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Proximate and ultimate drivers of variation in bite force in the insular lizards *Podarcis melisellensis* and *Podarcis sicula*

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Bite force is a key performance trait in lizards because biting is involved in many ecologically relevant tasks, including foraging, fighting and mating. Several factors have been suggested to impact bite force in lizards, such as head morphology (proximate factors), or diet, intraspecific competition and habitat characteristics (ultimate factors). However, these have been generally investigated separately and mostly at the interspecific level. Here we tested which factors drive variation in bite force at the population level and to what extent. Our study includes 20 populations of two closely related lacertid species, *Podarcis melisellensis* and *Podarcis sicula*, which inhabit islands in the Adriatic. We found that lizards with more forceful bites have relatively wider and taller heads, and consume more hard prey and plant material. Island isolation correlates with bite force, probably by driving resource availability. Bite force is only poorly explained by proxies of intraspecific competition. The linear distance from a large island and the proportion of difficult-to-reduce food items consumed are the ultimate factors that explain most of the variation in bite force. Our findings suggest that the way in which morphological variation affects bite force is species-specific, probably reflecting the different selective pressures operating on the two species.

ADDITIONAL KEYWORDS: bite force – head dimensions – intraspecific competition – island area – island isolation – lizard – *Podarcis melisellensis* – *Podarcis sicula* – resource use.

INTRODUCTION

Whole-organism performance has been defined as a measure of the ability of an animal to execute an ecologically relevant task (Huey & Stevenson, 1979; Arnold, 1983; Lailvaux & Irschick, 2006). Because whole-organism performance traits may increase survival or fitness (Wainright, 1991; Le Galliard *et al.*, 2004; Miles, 2004; Lailvaux & Irschick, 2006; Calsbeek & Irschick, 2007), it is generally considered that natural selection acts upon performance rather than on the underlying morphological or physiological traits (Irschick *et al.*, 2008). This view is supported by the concept of many-to-one mapping of form to function, which suggests that morphology and performance can sometimes be decoupled, with many morphologies giving rise to the same functional output (Wainwright *et al.*, 2005). Studying the performance of an animal in an ecological context thus contributes to a better understanding of evolutionary processes and helps to explain how variation in morphology arises in different ecological contexts (Arnold, 1983; Kingsolver & Schemske, 1991; Brodie *et al.*, 1995; Kingsolver & Pfenning, 2007).

Numerous studies have considered bite force to be a key performance trait because biting is involved in many essential tasks in vertebrates including feeding, mating (Leboeuf, 1972; Herrel *et al.*, 1996),

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*Corresponding author. E-mail: maxime.taverne@mnhn.fr inter- (Snekser *et al.*, 2008) and intraspecific competition (Blanchard *et al.*, 2001), food manipulation (Jones & Kamil, 1973; Reghem *et al.*, 2011), communication (Derryberry *et al.*, 2012), parental care (Balshine-Earn & Earn, 1998), predator defence, and even locomotion (Williams & Bunkley-Williams, 2006). Variation in bite force has been extensively studied as the acquisition of bite force data is relatively straightforward in small vertebrates and the measures are highly repeatable (Herrel *et al.*, 2005; Anderson *et al.*, 2008; Lappin & Jones, 2014). Biting is essential in resource acquisition and food processing and it has been previously shown that a high bite force is advantageous, rendering digestion more efficient by increasing the surface area available to digestive juices or microorganisms (e.g. in turtles: Bjorndal *et al.*, 1990; Bjorndal & Bolten, 1992). A direct association between the ability to deal with tougher food items and an increase in bite force has also been suggested for lizards (Verwaijen *et al.*, 2002; Herrel *et al.*, 2004a, b; Herrel & Holanova, 2008; Jones & Lappin, 2009), turtles (Herrel *et al.*, 2002) and mammals (Aguirre *et al.*, 2003; Fabre *et al.*, 2017). Moreover, studies have established that the inclusion of plant material in the diet is often associated with higher bite forces, especially in lizards (Herrel *et al.*, 1998a, b, 2004a, 2008; Herrel, 2007; Sagonas *et al.*, 2014).

In lizards, biting is also important in the context of several other fitness-relevant tasks. First, male lizards often display territorial behaviours when defending resources and sexual partners (Irschick, *et al.*, 2007), which may lead to male–male combat (Stamps, 1977). Bite force is a good predictor of the outcome of these interactions, with males that bite more forcefully typically winning fights (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006, 2009; Lailvaux & Irschick, 2007). Second, biting may allow males to immobilize females during mating by firmly gripping their necks or abdomens (Noble & Bradley, 1933; Herrel *et al.*, 1996). Higher bite forces may thus increase the reproductive success of males (Lappin & Husak, 2005; Herrel *et al.*, 2010). However, in some species females avoid males with the greatest bite forces, possibly to avoid injury (Huyghe *et al.*, 2012).

The drivers of variation in bite force in lizards are relatively well understood, at least at the proximate level. Indeed, numerous studies have established the morphological and anatomical basis for the variation in bite force. Lizards with taller and wider heads typically bite harder (Herrel *et al.*, 2001a, 2010; Verwaijen *et al.*, 2002; Lappin *et al.*, 2006; Huyghe *et al.*, 2009; Wittorski *et al.*, 2016). The morphological variation associated with variation in bite force has been often linked to an increase in space available for jaw muscles (Herrel *et al.*, 2007), the size and architecture of the jaw muscles (Huygue *et al.*, 2009), or the optimization of lever arms (Herrel *et al.*, 2001a). Although these previous studies have contributed to unravelling the drivers of variation in bite force, they have typically focused on interspecific studies (Herrel *et al.*, 2001b; Vanhooydonck *et al.*, 2010; Kaliontzopoulou *et al.*, 2012), ontogenetic variation (Herrel *et al.*, 2006), or variation between males and females within a species (Brecko *et al.*, 2008; Sagonas *et al.*, 2014; Lopez-Darias *et al.*, 2015). However, analyses dealing with variation across populations of the same species are relatively rare (but see Bonneaud *et al.*, 2016; Donihue *et al.*, 2016). Yet, population-level studies are especially insightful in helping understand the drivers of variation in performance given that they are not confounded by phylogenetic effects.

The present study aims to explore and quantify the drivers of variation in bite force across 18 insular and two continental populations of two *Podarcis* species (eight populations of *Podarcis sicula* Rafinesque-Schmaltz, 1810, and 12 of *Podarcis melisellensis* Braun, 1877). Taverne *et al.* (2019) have demonstrated that these populations differ in diet, ranging from an almost strictly insectivorous to a largely omnivorous diet. Moreover, the islands that these lizards inhabit are located in the southern Adriatic, off the coast of Croatia, and differ in size, habitat structure and substrate. Indeed, the islands range from very small rocky islets to bigger islands with greater and more complex vegetation cover and topography. The island structure may affect the type and the intensity of social interactions and intraspecific competition within each population (Svanbäck & Bolnick, 2007; Thomas *et al.*, 2009; Donihue *et al.*, 2016). The formation of these land bridge islands (Marjanac & Marjanac, 2004; Sikora *et al.*, 2014) as well as the time of isolation and genetic divergence have been partially resolved in the literature (Gorman *et al.*, 1975; Podnar *et al.*, 2004; Podnar *et al.*, 2005), allowing us to explore the historical factors that drive variation in morphology and performance in lizards across these islands.

First, we explored the impact of proximate factors such as head shape and size on variation in bite force. Second, we explored the relationships between the functional properties of the food items ingested by the lizards (data from Taverne *et al.*, 2019), food niche breadth and bite force. Intraspecific competition between males is common, and as a result males often display higher performance levels associated with a sexual dimorphism in head size and shape (Herrel *et al.*, 1996; Verwaijen *et al.*, 2002). Here, we calculated the degree of sexual dimorphism in head dimensions and use it as a proxy for the intensity of sexual selection (Vanhooydonck *et al.*, 2009, 2010) and tested its role as a driver of variation in bite force. Additionally, we tested whether two proxies for intraspecific competition (i.e. the number of regenerated tails and the number of missing toes; see Vervust *et al.*, 2009) impacted bite force. As insular populations typically experience an increase in the level of intraspecific competition compared to their mainland counterparts (Pafilis *et al.*, 2009) this may be an important driver of variation in bite force (Donihue *et al.*, 2016). Finally, island size and isolation have been shown to significantly impact the diversity and abundance of prey and vegetation (Itescu *et al.*, 2020), thus impacting the resources available and population densities (Polis & Hurd, 1996). As such, island size and isolation may also be drivers of variation in bite force. By comparing two closely related species living on geographically close islands of similar size and structure, we further aim to explore whether the drivers of variation in bite force are similar in different species under similar contexts, or whether species-specific patterns are observed.

We predict (1) that snout–vent length as well as head size and dimensions should be good predictors of bite force, (2) that the degree of sexual dimorphism should be correlated with increased bite force in males, (3) that bite force should be correlated with food niche breadth, (4) that island size and remoteness should be respectively negatively and positively correlated with bite force, and (5) that variation in bite force between populations should not be related to the phylogenetic relationships between populations.

MATERIALS AND METHODS

SPECIMENS

Twenty populations of *Podarcis* lizards were sampled: eight populations of the Italian wall lizard *Podarcis sicula* and 12 populations of the Dalmatian wall lizard *Podarcis melisellensis*, including one mainland site for each (Fig. 1). These populations are located in the Adriatic, off the coast of Croatia. In total, 535 adult animals (between 15 and 42 individuals per population) were captured by noose or by hand during the late summer of 2016 (Table 1), with permission from the Croatian Ministry of the Environment (permit no. 517-07-1-1-1-16-6). We measured all individuals using digital calipers (Mitutoyo absolute digimatic; ±0.01 mm; see Supporting Information, Fig. S1) and recorded snout–vent length (SVL) and linear head dimensions including head length (HL), head width (HW), head height (HH), lower jaw length (LJL), quadrate to jaw tip length (QT) and coronoid to jaw tip length (CT).

Two other functionally relevant variables were calculated: the in-lever for jaw opening (open = LJL – QT) and the in-lever for jaw closing (close = QT – CT).

IN VIVO BITE FORCE MEASUREMENTS

In vivo bite force was measured using an isometric Kistler force transducer (type 9203) connected to

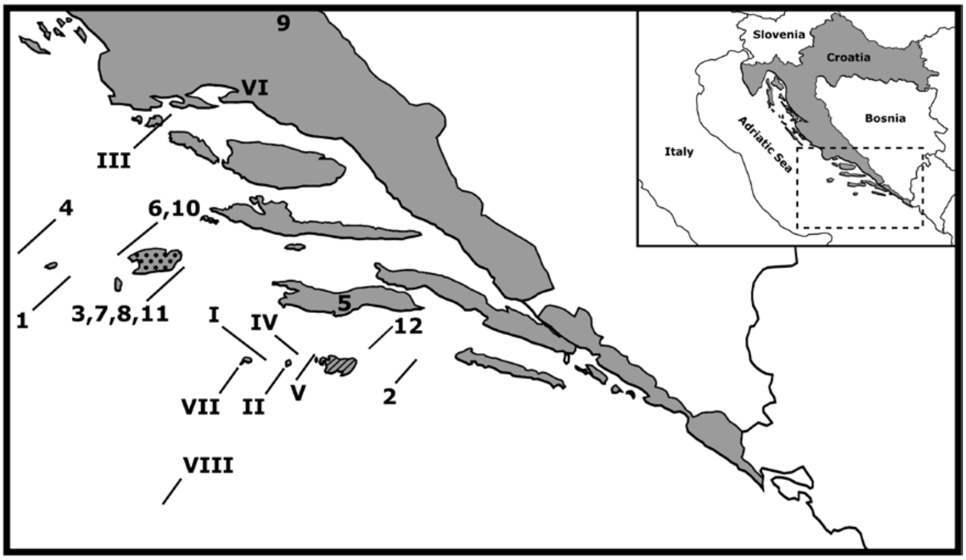

Figure 1. Location of the populations of *Podarcis sicula* (I: Bijelac, II: Kopište, III: Pijavica, IV: Pod Kopište, V: Pod Mrčaru, VI: Split, VII: Sušac, VIII: Mala Palagruža) and *Podarcis melisellensis* (1: Brusnik, 2: Glavat, 3: Greben, 4: Jabuka, 5: Korčula, 6: Mali Barjak, 7: Mali Paržanj, 8: Ravnik, 9: Sinj, 10: Veli Barjak, 11: Veli Budikovac, 12: Veli Tajan) included in the present study. Lines point to the locations of the islands that are too small to be represented on the map. The large islands Lastovo and Vis are respectively hatched and dotted.

