

Dietary analysis of *Homonota darwini* (Squamata: Gekkonidae) in Northern Patagonia

Marcelo E. KUN^{1*}, Carla PIANTONI², John D. KRENZ³, Nora R. IBARGÜENGOYTÍA^{1,4*}

¹Departamento de Zoología, Centro Regional Universitario Bariloche, Universidad del Comahue, Unidad Postal Universidad del Comahue, 8400 San Carlos de Bariloche, Argentina

²Smithsonian Institution, NHB, MRC 163, 10th St & Constitution Ave., NW, Washington, DC 20013-7012, USA

³Department of Biological Sciences, Minnesota State University, Mankato MN 56001, USA

⁴Instituto de Investigación en Diversidad y Medio Ambiente (INIBIOMA), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Argentina

Abstract Our study investigated the diet of the southernmost gecko in the world, *Homonota darwini*. Fifty-three specimens were captured during spring and summer in four locations in Patagonia, Argentina. The stomach contents of the specimens were identified, and we found that prey consisted of six main groups: Coleoptera, Hymenoptera, Homoptera and Araneae, and the adults and larvae of moth Lepidoptera. Lepidoptera was the major dietary component. The presence of ants and moths as common prey suggests an ambush feeding strategy. In spring, females consumed more ants than males although no other dietary differences between males and females were evident. We found nine geckos with empty stomachs and six parasitized by nematodes. Presence of empty stomachs corroborates previous observations of other nocturnal geckos and non-gecko lizards. Reduced foraging success of nocturnal lizards could be due to difficulty in prey detection due to dim light, reduced or erratic activity of insect prey at night, or shorter activity times of geckos relative to diurnal success. Sex and season were not associated with the incidence of empty stomachs. Principal component analysis showed that four food alternatives correlated with season. The constraint of nocturnality, coupled with low night-time temperatures restricting feeding to only a few hours after sunset, appear to have caused a generality of diet which may limit energy acquisition. We conclude that *H. darwini* is an arthropod generalist and likely an ambush forager, as are many other nocturnal gekkonids [*Current Zoology* 56 (4): 406–410, 2010].

Key words Nocturnal lizards, Diet, Gekkonidae, Patagonia, PCA

Although nocturnal behavior in most geckos exists because of phylogenetic constraints, its origin may have involved advantages such as greater prey availability, lower competition and lower predation pressure (Autumn and DeNardo, 1995). A number of physiological adaptations that allow resource acquisition at night may also have played a role. Previous studies have shown that many geckos are active over a wide temperature range that allows them to be active at night as well as during the day, when they can be found under rocks (Ibargüengoytía et al., 2007). Geckos forage for prey at night which requires locomotion and results in heat loss (Huey et al., 1989). Geckos may depend on diurnal temperatures while in burrows to perform physiological functions, and reach optimal metabolic and growth rates (Autumn and DeNardo, 1995; Piantoni et al., 2006). Geckos feed at temperatures that are suboptimal for sprinting, which are similar to those for diurnal lizards

(Huey et al., 1989). Nocturnality may have evolved as a means of predator avoidance, resulting in geckos foraging at low temperatures, which may influence their predation strategy and prey diet, especially for geckos at high latitudes or altitudes.

Homonota darwini is the world's southernmost gekkonid lizard with the widest distribution of the genus in South America, extending from the Atlantic Coast west to the Precordillera (32°–52° S, 63°–73° W; Cei 1986, 1993). It is a small nocturnal gecko with a maximum snout-vent length (SVL) of 55 mm. It is found in rocky areas of the steppe in Argentina and Chile. *H. darwini* hibernates during fall and winter when temperatures occasionally drop below freezing. In spring and summer, it is only active at night and uses flat rocks as burrows during the day. *H. darwini* is adapted to nocturnality, when opportunities for thermoregulation are limited (Autumn et al., 1994). The gecko's physio-

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* Corresponding author. E-mail: mkun@crub.uncoma.edu.ar; norai@bariloche.com.ar

