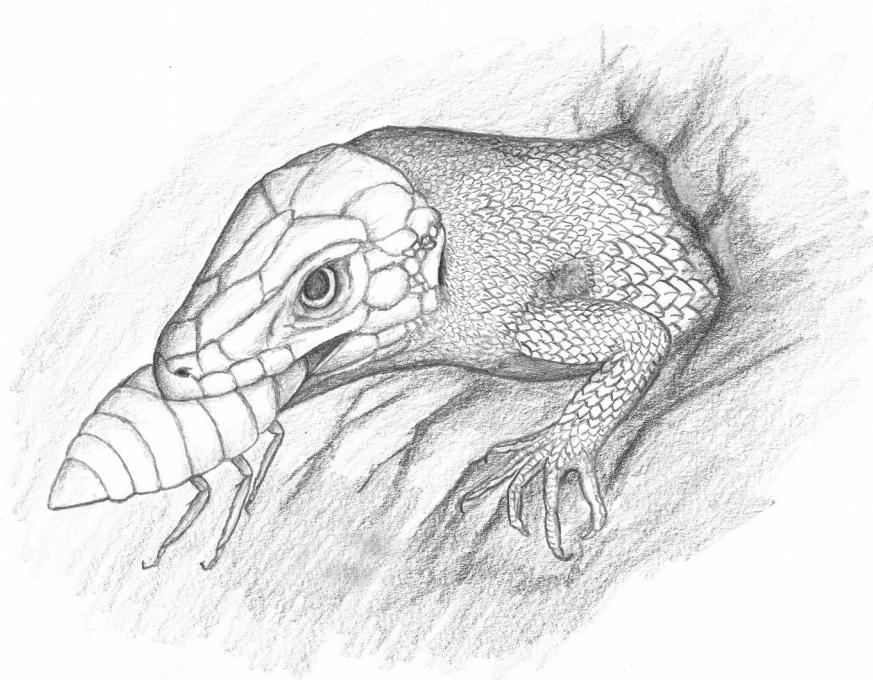

Capítulo IV

Diet composition and trophic ecology of three sympatric insectivorous lizard species in a highly anthropized area in the eastern Iberian peninsula

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Diet composition and trophic ecology of three sympatric insectivorous lizard species in a highly anthropized area in the eastern Iberian peninsula

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Abstract

Trophic ecology is one of the most important aspects of a species' ecology and it is crucial when trying to assess how different species interact in an ecosystem. Showing how the diet intraspecifically changes in different body sizes, sexes or habitats and how trophic resources are shared interspecifically allows to understand how the ecosystem functions. With this objective, we studied the diet and trophic ecology of *Acanthodactylus erythrurus*, *Psammodromus algirus* and *Psammodromus edwardsianus*, which are in syntropy in the Albufera de Valencia Natural Park. We collected a total of 485 faecal samples and could identify 18 different prey groups. The main prey groups in *A. erythrurus* were Hymenoptera, Coleoptera and Hemiptera; in *P. algirus*, Lepidoptera, Arachnida, Coleoptera, Diptera, Hemiptera and Orthoptera; and in *P. edwardsianus*, Coleoptera, Hemiptera and Arachnida. Our results show that *A. erythrurus* seems to be the most specialized species, having the lowest values of trophic niche amplitude and the lowest intraspecific diet variation. Although this species is known to feed mainly on ants, our results indicate that mirmecophagy seems to be especially important in juveniles. Indeed we observed in all three species a niche separation between small and big individuals, indicating that diet changes with age. We could also evidence a resource partitioning between *A. erythrurus* and *P. algirus*, presenting a niche overlap of only 51.6%. In conclusion, there are various factors playing together shaping the diet of a species in a certain environment: behavioural, ecological, environmental and physiological factors.

Keywords: Coastal habitat, Diet, Lizard, Trophic ecology, Spain.

Introduction

The Mediterranean region of the Iberian peninsula presents a typical clime, characterized by a noticeable seasonality, with hot and dry summers, cold winters and humid springs and autumns with softer temperatures, and

an important interannual variability (e.g. Lionello et al., 2006). These peculiar environmental conditions allowed the formation of a relatively rich and singular biodiversity which deserves to be conserved. Although the conservation of biodiversity is being a more and more complicated task. Human activity lead to the extinction of many species in the past decades and its effects can be noticed in nearly every ecosystem on the planet (Jordan et al., 1990). One of the most interesting aspects to consider in this context of biodiversity loss is the study of trophic webs in communities and the function each species has in them. The alteration of a single species' function can be transmitted to the rest of the ecosystem by the trophic web, which is known as trophic cascades (Pace et al., 1999). These negative effects of species loss by trophic cascades could be evidenced for example in tropical ecosystems, where the disappearance of insectivorous lizards lead to an uncontrolled increase in the density of herbivorous arthropods and, in consequence, to a higher leaf damage of the plants they consumed (Spiller & Schoener, 1994; Dial & Roughgarden, 1995). On the other side, there are also cases where the feeding of a species plays a major role in its conservation. In reptiles, we can cite the case of different elapid species in Australia, where the type of foraging is correlated with its vulnerability to extinction (Reed & Shine, 2002).

However, trophic ecology is not limited to only describing the diet of a species, it is much more complex. For example, there could be variations in the diet from one population to another of the same species (Vitt et al., 1997); or even within the same population, given that sex, different size ranges or the phenology could lead to diet variations (Best & Pfaffenberger, 1987; Perry, 1996; Verwijen et al., 2002). Thus, we have to contemplate trophic ecology studies of species from different perspectives. Also, the presence of other species with a similar trophic niche can result in a resource partitioning and a specialization in one particular food type or even a total change in diet. It has been proved that there is an inverse relation between resource partitioning, or the separation of trophic niches, and trophic competition between species (Pacala & Roughgarden, 1982).

