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RELATIONSHIPS BETWEEN PLANTS AND MEDITERRANEAN LIZARDS

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Different kinds of interactions between lizards and plants in the Mediterranean basin have been described. Lizards have shown to »use« plants as a refuge against predators, as a foraging site, as a thermal microhabitat or as a food resource. In the last case, they can either act as herbivores (+/– interaction, consuming vegetative and/or reproductive parts, and damaging the plant to a higher or lower degree) or as mutualists (+/+ interaction, by behaving as legitimate pollinators and/or seed dispersers).

Keywords: Mediterranean lizards, *Podarcis*, Lacertidae, pollination, seed dispersal, mutualism, herbivory, foraging behaviour

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U radu se opisuju različite vrste međudjelovanja biljaka i guštera u sredozemnom prostoru. Pokazalo se da gušteri »koriste« biljke kao zaklon od predatora, mjesto na kojem traže hranu, termalno mikrostanište ili izvor hrane. U posljednjem slučaju mogu se ponašati kao herbivori (+/– međudjelovanje, konzumiranje vegetativnih i/ili reproduktivnih dijelova, i oštećivanje biljke u većoj ili manjoj mjeri) ili kao mutualisti (+/+ međudjelovanje, ponašajući se kao pravi oprašivači i/ili raznositelji sjemena).

Keywords: sredozemni gušteri, *Podarcis*, Lacertidae, oprašivanje, raznošenje sjemena, mutualizam, herbivornost, traženje hrane

INTRODUCTION

Lizards have traditionally been considered as poor plant consumers due to their lack of particular adaptations to this type of food (SOKOL, 1967; POUGH, 1973). A set of constraints limit true herbivory in lizards. First, there are limitations directly re-

lated with plant processing. Lizards have a streptostylic mandibular suspension via quadrate bone that precludes the use of mandibles for chewing (OSTROM, 1963) and apparently lack the ability to fragment plant tissues (SZARSKI, 1962). Hence, only soft vegetal tissues are really available to them (KING, 1996). Small lizards, however, can take advantage of vegetative tissues by using a piercing technique (HERREL *et al.*, 1998) similar to the epidermal piercing of insects such as Homoptera and Heteroptera (HOWE & WESTLEY, 1988). This piercing of plant tissues decreases gut passage time and, in turn, digestive efficiency (BJORNDAL *et al.*, 1990).

Small lacertid lizards are also limited by their digestive and fermentation systems. They can use a wide range of plant nutrients (soluble carbohydrates, starch, organic acids, proteins, etc.) without any morphological or physiological adaptation. They are oligophagous herbivores, eating a limited variety of plants that they recognize. Lizards are adapted to eat fiber-poor components of plants like fruits, seeds, flowers and buds.

In this work we will summarize the present-day knowledge of plant uses of Mediterranean lacertid lizards that promote different types of interaction between lizards and plants.

PLANT CONSUMPTION BY LACERTID LIZARDS

The consumption of plants by animals has a long evolutionary history. A vast set of different adaptations to herbivory arose around 450 million years ago (HOWE & WESTLEY, 1988). In the case of Mediterranean lacertids, their interaction with plants is much more recent, probably beginning when these lizards colonized insular ecosystems and underwent a speciation process. Previously, the interaction between lacertid lizards and plants was probably restricted to the use of plants as refuges, foraging or thermoregulation sites, as indicated when examining the trophic ecology of lacertid lizards on the continent, where plant use is fairly frequent but never important as a main food resource (PÉREZ-MELLADO, 1991).

Enlarging the database employed in a previous survey on the feeding ecology of lacertid lizards (see PÉREZ-MELLADO, 1991, a full list of references employed will be provided by the first author upon request), we can determine the extent of plant use by this lizard group. Plant use seems to be uncommon in the Lacertidae, excluding the genus *Gallotia*, endemic to the Canary Islands (see, for example, MOLINA, 1986 for *Gallotia stehlini*; and PÉREZ-MELLADO *et al.*, 1999, for *Gallotia simonyi*). Plants are present only in 26.7% of stomach contents of *Lacerta* species, and in 33.3% of the genus *Psammodromus*. They are absent in *Acanthodactylus*, whereas *Podarcis* appears to be the genus with the highest frequency of plant material in the stomachs (57.1%). In the whole family Lacertidae, plant tissues represent on average 6% of the total prey types.

