

**The Cuban Treefrog
(*Osteopilus septentrionalis*)
Dampens Competitive
Superiority Between
Two *Hemidactylus* Gecko
Species on Buildings**

Walter E. Meshaka, Jr., Malcolm L. McCallum,
Connor Voirin, and Jon Moore



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Cover Photograph: A Cuban Treefrog, *Osteopilus septentrionalis*, eating a Wood Slave, *Hemidactylus mabouia*, that it caught near a light on a building in Palm Beach County, Florida. Photograph © Jon Moore.

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The Cuban Treefrog (*Osteopilus septentrionalis*) Dampens Competitive Superiority Between Two *Hemidactylus* Gecko Species on Buildings

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Connor Voirin³, and Jon Moore³

Abstract - A survey of the herpetofauna from buildings in southern Florida was conducted in 2005 and again during November 2015–March 2016. Associations among activity and abundance of the building-dwelling species were compared between the two surveys, one in 2005 for four buildings and a follow-up in 2016 for the same four buildings, plus five additional buildings. Two species, *Hemidactylus garnotii* (Indo-Pacific Gecko) and its superior competitor, *H. mabouia* (Wood Slave), overlap extensively with respect to habitat use and activity across various weather conditions. Our surveys, however, revealed larger populations of the Wood Slave among a wider subset of the buildings than in 2005, commensurate with its general replacement of the Indo-Pacific Gecko. The presence of their predator, *Osteopilus septentrionalis* (Cuban Treefrog), differentially impacted occurrence of these two species of geckos, perhaps as an adaptive predator avoidance strategy, the result of which maintained coexistence of these two ecological analogues on some buildings.

Introduction

Osteopilus septentrionalis (Duméril and Bibron) (Cuban Treefrog), is a highly successful colonizing species in Florida that has a nearly statewide distribution (Meshaka 2001, 2011). Buildings provide many features promoting its abundance (Meshaka 2001). Its diet includes vertebrates and it can suppress native treefrog populations (Meshaka 2001). Likewise, building-dwelling individuals often encounter geckos upon which they also feed (Fig. 1). Two of these geckos, *Hemidactylus mabouia* (Moreau de Jonnès) (Wood Slave, aka Tropical House Gecko) and, *H. garnotii* (Duméril and Bibron) (Indo-Pacific Gecko) are ecologically analogous and do not stably coexist when alone on buildings (Meshaka 2000, Meshaka and Moody 1996, Meshaka et al. 2006a, 2005). The Wood Slave, a superior competitor, quickly replaces its congener and often in far greater abundance (Meshaka 2000). Exceptionally, the presence of the Cuban Treefrog on buildings appears to maintain a stable coexistence of these geckos (Meshaka 2000, 2001; Meshaka et al. 2005). The Cuban Treefrog has been on the Florida Keys since at least the early 20th century (Barbour 1931), where its exotic status is debatable (Meshaka 2001). The Indo-Pacific Gecko was introduced to Florida in the 1960s (King and Krakauer 1966), and the Wood Slave arrived in the 1980s (Lawson et al. 1991).

By examining the relationships among these three species and the building structure, our goal was to quantify the impact of differential predation by Cuban Treefrogs on these geckos in southern Florida. We compared abundance data collected from a subset of these buildings over two time periods (2005 and 2015–2016) (Meshaka et al. 2006a) to test patterns of replacement

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and coexistence, and to build predictive models of abundance of the competitors and predator based on biotic and abiotic factors within this ever-expanding artificial urban ecosystem.

Materials and Methods

We conducted nine surveys on four buildings during 3 January–30 March 2005 (Meshaka et al. 2006a) located on the campus of Florida Atlantic University (FAU) (Jupiter, Palm Beach County, FL). We again surveyed those four buildings and an additional five structures during 19 November 2015–12 March 2016 (Table 1). The new surveys were conducted every 10–20 days for a total of 10 visits to each building during the follow-up survey ($n = 10$). Each survey began after the sun had fully set, at which time we counted the individual geckos and treefrogs that we observed during a single walk around each building (per Meshaka 2000, Meshaka et al. 2005).

