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Clutch size variability in an ostensibly fix-clutched lizard: effects of insularity on a Mediterranean gecko

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Abstract:	The island syndrome describes the evolution of slow life history traits in insular environments. Animals are thought to evolve smaller clutches of larger offspring on islands in response to release from predation pressure and interspecific competition, and the resulting increases in population density and intraspecific competition. These forces become more pronounced with diminishing island size, and life histories are thus expected to become slowest on small, isolated islands. We measured clutch sizes in 12 insular populations of Mediodactylus kotschyi, a small gecko from the Cyclades Archipelago, a set of land-bridge islands in the Aegean Sea (Greece). We analyse variation in clutch size in relation to island area, island age, maternal body size, the presence of putative competitors and nesting seabirds (which increase resource abundance in the form of marine subsidies), and richness of predators. Clutch size of M. kotschyi decreases with increasing island area, in depature from classic island syndrome predictions, suggesting the evolution of faster life histories on smaller islands. There are no relationships between clutch size and island age, maternal size, the presence of competitors or predator richness. Larger clutch sizes on small islands could reflect the beneficial effect of marine subsidies derived from resident seabird colonies. Indeed, populations of M. kotschyi on islands with nesting seabirds have clutch sizes 30.9% larger (1.82 versus 1.39 eggs) than populations on islands without nesting seabirds. Thus, our data suggest that bottom-up effects of marine subsidies may supersede the expression of a simple island syndrome in the Aegean M. kotschyi.

Research article

Clutch size variability in an ostensibly fix-clutched lizard: effects of insularity on a Mediterranean gecko

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ABSTRACT

The island syndrome describes the evolution of slow life history traits in insular environments. Animals are thought to evolve smaller clutches of larger offspring on islands in response to release from predation pressure and interspecific competition, and the resulting increases in population density and intraspecific competition. These forces become more pronounced with diminishing island size, and life histories are thus expected to become slowest on small, isolated islands.

We measured clutch sizes in 12 insular populations of *Mediodactylus kotschyi*, a small gecko from the Cyclades Archipelago, a set of land-bridge islands in the Aegean Sea (Greece). We analyse variation in clutch size in relation to island area, island age, maternal body size, the presence of putative competitors and nesting seabirds (which increase resource abundance in the form of marine subsidies), and richness of predators.

Clutch size of *M. kotschyi* decreases with increasing island area, in depature from classic island syndrome predictions, suggesting the evolution of faster life histories on smaller islands. There are no relationships between clutch size and island age, maternal size, the presence of competitors or predator richness. Larger clutch sizes on small islands could reflect the beneficial effect of marine subsidies derived from resident seabird colonies. Indeed, populations of *M. kotschyi* on islands with nesting seabirds have clutch sizes 30.9% larger (1.82 versus 1.39 eggs) than populations on islands without nesting seabirds. Thus, our data suggest that bottom-up effects of marine subsidies may supersede the expression of a simple island syndrome in the Aegean *M. kotschyi*.

Key-words: Cyclades, island biogeography, island syndrome, Kotschyi’s gecko, life history, reproduction.

INTRODUCTION

The evolution of life histories on islands has received much attention in the past two decades (e.g., Adler and Levins 1994; Adler 1996; Adamapoulou and Valakos 2000; Knapp et al. 2006; Salvador and Fernandez 2008; Raia et al. 2010; Pafilis et al. 2011; Novosolov and Meiri 2013; Novosolov et al. 2013). The life history of animals is defined by a wide set of traits associated with the timing and magnitude of reproductive and ontogenetic events (Stearns 1992). Much research has focused on the concept of life history strategies that describe the concerted evolution of various life history traits, originally conceived as *r* and *K* strategies (MacArthur and Wilson 1967; Pianka 1970). This theory generally distinguished between organisms that mature early and produce many small offspring (*r*-selected) and organisms that mature late and produce few large offspring (*K*-selected). The two strategies were traditionally interpreted as the outcome of density-dependent (at carrying capacity, *K*) or density-independent population growth (selected for a high intrinsic rate of increase, *r*). Lack of empirical findings to support this theory (see e.g., Stearns 1992; Reznick et al. 2002) has caused it to lose stature and the emphasis now lies with the covariations of life history traits on a “fast-slow” continuum (with “fast” life history similar to *r* strategy and “slow” life history to *K* strategy) in response to selection pressures acting on age-specific mortality rates (Stearns 1983; Read and Harvey 1989; Promislow and Harvey 1990; Stearns 1992; Reznick et al. 2002; Bielby et al. 2007).

Adler and Levins (1994) showed that insular rodent populations tend to have denser and more stable, populations, larger body sizes, delayed maturity, smaller litters and larger offspring. They suggested that, according to this pattern, which they termed "the island syndrome", increasing population density and changes in mortality rates due to lack of predators and interspecific competitors on islands (MacArthur et al. 1972), lead to selection for slower life histories (Adler and Levins 1994).