Significant differences in the importance of plant consumption, estimated as the volume of plant matter in faeces, are found when comparing two groups of lacertid lizards, those from the Mediterranean basin (including both continental and insular populations) with those of non-Mediterranean areas (one-way ANOVA, $F = 13.68$, $p = 0.003$; for the Mediterranean basin: $= 16.99 \pm 2.17\%$, n = 106 populations, range =

0–78%, whilst for the non-Mediterranean populations: = 0.06 ± 0.06%, n = 24, range = 0–15%). We found similar results when using the percentage of plant presence in individuals as the dependent variable ($F = 7.40$, $p = 0.008$; Mediterranean populations: = 19.97 ± 2.62%, n = 93, range = 0–83.33%, non- Mediterranean: = 4.43 ± 4.34%, n = 23, range: 0–100%). However, when we exclude the insular populations from the Mediterranean areas, the significant differences between the two groups disappear (volume of plant matter in faeces: U Mann-Whitney test, $U = 254.5$; $Z = -1.93$, $p = 0.052$; percentage of individuals with plant matter: $U = 238.5$, $Z = -0.71$, $p = 0.47$), which indicates that plant matter is not more important in the diet of continental lizards from the Mediterranean basin than in that of lizards from other continental areas in the distribution range of the family in Europe. We lack information on the trophic ecology of most lacertid lizards from Africa.

PLANT USE IN MEDITERRANEAN ISLANDS

Plant consumption by the two species of lizards endemic to the Balearic Islands, *Podarcis pityusensis* and *Podarcis lilfordi*, cannot be considered true trophic specialization. Several lines of evidence support this idea. First, the helminth infracommunities in the digestive tracts of both species do not differ much and are typical of insectivorous lizards, lacking any evidence of herbivorous specialization (HORNERO & ROCA, 1994; ROCA & HORNERO, 1994). From the point of view of morphological and physiological specialization, little work has been done so far. EISENTRAUT (1950) pointed out that *Podarcis lilfordi* has a longer intestine than other lacertid lizards, as an adaptation to herbivory. However, SALVADOR (1986) rejected these observations after measuring intestinal canals of several populations of *P. lilfordi* from Cabrera Archipelago. CARRETERO (1997) also failed to demonstrate a significant correlation between intestine length and degree of herbivory when performing a comparative study of different species of lacertids.

In the Aegean Sea area, insular populations of *Podarcis erhardii* and *Podarcis milensis* do not use plant material as a significant food item (VALAKOS *et al.*, 1997). Plant material is also apparently absent from the diet of *Podarcis peloponnesiaca* and *Lacerta graeca* (MARAGOU *et al.*, 1997). Thus, the case of Balearic lizards is the best known example of plant use in the Mediterranean basin.

According to published information (SÁEZ & TRAVESET, 1995; SALVADOR, 1976, 1986; TRAVESET, 1995, 1997 and unpub.), a variety of plant species are consumed by *Podarcis lilfordi* in Cabrera Archipelago (Tab. 1). Additionally, in a recent spring survey of plant consumption by *P. lilfordi* from ten islets around Menorca (PÉREZ-MELLADO *et al.*, unpub. data), a total of 45 plant species belonging to 26 different families have been recorded from a sample of 968 faeces.

SEED DISPERSAL BY LIZARDS

The study of seed dispersal by reptiles has received little attention compared to seed dispersal by either birds or mammals (e. g. HOWE & WESTLEY, 1988; JORDANO, 1992). Within lacertid lizards, GELINEO & GELINEO (1963, *in*: TIEDEMANN & HENLE,

Tab. 1. Plant use by *Podarcis lilfordi* in the Cabrera archipelago.

