NEW VISUAL RECORDS OF PLANTS CONSUMED BY 10 LIZARD SPECIES ON ISLANDS OF THE GULF OF CALIFORNIA, AND IMPLICATIONS FOR THE INSULAR ECOLOGY AND TROPHIC WEBS

NUEVOS REGISTROS VISUALES DE PLANTAS CONSUMIDAS POR 10 ESPECIES DE LAGARTIJAS EN ISLAS DEL GOLFO DE CALIFORNIA, E IMPLICACIONES PARA LA ECOLOGÍA INSULAR Y LAS REDES TRÓFICAS

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Resumen.– Presento una lista inédita de 59 especies de plantas de 19 familias que constituyen una fuente de alimento para los reptiles insulares *Ctenosaura conspicuosa, C. hemilopha, Sauromalus varius, S. hispidus, S. slevini, S. klauberi, S. ater, Dipsosaurus dorsalis, D. catalinensis,* y *Petrosaurus thalassinus* en 15 islas del Golfo de California basada en 711 observaciones directas de eventos alimenticios. Dos especies trepan a los ápices de las pencas de cardón con el propósito de alimentarse de sus flores y frutos, y al hacerlo accidentalmente desprenden partes de la planta que subsidian parcialmente a los organismos terrestres; el resto forrajea en el suelo, pero muestran tendencias evolutivas, ecológicas y conductuales marcadas para trepar a los arbustos y árboles para comer sus hojas, flores y frutos. Los hábitos alimenticios de estos reptiles repercuten hacia e influyen a otras poblaciones, especies, niveles tróficos e incluso a la comunidad insular completa, tanto hacia arriba (a depredadores) y hacia abajo (a productores y consumidores primarios) como horizontalmente (a competidores). Las lagartijas insulares herbívoras y omnívoras, en su papel de consumidores primarios y secundarios, e incluso como depredadoras, están en medio de complejas redes tróficas. En estas interacciones destaca el cardón por las masivas cantidades de biomasa y energía que proporciona a las comunidades insulares completas.

Palabras clave.– Lagartijas insulares herbívoras, lagartijas insulares omnívoras, redes tróficas, especies estructurales, subsidios marinos, cardón.

Abstract.– I present an unpublished list of 59 plant species of 19 families that constitute a source of food for the insular reptiles *Ctenosaura conspicuosa, C. hemilopha, Sauromalus varius, S. hispidus, S. slevini, S. klauberi, S. ater, Dipsosaurus dorsalis, D. catalinensis*, and *Petrosaurus thalassinus* on 15 islands of the Gulf of California based on 711 direct observations of feeding events. Two reptile species climb to the tops of cardon cacti branches to purposely eat flowers and fruits and accidentally dislodge plant parts that partially subsidize ground organisms; the rest forage mainly on the ground, but do show a strong evolutionary, ecological, and behavioral tendency to climb on low trees and bushes to eat leaves and flowers. The reptiles' food habits influence other populations, species, trophic levels, and even the whole insular communities, both up (to predators), down (to producers and primary consumers) and horizontally (to competitors). Insular herbivorous and omnivorous lizards, as primary and secondary consumers, and even as predators, are in the middle of complex food webs. In these interactions, the cardon cactus provides vast amounts of biomass and energy to the whole insular communities.

Keywords.– Insular herbivorous lizards, insular omnivorous lizards, food webs, structural species, marine subsidies, cardon cactus.

INTRODUCTION

The islands of the Gulf of California, Mexico, support diverse flora and fauna assemblages with interesting evolutionary histories that include plate tectonics-background settings, diverse paleogeographic scenarios, vicariance and dispersal events, adaptive radiations, convoluted phylogeographic and phylogenetic patterns, genetic and phenotypic diversity, cryptic diversity, endemism, varied habits and lifestyles, and evolutive trends (i.e. character release, change in form, secondarily adaptations) resulting in complex, even perplexing, distributions and ancestry relations with still unresolved taxonomies (Savage, 1960; Soulé & Sloan, 1966; Murphy & Otley, 1984; Murphy & Crabtree, 1985; Grismer, 1999; Riddle et al., 2000; Case et al., 2002; Douglas et al., 2006; Riddle & Hafner, 2006; Hafner & Riddle, 2011; Cruz-Andrés, 2014; Meik et al. 2015; Alencar et al., 2016; Harrington et al., 2017; Meik et al., 2018; Ruíz-Sánchez et al., 2019; Ramírez et al., 2020).

The reptiles, being abundant and conspicuous in these arid habitats, have attracted more attention than other vertebrates and today we have a reasonably complete picture of at least which species are on which islands (Case, 2002). Lovich et al. (2009) have noted that the Baja California Peninsula and associated gulf and Pacific islands contain 167 species of native amphibians and reptiles with native reptiles comprising 50 genera and 149 species (8 turtles, 86 lizards, one amphisbaenid, and 54 snakes). Among these, there are five species of sea turtles and the sea snake *Pelamis platurus* (Lovich et al., 2009). In addition, 54 islands in the gulf are inhabited by 276 populations of reptiles of 94 species, which represent an assemblage of continental and peninsular components, plus the endemics that have originated *in situ* (Murphy & Aguirre, 2002).

Studies on the cited topics at the beginning of this section have been conducted for diverse reptile taxa, especially genetic and molecular ones, e. g. on rattlesnakes of the genus *Crotalus* (in prep.), to the point of finding new species (*C. polisi* and *C. thalassophorus*) based on biological data including mitochondrial nSNP trees, as recently as 2018 (Meik et al., 2018).

However, natural history research related to Baja California reptiles has been slower and less often reported. Most studies have focused on the endemic, insular rattlesnakes (Avila-Villegas et al., 2007; Arnaud et al., 2008; Martins et al., 2008; García-Padilla, 2010). Many aspects of reproduction, growth, population dynamics, behavior and feeding are still unknown for most reptile species, although several researchers have studied and compiled information on various aspects of lizard biology and ecology, and Grismer (2002), in his book of Baja Californian reptiles and amphibians, included what was known about their Natural History up to 2002.

The food of insular lizards is the focus of this paper. A literature review on dietary habits and feeding behavior of Sonoran Desert lizards reveals that most research has been done on continental ones, although a few, very specialized studies have been done on insular ones (see below). Among the continental representatives that have been studied, two species that have island populations in the Gulf of California (*Sauromalus ater* and *Dipsosaurus dorsalis*), have attracted much attention. These two continental/insular species are useful to illustrate the broad spectrum of diets available for herbivorous and omnivorous lizards in the Sonoran Desert realm and are presented in a summarized form in Table 1.

In relation to feeding behavior, few authors have focused on the climbing behavior of lizards. Johnson (1965), in his ecological study of continental *Sauromalus ater*, noted that individuals of this species either ate small annuals and shrubs on the ground, or climbed onto the higher shrubs to get flowers. Lizards of both sexes were observed feeding on the same bush simultaneously, showing both the climbing tendency of the species and its gregariousness.

The island forms of widespread lizards have received much less attention than the continental ones. The dietary habits and feeding behavior of only four insular, endemic species have been studied (Table 1), though three have been studied intensively. For *Dipsosaurus catalinensis* on Santa Catalina island, Grismer (2004) reported that, at certain times of the year, groups of two to six animals feeding communally on the fallen fruits of *Pachycereus pringlei* was a common occurrence. Individuals feeding on ripened fruits of *Stenocereus gummosus* were observed as high as one meter above the ground.

Without any doubt the champion of intensive chuckwalla (*Sauromalus sp.*) research on islands of the Gulf of California was Ted J. Case. In 1979, he initiated the first, and to date the only, ecological study of *Sauromalus varius* and *Ctenosaura hemilopha* (= *C. conspicuosa* [Grismer, 1999, 2002]) on San Esteban Island, and *S. hispidus* on Angel de la Guarda and satellite islands. Case (1982) found on Ángel de la Guarda, that *Sauromalus hispidus* was the most arboreal chuckwalla of all *Sauromalus* species, with 45% of juveniles (in one of his studied locations) observed on *Dalea, Hyptis, Acacia* and other perennials bushes at a height of 1.5 to 3.0 m, maneuvering to the end of flowering stems to eat the blossoms, but the global arboreal preference of juveniles was unknown. Only 10% of the adults were sighted in arboreal situations and

Tabla 1. Dietas comparativas de seis especies de lagartos de tierra firme e islas según lo informado en la literatura revisada.

Table 1. Comparative diets of six lizard species of mainland and islands as reported in the reviewed literature.

Lizard species	Location	Technique	Plant food	Reference
Sauromalus ater	Borrego Mountains, California	Stomach analysis	*Phacelia* sp.	Shaw, 1939
			Ambrosia dumosa	
			Encelia farinosa	
			Erigonum	
			Ditaxis lanceolata	
			Larrea tridentata	
			Fouquieria splendens	
	Tubbs Canyon, California		*Encelia farinosa*	
			Lotus sp.	
			Phacelia sp.	
			Festuca sp.	
			Cryptantha sp.	
			Lotus strigosus	
	Palm Canyon		*Chenactis* sp.	
			Cryptantha sp.	
			Tropidocarpum gracile	
Sauromalus ater	Western Mojave Desert	Observation	*Cryptantha* sp.	Johnson, 1965
			Isomeris arborea	
			Eriogonum fasciculatum	
			Stephanomeria pauciflora	
Sauromalus ater	Grand Wash Cliffs, Grand Canyon	Fecal pellet analysis	*Sphaeralcea ambigua*	Hansen, 1974
			Ambrosia dumosa	
			Acacia gregii	
			Lotus strigosus	
			Coldenia hispidissima	
Sauromalus ater	Colorado Desert of Southern California	Observation	*Plantago insularis*	Abts, 1985
			Perityle emoryi	
			Phacelia crenulata, Erigonum inflatum	
			Mirabilis bigelovi	
			Sphaeralcea ambigua	
			Chaenictis carphoclina	
			Ambrosia dumosa	
			Fagonia chilensis	
			Bebbia juncea	
			Pectis papposa	
			Euphorbia polycarpa	

Tabla 1 (cont.). Dietas comparativas de seis especies de lagartos de tierra firme e islas según lo informado en la literatura revisada.

Table 1 (cont.). Comparative diets of six lizard species of mainland and islands as reported in the reviewed literature.

Lizard species	Location	Technique	Plant food	Reference
Sauromalus ater	Santan Mountains, South Mountains, and Phoenix Mountains, Arizona	Observation	*Cercidium microphylum* *Sphaeralcea ambigua* *Trixis califórnica* *Viguiera deltoidea* *Fouquieria splendens* *Hyptis emoryi* *Lycium* sp.	Kwiatkowski and Sullivan, 2002
Dipsosaurus dorsalis	Dry areas of California	Observation	*Lupinus sparsiflorus* *Chaenactis fremontii* *Larrea tridentata* *Olneya tesota*	Howland, 1988
Dipsosaurus dorsalis	Mainland	Observation, fecal pellet analysis	*Omnivorous (herbivorous and insectivorous)*	Norris, 1953
Dipsosaurus catalinensis	Santa Catalina Is., Gulf of California	Observation	*Pachycereus pringlei* *Stenocereus gummosus*	Grismer, 2004
Sauromalus varius	San Esteban Island	Observation	*Macrocereus* sp. *Cercidium* sp. *Prosopis* sp. *Olneya* sp. *Cactus fruits* *Assorted perennial flowers*	Case, 1982
Ctenosaura conspicuosa	San Esteban Island			
Sauromalus hispidus	Angel de la Guarda Island	Observation	*Dalea* sp. *Hyptis* sp. *Acacia* sp. *Jatropha* sp. Cholla Cardon	Case, 1982
Sauromalus varius	San Esteban Island	Fecal pellet analysis	22 plant species of 12 families, with "large amounts of shrubs, forbs and tree leaves and fruits"	Sylber, 1988
Sauromalus hispidus	San Lorenzo Sur, Angel de la Guarda and Mejia Islands		35 plants species of 20 families, including *Cressa truxilliensis, Amaranthus palmeri, Ferocactus peninsulae, Opuntia echinocarpa, Agave deserti, Asclepias subulata*	
Sauromalus hispidus	Rasa Island	Observation	*Cressa truxilliensis*	Velarde, pers. com., 2014
Sauromalus hispidus	Rasa Island	Fecal pellet analysis	*Cressa truxilliensis*	Cerdá, unpubl. data

usually at about 1 m in height in shorter, sturdier shrubs. On the other hand, *Sauromalus varius* adults were not inclined to climb vegetation, with only a 3% of his global sightings in such situations. A 53% of the individuals were sighted in vegetation. Like *S. hispidus* on Ángel de la Guarda island, ctenosaurs (members of the genus *Ctenosaura*) occasionally perched on the top of cardons to bask and feed.

