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Spatial, Ontogenetic, and Sexual Effects on the Diet of a Teiid Lizard in Arid South America

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Abstract.—Most lizard species feed on small arthropods, and although some are omnivorous, only a few species are strict herbivores. We studied the diet of *Dicrodon guttulatum*, a teiid lizard endemic to the arid coastal deserts and dry forests of northern Peru. Herbivory by this lizard has been identified as a potential limiting factor in the regeneration of plant communities in these dry ecosystems. We collected gastric and fecal samples of adult males, adult females, and juveniles of *D. guttulatum* in different plant communities. Based on the ontogenetic shift from insectivory to herbivory observed in other herbivorous lizards, we hypothesized that juvenile *D. guttulatum* would have an omnivorous or insectivorous diet. We found *D. guttulatum* to be almost exclusively herbivorous (78–100%) and to feed largely (12–95%) on mesquite (*Prosopis pallida*) leaves and flowers across all plant communities and locations. Contrary to our predictions, there was a large overlap in diet between adult males and juveniles, whereas adult females were most likely to include plant species other than *P. pallida* in their diet. The consistency of herbivory in both juveniles and adults makes the origin of herbivory in *D. guttulatum* very interesting. We discuss potential factors promoting the evolution of herbivory in this species and the importance of lizard herbivory in the dry ecosystems of northern Peru.

Most lizard species feed on small arthropods, mainly insects (Cooper and Vitt, 2002; Espinoza et al., 2004). Few species are omnivores, and less than 3% of all lizard species are strict herbivores. A lizard is considered strictly herbivorous when more than 90% of its diet is composed of plant material (Cooper and Vitt, 2002). Most herbivorous lizards consume fruits and seeds that are easily digestible (Valido and Nogales, 1994; Van Damme, 1999).

A strict leaf-eating habit requires physiological and behavioral adaptations that include specialized dentition, elongated intestines, colic valves for slowing down food processing, intestinal flora for digestion of cellulose, and maintaining high body temperature to enable fermentation (Van Damme, 1999; Cooper and Vitt, 2002; Vitt, 2004). These morphological and physiological adaptations are thought to be associated with large body size in most herbivorous lizards (Cooper and Vitt, 2002; Espinoza et al., 2004). However, current knowledge of lizard herbivory is biased toward larger herbivorous species (family Iguanidae). The adaptations developed in small herbivorous lizards are mostly unknown (Dearing, 1993; Schall and Dearing, 1994; but see Espinoza et al., 2004).

Lizard diet is often affected by ontogeny (Ballinger et al., 1977; Castilla et al., 1991; Rocha, 1998; Cooper and Lemos-Espinal, 2001). These changes in diet result from different requirements for growth as well as physiological developments during ontogeny. In general, only iguanid lizards are born herbivorous (Durtsche, 2000). Most other herbivorous and omnivorous lizards switch from consuming insects to consuming plants as they grow from juveniles to adults (Castilla et al., 1991; Rocha, 1998; Fialho et al., 2000). Consumption of protein-rich insects can probably cover the higher energetic requirements for growth of young individuals, which also lack the intestinal flora needed to digest cellulose (Cooper and Vitt, 2002).

Insectivory is the ancestral feeding habit in lizards (Cooper, 2002). Herbivory originated in many lizard families, especially among the Iguania (Vitt, 2004) and also evolved repeatedly within families, such as in the Liolaemidae (Espinoza et al., 2004). Herbivory is rare among the scleroglossan lizards, where only a few lineages within Scincomorpha contain strictly herbivorous species (Cooper and Vitt, 2002). Within the family Teiidae, herbivory has evolved independently in at least two clades (Espinoza et al., 2004). Herbivory in *Dicrodon* has evolved separately from other herbivorous teiid lizards (Cooper and Vitt, 2002), because *Dicrodon* forms an outgroup in the monophyletic tree that includes the genera *Ameiva* (omnivores and insectivores), *Kentropyx* (insectivores), and *Cnemidophorus* (insectivores, omnivores, and herbivores), with a common insectivorous ancestor (Cooper and Vitt, 2002; Giugliano et al., 2007). Many hypotheses have been advanced for the evolution of herbivory in lizards. For Teiidae, which are relatively small lizards (Espinoza et al., 2004; Vitt, 2004), possible factors promoting herbivory include aridity (Velásquez et al., 2007), insularity (the herbivorous *Cnemidophorus murinus* and *Cnemidophorus arubensis* are insular; Cooper and Vitt, 2002), and prey availability (Cooper and Vitt, 2002).