The physical and ecological characteristics of the islands are expected to affect the extent to which changes predicted by the island syndrome are expressed. As isolation increases (i.e. duration of separation or geographical distance from the mainland), islands are expected to become increasingly species-poor (MacArthur and Wilson 1967), and consequently poorer in predators and competitors. Adler and Levins (1994) therefore predicted that the expression of the island syndrome will be stronger on more isolated islands, as population density is expected to be highest there. Conversely, expressions of the island syndrome are expected to decrease with increasing island area (Adler and Levins 1994). As islands grow larger, they become more ‘mainland-like’ (Whittaker and Fernández-Palacios 2007), and therefore contain more species, more available niches, and more competitors and predators, cancelling out the effects of insularity (but see Meiri et al. 2005).

Support has been found for the island syndrome in mammals (e.g., Adler and Levins 1994; Adler 1996; Goltsman et al. 2005), birds (e.g., Covas 2012), amphibians (e.g., Wang et al. 2009), snakes (Tanaka and Mori 2010; Ajtić et al. 2013), and lizards (e.g., Adamopoulou and Valakos 2000; Novosolov and Meiri 2013; Novosolov et al. 2013). However, most of these studies either compared island-endemic species to mainland congeners (e.g., Adamopoulou and Valakos 2000), or compared a single insular population and a mainland population (e.g., Tanaka and Mori 2010). As such, they offer little insight on the effects of island area and insularity on evolution of life history traits. Novosolov et al. (2013) found that island endemic lizards have smaller clutches of larger hatchlings, but no effect of island area on the life history traits they examined.

A few intraspecific studies have also identified insular populations that appear to depart in their life history traits from the predictions of the island syndrome. Raia et al. (2010) found that an insular population of the Italian wall lizard, *Podarcis sicula*, display a “reversed island syndrome”, i.e. higher aggressiveness and a greater reproductive effort, where population densities were low or fluctuating due to environmental unpredictability (see also Monti et al. 2013). When studying *Podarcis gaigeae*, a wall lizard species endemic to the Skyros archipelago in the Aegean Sea, Pafilis et al. (2011) found that populations on smaller islands exhibited a higher reproductive effort, with no visible trade-offs between egg size and clutch size. Furthermore, the authors found that the differences in life history traits between populations were explained by maternal body size, i.e. the lizards on small islands grow larger, with proportional increases in clutch and egg sizes. One of the main drivers responsible for this counter-intuitive response to insularity is likely the elevated resource abundance resulting from “marine subsidies” (i.e. nutrients imported by seabirds from the surrounding marine ecosystems in the form of food scraps, carcasses and guano; see Anderson and Polis 1998). Such subsidies can have profound effects on insular lizard ecological and physiological traits and population densities (Sánchez-Piñero and Polis 2000; Barret et al. 2005; Pafilis et al. 2009b), and highlight how high food availability can release species from life history trade-offs (Pafilis et al. 2011). If so, the exact interaction between island characteristics and life history traits still has room for exploration.

Mediodactylus kotschyi (Kotschy's gecko) is a small (snout-vent length up to 56mm; Valakos and Vlachopanos 1987; and mass up to 5.5gr; our unpublished data), cathemeral, mainly insectivorous (Valakos and Polymeni 1990) gecko, highly abundant on the Aegean Sea islands, including extremely small islets (Valakos et al. 2008; and our pers. obs.). Insular populations of *M. kotschyi* have persisted since the islands were separated from the mainland as sea levels rose following the end of the Last Glacial Maximum (Kasapidis et al. 2005). These geckos show large morphological and life history variability across islands (Valakos et al. 2008; and our pers. obs.).

The reproductive biology of the species has been modestly studied: *M. kotschyi* has a fairly constant clutch size of one, two or three eggs, similar to other geckos (Kluge 1987; Goldberg 2012), but differences in mean clutch size between populations can still be discerned (Goldberg 2012), and egg volume is variable (Mollov 2011). While such studies give insight into the general reproductive biology of the species, we still lack comparative research at the population level, particularly on islands.

In this study, we examined clutch sizes of insular populations of *M. kotschyi* from different islands of varying size in the Cyclades archipelago, Greece. We predicted that, according to the island syndrome, clutch size of *M. kotschyi* would decrease with decreasing island area and increasing island age, the geckos having adopted a slower life history on small, isolated islands with few predators and competitors. We further explicitly tested predictions arising from the proposed causal mechanism of the island syndrome, i.e., the effects of release from predation pressure and interspecific competition, as well as effects of resource abundance on life history traits. We examined if clutch size of *M. kotschyi* increased with decreasing richness of predators and competitors, and with increasing resource abundance, using the presence of seabird nesting colonies, which deliver marine subsidies, as a proxy.

METHODS

During May and June 2014, we surveyed 17 islands of varying sizes in the Cyclades archipelago, Greece. We searched for *M. kotschyi* on the ground or dry stone walls, and under rocks and other items. All geckos were captured by hand.

