ROBERT HOLT (graduate student, Harvard University) reports on his recent field research:

I am interested in species border phenomena. During the summers of 1975 and 1976 I have studied the ecology and distribution of three species of Lesser Antillean Anolis that provide interesting material for the study of factors that limit species' distributions. Anolis aeneus and A. trinitatis are believed to be introduced onto the continental island of Trinidad from the oceanic islands of Grenada and St. Vincent. The Anolis richardi on Tobago are very similar to richardi from Grenada. The lack of morphological differentiation suggests that all three species are relatively recent colonizers. As compared with their Grenadan counterparts, the introduced aeneus and richardi show sharply circumscribed ranges; as discussed below, these limits are not due to competitive interactions with other lizards. By contrast, A. trinitatis exists on Trinidad as scattered enclaves within the range of aeneus; the two species are mutually exclusive with narrow bands of overlap, and aeneus appears to be slowly pushing trinitatis to extinction.

Anolis richardi. Several authors have noted that richardi on its native island of Grenada is ubiquitous, ranging through many habitats from xeric scrub forest at Pt. Saline to high wet forest near Grand Etang. There is one puzzling feature of its distribution that has not been noted. Since I wished to compare comparable habitats on Grenada and Tobago, I searched for patches of near-virgin habitat (with the assistance of local foresters). I found such patches on Mt. Delice (a dry forest) and in the Grand Etang Forest Reserve (a wet forest). Anolis richardi was conspicuously less common in these patches than in most other wooded habitats on Grenada. This is somewhat peculiar, since there are no obvious competitors or predators in virgin forest that are more common than in disturbed habitats. It is possible that insect productivity is less in these forests (Janzen, 1973). I suspect that the anoline abundance of the West Indies (at least in wet habitats of the Lesser Antilles) may in part be the result of massive disturbance during the last five centuries and may not accurately reflect the conditions in which these anoles evolved.

The distribution of richardi on Tobago presents quite a different pattern. As noted by Lazell (1972), richardi is common all along the southern coast. The animals can be observed in areas near human habitation, or in coconut groves. But in less disturbed habitats with more structural complexity, the anoles are markedly scarce. For example, at the Botanic Gardens in Scarborough a range of habitats varying in their disturbance is available. The anoles are present in some numbers within the gardens themselves. As one walks into the wooded hills behind the gardens, the density of visible anoles gradually decreases; a hundred yards or so inside the forest not a single anole is visible. The remarkable thing about this situation is that these wooded hillsides look similar to those Grenadan habitats in which richardi is most common; the woods are far from virgin, since many trees have been cut and there is a good deal of patchiness, clearings of varying size being scattered throughout. On one long hike in the highlands, I did not see a single richardi; at the Alefounder Estate in the lowlands (one of the few

areas left unharmed by the hurricane), richardi were common in the immediate vicinity of the estate buildings; only one anole was seen in the forest. Thus, there is a very clear large reduction in anoline densities between Tobago and Grenada in forested habitats; in habitats near human habitation, and in coconut groves, the densities on the two islands are comparable.

Diffuse interactions with other Tobagan species may have led to the reduction in the habitat range of richardi. Grenada and Tobago have the same overall climate, and the vegetation is similar, but Tobago has a substantially richer fauna of birds and snakes. Competition with other lizards cannot explain the habitat limitation; no other anole is present, and the only other arboreal lizard on Tobago is Iguana iguana - which is also on Grenada and is not likely to compete directly with richardi, anyway.

Anolis aeneus. The preferred habitat of aeneus in Grenada is scrubby woodland with plenty of small trunks; they are abundant in disturbed habitats all over the island. One might surmise that the introduced aeneus of Trinidad would be widespread over the island wherever second growth occurs. This is not the case. There are two striking differences between the distribution of aeneus on Trinidad and its distribution on Grenada. On Grenada, aeneus has a continuous distribution. On Trinidad a number of disjunct populations exist, some separated by many miles from their nearest neighbor. For example, the population at Maracas Bay is restricted to a small grove of coconuts at a public beach park; a tall heavily wooded mountain range separates this population from the main range of the species. Second, aeneus on Trinidad occupies a much narrower range of habitats than on Grenada. The species behaves as a vertebrate weed, its populations occurring only in artificial habitats provided by man - in his suburban gardens, in his public parks, in coconut groves and, sometimes, in overgrown, abandoned lots. This close association with man probably explains the haphazard, overall distribution of the species. The overall shape of the distribution is likely the result of passive dispersal by man. The habitat restriction on Trinidad as compared with Grenada is of greater intrinsic interest. The borders of populations are often surprisingly sharp. I have found numerous examples of populations thriving in backyards or parks immediately adjacent to bushy woodlots, in which not a single anole could be found in the woodlot. In superficially similar areas on Grenada, aeneus is swarming. The absence of aeneus from apparently accessible, suitable habitats is characteristic throughout the range of aeneus in Trinidad. I feel that this habitat restriction is caused by the cumulative effects of a large number of native species, particularly snakes and avian predators. My evidence for this is mostly indirect. Several other, alternate hypotheses can be eliminated. For example, the density of anoles might simply be tracing a gross pattern of insect abundance. By sampling insect density with Tanglefoot and sweep netting, I have shown that this is not the case. On Grenada, the density of aeneus seems to be correlated with insect density; in Trinidad, along a transect from an inhabited area into an adjacent patch of second growth, insect density increased but aeneus decreased to zero. Direct competition with another species of lizard cannot explain the limited habitat range;

the only native anole on Trinidad, chrysolepis, is not found in these habitats, and the other arboreal lizards either overlap extensively with aeneus (Gonatodes) or are also not found in these areas of bushy second growth (Polychrus and Plica).

