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Patterns of parasitism in insular lizards: effects of body size, condition and resource availability

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ABSTRACT

The spatial distribution of a population of lizards is influenced by the distribution of resources and the individuals' skills to gain access to them. On several Mediterranean islands with food scarcity and unpredictable resource availability, some resources can be extremely important during some periods of the year, as, e.g., the dead horse arum, *Dracunculus muscivorus*, on Aire Island, Spain. In this study, we analysed parasite infestation in an endemic lizard, *Podarcis lilfordi*, in relation to the distribution of *D. muscivorus* during spring. We found a higher prevalence of parasitism in males from a central area where the plant was significantly more abundant. Also, in this area, males were more abundant and larger than in two areas with lower plant densities. Moreover, overall differences appeared in the intensity of infection, which was higher in individuals from the central area, and we found a relationship between body size and parasite load, with more infected cells in larger individuals. Spatial distribution of individuals due to differential availabilities of *D. muscivorus* is proposed as an explanation for the observed differences.

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1. Introduction

Animals are not distributed randomly because some places are better than others in terms of resource availability when balanced against the risks or costs of acquiring the resource (Zug et al., 2001). If all resources were spread uniformly in the environment or even across different environments, it would be difficult for individuals or species to segregate spatially (Zug et al., 2001). In the case of lizards, Hews (1993) suggested that food resources influence their abundance, and that sexes differ in social behaviour and spatial distribution in response to food abundance. In some lizard species, territory acquisition is influenced by environmental quality, which affects the motivation to fight and defend territories (Hews, 1993). Individuals are assumed to gain possession of areas after winning fights or encounters, while conspecifics that lose agonistic interactions leave areas where they were defeated. In this sense, body size and aggressiveness are two of the most important traits that determine dominance status, and hence, priority access to resources (Civantos, 2000). Shifts in niche exploitation within a population may also arise as a result of ontogenetic constraints imposed by differences in body size, physiological capacities and allocation to age-associated behaviour (Durtsche et al., 1997). Dominant individuals secure the territory or a given resource, often excluding subordinates from optimal habitats (Krebs, 1971; King, 1973). Consequently, in resource-rich habitats the proportion of

dominant individuals increases, as well as the probability of aggressive encounters between them. Stamps (1977) argued that intraspecific aggression is a result of critically limited resources, and aggressive encounters may involve risk of damage, even death. Thus, individuals fighting to access resources are more exposed to stressful conditions. Now it is well known that stressful conditions have an immunosuppressive effect and may affect disease resistance (Oppliger et al., 1998). Stressed individuals may therefore be more prone to parasites and the prevalence and intensity of infections might rise among them. Accordingly, parasites could be considered a cost for individuals inhabiting resource-rich habitats. In addition, many studies in lizards show fitness-related effects of parasites, such as poorer body condition (Merino et al., 2000). The most infected individuals would be less able to compete for the access to resources. However, in favourable habitats, the host can accept the costs of being parasitised in exchange for gaining access to better resources (Bull and Burzacott, 1993; Weatherhead et al., 1995). Thus, in these habitats hosts are able to tolerate higher parasite intensities (Bouma et al., 2007). In addition, parasites can alter the hosts' spatial distribution (Price, 1980; Van Riper et al., 1986), as occurs in the case of the Australian sleepy lizard, *Tiliqua rugosa*, where infected individuals exhibit smaller home ranges than uninfected ones (Bouma et al., 2007).

Some populations of the Balearic lizard, *Podarcis lilfordi* (Günther, 1874), live on small islets in the vicinity of Menorca (Balearic Islands, Spain) that lack terrestrial predators and have very limited trophic resources (Pérez-Mellado, 1989). On small Mediterranean islets, food scarcity and unpredictability of resource availability is the norm (Pérez-Mellado and Corti, 1993). In this situation, some

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resources become extremely important during some periods of the year, as is the case with dead horse arum, *Dracunculus muscivorus* (Araceae). During spring, this plant is extremely important for the Balearic lizard on Aire Island. Spring is the blooming period of *D. muscivorus*, when these plants are excellent perching sites, aiding the lizards' thermoregulation and ambush foraging, because of their thermogenic capacity and the attraction of potential flying pollinators, mainly bow flies. Some of these pollinators are captured by basking lizards, sometimes directly from the floral chambers of the plant (Pérez-Mellado et al., 2000, 2007). Although the Balearic lizard is a non-territorial species (Pérez-Mellado, 1989), the exploitation of this resource leads the lizards to compete for blooming plants; these are generally monopolised by larger adult males (Pérez-Mellado et al., 2007). So, as it happens in other non-territorial species living in areas with resource scarcity (as, for example, *Darevskia* (Steward, 1965) and *Podarcis muralis* (Pianka and Vitt, 2003)), the spatial distribution of lizards on Aire Island is strongly influenced by dead horse arum density (Pérez-Mellado et al., 2007 and unpublished data).

In the present study we focus our attention on two delimited areas of Aire Island characterised by a different availability of dead horse arum during spring. Our hypothesis is that the distribution of this resource affects the distribution of adult males and their exposure to parasitic infection. We expect a rise in parasitic infections in the area of higher density of *D. muscivorus*, where lizards are subjected to higher stress and an increased competition for plant access.

