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# ECOLOGICAL RELATIONSHIPS AND SUCCESSION IN AN URBAN SOUTH FLORIDA HERPETOFAUNAL COMMUNITY DURING 2006–2021: A CASE STUDY

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Abstract.— Visual encounter surveys comprised a case study of urban ecology conducted along a 3.22 km sidewalk loop in a residential development in southern Florida during March 2006-June 2021. The Nautica, a gated residential development, was completed in the early 2000s and initial investigations of the herpetofauna began shortly thereafter. Species accumulation was rapid, with 10 native and 13 exotic species comprising the herpetofaunal community. The construction of Nautica occurred on a highly modified habitat in which many native species were marginalized and several exotic species, also already there, could take advantage of the subsequent structural and hydrological changes culminating in the creation of this subdivision. Colonization patterns, persistence, and abundance varied widely among species. Measurement of abiotic factors associated with standardized focal surveys provided information to predict the likelihoods of activity by members of the herpetofaunal community and the detection of interspecific interactions that affect their activity patterns. Exotic-species-dominated artificial systems are commonplace in southern Florida and bring with them a conservation need for awareness to understand the ways in which residential species interact with and impact their environment and other species, including avian predators and feral cats. To that end, in the nearly two decades since the construction of Nautica, the native terrestrial herpetofauna has remained depauperate, while exotic counterparts underwent accelerated colonization patterns, with one species possibly contributing to the persistence of a native lizard.

Keywords: colonization; ecology; herpetofauna; species succession; urban ecology

#### INTRODUCTION

The United States is home to 103 exotic species of amphibians and reptiles, 74 of which are not native to any part of the United States (Meshaka et al. 2022). Florida, like the world itself (Lever 2003, Kraus 2008), is replete with unparalleled exotic herpetofauna. Lizards, especially geckos and anoles, comprise most of Florida's 61 exotic herpetofauna (Meshaka et al. 2022), and most of the species excel around human-mediated disturbance, including human habitation (Meshaka 2011, Meshaka et al. 2022). Florida serves as a significant source area for human-mediated dispersal and faunal additions elsewhere in, as well as outside

of, the state. The present rate of exotic herpetofaunal species accumulation in the state and in the Southeast is indicative of a future of both greater range expansions of established exotic amphibians and reptiles, as well as colonizations of more new exotic species. Our study was initiated with the view of the importance of awareness to understand the ways in which residential species interact with and impact their environment and other species. Our case study aims to demonstrate one way in which these processes can operate within and among species in an overwhelmingly common urban development in a subtropical setting in southern Florida where exotic species can be successful.

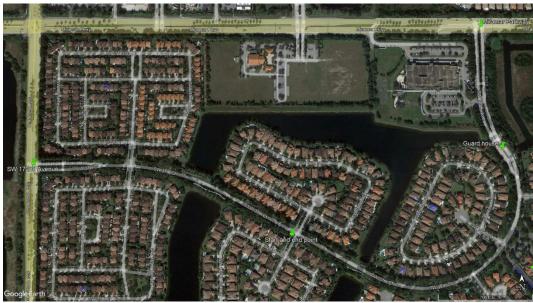


Figure 1. Google Earth image of Nautica, Miramar, Broward County, Florida.

In one such urban development in southeastern Florida, USA, Nautica, founders of an exotic herpetofaunal community existed in the disturbed habitat in advance of development in the early 2000s. Consequently, the colonization process was accelerated in establishment and success by some species, as the development was constructed concomitant with a pre-existing depauperate native fauna (Meshaka et al. 2008).

The same ecological principles at work in natural systems can be found in urban communities involving both native and exotic species. Within these communities, species replacement occurs in some of Florida's exotic geckos, often with many more individuals of the superior competitor (Meshaka 2000). Replacement can also be held at bay by the presence of an exotic treefrog differentially predatory to the geckos (Meshaka et al. 2020). In turn, many exotic amphibians and reptiles are eaten by native species (Meshaka 2011, Meshaka et al. 2022). Abiotic factors, such as structural changes in the habitat, can also lead to changes in the assemblage structure of anoles in southern Florida (Meshaka 2020, Meshaka et al. 2020). Our interest in the dynamics of the herpetofaunal community structure associated with interspecific interactions and habitat changes among resident and newly colonizing native and exotic species in an urban system led us to conduct a long-term ecological study of this site during 2006-2021; this is a case study heretofore unknown for urban south Florida.

# MATERIALS AND METHODS

## Habitat availability

The Nautica development, completed in 2001, is a private gated community in Miramar, Broward County, Florida (Figure 1), the herpetofauna of which was assessed from surveys during 2002–2007 (Meshaka et al. 2008). Prior to development of Nautica in the early 2000s, the habitat had been highly disturbed. In its place, the subdivision was lushly planted with native and exotic trees and bushes (Meshaka et al. 2008) (Figure 2). A mosaic of shaded and open areas comprises the urban habitat traversing the main road that connects the two entrances.

Interspersed along the way are canals and borrow pits of various sizes for flood control. Homes within named sections of Nautica vary in size and proximity to water. Over the ensuing decades, trees, such as West Indian Mahogany, *Swietenia mahagoni*, and, more so, Royal Poinciana, *Delonix regia*, have both grown into specimens that provide greater shade and have been cut back from a series of hurricanes. Thus, the survey area comprised a spatial and temporal mosaic of shade. Nearly continuous hedges were set back from the sidewalk, the base of which provided hunting and basking areas for Brown Anoles, *Anolis sagrei*. Trees interspersed among the hedges or apart from them provided vertical structure to all of the lizards observed in this study.

Private plantings varied, but most properties were little shaded. Grassy strips alongside the sidewalks are bare or planted primarily with Live Oak, *Quercus virginiana*. Circular cement borders placed around trees subsequently provided refuges for Curly-tailed Lizards, *Leiocephalus carinatus*, and Brown Anoles, which they include in their diet.

