Russian Journal of Herpetology Vol. 28, No. 4, 2021, pp. 225 – 230

SHORT COMMUNICATIONS

DOI: 10.30906/1026-2296-2021-28-4-225-230

THE ISLAND OF EXTREMES: GIANTS AND DWARFS ON A SMALL REMOTE ISLAND

Yuval Itescu,[1,2] Johannes Foufopoulos,[3] Rachel Schwarz,[2] Petros Lymberakis,[4] Alex Slavenko,[2] Ioanna-Aikaterini Gavriilidi,[5] Shai Meiri,[2,6] and Panayiotis Pafilis[5]

Submitted October 10, 2019

Body size evolution on islands is widely studied and hotly debated. Gigantism and dwarfism are thought to evolve under strong natural selection, especially on small remote islands. We report a curious co-occurrence of both dwarf and giant lizards on the same small, remote island (Plakida): the largest *Podarcis erhardii* (Lacertidae) and smallest *Mediodactylus kotschyi sensu lato*; Gekkonidae — the two commonest insular reptiles in the Aegean Sea. The geckos of Plakida have a peculiar tail-waving behavior, documented here for the first time in this genus. We suspect that *P. erhardii* evolved large size to consume geckos and the geckos evolved a unique tail-waving behavior as a defensive mechanism.

Keywords: Aegean Sea islands; body size; geckos; lizards; tail autotomy; tail waving.

Extreme body sizes (gigantism and dwarfism), have been widely documented on islands (Meiri et al., 2011). The evolution of body size on islands has been frequently studied and hotly debated (Lomolino, 2005; Itescu et al., 2014, 2018a; Lokatis and Jeschke, 2018). Body size changes are often hypothesized to become more extreme as island area diminishes and isolation increases, because species experience ecological release from predators and competitors (Dayan and Simberloff, 1998). However, several studies showed reptiles often do not follow this pattern (Meiri, 2007; Itescu et al., 2014, 2018a).

[1] Institute of Biology, Freie Universität Berlin, Berlin D-14195, Germany; e-mail: yuvitescu@gmail.com

[2] Department of Zoology, Tel Aviv University, Tel Aviv, 6997801, Israel.

[3] School for Environment and Sustainability, University of Michigan, Ann Arbor, MI 48109, USA.

[4] Natural History Museum of Crete, University of Crete, Knossos Av., P. B. 2208, Irakleio, Crete, 714-09, Greece.

[5] Department of Biology, National and Kapodistrian University of Athens, Athens 157-84, Greece.

[6] The Steinhardt Museum of Natural History, Tel Aviv University, Tel Aviv, 6997801, Israel.

The lizards *Mediodactylus kotschyi sensu lato* and *Podarcis erhardii*, are the two most widespread and abundant reptile species in the Aegean Archipelago (Greece) (Itescu, 2017). We report the curious co-occurrence of the most extreme-sized forms of these two species on a single small, remote islet. We further report an unusual behavior exhibited by the geckos.

Plakida (36°17′06″ N 26°44′42″ E) is a small (0.52 km^2) island in the southeastern Aegean Sea (Fig. 1). It comprises a low rounded limestone back, covered by a thin soil layer, mostly in the northern side of the island. The island is part of the Tria Nissia Cluster, in an arid (<300 mm/year) region of the Aegean Sea which is exposed to strong winds year-round. It is highly isolated both in space (70.5 km from the closest mainland; 6.5 km from the closest larger island: Syrna; Fig. 1) and in time: it is estimated to have last been connected to Syrna about 200,000 years ago, and not to have been connected to the mainland since the end of Messinian crisis, approximately 5.3 million years ago (see maps in Poulakakis et al., 2014). The vegetation comprises of low bushes (chiefly *Pistacea lentiscus* and *Juniperus phoenicea*) and

