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The effect of plant consumption in the overall diet of an omnivorous lizard

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Abstract. During the blooming period of the thistle *Carlina corymbosa* L. (Asteraceae) on Aire Island (Menorca, Balearic Islands, Spain), the Balearic lizard, *Podarcis lilfordi*, climbs the plant and forages on its inflorescences. We studied this foraging behaviour by means of observation. We collected data on fourteen variables belonging to three groups: movements and foraging strategy, use of *C. corymbosa* as a trophic resource, and foraging behaviour of *P. lilfordi* on this plant species. Analysis of these variables shows that *P. lilfordi* employs a mixed strategy of licking and plucking *C. corymbosa* flowers, probably due to a low nectar production and/or its difficulty of access. Interestingly, some behavioural traits are similar to those observed while foraging on carcasses. We also studied the diet of *P. lilfordi* through analysis of faecal samples. We found that *C. corymbosa* is a key food resource during summer. Foraging on *C. corymbosa* led to consumption not only of plant elements, but also of different proportions of flying and terrestrial prey by lizards living in areas of the island with or without *C. corymbosa*. In this manner, the consumption of a plant species during a short period of annual activity has an unexpected influence on the overall diet of these lizards.

Key words. Squamata, Lacertidae, Balearic lizard, *Podarcis lilfordi, Carlina corymbosa,* foraging, herbivory, Mediterranean islands.

Introduction

The study of foraging behaviour occupies a large part of the existing literature, especially since the seminal works by MacArthur & Pianka (1966) and Emlen (1966) that laid the theoretical basis of the optimal foraging theory. Optimal foraging entails maximizing the energy benefit while spending the least amount of time and energy. Early works on lizard foraging defined two foraging modes: sit-and-wait or ambush foraging, and wide or active foraging (Pianka 1966, Huey & Pianka 1981). Subsequent empirical studies have revealed that in some cases foraging patterns fall clearly within one of these two categories, and that such a bipolar view is appropriate and/or analytically very useful (e.g., McLaughlin 1989, Cooper & Whiting 2000, Cooper 2005, 2007). Nevertheless, foraging behaviour falls between these two extremes in other species, so that it would be a continuum (e.g., Magnusson et al. 1985, Perry et al. 1990, Perry 2007). When this is the case, there is no clear consensus among authors of the numerical threshold between these modes.

On several coastal islets off Mallorca and Minorca, the Balearic lizard, *Podarcis lilfordi* (Günther, 1874; Squamata: Lacertidae), is almost the only terrestrial vertebrate. This lizard has been living in the absence of competitors and with few predators for thousands of years prior to the arrival of people during the Holocene (Corti et al. 1999). *Podarcis lilfordi* has high population densities compared to continental lacertid lizards of similar body size (Pérez-Mellado et al. 2008), reduced clutch sizes (Perera & Pérez-Mellado 2002), marked sexual dimorphism in body size, with males being larger and more robust than females (Perera & Pérez-Mellado 2002), and a wide range of foraging behaviours (Pérez-Mellado & Corti 1993).

On small islands, food resources are usually scarce and their presence and abundance are unpredictable and strongly seasonal (Pérez-Mellado & Corti 1993). In continental areas, the higher density of invertebrate prey allows most lizards to be insectivorous. Furthermore, the higher predation pressure in continental areas may favour insectivory, because consuming insects allows lizards to acquire the most energy per unit of foraging time. On small islands, where predation pressure is lower, lizards have been able to develop a wide range of foraging behaviours on other sources of food, frequently incorporating into their diets plant matter (Pérez-Mellado & Corti 1993, van Damme 1999, Cooper & Vitt 2002), carrion, remains of marine animals that wash ashore, human leftovers, or even conspecifics (Pérez-Mellado & Corti 1993; authors' pers. obs.).

Omnivory is widespread in islet habitats, because specializing in the consumption of a particular food resource would give rise to dramatic consequences in the population during the year, or even the season, when that resource became less abundant (MacArthur & Pianka 1966). Although consumption of plants by *P. lilfordi* is frequent, this species exhibits none of the anatomical or physiological modifications that are typical of herbivores (Pérez-Mellado & Traveset 1999). Thus, omnivory and herbivory can be associated with body morphologies that are not directly related to the type of diet, which means that the morphology of a species of squamate reptile does not necessarily predict its diet (Schwenk 2000). Omnivorous island lizards select a wide range of food items, adopting a large variety of searching and handling strategies depending on the type of trophic resource. They may consume diverse plant products, including fruits, leaves, nectar, pollen or entire flowers. Typically, fleshy leaves, fruits and some flowers are plucked, while other flowers, probably with higher nectar production, are intensively licked (Pérez-Mellado 2009).

Aire Island (Minorca, Balearic Islands, Spain) only serves sea birds for breeding, as well as two or three passerine bird species in some years. The only mammal present in the island is the introduced rabbit, *Oryctolagus cunniculus*, and arthropod biomass is low in July and throughout the summer. In addition, very few plants flower during that period. One of them is the thistle *Carlina corymbosa* L. (Asteraceae). Over many years, we have been observing *P. lilfordi* climbing to the top of its inflorescences and foraging, either licking or tearing off flowers (Pérez-Mellado 2009; Fig. 1). This behaviour was different from the behaviour these lizards exhibit on other plants such as the sea fern, *Crithmum maritimum* L., which is much more intensively licked (Pérez-Mellado & Casas 1997). *Crithmum maritimum* blooms from late July or early August and has a higher nectar production than *C. corymbosa*.

