

Ecology and co-existence of two endemic day gecko (*Phelsuma*) species in Seychelles native palm forest

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Keywords

body size; herpetofauna; Indian Ocean; niche separation; Simpson's diversity index; specialist/generalist dichotomy.

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Abstract

In island ecosystems, reptiles play diverse ecological roles as a result of niche broadening, which increases potential niche overlap between species. Ecological niche partitioning is a means of reducing direct competition between coexisting species and differences in habitat use among island gecko species have been suggested as a by-product of specialization to feeding on certain resources. Here, we examine modes and drivers of niche partitioning of two endemic species of *Phelsuma* gecko (*Phelsuma sundbergi* and *Phelsuma astriata*) in relict native palm forest in the Seychelles to further understanding of congeneric reptile co-existence in native habitats. *Phelsuma* abundance, microhabitat use and habitat composition were quantified in different macrohabitat types. *P. sundbergi* showed a clear preference for habitat dominated by the coco de mer palm, *Lodoicea maldivica* and a strong association with male individuals of this dioecious species. *P. astriata* density increased significantly with arboreal biodiversity but did not display a relationship with a specific tree type. High levels of resource segregation were determined along the microhabitat axis, based on differential tree preference. Our results suggest that *P. sundbergi* and *P. astriata* may have evolved to co-exist in this habitat type through partitioning of microhabitat as members of a divergent specialist/generalist assemblage determined by consumption of *L. maldivica* pollen by *P. sundbergi*. Our findings concur with the hypothesis that differences in habitat use among island reptiles are a by-product of trophic specialization and support the conservation of native habitat for maintenance of reptile diversity.

Introduction

The contribution of islands and insular communities to global biodiversity is disproportionately high (Myers *et al.*, 2000; Whittaker & Fernández-Palacios, 2006) with geographically isolated systems providing optimal conditions for speciation of biota and, consequently, high levels of endemism. Reptiles are one group that benefited greatly from the mechanisms prevalent in insular settings. Endemic reptile species richness (Kier *et al.*, 2009) and density (e.g. Rodda & Dean-Bradley, 2002) tend to be higher on islands than mainland areas. Lizards, in particular, represent a highly abundant and diverse group of island reptiles (e.g. Williams, 1972; Whittaker & Fernández-Palacios, 2006), many having undergone niche broadening and conducting vital ecosystem functions on islands (e.g. pollination, seed dispersal; Whittaker, 1987; Olesen & Valido, 2003; Hansen & Müller, 2009; Kaiser-Bunbury, Memmott & Müller, 2009), which are commonly fulfilled by mammals, birds and insects in mainland systems (Proctor, Yeo & Lack, 1996; Levey, Silva & Galetti, 2002).

Niche broadening can lead to an increased habitat and trophic niche overlap, commonly resulting in mechanisms, that limit direct competition. In Mauritius, for example, niche broadening has resulted in selective habitat partitioning among *Phelsuma* day geckos depending on coexisting species (Harmon, 2005); Harmon, Harmon & Jones (2007) later raised the 'intriguing possibility' that differences in habitat use among *Phelsuma* species may be a by-product of specialization to feeding on certain resources, a suggestion that has not yet been investigated. In this study, we therefore aim to determine the driver(s) of habitat partitioning in two co-existing *Phelsuma* species in their native habitat in the Seychelles.

The herpetofauna of the Seychelles islands in the Indian Ocean is archetypal of evolution under isolated, oceanic conditions. The Seychelles is part of a global biodiversity hotspot with current reptile endemism of *c.* 40% (UNEP-WCMC, 2004). Evolutionary divergence of geckos across the archipelago has been affected by alternating periods of isolation and connection due to sea level rise and fall (Losos, 1986), which has resulted in varying body size

