp	49	6.16	0.51
Hymenoptera	Ichneumonidae	*Enicospilus* sp.	1	0.13	0.10
Lepidoptera	Cosmopterygidae	*Hyposmocoma* sp.	13	1.64	0.27
Lepidoptera	Geometridae	*Eupithecia* sp.	16	2.01	1.82
Orthoptera	Gryllidae	*Laupala* sp.	25	3.14	2.04

This study of *Chamaeleo jacksonii*, from a different form of native vegetation in Hawai'i (wet versus dry forest), supports several of these findings and expands on others. Chameleons investigated in this study contained fewer food items on average than did animals from the earlier dry-forest study (23.4 versus 41.8), and the numerical range of items (0–77 versus 0–352) and standard deviation of samples (3.18 versus 10.41) were both lower, but numbers of consumed items were still large. Size distribution of prey items, however, was virtually identical with that in the earlier study from dry-forest habitat, with (1) the large majority of dietary items being less than 9 mm in length (Figure 1), and (2) larger prey items being consumed at lower frequencies. Prey diversity was even higher in this study than in that on Maui (Shannon-Wiener index 3.01 versus 2.56), perhaps reflecting the greater structural and community diversity of vegetation at the wet-forest study site or its closer proximity to human activity, either of which could be expected to result in a larger community of invertebrate species. It is not explained by larger sizes of the Volcano lizards,

which do not differ significantly from those collected earlier on Maui (for males, Mann-Whitney $U = 392.0$, $n_{\text{Volcano}} = 21$, $n_{\text{Maui}} = 21$, $P = .18$; for females, Mann-Whitney $U = 392.0$, $n_{\text{Volcano}} = 11$, $n_{\text{Maui}} = 12$, $P = .81$).

The vast majority of prey in this study were arthropods, but land snails and lizards were also consumed. The latter confirms the observation of Holland et al. (2010), although the snails obtained in our study are alien introductions. Both the lizard (*Lampropholis delicata*) and snails (*Oxycheilus alliarius*) are of interest because they are leaf-litter inhabitants and must have been consumed while the chameleons were active on the ground. Although chameleons are primarily arboreal, they are often seen crossing roads in Hawai'i, and these prey items confirm their willingness to feed while crossing between patches of arboreal habitat. As found in our earlier study, homopterans, dipterans, and coleopterans were of greatest dietary importance, with percentages of prey items consumed of the first and last virtually the same between study sites (homopterans: 34.64% on Maui, 35.47% on Hawai'i Island; coleopterans:

14.57% on Maui, 16.10% on Hawaiʻi Island) but with far fewer flies consumed in this study (42.88% on Maui, 23.27% on Hawaiʻi Island). We presume that the reduced consumption of dipterans on Hawaiʻi Island reflects the lesser relative abundance of flies in this wet forest.

Also, as found earlier, hymenopterans formed a very small portion of the diet in both studies (1.69% of prey items on Maui, 4.03% on Hawaiʻi Island), in contrast to the usual expectations for iguanian lizards (Vitt et al. 2003, Vitt and Pianka 2005). In this instance, we found no ants at all in the diet, although two honey bees (*Apis mellifera*), one sphecid (*Ampulex compressa*), five ichneumonid wasps (4 *Barichneumon*, 1 *Enichospilus*), and 24 yellow jackets (*Vespula pensylvanica*) were present. Beetles also compose a large percentage of the diet of most iguanians (Vitt et al. 2003, Vitt and Pianka 2005) and, as already noted, composed a fair portion of chameleon diets in both dry forest on Maui and wet forest on Hawaiʻi Island, although in neither case did they approach constituting a majority of food items.

A larger percentage of prey in the diets of Volcano chameleons consisted of native species than was found in dry forest on Maui (46.9% versus 35.2%). The unexpected result that chameleons taken from native plants had fewer native prey species in their digestive tracts could reflect that (1) chameleons move frequently among perches, such that their final resting places for the night do not necessary reflect where they last foraged; (2) the native arthropods ingested are not particularly restricted to native plants; or (3) native insects are more vulnerable to predation when on alien plants. Given what we presume to be rapid digestion rates for these chameleons and their generally sedentary nature, we are inclined to view the first hypothesis as less likely than the other two.

