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## APPENDIX 1

Specimens examined. *Hyla cipoensis*.—UFMG 367, three tadpoles collected by P. C. Eterovick at the Serra do Cipó (19°16'S, 43°32'W), on 30 May 1999; UFMG 368, four tadpoles collected by P. C. Eterovick at the Serra do Cipó (19°15'S, 43°33'W), on 30 May 1999; UFMG 369, two tadpoles collected by P. C. Eterovick at the Serra do Cipó (19°15'S, 43°33'W), on 8 December 1998.

*Hyla goiana*.—UFMG 364, six tadpoles collected by R. A. Brandão and M. Bagno in the Rio Maranhão, Distrito Federal, Brazil, on 24 January 1996.

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### A Comparison of the Breeding and Nonbreeding Season Diets of *Agama aculeata* and *Agama planiceps* (Reptilia: Agamidae) in Windhoek, Namibia

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Lizard diets can be analyzed by examining stomach contents (Pianka and Huey, 1978; Floyd and Jenssen, 1983; Bauer et al., 1989), stomach and intestinal contents (Schoener, 1971; Robinson, 1987), fecal pellet

TABLE 1. Incidence (%) and index of relative importance (IRI) of prey items in the diet of *A. a. aculeata* males and females during the breeding and nonbreeding seasons. SVL is given as the mean  $\pm$  1 SD.

Prey items	Males Mean SVL: 93.3 $\pm$ 11.7 mm				Females Mean SVL: 85.4 $\pm$ 6.6 mm			
	Breeding season (N = 32)		Nonbreeding season (N = 61)		Breeding season (N = 32)		Nonbreeding season (N = 47)	
	%	IRI	%	IRI	%	IRI	%	IRI
Apoidea	46.9	0.67	42.6	0.63	40.6	0.36	19.1	0.07
Coleoptera	59.4	0.80	47.5	0.90	31.3	0.18	48.9	0.49
Diptera	0	0	11.5	0.05	0	0	6.4	0.007
Formicoidea	87.5	98.2	100	97.6	93.8	99.1	100	98.9
Hemiptera	15.6	0.03	18.0	0.041	25.0	0.10	19.1	0.05
Isoptera	15.6	0.21	16.4	0.75	15.6	0.24	19.1	0.36
Larvae	6.3	0.06	14.8	0.04	9.4	0.01	8.5	0.02
Odonata	12.5	0.03	8.2	0.04	6.3	0.004	8.5	0.009
Orthoptera	3.1	0.001	0	0	0	0	0	0

contents (Bruton, 1977; Mitchell et al., 1987), by stomach flushing (Pietruszka, 1987) or by actual observation of foraging (Henle, 1990). Of these, the first two methods appear most commonly used. Floyd and Janssen (1984) argued that examination of stomach contents alone provides a more accurate assessment of lizard diets than examination of the entire alimentary canal. In their opinion, digestion tends to remove soft-bodied food items, which are usually large, from the lower part of the alimentary canal so that small-bodied food items predominate in the hindgut, leading to an underestimation of large-bodied prey if contents of the entire alimentary canal are used. Schoener (1989), however, refuted their argument by showing that in general there is a nonsignificant decrease in both prey species diversity and size from fore- to hind gut. Schoener (1989) further contended that an analysis of the entire gut not only eliminates the possibility of larger food items being underestimated but in fact increases sample size. In this study, the diets of *Agama aculeata* and *Agama planiceps* were therefore analyzed by examining the contents of both the stomach and intestine.

*Agama aculeata* and *A. planiceps* are diurnal, oviparous agamids occurring syntopically in large parts of Namibia. *Agama aculeata* is widely distributed throughout southern Africa and inhabits sandveld areas in semidesert and savannah biomes (McLachlan, 1981; Branch, 1988). *Agama planiceps* is confined to Namibia and inhabits rocky outcrops in semidesert and arid savannah areas (McLachlan, 1981; Branch, 1988). The two species are common in and around Windhoek (22°34'S; 17°06'E), Namibia, which lies in the seasonal tropics at an altitude of approximately 1725 m above sea level, in a cool steppe region. Both species breed in summer (October through January), which is the rainy season, whereas their nonbreeding season coincides with autumn and winter (February through July), the dry season (Heideman, 1994; 1995). *Agama aculeata* is solitary during the nonbreeding season and monogamous during the breeding season, whereas *A. planiceps* is more social and becomes polygynous during the breeding season (Heideman, 1994; 1995). Herein, I present (1) a comparison of the diets of males and females in each species in the breeding and non-

breeding season, (2) a comparison of their breeding and nonbreeding season diets, and (3) an interspecific comparison of the diets of corresponding sexes in the breeding and nonbreeding season.

