

Island biogeography of Day Geckos (*Phelsuma*) in the Indian Ocean

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Summary. Step-wise multiple regression was employed to probe the determinants of species diversity of day geckos (*Phelsuma*) in the Indian Ocean. Independent variables were area, elevation, and two measures of isolation. Distance from Madagascar and island height (an indicator of habitat diversity) were the two most important predictors of species richness. Similar studies on other taxa rarely find isolation to be a major factor. The relatively poor dispersal abilities of reptiles may explain why isolation, rather than attributes of the islands, are more important in this case. The regressions also indicate that habitat diversity (assumed to correlate with maximum island elevation) is more important than area per se in determining species diversity. These results agree with predictions of the equilibrium theory of island biogeography, but historical processes have also greatly influenced species richness.

Islands have unique and depauperate faunas relative to mainland areas. Derivation of the species-area relationship by Preston (1962) and MacArthur and Wilson (1963, 1967), coupled with MacArthur and Wilson's equilibrium theory of island biogeography, led to renewed interest and investigation into the factors regulating diversity of a wide variety of taxa on islands surrounded by water or inhospitable habitat (for reviews, see Simberloff 1974; Connor and McCoy 1979; Gilbert 1980). Recently, a number of attempts have been made to apply equilibrium theory to the island biogeography of reptiles (e.g., Heatwole 1975; Case 1975, 1983; Kitchener et al. 1980a; Murphy 1983; Schoener and Schoener 1983a, b; Gardner 1984; Jones et al. 1985).

The distribution of the lizard genus *Phelsuma* (commonly known as day geckos) presents another opportunity to assess the applicability of the theory to the class Reptilia. Day geckos are widespread throughout the Indian Ocean (see Table 1 and Fig. 1), with more than 30 species currently recognized (Cheke 1981). Approximately half of the species occur on Madagascar, where the genus probably originated (Mertens 1962; Vinson and Vinson 1969). Brightly colored and diurnal, these lizards do not fit the customary gecko mold; instead, they fill otherwise unoccupied niches similar in many respects to those of West Indian *Anolis*. Focusing on the biogeography of a single genus differs from previous biogeographic work in two ways. First, important differences among disparate taxa in vagility and extinction rates are controlled. Second, by concentrating on a narrow tax-

onomic group distributed among islands that differ widely in degree of isolation, rather than on a broadly defined taxonomic group distributed among islands differing little in degree of isolation (as is often done, particularly with the avifauna of a given island group), the effect of isolation can more easily be discerned.

MacArthur and Wilson's theory of island biogeography was directed toward two observations: (1) the number of species on an island is positively associated with area (the species-area relationship), and (2) species richness is inversely related to degree of isolation (the distance effect). MacArthur and Wilson (1967), drawing on the work of Preston (1962) and Williams (1964), proposed two non-exclusive explanations to account for the widely observed species-area relationship: (1) the "area per se" hypothesis – greater population size on larger islands reduces the probability of extinction – and (2) the "habitat diversity" hypothesis – increased habitat heterogeneity accompanies larger island size and permits greater species diversity. A third explanation, the "increased immigration" hypothesis, consistent with the equilibrium theory, states that larger islands present a greater target for passively dispersing organisms, leading to a greater immigration rate (Whitehead and Jones 1969).

Experimental manipulations of island size among small mangrove patches in the Florida Keys have shown the effect of area independent of habitat diversity and immigration effects (Simberloff 1972, 1976; Rey 1981, 1984). Several studies have demonstrated higher immigration rate for larger areas (Osman 1978; Schoener and Schoener 1981; Toft and Schoener 1983).

