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Effects of season, sex and age on the diet of *Homonota fasciata* (Squamata, Phyllodactylidae) from Monte region of Argentina

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ABSTRACT. This study aimed to investigate the diet of the gecko *Homonota fasciata* (Duméril & Bibron, 1836) in a population from Monte of San Juan Province, Argentina, and to analyze possible temporal, sexual, and ontogenetic variations in feeding behavior. We determined the total volume, number, and occurrence frequency of each prey item and calculated the relative importance indexes. We also assessed trophic diversity and trophic equity. *Homonota fasciata* had a generalist and diverse diet based on arthropods, including insects and arachnids. Individuals adopted a passive 'sit and wait' foraging strategy. There were seasonal-, sex-, and age-related variations in the trophic spectra. The results of this study provide a valuable contribution to our understanding of the biology of this species, with implications for the establishment of management guidelines both for the species and its habitat.

KEYWORDS. Foraging ecology, gecko, trophic niche, trophic overlap.

RESUMEN. Efectos de la estacionalidad, el sexo y el grupo etario sobre la dieta de *Homonota fasciata* (Squamata, Phyllodactylidae) en una región del Monte de Argentina. El objetivo de este trabajo fue conocer y describir la dieta de *Homonota fasciata* (Duméril & Bibron, 1836) en una población del Monte de la provincia de San Juan Argentina, analizando posibles variaciones temporales, sexuales y ontogenéticas en la alimentación. Para examinar la dieta, se determinó volumen, numerosidad y frecuencia de ocurrencia para cada ítem-presa, y se calculó el Índice de Importancia Relativa (IRI). Se evaluaron diversidad y equidad trófica, además de variaciones estacionales, sexuales y etarias del espectro trófico. La dieta de *H. fasciata* es generalista, diversa, basada en artrópodos, incluyendo insectos y arácnidos. La estrategia de forrajeo exhibida fue pasiva ("sit and wait"). Se encontraron variaciones estacionales, sexuales y ontogénicas en la alimentación. Este estudio permite una valiosa contribución al conocimiento de la biología de esta especie, útil a la hora de fijar pautas de manejo para la misma, como así también para los ambientes que habita.

PALABRAS-CLAVE. Ecología trófica, gecko, nicho trófico, solapamiento trófico.

The diet of a species is closely related to ecological features such as food abundance, habitat conditions, and predation (Moreno & Acosta, 2011). The study of a species' trophic niche is necessary for understanding aspects of their nutrition in a population context, e.g., differences in food habits between sexes and correlations between prey and predator sizes (Aun *et al*., 1999; Teixeira-Filho *et al*., 2003). Moreover, dietary habits are known to be influenced not only by extrinsic biotic factors, such as seasonal variations in food availability, but also by intrinsic factors, such as ontogenetic changes that determine consumptions of different prey categories (Vidal & Labra, 2008). Understanding of these intrinsic and extrinsic factors allows an analysis of the possible existence of intraspecific competition for food resources, as well as the possible influence of phylogenetic constraints acting on prey consumption (Halloy *et al*., 2006).

The genus *Homonota* Gray, 1845 (Squamata, Phyllodactylidae) is distributed within Argentina from Bolivia (25°S) to Santa Cruz province (52°S), including the World's southernmost distribution of geckos. *Homonota fasciata* (Duméril & Bibron, 1836) is a small lizard with a snout-vent length SLV up to 60 mm. It has crepuscular habits and is common in rocky sites and building crannies (Cabrera, 2009), and occurs in the Monte and Chaco regions up to 2,500 masl.

Few studies have described the diet of *Homonota* species in Argentina (Aun & Martori, 1994; Blanco *et al*., 2009; Kun *et al*., 2010; V. Blanco Fager, unpubl. data). We therefore aimed to investigate the diet of the gecko *H. fasciata* in the Monte region of San Juan Province, with regard to possible seasonal, sexual, and ontogenetic variations in diet.

MATERIALS AND METHODS

The Médanos Grandes cover a large area in the southeast of San Juan Province, including 2,000 km^2 of the eastern foothills of Pie de Palo, 576 masl (31°44'S, 68°10'W). The area is a Quaternary wind-flood plain with temporary drains and dune chains. The climate is dry and warm, with an average annual temperature of 18°C and

average summer rainfall of 103 mm (De Fina, 1992).

