A complex case of interaction between lizards and plants. The dead horse arum (Dracunculus muscivorus) and the Balearic lizard (Podarcis lilfordi)

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In this work we describe the interaction of the dead horse arum and the Balearic lizard in Aire (Balearic Islands, Spain). In Aire Island, the dead horse arum, Dracunculus muscivorus, is particularly abundant. From 1999 to 2005 we studied the population of this plant species and its relationship with the Balearic lizard, Podarcis lilfordi. During blooming period, several lizards exhibited an intense foraging behaviour focused on open inflorescences. Lizards were able to capture flies attracted by the plants and those trapped in tubules as pollinators. The exploitation of pollinators was principally made by largest males of the population that actively excluded females and smaller males from plants, skewing lizard sex-ratio in areas of maximum plant density.

Lizards consumed fruits following the progressive fruit maturation. In two germination experiments, we detected an enhanced germination of seeds from lizards' faeces, in comparison with those directly taken from ripening fruits. Thus, the Balearic lizard is the main legitimate disperser of the dead horse arum.

From 1999 to 2005, the density of the dead horse arum increased from 4800 ind./ha to more than 25.000 ind./ha in some optimal areas of the islet, indicating a very positive balance of the interaction between plants and lizards.

Keywords: mutualism, interaction, Balearic lizard, islands.

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INTRODUCTION

Plants are the basis for animal radiation on earth and the dominance of flowering plants is directly linked with mutualistic relationships of plants, their pollinators and seeds dispersers (Price 2002). Hence, it is not surprising that a myriad of different interactions between plants and animals arose during biota evolution. At Mediterranean ecosystems these interactions are widespread. Even within lizards, several interactions are described (Pérez-Mellado & Traveset 1999, Olesen & Valido 2003).

Insular ecosystems of the Mediterranean basin are characterized by a low trophic availability and, consequently, a reduced number of terrestrial vertebrates. In addition, Mediterranean islands have a small number of autochthonous predators, at least, prior to human arrival during the Holocenic period (Corti *et al.* 2000, Pérez-Mellado 2002). It is the case of Balearic Islands (Spain). At several coastal islets, the Balearic lizard, *Podarcis lilfordi* (Squamata, Lacertidae), is the only terrestrial vertebrate, inhabiting islets without significant interferences from predators and/or competitors. This situation promotes the raise of a varied set of demographic and natural history traits, in some cases unique of one or more populations. Among these traits, we can mention a very high population density, generally higher than observed densities for continental lacertid lizards of similar body size (Pérez-Mellado 1989, Brown & Pérez-Mellado 1994 and a summary in Pérez-Mellado 1998). Another characteristic is a sharp sexual dimorphism, with bigger males than females, as well as an eclectic foraging behaviour (Pérez-Mellado & Corti 1993, Pérez-Mellado 1998, Pérez-Mellado & Traveset 1999).

Several examples of interaction between the Balearic lizard and different plant species has been already described, including the role of the lizard as the main pollinator of Crithmum maritimum and Euphorbia dendroides (Pérez-Mellado & Casas 1997, Traveset & Sáez 1997, respectively), as well as several cases of seed dispersal (see Pérez-Mellado & Traveset 1999 for a review). However, from 1997 a much more complex interaction between the dead horse arum and the Balearic lizard was detected at Aire Island (Menorca, Balearic Islands, Spain). The consumption of pollinators arriving to blooming plants, as well as an intense fruit consumption during the ripening period was shortly described in a preliminary paper (Pérez-Mellado et al. 2000). In the present work we summarize the findings of a deeper study made during the spring and summer 2003 (see also Pérez-Mellado et al. in press and Pérez-Mellado et al. in prep.). Starting from previous observations, we checked the role of the Balearic lizard in the pollination of the dead horse arum and the pattern of flower visitation by lizards. In addition, we studied the fruit consumption during the ripening period, the characteristics of fruits produced by the plant and the main cues used by lizards on fruit selection. Finally, we estimated the extent of seed dispersal and its influence on plant density.

MATERIAL AND METHODS

Study area and period

The study was carried out during the spring and summer 2003, with additional observations in 2002, 2004 and 2005. In 2003, intensive field work started on the first week of February till September.

Aire Island is located off the south-eastern coast of Menorca (Balearic Islands, Spain). The island has a surface of around 342500 m². It is probably the oldest and most remote of the islands that surround the coastline of Menorca. It is a fairly flat island, with a slow gradient rising to 15 m above sea level in the north to south axis. A jetty, suitable for dockings of small to medium boats, is located in the central zone of the northern coast. The constructions of the island are all in ruin with the exception of a small hut by the jetty and the lighthouse, which was maintained by a resident lighthouse keeper up until the 1960s and is now automatic (Fig. 1). A colony of the yellow-legged gull (*Larus michaellis*) is located in the western end of the island (Fig. 6); other nesting birds are the peregrine (one breeding pair, *Falco peregrinus*), storm petrel (*Hydrobates pelagicus*), Cory's Shearwater (*Calonectris di*-

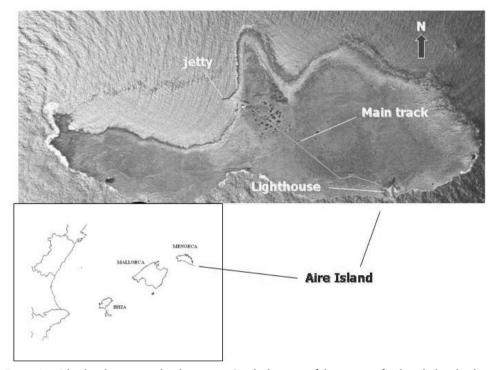


Fig. 1. Aire Island and its geographical situation. See the location of the main artificial track that divides the central area of the island in two distinct parts, with lower vegetal cover to the west of the track.

omedea), Balearic shearwater (*Puffinus mauretanicus*) and European shag (*Phalacro-corax aristotelis*).

Menorca, and therefore also Aire Island, has a mesomediterranean climate, characterised by mild temperatures with very seasonal precipitations, abundant rains in winter and very dry summers. There are frequent and strong winds principally from the north and the east. Aire Island is located in the driest zone of Menorca. Between 1945 and 1975 an average rainfall of 435 mm was recorded half yearly (lighthouse rain station from Aire Island). Yearly average temperature is 17.2 °C with a maximum of 27.5 °C in July and a minimum of 9.5 °C in January (weather station at Sant Lluís, the closest to the island, Jansà i Clar 1979).

