Frugivory and seed dispersal by the lizard Gallotia galloti (Lacertidae) in a xeric habitat of the Canary Islands

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The relationship between an endemic lizard (*Gallotia galloti*) and plants with fleshy fruits was examined in a xeric habitat on the island of Tenerife, Canary Islands. An analysis of 441 droppings collected in May 1991, showed that fruits are an important item in the diet of this omnivorous lizard; 92% and 56% of droppings contained fruits from two different areas. Fruits of seven plant species were found in the droppings: *Rubia fruticosa, Neochamaelea pulverulenta, Withania aristata, Lycium intricatum, Atriplex semibaccata, Opuntia dillenii* and *Scilla* cf. *haemorrhoidalis*. The number of fruit species consumed at each area by *G. galloti* was related to their availability.

Seed viability did not differ between control seeds and seeds from the droppings, except for *N. pulverulenta* and *L. intricatum*, where viability was higher in control seeds. The gut passage of seeds significantly reduced the germination of *R. fruticosa* and *N. pulverulenta*, increased that of *W. aristata* while no differences were found for the rest.

Gallotia galloti preferred rocky and grassy sites with less open ground and more shrub cover (> 50 cm in height). This should produce a non-random seed shadow in the habitats, potentially affecting the distribution of species with fleshy fruits.

Omnivorous lizards on islands can act as important seed dispersers over short distances for plant species with fleshy fruits, actively influencing both their relative abundance and vegetation structure in xeric habitats.

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Among vertebrates which disperse seeds, birds and mammals are most commonly associated with fleshy fruits (see review in Ridley 1930, van der Pijl 1972, Janzen 1983, Howe 1986, and Jordano 1992). In contrast, few studies have focused on the importance of reptiles as seed dispersal agents (Rick and Bowman 1961, Barquín and Wildpret 1975, Hnatiuk 1978, Iverson 1985, Whitaker 1987, Cobo and Andreu 1988, Traveset 1990, Milton 1992), despite their presumed role in the seed dispersal of the ancient gymnosperms during the Jurassic (cf. Howe 1986). This lack of studies may be due to the fact that the great majority of reptile species, particularly lizards in continental habitats (where most studies of seed dispersal

have been carried out), are basically insectivorous (e.g., Avery 1966, Pianka 1973, Pérez-Mellado 1982, Castilla et al. 1991), and unlikely to play an important role in seed dispersal.

Several studies, however, have emphasized the importance of omnivorous and vegetarian diets in island lacertids (e.g., Sadek 1981, Machado 1985, Fellers and Drost 1991) and noted fleshy fruits as part of the lizard's diet. These studies, however, were largely based on anecdotal information and results were not interpreted in the context of the plant-animal interaction.

In this study, we examine the importance of the Lacertidae, *Gallotia galloti* (Duméril and Bibron 1839), as an

Table 1. Composition of shrub species and percentage of plant cover in the two study areas. (+) species present in the area but not included in sampling. (−) species not present in the area. Species marked with an asterisk (*) have fleshy fruits.

Species	Vegetration cover (%)	
	Barranco	Llano
Rubia fruticosa Ait.*	28.9	0.3
Withania aristata (Ait.) Pauq.*	4.3	+
Neochamaelea pulverulenta (Vent.) Erdtm.*	1.2	4.0
Lycium intricatum Boiss.*	+	3.7
Opuntia dillenii (Ker-Gawl.) Haw.*	3.4	7.2
Atriplex semibaccata R. Br.*	−	+
Scilla cf. *haemorrhoidalis* Webb et Berth.*	+	−
Euphorbia obtusifolia Poir.	9.6	8.5
Euphorbia canariensis L.	6.8	+
Launaea arborescens (Batt.) Murb.	0.6	2.0
Artemisia thuscula Cav.	0.1	4.7
Periploca laevigata Ait.	0.3	3.6
Kleinia neriifolia Haw.	0.1	0.8

agent in seed dispersal. We sought to achieve the following objectives: 1) To document the importance of fleshy fruits in the diet of this species in the ripening period. 2) To test disperser legitimacy considering the differences in seed viability and germination between seeds which passed the lizard's guts and control seeds. 3) To study disperser efficiency taking into account the sites of seed delivery. Habitat use and the present vegetation distribution in the study area were compared to determine the role played by the lizard in the modification of its habitat (Livingston 1972, Herrera 1985).

