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

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

ADRIÁN CERDÁ-ARDURA
‘Lindblad Expeditions/National Geographic; Facultad de Ciencias, UNAM.
*Correspondence: adriancerda@ciencias.unam.mx.

Received: 2020-09-16. Accepted: 2021-09-10.
Editor: Leticia Ochoa-Ochoa, México.

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Abstract.— I present an unpublished list of 59 plant species of 19 families that constitute a source of food for the insular reptiles Ctenosaura conspicuosa, C. hemilopha, Sauromalus varius, S.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, endemicity, 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; Ruiz-Sánchez et al., 2019; Ramirez 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 Diposaurus 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 Diposaurus 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 gammosus 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 hemilophya (= C. conspicua) (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, manoeuvring 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
| Lizard species | Location | Technique | Plant food | Reference |
|----------------|----------|-----------|------------|-----------|
| Sauromalus ater | Borrego Mountains, California | Stomach analysis | Phacelia *sp.* <br> Ambrosia *dumosa* <br> Encelia *farinosa* <br> Erigonum *lanceolata* <br> Ditaxis *lanceolata* <br> Larrea *tridentata* <br> Fouquieria *splendens* <br> Encelia *farinosa* | Shaw, 1939 |
| Sauromalus ater | Tubbs Canyon, California | | Lotus *sp.* <br> Phacelia *sp.* <br> Festuca *sp.* <br> Cryptantha *sp.* <br> Lotus *strigosus* <br> Chenactis *sp.* <br> Cryptantha *sp.* <br> Tropidocarpum *gracile* | |
| Sauromalus ater | Palm Canyon | | | |
| Sauromalus ater | Western Mojave Desert | Observation | Cryptantha *sp.* <br> Isomeris *arborea* | Johnson, 1965 |
| Sauromalus ater | Grand Wash Cliffs, Grand Canyon | Fecal pellet analysis | Sphaeralcea *ambigua* <br> Ambrosia *dumosa* <br> Acacia *gregii* <br> Lotus *strigosus* <br> Coldenia *hispidissima* | Hansen, 1974 |
| Sauromalus ater | Colorado Desert of Southern California | Observation | Plantago *insularis* <br> Perityle *emoryi* <br> Phacelia *crenulata*, Erigonum *inflatum* <br> Mirabilis *bigelovii* <br> Sphaeralcea *ambigua* <br> Chaenictis *carphoclinea* <br> Ambrosia *dumosa* <br> Fagonia *chilensis* <br> Bebbia *juncea* <br> Pectis *papposa* <br> Euphorbia *polycarpa* | Abts, 1985 |
## 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 microphyllum, Sphaeralcea ambigua, Trigia californica, 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 |
| Sauromalus 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. | Case, 1982 |
| Ctenosaura conspicuosa | San Esteban Island | Observation | Cactus fruits, Assorted perennial flowers | |
| 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 | Fecal pellet analysis | 35 plant species of 20 families, including Cressa truxillenis, Amaranthus palmeri, Ferocactus peninsulae, Opuntia echinocarpa, Agave deserti, Asclepias subulata | |
| Sauromalus hispidus | Rasa Island | Observation | Cressa truxillenis | Velarde, pers. com., 2014 |
| Sauromalus hispidus | Rasa Island | Fecal pellet analysis | Cressa truxillenis | 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 truxillensis* 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,
isular 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

---

**Table 2.** List of the 15 islands visited during this long-term data recording, arranged by increasing area, and the numbers of plant and reptile species consumed by lizards. Researchers identified 711 feeding situations with 22 plant species and 48 species in 25 plant families. The insular lizards showed a wide range of food items for consumption along the seasons, and they probably displayed adaptive behaviors to do so. These lizards consumed 71% of plants identified, excluding halophytes, through visual observations and field identification. The insular lizards showed a wide range of food items for consumption along the seasons, and they probably displayed adaptive behaviors to do so.