The overall aim of this study is to describe the characteristics of the foraging behaviour of the Balearic lizard on *C. corymbosa* and the strategy adopted by the lizards in their consumption, as well as the importance of this relationship to the diet of the lizard. Even if there is abundant literature concerning the use of plant matter by lizards (van Damme 1999, Cooper & Vitt 2002, and references therein), the influence of plant consumption on the overall diet of omnivorous lizards has rarely been addressed. Our hypothesis is that during the short period of blooming of some plant species, acting as seasonal key resources, as is the case with *C. corymbosa*, foraging behaviour of lizards is substantially modified and will result in a significant difference between the remaining prey consumed by individuals living in areas with *C. corymbosa* and lizards living in areas without that plant species. We also hypothesize that differences in sex, age, body size, weight, strength, or experience may be associated with differences in foraging behaviour and diet.

Figure 1. An individual of *Podarcis lilfordi* foraging on an inflorescence of the thistle, *Carlina corymbosa*, on Aire Island (Minorca, Balearic Islands, Spain).

Materials and methods

We conducted this study on Aire Island, a 32-hectare islet off the coast of Minorca on sunny July days between 2008 and 2011. The main blooming species in July is *C. corymbosa*. We divided Aire Island into two study areas, one of them with a high density of *C. corymbosa*, and the other without it and dominated by *C. maritimum* and *Suaeda vera* instead.

Study species

Carlina corymbosa is a biannual thistle of dry and poor habitats of the Mediterranean region. It is 10–70 cm high. Blooming occurs between late June and early August, and the yellow florets are clustered in several flower heads at the end of the branches (Meusel & Kästner 1990). Its florets are primarily insect-pollinated, and the nectar production is low, and/or access to the nectarium is difficult (Hidalgo & Cabezudo 1995).

Podarcis lilfordi is a lacertid lizard endemic to the Cabrera Archipelago and the offshore islets of Mallorca and Minorca (Balearic Islands, Spain). It is medium-sized with a maximum SVL (snout–vent length) of 81 mm in males and 75 mm in females (Pérez-Mellado 1998). *Podarcis lilfordi* reaches high population densities on Aire (Pérez-Mellado et al. 2008). Its diet consists mainly of insects, although it frequently consumes vegetal matter as well, especially in summer when prey is scarce. Plant products ingested are leaves, fleshy fruits, pollen, nectar and whole flowers (Pérez-Mellado 1989, Pérez-Mellado & Corti 1993).

Field observations

The same observer (APC) made focal observations in July of 2008, at 07.00–10.00 h GMT, when the lizards were more active. We located a lizard on *C. corymbosa* by randomly searching. We then observed it through binoculars from a distance of 3–4 m. We used a digital voice recorder and additionally recorded the activity of the lizard including time spent on moving, estimated distances travelled, switching between plants or inflorescences, foraging behaviour, and any additional information that might be useful for comparative purposes among individuals and situations. At the end of each observation, we measured with a ruler the height of each inflorescence used by the lizard. Whenever possible, observation was continued while the lizard was on a *C. corymbosa* plant, for a minimum of 10 minutes (Perry 2007). In some cases, the lizard moved out of sight, and our observation was terminated before that time limit. We considered as valid only those observations that lasted for at least 90 seconds. We obtained 53 valid focal records with an average duration of 7.90 minutes (minimum: 90 seconds, maximum: 35.38 minutes, total: 6.98 hours). We obtained 16 focal records from subadult individuals and 37 from adults. Within adults, 10 were male and 27 female.

Data analysis

We calculated two quantitative indices of foraging behaviour: movements per minute (MPM) and proportion of time spent moving (PTM) (Cooper 2005, Perry 2007). We analysed 14 variables of two types: continuous variables with duration, which were later converted into a percentage of the total observation time (activity or occupation of a given substrate), and discontinuous behavioural variables of very short duration, which were counted as number of events per minute. We defined three groups of variables based on the information they provide:

Group 1: Movement variables commonly used to define the foraging mode: number of moves per minute (MPM), the percentage of the time spent moving (PTM) (Pianka et al. 1979, Huey & Pianka 1981), and distance covered per minute (DPM). Distance per minute was calculated as the total distance covered divided by the total duration of the focal record. MPM and PTM are the most commonly used measurements, and, although they are usually correlated, each provides distinct yet complementary information (Perry 2007). We recorded only two attacks on prey by subadults and four by adults. Due to this small sample size, we did not calculate the percentage of attacks while moving (PAM) (Cooper & Whiting 1999) or the proportion of attacks made while stationary (AWS) (McBrayer et al. 2007).

Group 2: Variables that describe the use of *C. corymbosa* as a trophic resource: percentage of time spent on *C. corymbosa*; percentage of time spent on inflorescences; number of inflorescences visited per unit of time; number of switches between different inflorescences per unit of time, and number of plants visited per unit of time. As each *C. corymbosa* plant can have several inflorescences, we counted the number of inflorescences and number of plants visited independently.

Group 3: Variables that describe the foraging behaviour of *P. lilfordi* on flowers: number of times the lizard ate per unit of time; percentage of time spent eating; number of tongue flicks per unit of time; number of licks on flowers per unit of time; number of bites into flowers per unit of time and number of flowers plucked per unit of time.

Diet study

We studied the diet of *P. lilfordi* by analysing faecal pellets. In July of 2008, 2009, 2010, and 2011, we collected samples from all over the island. We obtained 601 pellets in the area where *C. corymbosa* was present and 285 pellets in the area where it was absent. Furthermore, in 2008 and 2010, we collected some individual faecal samples directly from lizards perched on *C. corymbosa*. Faecal pellets were analysed using a binocular dissecting microscope with a micro-

Table 1. Results of different variables analysed from focal observations of the Balearic lizard (*Podarcis lilfordi*) on *Carlina corymbosa* (see details in the text) on Aire Island. The standard error is abbreviated SE.