Upon capture, we measured snout-vent length (SVL) and mass, and determined sex by visual examination of the cloacal region (Beutler and Gruber 1979). For female geckos, we determined whether they were gravid, and measured clutch size, by palpation of the abdomen and visual examination. This is possible thanks to their semi-transparent colouration, which makes the eggs readily visible in this species (Figure 1). After measuring the animals, we released them back into the wild, apart from a few specimens that were captured and transferred to a housing facility in the University of Athens for further research.

We calculated island areas using Google Maps. Times of separation of islands in the Aegean Sea have previously been estimated using bathymetric maps and charts that give the rates of sea level change (Foufopoulos and Ives 1998; 1999). We used updated times of separation for the 17 surveyed islands to construct a dendrogram of the island separation (Figure 2) and to calculate island age as a proxy for isolation, hereby considered as the time since separation from a larger landmass. The dendrogram was used for the phylogenetic analysis of the studied populations, in order to control for a phylogenetic signal in clutch size, under the assumption that the main mode of divergence of populations of *M. kotschyi* in the Cyclades is vicariance. This seems a reasonable assumption, as the timing of divergence of populations of *M. kotschyi* closely correlates with the timing of geological events related to the formation of islands and island clusters in the Aegean (Kasapidis et al. 2005). Furthermore, *M. kotschyi* seem to be poor dispersers (Scillitani et al. 2004), likely limiting gene flow between insular populations.

In order to account for the possible effects of maternal body size on clutch size (Meiri et al. 2012), we examined the effect of mean SVL on mean clutch size. We used SVL and not mass as our proxy for maternal body size due to the fact that clutch size and maternal mass are not statistically independent, because the clutch constitutes a relatively large fraction of a gravid female's body mass. We used log-transformed values of mean SVL, island area and island age as predictors, in order to linearize the relationship, normalise residuals, and reduce heteroscedasticity.

We used literature data (Valakos et al. 2008; Pafilis et al. 2009a, and references within; Brock et al. 2014), and our own observations from the field, to derive proxies for predation pressure, interspecific competition, and marine subsidies. The pooled number of potential avian (*Buteo buteo*, *B. rufinus*, *Circaetus gallicus*, *Falco tinnunculus*, *F. eleonorae*, *Athene noctua*, *Lanus senator*, *Corvus corax* and *C. corone*), mammalian (domestic cats, *Martes foina*, *Rattus norvegicus*, and *R. rattus*), and reptilian predators (*Dolichophis caspius*, *Elaphe quatuorlineata*, *Eryx jaculus*, *Macrovipera schweizeri*, *Natrix natrix*, *N. tessellata*, *Platyceps najadum*, *Telescopus fallax*, *Vipera ammodytes*, and *Zamenis situlus*) present on each island was our proxy for predation pressure (Table 1). As a proxy for interspecific competition, we used the presence of *Hemidactylus turcicus*, a similar-sized, insectivorous gecko, and the only other gecko species present on the Cyclades (Valakos et al. 2008). These two species are found on many of the same islands, and often their densities display inverse relationships, i.e., where one is abundant the other is not (Foufopoulos 1997). We used presence of nesting seabirds (mainly *Larus michahellis*) as a proxy for marine subsidies, as these gulls provide nutrients from marine ecosystems that indirectly enrich the arthropod fauna on islands (Anderson and Polis 1999; Sánchez-Piñero and Polis 2000), the main food resource for *M. kotschyi* (Valakos and Polymeni 1990).

Sample sizes from the islands were unequal (Table 1). We therefore omitted five islands, from which we had extremely low clutch sample sizes (although we still report them; Table 1), and divide the remaining data into two subsets, to control for data quality due to unequal sampling: (A) a subset of 12 islands where we sampled three or more geckos; and (B) a subset of nine islands where we sampled five or more geckos.

We performed a phylogenetic generalised least square (PGLS) regression (Freckelton et al. 2002) using the ‘caper’ package in R (Orme et al. 2012) to estimate the maximum likelihood value of the scaling parameter λ, and conducted two analyses. In one, we examined the effects of island traits (area and age) and maternal body size (SVL) on clutch size in *M. kotschyi* to determine the insular patterns in this species’ clutch size. In the second analysis, we used the presence of *H. turcicus* (yes/no), the presence of nesting seabirds (yes/no), and predator species richness as predictors, to examine the effects of interspecific competition, resource abundance, and predation pressure (possible causal mechanisms) on the same trait. Model selection was based on p values. All statistical analyses were performed in R v3.1.1 (The R Foundation for Statistical Computing 2014) using the RStudio v0.98.978 interface (RStudio Inc. 2013).

RESULTS

Clutch size of *M. kotschyi* varied between one and three eggs, and island means varied between one and 2.2 eggs, with a mean value of 1.5 (Table 1). These are smaller clutches than were previously reported for this species from the Aegean islands (1.86 eggs; Goldberg, 2012). We found no correlation, in either subset (i.e., A [n=12] and B [n=9]), between mean clutch size and either mean SVL or island age. There is no phylogenetic signal in the relationship between clutch size and any of the predictors ($\lambda = 0$ in both subsets), i.e. closely related populations do not have similar clutch sizes. Mean clutch size was likewise unaffected by either the presence of *H. turcicus* or by predator richness.