Teiidae is one of the dominant lizard families in South and Central America. *Dicrodon guttulatum* and *Dicrodon holmbergi* are the only mainland teiid lizards for which strict herbivory has been suggested (Holmberg, 1957; Vitt, 2004; Velásquez et al., 2007). *Dicrodon guttulatum* is endemic to the Sechura desert and coastal dry forests of northern Peru and southern Ecuador, between the Pacific Ocean and the foothills of the Andes (Schmidt, 1957). The morphologically similar *D. holmbergi* replaces *D. guttulatum* in the Chau valley in the Peruvian Departamento of La Libertad (Schmidt, 1957). The third species of the genus, *Dicrodon heterolepis*, is thought to be insectivorous (Schmidt, 1957), although empirical data are lacking. *Dicrodon guttulatum* reaches a maximum snout–vent length of 140 mm in males and 100 mm in females (Schmidt, 1957) and a maximum weight of 60 g and 40 g, respectively, for males and females (JPvL, pers. obs.).

Dicrodon guttulatum is an important and ubiquitous native herbivore in the Sechura desert, where it plays a key role in the regeneration of dry forests by limiting the establishment of *Prosopis pallida* seedlings (Holmgren et al., 2006a; Squeo et al., 2007). *Prosopis pallida* trees and shrubs provide lizards with foraging grounds, microhabitats, thermoregulation sites, and protection from predators (Holmberg, 1957). However, the lizards could potentially weaken the regeneration of their habitat in the long term by limiting *Prosopis* seedling establishment. Clearly, a better knowledge of the diet of *D. guttulatum* is important to understand this plant-animal interaction.

In this study, we investigated the diet of *D. guttulatum* in the dominant plant communities in the Sechura Desert and compared diet width and extent of herbivory between ontogenetic stages among different plant communities. We hypothesized that there would be a higher proportion of arthropods in the diet of juveniles as compared to adults, as suggested by Schmidt (1957) and Durtsche (2000).

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TABLE 1. Adult tree cover (%) at the sampled study sites (calculated sensu Sitters et al., 2011). Means ± SD of extent of herbivory (proportion of plant material) and diet width (Levin's *B*) for *Dicrodon guttulatum* are given.

Location	Coordinates		Total adult tree cover (%)	*Prosopis* cover (% of total)	Soil type	Extent of herbivory		Diet width	
	Latitude	Longitude				2006	2008	2006	2008
Tortuga-Sechura 2 (Bayovar)	−5.8999°	−80.9217°	4	0	Calcareous	78.3 ± 28.4 (*N* = 43)	93.2 ± 10.8 (*N* = 18)	2.15 ± 1.01 (*N* = 43)	1.73 ± 0.68 (*N* = 18)
Paraiso	−5.4455°	−80.6007°	75	100	Sandy	77.9 ± 16.6 (*N* = 50)	—	2.69 ± 0.97 (*N* = 50)	—
Mirador	−5.6601°	−80.5810°	71	94	Sandy	92.1 ± 16.6 (*N* = 50)	100.0 ± 0.0 (*N* = 3)	2.10 ± 0.59 (*N* = 50)	1.26 ± 0.22 (*N* = 3)
Tortuga-Sechura 1	−5.4042°	−80.7944°	9	100	Calcareous	85.0 ± 23.4 (*N* = 50)	85.2 ± 34.9 (*N* = 8)	1.84 ± 0.80 (*N* = 50)	1.64 ± 0.73 (*N* = 8)
Loma Negra	−5.2542°	−80.8880°	37	31	Sandy	—	85.5 ± 23.0 (*N* = 10)	—	1.86 ± 0.96 (*N* = 10)
Piura-Castilla	−5.1935°	−80.6248°	92	27	Sandy	—	77.6 ± 22.9 (*N* = 18)	—	2.54 ± 0.95 (*N* = 18)