Plant species	Family	Part	Locality	Source	R
Juniperus phoenicea	Cupressaceae	Fr	C	1,2	SD
Ephedra fragilis	Ephedraceae	Fr	C	1	SD
Ficus carica	Moraceae	Fr	C	1,2	SD
Arthrocnemum fruticosum	Chenopodiaceae	Fl	NP	1	C
Chenopodium murale	Chenopodiaceae	Fl,Fr	C	2	SD?
Suaeda vera	Chenopodiaceae	Fl,L	C,NPr,R,I	2	C
Capparis inermis	Capparaceae	Fr	R	2	SD?
Fumana ericoides	Cistaceae	Fl	C	1	C
Alyssum maritimum	Brassicaceae	Fl	C	1	C
Sedum sp.	Crassulaceae	Fl	C	2	C
Anthyllis fulgurans	Leguminosae	Fr	NF	2	SD?
Medicago arborea	Leguminosae	Fl	ED	2	C
Euphorbia characias	Euphorbiaceae	Fl	C	3	P?
Euphorbia dendroides	Euphorbiaceae	N	C	1	P
Rhamnus ludivici-salvatoris	Rhamnaceae	Fr	C	1,2	SD
Pistacia lentiscus	Anarcadiaceae	Fl, Fr	C,F	1,2	SD
Lavatera arborea	Malvaceae	Fl,N	RT,X	2	C
Cneorum tricoccon	Cneoraceae	Fl,Fr	C,CN	1,2	SD
Withania frutescens	Solanaceae	Fr	R	1	SD
Rosmarinus officinalis	Labiatae	Fl,N	C,F	1,2	C,P?
Daucus gingidium	Umbelliferae	Fl,Fr	F,NF	2	SD?
Limonium caprariense	Plumbaginaceae	Fl	ED	2	C
Phillyrea angustifolia	Oleaceae	Fr	C	1,2	SD
Phillyrea latifolia	Oleaceae	Fr	C	1	SD
Cuscuta epithymum	Convolvulaceae	Fl	NF	2	C
Globularia alypum	Globulariaceae	Fl	C	1,3	C
Helichrysum sp.	Compositae	Fl	ED	2	C
Dracunculus muscivorus	Araceae	Fr	C	4	SD
Asparagus stipularis	Liliaceae	Fr	C	1	SD

Part: Fr= Fruit, N=Nectar, Fl= Flowers; L= leaves

Sources: 1: SÁEZ & TRAVESET (1995) and TRAVESET (1995); 2: SALVADOR (1976, 1986); 3: TRAVESET (1997); 4: TRAVESET (unpub.).

R: Role. P= pollinator; SD= seed disperser; C= consumer.

Locality: C= Cabrera Island; CN= Conejera Island; F= Fonoll; I= Imperial islet; NP= Na Plana islet; NF= Na Foradada islet; Npr= Na Pobra islet; ED= Estell de dos Colls islet; R= Redona islet; RT= Ses Rates islet; X= Xapat gros islet.

1986) recorded the consumption of *Capparis rupestris* fruits by *Podarcis melisellensis*, as well as fruits of *Opuntia ficus-indica* (BUTZ & KUENZER, 1956) and of *Solanum nigrum* (BOLKAY, 1923, 1925 *in*: HENLE & KLAVER, 1986) by *Podarcis sicula*. VALIDO & NOGALES (1994) and NOGALES *et al.* (1998) studied seed dispersal by *Gallotia galloti* and *G. atlantica* in the Canary Islands. In the Western Mediterranean, HERNÁNDEZ (1990) showed the role of *Lacerta lepida* in seed dispersal of some plant species, although it is in the Balearic islands where the longest list of consumed fruits has been reported (see Tab. 1 and references therein).

In the Menorca islets we identified ten different plant species whose seeds appeared intact after passing through the intestines of lizards (PÉREZ-MELLADO *et al.*, unpub. data). Lizards are thus potentially seed dispersers, not destroying the seeds in their digestive tracts even if these seeds are of a large size.

In order to have an idea of the relative importance of seed dispersal by lizards in the Balearic Islands, we may compare our results found to date with lists of vascular plants dispersed by other vertebrates, such as carnivorous mammals, that have not received much attention as important frugivores and seed dispersers until recently (e.g. HERRERA, 1989). In Herrera's 10 year survey encompassing an area of 20,000 ha in Parque Natural de Cazorla (southeastern Iberian Peninsula), three species of carnivores (*Vulpes vulpes, Meles meles* and *Martes foina*) were found to disperse a total of 27 vascular plants. In the Balearics, with an area of approximately 500,000 ha, lizards consume the fruits (and presumably disperse the seeds) of a minimum of 26 species.

The viability of seeds after passing through the guts of lacertid lizards has been demonstrated in a variety of species such as *Cneorum tricoccon* (TRAVESET, 1995), *Phillyrea latifolia rodriguezii* (PÉREZ-MELLADO *et al.*, unpub. data), *Opuntia dillenii, Neochamaelea pulverulenta, Plocama pendula, Lycium intricatum, Withania aristata* (VALIDO & NOGALES, 1994 and NOGALES *et al.* 1998) and *Withania frutescens* (CASTILLA, unpubl.). Depending upon the plant species ingested, lizards can even modify the rate and/or percentage of seed germination (see review in TRAVESET, 1998).

