Reproductive Biology of Insular Reptiles: Marine Subsidies Modulate Expression of the "Island Syndrome"

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Differences in ecological conditions can result in the evolution of dramatic inter-population shifts in whole suites of traits. We studied variation in reproductive output in three lizard populations of the Skyros Wall Lizard (*Podarcis gaigeae,* Lacertidae) endemic to the Skyros Archipelago (Greece), which live under similar climatic conditions but differ in predation pressure and food availability. Based on the "island syndrome" hypothesis, we predicted that females from island populations would produce larger, but fewer offspring. The study populations differ conspicuously in average body size, with males from the satellite Lakonissi and Diavates islets being respectively 20% and 39% larger than males from the main Skyros Island. Lizards from these predator-free islets produced eggs of larger size than the main Skyros population; however, they also produced significantly larger clutches than the Skyros population (2.31 ± 0.83 and 2.73 ± 1.0 vs. 1.97 ± 0.58 eggs). All inter-population differences in clutch size, clutch volume, and egg size were explained by corresponding differences in average body size of the dams, revealing that across all populations, reproductive effort scaled similarly with maternal body size. There was no evidence of trade-offs between egg size and clutch size as generally encountered in many reptile taxa. The occurrence of this unusual pattern of reproductive investment among islet populations of giants is probably best explained by the occurrence of two underlying drivers: first, the substantial marine subsidies by resident seabird colonies and second, the existence of intense cannibalistic behaviors in the form of attacks to the tail and severe intraspecific predation on juveniles. This suggests that subsidies-driven gigantism in island endemics may free species from such trade-offs and allow a population to maximize reproductive output in multiple, normally conflicting dimensions.

THE reproductive output of an organism is the final outcome of multiple interacting aspects of life history that are themselves subject to trade-offs. Within-species variations in life history traits have been documented in many taxa (Sinervo, 1990; Niewiarowski, 1994) and are generally interpreted to be phenotypic adaptations to varying ecological and environmental conditions such as climate, food availability, predation pressure, and competition (Jones et al., 1987; Niewiarowski and Dunham, 1994).

Body size, clutch size, and egg size are basic components of an organism's life history (Dunham et al., 1988) and are tightly intertwined in reptiles (Shanbhag et al., 2000). Increases in female body size generally translate into greater clutch mass, as the latter can be constrained either by limits in maternal body volume (Vitt and Congdon, 1978) or shape (Forsman and Shine, 1995). Nonetheless, it is not always clear whether increased reproductive investment in larger females should translate into larger clutches of conventionally sized eggs (Sinervo et al., 2000) or into the same number of larger eggs (Parker and Begon, 1986).

Island populations have been frequently used for studies of ecological and evolutionary relationships (MacArthur and Wilson, 1967; Roughgarden, 1995). Multiple genetic and environmental processes act simultaneously to create combinations of unusual phenotypes often referred to as the "island syndrome" (Adler and Levins, 1994). Probably the most widely recognized hallmark of the "island syndrome" is a shift to the production of fewer, but larger offspring (Smith and Fretwell, 1974; Blondel, 2000). This near-universally observed decline in reproductive output in isolated island populations has been documented in reptiles (Knapp et al., 2006), birds (Clegg and Owens, 2002), as well as in marsupial (Sale et al., 2009) and placental mammals (Goltsman et al., 2005). The process underpinning this phenomenon is thought to be a relaxation in predation pressure leading to inflated population densities (Rodda et al., 2001), reduced food availability (Brown and Pérez-Mellado, 1994), and concomitant increases in intraspecific competition (Wu et al., 2006). The latter have been shown to elevate juvenile mortality (Wagner and Wise, 1996) and select for the production of larger juveniles at the expense of clutch size (Melton, 1982). Larger offspring perform better physiologically (Olsson et al., 2002), and are thought to be of better "quality" (Lack, 1954) and more competitive than smaller offspring (Stamps, 1988).

Recent research has shown that small islands receive important nutrient contributions termed "marine subsidies" from surrounding marine ecosystems (Anderson and Polis, 1999; Barrett et al., 2005). Such nutrients, imported by fish-eating seabirds in the form of guano, fish scraps, or bird carcasses to their nesting sites (Polis and Hurd, 1996), subsidize local plant, arthropod, and eventually lizard communities (Sanchez-Piñero and Polis, 2000). Despite recent recognition of the importance of such subsidies, their effects on the physiology and life history of resident island populations are not well understood.

