



Dietary analysis of the invasive lizard  
*Chamaeleo jacksonii* from a wet forest  
habitat in Hawaii

Hawaii  
Biological  
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Final Report

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**Dietary analysis of the invasive lizard *Chamaeleo jacksonii*  
from a wet forest habitat in Hawaii**

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**Honolulu, Hawai'i 96817**

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## Introduction

*Chamaeleo jacksonii* 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 Hawaii 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. This species is physiologically capable of colonizing most non-alpine habitats within Hawaii, occurs at high population densities, and occupies a novel predatory niche (Kraus et al., in review). An earlier study of animals from native dry forest on Maui demonstrated the species to feed on a wide diversity of invertebrates (Kraus et al., in review). This diet included a number of endemic Hawaiian invertebrates, which comprised 35% of all items eaten (Kraus et al., in review). It has also been shown on Oahu that the species consumes some species of endangered landsnails (Holland et al., 2009). The impression gained from this earlier dietary study 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 Hawaii Island.

## Materials and Methods

We obtained a sample of 34 lizards from Volcano Village and immediate vicinity, Hawaii 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. Six other animals were collected by others living in or near Volcano and given to us; some of these were obtained while crossing roads. Consequently, there is no perch information for any of these animals.

Animals were fixed in formalin or frozen within a few hours of collection in order to terminate digestion; frozen animals were later fixed in formalin. All were then stored in 65% ethanol at Bishop Museum. Digestive tracts were removed from specimens, opened, their contents removed, and these contents sorted by taxon, identified to the lowest taxonomic level possible, and counted under a binocular dissecting scope. Identifications of dietary items – whole specimens (when present) or diagnostic fragments – were determined by comparison to 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 would be partially or wholly disarticulated during consumption, these arthropod parts were counted separately and the total number of prey items/taxon was determined by choosing the identifiable part with the highest count. For example, if there were 20 pair of elytra from species A but only 5 legs, the total count of prey items for species A would be 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 ten 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 4 were so fragmented by digestion that we could not identify them or estimate their volume. Taxonomy and provenance for all identified dietary items followed Nishida (2002). All recovered and sorted material was labeled, stored in vials with 95% ethanol, and maintained in the collections of the Bishop Museum. Statistical differences were assessed with Mann-Whitney  $U$  tests implemented in Minitab 14. Comparisons of prey numbers relied on means; comparisons of prey volume relied on medians because of the additional order of magnitude observed in the range of those numbers.

## Results

A total of 795 dietary items from 48 taxa was retrieved from our sample of lizards. Twenty-six of these dietary taxa were identified 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 tracts (97.1%); all but four food items were arthropods. Non-arthropods included two landsnails (*Oxychilus alliarius*) and two lizards (*Lampropholis delicata*). Numbers of food items/chameleon ranged from 0–77 (mean = 23.4, SD = 3.18). For stomachs containing food, numbers of prey species/chameleon ranged from 1–12 (mean = 5.6, SD = 0.45), and prey volumes/lizard ranged from 0.009–5.10 ml (mean = 0.76 ml, SD = 0.17). For stomachs containing food, numbers of prey did not differ between sexes (Mann-Whitney  $U = 168.5$ ,  $n_F = 11$ ,  $n_M = 21$ ,  $p = 0.62$ ), nor did prey volume (Mann-Whitney  $U = 163.0$ ,  $n_F = 11$ ,  $n_M = 21$ ,  $p = 0.47$ ). 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 were 48 mm in length; however, most prey were of small size (Fig. 1).