Table 1. Origin of specimens and island characteristics

Species	Site	Symbol	Date	Number of females	Number of males	Area (m^2)	Distance from large island (m)	Distance from mainland (m)
Podarcis melisellensis	Brusnik	BR	08.27.2016	22	20	49 455	20 949	55 695
	Glavat	GL	09.09.2016	9	12	18 430	16 491	23 071
	Greben	GR	08.31.2016	12	18	51 690	1004	48 768
	Jabuka	J	08.28.2016	21	17	22 585	48 002	62 875
	Korčula	KR	10.08.2016	7	11	2.79×10^8	–	1367
	Mali Barjak	BM	08.26.2016	14	18	6232	725	46 643
	Mali Paržanj	PZ	09.01.2016	13	12	13 403	838	49 969
	Ravnik	RV	09.03.2016	6	11	226 605	489	51 456
	Sinj*	SI	09.12.2016	5	11	–	–	–
	Veli Barjak	BU	08.30.2016	19	21	18 116	255	46 679
	Veli Budikovac	BD	09.02.2016	17	17	316 748	748	50 844
	Veli Tajan	T	09.08.2016	7	8	20 127	6862	19 649
Podarcis sicula	Bijelac	BI	09.08.2016	7	13	5530	10 233	38 550
	Kopište	KO	09.06.2016	14	19	738 726	6544	36 747
	Mala Palagruža	PG	09.10.2016	8	12	26 510	60 280	91 549
	Pijavica	PI	09.14.2016	13	12	11 037	1799	1799
	Pod Kopište	K	09.06.2016	15	22	35 835	7340	36 152
	Pod Mrčaru	M	09.05.2016	12	24	13 514	2630	31 933
	Split*	ST	09.12.2016	9	7	–	–	–
	Sušac	SU	09.04.2016	15	5	4 025 460	23 013	48 958

*Mainland populations.

a Kistler charge amplifier (type 5995, Kistler Inc., Winterthur, Switzerland; see Herrel *et al.*, 1999a for a detailed description of the set-up). Lizards were made to bite the plates of the transducer (left bare), at least five times, and the greatest bite force across the five trials was retained as an estimate of an individual's maximum bite force. Gape angle was standardized across trials by adjusting the distance between the bite plates for each individual to maintain gape angle constant at around 30°. Bite position was standardized by ensuring that the tips of the jaws of each lizard were up against the metal stop mounted on the device. Bite force was $\log_{10}$-transformed before statistical analyses.

ISLAND CHARACTERISTICS

The values of the island area were taken from Duplančić *et al.* (2004). The shortest linear distance from the continent and the shortest linear distance from the nearest large island (here, either Lastovo or Vis) were calculated using Google Maps and ImageJ (Fig. 1; Table 1).

STOMACH CONTENT ANALYSIS

All individuals were stomach flushed immediately after capture using a syringe with a ball-tipped steel needle (Herrel *et al.*, 2006; Measey *et al.*, 2011) and stomach contents were analysed as described by Taverne *et al.* (2019). The lizards' diet consisted mostly of arthropods, arachnids, myriapods, gastropods and plant material (leaves, seeds, fruits and flowers) in various proportions. Diet across populations ranged from strictly insectivorous (e.g. Mali Barjak) to omnivorous, as some populations included a significant part of plant matter in their diet (e.g. Sušac, Pod Mrčaru). The maximum and minimum length, maximum and minimum width, and maximum volume of the food items in each stomach were recorded. The volume of a prey item was calculated following a spheroid equation [ellipsoid volume = $(4/3)\ \pi\ (L/2)\ (W/2)^2$, with L the length of the item and W its width]. Every prey taxon was then attributed to a functional group based on prey hardness and evasiveness as proposed by Vanhooydonck *et al.* (2007). The relative contribution of each of the six functional groups (soft prey, prey of medium hardness, hard prey, sedentary prey, prey of intermediate evasiveness and evasive prey) and of plant material to the total mass of the stomach contents was then calculated. The hardness of each food item was further estimated using the following regression equations proposed by Herrel & O'Reilly (2006) that relate prey length and hardness, according to the item hardness category:

$$(soft)\quad \log_{10}[prey\quad hardness\quad (N)] = 0.997\quad \times \log_{10}[prey\quad length\quad (mm)] - 1.379$$

$$(\mathrm{medium})\quad \log_{10}[prey\quad hardness\quad (N)] = 1.780 \times \log_{10}[prey\quad length\quad (mm)] - 1.942$$

$$(\mathrm{hard})\quad \log_{10}[prey\quad hardness\quad (N)] = 1.582\quad \times \log_{10}[prey\quad length\quad (mm)] - 1.365$$

The maximal and mean hardness of the prey items in each stomach were retained for further analyses.

A diet disparity metric was calculated for each sex of each population (see Taverne *et al.*, 2019). To do so the hyper-volume occupied by each of these subsets in the ecospace was estimated using the 'disparity.per.group' function from the 'dispRity' package (Guillerme, 2018). Finally, an estimate of the taxonomic diversity of prey found in the stomachs, Shannon's diversity index, was calculated for each individual following the equation:

$$H = -\sum_{i=1}^{S} \frac{n_i}{N} \log(\frac{n_i}{N})$$

where S is the total number of prey taxa found in a stomach, n_i the total number of prey items of taxon i and N the total number of items found in a stomach.

PHYLOGENETIC ANALYSIS

For phylogenetic analysis, mitochondrial cytochrome-*b* sequences were obtained from GenBank (accession numbers in Supporting Information, Table S1) for 14 out of the 20 populations used in this study (Table 1). DNA samples for three additional *P. sicula* populations (Bijelac, Kopište and Pod Mrčaru) and three *P. melisellensis* populations (Sinj, Veli Barjak and Veli Tajan) were collected during sampling in summer 2016. A piece of lizard tail tissue was taken from two individuals per population and preserved in 96% ethanol. DNA was extracted from ~15 mg of lizard tail tissue using a commercial DNA extraction kit and the provided protocol (Sigma-Aldrich GenElute Mammalian Genomic DNA Miniprep Kit). The quality and quantity of the extracted DNA were examined by agarose gel electrophoresis and spectrophotometric measurement on a Nanodrop device (Thermo Scientific 2000c).

Optimized protocols from Podnar *et al.* (2004, 2005) were used to obtain mitochondrial cytochrome-*b* sequences. For both *P. sicula* and *P. melisellensis* populations, 40–50 ng of extracted DNA was amplified in a 25-µL reaction containing 5× Iproof buffer, nfH20, 1.5 mM $MgCl_2$, 0.2 mM of each dNTP, 0.4 µM of each primer (Supporting Information, Table S2) and 0.5 U iProof Polymerase (Bio-Rad). PCR conditions included initial denaturation for 2 min at 98 °C, followed by 35 cycles of 10 s at 98 °C, 20 s at 50 °C and 90 s at 72 °C, and a final extension of 7 min at 72 °C.

Samples from Bijelac, Kopište and Pod Mrčaru were further reamplified to account for the presence of cytochrome-*b* nuclear pseudogene sequences (numts) in the *P. sicula* populations (Podnar *et al.*, 2005). Reamplification was performed using 1 µL of the amplification mix and included the same conditions as the amplification, apart from the primers used (Supporting Information, Table S2), reaction volume which was set to 50 µL and the PCR annealing temperature that was adjusted to 55 °C. All PCRs were performed in a Bio-Rad Gradient Thermal Cycler. Macrogen (Amsterdam, Netherlands) provided PCR product purification and bidirectional sequencing using the primers listed in Table S2.

The chromatograms from the 12 processed samples were loaded in Geneious 4.8.5 (Biomatters, Auckland, New Zealand), corrected manually, aligned and trimmed to the same length together with the sequences from the other previously published populations (Supporting Information, Table S1). The optimal nucleotide substitution model was determined with jModelTest 2.1.10 (Guindon & Gascuel, 2003; Darriba *et al.*, 2012). Likelihood scores were computed using the 'best' base tree topology search method (from both 'Nearest Neighbour Interchange' and 'Subtree Pruning and Regrafting'). MEGA-X 10.0.5 (Kumar *et al.*, 2018) was used to calculate nucleotide composition, nucleotide pair frequencies, and transition and transversion rates (R ratio) according to the chosen nucleotide substitution model. A cytochrome-*b* sequence of *Lacerta bilineata* from Krbavica (Croatia) was added as an outgroup before analysis (Table S1).

Phylogenetic trees were generated using three methods: maximum parsimony (MP) and maximum likelihood (ML) both implemented in PAUP 4.0a (Swofford & Sullivan, 2003), and a Bayesian inference analysis implemented in MrBayes 3.2.7a (Ronquist *et al.*, 2012). All analyses were performed after setting the calculated nucleotide substitution model and R ratio. MP and ML analyses were performed with a full heuristic search and allowing tree-bisection-reconnection (TBR) branch-swapping. MP starting trees were obtained via stepwise addition with ten replicates of each random addition sequence, and bootstrap replicates were set to 1000 for MP trees. ML starting trees were obtained by neighbour-joining (NJ), and bootstrap replicates were set to 100. Because the computational power and time required for ML is greater, the number of rearrangements was limited to 8×10^6, and time per replicate was limited to 2000 min. For the Bayesian inferred trees 6×10^6 generations were run, sampled every 100 (60 000 trees) and the first 6000 trees were discarded (burn).

The MP tree was preferred when correcting for the non-independence of the data in subsequent statistical analyses because this method maximizes the resolution of the relationships between *P. sicula* populations (Fig. 2). The trees which were generated by the other two methods are provided in Supporting Information, Table S2. The influence of phylogenetic heritage on the variation in bite force and every head dimension was investigated through calculation of Pagel's lambda (Pagel, 1999), using the 'phylosig' function from the 'phytools' package. This measure of phylogenetic signal was calculated on both raw and residual head dimensions.

PROXIES FOR INTRASPECIFIC COMPETITION

For both species separately, a principal component analysis (PCA) was run on head dimensions using the function 'prcomp' from the 'stats' package, allowing a reduction of dimensionality. The contribution of each specimen along the three first principal components (PCs) was extracted and used to calculate the mean contribution of each sex of each population on these axes. The sexual dimorphism in head dimensions (*SD*) for each site was determined as follows:

$$SD = \sqrt{(m_1 - f_1)^2 + (m_2 - f_2)^2 + (m_3 - f_3)^2}$$

where m_i and f_i refer respectively to the mean contribution of the males and females of the population of interest along with PC$_i$.

