

Can interspecific competition alter population dynamics? A possible case of three lizard species in a coastal area in Eastern Spain

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Abstract

There are many factors affecting population dynamics, both abiotic and biotic. One of the most important biotic factors affecting different ecological aspects of a species is competition. But there is relatively little research focussing on the effect of competition on population dynamics. Thus, we studied population dynamics of three insectivorous lizard species (*Acanthodactylus erythrurus*, *Psammodromus algirus* and *Psammodromus edwardsianus*) which cohabit in our study area. We carried out periodic censuses and samplings during 2015 and 2017. Our results seem to confirm that a high level of competition can alter some aspects of population dynamics. Also body size seems to play a role, as most adjustments we detected were related to small size classes and the most affected species was *P. edwardsianus*. Some possible responses to competition we detected were an advance of the reproduction period, increased growth rates and biasing the sex ratio notably towards males (as higher testosterone levels lead to more aggression and this improves success rates in interspecific encounters). However, our study area is highly anthropized and further research is needed to discern if these adjustments are really exclusively related to competition or if human disturbance also plays a role.

Keywords *Acanthodactylus erythrurus*, Competition, Ecology, Population dynamics, *Psammodromus algirus*, *Psammodromus edwardsianus*, Spain.

Introduction

The species in the Mediterranean region adapted their life cycles to the peculiarities of the Mediterranean climate, leading to very characteristic phenologies (Crucitti, 2012). This has also an effect on population dynamics, observing different reproductive strategies to grant the survival of the populations. Some species present annual cycles, so that nearly the entire population is renewed every year (Carretero & Llorente, 1991), others opt for a longer generation time, so that individuals reproduce various times during their life (Galán, 1999; Carretero, 2006).

However, in addition to climatic conditions and other abiotic factors, there are also biotic factors that can influence population dynamics. One of the most important is competition (Werner & Gilliam, 1984). For example, it has been described that a high level of (intraspecific) competition is one of the most important forces behind gigantism in isolated systems (e.g. Pafilis et al., 2009). Competition can also be responsible for changes in reproductive and phenotypic traits of a species (Svensson, & Sinervo, 2000; Du, 2006; Calsbeek & Cox, 2010). In interspecific relations, usually the larger species has higher competitive capacity (Werner & Gilliam, 1984). However, the recruitment of new individuals occurs through small size classes, so that the maximum level of competition can be expected in juveniles (Werner & Gilliam, 1984). One way to avoid this competition is using the plasticity of population dynamics, inherent to every species (Ford & Seigel, 1989; Carretero, 2006). This plasticity allows for example to advance or delay the hatching period or to enhance fertility in comparison to other populations, less exposed to the competitive pressure.

In our study area cohabit three lizard species *Acanthodactylus erythrurus* (Schinz, 1834), *Psammodromus algirus* (Linnaeus, 1758) and *Psammodromus edwardsianus* (Dugès, 1829). All three species share the same microhabitats and feed on the same prey (insects). Thus, we expect a high competitive pressure between them, maybe leading to alterations of their “normal” population dynamics. There were carried out some studies in the past regarding population dynamics and demography of the species, as show the information compilations from Belliure (2015) for *A. erythrurus*; Salvador (2011) for *P. algirus* and Fitze (2012) for *P. edwardsianus*. Especially for *P. algirus* and *P. edwardsianus* there is a good amount of information, however, the studies are basically descriptive and focussed on each species independently. In the case of *A. erythrurus* interactions with other species are completely unknown (Belliure, 2015). There are no studies which focus on the three species at once and the effect this coexistence could have on their population dynamics. Additionally, the studies show a great geographic variability of different aspects of population dynamics. For example, the body size at which *P. algirus* reaches sexual maturity varies from 55 to 67 mm snout-vent length (Busack et al., 2006 and Salvador & Veiga, 2001, respectively) and the mean number of eggs found per female varies from 4.5 (Carretero & Llorente, 1997) to 6 (Pollo & Pérez-Mellado, 1990). Another interesting case is *P. edwardsianus*, where important interannual fluctuations of population densities were described, passing from values of 60 individuals per hour to 2 individuals per hour between 2006 and 2010 (Fitze, 2012). This is associated to the fact that *P. edwardsianus* seems to be an opportunistic species, very abundant in highly altered areas and less abundant as habitat maturity increases (Fitze, 2012).

The hypothesis we want to test is, given the expected high competitive pressure and the high degree of variability of different aspects of population dynamics, we expect alterations of some of these aspects, with the objective to minimize the negative effects of such interactions, especially at the forest habitat where we expect the maximum values of lizard densities. Therefore, our main objective is to record these alterations and provide the first data regarding annual demographic variations of three sympatric lizard species in our study area.