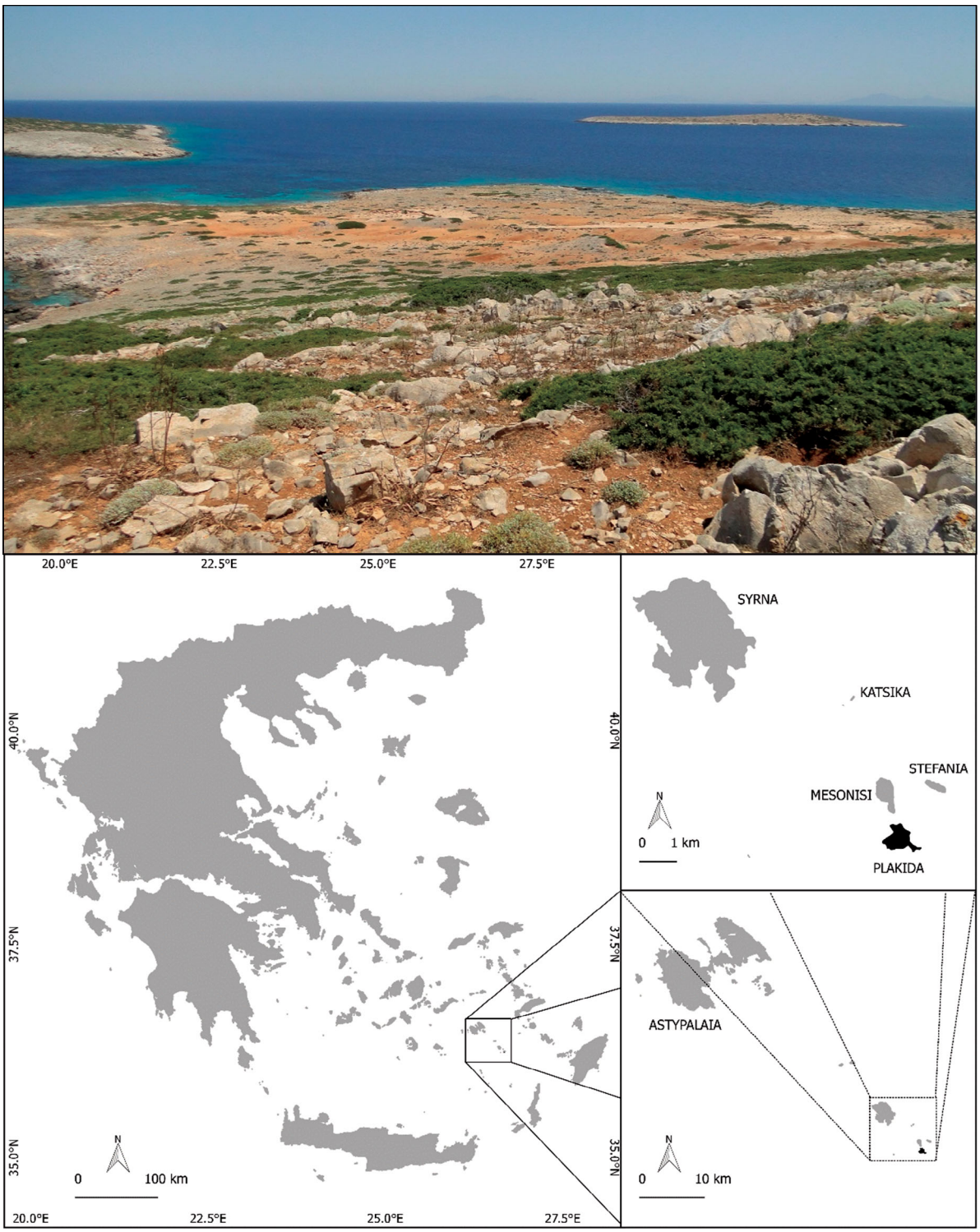

Fig. 1. A general view and the location of Plakida Island, photo: Johannes Foufopoulos.

annuals (Fig. 1). The island harbors a depauperate avifauna (authors' pers. obs.).

Because of the relatively low seabird breeding numbers the island probably receives relatively few nutrients

from marine sources ('marine subsidies', Polis and Hurd, 1996), which are often implicated in reptile gigantism (Pafilis et al., 2009; Richardson et al., 2019). The island is inhabited by invasive rabbits and goats, and according to locals, until recently, feral cats (now removed from the island, but possibly have had an impact on its ecology). Rats (*Rattus* spp.), which inhabit many small islets in the Aegean Sea (Masseti, 2012), are absent (authors' personal observation). Rabbits and goats severely overgrazed the island's vegetation, and much of the native vegetation is damaged. Consequently the island experiences strong levels of soil erosion and has lost ca. >10 cm of soil in the last 80 years.

Otto von Wettstein visited the island in May 1935 and provided the only report on the ecology and reptiles of Plakida to date (Wettstein, 1937). He reported that the only reptiles on this island were the gecko *M. kotschyi* and the lacertid *P. erhardii*. He further reported unusually large sizes (snout-vent length; SVL) of *P. erhardii* (up to 79.5 mm) from Plakida and very small sizes for *M. kotschyi* from nearby small islets (e.g., up to 36.5 mm in Megalo Zofrano) — but provided no data on geckos from Plakida.