**Cerdá Ardura - Plants consumed by lizards in islands**
Some of the reptile species were on of the islands visited with reported area and numbers of plant and reptile species (Carreño & Helenes, 2002). The maximum number of records of a single reptile species eating these 10 reptile species on the 15 islands of the Gulf of California. The 711 feeding observations correspond as follows: 81 to Ctenosaura conspicuosa, two to C. hemilopha, 51 to S. varius; 22 to S. ater; six to S. slevini; 100 to S. klauberi; 411 to S. ater; 20 to Diposaurus dorsalis; 16 to D. catalinensis, and eight to 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 where 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 Diposaurus 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 Pachycreus pringlei, followed by Sauromalus varius to P. pringlei in 41 times. Also meaningful are the records of S. klauberi with 18 feeding observations on Ferocactus diguetii, 19 times on Hypsiz 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 Perytle 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 Mardensia 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 truxillensis, 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

| Island          | Area in km² | 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 GUARDIA | 936.04 | 199                     | 15                       |
| 15 TIBURÓN      | 1223.53     | 298                     | 29                       |

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).
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.

| 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. hemilopa      | 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 truxilliiensis *           | 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 emory                      | 19 |                          |
|                  | Lysiloma candidum                  | 2 |                          |
|                  | Melochia tomentosa                | 8 |                          |
|                  | Pachycereus pringlei            | 15 |                          |
|                  | Parkinsonia microphylla            | 1 |                          |
|                  | Pythecellobium confine            | 3 |                          |
| S. klauberi      | Ruella californica                  | 13 | Santa Catalina |
|                  | Simmondsia chinensis              | 3 |                          |
|                  | Stenocereus gummosus              | 5 |                          |
|                  | Stenocereus thurberi              | 1 |                          |

Tabla 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                        |
|-----------------|--------------------------------------------|------------------------------------|--------------------------------|
| S. ater         | Acacia goldmanií                           | 1 | Espíritu Santo, San Francisco, San José, Danzante, Peninsula, San Marcos, Tiburón |
|                  | Amaranthus fimbriatus                        | 12 |                          |
|                  | Ambrosia dumosa                              | 2 |                          |
|                  | Antigonon leptopus                           | 5 |                          |
|                  | Atriplex sp.                                 | 3 |                          |
|                  | Bacharis salicifolia                        | 6 |                          |
|                  | Bajacalia grassiflora                       | 11 |                          |
|                  | Bebbia juncea                                | 17 |                          |
|                  | Bursera hindsiana                            | 4 |                          |
|                  | Bursera microphylla                          | 6 |                          |
|                  | Collinia californica                         | 15 |                          |
|                  | Celtis pallida                               | 1 |                          |
|                  | Cordia curassavica                           | 3 |                          |
|                  | Cotyledon capitata                           | 9 |                          |
|                  | Craton californicus                          | 3 |                          |
|                  | Cylindropuntia alcatae                       | 7 |                          |
|                  | Cylindropuntia cholla                        | 9 |                          |
|                  | Ditaxis lanceolata                           | 1 |                          |
|                  | Encelia farinosa                             | 11 |                          |
|                  | Euclidean aurea                              | 6 |                          |
|                  | Euclidean cordata                            | 5 |                          |
|                  | Euphorbia misera                             | 3 |                          |
|                  | Ficus palmeri                                | 3 |                          |
|                  | Gossypium davidsonii                         | 14 |                          |
|                  | Heliotropum curassovicum                     | 7 |                          |
|                  | Hoffmeisteria fasciculata                    | 9 |                          |
|                  | Hyptis emory                                 | 17 |                          |
|                  | Jacqemontia abutiloides                      | 11 |                          |
|                  | Jacquemontia eastwoodiana                    | 17 |                          |
|                  | Jatropha cuneata                              | 2 |                          |
|                  | Lophocereus schattii                         | 5 |                          |
|                  | Mammillaria albicans                         | 7 |                          |
|                  | Mammillaria dioica                           | 13 |                          |
|                  | Mardsenia sp. **                            | 1 |                          |
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                                |         |
|                 | Simmondsia chinensis    | 4                                 |         |
|                 | Stenocereus gymmosus    | 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* | Feracactus diguetii var. diguetii | 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).

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.