In this study we assess the effects of insularity on reproductive strategy in three populations of the Skyros Wall Lizard (*Podarcis gaigeae*), a lacertid lizard endemic to

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the Skyros Archipelago (Greece). These populations share the same climatic conditions but differ in crucial ecological factors such as predation pressure, food abundance, and intraspecific competition (Pafilis et al., 2009a). The particular physical setting, with the central island of Skyros being so much larger than the surrounding islets and acting as a *de facto* mainland, in combination with the wide range of body sizes found among the study populations (Pafilis et al., 2009a), offers the opportunity to investigate how insularity and changes in body size shape reproductive allocation in small populations. Here we compare females from three populations, one from the main land mass (Skyros) and two from small satellite islets (Lakonissi, Mesa Diavates). By comparing patterns of body size and reproductive allocation in these three populations, we evaluate whether reproductive strategies shaped by island gigantism follow the predictions of the ''island syndrome'' model. We also test whether widely accepted predictions of life history theory regarding trade-offs between size and number of offspring hold in island endemics.

MATERIALS AND METHODS

Study species and area.—*Podarcis gaigeae* is endemic to the Skyros Archipelago (Central Aegean Sea, Greece, Fig. 1). The species is a widespread small-bodied generalist lacertid (snout–vent length [SVL] around 60 mm, body mass 6.58±1.3 g) that feeds on a broad range of terrestrial arthropods (Valakos et al., 2008).

Our study focused on the main island of Skyros and two satellite islets, Mesa Diavates (hereinafter Diavates) and Lakonissi (Fig. 1, Table 1). All islands are covered with the same general type of thermo-Mediterranean vegetation. Skyros encompasses a variety of Mediterranean habitats including maquis, pine forest, farmland, and phrygana (xerophytic dwarf scrub) communities. The vegetation of Lakonissi is predominately shaped by goat grazing and consists of phrygana and some evergreen scrubs (*Pistacea lentiscus*; Snogerup and Snogerup, 2004). Diavates, which is not grazed, is covered by dense herbaceous vegetation characterized by nitrophilous species (Bohling et al., 2002).

Vertebrate species communities on the study islands.—Skyros is characterized by a general dearth of avian or mammalian predators (Table 1). The main lizard predators in Mediterranean islands are snakes (Pafilis et al., 2009b). Skyros hosts only four species that include lizards in their diet, in sparse populations (Cattaneo, 2010). Predation is even further relaxed on Lakonissi and Diavates: no snakes or mammalian predators exist on either of the islets. A small colony of Eleonora's falcons (*Falco eleonorae*) nests on Diavates; however, these falcons are specialized predators and generally do not feed on lizards. Competition is relaxed: the main other lizard taxa on Skyros are *Lacerta trilineata, Hemidactylus turcicus,* and *Cyrtopodion kotschyi*, though none of them competes directly with the study species (Valakos and Vlachopanos, 1989; Pafilis and Valakos, 2008).

Both islets, but not Skyros proper, harbor significant gull colonies (*Larus michahellis*) that breed in larger numbers on Diavates (more than 50 pairs) than on Lakonissi (approximately ten pairs). On both islets but especially on Diavates, seabirds deposit significant amount of nutrients in the form of guano, food scraps, and carcasses, and this deposition is reflected in the relatively luxuriant vegetation (Pafilis et al., 2009a). Although some seagull species may occasionally prey on lizards, *L. michahellis* is not known to do so (Castilla and Labra, 1998; Cooper et al., 2004 and references therein).

Laboratory and field methods.—We measured snout–vent length (SVL) on 175 preserved adult female *P. gaigeae* lodged at the herpetological collection of the Zoological Museum of Bonn (Germany): 87 males and 40 females from Skyros, 14 males and 6 females from Diavates, and 22 males and 6 females from Lakonissi. We also captured by noose and measured SVL in 324 adult lizards in the field (96 males and 62 females from Skyros, 55 males and 37 females from Diavates, and 42 males and 32 females from Lakonissi) during their reproductive period (early spring to midsummer).

A subset of 85 gravid females (33 from Skyros, 26 from Lakonissi, and 26 from Diavates) from field captures were transferred and held under species-appropriate conditions (Pafilis et al., 2007) in individual terraria at the laboratory facilities of the Biology Department at the University of Athens until oviposition occurred. Terraria were checked daily and any eggs found were immediately removed, measured, and placed in an incubator. We recorded egg volume, clutch size, total clutch volume, and abdominal cavity volume. Egg volume was calculated by first measuring egg size (along the longest and shortest axes) to the nearest 0.1 mm and using the equation for volume (V) of an ellipsoid: $V = (4/3) \pi a b^2$, where a is half the longest axis and b is half the shortest axis (Mayhew, 1963). Total clutch volume was calculated as the product of clutch size and egg volume. To determine abdominal cavity volume for each female, we measured the girth and length of the torso between fore- and hind limbs (interlimb length) to the nearest 0.5 mm. The volume of the abdominal cavity was calculated by applying the formula for volume of the cylinder, where interlimb length equaled the length of the cylinder and girth equaled the twice the radius (Shine, 1992).