	Age				Sex			
	Adults (N = 37)		Subadults (N = 16)		Males (N = 10)		Females (N = 27)	
Variable	mean	SE	mean	SE	mean	SE	mean	SE
Duration of observation (sec)	446.2	61.4	539.5	105.5	337.8	61.5	486.4	80.3
Distance travelled (cm)/min	27.2	4.1	31.9	3.5	22.3	4.7	29.1	5.4
PTM	10.5	0.9	17.0	2.5	8.9	1.8	11.2	1.1
MPM	1.8	0.2	2.2	0.2	1.5	0.4	1.9	0.2
% time spent on *C. corymbosa*	84.7	3.8	87.3	4.0	82.6	8.7	85.5	4.2
% time spent on flowers	58.4	4.3	56.0	5.0	59.8	10.2	57.9	4.6
Inflorescences visited/min	0.8	0.1	1.0	0.1	0.8	0.3	0.7	0.1
Changes between inflorescences/min	0.7	0.1	0.9	0.1	0.8	0.4	0.7	0.1
Plants visited/min	0.3	0.0	0.3	0.1	0.3	0.1	0.3	0.0
Eating bouts/min	1.6	0.2	1.6	0.2	1.7	0.5	1.5	0.2
% time spent eating	13.8	2.0	14.3	3.0	10.8	3.5	15.0	2.4
Number of tongue flicks/min	0.5	0.1	0.6	0.2	0.4	0.2	0.5	0.2
Number of licks/min	7.6	1.9	10.6	3.4	5.6	3.7	8.4	2.3
Number of bites/min	0.4	0.1	1.2	0.3	0.6	0.2	0.4	0.1
Number of pulls/min	2.2	0.5	1.4	0.5	2.8	1.5	1.9	0.4
Height on flowers above ground (cm)	37.4	2.3	38.4	2.8	37.6	5.9	37.3	2.3

meter, identifying prey items to family or order level. We measured characteristic body parts of prey to estimate the dry mass of each prey with regression equations. Where possible, we applied the regression equations we had developed from arthropods collected in the study area during previous years (Pérez-Cembranos et coll. unpubl. data). When no such equation was available for a prey group, we adopted a suitable substitute from Hódar (1996, 1997) or Díaz & Díaz (1990). When prey items were identified but measurements were not possible, we assigned the average dry mass recorded for that group in the study area. When we could not identify the group of arthropod remains, we assigned the average dry mass recorded in faeces for all arthropod groups. We only made statistical analyses of prey mass for those prey groups for which estimated dry mass values were available. Plant consumption was estimated as the percentage of plant volume in the total volume of the pellet. When possible, we identified the species and structures of plant remains by comparing them to a collection of several plant species from Aire Island. We carefully searched for remains of small and soft-bodied prey, such as larvae and spiders. In lizards, diet reconstruction based on this meticulous faecal pellet analysis is as accurate as one based on stomach content analyses from dissected lizards (Pérez-Mellado et al. 2011).

We carried out statistical tests with the raw data of prey frequency for each taxon (n), frequency of pellets in which each taxon was present (presence), and dry weight estimated for each taxon (biomass). We calculated prey abundance (%n) as the percentage of a given prey type in relation to the total prey number, and the relative prey or plant presence (%p) as the percentage of faeces containing a given type of prey or plant. The percentage of estimated biomass (%b) is the proportion of dry weight of each prey type relative to the total estimated biomass (Rosenberg & Cooper 1990). We estimated diet diversity using both Levins' niche breadth index (B) (Levins 1968) and its standardised form (B_a) (Hurlbert 1978). We calculated Pianka's index (O) (Pianka 1973) to estimate dietary overlaps between individuals in the area with *C. corymbosa* and the area where this plant was absent, as well as between age categories.

We categorized every taxon occurring in the diet of the lizards according to its mobility, following Perry (2007). We then used prey composition and movement index to calculate H_j, a single value that represents the weighted average of the locomotor tendencies of all items found in each faecal pellet (Perry 2007). This value can be expressed as $H_j = \Sigma M_i F_i$, where M_i is the movement index of prey type i, and F_i is the percentage of prey type i in the diet of lizard j. We also used the movement index M_i assigned to each prey item to construct a table of frequencies of overall mobility values for the area with *C. corymbosa* and the area without *C. corymbosa*. We proceeded in the same manner to compare the mobility of prey consumed for adult and subadult individuals.

Statistical analyses

Analyses were conducted within R framework and using the different available packages (R 2.15.1, R Core Team 2012). Because data showed non-normality and/or hetero-

Table 2. Diet of the Balearic Lizard (*Podarcis lilfordi*) each in July of 2008, 2009, 2010, and 2011 on Aire Island. n – prey frequency of each taxon; % n – percentage of prey of each taxon in relation to total prey number; Presence – frequencies of pellets in which each taxon is present; % Presence – percentage of pellets in which each taxon is present, in relation to total number of pellets; Biomass – dry weight (mg) estimated for each taxon; % Biomass – percent biomass consumed of each taxon in relation to total biomass. The *C. corymbosa* and plant matter rows show the average percentage volume per pellet (mean ± SE [standard error]) instead of prey frequency. The Total row shows the total number of prey items (n), sum of percentages (% n and % biomass), total number of pellets (presence), and total dry weight consumed (biomass). Abbreviations: B – Levins' niche breadth index; B_a – standardized form of Levins' index.

