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Island tameness: living on islands reduces flight initiation distance

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One of Darwin's most widely known conjectures is that prey are tame on remote islands, where mammalian predators are absent. Many species appear to permit close approach on such islands, but no comparative studies have demonstrated reduced wariness quantified as flight initiation distance (FID; i.e. predator–prey distance when the prey begins to flee) in comparison with mainland relatives. We used the phylogenetic comparative method to assess influence of distance from the mainland and island area on FID of 66 lizard species. Because body size and predator approach speed affect predation risk, we included these as independent variables. Multiple regression showed that FID decreases as distance from mainland increases and is shorter in island than mainland populations. Although FID increased as area increased in some models, collinearity made it difficult to separate effects of area from distance and island occupancy. FID increases as SVL increases and approach speed increases; these effects are statistically independent of effects of distance to mainland and island occupancy. Ordinary least-squares models fit the data better than phylogenetic regressions, indicating little or no phylogenetic signal in residual FID after accounting for the independent variables. Our results demonstrate that island tameness is a real phenomenon in lizards.

1. Introduction

Darwin [1] observed that animals on remote oceanic islands often are unafraid of people, permitting close approach. He believed that escape behaviour had diminished where predators were rare or absent on remote islands, which resulted in loss of costly escape responses [2–6] in the absence of strong natural selection to maintain them. Island tameness has been reported anecdotally in birds, lizards and other taxa [6–9]. If Darwin's island tameness hypothesis is correct, predation intensity and escape responses should be diminished on islands compared with the mainland and should also vary with distance from the mainland [10,11]. Mammalian predators are often absent from remote islands [1,7], but are able to visit or colonize islands nearer the mainland. Therefore, predation intensity should decrease as distance to the mainland increases (i.e. isolated islands should have lower predation intensity).

Recent evidence indicates that on islands where predation is reduced or absent, flocking of birds and group-size effects on vigilance in macropod marsupials are reduced [10,12]. In several cases, it has been shown for one or a few species that flight initiation distance (FID; i.e. predator–prey distance when the prey starts to flee) is shorter on islands having fewer predators (e.g. [6,13,14]). Despite such studies and the existence of many reports that some island species appear to be tame, the reality of island tameness as a general phenomenon has not previously been examined empirically in any diverse group of prey species, such as lizards, that are distributed widely on both continents and islands. Phylogenetic relationships that might affect estimates of correlations between escape behaviour and island occupancy have not been taken into account except in a single study of kangaroos and wallabies, for which no relationship was discovered between FID and island occupancy [12].

Escape behaviour is costly owing to loss of foraging, social and other opportunities, as well as to energetic expenditure [15,16]. To reduce escape costs when predation is relaxed or absent, shortened FID is expected to evolve over time. Several recent lizard studies have shown that FID is diminished in populations on islands where predation is relaxed [2,6,13] or is increased on islands where prey are exposed to feral cats and dogs [6,17]. In the lizard *Podarcis pityusensis*, which exists only on Ibiza, Formentera and nearby islets, FID increases as predation intensity on the islets increases [14]. On the other hand, Blumstein & Daniel [12] suggested that island tameness could be a consequence of aspects of living on islands other than predation.

Most species claimed to exhibit island tameness occur only on remote islands, but quantitative comparisons of escape behaviour between putatively tame animals and related mainland species are needed to eliminate the possibilities that (i) escape behaviour is not reduced on islands generally (barring anecdotal exceptions) or (ii) that it is reduced, but that lineages having short FID on islands also have short FID on the mainland. The latter might occur if species with minimal escape responses are more likely to become established and survive on remote islands. To test for island tameness in lizards, we conducted a phylogenetically informed analysis of variation in FID among 66 island and mainland lizard species from five continents and islands in the Atlantic and Pacific Oceans and the Caribbean and Mediterranean Seas.

Optimal escape theory [16,18] predicts that FID should increase as predation risk increases. Relative sizes of prey and predator affect risk, and FID should increase as predator size increases [19,20]. In the lizard *Sceloporus jarrovii*, FID when approached by a person is longer in larger individuals, presumably because larger lizards are more likely to be detected and attacked by (or less able to escape from) a large predator [21]. We predicted that FID increases as body size (snout–vent length; SVL) increases, as it does in birds [22] and macropod marsupials [9]. Because occupation of islands affects body size of lizards [23], we used multiple regression to examine the independent statistical influences of distance from the nearest mainland and body size on FID. Because FID increases as predator approach speed increases [24,25], it was included in the multiple regression models. Because predation pressure may be predicted to decrease with distance from the mainland and increase with island area (the latter effect owing to the increase in species diversity with island area [11]), we examined effects of these variables, as well as that of island versus mainland occupancy, on FID.

