

Evolution on a desert island: body size divergence between the reptiles of Nevada's Anaho Island and the mainland around Pyramid Lake

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resource availability; competition; dwarfism; gigantism; *Aspidoscelis*; Teiidae; *Callisaurus*; *Sceloporus*; Phrynosomatidae; *Crotalus*; Viperidae.

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Abstract

Patterns of body size evolution on islands provide compelling cases of rapid and dramatic phenotypic evolution in terrestrial vertebrates, yet debate remains over the relative roles of predation and resource availability in driving such evolution. We compared the morphology of five reptile species (four lizards, one snake) from Anaho Island, a desert island in Pyramid Lake, Nevada, and the nearby mainland, using museum and live-caught animals. We also examined head-shape allometries to make inferences about dietary shifts and recorded tail-regeneration frequencies (in lizards) to examine predation intensity. Compared with mainland samples, two phrynosomatid lizard species are larger on Anaho (*Callisaurus draconoides* and *Sceloporus occidentalis*), whereas the largest (*S. uniformis*) is not different on the island. Conversely, the teiid lizard *Aspidoscelis tigris* is smaller in body and head size on the island, and the pitviper *Crotalus oreganus* is especially diminutive on the island, with males and females 25 and 15% smaller, respectively. Our results appear consistent with the hypothesis that body size is related to resource availability. The change in body size of the two smaller phrynosomatids may be due to interference competition. The reduction in body and head size in *A. tigris* suggests a dietary shift, and the dramatic difference in *C. oreganus* is likely due to a switch in diet from mammals to lizards. Future work is needed to determine whether body size differences reflect genetic evolution or environmental differences in growth rates or resource use. Regardless, Anaho Island, although remarkably young (early Holocene), appears to harbour a unique community of reptiles with distinct morphologies and possibly divergent life histories.

Introduction

Body size is one of the most crucial aspects of an organism's morphology, with major implications for ecological interactions, resource requirements, physiology, and even extinction risk (Brown, Marquet & Taper, 1993; Cardillo *et al.*, 2005; White *et al.*, 2007). Various hypotheses for geographic patterns in body size have been put forth, from simple environmental influences on development (Van Voorhies, 1996), to specific thermal advantages in particular climates (Bergmann's rule), to changes in resource abundance (Eastman *et al.*, 2012). Islands offer ideal arenas in which the abiotic and biotic conditions thought to influence body size can be examined. Body size evolution is often dramatic on islands, with celebrated cases of both dwarfism and gigantism (Lomolino, 2005; but see Meiri, Raia & Phillimore, 2011). Furthermore, islands, particularly continental islands, are often closed and relatively simplified versions of nearby mainland communities, such that key drivers of body size evolution

might be more easily decomposed in island systems (Lomolino *et al.*, 2010). As such, phenotypic evolution on islands has long drawn the attention of evolutionary biologists (e.g. Darwin, 1845).

Theoretical work (Case, 1978) and empirical studies of body size evolution on insular terrestrial vertebrates (e.g. Foster, 1964; Case, 1976; Boback, 2003; Meik, Lawing & Pires-da Silva, 2010; Raia *et al.*, 2010a) suggest that predation pressure and resource availability are important drivers of body size evolution on islands. Nevertheless, there remains substantial debate over the relative roles of these mechanisms and their predicted outcomes. Repeated patterns of gigantism in some small-bodied mammal groups (e.g. rodents) and dwarfism in some large-bodied clades (e.g. artiodactyls) (the Island rule) hint that certain lineages or functional groups may be subject to different selective pressures; predator release is thought to allow the size increase in small-bodied mammals, whereas resource limitation is thought to pull large-bodied mammals to the other extreme on islands (Van Valen, 1973;

Lomolino, 1985, 2005). However, the ubiquity of these patterns has been questioned (Meiri, Dayan & Simberloff, 2006; Meiri, Cooper & Purvis, 2008; Raia, Carotenuto & Meiri, 2010b), and data from some mammal groups (e.g. carnivores) and from reptiles suggest that availability and competition for resources may be chiefly responsible for insular body size patterns (Case, 1976; Case & Schwaner, 1993; Boback, 2003; Meiri, 2007; Meik *et al.*, 2010; Raia *et al.*, 2010a). Furthermore, the behavioural ecology of species can impact resource use and competitive interactions in a community, and may play a major role in determining body size evolution on islands (Case, 1978; Palkovacs, 2003), yet behaviour is seldom considered (but see Case & Schwaner, 1993; Boback, 2003; Raia *et al.*, 2010a). Thus, studies that examine the relationship between insular body size and patterns of predation and resource availability should also consider how the behavioural ecology of species mediates these factors in contributing to patterns of size evolution.

Here, we examine whether body size evolution has occurred in a local community of insular reptiles, and whether patterns of body size change are consistent with predictions of the leading hypotheses of insular body size evolution. We investigated the reptiles of Anaho Island, a stark desert island in Pyramid Lake in the Great Basin Desert of Nevada. The island supports a modest community of reptiles that is similar to the mainland in lizard diversity, but includes only a small subset of mainland snake diversity (Woodbury, 1966; Gienger, Kuhn & Tracy, 2006). We focused on four common lizards and one snake species.

