



Competition and community structure in diurnal arboreal geckos (genus *Phelsuma*) in the Indian Ocean

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In this study, we investigate community structure in day geckos (genus *Phelsuma*) in the Indian Ocean. Much of what we know about communities of diurnal arboreal lizards comes from studies of Caribbean *Anolis*. *Phelsuma* in the Indian Ocean are ecologically similar to *Anolis* but not closely related. Using field observations and an experiment, we test three hypotheses for *Phelsuma* communities, all derived from work on *Anolis*: (1) *Phelsuma* species richness will be correlated with the diversity of available perches, (2) sympatric species will partition their habitat use, shifting their habitat use depending on which other species of *Phelsuma* are present, and (3) experimentally removing individuals of one species will lead to changes in the microhabitat use and/or abundance of sympatric congeners. We find support for all three hypotheses. We also describe some unique aspects of *Phelsuma* communities, such as partitioning of palm vs. non-palm trees. This study identifies some potentially general features of diurnal arboreal lizard communities, and suggests that some aspects of community assembly might be repeatable.

Ecologists would like to generalize from detailed studies of particular species assemblages; this is possible only to the extent that the processes influencing community evolution and assembly are repeatable (Schluter 2000). Competition among species within a guild is one of the main forces driving community structure (Tilman 1982, Connell 1983, Schoener 1983, Schluter 2000, Tilman 2004), with well-known ecological and evolutionary results, such as character displacement (Brown and Wilson 1956), habitat shifts (Schoener 1968), or competitive exclusion (Gause 1934). However, debate still exists over the extent to which these processes will result in repeatable patterns in communities (Cadle and Greene 1993, Schluter and Ricklefs 1993, Vitt and Pianka 2005). Some researchers have emphasized the role of historical differences among species and regions in determining the structure of present-day communities (Cadle and Greene 1993, Price et al. 2000, Vitt and Pianka 2005). Other studies have found repeated patterns of community structure among independently evolved taxa (Rüber and Adams 2001, Melville et al. 2006). This distinction is likely scale-dependent

(Schluter 2000); closely related taxa form communities where different species fill similar ecological roles (e.g. benthic and limnetic lineages of stickleback fish, Schluter 1996), while more distantly related taxa tend to show unique patterns of community structure and evolution (e.g. squamate families, Vitt and Pianka 2005).

One way to address the repeatability of community structure is to compare communities of distantly related organisms living in similar habitats (Samuels and Drake 1997, Price et al. 2000, Ben-Moshe et al. 2001, Melville et al. 2006). If ecological factors are strong enough to overcome any historical contingencies among clades or regions, these communities will show similar patterns of community structure. Previous researchers have approached this problem by comparing the morphological attributes and habitat use of species in potentially replicated radiations (Price et al. 2000, Ben-Moshe et al. 2001, Melville et al. 2006). However, this approach fails to address important aspects of these communities, such as species richness and the type, intensity, and results of species interactions.

Here, we test for the repeatability of community structure in assemblages of diurnal arboreal lizards, using observations and experiments to directly compare patterns of habitat use in natural communities. Although an extensive history of field observations and experiments documents the patterns and processes occurring in arboreal lizard assemblages (Williams 1972, Schoener 1974, Huey et al. 1983, Williams 1983, Losos 1994, Vitt and Pianka 1994), the majority of studies focus on one group, *Anolis* lizards in the Caribbean. In communities of these lizards, interspecific interactions result in habitat partitioning, such that different species of *Anolis* that occur in the same place use different habitat types. Although the particular niche axes partitioned can vary among islands, sympatric species tend to use perches of differing heights and/or diameters (reviewed by Losos 1994). Several experiments strongly implicate competition as the mechanism determining *Anolis* community structure (Pacala and Roughgarden 1982, Leal et al. 1998). For this study, we investigate communities of day geckos in the genus *Phelsuma* in the Indian Ocean region. *Phelsuma* are unusual (but not unique) among gekkonids in being diurnal and arboreal. They are territorial sit-and-wait predators that occupy a niche similar to that occupied by other diurnal arboreal lizards such as *Anolis* lizards in the Caribbean (Losos 1986). Thus, one might expect that *Phelsuma* geckos would have communities structured similarly to *Anolis* lizards (Pianka and Vitt 2003).

Alternatively, if species tend to be ecologically similar to their close evolutionary relatives through phylogenetic niche conservatism (Webb et al. 2002), then *Phelsuma* communities might be expected to resemble those of their nocturnal gekkonid ancestors (Thorpe and Crawford 1979). Nocturnal gecko communities differ substantially from those of other lizards (Vitt and Pianka 2005). For example, compared to other lizards, geckos have well-developed nasal olfaction (Schwenk 1993); the associated increased chemosensory discrimination may lead to distinct dietary preferences with little overlap among sympatric species in some cases (Pianka and Pianka 1976, Pianka and Huey 1978, Huey 1979, Thorpe and Crawford 1979, Schwenk 1993, but see Petren and Case 1996). Additionally, most geckos are nocturnal and consequently have lower active field temperatures, more efficient locomotion (Autumn et al. 1999), a higher frequency of empty stomachs (Huey et al. 2001), and more intense competition for retreat sites (Downes and Shine 1998, Kearney and Predavec 2000, Brown et al. 2002, Shah et al. 2004) than diurnal lizards.

In this study, we investigated the hypothesis that community structure in *Phelsuma* will be similar to structure in other diurnal arboreal lizard communities. We tested three hypotheses:

1) We predict that *Phelsuma* species richness will be correlated with the diversity of available perches.

In the Bahamas, Schoener and Schoener (1983) found that lizard species diversity was related to the diversity of available perches of varying heights and diameters; this study included several species of *Anolis*. We tested for a correlation between habitat diversity and species richness for five species of *Phelsuma* in communities of varying composition throughout Mauritius.

2) We predict that sympatric species of *Phelsuma* will partition their habitat use, with species shifting their habitat preferences in response to congeners.

Anolis species show both habitat partitioning and shifts in perch height and diameter in response to congeners (Schoener 1975). We compared habitat use of *Phelsuma* in communities of varying composition, and tested for microhabitat partitioning and habitat shifts among these communities.

3) We predict that experimentally removing individuals of one species (*Phelsuma ornata*) will lead to changes in the microhabitat use and/or abundance of sympatric *Phelsuma cepedianana*.

In *Anolis*, experimental removal of competitors significantly effects abundance (Leal et al. 1998) and habitat use (Pacala and Roughgarden 1982). We conducted a field removal experiment to test this hypothesis in *Phelsuma*.