2. Materials and methods

2.1. Study animals

P. lilfordi is a medium-sized lacertid lizard endemic to the Balearic Islands, with a snout–vent length (SVL) of up to 81 mm in males and 75 mm in females (Pérez-Mellado, 1989). The present study was conducted on Aire Island (39° 48' 3" N; 4° 17' 24" E), a small islet off Menorca (Balearic Islands, Spain), during the spring of 2007, 2008, 2009 and 2010. The island has a surface of around 342,500 m² and is about one mile from the south-eastern coast of Menorca. The vegetation is highly influenced by its environmental characteristics (strong winds, high salinity and long drought periods) and dominated by low shrubs and a variety of herbaceous plant species. Lizard densities can be very high, with over 4000 individuals per hectare (Pérez-Mellado et al., 2008).

P. lilfordi, just like other lacertid lizards on the Iberian Peninsula, may be infected with haemogregarines (Apicomplexa: Adeleorina), protozoan blood parasites of a wide variety of host species, including reptiles. Because the genera of this family can only be identified by oocyst stages within the invertebrate hosts (Levine, 1982; Barnard and Upton, 1994), we could not classify these parasites any further.

Haemogregarines have an indirect cycle, including at least two hosts: a final vertebrate host, where they appear in the form of gametocytes in the blood cells, mostly in erythrocytes (in many cases, this is the only known phase of the parasite; see Telford, 2008) and an invertebrate vector. For lizards, the most common vectors are ticks and mites (Telford, 2008), acquired when sharing suitable places for basking, foraging or hiding. There is another surmised method of transmission, via ingestion of another infected vertebrate host or of infected invertebrates (see, for example, Telford, 2008). The effects of haemogregarines on their carriers have been little studied, but we do know that they destroy red blood cells, causing anaemia (Caudell et al., 2002). Furthermore, the presence of gametocytes in blood cells indicates the presence of schizonts in internal organs, which cause additional damage

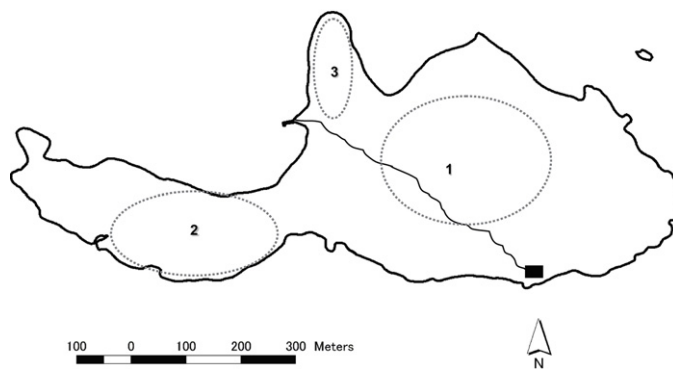


Fig. 1. Map of Aire Island according to the zoning used for the study: (1) central area, (2) western peninsula, (3) northern peninsula.

(Svahn, 1974), sometimes leading, even under laboratory conditions, to the death of the host (Schall, 1996). As haemogregarines are vector-borne parasites, we also checked for ectoparasites because they might be the decisive component.

2.2. Study area

Following Pérez-Mellado et al. (2007), we delimited two areas in relation to the distribution and abundance of *D. muscivorus*. Taking the middle track from dock to lighthouse (Fig. 1) as a reference, the first area, which we designated as “central area”, is located within the core of the island, to the east of the pathway. The artificial track marks a clear limit of vegetation. East of the track there is the area of densest shrub vegetation, dominated by *Suaeda vera* and featuring the highest recorded density of *D. muscivorus*, up to almost 11,000 plants per hectare (Pérez-Mellado et al., 2007). It is also the area of the island with the least influence of salinity.

The northern and western peninsulae of the islet are collectively considered the second area of our study, termed “peninsulae” (Fig. 1). During spring, the key difference in relation to the central area is the lower abundance of dead horse arum. In the northern peninsula, it is very scarce and Pérez-Mellado et al. (2007) did not record any individual plants during line transects, even if some plants may have been present. In the western peninsula the density is also significantly lower than in the central area (fewer than 5100 plants per hectare, see Pérez-Mellado et al., 2007).

2.3. Capture and blood analysis

Lizards were collected by noosing. For each individual, we recorded age, sex, SVL, tail length and body weight. We also counted the number of ectoparasites observed on the body surface immediately after capture. To obtain blood samples, we made a slight longitudinal cut in the dorsal and proximal side of the tail with a sterile scalpel. With the blood drop we obtained a blood smear in situ. Sometimes blood samples were also obtained by clipping off the tail tips (which were later used for DNA extraction). Specimens were always released at the site of capture.

Blood smears were made on microscope slides and air dried in the field. In the laboratory, the slides were fixed with absolute methanol for 10 min and then stained with modified Giemsa solution for 20 min. Samples were analysed using an optical microscope at 400×. The only blood parasites identified were haemogregarines (Fig. 2). The intensity of parasitism was estimated on the basis of a total of 2000 counted cells per sample. Prevalence was estimated as the percentage of infected individuals in each of the two areas under study.