In subset A, mean clutch size decreases with increasing island area (slope = $-0.06 \pm 0.03_{se}$, $F_{2,9} = 5.27$, $p = 0.047$; Figure 3). This model explains 37% of the variation in mean clutch size across populations of *M. kotschyi*. This correlation is similar, but even stronger in subset B, with an even steeper slope (slope = $-0.09 \pm 0.03_{se}$, $F_{2,6} = 10.17$, $p = 0.019$; Figure 3). This model explains 63% of the variation.

In subset B, mean clutch is 30.9% higher for islands with nesting seabirds (1.82 versus 1.39 for islands with and without nesting seabirds, respectively; $F_{2,6} = 8.645$, p =

0.026, $R^2 = 0.59$; Figure 4). However, presence of nesting seabirds is not correlated with mean clutch size in the less conservative subset A.

DISCUSSION

Mean clutch size of insular populations of *M. kotschyi* decreases with increasing island area. This correlation is evident in our liberal dataset A, and becomes even stronger in the smaller, more conservative B dataset, explaining more than half of the variation in gecko clutch size in that subset, despite the reduction in the sample size of analysed islands.

Decreasing clutch size with increasing island area is the opposite of what we predicted, and could be viewed as suggestive of faster life histories on smaller islands, i.e., a reverse island syndrome (Raia et al. 2010). There is also some evidence that the geckos from Naxos island in the Cyclades Archipelago, Greece have smaller egg volumes than geckos from mainland Europe (Mollov 2011) and Israel (Werner 1993), again suggestive of faster life histories in insular populations. Faster life histories are predicted to evolve in insular environments under low or fluctuating population densities (Raia et al. 2010). However, *M. kotschyi* populations are both highly abundant and appear overall stable on small Cycladic islands (pers. obs.). Furthermore, *M. kotschyi* from a mainland population in Bulgaria have mean clutch sizes of 2.25 eggs (Mollov 2011), larger than all mean clutch sizes in our dataset (Table 1). This is similar to the findings of another study held at Naxos, the largest island in the Cyclades (Valakos and Vlachopanos 1989; we have just one datum from Naxos, of a two-egg clutch). These data make difficult the claim that geckos on Cycladic islands have faster life histories than mainland populations. Therefore, while our results seem to correspond to at least some of the predictions of the reverse island syndrome (Raia et al. 2010), we still lack concrete data on life history traits of mainland populations of *M. kotschyi* and insular and mainland population densities to explicitly test the syndrome.

The observed negative correlation between island area and cutch size does not imply a causal mechanism in shaping the clutch size of geckos. Island area most often shapes a species' life history through its effects on the diversity of predators and competitors.

Surprisingly, we found no correlation between clutch sizes of *M. kotschyi* and either the presence of *H. turcicus* or predator richness, despite both being tightly correlated with island area (Foufopoulos et al. 2011). While this possibly suggests lack of support in our system for these particular causal mechanisms of the island syndrome, it is also possible that the presence of *H. turcicus* and predator richness are simply not reliable proxies for interspecific competition and predation pressure on *M. kotschyi* (Meiri et al. 2014).

While *H. turcicus* can frequently be found co-occurring in the same microhabitat patches (e.g., under the same rocks in Greece, or on the same trees in Israel; pers. obs.) it is significantly more nocturnal than *M. kotschyi* (Valakos et al. 2008; and our pers. obs.). Therefore, it is possible that *H. turcicus* does not exert strong enough competitive pressure to induce selection on life history traits in *M. kotschyi*. Likewise, although predator richness has often been used as a proxy for predation pressure (e.g., Brock et al. 2014), it may be an inadequate index in the case of *M. kotschyi*, as other factors such as individual predator foraging tactics, population density and activity time may more strongly shape predation pressure.