Methods

Community observations

We collected habitat use data for *Phelsuma* species in communities of varying composition throughout Mauritius. Mauritius has five extant endemic species of *Phelsuma*: *P. ornata*, *P. cepedianana*, *P. guimbeaui*, *P. rosagularis* and *P. guentheri*. Additionally, the Madagascan giant day gecko *P. madagascarensis* has been introduced into a small area in eastern Mauritius. Mauritius is a relatively young volcanic island; since Mauritian *Phelsuma* are a monophyletic group, they likely are all descended from a single dispersal event from Madagascar (Austin et al. 2004). We collected data at 12 sites throughout Mauritius that varied in the particular species of *Phelsuma* that were present. These represented seven distinct *Phelsuma* communities, five of which were replicated at distinct geographical locations (Fig. 1). One community combination (*P. ornata*, *P. cepedianana* and *P. guimbeaui*) is replicated but also includes introduced *P. madagascarensis* in one of the two localities. These introduced geckos were rare at the beginning of the field study (June 2002) but

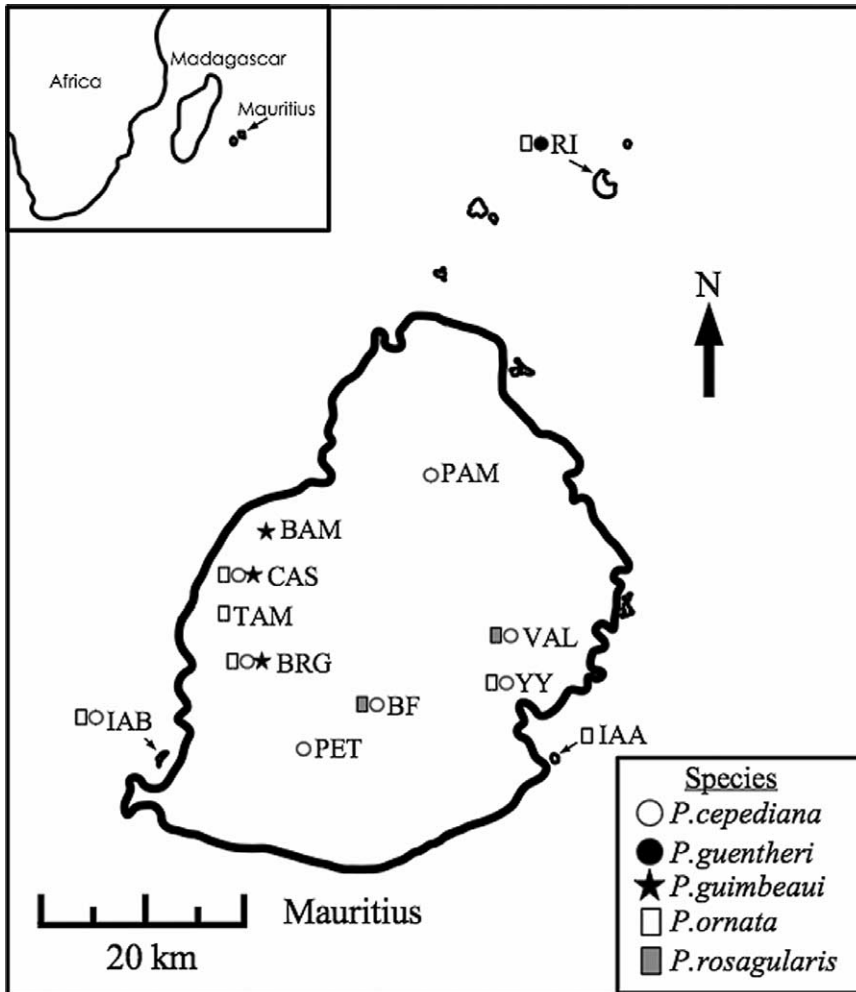


Fig. 1. Map of localities in Mauritius where we carried out community habitat observations, along with the native species of *Phelsuma* present at each locality. Locality abbreviations as follows: BAM = Bambous, BF = Brise Fer, BRG = Black River Gorges National Park (lowlands), CAS = Casela Bird Park, IAA = Ile aux Aigrettes, IAB = Ile aux Benitiers, PAM = Pamplemousses Botanical Gardens, PET = Le Petren, RI = Round Island, TAM = Tamarin mountain, VAL = Valée de l'Est, YY = Ylang Ylang Estate.

more common at the end (Sept. 2004; L. J. Harmon unpubl.). Most sites were in lowland areas, but two sites (Le Petren and Brise Fer) were at higher elevations (~500 m).

Phelsuma are by far the most abundant diurnal arboreal lizard seen in these communities, although introduced agamid lizards *Calotes versicolor*, which are mainly ground-dwellers, are also present at all localities except one (Round Island). Introduced nocturnal house geckos *Hemidactylus frenatus* were also encountered at some locations, although these lizards were only rarely seen during the day. Thus, we focus on only the *Phelsuma* species present at each locality in this study (Fig. 1).

We collected data on habitat availability at each locality for three habitat variables: tree type (palm or nonpalm), perch height, and perch diameter. To do this, we set up four 25 × 5 m transects at each locality. Transects were placed haphazardly in representative forest habitat. We categorized all trees within each transect as “palm” or “nonpalm” (trees with a diameter at breast height of <3 cm excluded). There are three non-palm plants in Mauritius that have palm-like features (i.e. smooth fronds with narrow, water-containing crevices); these plants (*Ravenala*, *Pandanus* and *Lomatophyllum*) were included in the “palm” category for the purposes of this study. This category was included because many *Phelsuma* species are

commonly found on palm trees and may be palm specialists, preferentially using the crevices in the palms for water, shelter, and egg-laying sites (Lehtinen 2002). We then used a random number generator to identify 25 random points within each transect. At each point, a pole was extended straight up in the habitat. At heights of 1, 3, 5 and 7 m the number and diameter of all branches intersecting a 1 m diameter sphere were visually estimated. Perch diameters were classified into one of four categories (0–5 cm, 5–10 cm, 10–20 cm and > 20 cm).

We calculated the Shannon-Weaver information statistic, H' (Levins 1968), a measure of habitat diversity, for the available habitats at each locality. We calculated both horizontal (perch heights and diameters) and vertical (proportion of trees of different types, palm vs nonpalm) habitat diversity. Since the height and diameters of available perches were related, we combined them into a single variable (4 height categories \times 4 diameter categories = 16 combined categories). We then tested for a positive relationship between each type of habitat diversity and the number of *Phelsuma* species found at each locality using linear regression, with p -value calculated for a one-tailed test.