Material and methods

The study area is located about 10 km South of Valencia city and is part of the Albufera de Valencia Natural Park (39°20'32"N 0°18'36"W). It represents a coastal line about 10 km long (N-S) and about 1 km wide (E-W).

The study area presents typical Mediterranean vegetation, with two distinct macrohabitat types. A “Dune” habitat with an area of mobile dunes with different degree of maturity and a vegetation formed by diverse herbaceous and shrub species, generally less than 1 m tall, like *Ammophila arenaria*, *Helichrysum stoechas*, *Euphorbia paralias*, *Medicago marina* or *Rhamnus alaternus*, among others; and a “Forest” habitat, an area of fixed dunes with an arboreal vegetation mainly formed by Aleppo pine (*Pinus halepensis*) and a dense undergrowth with species like *Smilax aspera*, *Asparagus officinalis*, *Chamaerops humilis* or *Pistacia lentiscus*.

The samplings were carried out between April and October (both included) of 2015 and 2017. In 2015 we carried out one sampling in each habitat every two weeks, and in 2017 we intensified the sampling effort to 2 times per week in each habitat. We only sampled on days with favourable weather conditions, starting approximately three hours after sunrise. We also measured the temperature with sunlight and with shade before and after each sampling.

Each sampling consisted in a census randomly walking the area for two hours, recording all detected individuals, annotating species, age class and sex every time possible. We also captured all possible individuals by hand or looping, putting all captures in individual cloth bags. After the census, we processed all captured individuals, measuring basic biometry (total length, SVL, weight) and counted abdominal eggs in females performing a gentle massage. We marked each individual with a code of amputated phalanges in order to control recaptures (Drechsler & Monrós, 2018). After the measuring, each individual was released near the capture point.

In the case of *A. erythrurus* we considered an individual as adult if its Snout-Vent Length (SVL) was over 60 mm (males) (Seva, 1982) or 55 mm (females) (minimum size we observed a gravid female); in the case of *P. algirus* we considered adults from SVL > 52 mm (males) or SVL > 53 mm (females); and in the case of *P. edwardsianus* we considered adults from SVL > 34 mm. These criteria were considered following results in previous studies in similar areas as our study area (Salvador, 2011; Fitze 2012; Belliure, 2015, Drechsler & Monrós, 2018). We considered an individual as hatchling if its body size was close to those described for newly hatched individuals for each species.

For the abundance estimation we standardized the counts by the duration of each census in hours, obtaining abundance values in individuals per hour. Then, we grouped the data by months and habitats, calculating the mean and standard error. We evidenced the statistical significance of the observed differences performing Kruskal-Wallis tests, given that the distribution of our data was not normal (Shapiro-Wilks Test, $W = 0.979$, $p = 0,039$ for *A.*

erythrurus; $W = 0.854$, $p < 0.001$ for *P. algirus* and $W = 0.930$, $p < 0.001$ for *P. edwardsianus*). Afterwards, we calculated the proportions of the different age classes for each month, each species and each habitat; and the sex ratio in each case. In the case of females, we also evaluated if there are differences in the amount of eggs produced per female between habitats, also performing Kruskal-Wallis test as these data did not have a normal distribution either (Shapiro-Wilks Test, $W = 0.849$, $p < 0.001$ for *A. erythrurus*; $W = 0.922$, $p = 0.141$ for *P. algirus* and $W = 0.827$, $p = 0.019$ for *P. edwardsianus*).

Results

The analysis of the abundance phenology of the three species showed significant differences between them (Kruskal-Wallis Test, $X^2 = 110.16$, $df = 2$, $p < 0.001$). While *A. erythrurus* presents two abundance peaks (one in May and one in September), the abundance of *P. edwardsianus* tends to increase throughout the year and *P. algirus* maintains similar (but relatively low) levels throughout the year (Fig. 1).

The comparison between the two habitat types also showed significant differences for all three species (Kruskal-Wallis Test, $X^2 = 6.607$, $df = 1$, $p = 0.010$ for *A. erythrurus*; $X^2 = 6.374$, $df = 1$, $p = 0.012$ for *P. algirus*; and $X^2 = 69.174$, $df = 1$, $p < 0.001$ for *P. edwardsianus*). In the case of *A. erythrurus* we observed a clear dominance in both habitats which was especially important in the “Dune” habitat. We recorded in all three species a preference for the “Forest” habitat, but especially for the two *Psammodromus* species, with higher abundance values in relation to the “Dune” habitat during the entire year. Although, in the case of *P. algirus* we observed a decrease in abundance in the “Forest” habitat going from values of about 4 ind./h in spring to 1 ind./h in autumn (Fig. 1).