Most prey items were endemic species (46.9%); most other dietary items were adventive or intentionally introduced alien species (41.6%), but the provenance of 11.6% of dietary items remained unknown because they could not be identified with sufficient precision. For animals with food in their stomachs, numbers of prey/lizard varied from 0–77 (mean = 24.1, SD = 3.20) and volume varied from 0.009–5.104 ml (mean = 0.758 ml, SD = 0.169). Numbers of endemic prey items/lizard varied from 0–58 (mean = 11.3, SD = 1.99) and volume endemic prey items/lizard varied from 0–0.405 ml (mean = 0.094

ml, SD = 0.019). Numbers of endemic prey did not differ between sexes (Mann-Whitney  $U = 186.0$ ,  $n_F = 11$ ,  $n_M = 21$ ,  $p = 0.87$ ), nor did volumes of endemic prey (Mann-Whitney  $U = 198.5$ ,  $n_F = 11$ ,  $n_M = 21$ ,  $p = 0.51$ ). Median numbers of endemic prey for males were nine and median numbers for 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 at which most of our prey items were identified (species or genus). Food items per lizard that could not have their provenance (endemic vs. alien) determined because of identification problems varied from 0–18. These numbers were sufficiently small that overall assessment of lizard impact on endemic prey is unlikely.

Analyzed taxonomically, homopterans comprised the greatest numbers of prey, followed by dipterans and coleopterans (Table 1). Together, these taxa formed 74.8% of all dietary items. Endemic Hawaiian taxa comprised 46.9% of dietary items, adventive aliens comprised 31.7%, intentionally introduced aliens comprised 9.8%, and taxa whose provenance could not clearly be identified comprised 11.6%. The large majority of endemic insects consumed at Volcano Village were homopterans of the genera *Oliarus* and *Nesophrosyne*, comprising 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 comprised significant volumes as well (16.9% and 13.7% of prey volume, respectively). Adventive aliens comprised 59.4% of food items by volume, endemic species comprised 12.5%, intentionally introduced aliens comprised 13.0%, and taxa whose provenance could not clearly be identified comprised 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 vegetation (12 on *Metrosideros polymorpha*, 4 on *Acacia koa*, 2 on *Coprosma ochracea*, 2 on *Dicranopteris linearis*, 1 on *Vaccinium calycinum*) and six were found in alien vegetation (4 on *Tibouchina urvilleana*, 2 on *Morella faya*). Unexpectedly, lizards found on alien vegetation had a higher percentage of endemic prey items in their digestive tracts than were animals collected on native vegetation (57.6% vs. 45.5%,  $G = 4.4877$ ,  $DF = 1$ ,  $p = 0.034$ ). Lizards found on alien vegetation also had a higher number of endemic species/lizard (1.33) than did animals found on native vegetation (0.90).

## 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 ranges (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., in review), 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 chameleons consumed a large number of small prey items, with a mean of 41.8 dietary items/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 comprised the predominant prey items. Third, ants, other hymenopterans, and beetles comprised small proportions of the chameleons' diets, which is unusual for an iguanian lizard, which are largely ambush predators reliant on visual cues for prey detection. Directly relevant to conservation concerns are that a large number of native insects (35.2% of total) was consumed, and cropping rates seemed likely to be high because of the high numbers of prey items in the lizards' digestive tracts and because chameleons have been reported to take 3-15 meals/day and to have high digestion rates that quickly clear their digestive tracts (Burrage, 1973).

The present study of *Chamaeleo jacksonii*, from a different native environment in Hawaii (wet vs. 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 vs. 41.8), and the range of items (0-77 vs. 0-352) and standard deviation of samples (3.18 vs. 10.41) were both lower. However, size distribution of prey items was virtually identical to the earlier study from dry-forest habitat, with (1) the large majority of dietary items being less than 9 mm in length (Fig. 1), and (2) larger prey items being consumed at lower frequencies. Prey diversity was even higher in the present study than in that on Maui (Shannon-Wiener index 3.01 vs. 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.

