Journal of Biogeography, **29**, 623–632

Excess density compensation of island herpetofaunal assemblages

Gordon H. Rodda* and Kathryn Dean-Bradley *US Geological Survey, McMurry Ave., Fort Collins, CO, USA*

Abstract

Aim Some species reach extraordinary densities on islands. Island assemblages have fewer species, however, and it is possible that island species differ from their mainland counterparts in average mass. Island assemblages could be partitioned differently (fewer species or smaller individuals) from mainland sites without differing in aggregate biomass (density compensation). Our objective was to determine the generality of excess density compensation in island herpetofaunal assemblages.

Location Our bounded removal plot data were obtained from Pacific Island sites (Guam, Saipan and Rota), the West Indies (British Virgin Islands), and the Indian Ocean (Ile aux Aigrettes off Mauritius). The literature values were taken from several locales. Other island locations included Barro Colorado Island, Bonaire, Borneo, Philippine Islands, Seychelle Islands, Barrow Island (Australia), North Brother Island (New Zealand), Dominica and Puerto Rico. Mainland sites included Costa Rica, Ivory Coast, Cameroon, Australia, Thailand, Peru, Brazil, Panama and the USA.

Method We added our thirty-nine bounded total removal plots from sixteen island habitats to fifteen literature records to obtain seventy-five venues with estimable density and biomass of arboreal or terrestrial herpetofaunal assemblages. These biomass estimates were evaluated geographically and in relation to sampling method, insularity, latitude, disturbance regime, seasonality, community richness, vegetative structure and climate. Direct data on trophic interactions (food availability, parasitism and predation pressure) were generally unavailable. Sampling problems were frequent for arboreal, cryptic and evasive species.

Results and main conclusions We found strong evidence that herpetofaunal assemblages on small islands (mostly lizards) exhibit a much greater aggregate density of biomass (kg ha^{-1}) than those of larger islands or mainland assemblages (small islands show excess density compensation). High aggregate biomass density was more strongly associated with the degree of species impoverishment on islands than it was on island area or insularity *per se*. High aggregate biomass density was not strongly associated with latitude, precipitation, canopy height or a variety of other physical characteristics of the study sites. The association between high aggregate biomass density and species-poor islands is consistent with the effects of a reduced suite of predators on depauperate islands, but other features may also contribute to excess density compensation.

Keywords
Density compensation, insularity, herpetofauna, island syndrome, *Sauria, Anura*.

*Correspondence: USGS Midcontinent Ecological Science Center, 4512 McMurry Avenue, Fort Collins, CO 80525, USA. E-mail: gordon_rodda@usgs.gov

© 2002 Blackwell Science Ltd

INTRODUCTION

Extraordinarily high densities of organisms are often associated with islands. Some of these high densities may represent breeding or resting aggregations, however, and may not be representative of the entire habitat. Nonetheless, there are a conspicuous number of reports of island herpetofauna in forested habitats reaching exceptional densities in habitat that appears representative. For example, Rodda *et al.* (2001) recently detected average population densities of $>50{,}000$ ha^{-1} for the tiny litter gecko *Sphaerodactylus macrolepis* Günther in coccoloba forest in the Virgin Islands, a density substantially higher than that reported for any mainland lizard. One might expect that the densities of single species would be higher in areas, such as islands, where few species were present and niche expansion was thereby facilitated. The few species present might be afforded a greater availability of food or space. This raises the question of whether the total density or biomass of all species in a guild is greater on islands.

MacArthur *et al.* (1972) coined the phrase 'excess density compensation' to describe the situation in which the aggregate density of a given guild or major taxon was higher on islands than in equivalent mainland habitats. Case (1975) concluded that diurnal terrestrial lizards of offshore islands in the Sea of Cortez showed excess density compensation when compared with their mainland counterparts. Recent advances in the sampling of herpetofaunal assemblages (Rodda *et al.*, 2001) have allowed us to extend Case's observations to include both ground-level and arboreal as well as nocturnal species from a variety of oceanic islands (Pacific, Atlantic, and Indian Ocean areas: see below). For small remote oceanic islands, however, there is no obvious mainland counterpart. It would be challenging to find exact mainland/landbridge pairs as did Case (1975). For example, the assemblages on Rota, Mariana Islands, can be compared with Guam, a nearby larger landmass that is also insular but has a higher species richness, Papua New Guinea or the Philippines, islands that have the same (greater) richness and (equivalent) insularity attributes but few species in common, or the Asian mainland, for which species analogues are difficult to recognize. Here we review literature for herpetofaunal assemblages throughout the world, facilitating a variety of island/mainland comparisons.

Our objective was to determine the generality of excess density compensation in island herpetofaunal assemblages. We tabulated information germane to identifying the causal factors responsible for excess density compensation or the lack thereof, but we recognize that a correlational study of this sort cannot decisively address causation. Furthermore, we found that vital biotic information was not available in the literature. MacArthur *et al.* (1972) identified reduced island predation and competition as two agents likely to be responsible for excess density compensation. Unfortunately, measures of the abundances of predators and competitors were not generally available from the literature records. Furthermore, estimation of the demographic significance of these roles could not be complete without substantial additional information on the intensity of competition/predation between the species of interest. These data were not available. We took the first step – determining whether the available data support the existence of excess density compensation in island herpetofaunas.

How can the densities of two assemblages be compared, if one is composed primarily of many tiny individuals and another is composed of a few large ones? For the purposes of this paper, we use aggregate fresh biomass of the entire species assemblage, recognizing that important biological questions about optimality of body size and life histories will be overlooked by use of this common currency.

METHODS

We sought all literature records that reported densities or biomasses of the major herpetofaunal components in a given terrestrial site. We found none that provided credible estimates of subterranean herpetofauna, so we limited our review to taxa usually found above-ground. We also did not find credible records that included terrestrial turtles or crocodilians along with the other terrestrial herpetofauna. Therefore, for each record we recorded documented densities and fresh biomasses of frogs, lizards, snakes, salamanders, and sphenodontians. For the purposes of this analysis we pooled the sphenodontians with the ecologically similar lizards. For comparison with the majority of records, which omitted arboreal species, we partitioned the reported densities/biomasses from the more complete studies into ground-level and arboreal strata based on the characteristic habits of the constituent species (not the stratum where captured, as capture position was generally unavailable and may reflect flight behaviour). In a few cases, the original records reported only biomass or only densities. Where necessary, we converted density estimates to biomass on the basis of estimated mean individual mass for comparable samples (i.e. including criteria such as comparability based on same species and whether young of year were included). We searched more than 1000 single-species density records in the literature to obtain estimates of the mean masses of various species (data sources available upon request). If several comparable literature records were available for a given estimate, we averaged the literature values to estimate the unknown mean mass. If no value for the species in question was available, we used data from congeners of similar size; failing that, we used confamilials of a similar size and body form.