The predator release hypothesis suggests that small-bodied island colonists eventually increase in body size in the absence of significant predation (Lomolino, 2005). The presumed mechanisms are twofold. One is that the anti-predator advantages of small size, such as lower detection or exposure probabilities and improved agility (Blanckenhorn, 2000), may no longer be selective advantages (Lomolino, 2005). The other is that small-bodied species may be at liberty to exploit resources at will, potentially increasing growth rates, and also experience higher survival, such that populations will contain a greater proportion of older (larger) individuals, leading to increases in overall mean body size (Lomolino, 2005). Under this model, we predict that all of our focal species will increase in body size on Anaho Island.

The resource availability hypothesis suggests that the optimal body size of an insular vertebrate is tied directly to food availability (Case, 1978). Species are expected to decrease in body size if resources are scarce, while they should increase in body size when resources are plentiful. However, food may be more or less available depending on competition within and between species (Case, 1978). Thus, considering interactions among conspecifics as well as other species with similar resource needs is important in evaluating the actual availability of resources (Case, 1978). While we do not have direct data on the availability of arthropod resources on Anaho Island compared with the mainland, our many visits to the island suggest that the insect community is less diverse and abundant, and likely more seasonal in nature (see below). Furthermore, the island possesses less habitat and structural

complexity than the mainland, so lizard species that spatially segregate on the mainland may be forced into closer proximity on Anaho Island. Thus, we expect competition for resources to be more intense among Anaho Island's lizards than on the mainland. Given these assumptions, we make different predictions of body size trends for the reptiles of Anaho Island based on their behavioural ecologies. We predict that non-territorial species will be smaller on Anaho Island than on the mainland, while we predict the opposite trend for territorial species, where intense interference (contest) competition should promote larger individuals that can hold and defend larger territories with greater food resources (Pianka, 1988; Abrams & Matsuda, 1994).

Materials and methods

Study site

Anaho Island rises ~180 m above the waters of Pyramid Lake, a large terminal lake (487 km²) in the Great Basin Desert of north-western Nevada (Washoe Co.). This small island (2.57 km²) lies only 1 km from the eastern shoreline, but is separated by relatively cool and slightly saline water (Fig. 1). The island is decidedly harsh and stark, with only a fraction of the plant community native to the mainland (Woodbury, 1966; Svejcar & Tausch, 1991); noticeably absent are many of the larger woody species that provide structural habitat and refuge for many desert lizards. The island is also fairly homogeneous, characterized by barren hillsides and only scattered rocky outcrops interspersed with gravelly or rocky flats (Woodbury, 1966). Despite this severe environment, Anaho Island is an important rookery for seabirds (e.g. American white pelicans *Pelecanus erythrorhynchos*). The seasonal occurrence of nesting seabirds attracts avian ectoparasites (Cimicidae) and other uncommon desert insects such as carrion (Silphidae) and hister (Histeridae) beetles that feed on rotting fish and dead nestlings (Woodbury, 1966), and these in turn likely support the island's lizard fauna.

Sampling and morphological measurements

We examined morphological variation and evidence of attempted predation in four lizard species and one snake species: western whiptail *Aspidoscelis tigris*, zebra-tailed lizard *Callisaurus draconoides*, western fence lizard *Sceloporus occidentalis*, yellow-backed spiny lizard *S. uniformis* and western rattlesnake *Crotalus oreganus*. We collected morphological data from 1262 specimens: 1148 museum specimens and 114 live specimens (Supporting Information Appendix S1). We captured live specimens by hand or noose, took measurements, determined sex, uniquely toe or scale-clipped each individual, and released specimens at their capture point. We sampled specimens located anywhere on the Island, and to represent the vicinity of the Pyramid Lake mainland, any site within 0–50 km of the lakeshore, as long as that site represented the same watershed or contiguous desert habitat (extended to 100 km for rattlesnakes).

