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Feeding ecology of the Tropical House Gecko *Hemidactylus mabouia* (Sauria: Gekkonidae) during the dry season in Havana, Cuba

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Abstract. The gecko *Hemidactylus mabouia* is an invasive species and a successful colonizer with a broad distribution in the tropics. The species is frequently associated with human buildings on which individuals profit from the availability of potential prey items attracted to artificial light sources. The feeding ecology of *H. mabouia* was studied in an urban area of Havana, Cuba, in order to evaluate diet composition and potential differences among adult males, adult females and juveniles during the dry season. The main prey items encountered consisted of non-flying arthropods (cockroaches, spiders and pill bugs). Cockroaches contributed most to the ingested volume. Snout-vent length did not significantly differ between adult males and adult females, whereas significant differences were recovered in head width among the three sex/age categories. No relationship between body and head size was found in relation to the number and volume of prey items. All analysed individuals tended to feed on small-sized prey. Microhabitat selection is suggested to be the main factor that determines diet composition in adult males and juveniles..

Keywords. Feeding ecology, diet composition, dry season, *Hemidactylus mabouia*, Havana, Cuba.

Introduction

The study of the feeding ecology of a given species generates information about the prey types, most frequent food items, relative importance of each prey, inter- and intraspecific relationships and strategies of food partitioning (Klawinski et al., 1994; Saenz, 1996; Aowphol et al., 2006; Bonfiglio, Balestrin and Cappellari, 2006). A high dietary niche breadth is characteristic for invasive species, which in combination with adequate ecological conditions, provides a solid basis for successful colonization of new environments (Powell, Parmerlee and Rice, 1990; Case, Bolger and Petren, 1994; Rödder, Solé and Böhme, 2008).

The Tropical House Gecko *Hemidactylus mabouia* (Moreau de Jonnés, 1818) (Fig. 1) belongs to the family Gekkonidae. It is a broadly distributed species in the tropics (Henderson and Powell, 2009) and has invaded the West Indies after being introduced from its native range, like other species of the genus, via slave ships coming from Africa during the European colonization (Weiss and Hedges, 2007). This species is an effective colonizer and nocturnal predator that is usually associated with human buildings. *Hemidactylus mabouia* is well known for using areas around artificial light sources as hunting grounds (Currat, 1980; Powell and Henderson, 1992; Daniells et al., 2008; Perry et al., 2008). Population densities can range between 0.04 and 0.21 individuals/ m^2 (Howard, Parmerlee and Powell, 2001). In Cuba, this species was first reported from Eastern Cuba (Schwartz and Henderson, 1991). However, in recent years, *H. mabouia* has gradually invaded central and western Cuba, displacing the closely related invasive species *H. angulatus* (Díaz, in prep.). Despite its current colonization in Cuban territory, there is no information regarding the ecology and especially the feeding habits of *H. mabouia*.

Figure 1. Male adult of *Hemidactylus mabouia* from Havana, Cuba. Photograph by Rubén Marrero.

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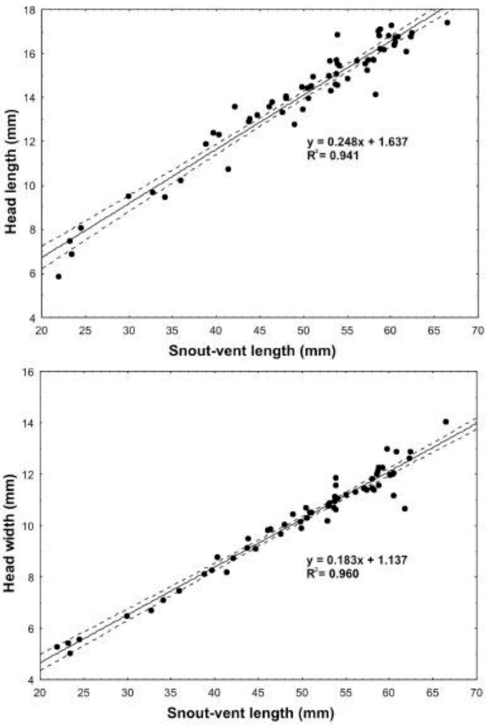

Figure 2. Linear regression between head length and snout-vent length (SVL); and between head width and SVL of juveniles and adult specimens of *Hemidactylus mabouia* from zoo Jardín Zoológico de La Habana "La Edad de Oro", Havana, Cuba. Solid line represents the regression line and dashed line represents 95% confidence intervals.