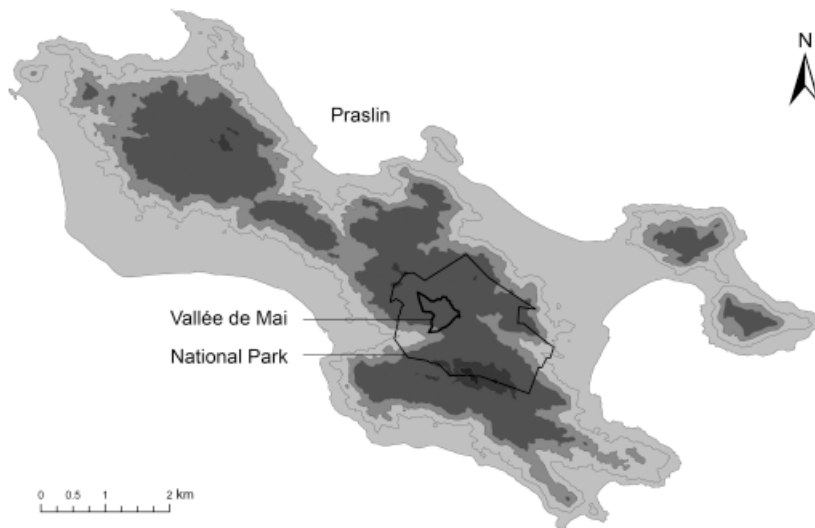


Figure 1 The island of Praslin, Seychelles, with the Praslin National Park (black line) and the Vallée de Mai (bold black line) shown. Different shades of grey indicate 100 m contours.

differentiation between two species of *Phelsuma* day gecko on islands where they co-occur (Radtkey, 1996). Body size difference between these endemic species *Phelsuma sundbergi* Rendahl, and *Phelsuma astriata* Törnier, is most marked on the island of Praslin, where they co-exist in remnant patches of native palm forest habitat. Both *P. sundbergi* and *P. astriata* are relatively abundant within the palm forest but there is a lack of information pertaining to their ecology in this native habitat as previous studies have concentrated mainly on secondary forest and plantation habitats (Thorpe & Crawford, 1979; Gardner, 1984). Genetic studies suggest that *P. sundbergi* and *P. astriata* initially evolved allopatrically from a single monophyletic lineage via adaptive radiation followed by secondary contact of sister species (Radtkey, 1996; Rocha *et al.*, 2009). Interspecific competition theory postulates that co-existence of phylogenetically similar species will result in resource use separation along one or more main axes of the multidimensional niche: spatial, temporal and dietary (Pianka, 1973) or exclusion of one species occurs either through habitat shift or extinction (Schoener, 1968).

In this study, we investigate the hypothesis that two sympatrically occurring *Phelsuma* species co-exist via niche partitioning in native palm forest habitat. We also aim to deepen our understanding of reptile diversity and conservation in this fragile endemic ecosystem. Specifically, we: (1) estimate relative densities of each species within different habitat types of the palm forest; (2) determine macro- and micro-habitat requirements and preferences for each species; (3) investigate the process by which these congeners achieve co-existence through niche partitioning of the spatial and temporal axes.

Materials and methods

Study site

The island of Praslin (4°19'S, 55°44'E; 0–367 m a.s.l.; 38 km²), is the second largest granitic island of the Seychelles

archipelago. Much of the island is now covered by degraded secondary vegetation (Procter, 1984), or dominated by alien invasive species. The last tract of native palm forest on the island is protected by a National Park (Fig. 1; Procter, 1973), in the centre of which lies the Vallée de Mai (VdM; 110–210 m a.s.l.; 19.5 ha) reserve. The VdM is a site of international conservation significance, having been inscribed as a UNESCO World Heritage site in 1983, and has been managed by the Seychelles Islands Foundation (SIF) since 1989. The area is composed of low–intermediate elevation palm forest. It is the only site to hold all six of the Seychelles' endemic palm species, including the largest population of the endemic dioecious coco de mer palm, *Lodoicea maldivica* Gmelin. The VdM is the most extensive example of intact native palm forest (Fleischmann *et al.*, 2005) and hosts a unique, and for its size, remarkably diverse fauna, including, most notably, numerous endemic reptiles.

Temperature range within the VdM is 27–31 °C and mean daily rainfall across the data collection period was 2 mm (± 5.1 SD), with a total rainfall of 130 mm (SIF, unpubl. data).

