Predation pressure as a determinant of locomotor performance: lizards run slower on islands without predators

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ABSTRACT

Endemic wildlife species confined to islands are both ecologically unique and tend to be severely endangered. More than 60% of the species known to have gone extinct to date used to occur on islands (Spatz et al. 2017). While there are several reasons why island taxa tend to be threatened, susceptibility to exotic species, such as invasive predators, is an important contributor. Earlier research has suggested that loss of antipredator defenses in island species is at least partially responsible for this. Locomotor abilities, including sprint speed and stamina, are traits that are essential to escape predation. Here we tested the hypothesis that island species that have evolved in predator-poor environments have lost their ability to run fast – a key trait for escaping invasive predators. We examined maximal sprint speed and maximal stamina in the Aegean wall lizard (*Podarcis erhardii*). The species is widespread throughout the Aegean archipelago (Greece, Mediterranean Basin) and is found on islands with varying levels of predation pressure making it an ideal study organism. We show that on islands with predators, lizards run at higher speeds relative to lizards on predator-free islands. Not all predator categories however are of equal importance: presence of mammalian - but not other - predators was significantly associated with higher sprint speeds in island lizards. In contrast to sprint speed, stamina was not related to predation environment suggesting that this is not a trait that is under selection by predators. Stamina may therefore be less useful for predicting endangerment by introduced predators. Differences in locomotor performance were not attributable to differences in limb lengths. The results of this study suggest that conservation funding may be best allocated to protect the most susceptible wildlife populations that live explicitly on low-predation islands as well as on islands isolated for long periods of time.

Key Words: Antipredator defenses, locomotor performance, sprint speed, predation, islands

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INTRODUCTION

The presence of predators in an ecosystem influences the ways in which potential prey respond to threats (Sih et al. 2010, Brock et al. 2015). Prey will deploy antipredator behaviors or physical responses that are key to survival, despite often being physically and energetically costly. Because most antipredator defenses are taxing, many species will only use them when the threat of death is imminent. In lizards, for example, tail autotomy is costly both physically and energetically. It leaves the lizard without a tail which can decrease locomotor ability while fleeing (Martin and Avery 1998) and requires substantial resources for regrowth. Other antipredator defenses demand fewer physical resources but are still energetically expensive; for example, retreating into a refuge decreases both the ability of lizards to thermoregulate and to feed (Martin and Lopez 1999, Downes 2001). Thus, because antipredator defenses incur such high costs, especially if deployed accidently, it is expected that the degree of their expression will reflect local predation risk in an area (Blumstein and Daniel 2005, Brock et al. 2015).

Island ecosystems, which may have been isolated over very long periods of time, often have low levels of predation (Alcover et al. 1994). Island endemics have often evolved special adaptations for island life. This “island syndrome” often involves differences in behavior, body size, and reproduction effort between island species and similar mainland taxa (Herrel et al. 2008, Novosolov et al. 2012). For example, island lizards are often substantially larger or smaller in size than their mainland counterparts; lay fewer eggs but larger eggs, and often lack or exhibit reduced antipredator defense mechanisms (Novosolov et al. 2012, Berger et al. 2007, Brock et al. 2015, Cooper and Perez-Mallado 2012, Blazquez et al. 1997, Li et al. 2014).

Some of the best studied aspects of the “island syndrome” are reduced antipredator defenses, often referred under the umbrella term “island tameness”. Such a relaxation in defense mechanisms, which are no longer useful in an island environment, is most often observed when species have been isolated from predator species for long periods of time (Sih et al. 2010, Blumstein and Daniel 2005). This lack of defenses makes island species particularly vulnerable to introduced novel predators (Berger et al. 2007, Sih et al. 2010). Indeed, colonization and invasion by novel predators, can lead to dramatic reductions and even extinctions in native species populations on islands (Spatz et al. 2017, Bellard et al. 2018). Introduced domesticated animals such as dogs, cats, or other human commensals like rats and mustelids have decimated native species populations worldwide (Duncan and Blackburn 2004, Blackburn et al. 2004). Feral cats alone are responsible for at least 48 documented global island species extinctions (Nogales et al. 2004). It has been postulated that prey naivete towards novel predators leads to insufficient escape responses and is responsible for increased mortality rates and concomitant declines and even prey population (Sih et al. 2010, Blackburn et al. 2004, Nogales et al. 2004).

One of the key antipredator defenses is the ability to flee from an approaching predator (Bauwens et al. 1995, Husak 2006, Husak and Fox 2006). Often summarized under the term locomotor performance, it can be distinguished as sprint speed (the ability to run quickly away under anaerobic conditions), versus endurance or stamina (the ability to run aerobically over extended periods of time) (Husak 2006, Losos 1990, de Albuquerque et al. 2015, Calsbeek and Irschick 2007). Sprint speed of a lizard can vary depending on the lizard’s body temperature, and is also influenced by body size (SVL), leg length, and the motivation for locomotion (Losos 1990, Bauwens et al. 1995, Avery et al. 1987b, Irschick 2000, Pinch et al. 2003). In the past, locomotor studies have focused on sprint speed as a measure of fitness for ecomorphs and the niches they occupy, focusing mainly on their ability to escape quickly in distinct habitats (Irschick and Losos 1999). Some studies have shown that elevated sprint speed is associated with survivorship in lizards (Avery et al. 1987b, Husak 2006, Irschick 2000). Sprint speed has only rarely been evaluated the context of predation pressure and duration of population isolation to determine whether locomotor performance declines in the wake of predator pressure (Vervust et al. 2007).

While sprint speed is the most common way in which scientists define locomotor ability, other measures like endurance or stamina are also important (Garland 1984, Calsbeek and Irschick 2007). Although endurance and stamina are similar in that they are both measures of sustained locomotion, they differ in the ways they are collected and measured. Endurance, which is measured on a motorized treadmill, collects data on how long an animal can run at a set speed (Garland 1984). Stamina is usually measured on circular tracks where the animals are encouraged to run continuously at their chosen speed for as long as possible (Pinch and Claussen 2003, Calsbeek and Irschick 2007). Stamina tests allow for a more natural gait in lizards, where the running pattern consists of bursts of movement followed by short pauses (Avery et al. 1987a, van Damme and Castilla 1995). Some studies have found that there are tradeoffs between sprint speed and sustained locomotion in lacertid lizards (Vanhooydonck et al. 2002, Vanhooydonck et al. 2014). This does not appear to be true for every species as is shown in de Albuquerque et al. (2015) which showed no tradeoff in phyrnosomatid lizards.

