Island Biogeography of Populations: An Introduced Species Transforms Survival Patterns

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Population phenomena, which provide much of the underlying basis for the theoretical structure of island biogeography, have received little direct study. We determined a key population trait—survival—in the Bahamian lizard *Anolis sagrei* on islands with an experimentally introduced predatory lizard and on neighboring unmanipulated islands. On unmanipulated islands, survival declined with several variables, most notably vegetation height: The island with the shortest vegetation had nearly the highest survival recorded for any lizard. On islands with the introduced predator, which forages mostly on the ground, *A. sagrei* shifted to taller vegetation; unlike on unmanipulated islands, its survival was very low on islands with the shortest vegetation but was higher on the others. Thus, species introduction radically changed a resident species' relation of survival to a key island-biogeographical variable.

When MacArthur and Wilson first proposed their highly influential equilibrium theory of island biogeography (*1*), a main objective was to predict patterns of species richness as a function of island area and distance. Subsequent research broadened the island properties to include variables such as habitat and elevation, but the focus on understanding species richness and related community characteristics remained (*2*–*6*). Likewise, experimental approaches to island biogeography dealt almost entirely with community rather than with population aspects (*7*). However, the equilibrium theory and its derivatives rely to a great extent on population phenomena for their underlying assumptions, making research on population traits necessary for mechanistic understanding. Here, we report an experimental study designed to examine how a prey population-level trait, in this case survival, relates to major island variables. We investigated not only island area, an original component of the island-equilibrium model, but also a habitat variable—vegetation height—because a number of previous studies have shown that such variables were better predictors of species richness than area. We also investigated a key ecological variable, population density of the subject species, the lizard *Anolis sagrei*.

We selected 12 neighboring islands varying in area, habitat, and *A. sagrei* population size (population size and population density are strongly correlated: $r = 0.86$). The islands are located near Snake Cay and Buckaroon Bay, Abaco, Bahamas. The islands range from 104

to 324 m^2 in vegetated area, at the small end of the continuum for islands that have *A. sagrei* (*8*). They are rather sparsely covered with trees (up to 3.8 m in height) and/or shrubs (many quite prostrate). On six islands, we introduced the larger lizard *Leiocephalus carinatus*, a predator on the smaller *A. sagrei*. To avoid strong predator density dependence, *L. carinatus* propagule size was scaled to the population size of *A. sagrei* (*9*). The introduction of the larger lizard caused *A. sagrei* to shift to higher perches (*10*). As the islands differed substantially in the availability of such perches, we selected a measure of vegetation height as the most relevant habitat variable.

The unmanipulated islands, containing *A. sagrei* with no introduced predator, showed negative relations of survival (percentage of the original cohort still alive by Date X) to all three variables (*9*). After 6 months (the time when about half the *A. sagrei* individuals had died), Pearson r for vegetation height was –0.90 (using the arcsin square-root transformation for survival and log transformation for height) and r values for *A. sagrei* population density and area (both log-transformed) were –0.75 and –0.37, respectively. Annual survival (*9*), highly related to the 6-month measure, gives similar results for vegetation ($r = -0.86$), density ($r = -0.81$), and area ($r = -0.28$). If we focused on a single one of these correlations, a Pearson r exceeding in magnitude –0.73 would be significant at the 5% level (one-tailed P). However, the results are highly related because the three island variables are positively intercorrelated: area/density $r = 0.34$, area/vegetation height $r = 0.55$, and vegetation height/density $r = 0.61$ (Fig. 1). Two of the variables are statistically confounded, and collinearity measured by the condition number is much too high (*11*) to perform multiple regression of survival with any two or all three island variables (*9*).

Rather, we accept as the best description the single island variable giving the strongest correlation with survival—namely, vegetation height (Fig. 2). Survival values over the six islands span the great majority of the possible range: Survival after 6 months varies from the nearly immortal (91.4% of individuals survived on the island that had the shortest vegetation, which was also the smallest island) to a very high mortality (25.6% of individuals survived on the island that had the tallest vegetation, which was also the largest island). Annual survival on the island with the shortest vegetation is still 80%, tied for the highest determined for any *Anolis* and only exceeded by one other lizard species population known to us (*12*).