At each locality, we walked through suitable habitat searching for adult geckos. To avoid pseudoreplication, each area in a particular site was only searched for lizards once, over the course of one or two days, by a single investigator (LJH). Habitat use data were only collected when the weather was sunny or partly cloudy (i.e. the sun was out at least 50% of the time). When an adult lizard was located, we collected the following habitat data: perch height (measured or estimated to the nearest 0.5 m, then classified into one of four categories: 0–2 m, 2–4 m, 4–6 m and >6 m), perch diameter (classified into one of four categories: 0–5 cm, 5–10 cm, 10–20 cm and >20 cm), percent canopy cover (visual estimate to the nearest 5%), thermal microhabitat (sun, shade, mix), the part of the vegetation on which the lizard was perched (trunk, side branch, palm frond, leaf, fruit, or rock/ground), substrate texture (categorized “rough” = significant visible texture present, otherwise “smooth”, all categorizations made by LJH), and, if the lizard was on a plant, whether it was a palm or a non-palm species. We attempted to observe at least 20 lizards of each species at each locality (see Appendix 1 Table A2 for sample sizes). For all tests, each of these aspects of habitat use was considered separately. To facilitate interpretations of these results, we tested for correlations among pairs of these categories using chi-squared tests, and interpret our results in light of these correlations.

We tested for habitat partitioning and habitat shifts using log-linear models (Heisey 1985, Manly et al. 1993). We first tested for habitat partitioning within each locality separately. Habitat availability was as-

sumed to be the same for all species. For each species occurring at a given locality, we calculated the selectivity (Manly 1974) for each resource category. Then, for each habitat variable, we created three nested log-linear models for these data, representing three hypotheses about resource use: H_0 , all species are using resources in proportion to their availability; H_1 , habitat-specific selectivities exist that are constant among species; and H_{full} , habitat-specific selectivities exist and are species-dependent. We evaluated differences among nested models using a likelihood-ratio test. For variables where habitat availabilities were not measured, we tested H_1 against H_{full} under the assumption that habitat availabilities, though unknown, are equal for all species in the community (Manly et al. 1993).

We also developed a log-linear version of Schoener's (1975) test for shifts in habitat use in response to potential competitors. This test incorporates the presence of potential competitor species occurring in sympatry with the species of interest. For this analysis, we constructed models for each species independently, including only those variables for which we had availability data. For each species occurring sympatrically with the species of interest, we created a dummy variable which was equal to “1” if the species occurred at that locality, and “0” otherwise. We then created nested log-linear models for these data, representing the following hypotheses about resource use for these lizards: H_0 and H_1 , as above; H_2 – H_n , selectivities depend on the presence or absence of competitor species; and H_{full} , as above. For hypotheses H_2 – H_n , potential competitor species were entered into the model one at a time; at each step, the species resulting in the most improved model fit (i.e. the greatest reduction in residual sums of squares) was retained. In some cases, the presence of two or more competitor species were confounded; for example, *Phelsuma guimbeaui* occurs alone and in combination with both *P. ornata* and *P. cepediana*, but never with just one of these two species. In such cases, confounded competitors were combined into a single dummy variable. We excluded recently introduced *Phelsuma madagascarensis* from these calculations. We again evaluated differences among nested models using a likelihood-ratio test.

Species removal experiment

We carried out an experiment to investigate the effect of the removal of *Phelsuma ornata* on *P. cepediana*. The experiment took place in low-elevation (<100 m) forest on Lion Mountain, Mauritius, where *P. ornata* and *P. cepediana* are the only common diurnal arboreal lizards. Habitat in these mountains is mainly dry tropical forest containing a mix of exotic and native plant species. We set up six square 10 \times 10 m

plots, three treatment and three control plots. We separated each plot from all others by at least 50 m, and made an effort to ensure consistency of habitat among plots within an experiment. Plots were open, and lizards could freely move into and out of the plot boundaries.

We set up plots during the week of 9–15 Sept. 2004. We then randomly assigned three plots to the treatment group, and the other three to the control. We also paired these plots into blocks, with each block including a single treatment and a single control group; in all cases, when counts were made, the two plots in each block were surveyed within 30 min. From 15 to 20 Sept. 2004, we removed as many *Phelsuma ornata* from the treatment plots as possible by noosing. Although we could not remove juvenile lizards from the plots in this manner, the treatment had an immediate and lasting negative effect on the abundance of adult *P. ornata* in the treatment plots (L. J. Harmon unpubl.). Captured lizards were released into a forest >1 km from the original capture sites. Over the course of the next month, we carried out four sets of counts in all of the plots (set 1: 26 Sept. 2004; set 2: 1 Oct.; set 3: 6 Oct., set 4: 12 Oct.). After each day's counts were concluded, we attempted to remove any additional *P. ornata* seen in the treatment plots; however, the vast majority of lizards that were removed (93%) were caught during the initial catching phase.

We surveyed lizard relative abundance and habitat use patterns in each plot using timed counts from four survey points in each plot, one in each corner. We counted lizards for three minutes at each survey point, using a tape recorder to record the following data on all adult lizards spotted: species, perch height (to the nearest 0.5 m), perch diameter (to the nearest cm), the part of the vegetation on which the lizard was perched (trunk, side branch, palm frond, leaf), thermal microhabitat (sun, shade, or a mix of both; this was not collected under overcast conditions), and tree type (palm or non-palm). Surveys were conducted three times for each plot, all in the same day whenever possible, for each of five survey periods. Surveys were not conducted when the sun was obscured by clouds more than 50% of the time. The first survey period took place before the experimental treatment was applied and provides a baseline for abundance and habitat use data for lizards in these plots; the four remaining survey periods took place after the treatment had been applied to the experimental plots.

We compared data on the abundance and habitat use of *Phelsuma cepediana* between treatment and control plots. For each plot, we calculated the average number of lizards seen, their average log-transformed perch height + 1 and perch diameter, and the proportion of sightings on various parts of the vegetation, as well as the proportion of sightings on “palm”-type

trees. We root-arcsin transformed and averaged all data for the three counts carried out in each set to avoid pseudoreplication. We used the average preliminary counts for each plot as a covariate, and analyzed the data using repeated measures ANCOVA with the following effects: treatment, preliminary count, time \times treatment and time \times preliminary count. Increased abundance in the treatment plots compared to the control plots could be associated with higher levels of intraspecific competition among *P. cepediana*. This could lead to differences in habitat use among treatment and control plots that are not directly due to the removal of *P. ornata*. To investigate this possibility, we used ANCOVA and linear regression to test for the effect of abundance on any habitat use variables that differed between experimental and control plots. Statistical analyses were carried out in R statistical software (Anonymous 2007) and SYSTAT 10.2

Results

Habitat diversity and species richness

A significant relationship existed between the height and diameter of available perches ($\chi^2 = 296.1$, $p < 0.001$), with lower perches tending to have wider diameters; these two variables were thus combined into a single measure of vertical habitat diversity. The number of *Phelsuma* species present at each locality was significantly positively correlated with the vertical habitat diversity of available perches ($r = 0.59$, one-tailed $p = 0.028$; Fig. 2), but not with the horizontal habitat diversity of available trees ($r = 0.1$, one-tailed $p = 0.40$).