This study focuses on locomotor performance as an antipredator defense in the Aegean wall lizard (*Podarcis erhardii*) a widespread species that occurs in numerous distinct populations throughout the Cyclades archipelago in the Aegean Sea, Greece. Because the species is a poor overwater disperser (Foufopoulos and Ives 1999, Santoanastaso et al. 2017), each population has evolved in isolation and reflects life history responses to locally prevailing conditions (Hurston et al. 2009). Varying degrees of predation pressure on the Cyclades islands provides the ideal environment to study the influence of predation on antipredator behaviors (e.g. Pafilis et al. 2009). Previous studies in this region have demonstrated differences in flight initiation distance among lizard populations inhabiting islands with varying degrees of predation pressure (Brock et al. 2014a). Loss of an important antipredator defense like flight initiation distance, shows that change in behavior and possibly physical responses to threats may already be taking place due to isolation (Brock et al. 2014a). The goals of this study are to: 1. Quantify the extent of variation of locomotor performance among different island and mainland populations in response to differing predation environments. 2. Determine which specific factors drive the evolution of locomotor abilities. 3. Assess morphological associates of locomotor performance, as well as, the existence of tradeoffs between maximum sprint speed and maximum stamina. Considering that the loss of locomotor ability determines the risk of a species to succumb to invasive predators and given the progressively pervasive nature of human activities on even remote island regions, it is becoming ever more important to be able to predict a species risk to invasive predator without time and energy-intensive measures of locomotor ability. A study like this which aims at determining species performance based on first principles, can help scientists make better predictions about the vulnerability of island endemic lizard species and therefore maximize benefit from the investment of scarce conservation dollars.

METHODS

Study system

The Cyclades archipelago is a cluster of land-bridge islands located in the central Aegean Sea (Greece). Since the end of the last glacial maximum approximately 18,000 years ago, rising sea levels has led to the formation of islands by fragmenting mainland coastal regions (Foufopoulos and Ives 1999). As Holocene sea level rise fragmented the area, populations of plants and animals also became increasingly isolated, thus setting the stage for the evolution of locally adapted island phenotypes (Foufopoulos and Ives 1999, Pafilis et al. 2009, Itescu et al. 2017).

The study area has warm, long, dry summers and mild, rainy winters as is typical of Mediterranean region climates (Poulos et al., 2009). Humans have inhabited the region for thousands of years, altering the vegetation through agriculture and animal grazing. Today island habitats consist mainly of agricultural fields delimited by dry, stone walls and embedded in a matrix of spiny, summer-deciduous, low-growing woody vegetation known as *phrygana* (Handrinos and Akriotis 1997, Watson 1964.)

The Aegean wall lizard *(Podarcis erhardii*, Lacertidae) is a medium-sized lizard, typically ranging in size from 48-78 mm from snout to vent (Valakos et al. 2008, Brock et al. 2014, 2015). *P. erhardii* is found throughout the southern Balkans, mainland Greece, and many Aegean islands (Gruber 1986, Brock et al. 2014, 2015). *P.erhardii* is common throughout the Cyclades island chain but can also encountered across large swaths of mainland Greece (Valakos et al. 2008). The species has – with the exception of closed canopy forests – catholic habitat preferences and can be found in particularly high densities in areas where appropriate refugia, like dry-stone walls are present. The diet of *P. erhardii* consists predominately of arthropods, but although it occasionally includes vegetation and fruit (Brock et al. 2014). The species is recognized into more than 20 island subspecies reflecting the broad morphological variation found in the different Aegean islands and pronounced adaptation to local environments (Gruber 1986).

Island Characteristics

Study sites (N=22 see Fig. 1) were selected to represent a range of island sizes and ages (i.e. periods of isolation), as well as predation environments (number of predator categories), all of which were obtained from the published literature and confirmed through field surveys (Pafilis et al. 2009; Brock et al. 2015). Predators were categorized based on taxonomic affiliation, life-history, and hunting strategy (Brock et al 2015, Pafilis et al. 2009). Using methods described in Brock et al. (2015) and Pafilis et al. (2009) we created indices of predation pressure based on the presence and absence of predator types and the summation of all predator types present on an island. Predator species were grouped into six categories: rats, sand boas, raptorial birds, vipers, other snakes, and mammals. Each predator category is characterized by distinct hunting strategies, which likely results in different antipredator behaviors (Brock et al. 2015). Rats (*Rattus rattus*), for example, are considered in a category distinct from “mammals” because in the Cyclades the rats are small, opportunistic predators that do not prey on lizards to the same effective capacity as feral cats (*Felis catus*) and stone martens (*Martes foina*) (Brock et al. 2015) which use burst speed to capture prey (Peck et al. 2008, Smith 1976). Snakes are separated into three categories based on hunting strategies. Vipers (*Vipera ammodytes*) are sitand-wait predators that use ambush and envenomation to immobilize prey (Pafilis et al. 2009). Sand boas (*Eryx jaculus*) mostly feed on lizard eggs but occasionally prey on adult and juvenile lizards (Brock et al. 2015). 'Other snakes' includes several diurnal colubrid taxa (e.g. *Natrix natrix*, *Elaphe quatuorlineata*, *Dolichophis caspius*) that use a distinctive active search hunting strategy (Pafilis et al 2009).

Fuller et al. (2011) had suggested that habitat openness is an important determinant of sprint speed. At each location, we calculated a measure of habitat openness along a 100 m long transect randomly laid out in habitat that was representative of the particular locale and was also occupied by *P. erhardii*. Habitat data were recorded at 1 m intervals along the transect. This included vegetation and substrate type as well as height above the ground. Areas with such structural complexity represent potential refugia for *P. erhardii*, while areas with height <5cm above were categorized as open habitat amenable to rapid bouts of running. Lizard population density measurements were taken at each site along a 100 m-long, 5 m-wide transect following established protocols (Brock et al. 2015). Lizards were counted by the same observer (SS) using visual or sounds detection while walking along the transect during peak hours of lizard activity (09:00-11:00, and 15:00-17:00 and under optimal environmental conditions (20-25 ^{o} C; sunny; windspeeds<2Bf).

Animal Methods and Morphology

Lizards were caught by noosing or baiting with *Tenebrio* larvae over the course of the early summer (May-early July) 2016. A sample size of 18-34 lizards were taken from each location. Each lizard was given a unique, temporary number on the back using a non-toxic marker. While in captivity, lizards were held in 60cm x 41.6cm x 33.7cm terraria, and were provided with water *ad libitum*, and fed once a day mealworms (*Tenebrio* sp. larvae). Lizards were returned to the place of capture after all morphological and performance measurements were recorded. Morphometric data, including snout to vent length (SVL), front and hind limb length, and hindleg span (hindspan) were measured using digital slide calipers following methodologies described in Donihue (2016a,b). Lizards were sexed and body mass measurements were collected using a spring-loaded scale, (Pesola 10020).

Sprint Trials

Sprint speed was measured using a 230 cm long and 40 cm wide wooden racetrack. Every lizard ran 3 sprint trials to ensure that at least one good measure of sprint speed was obtained. Before each sprint trial, lizards were allowed to thermoregulate at will for at least an hour along a temperature gradient. Temperatures were taken by cloacal thermometer immediately after each trial. Trials were spaced at least 1 hour apart to allow the lizards time to recover. Using a video camera (GoPro; Hero Black 4; 1280 x 720 px), video of each trial was recorded at 240 frames per second; the camera was positioned 1.5 m above the racetrack, so that a clear dorsal view of the running lizard was visible for at least one full meter of the racetrack. Using the video analysis tool SAVRA (code: https://github.com/bkazez/savra) custom-built for Donihue (2016b), a measurement of the distance travelled between every 5 frame sequence was calculated, and fit with a quintic spline using the SPAPI function in MatLab (MathWorks Inc. 20) as described in Donihue (2016b) in order to calculate velocity of the lizard in m/sec. The fastest of the three trials for each lizard was selected for use in analyses. Gravid females were excluded from the analysis, as were trials where individual lizards were judged not to be able to run normally. Stamina and sprint trials were run more than 12 hours apart to allow the lizards time to recover.