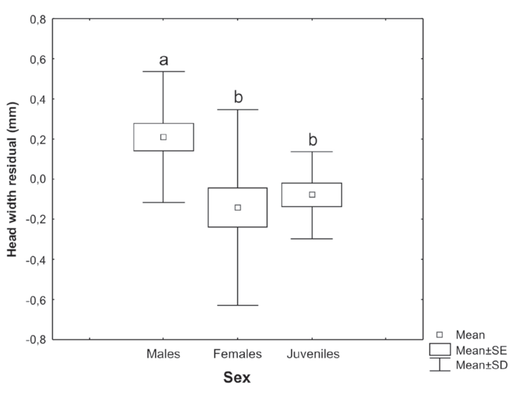

Figure 3. Comparisons of head width residual among adult males, adult females and juveniles of *Hemidactylus mabouia* from zoo Jardín Zoológico de La Habana "La Edad de Oro", Havana, Cuba. Means with different letters differed significantly (Tukey´s HSD post-hoc test, $P < 0.05$).

One of the limiting factors that prevents a better understanding of the problems caused by invasive species is the lack of information about aspects of their natural history and ecology (Rocha and Anjos, 2007; Caicedo-Portilla and Dulcey-Cala, 2011; Hoskin, 2011). Therefore, this article aims to study the diet composition of an urban population of *H. mabouia* from Havana, Cuba, during the dry season and to determine whether intraspecific food partitioning in trophic niches exists.

Materials and Methods

The study was carried out from November 2009 to February 2010 at the zoo Jardín Zoológico de La Habana "La Edad de Oro" (26° 06‘ 41.25“ N, 82° 23‘ 50.18“ W; elevation ca. 39 m SIU) in Havana, Cuba. During each month, 15 individuals of *H. mabouia* were captured which resulted in a total of 61 specimens. All geckos were collected by hand during the period between 18:30 and 22:00 h. Individuals were encountered on tree trunks, on the ground under rocks and human debris, and on the wall of human housing, but not under artificial lights. Specimens captured were immediately sacrificed and preserved in 70% ethanol. The snout-vent length (SVL), head length (HL) and head width (HW) were measured in each individual using a digital calliper (to 0.01 mm). Sex determination was performed based on secondary sexual characters, presence of preanal pores in adult males and endolymphatic sacs behind of the head in adult females, and finally by gonadal identification after dissection. The specimens were divided into three sex/age categories.

Specimens were dissected and their stomachs were removed for posterior content analyses under a stereomicroscope. Stomach contents were identified to the taxonomic level of Order. The contents that could not be identified were pooled into a "non-identified" category. The food items of each specimen were counted and measured (length and width) using digital calliper for larger prey and X15 eyepiece micrometre coupled to the binocular stereomicroscope (to 0.014 mm) for smaller prey.

The number of prey was defined as the amount of prey of a given item in the total diet, and the frequency as the total number of stomachs in which a given item was found. The volume of each item (mm^3) was estimated by the prolate spheroid volume: Volume= $4/3\pi \times (L/2) \times (W/2)^2$ where L= length and W= width (e.g. Colli et al., 2003; Bonfiglio, Balestrin and Cappellari, 2006). The importance of each food item consumed (*i*) was described by the index of relative importance (Pinkas et al., 1971), which was calculated as $IRI_i = \%F_i(\%N_i+\%V_i)$, where $\%F_i$ is the percent frequency (the number stomachs containing each item *i*); $\%N_i$ is the percent of the number of *i* items in all stomachs; and $\%V_i$ is the percent of the volume of items *i* in all stomachs. Levin´s standardized niche breadth index (Hurlbert, 1978), $B = (1/\Sigma p_i^2) - 1/n-1$, was used to determine niche breadth in number and volume of ingested prey, where pi is the proportion of occurrence of items *i* in the diet composition, and *n* is the total number of prey taxa. B ranges from 0 to 1; a value of near 1 means that every prey was used in same proportion, whereas a value near zero means that only one or a few food items were used in higher proportions and the rest in lower proportions. Pianka´s index of niche overlap

Table 1. Number (**N**), volume (in mm³) (**V**) and frequency of prey (**F**) and index of relative importance (**IRI$_i$**) in the diet of adult males, adult females and juveniles of *Hemidactylus mabouia* from zoo Jardín Zoológico de La Habana "La Edad de Oro", Havana, Cuba.