Sylber (1988) conducted the first and most comprehensive research on the feeding habits of insular lizards. He collected 1875 fecal pellets of *Sauromalus varius* and *S. hispidus* on four islands of the midriff region of the Gulf of California (Table 1). A total of 48 species representative of 25 plant families were in the diets of adult *Sauromalus*. For *S. varius* he found a diet consisting of 22 plant species of 12 families, whereas that of *S. hispidus* was made of 35 plant species from 20 families. When the diet was subdivided into plant types, shrubs were the most frequently eaten food item (40.4%), followed by forbs (32.4%), tree leaves and fruits (18.8%), cactus flowers and fruits (6.6%), and grasses (1.2%). If plants parts were considered, seeds made up the largest portion of the diet (46%), followed by leaves (36%), flowers (10%), and stem (7%). Notably, no halophytes (*i.e. Abronia* sp., *Artiplex* sp., *Suaeda* sp., and *Allenrolfea* sp.) were obtained in the fecal analyses, except *Cressa truxilliensis* and *Amaranthus palmeri*, consumed by *S. hispidus*.

Traditionally, analysis of stomach contents has been the main way to determine the dietary habits of many animal species, but this implied the killing of individuals, including rare, unique, scarce, or endangered ones; or the dissecting of museum specimens. More recently, scat collection and analysis has become the most effective technique (Hansen, 1974), but also requires enormous reference plant collections (with flowers, fruits and seeds) and laboratory work. Although still applicable and effective, the feces analyses can be complemented with direct observation of feeding events in the field (empirical evidence *ad oculos*), that may also render other valuable information like behavior. Photography can reinforce these observations. By simply observing, there is no need to collect, kill or disturb any of the insular lizards, which have in the past been catastrophically decimated by introduction of feral species and are now in the process of population recovery after eradication of invasive, non-native species on some islands (Cerdá-Ardura, 2019).

By previous observations (made in 1986 and 1987 during eight scientific, one month-long cruises), I assumed that native, insular lizards had a wide range of food items available for consumption along the seasons, and that they probably displayed adaptive behaviors to do so. Accordingly, the objectives of my research were: 1) to visually record the plant species the lizards consumed by direct, field observations and plant identification *in situ*; 2) the recording of feeding behavior; and 3) to make some assumptions, based on results, about lizards' position and importance into the insular food webs.

MATERIAL AND METHODS

Based on 711 visual records, I obtained the feeding habits for 10 lizard species from 24 years (from December 1995 to April 2019) of visiting diverse islands of the Gulf of California in winter, spring, early summer, and in some cases in mid-late summer. Most of the visits consisted in 4-hours long walks in the morning and/or afternoon on seven-day long trips, yielding a minimum observation time of 24 hours per week, 288 hours per season (year), and 6900 hours in the whole period of 24 years and more than 1500 days of navigation and exploration. I tried to cover most habitats and as many physiognomic landscapes as possible, e.g. arroyos, foothills, mountains, beaches, sand dunes, berms, and mangroves in different locations of the following 15 islands: Ángel de la Guarda, Carmen, Cerralvo, Coronado, Danzante, Espíritu Santo-Partida Sur (herein referred as Espíritu Santo), Monserrat, Rasa, San Francisco, San Esteban, San José, San Lorenzo Sur, San Marcos, Santa Catalina, and Tiburón.

All visits were made aboard touristic cruise ships belonging to Lindblad Expeditions/National Geographic. Disembarking was made on Zodiac-type and DIB rubber boats. The walks were of different lengths, but the majority was 2-4 km long following linear transects across different landforms (e.g. arroyos, foothills), and investing the same searching effort. Field notes on Natural History of the species (e.g. behavior, measurements, etc.), and photographs, when possible, were taken. Samples include N= >1000 individuals of the different chuckwalla species (*Sauromalus* sp.), N= >300 iguanas (*Ctenosaura* sp.), N= >200 desert iguanas (*Dipsosaurus* sp.) and N= <150 rock lizards (*Petrosaurus thalassinus*). No feces were collected for this report although feces have been collected in other, specifically oriented studies, but will not be reported here (*cf.* Cerdá & Langarica, 2018). Photographs are presented as a way of documenting the behavior of some of these species and their feeding habits, as well as to present aspects of morphology of buds, flowers, and fruits of some plants.

RESULTS

Plants and feeding preferences. Table 2 presents the list of the 15 islands visited during this long-term data recording, arranged by increasing area, and the numbers of plant and reptile species

Tabla 2. Islas visitadas con área informada y número de especies de plantas y reptiles (Case, Cody & Ezcurra, 2002).

Table 2. Islands visited with reported area and numbers of plant and reptile species (Case, Cody & Ezcurra, 2002).

	Island	Area in km^2	Number of plant species	Number of reptile species
1	RASA	0.68	14	2
2	SAN FRANCISCO	4.49	109	10
3	DANZANTE	4.64	128	16
4	CORONADO	9.13	127	15
5	MONTSERRAT	19.86	127	13
6	SAN MARCOS	30.07	142	22
7	SAN LORENZO SUR	33.03	82	7
8	SAN ESTEBAN	40.72	123	9
9	SANTA CATALINA	40.99	122	10
10	ESPÍRITU SANTO	96.26	249	21
11	CERRALVO	136.50	232	20
12	CARMEN	143.03	195	16
13	SAN JOSÉ	187.16	219	22
14	ÁNGEL DE LA GUARDA	936.04	199	15
15	TIBURÓN	1223.53	298	29

as reported in literature (from Carreño & Helens, 2002; Cody et al., 2002; and Murphy & Aguirre, 2002, respectively). The general geological, ecological and biogeographic features of these islands of the Gulf of California and their locations can be reviewed in Carreño and Helenes (2002) and Álvarez-Borrego (2002). For identification, measurements, morphology, taxonomy, distribution and natural history of the reptiles treated below, see Grismer (2002). All plants mentioned here were identified in situ using the Baja California Plant Guide by Rebman and Roberts (2012).

From Table 2 I must emphasize the great variation in size of these islands: they range from Rasa, with only 0.68 km^2 of extension and only 14 plant species (Velarde et al., 2014) and two reptile species (Murphy & Aguirre, 2002), to Tiburón, the largest island of Mexico, with 1223.53 km^2 (Carreño & Helenes, 2002) and as many as 298 plant species (Cody et al., 2002) and 29 reptiles (Murphy & Aguirre-León, 2002; Grismer, 2002). In addition to a small area, Rasa is low and flat, presenting few habitats for reptiles (Cerdá & Langarica, 2018), whereas Tiburón is high (1218 m) (Murphy et al., 2002) and with multiple habitats. These features make the future research on insular reptiles' diet highly promising.

I visually recorded 10 lizard species feeding directly on plants. From these, *Sauromalus* species are classically regarded as strict herbivorous lizards (Sylber, 1988; Hollingsworth, 2004), with the iguanas *C. conspicuosa, C. hemilopha, Dipsosaurus dorsalis* and *D. catalinensis*, and the rock lizard *Petrosaurus thalassinus* being omnivorous (Grismer, 2002, 2004). A total of 711 observations of exclusively feeding events were retrieved from my general records.

Table 3 gives a summarized, composite view of the reptile species recorded, the plants they consumed, the number of times they were observed feeding on each plant, and the island or group of islands were this behavior occurred. The 711 feeding observations correspond as follows: 81 to *Ctenosaura conspicuosa*; two to *C. hemilopha*; 51 to *S. varius*; 22 to *S. hispidus*; six to *S. slevini*; 100 to S. klauberi; 411 to S. ater; 20 to *Dipsosaurus dorsalis*; 16 to *D. catalinensis*, and eight to *Petrosaurus thalassinus*.

As many as 59 plant species were found to be consumed by these 10 reptile species on the 15 islands of the Gulf of California. The maximum number of records of a single reptile species eating a single plant species corresponds to *Ctenosaura conspicuosa*, with 52 feeding times on *Pachycereus pringlei*, followed by *Sauromalus varius* to *P. pringlei* in 41 times. Also meaningful are the records of *S. klauberi* with 18 feeding observations on *Ferocatus diguetii*, 19 times on *Hyptis emoryi*, and 15 times on *P. pringlei*; and *S. ater*, with 17 records of feeding on *Bebbia juncea*, 17 on *H. emoryi*, 21 on *P. pringlei*, 25 on *Perytile californica*, 17 on *Jacquemontia eastwoodiana*, and 17 on *Trixis californica*. Some of the reptile species were observed feeding on different plant species only once, and the one of *Mardsenia* sp. is uncertain as I had difficulties in correctly identifying the plant. Table 3 is also useful to compare the whole diversity of plants available for the reptiles, their preferences, and the intensity with which they feed on them. In the case of *Cressa truxilliensis*, the record correspond to what was published by Velarde el al. (2008), and Cerdá and Langarica (2018), plus 43 *Sauromalus hispidus* feces I collected on Rasa, feces that were not included in the general counting and are presented just as one plant record. Another interesting fact derived from Table 3 is that *S. ater*, as the reptile species with wider distribution

Tabla 3. Tabla compuesta para las 10 especies de reptiles encontradas durante este estudio, con las especies de plantas que consumieron, el número de veces que se observó que cada especie de reptil comía cada especie de planta y las islas donde se realizaron las observaciones combinadas.

Table 3. Composite table for the 10 reptile species found during this study, with the plant species they consumed, the number of times each reptile species was observed eating each plant species, and the islands where the combined observations were made.

Reptile species	Consumed plant species	No. of times seen eating the plant	Islands
Ctenosaura conspicuosa	*Lysiloma candidum*	9	San Esteban
	Olneya tesota	8	
	Pachycereus pringlei	52	
	Stenocereus gummosus	9	
	Stenocereus thurberi	3	
C. hemilopha	*Lysiloma candidum*	1	Cerralvo
	Pachycereus pringlei	1	
Sauromalus varius	*Ambrosia ambrosioides*	3	San Esteban
	Echinocereus grandis	2	
	Pachycereus pringlei	41	
	Stenocereus gummosus	5	
S. hispidus	*Atriplex sp.*	2	Ángel de la Guarda, San Lorenzo Sur, Rasa
	Cressa truxilliensis *	N/A	
	Encelia farinosa	12	
	Pachycereus pringlei	6	
	Suaeda nigra	2	
S. slevini	*Amauria rotundifolia*	4	Carmen, Monserrat, Coronado
	Pachycereus pringlei	2	
S. klauberi	*Bursera hindsiana*	3	Santa Catalina
	Bursera microphylla	2	
	Euphorbia polycarpa	3	
	Ferocactus diguetii diguetii	18	
	Gossypium davidsonii	4	
	Hyptis emoryi	19	
	Lysiloma candidum	2	
	Melochia tomentosa	8	
	Pachycereus pringlei	15	
	Parkinsonia microphylla	1	
	Pythecellobium confine	3	
S. klauberi	*Ruellia californica*	13	Santa Catalina
	Simmondsia chinensis	3	
	Stenocereus gummosus	5	
	Stenocereus thurberi	1	
S. ater	*Acacia goldmanii*	1	Espíritu Santo, San Francisco, San José, Danzante, Península, San Marcos, Tiburón
	Amarathus fimbriatus	12	
	Ambrosia dumosa	2	
	Antigonon leptopus	5	
	Atriplex sp.	3	
	Bacharis salicifolia	6	
	Bajacalia crassiflora	11	
	Bebbia juncea	17	
	Bursera hindsiana	4	
	Bursera microphylla	6	
	Calliandra californica	15	
	Celtis pallida	1	
	Cordia curassavica	3	
	Coulterella capitata	9	
	Croton californicus	3	
	Cylindropuntia alcahes	7	
	Cylindropuntia cholla	9	
	Ditaxis lanceolata	1	
	Encelia farinosa	11	
	Eucnide aurea	6	
	Eucnide cordata	5	
	Euphorbia misera	3	
	Ficus palmeri	3	
	Gossypium davidsonii	14	
	Heliotropum curassavicum	7	
	Hoffmeisteria fasciculata	9	
	Hyptis emoryi	17	
	Jacquemontia abutiloides	11	
	Jacquemontia eastwoodiana	17	
	Jatropha cuneata	2	
	Lophocereus schottii	5	
	Mammillaria albicans	7	
	Mammillaria dioica	13	
	Mardsenia sp. **	1	

Tabla 3 (cont.). Tabla compuesta para las 10 especies de reptiles encontradas durante este estudio, con las especies de plantas que consumieron, el número de veces que se observó que cada especie de reptil comía cada especie de planta y las islas donde se realizaron las observaciones combinadas.

