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Body condition and jumping predict initial survival in a replicated island introduction experiment

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Over-water dispersal to small islets is an important eco-evolutionary process. Most often, new arrivals on islets find the environment harsh or mate-less, making their footholds on these islets fleeting. Occasionally, introduced animals are able to survive the strong selection following their arrival, leading to subsequent propagation and, in several famous cases, adaptive radiation. What traits predict that initial survival? We established a replicated island introduction experiment to investigate this process in lizards. In 2014, we introduced 20 *Podarcis erhardii* lizards to each of five small islets in the Greek Cyclades Islands. We found that the lizards that survived were those with better initial body condition, longer distal portions of their limbs and a greater propensity for jumping. Contrary to our expectations, neither body size nor the strength of the lizards' bite – two traits positively related to competitive ability, which becomes important later in the colonization process in lizards – predicted survival. This is the first selection study of its kind investigating an experimental introduction of *Podarcis*, and whether the traits that determined initial survival are important in driving the future evolutionary trajectories of these populations remains to be determined.

ADDITIONAL KEYWORDS: Cyclades Islands – experimental evolution – functional morphology – Greece – island ecology – lizard – natural selection – *Podarcis*.

INTRODUCTION

Dispersal from source populations to surrounding habitat patches such as satellite islands is a dynamic and important eco-evolutionary process. Over-water dispersal has led to multiple adaptive radiations across island chains and to the origin of countless unique island endemics (Gillespie *et al.*, 2020). Whereas traits impacting over-water dispersal have been investigated (Vazacova & Munzbergova, 2014; García-Verdugo *et al.*, 2019), our understanding of the traits determining survival after dispersal remains limited. Studies on dispersal and the colonization of novel areas have suggested that traits related to body size (Clegg *et al.*, 2008; Van Bocxlaer *et al.*, 2010), locomotor capacity (Phillips *et al.*, 2006), behaviour (Cote *et al.*, 2010; Brodin *et al.*, 2013), life-history (Van Bocxlaer *et al.*, 2010) and fat reserves (Van Bocxlaer *et al.*, 2010) may all be related to their establishment success. However, the traits important in the survival of individuals on small islands may differ significantly from those identified in studies of mainland communities given the dramatic differences in competition, predation and resource availability.

Life on small islands can be challenging in many ways: food, shelter and access to mates are often limited, resulting in a highly competitive insular environment (Pafilis *et al.*, 2009; Donihue *et al.*, 2016; Taverne *et al.*, 2019). However, at the same time small islets rarely host terrestrial predators, thus resulting in lower predation pressures (Brock *et al.*, 2014; Li *et al.*, 2014; Donihue *et al.*, 2020). In ectotherms such

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*Corresponding author. E-mail: colindonihue@gmail.com as lizards, living on small islands has led to rapid and substantial evolutionary changes in diet (Cooper & Vit, 2002; Sagonas *et al.*, 2014), gut morphology (Herrel *et al.*, 2008; Wehrle *et al.*, 2020) and changes in performance (Van Damme *et al.*, 1997; Herrel *et al.*, 2001, 2008), possibly in response to the strong selection on animals in these harsh environments. The selection on animals that survive over-water dispersal to small islets can be expected to be strong, rapidly redirecting the evolutionary trajectory of the arriving individuals (Clegg *et al.*, 2008; Aubret & Shine, 2009).

Establishment in novel environments typically has two phases: initially, populations must acquire food and survive to reproduce, and later, a second phase is characterized by intraspecific competition for resources. The traits that determine initial survival after arrival on an islet remain largely unknown, yet these traits play an outsized role in directing the subsequent evolutionary trajectory of small-islet populations due to founder effects. The most direct approach to understanding these patterns is with *in situ* experiments, whereby measured animals are introduced onto experimental islands (Radovanovic, 1956; Nevo *et al.*, 1972), thus enabling the calculation of individual trait-based survival in an ecologically relevant setting. We set up just such an experiment with the Aegean wall lizard, *Podarcis erhardii*. This species is a common and ecologically important meso-predator that is widespread throughout the Greek Cycladic Islands (Valakos *et al.*, 2008; Fig. 1). Two ecological processes have largely determined the biogeography of *P. erhardii* in the Cyclades: first, when sea levels were lower during the last glacial maximum many of the islands of the Cyclades were connected by land bridges, forming a single contiguous landmass allowing for dispersal. Second, multiple islands separated by deep channels in the Mediterranean have been populated by lizard species via over-water dispersal (Foufopoulos & Ives, 1999), making this system relevant for testing the traits that determine colonization success.