	Adult Males (n=15)				Adult Females (n=21)				Juveniles (n=12)			
Item	**N (%)**	**V (%)**	**F (%)**	**IRI$_i$**	**N (%)**	**V (%)**	**F (%)**	**IRI$_i$**	**N (%)**	**V (%)**	**F (%)**	**IRI$_i$**
Arachnida												
Araneae	5 (11.36)	42.58 (6.12)	5 (21.74)	380.02	7 (14.89)	118.5 (4.93)	7 (18.42)	365.08	4 (13.79)	0.46 (0.08)	4 (16.67)	231.21
Crustacea												
Isopoda	2 (4.55)	-	2 (8.70)	-	8 (17.02)	167.53 (6.96)	5 (13.16)	315.58	7 (24.14)	60.4 (11.07)	5 (20.83)	733.42
Insecta												
Blattodea	4 (9.09)	466.39 (67.03)	4 (17.39)	1323.73	7 (14.89)	1675.73 (69.65)	6 (15.79)	1334.87	3 (10.34)	386.28 (70.84)	3 (12.5)	1014.75
Coleoptera	2 (4.55)	10.36 (1.49)	1 (4.35)	26.27	3 (6.38)	1.64 (0.07)	3 (7.89)	50.89	1 (3.45)	-	1 (4.17)	-
Diptera	-	-	-	-	1 (2.13)	-	1 (2.63)	-	2 (6.90)	-	2 (8.33)	-
Heteroptera	1 (2.27)	0.80 (0.11)	1 (4.35)	10.35	-	-	-	-	-	-	-	-
Hymenoptera	3 (6.82)	41.82 (6.01)	1 (4.35)	55.81	11 (20.4)	46.43 (1.93)	4 (10.53)	235.13	4 (13.79)	0.28 (0.05)	3 (12.5)	173.00
Isoptera	24 (54.55)	49.69 (7.14)	2 (8.70)	536.70	-	-	-	-	-	-	-	-
Lepidoptera (adult)	-	-	-	-	2 (4.26)	43.34 (1.80)	2 (5.26)	31.88	2 (6.90)	6.59 (1.21)	2 (8.33)	67.56
Lepidoptera (larvae)	1 (2.27)	84.15 (12.09)	1 (4.35)	62.47	-	-	-	-	2 (6.90)	26.34 (4.83)	1 (4.17)	48,91
Orthoptera	-	-	-	-	2 (4.26)	321.95 (13.38)	2 (5.26)	92.79	1 (3.45)	64.94 (11.91)	1 (4.17)	64,05
Psocoptera	-	-	-	-	4 (8.51)	4.22 (0.18)	3 (7.89)	68.56	1 (3.45)	-	1 (4.17)	-
Thysanura	-	-	-	-	1 (2.13)	1.21 (0.05)	1 (2.63)	5.73	-	-	-	-
Myriapoda												
Chilopoda	-	-	-	-	1 (2.13)	25.51 (1.06)	1 (2.63)	8,39	-	-	-	-
Other												
Plant material	uncountable	-	3 (13.04)	-	uncountable	-	3 (7.89)	-	-	-	-	-
Gecko skin	uncountable	-	1 (4.35)	-	-	-	-	-	-	-	-	-
not identified	2 (4.55)	-	2 (8.70)	-	-	-	-	-	2 (6.90)	-	1 (4.17)	-
Total	**44 (100)**	**695.79 (100)**			**46 (100)**	**2406.06 (100)**			**29 (100)**	**545.29 (100)**		

(Pianka, 1973) was used to determine diet similarity among adult males, adult females and juveniles: $O_{jk} = \sum P_{ij} P_{ik} / \sqrt{(\sum P_{ij}^2)(\sum P_{ik}^2)}$, where P_{ij} and P_{ik} is the proportion of use of food item i for the sex/age categories j and k, respectively.

