

## Does relaxed predation drive phenotypic divergence among insular populations?

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coloration;  
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variance.

### Abstract

The evolution of striking phenotypes on islands is a well-known phenomenon, and there has been a long-standing debate on the patterns of body size evolution on islands. The ecological causes driving divergence in insular populations are, however, poorly understood. Reduced predator fauna is expected to lower escape propensity, increase body size and relax selection for crypsis in small-bodied, insular prey species. Here, we investigated whether escape behaviour, body size and dorsal coloration have diverged as predicted under predation release in spatially replicated islet and mainland populations of the lizard species *Podarcis gaigeae*. We show that islet lizards escape approaching observers at shorter distances and are larger than mainland lizards. Additionally, we found evidence for larger between-population variation in body size among the islet populations than mainland populations. Moreover, islet populations are significantly more divergent in dorsal coloration and match their respective habitats poorer than mainland lizards. These results strongly suggest that predation release on islets has driven population divergence in phenotypic and behavioural traits and that selective release has affected both trait means and variances. Relaxed predation pressure is therefore likely to be one of the major ecological factors driving body size divergence on these islands.

### Introduction

Island populations are natural laboratories (Whittaker & Fernandez-Palacios, 2007) and are therefore useful model systems to understand the evolutionary and ecological processes that shape biological diversity (Mayr, 1963; Grant & Grant, 2008; Losos, 2009). Islands often differ markedly in their ecology from adjacent mainland localities; for example, islands are thought to have more empty niches due to the species poor faunas and floras and relaxed competition. This may provide opportunities for rapid diversification and adaptive radiations (Grant & Grant, 2008; Losos, 2009). MacArthur and Wilson's (1967) classical island model aimed to describe biogeographical patterns and the processes underlying these patterns, and this theory predicts lower species richness on islands compared with their

adjacent mainland localities. Animals on islands are hence expected to experience a lower predation risk due to the lower number of predator species (although not necessarily a lower number of individual predators). Reduced predation can make some mainland adaptations unnecessary, as seen, for example, in the higher occurrence of flightless birds on islands (McNab, 1994). More generally, predation is a strong selection pressure (Blanckenhorn, 2000) and has been shown to shape ecologies, life histories and morphology of prey species (Reznick & Endler, 1982; Reznick *et al.*, 1996; Losos *et al.*, 2004; Herczeg *et al.*, 2009).

Although divergent morphologies on islands, in particular patterns of body size divergence, have been extensively studied in the past (Foster, 1964; van Valen, 1973; Case, 1978; Palmer, 2002; Lomolino, 2005; Meiri *et al.*, 2006; Raia & Meiri, 2006; Meiri, 2007; Meiri *et al.*, 2008; Nosolov *et al.*, 2013), identifying the ecological causes driving the population divergence remains an empirical challenge. Past work in this area has mainly focused on changes in trait means and

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has tended to ignore changes in variances. Most previous work is based on large-scale interspecific comparisons that include few islands with little or no replication within species (but see Clegg *et al.*, 2002 and Frentiu *et al.*, 2007 for exceptions). The amount of between-population variance in phenotypic traits and recurrence of morphological change is also informative of the evolutionary processes driving divergence (Clegg *et al.*, 2002). To quantify variances and better understand the ecological causes driving the evolutionary processes affecting island phenotypes, we should either use experimental approaches (c.f. Losos *et al.*, 2004) or replicated and well-designed observational studies comparing multiple island and mainland populations with similar ecologies. Replication at the population level within-habitat categories (i.e. island vs. mainland populations) is therefore crucial in demonstrating the generality of island divergence and identifying the ecological factors and selective pressures that drive island divergence (Clegg *et al.*, 2002).

Removal of a selection pressure such as predation can result in (i) an overall flatter fitness landscape (ii) a flatter fitness landscape in only one direction (iii) a broader fitness peak or (iv) an increase in the influence of residual selection pressures. Alone or in combination, these four scenarios may result in fitness peak shifts (Lathi *et al.*, 2009). In the first two scenarios, an increase in between-population variation is expected as populations can drift freely (e.g. peaks can shift freely) in one or both directions. In addition, if there is variation in residual selection pressures, increased between-population variation is expected in the fourth scenario as well as peaks would then differ in position between populations. In the third scenario, within-population variation is also expected to increase. For an illustration and a more detailed description of the outcomes expected under a predation release, see Fig. S1. In summary, increased between-population variation is expected following a selective release. Comparisons of population variation between habitats that experience different selection regimes may provide insight into the phenotypic consequences of relaxed selection.

Body size is the classical trait used in studies of phenotypic divergence on islands (Foster, 1964; van Valen, 1973; Case, 1978; Lomolino, 2005; Meiri *et al.*, 2006) and is of central evolutionary interest, as size is often correlated with other physiological and life-history traits (Stearns, 1992; Herczeg *et al.*, 2009). Predation can favour small body size directly, due to reduced detection from size-selective predators (Quinn & Kinnison, 1999) or indirectly, as a correlated response to selection for early maturation in high-predation environments (Abrams & Rowe, 1996; Rodd & Reznick, 1997; Blanckenhorn, 2000). The 'Island rule' described by Foster (1964) and later coined by van Valen (1973) originally stated that small mammals evolved larger

body sizes, whereas large mammals become smaller on islands. This rule was later suggested to be applicable to all terrestrial vertebrates (Case, 1978). The generality of the island rule has, however, been re-examined and questioned (Lawlor, 1982; Meiri *et al.*, 2006, 2008; Meiri, 2007), and the evolutionary processes generating the patterns are not well understood. Moreover, data are scarce for other divergent morphological traits and behaviours on islands.

Studying the joint divergence in traits and behaviours should enhance our understanding of the evolution of aberrant phenotypes on islands. Although reduced vigilance (Robinson, 1997) and reductions or losses of other antipredator defences (McNab, 1994; Perez-Mellado *et al.*, 1997; Cooper *et al.*, 2004; Pafilis *et al.*, 2008; Raia *et al.*, 2010) have been found in insular environments, combined studies of antipredator defences and body size divergence are rare. Increased variation in colour (Hayashi & Chiba, 2004) and aberrant coloration (Doucet *et al.*, 2004) have been reported for insular populations, but few studies address colour divergence jointly with body size or behavioural divergence (but see Rudh, 2013 for an exception). Coloration is important for crypsis (Endler, 1984; Storfer *et al.*, 1999; Stuart-Fox *et al.*, 2004), and selection for cryptic coloration is expected when predators are visually guided (Rosenblum *et al.*, 2004, 2010; Stuart-Fox *et al.*, 2004; Rosenblum, 2006). Therefore, quantifying body size divergence jointly with antipredator defences and crypsis should provide multiple independent lines of inference that jointly improve our ability to elucidate the role of predation in insular population divergence.

