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Lizards on newly created islands independently and rapidly adapt in morphology and diet

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Rapid adaptive changes can result from the drastic alterations humans impose on ecosystems. For example, flooding large areas for hydroelectric dams converts mountaintops into islands and leaves surviving populations in a new environment. We report differences in morphology and diet of the termite-eating gecko *Gymnodactylus amarali* between five such newly created islands and five nearby mainland sites located in the Brazilian Cerrado, a biodiversity hotspot. Mean prey size and dietary prey-size breadth were larger on islands than mainlands, expected because four larger lizard species that also consume termites, but presumably prefer larger prey, went extinct on the islands. In addition, island populations had larger heads relative to their body length than mainland populations; larger heads are more suited to the larger prey taken, and disproportionately larger heads allow that functional advantage without an increase in energetic requirements resulting from larger body size. Parallel morphological evolution is strongly suggested, because there are indications that, before flooding, relative head size did not differ between future island and future mainland sites. Females and males showed the same trend of relatively larger heads on islands, so the difference between island and mainland sites is unlikely to be due to greater male–male competition for mates on islands. We thus discovered a very fast (at most 15 y) case of independent parallel adaptive change in response to catastrophic human disturbance.

rapid character change | islands | dietary shift | Brazilian Cerrado | lizards

Rapid evolution has been recorded recently for several taxa (1, 2), with rates of phenotypic change approaching, but not quite matching, rates of ecological change (3). Fast evolution is often driven by sudden anthropogenic environmental alteration, such as the flooding of large areas after the construction of hydroelectric dams. This inundation can convert mountaintops into islands, drastically shrinking continuous ranges of populations (4). The MacArthur–Wilson Species Equilibrium Model (5, 6) predicts that isolation and reduction of area will lead to species loss. In particular, a guild of competing species may lose some members, allowing those remaining to expand their niches (i.e., “ecological release”) (7). In this and other ways, island species may systematically differ from their mainland counterparts, phenomena that have been explored in various taxa (8), including lizards (9–12).

An example of rapidly human-created islands is at the lake resulting from the Serra da Mesa Hydroelectric Plant in central Brazil (Fig. S1). The reservoir is located within the Cerrado hotspot, a region of great conservation importance due to its combination of unique species and major human disturbance (13). The filling of the Serra da Mesa reservoir began in 1996 and flooded an area of 170,000 ha, comprising several valleys, forming ~290 islands (14). Periodic monitoring at island and mainland sites showed that lizard communities suffered significant impacts, including the extinction of most large-sized lizard species on many islands (refs. 15 and 16; Table S1 and *SI Methods*). We selected the termite-specializing gecko *Gymnodactylus amarali* (Gekkonidae) as the focus of this

study, because it was the most common lizard species in the area at the time of the field study.

We evaluated the effects of isolation (actually, insularization) on diet and morphology of *G. amarali* populations on islands formed by the Serra da Mesa reservoir. We collected data on lizard diet and morphology on five islands, as well as five nearby mainland areas, to evaluate the changes that occurred as a result of insularization. One of our studied island sites has been periodically connected to the mainland (Island IX), but the other four islands (I34, I35, I37, and I38) became and remained isolated since 1998, when the reservoir was filled (*SI Methods*). We proposed the following hypotheses:

- i) *Island populations of G. amarali have greater food niche breadth, based on prey size, than mainland populations.* Reduction of species richness on islands likely reduces interspecific competition, allowing a niche expansion of the remaining species. Because *G. amarali* specializes in termites (17), this expansion would probably not occur through the addition of nontermite taxa to their diet. However, increased availability of larger termites could increase niche breadth along the food-size dimension. This hypothesis was driven by the fact that four species of termite-eating lizards that became extinct on the islands, but not at the mainland

Significance

We report for island populations of the termite-eating common gecko species *Gymnodactylus amarali* rapid parallel morphological and ecological change in response to human-caused environmental disturbance. The islands were formerly part of an extensive terrestrial ecosystem; in 1997, the area was flooded to construct a reservoir, fragmenting the higher portions into separate islands. Populations on all five islands studied have proportionally larger heads than populations at five nearby mainland sites. The new island morphology is accompanied by an increase in dietary niche breadth, mainly via expansion toward larger prey. This expansion is likely due to the greater availability of such prey on the newly formed islands after the extinction there of four larger lizard species that typically also included termites in their diets.