Individuals were marked with different colour pens for each area. Throughout the study period, marked individuals from one

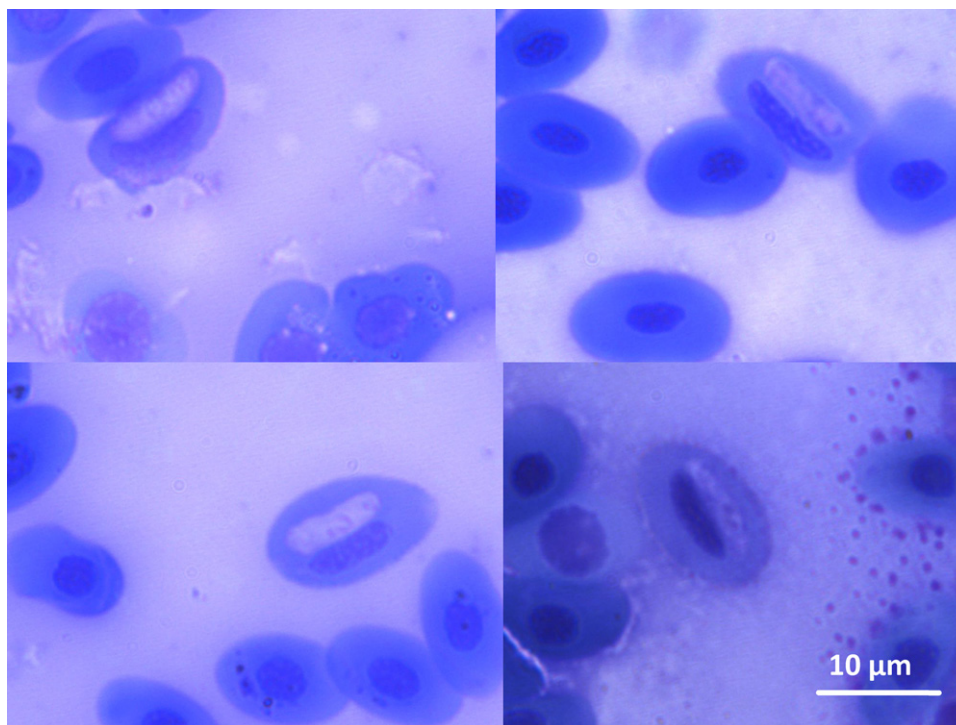


Fig. 2. Scaled microphotography of infected red blood cells, with the nuclei displaced by gametocytes of haemogregarines.

area were not seen in the other areas. Individuals already examined could be recognised by the cut in the tail. Lizards that had already been captured in previous years were discarded. Thus, during the study period of 4 years, each individual was studied only once.

2.4. Lizard distribution according to age/sex categories

Lizard abundances were estimated with line transects during April of 2009 and 2010. The width of transects was 2 m. Counting was carried out on sunny days, during the morning hours with highest lizard activity. All transects were surveyed by the same observer (V.P.-M.). Each individual was classified as adult male, adult female or juvenile. This method provides a relative abundance of lizards and sex and age ratios for each area under study.

Males, females and juveniles exploit open spathes of dead horse arum in a completely different way (Pérez-Mellado et al., 2007). Thus, we looked for differences between age/sex categories in each variable under study. Then, we applied generalised linear models (GLMs) for males, females and juveniles separately to understand which factors have a better predictive value. To compare the prevalence of infestation among age/sex classes or areas and the age and sex ratios among different areas or years we applied Fisher's test. To determine changes in the prevalence of haemogregarines between areas, years and body size (SVL) we used GLMs, with parasite prevalence as the dependent variable following a binomial distribution, and including the interactions between the three variables in the model (Crawley, 2007). As endoparasite load distributions had homogeneous variances, relations with area, year and body size (SVL) were analysed using a GLM with a Gaussian distribution. In the same way, mite load relations with age/sex categories and with area and body size (SVL) were analysed using a GLM with a Gaussian distribution (Crawley, 2007). Ectoparasite intensities were log-transformed when required. Using GLMs, the significance of each factor was estimated from the analysis of accumulated deviance and the associated statistic.

Sometimes it was necessary to calculate body condition separately for each age/sex category because differences in body

shape were present. We initially compared the body condition of adult males, adult females and juveniles with ANCOVA analyses, introducing log mass as the response variable, age/sex variable as a factor and log SVL as the covariate. Then, to analyse the effects that area and year have on body condition, we introduced both factors in a two-way ANCOVA, using log of mass as the response variable and log of SVL as the covariate. Following Crawley (2007), factors and interactions which had no significance were removed from the GLM and ANCOVA models until we obtained a minimal adequate model, taking Akaike's information criterion (AIC) into account at each step. In all cases, post hoc Tukey tests were made using the package 'multcomp' (Hothorn et al., 2008). The statistical analyses were done with R (ver.2.12.1; R Foundation for Statistical Computing, Vienna, Austria).

3. Results

No differences were found in the sex ratios of both areas among years (G -test: central area, $G=0.03$, $df=1$, $p=0.86$; peninsulæ, $G=0.44$, $df=1$, $p=0.50$). Thus, we pooled the data of the 2 years of study. In the peninsulæ, we found a 1:1 sex ratio (G -test, $G=0.49$, $df=1$, $p=0.50$), while in the central area the proportion was significantly skewed towards males (G -test, $G=10.67$, $df=1$, $p<0.01$). Accordingly, there were differences in the sex ratio between areas (G -test, $G=44.12$, $df=1$, $p=3.085 \times 10^{-11}$; see Table 1). Age ratio also varied among areas (G -test, $G=29.29$, $df=1$, $p=6.22 \times 10^{-8}$), the proportion of adults being higher in the central area (Table 1).

Table 1

Proportion of *P. lilfordi* adults (AD), adult males (M), adult females (F), juveniles (JUV) and sex and age ratio in the studied areas on Aire Island.