Stamina Trials

In addition to sprint trials, a subset of 20 lizards was randomly selected from each island sample to participate in stamina trials. Gravid females were further excluded from the analysis. Lizards were allowed to thermoregulate for an hour before each trial and temperatures were recorded by cloacal thermometer immediately before the start of each trial. Lizards were placed in a circular track, 2.71 m in circumference, with the floor covered with sand. Researchers worked in pairs, the animal handler encouraged the lizard to run for as long as possible by tapping it on the base of the tail or chasing it with a hand, and the observer used a stopwatch to record the length of each trial to the nearest second. Lizards were encouraged to run along the track by light tapping on the base of the tail. If an animal did not start running after ten tail taps or was unable right itself when flipped on its back, the trial was considered finished. Three stamina trials were performed on each lizard, with a minimum between trial waiting time of 90 min to allow for recovery between trials.

Statistical Analysis

Performance and morphological values were Log_{10}-transformed to ensure normality of residuals. Correlations (Pearson), unless stated otherwise, were used to explore relationships between locomotor performance and morphological characteristics (SVL, hindlimb length, and hindspan length), as well as island characteristics (island age, island area, % open habitat, lizard density, and number of predator categories). We also used a correlation analysis between sprint speed and stamina to explore whether there was a trade-off between sprint speed and stamina.

We used a linear mixed model approach to analyze how sprint speed and stamina were influenced by different ecological drivers. Fixed effects included predation variables, while sex, lizard body size (snout-vent length), and lizard body temperature were included as random effects in the model. These individual-level characteristics were chosen as random effects for the mixed model analysis based on known interactions with sprint speed. Snout-vent length is typically used as a measure of body size, which is linked to stride length and sprint speed, and body temperature has also been broadly linked to sprint speed (Bauwens et al. 1995, Garland 1984, Losos 1990, Avery et al. 1987b, Irschick 2000, Pinch et al. 2003). Island characteristics of predation and island age were chosen for further examination in the linear mixed model analysis because previous research in this study system suggested these were important to other similar antipredator mechanisms (Brock et al. 2015).

We compared 8 *a priori* models to identify which predator types were most important in shaping maximum sprint speed and maximum stamina. Models looked at the presence or absence of any predators, total predation, and individual predator types (Tables 2,3). The “0 Predation” model took into account the presence or absence of any predator on the islands. The “Sum Predation” model summed all the predator types found on each island, assuming each predator type added equal predation pressure to the system as described in Brock et al. (2015). Alternatively, another model looked at each predator type added individually and simultaneously (R+SB+V+B+OS+M). This model considers the fact that all predator types are not the same and do not contribute equally to sprint speed or stamina. Based on a priori knowledge, the other six models looked at individual predators and combinations of predators that would likely have the most influence on locomotor performance. These models emphasized the role of mammals (M) and predatory birds (B) on sprint speed and stamina. These two categories of predators are expected to have the most influence on locomotor performance based on the speed-based hunting strategies they utilize. In order to catch prey, mammals stalk and chase prey, often overcoming an animal in short bursts of speed (Peck et al. 2008, Nogales et al. 2004). Predatory birds utilize a similar approach: after locating prey from above they swoop down to overcome and capture an animal (Smith 1976). A category including other predators (OP), was used to see whether the presence of any other predator type beyond mammals and/or birds had an impact on sprint speed. In order to determine whether time of isolation influenced sprint speed and stamina, island age (Log_{10}-transformed) was added as another fixed effect to the 8 models stated above. Models were then compared using Akaike Information Criteria, using AICc values and the associated Akaike weights (Burnham and Anderson 2003).

RESULTS

Sprint Speed

Maximum sprint speed did vary between individual lizards and between islands (range: 1.04 - 4.37 m/s, $\bar{x}$=1.75±0.017 m/s, n=526). Lizard body temperature was positively correlated with sprint speed (r=0.239, P<0.0001, n=526). Lizard SVL was also positively, yet weakly, correlated with sprint speed values (r=0.081, P=0.045, n=526). Although body size (SVL) is thought to be positively correlated with sprint speed, mostly because of increases in stride length, in most island populations in our regions the slopes of Log_{10}-transformed sprint values against Log_{10}-transformed SVL were slightly negative (Losos 1990, Bauwens et al. 1995, Garland 1984). This suggests that sprint speed is particularly important for escape in smaller, younger lizards; with increasing age, survival may hinge more on early predator recognition and prior escape experience- rather than sprint speed. Indeed, Husak (2006) found similar evidence in collared lizards (*Crotaphytus collaris*), where sprint speed influenced survival in hatchlings but not adults. Sprint speed was negatively correlated with lizard density (Log_{10}-transformed) (r=-0.467, P=0.028, n=22), and island age (Log_{10}-transformed) (r=-0.494, P=0.019, n=22). In contrast, total predation (r=0.559, P=0.007, n=22) and island area (Log_{10}-transformed) (r=0.454, P=0.034, n=22) were positively correlated with sprint speed (Table 2).

On islands where predators were present lizards ran at a significantly faster sprint speed than lizards on islands without predators (Figure 2, linear mixed model). Indeed, lizards on islands with mammals ran an average of 32% faster than lizards on islands without predators; they also ran 14% faster than lizards on islands with other predators but not mammals present. Overall, sprint speed was best explained by the presence of mammalian predators on islands (Table 3). Lizards on islands with mammals ran at a higher velocity than lizards on islands without mammalian predators present. However, the AIC table (Table 3) reveals that the first two models perform similarly well, with an ΔAICc of 0.641 and an Akaike weight of 0.165 for the model with mammals and other predators present, compared to the Akaike weight of 0.228 for the model with just mammals, and the “0 Predation” model had an Akaike weight of 0.116. The relatively small differences in values (<2) of ΔAICc between the first six models suggest that any one of these models is just as good as the “best” model. In contrast the “Sum Predation” model that stated each predator type added the same amount of predation pressure to the system was not very predictive with an Akaike weight of 0.04. Similarly, the “R+SB+B+V+OS+M” model had the least predictive power.

Stamina

Maximum stamina values varied widely from individual to individual and from island to island (range: 24-825 s, $\bar{x}$=104.62±5.08 s, n=332). Lizard body temperature was negatively correlated with stamina values (r=-0.233, P<0.0001, n=332), but SVL was not correlated with maximum stamina (Table 2). Island averages of maximum stamina were positively correlated with lizard population density (Log_{10}-transformed) (r=0.440, P=0.041, n=22). Similarly, island average stamina and number of predator types (r=-0.425, P=0.049, n=22). In contrast island age (Log10-transformed), island area (Log_{10}-transformed), and % open habitat was not related to stamina. We also detected a negative correlation between individual stamina and sprint speed performances (r=-0.196, P<0.0005, n=332), although this relationship did not hold up when individual island average were compared (r=-0.400, P-value=0.065, n=22).