We test here whether traits predicted to be under selection in the introduced lizards impacted survival. First, we hypothesized that larger lizards would have a survival advantage; larger *P. erhardii* are known to be competitively dominant (Pafilis *et al.*, 2009) and so should be better able to gain access to scarce resources on the islets. Second, we hypothesized that animals with a better body condition (i.e. greater fat reserves for their body size) would be more likely to survive the introduction as they would be able to survive periods of food scarcity. Third, we hypothesized that lizards with a stronger bite force would survive better. Bite force in lizards dictates both an individual's competitive dominance (Lailvaux *et al.*, 2004; Huyghe *et al.*, 2005) and its ability to access a wider breadth of food resources including plant material or hard-shelled invertebrates (Verwaijen *et al.*, 2002; Aguirre *et al.*, 2003; Herrel *et al.*, 2006). Finally, we predicted that animals that showed increased locomotor performance and longer limbs would survive better as they should be able to gain easier and more rapid access to insular resources, thus dominating intraspecific competition.

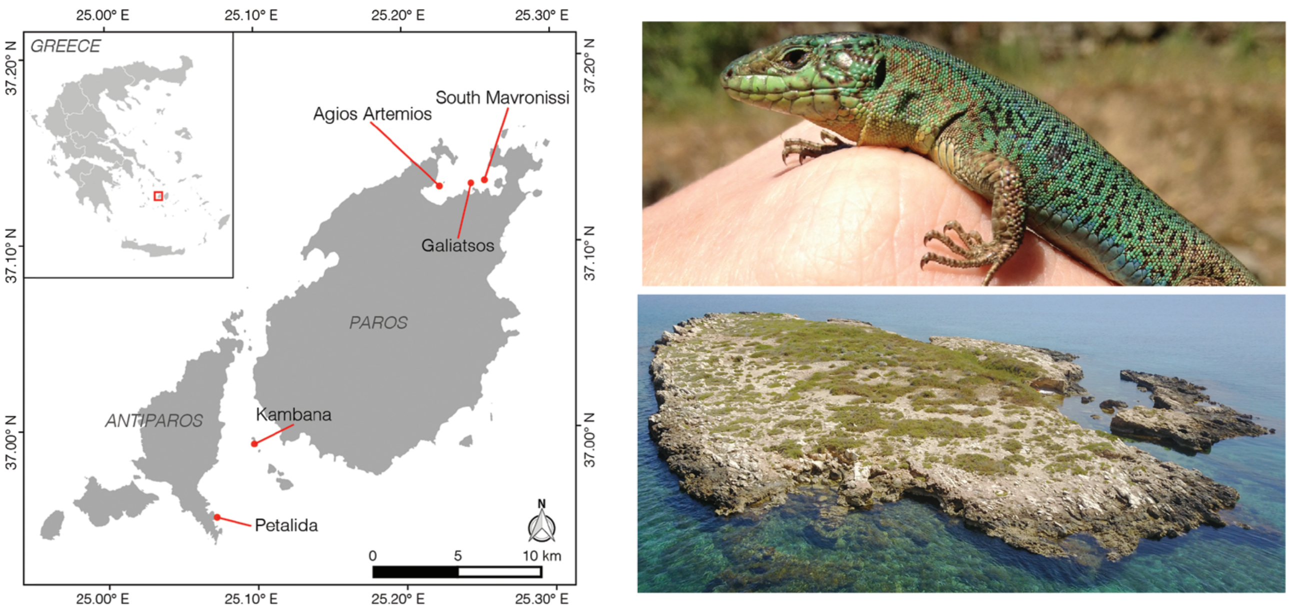

Figure 1. Map of Paros in the Greek Cyclades (inset) and its surrounding islands including the five small islets (red dots) used in this experiment. A picture of a male *Podarcis erhardii*, and an image of Agios Artemios, one of the introduction islands, are on the right.