Two other proxies for intraspecific competition were estimated: the proportion of individuals missing the longest toe on one of the hind feet (Vervust *et al.*, 2009) and the proportion of individuals with a regenerated tail (Brock *et al.*, 2014).

STATISTICAL ANALYSES

All analyses were performed in R (v.3.5.1, R Core Team, 2018). To ensure normality, the proportion data, values of which were between 0 and 1, were arcsin-transformed. For the same reason, prey dimensions, head dimensions, hardness, disparity, distance variables and island area were log$_{10}$-transformed. A Shapiro test and Bartlett's tests ('shapiro.test' and 'bartlett.test' functions from the 'stats' package) were used to test the normality and the homogeneity of residuals in each sub-dataset.

A two-way univariate analysis of covariance (ANCOVA) with SVL as the co-variable was carried out on the data for both species separately to test for a possible effect and interaction of sex and island on bite force. Similarly, a two-way multiple analysis of covariance (MANCOVA) with SVL as the co-variable

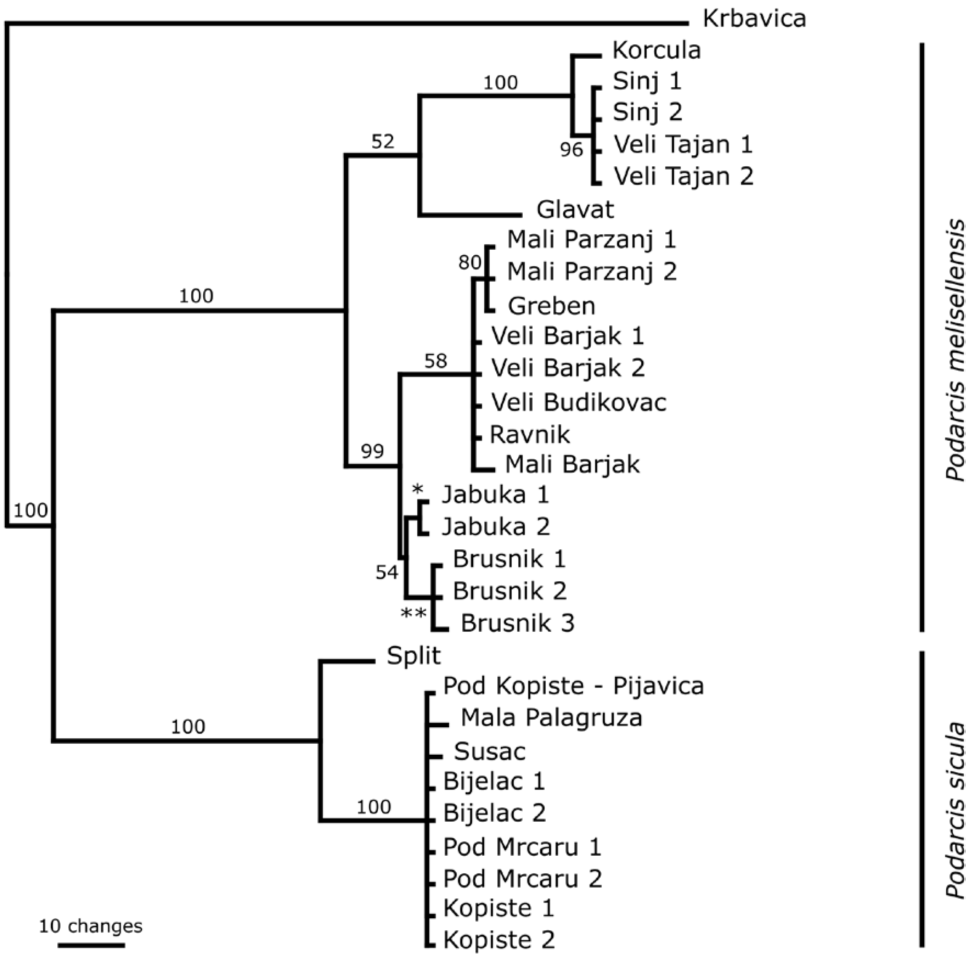

Figure 2. Phylogenetic relationships among the populations sampled in our study with one outgroup, generated using maximum parsimony (MP). Branch lengths are proportional to the number of changes in the DNA sequences. Bootstrap values for topology support are indicated and rounded (*96; **79). For precise values, see Figure S2a.

was performed to detect a possible effect of sex and island on head dimensions. Phylogenetic univariate analyses of variance, using Holm–Bonferroni's correction for multiple comparisons, were carried out to test for an effect of sex and species on residual bite force and head dimensions (obtained subsequent to phylogenetic linear regressions using the function 'phylolm' from the 'phylolm' package), by using the function 'phylANOVA' from the package 'phytools'.

Next, we explored associations between bite force and variables such as disparity, prey hardness or proxies for intraspecific competition through linear regressions (function 'lm' in the package 'stats'). Three different stepwise regressions (function 'stepAIC' in the package 'MASS') computed on prey dimensions, mass proportions or head dimensions enabled us to detect possible associations between bite force and these data. The best model was selected based on the minimal AIC value, and variables in the model were selected using both forward and backward procedures. A phylogenetic multiple regression was carried out to estimate the relationship between bite force and head dimensions when considering phylogeny (function 'phylostep' in the package 'phylolm'). Because a Shapiro test revealed diversity to be non-normally distributed, a Spearman-rank correlation test was used to detect a possible relationship between bite force and prey diversity. For this analysis the Shannon index of diversity was averaged by population to avoid *ex aequo* rankings in the Spearman test. Mean values of absolute and residual (against head length) bite force were also tested against island size, distance from the mainland and distance from the nearest large island using linear regressions. Other stepwise regressions were performed to test for a relationship between isolation metrics and the proportions and dimensions of food items. Additionally, a simple regression between isolation metrics and prey mean hardness was carried out. Finally, the ecological variables that were demonstrated to drive variation in bite force in these statistical analyses were combined in a final stepwise regression to compare the contribution of each relevant parameter to bite force. Standardized estimates of the stepwise regressions were given with the function 'summ' from 'jtools' to compare the relative contribution of each variable to the final model. Each of these statistical analyses includes all populations, except when excluding mainland populations was necessary (e.g. when testing the island area effect).

RESULTS

When considering the whole dataset, bite force appears to be influenced by phylogeny (Table 2). When considering sexes separately, phylogenetic relationships affected bite force, and raw and residual head dimensions in females only. At the intraspecific level, phylogeny influenced raw head dimensions (but not residuals) in females of *P. melisellensis* only. No signal was detected in raw or in residual data in males of *P. melisellensis*. The phylogenetic signal was not calculated for *P. sicula* separately due to the very weak differentiation among populations.

The two-way univariate ANCOVA revealed that in *P. sicula*, bite force was influenced by SVL ($P < 0.001$), sex ($P < 0.001$) and island identity ($P < 0.001$) but there was no interaction between sex and island ($P = 0.249$). This was also the case in *P. melisellensis*, but the interaction between sex and island identity was just significant ($P = 0.048$). The two-way multivariate ANCOVA indicated that head dimensions also differed between sexes and islands in both species. An interaction between sex and island was observed for *P. melisellensis* only ($P = 0.004$). The phylogenetic ANOVAs showed that when accounting for phylogeny, bite force and head dimensions differed between sexes but not between species. (Supporting Information, Table S3).

MORPHOLOGICAL TRAITS UNDERLYING VARIATION IN BITE FORCE

Bite force was highly correlated with body size (SVL) for each sex and species ($P < 0.001$). The stepwise regressions between bite force and residual head dimensions further showed that head shape also predicted bite force in each species and each sex. In male *P. sicula* ($P = 0.002$, $R^2 = 0.087$, $F_{1,112} = 350.1$), head height and lower jaw length were correlated with bite force (β coefficients: 1.13, −0.69). In female *P. sicula* ($P < 0.001$, $R^2 = 0.187$, $F_{2,90} = 11.59$), the in-lever for jaw-opening and the lower jaw length were correlated with bite force (β coefficients: −0.19, 1.26). In males of *P. melisellensis* ($P < 0.001$, $R^2 = 0.211$, $F_{3,172} = 16.56$), head height, head width and lower jaw length were related to bite force (β coefficients: 1.29, 1.27, −2.17). In female *P. melisellensis* ($P < 0.001$, $R^2 = 0.280$, $F_{3,148} = 20.57$), head height, head width and quadrate-to-tip length were correlated with bite force (β coefficients: 1.84, 0.91, −1.98). The two latter results still held when correcting for the phylogenetic relationships among populations of *P. melisellensis* (Supporting Information, Table S4).

INTRASPECIFIC COMPETITION

The three first axes of a PCA used to calculate sexual shape dimorphism jointly explained over 90% of the variance. In females, bite force did not correlate with the degree of sexual dimorphism in head dimensions, used here as a proxy for intraspecific competition and aggression (*P. melisellensis*: $P = 0.121$, *P. sicula*: $P = 0.985$). In males, bite force increased with the degree of sexual dimorphism in *P. sicula* ($P = 0.030$, $R^2 = 0.498$, slope = 0.423; Fig. 3), but not in *P. melisellensis* ($P = 0.185$). Except in females of *P. melisellensis* where a correlation between the proportion of individuals with missing toes was positively associated with bite force ($P = 0.031$, $R^2 = 0.394$, slope = 0.96) the proportion of individuals with missing toes and the proportion of individuals with regenerated tails did not predict bite force (all $P > 0.05$).

RELATIONSHIPS BETWEEN BITE FORCE AND FOOD PROPERTIES

The linear regression between bite force and maximum prey hardness was significant in female *P. sicula* only ($P = 0.039$, $R^2 = 0.04$, slope = 0.079) but explained little of the total variance (Fig. 4; Table 3). Bite force was also positively associated with mean prey hardness in female *P. sicula* ($P = 0.014$, $R^2 = 0.053$, slope = 0.149), female *P. melisellensis* ($P = 0.034$, $R^2 = 0.025$, slope = 0.161) and male *P. melisellensis* ($P = 0.026$, $R^2 = 0.024$, slope = 0.180). A stepwise regression on food item dimensions revealed that an increase in bite force in female *P. sicula* was associated with greater minimum prey width ($P = 0.019$, $R^2 = 0.048$, $F_{1,91} = 5.665$), and that greater bite force was associated with greater maximum prey length in female *P. melisellensis* ($P = 0.006$, $R^2 = 0.052$, $F_{2,149} = 5.216$). Stepwise regressions on the proportion of different food items in the diet also provided statistically significant models in *P. sicula* (males: $P = 0.010$, $R^2 = 0.080$, $F_{4,109} = 3.481$; females: $P = 0.021$, $R^2 = 0.081$, $F_{4,88} = 3.040$). In males, bite force was explained by the proportion of plant matter, the proportion of hard prey and the proportion of prey of intermediate evasiveness consumed (β coefficients: 0.05, 0.13 and −0.15). Similarly, in females an increase in bite force was associated with an increase in the proportion of plant

Table 2. Summary of the Pagel's lambda (λ)

			SVL	Bite force	HL	HW	HH	LJL	QT	CT
Raw data	All data	λ	0.554	0.556	0.732	0.486	0.244	0.828	0.784	0.766
		P	0.078	0.001*	0.004*	0.019*	0.189	0.003*	0.003*	0.004*
	All females	λ	0.930	0.822	0.944	0.915	0.955	0.950	0.948	0.942
		P	0.008*	0.001*	<0.001*	<0.001*	0.003*	<0.001*	<0.001*	<0.001*
	All males	λ	0.275	0.244	0.567	0.173	<0.001	0.670	0.637	0.608
		P	0.592	0.160	0.171	0.509	1	0.128	0.131	0.178
	Female *P. melisellensis*	λ	0.991	<0.001	0.976	0.980	<0.001	0.970	0.972	0.959
		P	0.016*	1	0.020*	0.081	1	0.018*	0.020*	0.026*
	Male *P. melisellensis*	λ	0.122	<0.001	0.300	<0.001	<0.001	0.389	0.376	0.337
		P	0.791	1	0.485	1	1	0.432	0.424	0.418
Residual data	All data	λ	–	–	0.310	0.671	0.896	0.203	0.299	0.258
		P	–	–	0.075	0.009*	0.049*	0.211	0.082	0.166
	All females	λ	–	–	0.523	0.912	0.891	0.388	0.502	0.369
		P	–	–	0.010*	<0.001*	0.005*	0.041*	0.017*	0.044*
	All males	λ	–	–	0.014	<0.001	<0.001	<0.001	0.025	<0.001
		P	–	–	0.921	1	1	1	0.866	1
	Female *P. melisellensis*	λ	–	–	<0.001	0.831	0.634	<0.001	<0.001	<0.001
		P	–	–	1	0.340	0.105	1	1	1
	Male *P. melisellensis*	λ	–	–	<0.001	<0.001	0.420	<0.001	<0.001	<0.001
		P	–	–	1	1	0.317	1	1	1

Asterisks indicate significant results ($P < 0.05$). SVL: snout–vent length, hl: head length, hw: head width, hh: head height, ljl: law-jaw length, qt: quadrate-to-tip length, ct: coronoid-to-tip length.