Here, we investigate the role of predator release as a driver of insular divergence in the Skyros wall lizard *Podarcis gaigeae*. We tested predictions from predation release to infer the role of predation in population and habitat divergence. If predation release is an important driver of insular divergence, insular populations are expected to have larger body sizes and be less cryptic and vigilant. Furthermore, we expect parallel divergence across replicated populations within environments because parallel phenotypic divergence between environments is indicative of natural selection (Reznick & Travis, 1996; Reznick *et al.*, 1996; Losos *et al.*, 1998; Schluter, 2000; Johannesson, 2001). We also predict between-population variation in phenotypes to increase under several scenarios of relaxed predator-mediated selection (Fig. S1; Clegg *et al.*, 2002; Lathi *et al.*, 2009; Des Roches *et al.*, 2011). To study the role of predation release and its effects on phenotypic divergence, we therefore quantified changes in means and variances in escape propensity, body size and dorsal colour in seven islet populations of the Skyros wall lizard lacking the most important predators (Pafilis *et al.*, 2009a,b, 2011). We compared patterns of population divergence among islets to a set of higher predation main island popula-

tions of this morphologically variable lizard species (Runemark *et al.*, 2010, 2011, 2012, 2013; Runemark & Svensson, 2012). Our results suggest that relaxed predation is indeed a major ecological factor that is likely to have driven the evolution of island gigantism in this system.

## Materials and methods

### Study species and geographical setting

The Skyros wall lizard *P. gaigeae* is an omnivorous lacertid lizard inhabiting maquis, sand dunes and bushy habitats on the island of Skyros, Greece, and its surrounding archipelago (Arnold & Ovenden, 2002; Valakos *et al.*, 2008). This small-bodied species (snout-vent length, SLV is about 6 cm; Valakos *et al.*, 2008) is morphologically very variable in both body size and throat colour (Runemark *et al.*, 2010; Runemark & Svensson, 2012). Islet populations have low effective population sizes (Runemark *et al.*, 2010, 2012) and are more genetically divergent than main island populations;  $F_{ST}$ -values between islet populations range between 0.08 and 0.33, whereas  $F_{ST}$ -values between main island populations are much lower: 0.0025–0.05 (Runemark *et al.*, 2010, 2012). There is a systematic ecological difference in predation pressure between islet and main island environments of this species as the studied islets lack the most important snake predators such as *Telescopus fallax* and *Zamenis situla* and avian predators, for instance *Lanius senator* and *Athene noctua*. This pattern has been reported by Pafilis *et al.* (2011) and confirmed for the remainder of the study islands by the authors of this study (Table S1). The lizards in this study were caught at 15 different localities (hereafter denoted populations), including seven islets and eight localities on the main island of Skyros (hereafter referred to as main island populations) during the peak reproductive period (March–May) of 2007–2009 (Fig. 1a,b; see Table S2 for coordinates and full population names). A mean of 58 lizards, with an approximately equal number of males (mean 30) and females (mean 28), were caught at each locality (see Table S3 for sample sizes per population and sex; in total 863 individuals).

### Flight initiation distances, morphological measurements and $F_{ST}$ estimation

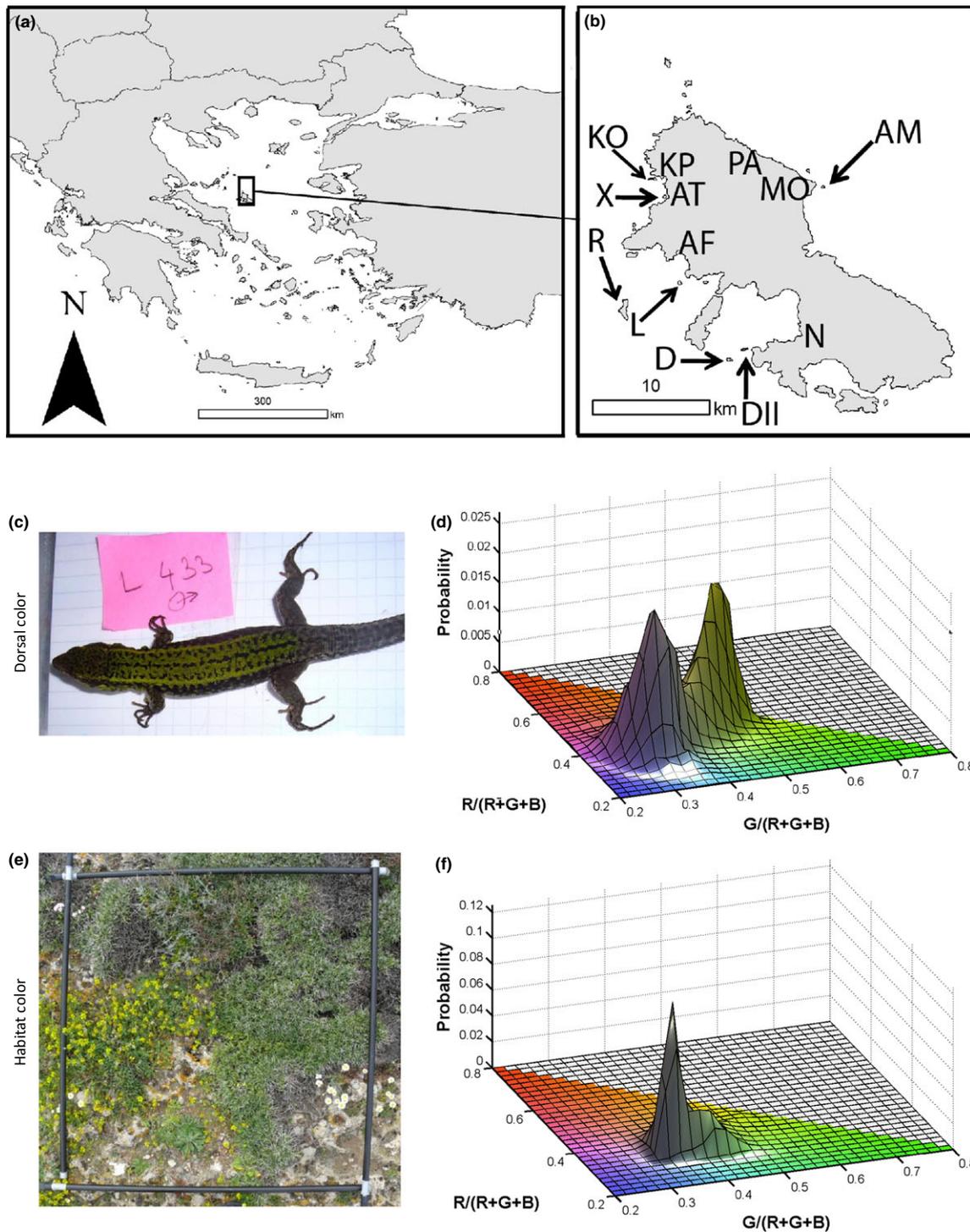
After lizards were caught in the field, we conducted field transects at the localities and recorded the distance between lizard and observer when the lizard first moved away (hereafter called flight initiation distance, FID, see Cooper & Perez-Mellado, 2012). We did not capture the lizards for which we recorded FIDs, but the transects were linear and we did not turn back to ensure that we did not observe the same lizard more

than once. As we did not catch the lizards, we were not able to classify all individuals to sex. A minimum of 50 (and a mean of 60) FIDs were recorded per population by 2–3 observers (see Table S3 for number of recorded FIDs per population). We recorded observer and tested for observer bias but found no significant differences between observers within any of the localities, and we therefore pooled the data. One observer (A. Runemark) performed transects at all localities to ensure that FIDs were comparable between sites and not only between observers within sites. Transects were performed when the weather was suitable for catching lizards, typically with the sun out, 20–25 °C and calm. All trials were conducted during peak lizard activity time, between 10 am and 4 pm.

