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ABSTRACT.—Microhabitat use is an important aspect of an organism's niche, often influencing both intra- and interspecific interactions such as competition. To reduce competitive interactions, species may shift their behavior when in sympatry to gain greater access to resources, resulting in patterns of habitat partitioning. Previous studies have described structural microhabitat partitioning in *Phelsuma* geckos with the likely cause being interference competition. Such interference competition also may lead to temporal microhabitat partitioning. We investigated the presence of temporal habitat partitioning in *Phelsuma* geckos from Mauritius and the relation of partitioning to competition. We found temporal variation in microhabitat use for Mauritian *Phelsuma*. However, this variation was not clearly associated with the presence of other focal *Phelsuma* species, suggesting competition may not be responsible for the observed pattern. Temporal habitat partitioning in Mauritian *Phelsuma* geckos may be attributable to historical competition or other factors such as thermoregulation, food availability, or predator avoidance. We encourage future studies to investigate the mechanisms of temporal microhabitat variation.

A species' microhabitat preferences are closely related to their role in the ecosystem, dictating the other organisms a species interacts with and possibly influencing long-term evolutionary patterns of trait evolution. Previous theoretical and empirical studies suggest lizards most often partition their environment based on structural habitat or diet to reduce competition among sympatric species (Schoener, 1974; Toft, 1985). Temporal partitioning, or diel differences in activity times of sympatric species, also can be effective mechanisms to reduce competition (Simon and Middendorf, 1976; Carothers and Jaksic, 1984).

Because of the nocturnal nature of most gecko species, nocturnal temporal partitioning of geckos has been considered in multiple studies (Pianka and Pianka, 1976; Pianka and Huey, 1978; Huey, 1979; Gordon et al., 2010); yet few studies have considered patterns of temporal partitioning in any of the multiple examples of secondarily diurnal geckos (but see Cole and Harris, 2011; Gamble et al., 2012). We consider temporal habitat partitioning of *Phelsuma* geckos, a secondarily diurnal genus of geckos endemic to Madagascar and island archipelagos in the Indian Ocean.

Phelsuma geckos are arboreal, insectivorous, and nectarivorous (Vinson and Vinson, 1969; NyHagen et al., 2001; Olesen and Valido, 2003) as well as occasionally cannibalistic and saurivorous, that is, eating other smaller gecko species (Vinson and Vinson, 1969; Cole and Harris, 2011). The ecological and behavioral patterns observed in *Phelsuma* geckos make them an excellent group to study habitat partitioning. Known structural habitat partitioning include species dividing their habitat by vegetation community, perch-tree species, perch height, perch diameter, and associations with flowers (Gardner, 1984; Harmon et al., 2007; Noble et al., 2011). For example, in Mauritius, Harmon et al. (2007) found patterns of structural partitioning in which *Phelsuma ornata* and *Phelsuma cepediana* used trees and bushes with palm-like fronds, including actual palm tree species and other vegetation with smooth fronds and narrow, water-containing crevices such as *Ravenala* (Strelitziaceae), *Pandanus* (Pandanaeae), and *Aloe* (Xanthorrhoeaceae). In contrast,

Phelsuma guimbeaui were most often found on non-palm trees. Exclusion experiments and comparisons between allopatric and sympatric populations further demonstrated that competition is likely driving these observed partitioning patterns (Gardner, 1984; Harmon et al., 2007). The prevalence of habitat partitioning in *Phelsuma* geckos may have contributed to their proliferation across Madagascar and associated island groups as an adaptive radiation (Radtkey, 1996; Rocha et al., 2007).

Although structural habitat partitioning has been documented in *Phelsuma*, temporal partitioning has not been previously described (Radtkey, 1996; Lehtinen, 2002; Noble et al., 2011). Anecdotal evidence suggests Mauritian *Phelsuma* also exhibit temporal microhabitat shifts during their diurnal activity periods (LJH and NC, pers. obs.). These shifts may be attributable to interspecific interference competition, similar to reported structural microhabitat partitioning, or other factors such as temporal variation in microhabitat temperature, prey availability, or predator activity. If competition were responsible for temporal microhabitat partitioning in Mauritian *Phelsuma* geckos, we would expect sympatric populations to have complementary activity patterns, reducing the time in which multiple species are active or using the same microhabitats. Alternatively, if competition is not responsible, we predict no relationship between the presence of heterospecifics and temporal activity patterns. We investigated the presence of temporal microhabitat shifts and their relationship to competition by comparing sympatric populations to populations found in allopatry, where interspecific competition is not present.