To understand whether the size of *P. erhardii* on Plakida is indeed extremely large, and whether the geckos are also small, and thus whether similar ecological conditions can result in inverse evolutionary trajectories of the same trait, we visited and surveyed Plakida on May 19, 2015, and May 17, 2018. In our first visit we searched for reptiles from 10:30 to 14:45 and in our second visit from 15:00 to 17:00. On both occasions, we searched for animals by flipping rocks and looking inside rock crevices. We measured the SVL (using a digital caliper to the nearest 0.1 mm) and body weight (using Pesola scales to 0.1 g precision) of each individual we caught and compared them to other Aegean island populations we studied (Itescu et al., 2018a).

Recently, Kotsakiozi et al. (2018) revised the phylogenetic relationship between populations of *M. kotschyi* across its distribution range, and concluded that *M. kotschyi* is a species complex in which they were able to delineate five distinct species. The populations of the islands in Southeastern Aegean Sea were found to belong to a species these authors named *M. oertzeni*. While the population of Plakida itself was not studied by Kotsakiozi et al. (2018), a recent analysis by Schwarz et al. (2020) showed the population of Plakida belongs to this lineage as well.

Our surveys confirmed that *M. oertzeni* (Fig. 2*a*) and *P. erhardii* (Fig. 2*b*) are the only reptiles inhabiting Plakida. We captured and measured 16 adult geckos and 8 adult *P. erhardii* lizards (thus 13 individuals were recorded and measured together with those in Wettstein,

Fig. 2. The reptiles of Plakida: A, two adult female *Mediodactylus kotschyi sensu lato*: *M. kotschyi* from Schinoussa Island (left) and *M. oertzeni* from Plakida Island (right), photo by Ioanna-Aikaterini Gavriilidi; B, two adult female *Podarcis erhardii*: the smaller is from Naxos Island (left) and larger from Plakida Island (right), photo by Johannes Foufopoulos.

1937; Table 1). Data for island populations of both species (Itescu et al., 2018a; Tables 1 and 2) confirms that the Plakida *Mediodactylus* have the smallest body size among the populations of this species and this genus, whereas the lizards of Plakida are the largest *Podarcis erhardii* anywhere (Itescu et al., 2018a; Fig. 2), and second largest of their genus (after *P. gaigeae* from Exo Diavates islet, Pafilis et al., 2009; as large as *P. levendis* from Pori islet, Lymberakis et al., 2008). On Plakida, *Podarcis* are 2.15 times longer and 6.5 times heavier than *Mediodactylus*, whereas on other islands the mean ratios are 1.4

in length (n = 34) and 2.03 in mass (n = 19) (authors' personal data).

Eighteen of the 19 geckos (16 adults and three juveniles) and five of the 13 *P. erhardii* recorded had amputated or regenerated tails (95 and 38.5%, respectively; including the five *Podarcis* reported by Wettstein, 1937, of which two had autotomized tails).

We also observed a peculiar behavioral display by the geckos. After their cover (the geckos hide usually under a rock) was lifted, the Plakida geckos, both in the field and later in the laboratory (where we kept some of the animals we captured for research purposes), stood still on the ground for a couple of seconds and vividly waved their tail before running for a different cover. This behavior was not reported (and we have not observed it) in any other *Mediodactylus* population that we are aware of.