The vast majority of prey were arthropods, but landsnails and lizards were also consumed. The last is of interest because the prey species (*Lampropholis delicata*) is terrestrial, and these lizards must have been consumed while the chameleons were active on the ground. Although chameleons are primarily arboreal, they are often seen crossing roads in Hawaii, and these prey items confirm their willingness to feed while crossing between habitat patches. 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 Hawaii Island; coleopterans: 14.57% on Maui, 16.10% on Hawaii Island), but with far fewer flies consumed in this study (42.88% on Maui, 23.27% on Hawaii Island). We presume the reduced consumption of dipterans on Hawaii 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 Hawaii Island), in contrast to the usual expectations for iguanian lizards (Vitt et al., 2003; Vitt and Pianka, 2005). In the present instance, we found no ants in the diet at all, although two honeybees (*Apis mellifera*), one sphecid (*Ampulex compressa*), five ichneumonid wasps (4 *Barichneumon*, 1 *Enichospilus*), and 24 yellow-jackets (*Vespula pensylvanica*) were present. Beetles also comprise a large percentage of the diet of most iguanians (Vitt et al., 2003; Vitt and Pianka, 2005), and, as noted above, comprised a fair portion of chameleon diets in both



dry forest on Maui and wet forest on Hawaii 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% vs. 35.2%). The unexpected result that chameleons taken from native vegetation had fewer native prey species in their digestive tracts suggests either that chameleons move frequently among perches, such that their final resting places for the night do not necessarily reflect where they have spent most of their day foraging, or that the native arthropods ingested are not particularly restricted to native vegetation.

One point of interest that we did raise in our earlier study is that these lizards clearly tolerate a diversity of prey with 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 the present study. Similarly, active motion would appear unnecessary to elicit feeding in these chameleons, as suggested by their consumption of landsnails (this study, Holland et al., 2010), which are largely inactive during daytime, and their consumption of bird eggs in captivity (cf. Kraus et al., in review). Lastly, the Maui study found that these lizards consumed species comprising virtually the entire range body sizes found in native arthropods in Hawaii. Thus, it would appear that few, if any, invertebrates found in Hawaii will prove invulnerable to predation by these lizards. The conservation implications of this conclusion, coupled with the chameleons' high population densities and wide projected range in Hawaii (Kraus et al., in review), should be obvious.

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Table 1. Composition of dietary items in gastrointestinal tracts of 33 *Chamaeleo jacksonii* from Volcano Village, Hawaii Island.

<b>ORDER</b>	<b>FAMILY</b>	<b># PREY ITEMS</b>	<b>% PREY ITEMS</b>	<b>% PREY VOLUME</b>
<b>Squamata</b>		<b>2</b>	<b>0.25</b>	<b>3.00</b>
	Scincidae	2	0.25	3.00
<b>Araneae</b>		<b>11</b>	<b>1.38</b>	<b>0.52</b>
	Tetragnathidae	9	1.13	0.44
	Thomisidae	2	0.25	0.08
<b>Blattodea</b>		<b>3</b>	<b>0.38</b>	<b>0.87</b>
	Blattellidae	3	0.38	0.87
<b>Coleoptera</b>		<b>128</b>	<b>16.10</b>	<b>17.66</b>
	Cerambycidae	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
<b>Dermoptera</b>		<b>1</b>	<b>0.13</b>	<b>0.03</b>
	Forficulidae	1	0.13	0.03
<b>Diptera</b>		<b>185</b>	<b>23.27</b>	<b>35.24</b>
	Calliphoridae	99	12.45	26.86
	Drosophilidae	1	0.13	0.00
	Stratiomyidae	37	4.65	5.49
	Syrphidae	48	6.04	2.89
<b>Heteroptera</b>		<b>35</b>	<b>4.40</b>	<b>3.15</b>
	Lygaeidae	2	0.25	0.01
	Miridae	14	1.76	0.24
	Nabidae	17	2.14	0.36
	Pentatomidae	2	0.25	2.53
<b>Homoptera</b>		<b>182</b>	<b>35.47</b>	<b>4.02</b>
	Cicadellidae	103	12.96	1.81
	Cixiidae	130	16.35	1.70
	Psyllidae	49	6.16	0.51
<b>Hymenoptera</b>		<b>32</b>	<b>4.03</b>	<b>16.94</b>
	Apidae	2	0.25	1.41
	Ichneumonidae	5	0.63	0.28
	Sphaecidae	1	0.13	0.40
	Vespidae	24	3.02	14.85
<b>Lepidoptera</b>		<b>38</b>	<b>4.79</b>	<b>3.96</b>
	Crambidae	8	1.01	0.92
	Cosmopterygidae	13	1.64	0.27
	Geometridae	17	2.14	2.76
<b>Orthoptera</b>		<b>29</b>	<b>3.64</b>	<b>13.74</b>
	Gryllidae	25	3.14	2.04
	Tettigoniidae	4	0.50	11.70