The background data that we sought for each venue were whether the site was on a geographic island (land surrounded by fresh or salt water), the size of the landmass from which data were taken (continents larger than Australia were arbitrarily assigned an area of 2×10^9 ha), overall species richness (operationally, the number of resident frogs and lizards), latitude, strata sampled, habitat type, seasonality (low, medium, high), disturbance regime (primary, secondary, agroforest and severely disturbed), canopy height, canopy cover, elevation and precipitation. Areas of

'low' seasonality had little annual modulation of rainfall; those with 'high' seasonality had little or no rain during the dry season; and 'medium' areas were similar to Barro Colorado Island in having substantial but incomplete annual modulation in rainfall (Rand & Rand, 1982). We defined species richness as the number of frog and lizard species because those data were available for every site, and their sum reflected community richness in both arid and mesic environments. We ascribe no particular importance to those particular taxa, but recognize that predation, competition and other biotic processes are likely to be more intense in areas of overall greater species richness.

To assess the adequacy of the sampling we noted whether any species was omitted, whether a barrier was used to impede the emigration of individuals during sampling, what attribute minimized immigration (usually brevity of the sampling period), the total area sampled, the number of taxa obtained and the number of focal taxa present in the area. We rejected records that sampled some special feature that was non-representative of natural ecological density (e.g. buildings, hibernacula, streamsides) or that failed to detect the bulk of the individuals present in the focal stratum.

To the records of the fifty-nine qualifying venues taken from the literature we added data from sixteen venues sampled by ourselves. These sixteen represent thirty-nine removal plots (usually two or three 100 m^2 plots for each venue) obtained following the methods specified in Rodda *et al.* (2001). Briefly, we censused the animals while removing all above-ground vegetation from demographically closed forest plots. The plots were artificially isolated from continuous forest by separating the canopy and installing a lizard and frog-proof fence at ground level (a greased 0.5 m high solid wall of aluminium flashing buried to sufficient depth to preclude burrowing escape by local species). The forest canopy was separated during the day, to minimize disturbance of arboreal species (most of which were nocturnal in the study sites). Installation of the ground-level barrier was carried out at night to minimize disturbance to ground-level species (most or all of which were diurnal in the studied sites). To further minimize disturbance, we allowed at least 6 h of daytime to elapse after completion of canopy clearing and before nightfall, to permit any displaced diurnal animals to return to their normal nocturnal retreats before demographically sealing the plot by installation of the fence.

Although the areas sampled by this total removal technique were relatively small (200–300 m^2 per site), the sites were carefully chosen on the basis of vegetative species composition and canopy cover to be representative of the habitat. Furthermore, they were information rich: a total of 4512 animals were detected, representing an average of 282 individuals per site.

RESULTS

Representativeness of sample

Study sites were fairly well-distributed in terms of longitude (Fig. 1a), but tightly clustered near the equator (Fig. 1b). Ninety-two per cent of the sites were at latitudes of 20° or less. All biogeographic realms except the Palaeractic are represented (Tables 1 and 2), although almost no data are available for mid- and high-latitude localities within any realms. The modal study sampled secondary forest (51% of sample), but primary forest was well represented (33%). Only 5% of the sample was of severely disturbed habitats, but an additional 11% was of agroforest lands, mostly abandoned or lightly managed coconut plantations. Because the sample of severely disturbed sites was small and potentially anomalous, it was omitted from most of the following analyses. Seasonality was fairly evenly distributed

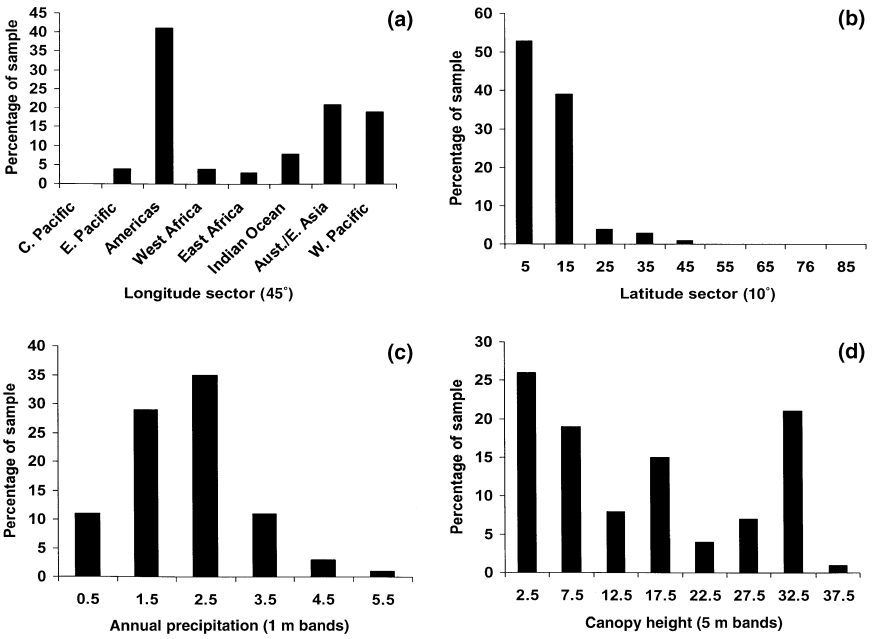

Figure 1 Distribution of sample venues with respect to (a) longitude, (b) latitude, (c) annual precipitation and (d) forest canopy height. Value labels on the abscissa denote interval centerpoints.