We suggest a number of hypotheses to explain these findings. Gigantism in *P. gaigeae*, a species endemic to the Skyros island cluster in northern Aegean Sea, has been linked to intense intraspecific competition and the presence of marine subsidies (Pafilis et al., 2009). There, on the small islet of Exo Diavates (38°47′20.4″ N 24°30′46.8″ E), where plenty of marine subsidies are available, the *Podarcis* population is very dense, and has evolved by far the largest body size of all the populations of this species (and indeed, the genus). On Exo Diavates, however, *M. kotschyi* are of intermediate size (adult SVL: 42.4 ± 5.6 mm, weight 2.7 ± 0.7 g; n = 17). We suspect that the mechanism that drove gigantism in Plakida's *P. erhardii* population is different from the one promoting gigantism in *P. gaigeae*. On Plakida *P. erhardii* is rare and marine subsidies are nearly absent. Wettstein (1937) reported that one of the individuals he captured (an adult male, 77 mm SVL) had consumed a gecko, the head of which hang out its mouth. Predation by *Podarcis* on *Mediodactylus* is not recorded elsewhere except for a single possible occurrence where a juvenile gecko was found in the stomach of a *P. erhardii* individual from Naxos (Valakos and Vlachopanos, 1989). An unpublished dataset collected by one of us (PP, together with Efstratios D. Valakos), of stomach contents of 1, 256 *P. erhardii* individuals from 63 Aegean island populations, including Naxos, but not Plakida, contains no gecko remains. Pafilis et al. (2009) reported that the giant *P. gaigeae* of Exo Diavates prey upon their own young, and suggested cannibalism can also drive the evolution of large size in that system. It is therefore possible that *P. erhardii* in Plakida regularly consume the much smaller geckos, which are the size of juvenile geckos from most other islands. We hypothesize they also consume their own young (considering anecdotal cannibalism in *P. erhardii*, Deem and Hedman, 2014; Madden and Brock, 2018). The nutritional advantage of this high quality food source (the geckos are still larger and more nutritious than most arthropods), may select for larger body size (Keogh et al., 2005; Meik et al., 2010), which in turn allows them to consume the geckos, resulting in a positive evolutionary feedback loop.

Alternatively, gecko dwarfism may have evolved in response to predation by *P. erhardii*. On the Plakida island cluster, geckos are ancestrally small (Kotsakiozi et al., 2018). When faced with large *Podarcis*, smaller size may allow geckos to squeeze into rock crevices the giant

TABLE 1. Body Size Measurements of Plakida lizards

Species	Sex	No. of specimens	Mean SVL, mm	SVL range, mm	No. of specimens	Mean body weight, g	Body weight range, g
Mediodactylus oertzeni	males	7	33.0 ± 0.7	30.0 – 35.8	7	1.1 ± 0.2	0.5 – 1.8
	females	9	34.3 ± 0.6	30.7 – 37.0	9	1.4 ± 0.1	1.0 – 2.0
Podarcis erhardii	males	9	71.8 ± 2.3	59.0 – 79.5	6	8.0 ± 0.6	5.7 – 9.8
	females	4	74.3 ± 3.9	63.0 – 81.0	2	7.2	5.4 – 9.0

SVL, snout-vent length.

TABLE 2. A Comparison of Lizard Populations with the Largest and Smallest Mean Body Size on Islands of the Aegean Sea

Species	Individuals in population	Size index	Largest population	No. of individuals	Mean size, mm	Smallest population	No. of individuals	Mean size, mm	Size ratio
Mediodactylus kotschyi sensu lato	86	SVL, mm	Schinoussa	57	47.9	Plakida	16	33.7	1.42
		Body weight, g			3.6			1.2	3.00
Mediodactylus oertzeni	17	SVL, mm	Megalo Pontikonissi	5	43.5	Plakida	16	33.7	1.30
Podarcis erhardii	118	SVL, mm	Plakida	13	72.6	Hydra	8	52.9	1.37

Note. Body weight comparison was possible only for *Mediodactylus kotschyi sensu lato* as we did not obtain mass data for *M. oertzeni* from Megalo Pontikonisi and for *Podarcis erhardii* from Hydra.

Podarcis cannot penetrate. The lack of stomach-contents data for Plakida reptiles does not allow us to adequately test these hypotheses.

The gecko population in Plakida has a high proportion of damaged tails (95%) and is relatively dense (7th highest in density out of 41 studied insular populations of *Mediodactylus*, Itescu et al., 2017). However, *P. erhardii* seem to be relatively rare on Plakida. The proportion of damaged tails in Plakida *Podarcis* is very low (the lowest rate among 32 other populations was 50%, Brock et al., 2015). These data are in line with findings that dense populations exhibit high tail-autotomy proportions (Brock et al., 2015; Itescu et al., 2017, 2018b) — regardless of body size (Itescu et al., 2018a). We suspect that the high autotomy rate of geckos results from inefficient predation by the lizards combined with intraspecific aggression. The gecko tail-waving behavior, which has never been reported for any other *Mediodactylus* geckos, has probably evolved to divert any potential threat from the gecko's body to its detachable tail allowing them to escape (Cooper, 1998). A similar behavior has been documented in other gecko species as a response to predation threat (e.g., Alonso et al., 2010). In some geckos, however, e.g., *Hemidactylus turcicus* which also inhabits many Aegean islands (but not Plakida), such a behavior was observed during aggressive male-male interactions and courtship (Saenz and Conner, 1996). We observed this behavior in the Plakida *Mediodactylus* population only in response to the removal of cover under which they hided, which we think the geckos interpret as posing predation threat. The common antipredator mechanisms of *Mediodactylus* geckos are camouflage (especially where they are arboreal, Schwarz et al., 2016) and tail autotomy (Itescu et al., 2017). Our observation thus potentially expands the known repertoire of antipredatory tactics in this species.