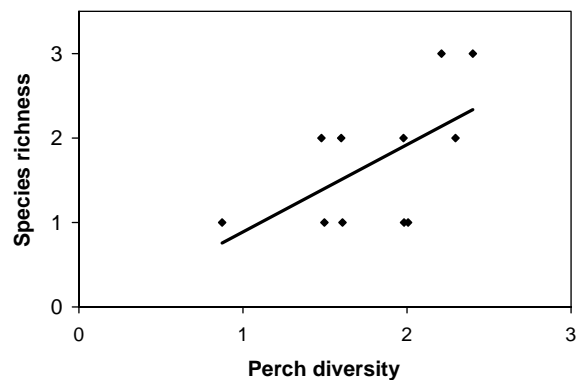


Fig. 2. Relationship between vertical vegetation diversity (calculated on perch height \times perch diameter categories, Shannon's diversity index) and species richness.

Habitat partitioning and shifts

There were significant relationships between all measured aspects of perches used by all geckos in this study (all chi-squared uncorrected $p < 0.01$, Appendix 1 Table A1). Perches on palm trees tended to be higher and narrower than perches on nonpalm trees, and higher perches tended to be narrower than low perches. Selectivities for all combinations of species, locality, and habitat variable are presented in Appendix 1 Table A2. In almost all cases, *Phelsuma* species' habitat use differs significantly from availability (indicated when models other than H_0 were selected in Table 1; see Appendix 1 Table A3 for detailed model selection results). In multi-species communities, each species tends to prefer perches within a certain range of heights: *P. ornata* close to the ground, *P. cepediana* at medium heights, and *P. guimbeaui* and *P. rosagularis* higher in the canopy. *Phelsuma* generally prefer broader perches over narrow twigs. Species also differ in their tree selection; some species (*P. ornata*, *P. cepediana*) tend to prefer palm trees, while others (*P. guimbeaui*, *P. rosagularis*) almost always occur on non-palm trees. *Phelsuma* occurring in sympatry tend to have significant differences in their habitat use (indicated when model H_{full} was selected in Table 1). Within each community, habitat partitioning often involves more than one habitat use variable. The most frequently partitioned axis was tree type (Table 1; significant in five of six communities), while perch height, perch diameter, and vegetation location each differed among species in four of six communities (Table 1). Other habitat use variables differed among sympatric species less often, although each was significantly different in at least one community (Table 1).

Table 1. Results of log-linear model selection for structural habitat partitioning. For each habitat use measurement in each community, we list the model selected using hierarchical likelihood ratio tests. Models: H_0 = species use habitat types in proportion to their availability, H_1 : species have preferences, but all species prefer the same habitat types, H_{full} : different species prefer distinct habitat types. For the last five variables, availabilities of different habitat categories were not measured, and H_0 cannot be distinguished from H_1 . Species abbreviations as follows: O = *Phelsuma ornata*, C = *P. cepediana*, G = *P. guimbeaui*, R = *P. rosagularis*, M = *P. madagascarensis* (introduced).

Community	Species present	Variable		Palm	Thermal	Texture	Vegetation type	Vegetation location	% canopy
		PH	PD						
IAA	O	H_1	H_1	H_1	–	–	–	–	–
TAM	O	H_1	H_1	H_0	–	–	–	–	–
PAM	C	H_1	H_1	H_0	–	–	–	–	–
PET	C	H_0	H_1	H_1	–	–	–	–	–
BAM	G	H_1	H_1	H_0	–	–	–	–	–
IAB	O+C	H_{full}	H_{full}	H_{full}	H_0	H_0	H_0	H_{full}	H_{full}
YY	O+C	H_1	H_{full}	H_{full}	H_{full}	H_0	H_0	H_{full}	H_{full}
BF	C+R	H_1	H_1	H_0	H_0	H_{full}	H_0	H_0	H_0
VAL	C+R	H_{full}	H_{full}	H_{full}	H_0	H_{full}	H_0	H_0	H_0
BRG	O+C+G	H_{full}	H_1	H_{full}	H_0	H_0	H_{full}	H_{full}	H_0
CAS	O+C+G(+M)	H_{full}	H_{full}	H_{full}	H_0	H_{full}	H_{full}	H_{full}	H_0

Significant habitat shifts related to the presence of sympatric congeners were seen in all three species that occur in communities of differing composition, *Phelsuma ornata*, *P. cepediana*, and *P. guimbeaui* (indicated when species-interaction models were selected in Table 2). *Phelsuma ornata* increased their use of palms in the presence of *P. guimbeaui*, a species that was never found on palm trees, and decreased their use of palms in the presence of *P. cepediana*, a species that tends to prefer palms. *Phelsuma ornata* also shifter onto narrower perches in the presence of *P. cepediana* and *P. guimbeaui*, both of which tend to occupy broader perches. Use of non-palm trees by *P. cepediana* was negatively affected by both *P. ornata* and *P. rosagularis*; the species occurs almost exclusively on palm trees in the presence of either of these mainly non-palm dwelling species. *P. cepediana* also showed shifts to higher perches in the presence of *P. ornata*, a low-perching species. *P. cepediana* also tended to select higher perches in the presence of *P. rosagularis*, also a high-perching species; this could potentially reflect the high-altitude habitat where these two species are found together. *Phelsuma cepediana* shifted onto narrower perches in the presence of both *P. guimbeaui*, a species with a strong preference for very wide perches, and *P. ornata*. Finally, *P. guimbeaui* shifted to higher perches when other day gecko species are present, generally becoming the highest-perching species in those habitats.

Removal experiment

Only perch height differed significantly among the six plots for the preliminary observations (ANOVA: abundance $F_{5, 12} = 2.51$, $p = 0.09$; perch height $F_{5, 11} =$

Table 2. Results of log-linear model selection for habitat shifts. Models correspond to the following: null: all lizards are using habitat types in proportion to their availability, selective: species prefer certain habitat types, and these preferences are constant across localities, species: species prefer certain habitat types, and these preferences depend on the selectivity of one particular species or list of species, full: species prefer certain habitat types, and these preferences differ among all localities. For goodness of fit tests, we report the G^2 statistic, the degrees of freedom for the model, and the delta statistic with associated p-value from a likelihood ratio test comparing each model to the next-simplest nested model. Asterisk denotes model selected by forward selection procedure using likelihood ratio tests.

