

The effects of predation risk, shelter, and food availability on the reproduction of Aegean Wall lizards (*Podarcis erhardii*) in the Greek islands

Yilun Zhao

A thesis submitted as partial completion of the requirements for the degree of
Master of Science (School for Environment and Sustainability) at the
University of Michigan
August 2018

Advisor:
Associate Professor Johannes Foufopoulos
Lecturer Shannon Brines

ABSTRACT

Reproductive investment, including the average number of offspring produced by an organism, is one of the fundamental characteristics of a species. Among other things, it predicts a species' resilience to environmental disruption: taxa that produce more offspring are able to recover more quickly from environmental perturbations and survive long-term environmental change. Despite the clear importance of this trait, ecologists do not have a good understanding of the primary drivers shaping the reproductive investment of each species. To answer this question, I compare the reproductive efforts of numerous island populations of the Aegean Wall Lizard (*Podarcis erhardii*), which differ in multiple key environmental characteristics. I test three hypotheses, namely that reproductive investment (measured as clutch size, clutch volume and egg volume) is: 1) positively associated with predation risk ['Predation Risk Hypothesis']; 2) positively associated with the presence of reliable vegetation cover that provides shelter ['Gravid Female Protection Hypothesis'], and 3) limited by (and hence positively correlated with) food availability ['Food Limitation Hypothesis']. Although field data are consistent with all three hypotheses, statistical analysis shows strong support for the Predation Risk Hypothesis. The result not only shed light on which fundamental forces shape reproductive investment in island vertebrates, but can also help set conservation priorities by identifying the most sensitive populations because reduced reproductive ability can be predicted based on easily quantifiable island characteristics (number of sympatric predator species).

Keywords: reproduction, reptile, conservation, island, predators, food.

ACKNOWLEDGEMENTS

I especially appreciate Dr. Johannes Foufopoulos for his professional guidance, invaluable help, and unwavering patience with this thesis. I am forever grateful for the time we worked together in both Greece and Ann Arbor.

Special thanks to Shannon Brines for all of his help and guidance on the data analysis, especially the NDVI analysis part. I could not have finished this thesis without taking NRE 540 GIS & Natural Resources Applications course and learning so much from him. My sincere thanks also go out to Dr. Kathleen Bergen, Dr. Panayiotis Pafilis, and Dr. Alison Davis Rabosky for their patient assistance with different part of my thesis.

I would also like to thank Chelsea Lisiecki, Kayla Hobby, Mike Rockwell, Michael Hostetler, and Graham Bevier for their help in the field. And, thanks to Chuying Lu, Zijun Yang and Feng-Hsun Chang for assistance with data interpretation and analysis.

Lastly, I would like to express my gratitude to Prof. W. Böhme for his encouragement and support to do this research and for making the University of Bonn Alexander König Museum collections available to us. Similarly, I would also like to thank M. Franzen and F. Glaw at the Zoologische Staatssammlung in Munich for providing us with access to their collections.

Financial support for this research was provided by the School for Environment and Sustainability (SEAS), the Program for Modern Greek, and the Weiser Center for Europe and Eurasia (WCEE), all at the University of Michigan. Field investigations were conducted under a permit from the University of Michigan IACUC (PRO00006987), the Greek Ministry for Environment and Energy (Permit Nr.: ΑΔΑ: Ω6ΛΝ4653Π8-ΤΨΑ) and were in full compliance with Greek National Law (Presidential Decree 67/81).

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INTRODUCTION

Island endemics constitute a significant component of earth's biodiversity. Despite the relatively small area they inhabit, these taxa also represent a disproportionate fraction of the planet's endangered biodiversity, with fully 41% of the world's endangered terrestrial species found predominately in island systems (Spatz et al., 2017). Island species face particularly high extinction rates (Case, Bolger, & Richman, 1992) as they are impacted by numerous threats including invasive species (Bellard, Cassey, & Blackburn, 2016; Wikelski et al., 2004) and global climate change (Foufopoulos, Kilpatrick, & Ives, 2011). The rapidly deteriorating conservation status of island vertebrates adds urgency to understanding the endogenous and exogenous factors that drive their decline.

Island vertebrates are often characterized by a distinct suite of life history changes referred to under the umbrella term 'island syndrome' (Adler & Levins, 1994). These changes have been observed across a broad range of disparate island organisms including mammals (Goltsman, et al., 2005), birds (Clegg & Owens, 2002), and reptiles (Novosolov & Meiri, 2013). Among reptiles, typical changes associated with the island syndrome include shifts in body size (Case, 1978; Meiri, 2007; Pafilis et al., 2011), modified limb length and head shapes (Herrel et al., 2008; Runemark, Hansson, Pafilis, Valakos, & Svensson, 2010), as well as longer life spans and lower growth rates (Andrews, 1976). Island lizards tend to achieve higher densities (Case, 1975; Novosolov et al., 2016) and may also display altered levels of intraspecific aggressiveness (Pafilis, Meiri, Foufopoulos, & Valakos, 2009), as well as attenuated morphological anti-predator behaviors (Brock, Bednekoff, Pafilis, & Foufopoulos, 2015a; Li et al., 2011; Stamps & Buechner, 1985) and adaptations (Pafilis et al., 2009). Probably the most widely recognized aspect of island syndrome is the altered pattern of reproductive investment, typically in the form of smaller clutches of larger eggs (Huang, 2007; Smith & Fretwell, 1974; Blondel, 2000). However, this pattern is neither universal (Galán, 2003) nor consistent (Novosolov et al. 2012), and it is not clear which factors drive reproductive investment.

Reproductive investment is a central aspect of a species' life history and can vary tremendously even across closely related taxa (Du et al., 2005; Mesquita et al., 2016). Studies over the last half century have revealed the multitude of factors that shape reproduction, including climate (Angilletta et al., 2004; Roitberg et al., 2013), latitude (Sinervo, 1990; Mesquitez et al., 2016), elevation (Ballinger, 1979; Cruz-Elizalde & Ramírez-Bautista, 2016), foraging mode (Vitt & Congdon, 1978), phylogenetic history (e.g. Mesquita & Colli, 2010; Werneck et al., 2009) and general body bauplan (Roitberg et al., 2013), but also proximate environmental conditions such as refugium shape (Vitt, 1981; Goodman et al., 2009), resource availability (Ballinger, 1977), and infection with parasites (Foufopoulos, 1999).

Chief among others, reproductive effort is thought to be subject to the constraints imposed by resource availability (Ballinger, 1977). Numerous studies have demonstrated the importance of both condition and seasonal nutrient intake in shaping both clutch size and clutch mass (Jordan & Snell, 2002; Hoy et al., 2016; Warne et al., 2012; Pafilis et al., 2011). In practice, comparisons made between high and lower quality habitats, or between high and low rainfall years have revealed that food availability can, but does not have to be, a driver of reproductive investment (Ballinger, 1977; Du, 2006). Moreover, it is not clear to which extent food availability modulates individual clutch size across years, and between

individuals of a population, or whether it acts as a long-term driver of macroevolutionary differences in reproductive output across different populations of a species.

Beyond resource availability, perhaps the most attention has been paid to the role of predation on reproductive investment. Both theoretical and empirical studies have revealed that predator-caused mortality can be a particularly important driver of an organism's patterns of reproduction (Schaffer, 1974; Vitt & Congdon, 1978; Stearns, 1977; 1992; Magnhagen, 1991). Indeed, according to classic life history theory, in areas of high mortality, selection should favor early onset of reproduction and high reproductive investment, even if that comes at the cost of future reproduction (Schwarzkopf, 1994). Nonetheless, whether predator-induced mortality affects reproductive investment in relatively isolated island populations have never been tested in a rigorous manner.

