SHORT COMMUNICATION

The densest terrestrial vertebrate

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An understanding of the abundance of organisms is central to understanding ecology, but many population density estimates are unrepresentative because they were obtained from study areas chosen for the high abundance of the target species. For example, from a pool of 1072 lizard density estimates that we compiled from the literature, we sampled 303 estimates and scored each for its assessment of the degree to which the study site was representative. Less than half (45%) indicated that the study area was chosen to be representative of the population or habitat. An additional 15% reported that individual plots or transects were chosen randomly, but this often indicated only that the sample points were located randomly within a study area chosen for its high abundance of the target species. The remainder of the studies either gave no information or specified that the study area was chosen because the focal species was locally abundant.

In many environments, lizards form important elements of the food web. In many cases, they have been used as model organisms with which to examine

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questions of community assembly or species coexistence. Caribbean islands have been among the most intensely studied locales for such work. Despite this, the number of absolute population measures for lizards is low even for this region. Data for entire assemblages are rarer yet. In this paper we report sampling of entire lizard assemblages conducted on Guana Island, British Virgin Islands. We chose two habitat types: early successional (dominated by *Leucaena leucocephala* (Lam.) de Wit and *Acacia macracantha* Humb. & Bonpl. ex Willd.), and mid-successional (dominated by *Coccoloba uvifera* (L.) L.). These habitats were chosen because they are representative of many habitats in the area. Additionally they are structurally (both habitats) and compositionally (*Leucaena* habitat) similar to habitats we have examined more extensively in the western Pacific, primarily on the island of Guam, Mariana Islands (Rodda & Fritts 1996, 1998). Though non-native in the Pacific, *Leucaena leucocephala* forests are extensive in the Mariana Islands where they have been purposefully seeded for erosion control (Falanruw *et al*. 1989). This species also dominates early successional landscapes in the Virgin Islands (Little & Wadsworth 1964). If vegetative composition determines the numerical success of the resident vertebrates, we would expect the members of comparable lizard guilds to have similar abundances on the two islands.

Through human-mediated species transport there is some artificial overlap in lizard species representation between Guam and Guana. *Anolis* lizards are a conspicuous native element in the West Indies (Lazell 1991); *A. carolinensis* has been introduced throughout the Pacific, including Guam (McCoid 1999). *Hemidactylus* geckos have been widely introduced in both the Pacific and Caribbean, including Guam and Guana (MacLean 1982, Rodda *et al*. 1991; Table 1). Thus, we might expect greater similarity in the abundances of lizards between Guam and Guana than would be the case if the assemblages had complete phylogenetic and historic independence.

We chose our sample sites on the basis of vegetative representativeness of the habitat (i.e. without advance knowledge of the population density of the target vertebrate taxa). We selected plots that were qualitatively similar to a

Table 1. Comparison of forest lizard assemblages between Guam (Mariana Islands, Pacific Ocean) and Guana (British Virgin Islands, West Indies).

Activity	Stratum	Guana Island	Guam Island
Diurnal	arboreal	*Anolis cristatellus* Duméril and Bibron *A. stratulus* Cope	*A. carolinensis* Voigt *Lipinia noctua* Lesson
	large terrestrial	*Ameiva exsul* Cope	*Varanus indicus* Daudin
	small terrestrial	*Mabuya sloanei* Daudin *Sphaerodactylus macrolepis* Günther	*Carlia fusca* Duméril and Bibron *Emoia caeruleocauda* de Vis
	folivore	*Cyclura pinguis* Barbour	—
Nocturnal	arboreal	*Hemidactylus mabouia* Moreau de Jonnès	*Hemidactylus frenatus* Duméril and Bibron *Lepidodactylus lugubris* Duméril and Bibron *Gehyra mutilata* Wiegmann
	terrestrial	—	*Nactus pelagicus* Girard

typical stand in terms of tree species composition, stem diameter, stem density, canopy height and canopy coverage. In each habitat, we censused all small, non-volant, non-fossorial vertebrates. Our total forest removal technique (see below) provides unbiased density estimates for all of the species, thereby allowing us to estimate representation of all species and thus the assemblage.