MATERIALS AND METHODS

We considered three sites in Mauritius, Casela, Bambous, and Ile aux Aigrettes (Fig. 1). Casela and Bambous are near the west coast of Mauritius, whereas Ile aux Aigrettes is an island off the east coast (Fig. 1). Previous studies have investigated habitat availability and structural habitat partitioning at these same sites (Harmon et al., 2007). These sites are home to different sympatric combinations of *Phelsuma* species. *Phelsuma ornata*, *P. cepediana*, and *P. guimbeaui* can all be found at Casela, as well as introduced *Phelsuma grandis*, at low frequency. At Ile aux Aigrettes, we observed only *P. ornata*. We note that *P. guentheri*

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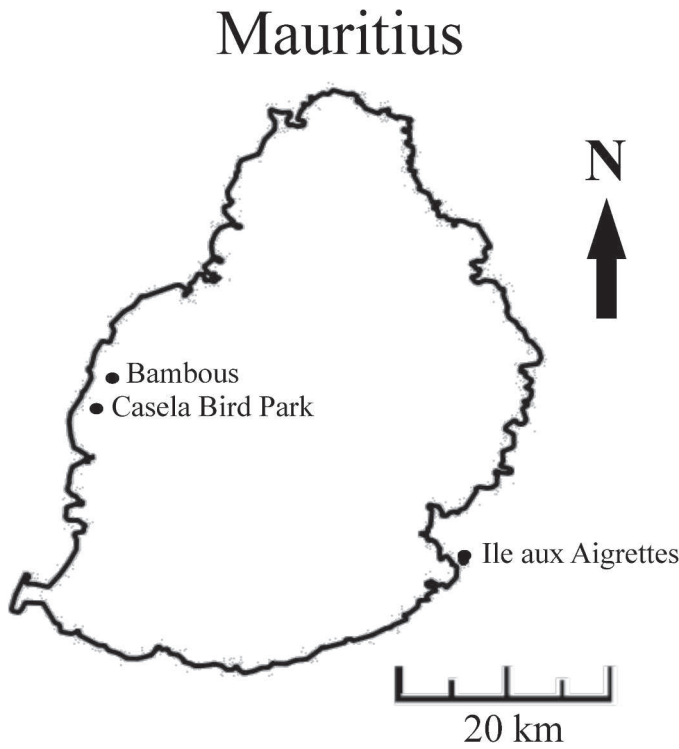


FIG. 1. Map of Mauritius. The Bambous and Casela sites are on the west coast with the Ile aux Aigrettes Island on the southeastern side of Mauritius. Image modified from Harmon et al. (2007).

were released on Ile aux Aigrettes in 2010, after this study was conducted. We found *P. guimbeaui* in allopatry at Bambous (Table 1). An introduced agamid lizard, *Calotes versicolor*, and introduced geckos, *Hemidactylus frenatus* and *Hemiphyllodactylus typus*, also were observed at all three sites in low frequencies (Table 1). Additional species that were not observed, but known to be present at low frequencies, include *Hemidactylus parvima- culatus* at the Bambous and Casela sites as well as *Lycodon capucinus* and *Gehyra mutilata* (mostly restricted to buildings) at all three sites (Table 1). Observations of introduced species were not included in our analyses.

We collected observations, conducted by LJH and LLH, over six warm sunny days in late June and early July 2002. We placed two rectangular 25 × 5-m transects haphazardly at each of three, typical forest-habitat sites. Each transect consisted of six observational points, one every 5 m. During our observations, we spent exactly 5 min at each observational point searching for adult geckos. When a gecko was identified, we recorded the

time of observation, perch height, and perch diameter, although we did not capture or mark observed individuals. We conducted 16 transect walks at Casela between 0930 and 1615 h on 17 June. We conducted 34 transect walks at Bambous between 0730 and 1620 h on 18 June, 5 July, and 6 July. At Ile aux Aigrettes, we conducted 20 transect walks between 0715 and 1630 h on 20 June and 21 June. Each site was sampled at least four times per 2-h time bin. We did not quantify microhabitat availability, but previous studies have found that *Phelsuma* geckos across sites in Mauritius do not randomly use microhabitats; instead, species show strong species-specific structural microhabitat preferences and shift microhabitat use in response to the presence of competing congeners (Harmon et al., 2007).