Species	Variable	Model	Goodness of fit test			p
			G^2	DF	Δ	
<i>ornata</i>	ph	null	160.9	18		
		selective*	25.7	15	135.2	0.00
		+G	22.8	12	2.9	0.40
		+C	22.2	12	3.5	0.32
		+GC	19.4	9	2.8	0.43
		full	0.0	0	19.4	0.02
<i>ornata</i>	pd	null	589.0	18		
		selective	75.9	15	513.1	0.00
		+G	49.6	12	26.3	0.00
		+C	48.7	12	27.2	0.00
		+GC	18.8	9	29.9	0.00
		full*	0.0	0	18.8	0.03
<i>ornata</i>	palm	null	202.2	6		
		selective	60.0	5	142.2	0.00
		+G	53.6	4	6.4	0.01
		+C	59.2	4	0.8	0.37
		+GC	48.1	3	5.6	0.02
		full*	0.0	0	48.1	0.00
<i>cepediana</i>	ph	null	84.2	24		
		selective	69.0	21	15.3	0.00
		+O	61.2	18	7.7	0.05
		+G	62.9	18	6.0	0.11
		+R	40.6	18	28.3	0.00
		+OR*	24.8	15	15.8	0.00
		+GR	34.2	15	6.4	0.09
		+OGR	23.4	12	1.5	0.69
		full	0.0	0	23.4	0.02
		<i>cepediana</i>	pd	null	472.1	24
selective	133.9			21	338.2	0.00
+O	115.4			18	18.5	0.00
+G	85.8			18	48.1	0.00
+R	128.0			18	6.0	0.11
+OG*	47.5			15	38.3	0.00
+GR	83.7			15	2.1	0.55
+OGR	43.0			12	4.6	0.21
full	0.0			0	43.0	0.00
<i>cepediana</i>	palm			null	238.1	8
		selective	73.1	7	165.0	0.00
		+O	66.2	6	6.9	0.01
		+G	69.5	6	3.6	0.06
		+R	54.8	6	18.4	0.00
		+OR*	24.6	5	30.1	0.00
		+GR	43.2	5	11.6	0.00
		+OGR	24.5	4	0.1	0.73
		full	0.0	0	24.5	0.00
		<i>guimbeui</i>	ph	null	85.2	9
selective	35.6			6	49.5	0.00
+OC	8.5			3	27.1	0.00
full*	0.0			0	8.5	0.04
<i>guimbeui</i>	pd	null	187.0	9		
		selective*	0.6	6	186.4	0.00
		+OC	0.3	3	0.3	0.96
		full	0.0	0	0.3	0.95

Table 2 (Continued)

Species	Variable	Model	Goodness of fit test			p
			G ²	DF	Δ	
<i>guimbeau</i>	palm	null	9.8	3		
		selective*	0.0	2	9.8	0.00
		+OC	0.0	1	0.0	1.00
		full	0.0	0	0.0	1.00

3.51, $p = 0.03$; all other variables $p > 0.1$, results not presented). We found no significant differences in abundance or microhabitat use between the control and experimental plots at the start of the experiment (t -test on means from three censuses, abundance $t_4 = -1.67$, $p = 0.2$; perch height $t_4 = 1.1$, $p = 0.3$; perch diameter $t_4 = 0.6$, $p = 0.6$). When pooling all preliminary observations within treatment and control plots, we found no differences in the proportion of time lizards spent in the sun ($\chi^2 = 1.72$, $p = 0.5$), in the proportion of time using palm trees (Fisher's exact test $p = 0.4$), or in the part of the plant occupied by lizards ($\chi^2 = 3.09$, $p = 0.23$).

After the experimental removals of *P. ornata*, experimental plots had significantly higher abundance of adult *P. cepediana* than control plots (Table 3, Fig. 3). Furthermore, these lizards were perching significantly lower in the experimental than the control plots after the low-perching *P. ornata* was removed (Table 3, Fig. 3), while perch diameters did not differ between plots (Table 3). No categorical variables (percentage of time in sun, on fronds, and on palm trees) differed between treatment and control plots (Table 3). There were no significant interaction terms in any of the above repeated-measures ANCOVAs (Table 3). Abundance and perch height were not correlated within treatments (ANCOVA on perch height, treatment effect $p < 0.001$, abundance $p = 0.5$, treatment \times abundance $p = 0.9$; interaction term omitted: treatment effect $p < 0.001$, abundance $p = 0.8$) or among plots in the experimental treatment ($r = 0.09$, $p = 0.8$).

Discussion

In this paper, we report three main results regarding the community ecology of *Phelsuma* species in Mauritius. First, the number of species in a particular habitat is positively correlated with the vertical diversity of available perches in that habitat. Second, this interaction among species results in microhabitat partitioning and habitat shifts among sympatric species in natural communities. Finally, experiments reveal that sympatric species interact, affecting both their abundance and microhabitat use. All of the main results of this paper confirm predictions made based on diurnal *Anolis* lizard communities in the Caribbean. This suggests that these two independently evolved communities of diurnal lizards share key similarities, with species interactions resulting in shared patterns of niche partitioning in the two groups.

Habitat complexity and species richness

Phelsuma species richness in Mauritius is positively correlated with an index of the diversity of available perches in a habitat. A relationship between habitat and species richness or diversity has been found for a wide range of taxa, although the particular aspect of the habitat that is correlated with species diversity varies (reviewed by Rosenzweig 1995). This is likely due to differences in the particular aspects of the habitat being exploited by different guilds (Holmes et al. 1979). Our result, that species richness is related to the complexity

Table 3. F-statistics from repeated-measures ANCOVA analysis of *Phelsuma cepediana* on removal of *P. ornata*. Means of each variable from preliminary counts in each plot before the experimental treatment were used as covariates. † DF of interaction effects reduced from 3 to 2 for perch height, perch diameter, percent sun, percent frond, and percent palm due to missing data; * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

	DF†	Abundance	Perch height	Perch diameter	% sun	% frond	% palm
Treatment	1	11.7*	109.2**	0.9	1.7	0.1	1.0
Preliminary data	1	2.0	309.7**	0.0	5.65**	2.0	0.2
Time \times Treatment	3	0.7	0.8	0.0	0.7	1.3	0.2
Time \times Preliminary	3	1.2	0.4	0.1	1.0	2.4	0.6

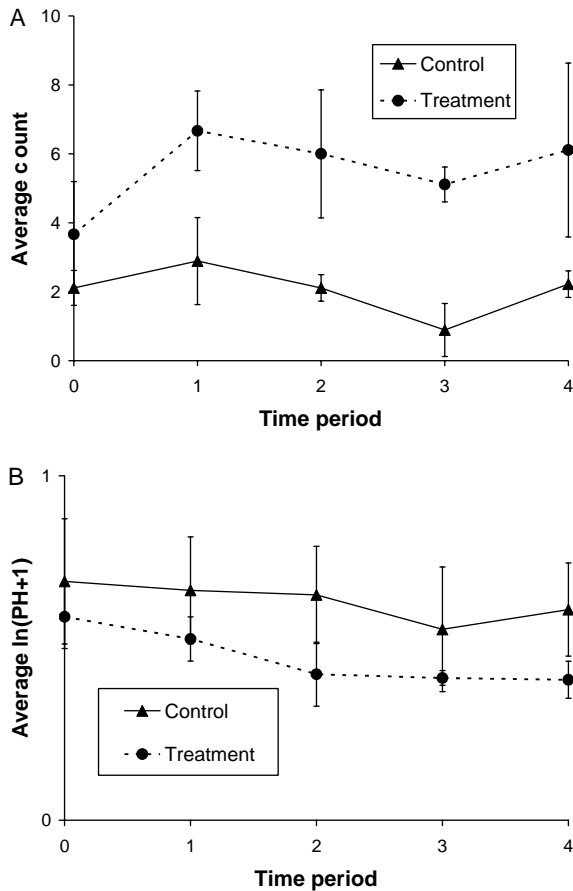


Fig. 3. (A) Abundance and (B) perch heights of *Phelsuma cepediana* during the removal experiment. Average of three counts for each of the six plots before the treatment was applied (time period 0) and after (time periods 1–4). Error bars represent ± 1 SD.

of tree branches in a particular habitat, has also been found in diurnal lizard communities in the Bahamas (Schoener and Schoener 1983), although the islands surveyed by Schoener and Schoener (1983) are much smaller and likely have less habitat diversity than Mauritius. The same pattern has also been recorded for diurnal arboreal bird communities (MacArthur and MacArthur 1961, Holmes et al. 1979).