Fieldwork was undertaken over a 3-month period (April–June 2009), during the drier season.

Study species

Phelsuma sundbergi is the larger [total length = ~20 cm, snout–vent length (SVL) = 8–9 cm; Crawford & Thorpe, 1981] and less abundant of the two *Phelsuma* species on Praslin. The subspecies *Phelsuma sundbergi sundbergi* is found across the Praslin group of islands and the total population size is currently estimated at 3663 ± 264 (Gerlach, 2008). *Phelsuma astriata* is smaller (total length = ~11 cm, SVL = 5 cm; Crawford & Thorpe, 1981) and the subspecies found in the Praslin group of islands *Phelsuma astriata semicarinata* has an estimated population of $26\,816 \pm 3862$ (Gerlach, 2008). Throughout the text, we refer

to the subspecies found on Praslin by the species name. On Praslin, the two species are readily distinguished by differences in body shape (*P. astriata* is noticeably more slender) and colour pattern (*P. sundbergi* has a finer 'sprinkling' of red dots while *P. astriata* has a more defined red line extending down the dorsal surface with larger red markings and a clear red 'chevron' between the eyes, plus 1–2 distinct red lines at back of the neck; see also Crawford & Thorpe, 1981).

Macrohabitat quantification

To ensure an even coverage of the VdM and all constituent habitat types, seven horizontal transects were placed at 50-m intervals, spanning the width of the reserve and running east–west. A total of seventy-five 10 × 10 m quadrats were placed 40 m apart along the length of each transect (*c.* 3.8% total area of VdM). Each quadrat was surveyed to quantify macrohabitat and vegetation variables, and GPS readings were recorded (Garmin eTrex, Garmin Ltd, Olathe, KS, USA). Variables were selected to account for the effects of vegetation composition, potential food sources and environmental factors on the distribution of arboreal reptiles.

All individual woody plants (>1 m total height) within each quadrat were identified with the VdM plant checklist and all adult palms (with distinct trunk) and juvenile *L. maldivica* palms without a trunk were recorded. Diameter at breast height (dbh; in cm) was measured and trunk height visually estimated (metres) by one of two surveyors following regular standardization exercises using a clinometer. The height of the tallest branch was recorded as a measure of dicotyledon canopy height. 'Juvenile' dicotyledons (dbh < 3 cm) and juvenile palms other than *L. maldivica* were excluded as *Phelsuma* geckos were not seen on these plants during the study.

Lodoicea maldivica was classified differently due to its disparate morphology at various developmental stages and because *P. sundbergi* are frequently observed upon male trees. We distinguished between 'adult' *L. maldivica* palms (males and females) and 'immature' trees, which are structurally similar to adults (with trunk) but lack reproductive organs. This distinction enabled us to infer the importance of palm structure versus food reward (i.e. nectar and pollen). Trunk height and dbh for adult and immature *L. maldivica* were recorded as in other palms. 'Juveniles' have no trunk but consist of robust vertical petioles up to 10 m in length, and hence were measured in the same way as other juvenile palms. 'Seedlings' (up to three leaves) were also recorded.

Mean canopy cover, which may affect gecko activity, was calculated for each quadrat by recording canopy cover measurements at each corner of the quadrat using a convex spherical densiometer.

Phelsuma surveys

We used the same quadrats as in the macrohabitat assessment and intensively searched all 75 quadrats once for *Phelsuma* geckos from ground to canopy level by two

surveyors for 30 min. We randomly surveyed 25 quadrats in each of three time periods (07:00–09:59, 10:00–12:59 and 13:00–15:59 h) to assess temporal activity partitioning. Geckos were only recorded if located on trees originating within the quadrat. *Phelsuma* sightings were identified to species (only by TN) and the following microhabitat and interaction variables were recorded: (1) tree species; (2) tree dbh (cm); (3) tree stage (adult/juvenile); (4) tree sex (if *L. maldivica*); (5) perch height (visually estimated in m); (6) perch diameter category (0–5, 5.1–10, 10.1–20 or >20 cm); (7) perch location (leaf, trunk, inflorescence, petiole, branch or nut); (8) microclimate (sun/shade/mix). In addition, proximity of the quadrat to the nearest waterway was recorded to investigate the influence of streams on habitat preferences.