Analyses were conducted in the R statistical environment (R version 3.0.1, Core Development Team 2013). Each transect walk was treated separately, for which we calculated summed species counts, species-specific mean perch height and diameter and assigned a 2-h time bin. We conducted multiple nested two-way analyses of variance using natural log-transformed species count, perch height, or perch diameter as our dependent variable. Transforming our dependent variables reduced the effect of variance heteroscedasticity on our analyses. We evaluated fully inclusive models including all focal species from all three sites, using site, species, and time bin as independent variables and considering all possible two- and three-way interactions. Also, we evaluated specific comparisons, only considering sympatric species at Casela, again using our count or perch measurements as dependent variables with species and time bin as independent variables. Finally, we evaluated models with only counts or perch measurements of *P. ornata* using the independent variables of site and time bin to investigate differences between sympatric (Casela) and allopatric (Ile aux Aigrettes) populations. A similar analysis was used to consider sympatric and allopatric populations of *P. guimbeaui* at Casela and Bambous. We conducted 12 analyses of variance. The need to account for multiple comparisons in statistical analyses is often debated (see Perneger, 1998; Pike, 2011), and as a result, we included information describing which results remained significant after using the Benjamini and Hochberg false discovery rate method (Benjamini and Hochberg, 1995) in our results section, although we discuss only our unadjusted analyses.

RESULTS

Here we report our calculated analyses of variance results. *P*-values with asterisks remained significant after corrections for

TABLE 1. List of lizard species found at each site. Numbers in parentheses indicate the number of observed individuals, including observations omitted from analyses such as juveniles and nonfocal species. We considered *Phelsuma guimbeaui* to be allopatric at the Bambous site, although NC has observed *Phelsuma cepediana* and *Phelsuma ornata* at these sites at very low frequencies.

	Casela Bird Park	Bambous	Ile aux Aigrettes
Endemic	<i>Phelsuma cepediana</i> (37) <i>Phelsuma guimbeaui</i> (26) <i>Phelsuma ornata</i> (48)	<i>Phelsuma cepediana</i> (0) <i>Phelsuma guimbeaui</i> (553) <i>Phelsuma ornata</i> (0)	<i>Phelsuma ornata</i> (463)
Introduced	<i>Calotes versicolor</i> (13) <i>Gehyra mutilata</i> (0) <i>Hemidactylus frenatus</i> (1) <i>Hemidactylus parvima- culatus</i> (0) <i>Hemiphyllodactylus typus</i> (0) <i>Lycodon capucinus</i> (0) <i>Phelsuma grandis</i> (10)	<i>Calotes versicolor</i> (41) <i>Gehyra mutilata</i> (0) <i>Hemidactylus frenatus</i> (5) <i>Hemidactylus parvima- culatus</i> (0) <i>Hemiphyllodactylus typus</i> (0) <i>Lycodon capucinus</i> (0)	<i>Calotes versicolor</i> (3) <i>Gehyra mutilata</i> (0) <i>Hemidactylus frenatus</i> (3) <i>Hemiphyllodactylus typus</i> (1) <i>Lycodon capucinus</i> (0)