We performed all statistical analyses with Microsoft Excel and MiniTab 13.0 (MiniTab, State College, PA). Data were tested for normality using the Anderson-Darling Normality Test ($\alpha = 0.05$). If data were non-normal, we transformed the data distribution using the Johnson Transformation (Johnson 1949) prior to application of parametric statistics.

We compared data collected between January and March from 2005 and 2016 to identify possible relationships among biotic and abiotic factors by constructing best fit models that predict abundance. These models were constructed using a combination of best-subsets regression, multiple regression, and general linear models. The initial run of each best-subsets regression included building area, weather, number of lights, and the opposing two species as predictors of abundance of the species in question. Weather parameters were comprised of air temperature and relative humidity during sampling and the dew point, maximum wind



Figure 1. A Cuban Treefrog, *Osteopilus septentrionalis*, eating a Wood Slave, *Hemidactylus mabouia*, that it caught near a light on a building in Palm Beach County, Florida. Photograph © Jon Moore.

Table 1. Locations and characteristics of nine buildings on the campus of Florida Atlantic University, Jupiter, Palm Beach County, Florida, surveyed for herpetofauna at night during November 2015–March 2016.

Building name	GPS latitude	GPS longitude	Building perimeter (m)	No. lights on building
Honors College Building	26° 53' 17.58"N	80° 07' 03.53"W	273.4	7
Administration Building	26° 53' 14.50"N	80° 07' 5.20"W	194.5	5
Hibel Fine Arts Building	26° 53' 20.36"N	80° 07' 1.92"W	107	9
College of Education Building EC	26° 53' 14.26"N	80° 06' 58.59"W	107.9	17
Wilkes Psychology Building	26° 53' 10.14"N	80° 07' 2.61"W	134.4	6
Research Facility	26° 53' 10.61"N	80° 06' 55.50"W	210.3	15
Hibel Museum of Art	26° 53' 20.28"N	80° 07' 0.45"W	82.3	7
Library	26° 53' 12.18"N	80° 06' 59.38"W	132.3	7
Pool House	26° 53' 12.13"N	80° 07' 2.90"W	41.5	4

speed, and air temperature maximum and minimum on that date, and growing degree days (GDD), all of which could influence activity. Lights were similar in type among buildings and variably distributed for coverage. We chose weather parameters based on their well-known impacts on ectotherms (Kristensen et al. 2006, Martínez-Meyer 2005) including amphibians (McCallum 2010) and reptiles (Gibbons et al. 2000, McCallum et al. 2009, Zug et al. 2001). Next, we compared standard error of the regression, Mallows statistic, r^2 , and the p-values following standard convention for this regression technique. We then ran multiple regression using the best models identified by best-subsets regression and compared the resulting r^2 , p-values, and predicted residual sum of squares (PRESS) to assess if the model was acceptable. If not, we repeated the process with different combinations of predictors until the best estimate was revealed. We performed these procedures on the entire 2015–2016 data set in isolation from the 2005 data to reinforce and further identify relationships among the species observed. We compared basic differences among buildings using a one-way ANOVA ($\alpha = 0.05$).

Results

2015–2016 Survey

All nine buildings surveyed were inhabited by at least one of the three exotic species (Fig. 2). The Wood Slave occurred on all buildings, the Cuban Treefrog occurred on eight buildings, and the Indo-Pacific Gecko occurred on five buildings (Fig. 2). The Indo-Pacific Gecko outnumbered the Wood Slave on only one building, the Museum of Art, where the Cuban Treefrog was most numerous, averaging 2.0 individuals (Fig. 2). The Wood Slave occurred often at high relative abundances to the exclusion or near exclusion of the Indo-Pacific Gecko where the Cuban Treefrog was either absent or in low abundances. Although the Squirrel Treefrog, *Hyla squirella* Bosc, was also recorded, its occurrence was too low to include in most of the analyses.