Adult male and female *A. aculeata* and *A. planiceps* were collected in Windhoek between January 1988 and December 1990 to analyze their reproductive biology. The diets of these specimens were analyzed at the same time. Sample size and mean snout-vent length (SVL) of specimens studied per season is given in Tables 1 and 2. Specimens were sacrificed within an hour of their capture, after which their alimentary canal was removed and its contents examined.

The contents of the alimentary canal of each specimen were examined and identified with the aid of a dissecting microscope. Although insects were identified mainly on the basis of head capsules and trophic apparatus, other identifiable body parts such as elytra and appendages were also used. I used the taxonomic keys of Skaife (1979), and Scholtz and Holm (1986). Larvae were counted but not identified. Plant matter (flower parts, leaves, and seeds) was also recorded but not identified. The incidence of each food item in samples of males and females examined per species, respectively, was calculated for both breeding and nonbreeding seasons. This was done by expressing number of lizards containing a particular item as a percentage of the total number of lizards examined of a particular sex in each species. An index of relative importance (IRI) was calculated for each food item as it occurred in the sample of each sex per species, for both breeding and nonbreeding seasons, respectively, using a modified version of the formula of Bjorndal et al. (1997):  $IRI = 100(F_i V_i) / \sum (F_i V_i)$ , where  $F_i$  = food item incidence;  $V_i$  = mean food item count.

Statistical analyses followed Sokal and Rohlf (1981), Zar (1984) and Littell et al. (1996) with differences between datasets considered significant at the level of  $P \leq 0.05$ . Although an ideal method for statistically comparing the count data of this investigation would have been analysis of variance with two seasons, two sexes, and two species factorial structure, the nonnormality of the data made this procedure invalid. Transforming the data did not remedy the situation as the data remained overdispersed and heavily skewed. Dif-

TABLE 2. Incidence (%) and index of relative importance (IRI) of prey items in the diet of *A. p. planiceps* males and females during the breeding and nonbreeding seasons.

Prey items	Males Mean SVL: 95.0 ± 8.7 mm				Females Mean SVL: 91.3 ± 6.4 mm			
	Breeding season (N = 24)		Nonbreeding season (N = 40)		Breeding season (N = 34)		Nonbreeding season (N = 36)	
	%	IRI	%	IRI	%	IRI	%	IRI
Apoidea	54.2	1.82	47.5	3.82	58.1	1.10	41.0	3.59
Coleoptera	45.8	1.06	65.0	4.40	29.0	0.19	61.5	3.31
Diptera	0	0	0	0	3.2	0.003	2.6	0.004
Formicoidea	91.6	95.9	87.5	86.7	96.8	97.9	74.4	85.6
Hemiptera	29.2	0.44	30.0	1.92	38.7	0.43	23.1	0.44
Isoptera	12.5	0.51	5.0	0.27	16.1	0.34	2.6	0
Larvae	4.2	0.007	5.0	0.27	3.2	0.005	3.2	0.08
Lepidoptera	0	0	2.5	0.01	0	0	3.2	0.02
Odonata	4.2	0.03	5.0	0.27	6.5	0.007	10.3	0.17
Orthoptera	0	0	2.5	0.13	3.2	0.002	0	0

ferences in variance and mean precluded use of the Poisson distribution. The procedure found to be appropriate was a generalized linear model with negative binomial distribution (Littell et al., 1996), the conditions of which were met by the data. This negative binomial distribution model provided better models of variation among the count data and hence of errors in linear models (Littell et al., 1996). The model treated diet and season (breeding and nonbreeding) as the same variable.

Ants (Formicoidea) eaten by the two species ranged from the small black *Pheidole* and *Crematogaster* spp. to the larger black and brown *Anoplolepis* spp. Beetles (Coleoptera) found in the diet were representatives of the families Coccinellidae, Curculionidae and Tenebrionidae, with the ladybird beetle, *Cheilomenes lunata*, the most commonly consumed species. The only honeybee (Apoidea) species consumed was *Apis mellifera*, whereas bugs (Hemiptera) in the diet represented the families Lygaeidae and Pentatomidae. The only termite (Isoptera) species consumed was *Hodotermes mossambicus*. The remainder of the food items comprised representatives of the Lepidoptera (absent in *A. acu-*

*leata*), Odonata, Orthoptera (absent in *A. aculeata* females), Diptera, and larvae.