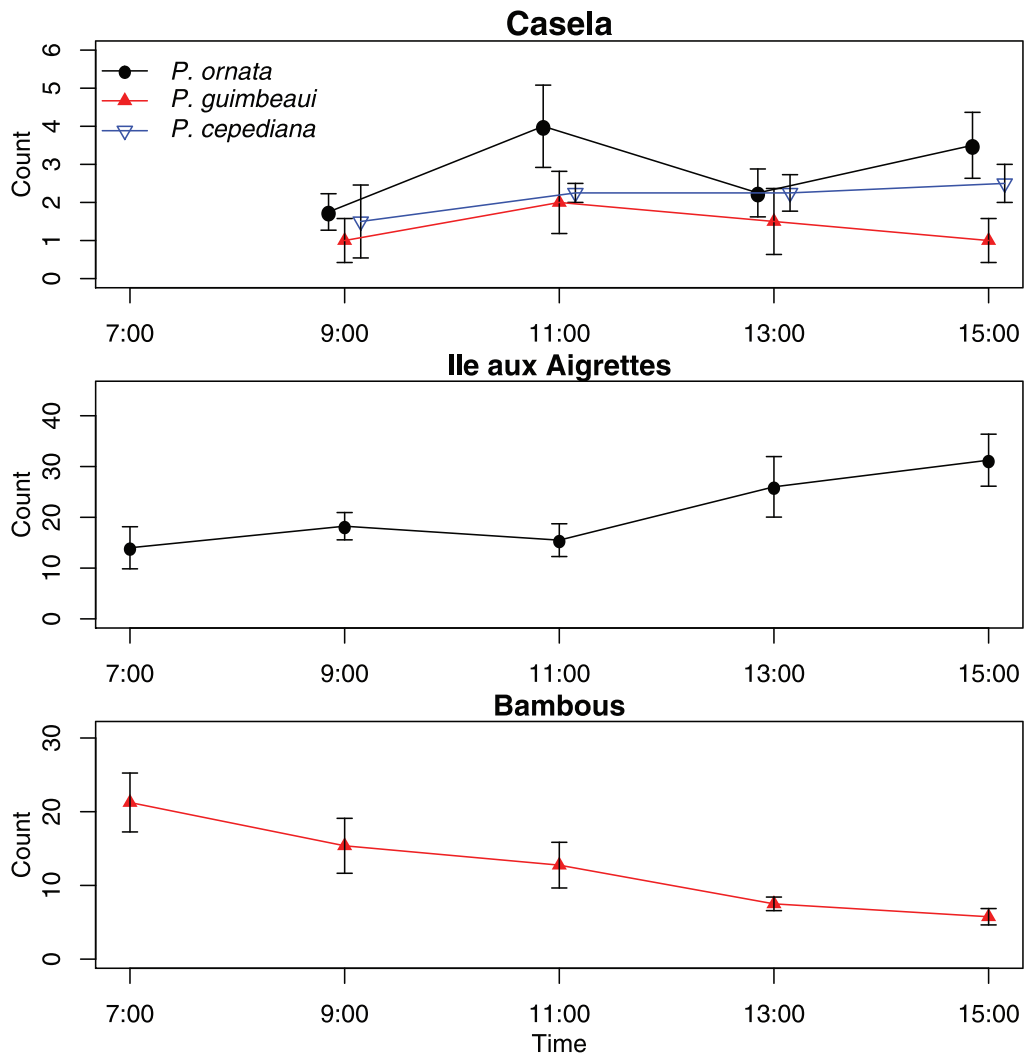


FIG. 2. Number of individuals observed (y-axis) against time (x-axis) for an average transect walk with standard error bars. *Phelsuma ornata* counts are displayed as black circles, *Phelsuma guimbeaui* as red triangles, and *Phelsuma cepediana* as inverted blue open triangles.

multiple comparisons. Across sites, we observed significantly different numbers of geckos, with fewer observations per unit time at Casela (Fig. 2). Species ($P < 0.001^*$) and site ($P = 0.017$) both significantly correlated with count. We observed different temporal patterns at each site. The number of observed focal individual lizards was consistent through time at Casela. Observations of *P. ornata* increased at Ile aux Aigrettes through the day, whereas observations of *P. guimbeaui* decreased through the day at Bambous (Fig. 2). Within Casela, we observed a different number of individuals from each species ($P = 0.012^*$), observing more *P. ornata*, but these differences were not related to the time that geckos were surveyed (Fig. 2). Observed counts of *P. ornata* in sympatry with other species of *Phelsuma* at Casela were lower than the observed counts on Ile aux Aigrettes ($P < 0.001^*$), where the species occurred in allopatry from the other *Phelsuma* (Fig. 2). Time of day affected how many individuals we observed ($P = 0.059$), but these temporal patterns were not different between sites (Fig. 2). A similar result was found for our *P. guimbeaui* observations from Casela and Bambous with more *P. guimbeaui* observed at Bambous as compared to Casela ($P < 0.001^*$, Fig. 2) and an effect of time of day on our *P. guimbeaui* observations ($P = 0.072$), but again, this did not interact with site (Fig. 2).

We observed different perch heights being used between sites ($P < 0.001^*$), with lower perches observed at Ile aux Aigrettes (Fig. 3). Also, we observed species using different perch heights ($P = 0.050$), with *P. guimbeaui* typically using higher perches than other species (Fig. 3). Within our observations from Casela, we did not observe differences in perch height related to species or time, although we did observe *P. ornata* using lower perches at Ile aux Aigrettes as compared to Casela ($P < 0.001^*$, Fig. 3). When comparing Casela and Bambous, *P. guimbeaui* was observed using different perch diameters ($P = 0.046$), with a significant interaction between site and time predicting *P. guimbeaui* perch height ($P = 0.031$, Fig. 3). Our data suggest this species moves to lower perches through the day at Casela, while decreasing and then increasing, perch height through the day at Bambous (Fig. 3).