Stamina was best explained by the presence of predatory birds on islands (Table 4). Thus counterintuitively, lizards on islands with aerial predators ran for shorter periods of time than lizards on islands with other predators present. The AIC table shows an Akaike weight of 0.469 for the model with birds. The “0 Predation” model had an Akaike weight of 0.169, Birds+OP follows with a weight of 0.103, and “Mammals” follows with a weight of 0.07. The “Sum Predation” model that stated each predator added the same amount of predation pressure to the system was not very predictive with an Akaike weight of 0.02. The “R+SB+B+V+OS+M” model had the least predictive power.

DISCUSSION

This study focused on the factors that determine the two primary types of locomotor performance that are relevant as antipredator defenses in reptiles. We predicted that sprint speed and stamina would vary across island populations of lizards, and that sprint speed would decline as the number of predator types decreased and as time of population isolation increased. We also predicted that mammals and bird predators would exert the strongest influence on sprint speed, because of the style these predators use to chase and capture prey. We also expected a tradeoff between sprint speed and stamina, with those populations where lizards ran the fastest also having the shortest stamina times.

The presence of mammals provided the best explanation for differences in sprint speed among the islands (Table 3). The main mammalian species on the islands, feral cats (*Felis cattus*) and stone martens (*Martes foina*) capture prey by stalking and then chasing down lizards. As a result, the ability to produce fast, anaerobically powered bursts, like the ones we measured are an excellent approach to reduce predation risk (Peck et al. 2008). We documented the highest sprint speeds from islands where mammals are present, and we saw significant declines in sprint speed between mammal islands and islands where predators other than mammals are present (Figure 2). Islands without mammalian predators but with other predator types present were inhabited by lizards with intermediate sprint speeds indicating that the ability to produce rapid sprint bursts is maintained when at least one predator is present (Figure 2). Hence the presence of any type of predator, effectively “keeps the lizards on their toes”. Islands with no predators had the slowest sprint speeds and seem to demonstrate that the lack of predation has led to a loss in sprinting ability (Figure 2).

Predation pressure was not the only island characteristic to have an effect on sprint speed, time of isolation (island age) was also linked to declines in sprint speed. Older islands, those that have been separated from the mainland the longest, had lower sprint speeds than younger islands These results suggest that islands that have been isolated from more diverse areas for longer have lost sprinting ability over time. Although there was significant effect of time of isolation, the AIC comparisons showed it was not the most important factor in determining sprint speed (Table 3), as the models that included island age were ranked lower than models without island age. This further suggests that predation pressure is highly important to the maintenance of sprint speed as an antipredator mechanism.

Stamina, in contrast to sprint speed, increased as the number of predator classes decreased (Figure 4). On average stamina was highest on islands without predators (166.22 s) and lower on islands with predators (93.71 s). Stamina was best explained by the presence of birds on islands, however, unlike the results for sprint speed there is not a visible pattern among the variation in stamina and predation pressure. The variation in stamina values that was not explained by island age either. These results and the fact that the lower end values of stamina are under a minute which may suggest that stamina is not relevant to escaping predators for *P. erhardii*.

The presence of a tradeoff between sprint speed and stamina is not obvious from the data collected (Figure 5). There was some evidence that lizards from populations with very high sprint speeds, tended to tire out quicker and achieve only modest stamina scores, and some of the populations with the highest stamina scores had only modest sprint speeds that allowed them to endure running for longer times. However, there were a lot of individuals and islands where a tradeoff was not apparent, as the sprint and stamina values were in the middle range. A tradeoff between sprint speed and stamina has been seen before in other lacertid species including other *Podarcis* species (Vanhooydonck et al. 2002, Vanhooydonck et al. 2014). However, there is much debate about whether this holds true for all species of lizards, as it has been shown that for 14 species of North American phrynosomatid lizards there was not a tradeoff between endurance and sprint speed (de Albuquerque et al. 2015). Although our data suggest that a trade-off between sprint speed and stamina does exist, more research should be conducted, possibly using a different technique, such as an electric treadmill, to measure both aerobically and anaerobically powered locomotion. Using an electric treadmill would allow for more direct comparisons with other studies on similar taxa and elucidate the existence of a tradeoff between sprint speed and endurance (Vanhooydonck et al. 2002, Vanhooydonck et al. 2014). Further research on the muscle fibers in *P. erhardii* may also be able to shed more light on whether there is likely a tradeoff, as certain muscle types are favored in anaerobic conditions and may be larger in species that favor that type of locomotion (Bonine et al. 2001, 2005).

The results of this study suggest that any attenuated running speeds get exacerbated by neophilic behaviors, reduced lack of predator recognition, and dramatically reduced FIDs (Brock et al. 2015, Li et al 2014). Lizards on islands where there are no predators present not only showed reductions in sprint speed, but they also displayed unique behaviors and an apparent lack of fear not present in predator diverse populations, as was seen in previous studies of the region (Brock et al. 2015, Li et al 2014, Sarah Semegen pers. obs.). Similar studies have noted that the inability to recognize predators has led to decreased sprint speed and flight initiation distances and increased predation on lizards (Vervust et al. 2007, Cooper and Pérez-Mellado 2012, Berger et al. 2007, Blazquez et al. 1997). This predator naivete is common in island species, especially species that have been isolated for millions of years such as the Galapagos islands (Cooper and Pérez-Mellado 2012, Röld et al. 2007, Sih et al. 2010).

The lack of natural predators on islands often means that energetically costly antipredator behaviors are lost over time (Sih et al. 2010). The results of this and similar studies suggest that attenuated predation conditions can lead to reductions in antipredator behaviors even over shorter periods of time (Brock at el. 2015, Vervust et al. 2007). Vervust et al. (2007) suggests that changes to responses to predators, such as, flight and speed can happen in a matter of decades. Analyses of time of isolation (island age) in our study showed that islands which have been isolated for longer periods of time (Figure 3) had the lowest sprint speeds. Unexpectedly, in combination with predator diversity models time of isolation did not further explain sprint speed values or stamina values. This may suggest that the main mechanism by which time of isolation acts on running speed is through progressive impoverishment of predator communities it causes. Indeed previous research in the Aegean has demonstrated that long-term isolation of species on islands leads via community relaxation to species loss (Foufopoulos and Ives 1999).

Alternatively, it is possible that the locomotor performance decline observed on small, old islands is not an adaptive response to reduced predation risk, but rather the result of loss of genetic diversity. Inbreeding depression, such as observed on small, old islands is known to undermine the physiological processes needed to run fast as sprint speed is known to be a heritable trait (Keller 1998, Garland et al. 1990, Manenti et al. 2014). In line with a possible role for inbreeding depression is the fact that we detected a strong negative relationship between sprint speed and duration of population isolation (island age), a known driver of genetic drift. (Figure 3),

Recent research shows that antipredator adaptations can be lost quickly, and once lost they may be lost permanently (Cooper and Pérez-Mellado 2012, Li et al. 2014). Some antipredator adaptations such as chemosensory processes appear to be persistent in recently predator free populations (van Damme and Castilla 1995), but predator shyness may be more labile and is lost quickly (Vervust et al. 2007). Furthermore, tameness may become fixed in the population if it is released from predation for long enough, as is suggested in the case of *Podarcis lilfordi* in Cooper and Pérez-Mellado (2012). Studies on Galapagos' marine iguanas produce similar findings, where even recent experience with introduced predators, while increasing flight distances, it was not enough to reduce predation by invasives (Berger et al. 2007, Rödl et al. 2007). This inability to adapt swiftly to increased predation and novel predators is thought to have led to a loss of island species all across the planes (Spatz et al 2017, Bellard et al. 2018). Our research suggests that on islands with a historic presence of mammalian predators, species may be less at risk of extinction or extirpation from a novel predator species. Island species without a historic presence of mammalian predators in general, and species from islands without any predators in particular, should be considered highly vulnerable to exotic predators.