2. Material and methods

(a) Dataset and phylogeny

We used published data on FID (m), SVL (mm), island occupancy, distance to mainland (km) and land area (km^2) for 66 lizard species, and included approach speed for all but three species (see electronic supplementary material, table S1). The species include two that currently have subspecific status, but are reproductively isolated. We included FID data only if based on continuous approaches towards researchers walking at fixed speeds of 0.4–1.2 m s^{-1}. We required that lizards be less than 1 m from the ground or be approached by a researcher walking at the height of the perch. We excluded data for populations habituated to human presence, in which individuals were approached more than once, and in which researchers pointed at lizards with arms or inanimate objects. Where sex differences in FID were reported, we calculated a grand mean FID using the data for both sexes and for populations or multiple studies, taking sample sizes into account by using weighted means. SVL values were the maximum for each species in field guides and original papers cited (see electronic supplementary material, table S1). Distances to mainland were taken from cited papers (see electronic supplementary material, table S1) or estimated from distances on maps viewed on the Internet, primarily Google maps. Approach speeds were obtained from the cited sources or, in a few cases, from the authors. Island areas were obtained from Wikipedia, other websites and atlases. In many birds, mammals and lizards, FID increases as starting distance (predator–prey distance when the predator begins to approach) increases, but this effect is absent or reduced in lizards at the slow approach speeds used [5,26,27]. Owing to our stringent requirements for inclusion to ensure comparability, data from some excellent studies of escape behaviour (e.g. [28,29]) were excluded.

There are 66 taxa for which data were available that were included in a recent phylogeny of Squamata [30], which was time-calibrated for phylogenetic comparative analysis in a recent study using several well-constrained node ages based on the fossil record [31]. The original tree contained 4161 species and was trimmed to the 66 in our dataset. FIDs were available for two subspecies of *Scelarcis* (*Lacerta*) *perspicillata*: *S. p. chabaudi* and *pellegrina*. To include both of these in the phylogeny, we simply broke the branch leading to the terminal *S. perspicillata* in half, and assigned that distance to each subspecies, grafted onto the final tree. The other branches were not modified. The pruned phylogeny is provided in the electronic supplementary material (appendix S1).

(b) Statistical analyses

We conducted multiple regressions of FID on SVL, approach speed, distance to the nearest mainland and land area (or a categorical variable indicating occupation of island versus mainland; see the electronic supplementary material) to assess possible independent effects of these variables. FID, SVL, distance to mainland and island area were logarithmically transformed to eliminate heterogeneity of variance between island and mainland taxa, and to linearize relationships. Prior to $\log_{10}$ transformation, 0.5 was added to distance to mainland to accommodate zero values. We conducted ordinary least-squares (OLS) analysis, the conventional analysis in which each species is assumed to provide an independent datum. OLS does not use phylogenetic information; it implies that all taxa originated simultaneously [32].

Other analyses were conducted using two phylogenetic scenarios with time-calibrated molecular branch lengths from our phylogeny. We conducted phylogenetic least-squares analyses (PGLS) and RegOU analyses, the latter using the Ornstein–Uhlenbeck transformation [33], which implies an elastically restrained random walk used to model stabilizing selection about an optimum value taken to be the mean for all taxa. Calculations were done in MATLAB using the Regressionv2.m program [33]. Alpha was 0.05. Akaike's information criterion corrected for sample size (AIC$_c$) was used initially to assess explanatory merits of the models [34].

For each of the three types of analysis (OLS, PGLS and RegOU), we performed regressions for 12 models, including various combinations of the island variables plus SVL and approach speed. Our initial analyses indicated that the OLS models always fit the data better than PGLS or RegOU models. We used adjusted r^2 and AICc to help choose among OLS models. In addition to the above tests, we conducted OLS regressions limited to island taxa, which greatly reduced multicollinearity of some of the independent variables. Although the phylogenetic models were poor for FID, we examined the possibility that phylogeny might affect SVL by conducting a maximum-likelihood test for the

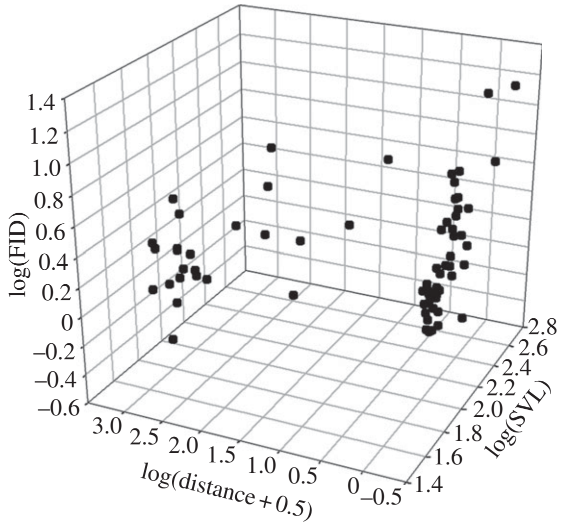

Figure 1. Three-dimensional scatter plot of FID on SVL and distance to mainland for all data. FID (m) decreases as the distance of the population from the mainland (km) increases, and increases as SVL (mm) increases. Note that mainland species are represented by a large cluster at log(distance + 0.5) having variable body length and FID.

phylogenetic tree fitted to log(SVL) and a randomization test for log(SVL) [35].