Grenada has six species of snake; Trinidad has about 40 species. There is an order of magnitude difference in bird species, too. Forty-one species of bird on Trinidad are known to include small lizards in their diet; several of these are common residents of second growth (e.g. antshrikes). Between Grenada and Trinidad there is a phenomenal increase in the diversity of small insectivorous birds which could both compete with adult aeneus and prey on juveniles; many of these are common in second growth and forage in just those places utilized by aeneus - along trunks and in the interior of foliage. It is a priori reasonable, therefore, to expect that aeneus on Trinidad faces a whole spectrum of enemies, absent on Grenada, that limit its distribution.

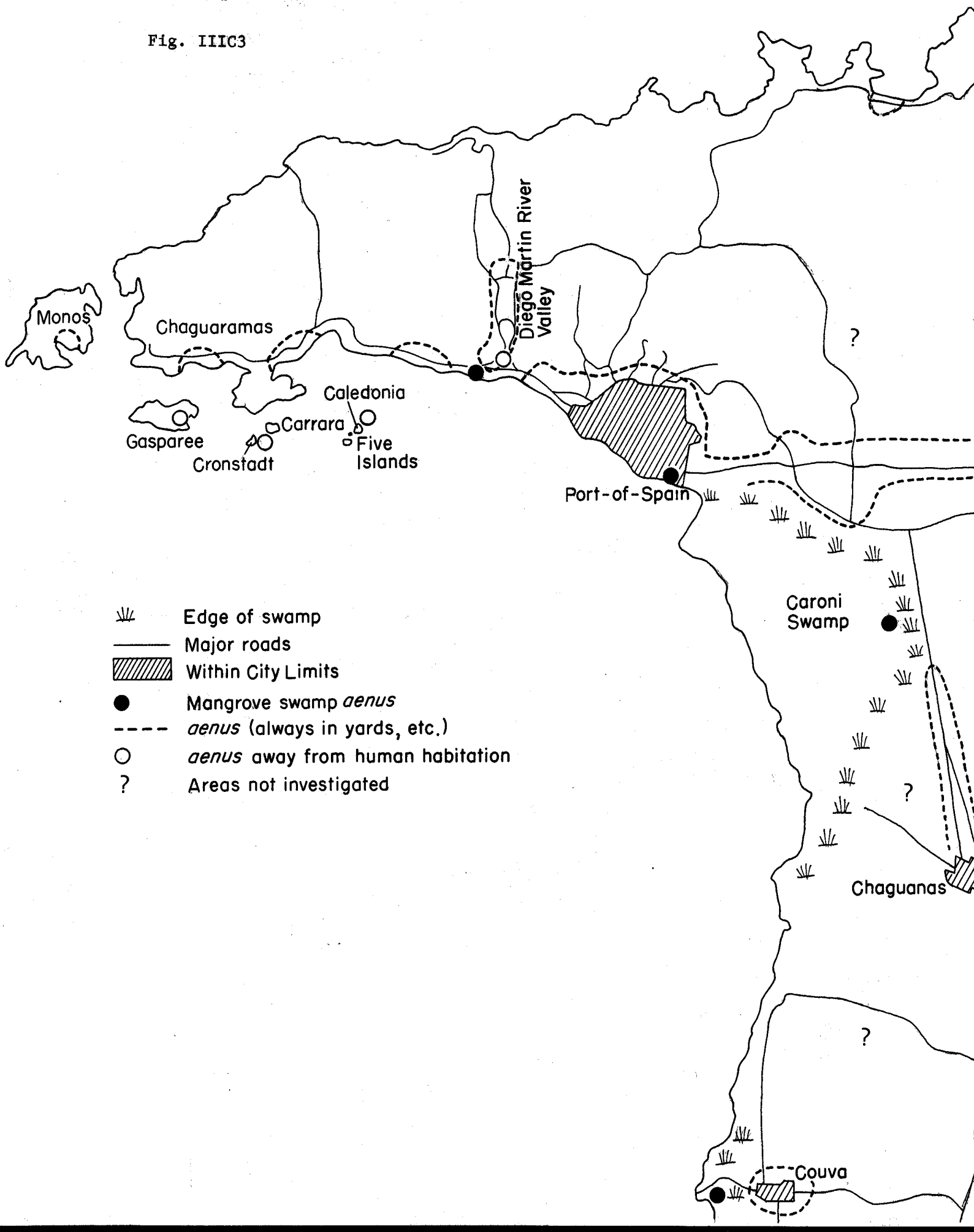
To provide indirect evidence for this hypothesis, I searched out sites which might be expected to have a depauperate fauna. I have found aeneus on a chain of islands west of Port-of-Spain (Fig. 1). The bird species of these islands follows the usual species-area relationship. As one goes down this island chain in order of decreasing island size, the density and habitat range of aeneus increases in a regular fashion. On Monos, anoles are restricted to near human habitation. On Gasparee, aeneus does penetrate roughly a hundred yards into wooded areas adjacent to yard populations, but in low densities. The entire surface of Cronstadt has resident anoles. On the small Five Islands, aeneus reaches its highest abundance. On Caledonia, as on Grenada, the density of anoles seems to roughly track insect abundance; this pattern does not hold on Gasparee. I also censused the birds at these sites. On Caledonia, the bird list is reminiscent of the Grenadan avifauna, with few foliage-gleaners or trunk-feeders, and no species likely to prey on aeneus. My mark-recapture data suggest that adult survivorship is lower on Cronstadt than on Caledonia; several species of presumed predators and competitors are present on Cronstadt. Thus, aeneus on these offshore islands shows a regular pattern of habitat expansion concordant with a decrease in bird species diversity.