In the study area cohabit three species of lizards: *Acanthodactylus erythrurus* (Schinz, 1834), *Psammodromus algirus* (Linnaeus, 1758) and *Psammodromus edwardsianus* (Dugès, 1829). These species share the same microhabitats as the same trophic resource. Thus, we would expect, if the resources are limited, a high level of competition between the species. In fact, there are studies that describe a higher specific aggression between species in syntropy (Ortiz & Jenssen, 1982). This competition, which clearly would reduce the fitness of involved species, could be avoided reducing the trophic niche amplitude (specialization) and the degree of niche overlap (Pacala & Roughgarden, 1982). There are previous works on the diet of the three study species (for example Busack & Jaksic, 1982, for *A. erythrurus*; Pérez-Mellado, 1982, for *P. algirus*; or Carretero-Llorente, 1991, for *P. edwardsianus*). In some cases the authors even considered the ecological interaction between *A. erythrurus* and *P. algirus* (Seva, 1984; Rouag et al., 2007). But these studies never considered *P. edwardsianus* and, in addition, were carried out in areas with low anthropic pressure.

The objective of this study is the description of the trophic ecology of three sympatric insectivorous lizard species (*Acanthodactylus erythrurus*, *Psammodromus algirus* and *Psammodromus edwardsianus*). Thus, on one hand, we

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will describe in detail the diet of each species and we will evaluate if there are interspecific differences. On the other hand, in each species we will study if there are intraspecific differences related to sex, size, gravidity, used macrohabitat type and month. Finally, we will analyse trophic niche amplitude and overlap.

Material and Methods

Study area

The study area is situated about 10km South from Valencia city and is part of the Albufera de Valencia Natural Park ($39^{\circ}20'20''N$ $0^{\circ}18'43''W$). It represents a coastal line about 10km long (N-S) and 1km wide (E-W). It is a very human-frequented area, in summer there is much activity related to touristic use of the beach, but it is also an area with a great interest in the ecotouristic and cycling sectors because of its distinct and naturalized landscapes.

The area presents a typical Mediterranean vegetation. It is a dune habitat with an area of mobile dunes with a variable degree of maturation and a vegetation formed mainly by herbaceous and bush species, generally less than 1m tall, like *Ammophila arenaria*, *Helichrysum stoechas*, *Euphorbia paralias*, *Medicago marina* or *Rhamnus alaternus*, among others (this is what we call “Dune” habitat). Behind this habitat there is an area of fixed dunes with an arboreal vegetation formed mainly by Aleppo pine (*Pinus halepensis*) and a dense undergrowth with species like *Smilax aspera*, *Asparagus officinalis*, *Chamaerops humilis* or *Pistacia lentiscus* (this is what we call “Forest” habitat).

Fieldwork

Field samplings were carried out between April and October (both included) of 2015 and 2017. In 2015 we did one sampling every two weeks in each habitat type, while in 2017 we intensified the sampling effort to four times a week (two in each habitat type).

In every sampling we captured lizards by hand or looping (e.g. Guillén-Salazar et al., 2007). We put the captured individuals in individual cloth bags until the later processing. At the end of the sampling, we measured basic biometric data (snout-vent length or SVL and weight), we identified the species, age class, sex (in females we annotated if they were gravid or not) every time possible. We obtained faecal samples deposited in the cloth bags or by performing a gentle abdominal massage on each individual. We kept the faecal samples friezed at -20°C until their processing in the laboratory.

Faecal sample processing and data analysis

All obtained samples were analysed in the laboratory. We put every sample on a petri dish with some drops of

water and carefully separated with tweezers the different items. Then, using a binocular magnifier and with the help of an arthropod identification guide (Melic, 2005), we tried to identify every item found in every sample, at least to the order level. Finally, we conserved every sample in an eppendorf with 70% ethanol.

We could distinguish a total of 18 groups (prey groups), which in general correspond to arthropod orders, except some lower levels, considered separately because of their peculiar characteristics. Thus, we considered the family Formicidae a part from the rest of Hymenoptera given their small size, very high abundance in the environment and the absence of wings; and scorpions from the rest of Arachnida given their harder exoskeleton, and generally bigger body size. With the obtained data we built a presence/absence matrix of each prey group in each sample, assigning 1 to presence and 0 to absence. Afterwards, we grouped the data by species, sex, size, habitat, gravidity and month. In the case of the size, we grouped the data by intervals of SVL (of 10mm for *A. erythrurus* and *P. algirus*, and 5mm for *P. edwardsianus*). In order to simplify the graphic representation of the proportions of the different prey groups in the detailed diet analysis for each species we unified all minor prey groups (with less than 5% presence in all species) in a single group called “Others”.

For the study of diet composition, in each comparison we calculated the proportion of presence of each prey group, respect the total of samples. In order to evidence statistical significance of the observed differences, we performed a non parametric Krushkal-Wallis (1952) test for each prey group in each comparison.

For the study of the trophic ecology we used the same method as in Sasa & Monrós (2000). We calculated niche amplitude in each case as the Levins (1968) niche amplitude index, using the following formula:

$$L = \frac{1}{\sum_{i=1}^n p_i^2}$$

Where p_i are the proportions of presence of each prey group respect the total.

Once we obtained the values of trophic niche amplitude, we proceeded to calculate the degree of niche overlap for each comparison, using the Pianka (1973) index, applying the following formula:

$$O = \frac{\sum p_1 * p_2}{\sqrt{\sum p_1^2 * \sum p_2^2}}$$

Where p_1 and p_2 are the proportion of a certain prey group in the grouping 1 and 2, respectively. For the percentages of niche overlap we followed Krebs (1989), applying the following formula:

$$\% \text{ Overlap} = 100 * \sum \text{minimum of } p_1, p_2$$

All statistical analysis were carried out using R (2016) v3.2.3.