### Survey methods

The standardized survey protocol of this study follows that of Meshaka et al. (2008). The 3.22 km roundtrip diurnal walks were followed along the semi-shaded SW 37th Court, a 1.60 km road bound between Miramar Parkway to the north and SW 172 Street to the west (Figures 1 and 2a-e). The start/end point was the intersection of SW 37th Court and SW 167th Terrace, the entrance to the Fantasy Isle neighborhood. Morning surveys commenced eastward from the point, and afternoon surveys commenced westward from the point. The edges of six shorelines were included in the surveys. Standardized survey data of Meshaka et al. (2008) are included with those of this study, resulting in 165 surveys during 25 March 2006-10 June 2021. All months except for August, when surveys were not possible, were sampled. Survey times across months and years began between 0841 and 1921 hrs, with most surveys taking place between 1000 and 2000 hrs (Figures 3 and 4).











Figure 2. (a) View of Nautica, Miramar, Broward County, Florida, from the main Miramar Parkway entrance. (b) View of Nautica, Miramar, Broward County, Florida, rear entrance at SW 172nd Avenue, October 2018. (c) View of hurricane damage at Nautica, Miramar, Broward County, Florida, October 2017. (d) Westward view of (southwest) pond at Nautica, Miramar, Broward County, Florida, October 2018. (e) Westward view of (southeast) pond at Nautica, Miramar, Broward County, Florida, March 2019. All photographs by W.E. Meshaka, Jr.

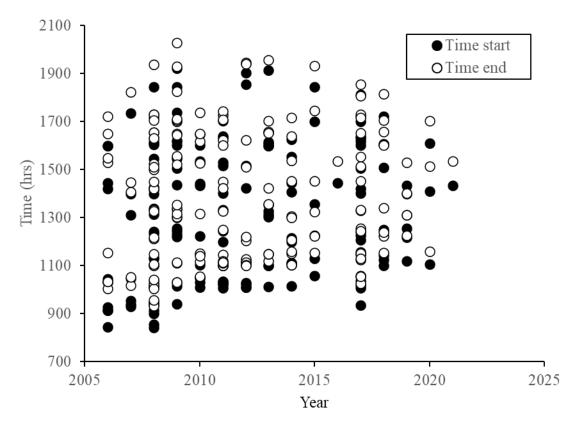


Figure 3. Time of day associated with surveys by year of Nautica, Miramar, Broward County, Florida.

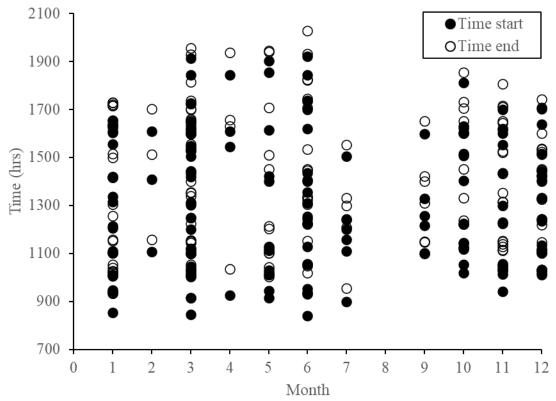


Figure 4. Time of day associated with surveys by month of Nautica, Miramar, Broward County, Florida.



Figure 5. Accumulation curve of 23 amphibian and reptile species detected at Nautica, Miramar, Broward County, Florida, during 2002–2021.

Records of the Greenhouse Frog, Eleutherodactylus planirostris, were represented exclusively by call on standardized walks. Calling by the Cane Toad, Rhinella marina, was noted, as were visits associated with the presence of tadpoles, and individuals, live or dead, were counted. Thus, The Greenhouse Frog and Cane Toad tadpoles are not included in the percentages of individuals of a given species. The Brahminy Blindsnake, Indotyphlops bramina, previously reported from the study site (Meshaka et al. 2008), was also excluded in survey numbers because of strongly fossorial habits. The Florida Brownsnake, Storeria victa, was also detected in the development and is included in the species list of Nautica; however, because it was never seen along the route, it is not included in survey numbers. Potential vertebrate predators of segments of the herpetofauna were also counted beginning 14 June 2007: Northern Mockingbird, Mimus polyglottos, Blue Jay, Cyanocitta cristata, American Crow, Corvus brachyrhynchos, Loggerhead Shrike, Lanius Iudovicianus, Red-shouldered Hawk, Buteo lineatus, and feral cat, Felis catus.

## Statistical Methods

We analyzed the data using applied linear models. The number of animals observed during each sampling period was divided by the amount of time spanned by each respective visit and expressed as observations/hour. Those factors were then ranked starting at 0=0 observations. All rankings were subsequently scaled by dividing each ranking by the value of the highest ranking for that species and multiplying the quotient by 100. The resulting value provided an output ranging 0–100 that could be analyzed for trends. These scaled ranked values were used as the response variable in best subsets regression with the assortment of potential predictors collected each period. The resulting selection of regression models was evaluated using  ${\bf r}^2,\ {\bf r}^2_{\rm adj},\ C_{\rm p},\ {\bf s},\ {\bf VIF},\ {\bf and}\ {\bf PRESS}.$  High

 $r^2,\ r^2_{adj,}$  and s were deemed supportive of the respective model, as was low VIF. A  $C_p$  with a value similar to the number of predictors in the model also supported acceptance of a model. If PRESS was less than or equal to the total sum of squares (SST) for the regression, it was considered acceptable.  $r^2=$  precision of the regression model. s= standard error of the regression for accuracy of the regression. Cp = Mallows' statistic. PRESS = predicted sums of squares. VIF = variance inflation factors. All of these statistics were used in consort to select the best model/s for each species. Where applicable, alpha < 0.05 was assessed for significance.

## **RESULTS**

Species Composition of the Herpetofaunal Community

Twenty-three species of amphibians and reptiles were detected at Nautica during 2002–2021 (Figure 5). Among them, 10 of the species were native, and 13 species were exotic. All three anurans were exotic. Eight of the ten lizard species were exotic. Only one of six snake species was exotic and one of four turtle species was exotic.