Table 3 (cont.). Composite table for the 10 reptile species found during this study, with the plant species they consumed, the number of times each reptile species was observed eating each plant species, and the islands where the combined observations were made.

Reptile species	Consumed plant species	No. of times seen eating the plant	Islands
S. ater	*Melochia tomentosa*	15	Espíritu Santo, San Francisco, San José, Danzante, Península, San Marcos, Tiburón
	Merremia aurea	6	
	Opuntia tapona	6	
	Pachycereus pringlei	21	
	Parkinsonia praecox	2	
	Passiflora palmeri	14	
	Perityle aurea	11	
	Perityle californica	25	
	Ruellia californica	14	
	Simondsia chinensis	4	
	Stenocereus gummosus	4	
	Stenotis mucronata	16	
	Trixis californica	17	
Dipsosaurus dorsalis	*Pachycereus pringlei*	18	Ángel de la Guarda, Carmen, San Marcos, San José, Espíritu Santo
	Simmondsia chinensis	2	
D. catalinensis	*Ferocactus diguetii var. diguetti*	7	Santa Catalina
	Pachycereus pringlei	9	
Petrosaurus thalassinus	*Ficus palmeri*	3	Espíritu Santo
	Pachycereus pringlei	5	

* Records from Velarde et al. (2008); Cerdá and Langarica (2018), and feces collection (Cerdá, unpubl. data).

* * Plant species identification uncertain.

(occupying naturally at least 14 islands; Grismer, 2002), repeated the consumption of plants species on different islands: nine plant species were consumed in series of two out of six islands, and 4 plant species were consumed in series of three out of six islands; the remaining 32 plant species were consumed on only one of the six single, different islands. These 59 plant species belong to 19 families arranged in alphabetical order in Table 4. All were Eudicots (Rebman & Roberts, 2012). Table 4 indicates the families represented in the 711 observations, the list of plant species per family, and the total number of species per family. Asteraceae is the best represented, with 12 species, followed by 11 species of the Cactaceae, and then Fabaceae (seven) and Euphorbiaceae (five).

This is not surprising as the sunflowers and daisies, either as annuals or perennials, can be abundant in most islands, especially after the winter rains, and produce numerous flowers and leaves (*pers. obs*.). Also, the Cactaceae, with 105 species in the area (Rebman and Roberts, 2012), can be abundant and more important than other type of plants.

Tabla 4. Especies de plantas consumidas por reptiles, ordenadas por familia.

Table 4. Plant species consumed by reptiles, arranged by family.

Family	Species	Number of plant species per family
ACANTHACEAE	*Ruellia californica*	1
AMARANTHACEAE	*Amarathus fimbriatus*	4
	Atriplex sp.	
	Suaeda niigra	
APOCYNACEAE	*Mardsenia sp.*	1
ASTERACEAE	*Amauria rotundifolia*	12
	Ambrosia ambrosioides	
	Ambrosia dumosa	
	Bacharis salicifolia	
	Bajacalia crassiflora	
	Bebbia juncea	
	Coulterella capitata	
	Encelia farinosa	
	Hoffmeisteria fasciculata	
	Perityle aurea	
	Perityle californica	
	Trixis californica	
BORAGINACEAE	*Cordia curassavica*	2
	Heliotropum curassavicum	
BURSERACEAE	*Bursera hindsiana*	2
	Bursera microphylla	
CACTACEAE	*Cylindropuntia alcahes*	11
	Cylindropuntia cholla	

Tabla 4 (cont.). Especies de plantas consumidas por reptiles, ordenadas por familia.
Table 4 (cont.). Plant species consumed by reptiles, arranged by family.

Family	Species	Number of plant species per family
CACTACEAE	*Echinocereus grandis*	11
	Ferocactus diguetii var. diguetti	
	Lophocereus schottii	
	Mammillaria albicans	
	Mammillaria dioica	
	Opuntia tapona	
	Pachycereus pringlei	
	Stenocereus gummosus	
	Stenocereus thurberi	
CANNABACEAE	*Celtis pallida*	1
CONVOLVULACEAE	*Cressa truxilliensis*	4
	Jacquemontia abutiloides	
	Jacquemontia eastwoodiana	
	Merremia aurea	
EUPHORBIACEAE	*Croton californicus*	5
	Ditaxis lanceolata	
	Euphorbia misera	
	Euphorbia polycarpa	
	Jatropha cuneata	
FABACEAE	*Acacia goldmanii*	7
	Calliandra californica	
	Lysiloma candidum	
	Olneya tesota	
	Parkinsonia microphylla	
	Parkinsonia praecox	
	Pithecellobium confine	
LAMIACEAE	*Hyptis emoryi*	1
LOASACEAE	*Eucnide aurea*	2
	Eucnide cordata	
MALVACEAE	*Gossypium davidsonii*	2
	Melochia tomentosa	
MORACEAE	*Ficus palmeri*	1
PASSIFLORACEAE	*Passiflora palmeri*	1
POLYGONACEAE	*Antigonon leptopus*	1
RUBIACEAE	*Stenotis mucronata*	1
SIMMONDSIACEAE	*Simmondsia chinensis*	1

Table 5 resumes the 10 reptile species with the total number of plant species consumed by each reptile species, and the families that the plants belong to. It is possible to observe that *S. ater* consumed 47 plants, representative of all the 19 families recorded, becoming the more varied diet of all the reptile species analyzed; and *S. klaubery* consumed 15 representatives of eight families. The remnant reptiles consumed two to five representatives of as much as four families, mostly of two, and *Dipsosaurus catalinensis* consumed only two plant species of one family (Cactaceae).

Tabla 5. Resumen de especies y familias de plantas consumidas por las 10 especies de reptiles.
Table 5. Summary of plant species and families consumed by the 10 reptile species.

Reptile species	Number of plant species consumed	Number of plant species per family
Ctenosaura conspicuosa	5	2
C. hemilopha	2	2
Sauromalus varius	4	2
S. hispidus	5	4
S. slevini	2	2
S. klauberi	15	8
S. ater	47	19
Dipsosaurus dorsalis	2	2
D. catalinensis	2	1
Petrosaurus thalassinus	2	2

Table 6 presents the number of single observations per plant, their relative frequency of occurrence, the number of reptile species feeding on them, and the individual reptile species that feed on each plant. As can be seen, *Pachycereus pringlei* was the most consumed plant, with 168 observations (frequency, f = 0.236), followed by *Hyptis emoryi* with 36 observations (f = 0.051), and six plant species with 23 to 27 records and f = 0.032 to 0.038. Also, 13 plant species were recorded between 11 and 19 times, with f = 0.015 to 0.025; and 37 species had less than 10 observations (1-9), and frequencies below 0.015 (= 1.5 % representation in the total sample of N = 711). In Table 6, *Pachycereus pringlei*, the elephant cactus or cardon, is consumed by all 10 reptile species, followed by *Stenocereus gummosus* (galloping cactus), consumed by four species, and *Lysiloma candidum* (Palo Blanco) and *Simmondsia chinensis* (Jojoba), both consumed by four reptile species. The other 55 plants are consumed by one or two lizard species. This table shows the relevance of the cardon and other seven plant species (with 18 to 36 records) as a source of food.

Tabla 6. Disposición jerárquica de plantas por número de veces que fueron consumidas (en orden decreciente), más frecuencia de consumo, número de especies de reptiles que consumieron cada especie de planta y especies de lagarto que consumieron cada especie de planta.

Table 6. Hierarchical arrangement of plants by number of times they were consumed (in decreasing order), plus frequency of consumption, number of reptile species that consumed each plant species, and lizard species that consumed each plant species.

	Plant species	Number of times observed being consumed	Frequency	Number of reptile species consuming the plant	Reptile species consuming the plant
1	*Pachycereus pringlei*	168	0.236	10	All 10 species
2	*Hyptis emoryi*	36	0.051	2	*S. ater, S. klauberi*
3	*Ruellia californica*	27	0.038	2	*S. ater, S. klauberi*
4	*Perityle californica*	25	0.035	1	*S. ater*
5	*Ferocactus diguetii var. diguetti*	25	0.035	2	*S. klauberi, D. dorsalis*
6	*Stenocereus gummosus*	23	0.032	4	*C. conspicuosa, S. ater, S. klauberi, S. varius*
7	*Melochia tomentosa*	23	0.032	2	*S. ater, S. klauberi*
8	*Encelia farinosa*	23	0.032	2	*S. ater, S. hispidus*
9	*Lysiloma candidum*	18	0.025	3	*C. conspicuosa, C. hemilopha, S. klauberi*
10	*Gossypium davidsonii*	18	0.025	2	*S. ater, S. klauberi*
11	*Trixis californica*	17	0.024	1	*S. ater*
12	*Jacquemontia eastwoodiana*	17	0.024	1	*S. ater*
13	*Bebbia juncea*	17	0.024	1	*S. ater*
14	*Stenotis mucronata*	16	0.022	1	*S. ater*
15	*Calliandra californica*	15	0.021	1	*S. ater*
16	*Passiflora palmeri*	14	0.020	1	*S. ater*
17	*Mammillaria dioica*	13	0.018	1	*S. ater*
18	*Amarathus fimbriatus*	12	0.017	1	*S. ater*
19	*Perityle aurea*	11	0.015	1	*S. ater*
20	*Jacquemontia abutiloides*	11	0.015	1	*S. ater*
21	*Bajacalia crassiflora*	11	0.015	1	*S. ater*
22	*Simmondsia chinensis*	9	0.013	3	*S. ater, S. klauberi, D. dorsalis*
23	*Hoffmeisteria fasciculata*	9	0.013	1	*S. ater*
24	*Cylindropuntia cholla*	9	0.013	1	*S. ater*
25	*Coulterella capitata*	9	0.013	1	*S. ater*
26	*Olneya tesota*	8	0.011	1	*C. conspicuosa*
27	*Bursera microphylla*	8	0.011	2	*S. ater, S. klauberi*
28	*Mammillaria albicans*	7	0.010	1	*S. ater*
29	*Heliotropum curassavicum*	7	0.010	1	*S. ater*
30	*Cylindropuntia alcahes*	7	0.010	1	*S. ater*
31	*Bursera hindsiana*	7	0.010	2	*S. ater, S. klauberi*

Tabla 6 (cont.). Disposición jerárquica de plantas por número de veces que fueron consumidas (en orden decreciente), más frecuencia de consumo, número de especies de reptiles que consumieron cada especie de planta y especies de lagarto que consumieron cada especie de planta.

Table 6 (cont.). Hierarchical arrangement of plants by number of times they were consumed (in decreasing order), plus frequency of consumption, number of reptile species that consumed each plant species, and lizard species that consumed each plant species.

	Plant species	Number of times observed being consumed	Frequency	Number of reptile species consuming the plant	Reptile species consuming the plant
32	*Opuntia tapona*	6	0.008	1	*S. ater*
33	*Merremia aurea*	6	0.008	1	*S. ater*
34	*Ficus palmeri*	6	0.008	2	*S. ater, P. thalassinus*
35	*Eucnide aurea*	6	0.008	1	*S. ater*
36	*Bacharis salicifolia*	6	0.008	1	*S. ater*
37	*Lophocereus schottii*	5	0.007	1	*S. ater*
38	*Eucnide cordata*	5	0.007	1	*S. ater*
39	*Atriplex sp.*	5	0.007	2	*S. ater, S. hispidus*
40	*Antigonon leptopus*	5	0.007	1	*S. ater*
41	*Stenocereus thurberi*	4	0.006	2	*C. conspicuosa, S. klauberi*
42	*Amauria rotundifolia*	4	0.006	1	*S. slevini*
43	*Ambrosia ambrosioides*	3	0.004	1	*S. varius*
44	*Pithecellobium confine*	3	0.004	1	*S. klauberi*
45	*Euphorbia polycarpa*	3	0.004	1	*S. klauberi*
46	*Euphorbia misera*	3	0.004	1	*S. ater*
47	*Croton californicus*	3	0.004	1	*S. ater*
48	*Cordia curassavica*	3	0.004	1	*S. ater*
49	*Suaeda nigra*	2	0.003	1	*S. hispidus*
50	*Parkinsonia praecox*	2	0.003	1	*S. ater*
51	*Jatropha cuneata*	2	0.003	1	*S. ater*
52	*Echinocereus grandis*	2	0.003	1	*S. varius*
53	*Ambrosia dumosa*	2	0.003	1	*S. ater*
54	*Mardsenia sp.*	1	0.001	1	*S. ater*
55	*Celtis pallida*	1	0.001	1	*S. ater*
56	*Parkinsonia microphylla*	1	0.001	1	*S. klauberi*
57	*Ditaxis lanceolata*	1	0.001	1	*S. ater*
58	*Acacia goldmanii*	1	0.001	1	*S. ater*
59	*Cressa truxilliensis*	N/A		1	*S. hispidus*
	Total frequency		**1.0**		
	Total observations	**711**			

Tabla 7. Especies de plantas por familia consumidas por cada especie de reptil. **/ Table 7.** Plant species per family consumed by each reptile species.