Notably, vegetation height gives a substantially stronger correlation with survival than does area. Islands with higher vegetation are especially attractive to birds: A study of more than 500 islands in the Bahamas showed that occurrences and diversity of bird species in-
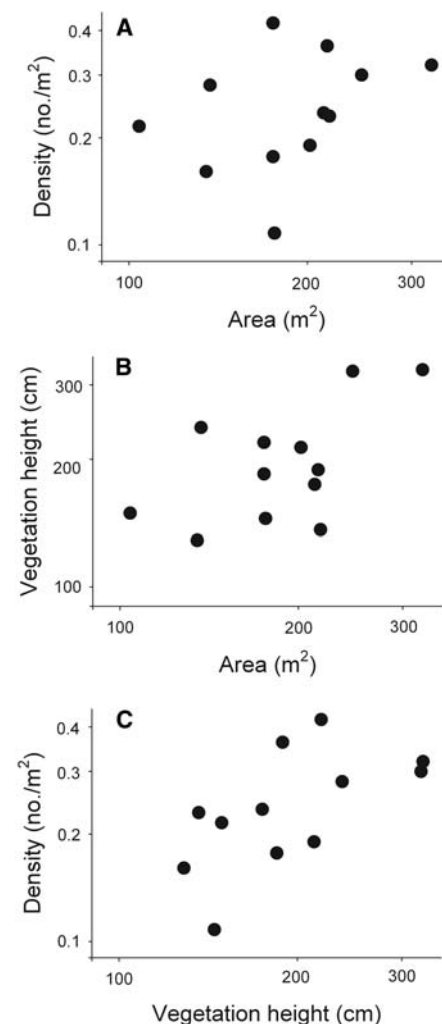
Fig. 1. Relationships between variables characterizing the 12 study islands. (**A**) *A. sagrei* population density versus area. (**B**) Vegetation height versus area. (**C**) Population density versus vegetation height.

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crease more with amount of higher vegetation than with other variables (8), including area. We would therefore expect this result if birds were the main natural predator on our 12 study islands. Prey density, however, is also strongly correlated with survival, which also suggests bird predation, particularly from itinerants. The larger the density of prey on an island, the more likely itinerant predators will be present, because it is profitable to spend more time there (13). This expectation is often supported by data (14). Furthermore, the greater the density, the more per capita interaction there is among prey individuals, leading to a greater likelihood of capture by predators (15).

How does the addition of a large predatory lizard species change this marked relation of survival to island vegetation height? The predator is substantially longer and stockier than *A. sagrei* and perches mainly on the ground and rocks. It only occasionally (and sometimes awkwardly) perches on the vegetation, but generally close to the ground and on relatively thick branches. Hence, a refuge from this predator for *A. sagrei* is the vegetation, particularly the higher branches and twigs (which tend to be thinner). One might expect, therefore, that availability of such perches would enhance survival in *A. sagrei* (16). If no other factors were involved, this would imply that islands with higher vegetation should have higher survival, the opposite of the trend expected from the other (e.g., bird) predators, which is indeed found on unmanipulated islands. As expected, results after introducing the large terrestrial predator give very different plots of survival versus vegetation height for the six manipulated islands than for the controls. First, the relation is now positive, not negative as it is for the unmanipulated islands (Fig. 2). Pearson *r* values are high but not quite statistically significant at the 5% level (6 months, $r = 0.65$; 1 year, $r = 0.71$). However, an analysis of covariance on the entire set of 12 islands gives a highly significant (treatment)*(vegetation height) interaction term (two-tailed $P = 0.005$ for both 6 months and 1 year). Second, the shapes of the curve are different (supporting online material text).

The difference in survival values between islands with and without the introduced predator varies substantially with vegetation height (Fig. 2). For islands with the shortest vegetation (which tend to be small), survival is much greater in the absence of the introduced predator. In particular, 80.0 to 91.4% of lizards on the two control islands with the shortest vegetation survived 6 months, whereas 6.3 to 15.2% did so on the two introduction islands that had the shortest vegetation (values of vegetation height are very similar between controls and introductions). In contrast, for moderate to large vegetation heights, little to no difference in survival exists; if mortality

factors were additive, one might expect that introduction islands with vegetation of these heights would have lower survival. Instead, the pattern found is consistent with compensatory mortality factors (17–19); no more lizards were killed on islands with moderate to large vegetation height in the presence of the introduced predator than were killed in its absence.