Numerous studies have shown that increases in reproductive investment in females come at the cost of declining running ability (VanDamme et al., 1989) and that this decline can also undermine longer-term survival (Mils et al., 2000) revealing a trade-off between current and future reproduction (Reznick, 1985; 1992). Gravid females can partially compensate for some of this loss in escape ability by modifying their foraging behavior (Cooper et al., 1990; Braña, 1993; Bauwens & Thoen, 1981) and initiating escape activities earlier (Brown & Shine, 2004; Lima & Dill, 1990; Magnhagen, 1991). Furthermore, gravid females stay closer to refugia (Braña, 1993; Bauwens & Thoen, 1981) and reduce their visibility through appropriate microhabitat selection (Cooper et al., 1990). Consequently, habitats that lack, or have only insufficient cover and refugia, may exert selective pressure on reduced reproductive investment (Cruz-Elizalde et al., 2017; Haenel, 2011). For example, in *Platynotus semitaeniatus*, an iguanid lizard species that seeks refuge in narrow rock crevices, females have evolved smaller clutches and reduced clutch mass which in turn allow them to squeeze into smaller crevices to avoid predation (Vitt, 1981; Goodman et al., 2009). Nonetheless, beyond this special case, the hypothesis that availability of cover can affect reproductive investment has, to our knowledge, never been explicitly tested.

While a steadily growing body of literature has described patterns of vertebrate reproduction on islands, very few studies have investigated which are the proximate drivers that have shaped the evolution of these patterns. Because so many co-varying factors have the potential to affect reproductive output in wildlife (Dunham & Miles, 1985) an increasing number of studies have taken an intraspecific approach and compared populations across a single widespread species (Niewiarowski et al., 2004; Díaz et al., 2012; Iverson et al., 1997; Roitberg et al., 2013). By comparing multiple locations within the circumscribed geographic range of a single species, investigators can control for many confounding factors such as climate, elevation, body architecture and phylogenetic effects and identify which microevolutionary processes are ultimately responsible for the observed variation in reproductive output. Focusing on island populations has the added benefit that they are evolutionarily discreet and, especially if small enough, can be considered homogenous in terms of prevailing environmental conditions.

In this study we describe and analyze the evolutionary patterns of reproductive investment in the Aegean Wall Lizard (*Podarcis erhardii*) - a lacertid species widely distributed across the Greek archipelago. By taking advantage of an unusual ecological setting where pronounced life-history differences exist between numerous well-characterized island populations both in reproductive investment and in the prevailing ecological

conditions, we test three fundamental hypotheses regarding the forces driving the evolution of reproductive effort in island taxa. Specifically, we test whether clutch size and clutch volume are determined by:

- (1) amount of food available to the lizards (Food Limitation Hypothesis),
- (2) amount of shelters available to the lizards, and (Gravid Female Protection Hypothesis)
- (3) species richness of the local predator community (Predation Risk Hypothesis).

By elucidating these relationships, we not only shed light on the drivers of the island syndrome but also help understand the fundamental causes of reproductive investment in ectothermic organisms.

METHODS

Study Sites

The study region lies predominantly in the Aegean Sea archipelago located between the southern Balkan peninsula in the west and the Anatolian mainland in the east. The study was conducted on 12 Aegean islands - 8 islands in the Cyclades Cluster and 4 islands in the Sporades Cluster, as well as 2 sites located in nearby mainland Greece (Figure 1). Island size ranges from 0.005 km² to 429 km². The climate of the region is typical Mediterranean, with long, dry and warm summers and mild, rainy winters (Giorgi & Lionello, 2008). The vegetation cover on the study sites consists mostly of xerophytic, summer-deciduous, coastal heaths termed 'phrygana' (comprised of diverse, spinose plant communities rich in aromatic taxa) as well as of agricultural fields, and sclerophyllous evergreen maquis (Fielding & Turland, 2008). The vegetation has been shaped by millennia of anthropogenic human activities including terraced agriculture and small ruminant grazing (Grove & Rackham, 2003).

Study Organism

The Aegean Wall Lizard (*Podarcis erhardii*) is a medium-sized lacertid lizard species with an adult SVL of 49-78 mm (Valakos et al., 2008). This species is widely distributed across the Greek mainland and the Aegean Sea islands (Brock et al., 2015). The species usually mates in spring and females lay their eggs in the period from April to July. Depending on the local conditions, eggs are hatched in middle to late summer (Valakos et al., 2008). Aegean wall lizards occur in a wide range of open habitats, with a preference for open, stony regions and tend to be absent from areas with dense vegetation and closed forest cover. They are particularly common in areas that provide refugia in the form of broken-up terrain and anthropogenic structures such as dry-stone walls and terraces (Brock et al., 2015b). *P. erhardii* consume a broad range of arthropods (Arnold, 1987), with a particular emphasis on Coleoptera, Orthoptera, and soft-bodied larvae (Adamopoulou, Valakos & Pafilis 1999). Additional secondary food items include snails (Adamopoulou, Valakos & Pafilis 1999) and even fruit (Brock, Donihue, & Pafilis, 2014), although the species is not known to consume nectar or vegetable matter like other island taxa. Recent observations suggest that the species displays at least occasionally cannibalistic tendencies (Adamopoulou, Valakos & Pafilis, 1999).

Reproductive Traits

Morphological traits were obtained from museum specimens. Snout-vent length (SVL) and reproductive traits, including clutch size, egg volume, and clutch volume were collected from specimens deposited at the Zoological Museum of Bonn (Germany) as well as from the Zoologische Staatssammlung in Munich (Germany). Following dissection, the number of oviductal eggs were recorded as clutch size. Size of oviductal eggs was recorded using digital calipers including the longest and shortest axes. Egg volume was determined by using the equation for volume (V) of an ellipsoid:

$$V = \frac{4}{3} \pi \alpha b^2$$

where α is half of the longest axis, and b is half of the shortest axis. Clutch volume for each female was calculated as the sum of the individual egg volumes (Mayhew, 1963).

Predation Pressure

Numerous types of predators feed on Aegean wall lizards, but their individual presence varies greatly across the range of *P. erhardii*, depending on ecological, vicariance and biogeographic factors. While mainland sites tend to harbor diverse communities of avian, mammalian, and reptile predators, some of the smallest islands fail to support even a single type of predator, hence creating a wide range of predation regimes. To obtain a more formal estimation of the predation environment that each population experiences, we follow the methodology of previous authors (Pafilis et al., 2009; Brock et al., 2015) and use predator species richness as a proxy of predation risk in each area. Predator presence data were obtained from the published literature and was often confirmed from our own field observations.