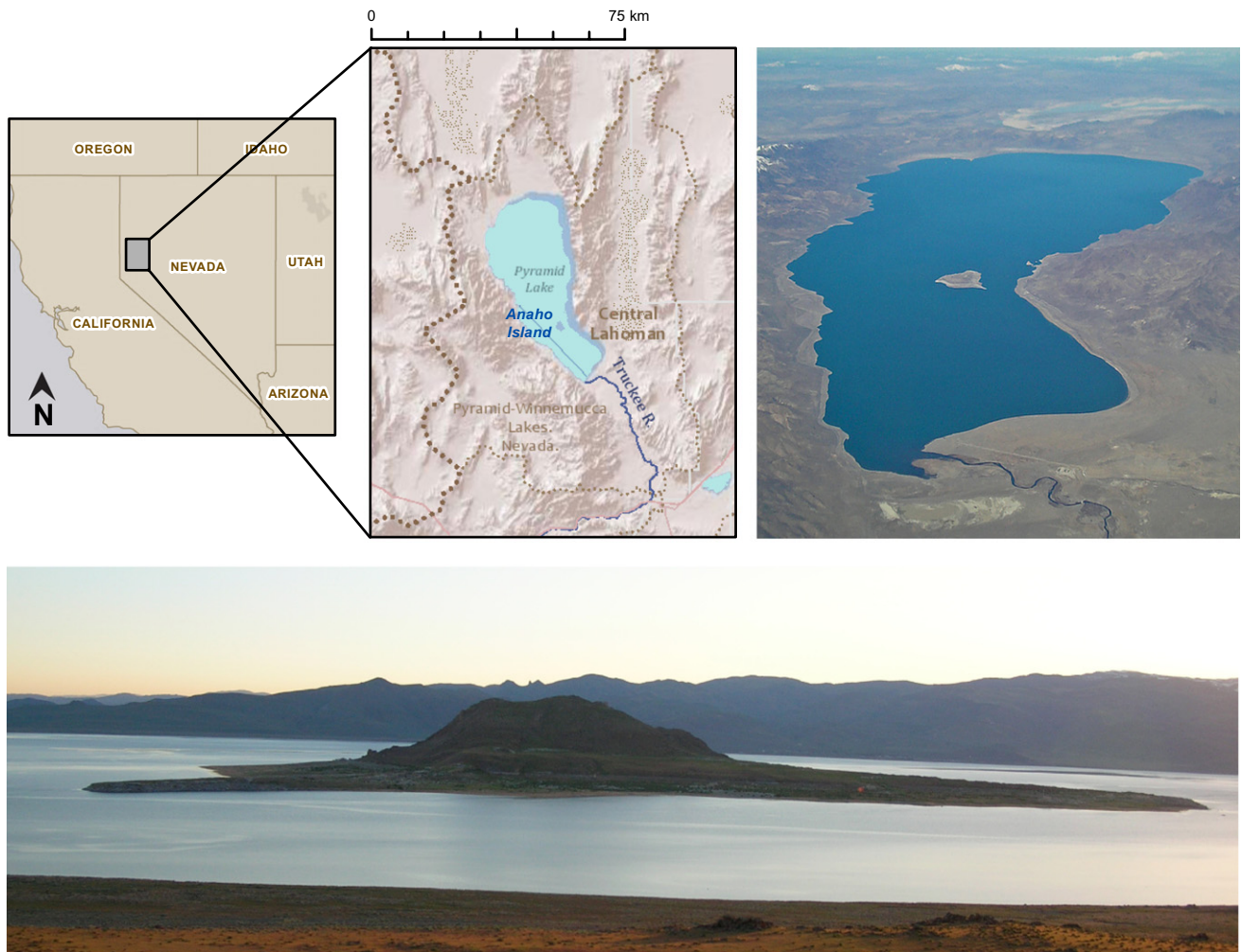


Figure 1 Pyramid Lake in the Great Basin Desert of north-western Nevada (Washoe Co.) is a terminal lake fed by the Truckee River which exits Lake Tahoe ~75 km to the southwest on the California-Nevada border. Anaho Island is the largest island in the lake (2.57 km²) and rises ~180 m above water level approximately one km from the eastern shore. Map shows lake location as well as major watersheds (dotted lines).

We recorded snout-to-vent lengths (SVL; tip of rostrum to vent) as a measure of overall body size (McDiarmid *et al.*, 2012). We used a ruler or meter stick for lizards (to nearest mm), and for snakes, we uncoiled specimens against a 45-cm wood hoop and used a string to measure SVL (McDiarmid *et al.*, 2012).

Differences in prey availability between Anaho Island and the mainland may have led to morphological changes in not just body size, but also in relative head size and shape because head morphology is tightly correlated with diet in both snakes and lizards (Herrel *et al.*, 1999; Meik *et al.*, 2010). If prey abundance is lower on Anaho than on the mainland, as is expected on small islands (MacArthur & Wilson, 1967), then snakes and lizards on the island may have proportionately larger heads, allowing these predators to exploit a wider variety of prey (Gravel *et al.*, 2011). Alternatively, if the availability of particular prey differs dramatically between island

and mainland (e.g. higher proportion of carrion and hister beetles), then other aspects of head shape may have changed to allow greater specialization on the most abundant resources (Meik *et al.*, 2010).

We therefore measured six head-shape variables (to nearest 0.01 mm with digital calipers): (1) head width (HW): between top of tympanic membranes for lizards; between widest part of head for rattlesnakes; (2) eye width (EW): between distal posterior base of supraoculars for lizards; between widest part of supraoculars for rattlesnakes; (3) head length (HL): tip of rostral scale to posterior margin of lower jaw (right side); (4) head height (HH): top of supraocular to margin of lower jaw below eye (not taken in rattlesnakes); (5) eye height (EH): top of supraocular to lower margin of upper labial below eye; (6) snout width (SW): between nostrils (not measured in *S. uniformis*), except in *A. tigris* measured as width of prefrontal at the posteriormost junction with internasals.

To determine whether differences in predation intensity exist between Anaho Island and the mainland, we examined the frequency of caudal autotomy in island and mainland lizards. In many lizards caudal autotomy or the shedding of a tail along a breakage plane, is a critical escape response to a predator attack (Arnold, 1988; Bateman & Fleming, 2009). If grasped by a predator, the tail is shed, allowing the lizard a quick getaway (Arnold, 1988; Bateman & Fleming, 2009). However, differences in caudal autotomy may also reflect differences in predator efficiencies or the intensity of intraspecific aggression across sites, and must therefore be interpreted with some caution (Bateman & Fleming, 2009, 2011).