A number of studies have employed step-wise multiple regression to distinguish the effect of area from that of habitat diversity with varied results. Area appears to be a better predictor of species number than habitat diversity in some cases (e.g., birds: Hamilton et al. 1964; Hamilton and Armstrong 1965; reptiles: Heatwole 1975; Case 1975, 1983; Jones et al. 1985; mammals: Kitchener et al. 1980b); some measure of habitat heterogeneity, however, has proven to be more important in other examples (e.g., birds: Power 1972; Harris 1973; Abbott 1974; Amerson 1975; Johnson 1975; reptiles: Case 1975; Kitchener et al. 1980a; mammals: Lawlor 1983; insects: Abbott 1974). A few studies have demonstrated that both area and habitat diversity significantly contribute to the explicative power of the regression (e.g., Vuilleumier 1970; Harris 1973; Amerson 1975). Interpreting these results is often difficult, however.

Table 1. Data for islands used in this study

Island	No. species	Area	Max. Elev.	D1	D2	Reference
<i>Seychelles</i>						
Praslin	2	40.40	367	1,111	3.6	1
Curieuse	2	2.83	172	1,127	0.8	1
Chauve Souris	2	0.006	10	1,115	0.2	1
Round (P)	1	0.20	75	1,119	0.4	1
Aride	1	0.39	135	1,119	6.9	1
Cousin	1	0.29	58	1,109	1.9	1
Cousine	1	0.25	77	1,107	4.1	1
La Digue	2	9.60	333	1,119	3.6	1
Felicité	2	2.68	231	1,125	2.6	1
Coco	2	0.008	10	1,127	0.6	1
Little Sister	2	0.34	106	1,127	4.6	1
Big Sister	2	0.85	113	1,129	4.9	1
Marianne	2	0.95	130	1,128	5.8	1
Frigate	2	2.20	122	1,107	19.1	1
Mahé	2	144.80	905	1,056	15.1	1
St. Anne	2	2.19	250	1,067	3.6	1
Cerf	2	1.26	108	1,065	2.0	1
Round (M)	1	0.01	30	1,067	3.4	1
Moyenne	2	0.09	61	1,067	4.0	1
Long	2	0.21	84	1,067	4.0	1
Cachée	2	0.02	10	1,065	2.1	1
Anonyme	2	0.10	37	1,064	0.4	1
Souris	1	0.004	10	1,063	0.2	1
Islette	2	0.04	30	1,058	0.2	1
Concepcion	2	0.66	132	1,055	1.3	1
Thérèse	2	0.72	160	1,056	0.8	1
Silhouette	2	16.00	621	1,064	15.1	1
North	1	2.01	198	1,072	5.6	1
<i>Comoros</i>						
Anjouan	3	424	1,595	405	70.7	2
Grand Comoro	3	1,148	2,360	500	43.1	2
Mayotte	5	371	660	310	70.7	2, 3
Moheli	2	290	790	429	43.1	2
<i>Mascarenes</i>						
Mauritius	4	1,865	828	921	182.3	4
Flat	1	2.0	95	954	11.7	5
Gabriel	1	0.5	21	956	11.7	5
Gunners' Quoin	1	0.7	163	950	3.8	5
Ile aux Aigrettes	1	0.3	11	965	0.6	5
Ile aux Bénitiers	2	1.2	5	925	1.2	5
Ile aux Cerfs	1	1.0	5	973	0.6	5
Ile d'Ambre	1	1.3	11	962	0.4	5
Ile de l'Est	1	0.3	5	973	0.3	5
Round (Maur)	2	1.5	317	968	19.8	4, 5
Reunion	2	2,512	3,069	722	182.3	4
Rodrigues	2	119	396	1,508	598.6	4
<i>Others</i>						
Andamans	1	5,525	732	5,400	4,412	6
Nossi Be	4	334	214	16	16.0	3, 6, 7
Pemba	1	984	95	1,270	49.4	6
Zanzibar	1	1,658	130	1,222	49.4	6

Notes: Height and area are in meters, distances in kilometers. D1 = distance to Madagascar; D2 = distance to nearest large (> 100 km²) island. Three Round Islands are included - one each near Praslin, Mahé, and Mauritius. One species on Round (P) is considered introduced (Gardner 1984) and is not included. References: 1. Gardner 1984; 2. Blanc 1972; 3. museum locality data; 4. Vinson and Vinson 1969; 5. Vinson 1976; 6. Loveridge 1942; 7. L. Hoeyers, pers. comm

because area and measures of habitat diversity are often strongly correlated (Simberloff 1976; Connor and Simberloff 1978). The confounding effect of correlated variables can be reduced by re-arranging the order in which variables are entered into the multiple regression. Variables that can explain part of the variation even after correlated variables have been considered are likely to be important determinants of species richness. Examination of the stability of the regression coefficients also can reveal confounding effects of correlated variables. In some cases, however, the lack of correlation between the measure of habitat diversity and area increases confidence that the effects of these two factors can be examined independently (e.g., Abbott 1974).