3. Results

Island tameness was apparent in the OLS analyses of the entire dataset and those restricted to island taxa. All RegOU models indicated that a star model is superior to the hierarchical phylogenetic tree that we used. These results indicate that ecological factors affect FID, but that the effects do not vary across species or clades in a predictable way based on their evolutionary relationships. The AIC$_c$ values of all PGLS models were very large (greater than 50) compared with those for OLS models (range 6–23). Therefore, we chose among OLS models. The superiority of OLS models for predicting log(FID) does not imply that the independent variables lack phylogenetic signal. The maximum likelihood for the phylogenetic tree fitted to log(SVL) was 30.14, far higher than that for a star phylogeny (3.71). The randomization test revealed a significant phylogenetic signal ($p < 0.0005$) and the K statistic ($K = 0.787$) indicates a fairly strong phylogenetic signal compared with those found for body size and other traits in various organisms.

For all data, including mainland and island species (figure 1), the five best OLS models included at least one of the three island-related variables plus SVL and approach speed; all five had adjusted r^2 values of 0.40–0.43 and had the lowest AIC$_c$ values (5.56–8.39; table 1). In the model having the lowest AIC$_c$ (second model in table 1), FID decreased significantly as distance to mainland increased (figure 2*a*). In the model having the second lowest AIC$_c$ (third model in table 1), FID increased significantly as land area increased. In the top model in table 1, distance to mainland and area were not significantly related to FID, but these variables were so tightly correlated ($r = 0.96$) that the assumption of independence between variables was seriously violated. In the fourth model, collinearity between island occupancy and area ($r = 0.96$) also occurred; neither variable was significantly related to FID. In the fifth model, which did not include distance to mainland or area as factors, FID was significantly shorter for island than mainland species. These findings for the three island variables show that island species have shorter FID than mainland taxa, demonstrating the existence of island tameness, but strong correlations among the island-related variables preclude conclusions regarding independent effects of the variables. However, distance to mainland had slightly greater explanatory power than the other two variables. For the entire dataset, FID increased significantly as SVL increased (figure 2*b*) and as predator approach speed increased in all OLS models in which they were included (table 1).

In the analyses restricted to island taxa (figure 3), two OLS models were clearly superior to the others, accounting for 65 and 63% of the variance of FID (table 1). None of the other models that we examined had adjusted $r^2 > 0.38$. In both models, FID increased significantly as both SVL and approach speed increased (table 1). Also in both models, FID decreased significantly as distance to mainland increased. One model did and the other did not include island area as a factor. In the model including both distance to mainland and area, the effect of island area was not significant. The best model (based on its having the lowest AIC$_c$) included distance to mainland as a factor, but not island area.

4. Discussion

Here, we demonstrate for the first time that island tameness exists as a general phenomenon in a large prey taxon by conducting analyses that take into account distance from the mainland, land area, island versus mainland occupancy, body size and predator approach speed in a large comparative dataset, and we account for possible phylogenetic effects. FID increases as distance from the nearest mainland increases, confirming the island tameness hypothesis for lizards. FID is greater in larger species and when approach speed is faster. The relationships between FID and both distance from mainland and island occupancy are robust, as indicated by their statistical significance in models for all taxa and those limited to islands. Thus, the suggestion by Darwin and others that prey on oceanic islands have diminished escape behaviour is supported for lizards, which are a geographically widespread prey clade [36].

The superiority of the OLS models to the phylogenetic models (PGLS and RegOU) suggests that ecological factors may drive changes in FID, forcing prey taxa to make escape decisions appropriate for predation regimes to which their populations have been exposed. This effect appears to eliminate any phylogenetic signal based on relatively ancient events. The relatively poor explanatory power of PGLS and RegOU models, and the utility of the OLS models, underscores this conclusion, which could not have been made without conducting phylogenetically informed analyses in addition to non-phylogenetic analyses. Although no phylogenetic signal was detected for FID, we detected a strong phylogenetic signal for SVL.