Statistical analyses

To test for macrohabitat type preferences, we classified macrohabitat using hierarchical cluster analysis on percentage data for: (1) *L. maldivica* (adults, immatures and juveniles with stem dbh >4 cm); (2) other adult palms; (3) dicotyledons.

We used the Simpson's diversity index, which accounts for species richness and abundance, to describe tree diversity of each quadrat using the equation

$$D = \frac{\sum n(n-1)}{N(N-1)},$$

where n is the total number of organisms of a particular species, and N is the total number of individuals of all plant species.

For analysis of niche partitioning, niche breadth (B) of *P. sundbergi* and *P. astriata*, and niche overlap (O) between the two species (j, k) were calculated for each spatial and temporal dimension, using Pianka's (1973) statistics, which are derived from MacArthur & Levins' equilibrium equation (1967), and in which the niche breadth of a single species is calculated using the equation:

$$B = \frac{1/\sum_i^n P_i^2}{n}$$

where P_i is the proportion of the i th resource used where the niche dimension is divided into n categories. Niche overlap between two species is quantified as

$$O_{jk} = O_{kj} = \frac{\sum_i^n P_{ij}P_{ik}}{\sqrt{\sum_i^n P_{ij}^2 \sum_i^n P_{ik}^2}}$$

where P_{ij} and P_{ik} are the proportions of the i th resource used by the j th and k th species.

Niche partitioning was further explored using χ^2 -tests to assess differences in macrohabitat use and diurnal activity patterns, and Fisher's exact test to investigate differences in tree type and perch type utilization. We determined

differences in preferred perch height using independent samples *t*-tests.

Generalized linear models with a Poisson distribution were used to investigate the effect of environmental and biotic variables on abundance of *P. astriata*, and *P. sundbergi*. We collected data on six environmental variables (mean canopy height, mean canopy cover, distance to river, time of day, tree species richness and tree density), which are relevant for both *Phelsuma* species. Additional species-specific variables were identified based on preliminary field observations including, for *P. sundbergi*, the number of male *L. maldivica* and for *P. astriata*, the number of *Phoenixophorium borsigianum* palms, number of *L. maldivica* juveniles, number of palms, plant species diversity and the density of *P. sundbergi*. Highly correlated variables were excluded *a priori* from the analysis to simplify the models; thus, the final models used different explanatory variables for *P. sundbergi* and *P. astriata*. We included the following variables in the *P. sundbergi* model: (1) canopy cover; (2) number of *L. maldivica* males; (3) time period; (4) distance to the stream. Variables included in the *P. astriata* model were: (1) abundance of *P. sundbergi*; (2) number of palm individuals, as a proxy of floral resource (pollen and nectar) availability; (3) abundance of *L. maldivica* juveniles; (4) number of *P. borsigianum*, to investigate a potential association with this palm species; (5) tree diversity expressed by the Simpson's diversity index; (6) time period; (7) canopy cover. Outliers were identified through residual plots and removed from the analysis (one sampling quadrat from *P. sundbergi* dataset, and four from *P. astriata*). Here, we present only statistically significant variables of the minimum adequate models. Models were generated using a step-wise technique following the improvement of AIC (Akaike's information criterion) after removal of the least significant variable. Models were checked, and where necessary, corrected for underdispersion, and Type III sums of squares were used.

All statistical analyses were conducted using SPSS v.16.0.