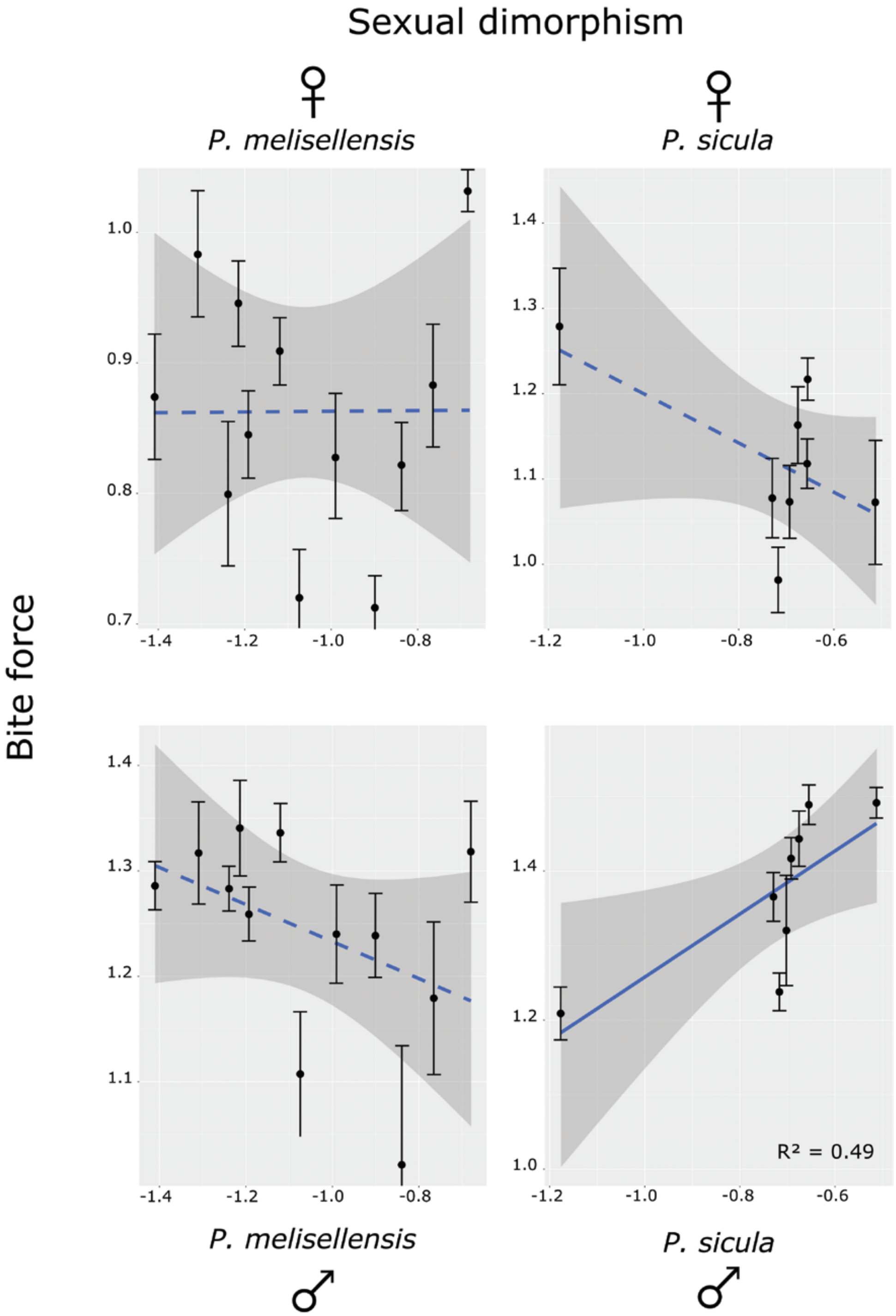

Figure 3. Linear regressions between bite force and sexual dimorphism in head dimensions at the population level. Full lines represent significant correlations ($P < 0.05$). Determination regression coefficients are also indicated when appropriate. Dashed lines represent non-significant correlations.

matter, medium prey and hard prey (β coefficients: 0.16, 0.23 and 0.23). No statistically significant model was detected for regression between bite force and the proportions of different prey types in *P. melisellensis*.

No statistically significant correlation was observed between bite force and dietary diversity, nor between bite force and diet disparity (all $P > 0.05$, see Table 3).

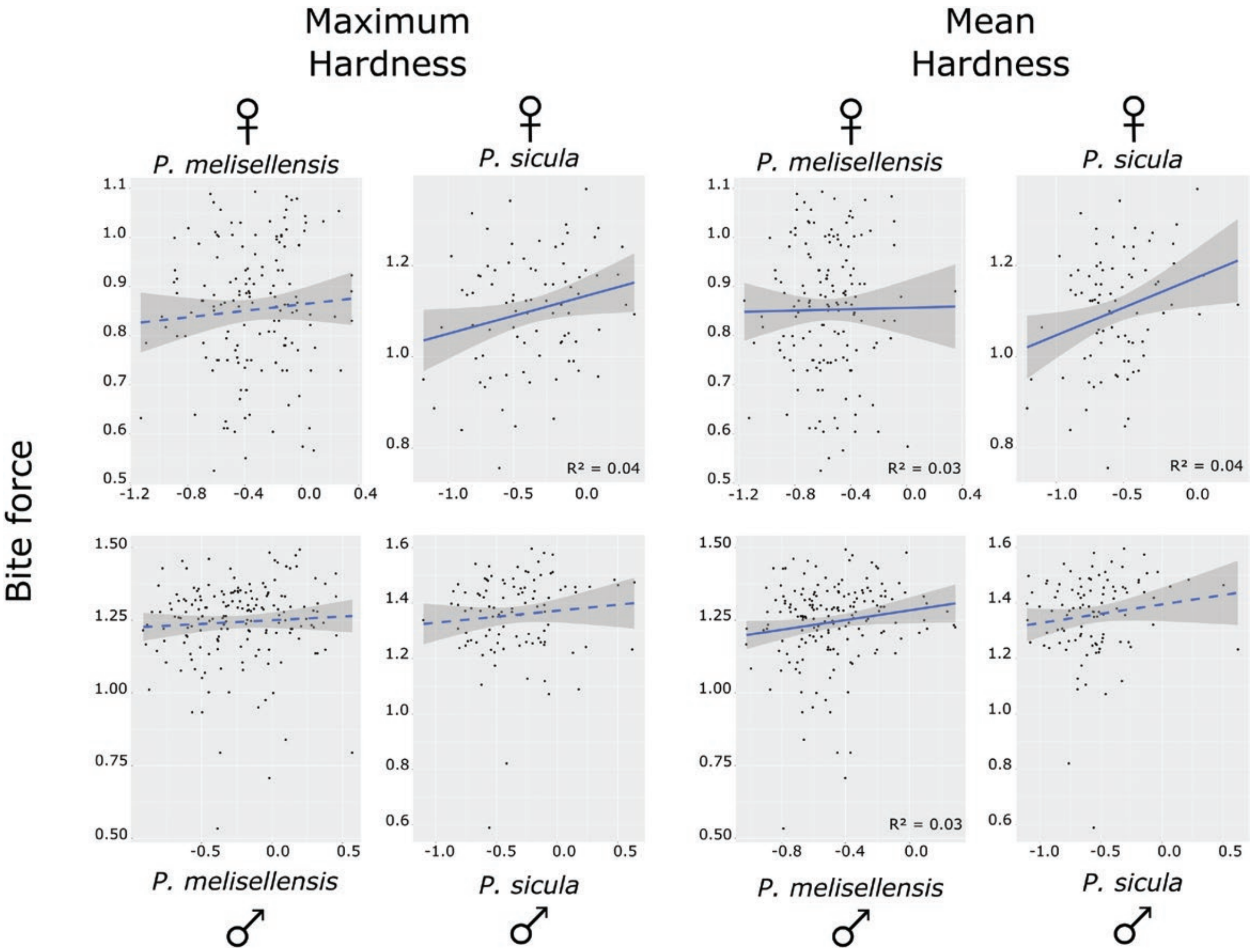

Figure 4. Linear regressions between bite force and prey hardness variables at the individual level. Full lines represent significant correlations ($P < 0.05$). Determination regression coefficients are also indicated when appropriate. Dashed lines represent non-significant correlations.

RELATIONSHIPS BETWEEN BITE FORCE, DIET AND ISLAND CHARACTERISTICS

Linear regressions showed that in *P. melisellensis* absolute bite force increased when the island was located further from the nearest large island (males: $P = 0.001$, $R^2 = 0.695$, slope = 0.077; females: $P = 0.009$, $R^2 = 0.540$, slope = 0.094) (Fig. 5; Table 3). In male *P. melisellensis* absolute bite force also increased when the island was located further from the continent ($P = 0.031$, $R^2 = 0.348$, slope = 0.135). This no longer held when considering residual bite force. Moreover, in neither species was absolute or residual bite force correlated with island area (all $P > 0.05$, see Table 3).

In female *P. sicula* only a significant model was retained for the stepwise regression between the distance from the nearest large island and prey proportions ($P = 0.01$, $R^2 = 0.99$). In *P. melisellensis* only a significant model was retained for the stepwise regression between the distance from the mainland and prey dimensions (females: $P = 0.001$, $R^2 = 0.732$; males: $P = 0.009$, $R^2 = 0.462$). Simple regressions carried out between isolation metrics and mean prey hardness revealed marginally significant results in *P. sicula* (females: $P = 0.08$; males: $P = 0.06$).