Taxon	n	% n	Presence	% Presence	Biomass	% Biomass
Gastropoda	47	1.32	44	4.97		
Pseudoscorpionida	14	0.39	14	1.58	1.7	0.03
Araneae	56	1.57	55	6.21	134.4	2.59
Isopoda	121	3.40	121	13.66	181.5	3.50
Crustacea	3	0.08	3	0.34		
Diplopoda	11	0.31	11	1.24	327.0	6.31
Dictyoptera	107	3.00	100	11.29	230.0	4.44
Isoptera	83	2.33	71	8.01	38.2	0.74
Dermaptera	13	0.36	12	1.35	170.7	3.29
Homoptera	100	2.81	89	10.05	11.3	0.22
Heteroptera	148	4.15	146	16.48	1965.3	37.92
Diptera	46	1.29	45	5.07	86.9	1.68
Lepidoptera	13	0.36	13	1.47	114.4	2.21
Coleoptera	207	5.81	184	20.77	829.5	16.01
Hymenoptera	387	10.86	156	17.61	717.3	13.84
Formicidae	2086	58.55	506	57.11	228.7	4.41
Unidentif. Arthrop.	34	0.95	34	3.84	83.6	1.61
Larvae	49	1.38	48	5.42	61.7	1.19
Seeds	31	0.87	27	3.05		
P. lilfordi	2	0.06	2	0.23		
Carrion	5	0.14	5	0.56		
C. corymbosa	10.96±0.93		159	17.95		
Plant matter	28.45±1.29		453	51.13		
Total	3563	100	886		5182.2	100
B	2.7469					
B_a	0.0873					

geneity of variances, we applied non-parametric tests. Data are showed as mean ± 1 SE. All tests were two-tailed, a = 0.05. Before applying G-tests, we grouped those taxa with frequencies < 3 to create classes of adequate sample size (Sokal & Rohlf 1995).

Results

Behaviour of *P. lilfordi* on *C. corymbosa*

Foraging mode: Both PTM and MPM were similar in adult males and females (Mann-Whitney test, U = 169, p = 0.257 for PTM values and U = 178, p = 0.148 for MPM values; see average descriptive data on Tab. 1). However, we found significant differences in PTM and MPM between adult and subadult individuals (U = 158, p = 0.007; U = 190, p = 0.040, respectively). Subadults spent a higher percentage of time moving and made more moves per minute. Distance travelled per unit of time showed no significant differences between adult males and females (U = 145, p = 0.749), or between adults and subadults (U = 227, p = 0.186).

We recorded eight cases in which two individuals were foraging on the same plant (with a distance of 10–20 cm between them). In three cases, there were two individuals of the same age class and sex, and in one, an adult female with a subadult. These lizards did not interact. In the remaining four cases, a female or another subadult individual displaced subadults from inflorescences.

Activity of lizards when foraging on *C. corymbosa*: Lizards observed during focal observations perched on inflorescences at 38 ± 2 cm height above the ground (range 0–70 cm). The number of plants visited per unit of time did not differ significantly between males and females (Mann-Whitney test, U = 140, p = 0.880; Tab. 1) or between adults and subadults (U = 333.5, p = 0.474). The proportion of time spent on *C. corymbosa* did not differ significantly between males and females (U = 142, p = 0.824) or between adults and subadults (U = 304.5, p = 0.877). As expected, we did not find significant differences in the number of inflorescences visited per unit of time by adult males and females (U = 154.5, p = 0.516) or by adult and subadult lizards (U = 219, p = 0.138). Males and females also showed a similar number of switches between inflorescences (U = 154.5, p = 0.516), as did adults and subadults (U = 208.5, p = 0.092). The proportion of time spent on inflorescences was similar in both sexes (U = 117.5, p = 0.561) and ages (U = 333, p = 0.480). In summary, the utilisation of the thistles was extremely uniform in *P. lilfordi* on Aire Island, and adults and subadults of both sexes employed a very similar strategy.

Feeding behaviour: The number of eating bouts on thistles per unit of time was similar for both sexes (Mann-Whitney test, U = 129.5, p = 0.864; Tab. 1) and ages (U = 282, p = 0.794), as well as the proportion of time they spent eating between sexes (U = 156, p = 0.451) and ages (U = 289, p = 0.900). The number of tongue flicks per unit of time was also similar in males and females (U = 122, p = 0.641), as well as in adults and subadults (U = 294, p = 0.975). We also found no significant differences in the number of licks per unit of time between sexes (U = 158, p = 0.436) or ages (U =

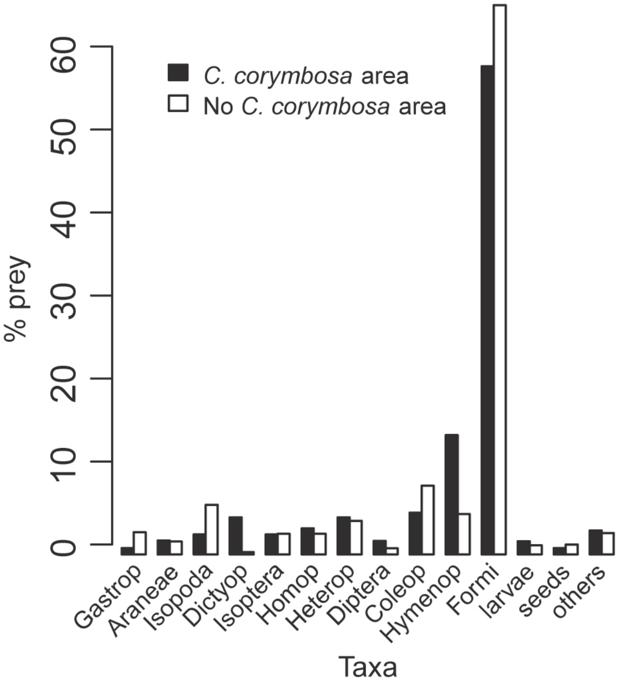

Figure 2. Percentage of prey items of each taxon in relation to the total number of prey items. We compared the percentage of prey present in faecal pellets from the Balearic lizard (*Podarcis lilfordi*) collected in areas where *Carlina corymbosa* is present (filled bars) and absent (open bars). Abbreviations: Gastrop – Gastropoda; Dictyop – Dictyoptera; Homop – Homoptera; Heterop – Heteroptera; Coleop – Coleoptera; Hymenop – Hymenoptera (excluding Formicidae); Formi – Formicidae; "Others" includes Pseudoscorpionida, Crustacea, Diplopoda, Lepidoptera, Dermaptera, unidentified arthropods, carrion remains, and *P. lilfordi*.