Results

A total of 112 *Phelsuma* geckos were recorded (49 *P. sundbergi*, 63 *P. astriata*) within the 75 quadrats, giving

overall minimum density estimates for our study of 65 and 84 individuals ha⁻¹ for *P. sundbergi* and *P. astriata*, respectively (Table 1). Hierarchical cluster analysis identified four macrohabitat types based on percentage composition of major vegetation groups, and minimum density estimates for both species of *Phelsuma* in each habitat type were calculated (Table 1). Minimum *Phelsuma* densities (hereafter 'density' refers to minimum density) were also calculated for combinations of clusters representing high and low cover of *L. maldivica*; *P. sundbergi* occurred at 92 individuals ha⁻¹ within habitat containing >20% *L. maldivica* (C1, C3), and 19 individuals ha⁻¹ in areas with <20% *L. maldivica* (C2, C4). *Phelsuma astriata* density did not differ between the two levels of *L. maldivica* cover with 87 (C1, C3) and 86 individuals ha⁻¹ (C2, C4).

The number of adult male *L. maldivica* individuals in a quadrat was positively correlated with the number of *P. sundbergi* individuals observed (GLM: Wald $\chi^2 = 44.8$, $P < 0.001$). Tree diversity (as calculated by Simpson's diversity index) was the only recorded variable to affect the density of *P. astriata*; higher tree diversity resulted in higher abundance of *P. astriata* (Wald $\chi^2 = 4.21$, $P = 0.04$).

Niche partitioning analysis for the two *Phelsuma* species showed that *P. sundbergi* preferred higher perches on average compared with *P. astriata* ($t_{85} = 5.96$, $P < 0.001$; Table 2) in the VdM. There was a difference in tree species ($P < 0.001$, Fisher's exact test) and perch type ($P < 0.001$) utilized by the two species (Table 2). *Phelsuma sundbergi* showed a marked preference for male inflorescences of *L. maldivica*, while *P. astriata* was observed on a wider variety of tree species, although most commonly on *L. maldivica* juveniles (Fig. 2a and b). Despite significant niche overlap in macrohabitat between the two species, the number of *P. sundbergi* and *P. astriata* individuals recorded in the various macrohabitat types differed ($\chi^2_3 = 16.1$, $P < 0.001$; Table 2), with *P. sundbergi* primarily recorded in macrohabitat type C3 (*L. maldivica* dominated; Table 1), and *P. astriata* more commonly associated with type C1 (mixed vegetation; Table 1). Diurnal activity patterns contrasted between the two species ($\chi^2_2 = 7.24$, $P = 0.027$), with *P. sundbergi* numbers decreasing and *P. astriata* numbers increasing throughout the course of the day (Fig. 2c).

Table 1 Macrohabitat types, number of quadrats (100 m²) per type, *Phelsuma* gecko species counts (and % of counts) and minimum density estimates in each macrohabitat type in the Vallée de Mai palm forest, Seychelles

Macrohabitat type	Plant species composition	Number of quadrats	<i>Phelsuma sundbergi</i>		<i>Phelsuma astriata</i>	
			N (%)	Density (/ha)	N (%)	Density (/ha)
C1	Mixed vegetation (<i>Lodoicea maldivica</i> >20%, other endemic palms, dicotyledons)	24	17 (34.7)	71	28 (44.4)	117
C2	Other (non- <i>L. maldivica</i>) endemic palm dominated (<i>Lodoicea</i> <20%)	18	5 (10.2)	28	11 (17.5)	61
C3	<i>L. maldivica</i> dominated (>50%)	23	26 (53.1)	113	13 (20.6)	57
C4	Mixed non-palm and other endemic palms	10	1 (2)	10	11 (17.5)	110
All		75	49 (100)	–	63 (100)	–

Macrohabitat types were defined by hierarchical cluster analysis.

Table 2 Niche breadth and overlap of *Phelsuma sundbergi* and *Phelsuma astriata* across spatial and temporal axes calculated using Pianka's statistics (1973)

Dimension ^a	Number of encounters (<i>Phelsuma sundbergi</i> / <i>Phelsuma astriata</i>)	Niche breadth		Niche overlap
		<i>P. sundbergi</i>	<i>P. astriata</i>	
Microhabitat				
Perch height	49/63	0.87	0.63	0.44
Perch type	46/62	0.52	0.35	0.42
Tree spp. ^b	47/55	0.19	0.54	0.30
Macrohabitat	49/63	0.61	0.83	0.67
Diurnal activity	49/63	0.98	0.87	0.88

Niche breadth reflects the diversity of resources used by a species; values closer to 1 indicate that approaching equal numbers of individuals were encountered in each category of the dimension (e.g. perch height). Niche overlap values closer to 0 indicate high partitioning, whilst overlap increases as values approach 1. Niche overlap is considered significant at >0.60.

