

Fleshy Fruits in the Diet of *Canarian Lizards Gallotia galloti* (Lacertidae) in a Xeric Habitat of the Island of Tenerife

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ABSTRACT.—We analyzed the frugivorous diet of the lizard *Gallotia galloti*, a Canary Island endemic, in relation to season and fruit availability in a xeric habitat from Tenerife. *Gallotia galloti* was omnivorous throughout the year (including >59% of plant material by volume in fecal pellets); only in the winter months (December and January) did invertebrates dominate the diet (>73% in volume). The most remarkable aspect of the diet was the high level of consumption of fleshy fruits, showing pronounced seasonal variation (from 30% in January to 95% in April in frequency of occurrence). Variation in fleshy fruit consumption was associated with seasonal patterns of fruits availability. A total of 4710 seeds were found in 1120 droppings analyzed during the entire year corresponding the majority to *Rubia fruticosa* and *Plocama pendula* (Rubiaceae). The extensive consumption of fleshy fruits during seven months of the year (>50% by volume) suggests *G. galloti* is an important seed disperser in the Canary Islands. These results contrast with the majority of continental lacertids that are insectivorous.

Lizards living on islands generally tend to be more herbivorous compared to lizards inhabiting mainland areas (e.g., van Damme, 1999; Cooper and Vitt, 2002 and references therein). This may be related to lower arthropod densities (Janzen, 1973), lower predation risk (Szarski, 1962), and larger body size (Szarski, 1962; Ostrom, 1963; Pough, 1973; Sokol, 1967; Cooper and Vitt, 2002) and is often associated with extremely high lizard abundance (Olesen and Valido, 2003).

Although fleshy fruits have low levels of nitrogen and protein (but high levels of easily digested sugars) and are seasonal in availability (Jordano, 2000), they have been cited as an important component of the diet of some herbivorous/omnivorous lizards on islands (see reviews in Whitaker, 1987; van Damme, 1999; Cooper and Vitt, 2002; Olesen and Valido, 2003). Omnivorous island lizards that feed on fleshy fruits must vary their diets according to seasonal availability of fruit. Therefore, it is of interest to study their diets for an entire annual cycle to assess how the degree of frugivory varies among seasons, especially because the

contribution of fruit to the annual diet could be underestimated by short-term studies.

Numerous studies of island lizard diets have been completed (see reviews in van Damme, 1999; Cooper and Vitt, 2002), but they were generally restricted to short periods (usually the wet and/or the dry season), and fruits (when present) were generally lumped into a general plant matter category so that their contribution to the overall diet was not emphasized. The *Canarian lizards* (genus *Gallotia*, Lacertidae) are not an exception, and currently, only incomplete information about the importance of fruits in their diet has been reported (e.g., Bischoff et al., 1979; Naranjo et al., 1991; Mateo and López-Jurado, 1992; Valido and Nogales, 1994; Nogales et al., 1998).

The genus *Gallotia* Boulenger is endemic to the *Canarian archipelago*, and it is represented by seven extant species (Hernández et al., 2001). *Gallotia galloti* is a medium-sized lizard (maximum SVL: 145 mm) that inhabits the islands of Tenerife and La Palma. This lizard occupies a wide variety of habitats, often occurring at high densities (population densities are lower in the laurel forest), and fruits are an important item of their diet (Valido, 1999).

In this paper, we document an extensive frugivorous diet of *G. galloti* during the entire year, from a xeric zone

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TABLE 1. Composition of lizard (*Gallotia galloti*) diet during the year (September 1993 through August 1994) in Teno Bajo (Tenerife). FO: frequency of occurrence (percentage of droppings with the taxon present), and P: percentage of the total fruits or invertebrates counted in the droppings. r_s indicates the Spearman correlation between the parameters FO and P. The highest values of each component/month appear in bold face. # indicates values lower than 0.006%. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: no significant. The percentage of plant material is given in volume (V). In Figure 2 the values obtained are indicated for each plant component: fruits remains, foliage and flowers.