The data were analysed using Statistica version 8.0 for Windows and GrasphPad Instat version 3.01 for Windows. The Kolmogorov-Smirnov test and Levene test were calculated to test if the data were normally distributed and had homogeneous variances, respectively. A Student-t test was performed to analyse differences in SVL between adult males and females. A Linear Regression analysis was used to test linear relationships between HW and HL with SVL. Calculated residuals from these regressions were used to compare among adult males, adult females and juveniles using a one-way ANOVA. Tukey´s HSD test (post-hoc) was applied to test the differences among particular sex/age categories. This approach minimizes the effect of body size and keeps the variation of response variable (Quinn and Keough, 2002). Kruskal-Wallis ANOVA by ranks for the mean number of consumed prey (the data did not fit a normal distribution) and a one-way ANOVA for mean volume of ingested prey were implemented to test for differences among the three sex/age categories. A Spearman Rank Correlation was performed to assess the relationship between the mean number of consumed prey with SVL and HW residuals. A Linear Regression was computed to test for a linear relationship between the volume of ingested prey with SVL and HW residuals. A Chi-square test was used to examine the variation of volume of ingested prey in diet among the three sex/age categories. The Volume of ingested prey was pooled in three groups: less 49 mm³, 50-99 mm³ and more 100 mm³.

Results

Among the captured geckos (n=61) during the sampling period, 48 specimens (15 adult males, 21 adult females and 12 juveniles) had stomach contents. The remaining stomachs were empty, representing 21.3% of the total sample.

No significant difference was found between SVL of adult males (51.56 ± 7.20 mm, range = 43.85-59.75 mm; n = 22) and adult females (54.47 ± 10.47 mm; range = 40.3-60.82 mm; n = 25) (Student-t; t = 0.878; P = 0.385,). Significant linear relationships were found between HW and SVL ($R^2 = 0.960$, $F_{1,59} = 1402.36$, $P < 0.0001$) and HL with SVL ($R^2 = 0.941$, $F_{1,59} = 945.88$, $P < 0.0001$) (Fig. 2). The one-way ANOVA test revealed significant differences in HW residuals among sex/age categories ($F_{2,58} = 5.272$, $P = 0.0079$, n = 61) where the adult males showed the higher values (Fig. 3). However, no differences were found in HL residuals ($F_{2,58} = 2.386$, $P = 0.101$, n = 61).

The diet was mainly composed of arthropods that comprised 10 orders of insects, one order of arachnids, one order of crustaceans and one order of myriapods (Table 1). In terms of number, the dominant prey in the diet of *H. mabouia* were termites (54.55%) for

Table 2. Standardized niche breadth and trophic niche overlap indexes based on proportions of prey number and volume, frequency and volume prey, respectively for adult males, adult females and juveniles of *Hemidactylus mabouia* from zoo Jardín Zoológico de La Habana „La Edad de Oro“, Havana, Cuba.

	Niche breadth		**Trophic niche overlap**					
	Prey	Prey	Prey frenquency			Prey volume		
	number	volume	Males	Females	Juveniles	Males	Females	Juveniles
Males	0.29	0.18	-	0.81	0.85	-	0.95	0.96
Females	0.66	0.11		-	0.90		-	0.99
Juveniles	0.78	0.11			-			-

adult males; ants (20.4%), pill bugs (17.02%), spiders (14.89%) and cockroaches (14.89%) for adult females and pill bugs (24.14%) for juveniles. In terms of volume, the order Blattodea (cockroaches) was the most important food item, with more than 50% of ingested volume in each sex/age category. The most frequent prey items were spiders and cockroaches for adult males and adult females, as were pill bugs and spiders for juveniles. According to the Index of Relative Importance (IRI_i), the most important food item consumed was cockroaches (more than 1000) for three sex/age categories. The pill bugs were the second most important item in the diet of juveniles (IRI_i = 733.42). For adult males termites (IRI_i = 536) and spiders (IRI_i = 380.02) were the second most important; whereas for adult females were spiders, pill bugs and ants (IRI_i = 365.08, IRI_i = 315.58 and IRI_i = 235.13, respectively). The rest of the prey had lower relative importance indexes (Table 1).

Items unusually found were fragments of vegetal material (in three stomachs) and shed gecko skins (one stomach) of adult males. Three non-identified arthropods were found in two stomachs of adult males and one of a juvenile.