Table 1 Terrestrial and arboreal herpetofauna biomass densities (kg ha^{-1}) for mainland venues

		Terrestrial			Arboreal		
Mainland assemblages venue	Source	Frog	Lizard	Other*	Frog	Lizard	Snake
Africa, Cameroon, Lac Tissongo, 1975	Scott (1982)	1	0				
Africa, Cameroon, Lombé 1975	Scott (1982)	1	0				
Africa, Ivory Coast, Lamto burned forest 1964–68	Barbault (1975b); Barbault (1977)	0	0. 1784	0.0646	0	0	0
Africa, Ivory Coast, Lamto burned savanna 1964–65	Barbault (1967); Barbault (1975a)	0. 1794	0.0822	0.0759	0.096	0.096	
Africa, Ivory Coast, Lamto non-burned savanna 1964–65	Barbault (1967); Barbault (1977)	0.095	0. 1793	0.02759			
Asia, Thailand, Sakaerat, deciduous 1969	Inger (1980)	0.02	0.1				
Asia, Thailand, Sakaerat, deciduous 1969 (2)	Inger (1979)	0.02	0.1				
Asia, Thailand, Sakaerat, evergreen 1969	Inger (1980)	0.01	0.1				
Australia, Alice Springs, spinifex dune field 1985–86	Morton & James (1988)		2.86				
C. America, Costa Rica, Braulio Carrillo NP, 1985	Fauth *et al.* (1989)	0.4	0.05				
C. America, Costa Rica, La Selva, New Cacao 1990	Heinin (1992)	2.3	0.6				
C. America, Costa Rica, La Selva, Old Cacao 1972–73	Lieberman (1986)	2.9	1	1			
C. America, Costa Rica, La Selva, Old Cacao, 1990	Heinin (1992)	1.5	0.5				
C. America, Costa Rica, La Selva, Primary forest 1972–73	Lieberman (1986)	1.1	0.3	0.3			
C. America, Costa Rica, La Selva, Primary forest 1990	Heinin (1992)	0.6	0.2				
C. America, Costa Rica, La Selva 1970–71	Scott (1976)	1.2	0.3	0.02*			
C. America, Costa Rica, Las Cruces, 1969	Scott (1976)	5	0.3				
C. America, Costa Rica, Las Cruces 1985	Fauth *et al.* (1989)	2	0.3				
C. America, Costa Rica, Las Vegas, incl. night 1985	Slowinski *et al.* (1987)	1.5	1.5				
C. America, Costa Rica, Las Vegas, 1985	Fauth *et al.* (1989)	1.2	0.8				
C. America, Costa Rica, Monteverde 1985	Fauth *et al.* (1989)	0.5	0.2				
C. America, Costa Rica, Osa, 1969–70	Scott (1976)	1	0.3	0.01*			
C. America, Costa Rica, Palo Verde 1985	Fauth *et al.* (1989)	2	0				
C. America, Costa Rica, Tortuguero, 1985	Fauth *et al.* (1989)	0.4	1.5				
C. America, Panama, Rio Canclon, 1961	Sexton *et al.* (1964)	0.4	0.3				
C. America, Panama, Silugandi 1962	Heatwole & Sexton (1966)	2.5	2				
N. America, USA, New Mexico, Mt Summerford, Bajada site 1971–74	Whitford & Creusere (1977)	0	0.74		0	0	0
N. America, USA, New Mexico, Mt Summerford, Playa site 1970–74	Whitford & Creusere (1977)	0	0.91		0	0	0
N. America, USA, Texas, Alpine, 1957	Milstead (1961)		1				
S. America, Brazil, Amazonas, Juruá River, dry land 1991–92	Gascon (1996)	0.15					
S. America, Brazil, Amazonas, Juruá River, flooded forest 1991–92	Gascon (1996)	0.15					
S. America, Brazil, Amazonas, Manaus INPA/ WWF 1983–84	Allmon (1991)	0.5	0.01	0.05			
S. America, Peru, Cuzco Amazonica, 1976	Duellman (1987)		2.2			0.2	

*All entries except the two marked with asterisks represent snakes; the two with asterisks in this Table represent salamanders.

within the sample (25% low, 48% medium and 27% high), as was total precipitation (Fig. 1c) and canopy height (Fig. 1d). Communities of low richness (less than ten frog and lizard species) constituted about 39% of the total sample, but communities from ten to seventy species were reasonably well represented (Fig. 2). Both island (56%) and mainland (44%) sites were well represented in the total sample, but only islands were found in the sample of sites for which both ground-level and arboreal strata were sampled.

Table 2 Terrestrial and arboreal herpetofauna biomass densities (kg ha^{-1}) for island venues