Natural history of Gallotia galloti

The genus *Gallotia* (Lacertidae) is endemic to the Canary Islands and is represented by four species. *G. galloti* is restricted to the islands of Tenerife, La Palma, La Gomera and El Hierro. For each of these islands, a different subspecies of *G. galloti* has been described (Bischoff 1985). It is a medium-sized species (135 and 126 mm, snout-vent-lenght for males and females, respectively) (Salvador 1985), and it is widely distributed from the coast to the mountains (Klemmer 1976), occupying all habitats except the evergreen laurel forest where it is scarce (Bischoff 1982). Densities of up to 500 individuals per ha have been recorded (Castanet and Báez 1988) in Tenerife.

G. galloti appears to be omnivorous (Klemmer 1976) and Díaz (1980) observed the presence of arthropods, shoots, leaves, flowers, etc. in its stomach contents. Barquín and Wildpret (1975) reported the presence of seeds of *Plocama pendula* Ait. (Rubiaceae) and *Solanum lycopersicum*. L. (Solanaceae) in the lizard's droppings.

Study area and methods

Field work was carried out at Teno Bajo (28°21'N, 16°54'W), north-western Tenerife (total surface of the island: 2 034 km²), Canary Islands. Teno Bajo is located in one of the three oldest geological sectors on the island (Carracedo 1990). The climate is typical of that of dry Canarian coastal habitats, with an annual average temperature of about 21°C and approximately 300 mm annual rainfall, falling mainly in the winter period November-January (Marzol-Jaén 1988).

Two adjacent sites, about 0.5 km apart were chosen. One was located in Barranco de Las Cuevas, 150 m a.s.l. (hereafter referred to as 'Barranco'), and the other was on an open plain, near Las Casas, 60 m a.s.l. (hereafter referred to as 'Llano'). The areas selected in the two sites were approximately one and two ha, respectively.

The isolation of this area has contributed to the good preservation of the vegetation and is thus one of the most representative areas of xerophytic shrub vegetation in the Canarian archipelago. This xeric vegetation consists mainly of low, sparse scrub, and is dominated by *Euphorbia* species (Euphorbiaceae). Other common species in this community are *Kleinia neriifolia* (Compositae), *Launaea arborescens* (Compositae), *Periploca laevigata* (Asclepiadaceae), as well as others with fleshy fruits, such as *Rubia fruticosa* (Rubiaceae), *Plocama pendula* (Rubiaceae), *Neochamaelea pulverulenta* (Cneoraceae), *Lycium intricatum* (Solanaceae) and the introduced species *Opuntia dillenii* (Cactaceae) which now grows wild, after being introduced for cultivation from Central America.

Whilst the species composition of the flora of the two sites was very similar, plant cover and relative abundance (estimated by tracing 10 intersecting lines 50 m long in each area) showed clear differences (Table 1), just as did the height of the plants ($\bar{x} = 1.5$ m, s = 0.50 m, n = 40 in Barranco and $\bar{x} = 0.9$ m, s = 0.38 m, n = 40 in Llano). Of the plant species listed in Table 1, 45.5% have fleshy fruits, making up a more important proportion (approximately double) of the vegetation cover in Barranco than they do in Llano.

Study material

The 441 lizard droppings (181 from Barranco and 260 from Llano) analyzed in this study were collected in the first fortnight of May 1991. It seems very likely that droppings had been recently deposited (no longer than approximately two months earlier) due to the fruiting period of the fleshy-fruit species. Random transects were used for dropping collection from the two kinds of substrates distinguished in this study (rocky and bare ground) in both Llano and Barranco during the same period. Time spent in dropping collection from the two substrates was the same (90 min in each). Spring was the richest period of fruit production for most of the species

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Table 2. Composition of the lizard (*G. galloti*) diet in the two habitats at Teno Bajo. % FAE: percentage of droppings with the species present. % F: percentage of the total fruits or insect prey in the droppings. % S: percentage of the total number of seeds. x̄: average number of seeds or animal prey items in droppings (only where present). sd: standard deviation.