We took nine morphological measurements on all captured lizards using digital callipers: SVL, humerus, radius, hind limb femur, hind limb tibia, head length, head width and head height. Body weight was measured using a pesola scale. From the nine morphological traits, we extracted principal components. The first principal component (PC1) had positive factor loadings on all traits and explained 86% of the variation in the data set [Fig. S2, see Tables S4 and S5 for factor loadings and eigenvalues from the principal component analysis (PCA)] and was therefore used as an index for body size. The rationale for using PC1 as a measure of body size rather than, for instance, SLV is that it incorporates multiple size measures and would reflect the development of both sturdier and longer bodies. A mean of 58 individuals per population were included in the analysis of body size (see Table S3 for sample sizes per population and sex; in total 863 individuals). We estimated  $F_{ST}$  for all population pairs using  $F_{STAT}$  version 2.9.3 (Goudet, 2001) using 16 highly variable microsatellite loci described in Runemark *et al.* (2010, 2012). All molecular procedures are as described in Runemark *et al.* (2010, 2012). A total of 798 individuals from all 15 study populations were analysed; see Table S3 for sample sizes per population.

### Colour measurements

The reflectance of 200 lizards' dorsal body surfaces was measured with an Ocean Optics USB4000 spectrometer/XeHg flash (Ocean Optics, Inc., Dunedin, FL, USA) in a 45° diffuse backscattering geometry, with a  $\emptyset$  5 mm field of view. No occurrences of UV features were found for dorsal coloration (see Fig. S3 for five representative example spectra). We therefore deemed RGB imaging appropriate. The use of RGB images and spatially resolved analysis which reflects the presence of discrete colours in the measured area rather than a mean (see e.g. the bimodal colour distribution reflecting the presence of both green and black scales in the histograms in Fig. 1c,e) is preferable if the spectral region of interest is covered by the RGB imager



**Fig. 1** Study localities and colour measurement methodology. (a) Map of the Greek archipelago with the island of Skyros marked with a box. (b) Enlarged map of the island of Skyros. Islet populations are demarcated by an arrow and their letter assignment, whereas main island populations are demarcated by only their letter assignment. We analysed colour from RGB images of the lizards' backs and from habitat squares. In c and e, we give representative examples of such RGB images. We sampled the chromaticity of each individual pixel and represented all pixels in a 2-D histogram representing the RGB colour space. In d and f, we present the histograms corresponding to image c and e, respectively.

(Brydegaard *et al.*, 2012). All lizards were photographed with a DMC FX01 Panasonic colour camera (a RGB imaging system) in an optical isolated box with a white background reference, using the built-in xenon flash. Specular reflections were avoided with crossed polarization filters in front of the flash and objective. We used a MATLAB script to isolate the dorsal area of interest. The head and back were included, but not the tail as regrown or lost tails could bias the results. The white background reference was used to calibrate a 2-D second-order polynomial function that corrects for the illumination profile. The correction algorithm and the colour analysis script have been deposited in Dryad. A mean of 41 individuals per population were included in the colour analyses, for breakdown sample sizes per population and sex see Table S3; a total of 621 individuals were included. All colour analyses in this study are based on the RGB data as this illustrates the patchy backs of the Skyros wall lizard better than single-point spectra.

### Environment measurements

To study lizard crypsis in their environments, we measured habitat coloration. At all field localities, we randomly selected four  $1 \times 1 \text{ m}^2$  (Fig. 1d,f) that were photographed using our DMC-FZ50 Panasonic colour camera (a RGB imaging system). The area of interest was removed from the picture using the same script as for dorsal coloration of the lizards.

### Statistical analyses

To capture the colour variance within each sample, the chromaticities of individual pixels were summarized in 2-D histogram planes (Drew & Au, 2003; Brydegaard *et al.*, 2012; Fig. 1e,f). The histogram's planes were decomposed using a PCA (Bro, 1998), and the expansion in principal component planes was truncated after analysing the eigenvalues. The truncation point was chosen based on where the eigenvalues deviated from the noise floor. The entire method for the colour analysis procedure is described in detail in Brydegaard *et al.* (2012). Matlab® (MathWorks, Natick, MA, USA) was used for all image analyses. To investigate whether populations differed in dorsal coloration, a discriminant function analysis based on the individual scores for the principal components included after truncation was performed.

To compare FID-, body size- and colour differences within and between islet and main island habitats, as well as between populations, we used mixed models with population as a random factor nested within the fixed factor habitat. For FID, only habitat and population nested within habitat was included as we could not record the sex of the escaping lizards, whereas sex and the interaction between sex and habitat also were

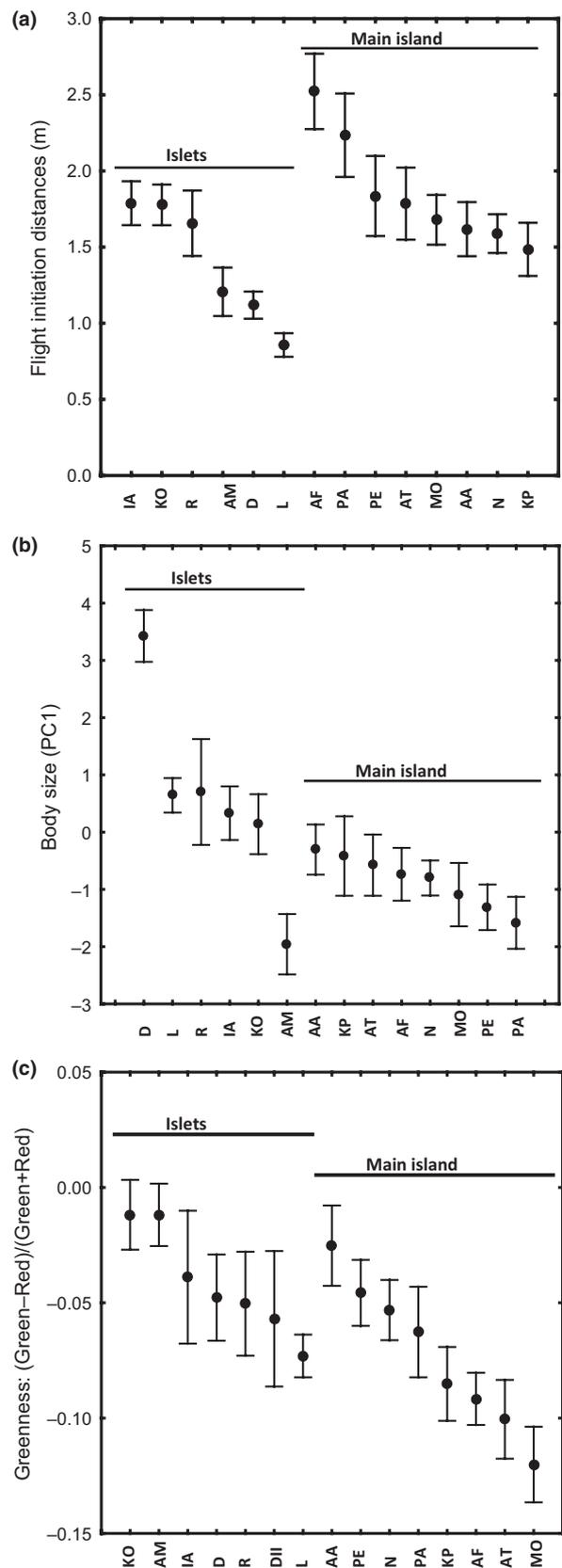
included for size and colour to investigate whether the sexes respond similarly to island habitat. We used PC1 as a proxy for body size and greenness – the value of  $(\text{Green} - \text{Red})/(\text{Green} + \text{Red})$  as a proxy for colour (See Tables S4 and S5 for factor loadings and eigenvalues of the PC's). We utilized the nlme package in R for the mixed models. For coloration, we also used a discriminant function analysis based on the PCs included after truncation (see e.g. Fig. S4 and Table S6) to test whether populations differed in dorsal coloration and whether the degree of divergence differed between habitats.