In summary, this study demonstrated that on islands with predators, lizards run at higher speeds relative to lizards on predator-free islands. Not all predator categories however were of equal importance: presence of mammalian - but not other - predators was significantly associated with higher sprint speeds in island lizards. In contrast to sprint speed, stamina was not related to predation environment suggesting that this is not a trait that is under selection by predators.

Stamina may therefore be less useful for predicting endangerment by introduced predators. The results of this study suggest that conservation funding should be preferentially allocated to protect the most susceptible wildlife populations that live explicitly on low-predation islands as well as on islands isolated for long periods of time.

TABLES

Island	Isolation Period (years)	Island Area (km)	Max Sprint (m/s)	Max Stamina (s)	SVL (mm)	Hindspan (mm)	Predators	Sum Predation	Percent Openness	Lizard Density Ind/100 m	Slope of Max Sprint vs. SVL
Amorgos (AM)	200,000	123	1.81	82.44	61.91	69.63	r,sb,b,os,m	5	47	4	0.01
Anafi (AN)	3,600,000	49	1.74	101.94	57.30	61.99	r,b,m	3	85	4	0.13
Andros (AD)	5800	379.95	1.89	53.13	68.49	77.60	r,sb,v,b,os,m	6	71	2	-1.06
Ano Antikeros (AA)	15150	1.05	1.57	110.69	59.16	62.50	r,sb,b	3	61	1	0.01
Aspronissi (AS)	5450	0.04	1.55	62.24	60.84	66.41	r	1	68	8	0.85
Fidussa (FI)	600	0.63	1.72	62.65	60.01	65.83	r,sb,b	3	77	6	-0.83
Glaronissi (GL)	5650	0.16	1.91	111.79	60.41	65.23	r,b	2	88	3	-0.34
Gramvoussa (GR)	6700	0.76	1.69	54.20	59.60	63.90	r,sb,b	3	60	1	-0.37
Ios (IO)	11750	109.03	1.83	81.00	64.40	71.61	r,sb,v,b,os,m	6	80	2	-0.81
Iraklia (IR)	9800	18.08	1.66	89.74	59.40	63.71	r,sb,v,b,os,m	6	70	4	-1.56
Kato Koufonissi (KK)	9100	4.30	1.84	75.46	58.46	67.17	r,sb,b	3	67	5	0.17
Keros (KE)	9150	15.05	1.60	208.83	56.52	60.45	r,sb,b	3	47	5	0.10
Kisiri (KI)	5700	0.01	1.56	54.59	56.31	61.69	r,b	2	83	2	-0.40
Lazaros (LA)	9100	0.01	1.39	225.29	68.75	73.43	None	0	61	13	-0.48
Makria (MA)	13500	0.5	1.68	133.67	56.49	63.22	r,sb,b	3	67	5	0.29
Mando (MN)	7	0.025	2.62	60.70	62.53	70.41	r,sb,b,m	4	71	2	1.30
Megalo Fteno (MG)	9580	0.06	1.40	76.94	59.91	62.13	None	0	57	20	-0.10
Mikro Fteno (MK)	5000	0.03	1.60	206.40	54.12	59.41	None	0	70	4	0.21
Naxos (NA)	8700	448	1.87	82.93	60.87	69.22	r,sb,v,b,os,m	6	74	6	0.01
Pachia (PA)	11850	1.36	1.92	140.53	55.92	58.71	r	1	61	7	0.54
Parnitha (Mainland) (PN*)	0	1000	2.09	115.06	65.22	82.86	r,sb,v,b,os,m	6	67	4	-0.79
Tinos (TI)	5800	194.5	2.11	48.70	67.36	77.69	r,sb,v,b,os,m	6	87	1	-0.75

Table 1: Summary Table. Island and lizard population characteristics. Islands are listed in alphabetical order. The isolation period is given in years. Island area is given in square kilometers. Sprint speed in given in meters per second. Stamina is given in seconds. Morphological characteristics of body size (SVL) and hindspan are given in *mm*. Predator categories for each island are listed (R=rats [*Rattus rattus*], SB=sand boas [*Eryx jaculus*], B=predatory birds, V=vipers [*Vipera ammodytes*], OS=other saurophagous Colubrid snakes, M=mammals). Sum predation is the summation of the predator categories found on each island. Percent openness is the percent of open habitat per a 100 m transect. Lizard density is the number of individual lizards seen along a 100 m X 5 m transect. The slope of maximum sprint vs. SVL for each island.

	Sprint Speed (Log$_{10}$-transformed)			**Stamina (Log$_{10}$-transformed)**		
Morphology	**Pearson r**	**P-value**	**n**	**Pearson r**	**P-value**	**n**
Body Temperature	0.239	<0.0001	526	-0.233	<0.0001	332
SVL (Log$_{10}$-transformed)	0.087	0.045	526	-0.018	0.741	332
Hindlimb (Log$_{10}$-transformed)	0.234	<0.0001	519	-0.089	0.108	329
Hindspan (Log$_{10}$-transformed)	0.195	<0.0001	526	-0.074	0.180	332
Island Characteristics						
Island Age (Log$_{10}$-transformed)	-0.494	0.019	22	0.143	0.526	22
Island Area (Log$_{10}$-transformed)	0.454	0.034	22	-0.200	0.373	22
Lizard Density (Log$_{10}$-transformed)	-0.467	0.028	22	0.440	0.041	22
Percent Openness	0.331	0.132	22	-0.377	0.084	22
Number of Predator Types	0.559	0.007	22	-0.425	0.049	22

Table 2: Results of univariate correlations.

Model	**AICc**	**ΔAICc**	**Akaike's weight**
Mammals	-1211.15	0	0.228
Mammals + OP	-1210.509	0.641	0.165
0 Predation	-1209.793	1.357	0.116
Mammals + OP+Log10Age	-1209.751	1.399	0.113
Birds+OP	-1209.734	1.416	0.112
Mammals+Log10Age	-1209.413	1.737	0.096
0 Predation+Log10Age	-1208.254	2.896	0.054
Sum Predation	-1207.919	3.231	0.045
Mammals + Birds	-1206.706	4.444	0.025
Birds	-1206.342	4.808	0.021
Mammals + Birds+Log10Age	-1204.619	6.531	0.009
Sum Predation+Log10Age	-1204.496	6.654	0.008
Birds+Log10Age	-1203.599	7.551	0.005
Birds + OP+Log10Age	-1203.161	7.989	0.004
R+SB+V+B+OS+M	-1194.534	16.616	5.61E-05
R+SB+V+B+OS+M+Log10Age	-1193.854	17.296	3.99E-05

Table 3: Selection criteria for the sixteen mixed models constructed to explain variation in maximum sprint speed of Cycladic populations of *P. ehardii*.