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sites, were all larger than *G. amarali* (*SI Methods*). Because these larger lizards are able to ingest larger termites, their extinction would reduce competition for this resource, increasing the availability of large-sized termites to *G. amarali*. Termite-nest mound number and volume showed no difference since 1996 between islands and the mainland (15, 16), suggesting that termite abundance has not changed significantly as a result of insularization.

ii) *Island populations consume larger termite sizes than mainland populations.* Because diet expansion is mainly expected toward larger prey for energetic reasons (ref. 18 and below), the increase in niche breadth hypothesized under hypothesis 1 would result in larger mean prey sizes being consumed on islands.

iii) *Island lizards have larger head lengths than mainland lizards.* We expect that island individuals would have larger head lengths than those at mainland sites for the same body size (i.e., would have disproportionately larger heads) for the following reasons. Lizards consuming larger prey should have a larger trophic apparatus. However, the energetic advantage of consuming larger prey would diminish if total energy requirements were to increase as well due to a larger body size. This disadvantage would be mitigated were island lizards to have larger heads for the same body size, allowing an increase in the size of prey taken without substantially increasing energy requirements.

All island populations had food-niche breadths (inverse of Simpson's diversity index; *Methods*) that were greater than all mainland populations (means 3.74 vs. 2.38 respectively, $t = 2.511$, $df = 4$, one-tailed $P = 0.033$; Table 1). Thus, lizards on islands ate prey with a broader distribution of body sizes than lizards of the nonisolated, mainland areas. These results confirmed that populations of *G. amarali* in Serra da Mesa did indeed increase their dietary niche breadth once isolated on islands, as hypothesized (hypothesis *i* above).

As hypothesized (hypothesis *ii* above), because of differential expansion along the food-size dimension toward larger prey, *G. amarali* on islands ate larger termites than individuals with the same body length on mainland areas (Fig. 1*A*; mixed model analysis: adjusted means 4.93 vs. 4.23 mm, respectively, $\chi^2 = 4.2$, $df = 1$, two-tailed $P = 0.041$). Two tests gave no indication that male and female lizards differed in prey size (sex effect: $\chi^2 = 2.2$, $df = 1$, two-tailed $P = 0.13$; sex \times location interaction: $\chi^2 = 1.2$, $df = 1$, two-tailed $P = 0.27$).

Lizards had a greater head length on islands than on the mainland for a given body size (adjusted means 10.2 vs. 9.8 mm, respectively, $\chi^2 = 11.0$, $df = 1$, two-tailed $P < 0.0001$; Fig. 1*B*; details are in *Methods*). Head length was correlated with mean termite length in stomachs (Pearson product-moment correlation coefficient = 0.32, $df = 48$, two-tailed $P = 0.025$). Analyses distinguishing the sexes gave no significant difference in relative head length or body size between males and females [sex effect on relative head length: $\chi^2 = 0.02$, $df = 1$, two-tailed $P = 0.88$; on

Table 1. Diet niche breadth (*B*) for populations of *G. amarali* in each island and mainland sites of the Serra da Mesa reservoir, using the inverse of Simpson's diversity index (34)

Site	<i>B</i>
Mainland B01	2.917
Mainland B02	2.259
Mainland B04	1.964
Island I34	3.399
Island I35	3.160
Island I38	4.645
Mean mainland	2.380
Mean island	3.735