^aDimension categories excluded where $n < 4$ (observations).

^b*Lodoicea maldivica* separated into four categories to account for key morphological differences.

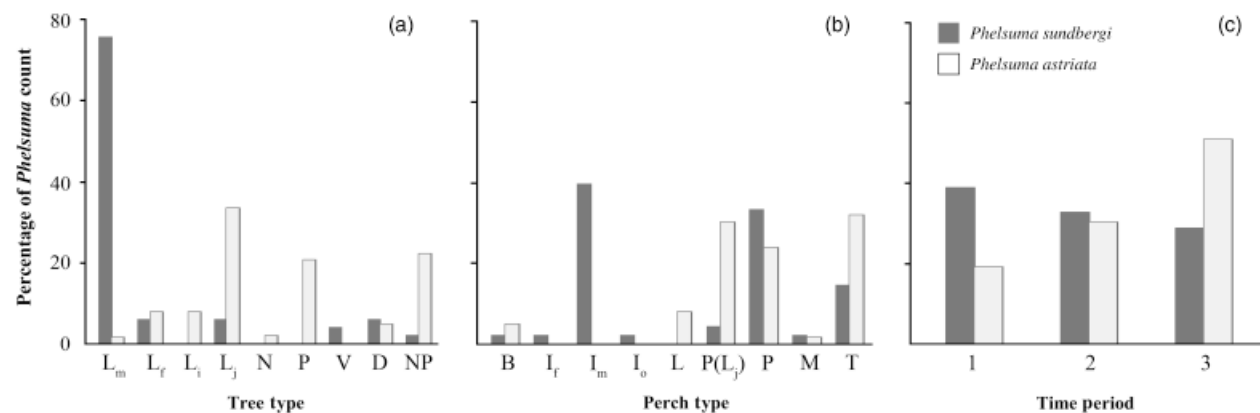


Figure 2 Variation in resource use between Seychelles day geckos *Phelsuma sundbergi* and *Phelsuma astriata* across categorical dimensions of the spatial and temporal niche axes in native palm forest. (a) Tree type: L_m = *Lodoicea* male, L_f = *Lodoicea* female, L_i = immature *Lodoicea*, L_j = *Lodoicea* juvenile, N = *Nephrosperma vanhoutteana*, P = *Phoenicophorium borsigianum*, V = *Verschaffeltia splendida*, D = *Deckenia nobilis*, NP = non-palm; (b) Perch type: B = branch, I_f = female *Lodoicea* inflorescence, I_m = male *Lodoicea* inflorescence, I_o = other inflorescence, L = leaf, $P(L_j)$ = petiole of *Lodoicea* juvenile, P = petiole other, M = midrib, T = trunk and (c) Time period: 1 = 07.00–09.59 h, 2 = 10.00–12.59 h, 3 = 13.00–16.00 h.

Discussion

Phelsuma sundbergi showed a clear preference for habitat dominated by the endemic coco de mer *L. maldivica*, with a 10-fold increase observed when comparing their density in *L. maldivica*-dominated habitat to other habitat types. In contrast, *P. astriata* density was 84% higher in diverse, mixed vegetation compared with assemblages dominated by *L. maldivica*. In Mauritius, *Phelsuma* species richness is positively correlated with habitat complexity, and *Phelsuma* species show flexible associations with palms or non-palms depending on the co-occurrence of congenics (Harmon *et al.*, 2007). In Madagascar, at least one *Phelsuma* species, *Phelsuma ravenala*, shows a close association with the travellers palm *Ravenala madagascariensis* (Raxworthy *et al.*, 2007). Our study is restricted to one area of palm forest but observations in other smaller patches of *L. maldivica*-dominated habitat confirm the dominance