The output of the best model is boldfaced, all models included maximal sprint speed as the dependent variable, with sex, SVL, and body temperature as covariates. The predator predictors were R=rats, SB=sand boas [*Eryx jaculus*], B=predatory birds, V=vipers [*Vipera ammodytes*], OS=other saurophagous Colubrid snakes, and M=mammals. Sum predation is the summation of all the predator categories found on the island, and 0 Predation is the presence of absence of any predator on the island.

Model	**AICc**	**ΔAICc**	**Akaike's weight**
Birds	-95.392	0	0.469
0 Predation	-93.390	2.002	0.172
Birds + OP	-92.368	3.024	0.103
Mammals + Birds	-92.324	3.068	0.101
Mammals + OP	-91.784	3.608	0.077
Birds+Log10Age	-89.481	5.911	0.024
Sum Predation	-89.121	6.271	0.020
0 Predation+Log10Age	-87.774	7.618	0.010
Birds + OP+Log10Age	-86.529	8.863	0.005
Mammals + Birds+Log10Age	-86.492	8.9	0.005
Mammals + OP+Log10Age	-86.150	9.242	0.005
Mammals+Log10Age	-84.865	10.527	0.002
Mammals	-83.532	11.86	0.001
Sum Predation+Log10Age	-83.499	11.893	0.001
R+SB+V+B+OS+M	-81.967	13.425	0.001
R+SB+V+B+OS+M+Log10Age	-76.787	18.605	4.28E-05

Table 4: Selection criteria for the sixteen mixed models constructed to explain variation in maximum stamina in the Aegean Wall lizard, *P. ehardii*.

The output of the best model is boldfaced, all models included maximal stamina as the dependent variable, with sex, SVL, and body temperature as covariates. The predator predictors were R=rats, SB=sand boas [*Eryx jaculus*], B=predatory birds, V=vipers [*Vipera ammodytes*], OS=other saurophagous Colubrid snakes, and M=mammals. Sum predation is the summation of all the predator categories found on the island, and 0 Predation is the presence of absence of any predator on the island.

FIGURES

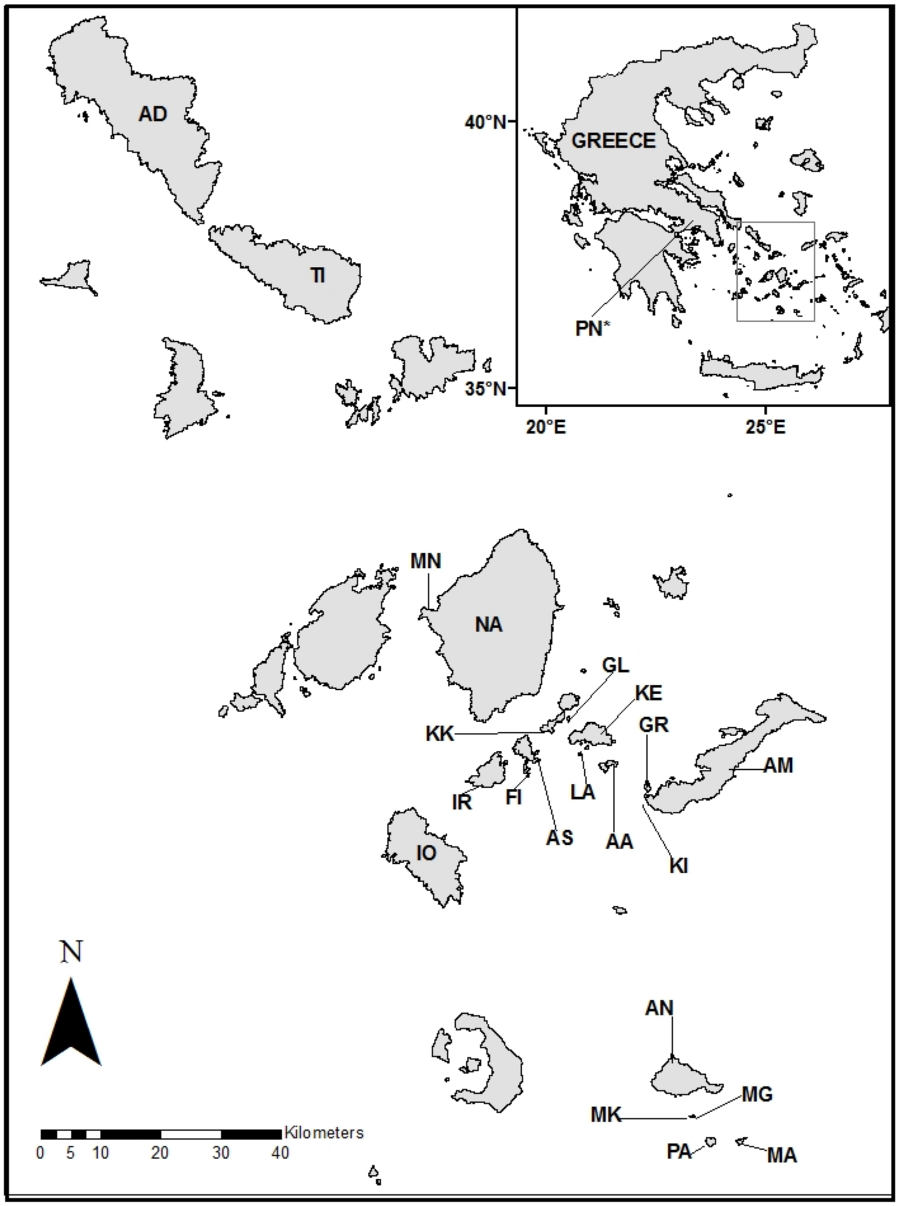

Figure 1: Map of Greece and study sites in the Aegean Sea. Amorgos (AM), Anafi (AN), Andros (AD), Ano Antikeros (AA), Aspronissi (AS), Fidussa (FI), Glaronissi (GL), Gramvoussa (GR), Ios (IO), Iraklia (IR), Kato Koufonissi (KK), Keros (KE), Kisiri (KI), Lazaros (LA), Makria (MA), Mando (MN), Megalo Fteno (MG), Mikro Fteno (MK), Naxos (NA), Pachia (PA), Tinos (TI), Parnitha (Mainland) (PN*). The mainland location is signified by an asterisk on the map.