Most multiple regression studies have employed some measure(s) of isolation or distance from a potential colonizing source to assess its importance in determining species number. Hamilton and Rubinoff (1967) found that geographic isolation was the most important predictor of species number for Darwin's finches (by contrast, Harris [1973] found number of plant species to be the most important factor, with isolation of secondary importance). Jones et al. (1985) found that distance to woodland habitat was the only significant predictor of reptile species richness for four riparian habitat islands in the American southwest. Isolation plays a subsidiary, but significant, role for the avifauna of the northern Andes (Vuilleumier 1970), California islands (Power 1972), and islands in the Gulf of Guinea (Hamilton and Armstrong 1965), and lizards (Case 1975) and mammals (Lawlor 1983) on oceanic islands in the Gulf of California.

Summing the results of a number of univariate analyses rather than employing multivariate procedures, Schoener and Schoener (1983a, b) found that island area, habitat diversity, and degree of isolation all were important in predicting lizard species richness on several island groups in the Bahamas, but that area was the most important predictor. Adler and Wilson (1985) employed multiple logistic regression to separately assess the factors determining species occurrence for each of nine small mammal species on Massachusetts islands. Island area and isolation were the most important variables.

Methods

In a manner similar to the studies just discussed, this analysis investigates how area, habitat diversity, and degree of isolation, alone or in combination, can explain the variation of *Phelsuma* species number on Indian Ocean islands. The number of species of *Phelsuma* present or known to be recently extinct on 48 granitic or volcanic Indian Ocean islands was obtained from Gardner (1984) for the Seychelles and from a number of sources for the other islands (Table 1). Sandy cay and raised atoll low islands, most significantly the Farquhar, Agalega, Aldabra and Amirantes groups, were excluded because they have been submerged relatively recently (within the last 10,000 years for sandy cays and 125,000 years for raised atolls [Taylor et al. 1979]) and may not have reached equilibrium (Peake 1971; Gardner 1984). These islands have depauperate faunas (Peake 1971; Gardner 1984) and only Denis in the Seychelles proper has more than one *Phelsuma* species. Madagascar, more than two orders of magnitude larger than the next largest island, was excluded because it has been the site of much in situ speciation and is assumed to be the

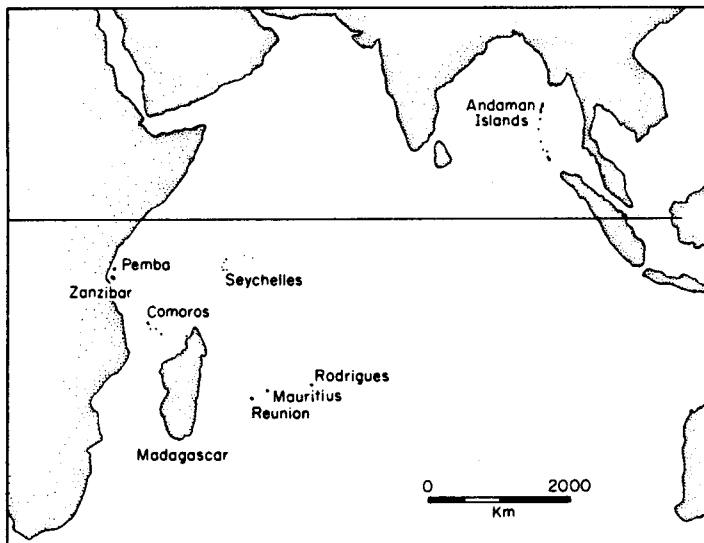


Fig. 1. The Indian Ocean. The Comoros are, from east to west, Mayotte, Anjouan, Moheli, and Grand Comore. Nossi Be lies off the northwest coast of Madagascar