Our study shows that island isolation reduces FID, but does not conclusively show that FID is related to island area. In analyses including mainland taxa, collinearity among distance to mainland, land area and island occupancy prevent us from concluding which of these variables is important. Mainland areas are so much larger than those of islands that any potential effect of area is conflated with island occupancy. However, the

Table 1. OLS regression analyses of effects of log body length, predator approach speed, log(distance to mainland + 0.5), occupancy of island versus mainland and log island area on log FID. The five best models for the entire dataset and two best for island taxa are shown, with *F*-values on the first line for each model and *p*-values on the second. Each model included a subset of the independent variables shown below. Where no value is printed, the factor was not included in a particular model. Degrees of freedom (d.f.) for the entire dataset are 1,58 for models including four independent variables and 1,59 for models with three independent variables. For the island taxa, d.f. = 1,19 for models with four independent variables and 1,20 for models with three. Distance represents log(distance to mainland +0.5), area is log(area), SVL is snout–vent length, and approach speed represents log(approach speed). AIC$_c$, Akaike's information criterion corrected for sample size. Adjusted R^2-values are for the entire model.

		independent variables included in model				
adjusted R^2	AIC$_c$	distance	area	island versus mainland	SVL	approach speed
entire dataset						
0.43	6.57	1.65	1.33		28.11	12.19
		>0.05	>0.05		<0.00001	0.00093
0.43	5.56	17.82			27.02	13.20
		0.000085			<0.00001	0.00059
0.42	5.89		17.41		29.62	10.96
			0.00010		<0.00001	0.0016
0.42	8.10		2.57	0.22	29.44	10.96
			>0.05	>0.05	<0.00001	0.0016
0.40	8.38			14.44	30.21	11.00
				0.00034	<0.00001	0.0016
island taxa only						
0.65	−9.64	17.21			10.83	24.11
		0.00050			0.0037	0.000085
0.63	−6.21	15.74	0.15		9.01	21.96
		0.00082	>0.05		0.0073	0.00016

analyses restricted to island species show a strong effect of distance to mainland on FID, but no effect of island area. Because the two independent variables are not strongly correlated in this subset of the data and we detected an effect of distance to mainland, but not island area, we conclude that FID does not covary with island area in our island dataset. Predator diversity is expected to be greater on larger islands [11], which would predict an increase in FID as island area increases. However, recently introduced predators on islands in the Galapagos Archipelago and Caribbean Sea may have distorted natural processes. Furthermore, our sample size for islands is small ($n = 25$). A larger sample size is needed to ascertain whether any consistent relationship exists between FID and island area.

In conjunction with frequent reports of decreased diversity and abundance of predators on islands [3,4,6,17,37], reduced FID in lizards on islands is consistent with the conjecture that island tameness evolves when predation is rare or absent, making benefits of fleeing low or non-existent, whereas costs of maintaining escape behaviour remain when predators are scarce. In lacertid lizards of the Mediterranean Basin, FID and other escape variables are reduced on islets with fewer predators [3,4,13,14]. Similar findings have been reported for iguanian lizards [2,6,17]. Antipredatory responses including FID and vigilance are weak where predation is relaxed in macropodid marsupials [9–12] and birds [8]. Our evidence strongly supports the existence of island tameness, but does not provide any direct evidence that it is a consequence of reduced predation.

Rates of evolutionary change in escape and related antipredatory behaviours under reduced predation intensity are largely unknown. However, evolution of island tameness sometimes proceeds rapidly, as shown by a decrease in FID within 30 years after introduction of a lizard population to an island having reduced predation intensity [13]. The lack of a strong phylogenetic effect in our dataset suggests that these differences in FID can evolve very quickly and are not strongly clade-specific. On the other hand, responses to a specific felid predator may be maintained by deer for thousands of years, while the predator has been absent [27]. According to the multipredator hypothesis, antipredator behaviours may be lost rapidly in the complete absence of predators, but are maintained if at least one predator is present [38]. More studies are needed to ascertain the importance of overall predation intensity exerted by local predator guilds, roles of predation by particular predators (and their similarity to other predators) in maintaining escape responses, generation time of prey species and the time scales across which antipredator behaviours evolve and persist.

Actively foraging and ambush foraging lizards differ in many aspects of ecology, behaviour and physiology [39–41]. However, additional analyses (see electronic supplementary material) show that FID did not differ between foraging modes or major taxonomic groups, consistent with the poor performance of the PGLS and RegOU models. Therefore, foraging mode and phylogenetic relationships are excluded as possible sources of bias affecting our conclusions regarding island tameness.