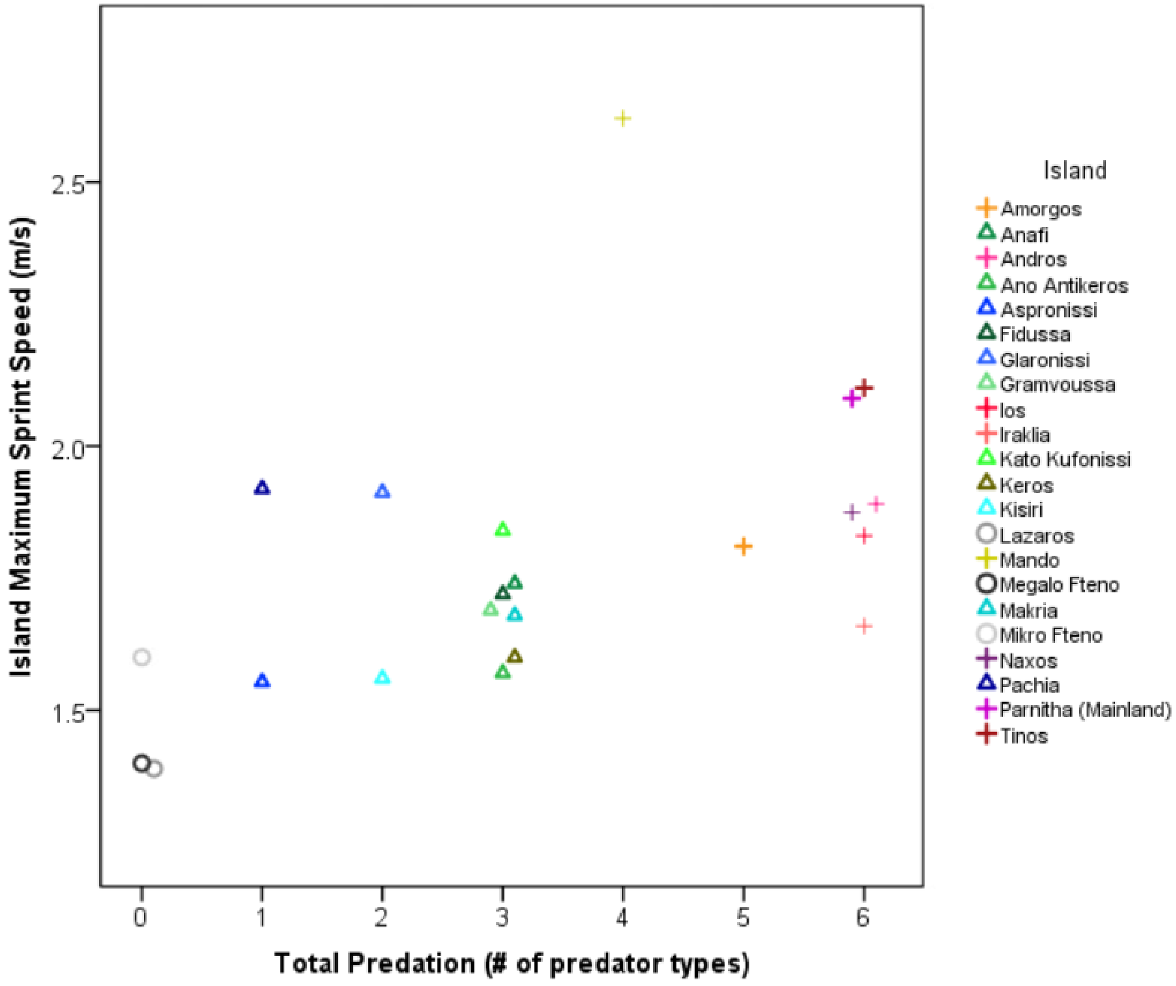

Figure 2: Scatterplot of island maximum sprint speed versus total number of predator categories found on each island. Circles represent islands without predators present, triangles represent islands with predators but not mammals present, and + represents islands with mammals present. Mean maximum stamina increases as predator categories increase.

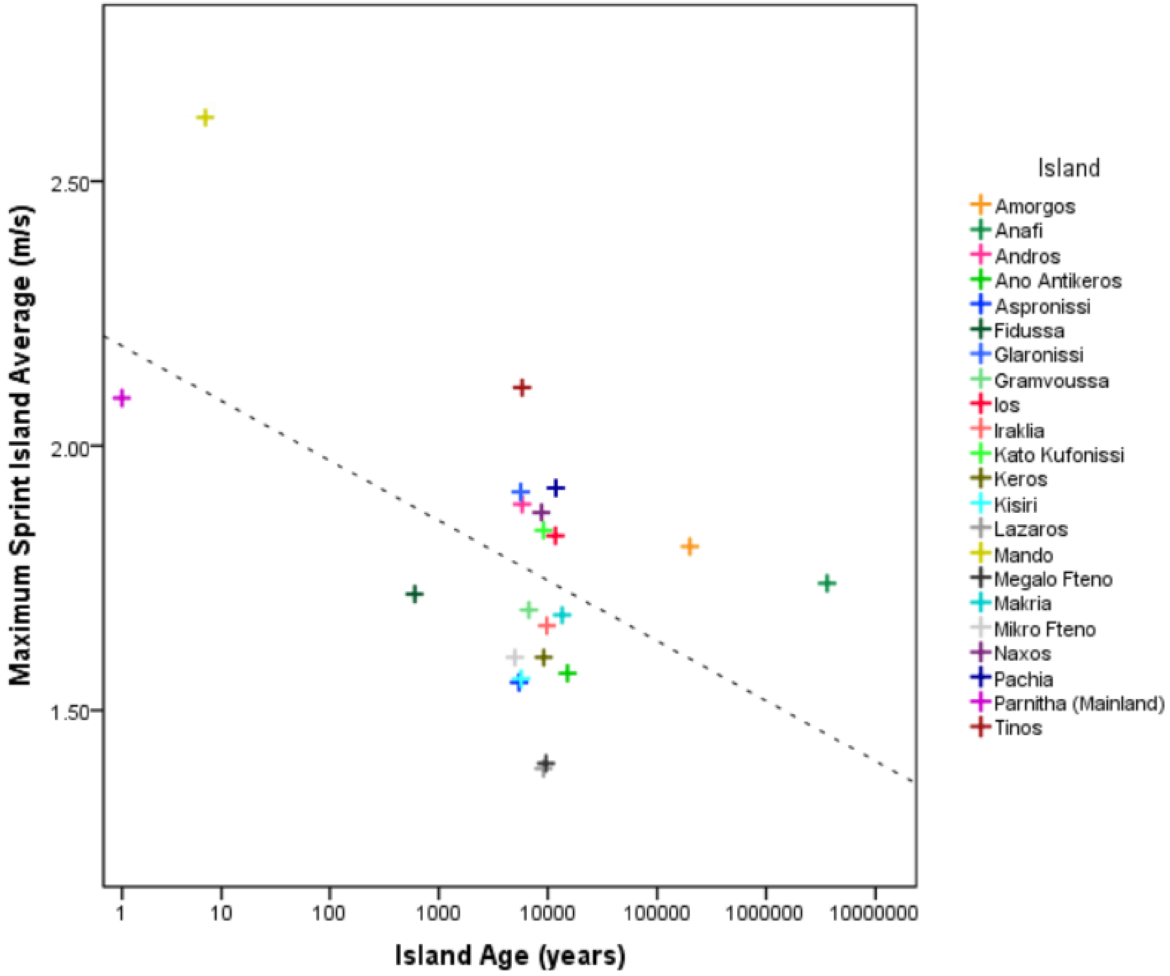

Figure 3: Scatterplot of island maximum sprint speed versus time of island isolation (Log_{10}-transformed). Each + represents an island.