	Barranco					Llano				
	% FAE	% F	% S	x̄	sd	% FAE	% F	% S	x̄	sd
Rubia fruticosa	80.5	97.1	80.3	4.8	4.1	1.1	1.1	0.4	1.0	0.0
Withania aristata	17.7	2.3	12.3	3.4	2.4	6.5	3.4	8.4	3.1	2.4
Neochamaelea pulverulenta	1.1	0.4	0.2	1.0	0.0	5.7	10.1	2.8	1.2	0.4
Lycium intricatum	0.5	–	0.1	–	–	6.9	13.4	24.5	8.8	13.2
Opuntia dillenii	14.4	0.2	6.3	2.2	1.4	38.7	1.1	29.9	1.9	1.5
Atriplex semibaccata	–	..	–	–	–	3.1	70.9	19.7	15.8	15.4
Scilla cf. *haemorrhoidalis*	–	–	–	–	–	1.9	–	2.2	2.8	2.2
Indetermined	1.1	–	–	–	–	7.2	–	–	–	–
Coleoptera	19.4	21.1	–	1.1	0.3	27.2	15.0	–	1.1	0.4
Hemiptera	3.8	3.9	–	1.0	0.0	4.2	2.2	–	1.0	0.0
Formicidae	34.4	52.2	–	1.5	0.9	57.9	74.4	–	2.5	2.9
Other Hymenopt.	6.6	7.8	–	1.1	0.6	5.0	2.9	–	1.1	0.5
Indetermined	13.8	15.0	–	1.1	0.3	9.5	5.5	–	0.5	0.6

	n		%		n		%	
Droppings with remains of fruits	165		91.7		148		56.7	
Droppings with remains of arthropods	90		50.0		186		71.3	
Droppings with only fruits	82		45.6		42		16.1	
Droppings with only arthropods	7		3.9		80		30.7	

which produce fleshy fruits in the study area (*R. fruticosa, N. pulverulenta, A. semibaccata, W. aristata* and *Scilla* cf. *haemorhoidalis*), except for *L. intricatum* (winter) and *O. dillenii* (spring–summer). The collected droppings are representative of a fruiting phenology period when all dominant species have ripe fruit available.

The droppings were analyzed in water and examined under magnification (16×). The various components were separated for subsequent quantification and identification. Seeds were identified to the species level, whereas insects were identified to the level of order (except the Formicidae). Comparative material collected at the study site was used in identification.

The diameters of fleshy fruits collected were measured by using a digital caliper, and were weighed (precision balance of 0.1 mg). Dry weight was obtained by drying the fruits in an oven (45–50°C) for 24–48 h. The minimum number of fruits consumed was estimated by using the average number of seeds counted in each dropping. This a conservative estimate because the largest fruits of *Neochamaelea pulverulenta* and fruits of *Opuntia dillenii* are eaten in pieces.

Seed germination and viability tests

Viability and germination of seeds were determined in order to find out whether the passage through the lizard's gut affected the seeds.

The undamaged seeds of the five most common species (seeds from *Atriplex* and *Scilla* were not used in this tests), both those collected from the plants (3–5 fruits per plant on different branches collected from approximately twenty plants per species on the same dates and from the same sites), as well as those found in the droppings were sown on a standard and sterilized substrate. The germination tests were performed in a greenhouse, starting for all species in mid-September (1991) through December (90 d) until no further germination was detected. This period coincides with the beginning of seed germination after the first rains in autumn. Petri dishes were not used because the seeds sown on soil better reflect ecological reality. Before the experiment, both lots of seeds (from droppings and plants) were stored in darkness for the same period of time. There was no influence of germinated seeds on the subsequent germinations because each seed was planted in an independent compartment. The night-day light period conditions were those naturally found in the study areas. Germinated seeds and emerging seedlings were recorded daily.