Measurement of Food Availability

We investigated the diet of *P. erhardii* across the study sites spanning a range of ecological conditions by studying biomass and abundance of arthropods in these sites during the key period during which females forage to form their clutches. From May to July 2017, 5 pitfall and sticky trap pairs were set on each island to collect crawling and flying arthropods. All pitfalls and sticky traps were set in randomly-selected areas with natural vegetation in the immediate vicinity of the sites where reproductive data specimens were collected. Crawling arthropods populations were analyzed by deploying five 400ml pitfalls containing antifreeze. To determine flying insect populations, we set up five 15.24cm x 30.48cm sticky traps placed on 30cm stakes over, or near, the pitfalls on each island. Following collection, all arthropods from pitfalls were washed with ethanol to remove dirt and antifreeze and stored in a 2oz. plastic wide-mouth jars for subsequent identification and measurement. All arthropods were identified to order and length was measured to the nearest *mm* using a ruler. Approximate biomass of each individual was then calculated using the length-to-biomass equation (Rogers, Hinds, & Buschbom, 1976):

$$W = 0.0305 \cdot L^{2.62}$$

The abundance and biomass of each sticky trap or pitfall trap was calculated and each island's abundance and biomass were calculated by averaging each sticky strip or pitfall. Because the deployment time of sticky strips and pitfalls from each island was different, the average abundance and biomass was standardized on a 48-hour basis.

Measurement of Vegetation

We measured vegetation cover by utilizing a Normalized Difference Vegetation Index (NDVI) ("Measuring Vegetation". NASA Earth Observatory.). For each island, we downloaded Landsat 8 OLI/ TIRS level 2 (surface reflectance) images from Earth Explorer, U.S. Geological Survey. To ensure accuracy of NDVI, we used only images with less than 10% cloud cover. NDVI of each surface reflectance image was calculated in Erdas Imagine 2016. Each image was then input in ArcGIS 10, and clipped to the sample area with 62.5m radius around sample site based on the size of the smallest of our field sites (Kokkinonisi). The NDVI of each pixel in sample area was exported and for each island, the NDVI of sample area was calculated by averaging the values of the corresponding pixels.

Statistical Analyses

Former studies show that island size influences vegetation, arthropods and predation risk (Kohn and Walsh, 1994; Shure and Phillips, 1991; Polis and Hurd, 1995). To test this hypothesis, we used linear models to find the relationship between island size (island area) and the amount of shelters (vegetation), food availability (biomass of arthropods) and predation risk (predator richness). Since island area has a highly skewed distribution, we used both island area and log-transformed island area as the independent variable when building linear regression models.

Because previous studies have shown that maternal SVL may affect reproductive traits, we included maternal SVL in some of the models as a covariate (Abell, Reyes, & Wiernasz, 1999; Pafilis et al., 2011). To avoid issues of collinearity we tested the correlations between all of the driving variables considered in this paper (maternal SVL, NDVI, predator richness, and biomass of arthropods) and excluded any complex models that had variables that were highly correlated with each other ($r > 0.5$). Since multiple lizards from each island were measured and individuals from the same island are assumed to be more similar with each other, we built linear models and linear mixed effect models to check the effect of shelter amount, predation risk, and food availability on reproductive traits.

Afterwards, Akaike information criterion (AIC) was used for comparison of the models. For each reproductive trait, same type of models (linear model or linear mixed effect model) were compared by AIC. Independent variables in the model with the lowest AIC value were considered to be the most important factor affecting reproductive traits.

RESULTS

Linear Models of Island Size and Independent Variables

Results of linear models show that log-transformed island area has a positive relationship with log-transformed predator richness ($r = 0.190$, $p < 0.001$, $R^2_{adj} = 0.942$) (Figure 2). The log-transformed biomass of arthropods has a positive correlation with log-transformed island area ($r = 0.152$, $p = 0.0018$, $R^2_{adj} = 0.531$) (Figure 3). NDVI shows a positive relationship with island area ($r = 0.0002752$, $p = 0.023$, $R^2_{adj} = 0.308$) (Figure 4). Hence larger islands tend to have higher predation risk, food availability, and extend of shelter-providing vegetation cover (Appendix 1).

Correlations

The correlation between predator richness and NDVI is 0.650 ($p < 0.001$), the correlation between predator richness and biomass of arthropods is 0.701 ($p < 0.001$), and the correlation between arthropods biomass and NDVI is 0.600 ($p < 0.001$). Because the correlations among predator richness, biomass of arthropods, and NDVI are all higher than 0.5 resulting in potential collinearity issues, we did not include them as independent variables in the same models during the model building process. The correlation between maternal snout-vent length and predator richness is 0.195 ($p = 0.002$); the correlation between maternal snout-vent length and NDVI is 0.102 ($p = 0.111$); the correlation between maternal snout-vent length and biomass of arthropods is -0.014 ($p = 0.826$). Therefore, maternal snout-vent length and one of other three independent variables were included in same models.

Effect of Predator Richness, Biomass of Arthropods, and NDVI on Reproductive Traits

Among three reproductive traits, clutch size was found significantly related to predator richness ($r = 0.087$, $P < 0.001$, $R^2_{adj} = 0.173$), biomass of arthropods ($r = 0.0034153$, $P < 0.001$, $R^2_{adj} = 0.07464$) and NDVI ($r = 1.7898$, $P < 0.001$, $R^2_{adj} = 0.06778$). Additionally, clutch volume has significant positive relationships with predator richness ($r = 44.52$, $P < 0.001$, $R^2_{adj} = 0.0673$) and biomass of arthropods ($r = 1.659$, $P = 0.00828$, $R^2_{adj} = 0.02424$). We also found significant positive effects from maternal snout-vent length on clutch size ($r = 0.06146$, $P < 0.001$, $R^2_{adj} = 0.08326$) and clutch volume ($r = 30.07$, $P = 0.00505$, $R^2_{adj} = 0.0278$). (Appendices 2, 3, 4)

Hypothesis Testing

Results of AIC comparisons are listed in Table 2, 3, 4, and 5 (Table 4 and Table 5 are in Appendix 6). Among all linear models and linear mixed effect models for explaining clutch size, the linear model contains predator richness and maternal SVL has the lowest AIC value (Table 2). For clutch volume, the linear mixed effect model including predator richness and maternal SVL as fixed terms, and location as the random term has the lowest AIC value, in terms of the highest explanation power (Table 3) although an alternative model that included NDVI, maternal SVL and location was only marginally worse (Appendix 5). Figure 5 and Figure 6 are the visualization of these two best models.

TABLES

Table 1. Summary Table including island name, coordinates, island size, predator richness, biomass of arthropods, NDVI, clutch size and clutch volume.

Island Name	Coordinates	Island Size (km ²)	Predator Richness	Biomass of Arthropods (mg)	NDVI	Clutch Size	Clutch Volume (mm ³)
Kokkinonisi	39°9'38.757"N, 23°54'7.129"E	0.005	2	16.734	0.387	1.7±0.3(10)	598±234(10)
Mikropsathoura (Mougia)	39°28'56.262"N, 24°10'51.691"E	0.014	2	20.724	0.511	1.6±0.2(11)	219±60(11)
Agios Ioannis	36°36'36.327"N, 24°57'23.118"E	0.033	2	125.727	0.108	1.4±0.2(10)	433±143(10)
Kopria	36°59'27.899"N, 25°38'14.122"E	0.138	2	100.870	0.164	1.6±0.2(10)	805±254(10)
Glaronisi	36°55'15.371"N, 25°36'15.286"E	0.188	2	57.548	0.200	1.9±0.1(8)	362±100(8)
Ano Koufonisi	36°56'49.45"N, 25°36'20.237"E	5.770	5	96.874	0.237	2.2±0.2(9)	386±120(9)
Gioura	39°23'46.899"N, 24°10'20.407"E	11.052	6	191.591	0.311	1.8±0.3(9)	549±149(9)
Santorini	36°22'59.326"N, 25°28'29.843"E	76.197	9	106.454	0.312	1.7±0.1(24)	612±121(24)
Skopelos	39°7'30.145"N, 23°39'10.323"E	96.229	11	333.154	0.542	2.5±0.4(12)	947±235(12)
Tinos	37°33'31.293"N, 25°7'40.568"E	194.500	12	77.232	0.213	2.7±0.2(23)	1268±269(23)
Andros	37°53'23.97"N, 24°43'25.309"E	380.000	13	286.327	0.363	2.2±0.4(9)	777±289(9)
Naxos	37°4'54.364"N, 25°29'16.147"E	429.785	11	121.837	0.289	2.4±0.1(42)	1008±139(42)
Olympiada	39°59'45.907"N, 22°14'0.477"E	1000.000	16	278.560	0.485	2.9±0.2(35)	1258±175(35)
Vevi	40°46'27.065"N, 21°36'53.896"E	1000.000	18	229.523	0.682	2.9±0.2(34)	951±165(34)