Clear interactions detected among variables were reflected in two highly significant p-values in pairwise comparisons of building denizens using regressions. Abundances of the Cuban Treefrog resulted in greater abundances of the Indo-Pacific Gecko ($r^2 = 0.796$) and fewer Wood Slaves ($r^2 = -0.468$). On the other hand, the Indo-Pacific Gecko was abundant when

the Wood Slave was scarce ($r^2 = -0.285$). Thus, the strongest relationships of interspecific abundances on buildings were negative between the Cuban Treefrog and the Wood Slave and positive between the Cuban Treefrog and the Indo-Pacific Gecko. Relationships were weakest between the geckos, indicating that despite predatory pressure by the Cuban Treefrog on both gecko species, the Indo-Pacific Gecko fared better in a pairwise arrangement with its predator than did its competitor, the Wood Slave, with the Cuban Treefrog (Fig. 3).

2005 (Meshaka et al. 2006a) vs. 2015–2016 Surveys

Cuban Treefrog. The Cuban Treefrog was less abundant in 2016 than in 2005 ($t = -2.24$, $p = 0.032$) (Fig. 4). Abundance of this species varied among buildings (ANOVA: $F = 2.91$, $df\text{-source} = 3$, $df\text{-error} = 41$, $p = 0.046$): Honors (mean = 0.1, SD = 0.316, SE = 0.1), Admin. (mean = 0.1, SD = 0.316, SE = 0.1), Hibel (mean = 0.1, SD = 0.316, SE = 0.1), College (mean = 2.07, SD = 3.58, SE = 0.923), Overall (mean = 0.756, SD = 2.24, SE = 0.334).

Warmer temperature ($t = 2.81$, $p = 0.009$) and higher humidity ($t = 2.06$, $p = 0.048$) increased sightings of the Cuban Treefrog on the buildings. Numbers of lights also increased sightings of Cuban Treefrogs ($t = 2.82$, $p = 0.008$). The Indo-Pacific Gecko did not directly reduce abundance of the Cuban Treefrog ($t = -0.88$, $p = 0.384$), but interacted with other predictors in the model to affect abundance of this predator ($F = 4.46$, $df\text{-source} = 5$, $df\text{-error} = 31$, $p = 0.004$).

The most accurate model based on standard error of regression ($s = 1.4770$) had an acceptable Mallows statistic ($C-P = 1.5$). This model included year, measured temperature during sampling, humidity, high temperature and low temperature on that date, GDD, the number of lights, and the abundance of the Indo-Pacific Gecko. However, the valence inflation factor was extremely high for growing degree days ($VIF = 1063$), and high for high temperature ($VIF = 233$) and low temperature ($VIF = 375$). Removal of the GDD lowered VIF for high temperature ($VIF = 5.4$) and for low temperature ($VIF = 6.0$). Removal of high temperature reduced VIF for low temperature ($VIF = 25.5$) and for GDD ($VIF = 24.3$),