MATERIAL AND METHODS

The Cyclades island group (Aegean Sea, Greece) contains hundreds of islands ranging in size from large islands like Naxos (440 km^2), to rocky islets measuring less than 0.1 km^2 (Valakos *et al.*, 2008). The islets of the Cyclades are arid, often with a rocky limestone substrate and little soil. Plant communities on these islets include *Juniperus* shrubs, small flowering forbs and grasses (Snogerup & Snogerup, 1987; Panitsa *et al.*, 2006). Many small islands are used by seabirds as nesting sites (Pafilis *et al.*, 2013; Lymberakis *et al.*, 2016). *Podarcis erhardii*, the Aegean wall lizard, is abundant throughout the Greek Islands (Fig. 1). It is moderately sized for the genus with adult snout-to-vent length (SVL) typically between 40 and 75 mm (Valakos *et al.*, 2008). Adults are sexually dimorphic, and they are largely generalist insectivores (Adamopoulou *et al.*, 1999; Donihue, 2016b), although some populations supplement their diet with fruits and conspecific eggs (Brock *et al.*, 2014).

During spring 2014, we identified several islets in the vicinity of the large islands of Naxos and Paros (Fig. 1) lacking *Podarcis* lizards and their primary predators: snakes and cats (Brock *et al.*, 2014; Li *et al.*, 2014). We selected five islets for this experiment due to their tractable small size (0.002–0.004 km^2 surface area) and the availability of habitat and food that we predicted could support an introduced lizard population (Fig. 1). To seed the experimental islets, we captured 60 adult female and 40 adult male *P. erhardii* from a low-lying coastal area, Alyko, on the nearby island of Naxos (Donihue, 2016a). We measured lizard body size (SVL) and the length of each segment of the right fore and hind limb using calipers (Mitutoyo 500-752). Body mass was measured using a spring scale (Pesola Light-Line).

Bite forces were measured by inducing lizards to bite on a purpose-built bite force meter (Kistler 9203, ±500 N connected to a Kistler 5995A charge amplifier) three times, the maximum force being retained for analyses (Herrel *et al.*, 1999; Donihue *et al.*, 2016). To assess locomotor performance lizards were chased along a track of 50 cm wide and 2 m long paved with large flagstones (see Donihue *et al.*, 2016a). Lizards were allowed to thermoregulate for 30 min and immediately before running temperature was recorded using a cloacal thermometer (Miller and Webber T6000). Each trial was recorded with a video camera (Sony HDRPJ260V; 1920 × 1080 pixels; 50 Hz) suspended directly over the track. Lizard position was digitized frame by frame and velocity was calculated as described by Donihue *et al.* (2016a). The number of times the lizards jumped from rock to rock was also counted.

Each animal was individually marked using toe clips and released on a randomly assigned study islet. Each introduction island received a total of eight males and 12 females at the beginning of June 2014. We intentionally female-biased the introduction to increase the likelihood of recruitment and because male-biased sex ratios in lacertids can cause aggression against females, sometimes leading to population collapse (Le Galliard *et al.*, 2005). In May 2015 we revisited each of the five islands and caught all of the lizards until the capture rate decreased to one lizard per two person-hours. After measuring the lizards, they were re-released on the islets for future investigation.

STATISTICAL ANALYSES

All analyses were conducted in R 3.6.0 (R Core Team, 2019). We first calculated body condition of the lizards using the scaled mass index (SMI) of Peig & Green (2009). The SMI has been demonstrated to better estimate body condition for small vertebrates than simple linear regression residuals (Peig & Green, 2009), and this estimate has previously been used for selection studies on lizard body condition (Cox & Calsbeek, 2015).