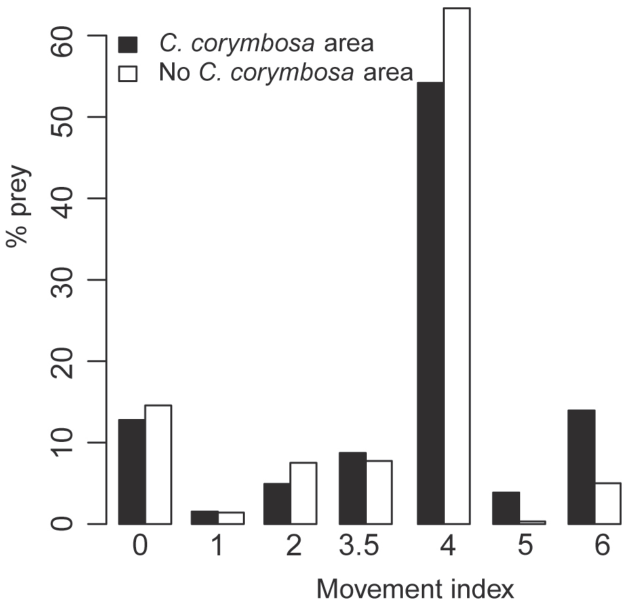

Figure 3. Overall distribution of prey mobility values in the diet of *P. lilfordi* in the areas with and without *C. corymbosa*. Values of movement index according to Perry (2007).

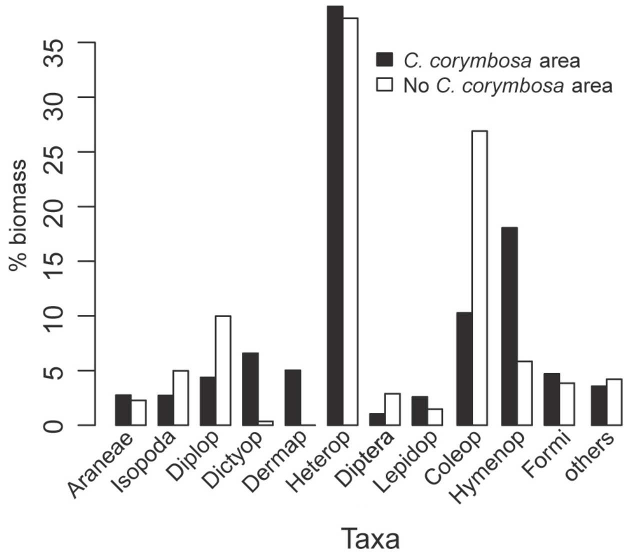

Figure 4. Percentage of the biomass of each taxon in relation to total biomass consumed by the Balearic lizard (*Podarcis lilfordi*). We compared the percentage of biomass consumed in areas where *Carlina corymbosa* is present (filled bars) and absent (open bars). Abbreviations: Diplop – Diplopoda; Dicty – Dictyoptera; Dermap – Dermaptera; Heterop – Heteroptera; Lepidop – Lepidoptera; Coleop – Coleoptera; Hymenop – Hymenoptera (excluding Formicidae); Formi – Formicidae; others includes Pseudoscorpionida, Isoptera, Homoptera, unidentified arthropods, and larvae.

261, df = 1, p = 0.499). Although we did not find differences in the number of bites into flowers per unit of time between sexes, (U = 115.5, p = 0.465), it was significantly higher in subadult individuals compared to adults (U = 162, p = 0.006). The number of flowers plucked per unit of time did not differ significantly between sexes (U = 126, p = 0.766) or age groups (U = 317.5, p = 0.678).

Carlina corymbosa in the diet of *P. lilfordi*

The diet of *P. lilfordi* was mainly insectivorous, even though it contained an important contribution by vegetal matter, which was present in more than 50% of the pellets examined (Tab. 2). In more than a third of the faecal pellets in which plants were identified, we found flowers of *C. corymbosa*, which therefore represented an important proportion in the volume of faeces (17.95%).

We found significant differences in the prey composition of the two areas, with and without *C. corymbosa* (G-test, G = 199.69, df = 17, p < 0.0001; Fig. 2). Ants were the most abundant item in both areas, although its consumption was higher in the area without *C. corymbosa*. In the area with *C. corymbosa*, the most commonly consumed types of prey were ants, Hymenoptera, Coleoptera, Heteroptera and Dictyoptera, whereas in the area without *C. corymbosa*, the prey with the highest frequency were ants, Coleoptera, Isopoda, Hymenoptera and Heteroptera. We found a higher consumption of Gastropoda, Isopoda and Coleoptera in the area without *C. corymbosa*. In contrast, Dictyoptera, Dermaptera and Hymenoptera were more abundant in the diet in the area with *C. corymbosa*. We found a significantly higher consumption of flying arthropods in the area where *C. corymbosa* was present (0.16% in the area with *C. corymbosa* and 0.06% in the area without the plant; binomial test of proportions, $\chi^2 = 71.05$, df = 1, p < 0.0001). During focal observations, we recorded five attempts, one successful, to capture flying hymenopterans. We found a significantly higher average prey mobility index in the area with *C. corymbosa* (Mann-Whitney test, U = 100355, p < 0.0001; *C. corymbosa* area, $H_j = 327.71 \pm 4.99$; area without *C. corymbosa*, $H_j = 290.52 \pm 7.02$), as well as a significant difference in the frequency distribution of mobility values in both areas (G-test, G = 152.98, df = 6, p < 0.001; Fig. 3).