In short, Mediterranean lacertid lizards are potentially important seed dispersers for a number of plant species, particularly in insular ecosystems, where they usually are the dominant group of terrestrial herbivores (IVERSON, 1985).

NECTARIVORY AND POLLINATION BY LIZARDS

The consumption of nectar by lizards within the family Lacertidae has been observed in insular populations of *Podarcis lilfordi* (PÉREZ-MELLADO, 1989; PÉREZ-MELLADO & CORTI, 1993; PÉREZ-MELLADO & CASAS, 1997; SÁEZ & TRAVESET, 1995; TRAVESET & SÁEZ, 1997), *Podarcis dugesii* (ELVERS, 1977, 1978; BEYHL, 1990), *Podarcis sicula* (HENLE, 1984) and *Gallotia caesaris* (BEYHL, 1997).

Foraging behavior can have a direct influence on the effect of lizard plant use. In the islands of Menorca and Cabrera, we detected at least four plant species in which foraging was performed by moving among inflorescences searching for nec-

tar, without apparent damage to the flowers. This was the case in *Crithmum maritimum* in all the islets of Menorca where its consumption was observed, in *Allium ampeloprasum* at Sanitja islet (Menorca, PÉREZ-MELLADO & CASAS, 1997), *Euphorbia dendroides* at Cabrera island (TRAVESET & SÁEZ, 1997) and *Launaea cervicornis* at Sargantana islet (Menorca, PÉREZ-MELLADO, unpub. data).

Pollination by lizards has been demonstrated only on two occasions, in *Podarcis lilfordi*, in the Cabrera Archipelago (TRAVESET & SÁEZ, 1997) and on a Menorcan islet (PÉREZ-MELLADO & CASAS, 1997). TRAVESET & SÁEZ (1997), in a two-year study of a typically entomophilous plant, *Euphorbia dendroides*, showed that in areas of Cabrera where lizards are abundant, they visit flowers much more frequently and stay longer on the inflorescences than insects, resulting in higher fruit sets. Lizards promote both geitonogamy and cross-pollination in that species. The other species in which effective pollination has been found is the sea fern, *Crithmum maritimum*, in the islet of Sanitja (PÉREZ-MELLADO & CASAS, 1997). The nectar usually acts as a medium of transport that enhances the probability of pollen load. In these two studies (and see also PÉREZ-MELLADO, 1989 and PÉREZ-MELLADO & CORTI, 1993), lizards were also observed consuming stamens of the plants they pollinated; thus nectaring might also lower male plant fitness to some degree (TRAVESET & SÁEZ, 1997).

TRAVESET & SÁEZ (1997) proposed that early flowering, with minimum temperatures, low insect activity and low number of plant species blooming and competing for pollinator attraction, could be the main factor that explains the time spent by lizards feeding on nectar of *Euphorbia dendroides*. Interestingly, similar factors are at work on Sanitja islet in Menorca, where strong nectaring behaviour and pollination of *Crithmum maritimum* take place during the second half of summer, at very high temperatures, also with very few flying insects and with the sea fern as the only plant species blooming (PÉREZ-MELLADO, 1989; PÉREZ-MELLADO & CASAS, 1997).

POLLEN TRANSPORT

ELVERS (1977) indicated that the smooth texture of lizard skin precludes an effective pollen transport. Nevertheless, TRAVESET & SÁEZ (1997) recorded an average of 209 ± 232 ($\pm$SD) pollen grains of *Euphorbia dendroides* attached to the snout of three lizard individuals. Pollen was up to 50% more abundant in the ventral part of the snout.

In Menorca, a first survey on pollen transport by lizards (PÉREZ-MELLADO *et al.*, submitted) shows that the Balearic lizard is able to transport large quantities of different pollen species. This survey was performed on three different islets: (1) Sanitja, where *P. lilfordi* pollinates the sea fern (PÉREZ-MELLADO & CASAS, 1997), (2) Aire, from which we have abundant information on plant use by lizards, and (3) Rei islet, with a great plant diversity but a smaller plant use by lizards (PÉREZ-MELLADO & CORTI, 1993). Four plant species, *Crithmum maritimum*, *Pancratium maritimum*, *Pistacia lentiscus* and *Carlina corymbosa* account for 99.55% of the 98,842 pollen grains attached to lizards, the sea fern alone accounting for 97.66% of the total amount. The remaining 435 pollen grains belong to 23 different plant species. In

Sanitja islet, the presence of sea fern pollen is even higher, accounting for 98.69% of the pollen transported by lizards. The quantities of pollen grains of *Allium ampeloprasum* in lizard snouts are also important. In the case of Rei island, very small quantities of pollen grains were recorded on lizards. The pollen of *Pistacia lentiscus* was the most abundant, representing 73.80% of the 252 counted pollen grains.