Selection on the suite of morphological and performance traits measured on the introduction animals were assessed using a binomial generalized linear model (GLM) with survival (1/0) in 2015 as the response. Before analysis, all continuous morphological traits (e.g. head length, not sex) were scaled to have a mean of zero and unit variance using the ‘scale’ function in R (Becker *et al.*, 1988). To assess whether each of the morphological traits measured predicted survival following colonization, we used a series of GLMs that incorporated body size (SVL) and the tested morphometric trait and we conducted a type III ANOVA on the factors to assess statistical significance. There were significant differences in survival between islands ($P < 0.001$) and marginally significant differences between sexes ($P = 0.056$); full model are given in the Results. We investigated incorporating nested random effects of sex within island but the models had insufficient power to evaluate the parameter space. We incorporated island identity as a random effect in the final models for analysis because the significant observed inter-island differences in survival were not a planned component of the experiment. We then tested whether sex significantly interacted with any of the potential explanatory variables – it did not – and so we removed sex from the analysis. We tested whether the performance traits predicted survival in the same way; however, in addition to incorporating differences in body size within the model, we also tested whether the performance traits alone – i.e. absolute performance as opposed to relative performance – predicted survival. We evaluated the models using the ‘glmer’ function in the '*lme4*' R package (Bates *et al.*, 2015) and assessed the significance of the factors using the 'Anova' function in the '*car*' package (Fox & Weisberg, 2019). As bite force typically varies between the sexes for many lizards, including *P. erhardii* (Donihue *et al.*, 2016), we separated the sexes and tested whether bite force residuals were a significant predictor of survival for either sex, again using island identity as a random effect in the GLM.

After identifying the suite of statistically significant predictors of survival, we then calculated linear selection coefficients for each factor. To do so, we used mean-standardized survival for each individual as the response in a single model that incorporated all of the significant factors so the coefficients could be interpreted relative to each other. Finally, we visualized selection surfaces using the 'gam' function in the '*mgcv*' R package (Wood, 2011) using REML as the smoothing parameter estimation method.

RESULTS

While in 2014 each island was seeded with 20 lizards, in 2015 an average of only 11 lizards remained per island. The pattern of lizard survival between islands differed significantly ($\chi^2 = 21.858$, d,f. = 4, $P < 0.001$). In subsequent analyses we pooled all 100 individuals and used island identity as a random effect in the analyses to account for unmeasured differences in the islands upon which lizards had been introduced.

We found that males had a slight survival advantage over females ($\chi^2 = 3.65$, d.f. = 1, $P = 0.056$). In total, 37% of females and 58% of males survived to 2015. We also found that body condition (SMI) was a strong predictor of survival ($\chi^2 = 8.92$, d.f. = 1, $P = 0.003$; Fig. 2B); lizards with higher body condition indices were more likely to survive. Contrary to our predictions, body size (SVL) was not a significant predictor of survival in the GLM ($\chi^2 = 2.85$, d.f. = 1, $P = 0.091$; Fig. 2A).

Moreover, the distal portions of the fore and hind limbs significantly predicted survival (forelimb: $\chi^2 = 7.208$, d.f. = 1, $P = 0.007$; hind limb: $\chi^2 = 5.226$, d.f. = 1, $P = 0.022$; Fig. 2C, D). Thus, lizards with relatively longer 'feet' experienced a survival advantage (Table 1).

When we tested whether performance predicted survival in the experiment, only the number of jumps was a significant predictor of survival (Fig. 2E, F); lizards that jumped more from rock to rock in the sprint track were significantly more likely to survive (Table 2).

Finally, we found that residual bite force was not a good predictor of survival in either females or males (females: $\chi^2 = 0.273$, d.f. = 1, $P = 0.601$; males: $\chi^2 = 0.854$, d.f. = 1, $P = 0.36$; Fig. 3).

DISCUSSION

Over-water dispersal is an important eco-evolutionary process underlying biogeographical patterns of diversity. While such dispersal has led to stunning evolutionary divergence and convergence across islands, the arrival and establishment in a new environment can be fraught with challenges. We experimentally reproduced the arrival of a small population of Aegean wall lizards onto five small islets in the Greek Cyclades to document the early stages of this process. We found that, indeed, these small islets posed a significant challenge to lizards introduced there from a large island; nearly 50% of the introduced lizards did not survive to the next year. Those that did survive were the individuals with particularly good body condition, that had long distal limb segments and that showed a propensity for jumping. In contrast to our predictions, body size and bite force, in both absolute and relative terms, did not predict survival. Altogether, after arriving on small islets, these five populations experienced strong selection and the subset that survived is now adapting to very different ecological circumstances from those on Naxos island.