Clutch sizes are significantly larger on islands with nesting seabirds, all of which are small (with an area of $<1\text{km}^2$; Table 1). This relationship, coupled with the failure of either presence of competitors or predator richness to explain variation in clutch sizes of *M. kotschyi*, suggests that clutch sizes of geckos may be linked to resource abundance. Nesting seabirds provide marine subsidies – nutrients from marine ecosystems (Anderson and Polis 1998). Cycladic islands are in general both nutrient poor and unproductive, though many small islands in the Cyclades support important nesting seabird colonies (e.g. *Phalacrocorax aristotelis, Calonectris diomedea, Puffinus yelkouan, Larus michahellis* and *L. audouinii*; Fric et al. 2012). Breeding colonies of the yellow-legged gull (*Larus michahellis*) can be particularly substantial (e.g., exceeding densities of 26 breeding pairs/ha on Aspronisi; pers. obs.) and strongly shape the food webs on these islets (Mulder 2011; Fric et al. 2012). It is unclear whether these gulls actually prey on reptiles (Pérez-Mellado et al. 2014). We have observed no attempts at such predation, and lizards (including the strictly diurnal, highly active *Podarcis erhardii*) occur in the immediate vicinity of nests but never seem nervous or vigilant around the birds. The influx of marine-derived nutrients, however, has been shown to greatly affect reptile life history in the Aegean (Pafilis et al. 2009b). In fact, earlier research revealed that marine subsidies were associated with a reversal of the island syndrome and dramatic increases in reproductive output (clutch size: 43.3%, clutch volume: 107%) in the Aegean lizard *Podarcis gaigeae* (Pafilis et al. 2011). While seabirds only nest on Cycladic islands during the spring and early summer (Fric et al. 2012) most species are present throughout the year and thus provide a steady source of nutrient inputs for the island food webs. Productivity of islet ecosystems is tied to seasonal precipitation patterns and thus varies strongly with the time of the year. Nonetheless this variation is highly predictable, with little apparent inter-annual variability (pers. obs.) and as such seems unlikely to satisfy the requirements for the evolution of the reverse island syndrome (Raia et al. 2010; Monti et al. 2013). As such, more data are needed to elucidate the conditions for reverse island syndrome evolution.

Mediodactylus kotschyi from Greek islands are known to produce multiple clutches per year (Goldberg 2012), and a shift to slower life histories in insular environments could also result in the laying of fewer clutches per year (Novosolov and Meiri 2013) rather than decreased clutch sizes. Such a case could potentially lead to our observed pattern (e.g., if the small clutches on larger islands may represent a second, smaller clutch, following an early large clutch that leaves females depleted, or clutch size may simply be compensated for by frequent laying). At the moment, however, the exact interplay between clutch size and brood frequency in this species remains difficult to unravel.

The island syndrome, which was originally observed in mammals (Adler and Levins 1994), has been widely studied in lizards in recent years (e.g., Raia et al. 2010; Pafilis et al. 2011; Monti et al. 2013; Novosolov et al. 2013), and results occasionally fail to fully support the predicted pattern, sometimes even finding evidence for a reverse trend. On the surface, our results may appear like they contradict the classical expression of the island syndrome and rather support the reverse pattern. A more thorough analysis instead suggests that the presence of marine subsidies, which are restricted to small islets ($<1\text{km}^2$ in area), may mask any expression of the island syndrome. Because of a relatively small sample size, we are not able to statistically disentangle island area effects from the presence of marine subsidies, and determine if a relaxation in life history constraints due to resource abundance, or selection for faster life histories following inconstant and unpredictable food supplies is responsible for the observed patterns. Our data, however, indicate that that life history traits of island lizards are subject to various selection pressures, and cannot be simply predicted by a straight-forward, directional response to insularity.

The land-bridge islands of the Cyclades constitute an interesting study system, with an abundant and diverse fauna and flora that allow for a detailed examination of the effects of insularity on evolution (Hurston et al. 2009). *M. kotschyi*, despite having a relatively fixed clutch size, still displays variation in this trait, and even an unexpected relationship with island area. Further research on other life history traits of these geckos (e.g., brood frequency or egg volume), or on similarly abundant animals with larger variation in clutch size (e.g., *Podarcis erhardii*), could shed considerable light on the causative mechanisms behind life history evolution on islands.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

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FIGURE LEGENDS

Figure 1 – A gravid female *Mediodactylus kotschyi* from Venetiko Isl., Greece. Encircled are two eggs, clearly visible in the abdomen.

Figure 2 – Map of the 17 surveyed islands (red) in the Cyclades archipelago, Greece, along with a dendrogram showing times of separation. The map was generated in ArcGIS 10.0 (ESRI, 2010), using a National Geographic Society basemap (ESRI, 2014).

Figure 3 – Linear regression of mean clutch size of *Mediodactylus kotschyi* against island area (km^2; log-transformed). White dots and dashed line represent subset B (islands with a sample size of five or more clutches); white and black dots together and continuous line represent subset A (islands with a sample size of three or more clutches). Islands on the left part of the graph (area <1km^2) harbor seabird populations.

Figure 4 – Mean clutch size of *Mediodactylus kotschyi* on islands with and without nesting seabirds (subset B: islands with sample size of five or more clutches, n = 9).