		Terrestrial			Arboreal		
Island assemblages venue	Source	Frog	Lizard	Other†	Frog	Lizard	Snake
Asia, Borneo, Sarawak, Nanga Tekalit 1962–63	Lloyd *et al.* (1968);	0.1	0.03	0.2			
Asia, Philippines, Negros Island, abaca grove 1963–64	Brown & Alcala (1964)	0.8	0.25	0.3	0.05	0.04	0
Asia, Philippines, Negros Island, City Park 1963–64	Brown & Alcala (1964)	0.005	0.05	0.04	0.01	0.15	0
Asia, Philippines, Negros Island, cloud forest 1958	Brown & Alcala (1961)	1.7	0.03	0.05	0.3		
Asia, Philippines, Negros Island, coconut grove 1963–64	Brown & Alcala (1964)	0.005	0.02	0.04	0	2	0
Asia, Philippines, Negros Island, dipterocarp forest 1958	Brown & Alcala (1961)	0.5	0.9	0.1	0	0.1	0
Asia, Philippines, Negros Island, mangrove 1963–64	Brown & Alcala (1964)	0	0.04	0.2	0	0.16	0
Asia, Philippines, Negros Island, montane 1958	Brown & Alcala (1961)	0.8	0.3	0.2	0.2	0.1	
Asia, Philippines, Negros Island, savanna 1963–64	Brown & Alcala (1964)	0	0.01	0.05	0.02	0.04	0
Asia, Philippines, Negros Island, strand 1963–64	Brown & Alcala (1964)	0	0.3	0.5	0	1.2	0
Asia, Philippines, Negros Island, swamp forest 1963–64	Brown & Alcala (1964)	0.5	0.12	0.25	0	0.88	0.05
Australia, Barrow Island (1977)	Heatwole & Butler (1981)		3	0			
C. America, Panama, Barro Colorado Island 1963	Heatwole & Sexton (1966)	0.2	1				
Indian Ocean, Mascarene Islands, Ile aux Aigrettes, Leucaena forest 1999	This study	0	0	0	0	2.36	0
Indian Ocean, Seychelle Islands, Cousin Island, 1978–79	Brooke & Houston (1983)	0	39.4		0		0
Indian Ocean, Seychelle Islands, Praslin Island, disturbed scrub forest 1976	Evans & Evans (1980)		0.7			0.44	
Indian Ocean, Seychelle Islands, Praslin Island, lowland forest 1976	Evans & Evans (1980)		1.21			1.04	
Indian Ocean, Seychelle Islands, Praslin Island, lowland primary forest 1976	Evans & Evans (1980)		3.11			4.1	
Indian Ocean, Seychelle Islands, Praslin Island, strand forest 1976	Evans & Evans (1980)		1.65			2.13	
Pacific Islands, Mariana Islands, Guam, former snake-free 1999	This study	0	16.3		0	7.51	0
Pacific Islands, Mariana Islands, Guam, NWFN snake-free 1995	This study	0	42.13		0	11.54	0
Pacific Islands, Mariana Islands, Guam, NWFN snake-ridden 1995	This study	0	19.39		0	4.46	0
Pacific Islands, Mariana Islands, Guam, NWFN snake-ridden 1999	This study	9.6	17.76		0	5.23	0
Pacific Islands, Mariana Islands, Guam, Ordnance Annex 1996	This study	50.41	8.94		0	6.38	0
Pacific Islands, Mariana Islands, Guam, strand forest 1997	This study	0	6.06		0	5.88	5.55
Pacific Islands, Mariana Islands, Guam, WAPA grassland 2001	This study	23.33	6.454		0	0.911	0
Pacific Islands, Mariana Islands, Guam, WAPA tangantangan 2001	This study	15.57	8.356		0	6.098	0
Pacific Islands, Mariana Islands, Rota, native forest 2000	This study	0	5			10.62	
Pacific Islands, Mariana Islands, Rota, pandanus forest 2000	This study	8.24	13.38			32.59	
Pacific Islands, Mariana Islands, Rota, tangantangan forest 2000	This study	1.93	2.44			2.63	
Pacific Islands, Mariana Islands, Saipan, native forest 1996	This study	0	0.87			13.34	
Pacific Islands, Mariana Islands, Saipan, tangantangan 1996	This study	6.72	5.09			9.38	
Pacific Islands, New Zealand, North Brother Island *c.* 2000	S. Keall, pers. comm., 2001	0	25	23†	0	4.75	0
West Indies, Greater Antilles, British Virgin Islands, Guana, acacia forest 1998	This study	0	4.9	3.05	0	1.31	0
W. Indies, Greater Antilles, British Virgin Islands, Guana, Coccoloba forest 1998	This study	0	15.26	0	0	2.67	0
W. Indies, Greater Antilles, Puerto Rico, Tabonuco forest 1958–59	Odum *et al.* (1970)	1.85	0		0.68	5	
W. Indies, Lesser Antilles, Bonaire, 1976	Bennett & Gorman (1979)	0	18.9		0	4.2	0
W. Indies, Lesser Antilles, Dominica, cultivated 1984	Bullock & Evans (1990)		6.3		0	2.2	0

Table 2 *continued*

Island assemblages venue	Source	Terrestrial			Arboreal		
		Frog	Lizard	Other†	Frog	Lizard	Snake
W. Indies, Lesser Antilles, Dominica, dry scrub woodland, 1984	Bullock & Evans (1990)		20		0	2.2	0
W. Indies, Lesser Antilles, Dominica, lowland rain forest 1984	Bullock & Evans (1990)		0.03		0	0.5	0
W. Indies, Lesser Antilles, Dominica, montane, 1984	Bullock & Evans (1990)		0		0	0.54	0
W. Indies, Lesser Antilles, Dominica, strand 1984	Bullock & Evans (1990)		1.5		0	5.3	0

†All entries except the one marked represent snakes; the marked entry represents tuatara (Sphenondontia).

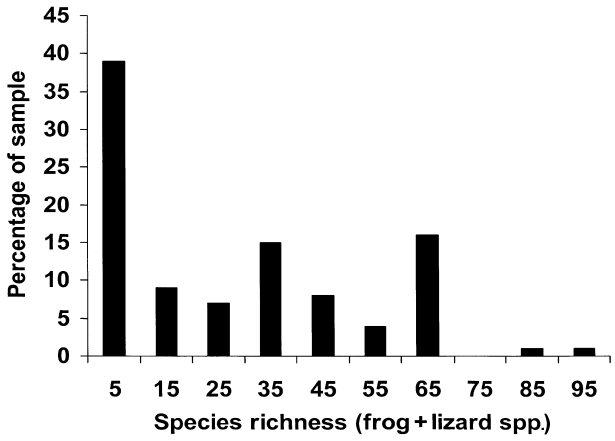

Figure 2 Distribution of sample venues with regard to richness of the sampled community, represented here by the sum of the number of frog and lizard species expected to be present in the sampled venue. Value label on the abscissa denotes interval centerpoint.

Completeness of sample within a site

Slightly more than half of the studies (57%) sampled all above-ground strata, whereas 33% sampled only the leaf litter, and an additional 9% sampled litter plus arboreal animals that could be reached from the ground. The latter were analysed only for ground-level species. The methods chosen for sampling ranged from the bounded total removal method highlighted in the methods section, to one study (Duellman, 1987) that based estimates on sightings along a strip transect. One study (Heatwole & Butler, 1981) used a variant on total removal plots that incorporated bulldozers and setting fire to grass clumps, and two studies (3%) used partially bounded litter plots, but the bulk of the records (39%) came from traditional litter plots (Heatwole & Sexton, 1966; Scott, 1976), or from a visual search of all strata (27%: Brown & Alcala, 1961, 1964). A small number (8%) used mark-recapture, but such studies tended to omit the rarer species. Mark-recapture studies sometimes sampled very large areas (up to 500,000 m^2), but other types of studies focused on smaller areas (75–73,300 m^2). We found it fairly difficult to assess the adequacy of the samples, as there does not appear to be any single or simple metric for assessing the highly variable sample quality.