Reptile species	Plant Family	Number of plants species per family consumed by each reptile species
Ctenosaura conspicuosa	Cactaceae	3
	Fabaceae	2
C. hemilopha	Cactaceae	1
	Fabaceae	1
Sauromalus varius	Asteraceae	1
	Cactaceae	3
S. hispidus	Amaranthaceae	2
	Asteraceae	1
	Cactaceae	1
	Convolvulaceae)	1
S. slevini	Asteraceae	1
	Cactaceae	1
S. klauberi	Acanthaceae	1
	Burseraceae	2
	Cactaceae	4
	Euphorbiaceae	1
	Fabaceae	3
	Lamiaceae	1
	Malvaceae	2
	Simmondsiaceae	1
S. ater	Acanthaceae	1
	Amaranthaceae	2
	Apocynaceae	1
	Asteraceae	10
	Boraginaceae	1
	Burseraceae	2
	Cactaceae	8
	Cannabaceae	1
	Convolvulaceae	3
	Euphorbiaceae	4
	Fabaceae	2
	Lamiaceae	1
	Loasaceae	2
	Malvaceae	1
	Moraceae	2
	Passifloraceae	1
	Polygonaceae	1
	Rubiaceae	1
	Simmondsiaceae	1
Dipsosaurus dorsalis	Cactaceae	1
	Simmondsiaceae	1
D. catalinensis	Cactaceae	2
Petrosaurus thalassinus	Cactaceae	1
	Moraceae	1

Finally, Table 7 presents a combined set of the 10 reptile species with the total number of plant species that they consume per plant family. *Sauromalus ater* stands out by eating 10 species of the family Asteraceae, eight of the Cactaceae, and four of Euphorbiaceae. None of the other lizard species consumes more than three species of a family, except *S. klauberi*, who consumes as many as four species of the Cactaceae.

Feeding behavior. The endemic San Esteban Island Spiny-Tailed Iguana (*Ctenosaura conspicuosa*) has become an icon of San Esteban Island for its behavior of climbing upon the cardon cactus branches (Figs. 1a, b and c); while on top, it is a main attraction for visitors because of its beautiful, sculptured poses (Fig. 2). This behavior was first reported by Banks and Farmer (1963) on Cerralvo, and later (as "occasional") by Case (1982, 2002) and then by Grismer (2002).

In this study, I observed that this climbing tendency is very strong and common among *Ctenosaura*. I found that this species also shows a remarkable capability to climb upon the *Stenocereus thurberi* (organ pipe) and galloping cacti. Mature and juvenile individuals show this climbing behavior for feeding purposes, protection and thermoregulation.

In many cases the juveniles are expelled (but not aggressively) from the cardon by occupant or arriving adults. Thus, juveniles move down to the ground and then climb upon galloping and organ pipe cacti (Fig. 3a), iron wood (*Olneya tesota*) (Fig. 3b), and palo blanco (*Lysiloma candidum*) (Fig. 3c). As famous for visitors to San Esteban as it has been, the behavior of the spiny-tailed iguana can also be taken as a symbol or a model of the reptile-cardon mutualist interaction and seed dispersal in some islands of the Gulf of California.

Ctenosaura conspicuosa consumes five plants species of two families on San Esteban. There is also another species, *Echinocereus grandis*, an endemic little cactus, whose flowers and fruits are available in spring-summer, but I have not been able to verify directly the consumption. I observed spiny-tailed

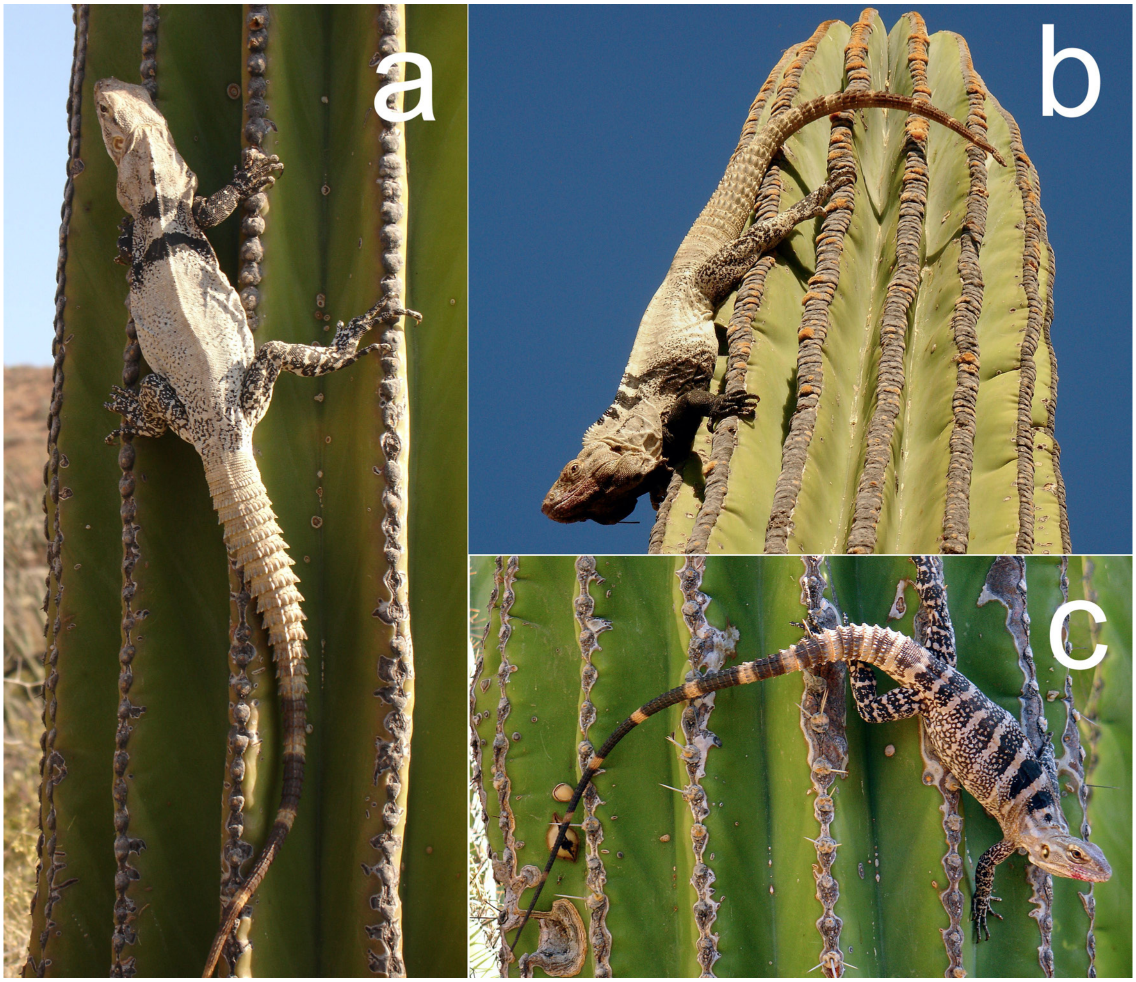

Figura 1. Son notables las capacidades escaladoras de *Ctenosaura conspicuosa*; a) hembra adulta subiendo; b) macho, descendiendo después de alimentarse; c) individuo inmaduro descendiendo después de alimentarse de los frutos del cardón.

Figure 1. The climbing capabilities of *Ctenosaura conspicuosa* are remarkable; a) adult female going up; b) male, descending after feeding; c) immature individual going down after eating on cardon fruit.

Figura 2. Los ctenosaurios de la isla San Esteban Island son icónicos, en parte por sus poses escultóricas sobre los ápices de las pencas de cardón.

Figure 2. Ctenosaurs on San Esteban Island are iconic partly for their sculptured poses on cardon tops.

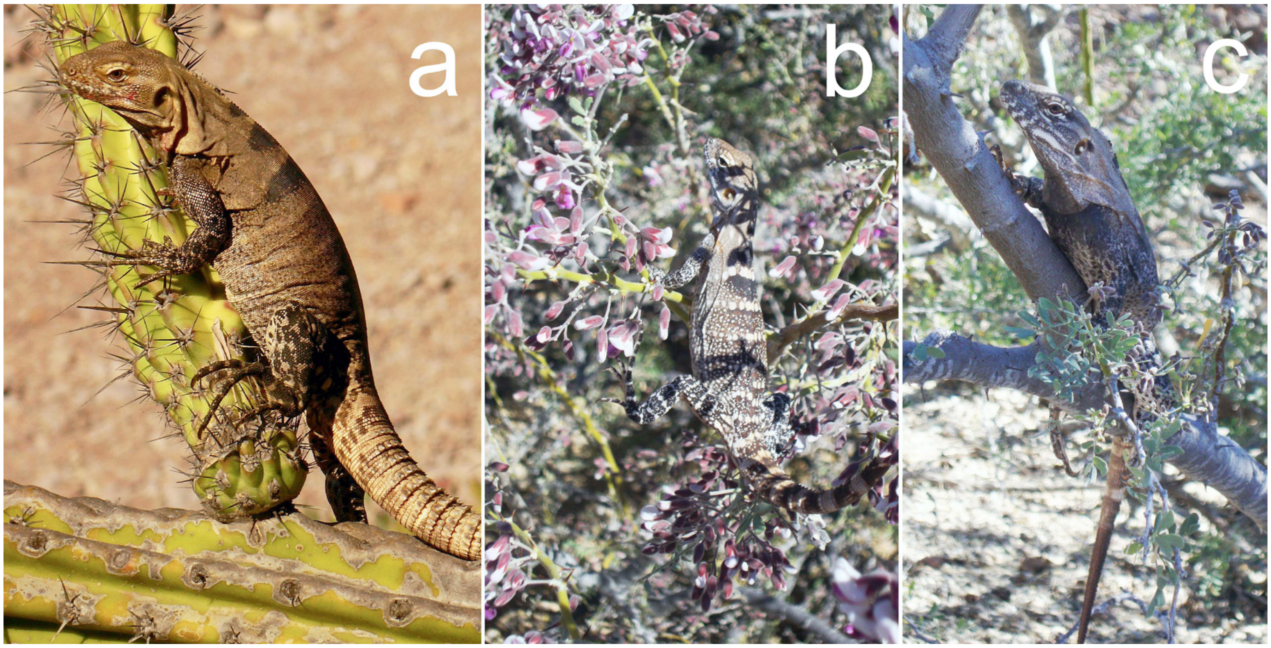

Figura 3. Usualmente, los ctenosaurios inmaduros se alimentan de diversas plantas, aunque los adultos también lo hacen; a) juvenil sobre pitahaya agria (*Stenocereus gummosus*); b) juvenil sobre palo fierro (*Olneya tesota*); c) adulto sobre palo blanco (*Lysiloma candidum*).

Figure 3. Usually, immature ctenosaurs are found feeding on diverse plants, but adults do so too; a) juvenile on galloping cactus (*Stenocereus gummosus*); b) juvenile on ironwood (*Olneya tesota*); c) adult on palo blanco (*Lysiloma candidum*).

iguanas, or ctenosaurs, climbing upon cardon branches but, in the way up, the individuals may feed on the lowest buds (Fig. 4). They take only the upper part of these buds, rejecting the rest, but they can dislodge, accidentally, the eaten buds, or the whole ones when moving around. When ctenosaurs get to a branch top, they feed on what is present at that moment (Fig.5). If they feed on opened flowers, they mostly eat the corolla with petals and the upper portions of sexual organs (Fig. 6). Rarely, the iguanas eat the whole flower structure. If there are fruits on the cardon branch top, the iguanas feed on the ripened ones, whose abundant pulp is crimson-colored. The evidence that they have been feeding on pulp is the color around the mouths of adults and juvenile iguanas (Fig. 7a), as with other lizard species (e.g. *Sauromalus klauberi* in Fig. 7b, and *S. slevini*, in Fig. 7c). A still undetermined number of flowers and fruits are dislodged in these ways and provide valuable food for juvenile iguanas and, importantly, for chuckwallas, which are not strict climbers.