We quantified the absolute population densities with 10 × 10 m forest removal plots (Rodda *et al.* in press). This technique is of value primarily for species that occur at moderately high density, and for such species is preferable to other estimates – because fewer assumptions are required. Details of this technique are reported elsewhere (Rodda *et al.* in press). Briefly, we sealed the 10 × 10 m plots to emigration or immigration of the target species by a combination of 1.5 m canopy separation (for non-volant arboreal species) and an unclimbable ground-level barrier of greased 0.5m-high aluminium flashing. The barrier is buried in the ground to preclude subterranean movements of all but specialized fossorial species. These measures were taken during the inactive period of the primary target species (thus the time-of-day varies from site to site according to species composition), to minimize disturbance and flight. In the British Virgin Islands we established the barriers at night.

Beginning on the following morning we then removed and dismantled all live and dead vegetation down to the level of mineral soil. We recorded the presence and mass of all vertebrates, as well as the fresh mass of aboveground vegetation.

During October 1998 we sampled four sites, two each in early successional (*Leucaena leucocephala*) and mid-successional (*Coccoloba uvifera*) forest on the sand flat of White Bay on Guana Island, British Virgin Islands (18.475°N, 64.578° W). For each plot we identified to species and measured all woody stems > 1 cm dbh, sampled ground-level vegetation with 20 uniformly spaced Daubenmire frame placements, measured litter depth in the centre of each of the 20 sampling points, estimated canopy height with reference to a measured rod, and judged canopy coverage on the basis of readings from a convex spherical densiometer read facing into the plot from each of the four corners. Each of our Virgin Island plots was cleared by 6–12 people in 1–2 d. We sampled two plots for each habitat type, which provided a reasonable estimate of absolute population density for species that exceed a density of about 500 ha^{-1}. We used the same technique in Pacific and Virgin Island sites, though this paper reports the results of only the Virgin Island samples.

The early-successional plots were composed almost exclusively of *Leucaena* and *Acacia* trees (Table 2), whereas the mid-successional plots had a greater diversity of woody species (the commonest, *Coccoloba uvifera*, averaged 42% of total basal area). There were a surprisingly high number of woody stems (up to 438), especially in the early successional plots, but medium and large trees (> 10 cm dbh) were generally absent (Table 2). Aside from species composition differences, the most distinct vegetation features of the two habitats were litter

Table 2. Plot characteristics for study areas on Guana Island, British Virgin Islands.

	Leucaena plots		*Coccoloba* plots	
	1	2	1	2
Dominant tree	*Acacia*	*Leucaena*	*Coccoloba*	*Coccoloba*
(% of total basal area)	(74)	(75)	(37)	(47)
Secondary tree	*Leucaena*	*Acacia*	*Acacia*	*Acacia*
(% of total basal area)	(26)	(25)	(31)	(10)
Total basal area (cm^2)	990	1617	1560	2675
Stems > 1 cm dbh	292	438	235	137
Stems > 10 cm dbh	0	0	0	3
Canopy height (m)	5	5.5	6.5	6
Canopy cover (%)	76	68	81	71
Litter > 1 cm	5	70	95	75
(% of 20 point samples)				
mean litter depth (cm)	0.31	1.75	3.33	4.89
Herb coverage	21	31	10	7
(mean of 20 Daubenmire samples)				
Vegetation wet mass (kg)	997	1231	2074	2366
Sphaerodactylus collected	6	262	676	380

amount (coverage and depth) and total wet mass of vegetation (range 997–2366 kg). In the earliest successional plot (*Leucaena*-1) litter was barely present (*c*. 5% of surface), whereas deep litter (mean = 4.9 cm) covered almost the entire forest floor in *Coccoloba* plot 1 (Table 2).

Faunal abundances were apparently related to these plot differences (Tables 2, 3). We obtained a total of seven snakes, 1401 lizards, and no amphibians, birds or mammals. The vast majority of individuals (94.5%) were of a single lizard species, *Sphaerodactylus macrolepis*, found in leaf litter. Statistical power is limited with four samples, but there was an obvious positive association (r^2 = 0.84) between the abundance of this diminutive diurnal gecko and the coverage of leaf litter. In the plots with extensive leaf litter this species was extraordinarily common (Table 3), reaching a higher density than has been reported for non-aggregated lizards (Figure 1). We project that this gecko attains densities of around 67 600 ha^{-1} in areas having continuous *Coccoloba* litter. Our average density in the *Coccoloba* plots was 52 800 ha^{-1}.