Given its flatness and its relative distance from the coast, the whole surface of the island is subjected, from the point of view of the vegetation, to the effect of the sea. Consequently, with the exception of communities of shallow rooting plants, virtually all of the vegetation is hallophyllous. In a straight transect along the islet can be seen various patches of vegetation. First, nearest to the sea, plant communities with marked hallophyllous characteristics appear. Typical of places strongly affected by the sea, species such as *Crithmum maritimum* and *Limonium* spp. can be found. A little further from the coast, the vegetation opens out into shrub communities dominated by *Suaeda vera*, typical of saline soils. On sites protected from the wind and sea by barriers of human origin (remains of walls and plantations of *Tamarix africana*), species of typical Mediterranean vegetation dominated by *Pistacia lentiscus* appear. Furthermore, *Carlina corymbosa* forms dense patches in the least saline areas. Beyond the communities previously mentioned unfold the communities of annual plants including especially abundant species such as *Bellis annua*, *Asteriscus maritimus* and *Valantia muralis*.

Between the dock and the lighthouse there is a narrow track of 465 m long that divides the island in two well differentiated areas. To the west of the track rock *sub-strata* is dominant and the vegetation is formed by coastal species, being the sea fern, *Crithmum maritimum* the dominant plant species. The eastern area can be divided in two portions, the westernmost part, with a shrub vegetation of *Suaeda vera* in the south and *Carlina corymbosa* in the north, together with some shrubs of *Pistacia lentiscus*. The easternmost area is covered by rocks and a scarce vegetation of sea ferns. We made a preliminary division of the island surface in different areas according with these differences in vegetation cover (Fig. 2).

Species under study

The dead horse arum, *Dracunculus muscivorus* Engler 1879 (Araceae, Aroideae), is a plant of Thyrrenian distribution, that is, an endemic species only present on West-

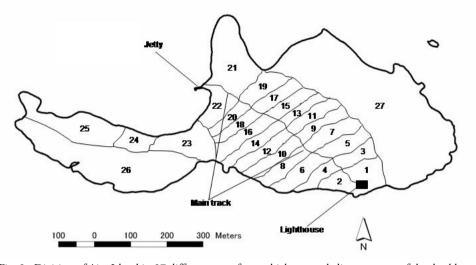


Fig. 2. Division of Aire Island in 27 different areas from which we made line transects of the dead horse arums and lizards.

ern Mediterranean islands, Corsica, Sardinia and the Balearic archipelago. This "very striking sinister-looking plant" (Polunin & Huxley 1981, Fig. 3), is considered the less common Araceae of Balearic Islands (Bonner 1994). Its natural habitat is formed by rocky areas with some degree of humidity (Collu & Dardani 1999). Some authors consider that differences on inflorescences, pollen grains and other morphological characteristics are sufficient to separate the dead horse arum in a different monotypic genus, *Helicodiceros* (Schott 1853).

Flowers are arranged around the floral axis or spadix, where male and female flowers are separated by a sterile portion of the spadix (Fig. 4). The spadix is surrounded by the basal portion of the spathe, a highly modified leaf that forms a narrow tubule, flanked by several filaments that can close the tubule above male or female flowers. The inner surface of the spathe is covered by short hairs and pigmented on red, pale pink or whitish. The outer portion of the spadix is yellowish with dark filaments and lacks flowers.

The dead horse arum has a highly sophisticated pollination mechanism. It produces an intense decaying meat odour, attracting flies (Diptera), especially from the family Calliphoridae. Some species are identified as pollinators, as *Lucilia caesar* and *Calliphora vicina* (Stensmyr *et al.* 2002). Female flies are attracted by the odour because they use carcasses as optimal laying sites. Recently it has been demonstrated that chemical composition of odours from *D. muscivorus* is extremely similar to the odour produced by decaying meat, eliciting almost identical neural responses on flies (Stensmyr *et al.* 2002). The plant odour, produced at the spadix, attracts flies coming from



Fig. 3. A blooming dead horse arum.

another plant, where they loaded pollen. Flies enter into the tubule and are trapped by a rosette of stiff hairs into the lower chamber with receptive female flowers. Flies' movements trying to escape sprinkles pollen grains on female flowers that close after pollination. Then, male flowers open and start pollen production to cover trapped flies. Pollen production takes place at night, followed by a fall on plants' temperatures, higher during diurnal period of female receptive flowers. In addition, the opening of male flowers stops the production of foetid odour by spadix (Bonner 1994). Finally, after two to several hours trapped, flies are released. This mechanism, with an asynchronous maturation of male and female flowers, precludes autopollination (Collu & Dardani 1999). *D. muscivorus* flowers remains open during no more than two days, while odour production is highest on the first day, when more pollinating flies are attracted (Stensmyr *et al.* 2002). Probably, the dead horse arum employs additional lures to attract flies as heat, because the plant is able to raise its temperature over more than 14 °C above air temperature (Pignatti 1982). Also the flashy colour of spathes can attract flies and other potential pollinators.

The Balearic lizard, *Podarcis lilfordi* (Günther 1874) (Lacertidae, Squamata) is a medium-sized lacertid lizard endemic to Balearic Islands. In some of the islands,

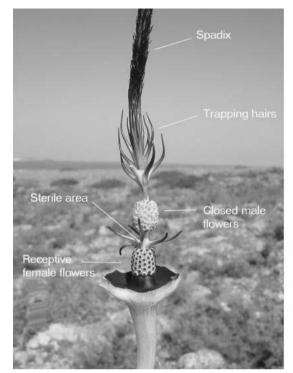


Fig. 4. Internal structure of a blooming dead horse arum after leaving the spathe.

extremely high population densities are found while in others the effective population has reduced to as little as just a few individuals (Pérez-Mellado 1989, 1998). Twenty-eight subspecies of *P. lilfordi* have been described, based on differences in morphometrics, design, colouration and scalation, but not all are accepted. In the most recent revisions (Pérez-Mellado 1997, 1998) 23 subspecies were recognised, with eight of them off the coast of Menorca, six off Mallorca and the rest present in Cabrera archipelago. The subspecies that occupies Aire Island is the nominal one, Podarcis lilfordi lilfordi. Along with the extinct population of Ratas Island, it is the most obviously differentiated of all the Menorcan populations (Pérez-Mellado & Salvador 1988, Pérez-Mellado 1998). P. lilfordi lilfordi is a melanistic lizard with a larger body size than any other Menorcan population and with characteristic biometrical and scalation traits (Fig. 5). It is a robust subspecies; the males have a head to tail length with an average of 69.98 mm and an average weight of 9.57 g, meanwhile the females are smaller with an average head to tail length of 61.73 mm and a weight of 6.34 g (Pérez-Mellado & Salvador 1988, Pérez-Mellado 1998). Lizards of Aire Island are active all year round. They are distributed throughout the island. The density reaches extremely high levels in certain areas around the moor and in the group of tamarinds situated in the eastern zone (Pérez-Mellado 1989, Brown &



Fig. 5. The Balearic lizard basking on a blooming dead horse arum.

Pérez-Mellado 1994 and pers. obs.). These densities fluctuate notably from one year to the next.

Density estimations and zonal stratification

Plant and lizard densities were estimated with line transects (Buckland *et al.* 2001). For plants, line transects had a length of 70 m with a width of 1 m at both sides of the line. Prior to plant line transects, we made lizard density estimations with transects on the same areas. In this case the width of transect was determined by the outermost individual recorded at each transect (Buckland *et al.* 1993).