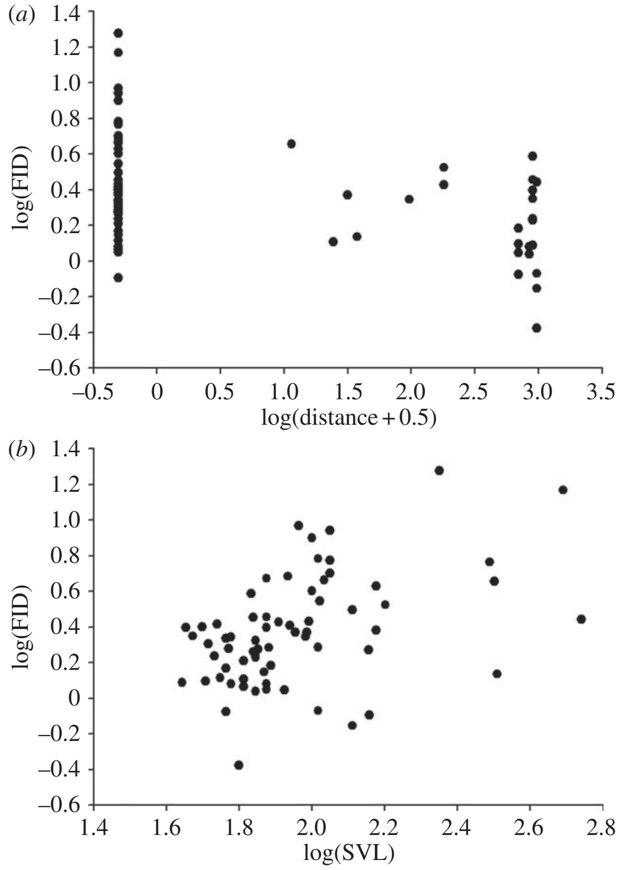

Figure 2. Two-dimensional scatter plots of FID on SVL and distance to mainland for all data. These graphs complement figure 1 in two-dimensional views. (*a*) FID (m) decreases as the distance of the population from the mainland (km) increases. (*b*) FID increases as SVL (mm) increases.

The increase in FID as body length increased establishes prey size as an important factor that affects escape behaviour, extending to lizards similar findings of a comparison among 150 avian species [22]. Although the relationship between FID and prey size is variable [19–21], our results suggest that larger prey may be more attractive to or more easily detected at greater distances by much larger predators. In a few other studies of single species, FID decreased as prey size increased [19], but body sizes of predator and prey were much more similar than in our study. Predation risk in such cases presumably decreased as prey size increased. In addition to the effect of body size on risk, other mechanisms may affect the relationship between prey size and FID, especially effects of body size on opportunity costs of fleeing.

Because frequency of attack, prey responses and survival are affected by predator–prey body size ratios, and these ratios vary over several orders of magnitude [42,43], the relationship between FID and prey size presumably is nonlinear over a wide range of predator–prey body size ratios. We hypothesize that when prey are very small relative to predators, predators do not attack isolated individual prey, resulting in the absence of fleeing or very short FID. As the ratio of prey size to predator size increases, prey are more likely to be attacked and FID presumably increases. With continued increase in prey size, FID may eventually decrease as the prey becomes less vulnerable if attacked. Alternatively, the magnitude of FID has a maximum value at some prey size and decreases at both smaller and larger prey sizes. As further increase in prey size relative to the predator occurs, prey may cease to flee and predator–prey relationships may be reversed.

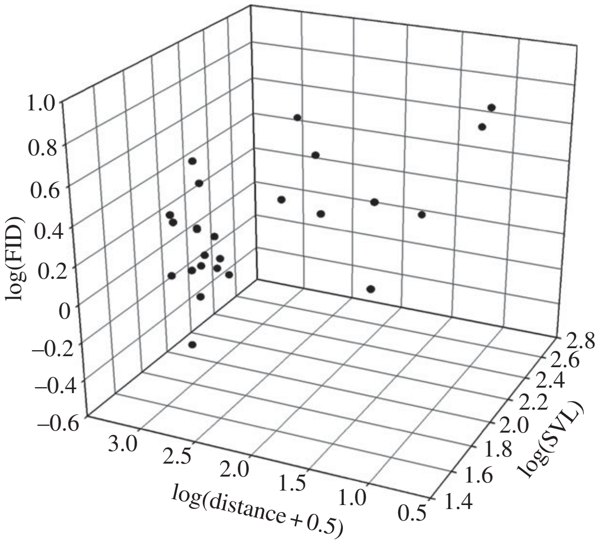

Figure 3. Three-dimensional scatter plot of FID on SVL and distance to mainland for island taxa. This figure complements figure 1, which includes data for mainland species in addition to the island species shown in figure 3. FID (m) decreases as the distance of the population from the mainland (km) increases, and increases as SVL (mm) increases.

Predator approach speed has been identified as a major risk factor that affects FID in lizards and other taxa [19]. The large effect of approach speed on FID in our study confirms the importance of approach speed in lizards in a comparative study using data from a phylogenetically diverse sample.