MATERIALS AND METHODS

Study Sites.—We worked at six sites in the Sechura desert, northwest Peru, that were representative of the diversity of vegetation types in the region (Table 1, Fig. 1, Sitters et al., 2011). The plant communities varied from sand dunes with sparse *P. pallida* trees to dry forests dominated by *P. pallida* and *Capparis scabrida*, interspaced with numerous saplings of both species and *Acacia macracantha* shrubs.

The climate is arid, with highly variable precipitation averaging 50 mm and ranging from 0 mm (1991) to 2,387 mm (1983; Meteorological Station at University of Piura). El Niño Southern Oscillation (ENSO) events are associated with higher precipitation, which in turn promotes vegetation growth and establishment (Block and Richter, 2000; Holmgren et al., 2006a). Precipitation was 76.5 mm in 2006 and 157 mm in 2008 (Meteorological Station at University of Piura). Maximum average temperatures range from 28.5°C (July to September) to 35.2°C (January to March). Daily temperatures at sites occupied by lizards in Tortuga-Sechura 2 (Bayovar) varied between 20.7°C and 39.3°C in July of 2004 (Catenazzi et al., 2005).

Lizard species that are sympatric with *D. guttulatum* in the Sechura desert include four species of geckos (*Phyllodactylus clinatus, Phyllodactylus kofordi, Phyllodactylus microphyllus, Phyllodactylus reissi*), three species of lava lizards (*Microlophus occipitalis, Microlophus peruvianus, Microlophus thoracicus*), and three other species of teiid lizards (*Ameiva edracantha, Callopistes flavipunctatus, D. heterolepis;* Huey, 1974; Catenazzi and Donnelly, 2007). Among these species, only *M. thoracicus* is known to supplement its mostly insectivorous diet with plant matter (Dixon and Wright, 1975).

Diet Composition.—To study the diet of *D. guttulatum,* we flushed stomach contents and collected fecal pellets. We preferred to use these techniques over stomach dissection for ethical reasons. According to Luiselli (2008), there is no significant difference in diet structure between stomach dissection and fecal analysis, although soft bodied insects might be lost during digestion (Pincheira-Dinoso, 2008). We think that our dietary analyses provided unbiased data, because we never found soft-bodied insects in flushed stomach contents. Moreover, dissection of deceased lizards revealed no difference between stomach content and flushed material.

We collected 191 fecal pellets of *D. guttulatum* from four sites (Tortuga-Sechura 2 (Bayovar), Paraiso, Mirador and Tortuga-Sechura 1, Fig. 1; Sitters et al., 2011) in December 2006 and 18 pellets from one site (Piura-Castilla) in January 2008. We flushed the stomachs of 39 lizards (3–18 lizards per site) at four sites in 2008 (Table 1). We measured snout–vent length (accuracy 0.1 mm) of lizards. Individuals were categorized as juveniles when snout–vent length was less than 75 mm, since none of the dissected lizards up to 75 mm had mature gonads. Most *D. guttulatum* were captured between 0900 and 1300 h, when they were most active. We flushed the lizard stomachs with water (Legler and Sullivan, 1979). When fatalities occurred during or after the flushing, lizards were dissected and stomach contents removed for analysis.