Aire Island was divided in different sectors to make density estimations of plants and lizards. Within the nucleus of previously observed highest plant density (Pérez-Mellado *et al.* 2000) we made narrow strips each 35 m from lighthouse enclosure to northern coast, taking as a reference the middle track from dock to lighthouse (Fig. 2). This artificial track marks a clear limit of vegetation. East to the track, the dominant plant is *Suaeda vera*, while at the western side the dominance corresponds to more coastal species as *Crithmum maritimum* and *Limonium* spp. Western area is also the main site of seagull breeding colonies (Fig. 6). Only three breeding pairs of *L*.

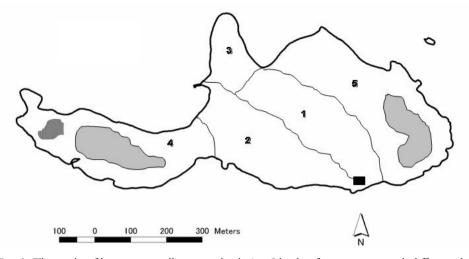


Fig. 6. The results of line transects allow us to divide Aire Island in five main areas with different plant and lizard density. Pale grey spots at areas 4 and 5 indicate the location of yellow-footed gull (*Larus michaellis*) colonies during 2003. Darker grey spot in area 4 was the site of Audouin's gull (*Larus audouinii*) colony.

michaellis were present close to the eastern side of the track during spring 2003. Then, another group of seagulls breed at the easternmost peninsula of islet. From the main track, parallel censuses of lizards and plants were made to both eastern and western sides heading to 220° and 40° compass courses respectively. In this way, 20 sectors of plant and lizard densities were defined. Then, four censuses covered the northeastern peninsula of the island (sector 21 of Fig. 2) were made. Finally, the western peninsula, a large rocky area with the largest seagull colony, was surveyed with four additional censuses (sectors 22 to 25 of Fig. 2) as well as the easternmost corner of the island. Thus, density of lizards and plants was estimated in the whole surface of the island, excepting from sector 27 for plants, with an extremely low density of *D. muscivorus*.

In addition, on 13th April 2003 and on 28th April 2005, we made four line transects of 25 m long and 100 cm to both sides of the line of transect each, at the same site of maximal plant density surveyed in 1999 (Pérez-Mellado *et al.* 2000 and Fig. 8) to make a direct comparison of plant density between 1999, 2003 and 2005.

Within the first 20 narrow sectors, where plant density is higher (see below), we made an additional estimation of rock, open ground and plant covers. We made 25 m censuses on each strip, recording the percentage covered by each shrub species, that is, by each vascular plant that can be used by lizards as a refuge or perching site. Plant cover was recorded in this way for *Asteriscus aquaticus, Carlina corymbosa, Crithmum maritimum, Euphorbia sagetalis, Pistacia lentiscus* and *Suaeda vera*. Rock cover was recorded in three categories, rocks of more than 50 cm high, less of 50 cm and rocky

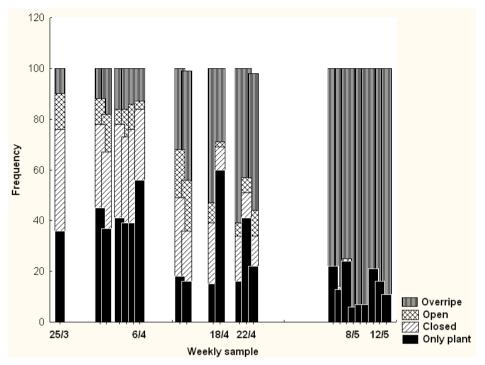


Fig. 7. Proportion of blooming *D. muscivorus* (open spathes), closed plants, plants after blooming period (overripe) and only plants (prior to blooming) during weekly sampling of spring 2003 at Aire Island. See the staggering of open spathes over a long period of almost two months.

ground. A comparative analysis of cover and its diversity was made at the first twenty areas surveyed. Diversity of vegetal and rock cover was estimated with Levins' niche breadth (Levins 1968), as well as its equitability according to Pielou's modification (Krebs 1989).

Plant characteristics, availability and lizard behaviour

Availability of open spathes of *D. muscivorus* was studied from 17th April till 12th May 2003. Sixty spathes were numbered with plastic labels recording their colour (whitish, pale pink, pink or reddish). The presence of flies as potential pollinators on spathes or trapped into the tubule, as well as the presence of lizards were also recorded. On additional 83 randomly selected open spathes the maximum height, spathe length and width, spathe orientation and distance to the nearest plant of the same species and to the nearest individual of *Suaeda vera* were measured.

Lizards on spathes were noosed. SVL and tail length was measured with a steel rule. Lizards were weighted with a spring balance and cloacal temperature was recorded with a digital thermometer (Pérez-Mellado *et al.* in prep.).

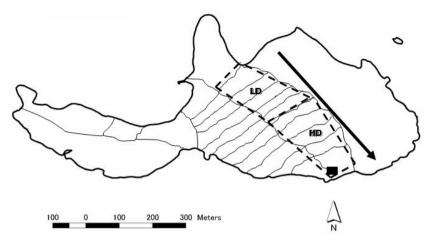


Fig. 8. Areas of low and high plant density to the east of the main track. The arrow indicates the general trend to higher plant and lizard density from north to south. A cross within high density area marks the point of identical line transects carried out in 1999, 2003 and 2005.

Potential role of lizards as pollinators

Potential role of *P. lilfordi* as a pollinator of *D. muscivorus* was studied with an exclusion experiment. From marked spathes (see above), we randomly selected six spathes, prior to their opening. Three spathes, to exclude flying pollinators (Calliphoridae flies), were covered with a cubic plastic mesh. Remaining three spathes were surrounded with a plastic enclosure open from the top. In this way, we precluded lizard access and allowed the access of flying pollinators. Ten of the remaining marked spathes acted as control, with a free access to flies and/or lizards. In addition, we evaluated the capacity of pollen load of this plant species by the lizard. Pollen grains of *D. muscivorus* are easily distinguishable for their spheroidal shape and spiny outer surface (Thanikaimoni 1969). Pollen load capacity was estimated using the same protocol of a previous study of the Balearic lizard and other plant species (see details in: Pérez-Mellado *et al.* 2000), extracting pollen grains from belly, dorsum and throat with cello-tape stripes. From April 2003 we obtained data of pollen load from 24 adult lizards. We added a sample of 10 lizards surveyed on May 1999.

Seed dispersal

Results of seed dispersal presented here are summarized from another work on this subject (Pérez-Mellado *et al.* in prep.). The study of available fruits was done from 500 ripening fruits obtained from 20 mature and intact infructescences in two different areas of Aire Island characterized by a very different plant density (see below). Thus, 10 infructescences were randomly collected for each density area. For each infructescence we obtained its total fruit number, fruit colour, that reflects its maturation state, and, from a random subsample of 25 fruits of each infructescence, fruit length, width and weight. In the same way, we recorded the number of seeds per fruit and their weight, length and width from a random subsample of 25 seeds from each infructescence.