What impact might be expected from *Chamaeleo jacksonii* on Hawaiʻi's native invertebrates? Three points are directly relevant to that question. First, as we discussed in our earlier study, these lizards clearly tolerate a diversity of prey having noxious defenses. In both studies, insects armed with painful stings (*Apis mellifera*, *Vespula pensylvanica*) or

bites (*Pheidole megacephala*) were eaten in sufficient numbers that their consumption cannot readily be ascribed to accidental ingestion. Similarly, a large number of prey items belonged to species having noxious chemical defenses: 36 *Nezara viridula* and 4 *Danaus plexippus* in the Maui study, 40 *Cylindroiulus latestriatus* in this study. Second, active motion appears to be unnecessary to elicit feeding in these chameleons, as suggested by their consumption of land snails (this study, Holland et al. 2010), which are largely inactive during daytime, and their consumption of bird eggs in captivity (cf. Kraus et al. 2012). Third, on both Hawaiʻi Island and Maui we found these lizards to consume species spanning virtually the entire range of body sizes found in native arthropods in Hawaiʻi. Thus, it appears that few, if any, native Hawaiian invertebrates will prove invulnerable to predation by these lizards. Coupled with the chameleons' high population densities and expected wide geographical range across Hawaiʻi (Kraus et al. 2012), the conservation implications of this conclusion for the largest component of Hawaiʻi's native biodiversity should be obvious.

Literature Cited

Blasco, M., J. Romero, J. M. Sánchez, and E. Crespillo. 1985. La biología alimentaria y reproductiva del camaleón común, *Chamaeleo chamaeleon* (L.) (Reptilia, Chamaeleonidae) de la Península Ibérica y norte de Africa. Monogr. Inst. Nac. Conserv. Nat. 43:121–148.

Burrage, B. R. 1973. Comparative ecology and behaviour of *Chamaeleo pumilus pumilus* (Gmelin) and *C. namaquensis* A. Smith (Sauria: Chamaeleonidae). Ann. S. Afr. Mus. 61:1–158.

Dimaki, M., E. D. Valakos, A. Legakis, B. Chondropoulos, and A. Bonetti. 2001. Preliminary results on the feeding ecology of the African chameleon *Chamaeleo africanus* Laurenti, 1768 from the southwestern Peloponnese, Greece. Pages 57–63 *in* P. Lymberakis, E. Valakos, P. Pafilis, and M. Mylonas, eds. Herpetologia Candiana. Societas Europaea Herpetologica, Irakleio, Greece.

Hagey, T. J., J. B. Losos, and L. J. Harmon. 2010. Cruise foraging of invasive chameleon (*Chamaeleo jacksonii xantholophus*) in Hawai‘i. Breviora 519:1–7.

Hofer, U., H. Baur, and L.-F. Bersier. 2003. Ecology of three sympatric species of the genus *Chamaeleo* in a tropical upland forest in Cameroon. J. Herpetol. 37:203–207.

Holland, B. S., S. L. Montgomery, and V. Costello. 2010. A reptilian smoking gun: First record of invasive Jackson’s chameleon (*Chamaeleo jacksonii*) predation on native Hawaiian species. Biodivers. Conserv. 19:1437–1441.

Keren-Rotem, T., A. Bouskila, and E. Geffen. 2006. Ontogenetic habitat shift and risk of cannibalism in the common chameleon (*Chamaeleo chamaeleon*). Behav. Ecol. Sociobiol. 59:723–731.

Kraus, F., A. Medeiros, D. Preston, C. S. Jarnevich, and G. H. Rodda. 2012. Diet and conservation implications of an invasive chameleon, *Chamaeleo jacksonii* (Squamata: Chamaeleonidae), in Hawai‘i. Biol. Invasions 14:579–593.

Luiselli, L., and L. Rugiero. 1996. Natural history notes: *Chamaeleo chamaeleon:* diet. Herpetol. Rev. 27:78–79.

Nishida, G. M., ed. 2002. Hawaiian terrestrial arthropod checklist. 4th ed. Bishop Mus. Tech. Rep. 22. http://hbs.bishopmuseum.org/hbsdb.html.

Pleguezuelos, J. M., J. C. Poveda, R. Monterrubio, and D. Ontiveros. 1999. Feeding habits of the common chameleon, *Chamaeleo chamaeleon* (Linnaeus, 1758) in the southeastern Iberian Peninsula. Isr. J. Zool. 45:267–276.

Rödder, D., W. Böhme, and S. Lötters. 2011. ‘Chamaliens’ on the Hawaiian Islands: Spatial risk assessment for the invasive Jackson’s chameleon (Chamaeleonidae). Salamandra 47:36–42.

Vitt, L. J., and E. R. Pianka. 2005. Deep history impacts present-day ecology and biodiversity. Proc. Natl. Acad. Sci. U.S.A. 102:7877–7881.

Vitt, L. J., E. R. Pianka, W. E. Cooper Jr., and K. Schwenk. 2003. History and the global ecology of squamate reptiles. Am. Nat. 162:44–60.

Wild, C. 1994. Ecology of the Western Pygmy Chameleon *Rhampholeon spectrum* Buchholz 1874 (Sauria: Chamaeleonidae). Br. Herpetol. Soc. Bull. 49:29–35.