Results

Comparison of the diet between species

During the samplings we obtained a total of 485 samples: 246 from *A. erythrurus*, 101 from *P. algirus* and 138 from *P. edwardsianus*. The analysis of diet composition of the three species showed significant differences in the consumption of the different prey groups (Table 1). In the case of *A. erythrurus* we can remark the proportions of Hymenoptera, ants, Coleoptera and Hemiptera, being the major groups present (Fig. 1). In the case of *P. algirus*, we observed maximum values in Lepidoptera and non-scorpion Arachnida, followed by a relatively equivalent composition of Coleoptera, Diptera, Hemiptera and Orthoptera. We can also remark that this species consumes the highest proportion of scorpions from the three studied lizards, finding remains in approximately 15% of the samples (Fig. 1). Finally, in the case of *P. edwardsianus*, the most consumed prey groups were Coleoptera, Hemiptera and non-scorpion Arachnida. This species was also the only one consuming cockroach oothecae (Fig. 1).

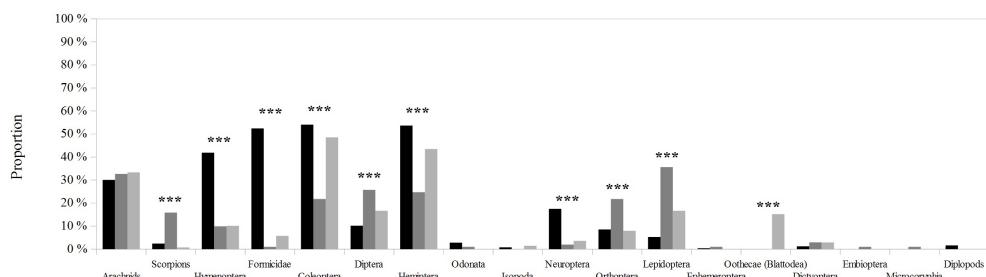


Figure 1: Representation of presence proportions in samples of the different prey groups, comparing the three lizard species (■ *A. erythrurus*; ■ *P. algirus*; ■ *P. edwardsianus*). We show significant results of the Krushkal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**); and $p < 0.001$ (***)

Diet analysis by species

The detailed diet composition analysis of *A. erythrurus* did not show significant differences in diet between sexes nor gravid and not gravid females (Table 1, Fig. 2). Although, we did find significant differences between the different SVL ranges in Hymenoptera, ants, Coleoptera and Odonata (Table 1). The most remarkable fact in this case is that there seems to be an increment in Hymenoptera consumption as the individuals grow, going from values of about 25% in small individuals to values of about 60% in big individuals. The opposite occurs in ants, where the proportions in small individuals lie by about 60%, while in big individuals it is reduced to 30%. In the case of Coleoptera we can remark the relatively low proportion in very small individuals (Fig. 2).

When comparing the diet of *A. erythrurus* in the two different habitat types, we found significant differences in the proportions of ants, Coleoptera and Diplopoda (Table 1), being ants more abundant in the Dune habitat and Coleoptera more abundant in the Forest habitat. Diplopoda was only found in the Forest habitat. Finally, the phenological analysis of diet composition showed significant differences in the consumption of scorpions, Hymenoptera, ants, Coleoptera and Hemiptera (Table 1). In this case, scorpions present maximum values in April; Hymenoptera are more consumed in spring and the beginning of summer; Coleoptera had also maximum values in spring (reaching values up to 90% in April) and Hemiptera, in contrast, are more consumed in summer (with values up to 80% in July). We did also detect individual cases of ingestion of vegetal items (small sticks, flowers, seeds), which were not included in the analysis as we think they were accidental ingestions while hunting prey sitting on the vegetation.

The detailed diet composition analysis of *P. algirus* did not show differences between sexes or by gravidity either (Table 1, Fig. 3). When comparing diet composition in the different SVL ranges we did observe some interesting differences, although most of them were not statistically significant (Table 1). The statistically significant differences correspond to the consumption of scorpions, being more consumed by large individuals, and Diptera, being more consumed by small individuals (Table 1, Fig. 3). In the comparison of diet composition between habitats we found significant differences in the consumption of Diptera, presenting higher values (about 35%) in the Dune habitat, and Hemiptera, presenting higher values in the Forest habitat (about 40%) (Table 1). Finally, the phenological analysis showed significant differences in Arachnida (being especially abundant in April, with about 65%), scorpions (being quite abundant in June, with more than 50%) and Coleoptera (being less abundant in June, August and October) (Table 1, Fig. 3). We also recorded individual ingestions of plant matter and some snail shells, what we interpret as accidental ingestions, and thus did not include it in the analysis. In addition, we recorded one case of interspecific predation: an adult male of *P. algirus* consumed a juvenile of *A. erythrurus*.

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Table 1: Krushkal-Wallis test results of the comparisons of the proportions between the different groupings. Values with a significance $p < 0.05$ are highlighted in bold.