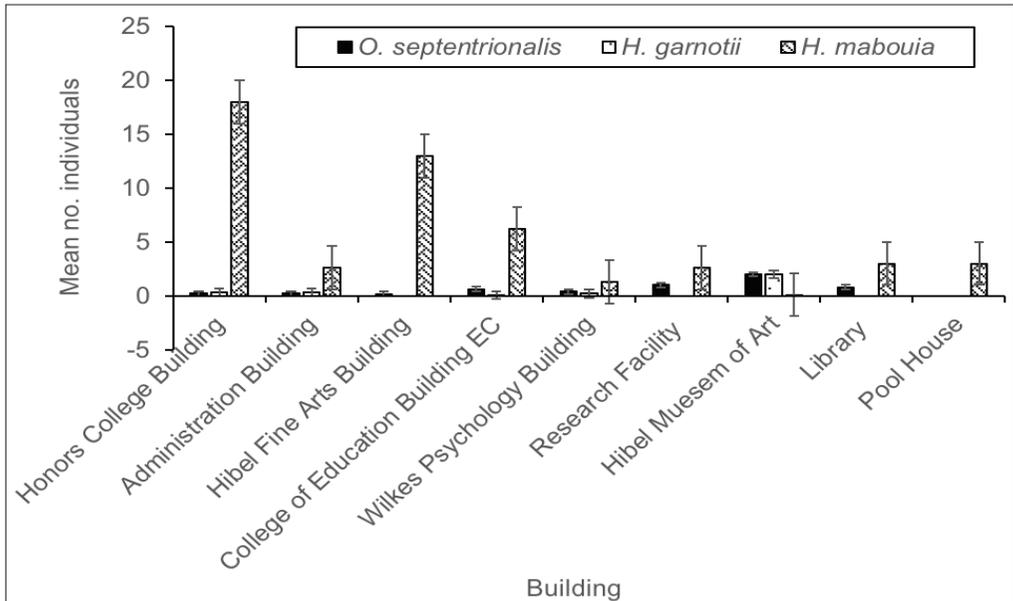


Figure 2. Mean numbers of the Cuban Treefrog, *Osteopilus septentrionalis*, Indo-Pacific Gecko, *Hemidactylus garnotii*, and Wood Slave, *H. mabouia*, counted on nine buildings on the campus of Florida Atlantic University, Jupiter, Palm Beach County, Florida, during November 2015–March 2016. Standard error bars are in association with mean values.

and removal of low temperature reduced VIF for high temperature (VIF = 15.8) and GDD (VIF = 17.2). The model without GDD also had the lowest PRESS (137.9 vs. 145.0, 145.0, 138.0). Removal of GDD and low temperature provided much lower PRESS (115.7), but similar VIF (all < 2.3), as did removal of GDD and high temperature (PRESS = 126, all VIF < 2.2), and removal of high and low temperatures (PRESS = 119.4, all VIF < 2.3). Removal of all three variables provided the lowest combination of PRESS (113.3) and VIF (all < 1.8). Best-subsets regression confirmed that this last model was the best (C-P = 6.0, S = 1.57). Using general linear regression, this model was selected to best predict Cuban Treefrog abundance on the buildings ($r^2 = 0.418$, S = 1.57):

$$\text{Cuban Treefrog abundance} = 276 - 0.142 \text{ year} + 0.232 \text{ temperature} + 0.0427 \text{ humidity} + 0.150 \text{ lights} - 0.115 \text{ Indo-Pacific Gecko abundance}$$

Best subsets regression revealed that 14.1% of the variance in Cuban Treefrog abundance was due to the abundance of lights, and 12.6% was due to the temperature at the time of the survey. Further, 5.6% of the variation was due to the year. The abundance of the Indo-Pacific Gecko (0.4%) and the humidity (0.4%) were minor predictors of Cuban Treefrog abundance.

Hyla squirella Bosc (*Squirrel Treefrog*). Sample size was insufficient to analyze abundances between sampling years of this diminutive treefrog. The Squirrel Treefrog was evenly distributed among buildings at FAU (Admin: Mean = 0.10, SD = 0.316, SE = 0.1; each of rest: mean = 0.0, SD = 0.0, SE = 0.0; overall mean: 0.025, SD = 0.158, SE = 0.025)