I have also studied the distributional pattern of aeneus on habitat 'islands' of second growth found scattered throughout settled areas near Port-of-Spain. These patches are usually sharply defined. Most of the land is kept clear of thick growth by the owners of the lots; abandoned lots, and those have never been cleared, are covered with dense vegetation. I characterized each patch by its area, distance to continuous vegetational cover, distance to yard populations of aeneus, and several indices of vegetational density, cover, and height; I also listed bird and lizard species seen. From equilibrium theories of island biogeography, it is to be expected that the diversity of potential predators or competitors will decrease as the size of the patch decreases or the distance of the patch from large, continuous tracts of similar vegetation increases. Given that this expectation is reasonable, I predicted that aeneus would be found in high densities in small

patches, absent from large patches (or present only along the edge, if adjacent to a yard population), and present in lower abundance in patches of intermediate size, particularly patches that are isolated. All these predictions were found to hold. Most patches less than 1000 m^2 are occupied by aeneus; those that are not occupied are either immediately adjacent to large areas of second growth, or are distant from yard populations of aeneus. Patches between 1000 and 5000 m^2 are less often occupied; those patches with aeneus tend to be more isolated. In those patches that are occupied, the density of aeneus is less than in patches below 1000 m^2 in size. I did not find aeneus in any patch above 5000 m^2 in size. There does not appear to be a correlation between aeneus' presence and any attribute of the vegetation I could measure. In like manner, I made a survey of habitat 'islands' near St. George's, Grenada. There, aeneus is present regardless of the size or degree of isolation of the patch.

Anolis trinitatis. Gorman has investigated several aspects of the interaction between Anolis aeneus and A. trinitatis on Trinidad. He has pointed out that the two species hybridize freely, the hybrids are sterile, or nearly so, and there is little overlap between the ranges of the two species. This situation is intriguing for two reasons. First, we expect strong selection for the development of reproductive isolating mechanisms, yet both anoles have been on Trinidad for a century or more, and their striking visual distinctness would seem to make them ideally pre-adapted for the development of such mechanisms - but they have not. Second, they provide a pleasing example of competitive exclusion in action. Victor Quesnel has kindly provided me with a set of maps that he and Garth Underwood had made during the late 1950's. These maps show in exquisite detail the distribution of both species in Port-of-Spain and St. Augustine. During August, 1976, I re-mapped the distribution of trinitatis in Port-of-Spain. Previously, it existed in four enclaves more or less surrounded by aeneus. I found that the smaller two of the four enclaves had disappeared; the larger two had shrunk considerably in size. From the apparent rate of shrinkage of the two larger enclaves, one would have predicted the disappearance of the two smaller ones. The largest enclave was bounded on the east by an enormous grassy field, on the west by a large concrete ditch, and on the other two sides by aeneus. The two edges bordered by aeneus had shrunk, the other two had not. This strongly suggests that the range contraction is due to interaction with aeneus rather than some unknown environmental change. The two species show great overlap in their structural niche, in the time of day at which they are active, and in size. In the narrow zone of spatial overlap, I observed many instances of interspecific aggression, both between males and between females. The density of lizards was correlated with the quantity of vegetation available. The width of the zone of overlap varied inversely with the total number of lizards observed.

Fig. IIIC3


Monos
Chaguaramas
Diego Martin River Valley
Caledonia
Carrara
Five Islands
Gasparee
Cronstadt
Port-of-Spain
Caroni Swamp
Chaguanas
Couva
?
?
?
Edge of swamp
Major roads
Within City Limits
Mangrove swamp aenus
aenus (always in yards, etc.)
aenus away from human habitation
? Areas not investigated