Our analyses of variance considering our whole data set suggest *Phelsuma* geckos use perches of significantly different diameters at different times of the day, with site ($P = 0.003^*$), species ($P = 0.001^*$), and time ($P = 0.007^*$) all separately correlating with perch diameter. We observed *Phelsuma* using the thinnest perches at Ile aux Aigrettes, followed by Bambous, and the largest diameter perches used at Casela (Fig. 4). At Casela, we observed *Phelsuma* geckos using different diameter

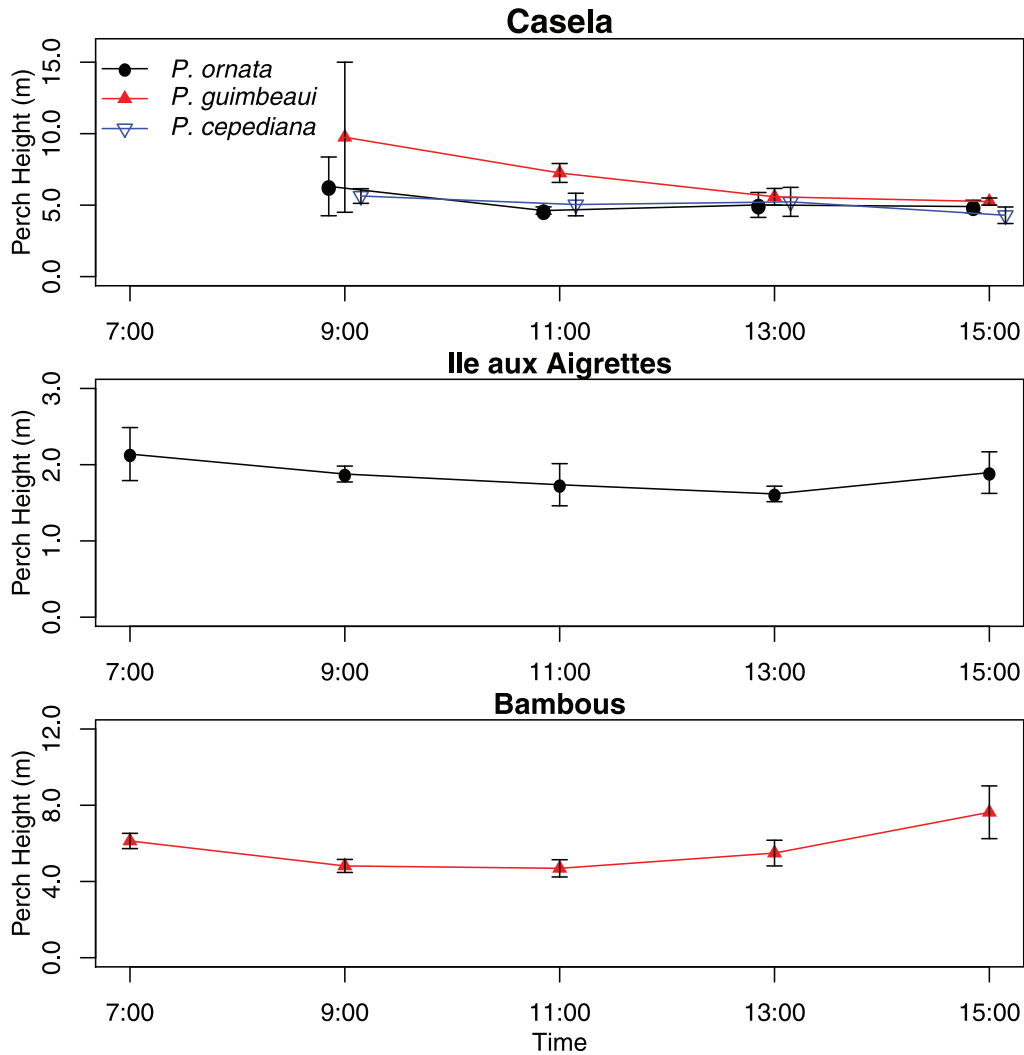


FIG. 3. Perch heights observed (y-axis) against time (x-axis) for an average transect walk with standard error bars. *Phelsuma ornata* results are displayed as black circles, *Phelsuma guimbeaui* as red triangles, and *Phelsuma cepediana* as inverted blue open triangles.