We calculated the amount of plant material in the diet as the sum of volumetric percentages of all plant items in the data for 2006 and 2008 separately. We identified leaves of *P. pallida,* *Acacia* sp. and other plant items whenever possible. A rarefaction curve was constructed with the cumulative number of dietary items as a function of sample size by using Mao Tau's index in the program EstimateS 8.2 (Colwell, 2009).

Ontogenetic Effects.—We used Kruskall-Wallis nonparametric tests to test for differences in the extent of herbivory between adult males, adult females, and juveniles. We calculated diet width based on Levin's formula (Pianka, 1973):

$$B = \frac{1}{\sum_{i=1}^{n} P_i^2},$$

where *B* stands for Levin's measure of diet width, and P_i is the proportion of volume of items of type *i* in the diet. *B* ranges from 1 (extreme dietary discrimination) to the total number of item types (*n*) when there is no discrimination between item types. We used Kruskall-Wallis nonparametric tests to test for differences in diet width between adult males, adult females, and juveniles. To determine diet similarity between adult males, adult females, and juveniles, we computed the diet
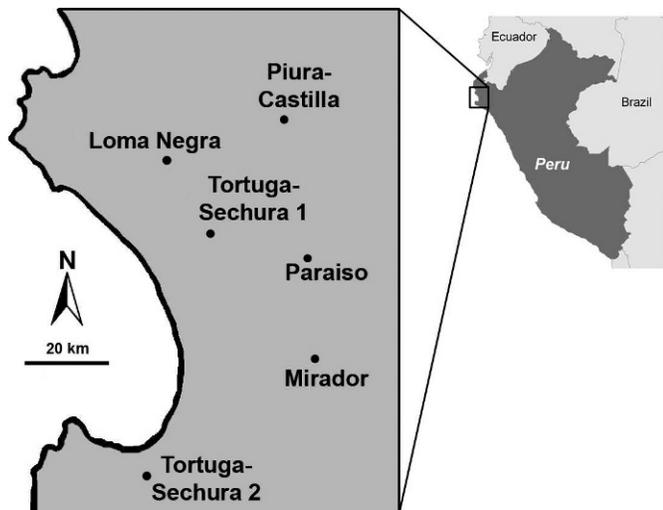

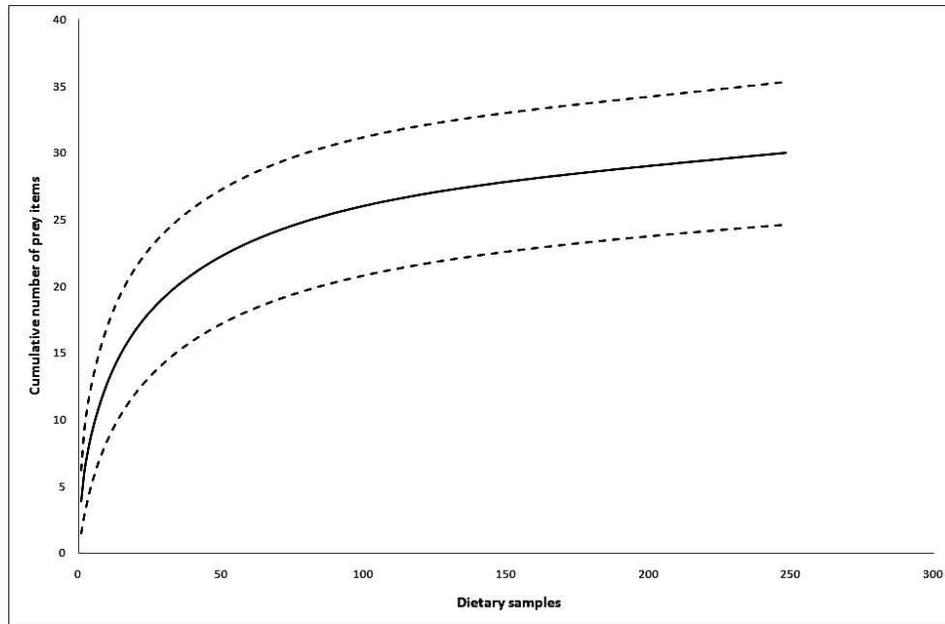FIG. 1. Map of study sites in northwest Peru.