Our study confirms Darwin's observations and numerous anecdotal reports of island tameness. Findings of several studies cited above support Darwin's proposals that escape responses are reduced on remote islands, because predators are scarce or absent there, and natural selection under reduced predation should favour prey that do not waste time and energy developing and performing needless escape. A similar reduction in response to predators that are absent occurs in isolated aquatic ecosystems, especially freshwater systems, where prey are highly vulnerable to introduced predators [44,45].

Some recent evidence suggests that FID is shorter where predation intensity is lower on islands than on the mainland or other islands [4,6,13,14]. However, the generality of this mechanism has not been assessed. To permit a broader assessment of the role of predation in the evolution of island tameness, we encourage comparative analyses that add quantitative estimates of predation intensity to the variables we studied. Despite the evidence for reduced predation on islands, it remains possible that other factors favour island tameness. For example, if food is scarce on islands, the cost of leaving food to flee would favour shortened FID. This would be likely to occur only when food is present, but lizards were not approached while eating in the studies cited. A final caveat: tameness might be learned within each generation, but antipredator responses are known to persist much longer [12]. We expect that genetic changes have occurred across generations, but we have not studied them.

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ELECTRONIC SUPPLEMENTARY MATERIAL

ESM 1. SUPPLEMENTARY ANALYSES: FORAGING MODE, HIGHER TAXA, AND FID

Foraging modes of insectivorous/carnivorous lizards strongly affect many aspects of lizard ecology and behaviour [1-3]. To exclude any bias of our main findings due to differences in foraging modes, we conducted a nonphylogenetic analysis of covariance using SVL as covariate and excluding herbivorous species (the iguanids in *Amblyrhynchus*, *Ctenosaura*, *Dipsosaurus,* and *Sauromalus*). Active foragers included 19 species of skinks in the genera *Carlia*, *Egernia*, *Plestiodon*, and *Trachylepis*, lacertids in the genera *Iberolacerta*, *Lacerta*, *Podarcis*, and *Psammodromus*, and teiids in the genera *Aspidoscelis* and *Cnemidophorus*; the remaining 40 species were ambush foragers. The analysis of covariance using logarithmic transformations of FID and SVL revealed no difference in FID between active and ambush foragers ($F_{1,56} = 0.62$, $P = 0.44$). Because foraging modes are stable within most lizard families (Cooper 1997) and our data set does not include cases of intrafamilial transitions between modes, it remains possible that foraging mode influences FID.

Our data set included more than one species of three higher taxa recognized in recent phylogenies (Vidal & Hedges 2005), Iguania (represented here by 43 species), Scinciformata (represented here by 8 species of Cordylidae and Scincidae), and Laterata (represented here by 14 species of Lacertidae and Teiidae). We conducted an analysis of covariance using log SVL as a covariate to assess any influence of clade membership on log (FID). Flight initiation distance did not differ significantly among the higher taxa ($F_{2,61} = 0.19$, $P = 0.83$). Although our data reveal no statistical differences in FID among these major taxa, it is important to note that several major groups were not included in the data set, especially Gekkota and Anguimorpha.

(c) *References*

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ESM 2. DATA

(a) *FID, distance from mainland, land area, SVL and predator approach speed*

Table ESM1. Taxa, flight initiation distance (FID), distance from mainland (km), land area (km^2)^, snout-vent length (SVL), and predator approach speed$^\#$.

Species	FID	Distance*	Area	SVL	Approach speed
Rhotropus boultoni	1.4[1]	0	30,370,000	74[2]	0.75
Cordylus niger	9.3[3]	0	30,370,000	92[2]	1.00
Platysaurus intermedius	3.1[4]	0	30,370,000	129[2]	0.80
Platysaurus broadleyi	4.8[5]	0	30,370,000	86[2]	1.08
Carlia scirtetis	1.2[6]	0	9,008,500	60[7]	1.10
Carlia mundivensis	2.5[6]	0	9,008,500	50[7]	1.10
Egernia cunninghami	2.4[8]	0	9,008,500	150[7]	0.62
Plestiodon laticeps	1.9[9]	0	24,490,000	143[10]	1.00
Trachylepis sparsa	4.6[3]	0	30,370,000	108[2]	1.08
Trachylepis acutilabris	2.2[3]	0	30,370,000	60[2]	1.08
Cnemidophorus murinus	3.3[11]	180	288	159[12]	0.77
Aspidoscelis tigris	5.9[13]	0	24,490,000	112[14]	0.60
Aspidoscelis exsanguis	2.7[15]	0	24,490,000	98[14]	0.70
Psammodromus algirus	2.5[16]	0	10,180,000	75[17]	NA
Lacerta viridis	1.9[18]	0	10,180,000	104[17]	0.5
Lacerta vivipara	1.2[19]	0	10,180,000	65[20]	0.75