The intensity of dispersal was estimated from weekly samples of 100 faeces of *P. lilfordi* collected at the areas of low and high plant density (50 faeces for each area). This sample took place from 18th May till 13th June 2003. Then, we obtained two additional samples on 28th June (eighth week) and 19th July (11th week). We also made an analysis of three consecutive years, 2002, 2003 and 2004 with additional samples of faeces from June 2002 and 2004 collected at both areas of high and low plant density (see below). We counted dead horse arum seeds, as well as the presence of elaiosomes on seeds.

Viability tests were performed in October 2003 on three samples of seeds from wild plants randomly selected that had free access to potential pollinators, another sample from plants isolated from flying pollinators (see Methods) and a third group from lizard faeces. We used tetrazolium test to check the viability of seeds. Seeds were cut so that the embryo is bisected. Then, seeds were placed in a 0.1% solution of 2, 3, 5-triphenyl-2H-tetrazolium chloride (TTC). Viable embryos release hydrogen ions during respiration, which combine with TTC, causing it to turn reddish (ISTA 1999).

We made two experiments on seed germination. First experiment was performed on 1999 and the second experiment, with a larger sample size on 2002. Seeds from faeces and plants were collected at Aire Island. In 1999 seeds were collected on 17th.

May 1999 and stored at 4 °C during two weeks. Prior to plantation, seeds were dried at room temperature during two days. The second experiment started on 29th June 2002 and finished after 182 days. In this case seeds were collected during June and May (see above). Seeds were buried on universal *substrata* and maintained during the whole duration of both experiments in open air at Menorca Island. Outdoor experiments on seed germination are better to detect effects (Traveset & Verdú 2002).

Seed predation

After fruiting period, we did an experiment to test post-dispersal seed predation intensity at Aire Island. We arranged two randomly selected samples of *D. muscivorus* seeds from lizard's faeces and ripening fruits, respectively. We checked seeds from faeces to assure the absence of elaiosomes, while in all seeds from ripening fruits elaio-somes were present. Both samples of seeds came from the two areas of high and low plant density (see above).

Lizards were placed in two series of 20 plastic Petri dishes of 9 cm of diameter at both areas of high and low plant density from 18th July 2003, when ripening fruits of *D. muscivorus* were not anymore available. In each series, we placed two parallel lines of Petri dishes 7 m apart each other and with 3.5 m between lines, one line with dishes covered with a wire mesh (6 per 6 mm) that precluded the access of vertebrates (lizards, granivorous birds or rabbits) to seeds and another line of uncovered dishes. On each Petri dish we placed 10 seeds. For each Petri dish, seeds were obtained from the high or the low plant density areas. A careful inspection of the 40 Petri dishes was done each three days during a trial of 30 days.

Data analysis

Data were analyzed with Statistica 6.0 package or with a handheld calculator for some likelihood tests. We employed parametric tests when data were normal and variances homogeneous or data log transformed. If data did not meet requirements for parametric tests after transformation, non-parametric alternative tests were employed. Frequency tables were analyzed with non-parametric test as G, McNemar or binomial tests (Zar 1999) or with log-linear models (Quinn & Keough 2002). In all cases we give the arithmetic mean (\bar{x}) followed by its standard error (± SE), maximum and minimum values of the distribution and sample size (n).

Results

General characteristics of Dracunculus muscivorus

The phenology of the dead horse arum can vary between years. In 2003, blooming period started earlier than in 1999 (Pérez-Mellado *et al.* 2000). During the first week of February we found several green plants at the central area of Aire Island. In March, several spathes were open, with the highest proportion during the four week of this month and the first two weeks of April (Fig. 7). Open spathes were present during a long period of more than five weeks, lacking synchronization of blooming plants.

Closed spathes of *D. muscivorus* are dark green and brownish spotted. Open spathes are white, yellowish, pink or reddish. Average length of spathes was $\bar{x} = 223.0123 \pm 3.8941$ mm (n = 81). We did not find significant differences between spathe lengths of different colours (one-way ANOVA, $F_{2,78} = 1.1899$, P = 0.3097, homogeneous variances, Levene's test, F = 0.5495, P = 0.5794). Maximal width of spathes was $\bar{x} = 184.0617 \pm 3.2268$ mm, range: 119-255 mm, n = 81, again without significant differences between colours (one-way ANOVA, $F_{2,78} = 1.1569$, P = 0.3198, homogeneous variances, Levene's test, F = 0.3860, P = 0.6810).

Density of lizards and plants

The dead horse arum is distributed over the whole Aire Island surface, but it is rare at sectors 26 and 27 from the eastern part of the island and was not detected at sectors 20, 21, 22 and 25 (Fig. 2) during line transects. These four sectors were during 2003 the sites of seagull breeding colonies.

Including sectors where the presence of plants was not detected, the average plant density for Aire Island is: 7186.54 ± 1979.71 plants/hectare, for n = 26 line transects (ranging from 0 to 32146 plants/ha, 95% confidence limits: 3109.25-11263.83).

These results allow us to group sectors in larger areas of similar plant density. Thus, we consider four large areas: 1: Central area east from the track to lighthouse, 2: Central area west from the track to the lighthouse, 3: Northeastern peninsula, 4: Western peninsula and 5: Eastern part of the island (Fig. 6).

For all line transects, the average density of lizards during spring 2003 was: 2188.89 ± 213.44 lizards/hectare (range: 398.67-5816.70, n = 35 line transects). Area 3, showed the highest lizard density (Table 1). Areas 2 and 4 are occupied by seagull breeding colonies (Fig. 6) and showed lower lizard densities, as well as the area 5, with a poor vegetal cover, very low density of dead horse arums (see below) and also a small seagull colony. Finally, area 1 has a high lizard density. We found significant differences between the density of these areas (one way ANOVA, $F_{4,30} = 3.9355$, P = 0.011, homogeneous variances, Levene test, $F_{4,30} = 2.5017$, P = 0.0633). A posteriori Duncan tests indicate significant differences between areas 5 and 1 (P = 0.03), with lowest and highest lizard density respectively, and between areas 3 and 4 (P = 0.0247), between

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Zone	$\overline{\mathbf{X}}$	± SE	Range	n
1	2825.88	346.22	2114.21-3537.55	10
2	1624.17	346.22	912.5-2335.84	10
3	3706.27	632.11	2406.94-5005.59	3
4	2110.01	413.81	1259.4-2960.62	7
5	1244.22	468.55	398.67-3002.10	5

Table 1. Lizard density at five different zones of Aire Island.