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

| Family            | Species                  | Number of plant species per family |
|-------------------|--------------------------|-----------------------------------|
| ACANTHACEAE       | Ruellia californica      | 1                                 |
| AMARANTHACEAE     | Amaranthus fimbriatus    | 4                                 |
| APOCYNACEAE       | Mardisia sp.             | 1                                 |
| ASTERACEAE        | Amauria rotundifolia     | 12                                |
|                   | Ambrosia ambrosioides    |                                   |
|                   | Ambrosia dumosa          |                                   |
|                   | Bacharis salicifolia     |                                   |
|                   | Bajacalia crassiflora    |                                   |
|                   | Bebbia juncea           | 12                                |
|                   | 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    |                                   |

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).
Tabla 5 resume los 10 reptiles especies con el total número de plantas consumidas por cada reptil especie, y las familias que las plantas pertenecen. Es posible observar que *S. ater* consumió 47 plantas, representativas de todas las 19 familias registradas, convirtiendo el más variado dieta de todas las especies de reptiles analizadas; y *S. klauberi* consumió 15 representantes de ocho familias. Los restantes reptiles consumieron dos a cinco representantes de hasta cuatro familias, principalmente dos, y *Dipsosaurus catalinensis* consumió solo dos especies de una familia (Cactaceae).

| 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. sievini           | 2                               | 2                                 |
| S. klauberi          | 15                              | 8                                 |
| S. ater              | 47                              | 19                                |
| Dipsosaurus dorsalis | 2                               | 2                                 |
| D. catalinensis      | 2                               | 1                                 |
| Petrosaurus thalassinus | 2                          | 2                                 |

Tabla 6 presenta el número de observaciones individuales por planta, sus frecuencias relativas de ocurrencia, el número de especies de reptiles que las consumen, y las especies de reptiles individuales que consumen cada planta. Como se puede observar, *Pachycereus pringlei* fue la planta más consumida, con 168 observaciones (frecuencia, f = 0.236), seguida por *Hyptis emoryi* con 36 observaciones (f = 0.051), y seis plantas con 23 a 27 registros y f = 0.032 a 0.038. Asimismo, 13 plantas especies se registraron entre 11 y 19 veces, con f = 0.015 a 0.025; y 37 especies tuvieron menos de 10 observaciones (1-9), y frecuencias por debajo de 0.015 (1.5% representación en el total de muestras N = 711). En Tabla 6, *Pachycereus pringlei*, el cactus de cardón o cardón, es consumido por todas las 10 especies de reptiles, seguido por *Stenocereus gummosus* (camelos), consumida por cuatro especies, y *Lysiloma candidum* (Palo Blanco) y *Simmondsia chinensis* (Jojoba), ambos consumidos por cuatro especies reptiles. Las otras 55 especies son consumidas por uno o dos especies de lagartos. Esta tabla muestra la relevancia del cardón y otros siete plantas especies (con 18 a 36 registros) como fuente de alimento.
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 |
|--------------------------------------|----------------------------------------|-----------|-----------------------------------------------|-------------------------------------|
| Pachycereus pringlei                 | 168                                    | 0.236     | 10                                            | All 10 species                      |
| Hyptis emoryi                        | 36                                     | 0.051     | 2                                             | S. ater, S. klauberi                |
| Ruellia californica                  | 27                                     | 0.038     | 2                                             | S. ater, S. klauberi                |
| Perityle californica                 | 25                                     | 0.035     | 1                                             | S. ater                            |
| Ferocactus diguetii var. diguetti    | 25                                     | 0.035     | 2                                             | S. klauberi, D. dorsalis            |
| Stenocereus gummosus                 | 23                                     | 0.032     | 4                                             | C. conspicuosa, S. ater, S. klauberi, S. varius |
| Melochia tomentosa                   | 23                                     | 0.032     | 2                                             | S. ater, S. klauberi                |
| Encelia farinosa                     | 23                                     | 0.032     | 2                                             | S. ater, S. hispidus               |
| Lysiloma candidum                    | 18                                     | 0.025     | 3                                             | C. conspicuosa, C. hemilopha, S. klauberi |
| Gossypium davidsonii                 | 18                                     | 0.025     | 2                                             | S. ater, S. klauberi                |
| Trixis californica                   | 17                                     | 0.024     | 1                                             | S. ater                            |
| Jacquemontia eastwoodiana           | 17                                     | 0.024     | 1                                             | S. ater                            |
| Bebbia juncea                        | 17                                     | 0.024     | 1                                             | S. ater                            |
| Stenotis mucronata                   | 16                                     | 0.022     | 1                                             | S. ater                            |
| Calliandra californica               | 15                                     | 0.021     | 1                                             | S. ater                            |
| Passiflora palmeri                  | 14                                     | 0.020     | 1                                             | S. ater                            |
| Mammillaria dioica                   | 13                                     | 0.018     | 1                                             | S. ater                            |
| Amarathus fimbratus                  | 12                                     | 0.017     | 1                                             | S. ater                            |
| Perityle aurea                       | 11                                     | 0.015     | 1                                             | S. ater                            |
| Jacquemontia abutiloides             | 11                                     | 0.015     | 1                                             | S. ater                            |
| Bajacalia grassilora                 | 11                                     | 0.015     | 1                                             | S. ater                            |
| Simmondsia chinensis                 | 9                                      | 0.013     | 3                                             | S. ater, S. klauberi, D. dorsalis   |
| Hoffmeisteria fasciculata            | 9                                      | 0.013     | 1                                             | S. ater                            |
| Cylindropuntia cholla                | 9                                      | 0.013     | 1                                             | S. ater                            |
| Cauterella capitata                  | 9                                      | 0.013     | 1                                             | S. ater                            |
| Olneya tesata                        | 8                                      | 0.011     | 1                                             | C. conspicuosa                     |
| Bursera microphylla                  | 8                                      | 0.011     | 2                                             | S. ater, S. klauberi                |
| Mammillaria albicans                 | 7                                      | 0.010     | 1                                             | S. ater                            |
| Heliantham cuassavicum               | 7                                      | 0.010     | 1                                             | S. ater                            |
| Cylindropuntia alcobes               | 7                                      | 0.010     | 1                                             | S. ater                            |
| Bursera hindsiana                    | 7                                      | 0.010     | 2                                             | S. ater, S. klauberi                |
| 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 Euclidean aurea  | 6                                      | 0.008     | 1                                           | S. ater                           |
| 36 Baccharis salicifolia | 6                                     | 0.008     | 1                                           | S. ater                           |
| 37 Lophocereus schottii | 5                                     | 0.007     | 1                                           | S. ater                           |
| 38 Euclidean 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 Amuria ratundifolia | 4                                     | 0.006     | 1                                           | S. elevini                        |
| 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
| Reptile species | Plant Family | Number of plants species per family consumed by each reptile species |
|----------------|--------------|---------------------------------------------------------------|
| *Ctenosaura conspicua*
  | Cactaceae    | 3                                                             |
|                 | Fabaceae     | 2                                                             |
| *C. hemilopa*   | 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                                                             |
|                 | Malvaece     | 2                                                             |
|                 | Simmondsiaceae | 1                                                        |
| *S. ater*       | Acanthaceae  | 1                                                             |
|                 | Amaranthaceae | 2                                                             |
|                 | Apocynaceae  | 1                                                             |
|                 | Asteraceae   | 10                                                            |