Once satisfied, the iguanas remain on the tops for as long as 30 minutes, or they jump to another branch to seek more food (Fig. 8). When feeding on fruits and flowers, the iguanas may inadvertently consume some of the insects present into those structures as well, especially *Drosophila* flies, wasps and bees, ingesting additional protein. The carnivorous habit of *C. conspicuosa* also has been recorded, especially the consumption of hatchlings and juveniles of the sympatric, gigantic chuckwalla (Case, 2002). Thus, the role of the iguana goes beyond a simple herbivory to a more complex trophic level.

Also endemic to San Esteban, the Piebald Chuckwalla (*Sauromalus varius*) (Fig. 9a) is not a climber but a ground and saxicolous lizard (Grismer, 2002). This is the largest of all chuckwalla species (Case, 1982; Hollingsworth, 2004) and is highly conspicuous for its yellow to orange and black coloration and its habit of seeking shelter under cholla cacti. *Sauromalus varius* benefits directly from cardon flowers and fruits either dislodged by iguanas or falling naturally, and feeds on leaves, flowers and fruits of other plant species (Case, 2002; Grismer, 2002). I have observed this species feeding on four plant species: leaves and flowers of canyon ragweed (*Ambrosia ambrosioides*),

Figura 4. En su camino a los ápices de los cardones, y en su descenso, los ctenosaurios se detienen a alimentarse de botones y flores bajos, de los que sólo comen las corolas, pero a veces pueden desprender las estructuras que serán consumidas por los organismos terrestres.

Figure 4. On their way up a cardon, and going down too, the ctenosaurs stop to feed on the lowest buds and flowers from which they only take the corolla and doing so they may dislodge some that eventually are eaten by ground organisms.

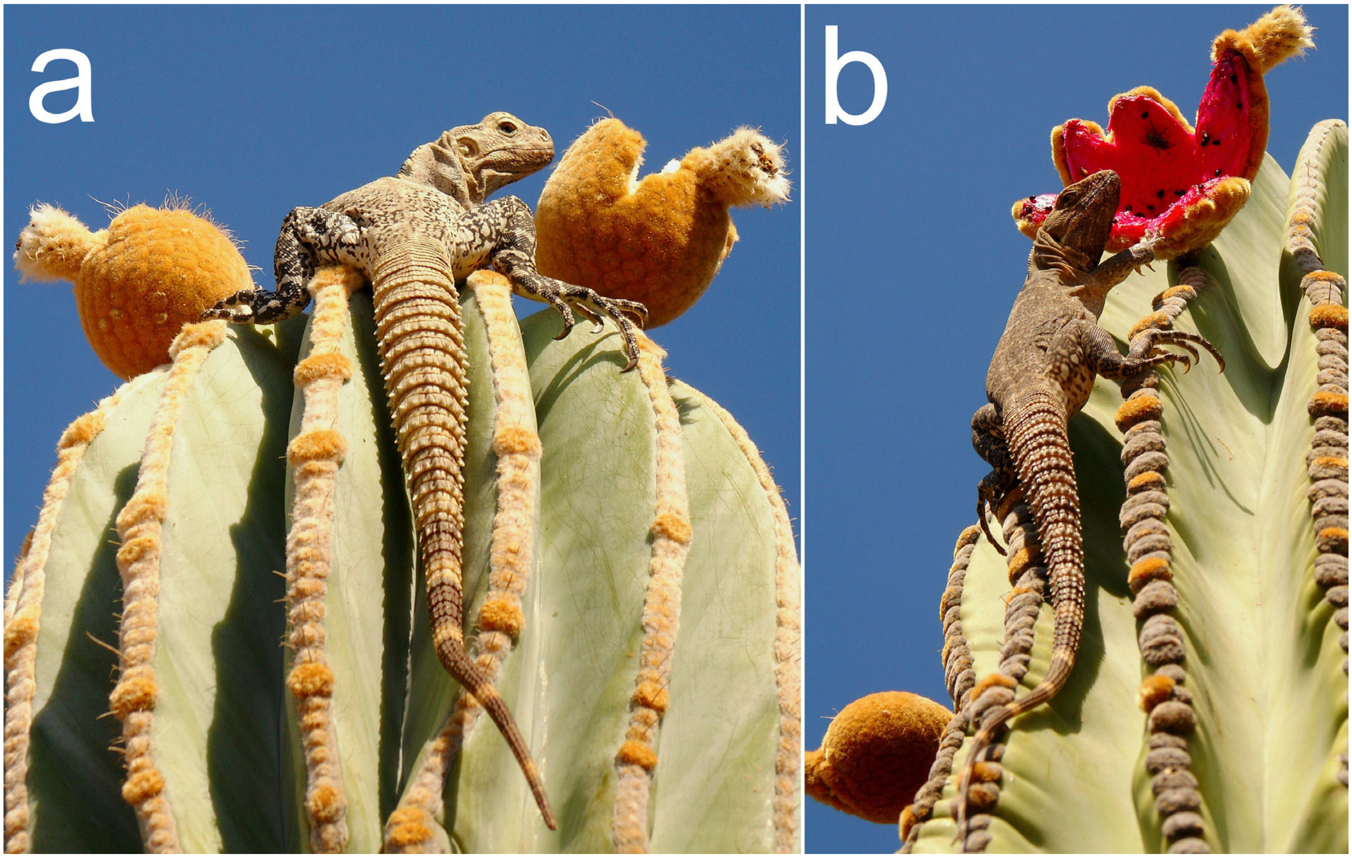

Figura 5. Iguanas de cualquier edad y sexos escalas los cardones para comer lo que está disponible al momento; a) juvenile listo para comer la pulpa de un fruto maduro y abierto; b) un pequeño juvenil ha comido casi toda la pulpa del fruto.

Figure 5. Iguanas of all ages and sexes climb cardon cacti to feed on what is available there; a) a juvenile ready to feed on a ripe fruit; b) a young juvenile has taken almost all the pulp from the cardon fruit.

flowers and fruits of the endemic San Esteban hedgehog cactus (*Echinocereus grandis*), which is small and within the reach of chuckwallas, and flowers and fruits from cardon and galloping cacti. Due to the presence of carotenoids in the fruit's pulp, a typical crimson coloration is also present in the chuckwalla's mouth.

This chuckwalla does not show aggressive behavior while feeding, neither towards their congeners nor towards iguanas. This tolerance contrasts with the behavior of *S. klauberi*, as will be described later. I have seen young *S. varius* as well as large adults (Fig. 9b) on the upper stems of densely stemmed cacti, behavior reported before (Case, 1982, 2002; Grismer, 2002).

Figura 6. Iguana adulta; a) ha mordido la corolla de una flor; b) deglutiendo la corola.

Figure 6. Adult iguana; a) it has bitten the corolla of a flower; b) swallowing the corolla.

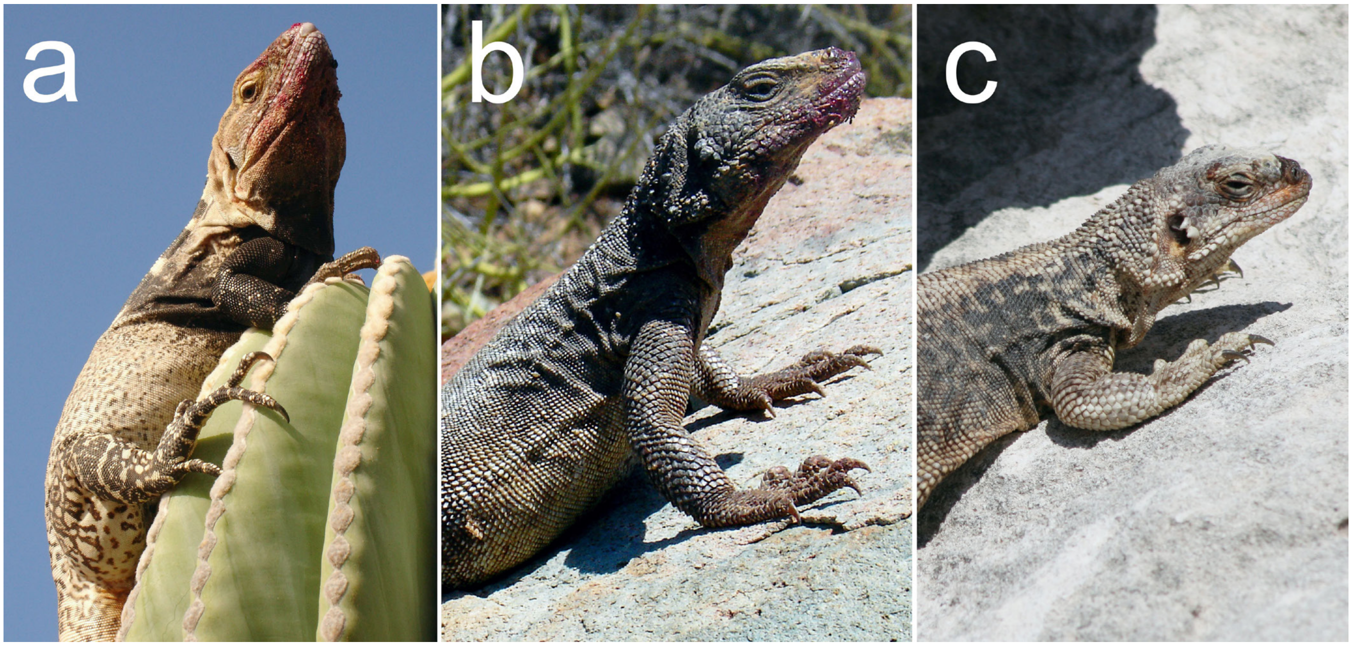

Figura 7. Después de comer la pulpa de un fruto, un color carmesí tiñe las escamas de la boca de los saurios; a) *Ctenosaura conspicuosa*; b) *Sauromalus klauberi*; c) *Sauromalus slevini*.

Figure 7. After eating the fruit's pulp, a crimson coloration remains on the scales around the mouth of lizards; a) *Ctenosaura conspicuosa*; b) *Sauromalus klauberi*; c) *Sauromalus slevini.*

Figura 8. Si las iguanas no obtienen suficiente comida en una rama de cardón, saltan a otra, haciendo que su comportamiento sea aún más llamativo. Foto: Carlos Navarro.

Figure 8. If the iguanas do not get enough food on a cardon branch, they jump to another, making their behavior even more attractive. Photo: Carlos Navarro.

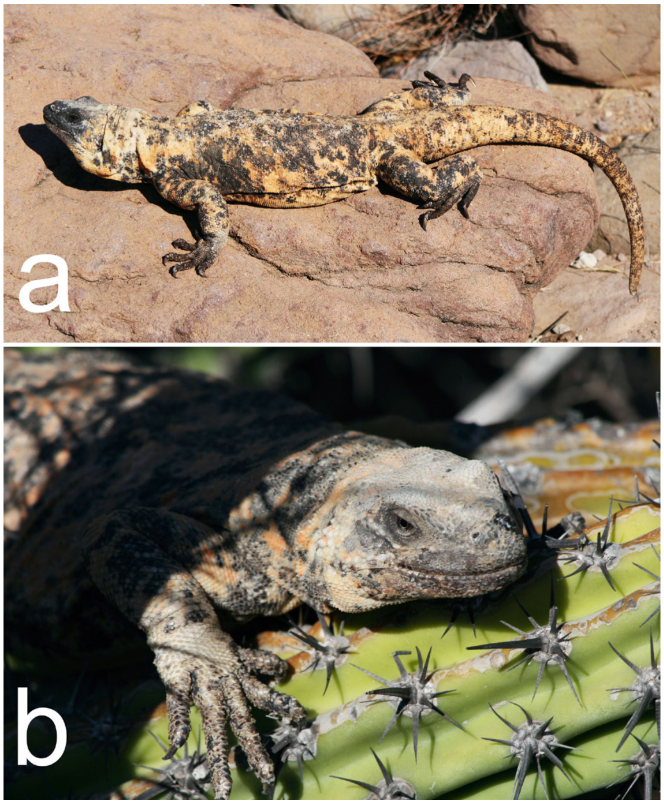

Figura 9. *Sauromalus varius* de la isla San Esteban Island es la especie más grande del género; a) es, básicamente, de hábitos terrestres; b) algunos individuos, en este caso un adulto, pueden ser vistos perchados en pitahayas agrias y otras cactáceas con el propósito de alimentarse.