Table 2. AIC for seven linear models constructed to explain clutch size

Model	AICc	Δ AICc	Akaike Weight
CS ~ P + SVL	695.691	0.000	0.998
CS ~ P	708.225	12.533	1.895x10 ⁻³
CS ~ B + SVL	712.715	17.024	2.007x10 ⁻⁴
CS ~ NDVI + SVL	719.651	23.959	6.257x10 ⁻⁶
CS ~ SVL	733.504	37.812	6.141x10 ⁻⁹
CS ~ B	735.805	40.114	1.943x10 ⁻⁹
CS ~ NDVI	737.624	41.933	7.826x10 ⁻¹⁰

CS = Clutch Size, P = Predator Richness, B = Biomass of Arthropods, SVL = maternal snout-vent length. Models were compared with their AICc values and their associated Akaike weight which is calculated by the equation:

$$W_i(AIC) = \exp(-0.5\Delta_i(AIC)) / \sum_{k=1}^k \exp(-0.5\Delta_k(AIC)) \text{ (Turkheimer et al. 2003).}$$

Table 3. AIC for seven linear mixed effect models constructed to explain clutch volume

Model	AIC	Δ AIC	Akaike Weight
CV ~ P + SVL + (1 Location)	4008.389	0	0.587
CV ~ NDVI + SVL + (1 Location)	4009.153	0.764	0.401
CV ~ P + (1 Location)	4017.407	9.018	6.461x10 ⁻³
CV ~ B+SVL + (1 Location)	4018.701	10.312	3.383x10 ⁻³
CV ~ NDVI + (1 Location)	4019.651	11.262	2.104x10 ⁻³
CV ~ SVL + (1 Location)	4022.031	13.642	6.401x10 ⁻⁴
CV ~ B + (1 Location)	4029.952	21.563	1.220x10 ⁻⁵

CV = Clutch Volume, P = Predator Richness, B = Biomass of Arthropods, SVL = maternal snout-vent length. Models were compared with their AICc values and their associated Akaike weight which is calculated by the equation:

$$W_i(AIC) = \exp(-0.5\Delta_i(AIC)) / \sum_{k=1}^k \exp(-0.5\Delta_k(AIC)) \text{ (Turkheimer et al. 2003).}$$

FIGURES

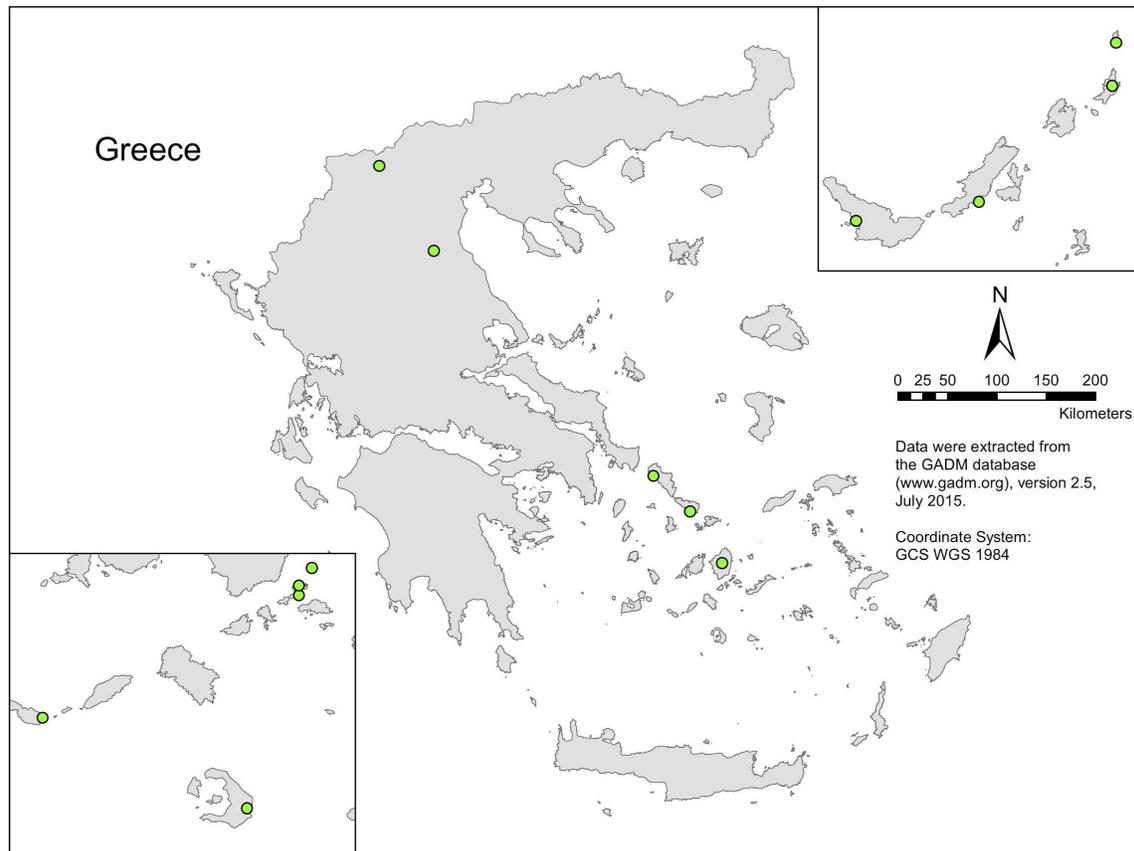


Figure 1. Map of the general area with the study sites marked in green circles.