of *P. sundbergi* on male *L. maldivica* (C. Kaiser-Bunbury, pers. obs.). This suggests a relatively consistent partitioning of this type of habitat between the two *Phelsuma* species on Praslin compared with the dynamic congeneric-dependent effects observed in Mauritius (Harmon *et al.*, 2007). *Phelsuma sundbergi* is also known to be in sympatry with *P. astriata* in habitats on Praslin with no *L. maldivica*, but these habitats have all been recorded to hold large palm species, dominated by either endemic species or native coconut (Thorpe & Crawford, 1979). It therefore appears that *P. sundbergi* is largely palm dependent on Praslin, a finding mirrored by the marked preference for *L. maldivica* shown by all three endemic *Ailuronyx* gecko species (Roberts, 2009).

Comparison with the low number of *P. sundbergi* observations on immature *L. maldivica*, which are structurally similar to adults, suggests that this association is resource-specific, and that male inflorescences are a driver of its

occurrence. Another study in Mauritius has shown that habitat preferences of *Phelsuma cepedianana* are driven by nearby floral resources (Hansen *et al.*, 2007). Our study provides strong evidence for this hypothesis in *P. sundbergi* in *L. maldivica* forest: frequent observations of *P. sundbergi* consuming pollen on male inflorescences and very few individuals on non-flowering males suggest that *P. sundbergi* distribution in native palm forest appears to be driven by availability of flowering male *L. maldivica* (which flowers year round), rather than the structure of the trees. Exploitation of *L. maldivica* pollen as a food resource is likely to drive this relationship, providing support for the hypothesis proposed by Harmon *et al.* (2007) that differences in habitat use of island gecko species are a result of trophic specialization. Further investigation is required, however, to determine territorial range and feeding ecology of this species within (and outside) palm forest.

Phelsuma astriata occurred at comparatively high densities (> 57/ha) in all habitat types and was more abundant in mixed vegetation. Tree diversity was the sole predictor for *P. astriata* density, indicating that this species is generalized in its habitat preference. An increased structural variety in ecologically diverse parts of the palm forest would increase the availability of microhabitats and other resources to the generalist. On Praslin, increased habitat biodiversity may reduce opportunities for specialists such as *P. sundbergi*, which would be a distinct advantage to the smaller *P. astriata* as resource exploitation is generally constrained by body-size-dependent control of large over small species (Bassett & Angelis, 2007).

Spatial and temporal partitioning

Microhabitat represents the most highly segregated niche dimension for *Phelsuma* species in the palm forest of the Vallée de Mai (Table 2). Although the two species largely occupied different perch types and heights, differential tree type preference shapes these divergences, for example *P. sundbergi* showed a strong association with male *L. maldivica* (76% of total count), which are the tallest trees in the area (Savage & Ashton, 1983), with the inflorescences situated high in the canopy. The majority of *P. sundbergi* was recorded on either the male inflorescence or leaf petiole of this species, both of which are linked to higher positions. In contrast, *P. astriata* were generalized in their tree choice, commonly found on most palms, *Pandanus* and dicotyledons, which is reflected by the broader perch height range.

The two *Phelsuma* species displayed the lowest degree of segregation in their diurnal activity patterns. Both species remained active throughout the day; however, diurnal activity pattern differed between the two species, with the frequency of *P. sundbergi* encounters declining through the course of the day. We propose that the observed decline in activity is due to depletion of *L. maldivica* pollen, because dehiscence of anthers occurs in the morning.

Pollination of *L. maldivica* by *Phelsuma* has long been postulated. We have shown that *P. sundbergi* spends a large amount of its time feeding on male inflorescences and

individuals have also been observed feeding on nectar from flowering females during targeted observations in another study (C. Kaiser-Bunbury, unpubl. data). Further research is underway to clarify the role of *P. sundbergi* in the reproduction of this vulnerable and culturally and economically important palm species.