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logical performance is sub-optimal at the low body temperatures it experiences in nature (Autumn et al., 1999; Ibargüengoytía et al., 2007) representing an appealing model for the study of life history adaptations to harsh environments. Some basic aspects of the ecology and physiology of *H. darwini*, including reproduction, growth and locomotion, have recently been reported (Piantoni et al., 2006; Ibargüengoytía et al., 2007; Ibargüengoytía and Casalins, 2007). Very little is known about the gecko's feeding ecology or natural diet, and this information is required to investigate broader ecological, energetic, and behavioral questions (Ceï 1986, 1993; Scolaro 2005). Here, we describe its diet by identifying and counting the prey contained in the guts of specimens captured over four years during spring and summer while in their burrows at multiple locations in Patagonia, Argentina. We discuss our results in relation to the evolution of life history traits as adaptations to cold and harsh environments.

1 Materials and Methods

Lizards were captured during their active season (October–March) in spring and summer over four years beginning Spring 1997. The first geckos were captured, at Ñirihuau (41°6'S, 71°7'W, 800 m asl; $n = 38$). Three geckos were caught in October, 2000, near Pilcaniyeu (41°S, 70°30'W; Rio Negro Province). One lizard was captured in November, 1997, and 10 more in March, 2000 at Sarmiento (45°S, 69°W; Chubut Province). Lizards were euthanized within 40 h of capture by intraperitoneal administration of sodium thiopental. Specimens were then fixed in Bouin's solution and preserved in ethanol before being deposited in the Colección Herpetológica del Departamento de Zoología del Centro Regional Universitario Bariloche, Universidad Nacional del Comahue. Digestive tracts were removed for examination and prey items were identified to the lowest possible taxonomic level and then counted.

To detect seasonal differences in diet, we ran t -tests for the differences in the mean number of prey per gecko, and a log-likelihood test (G-test) for differences in the proportional representation of prey taxa in spring (geckos collected between 1 October–20 December) and summer (geckos collected 21 December–31 March), and between sexes. We also compared the number of geckos captured with empty stomachs across seasons and sexes, and noted the presence of nematode parasites. To detect the existence of consistent prey taxa groupings in the diet, we conducted a Principal Component Analy-

sis (PCA) using an initial matrix of 34 individual geckos (rows) across 11 prey taxa (columns); for a full description of the method, see Howard (1991). We included only the Ñirihuau specimens for the PCA despite having collected geckos from two other populations, as the majority of geckos were captured there. Individuals containing only one prey item and individuals with unique prey taxa that was found only once were not used in the analysis. The shape of this matrix was a table of row profiles, such that columns did not sum to 100% but rows did. To conduct PCA, the matrix was transformed into a table of weighted values by dividing each cell value by the square root of each corresponding column. The table was then subjected to a non-standardized PCA as all the variables were measured in the same way using the program SPAD 3.5 (CISIA-CERESTA, Saint Mandé, France). Sex and season (spring and summer) were included as illustrative variables.

2 Results

We examined 53 geckos and found 195 prey items, or 4.43 items per lizard excluding the nine geckos with empty stomachs (Table 1). Prey consisted primarily of six groups: Lepidoptera larvae and adults, Hymenoptera (ants), Coleoptera, Homoptera and Araneae (Table 1). The average number of food items per lizard did not significantly differ as a function of season ($t_{39} = 1.31$, $P = 0.20$) or sex ($t_{35} = 2.03$, $P = 0.30$). Proportional representation of prey taxa was significantly different for seasons ($G_6 = 33.51$, $P < 0.001$), with fewer ants (Hymenoptera) in summer than in spring as the major difference. Repeating the test with ants excluded yielded no significant differences between seasonal diets ($G_5 = 9.65$, $P = 0.438$). The diets of male and female ants were also not significantly different. The proportional representation of prey taxa was significantly different between sexes ($G_6 = 25.85$, $P < 0.0005$), but no significant difference was found when ants were excluded ($G_5 = 6.74$, $P = 0.241$). When we analyzed only the Ñirihuau sample population ($n = 33$), there was a significant difference in the proportion of prey across seasons ($G_6 = 38.98$, $P < 0.0005$), even when Hymenoptera was excluded ($G_5 = 11.19$, $P = 0.048$), but not when both Hymenoptera and Araneae were excluded ($G_4 = 3.10$, $P = 0.542$) or when Hymenoptera and Homoptera were excluded ($G_4 = 6.60$, $P = 0.158$). The proportion of prey for the Ñirihuau population was significantly different between sexes ($G_6 = 24.81$, $P < 0.0005$) although there was no significant difference when the Hymenoptera were excluded from calculations ($G_5 = 5.33$, $P = 0.378$).