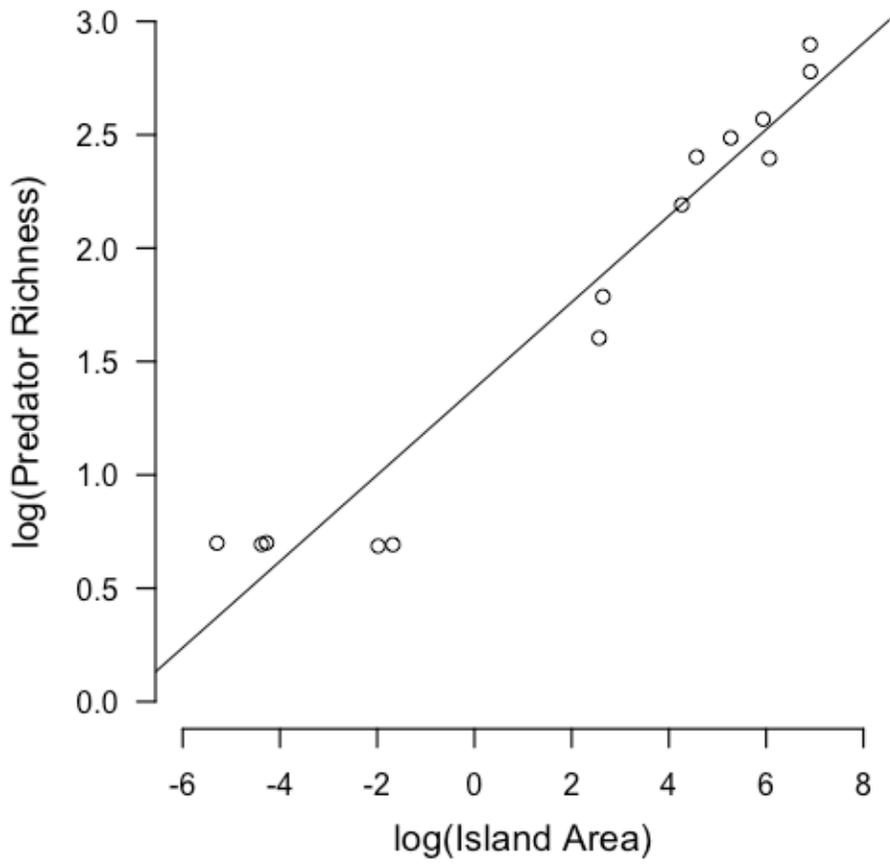


Figure 2. Linear regression between log-transformed Island Area and log-transformed Predator Richness. Each circle represents an island. Log-transformed predator richness has a positive relationship with log-transformed island area.

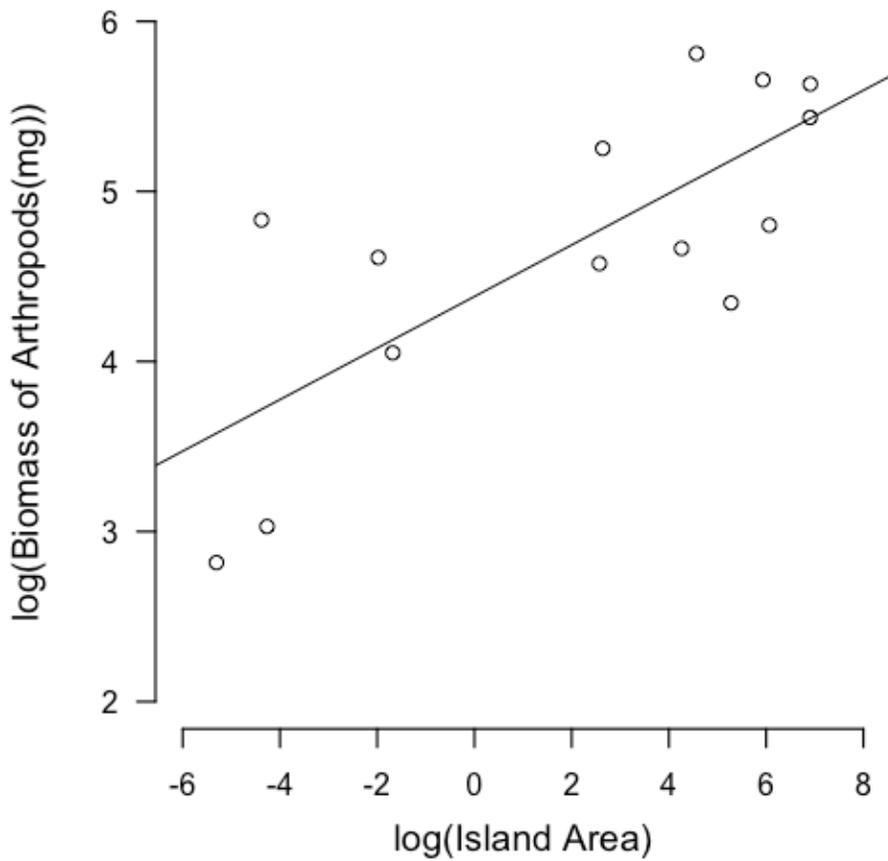


Figure 3. Linear regression between log-transformed Island Area and log-transformed Biomass of arthropods. Each circle represents an island. Log-transformed biomass of arthropods has a positive relationship with log-transformed island area.

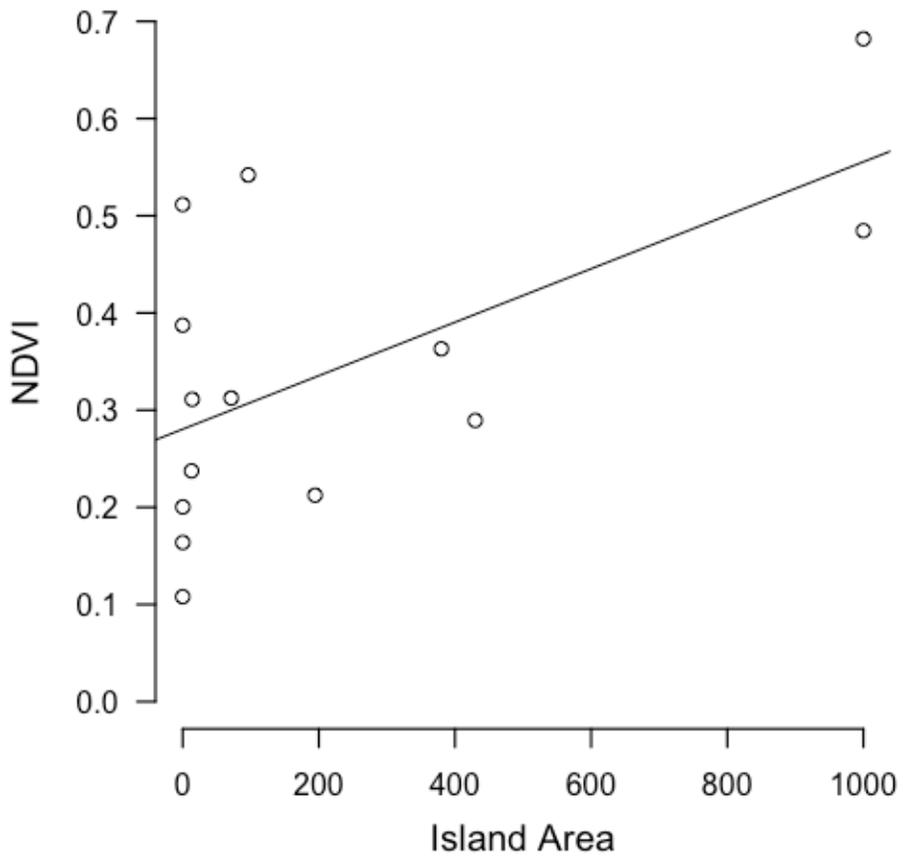


Figure 4. Linear regression between island area and NDVI. Each circle represents an island. NDVI has a positive relationship with island area.