FIG. 2. Rarefaction curve for prey items in dietary samples. The cumulative number of prey is plotted against the number of randomized dietary items (95% confidence interval depicted by dashed lines).

overlap index O_{jk} (Pianka, 1973):

$$O_{jk} = \frac{\sum\limits_{n=1} P_{ij}P_{ik}}{\sqrt{\sum\limits_{i=1}^{n} P_{ij}^2 \sum\limits_{i=1}^{n} P_{ik}^2}},$$

where P_{ij} and P_{ik} are proportions of item volume of type i in the groups j and k (which in this case can represent adult males, adult females, or juveniles). O_{jk} values range from 0 (no niche overlap) to 1 (complete overlap).

Spatial Effects.—We used Kruskall-Wallis nonparametric tests to test for differences in the extent of herbivory and diet width among sampled sites. We tested the relationship between *P. pallida* tree cover, estimated in December 2004, and the proportion of *Prosopis* parts in the diet of *Dicrodon,* using a Spearman rank correlation test. We used Mantel tests to test for relationships between geographic distances among sampled sites versus extent of herbivory and diet width of the lizards. Means are reported ± SD.

RESULTS

Diet Composition.—Overall, we identified 30 types of food items among 13,898 items in 248 fecal or stomach samples. The rarefaction curve (Fig. 2) shows that the sample size produced a good approximation of the diversity of food items in *D. guttulatum. Prosopis pallida* represented the most important component of the diet (between 12% and 95%) and was a minor component only at one location (Loma Negra; Table 2). Besides leaves, flowers, and seeds of *P. pallida*, the seeds of an unidentified species of grass (Poaceae) formed an important component of the diet in several study sites (Table 2). We also found leaves of *Acacia* sp. (<2%), *Capparis* sp. (<2%), and unidentified herbaceous plant species (Table 2). Insects formed only a small proportion (average 10%) of the diet.

We found that the efficacy of the flushing method varied between juveniles and adults. Juveniles suffered a higher number of fatalities than adults (25% vs. 7%). Stomachs of deceased adults ($N = 2$) contained a variable amount of food (15 and 90% of total content remained after flushing), whereas

stomachs of deceased juveniles were empty after flushing ($N = 3$).

Overall, 97.4% of *D. guttulatum* stomach contents (excluding empty stomachs) and 99.5% of all fecal pellets contained plant material. The proportion of plant material across years and sites averaged 91.0 ± 20.6% in stomach samples (excluding empty stomachs). In fecal pellets (where each individual lizard can be associated to one or more pellets), this proportion averaged 82.2 ± 22.2%.

Ontogenetic Effects.—The amount of plant material in the diet averaged 96.4 ± 6.1% for males ($N = 7$), 89.3 ± 18.0% for females ($N = 20$), and 87.9 ± 29.3% for juveniles ($N = 12$). Differences between the groups were not significant (Kruskall-Wallis, $\chi^2 = 0.983$, df $= 2$, $P = 0.642$). Diet width did not differ between males (2.00 ± 0.62), females (1.63 ± 0.57), and juveniles (1.66 ± 1.03; Kruskall-Wallis, $\chi^2 = 2.260$, df $= 2$, $P = 0.323$). Diet overlap based on volumetric data of stomach contents was large between males and juveniles ($O_{jk} = 0.87$) and between females and juveniles ($O_{jk} = 0.89$). Diets of males and females varied more ($O_{jk} = 0.56$). The differences in volumetric diet contents between the sexes were caused by the larger consumption of non-*Prosopis* (herbaceous) plant parts by females (73% of the diet) compared to males (26%) and juveniles (47%) (Kruskall-Wallis, $\chi^2 = 6.754$, df $= 2$, $P = 0.035$). Because of the difference in diet between males and females, niche overlap of adults (males and females combined) versus juveniles is almost complete ($O_{jk} = 0.97$).