Viability tests were carried out using 2, 3, 5 triphenil tetrazolium (TTC) (Heydecker 1965 and 1968, Scharpf 1970). Grease and oils were first removed from the seed surface by dipping seeds in 70% ethanol for 30 s. Thereafter, they were kept in water for 24 h, immersed in TTC, and kept in the dark. After a further 24 h, seeds with a wholly or partially colored embryo were considered viable.

Habitat use and plant distribution

Forty line transects (2 000 m in total) were recorded in the

Table 3. Results obtained in germination tests on seeds taken from droppings and seeds collected directly from plants (controls). Statistical value is for χ^2, except in the case of *O. dillenii*, where Fisher's exact test was used (p = 0.12).

Species	% Seed germination droppings	(n) from controls	χ^2-test	p
Rubia fruticosa	67.1(70)	92.9(70)	15.3	***
Neochamaelea pulverulenta	4.0(50)	32.0(50)	11.4	***
Withania aristata	55.7(70)	28.6(70)	9.5	**
Lycium intricatum	14.3(70)	20.0(70)	0.4	n.s.
Opuntia dillenii	0.0(70)	5.7(70)	–	n.s.

study area, by walking slowly so as not to disturb the lizards. At every point where a lizard was detected, two perpendicular lines (10 m long) were traced. The direction of the two lines was determined by the position of the sun (orientation of one of the lines to the sun). A wooden stick with a height scale was held vertically on the ground to determine the presence or absence of stones, bare ground, grass or shrubs at different heights so as to calculate the percentage cover for these variables. All these variables were recorded along the lines at 1-m intervals starting from the center, no notes being made at the intersection. This method allows 20 samples of substrate and vegetation variables to be taken for each individual lizard (n = 50 individual lizards). More details of the method used can be found in Carrascal et al. (1989) and Díaz and Carrascal (1990). Four sampling points were established in each of the 20 random line transects (50 m long) to make a total of 80 sampling points. Random selection of the position of the sampling point was achieved by dividing the transects into 12-m intervals and taking a point alternately 1 m to the right or to the left of the transect as the sampling point.

In order to check whether the plants which were being actively dispersed by *G. galloti* were more abundant in a particular kind of substrate, a total of 320 random sampling points were located on the rocky and bare ground substrates (160 at each site). Each point was chosen at random over a line with horizontal scale. A 0.5×0.5 m grid was centered over each sampling point. On each sampling point we counted the number of individuals of each fleshy-fruited species within the grid.

To test for differences in vegetation cover of each species on rocks and bare ground, we measured the diameter in 296 random individuals (157 on rocks and 139 on ground) of all species. No significant differences in vegetation cover between the two substrates for any of the species measured were found (U = 557, p > 0.05, Mann-Whitney U-test in the case of *N. pulverulenta*, and all p > 0.05, Student's t test for each one of the rest of the species). For a similar method see Tester et al. (1987).

Statistical analyses were carried out following Sokal and Rohlf (1981). Non-parametric tests were used for those data in which distribution did not meet the requirements of parametric tests, even after transformations (Siegel 1990).

Results

Composition of the diet

A total of 1 526 seeds were found in the 441 droppings analyzed. Most seeds corresponded to *R. fruticosa* in Barranco and *O. dillenii*, in Llano (Table 2). The diet in both places is clearly omnivorous, being composed of fruit remains, arthropod fragments, and other plant remains (leaves, stalks, flowers, etc.). In the first two weeks in May, lizards showed a clear tendency to eat fruits, whose seeds were found in 91.7% of droppings from Barranco and 56.7% from Llano. In 51.8% of the droppings, the number of seeds ranged from 1 to 5, in 14.7% between 6 and 11, and in 5.6% the number was even greater.

Five and seven plant species with fleshy fruits were consumed in the two zones respectively (Table 2). The most representative at Barranco was *R. fruticosa*, while at Llano *A. semibaccata* and *O. dillenii* were basic elements. Although *O. dillenii* had a higher frequency of appearance (38.7%) than *A. semibaccata* (3.1%), *A. semibaccata* fruits made up 70.9% of total number of fruits eaten at Llano. The fruits eaten by lizards are mainly taken on the plants.