The survey was carried out by four collectors from September 1999 to April 2000. Animals were captured using a grid of 100 Barber pitfall traps, 40 cm in diameter. The traps were randomly placed along eight transects, with 25 m between each trap. The traps were active permanently and sampling periodicity was weekly (see acknowledgments for collecting permits).

Forty-six individuals were collected, 23 females, 17 males and 6 juveniles. Animals were killed by freezing, fixed in 10% formalin and stored in 70% alcohol. Samples were incorporated into the scientific herpetological collection of the Universidad Nacional de San Juan, Argentina (Numbers: UNSJ 398-411, 430-442, 642-648, 1541-1556).

Individuals were dissected, sexed and their stomach contents were removed. Diet was analyzed using a binocular stereoscope lens to identify prey items. Systematic prey categories were determined following the classification of Bland & Jaques (2010). The maximum length and width of prey items were measured and their volume was calculated using the Dunham (1983) formula.

The relative importance index (IRI) was calculated for each prey category (Pinkas *et al*., 1971) to determine its contribution to the diet. In order to establish the hierarchy ranking of the diet, the highest value of IRI was considered as 100% and other values were calculated as relative percentages (Villavicencio *et al*., 2005; Cossovich *et al*., 2011). The IRI values of prey items were categorized as follows: 100–75% indicated fundamental prey items, 75–50% secondary prey items, 50–25% accessory prey items, and <25% indicated accidental prey items.

The Shannon–Wiener index was used to determine trophic diversity (Magurran, 1988) and the Pielou equity index was used to estimate trophic equity. The Jaccard similarity index for qualitative data was used to analyze differences in diet between seasons, sexes, and age groups. The Morisita–Horn similarity index (Magurran, 1988) was used to make quantitative comparisons between the variables.

RESULTS

Diet description. *Homonota fasciata* had a diet based on arthropods, including insects and arachnids. General IRI values indicated that Formicidae, Araneae, and Coleoptera were fundamental prey items, while Diptera species were accessory prey items. The remaining items were considered to be accidental. The Shannon–Wiener index was H'=1.96 (H^{max}=2.64) and the Pielou equity index was E=0.74.

Temporal variation in diet. Seasonal variation was observed in key prey items: Araneae were fundamental prey in spring, Formicidae in summer, and Coleoptera and Araneae again in the autumn (Tab. I).

Qualitatively, the stations had low similarity in prey categories consumed (Jaccard=0.14), however this index could have been influenced by small sample sizes. The greatest similarities were obtained in spring and autumn (Morisita-Horn I^{M-H}=0.86). The Shannon index indicated that the summer season was the most diverse in terms of numbers of prey items (H'=1.86), but the values differed slightly among the three seasons. The Pielou index was highest in the autumn, which was the most equitable season (E=0.96).

Sexual variation in diet. The IRI for males showed that Araneae and Formicidae were fundamental prey items, while Coleoptera and Araneae were fundamental prey items for females (Tab. II). The qualitative Jaccard index showed 50% similarity in diet between males and females (Jaccard=0.50), while the Morisita–Horn index indicated minimal differences between variables, so male and female diets were highly similar (I^{M-H}=0.86).

Males had a higher Shannon trophic diversity index (H'=2.04) than females (H'=1.73), and the diet equity value was also higher for males (E=0.82) than for females (E=0.79).

Ontogenetic variation in diet. Adult lizards had a diet composed of 14 prey items, while the juvenile diet was made up of only five prey items. Araneae, Formicidae, and Coleoptera were fundamental items in the adult diet, with scorpions as an accessory prey. Coleoptera and Formicidae were also fundamental for juveniles, while Araneae species were accessory prey items (Tab. III).

With respect to the trophic spectra of *H. fasciata*, adults and juveniles showed low qualitative similarities (Jaccard=0.36). Considering the Morisita–Horn quantitative index, we observed high similarities in numbers of prey items, occurrence frequency, and IRI between both age groups (I^{M-H}=0.85), but less similarity in prey volume (I^{M-H}=0.39).

The Shannon index demonstrated that adults had a more diverse diet (H'=1.99) than juveniles (H'=1.41), and trophic equity was higher in juveniles (E=0.88) than in adults (E=0.75).