| | Arachnids | Scorpions | Hymenoptera | Formicidae | Coleoptera | Diptera | Hemiptera | Odonata | Isopoda |
|------------------------|------------|------------|-------------|---------------|------------|-------------|------------|---------------|-----------|
| Between species | 0.762 | <0.001 | <0.001 | <0.001 | <0.001 | 0.001 | <0.001 | 0.094 | 0.476 |
| <i>A. erythrurus</i> | Sex | 0.432 | 0.595 | 0.163 | 0.073 | 0.969 | 0.772 | 0.201 | 0.963 |
| | Gravidity | 0.519 | 0.130 | 0.118 | 0.114 | 0.678 | 0.724 | 0.733 | 0.542 |
| | Habitat | 0.841 | 0.200 | 0.245 | <0.001 | 0.045 | 0.128 | 0.469 | 0.114 |
| | Size | 0.944 | 0.560 | 0.044 | 0.007 | 0.027 | 0.419 | 0.918 | 0.042 |
| | Phenology | 0.278 | 0.020 | 0.006 | 0.001 | 0.015 | 0.393 | 0.044 | 0.596 |
| <i>P. algirus</i> | Sex | 0.649 | 0.629 | 0.418 | NA | 0.930 | 0.418 | 0.420 | 0.306 |
| | Gravidity | 0.512 | 0.218 | 0.522 | NA | 0.892 | 0.121 | 0.221 | 0.178 |
| | Habitat | 0.800 | 0.074 | 0.201 | 0.493 | 0.041 | 0.002 | 0.014 | 0.493 |
| | Size | 0.064 | 0.014 | 0.670 | 0.530 | 0.154 | 0.016 | 0.400 | 0.406 |
| | Phenology | 0.021 | <0.001 | 0.340 | 0.602 | 0.007 | 0.070 | 0.892 | 0.462 |
| <i>P. edwardsianus</i> | Sex | 0.389 | NA | 0.668 | 0.827 | 0.734 | 0.516 | 0.780 | NA |
| | Gravidity | 0.335 | NA | 0.645 | 0.346 | 0.204 | 0.685 | 0.398 | NA |
| | Habitat | 0.903 | 0.409 | 0.058 | 0.042 | <0.001 | 0.009 | 0.413 | NA |
| | Size | 0.995 | 0.670 | 0.329 | 0.222 | 0.049 | 0.732 | 0.283 | NA |
| | Phenology | 0.964 | 0.959 | 0.724 | 0.195 | 0.508 | 0.867 | 0.694 | NA |
| | Neuroptera | Orthoptera | Lepidoptera | Ephemeroptera | Oothecae | Dictyoptera | Embioptera | Microcoryphia | Diplopods |
| Between species | <0.001 | 0.001 | <0.001 | 0.499 | <0.001 | 0.417 | 0.149 | 0.149 | 0.142 |
| <i>A. erythrurus</i> | Sex | 0.929 | 0.381 | 0.398 | 0.149 | NA | 0.325 | NA | NA |
| | Gravidity | 0.436 | 0.811 | 0.346 | 0.509 | NA | NA | NA | NA |
| | Habitat | 0.952 | 0.387 | 0.387 | 0.243 | NA | 0.753 | NA | NA |
| | Size | 0.372 | 0.565 | 0.988 | 0.305 | NA | 0.620 | NA | NA |
| | Phenology | 0.460 | 0.497 | 0.821 | 0.254 | NA | 0.813 | NA | 0.782 |
| <i>P. algirus</i> | Sex | NA | 0.234 | 0.563 | 0.340 | NA | 0.946 | 0.294 | NA |
| | Gravidity | NA | 0.437 | 0.181 | NA | NA | 0.286 | 0.458 | NA |
| | Habitat | 0.583 | 0.592 | 0.831 | 0.496 | NA | 0.951 | 0.496 | 0.496 |
| | Size | 0.171 | 0.077 | 0.422 | 0.330 | NA | 0.149 | 0.432 | 0.524 |
| | Phenology | 0.496 | 0.233 | 0.357 | 0.454 | NA | 0.655 | 0.116 | 0.595 |
| <i>P. edwardsianus</i> | Sex | 0.251 | 0.534 | 0.101 | NA | 0.510 | 0.192 | NA | NA |
| | Gravidity | 0.346 | 0.346 | 0.065 | NA | 0.432 | NA | NA | NA |
| | Habitat | 0.979 | 0.106 | 0.217 | NA | 0.225 | 0.698 | NA | NA |
| | Size | 0.264 | 0.132 | 0.504 | NA | 0.983 | 0.287 | NA | NA |
| | Phenology | 0.091 | 0.555 | 0.237 | NA | 0.136 | 0.914 | NA | NA |

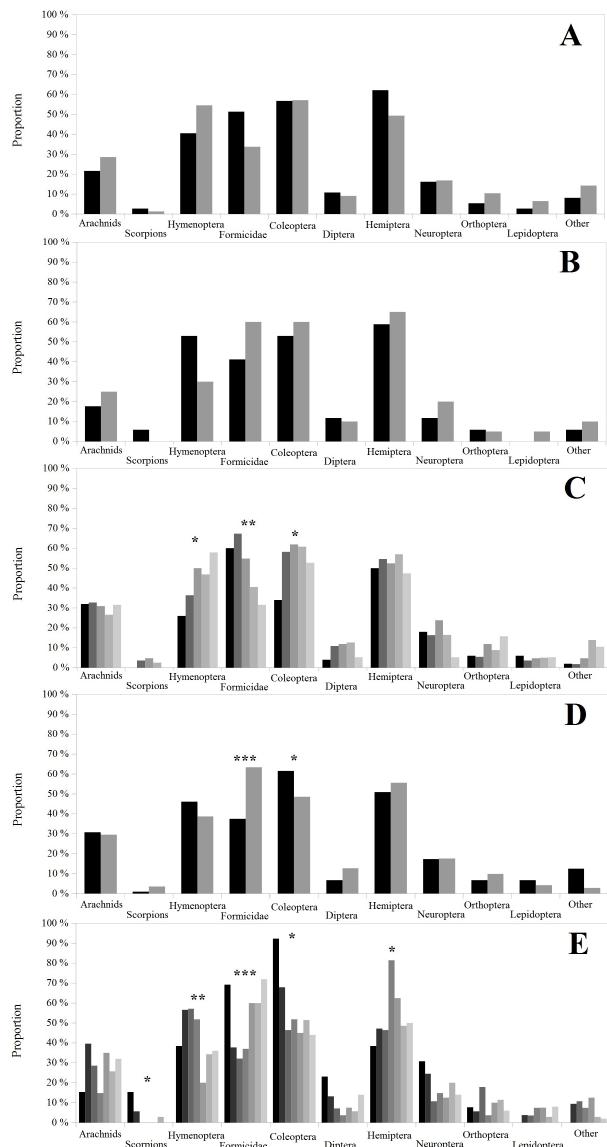


Figure 2: Representation of presence proportions in samples of the different prey groups in *A. erythrurus*. We show the comparison between sexes (A, ■ females; ■■ males), by gravidity in females (B, ■■ gravid; ■■ not gravid), SVL ranges in mm (C, ■■ 30-39; ■■ 40-49; ■■ 50-59; ■■ 60-69; ■■ 70-79), habitat types (D, ■■ Forest; ■■ Dunes) and months (E, ■■ April; ■■ May; ■■ June; ■■ July; ■■ August; ■■ September; ■■ October). We show significant results of the Krushkal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**); and $p < 0.001$ (***)

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Last but not least, in the detailed analysis of diet composition in *P. edwardsianus* as in the other two species we did not find significant differences between sexes nor by gravidity (Table 1, Fig 4). Considering body size ranges, we did only find significant differences in the consumption of Coleoptera, being more consumed by large individuals (Table 1, Fig. 4). The comparison of diet composition in the different habitat types showed significant differences in the consumption of ants, Coleoptera and Diptera (Table 1). While Coleoptera are especially abundant in the Forest habitat (about 65%), ants and Diptera are more abundant in the diet of individuals in the Dune habitat. The phenological analysis did not show any significant differences in any prey group (Table 1, Fig. 4).