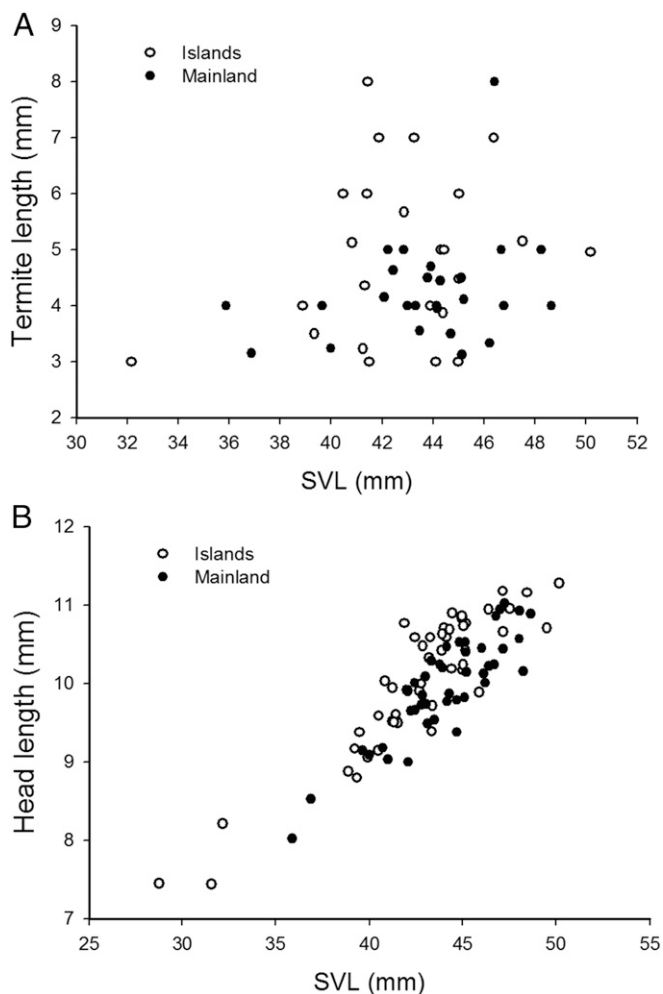


Fig. 1. Mean prey size (*A*) and head length (*B*) as a function of body size (SVL) for *G. amarali* on islands and mainland sites of the Serra da Mesa reservoir. Each point is a separate individual.

snout-vent length (SVL): $\chi^2 = 0.54$, $df = 1$, two-tailed $P = 0.46$], nor was there a significant interaction between sex and location (relative head length: $\chi^2 = 0.00$, $df = 1$, two-tailed $P = 0.95$; SVL: $\chi^2 = 1.5$, $df = 1$, two-tailed $P = 0.22$). These results were bolstered by the analysis of residuals that considered each site as a separate population; it showed that island populations have a larger mean head length relative to body length than mainland populations ($t = 4.216$, $df = 6$, two-tailed, $P = 0.006$)—in fact, there is a perfect ranking (Fig. 2).

According to the ecological release hypothesis, the loss of species on newly formed islands should result in reduced interspecific competition and, consequently, less consumption of certain resources, allowing the remaining species to eat a larger spectrum of prey (i.e., have larger dietary niche breadths) (19–21). In addition, island populations might be expected to evolve appropriate morphological changes, allowing them to use a greater resource availability. Our findings support these predictions. Populations of *G. amarali* in the Serra da Mesa islands increased their food-niche breadth by adding larger termites to their diet. They also exhibited larger heads, relative to body size, than their mainland counterparts. These two results are directly related, because lizards with larger trophic apparatuses are able to ingest larger prey, while still being able to ingest smaller prey (18), thereby adding new items to their diet and expanding their niche along the prey-size dimension.