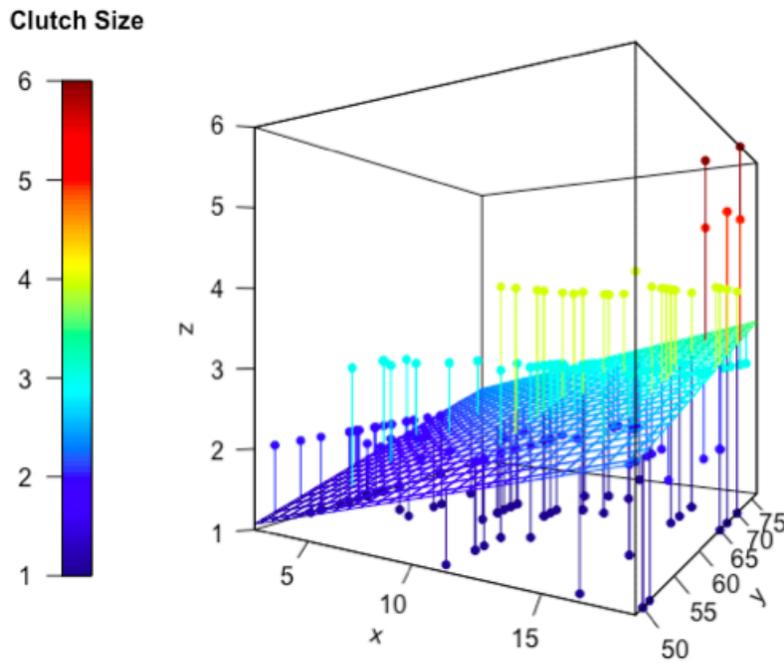


Figure 5. Lizard clutch size against predator species richness and maternal body size. Each dot represents one lizard clutch, and wire mesh represents the predictions of the best model as provided from the AIC model comparison. x : Predator Species Richness, y : Maternal snout-vent length (in mm), z : clutch size (number of eggs).

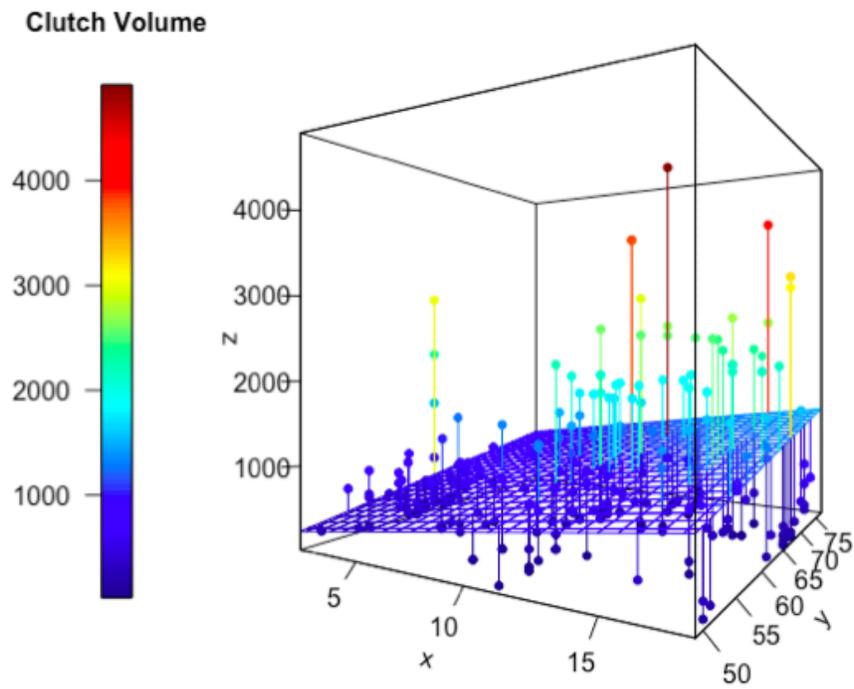


Figure 6. Lizard clutch volume against predator species richness and maternal body size (in *mm*). Each dot represents one lizard clutch, and wire mesh represents the predictions of linear model. *x*: Predator species richness, *y*: Maternal snout-vent length (in *mm*), *z*: Clutch volume (in mm^3).

DISCUSSION

Reproductive investment is a fundamental component of a species' biology and has been the focus of many fruitful life-history studies (Tinkle, 1969; Tinkle et al., 1970; Stearns, 1992). It is also of practical importance: for example, small clutch size has been shown to be a critical predictor of vulnerability to extinction in lizards (Siliceo & Díaz, 2010). Reptiles have emerged as particularly useful study systems to investigate the evolution of different reproductive investments because of the tremendous variety in reproductive modes that are made possible by ectothermy (Shine, 2005; Mesquita et al., 2016). Because reproduction entails multiple conflicting demands and organisms operate under limited resources, (e.g. nutrients –Ballinger, 1977; maternal body cavity volume - Qualls and Shine, 1995) it is impossible for an individual to optimize all aspects of its life history (Mesquita et al., 2016). This in turn creates important trade-offs such as present-season versus future-season reproduction (Shine, 2003; Schaffer, 1974; Schwarzkopf, 1994; Miles et al., 2000; Shine & Schwarzkopf, 1992; Olsson et al., 2001). Other well-recognized trade-offs exist within a single clutch e.g. the fundamental choice between number of offspring and size of individual offspring (Sinervo, 1990; Sinervo and Licht, 1991). Ultimately, a lot of variation exists between, as well as within species (e.g. Angilletta et al., 2004) and much of it remains unexplained.

In this study we tested the effect of different factors on three different reproductive traits, clutch size, clutch volume and egg volume. We found that while clutch size was significantly and positively correlated with predation risk, food availability, and vegetation amount, the latter two of these relationships were weaker than the first one and had little explanatory power. Similarly, we found that clutch volume was correlated with predation risk and food availability, but not with vegetation cover. Regarding clutch size, the model with the lowest AIC score included predator species diversity, as well as maternal snout-vent length as explanatory factors. Similarly, the marginally better model for clutch volume included predation risk and maternal snout-vent length as independent variables.

Our analyses indicate that the main factor associated the evolution of different clutch sizes in island lizards is predator diversity. As the diversity of syntopic predators' decreases, so does clutch size, declining from an average of 4.12 eggs per clutch on Naxos Isl. to 1.47 eggs per clutch on predator-poor Glaronissi Isl. Similarly, predator species richness was the most important driver (albeit marginally) of clutch mass with the smallest clutch masses found on one off the most predator-poor islands (529 mm³, on Mikropsathoura). These results underscore the seminal importance that predation pressure plays for Lacertid lizards and dovetail with recent investigations that highlight the importance of predation as a general driving force for the evolution of island lizards. For example, intraspecific comparisons across numerous island populations have demonstrated that wall lizards on reduced-predation islands have both slower sprint speeds and tend to have relatively shorter legs (Semegen, 2018; Vervust et al., 2017). Furthermore, lizards on low-predation islands have downregulated tail autotomy (Savvides et al., 2017), stray further away from refugia (Cooper et al., 2000; Li et al., 2014) and are more apt to let potential predators approach before initiating escape behaviors (Li et al, 2014; Brock et al., 2015) relative to lizards on predator-rich mainland regions.