Density compensation

Because arboreal samples were not available for mainland sites, it was possible to compare only the ground-level stratum between island and mainland sites. The overall average ground-level frog biomass density on islands was 2.91 kg ha^{-1}, over three times the corresponding average for mainland sites (0.90 kg ha^{-1}). The difference for lizards was even more extreme, with the island average (7.05 kg ha^{-1}) roughly 12.5-fold that from mainland sites (0.56 kg ha^{-1}). Summing frog, lizard and whatever other ground-level herpetofauna were sampled, the overall average for island sites was 10.63 kg ha^{-1}, about seven times that of mainland sites (mean = 1.51 kg ha^{-1}). Thus, there is little evidence for density equivalence in island herpetofaunas; the average condition is of 'excess density compensation'.

Correlates of herpetofaunal biomass density

Considerable variation in biomass density exists within island and mainland classes, even within archipelagos or islands (Figs 3 & 4). Little of the variation is removed by limiting the sample to the ground stratum only from tropical sites at low elevation (Fig. 3), or to samples with all strata, low elevation and low latitude tropical sites only, natural habitats only (Fig. 4). A plot of ground-level frog and lizard biomasses by precipitation reveals no clear pattern (Fig. 5), although the highest values are missing from the driest and wettest sites. Latitude does not appear to account for much of the variation (Fig. 6), as very high and very low biomass values were found at both extremes of the latitudinal range sampled.

Agroforest had more ground-level herpetofaunal biomass on mainlands (2.96 kg ha^{-1}) than on islands (1.02 kg ha^{-1}), although the samples included only five and three venues, respectively. Primary forest values were virtually identical [1.54 vs. 1.59 kg ha^{-1}, for mainlands ($n = 19$) and islands ($n = 6$), respectively], but the secondary forest values from islands (mean 14.7 kg ha^{-1}; $n = 29$) exceeded that of mainland sites (0.63 kg ha^{-1}; $n = 9$) by a factor of more than 20.

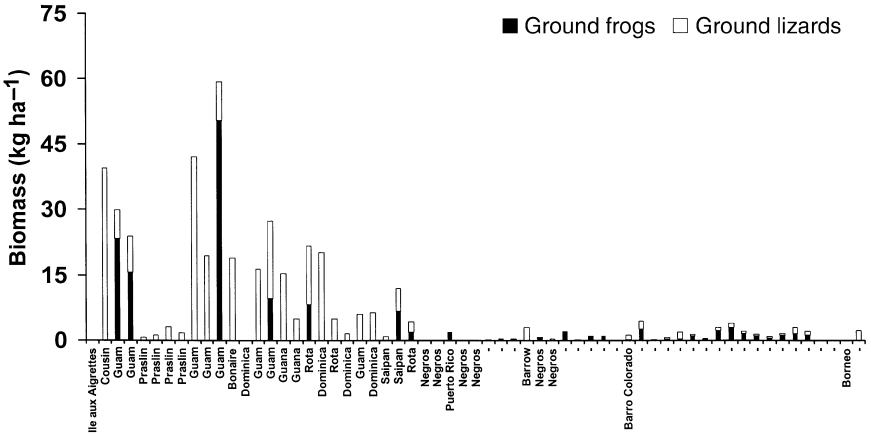

Figure 3 Biomass densities for ground-level frogs and lizards from sixty-one tropical lowland venues. Venues denoted on the abscissa by a '-' are mainland sites; other values indicate island names. Venues are arrayed (L to R) in order of increasing community richness.

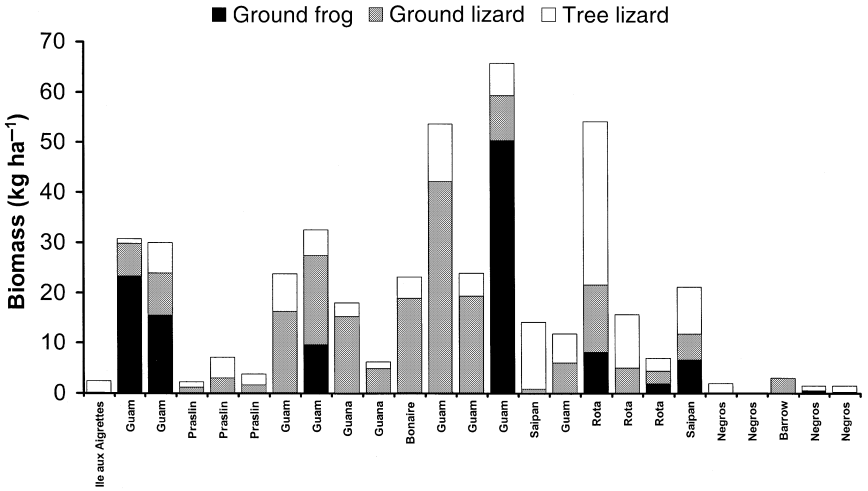

Figure 4 Biomass densities for frogs and lizards from twenty-five lowland tropical venues for sites in semi-natural habitats that were sampled for both ground-level and arboreal species. Arboreal frogs were sampled but did not constitute a large enough sector to be visible at this scale. Venues are arrayed (L to R) in order of increasing community richness. Mainland sites are not named, but denoted by a dash.

Seasonality had no predictive power within insularity classes for ground-level herpetofauna: mainland areas were indistinguishable on the basis of seasonality (low 0.62, medium 0.62 and high 0.59), as were islands (low 7.7, medium 7.6, high 8.1: all values kg ha^{-1}). The correlation between canopy height and overall ground-level herpetofaunal biomass was very weak ($r^2 = 0.127$), and the pattern was of extensive overlap in values up to canopy heights of about 20 m, above which no elevated biomass densities were observed (Fig. 7). Data for arboreal species were not analysed as they are not available for mainland sites.

The distribution of biomasses in relation to island size was more distinct (Figs 8 & 9), with a biomass mode at *c.* 80,000 ha, whether one considered ground-level biomass among all tropical lowland studies (Fig. 8) or all-strata tropical lowland studies (Fig. 9). Islands of size less than or greater than 80,000 ha appeared to attain reduced biomasses in comparison with islands of *c.* 80,000 ha.

The distribution of biomasses in relation to community richness (Figs 10 & 11) was the most distinct of the relationships considered. Assemblages in communities of richness less than about fifteen species were highly variable but often exceptionally dense (up to about 70 kg ha^{-1}) in biomass, whereas virtually all biomasses of richer communities were very low, rarely exceeding 3 kg ha^{-1}. This pattern was evident in both the analysis of ground-level herpetofauna (sixty-one island and mainland venues, Fig. 10), and in the subset of twenty-five natural, lowland tropical venues that provided data for all strata (Fig. 11).