DISCUSSION

The variety of prey items consumed indicates that *H. fasciata* has a generalist diet, with insects, such as formicids and beetles, and arachnids being fundamental prey items, and Diptera species as accessory prey items. These results are consistent with those for the same species in Córdoba, Argentina (Martori *et al*., 2002), *Homonota underwoodi* in San Juan, Argentina (V. Blanco Fager, unpubl. data), *H. andicola* in Catamarca, Argentina (Blanco *et al*., 2009), *H. darwini* in Patagonia, Argentina (Kun *et al*., 2010), and *H. uruguayensis* in Brasil (V. de Albuquerque Nunes, unpubl. data). These results demonstrate that different species of the genus select similar prey items, and only the hierarchy of each category within the diet varies among species. This difference could be attributed to differences in availability of prey items in the different environments that each species inhabits.

Homonota fasciata consumes high-mobility prey items using a 'sit and wait' feeding strategy. Huey & Pianka (1981) proposed that active predators (widely foraging) consume sedentary prey, while passive predators (sit and wait) are more likely to consume mobile prey. This behavior may be related to the idea that some species ambush their

Tab. I. *Homonota fasciata* (Duméril & Bibron, 1836) seasonal IRI values and their hierarchy rankings (DJ) in Monte region of Argentina.

	Spring n=19		Summer n=24		Autumn n=3	
Item	IRI	DJ	IRI	DJ	IRI	DJ
Formicidae	1134.28	40.69	2276.64	100	1225.22	20.19
Hemiptera	117.48	4.21	33.62	1.48	0	0
Coleoptera	1597.41	57.30	1260.77	55.38	4813.05	79.31
Diptera	1053.36	37.79	67.10	2.95	0	0
Lepidoptera larvae	106.92	3.84	46.27	2.03	0	0
Coleoptera larvae	0	0	7.18	0.32	0	0
Blattaria nymph	0	0	7.18	0.32	0	0
Araneae	2787.59	100	835.85	36.71	6068.52	100
Solifugae	0	0	9.44	0.41	0	0
Scorpiones	0	0	707.23	31.06	0	0
Homoptera	0	0	7.33	0.32	0	0
Ixodida	106.13	3.81	29.10	1.28	0	0
Hymenoptera	6.94	0.25	0	0	0	0
Lepidoptera	19.74	0.71	0	0	0	0

Tab. II. *Homonota fasciata* (Duméril & Bibron, 1836) males and females IRI values and their hierarchy rankings (DJ) in Monte region of Argentina.

	Males n=17		Females n=23	
Item	IRI	DJ	IRI	DJ
Formicidae	1571.53	96.95	1516.99	66.90
Hemiptera	36.23	2.23	88.94	3.92
Coleoptera	817.15	50.41	2267.67	100
Diptera	412.66	25.46	307.39	13.56
Lepidoptera larvae	54.25	3.35	79.47	3.50
Coleoptera larvae	7.58	0.47	0	0
Blattaria nymph	7.58	0.47	0	0
Araneae	1620.94	100	1905.39	84.02
Solifugae	0	0	9.35	0.41
Scorpiones	829.20	51.16	0.00	0
Homoptera	0	0	5.34	0.24
Ixodida	205.25	12.66	5.35	0.24
Hymenoptera	7.72	0.48	0	0
Lepidoptera	13.67	0.84	0	0

Tab. III. *Homonota fasciata* (Duméril & Bibron, 1836) juveniles and adults IRI values and their hierarchy rankings (DJ) in Monte region of Argentina.

	Adults n=40		Juveniles n=6	
Item	IRI	DJ	IRI	DJ
Formicidae	1334.21	86.73	2687.57	89.43
Hemiptera	52.19	3.39	153.62	5.11
Coleoptera	1160.75	75.45	3005.20	100
Diptera	372.92	24.24	252.92	8.42
Lepidoptera larvae	54.02	3.51	0	0
Coleoptera larvae	1.94	0.13	0	0
Blattaria nymph	1.95	0.13	0	0
Araneae	1538.39	100	1028.63	34.23
Solifugae	3.28	0.21	0	0
Scorpiones	397.76	25.86	0	0
Homoptera	2.03	0.13	0	0
Ixodida	77.43	5.03	0	0
Hymenoptera	2.01	0.13	0	0
Lepidoptera	4.97	0.32	0	0

prey near their shelters, and are therefore not active foragers (Cooper, 1995). This strategy may also be linked to reducing predation risk, while allowing visualization of moving prey.