These results suggest that perches of differing height and diameter play an important role in community structure of *Phelsuma*, such that a greater diversity of such perches provides more available niche space that can be partitioned by sympatric species (MacArthur and MacArthur 1961). However, this correlation is not perfect, and other aspects of the habitat uncorrelated with the diversity of available perches may play a role in determining gecko species richness (Holmes et al. 1979). For example, geographic differences in elevation,

a broad index of horizontal habitat diversity, have also been shown to influence species richness of *Phelsuma* on islands in the Indian Ocean (Losos 1986) and lizards in the Bahamas (Schoener and Schoener 1983).

Microhabitat partitioning in communities

Sympatric species of *Phelsuma* in Mauritius often differ among several different resource axes at the same time. Such habitat partitioning is common in ecological communities, and may result from a number of factors. These include, but are not limited to, interspecific competition, intraguild predation (Wissinger 1992), the effects of shared predators (Abrams and Matsuda 1996), and other indirect effects (Billick and Case 1994, Stanton 2003). Of course, intercorrelations among habitat use categories make it difficult to form definite conclusions about the particular axes of habitat that are actually being partitioned in this system.

We found evidence for significant shifts in habitat use in response to potential competitors in three species, where the presence of competitors was associated with shifts in their relative use of perches and palm vs nonpalm trees. In most cases, sympatric species shifted habitat such that they were using perches that were less similar than expected based on habitat use in allopatry. Similar shifts in perch microhabitats in response to competitors have also been observed in *Anolis* (Schoener 1975). These shifts are predicted to occur whenever different species are specialized to use different structural habitats (Rosenzweig 1991).

Two *Phelsuma* species (*P. ornata* and *P. cepediana*) shifted their preferences for palm trees, with *P. cepediana* using palm trees more frequently when the non-palm using *P. rosagularis* is present, and *P. ornata* and *P. cepediana* shifting habitat use patterns in opposite directions in sympatry with each other. Similar partitioning of tree types involving two types of palms occurs in *Phelsuma* communities in the Seychelles (Thorpe and Crawford 1979, Gardner 1984), and some Madagascan *Phelsuma* species have been referred to as specialists for living on *Pandanus* (Lehtinen 2002). Although habitat partitioning by tree type has been suggested for nocturnal gecko communities (Pianka and Pianka 1976, Pianka and Huey 1978, Huey 1979), we are not aware of any examples of a habitat shift involving tree type in *Anolis* or any other diurnal lizard community.

A possible explanation for this distinct pattern could be that these geckos, like their nocturnal ancestors, compete for refuge sites. Several studies have demonstrated that geckos prefer certain refuge sites due to their suitability for diurnal thermoregulation (Autumn and Denardo 1995, Downes and Shine 1998, Kearney and Predavec 2000, Rock et al. 2002) and that

sympatric species can compete for these refuges (Brown et al. 2002). *Phelsuma* species also use refuge sites, but their choice of sites is not likely to be based on thermoregulation; these lizards seem to be actively thermoregulating during the day using patches of sun (L. J. Harmon unpubl.). Instead, *Phelsuma* may choose refuge sites based on protection from predators, egg laying, or other factors. One intriguing possibility is that habitat use differences among day gecko species are a by-product of specialization to feeding on certain types of nectar, pollen, tree sap, and other non-arthropod resources. A number of species of *Phelsuma*, including the Mascarene species studied here, feed on nectar, pollen, and other plant products (Hansen et al. 2002, 2006). Any differences among species in these behaviors would be reflected in patterns of habitat partitioning.

In addition to ecological differences in habitat use, sympatric species of day gecko in Mauritius also tend to differ in morphology and body size. Body size may be related to prey size in *Phelsuma* (Gardner 1984), and body shape differences might reflect tradeoffs associated with distinct types of structural habitat, as in anoles. Future work in this system is needed to investigate the relationship between body form and ecological habitat use.

Interspecific interactions and community structure

Although the above results are suggestive of species interactions, such observational studies do not reveal much about mechanism. Results from the removal experiments provide strong evidence for interspecific interactions in the field between two of these species, *Phelsuma ornata* and *P. cepediana*. Removal of *P. ornata* results in an immediate and lasting increase in the abundance of *P. cepediana*. There are three possible explanations for this increase in abundance over such a short time scale: lizards could be moving into the plots from outside, those lizards already in the plots could be becoming more active, or lizards could be shifting into parts of the habitat where they were more visible to us. Since we did not mark individual lizards, we cannot distinguish between the first two alternatives. We consider the last alternative to be unlikely, since lizards higher in the canopy were often found on the fronds of palm trees, where they were readily spotted, whereas lizards perched lower on the trunks of these palms were generally more cryptic.

A second result of the experimental treatment was that *Phelsuma cepediana* in the experimental plots shifted their habitat use to include lower perches. These perches would normally be occupied by *P. ornata*, a species with a strong preference for perches near the

ground (selectivity for 0–2 m perches ranged from 0.51 to 0.8 for this species; Appendix 1). Because total lizard density was not controlled in this experiment, it is possible that only one of these two observed changes is the direct result of removal of *P. ornata*; the niche shift could have been caused by an increase in abundance of *P. cepediana* after removal of the second species, leading to higher levels of intraspecific competition and forcing some individuals onto otherwise less desirable perches (Fretwell and Lucas 1970). However, the lack of a significant abundance effect on habitat use within treatments argues against this explanation.