Ants had the highest incidence in *A. aculeata* and *A. planiceps* in both seasons, followed in general by honeybees and beetles (Tables 1–2). Ants also had the highest IRI throughout (Tables 1–2). The IRI of the rest of the prey items were not comparable to those of ants, but it should be borne in mind that they were much larger prey items and therefore represented substantial sources of energy. Items with an IRI greater than 1 were thus also regarded as important. On the basis of this, none of the remaining food items were important in *A. aculeata*, whereas only honeybees and beetles were important food items in *A. planiceps* in both seasons.

Consumed plant material usually consisted of fragmented pieces of flowers and leaves in both species. A comparison of the relative mean ( $\pm$  1 SD) wet mass of plant material found in 17 *A. planiceps* specimens and seven *A. aculeata* specimens showed no significant difference (*A. planiceps*: 0.253  $\pm$  0.239 g vs. *A. aculeata*: 0.115  $\pm$  0.066 g,  $t_{22} = 0.279$ ,  $P > 0.05$ ).

A generalized linear model with negative binomial distribution showed that significant seasonal differences with respect to consumption of honeybees were influenced by sex (Tables 3–4). The model also showed that consumption of beetles was significantly different between sexes and species, respectively, and there was no significant interaction with any of the other variables (Table 3). The highly significant differences in the consumption of ants were, however, influenced by sex, season, and species (Tables 3–5). Significant differences between sexes with respect to consumption of larvae were influenced by season (Tables 3–4), whereas significant differences in larvae consumption between species was not influenced by the other two variables (Table 3). Significant seasonal differences in consumption of representatives of Odonata were influenced by neither sex nor species (Table 3), whereas sex and species showed a significant interaction with respect to consumption of these prey items (Tables 3, 5).

*Agama aculeata* and *A. planiceps* are insectivorous lizards but also consume varying amounts of plant ma-

TABLE 3. *P*-values obtained following analysis of prey item data by generalized linear model with negative binomial distribution. <sup>a</sup> For example, consumption of Apoidea differed significantly by season but not between sexes.

Prey items	Season	Sex	Species	Season $\times$ sex	Sex $\times$ species
Apoidea <sup>a</sup>	0.001	0.677	0.217	0.003	0.919
Coleoptera	0.983	0.023	0.029	0.413	0.954
Diptera	0.331	0.704	0.549	0.656	0.980
Formicoidea	0.001	0.002	0.001	0.001	0.001
Hemiptera	0.454	0.207	0.131	0.600	0.123
Isoptera	0.253	0.259	0.259	0.425	0.402
Larva	0.215	0.019	0.019	0.034	0.368
Odonata	0.046	0.049	0.050	0.187	0.020
Orthoptera	1.00	0.907	0.907	0.940	0.884
Lepidoptera	0.826	0.852	0.852	0.999	0.999

TABLE 4. Two-way table of treatment means of sex-by-season interaction effects. The numbers given are the mean counts of food items for which there were significant interactions as shown in Table 3. BS = breeding season; NBS = nonbreeding season.

		Female	Male
<i>A. a. aculeata</i>			
Apoidea	BS	0.88	0.97
	NBS	0.34	1.08
Formicoidea	BS	104.88	75.28
	NBS	84.64	71.46
Larva	BS	0.13	0.63
	NBS	0.28	0.21
<i>A. p. planiceps</i>			
Apoidea	BS	1.06	0.92
	NBS	1.58	3.80
Formicoidea	BS	59.12	28.75
	NBS	20.83	47.00
Larva	BS	0.09	0.04
	NBS	0.47	2.55

terial. They are therefore carnivorous omnivores following the definition of Pough (1973). Vitt and Price (1982), and Pianka (1986) classified agamid lizards as primarily sit-and-wait predators, which is supported by my data showing a preponderance of ants in the diet of both species. In terms of numbers, ants form the bulk of their diet probably because of their high availability and ease of capture. Whether they constitute the most important source of energy for these lizards, however, remains to be determined. Apart from the absence of representatives of the Lepidoptera in the diet of *A. aculeata* and those of the Orthoptera in female *A. aculeata*, diets of the two species overlapped completely. This was not unexpected considering their overlapping distributional ranges and the fact that both are primarily sit-and-wait predators. The absence of the two more dispersed prey types from the diet of *A. aculeata* nevertheless suggests some widely foraging behavior by *A. planiceps* or superior ability by the latter species to capture such prey.