Statistical analyses.—We tested all variables for deviations from normality; if needed, variables were log-transformed appropriately (Zar, 1984). We used one-way analysis of variance (ANOVA) or analysis of covariance (ANCOVA) tests to evaluate the effects of population identity on various life history and reproductive biology traits. These were followed by Tukey *post-hoc* tests on specific inter-population differences. Morphological differences between sexes were evaluated using t-tests, relationships between different continuous variables using correlation analyses. All statistical analyses were conducted using PASW-18.0 (SPSS Inc., 2010).

RESULTS

Body size.—SVL differed significantly between the three islands populations for both females ($F_{2,180} = 172.44$, $P < 0.001$; Table 1) and males ($F_{2,315} = 592$, $P < 0.001$; Table 1). Both males and females from Lakonissi and especially Diavates attained very large body sizes that were significantly different from each other as well as from Skyros (females: $P < 0.001$ for all inter-population contrasts, Tukey; males: $P < 0.001$ for all inter-population contrasts, Tukey), and that were well outside the norm for lizards in the genus *Podarcis*. These inter-population differences in body size were also paralleled in significant differences among several metrics of body size for the gravid females we examined (for SVL: $F_{2,82} = 66.67$, $P < 0.001$; dam trunk length: $F_{2,82} = 29.34$, $P < 0.001$; and dam trunk volume $F_{2,82} = 17.292$, $P < 0.001$, one-way
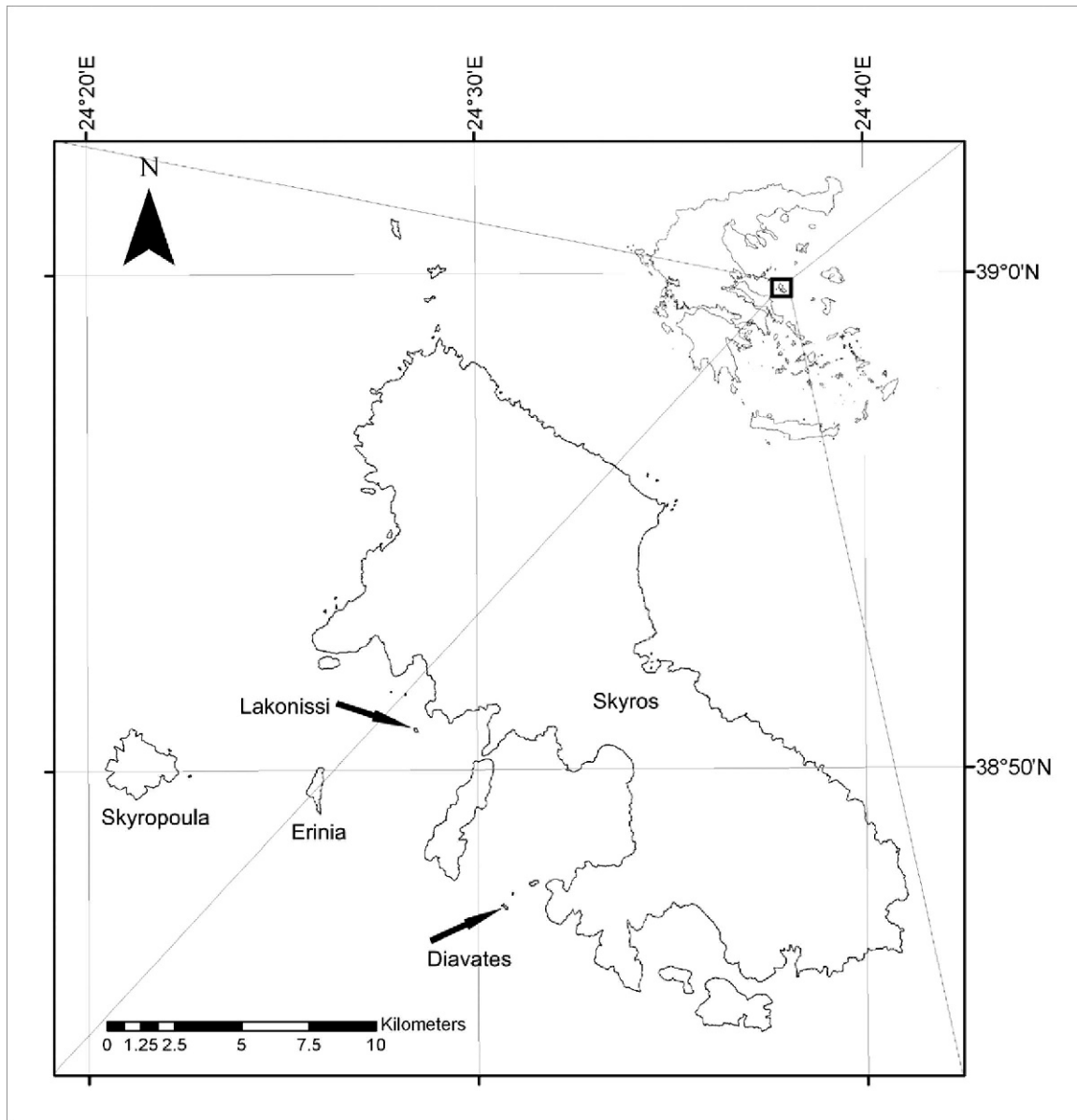
Fig. 1. Map of the study area. The Skyros cluster is located on a distinct shelf in the central Aegean Sea (Greece), NE Mediterranean Basin.