How might such compensation take place? A simple explanation is that mortality from predators other than *L. carinatus* is smaller on introduction than on control islands. But why would mortality from other predators decline? It seems likely that such predators would be mostly itinerant birds (rats are also possible), which include the study islands within their foraging range but only occasionally (if ever) nest on one of them. Were potential prey reduced by the introduced lizards on a particular island, such itinerant predators would feed there less, much as is depicted by optimal foraging conceptualizations (13). In other words, the predator that can select feeding sites over a broad region can avoid those islands to which the nonitinerant introduced predators are necessarily confined (20). Additionally, especially vulnerable prey individuals will mostly be eaten by the introduced lizard predator, leaving few prey that the itinerant predators can easily capture.

Losey and Denno (17) showed for an arthropod assemblage that when a predator caused a shift of prey to a different habitat, a synergistic effect arose in which the prey suffered from the predators in the original habitat and were more vulnerable to the predators in the new habitat. In this case, not only was compensatory predation not operating, but even additive predation underestimated the combined effect of the several predators. A similar phenomenon might have been expected for our system, with *A. sagrei* shifting upwards in the vegetation and thereby increasing their vulnerability to predation by birds. However, the pattern of survival that we found is inconsistent with this expectation, leading to the inference that predation by birds takes place mostly at lower sites, including the ground, perhaps because *A. sagrei* is in general much more vulnerable there. A trial (9) in which clay-model lizards were placed in low positions (on the ground or rocks) produced significantly fewer marks—plausibly the result of bird pecking (21, 22)—on the control island with the second-shortest vegetation (13%) than on the control island with the tallest vegetation (67%; $P = 0.007$). The difference is in line with Fig. 2 and implies substantial attempted predation at low sites on the nonintroduction island with the tallest vegetation.

The kind of compensation we are hypothesizing can provide the basis of a simple model giving the form (9) and positioning of the curve relating survival to vegetation height on introduction islands. Assume that itinerant bird
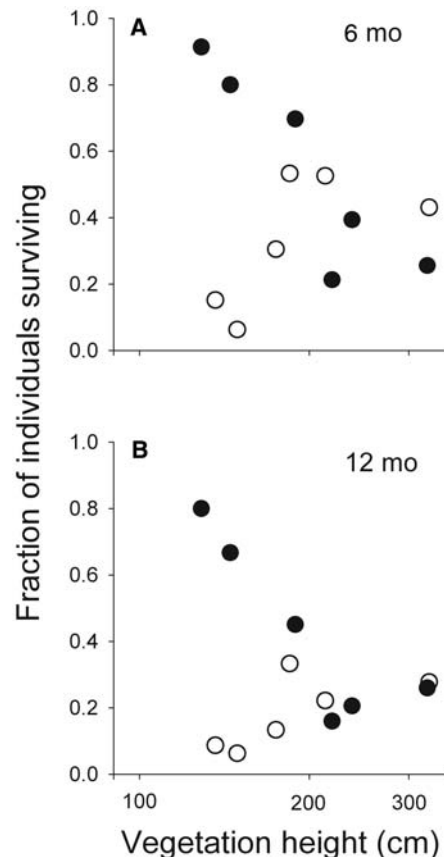
Fig. 2. Survival fractions versus vegetation height on control (solid) and introduction (clear) islands in November 2003, ~6 months after initiation of the experiment (**A**) and in May 2004, ~1 year after initiation of the experiment (**B**).