Species Accounts Anura: Bufonidae

Cane Toad (Rhinella marina)—The Cane Toad comprised 0.05% of all amphibians and reptiles and 83.3% of frogs and toads, with five standardized records of post-metamorphic individuals. The first detection of this species was opportunistic in 2002. Two dead individuals were seen on 6 January 2008. A smashed adult was found on 16 June 2009. An adult was seen in the water looking out of a culvert near the guard house between 1638 and 1709 hrs. on 9 December 2011. The last individual, of ca. 100 mm in snout-vent length, was seen between 1142 and 1238 hrs. on 13 October 2018. It was alert atop a Ficus sp. root in the shade. The toad had

the appearance of sweating. The ambient temperature was 30 °C, and wind speed was 4.83 km/hr. Cloud cover was 25%. Choruses were heard opportunistically at night on 14 March 2019. The ambient temperature was 27.2 °C, and wind speed was 24.1 km/hr. Tadpoles were seen during January-April, May, June, and July. At least two distinct size classes of tadpoles were seen on 24 March 2009 (Figure 6), 23 March 2018, and 12 March 2019. Large tadpoles were seen on 25 March 2011, and recently hatched but free-swimming tadpoles were seen on 30 April 2008. Multiple size classes of tadpoles were seen on 16 July 2017. The absence of August surveys precludes determination of breeding in that month; however, the absence of eggs or tadpoles on the 4-9 September 2013 and 4-7 September 2019 visits, and none in the remaining months, infers a low likelihood of new clutches in August.



Figure 6. Multiple size and age classes of the Cane Toad, *Rhinella marina*, at the Nautica development in Miramar, Broward County, Florida. 24 March 2018. Photo by W.E. Meshaka, Jr.

Anura: Hvlidae

**Cuban Treefrog (Osteopilus septentrionalis)**—The Cuban Treefrog comprised 0.01% of all amphibians and reptiles and 16.7% of frogs and toads. The single individual, represented by a dried carcass of a large female, was found on the raised base of a pole near the entrance quard house during a survey on 28 March 2013.

Anura: Leptodactylidae

**Greenhouse Frog (***Eleuthrodactylus planirostris***)**—The first detection of the Greenhouse Frog was opportunistic when seen at night on 18 January 2007 (Meshaka et al. 2008). This species was heard calling three times on surveys: 18 June 2009 at 1921–2029 hrs., sultry, 100% cloud cover, 28.9 °C ambient air temperature; 17 May 2012 at 1902–1945 hrs, sultry, 100% cloud cover, 25.6 °C ambient air temperature, wind speed of 11.1 km/hr; 9 July 2014 at 1200–1300 hr, 50% cloud cover, 31.7 °C ambient air temperature.

Testudines: Emydidae

Florida Red-bellied Turtle (*Pseudemys nelsoni*)—The Florida Red-bellied Turtle comprised 0.08% of all amphibians and reptiles and 43.75% of turtles, with seven standardized records. The first detection of this species was on a survey on 18 March 2010, when an adult was seen in the wetland near the Miramar Parkway entrance. Individuals were seen in February, March, May, September, and October during 1022–1648 hrs, active in ambient air temperatures of 20.0–33.4 °C, cloud cover of 0–75%, and wind speeds ranging 7.6–14.5 km/hr. Two

was the maximum number of individuals encountered in a survey. A pair was seen courting on 19 May 2012 between 1022 and 1113 hrs. An adult pair was seen next to one another on 13 October 2018 between 1604 and 1706 hrs. A large female was observed feeding at the water's surface on 4 September 2019 between 1218 and 1310 hrs. The ambient air temperature was 33.4 °C.

Peninsula Cooter (*Pseudemys peninsularis*)—The Peninsula Cooter comprised 0.03% of all amphibians and reptiles and 18.75% of turtles, with three standardized records. The first detection of this species was on a survey on 7 September 2013. Between 1101 and 1148 hrs, a large female was basking along the shoreline. Conditions were 25.0 °C, 100% cloud cover, and a wind speed of 7.56 km/hr. Another large female was seen on 24 January 2017 immediately out of the water by the wetland at the Miramar Parkway entrance. Conditions were 25.0 °C, 0% cloud cover, and a wind speed of 22.4 km/hr. The third individual was also a large female basking at the shore of the previous record. Conditions were 28.3 °C, 75% cloud cover, and a wind speed of 20.9 km/hr.

**Red-eared Slider (***Trachemys scripta elegans***)**—The Red-eared Slider comprised 0.05% of all amphibians and reptiles and 31.25% of turtles, with five standardized records. The first detection of this species was in a survey on 25 March 2006, when, between 1045 and 1145 hrs, two individuals were observed basking. The ambient air temperature was  $20.0\,^{\circ}\text{C}$ , and the wind speed was  $24.1\,^{\circ}\text{km/hr}$ . The next individual was seen on 16 July 2017. A juvenile was seen basking on 18 October 2017, when ambient air temperature was  $28.9\,^{\circ}\text{C}$ , and wind speed was  $14.5\,^{\circ}\text{km/hr}$ . in 75% cloud cover. A melanistic individual was seen on  $12\,^{\circ}\text{February}$  2020. Individuals were active in ambient air temperatures of  $20.0-29.5\,^{\circ}\text{C}$ , cloud cover of 75% (n = 1), and wind speeds ranging  $8.0-24.1\,^{\circ}\text{km/hr}$ .

Testudines: Trionychidae

**Florida Softshell (Apalone ferox)**—The Florida Softshell comprised 0.01% of all amphibians and reptiles and 6.25% of turtles, with one standardized record. The first detection of this species was in a survey on 25 January 2017. Between 1006 and 1054 hrs, a large adult was seen in shallow water. Conditions were 22.2 °C, 0% cloud cover, and a wind speed of 9.33 km/hr.