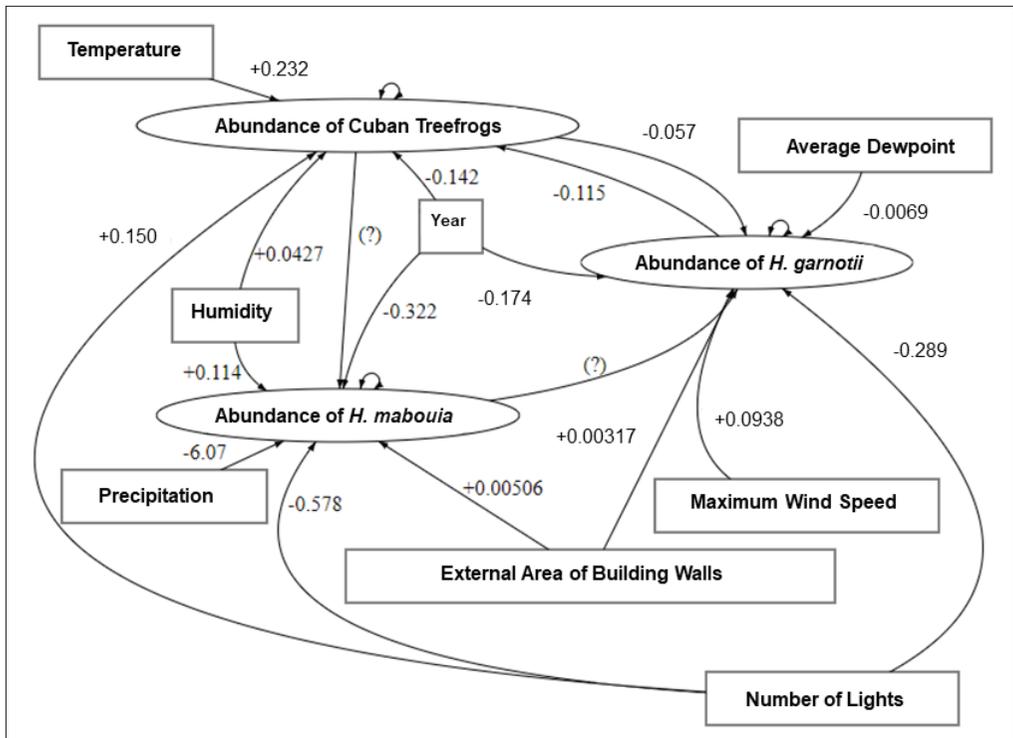


Figure 3. Structural Equation Model demonstrating interactions among the measured factors affecting abundance of the Cuban Treefrog, *Osteopilus septentrionalis*, Wood Slave, *Hemidactylus mabouia*, and Indo-Pacific Gecko, *H. garnotii*, on buildings of Florida Atlantic University, Jupiter, Palm Beach County, Florida. Numbers represent slopes from the regression.