| | Sept | | Oct | | Nov | | Dec | | Jan | |
|-------------------------------------|---------------|-------------|---------------|-------------|---------------|-------------|---------------|-------------|---------------|-------------|
| | FO | P | FO | P | FO | P | FO | P | FO | P |
| Frugivory component | | | | | | | | | | |
| <i>Atriplex semibaccata</i> | 1 | 0.3 | - | - | - | - | - | - | - | - |
| <i>Lycium intricatum</i> | - | - | - | - | - | - | - | - | - | - |
| <i>Neochamaelea pulverulenta</i> | - | - | 1 | 0.7 | - | - | 1.1 | 2.4 | - | - |
| <i>Opuntia dillenii</i> | 18 | 0.1 | 11 | 0.1 | 14 | 0.4 | 11.5 | 0.4 | - | - |
| <i>Plocama pendula</i> | 44 | 78.2 | 37 | 89.9 | 18 | 70.9 | 16.1 | 75.4 | - | - |
| <i>Rubia fruticosa</i> | 29 | 20.8 | 11 | 9.4 | 12 | 26.3 | 6.9 | 20.9 | 1.9 | 100 |
| <i>Withania aristata</i> | 4 | 0.6 | - | - | 2 | 2.3 | 2.3 | 1.2 | - | - |
| unidentified seeds | 6 | - | 3 | - | 2 | - | - | - | - | - |
| Animal component | | | | | | | | | | |
| Coleoptera | 9 | 14.5 | 6 | 5.3 | 5 | 2.9 | 12.6 | 13.5 | 17.3 | 7.9 |
| Hemiptera | 4 | 6.4 | 2 | 1.8 | - | - | 3.4 | 3.1 | 1.9 | 0.9 |
| Diplopoda | 2 | - | - | - | 1 | - | - | - | 1.9 | - |
| Diptera | - | - | - | - | - | - | 1.1 | 1.0 | 3.8 | 1.8 |
| Formicidae | 18 | 67.7 | 20 | 88.6 | 18 | 90.9 | 33.3 | 80.2 | 30.8 | 85.0 |
| Others Hymenoptera | - | - | 2 | 1.8 | 4 | 5.1 | - | - | - | - |
| Orthoptera | 2 | 3.2 | 1 | 0.9 | 2 | 1.1 | 1.1 | 1.0 | - | - |
| Araneae | - | - | - | - | - | - | - | - | - | - |
| Gasteropoda | - | - | 1 | - | 2 | - | - | - | 1.9 | - |
| Unidentified remains | 4 | 6.4 | - | - | - | - | 1.1 | 1.0 | 5.8 | 2.6 |
| No. droppings analyzed | 100 | | 100 | | 100 | | 87 | | 52 | |
| Mean droppings diameter (\pm SD) | 5.2 \pm 1.1 | | 5.1 \pm 1.1 | | 4.5 \pm 1.3 | | 3.9 \pm 1.3 | | 3.2 \pm 1.1 | |
| % (V) plant material (\pm SD) | 66.5 (22.1) | | 56.1 (31.8) | | 49.1 (32.5) | | 26.1 (31.8) | | 23.1 (33.3) | |
| No. species fruits/month | 5 | | 4 | | 4 | | 5 | | 1 | |
| % droppings with: | | | | | | | | | | |
| plant material | 99 | | 97 | | 92 | | 60.9 | | 44.2 | |
| plant material only | 8 | | 8 | | 8 | | 4.6 | | 3.8 | |
| leaves and flowers | 22 | | 31 | | 53 | | 35.6 | | 42.3 | |
| fruit remains | 79 | | 54 | | 40 | | 29.9 | | 1.9 | |
| Arthropods | 92 | | 92 | | 92 | | 95.4 | | 96.2 | |
| arthropods only | 1 | | 3 | | 8 | | 39.1 | | 55.8 | |
| r_s | 0.65* | | 0.69* | | 0.60 ns | | 0.68* | | 0.29 ns | |

in Tenerife (Canary Islands). We also quantify the contribution of fruits in the diet during different seasons and its relationship with fruit availability of the plant species consumed. We conclude that this species is an important seed disperser of Canarian vascular plants species (Valido and Nogales, 1994), comparable to other well-known frugivorous species (e.g., Mediterranean fall migrants and overwintering birds and mammals).

MATERIALS AND METHODS

Study Site.—Fieldwork was carried out in Teno Bajo (Barranco de Las Cuevas, northwest of Tenerife), which is one of the oldest geological sectors of the island (4.5–6.7 MYA, Ancochea et al., 1990). The climate is xeric, typical of the Canarian lowland, with an annual mean temperature of about 21°C and a mean annual rainfall of 204 mm, mainly between November and February.

May through September is the driest time of the year (<3 mm of precipitation). The study site (150 m a.s.l.) encompasses some of the most characteristic xerophytic shrub land of the Canaries.