The results of the PCA analysis showed that there are four common items for *H. darwini* in spring (caterpillars, moths, beetles and ants), and three in summer when the consumption of ants is less (Fig. 1, 2). Only the illustrative variable “season” was well represented, with a test value of 2.1 and the two alternatives spring and summer lying close to axis 1 (Fig. 1b). Variables “Araneae” and “Lepidoptera adults” contributed to axis 2 and correlate. The variable “Hymenoptera” contributed to axis 1,

whereas “Lepidoptera larvae” contributed to both axes (Fig. 1a). The variable “Coleoptera” was associated with axis 3 (Fig. 2a). Three groups appear in the factorial plane of axes 1 and 2. Furthermore, axis 1 separated spring and summer (Fig. 1b). In factorial planes 1 and 3, a fourth group of lizards appeared which is also associated with summer. As both males and females were present in every group, PCA showed no evidence of sex differences in diet.

Table 1 Prey information represented as number of prey (N), frequency of prey (%), and number of geckos that consumed each prey taxon (G)

	Combined (44)			Season				Sex			
				Spring (19)		Summer (24)		Males (17)		Females (26)	
	N	%	G	N	%	N	%	N	%	N	%
Prey order											
Lepidoptera larvae	48	24.6	21	22	22.9	26	27.1	22	32.8	26	20.8
Hymenoptera	36	18.5	13	30	31.3	4	4.2	2	3.0	32	25.6
Araneae	28	14.4	18	17	17.7	11	11.5	15	22.4	13	10.4
Lepidoptera adults	23	11.8	16	9	9.4	14	14.6	10	14.9	13	10.4
Coleoptera	23	11.8	20	7	7.3	15	15.6	8	11.9	14	11.2
Homoptera	20	10.3	13	4	4.2	16	16.7	4	6.0	16	12.8
Diptera	5	2.6	5	0	0.0	5	5.2	1	1.5	4	3.2
Orthoptera	2	1.0	2	1	1.0	1	1.0	0	0.0	2	1.6
Thysanura	2	1.0	2	1	1.0	1	1.0	1	1.5	1	0.8
Acari	2	1.0	2	2	2.1	0	0.0	1	1.5	1	0.8
Heteroptera	1	0.5	1	0	0.0	1	1.0	0	0.0	1	0.8
Phasmoda	1	0.5	1	1	1.0	0	0.0	0	0.0	1	0.8
Unidentified insects	4	2.1	3	2	2.1	2	2.1	3	4.5	1	0.8
Total	195			96		96		67		125	
Prey items per gecko	4.43			5.05		4.00		3.94		4.81	

The data were combined and partitioned by season and sex. Empty stomachs were observed in three males and six females (three in spring and six in summer). Nematodes were observed in one male and five females (four in spring and two in summer). The number of geckos examined, excluding those that had empty stomachs (nine of the 53 geckos), are shown in parentheses. Capture information (including date, location, and sex) was lost for one gecko whose stomach contained 3 food items, so it was included in the combined category only.