The high density we observed was unprecedented among all non-aggregated vertebrates. No mammals or birds are known to approach the high densities attained by reptiles and amphibians (Welty & Baptista 1988, Fa & Purvis 1997). A landmark study (Burton & Likens 1975) of leaf litter salamanders (*Plethodon cinereus* Green) in New Hampshire documented densities of around 2950 ha^{-1}. This value is near the upper reported limit of densities for salamanders that are not aggregated along water courses or in tiny rock refugia. The highest published density of non-aggregated frogs (20 570 ha^{-1}) is for the coqui frog, *Eleutherodactylus coqui* Thomas, in Puerto Rico (Stewart & Rand 1991). Although our density estimates for *Sphaerodactylus macrolepis* are near the cloud of densities reported for other lizard species in the logarithmic scale shown in Figure 1, the next highest value (23 600 ha^{-1}, for *Anolis stratulus* (Reagan 1992) is less

Table 3. Mean densities of species obtained from Guana Island removal plots (see also Table 2). Although six *Typhlops richardi* were obtained during sampling, the sampling technique is considered inappropriate for this fossorial species. The ground level barrier has not been tested on snakes such as *Liophis portoricensis*; if the barrier is not completely effective, the obtained results may be underestimates for that species.

|		*Leucaena* plots	*Coccoloba* plots
Numbers ha^{-1}	*Liophis portoricensis*	50	0
Snakes			
	Typhlops richardi	0	300
Lizards	*Ameiva exsul*	200	0
	Anolis cristatellus	1000	1100
	Anolis pulchellus	50	0
	Anolis stratulus	600	900
	Sphaerodactylus macrolepis	13400	52800
Biomass (kg ha^{-1})	*Liophis portoricensis*	3.05	0
Snakes			
	Typhlops richardi	0	0.71
Lizards	*Ameiva exsul*	1.22	0
	Anolis cristatellus	0.69	1.68
	Anolis pulchellus	0.09	0
	Anolis stratulus	0.63	1.00
	Sphaerodactylus macrolepis	3.60	15.26
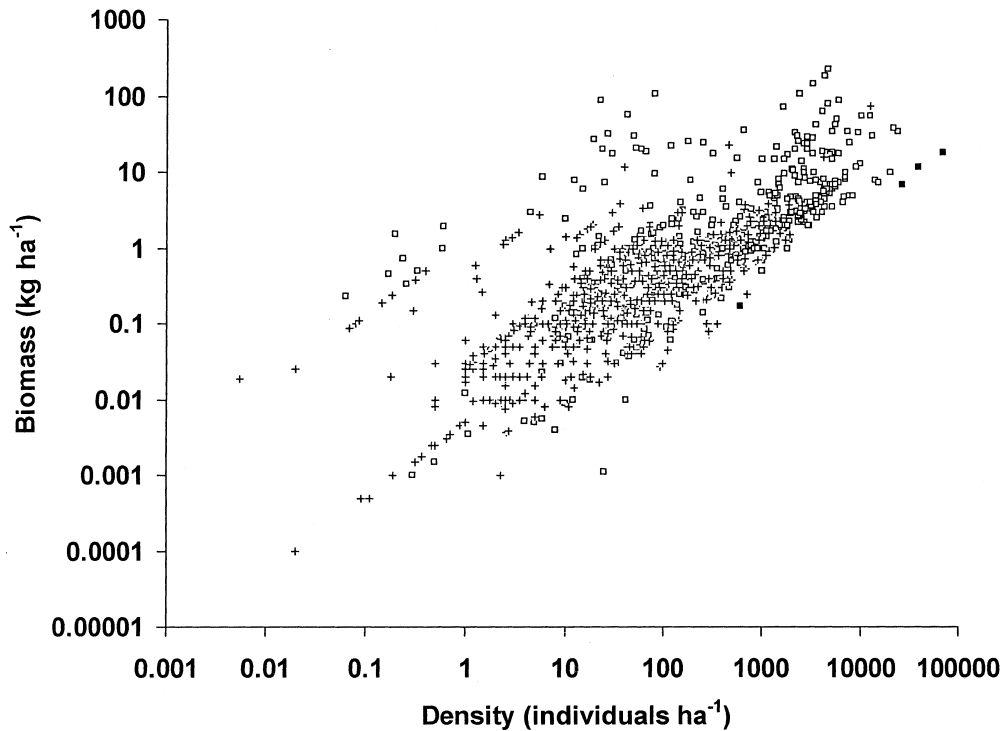
Figure 1. Density estimates of 1072 non-aggregated lizard species/venue combinations taken from our work and 228 literature sources (available upon request). Values marked with a + are from mainland sites; the others are from islands. The four filled symbols represent the *Sphaerodactylus macrolepis* samples reported here, three of which exceed prior records for numerical density, but none is exceptional in terms of biomass.

than half the average value we recorded in mid-successional forest (we also found *A. stratulus* in our plots, but at a much lower density: 600–900 ha^{-1}). Thus, our censuses of *S. macrolepis* constitute a new record, despite the choice of site without regard to focal species abundance.