The mean number of food items consumed by adult males was 1.92 ± 1.72, by adult females 2.24 ± 1.26 and juveniles 2.42 ± 1.16. There were no significant differences among them (Kruskal-Wallis ANOVA by ranks $H_{2,45}$ = 3.45; P = 0.178, n = 45). The highest number of ingested prey was that of an adult male, with 21 food items (all termites) in its stomach. The mean volume of ingested prey of adult males ranged between 86.97 ± 146.52 mm3, that of adult females between 169.34 ± 325.17 mm^3 and that of juveniles between 68.16 ± 81.11 mm^3. The differences among these were not significant in mean volume (one-way ANOVA, $F_{2,27}$ = 0.552; P = 0.582; n = 37). No significant relationships were found between the number of food items in each stomach and body size of geckos (Spearman Rank Correlation, r= 0.009, P = 0.515, n = 47) neither between mean volume of food items and SVL (Linear Regression, R^2 = 0.0014, $F_{1,28}$ = 0.039, P = 0.846). Additionally, no significant relationships were recovered between number of food items and HW residuals (Spearman Rank Correlation, r = -0.2776, P = 0.064, n = 47) nor between mean volume of ingested prey and HW residuals (Linear Regression, R^2 = 0.119, $F_{1,28}$ = 3.796, P = 0.062).

Food niche breadth was similar between adult females and juveniles, but higher in adult males. The trophic niche overlap in terms of prey frequency was similar among three sex/age categories, although between adult female and juveniles this overlap was slightly higher. The niche breadth and trophic niche overlap in terms of prey volume were similar (Table 2). No significant differences recovered among the three groups (χ^2 = 1.40;

Table 3. Volume groups of ingested prey by adult males, adult females and juveniles of *Hemidactylus mabouia* from zoo Jardín Zoológico de La Habana “La Edad de Oro”, Havana, Cuba.

Volume groups (mm^3)	**Adult Males**	**Adult Females**	**Juveniles**
0-49	8	12	7
	80%	75%	63.6%
50-99	1	1	2
	10%	6.2%	18.2%
≥ 100	1	3	2
	10%	18.8%	18.2%
Total	10	16	11

P > 0.05) regarding the volume of ingested prey (Table 3). Adult males, adult females and juveniles generally preferred small sized prey and the volume of consumed prey was similar among these classes during the dry season..

Discussion

The diet of *H. mabouia* in the study area consisted essentially of arthropods, coinciding with other studies on the species (Zamprogno and Teixeira, 1998; Bonfliglio, Balestrin and Cappellari, 2006; Rocha and Anjos, 2007). In general, the data indicated that this population is generalist and opportunistic. Cockroaches represented the most important dietary item for all of the three sex/age categories, followed by pill bugs for juveniles, termites and spiders for adult males and spiders, pill bugs and ants for adult females, which are non-flying arthropods. Capula and Luiselli (1994) comparatively found that diet of *Tarentola mauritanica* and *Hemidactylus turcicus* in an urban area from Rome, Italy was primarily composed of terrestrial prey. The low contribution of flying arthropods in the diet of *H. mabouia*, could be explained by the fact that all captures took place in microhabitats lacking any artificial lights. This approach was performed in order to be able to evaluate the availability of real prey and eliminate the bias of consumption of flying prey that are not usually present in the microhabitats of these geckos. Intraspecific diet composition of a nocturnal lizard is known to differ in terms of category of consumed prey between populations that inhabit urban environments and those living in natural ones (e.g., Bonfiglio, Balestrin and Cappellari, 2006; Rocha and Anjos, 2007). In urban environments, the flying groups (such as lepidopterans and dipterans) have a higher number and frequency of occurrence in the diet of geckos (e.g. Powell, Parmerlee and Rice, 1990; Klawinski et al., 1994; Saenz, 1996), because these are attracted by artificial light while sit-and-wait behaviour has been reported to be highly successful for gecko species (Aowphol et al., 2006). However, in natural environments the number and frequency of non-winged groups (such as spiders, orthopterans, ants, Lepidoptera larvae and termites) is comparatively higher (e.g., Vitt and Zani, 1997; Vitt, Zani and Monteiro de Barros, 1997; Zamprogno and Teixeira, 1998; Colli et al., 2003). The high number of termites predated by adult males of *H. mabouia* can be considered as an unusual result, because the frequency of this item in their diet composition was low. Probably, the analysed adult males found a termite nest and they profited from that opportunity. In arid areas of southern Africa, termites show a patchy distribution (not only temporal but also spatial) and are an irregular food resource fortuitously consumed by *Ptenopus garrulus* (Hibbitts et al., 2005). Fragments of vegetal material and shed gecko skins occasionally found in stomachs of adult males of *H. mabouia* were probably ingested by accidental (the first) or intentional (the latter).