Figure 1

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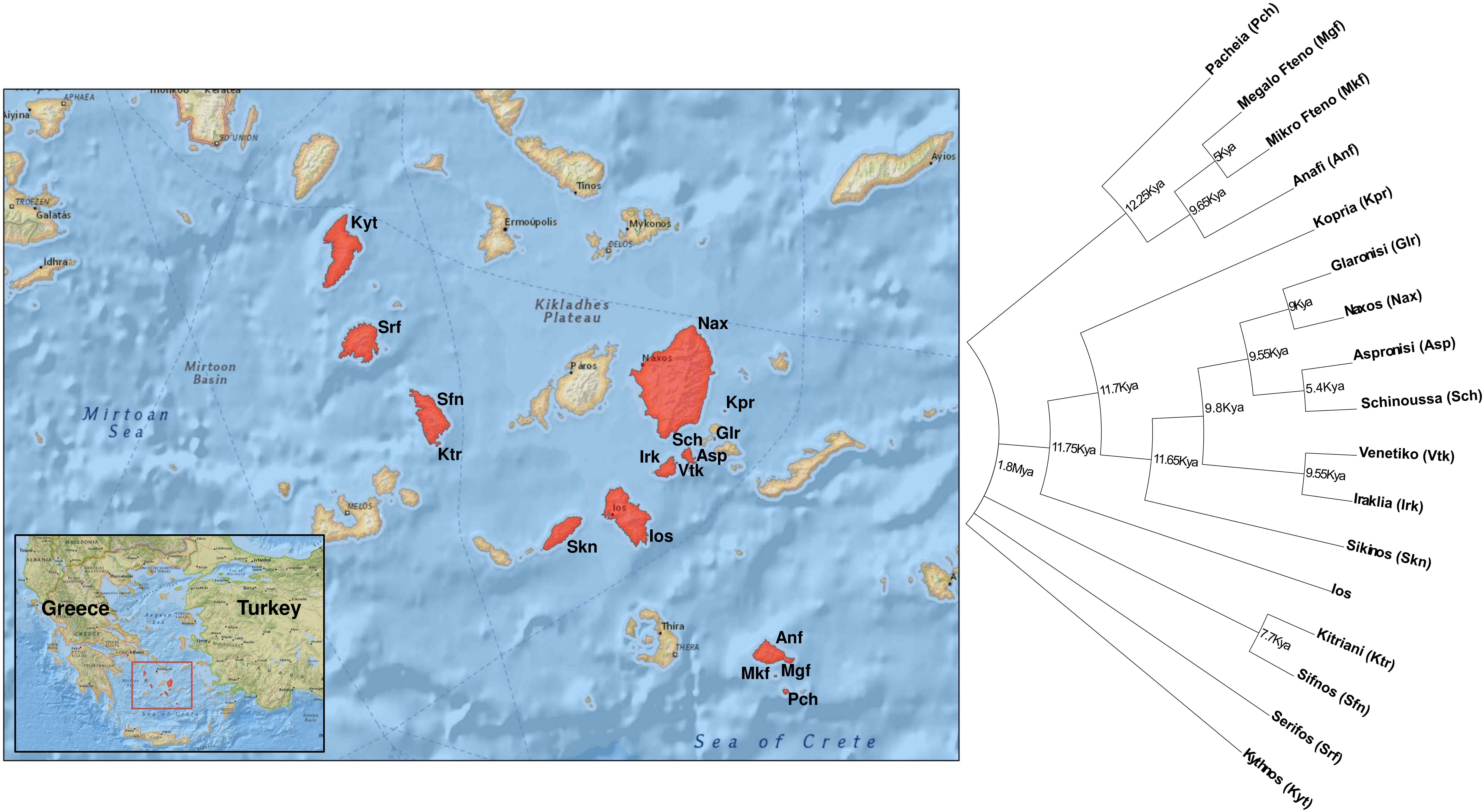
Figure 2


Kyt
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Vtk
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Anf
Mkf
Mgf
Pch
Greece
Turkey
Kikladhes Plateau
Mirtoon Basin
Mirtoan Sea
Sea of Crete
APHAEA
Aiyina
SOUNION
TROEZEN
Galatás
Idhra
Tinos
Ermoúpolis
Mykonos
DELOS
Páros
Naxos
Ios
MELOS
Thira
THERA
Ayios
Pacheia (Pch)
Megalo Fteno (Mgf)
Mikro Fteno (Mkf)
Anafi (Anf)
Kopria (Kpr)
Glaronisi (Glr)
Naxos (Nax)
Aspronisi (Asp)
Schinoussa (Sch)
Venetiko (Vtk)
Iraklia (Irk)
Sikinos (Skn)
Ios
Kitriani (Ktr)
Sifnos (Sfn)
Serifos (Srf)
Kythnos (Kyt)
12.25Kya
5Kya
9.65Kya
9Kya
9.55Kya
11.7Kya
5.4Kya
9.8Kya
11.75Kya
11.65Kya
9.55Kya
1.8Mya
7.7Kya