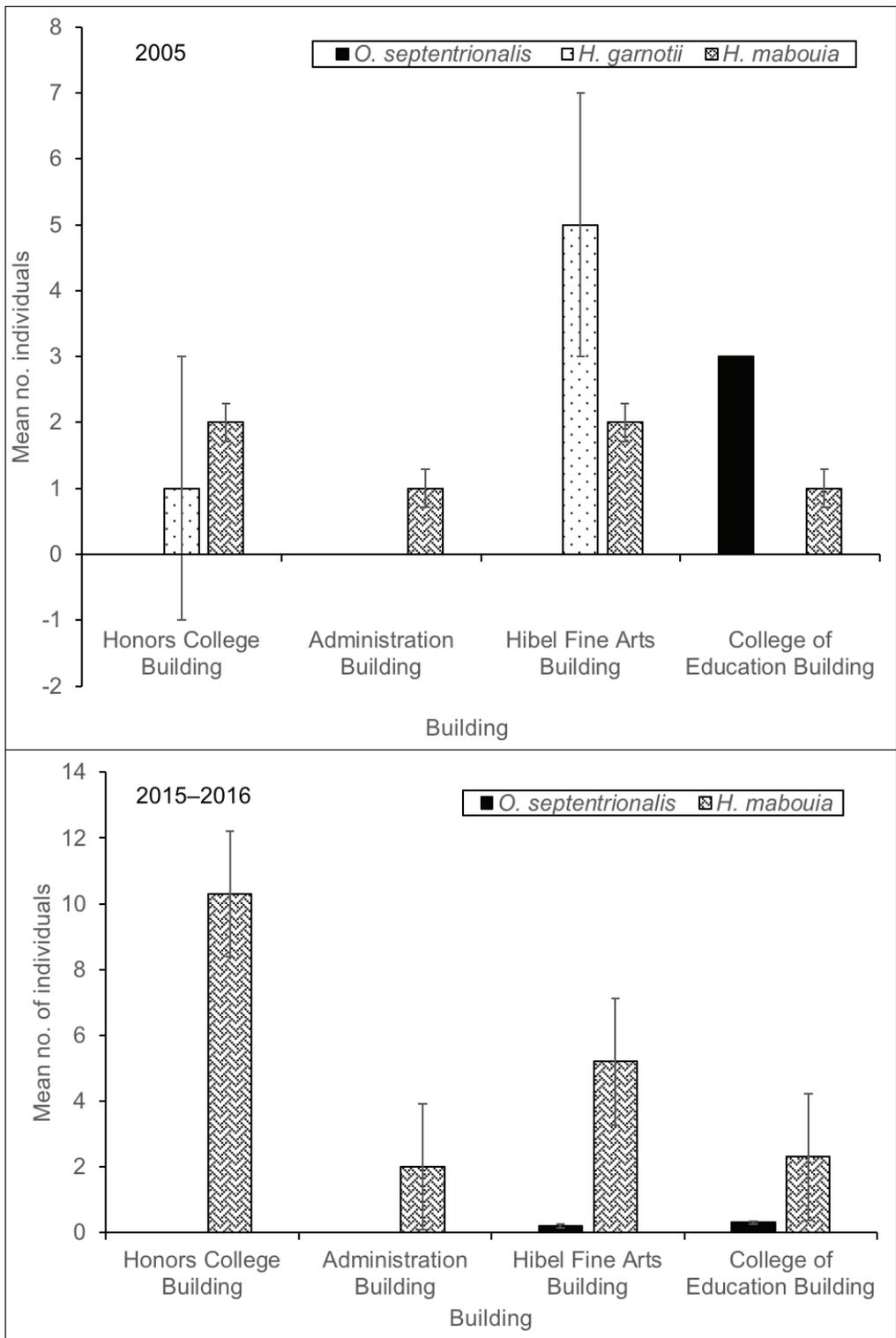


Figure 4. Mean number of the Cuban Treefrog, *Osteopinus septentrionalis*, Indo-Pacific Gecko, *Hemidactylus garnotii*, and Wood Slave, *H. mabouia*, counted on buildings on the campus of Florida Atlantic University, Jupiter, Palm Beach County, Florida, from overlapping buildings and in overlapping months of January–March in 2005 (Meshaka et al. 2006) and January–March 2015–2016 (this study). Standard error bars are in association with mean values.

(ANOVA: $F = 1.00$, df -source = 3, df -error = 36, $p = 0.404$). No meaningful relationships were observed between environmental variables and its activity.

Wood Slave. This species was more abundant in 2016 than in 2005 ($t = 2.58$, $p = 0.015$) (Fig. 4). The Wood Slave was not distributed differently among buildings between sampling years. Because those data were not normally distributed as determined using the Anderson-Darling Normality Test ($A^2 = 5.914$, $p < 0.000$), the data were transformed to meet the assumptions of the ANOVA ($F = 1.87$, $df = 44$, $p = 0.150$).

The Wood Slave abundance was inversely related to the number of lights ($t = -3.32$, $p = 0.002$), a resource exploited by its predator, the Cuban Treefrog. The larger buildings had more of these geckos ($t = 2.66$, $p = 0.12$). The Wood Slave was more common in later months than earlier ones ($t = 2.26$, $p = 0.031$). Individuals were more commonly observed when humidity was high ($t = 2.28$, $p = 0.30$), unless it rained, in which case more rain led to fewer observations ($t = -2.89$, $p = 0.007$).