Iberolacerta horvathi	1.6[21]	0	10,180,000	65[20]	0.75
Lacerta perspicillata pellegrina	1.5[22]	0	30,370,000	56[22]	0.45
Lacerta p. chabanaudi	2.2[22]	0	30,370,000	85[22]	0.45
Podarcis pityusensis	2.2[23]	96	94	96[17]	0.80
Podarcis lilfordi	2.7[23]	180	0	81[17]	0.83
Podarcis muralis	1.1[24-25]	0	10,180,000	75[17]	0.67
Podarcis sicula	2.3[26]	31	1	90[17]	0.56
Podarcis melisellensis	1.3[27]	24	47	65[20]	NA
Lophognathus temporalis	4.0[28]	0	9,008,500	104[7]	1.00
Agama planiceps	5.0[1]	0	30,370,000	112[2]	0.92
Liolaemus multimaculatus	2.1[29]	0	17,840,000	70[30]	V
Liolaemus lemniscatus	1.7[31]	0	17,840,000	54[32]	0.48
Liolaemus nigromaculatus	4.2[33]	0	17,840,000	150[34]	0.76
Liolaemus fuscus	1.9[31]	0	17,840,000	59[32]	0.48
Liolaemus monticola	1.9[31]	0	17,840,000	76[35]	0.48
Microlophus bivittatus	0.4[36]	972	558	63[37]	0.50
Microlophus delanonis	0.7[13]	972	60	129[37]	0.50
Microlophus albemarlensis	0.8[13]	972	1761	104[37]	0.50
Crotaphytus collaris	8.7[38]	0	24,490,000	112[14]	0.83
Leiocephalus carinatus	3.5[39]	0	24,490,000	105[40]	1.00
Dipsosaurus dorsalis	0.8[41]	0	24,490,000	144[14]	0.67
Amblyrhynchus cristatus	2.8[42]	972	1,035	550[43]	0.50
Ctenosaura hemilopha	5.8[44]	9	160	308[45]	0.50
Ctenosaura similis	14.7[46]	0	24,490,000	489[47]	1.00
Sauromalus ater	18.9[48]	0	24,490,000	224[48]	0.50

Sauromalus hispidus	4.5[48]	11	632	371[48]	0.50
Sauromalus varius	1.4[48]	37	45	323[48]	0.50
Urosaurus bicarinatus	2.0[49]	0	24,490,000	52[50]	0.62
Urosaurus ornatus	1.3[51]	0	24,490,000	56[14]	0.56
Holbrookia propinqua	1.9[52]	0	24,490,000	71[10]	0.85
Callisaurus draconoides	7.9[53]	0	24,490,000	101[14]	0.84
Cophosaurus texanus	4.7[53]	0	24,490,000	75[14]	0.84
Sceloporus gadoviae	2.8[49]	0	24,490,000	69[54]	0.62
Sceloporus grammicus	2.6[49]	0	24,490,000	68[55]	0.62
Sceloporus virgatus	1.8[56]	0	24,490,000	69[14]	0.75
Sceloporus occidentalis	2.6[57]	0	24,490,000	87[14]	NA
Sceloporus mucronatus	6.1[49]	0	24,490,000	104[58]	0.62
Sceloporus jarrovii	2.3[59-61]	0	24,490,000	97[14]	0.94
Anolis coelestinus	1.1[62]	700	76,480	84[40]	0.80
Anolis bahorucoensis	1.2[62]	700	76,480	51[40]	0.80
Anolis cybotes	1.5[62]	700	76,480	77[40]	0.80
Anolis lineatopus	1.1[63-64]	850	10,990	70[40]	0.92
Anolis grahami	1.2[64]	850	10,990	75[40]	1.01
Anolis distichus	0.8[62]	700	76,480	58[41]	0.80
Anolis evermanni	1.7[65]	900	8,959	70[66]	1.05
Anolis stratulus	1.2[65]	900	8,959	44[66]	1.05
Anolis cooki	1.7[65]	900	8,959	70[66]	1.05
Anolis cristatellus	2.8[65]	900	8,959	75[66]	1.05
Anolis gundlachi	3.8[65]	900	8,959	68[66]	1.05
Anolis krugi	2.5[65]	900	8,959	45[66]	1.05

Anolis pulchellus	2.2[66]	900	8,959	47[66]	1.05

Distances from mainland (km) were determined from the papers cited for FID (m) and SVL (mm) for mainland populations and from cited papers or estimated from maps for island populations. ^ Land areas (km^2) were obtained from the papers cited, Wikipedia and other web sources, and from geographic atlases. For mainland taxa the area of the continent was used. # Predator approach speeds (m/s) were taken from the cited papers or were obtained from their authors. NA – not available. V – Data not analyzed due to decreasing speed during approach.