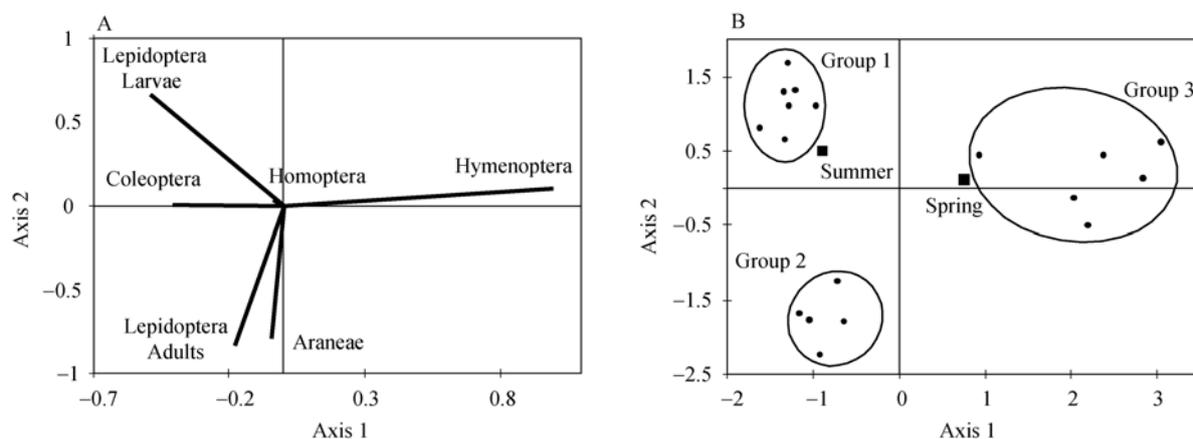


Fig. 1 PCA results for the diet of *Homonota darwini* captured at Ñirihuau, Patagonia, Argentina

Factorial plane 1-2. A. Percentage values indicate the inertia explained by each correspondence analysis axis. Lepidoptera larvae contribute to axis 1 as well as axis 2 and are positively correlated with both axes. Variables Araneae and Lepidoptera adults correlate negatively with axis 2. The variable Coleoptera negatively correlates with axis 1. The variable Homoptera is not related with any of the axes. B. Individual geckos and illustrative variables on the same plane. Three groups appear, one in spring and two in summer.

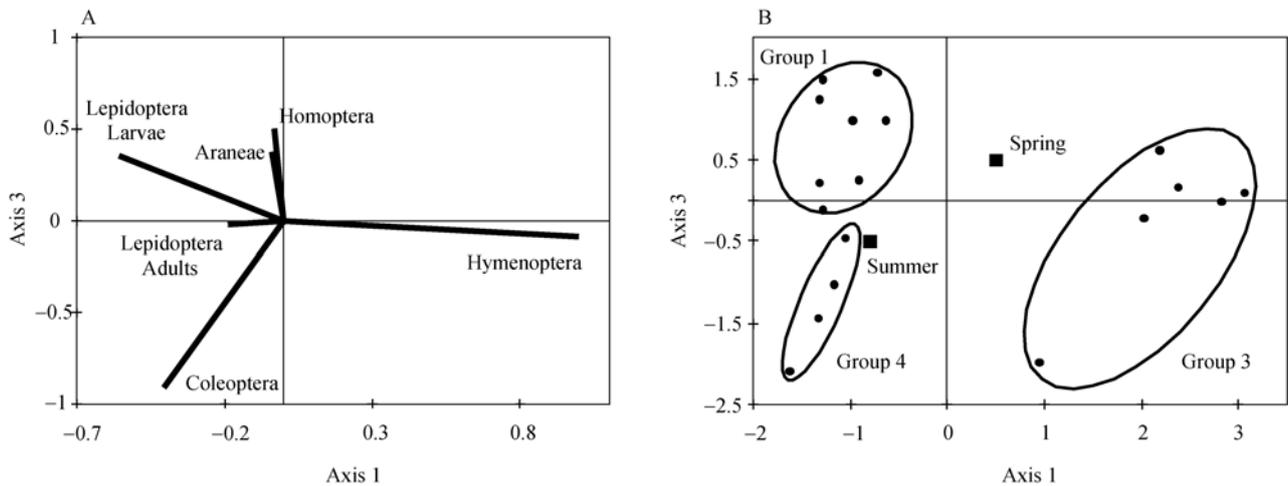


Fig. 2 PCA results for the diet of *Homonota darwini* captured at Ñirihuau, Patagonia, Argentina

Factorial plane 1-3. A. Variable vectors. Variables appearing in plane 1-2 are important, but the variable Coleoptera is not part of group 1 of plane 1-2. The Coleoptera variable is negatively correlated with axis 3. B. Separation of individuals in factorial plane 1-3. A fourth group is due to the variable Coleoptera.