We scored tails as damaged if they showed signs of regrowth posterior to the fracture plane (abnormal scale rows, coloration, etc.). We did not score missing tails or tails simply broken (not regenerated) because such breakage in museum specimens may result from postmortem examination or collection methods, rather than attempted predation (Bateman & Fleming, 2011).

We determined sex in lizards by presence/absence of enlarged post-anal scales (Stebbins, 2003) and in live snakes by eversion of hemipenes. In nearly all preserved snakes, sex had previously been established by dissection and examination of gonads (Glaudias, Goldberg & Hamilton, 2009). For those remaining snakes in which sex had not been documented (only 29), we assigned sex by shape of the tail base and by the ratio of tail length to SVL, using data from Glaudias *et al.* (2009).

Statistical analyses

To determine whether body size differs between conspecific reptiles on Anaho Island and the mainland vicinity of Pyramid Lake, we compared mean SVLs. We first assessed normality through standard probability plots of samples from each location. We also tested for sexual size dimorphism within populations using a *t*-test. All species except *S. occidentalis* exhibit significant sexual dimorphism, and thus, we analysed the sexes separately in all subsequent analyses (including *S. occidentalis* for consistency). To determine significant differences in mean body size (SVL) between island and mainland reptile populations, we used a Mann–Whitney *U*-test, which is more appropriate than a *t*-test when sample sizes are unbalanced (Zar, 2010).

To examine differences in relative head size and shape between Anaho Island and Pyramid mainland populations, we performed an analysis of covariance (ANCOVA) on log-transformed variables. We used the six head measurements as response variables (log HL, log HW, log EW, log HH, log EH, log SW) and location (island or mainland) and body size (log SVL) as predictor variables. This approach adjusts for individual variation in body size (log SVL). We excluded *S. occidentalis* because of small sample size.

To quantify potential differences in predator encounters between island and mainland communities, we calculated the frequency of tail regeneration for each species (and sex) in both locations. We used a Pearson's χ^2 test (proportions test)

to assess whether differences in the percentage of regenerated tails differed between populations.

Results

Body size

Body size comparisons between the reptiles on Anaho Island and their mainland counterparts around Pyramid Lake show significant differences in mean size in four of the five species (Table 1; Fig. 2). The zebra-tailed lizard (*C. draconoides*) appears larger on Anaho Island than on the mainland, although the trend is not quite significant in males (male \bar{x} = 74.0 vs. 69.8, z = 1.67, P = 0.09), but is in females (\bar{x} = 67.4 vs. 63.7, z = 2.12, P = 0.03). The western fence lizard (*S. occidentalis*) is also larger on Anaho Island than on the mainland (male \bar{x} = 76.0 vs. 69.9, z = 2.33, P = 0.02; female \bar{x} = 78.2 vs. 69.1, z = 2.00, P = 0.04). However, the yellow-backed spiny lizard (*S. uniformis*) is similar in size on island and mainland (male \bar{x} = 87.6 vs. 85.8, z = 0.93, P = 0.35; female \bar{x} = 78.5 vs. 80.1, z = 0.48, P > 0.5). The western whiptail lizard (*A. tigris*) is significantly smaller on Anaho Island (male \bar{x} = 76.5 vs. 80.5, z = 2.19, P = 0.03; female \bar{x} = 73.4 vs. 80.4, z = 3.52, P < 0.001). The western rattlesnake (*C. oreganus*), is especially diminutive on Anaho Island where males are nearly 25% smaller than their mainland counterparts (male \bar{x} = 565.3 vs. 749.3, z = 7.35, P < 0.001) and island females almost 15% smaller (female \bar{x} = 536.4 vs. 628.8, z = 4.05, P < 0.001).

Head shape

The ANCOVA adjusting for body size shows there are no consistent differences in head dimensions (e.g. wider, longer, etc.) between Anaho Island and mainland populations (Table 2) except for *A. tigris*, which has head-shape variables that are significantly smaller on Anaho Island compared with the mainland.

Tail regeneration

Frequencies of tail regeneration in lizards are similar between island and mainland populations of all species (Table 3) except for a significant difference in tail-regeneration frequency in male *S. uniformis*, with mainland males suffering greater tail loss than males on Anaho Island (17% vs. 37%, χ^2 = 6.19, P = 0.01). We did note bias in regeneration frequencies between males and females, with seven out of eight comparisons showing more frequent tail regeneration in males than in females (Table 3).

Discussion

Unique local conditions, boundaries to gene flow, confined space, often limited resources and unusual ecological communities are all thought to be important drivers of morphological novelty on islands (reviewed in Lomolino *et al.*, 2010).