THE IMPORTANCE OF INTERACTIONS TO ENDEMIC PLANT SPECIES

In Menorca, at least four plant species used by *Podarcis lilfordi* are endemic (CAO, 1996), either to this island (*Phillyrea latifolia rodriguezii*; Oleaceae and *Daphne rodriguezii*; Thymelaeceae), or to the Balearics (*Arum pictum*; Araceae and *Launaea cervicornis*; Compositae). Lizards have been observed consuming their pollen and/or fruits (PÉREZ-MELLADO, unpub. data). Of *Launaea cervicornis*, the Balearic lizard eats its pollen and also its small leaves. Finally, lizards have been observed feeding on the leaves of *Arum pictum* in Menorca (PÉREZ-MELLADO, pers. obs.) and might actually exert a negative effect on the plant; however, intact seeds of this species were found in lizard feces in the islet of Moltona (south of Mallorca) (SÁEZ & TRAVESET, 1995).

HERRERA (1989) stressed the importance of seed dispersal by carnivores for some Mediterranean plant species. Under some circumstances, modified habitats lacking the presence of these mammal species might have problems with seed dispersal of some vascular plants. In the case of small island populations, there is a similar or even more important effect of the seed disperser. In some microinsular ecosystems, the only terrestrial vertebrate able to disperse seeds is *Podarcis lilfordi*.

DISCUSSION

According to our results, the use of plant material as a food resource by lacertid lizards seems to be uncommon. Only in insular populations are plants a frequent food item. A significant variation in plant consumption was also detected when comparing western with eastern Mediterranean populations of lacertid lizards, finding a lower herbivory in the latter.

At least in the Balearic Islands, the endemic lacertid lizards play a potentially important role both as pollen vectors and as seed dispersers of several plant species. Our current knowledge, however, is still fairly poor. We need more studies on both the quantitative and qualitative relative importance of lizards as pollinators compared to insects that also visit the plants. Likewise, for seed dispersal studies, a wider quantification of the interaction between lacertid lizards and fleshy-fruited plants is necessary, of the kind that has been done for other vertebrate frugivores such as birds and mammals. In this sense, it is important to study what factors contribute to the selection of fruits by lizards (fruit size, color, maturation stage, fruit crop, accessibility, etc.) and know which are »preferred« by them. This, for instance, has been examined in the case of carnivores by HERRERA (1989), who found that these frugivores tended to select fruits with low fresh weight, number of seeds and

relative pulp weight. Moreover, we know almost nothing about the capacity of dispersion in terms of distances covered by lizards in their daily movements. Compared to birds or mammals, the distance dispersal for lizards is probably short. However, such distances may be essential in some cases to maintain local plant populations in small isolated localities, such as the Mediterranean islets, and it may also help in avoiding or reducing plant inbreeding in these populations.

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SUMMARY

Relationships between plants and Mediterranean lizards

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Different kinds of interactions between lizards and plants in the Mediterranean basin have been described. Lizards have shown to »use« plants as a refuge against predators, as a foraging site, as a thermal microhabitat or as a food resource. In the last case, they can either act as herbivores (+/- interaction, consuming vegetative and/or reproductive parts, and damaging the plant to a higher or lower degree) or as mutualists (+/+ interaction, by behaving as legitimate pollinators and/or seed dispersers).

The importance of plants as a food resource for Mediterranean lizards has been found to be high in insular habitats, especially in small islands, where the paucity of arthropod prey availability redirects the foraging activity of lizards towards other nutrient resources. In such small islands, plants may play a major role in the trophic ecology of lacertid lizards, as suggested by recent studies. Likewise, lizards may be important both as efficient pollen transporters and seed dispersers for a variety of plants. Some of these plant-lizard interactions are unique. The effect lizards have on the reproductive and dispersal success of some species may be very relevant for plant preservation, and in turn, the preservation of particular behavioral and ecological traits of the particular lizard populations depends, at least partly, on the plants they interact with.