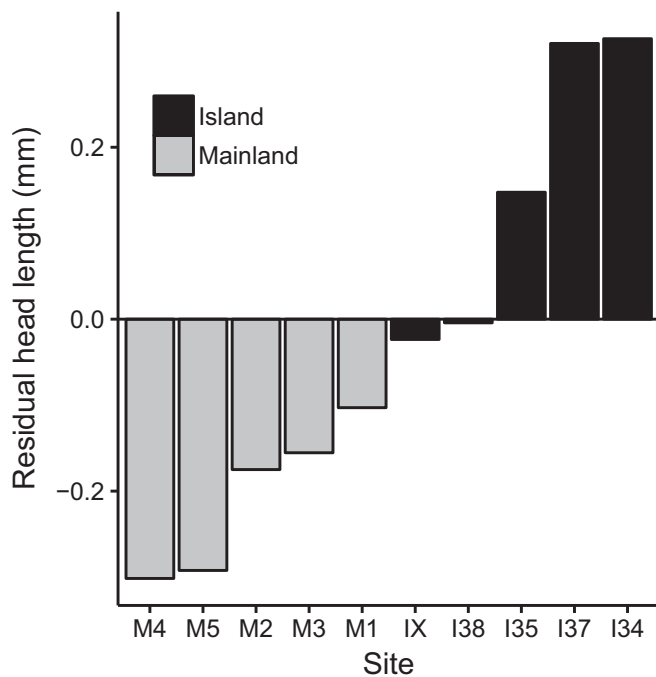


Fig. 2. Mean of the residual head lengths from linear regression of head length vs. SVL of *G. amarali* from five island and five mainland sites at the Serra da Mesa reservoir.

That lizards of a given size on islands consumed larger termites on average than did those on mainland may also be because, once lizards have a morphology that allows them to consume a variety of sizes of prey, they will prefer those that give them more energy per handling and swallowing time—in this case, larger prey (18, 22). Indeed, Cohen et al. (23) showed a positive correlation between prey and predator size for a wide variety of organisms. However, larger predators may not always consume their preferred prey. In particular, because of lower abundance of large food items, larger predators may be forced to eat small items if large food has not been available for a period. Moreover, larger predators should take small prey if they have to make only a minimum effort, such as when small prey occurs near a perched lizard. Note that this scheme implies much variation in the relation of predator to prey size calculated from short feeding bouts (as when stomach contents are analyzed). Such a “snapshot” could differ greatly from the long-term diet (e.g., the long term prey-size distribution). In particular, some larger predators in the present study seem to have consumed inappropriately small prey. Fig. 1A illustrates this variability: Whereas the smallest lizards never take large prey (presumably because they cannot consume it efficiently), the largest lizards frequently take small prey—notice how the cluster of points is both quite diffuse and expands outward on the right-hand side.

Perhaps the most interesting result of this study is the disproportionately larger heads on islands than on the adjacent mainland. In fact, the relation is a perfect separation: All of the island populations have disproportionately larger heads than all of the mainland populations (Fig. 2). Before the creation of the reservoir, gecko populations at future island and mainland sites likely had similar characteristics, because they belonged to the same continuous population before the rise in water level. In fact, although data are not abundant, we did not detect differences in relative head length between future island (13 individuals) and mainland (10 individuals) sites before flooding (1996–1998; $U_{1,23} = 69.0$; $P = 0.68$). Considering the island-formation process, the astonishing aspect of this morphological shift is that the five island populations developed larger heads independently of one another, because the islands quickly

separated before populations had much time to undergo change (SI Methods). Thus, each new population of *G. amarali* developed the same new traits independently on each island, driven by apparently similar changes in community structure in the newly isolated areas, such as the extinction of larger lizards on all studied islands. Specifically, the reduction in interspecific competition, and the consequent increased availability of certain resources, may have led to the observed dietary niche expansion in which larger prey were selected. Foraging for larger prey should have favored lizards with a disproportionately large head size, making them more efficient in the consumption of this resource. Note from Fig. 1 that the body-size range for island and mainland individuals is similar—the increase in relative head size is the key result. This set of results strongly indicates phenotypic parallelism.

An alternative hypothesis might be male–male competition for mates, with males hypothetically being sexually selected to have relatively larger heads on islands because of possible higher intraspecific densities there. Although Colli et al. (17) did find slightly larger heads for males than females in their study of the same species (but wide sexual overlap in overall morphological space), we found no significant sexual differences in our study for relative head length: First, in the mixed-model analyses with head length as the dependent variable, neither sex nor the sex \times location interaction was significant, although there was a tendency for males to have longer heads than females (adjusted means 10.03 vs. 9.92 mm, respectively; $P = 0.13$); second, when we performed the mixed-model analyses separately for each sex, both males and females had significantly greater relative head lengths on islands (males: $\chi^2 = 4.8$, $df = 1$, two-tailed $P = 0.03$; females: $\chi^2 = 11.4$, $df = 1$, two-tailed $P < 0.001$). If some sort of social hypothesis such as greater efficacy in aggression on islands were correct, it would have to apply to both males and females.