Niche amplitude and overlap

Our values regarding niche amplitude show that *A. erythrurus* is the species with the smallest trophic niche and *P. algirus* is the one with the biggest niche (Table 2). At the intraspecific level we can remark that, in the case of *P. algirus*, females tend to have considerably greater trophic niche than males. This is not the case in the other two species (Table 2). In all three species, gravid females seemed to have slightly greater trophic niche amplitudes than non gravid females (Table 2). Regarding body size ranges, in general smaller (younger) individuals in all three species seem to present wider trophic niches than older individuals (Table 2). Considering the habitat types, we found that both *Psammodromus* species had wider trophic niches in the Dune habitat than in the Forest habitat (Table 2). Finally, regarding the variations of the values during the year, we could not detect a clear pattern, but there is a light trend to increase trophic niche amplitude during hotter months (especially in both *Psammodromus* species) (Table 2).

Considering the values of trophic niche overlap, we found that the diets of *A. erythrurus* and *P. algirus* are the most different, with an overlap of only 51.6%. The other comparisons lay by about 67% (Table 3). At the intraspecific level, we observed results according to the described above (Table 3). In neither species we observed differences between sexes, with overlaps of more than 80% (Table 3). The analysis considering gravidity did not show great differences in *A. erythrurus*, but in *P. algirus* and *P. edwardsianus*, with overlaps of 68.3% and 71.0%, respectively (Table 3). Regarding body size ranges, we could see in all three species the same pattern: a trophic niche separation as individuals grow, that means the values of niche overlap are lower comparing small and big individuals (Table 3). Comparing both habitat types, we observed that trophic niche overlap values are relatively high for both *Psammoromus* species (about 70%), but are especially high for *A. erythrurus* (86.3%). Finally, considering the phenological analysis, in the case of *A. erythrurus* we observed relatively high values (>70%) in all comparisons. In the case of *P. algirus*, values were between 50% and 70%, and the lowest values in general correspond to summer months. In the case of *P. edwardsianus* all values were located above 75%, with the exception of May (Table 3).

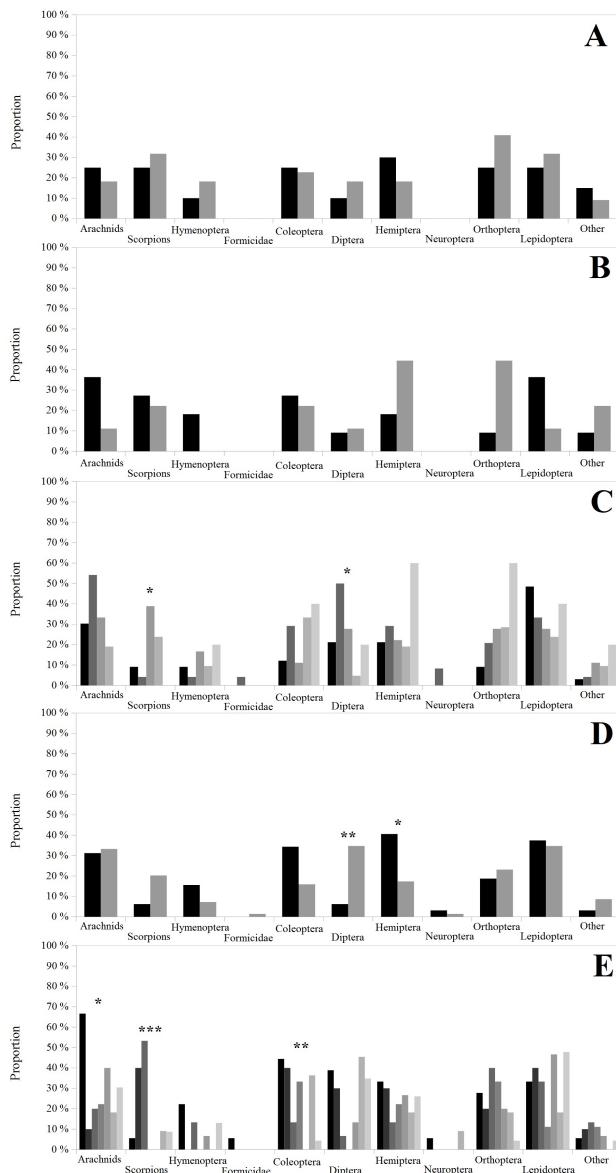


Figure 3: Representation of presence proportions in samples of the different prey groups in *P. algirus*. We show the comparison between sexes (A, ■ females; ■ males), by gravidity in females (B, ■ gravid; ■ not gravid), SVL ranges in mm (C, ■ 30-39; ■ 40-49; ■ 50-59; ■ 60-69; ■ 70-79), habitat types (D, ■ Forest; ■ Dunes) and months (E, ■ April; ■ May; ■ June; ■ July; ■ August; ■ September; ■ October). We show significant results of the Krushkal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**); and $p < 0.001$ (***)

Discussion

The global diet analysis accords to data obtained in previous studies in the case of *A. erythrurus* (Belluire, 2015). The major prey groups in this species were Hymenoptera, ants, Coleoptera and Hemiptera, the same as in a similar study carried out in Alicante (Seva, 1984), although our results show a higher diversity of minor prey groups. In the case of *P. algirus*, we observed some discrepancies with results obtained in previous works. The most remarkable is the relatively high proportion of Lepidoptera, a group which has not been described as such important in the diet of this species yet, in fact in the majority of studies it is not even mentioned (Salvador, 2011; Mamou et al., 2016). In addition, we found other minor prey groups which were not described previously in the diet of *P. algirus*, as scorpions and Neuroptera. Finally, in the case of *P. edwardsianus*, our results in general adjust to the ones obtained in previous studies, although we can remark some differences. On the one hand, Hymenoptera had been described as a very abundant prey group in this species (Fitze, 2012), but in our case it is more a minor prey group. On the other hand, in none of the previous studies the consumption of cockroach oothecae by *P. edwardsianus* was described, while in our case they appeared in about 15% of the samples.