This xeric vegetation consists of a low and sparse shrub cover. Species such *Rubia fruticosa* and *Plocama pendula* (Rubiaceae), *Euphorbia obtusifolia* and *E. canariensis* (Euphorbiaceae), *Withania aristata* (Solanaceae), *Periploca laevigata* (Asclepiadaceae) and the invasive *Opuntia dillenii* (Cactaceae) are the predominant plant species (for more information about the habitat of this area, see Valido and Nogales, 1994).

Diet Analysis.—We selected five linear transects in an area of approximately 1.3 ha, which were systematically visited every 15 days from September 1993 to August 1994. These transects were chosen to ensure that the main types of vegetation in the study area were present. Along each transect (2-m width), we collected only

TABLE 1. Extended.

| Feb | | March | | April | | May | | June | | July | | Aug | |
|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|-------------|
| FO | P | FO | P | FO | P | FO | P | FO | P | FO | P | FO | P |
| - | - | - | - | - | - | - | - | - | - | - | - | - | - |
| 2.5 | 15.1 | 1 | 3.4 | - | - | 5 | 12.1 | - | - | - | - | - | - |
| - | - | 1 | 0.3 | - | - | - | - | 2 | 1.3 | 12 | 6.3 | 3 | 1.2 |
| 1.2 | 0.01 | - | - | 1 | # | 1 | # | 19 | 0.2 | 23 | 0.2 | 27 | 0.2 |
| - | - | 1 | 0.9 | - | - | - | - | 1 | 0.2 | 9 | 8.3 | 40 | 58.4 |
| 23.5 | 84.7 | 72 | 94.8 | 94 | 98.4 | 84 | 86.9 | 68 | 95.3 | 52 | 84.1 | 33 | 38.8 |
| 2.5 | 0.2 | 8 | 0.5 | 10 | 1.5 | 9 | 1.2 | 12 | 2.9 | 5 | 0.9 | 7 | 1.3 |
| 27.2 | - | 15 | - | 4 | - | 11 | - | 5 | - | 3 | - | 1 | - |
| 14.8 | 42.8 | 9 | 34.6 | 11 | 17.2 | 15 | 12.8 | 12 | 11.3 | 16 | 7.6 | 18 | 14.4 |
| 1.2 | 3.6 | - | - | 5 | 9.4 | 9 | 8.0 | 5 | 5.2 | 4 | 1.9 | 6 | 4.0 |
| 1.2 | - | 1 | - | 4 | - | - | - | 1 | - | - | - | - | - |
| - | - | - | - | 1 | 1.6 | 1 | 0.8 | - | - | - | - | - | - |
| 11.1 | 50.0 | 9 | 53.8 | 20 | 62.5 | 27 | 71.2 | 30 | 74.8 | 51 | 86.6 | 37 | 81.1 |
| 1.2 | 3.6 | 1 | 3.8 | 2 | 3.1 | 3 | 2.4 | 7 | 6.1 | 3 | 0.8 | - | - |
| - | - | 2 | 7.7 | 3 | 4.7 | 4 | 3.2 | 1 | 0.9 | 4 | 1.9 | 1 | 0.6 |
| - | - | - | - | 1 | 1.6 | 1 | 0.8 | 1 | 0.9 | 1 | 1.9 | - | - |
| 1.2 | - | - | - | - | - | - | - | - | - | - | - | - | - |
| - | - | - | - | - | - | 1 | 0.8 | 1 | 0.9 | - | - | - | - |
| 81 | | 100 | | 100 | | 100 | | 100 | | 100 | | 100 | |
| 3.9 ± 1.6 | | 4.6 ± 1.1 | | 4.9 ± 1.1 | | 5 ± 1 | | 5.2 ± 1.3 | | 5.9 ± 1.4 | | 5.7 ± 0.9 | |
| 54.8 (37.6) | | 74.3 (23.8) | | 79.3 (19.1) | | 72.2 (23.3) | | 74.8 (23.8) | | 60.3 (30.2) | | 72.3 (22.5) | |
| 4 | | 5 | | 3 | | 4 | | 5 | | 5 | | 5 | |
| 81.5 | | 99 | | 100 | | 100 | | 100 | | 98 | | 99 | |
| 7.4 | | 11 | | 22 | | 14 | | 16 | | 8 | | 6 | |
| 54.3 | | 24 | | 7 | | 12 | | 23 | | 18 | | 17 | |
| 27.2 | | 67 | | 95 | | 89 | | 79 | | 82 | | 78 | |
| 92.6 | | 89 | | 78 | | 86 | | 84 | | 92 | | 94 | |
| 18.5 | | 1 | | 0 | | 0 | | 0 | | 2 | | 1 | |
| 0.83* | | 0.75* | | 0.79* | | 0.92** | | 0.66* | | 0.54 ns | | 0.72* | |