	M	F	AD	JUV	Sex ratio (M/F)	Age ratio (AD/JUV)
Central area	373	181	554	64	2.06/1	8.66/1
Peninsulæ	199	231	432	121	0.86/1	3.57/1

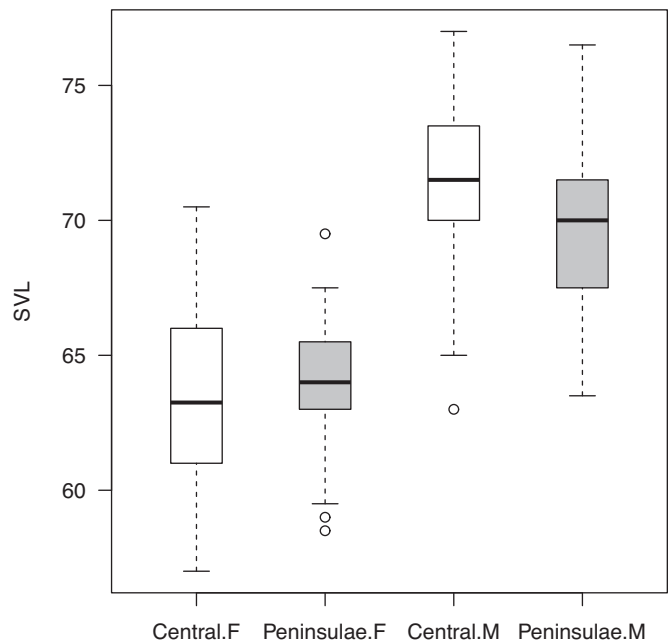
Table 2Prevalence of infection among *P. lilfordi* on Aire Island, with confidence intervals by sector and age/sex categories.

	Infected/total	Percentage	Conf. interval
Males			
Total	121/124	97.58%	93.09–99.50
Central area	78/78	100.0%	95.38–100.0
Peninsulæ	43/46	93.48%	82.10–98.63
Females			
Total	72/79	91.14%	82.59–96.36
Central area	44/46	95.65%	85.16–99.47
Peninsulæ	28/33	84.85%	68.10–94.89
Adults			
Total	195/205	95.12%	91.21–97.64
Central area	122/124	98.39%	94.30–99.80
Peninsulæ	71/79	89.87%	81.02–95.53
Juveniles			
Total	13/14	92.86%	66.13–99.82
Central area	1/8	87.5%	47.35–99.68
Peninsulæ	6/6	100.0%	54.07–100.0

Prevalence of infection was similar between adults and juveniles (Fisher's test, $p=0.53$; see Table 2), but in adults we found significant differences between the sexes (Fisher's test, $p=0.049$; see Table 2), with a higher prevalence in males than in females. For males, the GLM binomial model revealed only differences between areas ($\chi^2=6.08$, $df=1$, $p=0.01$), with more infected individuals in the central area (see Table 2). The year ($\chi^2=5.30$, $df=3$, $p=0.15$), body size ($\chi^2=0.31$, $df=1$, $p=0.57$) and the interactions between the three response variables had no effect (all $p>0.05$). In females (Table 2), prevalence varied significantly between years ($\chi^2=13.11$, $df=3$, $p<0.01$) because all non-infected females were captured in 2009. Body size had no influence on prevalence in females ($\chi^2=0.51$, $df=1$, $p=0.47$) and no differences appeared among areas ($\chi^2=2.76$, $df=1$, $p=0.10$). None of the interactions were significant (all $p>0.05$). Neither the variables year ($\chi^2=1.79$, $df=2$, $p=0.41$), size ($\chi^2=0.77$, $df=1$, $p=0.38$) and area ($\chi^2=1.18$, $df=1$, $p=0.28$) nor the interactions seemed to have any effect on the prevalence of infection in juveniles (all $p>0.05$).

We did not find any differences in the SVL of adult females (central area: $\bar{x} \pm SE = 63.51 \pm 0.49$; peninsulæ: $\bar{x} \pm SE = 63.19 \pm 0.45$; GLM, $F_{1,77}=0.16$, $p=0.69$) or juveniles (central area: $\bar{x} \pm SE = 58.62 \pm 2.40$; peninsulæ: $\bar{x} \pm SE = 58.33 \pm 3.39$; GLM, $F_{1,12}=0.005$, $p=0.94$) between areas. But for adult males, we found that the body size of individuals varied between areas (central area: $\bar{x} \pm SE = 71.47 \pm 0.31$; peninsulæ: $\bar{x} \pm SE = 69.41 \pm 0.44$; GLM, $F_{1,122}=14.98$, $p<0.001$), with larger males found in the central area (Fig. 3).

There was no difference in the parasite load between adults and juveniles (GLM, $F_{1,217}=0.61$, $p=0.43$), nor between adult males and females (GLM, $F_{1,204}=0.07$, $p=0.79$; see Table 5). The infection intensity among adult males (see Table 3) was significantly different between years (homogeneous variances, Fligner test: $\chi^2=9.80$, $df=81$, $p=0.21$; GLM, $F_{3,120}=3.50$, $p=0.02$) and areas (GLM, $F_{1,119}=5.37$, $p=0.02$), but the interaction between them was not significant (GLM, $F_{3,115}=1.07$, $p=0.36$), indicating that the relation among the areas was stable over the years. Thus, males from the central area showed higher infection intensity (Table 5), and post hoc comparisons revealed that the parasite load was statistically higher in 2010 ($\bar{x} \pm SE = 21.94 \pm 3.39$) than in 2008 ($\bar{x} \pm SE = 11.67 \pm 1.82$) (Tukey's test, $t=2.875$, $p=0.02$) and 2007 ($\bar{x} \pm SE = 11.94 \pm 1.36$) ($t=2.55$, $p=0.05$); other comparisons between years were not significant (all $p>0.05$). Body size was not related with infection intensity (GLM, $F_{1,118}=2.90$, $p=0.09$). All interaction terms in the GLM of males were not significant (all $p>0.05$). For adult females (see Table 4), none of the interaction terms between SVL, area and year were significant (Fligner test, $\chi^2=72.19$, $df=63$, $p=0.20$; all $p>0.05$). There were no differences