Body condition in animals is often considered a proxy for fitness: 'fatter' individuals with a higher body condition index are assumed to have underlying physiological advantages that would lead to higher reproductive success and/or survival (Jakob *et al.*, 1996; Cox & Calsbeek, 2015). For lizards, a higher body condition index may indicate an individual is better capable of surviving periodic fasts when food availability drops, and for females, better body condition may result in higher quality eggs. Despite the intuitive nature of this prediction, there is mixed evidence in the literature for positive selection on body condition. Examples exist in nature, for example among birds where better body condition predicts survival (Linden *et al.*, 1992; Merilä *et al.*, 2001), but counter examples with mixed or no evidence are just as prevalent (Hendry *et al.*, 2003; Dibattista *et al.*, 2007; Cox & Calsbeek, 2015) and may be underreported due to non-significant statistical publication biases (Kingsolver *et al.*, 2001). The most comprehensive multi-year analysis of survival selection on body condition by Cox & Calsbeek (2015) found no consistent evidence for selection on body condition for *Anolis sagrei* individuals. In contrast, our results show a strong positive trend for 'survival of the fattest'. This result, however, does not contradict that of Cox & Calsbeek (2015), but instead highlights the difference in experiments: Cox and Calsbeek investigated lizards in stable populations whereas we introduced lizards onto small islets; environments that were previously unknown to the lizards. Our experiment clearly shows the advantage of good body condition.