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
Cerdá Ardura  - Plants consumed by lizards in islands

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. conspicua 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),...
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 conspicua; 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 conspicua; 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.
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 Ángel de la Guarda island; b) Sauromalus hispidus upon a bush.
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.
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...
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 ($N_{\text{island}} = 10^{1.31\pm0.08}$; 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
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.

**Figura 14.** a-d. Aspidoscelis rubidus, de la 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.
**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 sexicolor*), Sansores (2016), from 90 fecal samples in Espiritu 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 Diposaurus dorsalis, D. catalinensis, and Petrobasaurus thalassinus benefit from inputs from other ecosystems, or subsidies. Barret et 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 et 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 et 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 31º 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 fruting 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 CO₂ 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 CO₂ uptake of 8 μmol·m⁻²·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. conspicua [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 conspicua 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 in 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.

Acknowledgements.— I deeply thank Lindblad Expeditions/National Geographic for the great logistic support, encouragement and freedom to explore the sea and the islands in the Gulf of California as a part of the Natural History Staff since 1995 to date. I am grateful to the following people too: Sven-Olof Lindblad, Jim Kelley, Rabb Cummings, Linda Burback, Steven Morello, Annie Fiske, John Mitchel, Sue Perin, Larry Prussin, Paula Tagle, Pete and Gretchen Pederson, Lee Moll, Betty Lou Krause, Sharon Grainger, Larry Hobbs, Alex and Kim Baldwin, Tom Bowen, and Emily Mount. I particularly thank my teacher, colleague and friend Dr. Oscar Flores-Villela for the review of the present paper, as well as for his critical suggestions. Oscar was the one that gave me the first opportunity to visit the Gulf of California as a herpetologist in those long-gone days when I was a Biology student in the Faculty of Sciences, UNAM. Finally, I am grateful to Dr. Michael Douglas for manuscript reviewing and for his useful suggestions to improve the whole text.