**Fig. 3.** Boxplot of male (M) and female (F) SVL (in mm) at each area.

between the years (GLM, $F_{3,75}=0.24$, $p=0.87$), but regarding the areas, females from the central area were more parasitised (GLM, $F_{1,77}=4.18$, $p=0.04$; see Table 5). Parasite intensity was strongly related with SVL (GLM, $F_{1,76}=7.20$, $p=0.01$). For juveniles we were not able to find any relation with the intensity of infection (all $p>0.05$), probably due to the small sample size.

Table 3Results of the GLM for blood parasite intensities in adult *P. lilfordi* males on Aire Island: minimal adequate model, F -values, degrees of freedom (df) and p -values of the variables and interactions when they were removed from the model.

	df	Resid. df	F	p
NULL		123		
Area	1	119	5.37	0.02*
SVL	1	118	2.90	0.099
Year	3	120	3.52	0.02*
Minimal adequate model of parasite intensity for males				
NULL		123		
Area:SVL	1	111	1.93	0.17
Area:year	3	115	1.07	0.37
SVL:year	3	112	0.86	0.46
Area:SVL:year	3	108	0.53	0.66

* $p<0.05$.**Table 4**Results of the GLM for blood parasite intensities in adult *P. lilfordi* males on Aire Island: minimal adequate model, F -values, degrees of freedom (df) and p -values of the variables and interactions when they were removed from the model.

	df	Resid. df	F	p
NULL		78		
Area	1	77	4.18	0.04*
SVL	1	76	7.20	0.01*
Minimal adequate model of parasite intensity for females				
NULL		78		
Year	3	75	0.24	0.87
Area:SVL	1	66	0.90	0.35
Area:year	3	70	1.08	0.36
SVL:year	3	67	0.48	0.70
Area:SVL:year	3	63	1.17	0.33

* $p<0.05$.

Table 5Mean infection intensity and standard error by area and age/sex categories (sample sizes in parentheses) in the *P. lilfordi* population on Aire Island.

	Males	Females	Adults	Juveniles
Total	16.90 ± 1.46 (126)	16.11 ± 2.93 (79)	16.60 ± 1.44 (205)	12.57 ± 1.46 (14)
Central area	19.04 ± 1.80 (78)	20.91 ± 4.71 (46)	19.73 ± 2.07 (124)	9.5 ± 3.49 (8)
Peninsulæ	13.67 ± 2.53 (48)	9.42 ± 2.07 (33)	11.9 ± 1.71 (81)	16.67 ± 4.54 (6)

Ectoparasite load did not differ between adults and juveniles (adults: $\bar{x} \pm SE = 125.44 \pm 9.99$; juveniles: $\bar{x} \pm SE = 85.00 \pm 19.64$; Fligner test, $\chi^2 = 0.81$, $df = 1$, $p = 0.37$; GLM, $F_{1,217} = 1.10$, $p = 0.30$), nor between adult males and females (males: $\bar{x} \pm SE = 134.54 \pm 14.45$; females: $\bar{x} \pm SE = 110.00 \pm 11.68$; Fligner test, $\chi^2 = 0.32$, $df = 1$, $p = 0.57$; GLM, $F_{1,203} = 1.34$, $p = 0.25$). We also searched for relations between mite and haemogregarine intensities and for differences in ectoparasite load between areas. We ran three models, one for males, one for females and a third one for juveniles. For adult males we find differences between areas (Fligner test, males, $\chi^2 = 77.50$, $df = 62$, $p = 0.09$; GLM, $F_{1,123} = 8.30$, $p = 0.005$), with higher mite loads in peninsulæ males ($\bar{x} \pm SE = 154.26 \pm 18.47$) than in central area males ($\bar{x} \pm SE = 116.59 \pm 20.05$), but mite load varied inversely with intensity of blood parasites (see above). We did not find any relation with haemogregarines (GLM, $F_{1,123} = 0.006$, $p = 0.94$) and no interaction (GLM, $F_{1,123} = 0.006$, $p = 0.94$). For females, no relation was statistically significant (Fligner test, $\chi^2 = 58.63$, $df = 48$, $p = 0.14$; GLM, area: $F_{1,76} = 2.64$, $p = 0.11$; haemogregarines: $F_{1,75} = 0.0002$, $p = 0.99$; interaction: $F_{1,74} = 0.42$, $p = 0.52$), the same as for juveniles (Fligner test, $\chi^2 = 13.00$, $df = 11$, $p = 0.29$; GLM, area: $F_{1,13} = 0.60$, $p = 0.46$; haemogregarines: $F_{1,13} = 0.0002$, $p = 0.99$; interaction: $F_{1,13} = 0.36$, $p = 0.85$).