ANOVA). This means that females from Diavates and Lakonissi were substantially larger than Skyros animals both for SVL (25.3% and 11.9%, respectively) and trunk length (23.8% and 9.39%, respectively). *Post-hoc* comparisons revealed that each population was significantly different from both others in respect to: SVL ($SVL_{Skyros} = 56.93 \pm 4.45$ mm, $n = 33$ vs. $SVL_{Lakonissi} = 62.13 \pm 4.95$ mm, $n = 26$ vs. $SVL_{Diavates} = 72.21 \pm 5.89$ mm, $n = 26$, $P < 0.01$, Tukey), and dam trunk length ($trunk_{Skyros} = 32.15 \pm 4.02$ mm, $n = 33$ vs. $trunk_{Lakonissi} = 35.17 \pm 2.95$ mm, $n = 26$ vs. $trunk_{Diavates} = 39.82 \pm 4.29$ mm, $n = 26$, $P \leq 0.01$, Tukey). However, in regard to dam trunk volume, Lakonissi females were not statistically different from Skyros females ($P = 0.546$, Tukey); all other pairwise comparisons were statistically significant ($P < 0.001$, Tukey; Table 1.)

Lizard clutch size.—Ln-transformed clutch size differed significantly between the three populations ($F_{2,82} = 5.210$, $P < 0.007$, one-way ANOVA). While clutches both on Lakonissi and especially on Diavates tended to be larger than on the Skyros (Table 1), *post-hoc* tests suggested that

only the difference between Diavates and Skyros was significant ($P < 0.005$, Tukey). Clutch size has been shown to depend closely on maternal SVL both in other (Barbault and Mou, 1988; Shanbhag et al., 2000), as well as in this species ($r = 0.447$, $P < 0.001$, $n = 85$, Pearson, Fig. 2). Since maternal body size differs strongly between islands, we repeated this analysis in an ANCOVA format correcting explicitly for SVL. Once differences in maternal body size were taken into account, inter-population differences in clutch size disappeared ($P_{Population} = 0.934$, $F_{2,85} = 0.068$, $R^2 = 0.175$, ANCOVA). Maternal body size appears hence to be the underlying factor explaining differences in clutch size between the study populations. However, in individual within-population analyses, this relationship was not significant (Skyros: $r = 0.068$, $P = 0.709$, $n = 33$, Lakonissi: $r = 0.319$, $P = 0.113$, $n = 26$, Diavates: $r = 0.369$, $P = 0.064$, $n = 26$, Pearson), instead suggesting that within each population, other factors, including health status, general condition, or reproductive history may be more important.

Table 1. Life-History Traits, Morphological Features, and Ecological Factors for the Three Populations. Predators include snakes: (1) *Zamenis situlus;* (2) *Elaphe quatuorlineata;* (3) *Telescopus fallax;* (4) *Natrix natrix* and birds: (1) *Buteo buteo;* (2) *Falco tinnunculus;* (3) *Falco eleonorae;* (4) *Athene noctua;* (5) *Lanius senator;* (6) *Corvus* sp. Supporting references for the main lizards predators: Watson, 1964; Handrinos and Akriotis, 1997; Cattaneo, 1998, 2010. Data on predator diversity, cannibalism, and tail damage are adapted from Pafilis et al. (2009a).