Significant differences in the frequency of appearance between the two sites were observed in the following species: *R. fruticosa* (χ^2 = 611.1, df = 1, p < 0.001), *N. pulverulenta* (χ^2 = 41.4, df = 1, p < 0.001), *L. intricatum* (χ^2 = 68.2, df = 1, p < 0.001) and *A. semibaccata* (χ^2 = 446.1, df = 1, p < 0.001). *R. fruticosa* was the most abundant species in the droppings from Barranco, whilst the others were more abundant at Llano, with the exception of *Scilla* cf. *haemorrhoidalis* and *A. semibaccata*, which were only present in the Llano droppings. No significant differences were found in the case of *W. aristata* (χ^2 = 0.24, df = 1, p > 0.05) and *O. dillenii* (χ^2 = 0.94, df = 1, p > 0.05).

With regard to the presence of other plant remains (stalks, leaves, flowers, etc.), 98% of droppings contained fragments of these materials.

The animal groups most frequently consumed were Formicidae and Coleoptera. Consumption of Formicidae was significantly lower in the Barranco site (χ^2 = 29.3, df = 1, p < 0.001). Between-site differences for the other animal prey groups were not significant. The possibility of certain soft-bodied insects (e.g. larvae of Coleoptera, Lepidoptera) being underestimated in the analysis of the droppings should be noted.

Table 4. Habitat utilization by *G. galloti*. x̄ = average mean and sd = standard deviation. ** p < 0.01, *** p < 0.001, n.s. = not significant. n = 50 and 80 for lizard and random samples, respectively.

| Structural variables | % Cover | | | | | |
| | Lizard sample | | Random sample | | | |
	x̄	sd	x̄	sd	t	p
Rock	39.7	23.59	29.1	18.70	2.63	**
Open ground	44.9	25.64	71.0	18.74	6.69	***
Litter cover	24.3	18.04	25.9	18.78	0.59	n.s.
Grass at ground level	8.1	10.39	9.9	11.15	1.17	n.s.
Grass (10 cm height)	20.0	13.21	17.7	11.36	0.96	n.s.
Grass (30 cm height)	15.5	15.91	7.9	8.77	2.95	**
Shrub (50 cm height)	7.3	9.16	1.6	3.24	5.31	***
Shrub (>50 cm height)	22.6	15.1	35.8	17.25	4.65	***

Germination and viability of the seeds

The seeds of *R. fruticosa* and *N. pulverulenta* showed a significantly lower ability of germination after being ingested by lizards (Table 3). In contrast, the seeds of *W. aristata* which had been eaten by lizards had a significantly higher percentage of germination than those collected from plants. No significant effects of digestive treatment were found for *L. intricatum* and *O. dillenii*.

The highest percentages of broken seeds appearing in the droppings occurred in *O. dillenii* and *L. intricatum*, with values as high as 16% and 28%, respectively. The percentage observed for the other species was less than 3%.

The seeds of *W. aristata* and *L. intricatum* from droppings germinated significantly earlier than the other species (Kolmogorov-Smirnov test, p < 0.001 for both species). In the case of *R. fruticosa* and *N. pulverulenta*, quite the opposite occurred (p < 0.001). None of the *O. dillenii* seeds from the droppings germinated.

Four of the species (*O. dillenii, W. aristata, A. semibaccata* and *R. fruticosa*) showed no significant differences in viability between the seeds found in the droppings and those collected from plants (G-test, p > 0.05 for all four species, n = 101, 108, 57 and 103, respectively). However, there were differences in *N. pulverulenta* (G = 11, p < 0.05, n = 59) and *L. intricatum* (G = 11.8, p < 0.01, n = 108), for which the percentage of viable embryos was higher in the seeds collected from fresh fruits than from those contained in droppings.