(b) *Sources for data in table*

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APPENDIX 1. NEXUS FORMAT OF THE RECOVERED PHYLOGENY SHOWING TAXA AND MOLECULAR BRANCH LENGTHS

(G1_Rhotropus_boultoni:168.832222,((((C2_Platysaurus_broadleyi:36.321531,C1_Platysaurs_intermedius:36.321531):30.861595,C3_Cordylus_niger:67.183125):84.624859,(S6_Plestiodon_laticeps:87.343384,((S3_Egernia_cunninghami:71.336135,(S2_Trachylepis_sparsa:32.10747,S1_Trachylepis_acutilabris:32.107469):39.228664):3.800332,(S5_Carlia_mundivensis:14.874649,S4_Carlia_scirtetis:14.874649):60.261818):12.20692):64.4646):14.80675,(((T5_Cnemidophorus_murinus:42.438233,(T4_Aspidoscelis_exsanguis:29.805591,T1_Aspidoscelis_tigris:29.805591):12.632641):111.54368,(L1_Psammodromus_algirus:84.808652,(LA_Lacerta_vivipara:51.107193,((L9_Lacerta_viridis:45.220753,((L7

_Lacerta_perspicillata_pellegtini:20.3730215,L8_Lacerta_perspicillata_chabanaudi:20.3730215):20.3730215,(L3_Podarcis_melisellensis:20.2741,((L4_Podarcis_sicula:13.480784,L2_Podarcis_muralis:13.480784):5.030651,(L5_Podarcis_lilfordi:6.562778,L6_Podarcis_pityusensis:6.562778):11.948657):1.762664):20.471944):4.47471):2.557182,LB_Iberolacerta_horvathi:47.777935):3.329258):33.701459):69.173261):8.230566,((A2_Lophognathus_temporalis:98.355928,A1_Agama_planiceps:98.355929):48.044071,((Z1_Microlophus_bivittatus:39.396408,(Z2_Microlophus_delanonis:18.84786,Z3_Microlophus_albemarlensis:18.84786):20.548548):65.223696,((I7_Dipsosaurus_dorsalis:66.283708,((I4_Sauromalus_ater:8.877658,(I6_Sauromalus_varius:2.872656,I5_Sauromaus_hispidus:2.872656):6.005002):26.971676,(I3_Amblyrhynchus_cristatus:26.362375,(I2_Ctenosaura_similis:18.877699,I8_Ctenosaura_hemilopha:18.877699):7.484675):9.486958):30.434376):33.20995,(W1_Leiocephalus_carinatus:96.243801,((N1_Crotaphytus_collaris:87.7674,((XB_Calllisaurus_draconoides:24.866111,(X1_Cophpsaurus_texanus:22.339153,X2_Holbrookia_propinqua:22.339154):2.526958):29.856636,((X3_Urosaurus_bicarinatus:35.78337,X4_Urosaurus_ornatus:35.783369):8.631643,(XA_Sceloporus_gadoviae:29.216999,(X9_Scelopororus_grammicus:18.321284,((X8_Sceloporus_jarrovii:16.395538,X7_Sceloporus_mucronatus:16.395538):1.066803,(X6_Sceloporus_occidentalis:10.998751,X5_Sceloporus_virgatus:10.998752):6.46359):0.858943):10.895716):15.198012):10.307734):33.044654):5.168531,(((R1_Liolaemus_lemniscatus:18.720367,(R2_Liolaemus_fuscus:15.951543,R3_Liolaemus_monticola:15.951543):2.768824):3.867377,R4_Liolaemus_nigromaculatus:22.587743):66.243868,((P1_Anolis_bahorucoensis:39.614992,PD_Anolis_coelestinus:39.614993):4.446784,(P2_Anolis_cybotes:39.197212,((P1_Anolis_distichus:29.887805,((P9_Anolis_evermanni:11.360637,P3_Anolis_stratulus:11.360637):13.760293,(

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((P7_Anolis_krugi:12.249602,P8_Anolis_pulchellus:12.249602):6.03237,P6_Anolis_gundlachi:18.281971):3.086306,(P4_Anolis_cooki:16.456944,P5_Anolis_cristatellus:16.456944):4.911334):3.752652):4.766875):8.044364,(PC_Anolis_lineatopus:27.454935,PB_Anolis_grahami:27.454934):10.477234):1.265043):4.864566):44.769833):4.104321):3.30787):3.249858):5.126445):41.779896):15.812478):4.402257):2.217488);
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