	Skyros	Lakonissi	Diavates
	Mean±SD; *n*; (range)	Mean±SD; *n*; (range)	Mean±SD; *n*; (range)
SVL males (mm)	61.43±4.92; 183; (51.7–73.3)	72.13±5.3; 64; (57.3–79.7)	85.34±2.9; 69; (77.9–90.3)
SVL females (mm)	55.7±4.2; 102; (45.1–65)	62.35±3.9; 38; (51–69.4)	69.8±5.5; 43; (53.7–79.3)
Trunk volume (mm³)	36,232±9,371; 33; (18,513–54,703)	39,555±5,947; 26; (29,307–49,796)	54,082±18,083; 26; (15,893–85,223)
Clutch size	1.96±0.6; 33; (1–3)	2.35±0.8; 26; (1–4)	2.81±1.0; 26; (1–5)
Egg volume(mm³)	369.7± 152.2; 33; (179.8–975.0)	468.3±177.8; 26; (234.3–1146.9)	515.6± 120.7; 26; (289.4–715.58)
Clutch volume (mm³)	706.5± 317.0; 33; (344.1–1653.0)	1083.9±466.3; 26; (360.8–1940.8)	1515.8± 774.1; 26; (406.6–2905.1)
Damaged tails	31.92%; 285	68.62%; 102	88.39%; 112
Cannibalism	1.15%; 87	4.54%; 22	21.42%; 14
Predators	Snakes: 1, 2, 3, 4	—	Birds: 3
	Birds: 1, 2, 3, 4, 5, 6		
Island size (km²)	210	0.016	0.019
Distance from Skyros (m)	—	666	1400

Egg volume.—Two unusual clutches consisting of exceptionally large (975 mm³ and 1146 mm³), irregularly shaped, and infertile (possibly because of damages caused by the pelvic girdle when the unusually large eggs were exiting the body cavity) single eggs were excluded from all analyses. Average egg volume differed significantly between the three study populations ($P = 0.003$, $F_{2,80} = 6.448$, one-way ANOVA). *Post-hoc* tests, however, indicated that the only significant difference was between the Diavates and Skyros populations ($P < 0.002$, Tukey; Table 1). Average egg volume from Skyros females was significantly smaller than that from islet (Lakonissi and Diavates) females ($EggVolume_{Skyros} = 354.7 \pm 116$ mm³ [$n = 32$] vs. $EggVolume_{Islets} = 475.6 \pm 130$ mm³

Fig. 2. Relationship of clutch size to maternal body size (measured as snout–vent length). Lines represent slope of the regression for each population.

[$n = 51$], t = -4.272, $P < 0.001$, indep. samples t-test). Average egg size from Lakonissi and Diavates was respectively 26.8% and 39.5% larger than from Skyros. Average egg volume was significantly correlated to maternal SVL for the pooled sample ($r = 0.465$, $P < 0.001$, $n = 83$, Pearson, Fig. 3), as well as for animals from Skyros and Lakonissi (Skyros: $r = 0.401$, $P = 0.023$, $n = 32$, Lakonissi: $r = 0.486$, $P = 0.014$, $n = 25$, Pearson), but not for those from Diavates ($r = 0.181$, $P = 0.377$, $n = 26$, Pearson). Once maternal body size was taken into account, egg volume differences between the three populations became non-significant ($P_{population} = 0.433$, $F_{2,80} = 0.846$, $R^2 = 0.331$, ANCOVA) suggesting that egg size scaled to maternal body size in the same fashion across populations.
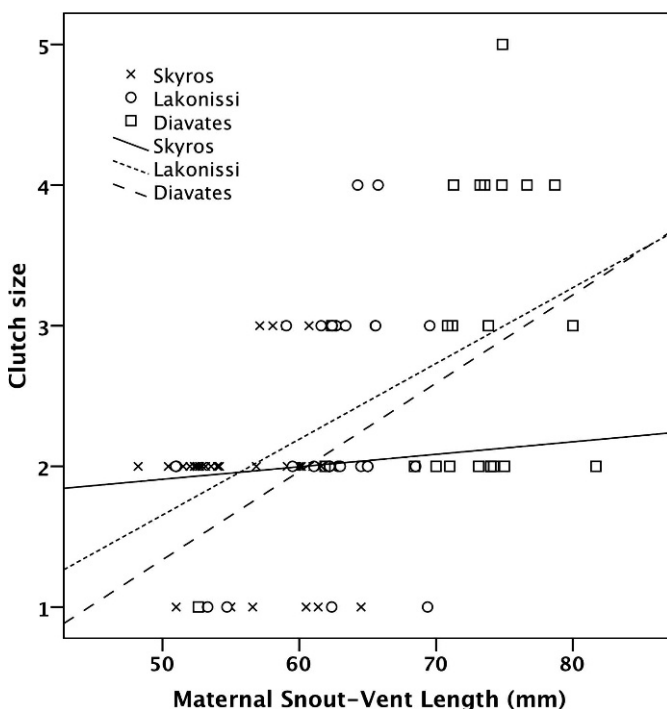
Clutch volume.—Log-transformed clutch volume differed significantly between the three populations ($P < 0.001$, $F_{2,82} = 14.6$, one-way ANOVA), with Skyros animals producing the least, and Diavates the most voluminous clutches (Table 1). *Post-hoc* analyses showed that all of these interpopulations differences were significant ($P < 0.02$, Tukey; Table 1), with the exception of the difference between Diavates and Lakonissi which was marginally non-significant ($P = 0.055$, Tukey). Average clutch volume from Lakonissi and Diavates animals was respectively 48.2% and 107% above that of the Skyros population. These increases were the result of corresponding increases in both clutch size and average egg volume in these populations (see above). Clutch volume was positively correlated to maternal body size for the aggregate sample ($r = 0.605$, $P < 0.001$, $n = 85$, Pearson), as well as for Skyros and Lakonissi populations, but not for the Diavates animals (Skyros: $r = 0.353$, $P = 0.044$, $n = 33$; Lakonissi: $r = 0.558$, $P = 0.003$, $n = 26$; Diavates:s $r = 0.311$, $P = 0.122$, $n = 26$; Pearson; Fig. 4).