Table 1 Body sizes (snout-to-vent length) of the focal reptile species on Anaho Island and the Pyramid Lake mainland along with sample sizes (*n*)

Clade Species	Sex	Pyramid Mainland (<i>n</i>)	Anaho Island (<i>n</i>)	z-value (d.f.)	<i>P</i> -value	Sig. Island Trend	Territorial	Prey	Foraging Mode
Phrynosomatidae									
<i>Callisaurus draconoides</i>	♂	69.8 (197)	74.0 (18)	1.67 (213)	0.09	–	Yes	Arthropod	Sit-and-wait
	♀	63.7 (126)	67.4 (21)	2.12 (145)	0.03	↑			
Phrynosomatidae									
<i>Sceloporus occidentalis</i>	♂	69.9 (122)	76.0 (23)	2.33 (143)	0.02	↑	Yes	Arthropod	Sit-and-wait
	♀	69.1 (90)	78.2 (6)	2.00 (94)	0.04	↑			
Phrynosomatidae									
<i>Sceloporus uniformis</i>	♂	85.8 (106)	87.6 (69)	0.93 (173)	0.35	–	Yes	Arthropod	Sit-and-wait
	♀	80.1 (74)	78.5 (18)	0.48 (90)	>0.5	–			
Teiidae									
<i>Aspidoscelis tigris</i>	♂	80.5 (104)	76.5 (19)	2.19 (121)	0.03	↓	No	Arthropod	Active
	♀	80.4 (76)	73.4 (26)	3.52 (100)	<0.001	↓			
Viperidae									
<i>Crotalus oreganus</i>	♂	749.3 (56)	565.3 (46)	7.35 (100)	<0.001	↓	No	Vertebrate	Sit-and-wait
	♀	628.8 (30)	536.4 (29)	4.05 (57)	<0.001	↓			

Initial comparisons of males and females indicated significant sexual size dimorphism in almost all species, thus sexes were examined separately using a Mann–Whitney *U*-test. Significant differences ($P < 0.05$) between body sizes of island and mainland reptiles are highlighted (bold), and the direction of size trend is indicated with arrows: smaller on Anaho Island (↓), larger on Anaho Island (↑), or no significant difference in mean body size (–). Information on the territoriality of the species (yes or no) along with the major clade (family) to which taxa belong is also provided. d.f., degrees of freedom.

However, there is an emerging consensus that patterns of body size evolution on islands are principally influenced by predation pressure and the availability of food (Foster, 1964; Case, 1978; Boback, 2003; Lomolino, 2005; Meiri, 2007). Here, we examine whether body size evolution has occurred in a community of reptiles on an island in the Great Basin Desert. We then consider whether patterns of body size change are consistent with either changes in predation pressure or changes in resource availability.

Body size trends on Anaho Island

Body sizes diverged significantly on Anaho Island in four of the five reptile species that we examined (Table 1; Fig. 2), but trends are not uniform in direction or magnitude. In response to release from predator pressure on islands, we expected all of our focal species to increase in body size on Anaho Island, but these predictions are not met. Furthermore, differences in tail-regeneration frequencies between island and mainland were minor, which might indicate similar predation pressures between island and mainland. Although mammal predators are absent or rare on Anaho Island (Woodbury, 1966), the major avian predators of the region should have easy access to the island. Additionally, the rattlesnakes on the island may have become the chief lizard predator (see later), so the intensity of lizard predation may be the same or even higher on Anaho Island. Regardless, we interpret the tail-loss data cautiously because different predators have different handling efficiencies, potentially biasing estimates of predation pressure (Bateman & Fleming, 2009, 2011).

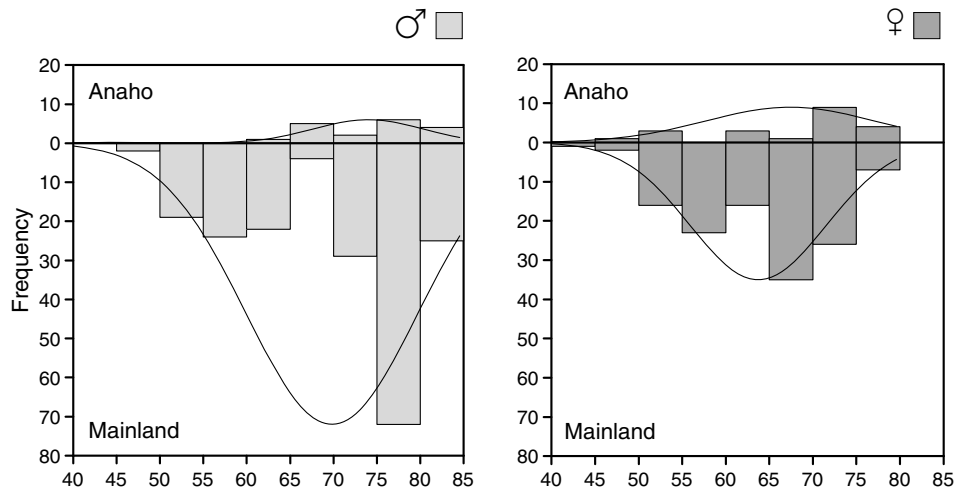
Our data appear consistent with the resource availability hypothesis, which suggests that the optimal body size of

an insular vertebrate is tied directly to food availability (Case, 1978). However, competition among conspecifics and heterospecifics may directly impact the availability of resources (Case, 1978). Furthermore, modes of competition can be different for species that are more or less territorial. In territorial species, access to resources often comes through the defence of a territory, thus selection should promote modifications that aid in resource defence and direct conflicts, such as increased body size or aggression (e.g. Raia *et al.*, 2010a). In non-territorial species experiencing resource limitation, selection should promote modifications that reduce resource demands (e.g. smaller body size) and possibly traits that aid in food-gathering efficiency. On Anaho Island, there are both territorial (phrynosomatids) and non-territorial (teiid, viperid) reptiles, and body size changes conform to these hypothesized predictions. We found the territorial zebra-tailed lizard *C. draconoides* and western fence lizard *S. occidentalis* are significantly larger on the island, while the western whiptail lizard *A. tigris* and the western rattlesnake *C. oreganus* are significantly smaller on Anaho Island (Table 1; Fig. 2).