Habitat use and vegetation distribution

Five out of eight habitat variables showed significant differences (p < 0.01) between their availability and actual use by the lizards (Table 4). Lizards tended to favor zones with rock cover and open ground with low shrub cover (>50 cm). They also showed a preference for places with greater grass cover with a height of 30 to 50 cm. No significant differences were observed in the re-

maining variables (plant litter cover, grass at ground level, and grass at 10 cm).

In the samples taken from the two substrates, bare ground and rocky places, in the two study sites, three plant species showed significant differences in frequency: *R. fruticosa* (χ^2 = 42.7, df = 1, p < 0.001, n = 150), *W. aristata* (χ^2 = 4.3, df = 1, p < 0.05, n = 150) and *N. pulverulenta* (χ^2 = 24.6, df = 1, p < 0.001, n = 150) are more frequent on rocky places than on bare ground; the opposite occurs for *O. dillenii* (χ^2 = 17.9, df = 1, p < 0.001, n = 150). No significant differences were obtained for *L. intricatum* (χ^2 = 0.7, df = 1, p > 0.05, n = 150).

Discussion

Frugivorous diet of the lizard Gallotia galloti

The important contribution that fruits play in the diet of *G. galloti* has been shown in the two habitats, in both of which this species is largely frugivorous. The unequal availability of plant species with fleshy fruits in the two habitats appears to determine the differences in the proportion of fruit remains found in the droppings (Barranco = 91.7%, Llano = 56.7%). However, an important seasonal difference in the contribution of fleshy fruits to the lizard's diet will depend upon the abundance of species with ripe fruits at each point in time.

The size of fruits consumed by lizards varied considerably (diameter: 2.64–34.6 mm, see Appendix). Fruits of *O. dillenii* and the largest fruits of *N. pulverulenta*, are eaten in pieces (Valido and Nogales pers. obs.). The lizards are thus able to make use of these larger fruits just as Whitaker (1987) observed for lizards in New Zealand.

Of the fruits consumed by lizards in xeric habitats in the Canary Islands, three of the main species eaten are *Plocama pendula* (Barquín and Wildpret 1975, Valido and Nogales, pers. obs.), *R. fruticosa* and *O. dillenii* (present study), all of which have a high water content (see Appendix). This fact might be explained by the

water requirements of a reptile living in a xeric island habitat with only a limited locomotive ability to move to the scarce watering points in this environment. Milton (1992) has arrived at the same conclusion with leopard tortoises, *Geochelone pardalis* (Bell), that feed on succulents plants and fruits of *Opuntia ficus-indica* (L.) Mill. and *Atriplex semibaccata* in South Africa.

G. galloti is an important disperser over short distances, within one vegetation type or across an ecotone (see also Barquín and Wildpret 1975 and Whitaker 1987 for other Lacertidae species). Sampling over a wider area would certainly increase the number of fruit species eaten by the lizards, such as *Plocama pendula* Ait. (Rubiaceae), observed by Barquín and Wildpret (1975), *Jasminun odoratissimum* L. (Oleaceae) and *Visnea mocanera* L. fil (Theaceae) (pers. obs.).

Most Lacertidae lizards are insectivorous (e.g., Avery 1966, Pérez-Mellado 1982, Valakos 1986), although a few appear omnivorous, such as *Lacerta lepida* (Hernández 1990). On islands, omnivory occurs in several species of this family, such as *Lacerta dugesii* (Sadek 1981) in the Madeira archipelago, *Gallotia simonyi* (Machado 1985) and *G. stehlini* (Barquín et al. 1986, Naranjo et al. 1991) in the Canarian archipelago. Frugivory also has been observed in nocturnal and diurnal geckoes and skinks in New Zealand (Whitaker 1987). Although few omnivorous reptile species are currently known, a great number of ancient reptiles were herbivorous (e.g. Benton 1991). This decline in numbers was possibly due to the fact that most reptiles did not undergo a process of adaptation which might favor this type of food, e.g. suspension mode in the buccal apparatus for handling plant food (Ostrom 1963), large size to provide the physical strength necessary for an adequate handling of vegetable matter and to provide better thermal conditions for endosymbiont (Sokol 1967). Szarski (1962) contends that a vegetarian diet is more generally associated with island conditions (where a process towards gigantism occurs) or in lizards species of great size.