major source pool for colonists. Islands without *Phelsuma* were also excluded because the range of *Phelsuma* spans the Indian Ocean; inclusion of all Indian Ocean islands would not be practical. Because most of these islands are remote from potential sources of colonization, their exclusion provides a bias against finding an effect of isolation. I obtained data on island areas and elevations from the literature and maps. Data on the islands near Mauritius, with the exception of Round Island, had to be estimated from topographic maps. Inter-island distances were obtained primarily from measurements taken from maps. The Andaman Islands were considered as one island. Combining these islands is justified because the separation between them is narrow and information is unavailable on them separately. Table 1 presents data for all islands included in this study.

I treated the number of species as the dependent variable for the step-wise multiple regressions. The independent variables were island area, maximum elevation (a rough indicator of insular habitat diversity [Hamilton et al. 1964; Vuilleumier 1970; Diamond and Mayr 1976]), and two estimates of distance from the two most likely potential colonizing pools, distance from Madagascar and distance from the nearest large (>100 km²) *Phelsuma*-bearing island. Without an established phylogeny for the genus, it is not possible in most cases to determine from where species colonized. Nonetheless, colonization has certainly been inter-island; there is no fossil record of *Phelsuma* on mainland Africa and the one species found there now, *P. dubia*, has probably colonized from Madagascar or the Comoros, where it is also found (whether the southwest African gecko *Rhoptropella ocellata* belongs in *Phelsuma*, as suggested by Russell [1977], is irrelevant here).

Step-wise multiple regression begins by regressing the independent variable against the dependent variable with which it is most highly correlated. At each subsequent step, the variable which produces the highest F-value is added to the regression. Variables can also be added to the regression out-of-order to investigate the effect of correlations between the independent variables. I performed three regressions for each data set using the data untransformed, independent variables log transformed, and all variables log transformed.

Results

The regression using semi-transformed data best accounted for the variation. Distance to Madagascar was the first variable selected by the stepwise procedure, explaining 33.6% of the variation ($F_{1,46} = 23.31$, $P \leq 0.01$). Island height added next, boosting the variation explained to 47.8% ($F_{2,45} = 12.21$, $P \leq 0.01$). Area was added before distance to nearest island, but neither provided a significant contribution. Forcing area as the second variable after distance to Madagascar also produced a significant regression accounting for 41.1% of the variation ($F_{2,45} = 5.72$, $P < 0.01$). Adding height then as the third variable also significantly accounted for a portion of the regression, increasing the explanatory power to 47.8% ($F_{3,44} = 5.66$, $P < 0.01$).

The regression employing untransformed data explained almost as much of the variation. In this regression, island height was the first variable selected, accounting for 13.6% of the variation ($F_{1,46} = 7.25$, $P < 0.01$). Distance to Madagascar added next, increasing the explanatory power to 24.4% ($F_{2,45} = 6.40$, $P < 0.01$). Distance to the nearest island added next, bringing the portion of variation explained to 46.0% ($F_{3,44} = 17.62$, $P \leq 0.01$). Area added last to the regression and did not significantly increase the explanatory power of the regression. If area is forced into the regression as the first variable, less than 1% of the variation is accounted for and the regression is not significant ($F_{1,46} = 0.07$). However, if area is forced into the regression as the third variable, before distance to the nearest island, it does have a significant effect ($F_{3,44} = 3.68$, $P < 0.05$). When distance to the nearest island is subsequently added to the regression, it still significantly increases the explanatory power ($F_{4,43} = 12.63$, $P \leq 0.01$).