MAIN DRIVERS OF THE VARIATION IN BITE FORCE

The final stepwise regressions using distance metrics, island area, proportion of plant matter, proportion of hard prey as well as mean prey hardness did not result in a statistically significant model in *P. sicula*. However, in males of *P. melisellensis*, the retained model ($P = 0.004$, $R^2 = 0.803$, $F_{3,6} = 13.29$) indicates that the proportions of plants and of hard prey, and the distance to the nearest large island drive variation in bite force (β coefficients: 0.30, −0.08, 0.08). In female *P. melisellensis*, the retained model ($P = 0.008$, $R^2 = 0.674$, $F_{2,7} = 10.3$) revealed that the proportion of

Table 3. Summary of the P-values and regression coefficients for each of the variables tested against bite force

	Simple regressions															
	Mean hardness		Maximum hardness		Diversity		Disparity		Island area		Dist. Island		Dist. Main.		Head dim.	
Bite force	P	R^2	P	R^2	P	R^2	P	R^2	P	R^2	P	R^2	P	R^2	P	R^2
Female *P. melisellensis*	**0.034**	**0.03**	0.366	–	0.852	–	0.978	–	0.66	–	**0.009**	**0.54**	0.865	–	0.985	–
Male *P. melisellensis*	**0.026**	**0.03**	0.436	–	0.142	–	0.326	–	0.166	–	**0.001**	**0.70**	**0.031**	**0.35**	0.185	–
Female *P. sicula*	**0.014**	**0.04**	**0.039**	**0.04**	0.405	–	0.156	–	0.822	–	0.333	–	0.421	–	0.121	–
Male *P. sicula*	0.097	–	0.338	–	0.293	–	0.623	–	0.854	–	0.747	–	0.351	–	**0.03**	**0.50**

	Stepwise regressions					
	Head shape		Prey dim.		Prey prop.	
Bite force	P	R^2	P	R^2	P	R^2
Female *P. melisellensis*	**0.001**	**0.28**	**0.006**	**0.05**	0.899	–
Male *P. melisellensis*	**0.001**	**0.21**	0.126	–	0.103	–
Female *P. sicula*	**0.001**	**0.19**	**0.019**	**0.05**	**0.021**	**0.08**
Male *P. sicula*	**0.002**	**0.09**	0.147	–	**0.01**	**0.08**

Significant values ($P < 0.05$) are in bold type.

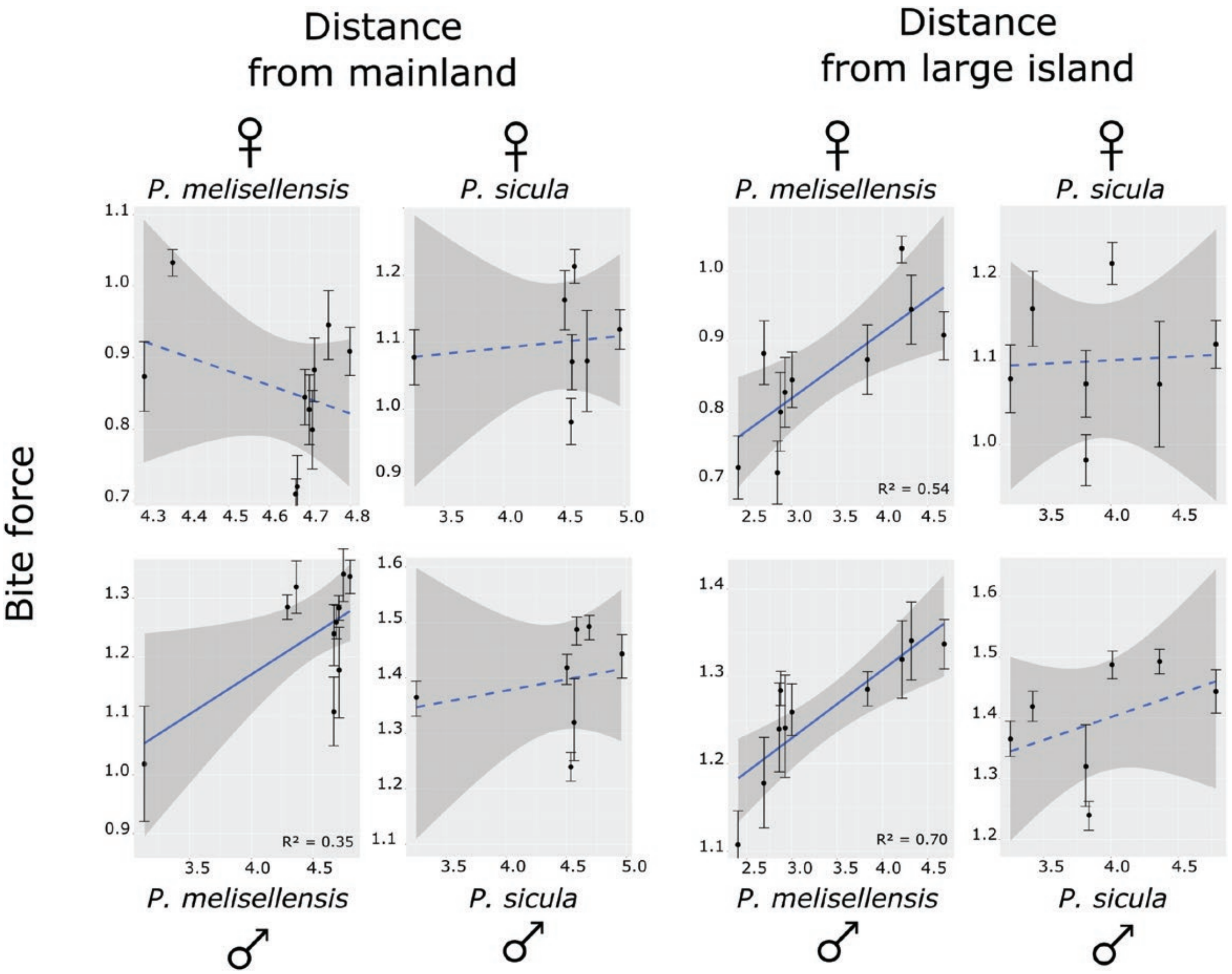

Figure 5. Linear regressions between bite force and island isolation metrics. Full lines represent significant correlations ($P < 0.05$). Determination regression coefficients are also indicated when appropriate. Dashed lines represent non-significant correlations.

hard prey and the distance to a large island were the main drivers of bite force (β coefficients: 0.30, 0.12).

DISCUSSION

Variability across populations and phylogenetic influence

We first investigated the effect of sex and island on the variation in bite force across populations. In *P. sicula* the lack of an interaction between the factors (sex and island) in the two-way ANCOVA and the two-way MANCOVA suggests that variation in bite force and head dimensions differs by island, irrespective of the sex considered. Differences between males and females are further independent of the variation between islands. In *P. melisellensis* the significant interaction between these factors suggests different effects of island and sex on the variation in bite force and head dimensions, and justifies the subsequent statistical analyses performed by sex and species separately.

Next, we investigated the influence of phylogenetic relationships between populations. The consistency of the results obtained with the phylogenetic ANOVAs suggests that differences in bite force and head dimensions between males and females are little impacted by phylogeny. By contrast, differences between species are impacted by phylogeny. At the interspecific level, bite force variation across populations can be partially explained by the history of colonization of the islands given that the divergence between the two species occurs relatively deep in the tree. The impact of phylogeny on interspecific levels of performance has, for example, also been demonstrated in *Anolis* lizards (Wittorski *et al.*, 2016). However, at the intraspecific level, bite force and head dimensions seem to be largely independent from the phylogeny, suggesting that local environmental characteristics strongly constrain these traits. This statement is supported by the fact that phylogenetic multiple regression of residual head dimensions on bite force provided similar results (Supporting Information, Table S3). Because no phylogenetic structure for *P. sicula* was detected among the examined island populations we could not test for phylogenetic effects (Fig. 2).

Proximate drivers of variation in bite force

Although morphology can sometimes be decoupled from performance (Wainwright *et al.*, 2005), the literature provides strong evidence that head shape and size are good predictors of bite force in vertebrates (Van Daele *et al.*, 2008; Chazeau *et al.*, 2013; Marshall *et al.*, 2014). In squamates (Penning, 2017), and especially in lizards (Herrel *et al.*, 2001a; Herrel & Holanova, 2008), dimensions such as height and length drive much of the variation in performance. The present study confirms this and shows that variation in bite force is mostly driven by variation in head height in the two species and the two sexes. Not only may a taller head allow the insertion of larger jaw adductor muscles (Herrel *et al.*, 2007), but it might also enhance bite force by increasing the moment arms of the muscles or by increasing the vertical component of the line of action of jaw muscles (Herrel *et al.*, 2002). In males, wider heads are also associated with higher bite forces, probably by providing more space for muscles. Some studies have suggested that bite force may trade-off with speed of prey capture (Herrel *et al.*, 2002, 2009). This trade-off is also found in lizards where fast jaw closing benefits from longer jaw out-levers as well as longer in-levers for jaw opening, whereas bite force benefits from longer in-levers for jaw closing and shorter out-levers (Herrel *et al.*, 2001a, b; Vanhooydonck *et al.*, 2007). Our results illustrate this trade-off between force and speed, as the length of the in-lever for jaw opening in female *P. sicula* is negatively correlated with bite force. This may allow females to capture faster and more evasive prey compared with males, as has been previously suggested for *Anolis carolinensis* (Herrel *et al.*, 2007). Accordingly, males of both *Podarcis* species with relatively shorter lower jaws had higher bite forces as this optimizes the out-lever for biting.

The present results show that relevant head dimensions correlated with bite force, yet accounted for a relatively low amount of the total variance (from 9 to 28%). Unexpectedly, in both species head dimensions are stronger predictors of bite force in females than in males. This is possibly because head width is strongly influenced by pterygoid muscles that are proportionally larger in males (Herrel *et al.*, 1996). Wider heads are thought to be a determining factor in the outcome of male–male encounters (Molina-Borja *et al.*, 1997; Huyghe *et al.*, 2005). We suggest that head dimensions possibly are poorer predictors of bite force in males than in females because some traits such as head width are shaped by sexual selection, resulting in investment in the size of the pterygoid muscles, which conversely contribute relatively little to the bite force for its size (Herrel *et al.*, 1999a, b).

Ultimate drivers

We tested whether sexual selection (i.e. the degree of sexual dimorphism) and resource use (i.e. functional properties of food items and food niche breadth) are drivers of variation in bite force. Sexual dimorphism in head dimensions may allow for food partitioning between males and females (Schoener, 1967; Herrel *et al.*, 1999a, b) but is generally considered to be maintained through male–male competition in lizards (Vincent & Herrel, 2007; Vanhooydonck *et al.*, 2010). Dimorphism in head dimensions was previously demonstrated to be decoupled from dimorphism in diet in this study system (Taverne *et al.*, 2019), hence suggesting that niche partitioning for limited resources probably does not explain the observed head dimorphism. This makes sexual dimorphism in head dimensions a good proxy for sexual selection, however. We found that the intensity of intra-sexual competition impacted bite force in male *P. sicula*. This makes sense because individuals with greater bite forces often win male–male interactions (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005; Husak *et al.*, 2006; Lailvaux & Irschick, 2007). Additional information on other populations are needed, however, because extreme populations appear to be driving the correlation between sexual dimorphism and bite force. Moreover, other proxies for intraspecific competition including the proportion of individuals missing the longest toe on the hind feet and the proportion of individuals with regenerated tails did not explain the variation in bite force across populations in contrast to what was has been observed in other systems (Lailvaux *et al.*, 2004; Lailvaux & Irschick, 2007; Donihue *et al.*, 2016). Data on population density would be informative in better understanding the relationship between intraspecific competition and performance in this system.