<b>Julida</b>		<b>40</b>	<b>5.03</b>	<b>0.27</b>
	Julidae	40	5.03	0.27
<b>Polydesmidae</b>		<b>2</b>	<b>0.25</b>	<b>0.17</b>
	Paradoxosomatidae	2	0.25	0.17
<b>Isopoda</b>		<b>5</b>	<b>0.63</b>	<b>0.38</b>
	Porcellionidae	5	0.63	0.38
<b>Gastropoda</b>		<b>2</b>	<b>0.25</b>	<b>0.04</b>
	Zonitidae	2	0.25	0.04
<b>TOTAL</b>		<b>795</b>	<b>100.00</b>	<b>100.00</b>

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Table 2. Endemic Hawaiian insects comprising dietary items in a sample of 33 *Chamaeleo jacksonii* from wet forest habitat on Hawaii Island.

ORDER	FAMILY	SPECIES	# PREY ITEMS	% PREY ITEMS	% PREY VOLUME
Araneae	Tetragnathidae	<i>Tetragnatha</i> sp. 1	6	0.75	0.26
Araneae	Tetragnathidae	<i>Tetragnatha</i> sp. 2	3	0.38	0.18
Araneae	Thomisidae	<i>Mecaphesa</i> sp.	2	0.25	0.08
Coleoptera	Cerambycidae	<i>Plagithmysus</i> sp. 1	2	0.25	0.72
Coleoptera	Cerambycidae	<i>Plagithmysus</i> sp. 2	1	0.13	0.09
Diptera	Drosophilidae	<i>Drosophila</i> sp.	1	0.13	0.00
Heteroptera	Lygaeidae	<i>Nysius</i> sp.	2	0.25	0.01
Heteroptera	Miridae	<i>Sarona</i> sp.	6	0.75	0.06
Heteroptera	Miridae	<i>Hyalopeplus pellucidus</i>	5	0.63	0.18
Heteroptera	Nabidae	<i>Nabis blackburni</i>	6	0.75	0.13
Heteroptera	Nabidae	<i>Nabis lusciosus</i>	1	0.13	0.04
Heteroptera	Nabidae	<i>Nabis</i> sp. nr. <i>blackburni</i>	10	1.26	0.20
Heteroptera	Pentatomidae	<i>Coleoticus blackburniae</i>	2	0.25	2.53
Homoptera	Cicadellidae	<i>Nesophrosyne</i> sp.	92	11.57	1.60
Homoptera	Cixiidae	<i>Oliarus</i> sp.	130	16.35	1.70
Homoptera	Psyllidae	<i>Megatrioza</i> sp.	49	6.16	0.51
Hymenoptera	Ichneumonidae	<i>Enicospilus</i> sp.	1	0.13	0.10
Lepidoptera	Cosmopterygidae	<i>Hyposmocoma</i> sp.	13	1.64	0.27
Lepidoptera	Geometridae	<i>Eupithecia</i> sp.	16	2.01	1.82
Orthoptera	Gryllidae	<i>Laupala</i> sp.	25	3.14	2.04

## Figure

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