The biomass values show the importance of Heteroptera in both areas (Fig. 4). In the area with *C. corymbosa*, the second most dominant prey items were Hymenoptera, Coleoptera, Dictyoptera, Dermaptera and Formicidae. In the area without *C. corymbosa*, the majority of biomass was made up by Coleoptera, Diplopoda, Hymenoptera, Isopoda and Formicidae.

Levins' index showed a wider variety of prey and more uniformly distributed frequencies in the *C. corymbosa* area (B = 2.8996, $B_a = 0.0873$) than in the area without *C. corymbosa* (B = 2.3981, $B_a = 0.0736$). The diet overlap between the lizards in the two areas was very high (Pianka's index O = 0.9814).

The average percentage volume of vegetal matter was similar in both areas (Mann-Whitney test, U = 86681, p = 0.756; area with *C. corymbosa*: 28.54 ± 1.55%; area without *C. corymbosa*: 28.26 ± 2.29%), as was the proportion of pellets in which vegetal matter appeared (binomial test of proportions, $\chi^2 = 0.21$, df = 1, p = 0.644, 95% CI = –0.05 to 0.09; area with *C. corymbosa*: 51.75%; area without *C. corymbosa*: 49.82%). The presence of remains of *C. corymbosa* was significantly higher in areas where this plant was present (binomial test of proportions, $\chi^2 = 66.92$, df = 1, p < 0.0001, 95% CI = 0.19 to 0.27; area with *C. corymbosa*: 25.29%; area without *C. corymbosa*: 2.46%), as was the average percentage of *C. corymbosa* consumption (Mann-Whitney test, U = 105122, p < 0.0001; area with *C. corymbosa*: 15.36 ± 1.29%; area without *C. corymbosa*: 1.68 ± 0.67%).

According to our results obtained from individual lizards, the diet was very similar in each age class, with no differences in the distribution of prey type frequencies (G-test, G = 9.08, df = 11, p = 0.614). None of the taxa consumed revealed differences between adults and subadults, and their niche overlap was very high (Pianka's index O = 0.9888). The mobility index H_j was also similar in both age classes (Mann-Whitney test, U = 3008.5, p = 0.816; adults, $H_j = 349.71 \pm 13.71$; subadults, $H_j = 354.24 \pm 13.98$). We did not find differences in prey mobility when the frequency of mobility values was compared between age classes (G-test, G = 3.09, df = 6, p = 0.798). In this particular analysis, all vegetal matter was identified as *C. corymbosa*. The proportion of pellets with *C. corymbosa* was relatively similar in the two age classes (binomial test of proportions, $\chi^2 = 3.14$, df = 1, p = 0.077, 95% CI = -0.01 to 0.32), as was the average volume consumed by adults and subadults (Mann-Whitney test, U = 3576, p = 0.065; adults: 35.07 ± 4.29%; subadults: 24.40 ± 4.20%).

Discussion

The Balearic lizard is an omnivorous reptile that exhibits a remarkable degree of plasticity in its foraging behaviour. Greef & Whiting (2000) argue that the opportunistic use of several food resources can lead to important changes in the foraging mode. Foraging behaviour varies greatly between populations of *P. lilfordi* and even between areas at the same locality, depending on the availability of food resources (Pérez-Mellado & Corti 1993 and authors' pers. obs.).

We found that subadults were foraging more actively than adult individuals. In other species, intraspecific differences in movement patterns were related to dietary differences (Greef & Whiting 2000). In our observations, the diet of individuals foraging on *C. corymbosa* was very similar in adults and subadults, implying that the difference in foraging mode may be due to their competing for *C. corymbosa*, as is suggested by the observed displacement of subadults from flowers by other lizards. Therefore, subadults foraging on *C. corymbosa* probably need to move more in order to avoid the pressure from other individuals.

Other plant species, such as the sea fern, *C. maritimum*, are exploited by *P. lilfordi* almost exclusively as food resources (Pérez-Mellado & Casas 1997). However, when foraging on *C. corymbosa*, the Balearic lizard exhibits a mixed strategy, since attempts to capture prey are relatively common and the proportion of flying arthropods in the diet is higher in the area with *C. corymbosa*.

Flowers of Asteraceae have a low production of nectar. In the case of *C. corymbosa*, the production is difficult to quantify because nectar is scarce and/or the position of nectaria makes it difficult to access the nectar (Hidalgo & Cabezudo 1995). Therefore, the nectar of *C. corymbosa* is either not quantitatively sufficient or not available to lizards. Moreover, the apical areas of *C. corymbosa* have a very high quantities of biomass with a high concentration of starch and oils (Meusel & Kästner 1990). *Podarcis lilfordi* discriminates between animal and plant elements in their diet based on the presence of fatty substances or sugars (Cooper et al. 2002a, 2002b).It is therefore possible that the Balearic lizard perceives the inflorescences of *C. corymbosa* and *C. maritimum* in a qualitatively different way. Consequently, *P. lilfordi* exhibits a feeding behaviour that is qualitatively different on thistles than on other flowering plants with a higher nectar production, such as *C. maritimum*. In this last case, lizards intensively lick up nectar and pollen of flowers, without destroying any part of them (Pérez-Mellado & Casas 1997). On *C. corymbosa*, lizards obtain floral elements not only by licking, but also biting and tearing them from the plant, in a similar manner to that used when feeding on a prey item that is too large to be swallowed whole. In fact, the consumption of large prey is exceptional in Lepidosauria and in the vast majority of non-mammalian Tetrapoda (Schwenk 2000). *Podarcis lilfordi* plucks *C. corymbosa* flowers by using the jaws like clamps (Pérez-Mellado 2009), a technique employed by many lepidosaurs. Sometimes, lizards will shake their heads violently when they try to dislodge pieces of a large prey item (Schwenk 2000, Metzger 2002). We observed several instances in which lizards appeared to lack the strength necessary to tear a flower from the plant. In these cases, the lizards applied another technique, biting flowers and rapidly rotating their bodies around the longitudinal axis. This technique has been described as rotational feeding, a way of handling large prey in Crocodilia (Cott 1961, Pooley & Gans 1976, Taylor 1987 in Schwenk & Rubega 2005), caecilians (Measey & Herrel 2006), and anguillid eels (Helfman & Clark 1986). Because few individuals displayed that behaviour during focal observations, we were unable to quantify it. This technique is very often employed to obtain small pieces from large vertebrate carcasses, which is a resource typically exploited by insular lizards (Pérez-Mellado 2009 and authors' pers. obs.).