perches and significantly moving to thicker perches midday (species $P = 0.044$, time $P = 0.012^*$, Fig. 4). Our analyses evaluating *P. ornata* perch diameter suggested similar results as our fully inclusive perch diameter model, with this species using narrower perches at Ile aux Aigrettes ($P = 0.006^*$, Fig. 4). Also corroborating our other results, our analysis of *P. guimbeaui* perch diameter suggested different temporal patterns between sites, with individuals moving to thicker perches midday only at Casela (interaction between site and time $P = 0.023$, Fig. 4).

DISCUSSION

Previous studies of *Phelsuma* geckos have found multiple examples of structural habitat partitioning that are likely driven by interactions and interference competition (Carothers and Jaksic, 1984; Richards, 2002). In this study, we collected abundance observations and microhabitat measurements at different time points through the day to investigate patterns of temporal partitioning and its relationship to competition. If temporal partitioning were present in Mauritian *Phelsuma* species as a result of aggressive competition, we would expect time of day to significantly affect abundance observations or microhabitat use, with different patterns present for populations in sympatric as compared to allopatric populations. In addition,

we would expect sympatric populations to reduce their temporal overlap by having distinct activity periods or microhabitat preferences throughout the day.

Although we did observe different abundance and microhabitat preferences for *Phelsuma* geckos with respect to time and site, these patterns did not appear to reduce interactions with sympatric species at Casela. These results suggest *Phelsuma* geckos change their activity levels and preferred microhabitat through the day, with *Phelsuma* geckos moving to larger diameter and lower perches later in the day, although these changes may not be to reduce antagonistic interspecific interactions. The reason for this daily cycle is not clear from our data. Possible mechanisms may include tracking optimal thermal environments, following invertebrate prey species, tracking diurnal patterns of flower nectar production, or avoiding predators. Differences in the available structural or thermal microhabitats between our sites also may have contributed to our observed differences (see Harmon et al., 2007). *Phelsuma* nest site temperatures on Ile aux Aigrettes have been recorded to change by an average of 15°C throughout the day (0700 to 1500 h; N. Cole, R. Mootoocurpen, and D. Vencatasamy, unpubl. data). These large temperature changes would likely require these small gecko species to actively