The diet analysis at the intraspecific level did not show significant differences between sexes in any species. This is not surprising, as this was already described in previous studies (Busack & Jaksic, 1982; Pollo & Pérez-Mellado, 1991; Fitze, 2012). Although we observed considerably higher values in niche amplitude for females than for males in the case of *P. algirus*. We found no significant differences between gravid and non gravid adult females in neither species. This seems to contradict the results of niche amplitude, but the lack of significance can also be due to a too low sample size. Moreover, the differences in niche amplitude are relatively subtle. Also the values of niche overlap in this case are low. Although it is not significant, there seems to be a very subtle trend of gravid *P. algirus* females to consume more soft preys (Lepidoptera, Arachnida, Hymenoptera) and less hard preys (Hemiptera, Orthoptera). We could not find any references regarding this issue, but it could be explained by a better digestion or an easier hunting of these types of prey, what would give a more positive energetic balance, important, as egg production and incubation is a very energetically demanding task. Another explanation could be that the eggs in the abdomen occupy much volume, leading to a more difficult digestion of very hard or very big preys (Weiss, 2001). The effect of gravidity on diet composition is a topic that should be more studied in the future, also in other reptile species.

The phenologic analysis of diet composition showed a nearly absent variation in diversity in the case of *A. erythrurus*, with trophic niche overlaps above 70% in nearly all cases. A similar result as in a previous study (Seva, 1984). Although we recorded variations in the proportions of the different prey groups. Coleoptera seem to be ingested more in spring, ants are consumed less during the dry period, opposed to Hemiptera. These variations could be the result of variations in abundance of the different prey groups in relation to changes in the physical conditions of the environment. Especially the preference for mirmecophagy in this species leads in this direction.

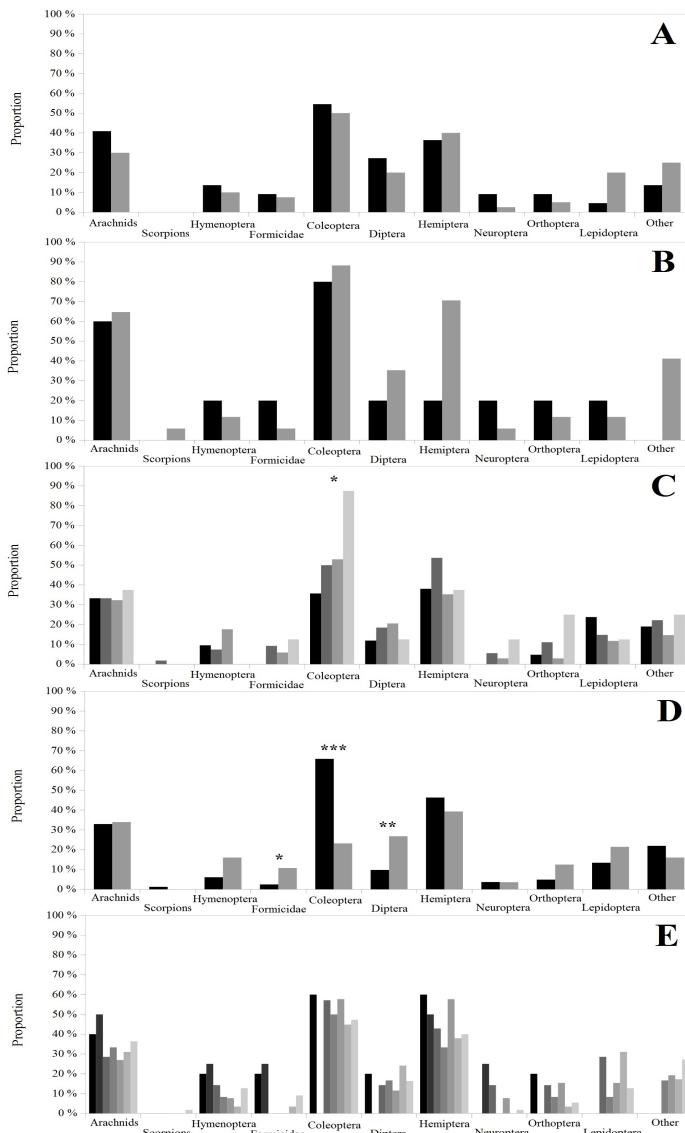


Figure 4: Representation of presence proportions in samples of the different prey groups in *P. edwardsianus*. We show the comparisons between sexes (A, ■ females; ■■ males), by gravidity in females (B, ■■ gravid; ■■ not gravid), SVL ranges in mm (C, ■ <35; ■■ 35-39; ■■■ 40-44; ■■■■ >44), habitat types (D, ■■ Forest; ■■ Dunes) and months (E, ■■ April; ■■ May; ■■■ June; ■■■■ July; ■■■■ August; ■■■■■ September; ■■■■■ October). We show significant results of the Krushkal-Wallis test (Table 1) with asterisks over the bars of each prey group: $p < 0.05$ (*); $p < 0.01$ (**); and $p < 0.001$ (***)

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In the case of *P. algirus*, we could record a higher variation in diet diversity, with some values below 60% of trophic niche overlap. This is coherent with the higher values in niche amplitude during summer months. Thus, it seems that *P. algirus* in fact presents a higher diet diversity in summer, resulting from a reduction in prey selectivity during less favourable periods.