Trade-offs between clutch size and average egg volume.—In lacertid lizards, both clutch size and egg volume are correlated to maternal SVL (in den Bosch and Bout, 1998). To evaluate trade-offs between clutch size and egg volume we therefore need to first account for the confounding effects of maternal body size. We follow Olsson and Shine (1997) and first regressed log$_e$-transformed clutch size on
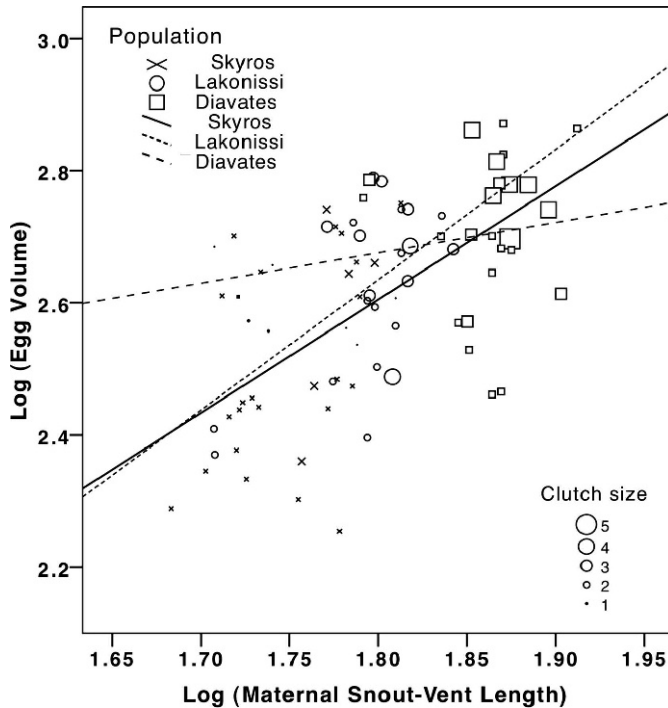
Fig. 3. Relationship between average egg volume (in mm³, Log_{10}-transformed) and maternal body size (measured as snout–vent length in mm, Log_{10}-transformed). Two exceptionally large single eggs are not shown in this graph. Lines represent slope of the regression for each population.

Fig. 4. Relationship between average clutch volume (in mm³, Log_{10}-transformed) and maternal body size (measured as snout–vent length in mm, Log_{10}-transformed). Lines represent slope of the regression for each population.

maternal SVL. We then correlated these residuals to log_e-transformed average egg volume. No significant relationship between these two variables was found for the combined sample size ($r = -0.013$, $P = 0.906$, $n = 83$, Pearson). We then repeated this analysis for each population; again we failed to detect any significant relationship indicative of trade-offs between clutch size and egg size (Skyros: $r = -0.096$, $P = 0.603$, $n = 32$; Lakonissi: $r = -0.028$, $P = 0.895$, $n = 25$; Diavates: $r = 0.334$, $P = 0.095$, $n = 26$, Pearson).

DISCUSSION

This study documents remarkable differences in body size, clutch size, egg volume, and clutch volume across three populations of *P. gaigeae*. We found a pronounced increase in clutch size in small islet populations, in a pattern that represents a striking departure from the classic ''island syndrome'' rule. We failed to detect the presence of a generally recognized clutch-size versus egg-size trade-off either within or between the island populations examined.