The two best models included year, month, humidity, lights, and area, with one model also including abundance of the Indo-Pacific Gecko. The difference in these two models was that the Indo-Pacific Gecko explained only 0.3% more of the variation than the model excluding it. Furthermore, the regression was actually more accurate ($S = 3.50$ vs. 3.54) and more precise ($C-P = 5.5$ vs 3.7) when Indo-Pacific Gecko abundance was excluded from the model. Using general linear regression, this model was selected to best predict Wood Slave abundance on the buildings ($r^2 = 0.390$):

$$\text{Wood Slave abundance} = -660 - 0.322 \text{ year} + 0.114 \text{ humidity} - 6.07 \text{ precipitation} - 0.578 \text{ lights} + 0.00506 \text{ area}$$

The Indo-Pacific Gecko. This gecko was less abundant in 2016 than in 2005 ($t = -2.74$, $p = 0.010$) (Fig. 4). There were differences among buildings (ANOVA: $F = 5.54$, df -source = 3, df -error = 41, $p = 0.003$): Admin. (mean = 0.2, $SD = 0.422$) had fewer geckos than Hibel (mean = 3.0, $SD = 3.59$; Tukey: -5.066, -0.535), College (mean = 0.07, $SD = 0.258$) had fewer than Hibel (Tukey: 0.865, 5.002), Overall: mean = 0.96/building, $SD = 2.163$, $SE = 0.322$).

Abundance of lights reduced occurrence of this species ($t = -3.07$, $p = 0.004$), a finding contrary to that of its predator, the Cuban Treefrog. Larger buildings had more of these geckos ($t = 3.33$, $p = 0.002$). The presence of the Cuban Treefrog ($t = -0.39$, $p = 0.70$), the maximum wind speed ($t = 0.95$, $p = 0.349$), and dew point ($t = 0.24$, $p = 0.81$) did not independently influence abundance of this species. However, these factors interacted to provide a well-fit model predictive of Indo-Pacific Gecko abundance ($F = 3.83$, df -source = 6, df -error = 36, $p = 0.005$), such that this species was predictably distributed based on physical characteristics of the habitat. This regression model was selected to best predict Indo-Pacific Gecko abundance on buildings ($r^2 = 0.390$):

$$\text{Indo-Pacific Gecko abundance} = 344 - 0.174 \text{ year} + 0.0938 \text{ maximum wind speed} - 0.057 \text{ Cuban Treefrog abundance} - 0.289 \text{ lights} + 0.00317 \text{ area} + 0.0069 \text{ average dew point}$$

Discussion

The community structures examined on these buildings within and between years were strongly and differentially affected by combinations of their members and the structural variations of the building habitat. To those variables, we factored in physical conditions and time to provide predictive regression models and a flow chart (Fig. 3) that weighed the inter-

related biotic and abiotic factors to quantify outcomes in predator-competitor abundances. In that regard, each additional Cuban Treefrog resulted in a loss of 0.057 Wood Slaves.

Data from the 2015–2016 surveys corroborated the instability of an assemblage comprised of the Wood Slave and Indo-Pacific Gecko, the former of which is a superior competitor, a predator of very small geckos, and capable of quickly replacing its congener on buildings and in greater abundances (Meshaka and Moody 1996; Meshaka 2000; Meshaka et al. 2004, 2005, 2006a). Our study also supports the theory that the Cuban Treefrog, when present in sufficient numbers, has a dampening effect on the replacement of the Indo-Pacific Gecko by the Wood Slave. Our survey also corroborated the dampening effect to replacement by the predatory Cuban Treefrog when present in suitable numbers (Meshaka 2000, 2001; Meshaka et al. 2004, 2005).