recent fecal pellets from *G. galloti* (the only lacertid). Prior to the first census, we removed all fecal pellets found along our transects to ensure that we would collect recent pellets in subsequent census. We tried to find at least 50 pellets per month, but in some months (December through February) it was impossible to collect this quantity because lizards were less active as a consequence of weather conditions. Each pellet was collected separately, and its diameter and length were measured using a digital calliper. Each pellet was then dissected in water with a few drops of alcohol, the content was inspected under magnification (16×), and plant and animal components were identified. Seeds were identified to species level, whereas invertebrates were identified to order (except the Formicidae).

The relative abundance of each component in the fecal pellets was quantified in several ways: (1)

frequency of occurrence of each component (FO); (2) percentage of fruits or invertebrates in relation to the total number of these two items counted each month (P); and (3) percentage by volume (V), estimated to the nearest 10%, for fleshy fruit, foliage, flowers, and animal items. To calculate the minimum number of invertebrates, we did not take into account Diplopoda and Gastropoda because of their high degree of fragmentation. However, these components were less common in the diet, and the percentage we estimated is probably close to the actual value. The number of morphologically damaged seeds was also noted.

To assess the relationship between content in digestive systems of lizards and content in fecal pellets, we captured 60 lizards and sampled fecal pellets at the same site on two consecutive days in August 1994. To avoid sampling bias, these captured lizards had no

access to bait inside the traps. We introduced a canula (coated with vaseline) into the esophagus and administered a saline solution. After a few minutes, the lizards regurgitated their stomach contents and often ejected feces. We analyzed these samples in the same way as described above. Once the lizard ejected the content of its digestive tract, it was immediately released into environment (less than 24 h).

Fruits Seasonal Availability.—We counted the total number of fruits in ten branches (cladodes in the case of *O. dillenii*) in about 20 plants of each of the fleshy-fruited species present in the study area. On these randomly selected branches, we made a follow-up count 15 days later to obtain data on the number of green, ripe and dry fruits, and how this varied during the year.

Statistical Analysis.—The temporal variation of animal and plant components in the diet was analyzed by ANCOVA (using the fecal pellet diameter as covariate, logarithmically transformed). This calculation was used to control for the effect of lizard body size. There is a significant relationship between the amount of plant items and lizard size (e.g., Mateo and López-Jurado, 1992; López-Jurado and Mateo, 1995, for data on *Gallotia* spp.). In this analysis, we used fecal pellet size as a predictor of lizard body size. There was a significant correlation between pellet diameter and lizard size (SVL; logarithmical transformation; Pearson correlation: $r_p = 0.79$; $P = 0.036$; $N = 24$ mean size of droppings obtained from 24 captive lizards a fed with omnivorous diet; Valido and Nogales, in press.).

Statistical analyses were done with the SPSS computer program (vers. 9.0), following the protocols given by Sokal and Rohlf (1979) and Siegel (1990). Means \pm SD are provided, but standard errors are reported in the figures.

RESULTS

Temporal Variation in Diet and Frugivory.—Lizards from Barranco de Las Cuevas were omnivorous throughout the year (Table 1). The total plant components of the diet (average = 59.1%, $N = 1120$) varied strongly among months (from 23.1% in January to 79.3% in April); fecal pellets collected in December and January included mostly invertebrates (>73% in volume). Ants were the most common element throughout the year, although Coleoptera were more frequent in February (42.8%) and were equal to ants in March. Ants and beetles were present in the diet every month of the year; these two insect groups constituted a total of 91.2% of all invertebrates in the fecal pellets (Table 1).