A previous study revealed great diversity and disparity in the functional properties of food items eaten by insular Croatian *Podarcis* lizards (Taverne *et al.*, 2019). Whereas this was not the case for diet diversity, diet disparity was shown to be impacted by island area, possibly because competition for food and population density tend to increase on smaller islands (Case, 1995; Buckley & Jetz, 2007). Variation in bite force has further been demonstrated to be associated with competition in similar insular systems (Donihue *et al.*, 2016). For these reasons, a greater bite force can be expected to enable lizards to widen their dietary breadth, but this is not confirmed by the present study. However, our results do show that female *P. sicula* that incorporate more plant items in their diet also bite more forcefully. Plants are considered very tough and fibrous (Lucas & Luke, 1984; Hiiemae & Crompton, 1985), their reduction requiring greater bite force (Herrel *et al.*, 1998a,b). A greater bite force thus enables lizards to rely on alternative food sources when resources are scarce. Moreover, in both sexes of *P. sicula*, animals that bite harder also include a proportionally greater proportion of hard prey items in their diet. Higher bite forces would thus enable them to gain access to other, harder resources such as beetles or snails.

The bite force of all individuals typically exceeds the maximum hardness of any prey item eaten, yet mean hardness is generally correlated with bite force (with the exception of male *P. sicula*). In bats (Aguirre *et al.*, 2003) maximum food size and hardness correspond well with the maximum bite force of an individual, suggesting that functional prey properties may be important drivers of bite force in some cases. In lizards and bats the mechanisms underlying variation in bite force thus seem to differ. On the one hand, bats are endotherms that need to maintain a high metabolic rate (Pough, 1980; Nagy, 2005). To fulfil their energetic needs, they select large food items to optimize their food intake and reduce foraging costs (optimal foraging, Stephens & Krebs, 1986; see also Hawlena & Pérez-Mellado, 2009). Prey hardness increases with size and thus may become a limiting factor driving an increase in bite force. In ectothermic organisms such as lizards, maximum hardness does not appear to drive an increase in bite force. Rather, a higher level of performance allows them to eat more hard items on average (see also Verwaijen *et al.*, 2002). From an energetic point of view, processing large or tough items requires more time and costs more energy than processing soft and small items (Preest, 1994; Herrel *et al.*, 1999b, 2001a, b; Verwaijen *et al.*, 2002). During this period, lizards are exposed to predation (Hawlena & Pérez-Mellado, 2009) and competition. Reducing handling time while foraging is consequently probably important for these lizards. A greater bite force enables them to reduce the intraoral transport time (Verwaijen *et al.*, 2002) which may provide enough of an advantage to select for higher bite forces. However, the mechanical resistance of plant material was not considered here. A previous study (Herrel *et al.*, 1999b) established that the hardness of plant material was far beyond those of arthropods of comparable size, so including these quantitative data into account in future studies would be of particular interest because (1) it might reveal some direct correlation between maximum hardness and bite force in our study system, and (2) it might explain the low yet significant amount of variance in bite force explained by prey hardness (Fig. 4).

We expected island area to be correlated with variation in bite force because this is an important feature that impacts the ecology of insular ecosystems (Hamilton & Armstrong, 1965; Whittaker & Fernández-Palacios, 2006; Santos *et al.*, 2016; Itescu *et al.*, 2020). First, islands are isolated environments hosting simpler communities that often lack top-predators (Losos & De Queiroz, 1997). Ecological release then often favours higher densities of meso-predators such as lizards (Litvaitis & Villafuerte, 1996; Ritchie & Johnson, 2009). Higher rates of intraspecific competition (Pafilis *et al.*, 2009; Itescu *et al.*, 2017) for territories and resource access due to food scarcity are also observed on the smallest islands. In contrast to a previous study that demonstrated a direct relationship between island area and bite force in *Podarcis* lizards (Donihue *et al.*, 2016), our results did not show this pattern. Why this is the case remains unclear, but possibly the proximity of many of these islands to large islands or to the mainland may perturb the expected relationships.

Island isolation (linear distances of the island from the nearest large island and/or from mainland) was also predicted to be correlated with bite force because the most remote islands are thought to host the poorest species diversity (Whittaker *et al.*, 2008; Santos *et al.*, 2016). Distance from the mainland is a very common isolation metric because the mainland is assumed to be the richest source (Weigelt & Kreft, 2013), whereas the distance from the nearest large island is typically used when predicting plant species richness (Diver, 2008). We did find a positive correlation between island isolation and absolute bite force, but only in *P. melisellensis*. Stepwise regressions further suggested a direct relationship between isolation metrics and diet variables (Fig. 6). The combined results reveal that island remoteness is correlated with the functional characteristics of diet in both species (marginally significant in *P. sicula*), including prey dimensions, mean prey hardness and the proportions of different prey. Subsequently, these correlate with variation in bite force. The present results suggest that island remoteness may impact bite force by constraining the functional properties and abundance of the available resources to meso-predators such as lizards, and that lizards can access these resources by increasing bite force along with their head size.

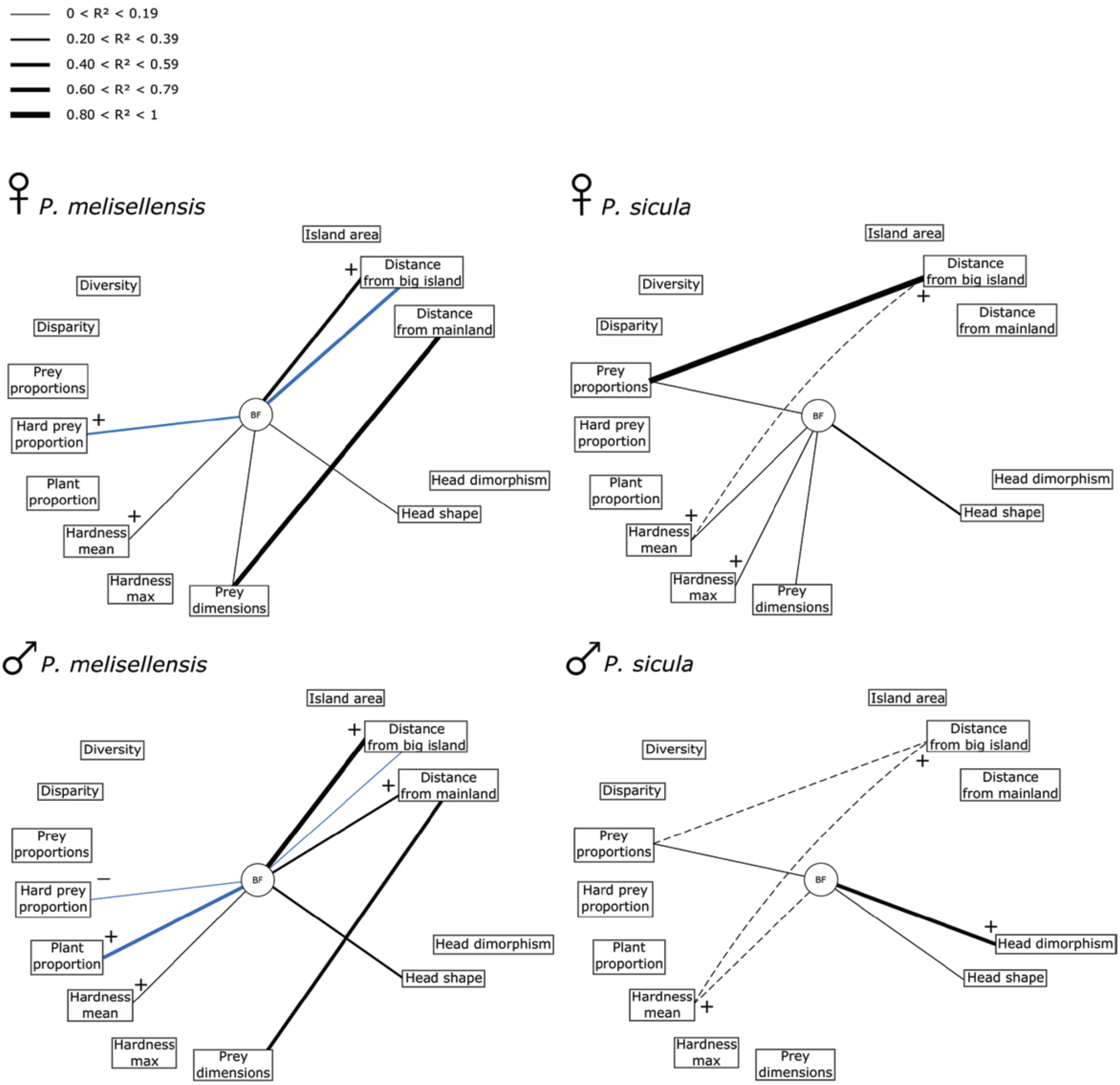

Figure 6. Summary of the significant correlations between the different factors tested and bite force (BF). Factors are grouped by diet, and morphological and habitat features. Line thickness is proportional to the determination coefficient (R^2), except for the blue lines which summarize the results of the final stepwise regression and for which line thickness is proportional to the standardized β coefficients. Dashed lines represent marginally significant correlations ($P < 0.1$). The direction of correlations found with simple regressions are indicated with plus and minus symbols.

CONCLUSIONS

Variation in bite force appears to be driven by different factors in the two species considered here. Indeed, whereas head width seems to be a fair predictor of bite force in *P. melisellensis*, it appears to be decoupled from bite force in *P. sicula*. Moreover, whereas patterns are consistent between males and females within *P. melisellensis*, this does not hold in *P. sicula*. Given that the intensity of sexual competition in this study system was shown to impact bite force in males of *P. sicula* only, we assume that strong competition between males in this species may be driving the different evolutionary response. Greater bite forces were not associated with a wider niche breadth (estimated by the prey taxonomic diversity and the dietary disparity) in either of the two species. Nevertheless, greater bite force enables the inclusion of greater amounts of difficult-to-reduce items (i.e. mean prey hardness, the proportion of hard prey or plant material) in males and females of both species, suggesting that diet is an important driver of variation in bite force. The results of the present study also show that in *P. sicula* island remoteness indirectly impacts bite force by influencing food resource availability. On the other hand, a more direct correlation between island isolation and bite force was demonstrated in *P. melisellensis*. In summary, the present study suggests that different evolutionary responses between species might originate from different levels of intrasexual competition. Future studies exploring these patterns in other island systems with other lizards are, however, needed to confirm the generality of these observations.

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REFERENCES

Aguirre LF, **Herrel A**, **Van Damme R**, **Matthysen E. 2003.** The implications of food hardness for diet in bats. *Functional Ecology* **17:** 201–212.

Anderson RA, **McBrayer L**, **Herrel A. 2008.** Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society* **93:** 709–720.

Arnold SJ. 1983. Morphology, performance and fitness. *American Journal of Zoology* **23:** 347–361.

Balshine-Earn S, **Earn DJE. 1998.** On the evolutionary pathway of parental care in mouth-brooding cichlid fish. *Proceedings of the Royal Society of London* **265:** 2217–2222.

Bjorndal KA, **Bolten AB. 1992.** Body size and digestive efficiency in a herbivorous freshwater turtle: advantages of small bite size. *Physiological Zoology* **65:** 1028–1039.

Bjorndal KA, **Bolten AB**, **Moore JE. 1990.** Digestive fermentation in herbivores: effect of food particle size. *Physiological Zoology* **63:** 710–721.

Blanchard RJ, **Ohl F**, **van Kampen M**, **Blanchard DC**, **Fuchs E. 2001.** Attack and defense in conspecific fighting in Tree Shrews *Tupaia belangeri*. *Aggressive Behavior* **27:** 139–148.

Bonneaud C, **Marnocha E**, **Herrel A**, **Vanhooydonck B**, **Irschick DJ**, **Smith TB. 2016.** Develomental plasticity affects sexual size dimorphism in an anole lizard. *Functional Ecology* **30:** 235–243.