The results of the regression employing transformed data were qualitatively identical to those in the semi-transformed regression, but less of the variation was explained. In order to examine the possibility that the preponderance of small islands in the Seychelles and Mascarenes biases the results, regressions were also conducted excluding data from the Seychelles and including only Reunion, Mauritius, Round, and Rodrigues from the Mascarenes. Distance to Madagascar and island height, in that order, were again the only significant variables. The Andamans, grouped as

one island, is an outlier both in size and isolation. Excluding them before performing the regressions does not qualitatively alter the results either.

Discussion

Studies conducted on a wide range of organisms (see the introduction) indicate that physical attributes of islands (e.g., area and height) are of primary importance in determining species richness. Analysis of these data, however, reveals that distance from a source of potential colonizers is the most important element affecting *Phelsuma* distribution in the Indian Ocean. These results come as no surprise given the relatively poor overwater dispersal abilities of non-marine reptiles (Williams 1969; Case 1975; Murphy 1983). More vagile organisms (e.g., some bird, insect, and plant species) can colonize islands with greater ease; for these groups, attributes of the islands, such as the number of habitats and competitors present, should be of greater importance in determining the numbers of species present (Diamond 1969; Lawlor 1983; see Fig. 2a and b). By contrast, the probability of colonization will be of greater importance in determining species richness for relatively poor dispersers such as reptiles.

The ability of lizard species to persist on all but the smallest islands also helps explain the importance of distance in determining species numbers. Small poikilothermic organisms such as lizards, with low energy demands and small space requirements, are often able to maintain high population densities (Schoener and Schoener 1983b). Large populations can be found even on very small islands, which decreases the likelihood of extinction due to stochastic events or inbreeding (Schoener and Schoener 1983a, b, c; Gardner 1984). Lessened competition or predation from homeotherms unable to persist on such small islands may enhance this effect (Wright 1979, 1981; Waide and Reagan 1983). Both species in the Seychelles occur on some islands considerably less than 1 km² in area. At least one species (either *P. astriata* or *P. sundbergi*) is able to persist on several extremely small islands (see Table 1).

If the extinction curve is not greatly affected by island area, then differences in the position of the immigration curve – resulting, for example, from differences in distance from the species source pool – would be of greatest importance in determining the number of species at equilibrium (Fig. 2c). Furthermore, to the extent that lizard populations on all but the smallest islands are buffered against extinction, any observed effect due to increase in area is likely to be the result of increased habitat diversity or immigration rate, rather than a lowering of the probability of extinction. This is not to say that species will never disappear from larger islands, however; environmental changes or colonization by new predators or competitors can also lead to extinction.

Assuming that island elevation serves as at least a rough indicator of habitat diversity (Peake 1971; Mühlenberg et al. 1977; Nussbaum 1984), the data from the regressions supports the contention that habitat diversity, not area per se or increased immigration, is more responsible for the species-area relationship. In all three regressions, height added before area; when area was forced before height in the regression, height still explained significant portions of the remaining variation.

Species number on the low-lying coralline and sandy

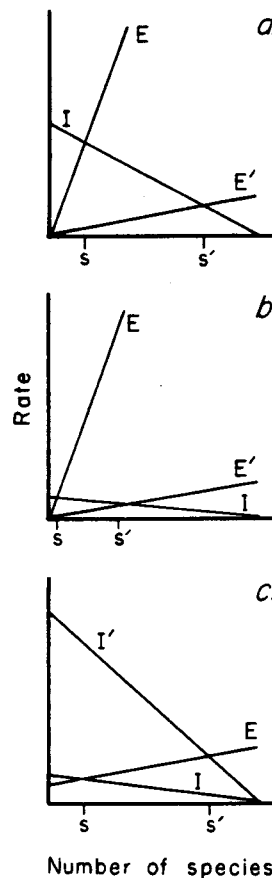


Fig. 2a-c. A simplified representation of the importance of dispersal ability. The top two graphs illustrate the effect of dispersal ability in determining the equilibrium species number (S). In a the immigration curve (I) is high, as it would be for a relatively good disperser. Variation in S is determined to a large extent by attributes of the island, which are expressed in the slope of the extinction curves (E and E'). In b, by contrast, the same change in S as a result of the lower immigration curve leads to a much smaller change in S as a result of the lower immigration curve, which reflects a poorer dispersal capability. However, this effect disappears and even reverses as S approaches its maximum value, equal to the total number of species in the colonizer pool. In c, a relatively flat extinction curve allows differences in the immigration curve to greatly change S .