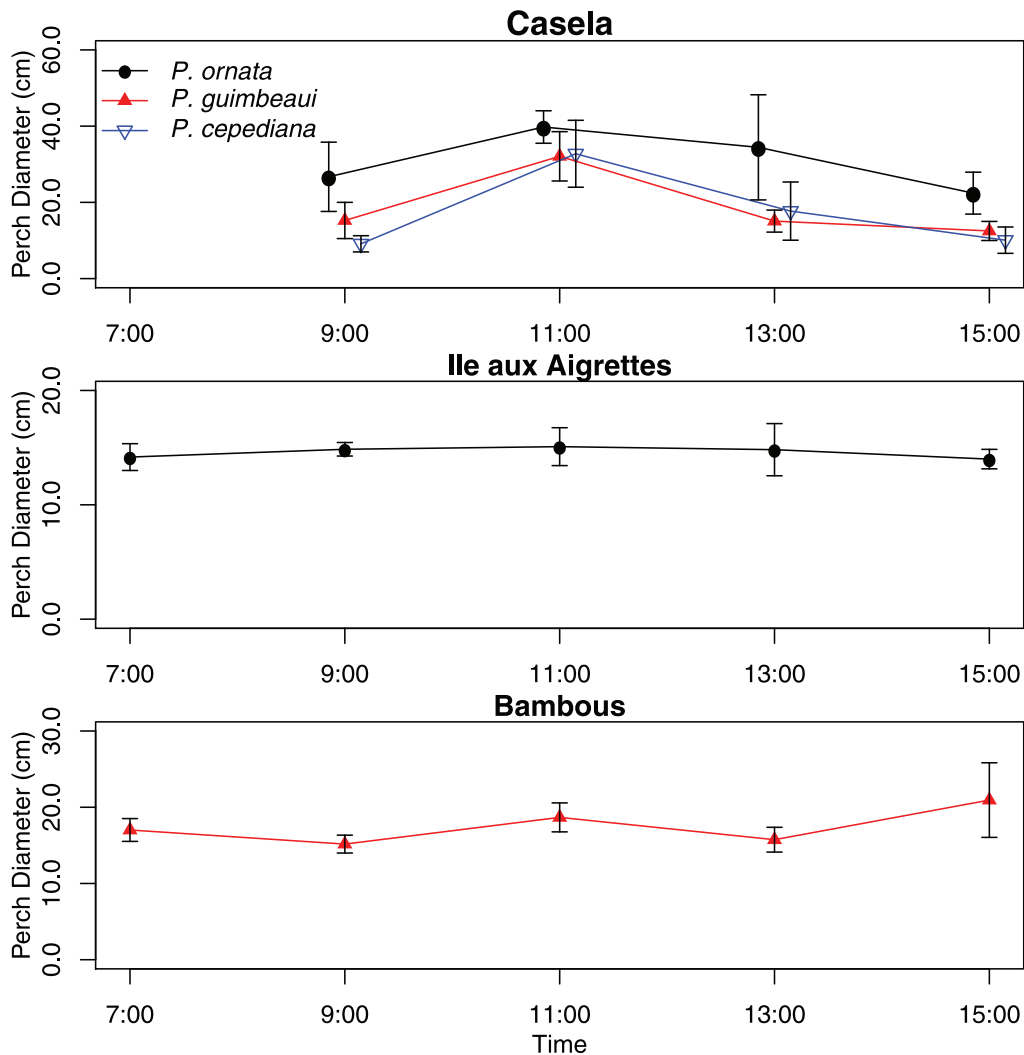


FIG. 4. Perch diameters observed (y-axis) against time (x-axis) for an average transect walk with standard error bars. *Phelsuma ornata* results are displayed as black circles, *Phelsuma guimbeaui* as red triangles, and *Phelsuma cepediana* as inverted blue open triangles.

change microhabitats to properly thermoregulate. Larger diameter perches are typically lower and capture more sun either earlier or later in the day, depending upon the specific structure of the site. Hansen and Muller (2009) note differences in diurnal and nocturnal nectar production in the Mauritian endemic plant *Roussea simplex* (Rousseaceae), a plant in which *Phelsuma* are known to visit and pollinate. Our Casela site also had a higher abundance of *Haematoxylum campechianum* (Fabaceae) in comparison to the other sites. These abundant nectar and sap feeding opportunities may reduce competitive interactions between species. In addition to potential thermoregulatory and dietary mechanisms, predation may influence microhabitat use. Mammalian predators of Mauritian *Phelsuma* are present on the mainland (Casela and Bambous) yet absent on Ile aux Aigrettes Island. This difference may be associated with the change in perch heights used by *P. ornata* between sites. The introduced *C. versicolor* also may be competing or preying upon *P. ornata* because of their similarity in preferred perch heights.

Another factor to consider is our ability to detect geckos in different habitats, at different times and under different environmental conditions. Imlay et al. (2012) suggest the best technique to accurately gather *Phelsuma* abundance data is to

use elevated survey positions. Although we did not use elevated survey positions in this study, any under-sampling that occurred in this study was distributed equally across our focal species and did not affect our relative abundance estimates. In addition, Imlay et al. (2012) observed differences in the number of observed *Phelsuma* at different time points at different sites, possibly suggesting divergent activity patterns across their survey sites. While collecting our observations, we did not disturb, capture, or mark our observed individuals and, as a result, cannot rule out repeated sampling of individuals, although the use of two transects per site likely reduced the potential for pseudoreplication.

Although our study did not find evidence of divergent temporal habitat partitioning for Mauritian *Phelsuma* geckos, we did find evidence of diurnal microhabitat variation through time. Additional research including tracking microhabitat thermal characteristics, diurnal variation in arthropod activity, floral nectar production, and potential predator activity patterns may shed light on the mechanisms responsible for our observed *Phelsuma* abundance and microhabitat patterns. Further sampling across additional sites and seasons would determine whether our observed patterns illustrate a general pattern across different communities of *Phelsuma* geckos. Since our

observations were collected, the sites considered here have been affected by habitat deforestation or habitat restoration, in the case of Ile aux Aigrettes, and new sympatric and allopatric sites may be needed for future studies. The proposed additional studies would greatly increase our understanding of how arboreal lizards use their environment through time. Temporal microhabitat and activity variation is not often considered when quantifying a species' microhabitat preferences yet may be important aspects of a species niche.

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