To further visualize within both population and habitat variation in body size, shape and colour, we used 3-D plots where size, shape (PC1, PC2 and PC3) and coloration (PC1, PC2 and PC3) were on the  $X$ ,  $Y$  and  $Z$  axes, respectively. For size, a higher value of PC1 represents larger overall size, whereas higher PC2 values reflects a transition to relatively longer limbs, and higher PC3 values represents a transition to relatively smaller heads and shorter hindlimbs (see Fig. S4 and Table S4-5 for factor loadings and eigenvalues of the PC's for body size). The use of PCs here is motivated by their ability to illustrate the main axes of variance and hence allow for comparisons of the within-population variance between populations. The spheres are centred at the mean and their sizes reflect standard deviation in the size, shape and coloration variables. To investigate whether body sizes and dorsal colour varied more between islet populations than between main island populations, we used a variance components test to decompose variation as between- and within-population variation. To test whether between-population variation is greater among island than among main island populations, we used  $F$ -tests to comparing body size and dorsal coloration between islet and main island populations. We also used similar  $F$ -tests to investigate whether the amount of total variation differed among islet and main island populations for body size and dorsal coloration, respectively. To determine whether differences in population variation between habitats could be the result of higher genetic relatedness within the main island, we tested whether between-population divergence in body size and greenness measured as  $P_{ST}$  was correlated with  $F_{ST}$ .  $P_{ST}$  was calculated using eqn 3 in Brommer (2011) which takes into account the proportion of the total variance presumed to be due to additive genetic effects across populations ( $c$ ), in addition to heritability ( $h^2$ ); we used several ratios between  $h$  and  $c$  (0.05, 0.25, 0.5, 0.75 and 1) to ensure that the results from the  $P_{ST} - F_{ST}$  comparison were not affected by assumptions regarding  $h$  and  $c$ . As  $F_{ST}$  and  $P_{ST}$  are properties of population pairs, we used Mantel tests (Isolde application in GenePop on the web; Raymond & Rousset, 1995; Rousset, 2008) to test whether genetic relatedness drives the patterns of phenotypic divergence.

A matrix correlation of the entire colour distributions was used to investigate whether islet populations differ more in dorsal coloration than main island populations. We compared the pairwise similarities between the mean chromatic histograms by correlating all the colour elements in the chromatic histogram of one population to the corresponding element from the other population involved in each comparison. Two identical populations would have a matrix correlation of one, whereas two populations with entirely nonoverlapping colour distributions would have a correlation of zero. As these correlations coefficients are pairwise and every population is involved in several comparisons and the comparisons are strictly speaking not independent, we used a resampling procedure in R (R Core Team, 2012) to compare the degree of lizard–lizard and lizard–habitat matching (average pairwise correlation coefficient between populations within each habitat category) between the habitats.

We also quantified phenotype–environment matching. We first tested whether the main island lizards are better matched to the main island environments than islet lizards to islet environments using the same type of matrix correlation of the colour histograms as described above (here for lizard and environment, respectively) and applying the same resampling procedure as described above. We then used a GLM with the lizard–environment correlation coefficients as dependent variables to test whether lizards in general are better matched to their own localities than other localities. Finally, we tested whether the magnitude of within-locality lizard–habitat correlation coefficients differs between islet and main island habitats using a GLM, to see whether islet lizards have reduced colour matching to their own localities. Statistical analyses were performed in Statistica (Statsoft Inc, 2004) and ‘R’ (R Core Team, 2012).

**Fig. 2** (a) Mean flight initiation distance (FID) by population and habitat. Islet populations are shown to the left side of the panel and main island populations to the right. Although there is an overall islet effect on FIDs ( $P < 0.001$ ), there is also substantial and significant between-population variation within both habitat categories ( $P < 0.001$ ). (b) Mean body size (PC1) separated by population for the Skyros wall lizard. There is a significant islet effect on body size ( $P < 0.001$ ), but also significant variation within both habitat categories ( $P < 0.001$ ). Note that the smallest islet population (AM) is not significantly smaller than its most proximate main island population (MO). (c) Mean greenness ( $((\text{Green} - \text{Red})/(\text{Green} + \text{Red}))$ ) by population for the Skyros wall lizard. Islet populations are significantly greener than main island populations ( $P < 0.001$ ), but there was also significant within-habitat variation ( $P < 0.001$ ). Note that although the patterns of population divergence in greenness are more continuous among the main island populations, some of the islet populations show more disparate measures of greenness.