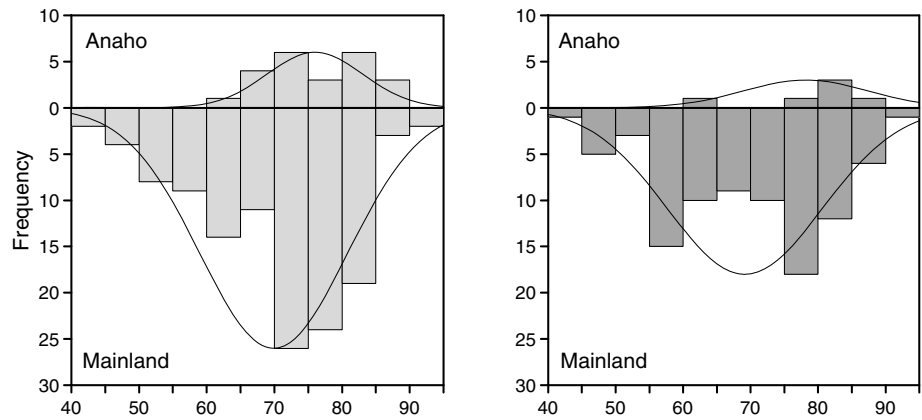
We posit that limited resources on Anaho Island may have intensified competition within and among the three phrynosomatids because they are close in size, consume similar prey, hunt by the same sit-and-wait strategy, and defend territories that provide them with access to food resources (Pianka, 1986). Furthermore, the relatively homogeneous habitat on the island may heighten interactions among these three species. On the mainland, these species segregate spatially, with *C. draconoides* along open flats, *S. occidentalis* along boulder-strewn slopes, and *S. uniformis* in trees and rocky outcrops (Stebbins, 2003). On the island, such a diversity of habitats is uncommon (Woodbury, 1966), and

Phrynosomatidae

Callisaurus draconoides



Sceloporus occidentalis



Sceloporus uniformis

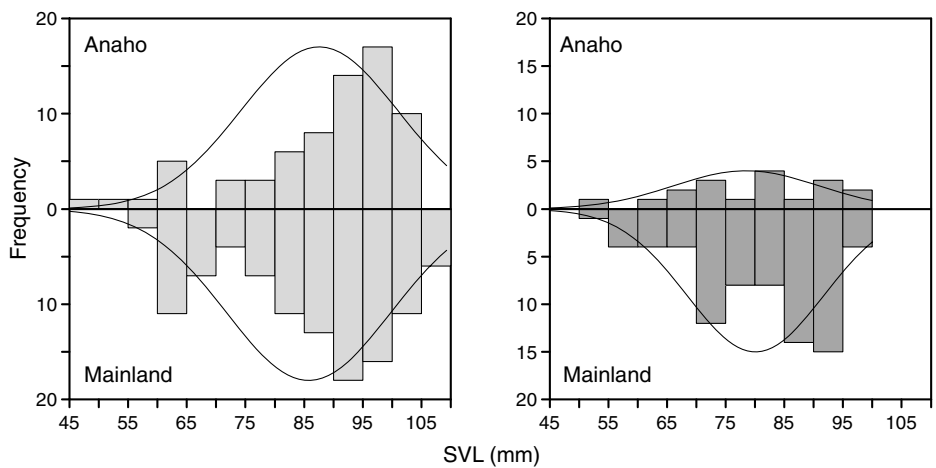
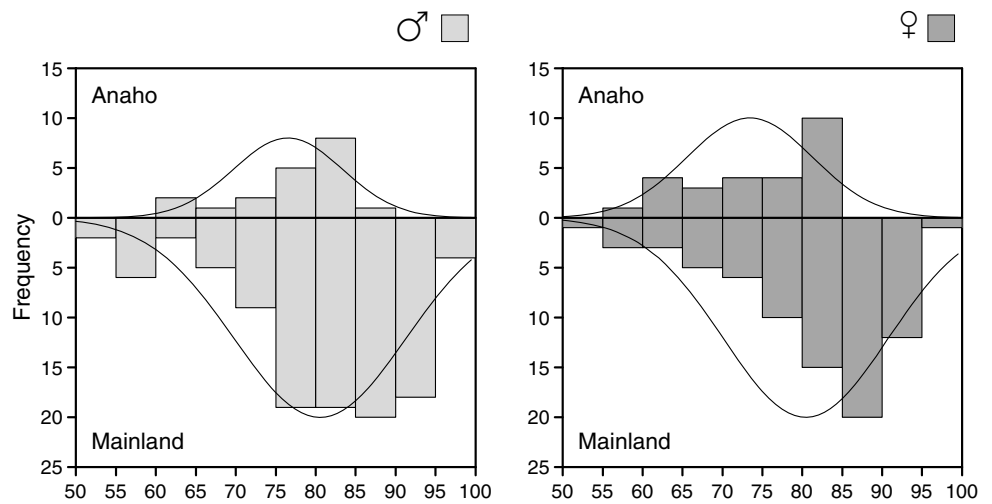


Figure 2 Body size [snout-to-vent length (SVL)] frequency histograms for each species on Anaho Island (upper) and the mainland area surrounding Pyramid Lake (lower), separated by sex (male: light grey; female: dark grey).