Squamata: Corytophanidae

Brown Basilisk (Basiliscus vittatus)—The Brown Basilisk (Figure 7) comprised 2.21% of all amphibians and reptiles and 2.22% of lizards, with 204 standardized records. The first detection of this species was opportunistic in April 2005, the first warm month of the study (Meshaka et al. 2008). Individuals were seen in every month of the study, with the highest numbers during June-October (Figure 8). The greatest activity was during the middle of the afternoon (Figure 9a), when the air temperature was warm (21.7–35.0  $^{\circ}$ C), especially when ranging 29.4–31.7  $^{\circ}$ C (Figure 9b), and in a wide range of cloud cover (Figure 9c). However, activity dropped off in wind speeds exceeding 22.5 km/hr (Figure 9d). Ten was the maximum number of individuals encountered on a survey. Young of the Year (YOY) were seen on 15 and 31 October 2017 and 12-13 November 2010. Five individuals were hanging face-upwards on a tree above water on 25 January 2017 between 1637 and 1722 hrs, with a clear sky, 24.4 °C ambient temperature, and 18.3 km/hr wind speed. All appeared to be sub-adults and seemed to be resting with the sun facing their backs. Throughout



Figure 7. An adult male Brown Basilisk, *Basiliscus vittatus*, at Nautica, Miramar, Broward County, Florida. Photo by W.E. Meshaka, Jr.

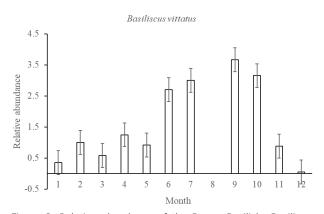


Figure 8. Relative abundance of the Brown Basilisk, *Basiliscus vittatus*, expressed per no. survey days per month from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

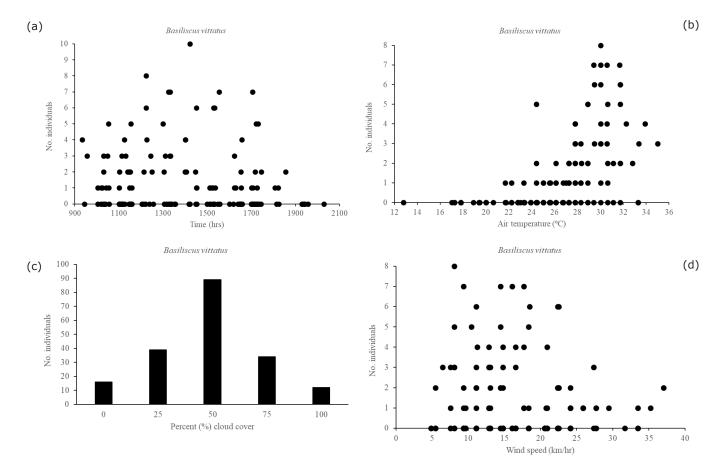


Figure 9. Activity of the Brown Basilisk, *Basiliscus vittatus*, from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. (a) Time of the day; (b) ambient air temperature; (c) percent cloud cover; (d) wind speed.

the study, individuals were seen along the east side of SW 172nd Avenue between the guard house and the Miramar Parkway entrance, which was bordered by water. Individuals were occasionally seen on the west side of the main entrance, across the street opposite the main colony and nearest water source. Associated with a water source, individuals were also occasionally seen on the west side of the guard house. Sightings elsewhere along the survey route increased over time. The first evidence of dispersal along the route was on 19 May 2012, when an adult Brown Basilisk was seen almost directly across from the clubhouse, 0.21 km west of the closest main entrance water, 0.23 km from water west of the sighting, and 0.15 km from water behind the clubhouse. On 16 July 2017, a large male Brown Basilisk was at the far end for the route at SW 172nd Avenue, 0.06 km from water to the west on the other side of 172nd Avenue and 0.34 km from the pond east in development. On 13 October 2018, an adult was seen 0.05 km from the rear entrance. On 12 March 2019, a Brown Basilisk was seen at a pond 0.58 km west of entrance colony. On 7 September 2019, two individuals were seen near the rear entrance on the south side. On 10 June 2021, an individual was seen on the sidewalk near a pond 0.97 km from water at main entrance, and on 10 June 2021, an individual was seen along the route at 36th Drive, 0.11 km from the nearest water. Best subsets regression provided several models with high precision ( $r^2 > 0.410$ ), but we settled on a five-predictor model because it had high initial precision ( $r^2 = 0.412$ ) that remained high after adjustments  $(r_{adj}^2 = 0.390)$ . This subset was also highly accurate (s = 24.901) and provided an acceptable Mallows statistic  $(C_n = 4.2)$ . This included the year, month, ambient temperature, wind speed, and feral cat observations. This model was:

scaled rank = 4589 + 2.25 year - 0.725 month + 3.96 ambient temperature - 0.340 wind speed - 3.18 feral cat

Observations of the brown Basilisk increased during the study (T = 4.02, p < 0.001). Observations declined as the year went on, although it was most abundant in summer, leading to a non-significant relationship (T = -1.33, p = 0.185). Observations were closely tied to warmer temperatures (T = 7.00, p < 0.001). Higher wind speeds tended to reduce observations, but not significantly (T = -1.09, p = 0.277). Feral cat abundance superficially appeared to directly reduce observations, but the relationship is probably hampered by complex interactions among other variables (T = -1.10, p = 0.273).

## Squamata: Dactyloidae

North American Green Anole (Anolis carolinensis) — The North American Green Anole (Figure 10) comprised 0.35% of all amphibians and reptiles and 0.36% of anoles, with 32 standardized records. The first detection of this species was opportunistic in 2003 (Meshaka et al. 2008). Individuals were seen in almost every month of the study, with the highest numbers in February and September (Figure 11). The greatest activity was between 1000 and 1700 hrs (range = 0933-1723 hrs) (Figure 12a), when air temperature was warm (21.7-35.0 °C), especially 23.9-33.9 °C (Figure 12b), and somewhat cloudy (Figure 12c). Individuals were most apt to be active in wind speeds ≤ 17.7 km/hr, and none were seen in wind speeds in excess of 27.7 km/hr (Figure 12d). Three was the maximum number of individuals encountered on a survey. Observance of this species was somewhat as-



Figure 10. A displaying male North American Green Anole, *Anolis carolinensis*, at Nautica, Miramar, Broward County, Florida. Photograph by W.E. Meshaka, Jr.