Comparing the data from 2015 and 2017, we detected a very subtle increase of abundance in 2017 for all three species, but in neither case it was statistically significant. Considering the global data (without distinguishing between both habitat types or seasons), *A. erythrurus* went from a mean value of 6.2 ind./h to 6.4 ind./h (Kruskal-Wallis Test, $X^2 = 0.444$, $df = 1$, $p = 0.505$); *P. algirus* went from 1.6 ind./h to 1.9 ind./h (Kruskal-Wallis Test, $X^2 = 1.018$, $df = 1$, $p = 0.313$) and *P. edwardsianus* went from 3 ind./h to 3.9 ind./h (Kruskal-Wallis Test, $X^2 = 2.886$, $df = 1$, $p = 0.089$).

The demographic analysis of *A. erythrurus* showed that at the beginning of the year, slightly over the half of the population is composed by immature individuals (Fig. 2). This proportion is reduced to <10% at the beginning of the hatching period in July. In the “Dunes” habitat, we observed the first gravid female on the 4th of May and the last on the 8th of July; while in the “Forest” habitat, the first gravid female appeared on the 12th of May and the last was observed on the 6th of August. The mean number of palpated eggs per female was 3.25 ± 0.62 ($n = 12$) in the “Forest” habitat and 3.33 ± 0.84 ($n = 18$) in the “Dunes” habitat (Kruskal-Wallis Test, $X^2 = 0.104$, $df = 1$, $p = 0.748$). The first hatchling of *A. erythrurus* appeared on the 13th of July in the “Dunes” habitat and on the 14th of July in the “Forest” habitat, being the maximum of hatchlings in August. This maximum was especially important

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in the “Forest” habitat. At the end of the year, the proportion of immature individuals in the population was >90% (Fig. 2). The sex ratio was practically identical between both habitat types, with 64.7%/35.3% (M/F) in the “Forest” habitat and 65.6%/34.4% (M/F) in the “Dunes” habitat.

The demographic analysis of *P. algirus* showed a high proportion of adults in the population during the first half of the year, which is reduced at the beginning of the hatching period in July (Fig. 3). The first gravid female appeared in the “Forest” habitat on the 22nd of April and the last on the 23rd of July; while in the “Dunes” habitat we observed the first one on the 2nd of May and the last one on the 10th of July. The mean number of palpated eggs per female in the “Forest” habitat was 3.73 ± 1.68 ($n = 11$) and in the “Dunes” habitat 3.86 ± 0.69 ($n = 7$) (Kruskal-Wallis Test, $X^2 = 0.020$, $df = 1$, $p = 0.886$). We observed the first hatchling of *P. algirus* on the 14th of July in the “Forest” habitat and on the 12th of August in the “Dunes” habitat. Regarding the phenology of the appearance of hatchlings, we observed a difference between both habitat types, as in the “Dunes” habitat hatching seems to occur later (August) than in the “Forest” habitat (July). In both cases the proportion of immature individuals increased to the end of the year to values >80% (even 100% in the “Dunes” habitat) (Fig. 3). The sex ratio is very similar between both habitat types, with 54.5%/45.5% (M/F) in the “Forest” habitat and 57.1%/42.9% (M/F) in the “Dunes” habitat.

Finally, the demographic analysis of *P. edwardsianus* showed that in both habitats at the beginning of the year the entire population is adult (Fig. 4). In the “Forest” habitat, the first gravid female appeared on the 7th of April and the last on the 17th of July; while in the “Dunes” habitat, we observed the first one on the 5th of April and the last one on the 9th of June. The mean number of palpated eggs per female was 2.25 ± 0.89 ($n = 8$) in the “Forest” habitat and 2.75 ± 1.50 ($n = 4$) in the “Dunes” habitat (Kruskal-Wallis Test, $X^2 = 0.302$, $df = 1$, $p = 0.583$). The first hatchling of *P. edwardsianus* appeared on the 22nd of June in the “Dunes” habitat and on the 13th of August in the “Forest” habitat. Although, due to the very low detectability of *P. edwardsianus* hatchlings we only observed these two individuals the entire sampling period, so that we can not infer on the hatching phenology of this species. The posterior increase of immature individuals in the population reaches maximum values in August with about 80%. Until the end of the year, the proportion of adult individuals increases to 50% in the “Forest” habitat and even 70% in the “Dunes” habitat (Fig. 4). The sex ratio showed differences between both habitat types, being in the “Forest” habitat 67.4%/32.6% (M/F) and in the “Dunes” habitat 80.3%/19.7% (M/F).