Although ants quantitatively dominated the diet in areas of Aire having and lacking *C. corymbosa*, there were some striking differences between these areas in other taxa frequencies. Our results show that during its flowering season, the thistle *C. corymbosa* will be an important trophic resource in the areas of the island where it is present. Its consumption appears to be associated with a lower percentage of other plant species present in the diet, at least during this time of the year. In addition, the consumption of thistle flowers appears to have a secondary effect on foraging, i.e., the use of *C. corymbosa* as a perch to capture flying insects from. Consequently, in the area without *C. corymbosa,* consumption of some terrestrial invertebrates, including gastropods, isopods, coleopterans and ants, was greater than in the area where the thistle was present, whereas some other insects, dictyopterans and dermapterans, were more abundant in the diet in the area with *C. corymbosa*. The greatest difference was that the proportional consumption of hymenopterans (excluding ants) was three times higher in areas covered by *C. corymbosa*. Other flying insects, like Diptera and Lepidoptera, were also more abundant in the diet of the area with *C. corymbosa*. Therefore, it seems that *P. lilfordi* foraged for both plant and animal prey on the thistle. Where *C. corymbosa* was present, the lizards obtained most of their food while foraging on this plant, obtaining not only a great amount of flower material, but also an important number of flying prey, which probably were attracted by the *C. corymbosa* flowers.

In conclusion, *P. lilfordi* on Aire Island employs a wide range of techniques to forage on *C. corymbosa*, with some of them being otherwise used to feed on other plant species and some typically employed to forage on carcasses. Moreover, our analysis of the diet of *P. lilfordi* shows that lizards use *C. corymbosa* both as an important trophic resource and a perch site to capture flying insects. Consequently, during the flowering period of *C. corymbosa* and in areas where the plant is present, the overall diet and foraging behaviour of these lizards are significantly influenced by the status of the plant. While a true active forager in other areas and during other seasons, *P. lilfordi* partly and temporarily turns into a sit-and-wait forager in areas with *C. corymbosa*. This is an unexpected result that shows the role of key food resources as a modifier even if they are available only during a short period.

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References

Cooper, W. E. (2005): The foraging mode controversy: both continuous variation and clustering of foraging movements occur. – Journal of Zoology **267**: 179–190.

Cooper, W. E. (2007): Foraging modes as suites of coadapted movement traits. – Journal of Zoology **272**: 45–56.

Cooper, W. E. & L. J. Vitt (2002): Distribution, extent, and evolution of plant consumption by lizards. – Journal of Zoology **257**: 487–517.

Cooper, W. E. & M. J. Whiting (1999): Foraging modes in lacertid lizards from southern Africa. – Amphibia-Reptilia **20**: 299–311.

Cooper, W. E. & M. J. Whiting (2000): Ambush and active foraging modes both occur in the scincid genus *Mabuya*. – Copeia **2000**: 112–118.

Cooper, W. E., V. Pérez-Mellado & L. J. Vitt (2002a): Lingual and biting responses to selected lipids by the lizard *Podarcis lilfordi*. – Physiology & Behavior **75**: 237–241.

Cooper, W. E., V. Pérez-Mellado & L. J. Vitt (2002b): Responses to major categories of food chemicals by the lizard *Podarcis lilfordi*. – Journal of Chemical Ecology **28**: 709–720.

Corti, C., M. Masseti, M. Delfino & V. Pérez-Mellado (1999): Man and herpetofauna of the Mediterranean islands. – Revista Española de Herpetología **13**: 83–100.

Díaz, J. A. & M. Díaz (1990): Estimas de tamaños y biomasas de artrópodos aplicables al estudio de la alimentación de vertebrados insectívoros. – Doñana Acta Vertebrata **17**: 67–74.

Emlen, J. M. (1966): The role of time and energy in food preference. – The American Naturalist **100**: 611–617.

Greeff, J. M. & M. J. Whiting (2000): Foraging-mode plasticity in the lizard *Platysaurus broadleyi*. – Herpetologica **56**: 402–407.

Günther, A. (1874): Description of a new European species of *Zootoca*. – The Annals and Magazine of Natural History; zoology, botany and geology 4th ser., **14**: 158–159.

Helfman, G. S. & J. B. Clark (1986): Rotational feeding: overcoming gape-limited foraging in Anguillid eels. – Copeia **1986**: 679–685.

Hidalgo, M. I. & B. Cabezudo (1995): Producción de néctar en matorrales del sur de España (Andalucía). – Acta Botanica Malacitana **20**: 123–132.

Hódar, J. A. (1996): The use of regression equations for estimation of arthropod biomass in ecological studies. – Acta Oecologica **17:** 421–433.

Hódar, J. A. (1997): The use of regression equations for the estimation of prey length and biomass in diet studies of insectivore vertebrates. – Miscel·lània Zoològica **20**: 1–10.

Huey, R. B. & E. R. Pianka (1981): Ecological consequences of foraging mode. – Ecology **62**: 991–999.

Hurlbert, S. H. (1978): The measurement of niche overlap and some relatives. – Ecology **59**: 67–77.