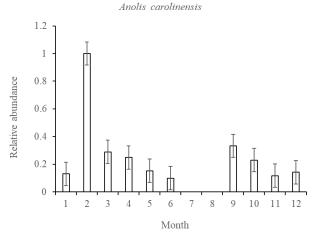


Figure 11. Relative abundance of the North American Green Anole, *Anolis carolinensis*, expressed per no. survey days per month from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

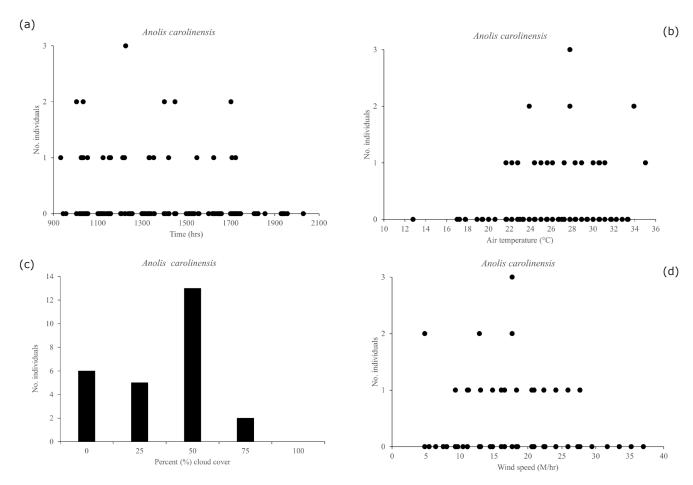


Figure 12. Activity of the North American Green Anole, *Anolis carolinensis*, from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. (a) Time of the day; (b) ambient air temperature; (c) percent cloud cover; (d) wind speed.

sociated (F = 4.58, df<sub>predictor</sub> = 7, df<sub>error</sub> = 137, p < 0.001) with the complex interaction of several predictors ( $r^2 = 0.190$ , s = 0.4259) in the following regression equation (PRESS = 29.40, SST = 30.66):

Anolis carolinensis (n) = 0.277 - 0.002 (% cloud cover) - 0.159 (cats present) - .001 (scaled ranked Anolis sagrei [n]) + 0.008 (scaled ranked Hemidactylus mabouia [n]) - 0.001 (scaled ranked Basilicus vittatus [n]) - 0.003 (scaled ranked Northern Mockingbirds [n]) + 0.007 (scaled ranked Blue Jay [n])

This species was observed more frequently when there was less cloud cover and smaller numbers of the feral cat, Brown Anole, Brown Basilisk, and Northern Mockingbird, but higher numbers of the Blue Jay and Wood Slave were observed. The effects of the Northern Mockingbird, Brown Basilisk, and Brown Anole were not in and of themselves significantly impacting observations/numbers of the North American Green Anole. There appears to be a complex interaction among these variables that we are not yet able to elucidate. This is the only species that was influenced by observations of other members of the herpetofauna or avifauna. Displaying males were seen 12 March 2019 between 1120 and 1226 hrs. A juvenile was seen on 7 September 2019. An adult was found

squished on the sidewalk on 25 January 2017 between 1006 and 1054 hrs. **Bark Anole (***A. distichus***)**—A single adult Bark Anole

was observed on 9 January 2008. It was greenish in col-

or. No other records exist for this species in this study. Knight Anole (A. equestris) - The Knight Anole (Figure 13a and b) comprised 3.30% of all amphibians and reptiles and 3.39% of anoles, with 303 standardized records. The first detection of this species was opportunistic in April 2005 (Meshaka et al. 2008). Individuals were seen during March-December, with the highest numbers peaking unimodally in the hottest months (Figure 14). The greatest activity was between 1029 and 1619 hrs (Figure 15a), when the air temperature was at least 23.3 °C, and especially  $\geq$  30.0 °C to a maximum of 35.0 °C (Figure 15b), and with light to moderate cloud cover (Figure 15c). Activity diminished quickly when wind speed exceeded 22.4 km/hr (Figure 15d). Fourteen was the maximum number of individuals encountered during a survey. Best subsets regression returned three models with strong precision ( $r^2 > 0.525$ ). Of these, three models had identical adjusted precision ( $r^2 = 0.507$ ). One had five predictors, whereas the other two had six predictors. We chose the model with fewer predictors (n =5) because the added predictors provided no increase in





Figure 13. Adults of the Knight Anole, *Anolis equestris*, hunting at different heights from the ground (a, b). Photograph by W.E. Meshaka, Jr.

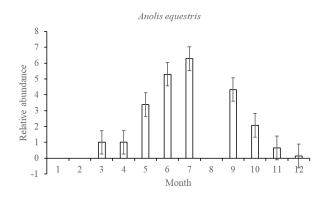


Figure 14. Relative abundance of the Knight Anole, *Anolis equestris*, expressed per no. survey days per month with 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

precision and one six-predictor model had the same accuracy (s=22.490) while the other only improved accuracy 0.8% (s=22.490 vs. 22.498). The selected model had acceptable VIF (all < 1.21) and its PRESS (=79,792) was in line with the regression error (SST = 153,206). The model was:

scaled rank = 3424 - 1.76 year - 1.50 month + 5.99 ambient temperature - 0.503 km/hr wind speed - 1.40 feral cats