Effects on germination by the lizard

There are numerous papers investigating the effect of seed passage through the disperser's gut, showing very variable results depending on the species that interact. In some plant species, an increase in germination has been observed (e.g. in reptiles: Rick and Bowman 1961, Cobo and Andreu 1988; in birds: Krefting and Roe 1949, Barnea et al. 1990 and 1991; in mammals: Lieberman et al. 1979, Rogers and Applegate 1983), while in other species no germination differences have been detected (e.g. in reptiles: Whitaker 1987, Traveset 1990; in birds: McDiarmid et al. 1977, Howe and Vande Kerckhove 1979, Lieberman and Lieberman 1986; in mammals: Alexandre 1978, Pigozzi 1992).

Looking at our overall results for the germination and viability tests and the dormancy period of the species in

question, it can be seen that two species, endemic to the Macaronesian archipelagoes, *N. pulverulenta* and *R. fruticosa* are those which are negatively affected by *G. galloti*. The opposite is observed for *W. aristata*, a non-endemic species. No differences were found for *O. dillenii* and *L. intricatum*, suggesting that *G. galloti* is a legitimate disperser for *W. aristata*, *O. dillenii* and *L. intricatum*, while it is an illegitimate disperser for *N. pulverulenta* and just less effective for *R. fruticosa* (67% vs 93%; see Table 3). *W. aristata* seeds also germinated earlier and at a higher percentage level than the control seeds.

In the case of *O. dillenii*, its expansion has been favored by its ecological interactions with the lizard, in much the same way as described by Walker (1990) for the introduced plant *Myrica faya* Ait., which is dispersed by autochthonous birds in Hawaii.

What must be considered in the case of *N. pulverulenta* and *R. fruticosa* is the fact that although the interaction has been going on for much longer on an evolutionary time scale there is still a drop in germination percentage, which brings home the independence of direct selection pressure and germination. Nevertheless, many other factors may be contributing to these interactions, such as the characteristics of the seeds (size, consistency, shape, etc), differential selection of fruits by the disperser or the existence of a high percentage of aborted seeds.

It is known that the germination ability of seeds is affected by the enzymatic action within the disperser's guts (Rick and Bowman 1961, Janzen 1981). Retention time in the gut of each species is important to consider also in relation to seed size (Levey 1986, Barnea et al. 1992) and the morphological features of the seed coat (Barnea et al. 1990, Barnea et al. 1991). Futher investigations are neccesary to clarify the relationship between retention time in the gut and germination success.

However, the effect of the dispersers can be observed in the non-random seed shadow in the habitat as a result of habitat use by the species (Livingston 1972, Herrera and Jordano 1981).

Habitat selection pattern

The study of the lizard's habitat choice reveals that structural variables, both of the vegetation profile and surface structure, are the factors responsible for the appearance and distribution of this species (Table 4). *G. galloti* shows a preference for rocky places over bare ground and for reduced shrub cover. These preferences reflect the importance of thermoregulation in reptiles. Grass cover 30 to 50 cm in height influences the species' habitat use because low shrub cover generates a continuous sun/shade gradient suitable for basking (Carrascal et al. 1989). This holds true for both heliothermic regulation, for which little shrub cover is sought, and for thigmothermic regulation, where the requirement is for greater basaltic rock cover (Spellerberg 1982). Rocky areas also offer a suit-

able refuge from predators. This is important as lizards are often taken by feral cats (*Felis catus*) (Nogales et al. 1990) and the common kestrel (*Falco tinnunculus*) (Martín 1987).

The preference for areas of greater grass cover, between 30 and 50 cm high, benefits the lizard since it minimizes the distance and length of movement between sun and shade in favor of optimum temperature and reduction of predation risk (Díaz and Carrascal 1990).

The results confirm the importance of vegetation structure (Pianka 1967, Díaz and Carrascal 1990) and that of the substrate on various vital parameters such as thermoregulation and predator avoidance.