DISCUSSION

If one assumes that the non-representativeness of the samples produced only relatively small biases in the assessment of biomass, excess density compensation would appear to be geographically and taxonomically widespread within terrestrial herpetofauna. Very high biomasses are characteristic of some but not all tropical islands (data for temperate islands are too sparse to judge). Environmental factors such as precipitation or canopy height do not appear to have much direct explanatory value. The relationship between biomass density and land area exhibits a nonlinearity that could reflect increasing herpetofaunal coverage of available niche space as islands increase in size up to around 80,000 ha and presumably gain species richness. Another possible explanation is inadequate sampling of very small islands.

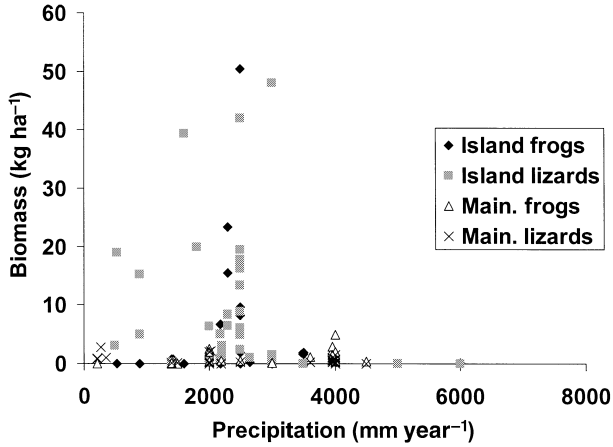

Figure 5 Biomass densities for frogs and lizards from seventy-five venues, in relation to estimated total annual precipitation.

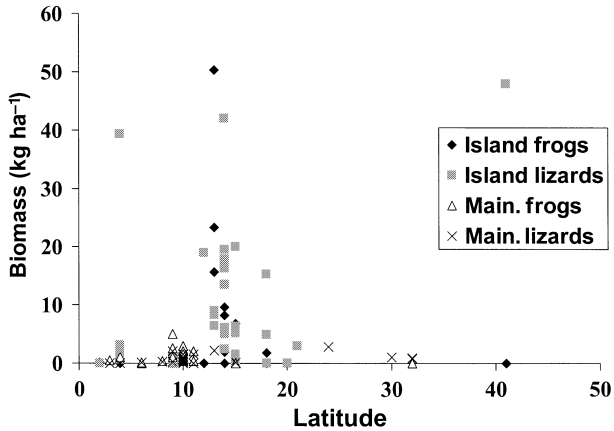

Figure 6 Biomass densities for frogs and lizards from seventy-five venues, in relation to latitude.

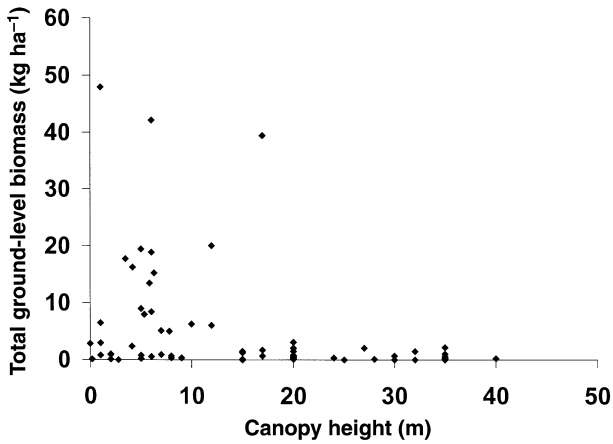

Figure 7 Total ground-level herpetofaunal biomass from seventy-five venues, in relation to forest canopy height.

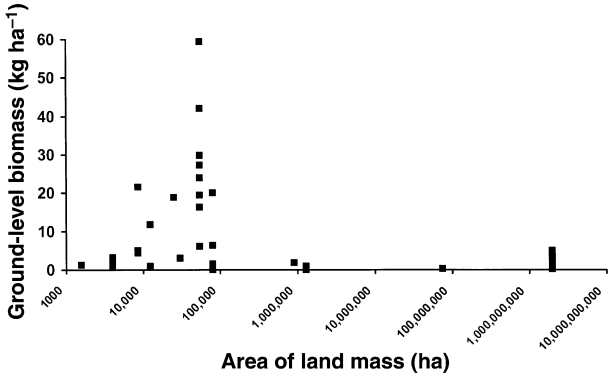

Figure 8 Total ground-level herpetofaunal biomass for sixty-one lowland tropical venues, in relation to land area. Continents larger than Australia were assigned an area of 2,000,000,000 ha.

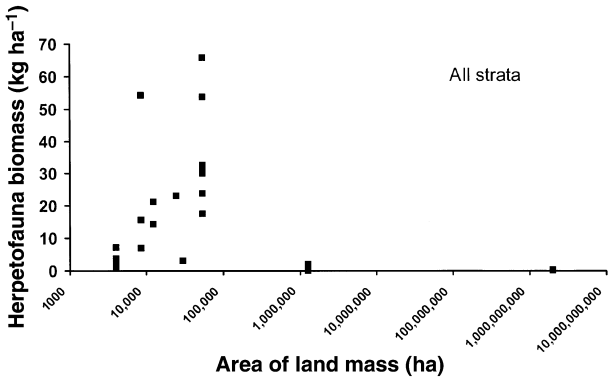

Figure 9 Total herpetofaunal biomass for twenty-five natural habitats in the tropical lowlands, in relation to land area.

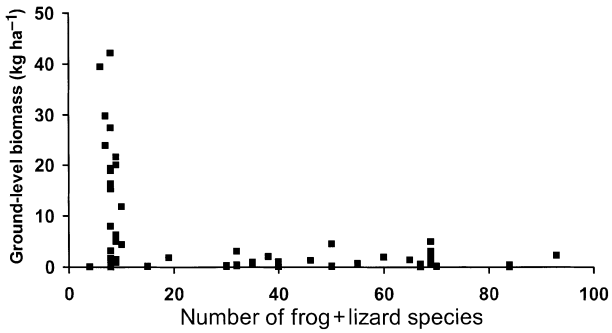

Figure 10 Total ground-level herpetofaunal biomass for sixty-one lowland tropical venues, in relation to community richness, quantified here as the sum of frog and lizard species expected to occur in the sampled habitat.