A substantial body of research has documented the close relationship between maternal body size and total reproductive output in reptiles (Vitt and Congdon, 1978; Shine, 1992). Our data mirror these findings with maternal body size being highly correlated with total clutch volume both between and within the populations studied, with the exception of Diavates females. For the Diavates population, some females clearly do not produce large enough clutches as can be accommodated by the space available in their body cavity, possibly because of variation in previous reproductive investments. A possible explanation for this is that reproductive investment in not limited by the space available in the body cavity, but rather other factors such as food availability or infection with pathogens or parasites (Foufopoulos, 1999).
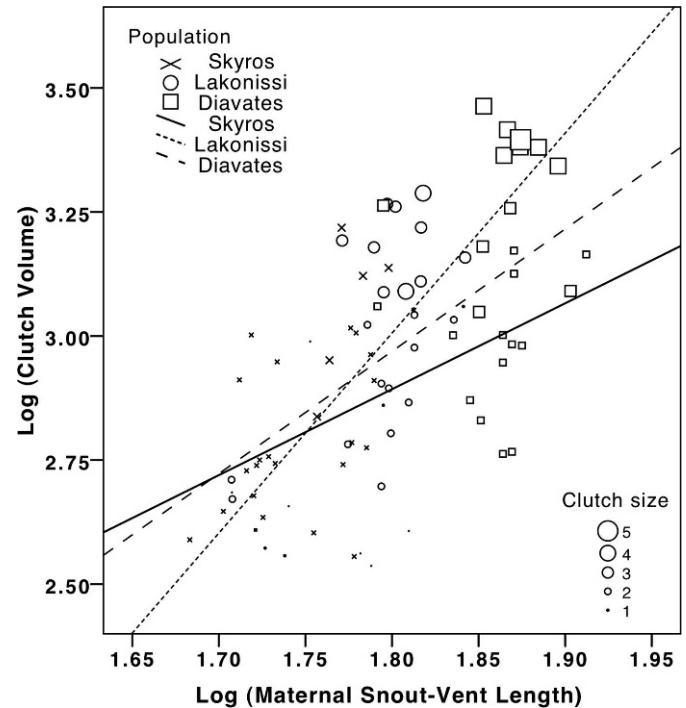
Both empirical data (Brown and Shine, 2009) and theoretical considerations (McGinley, 1989) suggest a positive relationship between maternal body size and average egg volume in squamates. When we analyzed all three populations together, a broad pattern emerged with larger-bodied populations also producing larger young (Fig. 3), suggesting that there is no species-wide optimal offspring size. Even within individual populations, the average egg volume varied widely (e.g., 59.6% in the case of Diavates), indicating that even if there is an optimum size for each population it is perhaps not easily achievable. When each population was considered individually, a positive correlation between dam size and average egg volume was found in the Skyros and Lakonissi animals but not in the giant Diavates population. It is possible that for the Diavates females, located at the far end of the size spectrum, production of even larger offspring does not bestow increased reproductive success.

If larger offspring are more fit as suggested in the literature (Stamps, 1988; Sinervo and Huey, 1990), then why don't more small-bodied females produce larger eggs? One hypothesis put forth in the literature (Stewart, 1984; Congdon and Gibbons, 1987) is that physical limitations such as pelvic girdle structure may prevent a female from producing offspring of the optimal size. Although we can't completely rule out this possibility, it appears that for *P. gaigeae,* this is unlikely to be important, as we documented at least two cases where relatively small-bodied females produced normal-volume clutches consisting of single, extraordinarily large eggs. Therefore it seems unlikely that dimensional limits keep small-bodied females from producing large eggs. Alternatively it is possible that smaller-bodied females preferentially allocate resources towards somatic growth, and thus future reproduction, rather than large offspring size.

Multiple studies have shown that in lizards (with a few important exceptions) clutch size is positively related to dam SVL (Bauwens and Verheyen, 1987; Castilla and Bauwens, 1989; Shanbhag et al., 2000). In *P. gaigeae*, the prominent inter-population differences in clutch size can be attributed to equally striking differences in SVL, although within each population this relationship largely disappears. This lack of a relationship was particularly notable on Skyros where we found clutch size to be largely invariant (two eggs in 67% of clutches). Similarly small clutch sizes also have been reported for the sister taxon *P. milensis* (Adamopoulou and Valakos, 2000).