where year, month, temperature, and feral cats were handled as reported with the Brown Anole, and wind speed was in km/hr. Observations of the Knight Anole markedly declined throughout the study (T = -3.40, p =0.001). Individuals were more commonly observed early in the year than later (T = -2.99, p = 0.003), and warmer temperatures led to more observations (T = 11.46, p< 0.001). Feral cat abundance appeared to reduce observations, but insufficient data precluded any confirmation of a statistically significant relationship. Displaying males were observed on 18 May 2012, 9 July 2014, 6 September 2013, and 7 September 2019. A male was opportunistically seen displaying on 4 September 2019. On 10 June 2015, between 1700 and 1746 hrs, a young pair of Knight Anoles was moments from copulating, with male behind and on top of the female on a horizontal branch of a Mahogany in the shade. The ambient air temperature was 28.9 °C, with 50% cloud cover and a 11.1 km/ hr wind speed. A young individual in a Ficus sp. hedge was captured by a cat, which then ran across the street with its prey. An adult was observed stalking a conspecific YOY on 18 November 2009 during 1230-1317 hrs. Brown Anole (A. sagrei)-The Brown Anole (Figure 16) comprised 92.90% of all amphibians and reptiles and 96.24% of anoles, with 8597 standardized records. The first detection of this species was opportunistic in 2002 (Meshaka et al. 2008). Individuals were seen in every month of the study, with the highest numbers during September-February (Figure 17). The greatest activity was between 1000 and 1700 hrs (Figure 18a), and across a broad range of air temperatures (17.2-35.0 °C), especially 23.9-31.1 °C (Figure 18b). Activity oc-

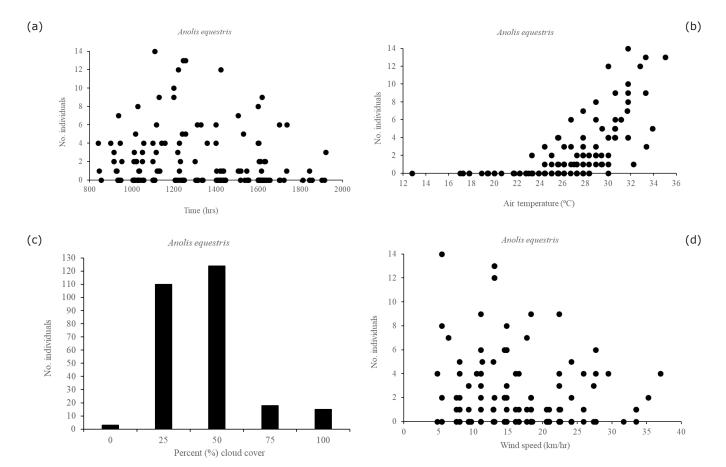


Figure 15. Activity of the Knight Anole, *Anolis equestris*, from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. (a) Time of day; (b) ambient air temperature; (c) percent cloud cover; (d) wind speed.

curred through a broad range of cloud cover, with most activity at 50% cloud cover (Figure 18c); activity tapered off at wind speeds > 25.9 km/r (Figure 18d). Two hundred thirty-three was the maximum number of individuals encountered on a survey. Best subsets regression returned four models with relatively high precision (r<sup>2</sup> > 0.20). All of these had reasonable accuracy (26.76 < s < 26.96). The Mallows statistic narrowed this to two equations. The first of these left off wind speed and the second excluded the year in which data were collected  $(C_n = 6.1)$  from among the predictors. We selected the model excluding wind speed because it had the marginally higher precision ( $r^2 = 0.224$  vs. 0.223) and adjusted precision ( $r_{adj}^2 = 0.188$  vs. 0.187), a smaller Mallows statistic ( $C_p = 6.1$  vs. 6.0), and higher accuracy (s = 26.859vs. 26.866). This model also had acceptable PRESS (= 107888) compared to the total error (TSS = 122381). The model produced was:

scaled rank = 104 - 0.049 year + 2.30 month + 0.077 cloud cover - 25.9 raining + 1.13 ambient temperature + 2.24 feral cats

where the year is that year in which observations were made, the month (January = 1) is the month expressed numerically in which observations were made. Cloud cover is expressed as a percentage, raining is posed as yes = 1, no = 0, the ambient temperature is in Celsius,

and the number of cats observed = feral cats. Complex interactions undetected among the variables studied are presumed to be responsible for the decline in numbers since the beginning of the study. This species was less detectable when it was raining and more detectable as cloud cover and air temperatures increased. The number of feral cats increased as lizard numbers increased, suggesting they were attracted to the easy prey, but there is insufficient evidence that the number of cats present was sufficient to reduce the population size.

Displaying males were seen along the survey route on the following dates: 22 March 2018, 17–21 May 2012, 10 June 2021, 16 June 2009, 9 July 2014, 12 October 2018, 2 and 3 November 2017, 17 and 18 November 2009. One opportunistic record exists for 4 September 2019. Pairs in copula were observed 29 March 2011 between 1007 and 1101 hrs, and 30 April 2008 at 1900 hrs. On 6 September 2013, two males appeared to have squared off in an agonistic encounter. YOY were seen and in abundance 18 May 2012, 6 June 2013, 16 July 2017, 6 September 2013, 16 and 17 November 2009.

# Squamata: Gekkonidae

**Wood Slave** (*Hemidactylus mabouia*)—The Wood Slave comprised 0.27% of all amphibians and reptiles and 0.27% of all lizards, with 25 standardized records. The first detection of this species was opportunistic in 2002 (Meshaka et al. 2008). Individuals were seen in



Figure 16. An adult male Brown Anole, *Anolis sagrei*, displays at Nautica, Miramar, Broward County, Florida. Photograph by W.E. Meshaka, Jr.