Spatial Effects.—The extent of herbivory in 2006 (fecal pellets) was largest in Mirador (92%, Fig. 1, Table 1, Kruskall-Wallis, $\chi^2 = 31.580$, df $= 3$, $P < 0.001$), whereas there were no differences among the other sites. In 2008, the amount of plant material in the diet ranged from 78% (Piura-Castilla) to 100% (Mirador). We found no relationship between geographic distance among sampled sites and extent of herbivory (Mantel test, $r = -0.138$, $P = 0.380$). In contrast with geographic distance, *P. pallida* tree cover had a positive relation with the proportion of *Prosopis* parts in the diet of *D. guttulatum* (Spearman, $r = 0.137$, $P = 0.031$). Diet width in 2006 differed significantly between Tortuga-Sechura 1 and Paraiso (Kruskall-Wallis, $\chi^2 = 27.637$, df $= 4$, $P < 0.001$; Table 1). Diet width in 2008 did not differ among sampled sites (Kruskall-Wallis, $\chi^2 = 1.776$, df $= 3$, $P = 0.620$) and varied from 1.26 ± 0.22 for Mirador to 2.54 ± 0.95

TABLE 2. Diet of *Dicrodon guttulatum*. Values represent volumetric percentages of food items, arranged by location and year.

Food item	Tortuga-Sechura 2 (Bayovar) 2006 (N = 43)	2008 (N = 18)	Mirador 2006 (N = 50)	2008 (N = 3)	Tortuga-Sechura 1 2006 (N = 50)	2008 (N = 8)	Piura 2008 (N = 18)	Paraiso 2006 (N = 50)	Loma Negra 2008 (N = 10)	Male 2008 (N = 7)	Female 2008 (N = 20)	Juvenile 2008 (N = 12)
Prosopis, leaf	34.5	29.6	63.3	67.0	31.5	45.1	47.2	32.0	11.9	52.2	17.8	40.9
Prosopis, flower	—	—	—	—	—	6.0	—	27.6	—	6.9	—	—
Prosopis, seed	1.4	—	—	27.7	0.8	—	2.3	1.7	—	11.9	—	—
Prosopis total	35.9	29.6	63.3	94.7	32.3	51.1	49.4	61.3	11.9	71.0	17.8	40.9
Acacia, flower	—	4.7	—	—	—	—	—	—	—	2.7	3.0	0.6
Acacia, seed	—	—	—	—	—	—	6.9	—	—	—	—	—
Capparis, seed	0.1	—	1.3	—	1.9	—	—	9.3	—	—	—	—
Poaceae, leaf	—	—	0.0	—	0.7	—	—	0.2	—	—	—	—
Poaceae, seed	24.3	58.8	26.1	—	44.6	31.0	1.7	—	25.3	19.3	46.7	40.9
Boerhavia, seed	—	—	—	—	—	—	9.0	—	—	—	—	—
Unidentified herb, leaf	—	—	—	1.2	0.6	3.1	4.3	1.5	35.6	3.5	15.9	3.5
Unidentified herb, fruit	—	—	—	—	—	—	0.3	0.4	—	—	—	—
Unidentified herb, seed	1.7	—	1.3	4.2	—	—	—	1.6	11.2	—	5.0	2.0
Unidentified plant part	17.8	2.0	0.2	—	5.0	—	6.0	3.8	1.6	1.0	2.3	—
Other plants total	43.9	65.6	28.9	5.3	52.7	34.1	28.2	16.9	73.7	26.4	72.8	47.0
Insect parts	14.7	4.9	5.4	0.0	6.8	14.8	16.0	13.9	14.5	2.6	9.4	12.1
Stone	4.8	—	1.6	—	4.9	—	—	0.3	—	—	—	—
Piece of wood/bark	0.7	—	0.8	—	3.3	—	6.3	7.7	0.0	0.0	0.0	0.0

for Piura-Castilla (Table 1). We found no relationship between geographic distance among sampled sites and diet width (Mantel test, $r = -0.192$, $P = 0.276$).