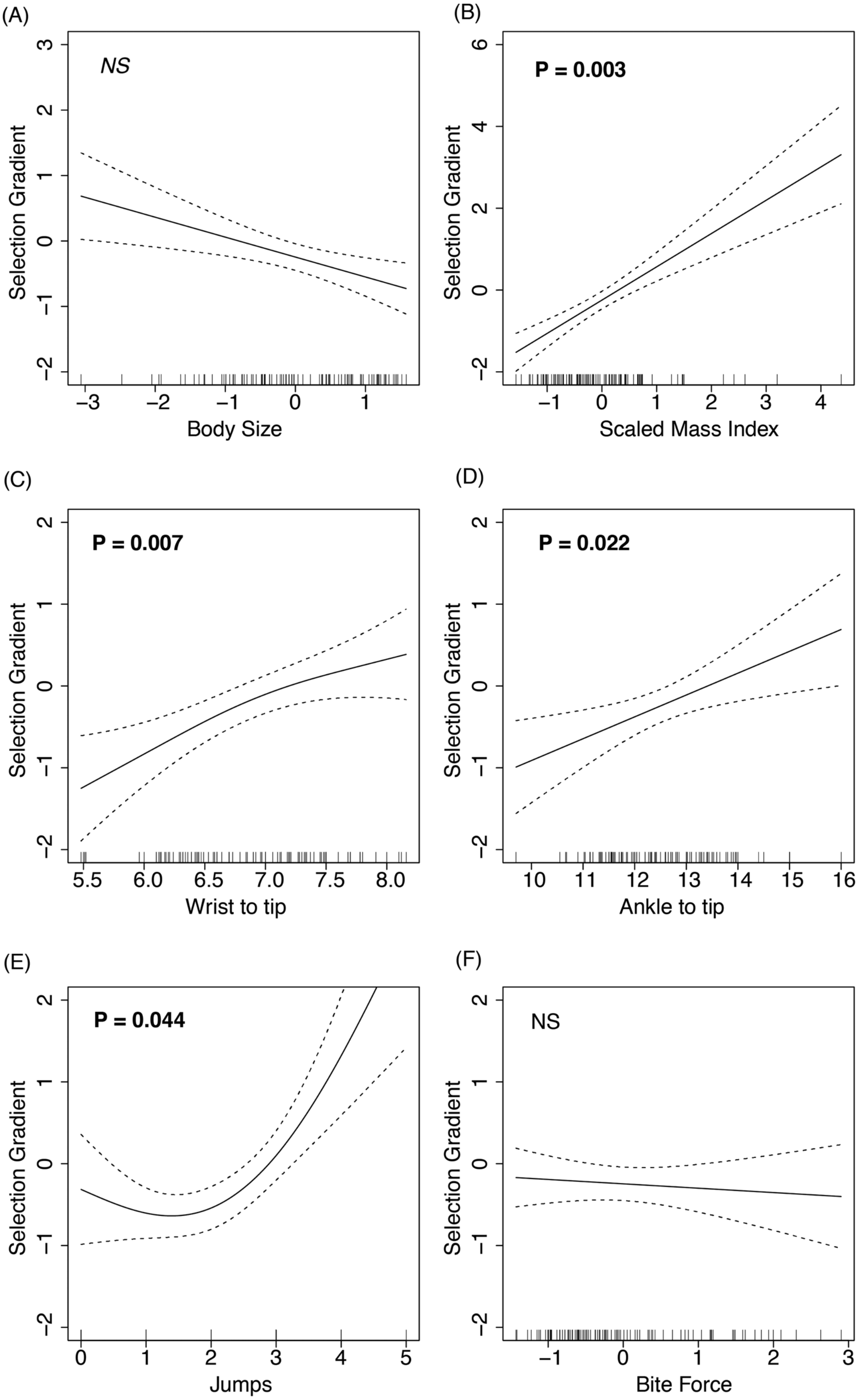

Figure 2. The selection gradients of body size, body condition (scaled mass index), distal limb segments, bite force and jumping propensity. All of the traits, with the exception of body size and bite force, were significant positive predictors of survival. Tick marks above the *x*-axis reflect individuals in the experiment. Trend lines and dotted confidence intervals are estimated using the 'gam' function in the '*mgcv*' R package – see Material and Methods.

Table 1. Morphological predictors of survival

	χ^2	d.f.	Pr($>\chi^2$)	
Survival (1/0) ~ trait				
Body size (SVL)	2.850	1	0.091	
Body condition (SMI)	**8.917**	**1**	**0.003**	**
Survival (1/0) ~ SVL + trait				
Head length	2.084	1	0.149	
Head width	3.175	1	0.075	
Head height	1.893	1	0.169	
Jaw length	2.555	1	0.110	
Humerus length	0.014	1	0.905	
Radius length	0.084	1	0.772	
Wrist to tip of longest finger	**7.208**	**1**	**0.007**	**
Femur length	3.790	1	0.052	
Tibia length	1.319	1	0.251	
Ankle to tip of longest toe	**5.226**	**1**	**0.022**	*

Table 2. Performance predictors of survival with and without accounting for differences in body size (SVL)

	Survival (1/0) ~ SVL + trait			Survival (1/0) ~ trait		
	χ^2	d.f.	Pr($>\chi^2$)	χ^2	d.f.	Pr($>\chi^2$)
Bite force	0.727	1	0.394	0.185	1	0.667
Sprint speed over rock	0.284	1	0.594	0.090	1	0.764
Sprint speed over sand	0.016	1	0.899	0.000	1	0.988
Number of jumps	3.545	1	0.060	**4.064**	**1**	**0.044**

In many lizards, including those in the genus *Podarcis*, body size is a reliable proxy for competitive ability (Tokarz, 1985; Olsson, 1992; Pafilis *et al.*, 2009). We thus hypothesized that larger lizards would survive better on the introduction islands due to their ability to competitively exclude conspecifics for access to scarce resources on the islets. Additionally, our hypothesis was informed by previous surveys of *P. erhardii* populations that found adult lizards on small islands tend to be larger than lizards from big islands (Donihue *et al.*, 2016; but see Itescu *et al.*, 2018). In our experiment, we did not find evidence for this hypothesis: body size was not a significant predictor of survival and, if anything, smaller lizards experienced a slight advantage. As body size is a reliable proxy for age in animals with continuous growth, it is possible that the largest individuals perished in the year following introduction simply because of old age. Furthermore, younger individuals are probably more behaviourally flexible, presumably allowing them to flexibly adapt to a novel environment. Lastly, larger bodied lizards have greater absolute nutritional requirements. It is conceivable that they would be unable to acquire sufficient resources to support themselves on the islets. Neither of these explanations are entirely satisfying and go counter to the fact that males (the larger of the sexes) survived better than females. Ultimately, the discrepancy between our hypothesis, survey observation (Donihue *et al.*, 2016) and result may simply be a matter of temporal scale: body size may become more relevant for competition and survival years and/or generations after an initial survival filter dictated by body condition is overcome.