## Results

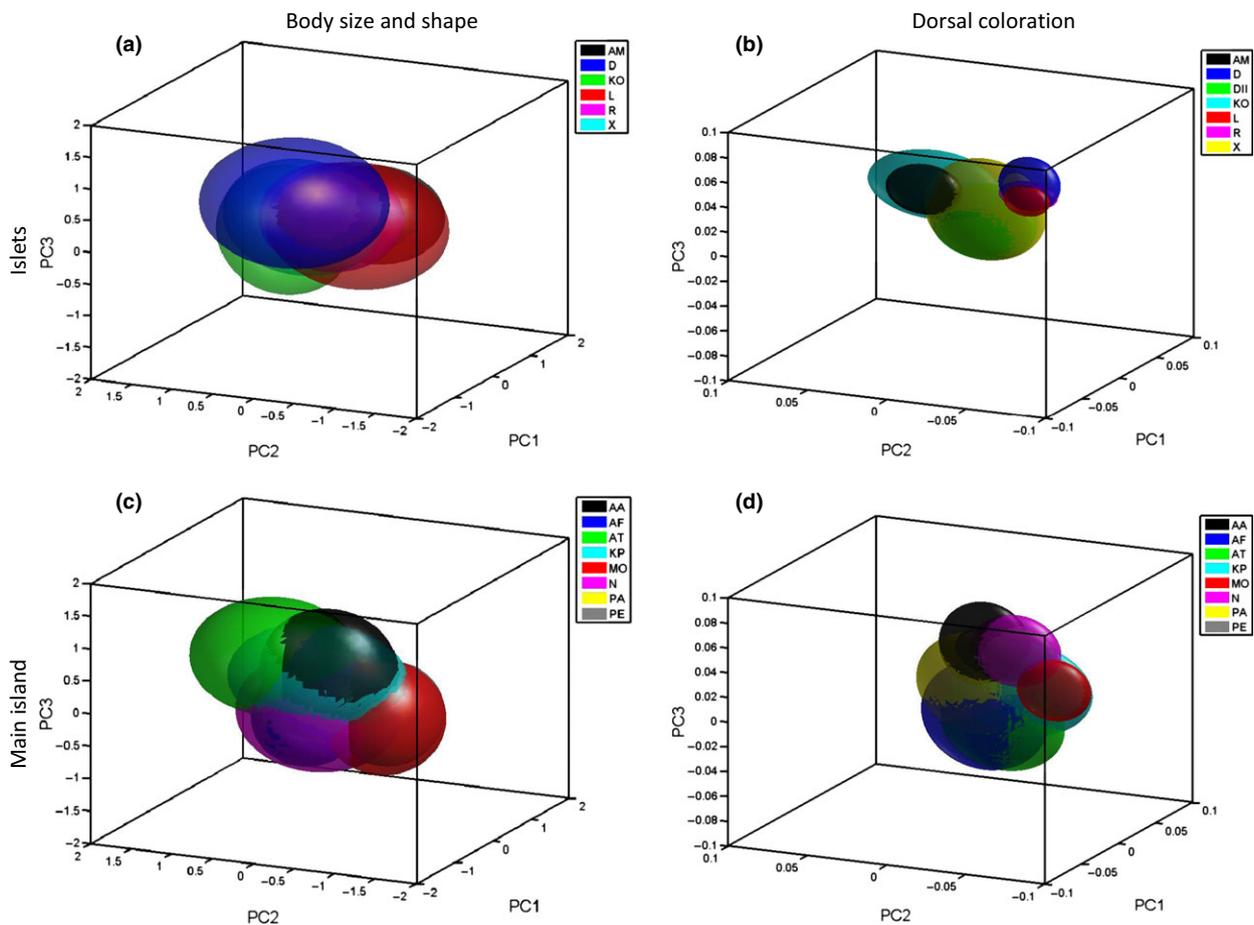
### Population divergence in escape propensity

Islet lizards escaped at significantly shorter distances (1.38 m; 95% CI 1.32–1.44 m) than did main island lizards (1.5 m; 95% CI 1.44–1.56 m;  $b = 0.44$ ;  $F_{1,12} = 4.68$ ;  $P = 0.05$ ). There was also substantial variation between populations within each habitat category (Fig. 2a). Pairwise population differences are reported in Table S7.

### Population divergence in mean body size

Islet lizards were on average 16% larger than main island lizards, with a mean SVL of 66.9 mm in comparison with the main island mean of 57.4 mm. In addition

to the inspection of the femoral pores (secretory glands found on the inside of the thighs of *Podarcis* lizards), we also plotted the distribution of main island individuals to ensure that only adults were caught. If the distribution was not bimodal, this indicated that no juveniles were caught and hence that the body size differences between habitats cannot be explained by a larger proportion of juveniles being caught on the main island (see Fig. S5). Both habitat and sex influenced body size. Overall, islet lizards were significantly larger (mean PC1 = 1.12; 95% CI: 0.73–1.51) than mainland lizards (mean PC1 = -0.99; 95% CI: -0.77 to -1.21;  $b = -1.46$ ;  $F_{1,11} = 5.93$ ;  $P = 0.03$ ; Fig. 3a), and males were significantly larger than females ( $b = 3.73$ ;  $F_{1,544} = 602.7$ ;  $P < 0.001$ ). In addition, there was a significant interaction between habitat and sex



**Fig. 3** Within- and between-population variation in morphology (a, c) and dorsal coloration (b, d). To illustrate the patterns of divergence in body size and shape (PC1–3) and coloration (PC1–3) between populations, we have plotted the population means and distributions of these characters for islet and main island populations. (a, b) show variation between islet populations in size and shape and dorsal coloration, respectively. (c, d) show the same data, but for main island populations. The centres of the spheres denote the mean of the populations, and the size of the spheres equals the standard deviation. A larger proportion of the variation is between-population variation in the islets (a, b: well-defined spheres), whereas within-population variation is relatively larger in the main island populations (c, d: more overlapping spheres).

( $b = -1.10$ ;  $F_{1,544} = 18.66$ ;  $P < 0.001$ ), revealing that the extent of sexual dimorphism differed between habitats and that islet populations were more sexually dimorphic. Pairwise population differences are reported in Table S7.

### Differences in dorsal coloration

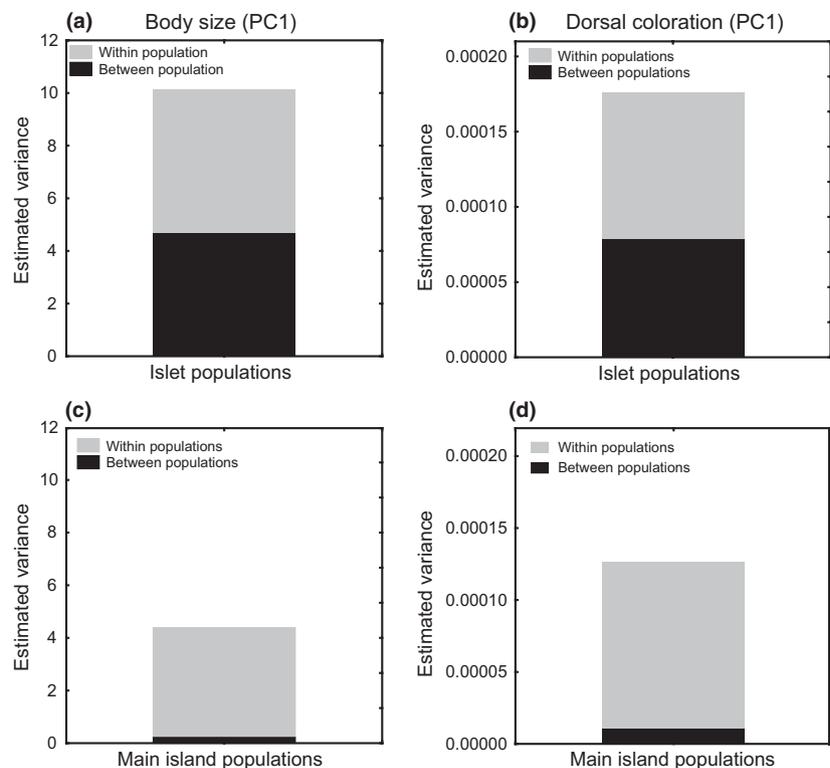
Populations differed strongly in dorsal coloration (discriminant function analysis based on the six-first PCAs illustrated in Fig. S6;  $F_{84,3350} = 13.03$ ;  $P < 0.001$ ; Figs 2c and 3b,d). Only eight of 105 between population comparisons were nonsignificant. Squared Mahalanobis distances ranged between 0.23 and 16.62, and most populations differed significantly from each other (Tables S8 and S9). In spite of large differences, classification to the correct population was quite low, ranging between 0% and 85% with a mean of 34% correct classifications (Table S10). The low classification success is likely due to the large overlap in colour between populations despite their distinct distributions (see Fig. 3a,b). There were no significant differences between the classification success of islet and main island populations ( $T_{13} = 0.44$ ,  $P = 0.66$ ). The islet lizards were greener than main island lizards ( $b = -0.03$ ;  $F_{1,13} = 5.05$ ;  $P = 0.04$ ). We also found sexual dimorphism: males were significantly greener than females ( $b = -0.01$ ;  $F_{1,604} = 9.46$ ;  $P = 0.002$ ). However, the interaction between habitat and sex was not