The significantly higher consumption of ants by *A. aculeata* males and females during the breeding season suggests greater engagement in sit-and-wait foraging during that time. In males, it is probably also indicative of less time spent widely foraging because of time spent engaged in breeding related activities (e.g., territoriality, mating; Heideman, 1993a, 1995). This is supported by the significantly lower consumption of dispersed prey such as honeybees but not by the significantly higher consumption of larvae. In females, more sit-and-wait foraging was expected because the associated reduction in movement might enhance the effectiveness of their cryptic coloration in predator avoidance (Heideman, 1993b). This may be particularly important during that time considering the fact that relative clutch mass is quite high thus constraining their ability to run away from predators (Heideman, 1994). Their significantly lower consumption of more dispersed prey such as larvae supports this suggestion but not the significantly higher consumption of honeybees. However, being large prey items and presumably also large sources of energy, the higher con-

TABLE 5. Two-way table of treatment means of species-by-sex interaction effects. The numbers given are the mean counts of food items for which there were significant interactions as shown in Table 3.

		<i>A. a.</i> <i>aculeata</i>	<i>A. p.</i> <i>planiceps</i>
Breeding season			
Formicoidea	Female	104.88	59.12
	Male	75.28	28.75
Odonata	Female	0.05	0.06
	Male	0.13	0.21
Nonbreeding season			
Formicoidea	Female	84.64	20.83
	Male	71.46	47.00
Odonata	Female	0.09	0.31
	Male	0.08	2.58

sumption of honeybees during this time may be vital for females to cope with the high-energy demands of egg production. The effect of breeding activities on foraging behavior would also explain significant differences in prey consumption in *A. planiceps* males during the breeding season, whereas female foraging behavior is also expected to be constrained by the effect of heavy egg loads on their locomotor ability.

Significant differences in prey consumption by males and females in the two species during the nonbreeding season is presumably the result of differences in the extent to which they engage in sit-and-wait and widely foraging behavior. Males and females may also differ in their ability to capture certain prey types.

The significantly higher consumption of ants by *A. aculeata* males compared to *A. planiceps* males in the breeding season was not unexpected, breeding behavior in the monogamous *A. aculeata* being much less intensive than that of the polygynous *A. planiceps* (Heideman, 1993a, 1995). The significantly higher consumption of ants by *A. aculeata* than *A. planiceps* females in both seasons suggests greater overall involvement in sit-and-wait foraging on part of the former. This was also not unexpected, particularly in the breeding season, considering that its relative clutch mass is about twice that of *A. planiceps* females (Heideman, 1994). The significantly higher consumption of Odonata by *A. planiceps* females, on the other hand, may also result in a more energy-rich diet which may offset their apparently higher predation pressure (Heideman, 1993b) by enabling them to reach reproductive maturity within a shorter time span. Nagy et al. (1984), for example, found that the widely foraging *Eremias lugubris* of the Kalahari Desert not only obtained a substantially higher amount of energy per hour than the sympatric sit-and-wait *Eremias lineoocellata* but also grew twice as fast. Karasov and Anderson (1984), in fact, speculated that, if high growth rates are synonymous with high rates of reproduction, species with these characteristics should have a high turnover rate in terms of population dynamics.

The presence of plant material in the stomachs of both species may have several explanations. Many of their insect prey occur in foliage, which is therefore probably ingested incidentally; the plant material usu-

ally showed little sign of mastication or digestion and was still fairly intact in both the stomach and hindgut. On numerous occasions members of both species were seen climbing into trees and shrubs to grab insects sitting on leaves and flowers (pers. obs.). In the case of *A. planiceps*, herbivory has been mentioned in a number of sources (e.g., Fitzsimons, 1943; Branch, 1988) without details on the quantity, state, or nutritional value of the ingested material. The fairly intact condition of the plant material in the stomach and hindgut of the species of this study, however, raises doubt about its nutritional value; it possibly serves only as a source of water, but this will have to be verified in follow-up studies. Bruton (1977) found that large *Agama atra* individuals readily consumed cabbage leaves in captivity, even though no plant material occurred in the guts of wild specimens. Marshall and Hook (1960) reported the presence of grass, berries, seeds, and flowers in the stomach of *Agama agama lionotus* from equatorial Africa but did not discuss the possible nutritional value of these materials to these agamids.