Regarding body condition, we first performed an ANCOVA analysis to look for differences between males, females and juveniles (see Section 2.4). As expected, there was a significant and positive correlation between body mass and SVL (one-way ANCOVA, $r^2 = 0.84$, $F_{1,207} = 266.11$, $p < 2.2 \times 10^{-16}$), and a significant difference between age/sex groups ($F_{2,207} = 218.5$, $p < 2.2 \times 10^{-16}$). Because body condition must be estimated separately for males, females and juveniles, we ran separate ANCOVAs for each group with area and year as factors and using log of mass as the response variable and log of SVL as the covariate. For males, the minimal adequate model showed a significant difference when the three variables were taken into account. As expected, SVL was positively and strongly correlated with body mass ($F_{1,115} = 123.82$, $p < 2.2 \times 10^{-16}$). We also found a significant influence of area on body condition ($F_{1,115} = 7.79$, $p = 0.006$), that is, individuals from the central area showed better body condition than those from the peninsulæ. Body condition differed significantly between years ($F_{3,115} = 9.03$, $p = 2.03 \times 10^{-5}$) and Tukey's post hoc test revealed that lizards had a better body condition during 2008 than during 2007 ($t = 2.65$, $p = 0.04$) and lizards from 2010 had a lower body condition than those from 2008 ($t = -5.11$, $p < 0.001$) and 2009 ($t = -0.33$, $p = 0.008$).

For females, the minimal adequate model also showed significant differences for the three variables. SVL was positively and strongly correlated with body mass ($F_{1,70} = 64.26$, $p = 1.71 \times 10^{-11}$). We found only a marginal influence of area on body condition ($F_{1,70} = 3.91$, $p = 0.05$), that is, individuals from the central area showed a better body condition than those from the peninsulæ. Body condition differed significantly between years ($F_{3,70} = 11.64$, $p = 2.83 \times 10^{-6}$) and Tukey's post hoc test revealed that during 2010 females had a poorer body condition than during 2007 ($t = -4.85$, $p < 0.001$), 2008 ($t = -3.86$, $p = 0.001$) and 2009 ($t = -2.62$, $p = 0.048$), and individuals from 2009 presented a poorer body condition than those from 2007 ($t = -0.14$, $p = 0.01$).

4. Discussion

The population structure differed strongly between areas. In the central area, where *D. muscivorus* is very abundant and exploited by *P. lilfordi*, the proportion of juveniles and females was almost 2.5 times lower than in the peninsulæ. Critically limited resources may be the cause of intraspecific aggression (Stamps, 1977) and, therefore, the population structure may be temporarily modified. There are other examples where the foraging of lizards on a particular plant species strongly affects their spatial distributions, e.g., *Niveoscincus microlepidotus* foraging on blooming shrubs of *Richea scoparia* (Olsson et al., 2000). On Aire Island, Pérez-Mellado et al. (2007) observed that adult males actively excluded juveniles and adult females from open spathes of *D. muscivorus*, thus effectively displacing them from the best places of the plants. Since these authors were unable to detect any changes in other available resources during spring and summer, the most parsimonious explanation for their results is that the site fidelity of adult males is a consequence of *D. muscivorus* flowering over spring. Once adult males monopolise the central area, the exclusion of adult females and juveniles becomes stronger. The high concentration of adult males had direct consequences for the adult sex ratio due to an increased aggression towards adult females, whose survival and emigration rates dropped (Le Galliard et al., 2005). This behaviour seems paradoxical, especially since it occurs during the breeding season. Perhaps females were of lower priority (as compared to food) in the males' choice system during the period in which the monopolisation of *D. muscivorus* explained their spatial distribution.

Furthermore, males from the central area were larger than those from the peninsulæ. Differences in SVL between areas were only found in adult males. This is a consequence of intraspecific competition to gain possession of better areas, because body size is an important factor in winning contests (Tokarz, 1985; Olsson, 1992). Dominant individuals acquire territory (review in Stamps, 1994) and exclude subdominants from optimal habitats (Krebs, 1971; King, 1973). Where the proportion of dominant males increases, aggressive encounters are more likely. Thus, the degree of aggressiveness or relative dominance may mirror the quality of a territory where an individual lives (Civantos, 2000). For example, more aggressive side-blotched lizards (*Uta stansburiana*) increased the size and quality of their home ranges (Fox, 1983).

As expected, our results showed differences in the patterns of parasitism between the two defined areas of Aire Island during spring. We propose that the observed differences in the distribution of *D. muscivorus* between areas are closely related to the differential distribution and behaviour of lizards (Pérez-Mellado et al., 2007), and, ultimately, with differences in parasitic load. Differences in parasite prevalence between areas were only found for adult males. During spring, the central area was mostly occupied by adult males, and those males were larger than males from the peninsulæ. But what drives these differences in parasite infestation? Mites act as vectors for haemogregarines, but for males, mite load was higher in the peninsulæ and no differences between areas were found for females. Therefore, we propose another mechanism of infection: parasite transmission between hosts increases with aggressive encounters. Body size and aggressiveness are important traits determining the dominance status, and, consequently, access

to resources. The higher proportion of adult and larger males in the central area implies more male–male aggressive encounters, especially if we take into account that dominant males show higher activity levels than females and juveniles (Martín and López, 2000). In male–male interactions, lizards commonly bite each other's tail and even caudal autotomy and tail consumption by the opponent may occur (Pérez-Mellado, 1997). Therefore, the ingestion of infected blood and mites on the tail may increase the probability of transmission of blood parasites between males.

In adults, prevalence of infection was higher for males. Differences in the rate of parasitism between the sexes are well documented (see, for example, Salvador et al., 1996). Two hypotheses have been proposed to explain these differences: (i) ecological, because males of *P. lilfordi* show more activity than females, as also proposed for *Sceloporus occidentalis* (Zuk and McKean, 1996), more aggressive behaviour and male–male interactions (frequently observed on Aire Island); and (ii) physiological, usually hormonal in origin as the level of aggressiveness is mediated by high levels of testosterone. Due to the immunosuppressive effects of testosterone, males are more likely to be infected than females (Zuk and McKean, 1996).