The reptiles on the small remote Plakida Island, exhibit both gigantism and dwarfism. These species co-exist on many dozens of islands in the region, and are always much more similar in size. This suggests that, even under similar environmental conditions, inverse evolutionary trajectories may develop, even in relatively simple ecosystems. It further suggests that biotic interactions have a stronger effect than abiotic conditions on body size evolution (because abiotic conditions would affect all species in a similar manner; Meiri et al., 2008). The common ecological expectation is that species that share the same habitat and ecological niche, as *P. erhardii* and *M. kotschyi* sensu lato often do, will show character displacement when co-occurring (Schoener, 1965, 1970). This seems to be happening on Plakida, while showing inverse pattern to that expected by the island rule (Lomolino, 2005). We suspect, however, that predation rather than competition, is the likely driving force in this system.

REFERENCES

Alonso M. L. B., Cotrina, J. M., Pardo D. A., Font E., and Molina-Borja M. (2010), "Sex differences in antipredator tail-waving displays of the diurnal yellow-headed gecko *Gonatodes albogularis* from tropical forests of Colombia," *J. Ethol.*, **28**(2), 305 – 311.

Brock K. M., Bednekoff P. A., Pafilis P., and Foufopoulos J. (2015), "Evolution of antipredator behavior in an island lizard species, *Podarcis erhardii* (Reptilia: Lacertidae): The sum of all fears?" *Evolution*, **69**(1), 216 – 231.

Cooper, Jr., W. E. (1998), "Reactive and anticipatory display to deflect predatory attack to an autotomous lizard tail," *Can. J. Zool.*, **76**(8), 1507 – 1510.

Dayan T. and Simberloff D. (1998), "Size patterns among competitors: ecological character displacement and character release in mammals, with special reference to island populations," *Mammal Rev.*, **28**(3), 99 – 124.

Deem V. and Hedman H. (2014), "Potential cannibalism and intraspecific tail autotomization in the Aegean wall lizard, *Podarcis erhardii*," *Hyla*, **2014**(1), 33 – 34.

Itescu Y. (2017), *Evolution on Islands: Testing the Extent and Consistency of the Effects of Island Characteristics. Ph.D. Thesis*, Tel Aviv University, Israel.

Itescu Y., Karraker N. E., Raia P., Pritchard P. C. H., and Meiri S. (2014), "Is the island rule general? Turtles disagree," *Global Ecol. Biogeogr.*, **23**(6), 689 – 700.

Itescu Y., Schwarz R., Donihue C. M., Slavenko A., Roussos S. A., Sagonas K., Valakos E. D., Foufopoulos J., Pafilis P., and Meiri S. (2018a), "Inconsistent patterns of body size evolution in co-occurring island reptiles," *Global Ecol. Biogeogr.*, **27**(5), 538 – 550.

Itescu Y., Schwarz R., Meiri S., and Pafilis P. (2017), "Intraspecific competition, not predation, drives lizard tail loss on islands," *J. Anim. Ecol.*, **86**(1), 66 – 74.

Itescu Y., Schwarz R., Meiri S., and Pafilis P. (2018b), "Lizard tail-loss rates on islands are not governed by longer life spans," *Isr. J. Ecol. Evol.*, **63**(2), 53 – 56.

Keogh J. S., Scott I. A., and Hayes C. (2005), "Rapid and repeated origin of insular gigantism and dwarfism in Australian tiger snakes," *Evolution*, **59**(1), 226 – 233.

Kotsakiozi P., Jablonski D., Ilgaz Ç., Kumlutaş Y., Avcı A., Meiri S., Itescu Y., Kukushkin O., Gvoždík V., Scillitani G., Roussos S. A., Jandzik D., Kasapidis P., Lymberakis P., and Poulakakis N. (2018), "Multilocus phylogeny and coalescent species delimitation in Kotschy's gecko, *Mediodactylus kotschyi*: hidden diversity and cryptic species," *Mol. Phylogen. Evol.*, **125**, 177 – 187.