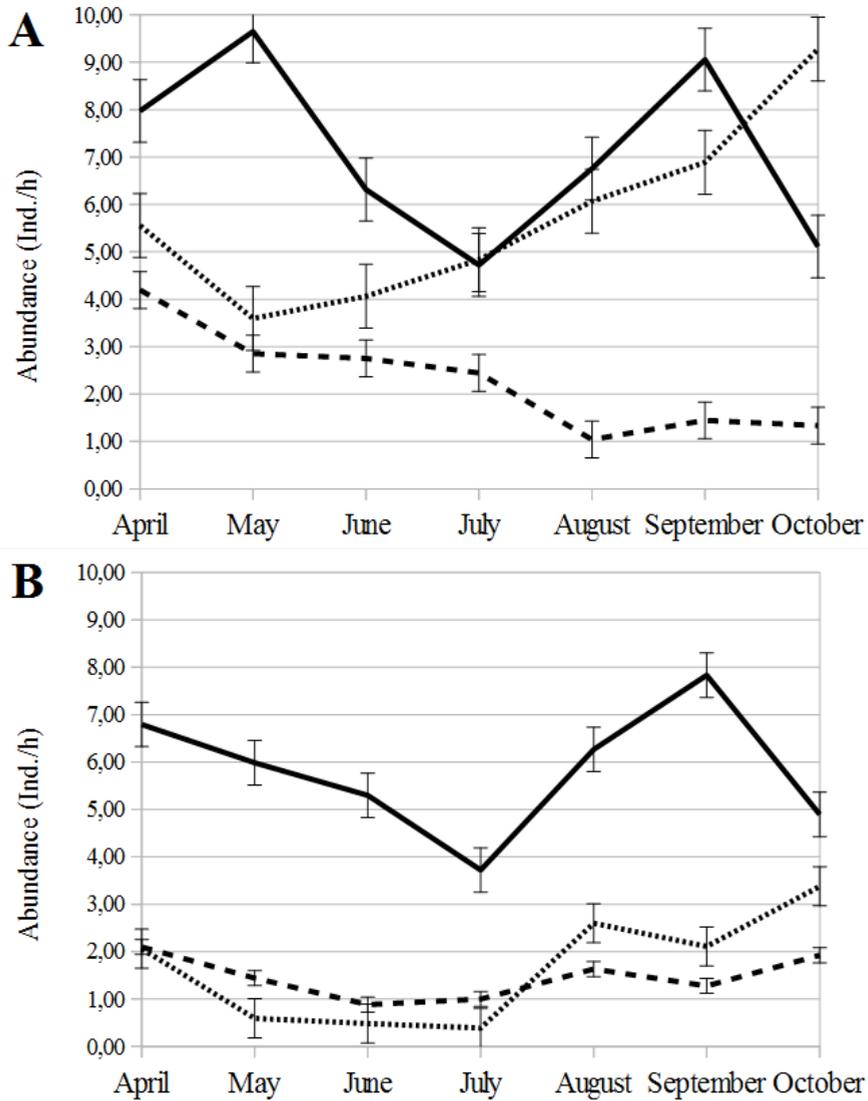


Figure 1: Representation of the abundance variation of *A. erythrurus* (continuous line), *P. algirus* (large dashed line) and *P. edwardsianus* (small dashed line) in the “Forest” habitat (A) and the “Dunes” habitat (B) during the sampling period. We represent the mean value and the standard error in each case.