Finally, in the case of *P. edwardsianus*, we did not detect differences except for May, but this month is only represented by 4 samples, what let us doubt on its representativeness. However, that we did not detect great variations in diet composition is an interesting result, given that this species was previously described as euriphage and opportunistic (Carretero & Llorente, 1991). In this case, seasonal variations in prey group abundance should be reflected in the diet of this species. This indicates that *P. edwardsianus* seems to be more selective as previously thought, given that it is hard to imagine that arthropod abundance and composition does not change during the year.

The values of trophic niche amplitude seem to indicate that *A. erythrurus* is the species with the most specialized diet. On the one hand, it presents the lowest values of niche amplitude of all three species. But it also has the lowest intraspecific variability in all comparisons. This is coherent with previous studies (Seva, 1984). That in all three species we recorded that gravid females have wider trophic niches also leads to the conclusion that gravidity has indeed an effect on the females' diet (Van Leeuwen et al., 2011). Another interesting result regarding niche amplitude is that in all three species the smallest (youngest) individuals have the largest trophic niches. This can basically be explained in two ways: 1) a higher diversity of small preys which for adult individuals result to be not profitable to hunt; or 2) neophilia, a young individual instinctively tends to try a greater diversity of preys and with time it specialises on certain types of prey. Considering our results for trophic niche overlap, indicating a separation of niches between small and large individuals, the first explanation seems to be the most correct. In the second case an individual would still be predating on (a reduced part of) the same pool of prey, thus we would expect higher niche overlap values. In fact, a shift in diet related to age had been observed in various lizards and it is mostly related to changes in energy requirements of the individual (e.g. Ballinger et al., 1977; Troyer, 1984; Mautz & Nagy, 1987).

Regarding the comparison between both habitat types, our results show that *A. erythrurus* presents very similar values in both habitats and in the other two species the most diverse diet is found in the Dune habitat. This is curious, as this habitat presents extremer environmental characteristics, with less vegetation and a high degree of insulation what leads to higher temperatures, especially in summer. It is known that abundance and diversity of arthropods tends to increase in dune systems with the increasing complexity of the vegetation (McLachlan, 1991). Our data, in contrast, show the complete opposite. As *A. erythrurus* is a more thermophile species (Carretero & Llorente, 1995; Belliure et al., 1996), a dune environment is an optimal environment for this species. But, the other two species are less thermophile and this type of habitat presents suboptimal conditions (Patterson & Davies, 1984). Thus, our conclusion is that an extremer environment induces a lower selectivity in the diet of these

Table 2: Trophic niche amplitudes, calculated as the niche amplitude index from Levins (L), with the sample size in each case (n). In the case of size ranges, the values in brackets refer to *P. edwardsianus*.

| Species | n | L | | | | |
|------------------------|----------------------|------|-------------------|------|------------------------|------|
| <i>A. erythrurus</i> | 246 | 0.85 | | | | |
| <i>P. algirus</i> | 101 | 2.03 | | | | |
| <i>P. edwardsianus</i> | 138 | 1.57 | | | | |
| | <i>A. erythrurus</i> | | <i>P. algirus</i> | | <i>P. edwardsianus</i> | |
| Sex | n | L | n | L | n | L |
| F | 37 | 0.81 | 20 | 2.33 | 22 | 1.38 |
| M | 77 | 0.89 | 22 | 1.79 | 40 | 1.59 |
| Gravidity | | | | | | |
| Gravid | 17 | 0.87 | 11 | 1.98 | 5 | 0.78 |
| Not gravid | 20 | 0.74 | 9 | 1.80 | 17 | 0.50 |
| Size (mm) | | | | | | |
| 30-39 (<35) | 50 | 1.07 | 33 | 2.19 | 42 | 2.05 |
| 40-49 (35-39) | 55 | 0.73 | 24 | 1.13 | 54 | 1.31 |
| 50-59 (40-44) | 42 | 0.72 | 18 | 1.70 | 34 | 1.60 |
| 60-69 (>44) | 79 | 0.83 | 21 | 2.53 | 8 | 0.83 |
| 70-79 | 19 | 0.93 | 5 | 0.86 | - | - |
| Habitat | | | | | | |
| Forest | 104 | 0.88 | 32 | 1.69 | 82 | 1.21 |
| Dunes | 142 | 0.80 | 69 | 1.96 | 56 | 1.97 |
| Phenology | | | | | | |
| April | 13 | 0.55 | 18 | 0.87 | 5 | 0.96 |
| May | 53 | 0.72 | 10 | 1.39 | 4 | 1.45 |
| June | 28 | 1.00 | 15 | 1.51 | 7 | 1.32 |
| July | 27 | 0.72 | 9 | 2.89 | 12 | 1.87 |
| August | 40 | 0.86 | 15 | 1.94 | 26 | 1.21 |
| September | 35 | 0.91 | 11 | 2.05 | 29 | 1.61 |
| Octobre | 50 | 0.80 | 23 | 1.85 | 55 | 1.53 |

species, favouring opportunism. This had been described in other organisms, like the snake *Natrix tessellata* (Weiperth et al., 2014), but we could not find any reference describing it in lizards. Although, it would also explain the tendency of the *Psammodromus* species to increase trophic niches during summer.

Our results regarding trophic niche overlap show that there is a resource partitioning between the species, at least between *A. erythrurus* and *P. algirus*. While the first tends to consume a greater proportion of hard preys like Coleoptera and Hemiptera, the second one, although it also consumes these prey groups, it tends to consume more soft preys like Lepidoptera, Arachnida or Diptera. These results are curious given that in another area where both species coexist a high degree of trophic niche overlap and diet similarity was described (Rouag et al., 2007). But in older studies (Pérez-Mellado, 1982; Seva, 1984) the authors found niche overlaps of 63% and 66%, respectively, more similar values to our case (51.6%), but still greater values. In Seva (1984) the author explains these

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differences in diet composition by differences in feeding strategies. *A. erythrurus* is more specialized (mirmecophagy) and *P. algirus* is more opportunistic. In addition to a behavioural factor, as *P. algirus* tends to climb through the vegetation, while *A. erythrurus* remains mostly on the ground.