significant ( $b = -0.0005$ ;  $F_{1,604} = 0.004$ ;  $P = 0.95$ ), implying that sexual dimorphism in greenness does not differ between habitats. We therefore removed this habitat  $\times$  sex interaction from the model. In this reduced model, islet lizards (greenness =  $-0.04 \pm 0.006$  95% CI) were significantly greener than mainland lizards (greenness =  $-0.075 \pm 0.008$  95% CI;  $b = -0.032$ ;  $F_{1,13} = 5.05$ ;  $P = 0.04$ ) and males were significantly greener than females ( $b = -0.13$ ;  $F_{1,604} = 9.47$ ;  $P = 0.002$ ).

### Increased between-population variance on islets

Consistent with predictions from predation release, we found that between-population variation was significantly larger among islet populations than among main island populations. This was true for both body size ( $F$ -tests;  $F_{288,319} = 21.11$ ;  $P < 0.001$ ) and dorsal coloration ( $F_{219,401} = 7.51$ ;  $P < 0.001$ ). Moreover, total variation (including both within- and between-population variation) was higher on the islets (body size:  $F_{288,319} = 2.31$ ;  $P < 0.001$ , and dorsal coloration:  $F_{219,401} = 1.39$ ;  $P = 0.0024$ ). The variance decomposition is illustrated in Fig. 4.

To investigate whether the increased between-population of the phenotypic traits on the islets could be explained simply as a correlated effect and confounded by higher background neutral genetic divergence



**Fig. 4** Variance component decomposition of body size (a and c for islet and main island populations, respectively) and dorsal coloration (b and d for islet and main island populations, respectively). The between-population component of variation is significantly larger among islets populations than among main island populations ( $P < 0.001$  for both body size and dorsal coloration). The total amount of variation (including both within- and between-population variation) was also significantly higher among the islet populations, both for body size and coloration ( $P < 0.001$  for body size and  $P = 0.0024$  for dorsal coloration).

between the islet populations than between the main island populations, we used Mantel's tests to estimate the correlations between genetic and morphological divergence. To ensure that the effects of similarity within category did not confound our analyses, we performed these tests separately for the main island and islet categories. We used a measure for  $P_{ST}$  which takes both assumptions about heritability and the proportion of the total variance that might be expected to be due to additive effects across populations (e.g. eqn 3 in Brommer 2011). Assuming an intermediate  $c/h^2$  ratio of 0.25, we found no significant relationships neither between  $F_{ST}$  and  $P_{ST}$  for size neither for islet ( $F_{ST} = 0.89 + 0.0004 \times P_{ST}$ ;  $P = 0.99$ ) or main island populations ( $F_{ST} = -68 + 554.6 \times P_{ST}$ ;  $P = 0.48$ ). There were no significant correlations between  $F_{ST}$  and  $P_{ST}$  for greenness either; islets ( $F_{ST} = 1.78 - 4.57 \times P_{ST}$ ;  $P = 0.98$ ) and mainland ( $F_{ST} = 0.19 - 1.0 \times P_{ST}$ ;  $P = 0.85$ ). None of the tests for other  $c/h^2$  ratios were significant (Table S11). Pairwise population differences are reported in Table S7.

### Within-habitat variation in dorsal coloration and background matching

Main island populations were significantly more similar to each other with respect to dorsal coloration than were islet populations (islet–islet correlations  $R^2 = 0.81$ ; 95% CI: 0.78–0.84; main island–main island correlations  $R^2 = 0.90$ ; 95% CI: 0.89–0.91;  $P < 0.05$ ; Fig. 5a,c). The two habitat categories also differed in degree of matching between environments and phenotypes, revealed by lower correlation coefficients between the islet than between the main island populations. Main island lizards were better matched to the generalized main island habitat than islet lizards to the generalized islet habitat (islet–islet correlation  $R^2 = 0.74$ ; 95% CI: 0.71–0.77; main island–main island correlation  $R^2 = 0.88$ ; 95% CI: 0.86–0.90;  $P < 0.05$ ; Fig. 5b,d).

To further investigate whether the differences in dorsal coloration between populations were likely to reflect adaptations to be cryptic in the habitat, we tested whether mean lizard–mean habitat correlations were higher within localities than between localities. This was not the case ( $F_{1,89} = 0.34$ ;  $P = 0.56$ ; Fig. 5d). However, the within-locality phenotype–environment matching was significantly higher for main island populations than for islet populations ( $F_{1,11} = 6.32$ ;  $P = 0.029$ ; Fig. 5d). This implies that islet populations are less cryptic in their environments.