In reptiles, trade-offs between egg size and clutch size are widespread though not universal (Dunham et al., 1988; Uller et al., 2009); the most common factors underlying such trade-offs are thought to be either space constraints or nutritional/ energetic limitations occurring during clutch production. Whether examining each population separately or all together, we did not detect any evidence for trade-offs between egg and clutch size. The most likely explanation for this pattern is that there is high variation in resource acquisition, since the study islands are inhomogeneous in terms of food availability. Thus energy input in each island varies, and the same goes for the proportion of energy that would be allocated for reproduction (Uller and Olsson, 2005).

The "island syndrome" is a term used to describe a loose constellation of life history traits commonly observed in lineages that have evolved in island environments. Typically, they encompass sharp reductions in the number and an increase in the size of egg size produced. Although our study populations follow in many aspects the predictions of this model, they fail to conform to the basic tenant of the syndrome, thus the reduction in the number of offspring from mainland to island populations (Castilla and Bauwens, 2000; Galán, 2003; Galán and Vicente, 2003). Such a reduction is generally interpreted as the price paid for shifting reproductive effort toward the production of larger, higher-quality offspring (Sinervo and Huey, 1990). Here, while the islet populations of *P. gaigeae* produce significantly larger eggs than those on Skyros, the dramatic increases in maternal body size have apparently allowed for a relaxation of the egg size vs. clutch size trade-off and have allowed for the production of both larger clutches and larger offspring. Hence in the islet populations, increases in maternal body size are so pronounced that they override the generally observed pattern of clutch reduction in small island environments.

What factors might be responsible for the observed patterns in morphology and reproduction in Lakonissi and Diavates? A recent analysis (Pafilis et al., 2009a) revealed that increases in average body size of *P. gaigeae* are tightly correlated with the amount of marine subsidies transferred to an island ecosystem through nesting seabirds, as well as with the degree of intraspecific predation and cannibalism.

Seabirds transport nutrients from sea by feeding on fish and then nesting on islands where they enhance the system with their dead bodies, fish scraps, and large amounts of nitrogen-rich guano (Polis and Hurd, 1996; Sanchez-Piñero and Polis, 2000). Nitrogen is believed to be the key factor for terrestrial systems (Huberty and Denno, 2006), affecting primary productivity and plant nutrient content (Wait et al., 2005; Kolb et al., 2010). Herbivore and detritivore invertebrates develop dense populations since they have access to highly abundant food sources and consequently subsidize consumers of higher levels, like lizards (Barrett et al., 2005). Marine nutrient subsidies vary substantially between the populations. Every spring Diavates hosts a thriving breeding colony of seagulls, which outnumbers that of Lakonissi, while no nests were found at the main island of Skyros (Pafilis et al., 2009a). Guano accumulation, seafood remains, and gull carcasses are naturally fertilizing soil at Diavates, thus augmenting food availability. Access to abundant resources is associated in reptiles with both enhanced somatic growth (Stamps and Tanaka, 1981) and egg size (Doughty, 1996), and in island populations high food availability is associated with gigantism (Goltsman et al., 2005). It is thus likely that the combination of seabird subsidies and reduced grazing by goats ease nutritional constraints that select against large body sizes and extravagant reproductive investments.

Reduced predation pressure on island reptiles translates frequently into very high reptile population densities, intense food competition, and evolution of aggressive foraging strategies and cannibalism behaviors (Pafilis et al., 2008; Vervust et al., 2009). In lacertids, cannibalistic behaviors include preying on autotomizable tails and attacks on conspecific juveniles (Castilla and Van Damme, 1996). Whereas only very low-level cannibalism had been recorded in *P. gaigeae* on Skyros (Adamopoulou et al., 1999), very high levels were recently discovered in the Lakonissi and Diavates populations (Pafilis et al., 2009a). Examination of stomach contents from Diavates revealed the regular occurrence of both entire juveniles and semi-digested body parts. These findings dovetailed with a parallel rise in the levels of autotomized and regenerated tails, which range from very low rates on Skyros to extremely high ones on Diavates (Table 1). Because cannibalism is generally a size-dependent process, it favors the evolution of gigantism through several discrete pathways: larger juveniles have better chances to escape infanticide and survive while larger male adults are more effective in attacking offspring and also have access to females (Pafilis et al., 2009a). In turn, the evolution of larger adult body sizes removes any morphological constraints for larger reproductive investments in females. Simultaneously because cannibalism is also a probabilistic process, it maintains strong selective pressure for the production of many offspring, thus setting the stage for the larger clutch sizes documented in the Lakonissi and Diavates populations.

MATERIAL EXAMINED

Podarcis gaigeae (Skyros Archipelago, Greece) from the Herpetological Collections of the Zoological Museum Alexander Koenig at Bonn, Germany. Skyros Island, ZFMK 10903–11031; Lakonissi, ZFMK 11032–11059; Mesa Diavates, ZFMK 11060–11080.

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