Of the five sampled islands, four (I38, I35, I37, and I34; Fig. S1 and Fig. 2) were created immediately after the start of the reservoir filling. The fifth island sampled, island IX (Fig. 2), was isolated from other islands since the beginning of flooding, but for a while remained connected to the mainland. According to satellite images, it separated only when the reservoir reached its maximum capacity, which occurred a few times during the entire period. Hence, isolation time is shorter for this island than the others. Therefore, island IX may receive more immigration from the mainland in those periods when they are connected. For these reasons, changes in traits on IX should not be as extreme as on the other islands. In fact, that is the case: Fig. 2 shows that, of all of the islands, IX is the most similar in relative head size to the mainland.

Classic studies of natural, nonexperimental character change show some similarity to our discoveries. A major example of predictable and repeatable morphological change are Fenchel’s (24) *Hydrobia* gastropods in Denmark. The ranges of two species of these deposit-feeders have come together repeatedly and independently over approximately a 150-y period after the collapse of a sea wall. In each area of sympatry, the species have evolved about the same body-size difference (always with the same species being larger), in turn correlated with food-size difference, a striking example of parallel character displacement. A second well-known such example is the lake-inhabiting sticklebacks studied by Schluter (25): Solitary species are intermediate in gill-raker length and other morphological traits compared with coexisting pairs of species, traits related to habitat and correlated dietary differences. On a much larger scale, Caribbean *Anolis* lizards exhibit independent parallel evolution: the four largest islands (the Greater Antilles) have much the same set of “ecomorphs”—species specialized to use particular perch heights and diameters—and these evolved largely independently and repeatedly on each island (26–28). A perhaps even more diverse system is the cichlids of African lakes, which evolved often repeated morphologies associated with feeding mode and/or habitat (29). Finally, Huey et al. (30) showed predictable character displacement in the termite-specializing fossorial lizard *Acontias* (*Typhlosaurus* in ref. 30), including prey-size changes precisely corresponding to the

morphological changes. It should be recalled that what we have shown statistically for geckos is character change in head size relative to body size.

The above studies are all ones in which the character change of a given species in response to other similar species was known to be slower than in our gecko system, or not precisely known, but inferred to be slower. Two studies, however, show character change over comparable periods of time. One is the classic case reported by Grant and Grant (31) of *Geospiza* on Daphne Island, in which the invasion of a larger-beaked second species caused the resident species to shift toward smaller beak sizes in a few months. This study is, of course, a single instance, rather than a parallel and replicated change over several islands. A second study that is more comparable with ours focuses on *Anolis carolinensis* on small islands in Florida invaded by the conspecific *Anolis sagrei*. Using a combination of experimentally and naturally invaded islands, Stuart et al. (32) showed that the resident, more arboreal *A. carolinensis* shifted its height upward and evolved larger toe pads after 20 y.

Our results provide strong evidence that particular circumstances predictably and precisely shape traits of species in ecological communities and illustrate that populations can respond both rapidly, and in parallel, to ecological change—results of basic scientific interest. In addition, they may have applied significance, because understanding rapid evolution in fragmented populations is important for conservation purposes (e.g., ref. 33). Indeed, whereas the subject gecko of this study persisted and adapted in newly created habitat fragments, a number of other lizard species were extirpated, illustrating the potential consequences of insufficient responses to rapid environmental changes.

Methods

Laboratory Procedures. We recorded SVL and head length (anterior edge of tympanum to the nose tip) to the nearest 0.01 mm, using Mitutoyo digital calipers. All measurements were performed by the same person (A.C.R.L.). To determine diets, we analyzed stomach contents of each individual under a stereoscopic microscope, identifying prey items to order. *G. amarali* is highly specialized on termites (17), and 90% percent of all items in this study were termites. Therefore, we used only that taxon in our analysis. We recorded prey length (millimeters) of intact items with graph paper.

Statistical Analyses. Diet niche breadth was calculated by using prey size as the dimension. We analyzed the contents of 50 *G. amarali* stomachs with three or more prey items—24 from island and 26 from mainland sites. Each study area was considered a distinct population. We sampled 10 areas (5 islands and 5 mainland sites), but 2 mainland and 2 island sites were omitted from niche-breadth analysis due to small sample size (<50 prey items), leaving a total of 3 island and 3 mainland sites. Animals were collected under Brazilian Permanent Permit 28190-1; our study follows the Brazilian law on ethical use of animals for research and education (Federal Law 6899/2009), being supported by permanent license from the Brazilian System of Access to Biological Information (SISBIO) and approved by the University of Brasília institutional review board [Commission on Animal Ethical Use (CEUA), Process #69/2010].