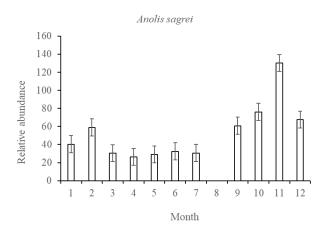


Figure 17. Relative abundance of the Brown Anole, *Anolis sagrei*, expressed per no. survey days per month from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

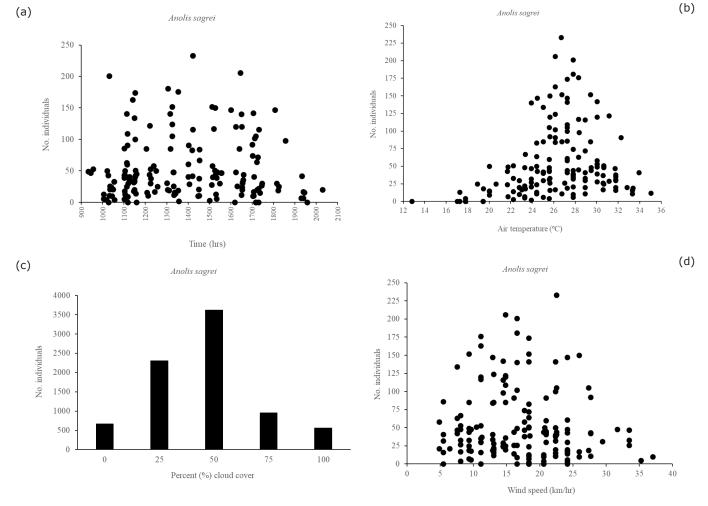


Figure 18. Activity of the Brown Anole, *Anolis sagrei*, from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. (a) Time of the day; (b) ambient air temperature; (c) percent cloud cover; (d) wind speed.

almost every month of the study, with the highest numbers in September (Figure 19). The greatest activity was between 1102 and 1730 hrs and when the air temperature was warm (24.5-31.8 °C); however, three individuals were seen when air temperature was 12.8 °C. The most activity occurred in somewhat cloudy conditions, and nearly all individuals were seen in wind speeds  $\leq$ 22.5 km/hr, and none in wind speeds in excess of 27.7 km/hr (Figure 20). Three was the maximum number of individuals encountered on a survey. Individuals basked occasionally. Two individuals were basking on trees on 20 May 2012 (27.8 °C, with 50% cloud cover, and a wind speed of 9.3 km/hr). Shade was used in hot weather. An individual was resting in a shady spot on 6 September 2013 (31.7 °C, 50% cloud cover, and wind speed of 14.8 km/hr). An adult male and a juvenile were each sitting alongside their respective retreats in the shade on 11 June 2015 (31.7 °C, 50% cloud cover, and wind speed of 22.4 km/hr). One individual was perched face-down on a palm tree on 12 December 2011 (24.5 °C, 50% cloud cover, and wind speed of 12.9 km/hr), perhaps to ambush prey (Persaud et al. 2003). We do not know the purpose of this behavior. A YOY was seen on 15 October 2017. Best subsets regression revealed no relationships with sufficient precision (all  $r^2 < 0.029$ ) to deduce relationships, likely due to an insufficient number of observations.

#### Squamata: Iquanidae

Green Iguana (Iguana iguana) - The Green Iguana comprised 0.08% of all amphibians and reptiles and of all lizards, with seven standardized records. The first detection of this species was opportunistic in 2004 (Meshaka et al. 2008). A YOY was seen on a pink Trumpet Tree, Tabebuia heterophylla, in November 2005, and a young male was seen basking on a Ficus sp. hedge on 21 January 2007. No other Green Iguanas were seen until 24 January 2017, when a large male was seen near water at the main entrance. On 15 October 2017, the first visit since Hurricane Irma, a ca. 60 cm TL individual was seen basking on a fallen branch (Figure 21). On 12 October 2018, two adults were basking near the shore of the southwest lake. On 14 March 2019, at the same lake, a large and very spiny male was seen soaking in the grassy shallow water near shore. On 18 February 2020, an adult dropped into the water from a Cocoplum, Chrysobalanus icaco, near the Miramar Parkway entrance. No individuals were seen on the last visit of 10 June 2021. Individuals were active in ambient air temperatures of 21.7-32.3 °C, during 1020-1630 hrs, with a cloud cover of 0 and 75%, and wind speeds ranging 16.1-27.7 km/hr. Three was the maximum number of individuals encountered on a survey.

#### Squamata: Leiocephalidae

Northern Curly-tailed Lizard (Leiocephalus carinatus)—The Northern Curly-tailed Lizard comprised 0.26% of all amphibians and reptiles, and of lizards, with 24 standardized records. The first detection of this species was opportunistic on 10 November 2010; a young adult perched on a rock on the north side of the rear entrance. New mulch applied to the area may have been the source of its dispersal. Subsequent sightings took place during 2017–2021 (Figure 22). A young adult was seen on 1 and 2 November 2017 a few blocks east of the rear entrance, also on the north side, and a large adult was seen perched at the entrance to the neighborhood directly across the street from the survey start and end point

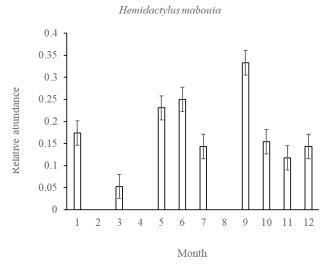


Figure 19. Relative abundance of the Wood Slave, *Hemidactylus mabouia*, expressed per no. survey days per month from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

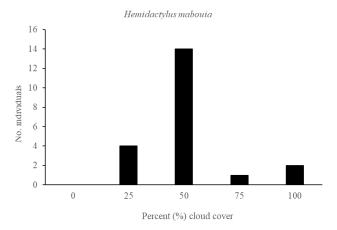


Figure 20. Percent cloud cover associated with activity of the Wood Slave, *Hemidactylus mabouia*, from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021.

on 2 November 2017. Two juveniles were seen on rocks on the north side of the rear entrance, and an adult was on the sidewalk near the rear entrance gate on 13 October 2018 (1142–1238 hrs). On the same day, between 1604 and 1706 hrs, three juveniles were perched on the same rock, an adult was on the sidewalk near the gate, and a fourth individual was seen on the west side of the Miramar Parkway entrance. On 12 March 2019, an adult was perched on a palm tree near the rear entrance, and two days later, an adult was perched on the median strip directly across the street from the start and end point. On 12 February 2020, one, and later in the day, two individuals were seen perched on rocks on the north side of the rear entrance. Two individuals were at the same site on 18 February 2020. On 10 June 2021, an adult



Figure 21. A young Green Iguana, *Iguana*, rests on fallen branches from a hurricane, at Nautica, Miramar, Broward County, Florida, 15 October 2017. Photograph by W.E. Meshaka, Jr.

was seen perched ca. 65 cm above ground on a Coconut Palm, *Cocos nucifera*, near the first lake immediately west of the start–end point, and a large individual was seen near the rear entrance gate on the south side, and another on the north side.