Figure 3

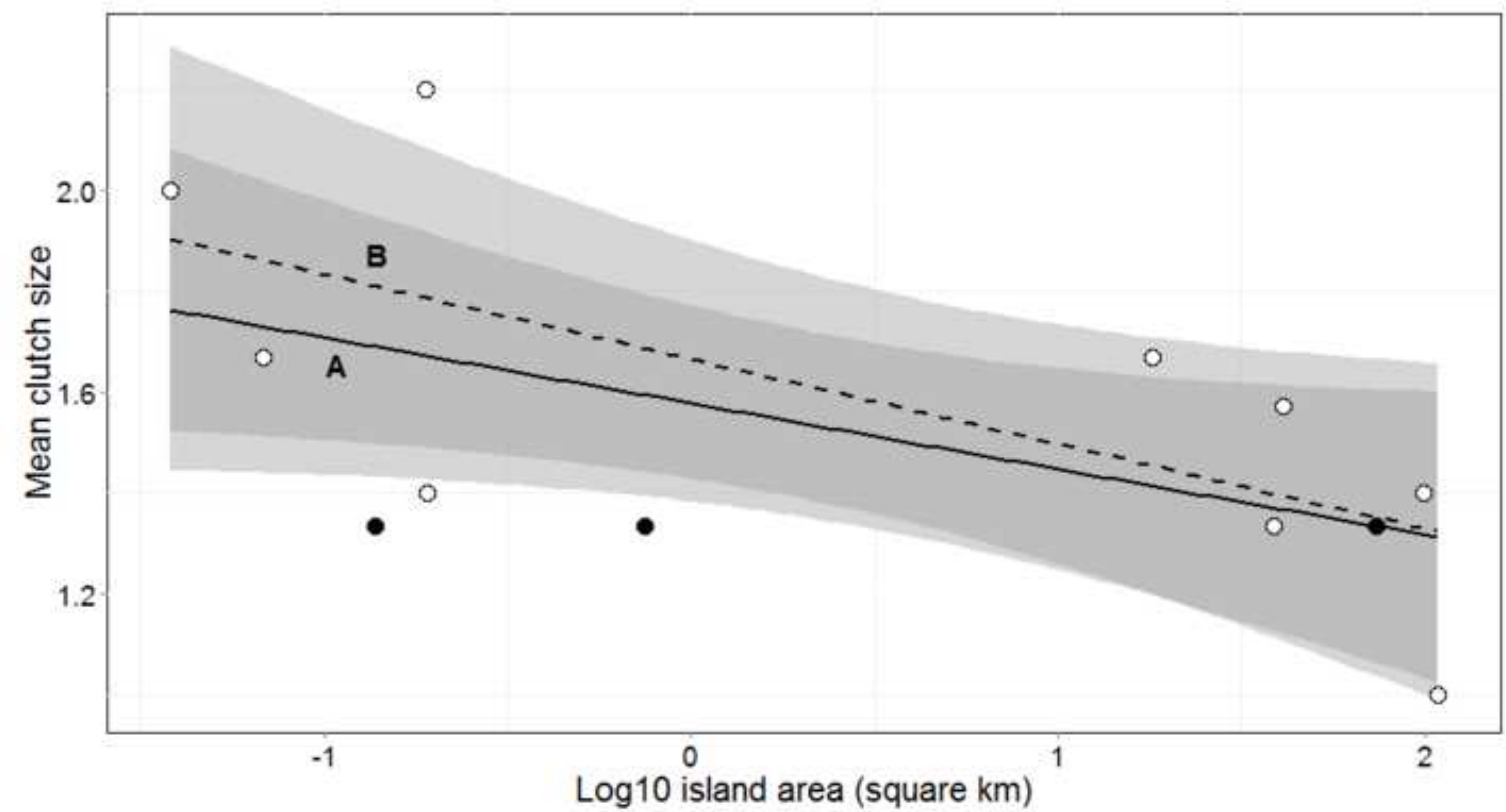

Figure 4

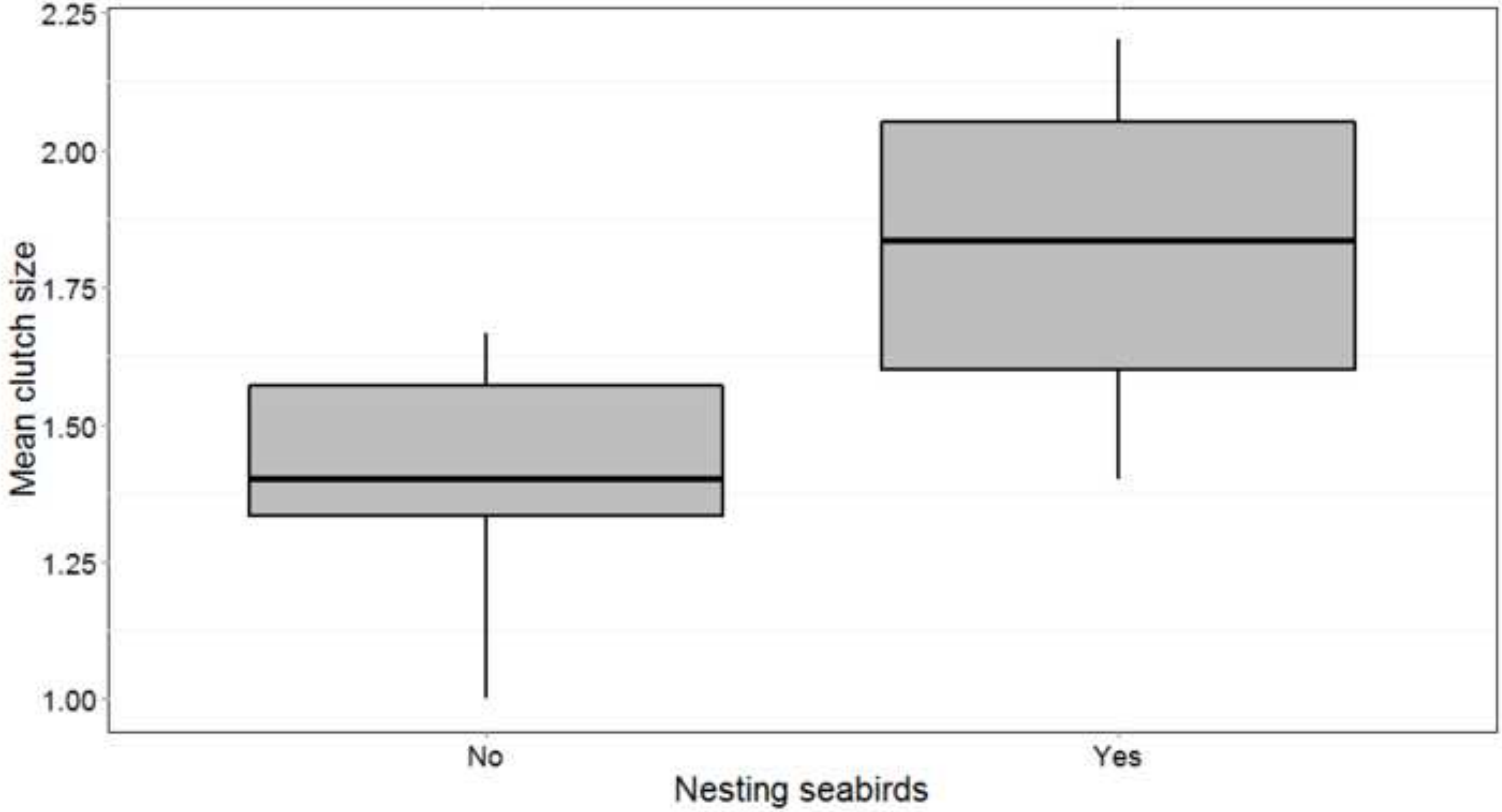
2.25
2.00
1.75
1.50
1.25
1.00
Mean clutch size
No
Yes
Nesting seabirds

Table 1. Mean clutch sizes of *Mediodactylus kotschyi* from 17 different islands in the Cyclades archipelago, Greece, along with island area, island age (regarded as time since separation from larger landmass), geographic coordinates, and data on predator richness (b = birds, m = mammals, s = snakes), presence of *Hemidactylus turcicus*, and presence of nesting seabirds.

Island	**Mean clutch size**	**Sample size**	**Island area (km^2)**	**Island age (years)**	**# of Predator species**	***Hemidactylus turcicus***	**Nesting seabirds**	**Coordinates (datum: WGS84)**
Anafi	1.33	9	38.64	1800000	2 (b, m)	Yes	No	36.3627°N, 25.7689°E
Aspronisi	2	11	0.04	5450	2 (b, m)	Yes	Yes	36.8553°N, 25.5461°E
Glaronisi	2.2	5	0.19	5600	2 (b, m)	No	Yes	36.9165°N, 25.6048°E