While bite force is an important trait that determines a lizard's competitive ability and capacity for consuming hard prey, it does not appear to have conferred a survival advantage in the initial year of this experiment. Contrary to our predictions, neither the absolute hardest biting nor the relatively hardest biting lizards experienced a survival advantage. One potential explanation is that the small number of lizards, relative to the size of the island, resulted in individuals dispersing sufficiently such that fights for space or food resources did not occur or that resources were sufficient. However, the latter is unlikely as roughly half of the lizards did not survive to the next spring. In contrast to bite force, jumping propensity provided a significant survival advantage. In line with this result, lizards with longer distal segments also survived better. Longer distal limb segments provide a performance advantage as they allow animals to continue to accelerate the centre of mass longer, thus achieving higher take-off velocities (James *et al.*, 2007) and resulting in an increase in jump height or distance. The distal limb segments weigh less than proximal segments and as such an elongation of distal segments does not increase the total mass of the animal as much allowing for greater jumping performance (Marsh, 1994). Thus, our results suggest that jumping performance was a key trait in allowing animals to survive the introduction onto these islands. Possibly, a better jumping capacity and a greater propensity to jump may have provided lizards with access to a unique food resource: flying prey. Indeed, although vegetation is limited on these islets, they do have flying insects visiting flowering plants or using the islands as stepping stones while crossing large distances over water. Yet, flying insects are notoriously hard to capture and possibly the greater jumping tendency and capacity may have provided a survival advantage to the lizards.

The five introduction islets used in this experiment are similar in island area, plant species composition

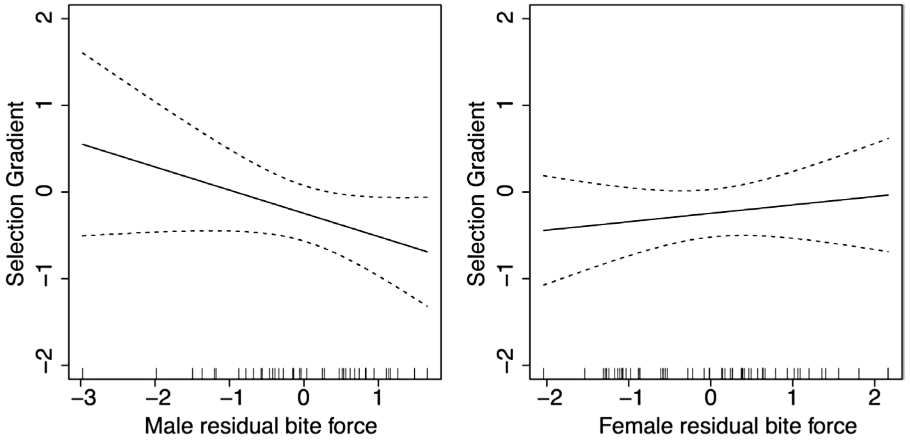

Figure 3. Size-corrected bite force was not a significant predictor of lizard survival. Tick marks above the x-axis reflect individuals in the experiment. Trend lines and dotted confidence intervals are estimated using the 'gam' function in the '*mgcv*' R package – see Material and Methods.

and substrate, and are typical of the small islets found throughout the Greek Archipelago. Nonetheless, the responses of the survivors to selection across the five islands varied significantly. Whether that difference is due to ecological differences in the islets, differences in the randomly assigned individuals introduced to each island or a combination thereof cannot be confidently determined with this experimental design. The analytical methods for detecting selection are sensitive to outliers, particularly with low sample sizes (Lande & Arnold, 1983; Arnold & Wade, 1984). Therefore, the fate of individuals with extreme phenotypes may have had disproportionate effects on inter-island differences in selection. This is the first selection study of its kind investigating an experimental introduction of *Podarcis*, and much remains to be learned about the strength and consistency of selection on morphology, performance and body condition following introduction to small islets. Whether the traits that determined initial survival are important in driving the future evolutionary trajectories of these populations remains to be determined.

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DATA AVAILABILITY

The data underlying this article are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.8931zcrs6 (Donihue *et al.*, 2021).

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