Figure 9. *Sauromalus varius* of San Esteban Island is the largest of all chuckwalla species; a) it is, basically, a ground dweller; b) some individuals, in this case an adult, can be seen perched on galloping and other cacti for feeding purposes.

I have recorded the black chuckwalla (*Sauromalus hispidus*) (Fig. 10a) more often on Ángel de la Guarda island, especially in the northern part (called Puerto Alcatraz), where *P. pringlei* is moderately abundant. My views of *S. hispidus* (both adults and juveniles) are while feeding on cardon fallen products and eating saltbush (*Atriplex* sp.) and flowers of brittlebush (*Encelia farinosa*) and *Suaeda nigra*, in which they tend to climb upon (Fig. 10b). On Rasa island, where the species never existed but has been reported recently (Velarde et al., 2008; Reynoso et al., 2017; Cerdá & Langarica, 2018), the single extant individual feeds on alkali weed (*Cressa truxilliensis*), which abounds in a small patch of the Tapete Verde Valley. In San Lorenzo Sur my records represent the feeding on cardon fruits only.

The Slevin's Chuckwalla (*S. slevini*) is inhabitant of Carmen, Monserrat and Coronado islands (Fig. 11a) and feeds on leaves and flowers of different perennial and annual shrubs and bushes on the three islands, but unfortunately, I was able to identify only the Baja California Rock Daisy, *Amauria rotundifolia* and the cardon flowers and fruits on the ground, so I provide only six feeding records. This species has a strong tendency to climb upon bushes and small cacti and trees, regardless of its saxicolous habit (Fig. 11b and c), and also can be gregarious.

The Santa Catalina island holds the one-island endemic Santa Catalina Island Chuckwalla (*Sauromalus klauberi*) (Fig. 12a), for which I have records of feeding on fallen cardon buds, flowers and fruits (Fig.12b), as well as on leaves, flowers and fruits of the plants listed in Table 3, for a total of 15 plant species in eight families. The special fact, not previously reported, was the observation of feeding on fallen flowers and fruits of the endemic Santa Catalina Barrel Cactus (*Ferocactus diguetii* var. *diguetii*), that ravens or other organisms may accidentally dislodge from this up-to-four-meters high cactus, or may fall naturally.

The chuckwallas can also reach fruits by climbing on the smaller cacti (from 0.70 m to 2.60 m) *Stenocereus gumossus* and *S. thurberi*. *Sauromalus klauberi* has a strong tendency to climb upon bushes too, and I recorded their efforts to climb upon the cardon cactus (Fig. 12c). This is the only chuckwalla species from which I have seen agonistic behavior towards congeners in association to the feeding of cardon structures on the ground (Fig. 12b), behavior not previously reported by other researchers: when an adult finds a good spot with buds, flowers and/or fruits, it chases away other individuals, either adults or juveniles, that may come close. The aggressive chase is short in distance (1-4 m maximum) and in time (few seconds). Then, the individual concentrates itself in a fast feeding event, being always alert. This species seems to be more solitary than the others, for all records made on Santa Catalina Island by the author are of single individuals, and never have seen it sharing a rock or a crack like in other species.

For *Sauromalus ater* (Fig. 13a), *Dipsosaurus dorsalis* (Fig. 13b) and *D. catalinensis* (Fig. 13c) my records showed a strong tendency for arboreal feeding on the different islands they inhabit, apart from the ground foraging. For *Petrosaurus thalassinus* (Fig. 13d) I recorded individuals feeding on several unidentified plants plus flowers and fruit of cardon and figs of *Ficus palmeri* (that usually grows on the boulders the lizards use as home and territory).

DISCUSSION

Plants consumed. To my knowledge, this report constitutes to date the only first-hand, totally field-based and non-invasive, extant list on the dietary habits of 10 lizard species on islands

Figura 10. a) Un adulto de *Sauromalus hispidus* de la isla Ángel de la Guarda; b) *Sauromalus hispidus* sobre un arbusto.

Figure 10. a) An adult *Sauromalus hispidus* from Angel de la Guarda Island; b) *Sauromalus hispidus* upon a bush.

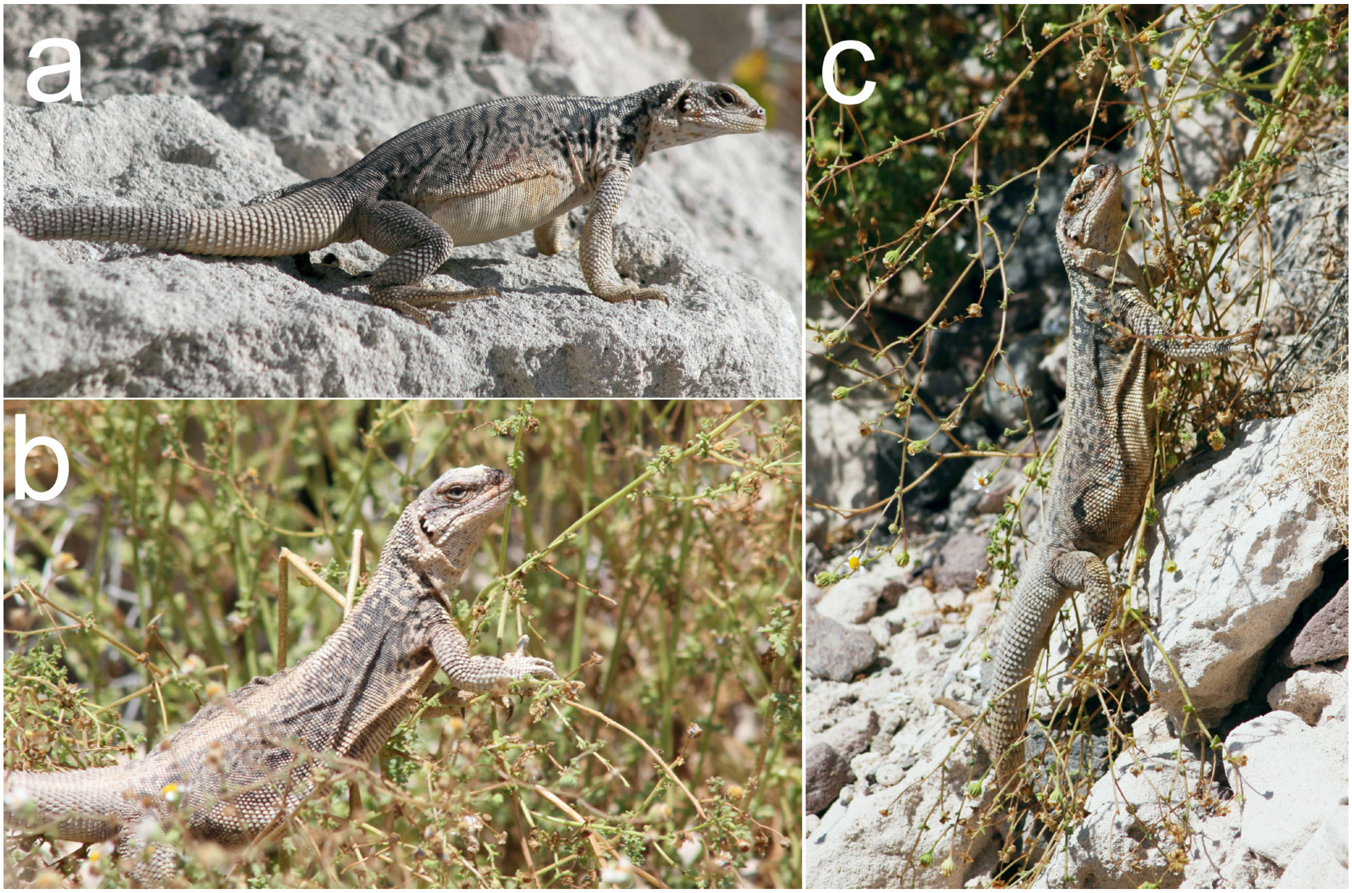

Figura 11. *Sauromalus slevini* de la isla Carmen. A pesar de sus hábitos saxícolas (a) esta especie muestra una fuerte tendencia a escalar sobre los arbustos de los que se alimenta, especialmente margaritas (b y c).

Figure 11. *Sauromalus slevini* from Carmen island. Despite its saxicolous habits (a), this species shows a strong climbing tendency upon bushes it feeds on, especially daisies (b and c).

of the Gulf of California observed directly. Certainly, this is not a finite list; with time, more plant species will be added up. For example, there is a great number of plants that, because of time constraints and my own lack of professional training in botanical taxonomy, I was unable to identify, but may account for several dozen more species to be included in this list; or the new records I obtained in the winter 2019-2020 (which was extremely wet due to summer storms and winter rains) that are not included here but may account for other 10 to 15 plant species, mainly Asteraceae (both annuals and perennials), that were extremely abundant and flowering on islands and the peninsula of Baja California.

For the plant diversity, Table 2 summarizes the number of species that have been recorded in the 15 islands I visited (from Cody et al., 2002). Reptiles have much more options for feeding in the medium-to-large islands, so my contribution here is just a minimal part of what can be expected. As an example, in San Esteban island a total of 123 plants have been recorded; I only report seven species (5.7%) being consumed by *C. conspicuosa* and *S. varius*. On Santa Catalina Island, of a total of 122 plants recorded, 15 species (12.3%) are reported here to be consumed by *S. klauberi* and *D. catalinensis*. For an estimate of 3000 to 4000 plant species for the peninsula and adjacent islands (Rebman & Roberts, 2012), the 59 plants recorded in this study account for only 1.5 to 2%. And for the 649 plant species reported solely for the gulf islands by Cody et al. (2002), my list accounts for a 9% plant species consumed by 10 lizard species. Taking into consideration all my unidentified plant species, and the new records from the winter 2019-2020, I estimate that the herbivorous and omnivorous lizards could eat a minimum of 20 to 30 % of the 649 plant species reported on islands.

Figura 12. a) El cachorón de roca *Sauromalus klauberi* de isla Santa Catalina, y de hábitos saxícolas, muestra una gran preferencia a ser solitario. b) *Sauromalus klauberi* alimentándose de un fruto de cardón en el suelo, situación en la que los individuos muestran comportamiento agresivo hacia sus congéneres. c) Algunos cachorones de Santa Catalina a veces tratan de subir sobre un cardón; a veces son exitosos, otras veces fracasan.

Figure 12. a) The saxicolous chuckwalla *Sauromalus klauberi* from Santa Catalina Island, shows a strong tendency to be solitary. b) *Sauromalus klauberi* feeding on a fallen cardon fruit on the ground, situation in which individuals show aggressive behavior towards congeners. c) Chuckwallas from Santa Catalina Island sometimes try to climb upon cardon cacti; sometimes they are successful, sometimes they are not.

Feeding behavior. The strong climbing tendency detected in chuckwallas must be emphasized. All the species of *Sauromalus* described in this report, at least in the juvenile stage, have been observed climbing upon small bushes and even small trees and cacti. In most circumstances, the animals stand up on their hind limbs to reach leaves, flowers and fruits, climbing upon most plants. Medium-sized *Sauromalus varius* and *S. hispidus* have been seen perched on branches of galloping cacti at more than 1.5 m from the ground. *S. klauberi* has shown a peculiar and strong tendency to climb upon cardon. I have seen its efforts repeatedly in Santa Catalina (Fig. 12c). Not all individuals doing this could climb at all, although many were successful, by holding the cardon's cuticle with their claws. The other chuckwalla species climb a lot too. *Dipsosaurus* species do not hesitate in climbing bushes in order to get food as well (Fig. 13b).