Ios	1	8	108.71	11750	3 (b, m, s)	Yes	No	36.7262°N, 25.3255°E
Iraklia	1.67	6	18.12	9800	3 (b, m, s)	Yes	No	36.8412°N, 25.4546°E
Kitriani	1.33	3	0.75	7700	1 (m)	No	Yes	36.9050°N, 24.7265°E
Kopria	1.33	3	0.14	11700	2 (b, m)	No	Yes	36.9858°N, 25.6387°E
Kythnos	1.4	10	99.42	1800000	3 (b, m, s)	Yes	No	37.4034°N, 24.4288°E
Megalo Fteno	1.67	6	0.07	9650	1 (b)	No	Yes	36.3111°N, 25.7999°E
Mikro Fteno	1	1	0.03	9650	1 (b)	No	Yes	36.3116°N, 25.7954°E
Naxos	2	1	430.17	8700	3 (b, m, s)	Yes	No	37.0551°N, 25.4526°E
Pacheia	2	2	1.41	12250	2 (b, m)	No	No	36.2727°N, 25.8317°E
Schinoussa	1.5	2	8.13	9550	3 (b, m, s)	Yes	No	36.8718°N, 25.5202°E
Serifos	1.33	3	74.09	1800000	3 (b, m, s)	Yes	No	37.1543°N, 24.4851°E
Sifnos	1	1	77.38	1800000	3 (b, m, s)	Yes	No	36.9674°N, 24.7041°E
Sikinos	1.57	7	41.23	11650	3 (b, m, s)	Yes	No	36.6805°N, 25.1202°E
Venetiko	1.4	10	0.19	9550	2 (b, m)	No	Yes	36.8560°N, 25.4849°E