Table 2. Dead horse arum density at different zones of Aire Island

Zone	$\overline{\mathbf{X}}$	± SE	n
1	10924.84	3846.21	10
2	6921.76	3206.91	9
4	5095.25	4385.73	3

3 and 2 (P = 0.005) and between 3 and 5 (P = 0.001). Thus, both island areas with breeding colonies of seagulls showed significantly lower lizard densities. It is also the case of area 5, with a smaller seagull colony and, probably, a suboptimal plant cover.

Regarding the dead horse arum, we restricted our analysis to areas 1, 2 and 4, because at the north-eastern peninsula (area 3) and area 5 we did not detect plants during transects, even if some individuals were present (pers. obs.). Densities are clearly higher at area 1 (Table 2), even if we did not detect significant differences among the three areas (one way ANOVA, $F_{2,19} = 0.5042$, P = 0.61, homogeneous variances, Levene's test, $F_{2,19} = 0.8164$, P = 0.4569).

Taking into account all sectors of the island, we did not find any significant correlation between dead horse arum and lizard density (Spearmann rank correlation, $R_s = 0.00123$, P = 0.99, n = 30). If we consider only those sectors with detected plants, the correlation is still non significant ($R_s = 0.2377$, P = 0.2866, n = 25).

However, at the central area of maximal plant density, east from the main track to the lighthouse (see above and Fig. 8), we found a significant correlation between plant and lizard density ($R_s = 0.6322$, P = 0.0498, n = 10) with a decreasing density gradient from south to north. This correlation does not exist at the western side of the main track ($R_s = -0.358$, P = 0.3096, n = 9) probably because these areas enter, at least partially, within the range of the breeding colony of seagulls.

Results from the central area of maximal plant density showed a clear north-south density gradient, suggesting and additional analysis. We grouped the twenty narrow areas east and west to the main track into four groups, southeast, southwest, northeast and northwest (Fig. 8) to compare these larger areas with fruit consumption and seed dispersal intensity. Densities of plants and lizards were again estimated for these four groups.

In the case of plants, we did not find significant differences in density between south-western and north-western groups (one way ANOVA for log-transformed data, $F_{1,7} = 1.504$, P = 0.2598, homogeneous variances, Levene's test, $F_{1,8} = 0.2584$, P = 0.6268). However, we found significant differences between south-eastern and north-eastern groups, with a higher plant density at south-eastern group (density = 19134.64 ± 4055.004 plants/hectare, n = 5 line transects) than at north-eastern groups (density = 2729.05 ± 4055.004, n = 5 line transects, one way ANOVA, $F_{1,7} = 10.90$, P = 0.011, homogeneous variances, Levene's test, $F_{1,8} = 0.0766$, g.l. = 1,8, P = 0.7889, Fig. 8). In next analyses we compare fruit availability and dispersal intensity by lizards between those south-eastern and north-eastern areas (Fig. 8). In addition, at the south-eastern area, where the four line transects of 1999 were done, 2003 and 2005 transects showed a constant increase of plant density (Fig. 9).

Regarding lizard density, again we did not find significant differences between south-western and north-western areas (one-way ANOVA of log-transformed da-

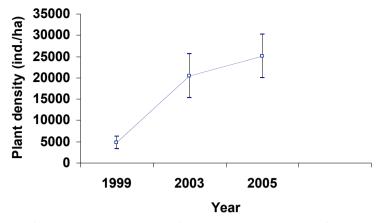


Fig. 9. Increase of plant density over a period of six years at the central area of Aire Island (average number of plant per hectare ± SE).

ta, $F_{1,7} = 0.082$, P = 0.782, homogeneous variances, Levene's test, F = 3.4380, P = 0.1061). A similar result was obtained in the comparison of south-eastern and north-eastern areas (Mannn-Withney U-test, Z = 1.1489, P = 0.2506).

At the twenty central sectors of density estimation, rocks and open grounds cover 59.62% of the surface and the remaining 40.38% corresponds to plant cover, with *Suaeda vera* as the main plant species (14.51%). We did not find significant differences between south-western, north-western from one side and north-eastern and south-eastern groups from the other side, excepting for *Suaeda vera* cover, higher at south-western area (Mann-Withney U-test, Z = 2.2045, P = 0.0275; south-western = 33.30 ± 4.8191%, range: 17.14-42.10%, north-western = 6.68 ± 4.2748 %, range: 0-19.17%). In fact, taking into account all cover plant species and substrates, we found only a significant correlation between the density of *D. muscivorus* and the percentage of *S. vera* cover (Spearmann rank correlation, $R_s = 0.4851$, P = 0.04, n = 19).

Lizard population structure

During the morning hours of highest lizard activity, we made line censuses over total length of the twenty central areas of maximal densities of *D. muscivorus* counting the number of adult males, adult females and juveniles of *P. lilfordi*. Then, we compared sex and age ratios with dead horse arum and lizard densities. We did not find any significant correlation between lizard densities and lizard sex or age ratios. However, we found a significant correlation between age ratios and plant densities (Spearmann rank correlation, $R_s = 0.6042$, d.f. = 19, P = 0.00614). Hence, areas of maximum plant density had a significantly lower proportion of juvenile lizards.

Lizard activity during the blooming period

During the blooming period visits of lizards to open spathes of *D. muscivorus* were regular. In some cases only the outer surface of spathe was explored, basking during a long time there. In other cases, tubules were explored and trapped flies captured (see also Pérez-Mellado *et al.* 2000). We did at least four isolated observations of lizards basking on adjacent rocks, close to open spathes, that rapidly turned their heads after a clear trapped flies' noise inside the tubule. Then, lizards inspected the tubules and captured trapped flies.

Visits to spathes were done mainly by adult individuals. From 24 recorded visits, 22 were from adult lizards and 2 from juveniles. In addition, during censuses of age and sex ratios (see above), the proportion of juveniles basking on spathes (8.33%) was significantly lower than the total proportion of juveniles recorded during censuses (24.39%, G test, G = 3.946, P = 0.0497).

Moreover, the proportion of adult males on spathes was also significantly higher than observed adult males proportion during censuses (G test, G = 5.04, *P* = 0.0276). Adult males visiting spathes had significantly larger body sizes than a random sample of adult males from Aire island (Mann-Withney U test, U = 1230, *P* = 0.0107; SVL for adult males observer on spathes: $\bar{x} = 71.1471 \pm 0.6165$ mm, range: 68-76 mm, n = 17; SVL of adult males of Aire Island, $\bar{x} = 68.2591 \pm 0.3122$ mm, range: 51.50-80 mm, n = 230).

Potential role of lizards as pollinators

Two of the three spathes isolated from flying pollinators were totally dry on 18th May 2003. In addition, from the third spathe only one seed of 66 was viable. Thus, the proportion of viable seeds was significantly lower than from control sample (G = 57.858, P < 0.001). These results confirm the absence of autopollination in *D. muscivorus*.

Regarding pollen transport capacity of *P. lilfordi*, Table 3 summarize the results from 1999 and 2003 samples. For ventral and dorsal regions, pollen load was significantly different on 1999 and 2003 samples (dorsal pollen, U Mann-Whitney test,

Table 3. Pollen load of *Dracunculus muscivorus* at dorsal, ventral y gular regions of *Podarcis lilfordi* individuals during April 1999 and May 2003 (see more details in the text).