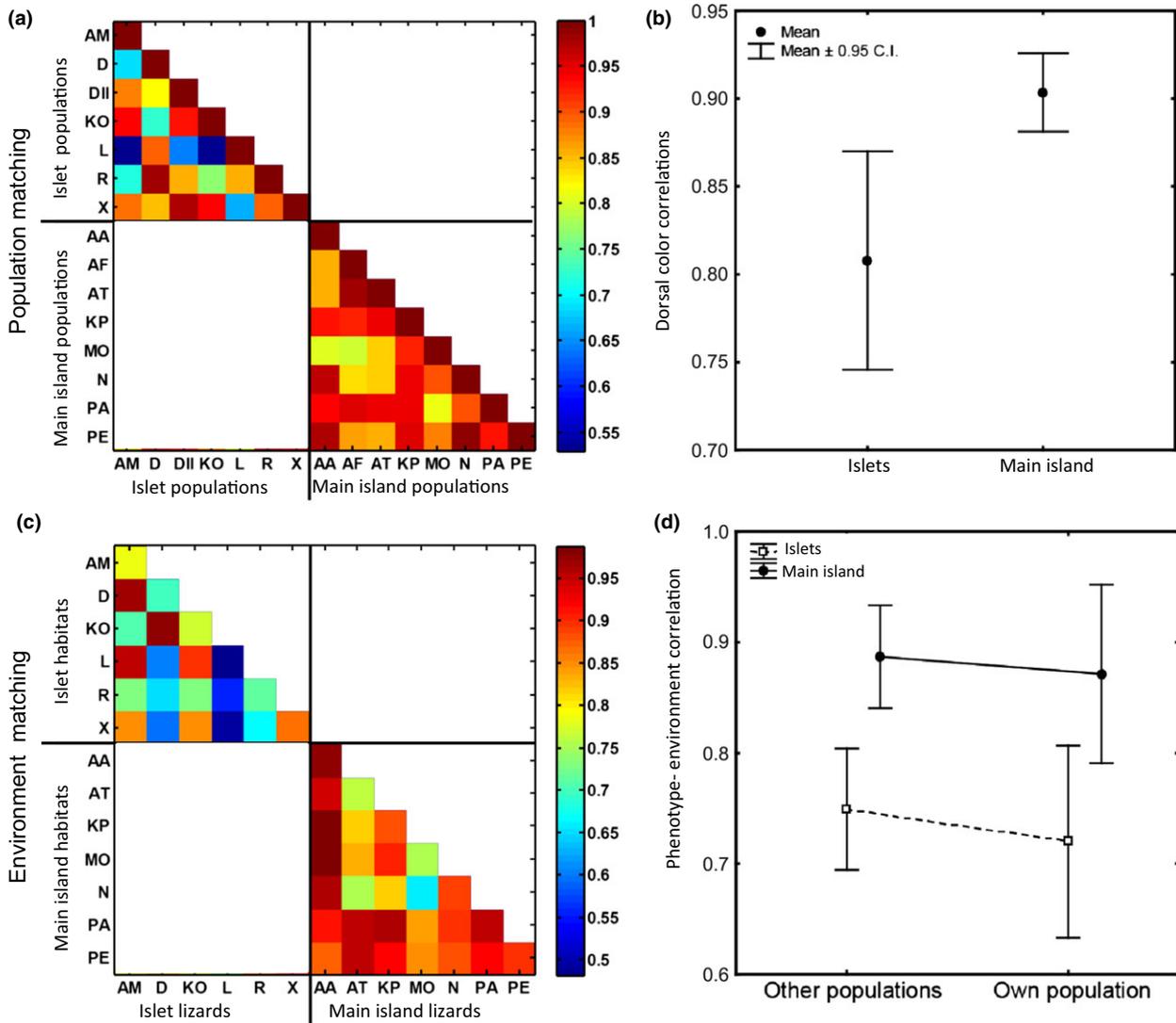
### Discussion

Here, we have demonstrated that insularity affects not only body size, a classical study trait in island biology and island biogeography, but also dorsal coloration and escape behaviour. Collectively, our results suggest

that predation release is one of the major ecological factors behind insular population divergence in the Skyros wall lizard. This is consistent with the findings of that predation affects behaviour and morphology in some other lizard species, such as *Anolis sagrei* (e.g. Losos *et al.*, 2004). Several independent lines of evidence suggest that predation release is a major explanation for population divergence and island gigantism in this system.

First and foremost, the differences between islet and main island habitats in FIDs revealed that islet lizards were less prone to escape than main island lizards. Lower escape propensity on the islets is certainly consistent with loss of defences following a predation release, (c.f. McNab, 1994; Robinson, 1997). The predator faunas on the islets surrounding Skyros are depauperate compared with the main island of Skyros (Pafilis *et al.*, 2011; Table S1). As lower shrubs and herbs where the lizards can hide below are present both on the islets and main island, the presence of and proximity to shelter is not likely to influence escape propensity.

Predation release has been suggested as one of the main factors responsible for the development of island gigantism (Blanckenhorn, 2000; Herczeg *et al.*, 2009). Here, we documented significantly larger body sizes across several insular populations of the Skyros wall lizard, compared with the main island, consistent with evidence from *Podarcis sicula* (Vervurst *et al.*, 2007), and some earlier studies on this species (Gruber & Schultze-Westrum, 1971; Gruber, 1986; Pafilis *et al.*, 2009a,b, 2011). The increased between-population variance in body size (Figs 3 and 4) on the islets likely reflects an ecological release following relaxed predation (Abrams & Rowe, 1996; Rodd & Reznick, 1997; Quinn & Kinnison, 1999). There are several alternative selective mechanisms that could contribute to this (see e.g. Fig. S1; Box 2 in Lathi *et al.*, 2009). For instance, relaxed predator-mediated selection could result in a more pronounced role for sexual selection. Secondary sexual traits often change quickly in response to reduced predation (see Svensson & Gosden, 2007 for a review). Sexual selection could select for a different trait optimum, and sexually selected traits and the preferences for them can then evolve along a neutral line of equilibrium (c.f. Uyeda *et al.*, 2009), thereby increasing between-population variation. Body size has been demonstrated to be important for male reproductive success in lizards (Fitze *et al.*, 2010), although we find no net directional selection for large males in no-choice trials in this species (Runemark & Svensson, 2012). In line with the expectation of an increased scope for sexual dimorphism following a predation release, we found significantly stronger body size dimorphism in islet populations than main island populations, and the stronger differences between males which suggest that they are the sex under stronger selection (c.f. Herczeg *et al.*, 2010). Alternatively, lower predation levels on islets



**Fig. 5** Colour similarity between populations within each habitat category (a and c) and colour matching between lizards and their local habitats (b and d). In (a, b), the colour of the square denotes how similar coloration of lizards from different populations are (a) and how well the lizards match their local habitats (BB). Red colours, implying a higher value of the correlation coefficient, indicate that lizards are more similar/more well matched to their habitats, whereas blue colours indicate a lower match. In the upper-left squares, the similarity between islet populations (a) and matching between islet populations and islet habitats (b) are shown, whereas main island populations and their matching to other populations (a) and matching to habitats (b) are shown in the lower-right square. As can be seen from the overall redder colour of the lower-right squares, main island populations are more similar to each other in terms of coloration than are islet populations (a). The main island lizards are also more closely matched to the coloration of the main island habitat than the islet lizards are to the islet habitats (b). (c) and (d) are alternative ways to illustrate the data from a and b, respectively; here, the mean of the correlation coefficients between mainland and islet populations (c) and the mean of the correlation coefficients between mainland populations and mainland habitat (filled circles), and islet population and islet habitat (open squares) (d). In d, we have divided the data by own population (how well the lizards match their home locality) and other population (how well the lizards match the other populations from their habitat). Error bars denote 95% C.I.

can also relax natural selection for early maturation, allowing more time for the development of larger body size (Rodd & Reznick, 1997; Ab Ghani *et al.*, 2013). If the selective advantages of an early onset of reproduction are relaxed on the islets, a larger spectra of body

sizes could then become selectively neutral or nearly neutral (case a, Fig. S1). Moreover, a theoretical model by Aikio *et al.* (2013) predicts larger optimal body sizes in low predation environments. We can, however, not rule out that lower predation potentially could have

caused islet lizards to live longer and thereby attain larger body sizes than main island lizards. However, hatchlings from islet eggs have larger initial body sizes and faster growth rates than these from main island eggs in a common garden environment (Runemark, 2012), which suggests that there are some intrinsic size- and growth differences between main island and islet environments.