CITED LITERATURE

Abts, M.L. 1985. The life history strategy of the saxicolous desert lizard, Sauromalus obesus. Ph. D. Thesis, Portland State University, Portland, Oregon, USA.

Alencar, L.R.V., T.B. Quental, F.G. Grazziotin, M.L. Alfaro, M. Martins, M. Venzon & H. Zaber. 2016. Diversification in vipers: Phylogenetic relationships, time of divergence and shifts in speciation rates. Molecular Phylogenetics and Evolution 105:50-62.

Álvarez-Borrego, S. 2002. Physical oceanography. Pp. 41-59. In T.J. Case, M.L. Cody & E. Ezcurra (Eds.). A New Island Biogeography of the Sea of Cortes. Oxford University Press, New York, USA.

Arnaud, G., M. Martins, I. Burguete-Trujillo, I. Hernández-Rodríguez, H. Ávila-Villegas, R. Murillo-Quintero & A. Quijada-Mascaréñas. 2008. Historia Natural de la serpiente de cascabel, Crotalus catalinensis, endémica de la isla Santa Catalina, Golfo de California, México. Pp. 93-100. In L.M. Flores-Campaña (Ed.) Estudios de las islas del Golfo de California. Universidad Autónoma de Sinaloa, Gobierno del Estado de Sinaloa, Consejo Nacional de Ciencia y Tecnología, D.F., México.

Ávila-Villegas, H., M. Martins & G. Arnaud. 2007. Feeding ecology of the endemic rattleless rattlesnake, Crotalus catalinensis, of Santa Catalina Island, Gulf of California, Mexico. Copeia 2007:80-84.

Banks, R.C. & W.M. Farmer. 1963. Observations on reptiles of Cerralvo Island, Mexico. Herpetologica 18:246-250.

Barret, K., W.B. Anderson, D.A. Wait, L.L. Grismer, G.A. Polis & M.D. Rose. 2005. Marine subsides alter the diet and abundance of insular and coastal lizard populations. Oikos 109:145-153.

Berry, K.H. 1974. The ecology and social behavior of the chuckwalla, Sauromalus obesus obesus Baird. University of California Press, Vol. 101.

Buckley, L.B. & W. Jetz. 2007. Insularity and the determinants of lizard population density. Ecology Letters 10:481-489.

Carriquisten, S. 1965. Island life: a natural history of islands of the world. Natural History Press, American Museum of Natural History, New York, USA.

Carriquisten, S. 1974. Island biology. Columbia University Press, New York, USA.

Carreño, A.L. & J. Helenes. 2002. Geology and ages of the islands. Pp. 14-40. In T.J. Case, M.L. Cody & E. Ezcurra (Eds.). A New Island Biogeography of the Sea of Cortes. Oxford University Press, New York, USA.

Case, T.J. 1975. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. Ecology 56:3-18.

Case, T.J. 1976. Body size differences between populations of the chuckwalla, Sauromalus obesus. Ecology 57:313-323.

Case, T.J. 1978. A general explanation for insular body size trends in terrestrial vertebrates. Ecology 59(1):1-18.

Case, T.J., 1982. Ecology and evolution of the insular gigantic chuckwallas, Sauromalus hispidus and S. varius. Pp. 184-212. In G.M. Burghardt & A.S. Rand (Eds.). Iguanas of the world. Their behavior, ecology, and conservation. Noyes Publications, New Jersey, USA.

Case, T.J. 1983. Niche overlap and the assembly of lizard communities. Oikos 41:427-433.
Cerdá Ardura - Plants consumed by lizards in islands

Case, T.J. 2002. Reptiles. Ecology. Pp. 221-270. In T.J. Case, M.L. Cody & E. Ezcurra (Eds.). A New Island Biogeography of the Sea of Cortes. Oxford University Press, New York, USA.

Case, J.T., Cody, M.L. & E. Ezcurra (Eds.). 2002. A New Island Biogeography of the Sea of Cortes. Oxford University Press, New York, USA.