Lokatis S. and Jeschke J. M. (2018), "The island rule: An assessment of biases and research trends," *J. Biogeogr.*, **45**(2), 289 – 303.

Lomolino M. V. (2005), "Body size evolution in insular vertebrates: generality of the island rule," *J. Biogeogr.*, **32**(10), 1683 – 1699.

Lymberakis P., Poulakakis N., Kaliontzopoulou A., Valakos E., and Mylonas M. (2008), "Two new species of *Podarcis* (Squamata; Lacertidae) from Greece," *Syst. Biodivers.*, **6**(3), 307 – 318.

Madden I. E., and Brock K. M. (2018), "An extreme case of cannibalism in *Podarcis erhardii mykonensis* (Reptilia: Lacertidae) from Siros island, Cyclades, Greece," *Herpetol. Notes*, **11**, 291 – 292.

Masseti M. (2012), *Atlas of terrestrial mammals of the Ionian and Aegean islands*, Walter de Gruyter, Berlin.

Meik J. M., Lawing A. M., and Pires-daSilva A. (2010), "Body size evolution in insular speckled rattlesnakes (Viperidae: *Crotalus mitchellii*)," *PLOS One*, **5**(3), e9524.

Meiri S. (2007), "Size evolution in island lizards," *Global Ecol. Biogeogr.*, **16**(6), 702 – 708.

Meiri S., Meijaard E., Wich S., Groves C., and Helgen K. (2008). Mammals of Borneo — small size on a large island," *J. Biogeogr.*, **35**(6), 1087 – 1094.

Meiri S., Raia P., and Phillimore A. B. (2011), "Slaying dragons: limited evidence for unusual body size evolution on islands," *J. Biogeogr.*, **38**(1), 89 – 100.

Pafilis P., Meiri S., Foufopoulos J., and Valakos E. (2009), "Intraspecific competition and high food availability are associated with insular gigantism in a lizard," *Naturwissenschaften*, **96**(9), 1107 – 1113.

Polis G. A. and Hurd S. D. (1996), "Linking marine and terrestrial food webs: allochthonous input from the ocean supports high secondary productivity on small islands and coastal land communities," *Am. Naturalist*, **147**(3), 396 – 423.

Poulakakis N., Kapli P., Lymberakis P., Trichas A., Vardinoyiannis K., Sfenthourakis S., and Mylonas M. (2014), "A review of phylogeographic analyses of animal taxa from the Aegean and surrounding regions," *J. Zool. Syst. Evol. Res.*, **53**(1), 18 – 32.

Richardson K. M., Iverson J. B., and Kurle C. M. (2019), "Marine subsidies likely cause gigantism of iguanas in the Bahamas," *Oecologia*, **189**(4), 1005 – 1015.

Saenz D. and Conner R. N. (1996), "Sexual dimorphism in head size of the Mediterranean gecko *Hemidactylus turcicus* (Sauria: Gekkonidae)," *Texas J. Sci.*, **48**(3), 207 – 212.

Schoener T. W. (1965), "The evolution of bill size differences among sympatric congeneric species of birds," *Evolution*, **19**(2), 189 – 213.

Schoener T. W. (1970), "Size patterns in West Indian Anolis lizards. II. Correlations with the sizes of particular sympatric species-displacement and convergence," *Am. Naturalist*, **104**(936), 155 – 174.

Schwarz R., Gavriilidi I.-A., Itescu Y., Jamison S., Sagonas K., Meiri S., and Pafilis P. (2016), "*Mediodactylus kotschyi* in the Peloponnese peninsula, Greece: distribution and habitat," *Acta Herpetol.*, **11**(2), 179 – 187.

Schwarz R., Itescu Y., Antonopoulos A., Gavriilidi I.-A., Tamar K., Pafilis P., and Meiri S. (2020), "Isolation and predation drive gecko life-history evolution on islands," *Biol. J. Linn. Soc.*, **129**(3), 618 – 629.

Valakos E. and Vlachopanos A. (1989), "Note on the ecology of *Cyrtodactylus kotschyi* (Reptilia, Gekkonidae) in an insular ecosystem of the Aegean," *Biol. Gallo-Hellen.*, **15**, 179 – 184.

Wettstein O. v. (1937), "Vierzehn neue Reptilienrassen von den südlichen ägäischen Inseln," *Zool. Anz.*, **118**, 79 – 90.