Brecko J, **Huyghe K**, **Vanhooydonck B**, **Herrel A**, **Grbac I**, **Van Damme R. 2008.** Functional and ecological relevance of intraspeciic variation in body size and shape in the lizards *Podarcis melisellensis* Lacertidae. *Biological Journal of the Linnean Society* **94:** 251–264.

Brock KM, **Bednekoff PA**, **Pafilis P**, **Foufopoulos J. 2014.** Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): the sum of all fears? *Evolution* **69:** 216–231.

Brodie ED, **Moore AJ**, **Janzen FJ. 1995.** Visualizing and quantifying natural selection. *Trends in Ecology and Evolution* **10:** 313–318.

Buckley LB, **Jetz W. 2007.** Insularity and the determinants of lizard population density. *Ecology Letters* **10:** 481–489.

Calsbeek R, **Irschick D. 2007.** The quick and the dead: correlational selection on morphology, performance and habitat use in insular lizards. *Evolution* **61-11:** 2493–2503.

Case TJ. 1995. Species numbers, density compensation, and colonizing ability of lizards on islands in the Gulf of California. *Ecology* **56:** 3–18.

Chazeau C, **Marchal J**, **Hackert R**, **Perret M**, **Herrel A. 2013.** Proximate determinants of bite force capacity in the mouse lemur. *Journal of Zoology* **290:** 42–48.

Darriba D, **Taboada GL**, **Doallo R**, **Posada D. 2012.** jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* **9:** 772.

Derryberry EP, **Seddon N**, **Claramunt S**, **Tobias JA**, **Baker A**, **Aleixo A**, **Brumfield RT. 2012.** Correlated evolution of beak morphology and song in the neotropical woodcreeper radiation. *Evolution* **66:** 2784–2797.

Diver KC. 2008. Not as the cow flies: assessing effective isolation for island biogeographical analysis. *Journal of Biogeography* **35:** 1040–1048.

Donihue CM, **Brock KM**, **Foufopoulos J**, **Herrel A. 2016.** Feed or fight: testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. *Functional Ecology* **30:** 566–575.

Duplančić TL, **Ujević T**, **Čala M. 2004.** Coastline lengths and areas of islands in the Croatian part of the Adriatic Sea determined from the topographic maps the scale of 1:25000. *Geoadria* **9:** 5–32.

Fabre PH, **Herrel A**, **Fitriana Y**, **Meslin L**, **Hautier L. 2017.** Masticatory muscle architecture in a water-rat from Australasia (Murinae, *Hydromys*) and its implication for the evolution of carnivory in rodents. *Journal of Anatomy* **231:** 380–397.

Gorman GC, **Soulé M**, **Yang SY**, **Nevo E. 1975.** Evolutionary genetics of insular Adriatic lizards. *Evolution* **29:** 52–71.

Guillerme T. 2018. dispRity: a modular R package for measuring disparity. *Methods in Ecology and Evolution* **9:** 1755–1763.

Guindon S, **Gascuel O. 2003.** A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Systematic Biology* **52:** 696–704.

Hamilton TH, **Armstrong NE. 1965.** Environmental determination of insular variation in bird species abundance in the Gulf of Guinea. *Nature* **207:** 148–151.

Hawlena D, **Pérez-Mellado V. 2009.** Change your diet or diet: predator-induced shifts in insectivorous lizard feeding ecology. *Behavioral Ecology* **161:** 411–419.

Herrel A. 2007. Herbivory and foraging mode in lizards. In: Reilly SM, McBrayer LB, McBrayer LD, Miles ,DB eds. *Lizard Ecology*, **Vol. 7**. Cambridge, UK: Cambridge University Press, 209–236.

Herrel A, **Aerts P**, **De Vree F. 1998a.** Ecomorphology of the lizard feeding apparatus: a modelling approach. *Netherlands Journal of Zoology* **48:** 1–25.

Herrel A, **Aerts P**, **De Vree F. 1998b.** Static biting in lizards: functional morphology of the temporal ligaments. *Journal of Zoology* **244:** 135–143.

Herrel A, **De Grauw ED**, **Lemos-Espinal JA. 2001a.** Head shape and bite performance in xenosauzid lizards. *Journal of Experimental Biology* **290:** 101–107.

Herrel A, **Holanova V. 2008.** Cranial morphology and bite force in *Chamaeleolis* lizards – adaptations to molluscivory? *Zoology* **111:** 467–475.

Herrel A, **Huyghe K**, **Vanhooydonck B**, **Backeljau T**, **Breugelmans K**, **Grbac I**, **Van Damme R**, **Irschick DJ. 2008.** Rapid large-scale evolutionary divergence in morphology and performance associated with exploitation of a different dietary resource. *Proceedings of the National Academy of Sciences of the United States of America* **105:** 4792–4795.

Herrel A, **Joachim R**, **Vanhooydonck B**, **Irschick DJ. 2006.** Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal of the Linnean Society* **89:** 443–454.

Herrel A, **McBrayer LD**, **Larson PM. 2007.** Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society* **91:** 111–119.

Herrel A, **Moore JA**, **Bredeweg EM**, **Nelson NJ. 2010.** Sexual dimorphism, body size, bite force and male mating success in tuatara. *Biological Journal of the Linnean Society* **100:** 287–292.

Herrel A, **O'Reilly JC. 2006.** Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology* **79:** 31–42.

Herrel A, **O'Reilly JC**, **Richmond AM. 2002.** Evolution of bite performance in turtles. *Journal of Evolutionary Biology* **15:** 1083–1094.

Herrel A, **Podos J**, **Huber SK**, **Hendry AP. 2005.** Bite performance and morphology in a population of Darwin's finches: implications for the evolution of beak shape. *Functional Ecology* **19:** 43–48.

Herrel A, **Podos J**, **Vanhooydonck B**, **Hendry AP. 2009.** Force–velocity trade-off in Darwin's finch jaw function: a biomechanical basis for ecological speciation? *Functional Ecology* **23:** 119–125.

Herrel A, **Spithoven L**, **Van Damme R**, **De Vree F. 1999a.** Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence. *Functional Ecology* **13:** 289–297.

Herrel A, **Van Damme R**, **De Vree F. 1996.** Sexual dimorphism of head size in *Podarcis hispanica atrata*: testing the dietary divergence hypothesis by bite force analysis. *Netherlands Journal of Zoology* **46:** 253–262.

Herrel A, **Van Damme R**, **Vanhooydonck B**, **De Vree F. 2001b.** The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* **79:** 662–670.

Herrel A, **Vanhooydonck B**, **Joachim R**, **Irschick DJ. 2004b.** Frugivory in polychrotid lizards: effects of body size. *Oecologia* **140:** 160–168.

Herrel A, **Vanhooydonck B**, **Van Damme R. 2004a.** Omnivory in lacertid lizards: adaptive evolution or constraint? *Journal of Evolutionary Biology* **17:** 974–984.

Herrel A, **Verstappen M**, **De Vree F. 1999b.** Modularity complexity of the feeding repertoire in scincid lizards. *Journal of Comparative Physiology A* **184:** 501–518.

Hiiamae KM, **Crompton AW. 1985.** Mastication, food transport and swallowing. In: Hildebrand M, Bramble DM, Liem KF, Wake DB, eds. *Functional vertebrate morphology*. Cambridge, USA: Harvard University Press, 262–290.

Huey RB, **Stevenson RD. 1979.** Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Journal of Zoology* **19:** 357–366.

Husak JF, **Lappin AK**, **Fox SF**, **Lemos-Espinal JA. 2006.** Bite-force performance predicts dominance in male Venerable Collared lizards *Crotaphytus antiquus*. *Copeia* **2:** 301–306.

Husak JF, **Lappin AK**, **Van den Bussche RA. 2009.** The fitness advantage of a high-performance weapon. *Biological Journal of the Linnean Society* **96:** 840–845.

Huyghe K, **Herrel A**, **Adriaens D**, **Tadić Z**, **Van Damme R. 2009.** It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard. *Biological Journal of the Linnean Society* **96:** 13–22.

Huyghe K, **Vanhooydonck B**, **Herrel A**, **Tadić Z**, **Van Damme R. 2012.** Female lizards ignore the sweet scent of success: male characteristics implicated in female mate preference. *Zoology* **115:** 217–222.

Huyghe K, **Vanhooydonck B**, **Scheers H**, **Molina-Borja M**, **Van Damme R. 2005.** Morphology, performance and fighting capacity in male lizards, *Gallotia galloti*. *Functional Ecology* **19:** 800–807.

Irschick DJ, **Herrel A**, **Vanhooydonck B**, **Van Damme R. 2007.** A functional approach to sexual selection. *Functional Ecology* **21:** 621–626.

Irschick DJ, **Meyers JJ**, **Husak JF**, **Le Galliard J-F. 2008.** How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research* **10:** 177–196.

Itescu Y, **Foufopoulos J**, **Pafilis P**, **Meiri S. 2020.** The diverse nature of island isolation and its effect on land bridge insular faunas. *Global Ecology and Biogeography* **29:** 262–280.

Itescu Y, **Schwarz R**, **Meiri S**, **Pafilis P. 2017.** Intraspecific competition, not predation, drives lizard tail loss on islands. *Journal of Animal Ecology* **86:** 66–74.

Jones TB, **Kamil AC. 1973.** Tool-making and tool-using in the Northern Blue Jay. *Science* **180:** 1076–1078.

Jones ME, **Lappin AK. 2009.** Bite-force performance of the last rhynchocephalian (Lepidosauria: Sphenodon). *Journal of the Royal Society of New Zealand* **39:** 71–83.

Kaliontzopoulou A, **Adams DC**, **van der Meijden A**, **Perera A**, **Carretero MA. 2012.** Relationships between head morphology, bite performance and ecology in two species of *Podarcis* wall lizards. *Evolutionary Ecology* **26:** 825–845.

Kingsolver JG, **Pfenning DW. 2007.** Patterns and power of phenotypic selection in nature. *Bioscience* **57:** 561–572.

Kingsolver JG, **Schemske DW. 1991.** Path analysis of selection. *Trends in Ecology and Evolution* **6:** 276–280.

Kumar S, **Stecher G**, **Li M**, **Knyaz C**, **Tamura K. 2018.** MEGA X: molecular evolutionary genetics analysis across computing platforms. *Molecular Biology and Evolution* **35:** 1547–1549.

Lailvaux SP, **Herrel A**, **Vanhooydonck B**, **Meyers JJ**, **Irschick DJ. 2004.** Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard *Anolis carolinensis*. *Proceedings of the Royal Society of London B* **271:** 2501–2508.

Lailvaux SP, **Irschick DJ. 2006.** A functional perspective on sexual selection: insights and future prospects. *Animal Behaviour* **72:** 263–273.

Lailvaux SP, **Irschick DJ. 2007.** The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *The American Naturalist* **170:** 573–586.

Lappin AK, **Hamilton PS**, **Sullivan BK. 2006.** Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla *Sauromalus ater*. *Biological Journal of the Linnean Society* **88:** 215–222.

Lappin AK, **Husak JF. 2005.** Weapon performance, not size, determines mating success and potential reproductive output in the collared lizard *Crotaphytus collaris*. *The American Naturalist* **166:** 426–436.

Lappin AK, **Jones ME. 2014.** Reliable quantification of bite-force performance requires use of appropriate biting substrate and standardization of bite out-lever. *Journal of Experimental Biology* **217:** 4303–4312.

Leboeuf BJ. 1972. Sexual behavior in the Northern Elephant Seal *Mirounga angustirostris*. *Behaviour* **41:** 1–26.

Le Galliard J-F, **Clobert J**, **Ferriere R. 2004.** Physical performance and Darwinian fitness in lizards. *Nature* **432:** 502–505.