	0 1		,		,	
1999			2003			
Dorsal	$\overline{x} = 113 \pm 21.58$	39-234	10	$\overline{x} = 10.04 \pm 2.13$	0-40	24
Ventral	$\overline{x} = 36.20 \pm 9.66$	4-93	10	$\overline{x} = 7.15 \pm 1.72$	0-28	24
Gular	$\overline{x} = 17.00 \pm 5.03$	2-58	10	$\overline{x} = 15.83 \pm 7.10$	0-171	24

U = 1.0, Z = -4.4978, P = 0.000007, ventral pollen: U = 30.50, Z = -3.3828, P = 0.000686). We did not find differences for gular pollen between both samples (one way ANOVA, F = 0.0102, d.f. = 1, 32, P = 0.9201, homogeneous variances, Levene test, F = 0.5967, P = 0.4455).

Fruit availability and lizard's access

Fruits of *D. muscivorus* are approximately pyriform or spheroidal. They are arranged in a helicoidal way around the spadix. According to maturation stage, fruits changed from an initial green colour to whitish or yellowish and, finally, to intense orange or reddish colour in ripening fruits. Maturation is clearly enhanced by sun exposure. Thus, last ripening is reached after the opening of the infructescence and direct solar incidence on fruits. Infructescence opening can be produced by the plant itself, from apical zone of the infructescence or along the spathe' closing line. But in Aire Island, the opening is frequently the result of lizards' activity. Lizards bite the outer surface of apical zone or dig a lateral hole in the infructescence (Pérez-Mellado *et al.* in prep.). In this way, maturation was probably accelerated, allowing an earlier sun exposure. Then, foraging behaviour of lizards is quite similar in most of the observed cases. Lizards approach ripening infructescences, exploring them and eating only fully mature fruits of orange or reddish colour. We never observed the consumption of green or whitish fruits. Additional experiments confirmed these observations (Pérez-Mellado *et al.* in prep.).

From a random sample of 20 infructescences, we found an average of $\bar{x} = 92.35 \pm 4.15$ fruits per infructescence, varying between 45 and 132 fruits (n = 20, 95% limits of confidence: 83.65-101.04). Their dimensions were: $\bar{x} = 9.3608 \pm 0.0824$ mm of maximal width (range between 4.92 and 14.97 mm, n = 500) and $\bar{x} = 14.4224 \pm 0.1122$ mm of maximal length (range between 9.12 and 22.32 mm, n = 500). Average fruit weigth was estimated for a random subsample of 100 fruits from the area of high plant density ($\bar{x} = 0.2097 \pm 0.015$ g, range: 0.025-0.7089 g, n = 100).

Because the dead horse arum was not uniformly distributed over Aire island (see above), we made a comparative analysis of fruit availability between the areas of high and low plant density at the eastern part of the main track. We did not find significant differences in the average number of fruits per infructescence between these two areas (Mann-Whitney test, U = 48, Z = 0.1511, P = 0.8798). Nor in the fruit weight (Mann-Whitney test, U = 29267.50, Z = 1.2272, P = 0.2197), fruit length (one way ANOVA, F = 0.2780, d.f. = 1, 498, P = 0.5982, homogeneous variances, Levene test, F = 1.6898, P = 0.1942), or fruit width (one way ANOVA, F = 0.5054, P = 0.4774, homogeneous variances, Levene's test, F = 0.5598, P = 0.4546).

The average number of seeds per fruit varies between 1 and 8 (\bar{x} = 2.4809 ±

0.0609, n = 499 fruits). It is significantly larger at the area of high plant density (one way ANOVA, F = 16.1812; d.f. = 1, 497; *P* = 0.000067; high plant density area: \bar{x} = 2.7229 ± 0.0926, range: 1-8, n = 249; low plant density area: \bar{x} = 2.24 ± 0.0764, range: 1-6, n = 250).

However, even if the number of seeds per fruit is significantly higher at the area of high plant density, the average number of seeds per infructescence is similar in both areas (one way ANOVA, F = 0.6724, d.f. = 1, 15; P = 0.4250, homogeneous variances, Levene's test, F = 0.0076, P = 0.9316). That is, seeds from high plant density area are smaller than in low plant density area (for seed length: one way ANOVA, F = 39.1377, d.f. = 1.1236, P < 0.00001, homogeneous variances, Levene test, F = 0.6307, P = 0.4272; high plant density area, $\bar{x} = 4.7459 \pm 0.0235$ mm, range: 2.92-6.34 mm, n = 678; low plant density area, $\bar{x} = 4.9618 \pm 0.0251$ mm, range: 3.18-6.53 mm, n = 560; for the whole sample: $\bar{x} = 4.8436 \pm 0.0174$ mm, range: 2.92-6.53 mm, n = 1238, and for seed width, Mann-Whitney test, U = 104728.5, Z = -13.5936, P < 0.001; high plant density area: $\bar{x} = 3.6589 \pm 0.0213$ mm, range: 1.21-5.50 mm, n = 678; low plant density area: $\bar{x} = 4.0275 \pm 0.0162$ mm, range: 2.68-4.88 mm, n = 560; for the whole sample: $\bar{x} = 4.0275 \pm 0.0127$ mm, range: 1.21-5.50 mm, n = 1238).

Fruits' water weights were in average: $\bar{x} = 0.1599 \pm 0.011$ g, range: 0.0231-0.5306, n = 100) that corresponds to an average percentage of the total fruit weight of: $\bar{x} =$ 77.88 ± 0.46% (range: 63.76-91.97% of water, n = 100). We did not find significant different in water content of fruits of different colour. That is, of fruits with a different maturation state (one way ANOVA, F = 1.4302, d.f. = 2,96, *P* = 0.2443, homogeneous variances, Levene test, F = 1.4769, *P* = 0.2335).

Seed dispersal

Timing and intensity of seed dispersal

In the three years surveyed (2002, 2003 and 2004), faeces from high plant density zone contained significantly more seeds than faeces from low plant density zone (Table 4). In 2003, we studied seed dispersal intensity throughout eight weekly samples. We

Table 4. Percentage of lizard faeces with seeds of <i>D. muscivorus</i> in May 2002 and June 2002 and 2004.							
Sample size within parentheses.							