Pellet diameters suggested that those collected during winter came from smaller lizards (Table 1), and these smaller pellets included a high fraction of insects. There was a significant negative correlation between fecal pellet diameter and percentage (in volume) of invertebrate remains (Pearson correlation, $r_p = -0.27$, $P < 0.001$). Elimination of the variation of plant material based on the dropping diameter (using a covariate analysis), revealed significant differences among months (angular transformation, ANCOVA, $F_{11,1019} = 30.39$, $P < 0.001$). This indicates that although fecal pellet size varied among months (logarithmic transformation; ANCOVA, $F_{11,1019} = 36.3$, $P < 0.001$), a pronounced variation existed in the importance of

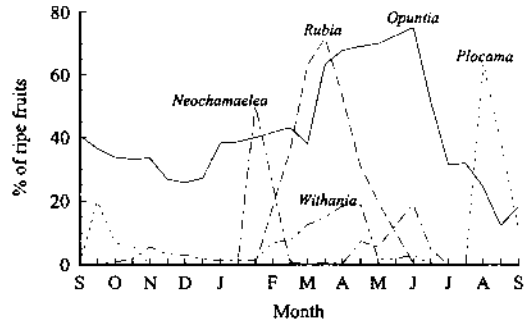


FIG. 1. Availability of ripe fruits (% of the crop size) during a year (September 1993 through August 1994) in Teno Bajo (Barranco de Las Cuevas, Tenerife).

plant material throughout the year. This seasonal variation was probably associated with seasonal changes in availability of fleshy-fruits (Fig. 1). For example, fecal pellets collected in December and January had the lowest levels of plant components (<60% FO), whereas in the other months (with the exception of February), fruits were present in >90% of the samples, reaching the maximum 100% (FO) in April, May and June (Table 1). Fecal pellet samples from November to February had a high frequency of leaves and flowers in contrast to fleshy-fruits, whereas fruits were the most abundant plant component during the rest of the year (Fig. 2).

In the 1120 fecal pellets analyzed throughout the year, a total of 4710 seeds were from fleshy fruits; 49.8% *R. fruticosus*, 28.3% *P. pendula*, 9.7% *L. intricatum*, 5.6% *W. aristata*, 4.7% *O. dillenii*, and 0.5% *N. pulverulenta* (their correspondence in fruit's number consumed are 71.2%, 23.6%, 2.9%, 1.2%, 0.1%, and 0.9%, respectively). The number of different fleshy-fruited plant species in the fecal pellets ranged from one in January to five in September, December, March, and June through August. This indicates that lizards consume a greater variety of fruits at the same time when they are available. Despite the temporal overlap in fruit availability of the different plant species (see Fig. 1), most fecal pellets (83.7%) had seeds from only one plant species; 16.2% of the droppings contained seeds from two plant species and 1.9% of the droppings presented seeds from three species (Fig. 3).

Mean number of seeds per fecal pellets ranged between 0.02 ± 0.1 (January) and 6.6 ± 9.8 (September). The highest value was recorded in one fecal pellet collected in May ($N = 154$ seeds of *L. intricatum*). Only 2.7% ($N = 126$ seeds) of the 4710 inspected seeds of all species appeared damaged externally (3.4% for *P. pendula*, 1.8% for *R. fruticosus*, 9.9% for *O. dillenii*, 4.9% for *W. aristata* and 0.4% for *L. intricatum*).

The high positive correlations between frequency of appearance and number of prey items of a particular species which were statistically significant, in nine months of the year, indicates that components consumed frequently (i.e., by many individual lizards) also tend to make up the highest proportion of diet volume (Table 1).

Validation of Fecal Pellets.—To assess whether fecal pellet analysis accurately reflected the make-up of the diet, we compared these results with those from

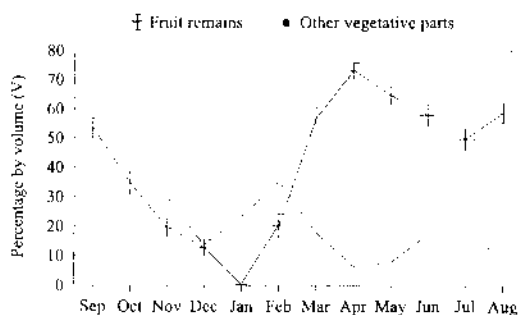


FIG. 2. Volume percentage of fleshy-fruit remains and other plant parts (flowers and foliage) in the droppings of *Gallotia galloti* (September 1993 through August 1994). In the case of fruit remains, figures indicate mean (\pm SE). Only mean values of other plant remains are shown to simplify the figure. See Table 1 for sample sizes and total percentage of plant matter (V) in each month.

analyses of the digestive tract content (stomach and intestine) obtained in August. This showed no differences either in percentage of plant material (angular transformation, ANOVA, $F_{1,115} = 0.016$, $P = 0.89$) or number of seeds (primarily *P. pendula*; logarithmic transformation, $F_{1,115} = 0.44$, $P = 0.51$) between fecal pellets and digestive tract contents. Furthermore, the relative consumption of plant material measured did not increase significantly with lizard size ($r_p = 0.22$, $P = 0.09$, $N = 60$), although number of seeds recorded in the digestive tract increase with lizard size ($r_p = 0.28$, $P = 0.036$, $N = 60$; Valido and Nogales, 2003).