Potential effects on vegetation distribution

Although our data do not show the differences in seed shadows between the two substrates very clearly, our habitat use results could indicate that non-random seed shadows will be produced in the habitat.

We assumed that the patterns observed in the lizards (see Table 4), as a result of their preference for certain areas (greater numbers of rocks and lower shrub cover), would cause a clear differential increase in seed density (per surface unit) in each of the substrates. The rocky areas show certain physical characteristics, such as higher humidity, less desiccation and predation (Livingston 1972), which are thought to create suitable microhabitats for the germination and settlement of plants in this xeric environment. This phenomenon has also been noted by Livingston (1972) and Whitaker (1987), who consider that microhabitats with rocky outcrops also provide greater protection from herbivores and trampling by animals. They may also favor the growth of plants because they offer a suitable microenvironment (greater humidity, smaller temperature variations, etc.). Despite the fact that some frugivores have been described as inefficient dispersers (see e.g. Bustamante et al. 1992), *G. galloti* could be considered an equally efficient disperser as the lizards observed by Whitaker (1987), the birds studied by Livingston (1972) and the mammals studied by Pigozzi (1992) and Tutin et al. (1991).

These suggestions are supported by the current distribution of plants (both indigenous, non-endemic and endemic) considered in this study. All fleshy-fruit species tend to be concentrated in this kind of microenvironment (rocky sites), except for *O. dillenii*, introduced around the middle of the last century (Rodríguez Delgado, pers. comm.), which is the only species detected more frequently on bare ground than in rocky areas. This fact is difficult to explain properly because the distribution could be the result of human agricultural practices and lizards' dispersion.

Birds and mammals have been shown to be important in determining vegetation structure, diversity and forestal dynamics (Smith 1975, Herrera 1984, Debussche et al. 1985, Stiles 1985, Lewis 1987, Dinerstein 1991, etc.). In the present case, the dispersal of seeds by *G. galloti* could be responsible for the current composition of the xerophytic scrub in the study area. The relative abundance and distribution of each species with fleshy fruits may well depend on the consumption of these fruits by the lizard. However, it is important to consider differences in seed survival, germination probability and herbivore risk on seedlings from one microhabitat to another in order to evaluate the role of Canary lizards on patterns of vegetation distribution. Futhermore, in order to know the dispersal role of the lizard, it should be necessary to compare with the other dispersal agents present in the study area (*Sylvia* spp. and *Corvus corax*), despite their lower density.

As shown by this study, fruits are an important part of the diet of lizards in scrub areas in the Canary Islands. More extensive studies are needed to quantify the selection pressures and fitness effects of lizards on fleshy-fruited species.

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Appendix

Characteristics of fruits and biogeographic range of the species dispersed by G. galloti. (*): Nogales unpubl. data. CE: Canary endemism. ME: Macaronesian endemism. INE: indigenous non-endemic. IM: introduced by man. All species are shrubs except A. semibaccata that is herbaceous.

Species	Color	Fruit type	Biogeography range	Length (mm)	Diameter (mm)	Fresh weight (g)	Dry weight (g)	% of water	Average seeds/fruit (±s.d.)	Seed weight (g)	N
Rubia fruticosa	translucent	berry	ME	7.50	5.60	0.20	0.037	81.50	1.4± 0.2	0.0074	40
Whitania aristata	orange-red	berry	INE	9.32	9.63	0.51	0.190	62.70	9.3± 1.5	0.0100	35
Neochamaelea pulverulenta	purple-red	drupe	CE	9.82	10.58	0.64	0.400	37.50	1.0± 0.0	0.3780	35
Lycium intricatum (*)	red	berry	INE	7.40	4.85	–	–	–	6.5± 0.9	0.0031	20
Opuntia dillenii	purple-red	berry	IM	45.60	34.60	30.37	6.250	80.00	89.6±18.4	0.0369	19
Atriplex semibaccata	red	drupe	INE	3.67	2.64	0.0096	0.0030	68.75	1.0± 0.0	0.0005	28
Plocama pendula	translucent	berry	CE	3.17	3.53	0.027	0.0080	70.24	2.4± 0.4	0.0007	45