1 1						
	May 2	2002	June 2002			
High density	37.05% (170)	G = 5.54	49.79% (492)	G = 64.04		
Low density	15.78% (57)	P = 0.018	11.45% (262)	P < 0.001		
			June 2	June 2004		
High density			92.30% (65)	G = 29.77		
Low density			50% (62)	P < 0.001		

examined the frequency of faeces with or without seeds in relation with two factors: the weekly sample and plant density zone; thus, considering the absence or presence of seeds in the faecal sample as the response variable (Quinn & Keough 2002). All tested models included the interaction between the two variables (week of sample and plant density). Sample week was variable 1 and plant density variable 2. The presence or absence of seeds in the faeces (response variable) was variable 3. Model 1 included the two interactions, 12 and 13, so we tested the null hypothesis of the independence of the presence/absence of seeds in relation to variable 2 (plant density zone). For this model we obtained a likelihood χ^2 = 248.30, d.f. = 8, *P* < 0.001. Thus, we rejected the null hypothesis of an independence of dispersal intensity and plant density zone. With model 2, including the interactions 12 and 23, we explored the null hypothesis of the independence of seed presence/absence and the week of sample. In this case, likelihood χ^2 = 227.62, d.f. = 14, P < 0.001. Thus, also in this case we rejected the null hypothesis of independence. Finally, model 3 of three way interaction: 12, 13 and 23 gave a χ^2 = 15.326, *P* = 0.03204, indicating a significant interaction between the three variables.

Figs 10 and 11 summarize the results of seed dispersal intensity during 2003 fruiting period. Seed dispersal started during the first half of May at the area of high plant density and around one or two weeks later at the area of low plant density.

In the area of high plant density dispersal finished almost completely between the second and the third week of July, while at the area of low plant density it was earlier.

Thus, as the results from log-linear analyses indicate, the intensity of seed dispersal was radically different between the areas for high and low plant density. In fact, in the area of high plant density, lizards include fruits in their diet from the beginning of the ripening period. Thus, the proportion of faeces with seeds was always higher than those without seeds. In addition, the analysis of three consecutive years indicates that the importance of *D. muscivorus* fruits in the diet of *P. lilfordi* had a continuous increase for both plant density areas.

Seed viability and seed germination

We detected 27 viable seeds from 30 seeds coming from lizard faeces, while form the control sample, coming from wild infructescences, 79 of 91 seeds were viable. Thus, we did not detect significant differences between seed from plants and faeces (G test, G = 0.014, P = 0.9064).

Regarding germination tests, in 2002 experiment we did not find significant differences between collected in May (33 germinated of 66 seeds) or June (125 germinated of 227 seeds, G = 0.162, P = 0.687). We found significant differences in the proportion of germinated seeds between those from plants and those from lizard faeces in both experiments of 1999 and 2002 (Table 5).

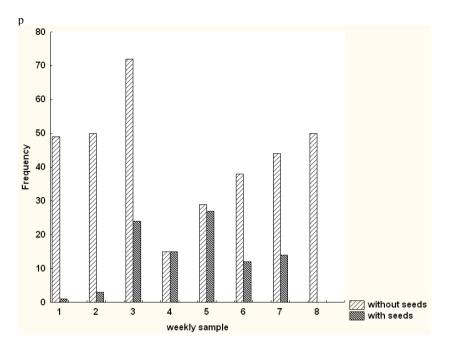


Fig. 10. Proportion of lizard's faeces with and without seeds of *D. muscivorus* at the area of low plant density.

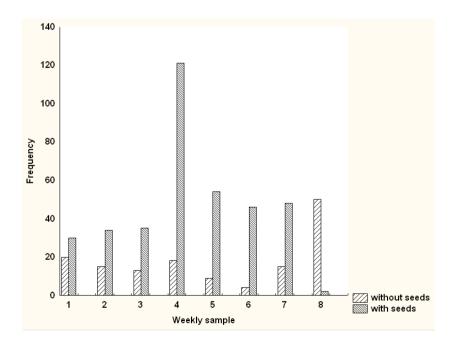


Fig. 11. Proportion of lizard's faeces with and without seeds of *D. muscivorus* at the area of high plant density.

	1999			20	2002		
	% germinated	G test	Р	% germinated	G test	Р	
Seed origin							
Faeces	63.63 (66)	15,14	0.001	55.06 (227)	24.67	< 0.001	
Plants	33 (100)		< 0.001	19.38 (294)	34,67		

Table 5. Germination experiments carried out in 1999 and 2002. Sample size of each group within parentheses.

Seed predation

The results of seed predation experiments were similar at areas of high and low plant density. In both cases we found significant differences in the number of seed predated from covered or uncovered Petri dishes. Seeds from covered dishes were scarcely predated, while those from uncovered dishes were intensively consumed (for high plant density area: McNemar test, $\chi^2 = 89.48$, P < 0.001 and for low plant density area, $\chi^2 = 95.09$, P < 0.001).

Seeds with or without elaiosomes disappeared in a similar way from uncovered dishes. However, the rate of disappearance was significantly higher from the high

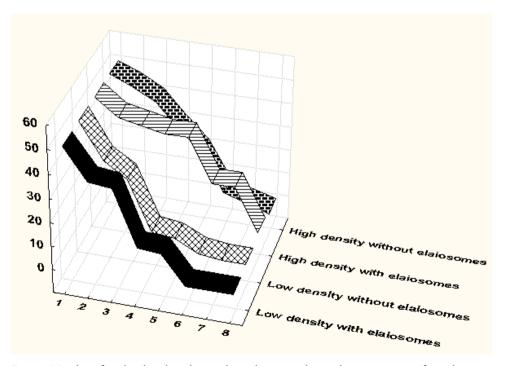


Fig. 12. Number of predated seeds with or without elaiosomes during the eperiments performed at areas of low and high plant density (see more details in the text).

plant density area in the case of seeds without elaiosomes ($\chi^2 = 160.89$, P < 0.001, see Fig. 12). We did not detect such differences at low plan density area ($\chi^2 = 12.50$, P = 0.0852).

Discussion

Lizard densities estimated during this study at Aire Island are similar to those recorded from previous years (Pérez-Mellado 1989, Pérez-Mellado *et al.* 2000 and unpub. data). But it is interesting to observe local variations of these values.

From one side, we detected very high densities at the north-eastern peninsula, with sandy substrates, lacking *Suaeda vera* and with the presence of Liliaceae and sea ferns as dominant plants. It is noteworthy that *D. muscivorus* is very rare at this zone and was not recorded during line transects. In addition, the high lizard density was linked with the presence of a large number of adult females and juveniles, indicating that probably this area is employed as a main laying site (pers. obs.) of Aire Island.

From another side, lizard density is lower at the area of breeding colonies of seagulls (western peninsula, some central areas and the easternmost area), probably as a consequence of seagull aggressiveness during breeding season and the sporadic capture of lizards (pers. obs.).

The existence of island zones with a high lizard density and almost absence of deadhorse arums precludes an overall correlation of lizard and plant density in the whole island. For this reason, only at central area of maximal plant density, east to the main track, we observed a significant correlation, in the part of the island densely covered by *Suaeda vera*, that permits optimal conditions for the development of *D. muscivorus*.

At the western peninsula we observed a much lower plant density than in the central zone, probably due to the rocky nature of the ground and a lower density of *Suaeda vera*. This western peninsula is also the site of the main breeding seagull colony. Thus, within Aire Island, we cannot confirm the supposed correlation of seagull breeding colonies and the presence of *D. muscivorus* (Meeuse & Morris 1984), apparently due to the abundance of calliphorid flies, attracted by organic matter and carcasses.