What is responsible for the high densities we found? Our impression is that many of the 73 *Sphaerodactylus* species recorded from the West Indies (Schwartz & Henderson 1991) are likely to occur at high densities. The previously published density values for *S. macrolepis* on Guana Island (Lazell 1991) include a conversion error, which when corrected (to 16 000 and 26 000 ha^{-1}) indicates a higher density than had been previously recorded. Despite these high densities, *Sphaerodactylus* have apparently not engendered much interest from ecologists, probably because of their secretive habits and small size (*S. macrolepis* mean mass = 0.285 g in our samples). One commonality among the species that exhibit the highest absolute densities (Figure 1) is their presence on islands. Presumably predation is reduced on islands, though other factors may also play a role (Andrews 1976). Fauth *et al.* (1989) found a strong association between leaf litter depth and the diversity and abundance of herpetofauna in tropical leaf litter. Several of the high density species mentioned above (temperate salamanders, tropical frogs) have also been associated with leaf litter, though a proximate cause for high density in leaf litter is not obvious.

Most dense terrestrial vertebrates are small. A more equitable basis for comparison among species might be biomass density (Table 3). *S. macrolepis* has the highest biomass density of the species recorded in our Guana Island plots, but its biomass is unremarkable. A variety of lizards exhibit values near 100 kg ha^{-1} (Figure 1). The two lizard species with the highest documented biomass densities are *Gallotia stehlini* Schenkel, for which the four highest values are 109–228 kg ha^{-1}, all in the Canary Islands (Vernet *et al.* 1997) and *Iguana iguana* L., which was documented at 107 kg ha^{-1} on an island in Colombia (Müller 1972). These are roughly an order of magnitude higher than that of *S. macrolepis* or *Loxodonta africanus* Blumenbach, the African elephant, two species at opposite ends of the size spectrum which both exhibit biomass densities of around 10 kg ha^{-1} (Fa & Purvis 1997, Prins & Reitsma 1989; present study). Due to their great mass, a few mammals attain biomass densities higher than that of *Sphaerodactylus*, but none approaches that of some island lizards (Figure 1).

Does the high density of *Sphaerodactylus* have an analogue in the lizard assemblages of Pacific islands? Litter insectivores are also the densest species in our Pacific samples. In *Leucaena* habitat in northern Guam, for example, litter dwelling insectivores outnumbered those from all other guilds, averaging 10 275 ha^{-1} (23.9 kg ha^{-1}) in our eight samples (unpubl. data). Aside from the importance of litter insectivores, there was little overall functional similarity between Guam and Guana lizard assemblages. Though arboreal diurnal lizard species occur in both places, they were absent from 11 of 12 samples on Guam, but numerous in all Guana samples. This was unexpected given that *Anolis*

occur in both places. While the Brown Tree Snake (*Boiga irregularis* Merrem in Bechstein) could be responsible for the low density of arboreal diurnal lizards, especially anoles, on Guam (Rodda & Fritts 1992), it does not explain the similar results obtained on nearby, snakeless islands (unpubl. data). No reptilian folivore has emerged in the Marianas.

The most striking difference between the two islands was in the nocturnal niches, however. We detected no individuals of nocturnal species on Guana Island, whereas about half of all terrestrial vertebrate individuals on Guam are from nocturnal species (Rodda & Fritts 1996, 1998). This is especially surprising in light of the presence of introduced *Hemidactylus* sp. in both places. Apparently the failure of *Hemidactylus mabouia* to proliferate away from human habitation on Guana Island is unrelated to the presence of native lizard competitors, since none is known from the island. This example suggests caution in invoking competition to explain the abundance or distribution of *Hemidactylus frenatus* in the Pacific (Case & Bolger 1991a, b; Case *et al*. 1994).

The pattern of gross dissimilarity between guild abundances that emerges from this comparison of assemblages in Pacific and West Indian islands differs from the relatively high overlap in assemblage structure detected on the basis of species composition (Table 1). The addition of information about species abundances strengthens the impression that historical factors or some process other than community adaptation severely constrains ecological roles and potential abundances. Although population densities are often difficult to quantify, they appear to provide considerable insight into the functioning of ecosystems.

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