Since both species are known to feed on similar food sources, including small insects and nectar, these lizards may be exploitatively competing for food, water, or other resources in the local habitat. However, two factors suggest that interference competition may be a more likely cause for the results of this experiment. First, shifts in abundance were seen on the first observation after the initial removal, and did not increase over the course of the experiment (Fig. 3). Exploitative competition seems unlikely to generate such immediate results, since it would likely take a substantial amount of time for resource levels to respond to the removal of one species from the plots. Second, we frequently observed antagonistic behavior between both conspecific and heterospecific males (L. J. Harmon unpubl.). These lizards are highly territorial (Murphy and Myers 1996, Ikeuchi et al. 2005), and may be defending particular parts of palm trees that provide food, access to mates, or shelter from predators (Evans and Evans 1980, Gardner 1984, Radtkey 1996). One alternative, noncompetitive explanation for these results, the shared predator hypothesis (Holt and Lawton 1994), seems unlikely. Given the small size of the plots, and lack of boundaries, it seems very unlikely that removing *Phelsuma ornata* from the plots could affect the abundance of birds, the main predators of these lizards (Nicoll et al. 2003).

One drawback of the experimental removal is that we only considered the effects of removal of one species (*Phelsuma ornata*) on another (*P. cepediana*); the reciprocal experiment was not carried out, and no other species were subject to field experiments. However, observational results above suggest that there are similar patterns of interaction among all sympatric species in Mauritius. Alternatively, the strength of competition might depend on the extent to which species differ (Connell 1980). For example, Pacala and Roughgarden (1982) found significant experimental effects on perch height and growth rate only with ecologically similar species. The concordance of our observational and experimental results suggests that the short-term behavioral effects seen in this experiment translate into longer-term consequences for day gecko populations. It

is likely that competition among species has led to the patterns in community structure described above.

Conclusions

This study shows that *Phelsuma* species are competing in Mauritian forests, with the main axes involving perch height, perch diameter, and tree type (palm vs nonpalm). Furthermore, these geckos show responses to competition that are similar to those seen among communities of *Anolis*, such that the two groups represent similar communities on island systems halfway around the world. Perhaps this diurnal, arboreal adaptive zone, filled by *Anolis* in the Caribbean and geckos in the Indian Ocean, leads to similar responses in independently evolving clades (Harmon et al. 2005). Further studies of community-wide convergence are needed to assess just how analogous these arboreal communities are. In particular, detailed studies of other diurnal arboreal geckos (e.g. *Lygodactylus*, Simbotwe 1983, *Pristurus*, Arnold 1993, sphaerodactylines, Kluge 1995, *Gonatodes*, Vitt et al. 2000) would be especially valuable in testing the generality of these results.

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Appendix 1.

Table A1. Chi-squared association test between habitat use variables. Significance based on 9999 random permutations of the data, with all p-values are Bonferroni-corrected; * = $p < 0.05$, ** = $p < 0.01$.

	PH	PD	% canopy	Thermal microhabitat	Vegetation location	Texture
PD	23.1					
% canopy	24.9	12.5				
Thermal microhabitat	9.4	4.6	32.6**			
Vegetation location	172.7**	171.**	65.1	35.7		
Texture	10.2	61.6**	7.5	7.5	197.3**	
Palm	107.3**	13.6	15.4	5.9	399.8**	13.6**

Table A2. Selectivities for habitat use variables among species and localities, along with sample sizes for habitat measurements of perches used (N_u) and available (N_a) to lizards. For some variables, the availability of perch types was not quantified; in these cases, we present the proportion of use for each habitat category. These equal selectivities if all perch categories are equally available. Locality abbreviations as follows: BAM = Bambous, BF = Brise Fer, BRG = Black River Gorges National Park (lowlands), CAS = Casela Bird Park, IAA = Ile aux Aigrettes, IAB = Ile aux Benetiers, PAM = Pamplémousses Botanical Gardens, PET = Le Petrin, RI = Round Island, TAM = Tamarin mountain, VAL = Valée de l'Est, YY = Ylang Ylang Estate.

Locality	Species	N_a	N_u	Perch height		4–6	6+	Perch diameter			30	Tree type	
				0–2	2–4			5	10	20		nonpalm	palm
BAM	<i>guimbeui</i>	302	66	0.04	0.31	0.50	0.15	0.01	0.18	0.47	0.34	1.00	0.00
BF	<i>cepediana</i>	505	26	0.09	0.21	0.47	0.23	0.01	0.08	0.14	0.76	1.00	0.00
BF	<i>rosagularis</i>	505	30	0.00	0.08	0.42	0.50	0.01	0.08	0.22	0.69	1.00	0.00
BRG	<i>cepediana</i>	348	19	0.11	0.33	0.29	0.28	0.04	0.18	0.22	0.56	0.00	1.00
BRG	<i>guimbeui</i>	348	26	0.04	0.09	0.14	0.73	0.01	0.13	0.41	0.44	1.00	0.00
BRG	<i>ornata</i>	348	26	0.81	0.08	0.08	0.03	0.01	0.05	0.67	0.27	0.00	1.00
CAS	<i>cepediana</i>	342	40	0.16	0.59	0.14	0.11	0.12	0.34	0.43	0.11	0.06	0.94
CAS	<i>guimbeui</i>	342	34	0.00	0.35	0.20	0.45	0.01	0.18	0.43	0.37	1.00	0.00
CAS	<i>madagascarensis</i>	342	11	0.13	0.58	0.19	0.10	0.09	0.27	0.30	0.35	0.30	0.70
CAS	<i>ornata</i>	342	33	0.41	0.33	0.22	0.04	0.03	0.20	0.36	0.41	0.22	0.78
IAA	<i>ornata</i>	439	53	0.50	0.50	0.00	0.00	0.00	0.01	0.80	0.19	0.04	0.96
IAB	<i>cepediana</i>	832	23	0.09	0.32	0.36	0.22	0.00	0.13	0.16	0.71	0.00	1.00
IAB	<i>ornata</i>	832	54	0.68	0.22	0.10	0.01	0.00	0.03	0.08	0.88	0.01	0.99
PAM	<i>cepediana</i>	797	25	0.60	0.15	0.05	0.19	0.00	0.23	0.23	0.54	0.57	0.43
PET	<i>cepediana</i>	146	27	0.40	0.60	0.00	0.00	0.04	0.05	0.39	0.52	0.06	0.94
RI	<i>guentheri</i>	–	26	0.81	0.12	0.08	0.00	0.00	0.27	0.65	0.08	0.00	1.00
RI	<i>ornata</i>	–	50	0.82	0.18	0.00	0.00	0.28	0.46	0.12	0.14	0.00	1.00
TAM	<i>ornata</i>	224	35	0.67	0.19	0.10	0.04	0.01	0.03	0.16	0.80	0.48	0.52
VAL	<i>cepediana</i>	599	22	0.00	0.24	0.72	0.04	0.00	0.11	0.09	0.80	0.00	1.00
VAL	<i>rosagularis</i>	599	2	0.00	1.00	0.00	0.00	0.00	0.00	1.00	0.00	1.00	0.00
YY	<i>cepediana</i>	758	25	0.32	0.48	0.20	0.00	0.00	0.14	0.02	0.84	0.04	0.96
YY	<i>ornata</i>	758	25	0.54	0.35	0.11	0.00	0.00	0.11	0.09	0.79	0.41	0.59

Table A2. (continued).