Differences in the breeding and nonbreeding season diets of *A. aculeata* and *A. planiceps* males can thus be explained in terms of variation in the time spent foraging because of breeding behavior in the former season. In females, on the other hand, greater reliance on sit-and-wait foraging in the breeding season caused by heavy egg burdens may be the primary causal factor. Differences in prey item availability in the wet (breeding) and dry (nonbreeding) periods probably also contribute to seasonal variation in diet.

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### Male-Male Combat and Head Morphology in a Fanged Frog (*Rana kuhlii*) from Taiwan

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In anurans, males and females usually differ in body size; typically females are larger than males (Shine, 1979). Adaptive explanations for the evolution of sexual size dimorphism (SSD) in anurans have included both natural and sexual selection (e.g., Shine, 1979; Woolbright, 1983; Halliday and Verrell, 1986). Why the common SSD is reversed in a few anuran species is an especially interesting problem. More than two decades ago, Wells (1978) proposed that large male body size in anurans may be an adaptation for fighting. Based on an extensive literature survey, Shine (1979) also suggested that large male body size in anurans is associated with physical combat between males and that spines and tusks that develop only in males may be used in male-male combat. Empirical data to support this hypothesis, however, have been rarely obtained for the last 20 yr. Recently, Katsikaros and Shine (1997) demonstrated that in the Australian tusked frog, *Adelotus brevis*, larger body and tusk sizes in males are related to male-male agonistic behavior, including vigorous biting.

The ranid fanged frogs, inhabiting tropical and subtropical Asia, are unusual among anurans in that males are larger than females (Inger, 1966; Emerson and Berrigan, 1993). Male fanged frogs also have a

derived suite of secondary sexual characteristics, such as odontoid processes (fangs) in the lower jaw, hypertrophied jaw muscles, and enlarged heads (Inger, 1966; Emerson and Berrigan, 1993). In the light of Shine's (1979) hypothesis, occurrence of male-male combat has been expected in ranid fanged frogs (Emerson and Inger, 1992). However, with the exception of a brief observation by Orlov (1997), there are no reports of male-male combat in ranid fanged frogs. For this reason, we made detailed observations of naturally occurring agonistic interactions between males in a population of *Rana kuhlii*, a fanged frog from Taiwan. Herein, we describe male agonistic behavior and sexual dimorphism in head morphology of this species.

The study was conducted at two sites (Tonghou and Hsingsien) near Wulai (24°52'N, 121°33'E; 150 m elevation), about 25 km south of Taipei in northern Taiwan, Republic of China. Preliminary fieldwork was done by one of us (HT) at a 35 cm wide and 28 cm deep roadside concrete ditch (water depth = 0–3.0 cm) at Tonghou from August to November 1992. Intensive fieldwork was done by one of us (HT) at a permanent small creek below a forest cliff at Hsingsien, about 5 km southwest of Tonghou, from 12 June to 31 August 1993. This creek was 30–50 cm wide and 0–2.0 cm deep, and the flow was gentle, except after heavy rains. The creek bed consisted of gravel and mud, covered with fallen leaves, and was mostly shaded by ferns. An 81-m transect, marked every 1 m, was set along this creek. The climate at the study sites is subtropical, and nightly water temperatures from June to August at Hsingsien were nearly constant (22–25°C).

A total of 38 adult males and 14 adult females were captured and marked along the transect during the study period at Hsingsien. Individuals were considered adults if they exhibited reproductive behavior or the presence of secondary sexual characteristics. Adult males were identified by amplexus position or courtship approaches to females, or dark-colored nuptial pads. Adult females were identified by egg laying or amplexus position. Three females did not exhibit reproductive behavior but were confirmed gravid by dissection. Following initial capture, body size (snout-vent length, SVL) and head width (across the base of the head at its widest point, HW) of each individual were measured to the nearest 0.1 mm using slide calipers, and body mass (BM) was measured to the nearest 0.1 g using a spring balance (after first blotting animals with a dry towel). Frogs were marked individually by toe-clipping and given a numbered waist band to facilitate recognition during behavioral observations. Numbered waist bands were replaced whenever they came undone, and on such occasions the individuals were measured again. Additionally, male BM was measured at each recapture.

At Hsingsien, censuses were carried out by one of us (HT) along the study transect several times each night from 1900 h until 2400–0300 h during 50 nights surveyed. During each census, the positions of males and females were recorded to the nearest 0.1 m, and interactions between individuals were noted. Observations were made directly at a distance of less than 1 m at night using a 4.5-volt battery head lamp, which seemed not to disturb the frogs' behavior.

For analysis of sexual dimorphism, individual SVL,

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