Other natural selection pressures, apart from predation, can of course also be important, and a role for predation release is by no means mutually exclusive with such other selective pressures. In lizards, the patterns of body size evolution on islands correlates with feeding ecology: carnivorous lizards become smaller on islands, whereas there is a trend for omnivorous and herbivorous lizards becoming larger (Meiri, 2007). The between-islet variation in body size also suggests that although the islet environment is necessary for the development of gigantism, it is obviously not sufficient to result in island gigantism in every potential situation of relaxed predation. Hence, other local selective factors such as local feeding ecology (Aubret, 2012) and sexual selection are likely to interact with predation release and jointly affect selection on body size. We have also found evidence for stronger bite force among islet lizards, presumably to cope with harder diets in islet environments (Runemark, 2012), although selection for stronger bite force to hold females during copulation has been reported in other species (Herrel *et al.*, 2002). Regurgitates, carcasses and faeces from nesting yellow-legged gull (*Larus michahellis*) could serve as food for arthropod prey and contribute to body size divergence as nest densities and lizard body size are correlated across study sites (Pafilis *et al.*, 2009b). The high density of gull nests on Mesa Diavates (d in Fig. 1a; Pafilis *et al.*, 2009b) where the lizards obtain very large body sizes is consistent with some effect of nesting gulls. Releases from interspecific competition can also result in niche- and body size shifts (Lomolino, 1985; Simberloff *et al.*, 2000); hence, the absence of the larger Lacertiid species Balcan green lizard (*Lacerta trilineata*) on the islets could imply that *P. gaigeae* can exploit parts of its niche there. Potentially, higher intraspecific aggression and cannibalism on islets relative to the main island could also contribute to the observed island gigantism (see e.g. Pafilis *et al.*, 2011). Interestingly, both in our data set and in Pafilis *et al.* (2011), body sizes are small on islets located closer to the main island, with the most compelling case being population AM. The short distance between the main island and such islets means that some predators could potentially cross the strait. Moreover, time since divergence and low levels of gene flow are other important factors to consider when predicting body size on particular islets. Even moderate levels of gene flow can limit population divergence and local adaptation (Garcia-Ramos & Kirkpatrick, 1997; Bolnick & Nosil, 2007; Räsänen & Hendry, 2008).

In further support of predation release, islet lizards were significantly greener than main island lizards and dorsal coloration was also more diverged between the islet populations than between the main island populations. This higher population divergence in dorsal coloration among islets was largely caused by the lower within-population variation on the islets compared with the situation on the main island (see e.g. the smaller sizes of the population spheres in Fig. 3b compared with 3d). Coloration is important for crypsis (Endler, 1984; Storfer *et al.*, 1999; Stuart-Fox *et al.*, 2004), and dorsal coloration in *Podarcis* lizards is likely to be subject to strong selection in order to reduce detection risk from birds and other visually guided predators.

We addressed the issue whether the larger differences in dorsal coloration between islet populations are due to selection for local background matching on the islets. Briefly, our results do not support selection for crypsis as the cause for the elevated population divergence between the islets. In stark contrast to the expectation from selection for crypsis, islet populations match their habitats less well than main island populations. The larger between-population variation in dorsal coloration on the islets in combination with the lack of environment matching in dorsal coloration strongly suggests selective release due to lower predation on the islets (see e.g. Fig. S1, case a). Furthermore, there is some evidence for sexual selection on the green coloration of lacertids (see e.g. Olsson, 1994a,b; Galán, 2009), and islet lizards being greener would be consistent with an increased role for such sexual selection as crypsis is becoming less important in the island environments. Although we found evidence for significant sexual dimorphism in greenness with males being greener, there was no significant interaction between habitat and sex. If the sexual dimorphism in greenness has arisen from selection on males to become greener, such an interaction would have been consistent with an increased scope for sexual selection on islets. However, the absence of a significant interaction does not necessarily imply that there is not a stronger role for sexual selection on the islets. For instance, green colour could be subject to mutual sexual selection, or an intersexual genetic correlation for green colour and intralocus sexual conflict could have resulted in a correlated response to sexual selection in females (cf. Bonduriansky & Chenoweth, 2009; Svensson *et al.*, 2009).

Much past research in island biology and studies of island gigantism has focused on changes in trait means, such as the increase or decrease in body size as animals invade island habitats (Lomolino, 2005; Meiri *et al.*, 2006, 2008; Meiri, 2007; Novosolov *et al.*, 2013). The results in this study underscore that not only trait means, but also variances, particularly between-population variance, differ between islands and mainland. This insight is of fundamental importance to understand the ecology and evolution of insular populations. We found

a general pattern of increased between-population variation between islets in both body size and dorsal colour, compared with the situation on the main island (Figs 3–5). This increased between-population variation in dorsal coloration cannot be explained by increased crypsis on the islets (Fig. 5b,d). Rather, these results strongly suggest that the increased variation is a consequence of relaxed predator-mediated selection on the islets; a larger spectrum of traits become selectively neutral (Fig. S1, case a and b; see also Lathi *et al.*, 2009) or the selective optimum of the residual selective forces vary more between populations (which is expected for sexually selected traits; c.f. Uyeda *et al.*, 2009). This is analogous with the classical process of ecological release, which has traditionally been used exclusively for processes within islands (Des Roches *et al.*, 2011). In support for the validity of our analysis of variances, we found no significant correlation between genetic and morphological divergence neither for body size nor greenness, and the degree of variation is hence not merely a reflection of degree of genetic differentiation.

In summary, our study has three main findings. First, we found that islet lizards show lower escape propensity than main island lizards, which is consistent with predation release. These behavioural data provide an independent and more quantitative line of evidence for previous natural history observations on the lack of predators on these islets (Pafilis *et al.*, 2009a,b, 2011). Second, we found evidence for parallelism in larger body size on islets. Increased longevity could also potentially contribute, although it is unlikely to solely explain the large size differences. Third, islet populations show greater between-population variation in dorsal coloration and match their local habitats less than main island populations, which is consistent with predation release and relaxed selection for local crypsis. These three patterns are likely to be adaptive, although we are not able to address whether this is a genetic adaptation or a result of adaptive phenotypic plasticity in the current study. Based on these three lines of evidence, we conclude that relaxed predator-mediated selection on islets has been an important ecological factor in driving pronounced changes in size, coloration and behaviour. Selective release has probably also resulted in increased scope for selection pressures on these characters that were previously held in check by predation, such as diet. We conclude that predation release can be an important selective force explaining the evolution of larger body sizes on islands.

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## Supporting information

Additional Supporting Information may be found in the online version of this article:

**Figure S1** Predictions for between-population variation following a selective release.

**Figure S2** Eigenvalues for successive Principal Components for body size.

**Figure S3** Representative example spectra of the dorsal area of a lizard.

**Figure S4** Eigenvalues for successive Principal Components for coloration.

**Figure S5** Histograms of size distributions for main island lizards.

**Figure S6** Visual representation for the Principal Components for coloration.

**Table S1** Predators present at the different localities.

**Table S2** Full population names, geographical information and predators present for all study populations.

**Table S3** Sample sizes per population and sex for FIDs, body sizes and colour analyses.

**Table S4** Factor loadings from morphological characters on Principal Components for body size.

**Table S5** Eigenvalues for successive Principal Components for body size.

**Table S6** Eigenvalues for successive Principal Components for coloration.

**Table S7** Pairwise population differences for FID, size and colour.

**Table S8** Pairwise squared Mahalanobis distances illustrating multivariate differences in dorsal coloration between population pairs.

**Table S9** Pairwise significances for differences in dorsal coloration based on multivariate Mahalanobis distances.

**Table S10** Classification matrix based on colour similarity.

**Table S11**  $F_{ST} - P_{ST}$  correlations for the entire range of  $c/h^2$  ratios.

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