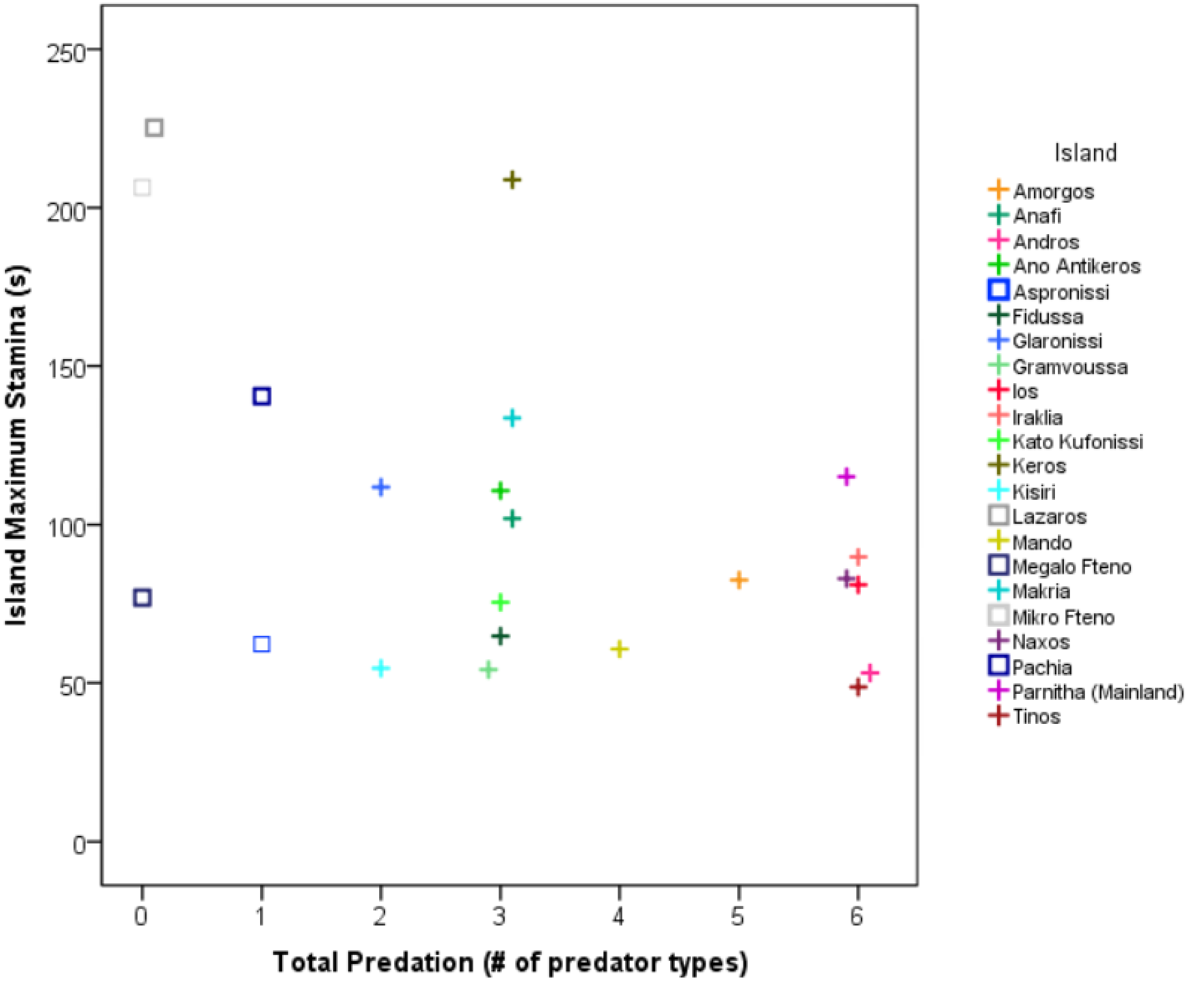

Figure 4: Scatterplot of island maximum stamina versus total number of predator categories per island. Each square represents an island without predatory birds present, and each + represents islands with predatory birds.

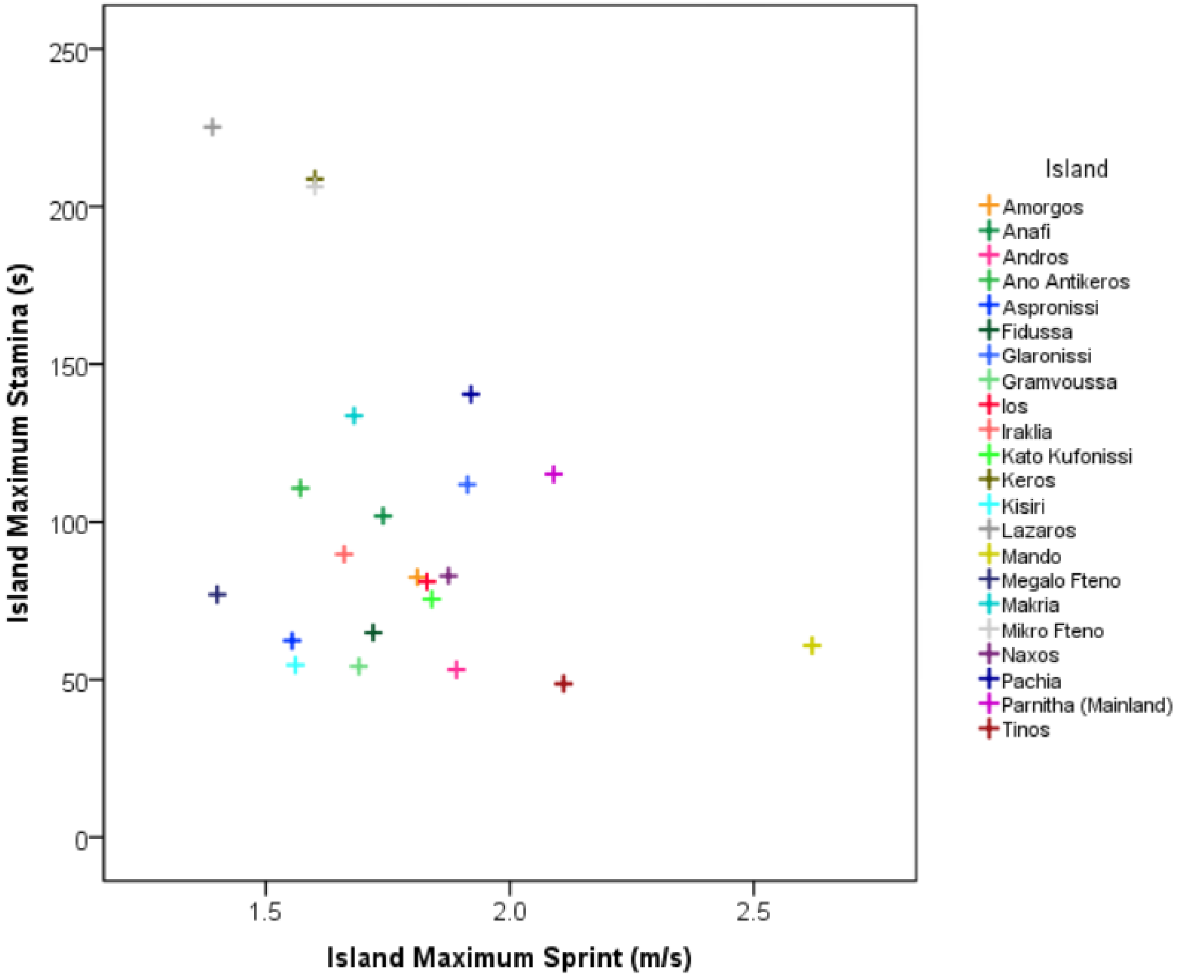

Figure 5: Scatterplot of maximum sprint speed for each island versus maximum stamina for each island.

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