Support for the latter interpretation comes from the absence of any apparent increase in biomass associated directly with species richness. Islands with as few as six herpetofaunal species exhibit near-maximum biomasses.

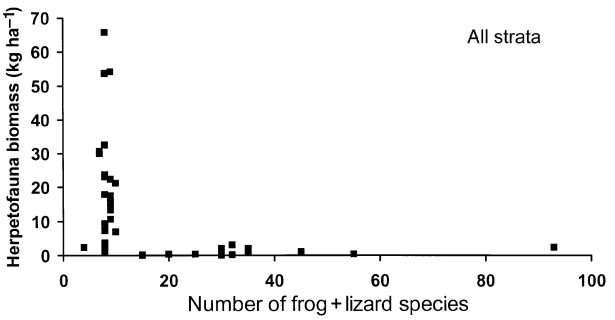

Figure 11 Total herpetofaunal biomass for twenty-five natural habitats in the tropical lowlands, in relation to community richness, operationalized as in Fig. 10.

Equally striking to us is the apparently sharp decline in biomass at community richnesses greater than about twelve frog and lizard species. Many more data, especially from communities of ten to thirty species, are needed to delineate the relationship between biomass and community richness.

One of the original suggestions for the cause of excess density compensation was the relative absence of predation on islands. The data set we analysed was unable to provide insight on this vital issue, but we did casually note that all venues except one (Pacific Islands, New Zealand, North Brother Island) possessed at least one 'carnivore' – introduced rats. We put 'carnivore' in quotation marks because many of the nominally insectivorous lizard and frog species are capable of eating smaller herpetofauna, at least opportunistically. The rats in question also consume plant material for the bulk of their diet. Nonetheless, they are capable of preying on small or relatively defenseless vertebrates such as juveniles or eggs (see below). It is perhaps notable that biomass density on North Brother Island was exceptionally high, consistent with a number of observations that introduced rats are capable of significant reduction in island herpetofaunal abundances (Whitaker, 1973; Atkinson, 1978, 1985; Day & Daltry, 1996). Our data set cannot directly address the impact of predators on island herpetofaunal abundances, but our inability to extract useful information from the literature is a testament to the paucity of studies that seek to tease apart the influences of various biotic factors influencing herpetofaunal abundances.

In the course of compiling these data, we realized the possibility that many of the differences in herpetofaunal abundances may be an artefact of inadequate sampling. We suspect that many of the studies using traditional 'litter plots' may be grossly undersampling true abundances. Evidence for this comes from three sources: a single comparison (Reynolds *et al.*, 1997) between a bounded removal plot and a nearby traditional litter plot (unbounded), a comparison between small leaf-removal plots (Rocha *et al.*, 2001) and traditional litter plots, and the distribution of abundance scores vis-à-vis the total removal method. Rodda *et al.* (2001) discussed additional evidence for the undersampling of traditional litter plots. Reynolds *et al.* (1997) detected three frogs per 100 m^2 traditional litter plot in a sample in Amazonian Peru, whereas a matched nearby – but bounded – removal plot (trees not felled) produced twenty-nine frogs and one snake. Rocha *et al.* (2001) found about six times the density and twice the biomass of frogs in ninety 2 m^2 leaf removal plots compared with twenty-four 64 m^2 traditional litter plots. These types of comparisons desperately need replication in a variety of contexts.

Further evidence that total removal sampling more completely censuses the herpetofauna is the observation that the sixteen total removal plots accounted for fifteen of the twenty highest biomasses reported in this study (both mainland and islands). Until more validation studies are conducted on herpetofaunal sampling methods, it will not be possible to determine the extent to which apparent island/mainland differences are the result of confounded differences in sampling method.

ACKNOWLEDGMENTS

This work was supported by grants from the US Departments of Interior (Office of Insular Affairs and National Park Service) and Defense. It would not have been possible without the generous support of Thomas Fritts and more than forty hard-working field assistants, whose compensation, if any, was little match for the trying field conditions. Their efforts are greatly appreciated. Teri Kman assisted with data management.

R. Rondeau, T. Kman, and T. Fritts suggested improvements to the manuscript.

REFERENCES

Allmon, W.D. (1991) A plot study of forest floor litter frogs, Central Amazonas, Brazil. *Journal of Tropical Ecology*, **7**, 503–522.

Atkinson, I.A.E. (1978) Evidence for effects of rodents on the vertebrate wildlife of New Zealand islands. *The ecology and control of rodents in New Zealand nature reserves* (eds P.R. Dingwall, I.A.E. Atkinson and C. Hay), pp. 7–30. New Zealand Department of Lands and Survey Informational Series 4. Wellington, New Zealand.

Atkinson, I.A.E. (1985) The spread of commensal species of *Rattus* to oceanic islands and their effects on island avifaunas. *Conservation of island birds* (ed. P.J. Moors), pp. 35–81. International Council for Bird Preservation, Technical Publication no. 3, Cambridge.

Barbault, R. (1967) Recherches écologiques dans la savane de Lamto (Côte-d'Ivoire): Le cycle annuel de la biomasse des amphibiens et des lezards. *La Terre et la Vie*, **3**, 297–318.

Barbault, R. (1975a) Les peuplements de lezards des savanes de Lamto (Côte-d'Ivore). *Annales de l'Université d'Abidjan Série E*, **8**, 149–221.

Barbault, R. (1975b) Place des Lézards dans la biocénose de Lamto: relations trophiques; production et consommation des populations naturelles. *Bulletin de l'Institut Fondamental d'Afrique Noire Série A*, **37**, 467–514.

Barbault, R. (1977) Structure et dynamique d'une herpetocenose de savane (Lamto, Côte-d'Ivoire) [in French w/English summary]. *Geo-Eco-Trop*, **1**, 309–334.

Bennett, A.F. & Gorman, G.C. (1979) Population density and energetics of lizards on a tropical island. *Oecologia*, **42**, 339–358.

Brooke, M.D.L. & Houston, D.C. (1983) The biology and biomass of the skinks *Mabuya sechellensis* and *M. wrightii* on Cousin Island, Seychelles. *Journal of Zoology (London)*, **200**, 179–195.

Brown, W.C. & Alcala, A.C. (1961) Populations of amphibians and reptiles in the submontane and montane forests of Cuernos de Negros, Philippine Islands. *Ecology*, **42**, 628–636.