Therefore, climbing by lizards is only one of their many amazing adaptations to the harsh, insular environments of the gulf, and may have important evolutionary implications. Just like what has happened to some reptile species (e.g. insular chuckwallas) in terms of body change (i.e. gigantism, dwarfism [Case, 1976, 1978, 1982, 2002; Tracy, 2004]), to plants (habit

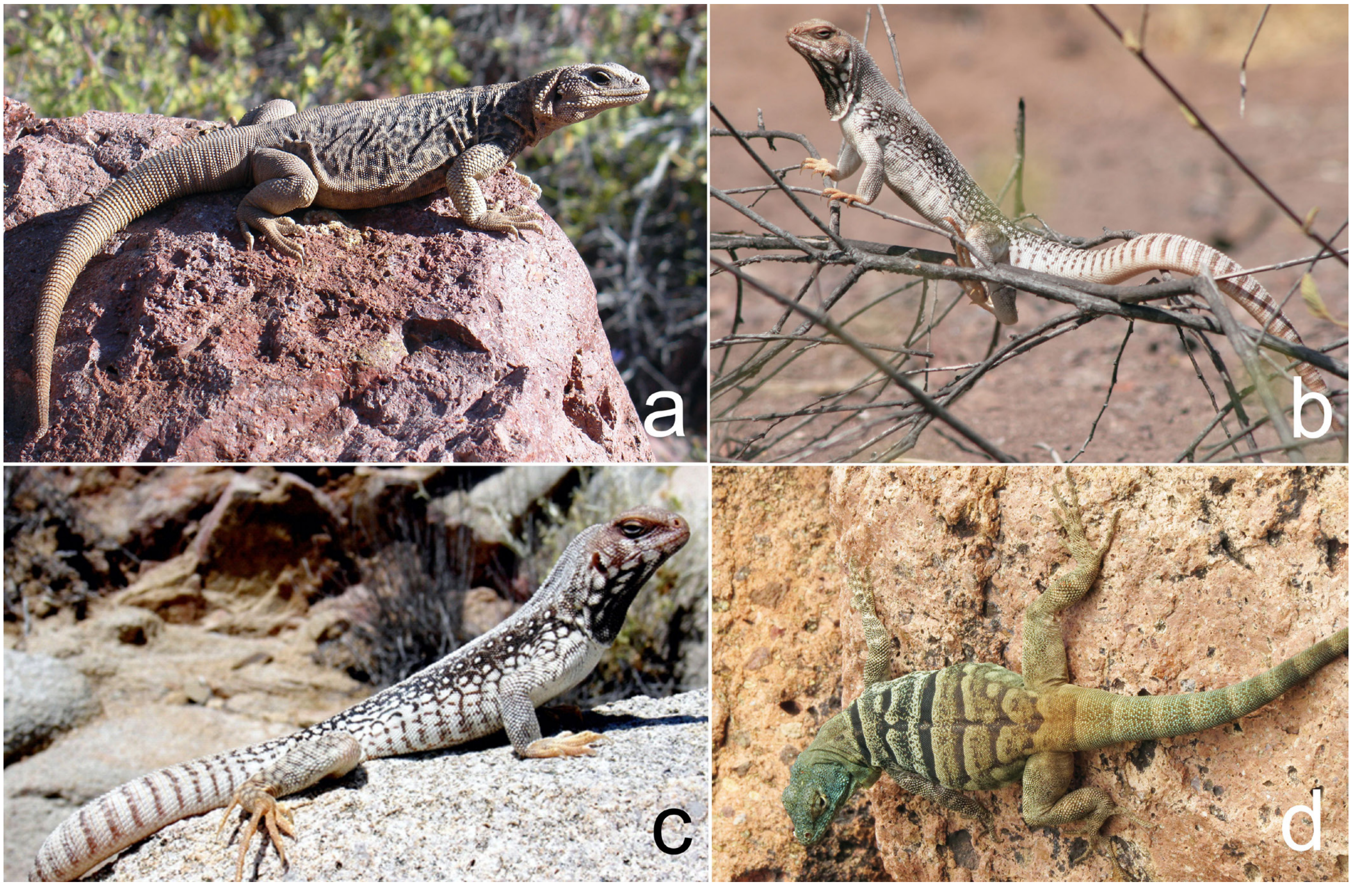

Figura 13. a) *Sauramalus ater*, isla Danzante; b) *Dipsosaurus dorsalis*, isla Carmen; c) *D. catalinensis*, isla Santa Catalina; y d) *Petrosaurus thalassinus* de la isla Espiritu Santo.

Figure 13. a) *Sauramalus ater*, Danzante island; b) *Dipsosaurus dorsalis*, Carmen Island; c) *D. catalinensis*, Santa Catalina Island; and d) *Petrosaurus thalassinus* from Espiritu Santo Island.

change, i.e. bush to tree, woodiness [Carlquist, 1965, 1974]), to tortoises (gigantism [Carlquist, 1965, 1974]), beak shape and size in Darwin's finches (Grant, 1986), changes in mammalian body size and shape on Mediterranean islands (Van der Geer et al., 2010), or change from terrestrial to aquatic as a secondarily adaptation in Mexican box terrapin (Pritchard, 1979), I hypothesize that insular chuckwallas as well as desert iguanas (*Dipsosaurus*) have a tendency to climb because they are passing through a process of shifting from terrestrial to partially arboreal habit as a secondarily adaptation (or a new one) for exploitation of a new ecological space through habitat partitioning that may explain too their high densities.

Habitat partitioning has been demonstrated to be a driver of population densities on small and isolated islands by 'density compensation' (Case, 1975, 1983), a result of the depressed number of predator and competing species that lead to ecological release and increased population densities (MacArthur & Wilson, 1967; Buckley & Jetz, 2007). Density compensation is a general and global phenomenon: it has been found that, on average, lizards on islands have population densities that are over an order of magnitude higher than on the mainland ($N_{island} \approx 10^{1.31\pm0.08}$; Buckley & Jetz, 2007). Lizards may have an exceptional potential to reach high densities following predator and competitor release due to their relative low energetic costs (up to 10 times lower than those of endotherms), and may also increase their densities by diversifying their diets (Buckley & Jetz, 2007) and by habitat partitioning.

Diversification of diets has been investigated by Olesen and Valido (2003) as well, finding that this island phenomenon occurs because island lizards reach very high densities by experiencing a lower predation risk than do those on the mainland (density compensation). Consequently, they can expand their diet to include nectar, pollen and fruit.

Olesen and Valido also stated that there are four potential reasons for why island lizards might include more floral

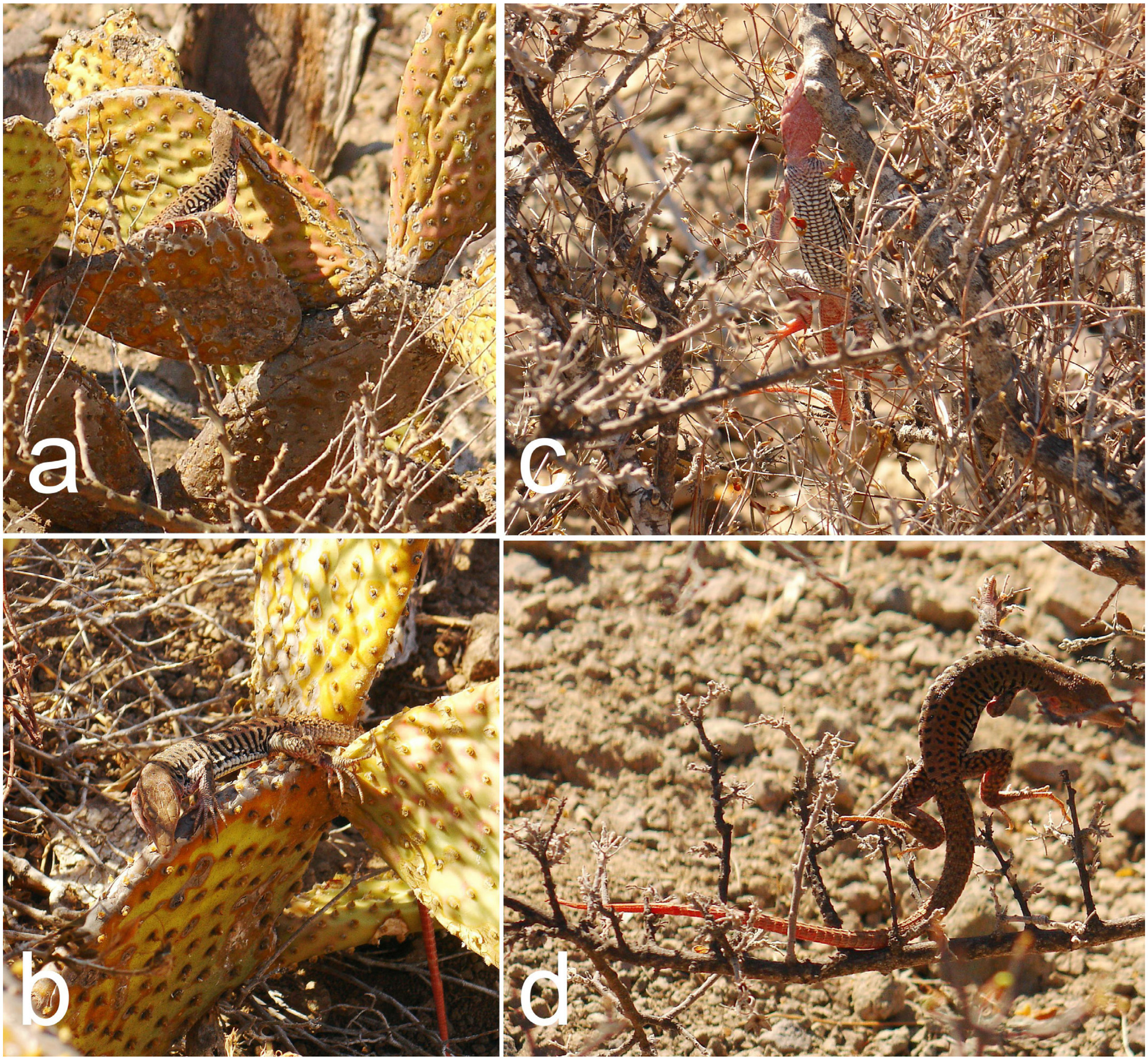

Figura 14. a-d. *Aspidoscelis rubidus*, de isla Danzante, frecuentemente se encarama sobre los arbustos y cactáceas buscando insectos y agallas de insectos. Este comportamiento incrementa sus posibilidades de encontrar alimento y expande su nicho terrestre típico hacia uno arbóreo.

Figure 14. a-d. *Aspidoscelis rubidus*, from Danzante Island, frequently climbs upon bushes and cacti while looking for insects and insect galls. This behavior increases its possibilities to find more food and expands its typical ground niche to an arboreal one.

resources and fruit into their diet compared with adjacent mainland species. Islands might have: (1) a surplus of floral food and fruit for herbivorous lizards (2) a scarcity of arthropod for insectivorous lizards; (3) larger lizards pre-adapted to a herbivorous diet; and (4) a reduced predation risk (Olesen & Valido, 2003). All these topics are still open for investigation on the gulf islands.

As an interesting example of an arboreal habit tendency in mostly ground lizards, in 2006 I observed an individual of *Aspidoscelis rubidus* on Danzante Island, climbing upon prickly pears and other plants in search of insects and insect galls (Fig. 14a-d), which is reported here for the first time. I have recorded this behavior some other times too.

Ecological implications. From literature data and the results of this study it seems clear that saurian communities on islands consume much more plant species than was known, and the niches they occupy are varied and complex, both temporarily and spatially. The plants consumed by lizards at different times of the year have different impacts on different stages of the lizards' life cycles. Some plants may be important for growing and re-gaining weight and a good health condition after the dry portion of the year, and others might be important for reptiles' reproduction, especially in the summer months (Case, 2002). Berry (1974) reported on the importance of food availability for growing of hatchlings during their first winter for *S. ater* at Lone Butte, California. Unfortunately, information about ontological parameters is still nonexistent for most insular reptiles (but see Cerdá-Ardura, 2019).

The ecological implications of the reptiles' feeding habits also go far beyond their own ontogenetic development and life cycles: I show here that their food habits have spatial, wide-range importance since they influence other populations and species, and even the whole insular community, both up (to predators) and down (to producers and primary consumers), as well as horizontally (to competitors and symbionts) for the reasons given below with one single example. Before going further, it is useful to remember that food webs are special descriptions of biological communities focusing on trophic interactions between consumers and resources, and ultimately represent transfer rates of energy and matter, thus they require tools to translate resource availability to energy supply, *i.e.* known biomass of both producers and consumers should be translated into growing and respiration rates (De Ruiter, Wolters and Moore, 2005). For insular reptiles, food webs have not been analytically constructed yet due to the lack of physiological studies.

I can exhibit the complexity of food webs in insular lizards with the single example of ctenosaurs by three observations. First, in a small, local scale, *Ctenosaura conspicuosa* of San Esteban Island feeds profusely on cardon buds, flowers and fruits on the highest branches, playing the role of a primary arboreal consumer and seed disperser in this niche that is shared with frugivorous and nectarivores birds, insects, and pollinating bats; in consequence, *C. conspicuosa* establishes horizontal, symbiotic interactions with the other animals by competition, and acts as a symbiotic seed disperser for the cardon but also altering or controlling consumption, pollination and seed dispersal rates of the plant.