As expected, both males and females from the central area showed a higher parasitic load. It might be assumed that the abundance of larger males or females drives the differences in blood parasite intensity among sites, and that the size effect confounds the differences in intensity among areas. Yet, for adult males, body size was not related with parasite load. SVL was related to parasite load in females, but average SVL was similar between areas. Nor did the occurrence of mites explain the differences between areas as their numbers were not related with haemogregarine load. Moreover, mites were more abundant in peninsular males and there was no difference between areas for females. Another factor that has been related with parasite infection is poor body condition (Sorci and Clobert, 1995; Merino et al., 2000). However, in our study, males and females of the central area had a better and slightly better condition, respectively, than the less infected individuals from the peninsular.

From our results, it may be surmised that the higher intensity of infection in the central area was due to an increased competition for access to resources and, consequently, to a higher exposition to aggressive encounters with dominant males. These encounters could, per se, result in re-infections. Moreover, agonistic interactions lead to social stress, which might be the factor driving differences in the intensity of infection. It is well known that stressful conditions have an immunosuppressive effect and may affect disease resistance (Oppliger et al., 1998). In the central area, agonistic interactions were more frequent, so this social stress may have induced an increase in parasite load, as has been observed in *Zootoca vivipara* (Oppliger et al., 1998) and *Iberolacerta monticola* (Amo et al., 2004). There is an alternative but less convincing explanation, according to which the impact of parasites may be spatially dependent, that is, parasitic loads would be higher in more favourable habitats (such as the central area during spring) because in these habitats, hosts could compensate for the costs of being parasitised by gaining access to more favourable resources (Bull and Burzacott, 1993; Weatherhead et al., 1995).

In conclusion, the temporal availability of a valuable resource, the dead horse arum, strongly influences the structure of the *P. lilfordi* population on Aire Island. Dominant individuals, mainly males, monopolise the central area where the resource is, relegating subdominant individuals to other parts of the island. Thus, as dominant and more aggressive individuals are concentrated in this area, the probability of agonistic encounters increases, leading to an increase of parasitism either directly, by the ingestion of infected tissues or vectors by eating opponents' tails, or indirectly, as stress increases and suppresses the immune function.

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References

- Amo, L., López, P., Martín, J., 2004. Prevalence and intensity of haemogregarinid blood parasites in a population of the Iberian rock lizard, *Lacerta monticola*. *Parasitol. Res.* 94, 290–293.
- Barnard, S.M., Upton, S.J., 1994. A Veterinary Guide to the Parasites of Reptiles, vol. 1. Protozoa. Krieger Publishing, Malabar, FL.
- Bouma, M.J., Smallridge, C.J., Bull, C.M., Komodeur, J., 2007. Susceptibility to infection by a haemogregarine parasite and the impact of infection in the Australian sleepy lizard, *Tiliqua rugosa*. *Parasitol. Res.* 100, 949–954.
- Bull, C.M., Burzacott, D., 1993. The impact of tick load on the fitness of their lizard hosts. *Oecologia* 96, 415–419.
- Caudell, J.N., Whitter, J., Conover, M.R., 2002. The effects of haemogregarine-like parasites on brown tree snakes (*Boiga irregularis*) and slatey-grey snakes (*Stegonotus cucullatus*) in Queensland, Australia. *Int. Biodeterior. Biodegradation* 49, 113–119.
- Civantos, E., 2000. Home-range ecology, aggressive behavior, and survival in juvenile lizards, *Psammotromus algirus*. *Can. J. Zool.* 78, 1681–1685.
- Crawley, M.J., 2007. The R Book. John Wiley and Sons Ltd., Chichester, UK.
- Durtsche, R.D., Gier, P.J., Fuller, M.M., Lutterschmidt, W.L., Bradley, R., Meier, C.K., Hardy, S.C., 1997. Ontogenetic variation in the autecology of the greater earless lizard *Cophosaurus texanus*. *Ecography* 20, 336–346.
- Fox, S.F., 1983. Fitness, home range quality and social rank in *Uta stansburiana*. In: Huey, R.B., Pianka, E.R., Schoener, T.W. (Eds.), *Lizard Ecology: Studies on a Model Organism*. Harvard University Press, Cambridge, pp. 149–168.
- Hews, D.K., 1993. Food resources affect female distribution and male mating opportunities in the iguanian lizards *Uta palmeri*. *Anim. Behav.* 46, 279–291.
- Hothorn, T., Bretz, F., Westfall, P., 2008. Simultaneous inference in general parametric models. *Biomet. J.* 50, 346–363.
- King, J.A., 1973. The ecology of aggressive behavior. *Annu. Rev. Ecol. Syst.* 4, 117–138.
- Krebs, J.R., 1971. Territory and breeding density in the great tit, *Parus major*. *Ecology* 52, 1–22.
- Le Galliard, J.F., Fitze, P.S., Ferriere, R., Clobert, J., 2005. Sex ratio bias, male aggression, and population collapse in lizards. *Proc. Natl. Acad. Sci. U. S. A.* 102, 18231–18236.
- Levine, N.D., 1982. Some correction in haemogregarine (Apicomplexa: Protozoa) nomenclature. *J. Protozool.* 29, 601–603.
- Martín, J., López, P., 2000. Social status of male Iberian rock lizards (*Lacerta monticola*) influences their activity patterns during the mating season. *Can. J. Zool.* 78, 1105–1109.
- Merino, S., Moreno, J., Sanz, J.J., Arriero, E., 2000. Are avian blood parasites pathogenic in the wild? A medication experiment in blue tits (*Parus caeruleus*). *Proc. R. Soc. B* 267, 2507–2510.
- Olsson, M., 1992. Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Anim. Behav.* 44, 386–388.
- Olsson, M., Wapstra, E., Madsen, T., Silverin, B., 2000. Testosterone ticks and travels: a test of the immunocompetence handicap hypothesis in free-ranging male sand lizards. *Proc. R. Soc. B* 267, 2339–2343.
- Oppliger, A., Clobert, J., Lecomte, J., Lorenzon, P., Boudjemadi, K., John-Alder, H.B., 1998. Environmental stress increases the prevalence and intensity of blood parasite infection in the common lizard *Lacerta vivipara*. *Ecol. Lett.* 1, 129–138.
- Pérez-Mellado, V., 1989. Estudio ecológico de la lagartija balear *Podarcis lilfordi* (Günther, 1874) en Menorca. *Rev. Menorca* 53, 455–511.
- Pérez-Mellado, V., 1997. *Podarcis lilfordi* (Günther, 1874). In: Pleguezuelos, J.M. (Ed.), *Distribución y biogeografía de los anfibios y reptiles en España y Portugal*. Monografías de Herpetología, vol. 3. Colección Monográfica Tierras del Sur, Universidad de Granada. Asociación Herpetológica Española, Granada, pp. 361–363.
- Pérez-Mellado, V., Corti, C., 1993. Dietary adaptations and herbivory in lacertid lizards of the genus *Podarcis* from western Mediterranean islands (Reptilia: Sauria). *Bonn. Zool. Beitr.* 44, 193–220.
- Pérez-Mellado, V., Cortázar, G., López-Vicente, M., Perera, A., Sillero, N., 2000. Interactions between the Balearic lizard *Podarcis lilfordi* and the plant *Dracunculus muscivorus*. *Amphibia – Reptilia* 21, 223–226.
- Pérez-Mellado, V., Riera, N., Hernández-Estévez, J.A., Piccolo, V., Potter, C., 2007. A complex case of interaction between lizards and plants: the dead horse arum (*Dracunculus muscivorus*) and the Balearic lizard (*Podarcis lilfordi*). In: Corti, C., Lo Cascio, P., Biaggini, M. (Eds.), *Mainland and Insular Lacertid Lizards: A Mediterranean Perspective*. Firenze University Press, pp. 133–160.
- Pérez-Mellado, V., Hernández-Estévez, J.A., García-Díez, T., Terrassa, B., Ramón, M.M., Castro, J., Picornell, A., Martín Vallejo, J., Brown, R., 2008. Population