Levins, R. (1968): Evolution in Changing Environments; Some Theoretical Explorations. – Monographs in Population Biology, No 2. Princeton University Press, USA.

MacArthur, R. H. & E. R. Pianka (1966): On optimal use of a patchy environment. – The American Naturalist **100**: 603–609.

Magnusson, W. E., L. Junqueira de Paiva, R. Moreira de Rocha, C. R. Franke, L. A. Kasper & A. P. Lima (1985): The correlates of foraging mode in a community of Brazilian lizards. – Herpetologica **41**: 324–332.

McBrayer, L. D, D. B. Miles & S. M. Reilly (2007): The evolution of the foraging mode paradigm in lizard ecology. – pp. 508–521 in: Reilly, S.M., L.D. McBrayer & D.B. Miles (Eds): Lizard Ecology: The Evolutionary Consequences of Foraging Mode. – Cambridge University Press, UK.

McLaughlin, R. (1989): Search modes of birds and lizards: evidence for alternative movement patterns. The American Naturalist **133**: 654–670.

Measey, J. & A. Herrel (2006): Rotational feeding in caecilians: putting a spin on the evolution of cranial design. – Biology Letters **2**: 485–487.

Metzger, K. (2002): Cranial kinesis in lepidosaurs: skulls in motion. – pp. 15–46 in: Aerts, P., K. D'Août, A. Herrel & R. van Damme (Eds) – Topics in Functional and Ecological Vertebrate Morphology. – Shaker Publishers, Netherlands.

Meusel, H. & A. Kästner (1990): Lebensgeschichte der Gold- und Silberdisteln: Monographie der mediterran-mitteleuropäischen Compositen-Gattung *Carlina*, Band I. Merkmalsspektren und Lebensräume der Gattung. – Österreichische Akademie der Wissenschaften. Mathematisch-Naturwissenschaftliche Klasse, Austria.

Perera, A. & V. Pérez-Mellado (2002): Ausencia de plasticidad fenotípica en las estrategias reproductoras de la lagartija balear, *Podarcis lilfordi* (Squamata, Lacertidae). – Revista de Menorca **86**: 159–171.

Pérez-Mellado, V. (1989): Estudio ecológico de la lagartija balear *Podarcis lilfordi* (Günther, 1874) en Menorca. – Revista de Menorca **80**: 455–511.

Pérez-Mellado, V. (1998): *Podarcis lilfordi* (Günther, 1874). – pp. 272–282 in: Salvador, A. (Ed.): Fauna Ibérica, vol 10. – Museo Nacional de Ciencias Naturales, Spain.

Pérez-Mellado, V. (2009): Les sargantanes de les Balears. – Documenta Balear, Spain.

Pérez-Mellado, V. & J. L. Casas (1997): Pollination by a lizard on a Mediterranean island. – Copeia **1997**(3): 593–595.

Pérez-Mellado, V. & C. Corti (1993): Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). – Bonner Zoologische Beitrage **44**: 193–220.

Pérez-Mellado, V. & A. Traveset (1999): Relationships between plants and Mediterranean lizards. – Natura Croatica **8**: 275–285.

Pérez-Mellado, V., J. A. Hernández-Estévez, T. García-Díez, B. Terrassa, M. M. Ramón, J. Castro, A. Picornell, J. Martín-Vallejo & R. Brown. (2008): Population density in *Podarcis lilfordi* (Squamata, Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). – Amphibia-Reptilia **29**: 49–60.

Pérez-Mellado, V., A. Pérez-Cembranos, M. Garrido, L. Luiselli & C. Corti (2011): Using faecal samples in lizard dietary studies. – Amphibia-Reptilia **32**: 1–7.

Perry, G. (2007): Movement patterns in lizards: measurement, modality, and behavioral correlates. – pp. 13–48 in: Reilly, S.M., L.D. McBraver & D.B Miles (Eds): Lizard Ecology: The Evolutionary Consequences of Foraging Mode. – Cambridge University Press, UK.

Perry, G., I. Lampl, A. Lerner, D. Rothenstein, E. Shani, N. Sivan & Y. L. Werner (1990): Foraging mode in lacertid lizards: variation and correlates. – Amphibia-Reptilia **11**: 373–384.

Pianka, E. R. (1966): Convexity, desert lizards, and spatial heterogeneity. – Ecology **47**(6): 1055–1059.

Pianka, E. R. (1973): The structure of lizard communities. – Annual Review of Ecology and Systematics **4**: 53–74.

Pianka, E. R., R. B. Huey & L. R. Lawyor (1979): Niche segregation in desert lizards. – pp. 67–115 in: Horn, D.J., R. Mitchell & G.R. Stairs (Eds): Analysis of Ecological Systems. – Ohio State University Press, USA.

R Core Team (2012): R: A language and environment for statistical computing. Version 2.15.1. – R Foundation for Statistical Computing, Vienna, Austria, http://www.R-project.org, downloaded on 2013-06-06

Rosenberg, K. V. & R. J. Cooper (1990): Approaches to avian diet analysis. – Studies in Avian Biology **13**: 80–90.

Schwenk, K. (2000): Feeding in lepidosaurs. – pp. 1–41 in: Schwenk, K. (Ed.): Feeding: form, function and evolution in tetrapod vertebrates. – Academic Press, California, USA.

Schwenk, K. & M. Rubega (2005): Diversity of vertebrate feeding systems. – pp. 1–41 in: Starck, J. M. & T. Wang (Eds): Physiological and ecological adaptations to feeding in vertebrates. – Science Publishers, USA.

Sokal, R. R. & F. J. Rohlf (1995): Biometry. – 3rd edition. – Freeman, New York.

van Damme, R. (1999): Evolution of herbivory in lacertid lizards: Effects of insularity and body size. – Journal of Herpetology **33**: 663–674.