DISCUSSION

The results of this study indicate that the diet of *G. galloti* in Teno Bajo includes a large proportions of plant material, similar to diets reported for other populations of *G. galloti* in Tenerife (Barquín and Wildpret, 1975; Díaz, 1980; Valido and Nogales, 1994; Valido, 1999), and other *Gallotia* species from the Canary Islands (Naranjo et al., 1991; Mateo and López-Jurado, 1992; López-Jurado and Mateo, 1995; Nogales et al., 1998; Pérez-Mellado et al., 1999; Valido, 1999). The overall data for *Gallotia* contrast with studies of the great majority of lacertids for which an insectivorous diet has been described (see review in van Damme, 1999).

One of the most striking features of *G. galloti* in Teno Bajo is the frequent use of fleshy fruits through the year. Fruit remains were recorded as an important percentage of the whole sample (60.2% and 41.8% in mean values in frequency of occurrence and percentage by volume, respectively), and peaking in April and May with volume values over 64%. In January, fruits were less important (only one seed from fleshy-fruit was detected), probably because in this month only juvenile lizards (with a more insectivorous diet; Valido, 1999) were active (pers. obs., and see also the lowest value in mean diameter of droppings, Table 1). Furthermore, one important consideration in this study is that fecal pellets collected in seven months had values of more than 50% of fleshy-fruit remains, both in FO and percentage by volume (V).

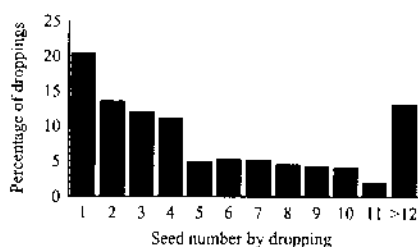


FIG. 3. Frequency distribution of number of seeds found in the droppings of *Gallotia galloti* in Teno Bajo (Barranco de Las Cuevas, Tenerife). Percentages calculated from a total of 1120 fecal pellets analyzed during a year.

Presence of fruit in the diet varied with fruit availability in the study area. Fruits of *R. fruticosus* and *P. pendula* had the highest values of FO: 98.4% (*R. fruticosus* in March) and 89.9% (*P. pendula* in September). Moreover these fruits were also consumed after the period when they were first available, since lizards ate these dried-fruits directly from branches (*R. fruticosus*) or from the ground (*P. pendula*).

Although all Canarian lacertid species feed regularly on fleshy-fruits, only three previous studies have reported (in FO) the quantitative importance of fleshy-fruits in their diet: *G. atlantica* from Alegranza islet (32%; Nogales et al., 1998), and Fuerteventura (12%; Valido and Nogales, in 2003), and in an introduced population of *G. stehlini* in Fuerteventura (49%; Naranjo et al., 1991). In other lacertids some authors have reported separate values for fruits, showing the quantitative importance of this component, but especially in insular species and populations (Sadek, 1981; Salvador, 1986a,b; Hernández, 1990; Castilla and Bawens, 1991; Pérez-Mellado and Corti, 1993; Hódar et al., 1996). This island phenomenon in lacertids is also in accordance with other island species of other lizard families (e.g., Auffenberg, 1979; Schoener et al., 1982; Whitaker, 1987; Sylber, 1988; Shea, 1989; Fellers and Drost, 1991; Dearing and Schall, 1992; Willson et al., 1996; Mitchell, 1999).

In conclusion, the population of *G. galloti* we studied showed extensively, and seasonally variable, frugivorous food habits, including primarily fleshy fruits most of the year. These results are comparable to those obtained from studies of other well-known and classical frugivorous birds and mammals (Heithaus, 1982; Wheelwright, 1986; Herrera, 1989, 1995; Charles-Dominique, 1991; Willson, 1993). These omnivorous insular species may be fulfilling similar to roles birds and mammals in the seed dispersal process (Valido and Nogales, 1994; Traveset, 1995; Willson et al., 1996; Wotton, 2002). For these reasons, we emphasize the need for more exhaustive studies to demonstrate the importance of this vertebrate group as seed disperser on islands, where this mutualistic phenomenon may occur more frequently (Olesen and Valido, 2003).

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