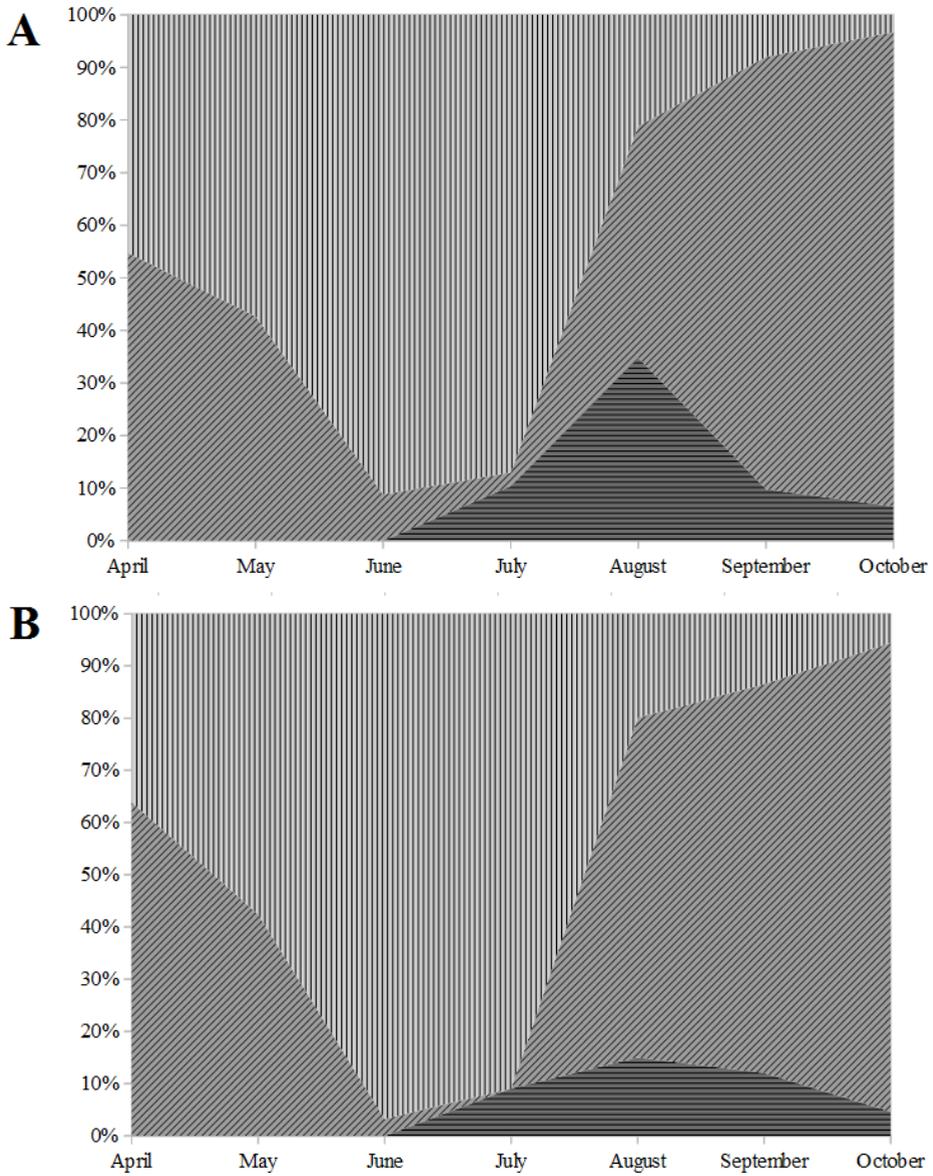


Figure 2: Representation of the variation of the proportions of adults (□), juveniles (▨) and hatchlings (▩) of *A. erythrus* during the sampling period in the "Forest" habitat (A) and the "Dunes" habitat (B).