DISCUSSION

Diet Composition: Ontogenetic and Sex Differences.—The diet of *D. guttulatum* in different plant communities in northwestern Peru consisted mainly of plants. We are confident that our study provided an accurate description of the diet based on the rarefaction curve of the cumulative number of prey items (Fig. 2). Most of the diet was composed of *P. pallida*, followed by grass seeds and small quantities of unidentified herbaceous plants. Insects were rare in the diet, regardless of year, location, or ontogenetic stage (Table 2).

The extent of herbivory in *D. guttulatum* ranged between 78% and 100%, regardless of sex and age, which is consistent with the study of Velásquez et al. (2007). The values are comparable to those of herbivorous iguanids (Mautz and Nagy, 1987; Durtsche, 2000). Within Teiidae, two species of Caribbean *Cnemidophorus* are considered to be strict herbivores as adults, whereas juveniles are insectivorous (Vitt et al., 2005). Therefore, our study makes *D. guttulatum* the only species in the family known to be herbivorous throughout its whole life (Vitt, 2004). Omnivorous teiid species supplementing insectivorous diets with fruits include species of *Tupinambis* (Williams et al., 1993) and *Cnemidophorus* (Cooper and Vitt, 2002; Dias and Rocha, 2007). Species of *Ameiva* and *Kentropyx* occasionally include plant material in their diet (Magnusson and da Silva, 1993; Vitt and de Carvalho, 1995).

Although diet width and extent of herbivory did not differ between adult males, adult females, and juveniles, the diet of adult females showed reduced overlap with adult males. This difference was caused by a dietary shift in adult females from *P. pallida* to herbaceous plants, which could reflect differences in behavior or dietary requirements. Pregnancy requires higher energy, protein, and fat assimilation in female lizards (Lourdais et al., 2004). Rocha (1989, 2000) showed that lizards can selectively consume highly nutritious food. Cappellari et al. (2007) suggested that differences in diet between adult females and adult males or juveniles of the insectivorous *Teius oculatus* (Teiidae) could be a result of the behavior of gravid females, which are less mobile during pregnancy (Shine, 1980). Durtsche (1995) also found a difference in diet between adult

males and females during the reproductive season in the omnivorous *Uma inornata,* but no differences have been detected in other lizard species (e.g., Magnussen and da Silva, 1993; Znari and El Mouden, 1997).

Diet Specialization.—The total amount of plant material in the diet was high in all sites. However, the relative importance of *Prosopis* parts in the diet was more variable (12–95%) among sites and between years, and positively related to the cover of *P. pallida* trees in each study site. Velásquez et al. (2007) examined the diet of *D. guttulatum* in the absence of *P. pallida* and found that lizards mainly consumed leaves of *Acacia* sp. and fruits of *Scutia spicata* and *Capparis* sp. These plants were rarely encountered in our stomach and fecal samples, although they are present at our study sites. These data suggest that *D. guttulatum* prefers *P. pallida* when it is available. Interestingly, the herbivorous teiid *C. murinus*, on Bonaire, generally avoids leaves of *Prosopis juliflora* (Dearing and Schall, 1992), possibly because of their high saponin content (Dearing and Schall, 1992). *Prosopis juliflora* is closely related to *P. pallida* (Harris et al., 2003; Burghardt and Espert, 2007), but little is known about the presence and abundance of saponin and other secondary metabolites in *P. pallida*. *Prosopis pallida* is a nitrogen fixing tree species (Ramírez-Orduña et al., 2005), and its leaves are rich in nitrogen (concentration of 3.24 ± 0.32%, compared with only 1.50 ± 0.30% for the sympatric *Capparis scabrida*; Havik, 2010). Leaves of *P. juliflora* had a high gross energy content of 19.1 KJ g^{-1} DM (M. D. Dearing, unpubl. data). If leaves of *P. pallida* have a similarly high gross energy content, then this together with their high nitrogen content could promote dietary specialization on *P. pallida* leaves.