Cerdá-Ardura, A. & E. Langarica-Andonegui. 2018. On the presence of the Spiny Chuckwalla Sauromalus hispidus (Stejneger, 1891) in Rasa Island, Mexico. Revista Latinoamericana de Herpetología 1(2):17-28.

Cerdá-Ardura, A. 2019. Records of Sauromalus ater (Duméril, 1856) hatchlings and subadults on San Francisco Island, Gulf of California, Mexico. Revista Latinoamericana de Herpetología 2(2):15-22.

Cody, M., R. Moran, J. Rebman & H. Thompson. 2002. Plants. Pp. 63-111. In T.J. Case, M.L. Cody & E. Ezcurra (Eds.). A New Island Biogeography of the Sea of Cortes. Oxford University Press, New York, USA.

Cruz-Andrés, O.R. 2014. Filogenia de las serpientes de cascabel endémicas de las islas del Golfo de California, México. Tesis de Maestría. Centro de Investigaciones Biológicas del Noroeste, La Paz, BCS.

De Ruiter, P.C., V. Wolters & J.C. Moore. 2005. Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change. Utrecht University, Utrecht, The Netherlands.

Delgado-Fernández, M., J.G. Escobar-Flores & K. Franklin. 2017. El cardón gigante (Pachycereus pringlei) y sus interacciones con la fauna de la península de Baja California, México. Acta Universitaria 27(5):11-16.

Douglas, M.E., M.R. Douglas, G.W. Schuett & L.W. Porras. 2006. Evolution of rattlesnakes (Viperidae: Crotalus) in the warm deserts of western North America shaped by Neogene vicariance and Quaternary climate change. Molecular Biology 15:3353-3374.

Fleming, T.H. 2002. Pollination biology of four species of Sonoran Desert columnar cacti. Pp.207-224. In T.H. Flemming & A. Valiente-Banuet (Eds.). Columnar cacti and their mutualists. The University of Arizona Press, Tucson, Arizona, USA.

Franklin, K.A., P.N. Sommers, C.E. Aslan, B.R. López, L. Bronstein, E. Bustamante, A. Búrquez, R.A. Medellin & B. Marazzi. 2016. Plant biotic interactions in the Sonoran Desert: current knowledge and future research perspectives. International Journal of Plant Science 177(3):217-234.

García-Padilla, E. 2010. Caracterización del hábitat, distribución y abundancia de la víbora de cascabel Crotalus muertensis (Grism, 1999), microendémica de la isla El Muerto, Golfo de California, México. Tesis de Licenciatura, Laboratorio de Herpetología, Universidad Autónoma de Nuevo León, Nuevo León, México.

Grant, P.R. 1986. Ecology and Evolution of Darwin's Finches. Princeton University Press, New Jersey, USA.

Grism, L.L. 1999. An evolutionary classification of reptiles on islands in the Gulf of California, México. Herpetologica 55(4):446-469.

Grism, L.L. 2002. Amphibians and reptiles of Baja California, including its Pacific islands and the islands in the Sea of Cortes. University of California Press, Berkeley, California, USA.

Grism, L.L. 2004. Santa Catalina Island Desert Iguanas, Dipsosaurus catalinensis: an evolutionary experiment in progress. Iguana 11(1): 3-7.

Hafner, D.J. & B.R. Riddle. 2011. Boundaries and Barriers of North American warm deserts. An evolutionary perspective. Pp. 75-114. In P. Upchurch, A.J. McGowan & C.S.C. Slater (Eds.). Paleogeography and Paleobiogeography. Biodiversity in space and time. The Systematics Association Special Volume Series 77. CRC Press, Boca Raton, California, USA.

Hansen, R.M. 1974. Dietary of the chuckwalla, Sauromalus obrusus, determined by dung analysis. Herpetologica 30:120-123.

Harrington, S.M., B.D. Hollingsworth, T.E. Higham & T.W. Reeder. 2017. Pleistocene climatic fluctuations drive isolation and secondary contact in the red diamondback rattlesnake (Crotalus ruber) in Baja California. Journal of Biogeography 45:64-75.

Hollingsworth, B.D. 2004. The evolution of iguanas. An overview of relationships and a checklist of species. Pp. 19-44. In A.C. Alberts, R.L. Carter, W.K. Hayes & E.P. Martins (Eds.). Iguanas: biology and conservation. University of California Press, Berkeley, California, USA.
Howland, J.M. 1988. Natural History of the desert iguana Dipsosaurus dorsalis. Pp. 51-59. In H.F. De Lisle, P.R. Brown, B. Kaufman & B.M. McGurty (Eds.). Proceedings of the Conference on California Herpetology. The Southwestern Herpetologist League.