Seven size categories of termite length (in millimeters) were defined: 2–2.9; 3–3.9; 4–4.9; 5–5.9; 6–6.9; 7–7.9; and 8–8.9. We computed niche breadths (B) of each population using the inverse of Simpson's diversity index (34):

$$B = \frac{1}{\sum_{i=1}^n p_i^2}$$

where p_i is the proportion of individuals of a given size (length) i found in the population diet, and n is the number of categories. Calculation of niche breadth using this index generates values ranging between 1 and n ; values close to 1 have a narrower niche (the population commonly consumes few

sizes of prey), whereas values close to n represent a broader niche (the population commonly consumes many sizes of prey).

A one-tailed t test for independent samples was performed on the mean island vs. mainland B values to detect differences in niche breadth between the two kinds of sites; the test is one-tailed because a change in the opposite direction is not predicted. All other analyses in this work use two-tailed tests.

We chose head length as the focal morphological variable, because it is functionally expected to relate to prey size and, in fact, was found to do so in many previous studies (22, 35–37). Individuals with larger heads can eat larger prey, and this capability also results in a potentially wider range of prey sizes for larger-headed lizards (18, 23). We used linear mixed models to evaluate differences in head length of *G. amarali* between islands and mainland sites. Head length was the dependent variable; location (island vs. mainland) and SVL were fixed predictor variables (the latter was included to account for the fact that larger lizards have longer heads); and study site (each of the five islands and five mainland areas) was included as a random effect to account for the nonindependence of lizards collected at the same study site. The analysis of head length featured 49 individuals from the five islands and 43 individuals from the five mainland sites.

We ran a second linear mixed model to test whether lizards of the same body size were consuming different prey sizes on islands vs. mainland. Mean termite length in an individual's diet was the dependent variable, and the independent variables were the same as those in the analysis of head length. Examination of residual plots from preliminary analyses of termite length suggested that differences in residual variation between islands and mainland may violate assumptions of homoscedasticity. This pattern is not surprising, given that our analysis of niche breadth showed a greater breadth of prey size used on islands than on mainland, consistent with hypothesis 1 (Table 1; the difference in the variation of termite length between islands and mainland is also apparent in Fig. 1A). To account for this heteroscedasticity, we included an additional parameter in our model that allowed islands and mainland to have different variance; the model with the additional parameter accounting for heteroscedasticity had a lower Akaike information criterion than the model without the adjustment for heteroscedasticity (1,775.4 vs. 177.2). The analysis of termite length featured 24 individuals from islands and 26 individuals from mainland sites.

We used likelihood ratio tests to assess the significance of fixed effects in linear mixed models. Preliminary analyses of both head length and termite length showed no significant interactions between the location (mainland vs. island) and SVL ($P > 0.99$ in both cases), and no effect of sex ($P > 0.13$ in both cases) or location \times sex interaction ($P > 0.27$ in both cases), so these terms were dropped from the final model.

To further explore our data, we performed an analysis based on residuals: We calculated from the general regression (all data combined including both sexes because no significant difference between males and females was found) the residual head lengths for each individual and then took the average (signed) residual for the individuals at each site, giving five mainland and five island values of mean residuals. We then performed a t test on those means. Because of inadequate prey sample sizes for some individuals at some of the sites, a similar analysis could not be performed using residual prey sizes. We performed the same analysis separately for males and females, using only sites having at least five individuals (three each for island and mainland).

Only sexually mature individuals were used in all analyses—minimum 27-mm SVL (17) for both sexes. Three outliers were damaged during collection to the point of increasing the likelihood of measurement error; these lizards were not included in our analyses.

We carried out statistical analyses of diet breadth using SPSS Statistics 21 for Macintosh (38); mixed modeling and analysis of residuals were conducted by using the nlme package in R (39, 40).

Data are available at datadryad.org.

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