Lizard Grazing Pressure.—To gain a better understanding of the role of *D. guttulatum* in the Sechura desert, we calculated the lizard grazing pressure on *P. pallida*. For a crude approximation of the energetic needs of *D. guttulatum*, data from other species had to be used, since specific data on *D. guttulatum* are not available. Body temperature of *D. guttulatum* was on average 32.2 ± 1.8°C during activity in Bayovar. The similar-sized herbivorous iguanid *Dipsosaurus dorsalis* has an energy expenditure of 3.66 kJ day^{-1} for adults with body temperature of 30°C and 6.2 kJ day^{-1} with a body temperature of 35°C (Mautz and Nagy, 1987). Assuming that energetic requirements of *D. guttulatum* do not differ substantially from those of *D. dorsalis*, we can estimate that adult *D. guttulatum* will need approximately 0.5 g DM of *P. pallida* leaves (metabolizable energy content 9.2 kJ g^{-1}; van den Bosch et

al., 1997; M. D. Dearing, pers. comm.) to fulfill their daily energetic needs, if only consuming leaves of this plant. Considering the average proportion (40.4%) of *P. pallida* leaves in the diet, grazing pressure of an adult *D. guttulatum* on *P. pallida* would be on average 0.2 g DM day^{-1}, with the assumption that the energetic content of other diet items combined is equal to that of *P. pallida* leaves on average. *Prosopis pallida* seedlings in Piura had an aboveground growth rate of only 0.009–0.016 g DM day^{-1} (Squeo et al., 2007; Havik, 2010). These values indicate that grazing pressure by *D. guttulatum* on *P. pallida* can be considerable, especially during the first weeks after germination. This is supported by Holmgren et al. (2006a), who experimentally showed that lizard herbivory can reduce *P. pallida* seedling survival by 69%. The ubiquity of these lizards combined with our estimates of individual grazing pressure indicates that lizard herbivory plays a major role in these plant communities. Indeed, Sitters et al. (2011) found that long-term success of reforestation projects, coupled with ENSO events in the Piura region, was larger when *P. pallida* seedlings were protected against lizards. To further improve our understanding, we will need to assess plant-herbivore interactions temporally, to account for the large interannual variability in precipitation and productivity that characterizes dry ecosystems (Holmgren et al., 2006b). Actually, theoretical models show that the rate of herbivore population growth, in response to plant growth during a pulse of productivity, can determine whether an ecosystem can be forced into an alternative state with higher plant biomass (Scheffer et al., 2008). To survive lizard herbivory pressure, *P. pallida* plants may need to reach a safe size. This may occur during a mass germination event in a rainy year or under environmental conditions that reduce lizard abundance.

Evolution of Herbivory.—We found that *D. guttulatum* is strictly herbivorous, despite being a medium-sized lizard without known morphological or physiological adaptations to herbivory. Further research is needed to understand how herbivory evolved in this genus, for example by evaluating the presence and role of fermentation. The presence of fermentation in the gut was hypothesized, but not tested, for *C. murinus* (Dearing and Schall, 1992). Our finding that both juveniles and adults are strict herbivores, without having morphological adaptations, makes the independent origin of herbivory in *Dicrodon* (Giugliano et al., 2007) very interesting. Aridity could have played a role in the evolution of herbivory in *D. guttulatum* in the Sechura desert. If aridity was an important selective pressure promoting herbivory, we could hypothesize that the extent of herbivory varied along a rainfall gradient from the Sechura desert to southern Ecuador. Testing this hypothesis will require a comparison of *D. guttulatum* diets and dietary preferences across this gradient.

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