The results of trophic diversity analysis indicated that *H. fasciata* is a generalist; it has no single predominant prey item and consumes several different main categories of prey, giving it a diverse diet. This is consistent with the results of Aun & Martori (1994) for the same species, Martori *et al.* (2002) for *H. whitti*, and V. Blanco Fager (unpubl. data) for *H. underwoodi.*

Similar patterns, as those found here, have been documented in diet studies of other species of geckos outside the genus *Homonota*. This fact allows to state that dietary patterns are preserved in most of geckos' species around the world, being phylogenetically fixed and varying according to the climates and features of different habitats that determine the presence and abundance of prey items. (Hibbitts *et al*., 2005; Rugiero *et al*., 2007; Aurich *et al.*, 2011; Bauer & Sadlier, 2011; Perez & Balta, 2011; Barragan-Ramirez *et al.*, 2015; Villegas *et al.*, 2016).

Temporal variation in diet. The IRI index indicated seasonal variation in fundamental prey items, with differences among spring, summer, and autumn. Only in autumn and spring the diet of *H. fasciata* shared a fundamental prey, as supported by the similarity index. Pianka (1973) proposed that there were temporal variations in the supply of trophic resources. However, our results differed from those of Aun & Martori (1994) who found no temporal variation in the diet of *H. fasciata* in the Chaco region of Córdoba, Argentina. Kun *et al*. (2010) found temporal differences in the diet of *H. darwini* in Patagonia, Argentina. Moreover, seasonal analysis in geckos outside the genus showed significant temporal shifts in diet (Gil *et al*., 1994; Aowphol *et al*., 2006; Hodar *et al*., 2006).

The diversity index showed no significant variation in the numbers of prey items consumed at the different sampling stations. The diversity index was only slightly lower in autumn, thus maintaining trophic diversity over time. The diet equity was higher in the autumn, and lower and similar in spring and summer respectively.

Sexual variation in diet. Males and females differed in their prey consumption hierarchies, sharing only one fundamental prey. Scorpions were eaten by males, but not by females (Tab. II). A reason of this difference could be associated to different nutritional needs. For example, females could need the ingestion of preys richer in fat or calcium for developing the eggs. Males in some species of lizards consume a carotenoid-enhanced diet which is associated to their coloration and reproductive success (Kodric-Brown, 1989). Our results agree with those of Blanco *et al*. (2009) for *H. andicola*, Kun *et al.* (2010) for *H. darwini*, Miranda & Andrade (2003) and Hibbitts *et al*. (2005) for other species of geckos outside the genus, which studies also found trophic differences between the sexes. In contrast, *H. underwoodi* showed no sex-related differences in diet (V. Blanco Fager, unpubl. data).

Males and females shared 50% qualitative similarity and 86% quantitative similarity, indicating high trophic overlap, which could lead to intraspecific competition between the sexes (Pianka, 1973). Males and females may therefore reduce competition by using different spatial or temporal niches, or by using common prey items but with different consumption hierarchies. Males showed a slightly higher trophic diversity index than females, having a greater number of prey items in their diet. According to the Pielou index, the diets of males and females were substantially equitable.

Ontogenetic variation in diet. *Homonota fasciata* showed little variation in diet between adults and juveniles. They shared fundamental items and only varied in terms of Araneae, which was a fundamental prey item for adults but only an accessory prey for juveniles (Tab. III). This difference may be associated with the inability of juveniles to consume sizeable spiders of the genus *Sicarius*, which were found in stomachs. These results agree with those of Aowphol *et al*. (2006) for *Gekko gecko* but contrast with V. de Albuquerque Nunes (unpublish. data), who found significant ontogenetic differences in *H. uruguayensis* feeding in Brazil, both in terms of prey size and consumption proportion.

The diets of the two age groups showed a low qualitative similarity index because of the larger trophic spectrum in adults. However, the quantitative similarity was high for most variables, with 85% overlap in the diets of the two age groups. Adult individuals have a more diverse diet than juveniles, while juveniles have a more equitable diet. These contrast with V. Blanco Fager (unpubl. data) for *H. underwoodi*.

The results of this study provide an important contribution to our knowledge of the biology of *H. fasciata*, which has rarely been studied in the Monte of Argentina. The data will provide the basis for future ecological and conservation-based studies.

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