Table 3: Trophic niche overlap, calculated as the Pianka index below the diagonal and as the percentage of overlap above the diagonal for all three species and intraspecific comparisons. In the case of size ranges, the values in brackets refer to *P. edwardsianus*.

| Species | <i>A. erythrurus</i> | | <i>P. algirus</i> | | <i>P. edwardsianus</i> | | |
|---|----------------------|--------------------|--------------------|--------------------|------------------------|--------------------|--------------------|
| <i>A. erythrurus</i> | 1 | | 51.6 | | 67.7 | | |
| <i>P. algirus</i> | 0.61 | | 1 | | 67.8 | | |
| <i>P. edwardsianus</i> | 0.82 | | 0.81 | | 1 | | |
| <i>A. erythrurus</i> <i>P. algirus</i> <i>P. edwardsianus</i> | | | | | | | |
| Sex | F | M | | | | | |
| F | 1 1 1 | 86.4 80.4 83.6 | | | | | |
| M | 0.97 0.93 0.96 | 1 1 1 | | | | | |
| Gravidity | G | NG | | | | | |
| G | 1 1 1 | 86.1 68.3 71.0 | | | | | |
| NG | 0.96 0.63 0.88 | 1 1 1 | | | | | |
| Habitat | Forest | Dunes | | | | | |
| Forest | 1 1 1 | 86.3 71.9 72.8 | | | | | |
| Dunes | 0.96 0.82 0.84 | 1 1 1 | | | | | |
| Size (mm) | 30-39 (<35) | 40-49 (35-39) | 50-59 (40-44) | 60-69 (>44) | 70-79 | | |
| 30-39 | 1 1 1 | 88.8 73.8 85.2 | 82.8 74.9 82.3 | 80.3 63.0 67.2 | 75.4 56.4 - | | |
| (<35) | | | | | | | |
| 40-49 | 0.98 0.87 0.96 | 1 1 1 | 90.4 59.9 85.1 | 88.3 62.9 78.5 | 80.9 56.0 - | | |
| (35-39) | | | | | | | |
| 50-59 | 0.95 0.83 0.95 | 0.98 0.82 0.96 | 1 1 1 | 91.1 74.4 75.7 | 84.7 59.0 - | | |
| (40-44) | | | | | | | |
| 60-69 | 0.93 0.75 0.86 | 0.96 0.73 0.91 | 0.99 0.85 0.92 | 1 1 1 | 84.3 65.4 - | | |
| (>44) | | | | | | | |
| 70-79 | 0.88 0.92 - | 0.92 0.65 - | 0.96 0.67 - | 0.97 0.80 - | 1 1 - | | |
| Phenology | April | May | June | July | August | September | October |
| April | 1 1 1 | 85.7 67.5 58.3 | 67.2 55.3 78.3 | 68.4 59.7 78.6 | 70.7 68.3 78.1 | 81.3 73.9 71.5 | 76.9 81.4 78.7 |
| May | 0.92 0.74 0.71 | 1 1 1 | 84.7 64.1 46.7 | 81.1 53.8 42.9 | 77.3 58.0 45.6 | 83.5 71.8 38.6 | 80.6 62.5 47.4 |
| June | 0.86 0.62 0.90 | 0.97 0.81 0.59 | 1 1 1 | 81.8 50.3 80.0 | 78.7 52.2 84.6 | 82.2 53.0 79.0 | 80.3 51.9 76.9 |
| July | 0.83 0.79 0.94 | 0.92 0.67 0.58 | 0.94 0.60 0.94 | 1 1 1 | 78.0 54.2 79.5 | 78.2 61.0 77.2 | 76.8 45.0 79.4 |
| August | 0.87 0.82 0.94 | 0.89 0.65 0.61 | 0.88 0.63 0.96 | 0.91 0.63 0.94 | 1 1 1 | 87.9 50.4 77.2 | 86.9 77.5 77.2 |
| September | 0.94 0.85 0.86 | 0.94 0.84 0.55 | 0.93 0.57 0.94 | 0.92 0.69 0.92 | 0.97 0.60 0.92 | 1 1 1 | 89.4 61.6 84.1 |
| October | 0.90 0.82 0.92 | 0.91 0.75 0.66 | 0.90 0.61 0.90 | 0.89 0.48 0.92 | 0.97 0.91 0.94 | 0.98 0.74 0.95 | 1 1 1 |

Although we would like to remark another (physiological) factor that affects diet composition: bite force. It is already known that *A. erythrurus* has generally a higher bite force than *P. algirus* (Verwaijen & Van Damme, 2007) and this grants it better access to harder prey types. This factor also allows to explain some of the other tendencies we observed regarding diet shifts related to body size. In *P. algirus* the proportions of hard preys (Orthoptera, Hemiptera, Coleoptera) increase with body size, while soft preys (Diptera, Arachnida, Lepidoptera) decrease with body size. The same can be observed in *P. edwardsianus*, where the proportion of Coleoptera increases with body

size and the proportion of Lepidoptera decreases. In this context, we can also remark that, although it had been described that *A. erythrurus* has a marked tendency to mirmecophagy (Pérez-Mellado, 1982; Seva, 1984), the consumption of ants seems to be especially important for juvenile individuals, appearing in over 60% of the samples. In adult individuals (>60mm SVL) the proportion of ants in the diet decreases about 20-30%.

In conclusion, we can say that there are multiple factors (environmental, behavioural, physiological, competition...) that affect diet composition of a species. Some of these factors had not been considered yet when describing the diet of the object species (like bite force). This may open a path for future studies which consider all these factors together and evaluate the importance each factor has on shaping such an important part of the ecology of a species like the trophic niche.

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