Locality	Species	N	Thermal environment			Texture		Vegetation location							Canopy					
			dapple	shade	sun	rough	smooth	burlap	frond	fruit	leaf	rock	side_branch	stem	trunk	0–20	20–40	40–60	60–80	80–100
BAM	<i>guimbeui</i>	66	0.14	0.12	0.74	0.12	0.88	0.00	0.00	0.00	0.00	0.00	0.82	0.00	0.18	0.10	0.13	0.60	0.17	0.00
BF	<i>cepediana</i>	26	0.15	0.04	0.81	0.58	0.42	0.00	0.00	0.00	0.00	0.00	0.23	0.00	0.77	0.12	0.19	0.35	0.35	0.00
BF	<i>rosagularis</i>	30	0.17	0.03	0.80	0.83	0.17	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.50	0.37	0.23	0.17	0.23	0.00
BRG	<i>cepediana</i>	19	0.05	0.21	0.74	0.11	0.89	0.00	0.21	0.00	0.37	0.00	0.11	0.00	0.32	0.05	0.53	0.32	0.11	0.00
BRG	<i>guimbeui</i>	26	0.08	0.04	0.88	0.19	0.81	0.00	0.00	0.00	0.00	0.00	0.69	0.00	0.31	0.15	0.23	0.42	0.19	0.00
BRG	<i>ornata</i>	26	0.12	0.04	0.85	0.04	0.96	0.00	0.00	0.00	0.77	0.00	0.04	0.00	0.19	0.27	0.50	0.15	0.08	0.00
CAS	<i>cepediana</i>	40	0.17	0.11	0.71	0.05	0.95	0.00	0.58	0.03	0.13	0.00	0.13	0.00	0.15	0.24	0.68	0.04	0.04	0.00
CAS	<i>guimbeui</i>	34	0.18	0.00	0.82	0.41	0.59	0.00	0.00	0.00	0.00	0.00	0.85	0.00	0.15	0.33	0.53	0.13	0.00	0.00
CAS	<i>madagascarensis</i>	11	0.13	0.25	0.63	0.18	0.82	0.00	0.09	0.00	0.18	0.00	0.36	0.00	0.36	0.00	0.40	0.20	0.40	0.00
CAS	<i>ornata</i>	33	0.20	0.04	0.76	0.21	0.79	0.00	0.39	0.00	0.03	0.09	0.24	0.06	0.18	0.48	0.40	0.08	0.04	0.00
IAA	<i>ornata</i>	53	0.25	0.18	0.58	0.09	0.91	0.00	0.00	0.00	0.73	0.04	0.08	0.04	0.12	0.42	0.19	0.13	0.21	0.06
IAB	<i>cepediana</i>	23	0.24	0.00	0.76	0.30	0.70	0.04	0.39	0.30	0.00	0.00	0.00	0.00	0.26	0.04	0.57	0.13	0.26	0.00
IAB	<i>ornata</i>	54	0.28	0.09	0.63	0.46	0.54	0.04	0.23	0.08	0.17	0.00	0.00	0.00	0.49	0.22	0.35	0.31	0.11	0.00
PAM	<i>cepediana</i>	25	0.17	0.04	0.79	0.16	0.84	0.00	0.28	0.04	0.08	0.00	0.20	0.00	0.40	0.32	0.48	0.20	0.00	0.00
PET	<i>cepediana</i>	27	0.00	0.00	1.00	0.33	0.67	0.00	0.37	0.00	0.00	0.04	0.56	0.00	0.04	0.48	0.41	0.07	0.04	0.00
RI	<i>guentheri</i>	26	0.23	0.15	0.62	0.88	0.12	0.00	0.12	0.00	0.04	0.00	0.42	0.00	0.42	0.04	0.35	0.46	0.12	0.04
RI	<i>ornata</i>	50	0.31	0.04	0.65	0.16	0.84	0.00	0.32	0.02	0.50	0.00	0.10	0.00	0.06	0.20	0.22	0.40	0.18	0.00
TAM	<i>ornata</i>	35	0.11	0.00	0.89	0.37	0.63	0.00	0.00	0.00	0.08	0.00	0.58	0.00	0.35	0.26	0.23	0.40	0.09	0.03
VAL	<i>cepediana</i>	22	0.00	0.00	1.00	0.09	0.91	0.00	0.55	0.05	0.00	0.00	0.14	0.00	0.27	0.59	0.27	0.14	0.00	0.00
VAL	<i>rosagularis</i>	2	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.50	0.00	0.50	0.50	0.50	0.00	0.00	0.00
YY	<i>cepediana</i>	25	0.08	0.00	0.92	0.24	0.76	0.04	0.44	0.32	0.00	0.00	0.12	0.00	0.08	0.40	0.56	0.04	0.00	0.00
YY	<i>ornata</i>	25	0.12	0.16	0.72	0.40	0.60	0.04	0.12	0.04	0.04	0.04	0.64	0.00	0.08	0.16	0.48	0.32	0.00	0.04

Table A3. Detailed results of log-linear goodness of fit tests for differences in resource selectivity in communities. Hypotheses tested: H_0 : all lizards are using resources in proportion to their availability, H_1 : Habitat-specific selectivities exist that are constant among species, H_2 : habitat-specific selectivities exist and are species-dependent. For communities with only one species, only H_0 vs H_1 could be tested, and for variables where availabilities were not measured, only H_1 vs H_2 could be tested. Numbers presented are G^2 values for comparison of stated model with the respective simpler model. Asterisks indicate support for the more complex model from a likelihood-ratio test: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. Locality abbreviations as in Table A2.

Community	PH		PD		Palm		Thermal habitat	Texture	Vegetation type	Vegetation location	Canopy
	H1	H2	H1	H2	H1	H2	H2	H2	H2	H2	H2
BAM	30.7***		99.5***		0.0						
BF	20.0***	8.1	78.5***	2.1	0.0	0.3	0.0	4.5*	0.0	4.4	6.3
BRG	9.0*	57.9***	106.1***	13.2	91.2***	44.8***	5.0	3.3	43.2***	61.6***	11.8
CAS	15.4**	66.8***	55.2***	38.0***	6.0*	80.8***	8.9	15.4**	34.0***	82.6***	15.5
IAA	13.1**		102.5***		54.7***						
IAB	40.6***	39.2***	285.8***	19.7***	44.7***	13.6**	3.6	1.7	5.3	15.4*	10.1*
PAM	16.6***		98.9***		0.4						
PET	0.4		13.8**		14.9***						
TAM	27.1***		83.6***		1.7						
VAL	31.0***	24.9***	62.6***	26.5***	73.3***	22.8***	0.0	8.2**	0.0	3.5	0.8
YY	17.6***	1.9	201.8***	12.3*	15.7***	19.0***	6.4*	1.5	1.4	23.6**	10.4*