predators kill those prey not killed by the introduced lizard predator, but only up to the point that the number they kill plus the number the introduced lizard predator kills equals the number the itinerants would kill if the island did not have the introduced lizard predator. The rule is roughly consistent with the marginal value theorem (13), whereby all patches (regardless of the value when entered by the predator) are left at the same marginal intake rate, corresponding to the same giving-up density (23). Such marginals are unlikely to change much for the entire site by manipulation of six islands, so the departure rule should be about the same with and without the introduced predator. Thus, on islands where the introduced predator kills a relatively large percentage of the prey, itinerants would kill no additional prey. On islands where prey are better able to avoid the introduced predator, itinerants kill some prey, but fewer than they would in the absence of the introduced predator. Figure 3 gives hypothetical examples. Assume (Fig. 3A) that the percentage of prey killed on control islands by itinerant birds rises linearly with vegetation height and then asymptotes, approximately as the data for control islands behave (Fig. 2). The curve representing
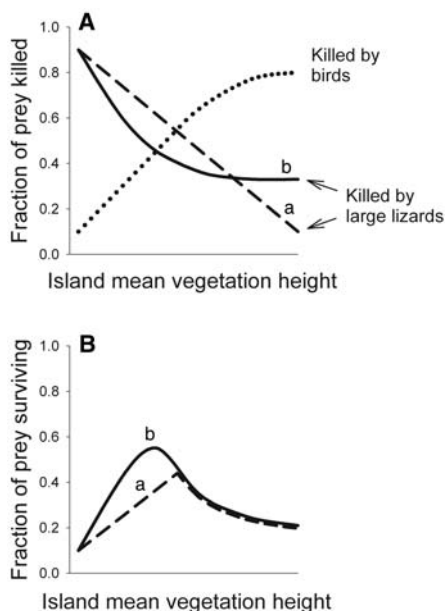
Fig. 3. (A) Hypothetical mortality curves as a function of vegetation height. The fraction of prey killed by the large introduced lizard predator decreases with vegetation height, either linearly (a) or asymptotically (b). The fraction of prey killed by natural predators such as itinerant birds increases with vegetation height, with a small asymptotic portion at the end. **(B)** Predicted survival curves as a function of vegetation height. These curves consist of two segments, the first of which is the complement (1 − fraction killed) of the large lizard predator curve to the left of the intersection, and the second is the complement of the itinerant bird predator curve to the right of the intersection.

predation by the large lizard is assumed to decline monotonically with vegetation height, either linearly (curve A) or asymptotically (curve B). The actual number killed by both predators is then the number killed by the introduced large lizard or the number killed by itinerant birds on the control island, whichever is larger. The resulting survival curves for introduction islands are depicted in Fig. 3B, which should be compared with the actual curves of Fig. 2. Although consistent with the data and hypothesized mechanisms involving itinerant birds, definitive evaluation awaits further investigation.

By using an archipelago of small islands as a laboratory for both comparative study and manipulative experiment, we showed a notable natural relation of survival rate to island characteristics—especially vegetation height—and the ability of an introduced predator to transform that relation. Implications of this study extend beyond islands: Vegetation structure over much of Earth's surface is being precisely characterized, in part to understand how species populations respond to anthropogenic changes in land use or in climate (*24–26*). However, information beyond vegetation structure may be crucial. Thus, in our study, sur-

vival is unrelated to vegetation height if data from all 12 islands are considered together (r = –0.23, –0.24), yet knowing which islands have the introduced predator makes the latter a good predictor of survival rates.

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A. sagrei, it is unlikely that such effects—intraspecific competition for food and consequences of aggressive interactions—would by themselves result in mortality, because the lizards marked for this study were relatively large.
16. Moreover, *L. carinatus* is thermophilic, depending on sufficient sunlight for its activity during cooler times of the year. Islands having taller vegetation on average have less sunlight striking the ground, which is where *L. carinatus* mostly forage. Hence, their average predation rate should be lower on such islands.
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Long-Term Modulation of Electrical Synapses in the Mammalian Thalamus

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Electrical synapses are common between inhibitory neurons in the mammalian thalamus and neocortex. Synaptic modulation, which allows flexibility of communication between neurons, has been studied extensively at chemical synapses, but modulation of electrical synapses in the mammalian brain has barely been examined. We found that the activation of metabotropic glutamate receptors, via endogenous neurotransmitter or by agonist, causes long-term reduction of electrical synapse strength between the inhibitory neurons of the rat thalamic reticular nucleus.

Connexin36 (Cx36)-containing gap junctions are a major mechanism of communication between the inhibitory neurons of the rodent thalamic reticular nucleus (TRN) (*1, 2*). More than 50% of neighboring TRN neurons interact via electrical coupling. TRN neurons, which provide feedback inhibition to the thalamus, also receive strong glutamatergic synaptic in-

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puts from neurons in the deep layers of neocortex (*3*). These corticothalamic fibers can activate metabotropic glutamate receptors (mGluRs) on TRN neurons (*2, 4–7*).

We used dual whole-cell recordings in rat thalamocortical slices under infrared–differential interference contrast (IR-DIC) visualization (Fig. 1A) to measure the strength of electrical synapses interconnecting adjacent neuron pairs [coupling coefficient (cc) = 0.08 ± 0.06, mean $\pm$ SE, $n = 30$ pairs]. The strength of electrical coupling was tested before and after briefly tetanizing corticothalamic (CT) fibers or applying the mGluR agonist (1S,3R)-1-aminocyclopentane-1,3-dicarboxylic