Co-evolution and niche partitioning

Our findings describe a possible mechanism for character displacement between the sympatric *Phelsuma* species following allopatric speciation on different islands (Radtkey, 1996; Rocha *et al.*, 2009). Although *P. astriata* are known to regularly consume pollen when co-occurring with other *Phelsuma* species (Gardner, 1984), we did not observe *P. astriata* feeding on pollen despite its widespread availability throughout the study (Noble, 2009). It is therefore likely that the observed morphological divergence between these two species on Praslin evolved due to *P. sundbergi* (the larger species) defending abundant floral resources of male *L. maldivica*, thus competitively excluding *P. astriata* from this temporally and spatially reliable food source. Both species may have evolved in palm forest vegetation dominated by *L. maldivica*, which historically covered the extent of Praslin and neighbouring islands (Edwards, Kollmann & Fleischmann, 2003). On other islands, additional drivers for size divergence may play a role. For example, on La Digue, *P. sundbergi* is relatively large in comparison to the sympatric *P. astriata* despite the absence of *L. maldivica*. Since human settlement in the 17th century, the Seychelles' native vegetation has been subject to intense disturbance (Vesey-Fitzgerald, 1940; Fleischmann *et al.*, 2005), disrupting *Phelsuma* assemblage dynamics. Interspecific competition is thus likely to have increased in homogeneous human-modified habitats such as plantations, where the niches of the dichotomy are not clearly defined. Our findings concur with those of studies on *Phelsuma* and analogous *Anolis* communities, which deduce that microhabitat partitioning is fundamental for the co-existence of these species (Schoener, 1974; Harmon *et al.*, 2007).

Phelsuma density on Praslin

The density of *P. astriata* was higher than that of *P. sundbergi* across the Vallée de Mai, as expected from previous population estimates (Gerlach, 2008) although the difference in abundance between the two species was not as marked in our counts. In a previous study, Thorpe & Crawford (1979) calculated estimates of *Phelsuma* density in a variety of macrohabitat types on Praslin. Although densities are likely to have been underestimated – Thorpe and Crawford found that three observers searching a 30 × 30 m quadrat for 1 h are only likely to see 60% of the *Phelsuma* individuals present – and the methodologies used were similar in both studies (ground-level quadrat counts), a direct comparison of density estimates is not possible. The majority of the macrohabitat types investigated by Thorpe & Crawford (1979) were human-modified, for example

plantation; density estimates were calculated for tracts of 'hillside forest' in which the density of *P. sundbergi* was estimated at 75/ha, and *P. astriata* at 225/ha. Their figures are considerably higher than the estimates of this study, where *P. sundbergi* and *P. astriata* were encountered at densities of 19 and 86/ha, respectively, in endemic palm and broadleaf forest. These differences could be due to factors including seasonality, different observers, varying methods and the difficulties of spotting geckos in a dense palm canopy. For example, the apparent decline may be partly due to seasonal fluctuations in abundance. Watson (1992) recorded *Phelsuma* abundance on Mahé, noting an increase from August onwards and a peak during October–December. Thorpe and Crawford estimated abundance between July and September, which may account for their higher density estimates. Although these methodological limitations prevent a direct comparison, declining *Phelsuma* populations on Praslin are still possible given the widespread destruction of native habitat on Praslin over the past 30 years (e.g. through burning and development).

Conclusion

This study has explored aspects of co-existence and niche partitioning in two species of gecko in an area of native habitat. *Phelsuma sundbergi* and *P. astriata* persist as a sympatric assemblage within palm forest habitat through extensive partitioning of microhabitat, where body size-mediated competition for *L. maldivica* pollen is likely to have led to a specialist/generalist dichotomy. Both species have co-evolved to exploit the resources of natural habitats through strong microhabitat partitioning. The dependency of *P. sundbergi* on male *L. maldivica* trees underlines the importance of conserving key species in native forest to maintain biodiversity. The marked niche partitioning observed in our study may explain why, on Praslin, *P. sundbergi* is almost absent from degraded areas without mature trees (Thorpe & Crawford, 1979) – an increasingly common habitat type on the island. If different ecological niches are not maintained through habitat protection, high reptile diversity cannot be sustained. The acquisition of information on the ecology of island species, particularly on reptiles, is crucial for safeguarding biodiversity and creating long-term conservation strategies.

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