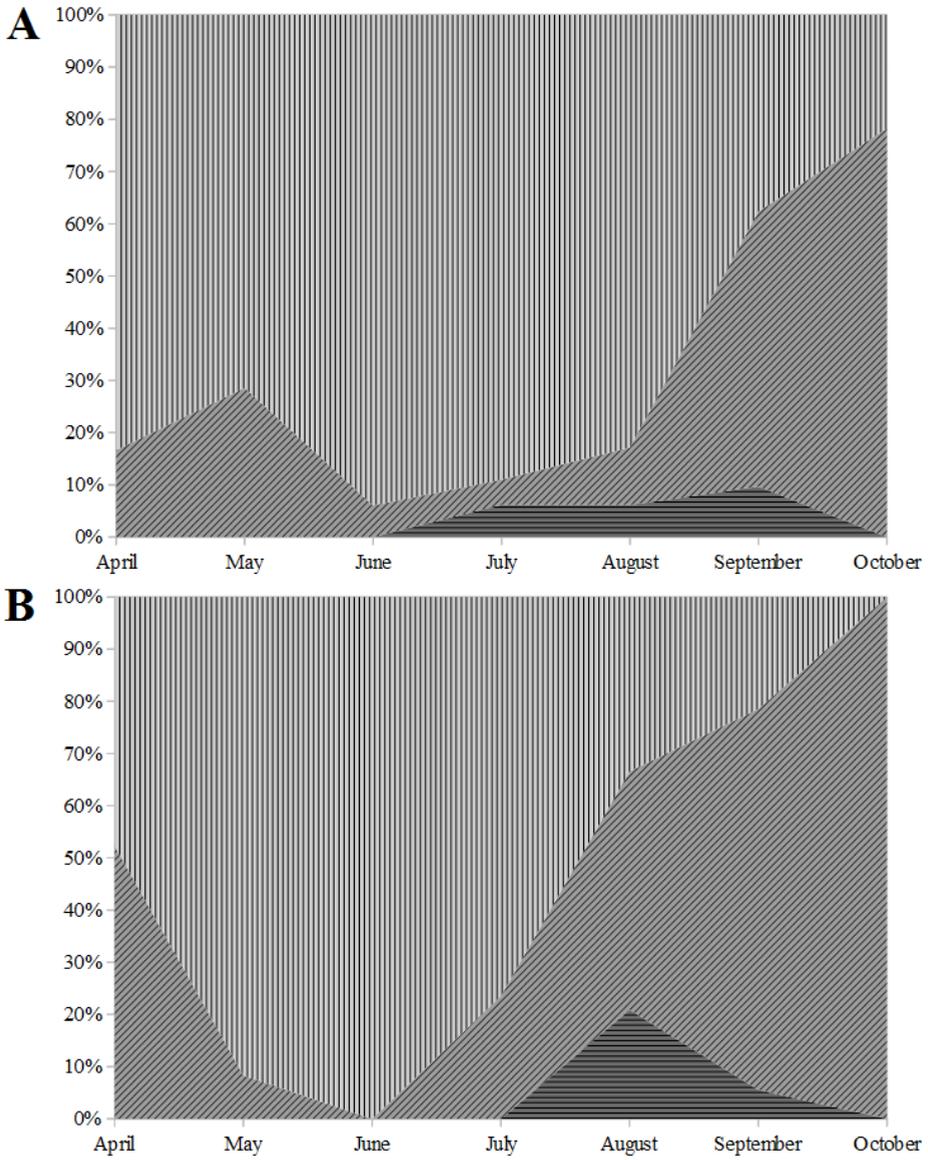


Figure 3: Representation of the variation of the proportions of adults (▨), juveniles (▧) and hatchlings (▩) of *P. algirus* during the sampling period in the “Forest” habitat (A) and the “Dunes” habitat (B).