Second, the ctenosaurs dislodge flowers and fruits adding biomass to ground dwellers (other reptiles species and, possibly, rodents and insects); with this, ctenosaurs partially subsidize the trophic level of the totally ground-based primary consumers in the same ecosystem but in a different niche. Subsidies of different types play an important role in general feeding ecology (sensu Huxel & McCann, 1988; Leroux & Loreau, 2008). As Barret el al. (2005) pointed out, ecosystems, even those with seemingly distinct borders, rarely function independently of other adjacent ecosystems, and ecologists are increasingly recognizing the important effects that cross-ecosystem transport of energy and nutrients have on plant and animal population, food webs and community patterns. The transport of energy and nutrients occurs from organisms that travel across ecosystem boundaries or from abiotic factors such as wind, tidal action, or watershed drainage. When materials move from a highly productive system to a relatively unproductive system, they have the greatest potential to alter plant and animal population and community dynamics.

Third, ctenosaurs are partially carnivorous of chuckwallas hatchlings and juveniles (Case, 1982, 1992), controlling at least minimally the *Sauromalus*' population recruitment and its juveniles' ecological distribution by displacing them to other niches, a consequence of predatory avoidance (i.e. to foothills). Therefore, I propose that ctenosaurs move in a tri-dimensional habitat with two functional niches: one niche represented by the ground (where they consume primary producers, and prey upon chuckwallas), and the other niche represented by the cardon, other cacti and non-cactus species (where ctenosaurs act as arboreal consumers and competitors for pollinating bats, birds and arthropods), providing important subsidies to the ground dwellers.

In turn, ctenosaurs, chuckwallas, desert iguanas and banded-rock lizards are subject to predation by raptors (i.e. red-tailed hawks, kestrels), owls, ravens, great blue herons, gulls, snakes, other lizards (e.g. the predatory genus *Gambelia*, *per. obs.*) and ring-tailed cats. For ring-tailed cats (*Bassariscus astutus sexicolus*), Sansores (2016), from 90 fecal samples in Espíritu Santo island, recorded the following reptiles as part of its diet: *Chilomeniscus punctatissimus*, *Masticophis* sp., *Aspidoscelis* sp., *Dipsosaurus dorsalis*, *Sauromalus ater*, *Sceloporus* sp., *Urosaurus nigricaudus*, and *Uta stansburiana*). Ctenosaurs do not occur on this island.

It is then not an excess to state that herbivorous and omnivorous insular lizards, as primary and secondary consumers and in some cases also predatory, are in the middle of complex food webs (*sensu* Lindeman, 1942), topology strengthened by the arboreal tendency that most of the studied species show, and the occurrence of subsidies. The arboreal habit, strong in ctenosaurs and less marked in chuckwallas, may be an expansion of their ecological and evolutionary adaptations to survive, and in this way the reptiles get involved in more complex energy transfers that exert influences on: (1) the plants' cycles by means of consumption; (2) the ecological symbiosis with plants, either as pollinators or seed dispersers, influencing their phenology and population dynamics; (3) the ecological symbioses with other organisms that share the same habitats (i.e. by competing with frugivorous bats, birds and insects, and with bird and mammalian seed dispersers; and with insectivorous bats and birds); (4) the ecosystem functioning, possibly controlling parts of it (*sensu* Paine, 1966, 1980).

Simultaneously, strict insectivorous invertebrates and vertebrates, and omnivorous lizards like *Dipsosaurus dorsalis, D. catalinensis*, and *Petrosaurus thalassinus* benefit from inputs from other ecosystems, or subsidies. Barret el al. (2005) demonstrated that materials are transferred from the ocean onto the islands and mainland coast by two mechanisms: 1) tidal activity, that washes large algal mats and marine carrion onto the beaches of the islands and mainland; and 2) seabirds, which feed exclusively in the marine system and transport marine derived nutrients onto the islands when they return to roost and nest. These nutrients may be in the form of guano, fish scraps, eggs, or bird carcasses. Marine materials have been found to subsidize insular and coastal communities including plants, detritivores beetles, rodents, spiders, and scorpions.

Barret el al. found that populations of *Uta stansburiana*, from 20 islands in the Gulf of California and coastal mainland of Mexico, benefit by consuming materials derived from the extremely productive marine system, and these food subsidies alter lizard abundance, as was derived from analyses of stable isotopes of C and N from lizard tissues to determine if lizard diets are ultimately based in the marine food web where subsidies are available (Barret el al., 2005). Polis and Hurd (1995) provided a notable example of these subsidies by marine input in relation to the extraordinary abundance of spiders on island of the Gulf of California, and Cerdá-Ardura (*in prep*.) shows the importance of marine subsidies for coyotes (*Canis latrans*) on Magdalena island.

The cardon cactus as a structural species. It has been found that, in food webs, there are few 'structural species' (Winemiller & Layman, 2005) which determine the production dynamics and ecosystem processes. In many ecosystems, according to these authors, certain plants and herbivores clearly support most of the consumers biomass, and certain consumers strongly influence biomass and production dynamics at lower levels. In many of the gulf islands, one conspicuous plant dominates the biomass of the whole land system: it is the cardon cactus. Therefore, this cactus can be considered as such.

The cardon dominates the landscape from the southern ranges in latitude 22° 54' N to 31° N on both sides of the Gulf of California to many of its islands (Medel-Narváez, 2003). The cardon possesses great symbiotic relevance (Franklin et al., 2016). For example, Delgado-Fernández et al. (2017) recorded 61 species of different taxonomic groups involved in 83 types of interactions with cardon as a source of food and shelter on the peninsula of Baja California. It is important to notice that these authors recorded only two reptile species involved in those biotic relations.

According to results in this study, the cardon is the most consumed plant by all the reptile species accounted for, at least during the flowering and fruiting seasons, with 168 observations. As a consequence of the great density of cardon, and the number of buds, flowers, fruits, pollen and nectar it produces (Fleming, 2002; Medel-Narváez, 2008), this plant constitutes one of the structural species for many herbivorous reptiles, birds, insects and mammals, including nectarivores and fruit-eaters of all sorts (*pers. obs.*).

By taking the figures provided by Fleming (2002) for this cactus (all averages: fruit mass = 78.9 g; seed mass = 52.2 mg; seeds per fruit = 1,329; flowers per season per plant = 872; fruits per season per plant = 170; seeds per season per plant = 225,930), and applying basic math to them, we can then obtain the following (all calculations mine): from a simple flower mass of 40.9 g existent in 1,329 flowers produced per season per plant, we obtain 54.3 kg of flower mass per plant per season. If we take the average 288 cardon/ha given by Medel-Narváez (2008), it results that, in a hectare, there are 15,638.4 kg of flowers available for herbivorous organisms.

Given the 170 fruits per season per plant contained in 288 ind./ha, we obtain 48,960 fruits/ha/year, or a fruit mass of 3,862.9 kg per ha/year. Thus, these 3,862.9 kilograms of fruit would theoretically be available for 1.4 to 44.3 *S. hispidus* per ha found by Case (2002), and to 8.3 to 45.4 individuals per ha of *S. varius.* In other words, for the lowest density of *S. hispidus* (1.4 indiv./ha), there would be 2,759 kg of fruit mass/year/ha per individual, and 465 kg of fruit mass/year/ha/ per individual for *S. varius* (8.3 indiv./ha); on the other hand, for the highest number of *S. hispidus* (44.3 indiv./ha), there would be 87 kg of fruit mass/year/ha per individual, and 81 kg of fruit mass/year/ha per individual of *S. varius* (45.4 indiv./ha).

This great theoretical amount of food potentially available for herbivorous lizards and for fruit flies, bees, wasps, lepidopterans, birds, bats, rodents, lagomorphs, deer and bighorn sheep, among many other, can be significantly increased by obtaining, from field data, the contributions of the other cacti and plant species. Thus, the energy that circulates from insular producers to primary consumers could be very large from an estimate of 649 species of plants reported for islands in the gulf (Cody et al., 2002). Unfortunately, for none, except cardon and cholla, biomass has been estimated in the field. The same occurs with physiological characteristics, like CO_2 consumption and conversion rates, which are necessary parameters that can be obtained either in the field or in laboratory. For some cacti, Nobel (2002) offers an excellent overview on physiological ecology of columnar cacti, and among other things, estimated a maximal rate of net CO_2 uptake of 8 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for *Stenocereus queretaroensis*, *Carnegiea gigantea* and *P. pringlei* at night, which is immediately incorporated into phosphoenolpyruvate which leads to the formation of an organic acid such as malate, and only fixed during the day into photosynthetic products such as the sugars glucose and sucrose.

Case (1982, 2002) reported that, for *Sauromalus hispidus*, population density in one locality was around 52 animals/hectare (about 1/3 were juveniles); on San Esteban was about 12.4 animals/hectare with no juveniles. The biomass maintained by the insular endemic chuckwallas was large: 20.8 kg/hectare for *S. hispidus* and 7.8 kg/hectare for *S. varius*. The *Ctenosaura* of San Esteban probably added at least another 5 kg/hectare. In relation to plants, in the same studies, Case found that the average number of buds, flowers and fruits on individual cholla in 1979 yielded 205 potential fruit/cholla. The average number of ripe edible fruits produced per cholla was 305. Using 18 gr/fruit and 1.8 Kcal/g dry weight and 41 plants/ha over a 6-month period, 122,500 Kcal of cholla fruit would be produced by hectare. The amount of this energy consumed by *Sauromalus* (assuming cholla fruit is all that they ate) was only about 23% of that produced. Since at least 30% of the chuckwallas diet consisted of other plant species, they alone did not appear to be making a severe dent in the total food supply. The diet of sympatric *Ctenosaura hemilopha* (= *C. conspicuosa* [Grismer, 1999]) was nearly identical to that of *S. varius*. *Ctenosaura* appeared to be almost as numerous. Both iguanids together may have eaten at most 46 % of the available energy tied up in cholla fruit during the moderately 1979 activity season.

As it can be derived from the above calculations, the flora of the islands of the Gulf of California holds a huge amount of energy available for organisms, and represent a treasure to be investigated by field biologist to fully understand the food webs, energy flux, population dynamics, and other topics in ecology and Natural History. This knowledge may have a great impact in the conservation actions for the insular environments.

CONCLUSIONS

A list of 59 plants of 19 families consumed by 10 herbivorous and omnivorous lizard species on 15 islands of the Gulf of California is available for the first time in literature, number that represents a 9.1% of the 649 plant species reported for these islands. *Sauromalus ater*, a widespread species with insular, peninsular and mainland representatives, has the most varied diet, consuming 47 plants of 19 families. All lizard species normally forage in the ground, but nine (the exception being *Petrosaurus thalassinus*) show a very marked tendency to climb upon bushes and small trees to get food, thus exploiting temporarily a new niche by becoming partially arboreal as a secondary, or maybe totally new, adaptation for survival.

The spiny-tailed iguana *Ctenosaura conspicuosa* from San Esteban Island, a mostly ground dweller but also with semiarboreal habits climbs to the cardon branches to feed, but frequently and accidentally dislodges buds, flowers and fruits that fall to the ground. Therefore, ctenosaurs function as important food-suppliers or subsidizers for other saurian species that forage on the ground, impacting their population biology and possibly their evolutionary histories. For their herbivory and for their habit of preying on chuckwalla hatchings, the iguanas occupy an important position in the insular food web, inhabiting a tri-dimensional habitat with ground and arboreal niches. The insular herbivorous and omnivorous lizards may also exploit other resources subsidized by the sea and may be preyed by different island predators. As a result, the 10 reptile species are entangled into complex food webs.

The cardon cactus, the most consumed plant in this study, produces vast amounts of flowers and fruits (representing vast amounts of biomass, energy, and water), and thus I consider it a structural species that support many different organisms, including herbivorous reptiles, at least during 3 to 4 months, time period that embraces the breeding season for some of the lizards reported here. The other 58 plant species, belonging to diverse families of vascular plants, also play a vital role in providing a still unknown amount of biomass whose availability throughout the year may substantially influence the rate of growing of hatchlings and juvenile herbivorous lizards before reaching sexual maturity.

Field observation is still a very powerful tool to understand the biology and ecology of organisms and provide qualitative and quantitative information that can be used for modelling and testing, and for conservation.

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