Huxel, G.R. & K. McCann. 1988. Food web stability: the influence of trophic flows across habitats. The American Naturalist 152(3): 460-469.

Johnson, S.R. 1965. An ecological study of the Chuckwalla, Sauromalus obesus Baird, in the Western Mojave Desert. The American Midland Naturalist 73(1): 1-29.

Kwiatkowski, M.A. & B.K. Sullivan. 2002. Mating system structure and population density in a polygynous lizard, Sauromalus obesus (= atar). Behavioral Ecology 13(2):201-208.

Leroux, S.J. & M. Loreau. 2008. Subsidy hypothesis and strength of trophic cascades across ecosystems. Ecology Letters 11:1147-1156.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. Ecology 23(4):399-417.

Lovich, R.E., L.L. Grismer & G. Danemann. 2009. Conservation status of the herpetofauna of Baja California, Mexico and associated islands in the Sea of Cortez and Pacific Ocean. Herpetological Conservation and Biology 4(3):358-378.

MacArthur, R.H. & E.O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, New Jersey, USA.

Martins, M., G. Arnaud & R. Murillo-Quero. 2008. Exploring hypothesis about the loss of the rattle in rattlesnakes: how arboreal is the isla Santa Catalina rattleless rattlesnake, Crotalus catalinensis. South American Journal of Herpetology 3(2):162-167.

Medel-Narváez, A. 2003. Biología floral y estructura poblacional de cardón (Pachycereus pringlei (S. Wats.) Briton & Rose (Cactaceae)) en el Comitán, Baja California Sur. Tesis de Maestría. Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, México.

Medel-Narváez, A. 2008. Estudio ecológico y genético del cardón (Pachycereus pringlei) en el Desierto Sonorense. Tesis de Doctorado. Centro de Investigaciones Biológicas del Noroeste, La Paz, Baja California Sur, México.

Meik, J.M., J.W. Streicher, A.M. Lawing, O. Flores-Villela & M.K. Fujita. 2015. Limitations of climatic data for inferring species boundaries: Insights from Speckled Rattlesnakes. PLoS ONE 10(6): e013435.

Meik, J.M., S. Schaack, O. Flores-Villela & J.W. Streicher. 2018. Integrative taxonomy at the nexus of population divergence and speciation in insular speckled rattlesnakes. Journal of Natural History 52(13-16):989-1016.

Murphy, R. & G. Aguirre. 2002. The nonavian reptiles. Pp. 181-220. In T.J. Case, M.L. Cody & E. Ezcurra (Eds.). A New Island Biogeography of the Sea of Cortes. Oxford University Press, New York, USA.

Murphy, R.W. & B. Crabtree. 1985. Genetic relationships of the Santa Catalina island rattleless rattlesnake, Crotalus catalinensis (Serpentes: Viperidae). Acta Zoológica Mexicana 9.

Murphy, R.W., F. Sánchez-Piñero, G.A. Polis & R. Aalbu. 2002, New measurements of area and distance for islands in the Sea of Cortes. Pp. 447-464. In T.J. Case, M.L. Cody & E. Ezcurra (Eds.). A New Island Biogeography of the Sea of Cortes. Oxford University Press, New York, USA.

Murphy, R.W. & J.R. Otley. 1984. Distribution of amphibians and reptiles on islands of the Gulf of California. Annals of Carnegie Museum 53(8): 207-230.

Nobel, P.S. 2002. Physiological Ecology of Columnar cacti. Pp. 189-204. In T.H. Fleming & A. Valiente-Banuet (Eds.). Columnar Cacti and Their Mutualists. The University of California Press, Berkeley, USA.

Norris, K.N. 1953. The ecology of the desert iguana Dipsosaurus dorsalis. Ecology 34(2): 65-287.

Olesen, J.M. & A. Valido. 2003. Lizards as pollinators and seed dispersers: and island phenomenon. Trends in Ecology and Evolution 18(4):177-181.

Paine, R.T. 1966. Food web complexity and species diversity. The American Naturalist 100(910): 65-75.

Paine, R.T. 1980. Food webs: linkage, interaction strength and community infrastructure. Journal of Animal Ecology 49:667-685.