Brown, W.C. & Alcala, A.C. (1964) Relationship of the herpetofaunas of the non-dipterocarp communities to that of the dipterocarp forest of southern Negros Island, Philippines. *Senckenbergiana Biologica Frankfurt*, **45**, 591–611.

Bullock, D.J. & Evans, P.G.H. (1990) The distribution, density, and biomass of terrestrial reptiles in Dominica, West Indies. *Journal of Zoology (London)*, **222**, 421–443.

Case, T.J. (1975) Species numbers, density compensation and colonizing ability of lizards on islands in the Gulf of California. *Ecology*, **56**, 3–18.

Day, M. & Daltry, J. (1996) Rat eradication to conserve the Antiguan Racer. *Aliens*, **3**, 14–15.

Duellman, W.E. (1987) Lizards in an Amazonian rain forest community (Peru): Resource utilization and abundance. *National Geographic Research*, **3**, 489–500.

Evans, P.G.H. & Evans, J.B. (1980) The ecology of lizards on Praslin Island, Seychelles. *Journal of Zoology (London)*, **191**, 171–192.

Fauth, J.E., Crother, B.I. & Slowinski, J.B. (1989) Elevational patterns of species richness, evenness, and abundance of the Costa Rican leaf-litter herpetofauna. *Biotropica*, **21**, 175–185.

Gascon, C. (1996) Amphibian litter fauna and river barriers in flooded and non-flooded Amazonian rain forests. *Biotropica*, **28**, 136–140.

Heatwole, H. & Butler, H. (1981) Structure of an assemblage of lizards on Barrow Island, Western Australia. *Australian Journal of Herpetology*, **1**, 37–44.

Heatwole, H. & Sexton, O.J. (1966) Herpetofaunal comparisons between two climatic zones in Panama. *American Midland Naturalist*, **75**, 45–60.

Heinen, J.T. (1992) Comparisons of the leaf litter herpetofauna in abandoned cacao plantations and primary rain forest in Costa Rica: some implications for faunal restoration. *Biotropica*, **24**, 431–439.

Inger, R.F. (1979) Abundance of amphibians and reptiles in tropical forests of Southeast Asia. *University of Hull, Department of Geography, Miscellaneous Series*, **22**, 93–112.

Inger, R.F. (1980) Densities of floor-dwelling frogs and lizards in lowland forests of southeast Asia and Central America. *American Naturalist*, **115**, 761–772.

Lieberman, S.S. (1986) Ecology of the leaf litter herpetofauna of a Neotropical rain forest: La Selva, Costa Rica. *Acta Zoologica Mex. (n.s.)*, **15**, 1–72.

Lloyd, M., Inger, R.F. & King, F.W. (1968) On the diversity of reptile and amphibian species in a Bornean rain forest. *American Naturalist*, **102**, 497–515.

MacArthur, R.H., Diamond, J.M. & Karr, J.R. (1972) Density compensation in island faunas. *Ecology*, **53**, 330–342.

Milstead, W.W. (1961) Observations of the activities of small animals (Reptilia and Mammalia) on a quadrat in southwest Texas. *American Midland Naturalist*, **65**, 127–138.

Morton, S.R. & James, C.D. (1988) The diversity and abundance of lizards in arid Australia: a new hypothesis. *American Naturalist*, **132**, 237–256.

Odum, H.T., Abbott, W., Selander, R.K., Golby, F.B. & Wilson, R.F. (1970) Estimates of chlorophyll and biomass of the tabonuco forest of Puerto Rico. *A tropical rain forest, section I* (ed. H.T. Odum), pp. 3–19. US Atomic Energy Commission, Oak Ridge, TN.

Rand, A.S. & Rand, W.M. (1982) Variation in rainfall on Barro Colorado Island. *The ecology of a tropical forest* (eds E.G. Leigh Jr, A.S. Rand and D.M. Windsor), pp. 47–59. Smithsonian Institution Press, Washington DC.

Reynolds, R., Fritts, T.H., Gotte, S., Icochea, J. & Tello, G. (1997) Amphibians and reptiles I: biodiversity assessment in the Lower Urubamba region. *Smithsonian/Biodiversity assessment and monitoring plan (Phase II–1997)* (eds F. Daullmeir and A. Alonzo), pp. 255–261. Smithsonian Institution, Washington, DC.

Rocha, C.F.D.D., Van Sluys, M., Alves, M.A.S., Bergallo, H.G. & Vrcibradic, D. (2001) Estimates of forest floor litter frog communities: a comparison of two methods. *Austral Ecol.*, **26**, 14–21.

Rodda, G.H., Campbell, E.W. III, & Fritts, T.H. (2001) A high validity census technique for herpetofaunal assemblages. *Herpetological Review*, **32**, 24–30.

Scott, N.J. Jr (1976) The abundance and diversity of the herpetofaunas of tropical forest litter. *Biotropica*, **8**, 41–58.

Scott, N.J. Jr (1982) The herpetofauna of forest litter plots from Cameroon, Africa. *Herpetological communities* (ed N.J. Scott Jr), pp. 145–150. US Department of the Interior, Fish & Wildlife Service, Wildlife Research Report 13, Washington, DC.

Sexton, O.J., Heatwole, H. & Knight, D. (1964) Correlation of microdistribution of some Panamanian reptiles and amphibians with structural organization of the habitat. *Caribbean Journal of Science*, **4**, 261–295.

Slowinski, J.B., Crother, B.I. & Fauth, J.E. (1987) Diel differences in leaf litter abundances of several species of reptiles and amphibians in an abandoned cacao grove in Costa Rica. *Revista de Biologia Tropical*, **35**, 349–350.

Whitaker, A.H. (1973) Lizard populations on islands with and without Polynesian Rats, *Rattus exulans* (Peale). *Proceedings of the New Zealand Ecological Society*, **20**, 121–130.

Whitford, W.G. & Creusere, F.M. (1977) Seasonal and yearly fluctuations in Chihuahuan desert lizard communities. *Herpetologica*, **33**, 54–65.

BIOSKETCH

The authors' focus is research and development of tools for containing and reversing the ecological, social and economic damage wrought by introduction to Guam of the brown treesnake, *Boiga irregularis*. The abundance of the snake is closely associated with abundance of the island lizards analysed in this paper.