Litvaitis JA, **Villafuerte R. 1996.** Intraguild predation, mesopredator release, and prey stability. *Conservation Biology* **10:** 676–677.

Lopez-Darias M, **Vanhooydonck B**, **Cornette R**, **Herrel A. 2015.** Sex-specific differences in ecomorphological relationships in lizards of the genus *Gallotia*. *Functional Ecology* **29:** 506–514.

Losos JB, **De Queiroz K. 1997.** Evolutionary consequences of ecological release in Caribbean *Anolis* lizards. *Biological Journal of the Linnean Society* **61:** 459–483.

Lucas PW, **Luke DA. 1984.** Chewing it over: basic principles of food breakdown. In: Chivers DJ, Wood BA, Bilsborough A, eds. *Food acquisition and processing in primates*. Boston: Springer, 283–301.

Marjanac L, **Marjanac T. 2004.** Glacial history of the Croatian Adriatic and coastal Dinarides. In: Ehlers J, Gibbard PL, eds. *Quaternary glaciations - extent and chronology, Volume 2, Part 1: Europe*. Amsterdam: Elsevier, 19–26.

Marshall CD, **Wan J**, **Rocha-Olivares A**, **Godinez-Reyes C**, **Fisler S**, **Narazaki T**, **… Sterba-Boatwright BD. 2014.** Scaling of bite performance with head and carapace morphometrics in green turtles *Chelonia mydas*. *Journal of Experimental Marine Biology and Ecology* **451:** 91–97.

Measey GJ, **Rebelo AD**, **Herrel A**, **Vanhooydonck B**, **Tolley KA. 2011.** Diet, morphology and performance in two chameleon morphs: do harder bites equate with harder prey? *Journal of Zoology* **285:** 247–255.

Miles DB. 2004. The race goes to the swift: fitness consequences of variation in sprint performance in juvenile lizards. *Evolutionary Ecology Research* **6:** 63–75.

Molina-Borja M, **Padrón-Fumero M**, **Alfonso-Martin MT. 1997.** Intrapopulation variability in morphology, coloration, and body size in two races of the lacertid lizard, *Gallotia galloti*. *Journal of Herpetology* **31:** 499–507.

Nagy KA. 2005. Field metabolic rate and body size. *Journal of Experimental Biology* **208:** 1621–1625.

Noble GK, **Bradley HT. 1933.** The mating behavior of lizards; its bearing on the theory of sexual selection. *Annals of the New York Academy of Sciences* **35:** 25–100.

Pafilis P, **Meiri S**, **Foufopoulos J**, **Valakos E. 2009.** Intraspecific competition and high food availability are associated with insular gigantism in a lizard. *Naturwissenschaften* **96:** 1107–1113.

Pagel M. 1999. Inferring the historical patterns of biological evolution. *Nature* **401:** 877.

Penning DA. 2017. The scaling of bite force and constriction pressure in kingsnakes *Lampropeltis getula*: proximate determinants and correlated performance. *Integrative Zoology* **12:** 121–131.

Podnar M, **Mayer W**, **Tvrtković N. 2004.** Mitochondrial phylogeography of the Dalmatian wall lizard, *Podarcis melisellensis* Lacertidae. *Organisms, Diversity and Evolution* **4:** 307–317.

Podnar M, **Mayer W**, **Tvrtković N. 2005.** Phylogeography of the Italian wall lizard, *Podarcis sicula*, as revealed by mitochondrial DNA sequences. *Molecular Ecology* **14:** 575–588.

Polis GA, **Hurd SD. 1996.** Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities. *The American Naturalist* **147:** 396–423.

Pough FH. 1980. The advantages of ectothermy for tetrapods. *The American Naturalist* **115:** 92–112.

Preest MR. 1994. Sexual size dimorphism and feeding energetics in *Anolis carolinensis*: why do females take smaller prey than males? *Journal of Herpetology* **28:** 292–298.

R Core Team. 2018. *R: a language and environment for statistical comuping*. Vienna: R Foundation for Statistical Computing. Available at: https://www.R-project.org/.

Reghem E, Tia B, Bels V, Pouydebat E. 2011. Food prehension and manipulation in *Microcebus murinus* Prosimii, Cheirogaleidae. *Folia Primatologia* **82:** 177–188.

Ritchie EG, Johnson C. 2009. Predator interactions, mesopredator release and biodiversity conservation. *Ecology Letters* **12:** 982–998.

Ronquist F, Teslenko M, Van Der Mark P, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck JP. 2012. MrBayes 3.2: efficient Bayesian phylogenetic inference and model choice across a large model space. *Systematic Biology* **61:** 539–542.

Sagonas K, Pafilis P, Lymberakis P, Donihue CM, Herrel A, Valakos ED. 2014. Insularity affects head morphology, bite force and diet in a Mediterranean lizard. *Biological Journal of the Linnean Society* **112:** 469–484.

Santos AM, Field R, Ricklefs RE. 2016. New directions in island biogeography. *Global Ecology and Biogeography* **25:** 751–768.

Schoener TW. 1967. The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science* **155:** 474–477.

Sikora M, Mihanović H, Vilibić I. 2014. Paleo-coastline of the central eastern Adriatic Sea, and paleo-channels of the Cetina and Neretva rivers during the last glacial maximum. *Acta Adriatica* **55:** 3–18.

Snekser JL, Leese J, Ganim A, Itzkowitz M. 2008. Caribbean damselfish with varying territory quality: correlated behaviors but not a syndrome. *Behavioral Ecology* **20:** 124–130.

Stamps JA. 1977. Social behavior and spacing patterns in lizards. *Ecology and Behavior A* **7:** 256–334.

Stephens DW, Krebs JR. 1986. *Foraging theory*. Princeton: Princeton University Press.

Svanbäck R, Bolnick DI. 2007. Intraspecific competition drives increased resource use diversity within a natural population. *Proceedings of the Royal Society B* **274:** 839–844.

Swofford DL, Sullivan J. 2003. Phylogeny inference based on parsimony and other methods using PAUP*. In: Marco Salemi A-MV, ed. *The phylogenetic handbook: a practical approach to DNA and protein phylogeny*. Cambridge: Cambridge University Press, 160–206.

Taverne M, Fabre A-C, King-Gillies N, Krajnović M, Lisičić D, Martin L, Michal L, Petricioli D, Štambuk A, Tadić Z, Vigliotti C, Wehrle BA, Herrel A. 2019. Diet variability among insular populations of *Podarcis* lizards reveals diverse strategies to face resource-limited environments. *Ecology and Evolution* **9:** 12408–12420.

Taverne M, King-Gillies N, Krajnović M, Lisičić D, Mira O, Petricioli D, Sabolić I, Štambuk A, Tadić Z, Vigliotti C, Wehrle B, Herrel A. 2020. Data from: Proximate and ultimate drivers of variation in bite force in insular lizards *Podarcis melisellensis* and *Podarcis sicula*, v5, Dryad, Dataset. Available at: https://doi.org/10.5061/dryad.1jwstqjrv.

Thomas GH, Meiri S, Phillimore AB. 2009. Body size diversification in *Anolis*: novel environment and island effects. *Evolution* **63:** 2017–2030.

Van Daele PAAG, Herrel A, Adriaens D. 2008. Biting performance in teeth-digging African mole-rats *Fukomys*, Bathyergidae, Rodentia. *Physiological and Biochemical Zoology* **82:** 40–50.

Vanhooydonck B, Cruz FB, Abdala CS, Moreno Azócar DL, Bonino MF, Herrel A. 2010. Sex-specific evolution of bite performance in *Liolaemus* lizards Iguania: Liolaemidae: the battle of sexes. *Biological Journal of the Linnean Society* **101:** 461–475.

Vanhooydonck B, Herrel A, Irschick DJ. 2007. Determinants of sexual differences in escape behavior in lizards of the genus *Anolis*: a comparative approach. *Integrative and Comparative Biology* **47:** 200–210.

Vanhooydonck B, Herrel A, Meyers JJ, Irschick DJ. 2009. What determines dewlap diversity in *Anolis* lizards? An among-island comparison. *Journal of Evolutionary Biology* **22:** 293–305.

Vanhooydonck B, Herrel A, Van Damme R. 2007. Interactions between habitat use, behavior, and the trophic niche of lacertid lizards. In: Reilly SM, McBrayer LB, McBrayer LD, Miles DB, eds. *Lizard Ecology*, **Vol. 14**. Cambridge, UK: Cambridge University Press, 427–449.

Vervust B, Van Dongen S, Grbac I, Van Damme R. 2009. The mystery of the missing toes: extreme levels of natural mutilation in island lizard populations. *Functional Ecology* **23:** 996–1003.

Verwaijen D, Van Damme R, Herrel A. 2002. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* **16:** 842–850.

Vincent SE, Herrel A. 2007. Functional and ecological correlates of ecologically-based dimorphisms in squamate reptiles. *Integrative and Comparative Biology* **47:** 172–188.

Wainwright PC. 1991. Ecomorphology: experimental functional anatomy for ecological problems. *American Zoologist* **31:** 680–693.

Wainwright PC, Alfaro ME, Bolnick DI, Darrin Hulsey C. 2005. Many-to-one mapping of form to function: a general principle in organismal design? *Integrative and Comparative Biology* **45:** 256–262.

Weigelt P, Kreft H. 2013. Quantifying island isolation – insights from global patterns of insular plant species richness. *Ecography* **36:** 417–429.

Whittaker RJ, **Fernández-Palacios JM. 2006.** *Island biogeography: ecology, evolution and conservation*, 2nd edn. Oxford: Oxford University Press.

Whittaker RJ, **Triantis KA**, **Ladle RJ. 2008.** A general dynamic theory of oceanic island biogeography. *Journal of Biogeography* **35:** 977–994.

Williams EH, **Bunkley-Williams L. 2006.** Rapid beak-swinging locomotion in the Puerto Rican *Spindalis*. *The Wilson Journal of Ornithology* **118:** 563–569.

Wittorski A, **Losos JB**, **Herrel A. 2016.** Proximate determinants of bite force in *Anolis* lizards. *Journal of Anatomy* **228:** 85–95.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Table S1. Population, sequence origin, species and GenBank accession numbers of the samples used in the analyses.
Table S2. List of primers used for cytochrome *b* sequence analysis. Primer use: A – PCR amplification, R – PCR reamplification, and S – sequencing.
Table S3. Results of the phylogenetic multiple regression of residual head dimensions on bite force (hl: head length, hw: head width, hh: head height, ljl: lower-jaw length, qt: quadrate to tip length, ct: coronoid to tip length).
Figure S1. Linear head dimensions. HL: head length, HW: head width, HH: head height, CT: coronoid to tip length, QT: quadrate to tip length, LJL: lower-jaw length, ilJO: in-lever for jaw opening, ilJC: in-lever for jaw closing.
Figure S2a. *Podarcis* MP bootstrap 50% majority-rule consensus phylogram tree (top) with the length of each branch according to the number of changes, and consensus cladogram tree (bottom) with percentage of trees supported (1000 bootstrap repetitions).
Figure S2b. *Podarcis* ML bootstrap 50% majority-rule consensus phylogram tree (top) with the length of each branch according to the substitution rate, and consensus cladogram tree (bottom) with percentage of trees supported (100 bootstrap repetitions).
Figure S2c. *Podarcis* 50% majority rule phylogram tree calculated with MrBayes with the length of each branch according to the substitution rate (top), and consensus cladogram tree (bottom) with posterior probability associated with each clade.

SHARED DATA

The data from this study may be downloaded from the Dryad Digital Repository (Taverne *et al*, 2020).