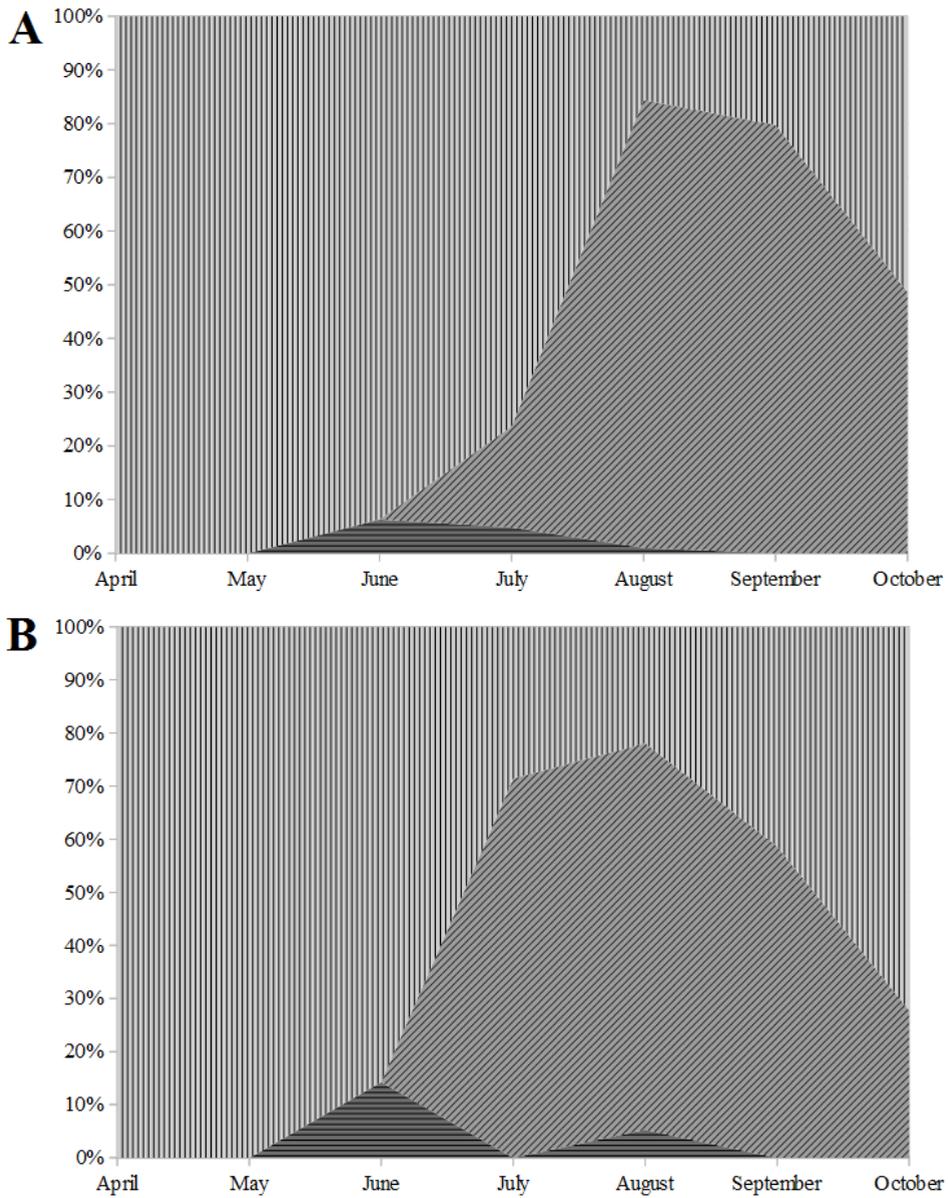


Figure 4: Representation of the variation of the proportions of adults (▨), juveniles (▧) and hatchlings (▩) of *P. edwardsianus* during the sampling period in the "Forest" habitat (A) and the "Dunes" habitat (B).

Discussion

Our results show several independent hints favouring our hypothesis. In the “Forest” habitat, where we expected a higher competitive pressure due to maximum abundance values, each species showed a different phenologic pattern. We found that *A. erythrurus* presented two abundance peeks, the first one can be explained by an increased activity during mating season (Busack & Klosterman, 1987), and the second one by the appearance of hatchlings (Pérez-Quintero, 1996). In the case of *P. edwardsianus*, we observed a clear tendency to increase abundance throughout the year. To explain this fact we have to take into account that the life cycle of this species is annual (Carretero & Llorente, 1991). This annuality also leads to high interannual fluctuations of the abundance of this species (Fitze, 2012), as the effect of environmental conditions on the population levels is much more direct than in other species. The fluctuations in abundance of *P. edwardsianus* were also associated to the ecological succession, as this species tends to occupy preferably the initial states (Fitze, 2012). Thus, reduced densities in mature environments could be, at least partly, related to interspecific competition. As new species colonize the habitat, *P. edwardsianus* keeps “loosing terrain”, being less competitive, maybe because of their small body size, especially juveniles. The unique reproduction of most individuals also implies a higher susceptibility to adverse periods and even spontaneous local extinctions (e.g. Jonsson & Ebenman, 2001; Jeppsson & Forslund, 2012). In the case of *P. algirus*, in neither of the two habitats we detected an abundance peek related to hatchling appearance. This could also be interpreted as a response to high competition levels between individuals of small body sizes, given the massive input of juveniles in summer, especially from *A. erythrurus*.

Another detail supporting the theory of competition between small size classes is that in the case of *P. edwardsianus*, the proportion of adults increases at the end of the year, indicating that some individuals reach sexual maturity the same year they hatched. If this is confirmed, it would be very interesting, as previous studies indicate that individuals reach sexual maturity in spring (Carretero & Llorente, 1991). An increased growth rate could be associated with competitive pressure. Moreover, the relatively small body size of *P. edwardsianus* also implies that adult individuals compete with juveniles of the other two species. In these conditions, an accelerated growth rate could be a great advantage. In addition, our results show that *P. edwardsianus* has an advanced phenology in comparison to the other two species. Juveniles hatch between one to two months earlier and also the appearance of gravid females indicates that the reproduction of this species is previous to the other species. In fact, in our case the hatching period is even earlier than the periods described for other *P. edwardsianus* populations, beginning in June (Fitze, 2012). This could be an important advantage for *P. edwardsianus* hatchlings regarding resource use, microhabitat occupation and territory knowledge.

Also in the case of *A. erythrurus* we evidenced a considerably higher growth rate than in previously described populations (Drechsler & Monrós, 2018). In our case, the variations of age class proportions indicates a mainly annual cycle of the population, very different results from previous studies, where the authors stated that individuals reach sexual maturity at 1.5 years of age (Busack & Jaksic, 1982; Belliure, 2015). Additionally, we

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detected an extreme peak of hatchlings in August in the “Forest” habitat. We could exclude that it is an artefact related to the representation of proportions (that in reality it is a low proportion of another age class), given that the mean values of abundance for the other age classes are practically identical in both habitats. Considering our hypothesis, this massive input of juveniles to the population can be advantageous for *A. erythrurus*.