Our findings identify the differential susceptibility of the Wood Slave to negative impacts by the Cuban Treefrog around lights as an important mechanism responsible for hindrance of faunal turnover by the Cuban Treefrog. Both gecko species are attracted to lights and consume many light-attracted prey (Meshaka 2000, 2001). The greater negative relationship to lights by the Wood Slave than the Indo-Pacific Gecko in the presence of the Cuban Treefrog, the counterintuitive positive relationship between the Indo-Pacific Gecko and the Cuban Treefrog in the presence of the Wood Slave, and the stabilizing effect of the Cuban Treefrog on the assemblage dynamics of the two geckos indicate that a differentially negative effect on numbers of the Wood Slave by predation, interference with foraging, or both occur in meaningful measure around lights. To that end, the Indo-Pacific Gecko is not territorial, it does not aggregate (Frankenberg 1982), it has a greater flight distance than the Wood Slave, and once startled runs farther away than the Wood Slave (Eifler et al. 2004). Adults of the Indo-Pacific Gecko are larger in body size, and juveniles are fewer on buildings with the Cuban Treefrog than on those without it (Meshaka et al. 2004). Consequently, the Cuban Treefrog may have a more difficult time capturing this species, especially adults, than the Wood Slave. The effect in dampening the otherwise negative outcome between the two species is all the more striking in light of the inclusion of small geckos in the diet of the Wood Slave. In the Cuban Treefrog, it would seem that the Indo-Pacific Gecko has an unexpected bodyguard, mediating competition and predation that follow colonization by the Wood Slave.

It remains to be seen what sort of effect the Cuban Treefrog has on other pairwise gecko assemblages comprised of the Wood Slave with either *H. frenatus* (Duméril and Bibron) (Common House Gecko) or *H. turcicus* (Linnaeus) (Mediterranean Gecko), both of which are also exotic to Florida and are both quickly replaced by the Wood Slave (Meshaka et al. 1994, 2004). The Mediterranean Gecko is now rare, if even present, in southern Florida (WEM and JM, pers. obs.), and, like the Indo-Pacific Gecko, also takes flight sooner and runs farther away than the Wood Slave from a perceived threat (Eifler et al. 2004). This behavioral trait should also be considered in evaluating the outcome of such an interaction with this species. As well, given the importance of lights in the Cuban Treefrog's neutralizing effect in Indo-Pacific Gecko replacement, we wonder if the Mediterranean Gecko's aversion to lights (Meshaka et al. 2006b) would be advantageous to its persistence on buildings with the Wood Slave and Cuban Treefrog or, for that matter, even with the Indo-Pacific Gecko by which it is also replaced (Meshaka 1994, 1995).

Lastly, we consider similar comparisons that could be explored where both the Cuban Treefrog and Wood Slave encounter native edificarian geckos. One such community might be Curaçao. There, mirroring its Florida history, the Wood Slave is well established since its initial introduction in the 1980s (Van Buurt 2005). The Wood Slave has all but replaced the

native *Phyllodactylus martini* Lidth de Jeude (Dutch Leaf-toed Gecko) on buildings, a habitat in which it was once common (Van Buurt 2010), with many more individuals (Hughes et al. 2015). Notably, this species was more often found away from lights, even if alone and could persist on Wood Slave-occupied buildings that were adjacent to forests (Hughes et al. 2015). *Gonatodes antillensis* (Lidth de Jeude) (Antilles Gecko), also native to Curaçao, is eaten by the Wood Slave (Dornburg et al. 2011) and partially excluded by it as well (Van Buurt in Hughes et al. 2015). The Wood Slave is no longer free of its competitor and predator on Curaçao, as a breeding population of the Cuban Treefrog was reported on the island in 2007 (Joubert-Bensink 2007). The population was derived from shipments of exotic plants from Miami, Florida, and palm trees from Cuba to a nursery. Unless eradication and prevention of imports are undertaken, island-wide colonization by the Cuban Treefrog seems inevitable to us. Should this occur, the population size response of native edificarian geckos to depredations by the Cuban Treefrog is uncertain, even as a drop in Wood Slave numbers is likely.

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