Compared to previous studies, the proportion of empty stomachs among the analysed individuals was relatively high. While this result is in agreement Bonfiglio, Balestrin and Cappellari (2006), it differs in respect to other populations of *H. mabouia* (Zamprogno and Teixera, 1998; Rocha and Anjos, 2007) and populations of the congeneric species *H. turcicus* (Capula and Luiselli, 1994; Saenz, 1996). According to Huey, Pianka and Vitt (2001), the energetic balance of a particular lizard population can be estimated by the rate of individuals with empty stomachs. Nocturnal lizard species tend to show higher proportions of empty stomachs among their individuals (more than 20%), when compared to diurnal species (less than 10%; Huey, Pianka and Vitt, 2001). The high percentage of empty stomachs can be explained by two reasons. First, this study was performed during the dry season. Population densities of arthropods difference significantly between the dry season and wet season in Cuba, where a reproductive explosion and increased prey availability extraordinarily increases during the latter (Núñez and Barro, 2003). Second, due to the fact that most of the captures took place in the early hours of the night, the geckos were emerging and did not have enough foraging time to catch prey. Howard, Parmerlee and Powell (2001) reported that the peak of foraging activity occurred in late night hours, between 20:00 and 01:00 h, in a population of *H. mabouia* from Angilla Island, Lesser Antilles.

Snout-vent length did not significantly differ between sexes, which is in agreement with studies of other populations of the same species (Howard, Parmerlee and Powell, 2001; Bonfiglio, Balestrin and Capellari, 2006; Rocha and Anjos, 2007) and populations of *H. turcicus* (Klawinski et al., 1994; Saenz and Conner, 1996). A possible explanation for this observation is the ecological advantage of a larger body size in females (positive correlation with fecundity), which might result in parallel increase of body size in both sexes. Subsequently, both sexes reach their maximum size by varying niche- and habitat constraints (Saenz and Conner, 1996). Alternatively, Colli et al. (2003) stated that a larger size of females in *Gymnodactylus geckoides* *amarali* could be associated with increased clutch and offspring size. The HW was shown to be being broader in adult males. Similar results were recovered by Saenz and Conner (1996) and Colli et al. (2003). Head-size dimorphism is a common trait in squamate reptiles that may be influenced by ecological segregation and sexual selection. The first explains intersexual differences as a mechanism to reduce competition for food resources both at intra- and interspecific levels (Klawinski et al., 1994; Gifford, Powell and Steiner, 2000; Dame and Petren, 2006); whereas the second invokes intrasexual competition among males for access to females (Colli et al., 2003; Dame and Petren, 2006).

The high dietary composition overlap between adults of *H. mabouia* can be explained by the high availability of prey (cockroaches and spiders) in the study area, while both adult sexes utilize similar microhabitats. High availability of prey either in urban or natural environments minimizes intraspecific competition of food resources (e.g., Colli et al., 2003; Hibbitt et al., 2005; Rocha and Anjos, 2007). The adult females also showed dietary overlap with juveniles. Therefore, adult females seem occupy the widest trophic niche breadth of the three age/sex classes. Possibly, this is related to guarantee energy for reproduction (Vitt and Caldwell, 2009). During the study period, seven adult females captured had oviductal eggs and four other individuals showed vitellogenic ovaries. The main difference in diet observed among the three sex/age categories represented the consumption of ground-dwelling prey (pill bugs) by juveniles.

During this study, surface-dwelling juveniles were commonly observed. Microhabitat selection therefore seems to be a major factor in determining diet composition. A similar use of microhabitat implicates higher dietary overlap (Rocha and Anjos, 2007) but different habitat associations can lead to consumption of different prey items (Saenz, 1996; Howard, Parmerlee and Powell, 2001). Possibly, the high frequency of juveniles encountered on or near the ground is driven by avoidance behaviour in relation to aggression by adult males. Several examples have been described concerning juvenile predation by geckos, due to which juveniles tend to be in or near the ground to avoid such behaviour by adults (e.g., Gifford, Powell and Steiner, 2000; Howard, Parmerlee and Powell, 2001; Bonfiglio, Balestrin and Cappellari, 2006). Summing up, the diet of *H. mabouia* in an urban area of Havana is composed of arthropods, mainly non-flying groups (cockroaches, spiders and pill bugs). Adult females show diet overlap with adult males and juveniles. No significant relationships were recovered between body size and head size, in relation to the number and volume of food items. There is a structural partitioning between juveniles and adult males that determines the consumption of ground-dwelling- prey by the former and avoids predation by the latter.

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