- density in *Podarcis lilfordi* (Squamata Lacertidae), a lizard species endemic to small islets in the Balearic Islands (Spain). *Amphibia – Reptilia* 29, 49–60.
- Pianka, E.R., Vitt, L.J., 2003. *Lizards: Windows to the Evolution of Diversity*. University of California Press, Berkeley.
- Price, P.W., 1980. *Evolutionary Biology of Parasites*. Princeton University Press, Princeton.
- Salvador, A., Veiga, J.P., Martín, J., López, P., Abelenda, M., Puerta, M., 1996. The cost of producing a sexual signal: testosterone increases the susceptibility of male lizards to ectoparasitic infestation. *Behav. Ecol.* 7, 145–150.
- Schall, J.J., 1996. Malarial parasites of lizards. *Adv. Parasitol.* 37, 255–333.
- Sorci, G., Clobert, J., 1995. Effects of maternal parasite load on offspring life-history traits in the common lizard (*Lacerta vivipara*). *J. Evol. Biol.* 8, 711–723.
- Stamps, J.A., 1977. The relationship between resource competition, risk and aggression in a tropical territorial lizard. *Ecology* 58, 349–358.
- Stamps, J., 1994. Territorial behavior: testing the assumptions. *Adv. Stud. Behav.* 23, 173–232.
- Steward, J.W., 1965. Territorial behavior in the wall lizard *Lacerta muralis*. *Br. J. Herpetol.* 3, 224–229.
- Svahn, K., 1974. Incidence of blood parasites of the genus *Karyolysus* (Coccidia) in Scandinavian lizards. *Oikos* 25, 43–53.
- Telford, S.R., 2008. *Hemoparasites of the Reptilia: Color Atlas and Text*. CRC Press, Boca Raton, FL.
- Tokarz, R.R., 1985. Body size as a factor determining dominance in staged agonistic encounters between male brown anoles (*Anolis sagrei*). *Anim. Behav.* 33, 746–753.
- Van Riper, C., Van Riper, S.G., Goff, M.L., Laird, M., 1986. The epizootiology and ecological significance of malaria in Hawaiian land birds. *Ecol. Monogr.* 56, 327–344.
- Weatherhead, P.J., Barry, F.E., Brown, G.P., Forbes, M.R., 1995. Sex ratios, mating behavior and sexual size dimorphism of the northern water snake, *Nerodia sipedon*. *Behav. Ecol. Sociobiol.* 36, 301–311.
- Zug, G.R., Vitt, L.J., Caldwell, J.P., 2001. *Herpetology. An Introductory Biology of Amphibians and Reptiles*. Academic Press, San Diego.
- Zuk, M., McKean, K.A., 1996. Sex differences in parasite infections: patterns and processes. *Int. J. Parasitol.* 26, 1009–1023.