Teiidae

Aspidoscelis tigris



Viperidae

Crotalus oreganus

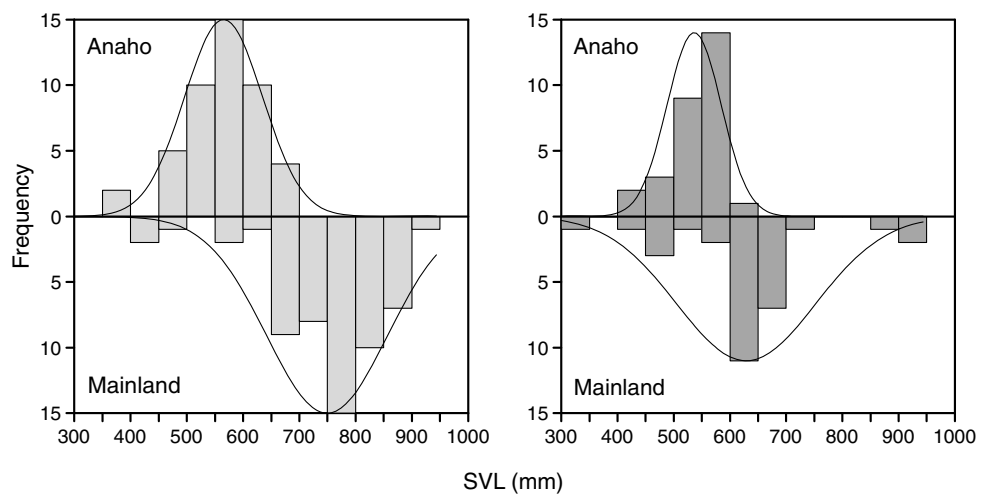


Figure 2 Continued.

Table 2 Results of analysis of covariance examining differences in six head-shape variables between Anaho Island and Pyramid Lake mainland reptiles

Morphological trait	<i>Callisaurus draconoides</i>		<i>Sceloporus uniformis</i>		<i>Aspidoscelis tigris</i>		<i>Crotalus oreganus</i>	
	♂	♀	♂	♀	♂	♀	♂	♀
Head length	-	-	-	↓	↓	↓	-	-
Head width	-	↑	↑	-	-	↓	↑	-
Snout width	↑	-	NA	NA	↓	↓	-	-
Eye width	-	↑	↑	-	-	-	↑	↑
Eye height	↓	↓	-	-	↓	↓	-	-
Head height	↓	↓	-	-	↓	↓	NA	NA

Analysis performed separately on sexes, and with log-transformed data, using body size (log SVL) as the covariate. The direction of size trend is indicated with arrows: significantly ($P < 0.05$) smaller on Anaho Island (↓), larger on Anaho Island (↑), or no trend (-). Note that some variables were not measured in particular taxa (NA), and that *S. occidentalis* populations were not compared because of low sample size. SVL, snout-to-vent length.

Table 3 Frequencies of tail regeneration and sample sizes (*n*), separated by sex and location (Anaho Island and Pyramid Lake mainland) for each lizard species

Species	Sex	Pyramid Mainland (<i>n</i>)	Anaho Island (<i>n</i>)	χ^2 (d. f.)	<i>P</i> -value	Sig. Island Trend
<i>Callisaurus draconoides</i>	♂	0.17 (178)	0.17 (18)	0.00 (194)	1.00	–
	♀	0.15 (112)	0.05 (21)	0.87 (131)	0.35	–
<i>Sceloporus occidentalis</i>	♂	0.28 (109)	0.22 (23)	0.16 (130)	0.69	–
	♀	0.20 (81)	0.17 (6)	0.00 (85)	1.00	–
<i>Sceloporus uniformis</i>	♂	0.37 (100)	0.17 (63)	6.19 (161)	0.01	↓
	♀	0.24 (71)	0.12 (17)	0.59 (86)	0.44	–
<i>Aspidoscelis tigris</i>	♂	0.33 (100)	0.11 (19)	2.88 (117)	0.09	–
	♀	0.23 (70)	0.38 (24)	1.28 (92)	0.26	–

A Pearson's χ^2 test was used to assess significant differences ($P < 0.05$) in tail-regeneration frequencies (bold) between Anaho Island and Pyramid Lake mainland for each sex separately.

although some spatial segregation is seen, these species may be forced to interact to a much greater degree on Anaho Island. Thus, competition for shared resources is likely more intense, leading to direct conflict over space (interference). We hypothesize that these direct contests over resources could have promoted the size differences in *C. draconoides* and *S. occidentalis* because larger individuals can hold and defend larger territories (Pianka, 1988). These taxa have converged on the size of the island's largest and most aggressive phrynosomatid, *S. uniformis* (Table 1). *Sceloporus uniformis* may not have changed in size because it easily dominates the other two species, and imposed selection for a larger body size on *C. draconoides* and *S. occidentalis* through aggressive conflicts. It is interesting to note that the evolutionary response of *C. draconoides* and *S. occidentalis* does not appear to involve any character displacement to minimize competition (Pianka, 1988; Pfennig & Murphy, 2000). The general lack of habitat diversity on Anaho Island may preclude any sort of specialization among these phrynosomatids.