islands of the Agalega, Aldabra, and Farquhar groups also lends support to this argument. Although surveyed *Phelsuma*-bearing islands in these groups range in area from 0.53 to 160 km², none has a maximum elevation greater than 28 m, or displays much habitat diversity (Stoddart 1967; Fosberg 1971), and all have but one species (not the same species on each island, even within island groups). Of course, equilibrium may not have been attained in these recently submerged islands, yet it is striking that no island has more than one species. Gardner (1984) found that on the smallest and lowest islands in the granitic Seychelles, species' occurrences are clearly dependent on the presence of appropriate habitat (i.e., trees). Heatwole (1975) and Kitchener and How (1982) similarly conclude that the depauperate reptilian faunas of sandy cays near New Guinea and coral islands near Australia, respectively, are due to habitat homogeneity on these islands.

Although the regressions provide significant results, they leave unaccounted more than half of the variation. By contrast, many similar studies have been able to explain more than 90% of the variation (e.g., Abbott 1974; Amerson 1975; Hamilton and Armstrong 1965; Hamilton et al. 1964; Harris 1973; Vuilleumier 1970). The relative imprecision of several of the indices used in this study may partially be responsible. For example, maximum elevation only approximates the habitat diversity of an island and assumes that the relationship is constant between island groups. Using linear distance to Madagascar as a measure of distance from the colonizing source pool assumes that all species emanate from there and ignores the effects of ocean current direction and seasonality (Taylor et al. 1979; Cheke 1984).

Also, biogeographic studies must consider the recent disruption of naturally evolved communities due to the activities of man (Lynch and Johnson 1974; Olson and James 1982; Steadman et al. 1984). Many species have vanished from Indian Ocean islands in the past 1500 years (Arnold 1980; Dewar 1984; Durrell 1977) including at least three *Phelsuma* (Vinson and Vinson 1969). Arnold (1980) suggests that this may be the cause of the depauperate reptilian fauna of Reunion.

Because most of the islands considered here have few diurnal arboreal lizards other than *Phelsuma* (Vinson and Vinson 1969; Blanc 1972; Gardner 1984), intergeneric competition is not likely to be a major factor in determining *Phelsuma* richness. However, on the large one-species islands of the Andamans, Pemba, and Zanzibar, *Phelsuma* may compete with various agamids and gekkonids. These islands then may harbor fewer *Phelsuma* than would be expected on the basis of their height and isolation.

Recent geological history of these islands is also probably reflected in present species distributions (Gardner 1984). As recently as the last glacial period (15,000 years ago), the lowered sea-level exposed the entire Seychelles bank, forming an island of approximately 43,000 km² in area (Taylor et al. 1979). The Comoros were also united in one land mass, and Mauritius and Rodrigues were much larger. If the lowered sea-levels persisted long enough for more species to accumulate on the larger and more habitat-rich landmasses, and if the relaxation time (Diamond 1972) of *Phelsuma* is greater than the time since the islands became distinct or decreased in size, then the species richness of the islands may be greater than the equilibrium number (i.e., the islands may be supersaturated). Thus, Reunion's depauperate reptilian fauna (relative to other large Mascarene islands) may be readily interpretable; Reunion has no shallow bank and did not increase in size during the last glacial period (Vinson and Vinson 1969). The presence of two species on some of the smaller and lower Seychelles may also be understandable in this light.

Despite the unexplained variation, the results indicate that both isolation and habitat diversity play a role in determining *Phelsuma* species richness, a finding which is in accord with predictions of the equilibrium theory of island biogeography. The large residual of unexplained variation suggests that historical factors have been an important factor determining species richness as well. To determine the dynamics and relative importance of equilibrium and historical processes will require long-term field research.

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