In a similar way, the analysis of correlation between vegetal cover, rock cover, lizard density and dead-horse density at the 20 central zones of the island (Fig. 8) revealed that only the percentage of *Suaeda vera* cover was significantly correlated with dead-horse arum density. This correlation is particularly important at the area to the west of the main track, where the overall density of *S. vera* is lower and, consequently, its presence is even more important for the development of *D. muscivorus*. Thus, we confirm the important role of *Suaeda vera* at Aire Island, probably as a protective shield for the development of the dead-horse arum.

In summary, lizard density is probably related to multiple factors as suitable laying sites for females, proximity of food resources as human visitors around the northern jetty, and the scarcity or absence of breeding seagulls, as occasional predators. On the other hand, dead-horse arum density depends on factors as the presence of protective plants against wind and sea influence, as *Suaeda vera*, as well as a certain distance from the shore, that mitigates that influence.

However, at better areas for lizards and plants, as the central zone, east from the main track, densities of both species were significantly correlated, indicating an interaction between the lizards and the plants, with a clear north-south gradient. In the case of lizards, such gradient is weaker, without significant differences, while for plants the gradient marks significant differences between higher densities in the south and lower in the north part of the zone.

The density of *Dracunculus muscivorus* at Aire Island can be viewed as extraordinary. In some particular spots it reaches more than 30,000 individuals per hectare! Within its reduced range, the dead-horse arum is considered a rare species (Corrias 1981) and, according to Boyce (2000), *Dracunculus muscivorus* is restricted to a few sites in Balearics, Corsica and Sardinia. Even if we lack estimations from other locations, probably Aire Island exhibits the highest known densities for the entire distribution range of this plant species. Moreover, identical censuses performed in 1999 (Pérez-Mellado *et al.* 2000), 2003 and 2005 indicate an amazing increase of density (Fig. 9), obviously as a result of the strong interaction with the Balearic lizard as its main seed disperser.

The activity of lizard on open spathes was intense during the whole blooming period. The peak of highest availability of open spathes took place during the fourth week of March and the two first weeks of April. However, open spathes were staggered during more than one month (Fig. 7). One of the most interesting results is the negative correlation between juvenile abundance and plant density. That is, the zones of maximal plant density have a higher proportion of juvenile lizards, probably indicating the active exclusion of juveniles from blooming spathes by adult lizards. Moreover, it was a higher proportion of adult males observed on spathes. In fact, the proportions of juveniles and adult males recorded on spathes were significantly lower and higher, respectively, to proportions recorded during ground visual censuses at the same areas. This result could indicate a displacement from this optimal zone of dead horse arums of adult females and juveniles by adult males. Thus, the access to open spathes, as a site for food (arrival of potential pollinators) and, probably, as an optimal thermoregulation site (Pérez-Mellado et al. 2000) is different for each sex and age class. Age and sex classes distribution at the zones of maximal plant density indicate that adult males actively preclude the access of juveniles to open spathes. Moreover, those adult males have significantly larger body sizes than the average of adult males from Aire Island. These results confirm the importance of open spathes as optimal sites from which big adult males exclude the access to smaller males, juveniles and most of the adult females.

Regarding pollination, our results demonstrate a negligible role of lizards as pollinators of the dead horse arum. In fact, the number of pollen grains loaded by lizards is clearly lower than in the cases of a proved role in pollination (Pérez-Mellado & Casas 1997, Pérez-Mellado *et al.* 2000). Also we can confirm the apparent absence of autopollination in this plant species (Collu & Dardani 1999).

The size of available fruits is similar at zones of high and low plant density. In addition, at the area of high plant density we detected fruits with more and smaller seeds. It is extremely difficult to construct a reliable hypothesis to explain such differences, also present on dispersed seeds. Apparently, plant density is the most relevant factor to explain dispersal intensity. Thus, dispersal is significantly higher at the area of high plant density, where ripening fruits of *D. muscivorus* is the major food resource of many lizards during fruiting period of the dead horse arum. In addition, studying a larger sample size, we were unable to confirm the selection of fruits with larger seeds by the Balearic lizard (Pérez-Mellado *et al.* 2000). There is a continuous increase of seed dispersal intensity during the three consecutive years under study, indicating a rapid spread of foraging behaviour on *D. muscivorus* fruits within lizard population.

Germination of fruits was significantly higher from those coming from lizard faeces indicating that the Balearic lizard is, not only a legitimate seed disperser of *D. muscivorus*, but also a disperser that increase germination probabilities of the seeds passing throughout its digestive tract.

Regarding seed predation, our results apparently indicate a very low predation pressure from arthropods, as well as a poor dispersal by members of this group as ants, that normally represent a coevolutionary unit with plants bearing elaiosomes on seeds, as it is the case for *D. muscivorus*. In addition, the high proportion of disappearance of seeds from uncovered Petri dishes probably indicates a strong predation pressure from granivorous or omnivorous vertebrates. At Aire Island, we can mention, among birds, the linnet, *Acanthis cannabina* and the rock dove, *Columba livia* or the rabbit, *Oryctolagus cuniculus* as the only introduced mammal present in the islet. We cannot discard also the consumption of seeds by non breeding granivorous birds that land time to time on the island. The practical absence of seed dispersal by ants increases the significance of lizards as seed dispersers. Moreover, the strong seed predation by other vertebrates was counterbalanced by seed dispersal within lizards' faeces, where seeds probably have a higher survival probability, remaining undetected by seed predators during some time.

Mutualism exists when two or more species enhance each other's fitnesses (Howe & Westley 1988). But, in the case of the Balearic lizard and the dead horse arum, we are in front of a more complex interaction where mutualistic relationship is mixed with an asymmetrical interaction during the blooming period, with the sole benefit

of lizards, consuming potential pollinators. Anyhow, benefit for plants seems to be higher than detrimental effects, according to the spectacular increase of plant density during a period of six years. As in other mutualistic relations (Thompson 1982), the interaction of these two species probably began as an antagonistic relationship where lizards acted only as pollinator's predators. Later, the use of blooming plants and optimal sites for thermoregulation (Pérez-Mellado *et al.* 2000) and/or foraging sites became general very rapidly among lizard population allowing the next step, the discovery of ripening fruits as a suitable food.

Even if plant-animal seed dispersal systems are characterized by the absence of obligate partnership and a weak mutual dependence between animals and plants (Herrera 2002), the case of the dead horse arum and the Balearic lizard is surprising in the sense of a strong effect of lizard' foraging behaviour on plant density and its extremely rapid spread over the island. Even if it is clear that a reduced population of the dead horse arum can be maintained without any interaction with lizards, the emergence of the strong interaction observed at Aire Island could be the only explanation for the extraordinary density reached by plants during a short period of six years.

Acknowledgments

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