3 Discussion

There is strong evidence of philopatry for *Homonota darwini*, and most of their activity occurs under or close to Rocks (Ibargüengoytia et al., 2007). This supports the idea that the species ambushes prey near their burrows and are not active foragers (Cooper, 1995). An ambush strategy may reduce predation risk while allowing visual detection of moving prey. Ambush behavior seems to be linked to the lizards' microhabitat underneath rocks which are moist even during the dry season, rich in organic matter and intensively used by ants and larvae of other insects (C. Piantoni, personal observation). However, the ambush strategy limits their opportunities to select prey; individual variation in stomach contents and a wide spectrum of prey can indicate such a strategy as shown for *Homonota whitti* (Martori et al., 2002). Geckos seldom eat Araneae, but we observed this prey as a common component of *darwini* stomachs. Araneae can be caught while they are on their webs. *Homonota underwoodi* has been found under rocks and is associated with burrows dug between plant roots, along with scorpions and Araneae (Sicariidae; Cei, 1993). *Homonota fasciata* has been observed feeding mainly on Araneae, which suggests ambush behavior (Martori et al., 2002). Although geckos typically eat fewer ants than other clades of lizards (see review by Hibbitts et al., 2005), the presence of spiders and ants in their diet agrees with other studies of gekkonids (Dial, 1978; Huey and Pianka, 1981; Henle, 1990), and suggests predation in or near rock burrows. Empty stomachs may

indicate an ambush strategy, with Huey et al. (2001) reporting empty stomachs in 21% of cases for a neotropical species, which is similar to our result of 17%. We believe that this phenomenon in diurnal lizards could be due to the difficulty of detecting prey in dim light. For nocturnal geckos such as *Homonota darwini* it may be due to stationary behavior and fewer hours of activity. However, we did observe Homopteran plant lice which suggests feeding on plants outside of burrows (Kun et al., 2004), a result similar to the report of both active and sedentary prey in *Homonota horrida*. This is suggestive of an intermediate feeding behavior (Aun and Martori, 1994), and we conclude that the diet information for congeners shows that the sit-and-wait ambush strategy is more common than intermediate feeding. Our data suggest that *H. darwini* is an ambush forager and an arthropod food generalist whose diet composition is largely determined by the prey availability.

The proportional representation of prey taxa differed significantly for sex and season, and these differences were principally caused by the presence of ants. There were no significant differences when ants were excluded. We found ants in the digestive tracts of approximately 30% of geckos, consisting of ten females and two males. This suggests food-niche segregation by sex which is consistent with the observation of Hibbitts et al (2005) of corresponding sexual dimorphism. Males of *H. Darwini* have wider heads (Piantoni et al., 2006; Ibargüengoytia and Casalins, 2007) but this has not been observed to be related to mate competition.

The amount of assimilated energy allocated to reproduction or other functions is determined not only by prey acquisition rates but also by digestive and metabolic processes, both of which are temperature dependent (Angilletta and Werner, 1998). In cooler climates, a large proportion of the year is unsuitable for growth and reproduction for most organisms, and this is particularly true for ectotherms. The reproductive cycles of temperate ectotherms must be completed within seasonal limits, and the timing of life history events has a strong influence on fitness (Gotthard, 2001). Breeding is restricted to the summer months for *H. darwini*, and the female cycle is annual or biennial, because post-partum females, faced with a short activity season with limited thermal opportunities, are typically unable to acquire and store sufficient energy for an one-year cycle (Ibargüengoytía and Casalins, 2007). Feeding habits and diet composition have a strong influence on life history traits such as reproduction timing and fecundity. Nevertheless, we found no dietary differences between ovigerous and non-ovigerous females. The higher prevalence of ants in females could be due to a more rapid adoption of a sit-and-wait foraging strategy compared to males, particularly once an ant path has been found. Males may be more likely to move as they search for mates. Despite the fact that more ants were found in female digestive tracts, there were no other significant dietary differences related to gecko sex or reproductive state, and this could be due to relative availability of prey within the population. Our results indicate that *H. darwini* is a generalist feeder, without a significant selectivity for prey.

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