Previous studies have argued that food availability is a critical driver of reproductive output in vertebrates (Ballinger, 1977; Du, 2006; Mugabo et al., 2017). While in temperate lizards and in species living in strongly seasonal environments, increased food availability generally translates into larger clutches (Ballinger, 1977), in more tropical or aseasonal

environments it may instead result in more frequent clutches of the same size (Du, 2006). Although the Aegean Sea region is a strongly seasonal environment and *Podarcis* lizards tend to produce only one, or at most, two clutches annually, none of the models including food availability emerged as being best in explaining the observed clutch size variation. While there were significant correlations between food availability and both clutch size and clutch volume, the explanatory power was very small ($R^2_{\text{adj.}} = 0.024$ and 0.075 respectively). Part of this may be because the field methods did not allow us to adequately sample the preferred foods of the species. For example, *P. erhardii* appears to prefer to feed on larval Coleoptera and Orthoptera (Valakos, 1986), two groups of arthropods that are hard to sample either in pitfall or in sticky traps. Alternatively, it is known that clutch investment represents not just nutrients available during the reproductive season that are then shunted towards reproduction, but instead does also integrate stored lipids and is a reflection of the general longer-term nutritional status of an animal rather than recent nutritional income. Lastly, it is possible that the average clutch size and volume is a phylogenetically conservative trait that represents the long-term optimum for a population, rather than mapping tightly onto the local food availability in a given year. Either one of these may be the reason why we failed to detect a relationship between food availability and clutch size or volume.

Numerous earlier studies have shown that increased reproductive output, whether in mammals (McLean & Speakman, 2000), birds (Lee et al., 1996; Veasey et al., 2001) or reptiles (Seigel et al., 1987) incurs multiple costs that can affect future survival. Such costs stem from impaired thermoregulation (Shine, 1980) but especially from reduced locomotor performance which in turn impairs escaping ability from predators (Magnhagen, 1991; Brown & Shine, 2004). While the proximate drivers of reduced running speed in gravid females are complex (Olsson et al., 2000), much of the costs center on the need to escape rapidly while carrying additional offspring mass along (Seigel et al., 1987; Shine, 1980). As a result, gravid females tend to stay close to hiding places, and presence of sufficient cover and refugia can help females escape predation and perhaps thermoregulate more efficiently (Vervust et al., 2017). While *P. erhardii* generally prefers open areas it requires the presence of hiding places such as sclerophyllous *phrygana* and maqui vegetation. As a matter of fact, lizard population density is related to the extent of sclerophyllous bush cover on an island (Foufopoulos *et al. in prep.*). As a result, we predicted that presence of cover in the form of evergreen shrubby vegetation and measured as an island's NDVI would be positively related to a population's reproductive investment. Instead, we found that there was no strong relationship between clutch size and NDVI. We also found that there was some support for a model incorporating NDVI to explain clutch volume, although this model was not the best (Table 2.).

In summary, when it comes to reproductive investment, wall lizard populations found in the Aegean Sea region constitute a textbook example of local adaptation showing different degrees of expression of the island syndrome depending on the extend of insularity of a particular population. Number of eggs produced by a female is not just a function of maternal SVL but is also strongly shaped by the richness of the resident predator community: lizard populations living on islands with the fewest predators showed a >64% reduction in clutch size, as well as corresponding reductions in clutch volume. At the same time, food availability appears to be significant factor for both clutch size and clutch volume: lizards living on islands with higher food availability have more eggs and larger clutches. Presence of vegetation appears to be positively associated with clutch size (but not clutch volume), presumably because more plant cover allows for slower-moving gravid females to avoid being preyed on and perhaps because of

thermoregulatory benefits. Traditional life history theory posits that the observed reductions in clutch size stem from a trade-off between clutch size and average egg (and therefore offspring) size. While in predator-rich environments selective pressures favor the production of large number of small-bodied offspring, high intraspecific competition among young lizards in low-predation, but high lizard density environments, is expected to favor investment in large-bodied offspring. Instead we find that low-predation populations produce *both* small clutches and eggs with relatively unchanged size. There are at least two possible explanations for this pattern. First, it is possible that low-predation islands are also low-productivity environments that do not provide resources for the production of large clutch numbers and volumes. Alternatively, it is possible that selection in low predation islands favors the evolution of long-lived life histories that produce small annual reproductive investment across many years. It is notable that these evolutionary patterns appear to have evolved several times and relatively rapidly. Some of the strongest inter-population differences occur on neighboring islands (e.g. on Naxos and Glaronissi which are <5km away from each other and have been separated for <5,000years) indicating that such differences can evolve quite quickly.

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APPENDICES

1. R outputs of linear regression between island area and independent variables

Call:

```
lm(formula = log(datasum$PredatorSpeciesNumber) ~ log(datasum$IslandArea))
```

Residuals:

Min	1Q	Median	3Q	Max
-0.36920	-0.12622	0.06443	0.14174	0.32167

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	1.38070	0.06256	22.07	4.40e-11 ***
log(datasum\$IslandArea)	0.19048	0.01308	14.56	5.47e-09 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.2134 on 12 degrees of freedom

Multiple R-squared: 0.9464, Adjusted R-squared: 0.942

F-statistic: 212 on 1 and 12 DF, p-value: 5.466e-09

Call:

```
lm(formula = log(datasum$FoodBiomass) ~ log(datasum$IslandArea))
```

Residuals:

Min	1Q	Median	3Q	Max
-0.83461	-0.46454	-0.03503	0.44819	1.11602

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	4.38242	0.18285	23.967	1.67e-11 ***
log(datasum\$IslandArea)	0.15160	0.03824	3.964	0.00188 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.6237 on 12 degrees of freedom

Multiple R-squared: 0.567, Adjusted R-squared: 0.5309

F-statistic: 15.72 on 1 and 12 DF, p-value: 0.001879

Call:
lm(formula = datasum\$NDVI ~ datasum\$IslandArea)

Residuals:
Min 1Q Median 3Q Max
-0.17240 -0.10198 -0.03417 0.08694 0.23513

Coefficients:
Estimate Std. Error t value Pr(>|t|)
(Intercept) 0.2803522 0.0435775 6.433 3.24e-05 ***
datasum\$IslandArea 0.0002752 0.0001057 2.605 0.023 *

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 0.1357 on 12 degrees of freedom
Multiple R-squared: 0.3611, Adjusted R-squared: 0.3079
F-statistic: 6.784 on 1 and 12 DF, p-value: 0.02303

2. R outputs of linear regressions between clutch size and independent variables

Call:
lm(formula = data\$ClutchSize ~ data\$PredatorSpeciesNumber)

Residuals:
Min 1Q Median 3Q Max
-1.9741 -0.5894 0.0259 0.6317 3.1990

Coefficients:
Estimate Std. Error t value Pr(>|t|)
(Intercept) 1.41627 0.14093 10.050 < 2e-16 ***
data\$PredatorSpeciesNumber 0.08655 0.01198 7.223 6.45e-12 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.013 on 244 degrees of freedom
Multiple R-squared: 0.1762, Adjusted R-squared: 0.1728
F-statistic: 52.18 on 1 and 244 DF, p-value: 6.449e-12

Call:

```
lm(formula = data$ClutchSize ~ data$FoodBiomass)
```

Residuals:

Min	1Q	Median	3Q	Max
-1.9134	-0.8464	-0.1133	0.8083	3.4405

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	1.7756044	0.1378230	12.883	< 2e-16 ***
data\$FoodBiomass	0.0034153	0.0007495	4.557	8.22e-06 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.071 on 244 degrees of freedom

Multiple R-squared: 0.07842, Adjusted R-squared: 0.07464

F-statistic: 20.76 on 1 and 244 DF, p-value: 8.218e-06

Call:

```
lm(formula = data$ClutchSize ~ data$NDVI)
```

Residuals:

Min	1Q	Median	3Q	Max
-1.8637	-0.9180	-0.1144	0.8392	3.4897

Coefficients:

	Estimate	Std. Error	t value	Pr(> t)
(Intercept)	1.6429	0.1707	9.624	< 2e-16 ***
data\$NDVI	1.7898	0.4126	4.337	2.11e-05 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.075 on 244 degrees of freedom

Multiple R-squared: 0.07158, Adjusted R-squared: 0.06778

F-statistic: 18.81 on 1 and 244 DF, p-value: 2.111e-05

3. R outputs of linear regressions between clutch volume and independent variables

Call:
lm(formula = data\$ClutchVolume ~ data\$PredatorSpeciesNumber)

Residuals:
 Min 1Q Median 3Q Max
-1117.4 -648.8 -159.5 431.8 3974.1

Coefficients:
 Estimate Std. Error t value Pr(>|t|)
(Intercept) 400.42 121.17 3.305 0.00109 **
data\$PredatorSpeciesNumber 44.52 10.30 4.322 2.26e-05 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 870.5 on 244 degrees of freedom
Multiple R-squared: 0.0711, Adjusted R-squared: 0.0673
F-statistic: 18.68 on 1 and 244 DF, p-value: 2.255e-05

Call:
lm(formula = data\$ClutchVolume ~ data\$FoodBiomass)

Residuals:
 Min 1Q Median 3Q Max
-1129.4 -651.7 -305.3 481.8 4179.7

Coefficients:
 Estimate Std. Error t value Pr(>|t|)
(Intercept) 600.8882 114.5931 5.244 3.41e-07 ***
data\$FoodBiomass 1.6590 0.6232 2.662 0.00828 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 890.4 on 244 degrees of freedom
Multiple R-squared: 0.02823, Adjusted R-squared: 0.02424
F-statistic: 7.087 on 1 and 244 DF, p-value: 0.008279

4. R outputs of linear regressions between clutch size or clutch volume and maternal snout-vent length

Call:
lm(formula = data\$ClutchSize ~ data\$SVL)

Residuals:
 Min 1Q Median 3Q Max
-2.25142 -0.88268 -0.08376 0.73187 3.11732

Coefficients:
 Estimate Std. Error t value Pr(>|t|)
(Intercept) -1.48067 0.79135 -1.871 0.0625 .
data\$SVL 0.06146 0.01274 4.822 2.5e-06 ***

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 1.066 on 244 degrees of freedom
Multiple R-squared: 0.087, Adjusted R-squared: 0.08326
F-statistic: 23.25 on 1 and 244 DF, p-value: 2.502e-06

Call:
lm(formula = data\$ClutchVolume ~ data\$SVL)

Residuals:
 Min 1Q Median 3Q Max
-1202.4 -659.4 -347.7 577.5 3798.2

Coefficients:
 Estimate Std. Error t value Pr(>|t|)
(Intercept) -994.31 659.85 -1.507 0.13313
data\$SVL 30.07 10.63 2.830 0.00505 **

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Residual standard error: 888.8 on 244 degrees of freedom
Multiple R-squared: 0.03177, Adjusted R-squared: 0.0278
F-statistic: 8.007 on 1 and 244 DF, p-value: 0.005048

5. R outputs of selected models to explain clutch size and clutch volume

Linear mixed model fit by REML. t-tests use Satterthwaite's method [`'lmerModLmerTest'`]
 Formula: `data$ClutchSize ~ data$PredatorSpeciesNumber + data$SVL + (1 | data$Location)`

REML criterion at convergence: 704.7

Scaled residuals:

Min	1Q	Median	3Q	Max
-2.3326	-0.7350	0.1262	0.6095	2.7431

Random effects:

Groups	Name	Variance	Std.Dev.
data\$Location	(Intercept)	0.02392	0.1546
	Residual	0.95159	0.9755

Number of obs: 246, groups: data\$Location, 14

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	-1.48402	0.75195	168.12000	-1.974	0.050070 .
data\$PredatorSpeciesNumber	0.07505	0.01429	9.73000	5.253	0.000407 ***
data\$SVL	0.04875	0.01229	186.99000	3.966	0.000104 ***

 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	dt\$PSN
dt\$PrdtrSpN	-0.009	
data\$SVL	-0.978	-0.173

Linear mixed model fit by REML. t-tests use Satterthwaite's method [`'lmerModLmerTest'`]
 Formula: `data$ClutchVolume ~ data$PredatorSpeciesNumber + data$SVL + (1 | data$Location)`

REML criterion at convergence: 3998.4

Scaled residuals:

Min	1Q	Median	3Q	Max
-1.4845	-0.7438	-0.2338	0.5773	4.3531

Random effects:

Groups	Name	Variance	Std.Dev.
data\$Location	(Intercept)	14009	118.4
	Residual	735291	857.5

Number of obs: 246, groups: data\$Location, 14

Fixed effects:

	Estimate	Std. Error	df	t value	Pr(> t)
(Intercept)	-970.72	656.43	183.32	-1.479	0.14091
data\$PredatorSpeciesNumber	40.77	12.08	14.43	3.376	0.00436 **
data\$SVL	22.68	10.74	197.54	2.111	0.03600 *

 Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Correlation of Fixed Effects:

	(Intr)	dt\$PSN
dt\$PrdtrSpN	-0.001	
data\$SVL	-0.979	-0.177

6. *AIC tables of linear mixed effect models of clutch size and linear models of clutch volume*

Table 4. AIC for seven linear mixed effect models constructed to explain clutch size

Model	AICc	Δ AICc	Akaike Weight
CS ~ P + SVL + (1 Location)	714.703	0.000	0.687
CS ~ NDVI +SVL+ (1 Location)	716.997	2.293	0.218
CS ~ SVL + (1 Location)	719.623	4.920	5.871x10 ⁻²
CS ~ P + (1 Location)	720.750	6.047	3.342x10 ⁻²
CS ~ NDVI + (1 Location)	727.220	12.517	1.315x10 ⁻³
CS ~ B + SVL + (1 Location)	727.674	12.971	1.049x10 ⁻³
CS ~ B + (1 Location)	739.570	24.867	2.737x10 ⁻⁶

CS = Clutch Size, P = Predator Richness, B = Biomass of Arthropods, SVL = maternal snout-vent length. Models were compared with their AICc values and their associated Akaike weight which is calculated by equation:

$$W_i(AIC) = \exp(-0.5\Delta_i(AIC)) / \sum_{k=1}^k \exp(-0.5\Delta_k(AIC)) \text{ (Turkheimer et al. 2003).}$$

Table 5. AIC for seven linear models constructed to explain clutch volume

Model	AIC	Δ AIC	Akaike Weight
CV ~ P + SVL	4030.073	0	0.753
CV ~ P	4032.505	2.432	0.223
CV ~ B+SVL	4037.205	7.132	2.128x10 ⁻²
CV ~ SVL	4042.707	12.634	1.359x10 ⁻²
CV ~ B	4043.606	13.533	8.668x-10 ⁻⁴
CV ~ NDVI + SVL	4043.926	13.853	7.386x10 ⁻⁴
CV ~ NDVI	4049.325	19.252	4.967x10 ⁻⁵

CV = Clutch Volume, P = Predator Richness, B = Biomass of Arthropods, SVL = maternal snout-vent length. Models were compared with their AICc values and their associated Akaike weight which is calculated by equation:

$$W_i(AIC) = \exp(-0.5\Delta_i(AIC)) / \sum_{k=1}^k \exp(-0.5\Delta_k(AIC)) \text{ (Turkheimer et al. 2003).}$$