Polis, G.A. & S.D. Hurd. 1995. Extraordinary high spider densities on islands: flow of energy from the marine to terrestrial food
webs and the absence of predation. Proc. National Academy of Science 92:4382-4386.

Pritchard, P. C. H. 1979. Encyclopedia of turtles. T. H. F. Publications, Miami, USA.

Ramírez-Reyes, T., C. Blair, O. Flores-Villela, D. Piñero, A. Lathrop & R. Murphy. 2020. Phylogenomics and molecular species delimitation reveals great cryptic diversity of leaf-toed geckos (Phyllodactylidae: Phyllodactylus), ancient origins, and diversification in Mexico. Molecular Phylogenetics and Evolution 150:106880.

Rebman, J. P. & N. C. Roberts. 2012. Baja California Plant Field Guide. 3rd Edition. San Diego Natural History Museum & Sunbelt Publications, San Diego, California, USA.

Reynoso, V. H., M. J. Monteverde, C. Martinez, E. Zarza & A. Cerdá. 2017. *Sauromalus hispidus* (Spiny Chuckwalla). Geographic Distributions, Herpetological Review 48:126.

Riddle, B. R., D. J. Hafner, L. F. Alexander & J. R. Jaeger. 2000. Cryptic vicariance in the historical assembly of a Baja California Peninsular Desert biota. PNAS 97(26):14438-14443.

Riddle, B. R. & D. J. Hafner. 2006. Biogeografía histórica de los desiertos cálidos de Norte América. Pp. 57-65. In E. Vázquez-Domínguez y D. J. Hafner. Genética y mamíferos mexicanos: presente y futuro. New Mexico Museum of Natural History and Sciences Bulletin No. 32.

Ruiz-Sánchez, E., G. Arnaud, O. R. Cruz-Andrés & F. J. García-De León. 2019. Phylogenetic relationships and origin of the rattlesnakes of the Gulf of California islands (Viperidae; Crotalinae: Crotalus). Herpetological Journal 29:162-172.

Sansores, R. E. 2016. Influencia de los recursos antropogénicos en la abundancia y dieta del babísuri (*Bassariscus astutus saxicola* Merriam, 1897) en el complejo insular Espíritu Santo, B. C. S., México. Tesis de Maestría. Conacyt, D. F., México.

Savage, J.M. 1960. Evolution of a peninsular herpetofauna. Systematic Zoology 9:184-212.

Shaw, C. E. 1939. Food habits of the chuckwalla, *Sauromalus obesus*. Herpetologica 1:153. Reprinted in Iguana 11(2), June 2004.

Soulé, M. & A. J. Sloan. 1966. Biogeography and distribution of the reptiles and amphibians on islands in the Gulf of California, Mexico. Transactions of the San Diego Society of Natural History 14:337-156.

Sylber, C. K. 1988. Feeding habits of the lizards *Sauromalus varius* and *S. hispidus* in the Gulf of California. Journal of Herpetology 22(4):413-424.

Tracy, C. R. 2004. Environmental influences on body size of two species of herbivorous desert lizards. Pp. 158-175 In A. C. Alberts, R. L. Carter, W. K. Hayes & E. P. Martins (Eds.). Iguanas: biology and conservation. University of California Press, Berkeley, California, USA.

Van der Geer, A., G. Lyras, J. de Vos & M. Dermitzakis. 2010. Evolution of island mammals. Adaptation and extinction of placental mammals on islands. Wiley-Blackwell, Chichester, West Sussex, United Kingdom.

Velarde, E., B. D. Hollingsworth & J. P. Rebman. 2008. *Sauromalus hispidus* (Spiny chuckwalla). Geographic Distribution. Herpetological Review 39(3):368.

Velarde, E., B. Wilder, R. Felger & E. Ezcurra. 2014. Floristic diversity and dynamics of Isla Rasa, Gulf of California, a globally important seabird island. Botanical Sciences 92(1):89-101.

Winemiller, K. O. & C. A. Layman. 2005. Food web science: moving on the path from abstraction to prediction. Pp. 10-23. In P. C. de Ruiter, W. Wolters & J. C. Moore (Eds.). Dynamic food webs: multispecies assemblages, ecosystem development, and environmental change. Utrecht University, Utrecht, The Netherlands.