The sex ratio also hints in favour to our hypothesis, as in all three species it is biased towards males. Higher levels of testosterone in males lead to higher aggression and, thus, a higher probability of success in interspecific encounters. Following our hypothesis, the smallest species (*P. edwardsianus*) would be the most affected, and that is exactly what we observed, although a higher proportion of males had been described previously in other populations, it did not reach such extreme values (Carretero, 1992). In the case of *A. erythrurus*, the sex ratio seems to be 2:1 biased towards males, which is also a higher proportion of males than previously described for this species (Busack & Jaksic, 1982). However, the sex ratio of *P. algirus* is very similar to those described in other populations (Salvador & Veiga, 2001).

We could not detect an possible effect of competition on the other aspects of population dynamics. In the case of *A. erythrurus*, hatching occurs between July and October, a period traditionally described for this species (Pérez-Quintero, 1996). The period we observed gravid females indicates that egg laying takes place from mid May to mid August, which also accords to previous results (Castilla et al., 1992, Carretero & Llorente et al., 1995). The fact that we only observed one hatchling peak indicates that in our population the majority of females only lays eggs once per year, although in other populations the capacity of various clutches per year was described (Castilla et al., 1992). The mean number of eggs per female (3.25 ± 0.62 for “Forest” and 3.33 ± 0.84 for “Dunes”) is a bit lower than in other populations (Belluire, 2015).

In the case of *P. algirus*, the variation of age class proportions showed differences between habitats. In the “Forest” habitat the obtained pattern seems to be similar to other populations, with a high proportion of adults until August, which is then reduced due to the input of juveniles to values of about 25% at the end of the year. In fact, this is exactly the percentage a previous study described for individuals surviving from spring to autumn (Civantos & Forsman, 2000). The period we observed gravid females is the same as described in other populations (Salvador & Veiga, 2001). However, the values of eggs per female (3.73 ± 1.68 for “Forest” and 3.86 ± 0.69 for “Dunes”) are among the lowest registered for this species, but very similar those described in the Ebro Delta, a habitat very similar to our study area (Salvador, 2011). Finally, in the case of *P. edwardsianus*, the variation of age class proportions throughout the year clearly reflects the annual character of this species, and the mean number of eggs per female (2.25 ± 0.89 for “Forest” and 2.75 ± 1.50 for “Dunes”) is similar to values described in other populations (Fitze, 2012).

Regarding the variation of abundance, the analysis showed differences between species and between habitats. In the “Dunes” habitat, *A. erythrurus* is clearly the dominant species, with values that generally triplicate the values

of the other two species. This is expectable, as previous studies described that *A. erythrurus* prefers more open areas and that it is more thermophile than the other two species (Belliure et al., 1996). These, in contrast, prefer denser habitats (Camacho, 1980; Bons, 1989; Martín & López, 2002). However it is curious that *A. erythrurus* also dominates in the “Forest” habitat, even with higher abundance values than in “Dunes”. This in some way contradicts the previously described preference. Although the comparison of our abundance results with other studies is difficult as they are usually expressed in individuals per hectare, and not individuals per hour. In addition, they refer to other habitat types, different from our study area. In fact, in the case of *P. algirus* we did not find any values for coastal or dune habitats, only for oak forests (Salvador, 2011). But given the high heterogeneity on a small scale in our study area, the estimation of abundance in relation to time is more reliable than in relation to surface, and this method is also more suitable for long term monitoring.

In conclusion, the detailed analysis of population dynamics of the three lizard species in the study area showed several hints favouring our hypothesis. However, there could also be other factors we did not consider playing a role. We have to take into account that the study area presents a high anthropic pressure, especially the “Forest” habitat, being a very frequented area by bicycles, cars and even buses, which imply an additional mortality. Although comparing 2015 and 2017 there was a subtle increase in abundance of all species, in neither case it was significant. Previous studies also showed that human alteration of a dune habitat can affect each lizard species differently (e.g. Vega et al., 2000). Thus we suggest to carry out similar studies in other areas where the three lizard species cohabit in order to discern if the described effects are really caused by competition or if they are more a local effect related to human activity.

Acknowledgements

We would like to thank all the people who helped during fieldwork and the Albufera de Valencia Management Team for the permissions to carry out this study. The main author is supported by a Val I+D predoctoral grant (ACIF/2016/331) of the Ministry of Education, Investigation, Culture and Sport of the Regional Government of Valencia and the European Social Fund.

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