Teiid lizards are highly active reptiles, constantly foraging, even at high temperatures when most other desert lizards have sought refuge from the heat (Cowles & Bogert, 1944; Pianka, 1986; Anderson & Karasov, 1981). For example, *A. tigris* spends more than 90% of their daily activity period moving, while *C. draconoides* spends just 2% of their activity period moving (Anderson & Karasov, 1981). Thus teiids have particularly high metabolisms and energetic demands compared with other local lizards (Anderson & Karasov, 1981), and we interpret the smaller body size of *A. tigris* on Anaho as evidence that limited resources may have favoured smaller individuals with lower food requirements. While a reduction in body size might also suggest character displacement to ease interspecific interactions with the island's phrynosomatid lizards, we doubt this is the case. Whiptails forage in a different manner than other lizards on the island, and they use a chemosensory tongue to detect cryptic prey (Pianka, 1986). Diet analyses of whiptails shows they are able to specialize on termites, insect eggs and larvae, and other buried or hidden prey that sympatric phrynosomatids do not (or cannot) exploit (Pianka, 1986). Thus, there may be little overlap in resource use between the teiid and phrynosomatids of Anaho Island.

In the case of the western rattlesnake *C. oreganus*, those on Anaho Island are substantially smaller than on the mainland, with males 25% and females 15% smaller (Table 1; Fig. 2), as suggested by Ashton (2000). Mammals are the primary prey of most adult *Crotalus*, while juveniles chiefly take lizards (Klauber, 1956). Given the scarcity of mammals on the island – only a single species (*Peromyscus maniculatus*) found at low densities (Woodbury, 1966; Kuhn, Gienger & Tracy, 2008) – and the multitude of lizards, it is easy to envision a simple retention of the juvenile diet (lizards) in island rattlers. Indeed, a recent diet analysis of *C. oreganus* throughout the Great Basin found only lizards in the stomachs of rattlesnakes from Anaho Island (Glaudias, Jezkova & Rodríguez-Robles, 2008). A reduction in body size is thus expected to accompany this exploitation of smaller prey (Case, 1978; Boback, 2003; Meik *et al.*, 2010). However, we cannot say whether body size reduction is due to any advantages smaller snakes might gain in hunting smaller prey, or whether a shift to smaller prey no longer requires these rattlesnakes to attain the large body size needed to prey on mammals. Regardless, the dietary shift from mammals to lizards and attendant reduction in body size is common in insular rattlesnakes (Case, 1978; Grismer, 2002; Meik *et al.*, 2010).

Finally, we note that these mechanisms (predation and resource limitation) may not be mutually exclusive (Palkovacs, 2003). For example, a decrease in predation pressure might lead to an increase in population density, which might then depress resources, leading to an increase in intraspecific competition (Palkovacs, 2003). A novel hypothesis, the 'reverse island syndrome', suggests that under similar conditions with unstable resources, aggressive individuals with rapid growth rates and early reproductive efforts will be favoured (Raia *et al.*, 2010a). It remains to be seen whether changes in disposition, growth rates, and fecundity, have accompanied body size evolution in the reptiles of Anaho Island. Further investigation of individual traits such as temperament, growth, age of first reproduction and fecundity, need to be linked to population dynamics and measures of predation pressure and resource use. Regardless, the behavioural ecology of species is key to understanding ecological interactions, and how these interactions can impact body size evolution in this system.

Conservation implications

Anaho Island clearly harbours a unique assemblage of reptiles morphologically distinct from their mainland counterparts. Remarkably, this diversity has accumulated rapidly, because Anaho Island first emerged from Pyramid Lake only ~11 000 years ago and may have been connected to the mainland at various times in the Holocene because of extreme droughts (Mensing *et al.*, 2004). Further work is needed to determine if such morphological divergence is the result of phenotypic plasticity or genetic evolution. Work is also needed to determine the degree of isolation of Anaho populations by estimating the frequency of new migrants from the mainland (if any). Gene flow may be critical in providing the genetic resources needed for island populations to respond to selection or, alternatively, may hamper local adaptation. Such movement also needs to be considered in light of increasing water demands from a growing urban population (Reno, NV) upstream that might threaten water levels in Pyramid Lake (Murphy & Tracy, 2005). If water levels decrease substantially, a land bridge could resurface between the island and the lakeshore (Woodbury, 1966), firmly linking reptile populations. Given the potentially distinct evolutionary history and trajectory of Anaho reptiles, such a connection could ultimately erase the unique biological heritage of Anaho Island.

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Supporting information

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Appendix S1. List of material examined. Institutional abbreviations follow the American Society of Ichthyologists and Herpetologists standard codes for institutional resource collections, except for live material (captured, marked, measured, and released) where the first two letters of genus and species and the order of first capture were used as unique identifiers (e.g. *Sceloporus occidentalis* capture 11, SCOC.011).