The temporal-spatial pattern of records points to the colonization of the route moving eastward from the establishment of a colony at the north side of the rear entrance during the last five years of the study. To that end, a thriving population of this species was detected on 14 October 2018 at 1720-1735 hrs, in the neighborhood of 170th, which is directly behind the north side rear entrance upon whose rocks and sidewalk individuals were most commonly encountered on surveys. Steady observations along the survey route since 2017 also coincided with the detection of a small colony in July 2017 in adjoining Fantasy Isle, located close to the survey starting point. Two adults and five or six juveniles remained in close proximity to the cover of a water meter alongside the sidewalk. This isolated group persisted through subsequent surveys conducted in Fantasy Isle during October 2018-June 2021. There, the main population of up to 37 individuals/≤ 20 min walk was located in a clumped distribution towards the rear of the neighborhood, and was otherwise unseen on the walk to the main study area. By the end of the Fantasy Isle survey, individuals were seen throughout the neighborhood, including its entrance near the starting point of the main route of this survey.

Individuals along the route were seen during 1057–1604 hrs, with ambient air temperatures of 25.6–30.0 °C, in all but complete cloud cover, and with wind speeds of  $\leq 24.1$  km/hr. However, because of the uncertainty associated with its status, few conclusions can be derived from its activity data along the route.

Squamata: Scincidae

**Southeastern Five-lined Skink (***Plestiodon inexpectatus***)**—The Southeastern Five-lined Skink comprised 0.04% of all amphibians and reptiles and of lizards, with four standardized records. The first detection of this species was during a survey on 20 March 2006. Subsequent records were 17 June 2007 (n = 1) and 24 March 2009

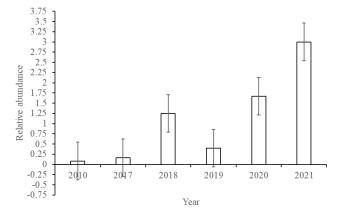


Figure 22. Relative abundance of the Northern Curly-tailed Lizard, *Leiocephalus carinatus*, expressed per no. survey days per year from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

(n = 2). A single individual was active in an ambient air temperature of  $28.9\,^{\circ}$ C. Individuals were active during 953-1505 hrs, in cloud cover of 50 and 100%, and wind speeds ranging from 8.1-33.5 km/hr.

Squamata: Teiidae

**Giant Ameiva** (*Ameiva ameiva*)—The Giant Ameiva comprised 0.11% of all amphibians and reptiles, and of lizards, with 10 standardized records. This species was first seen during an opportunistic visit in April 2005. An individual was next seen on 25 March 2006. Individuals were not seen again until 2008: 6–8 January (n = 3), 30 April 2008 (n = 2), and 14–16 December (n = 3). All but one 2008 individual (ca. 40–50 mm SVL) were adults. The next and last sighting was of a large juvenile between the gate and rear entrance on 10 June 2021. Individuals were active in ambient air temperatures of  $20.0-30.0~^{\circ}\text{C}$ , with cloud cover of 25-100%, and wind speeds ranging 13.0-33.5~km/hr.

Squamata: Colubridae

Everglades Racer (*Coluber constrictor paludicola*)—The Everglades Racer comprised 0.11% of all amphibians and reptiles and 40.00% of snakes, with 10 standardized records. The first detection of this species was opportunistic in November 2005 (Meshaka et al. 2008). Activity may have peaked in July (Figure 23). One individual was chopped up by a mower near behind the wall of the Miramar Parkway entrance on 12 March 2019. Individuals were active at 0915–1924 hrs, with ambient air temperatures of 17.2–31.8 °C, cloud cover of 0–75%, and wind speeds ranging 5.5–22.5 km/hr. One was the maximum

number of individuals encountered in a survey.

Squamata: Dipsadidae

**Southern Ring-necked Snake** (*Diadophis punctatus punctatus*)—The Southern Ring-necked Snake comprised 0.01% of all amphibians and reptiles and 4.00% of snakes, with one standardized record. The first detection of this species was opportunistic on 18 January 2007, as seen basking at 1130 hrs (Meshaka et al. 2008). The only standardized record of this species was that of a headless specimen seen on the sidewalk on 16 June 2009.

Squamata: Natricidae

Florida Watersnake (Nerodia floridana)—The Florida Watersnake comprised 0.12% of all amphibians and reptiles and 44.00% of snakes, with 11 standardized records. The first detection of this species was opportunistic in 2003 (Meshaka et al. 2008). Individuals were seen in most months between October and April, with most sightings in March and April (Figure 24). Snakes were seen during 1155-1929 hrs, in air temperatures of 20.0-27.8 °C. Activity was associated with variable cloud cover of 0% (n = 3), 25% (n = 1), 50% (n = 4), and 100% (n = 1), and wind speeds of 9.3-33.5 km/hr. Two was the maximum number of individuals encountered during a survey. All but one snake were observed in shallow water near the shoreline. A single individual was basking on top of a culvert on 6 January 2014 between 1555 and 1640 hrs. The air temperature was 25 °C, the wind speed was 8.33 km/hr, and the sky was dark in advance of a storm. One captured individual was reddish and well patterned. Florida Brownsnake (Storeria victa)-The Florida Brownsnake is represented by one record obtained during a systematic survey in the Fantasy Isle neighborhood on 9 September 2019. The individual was a freshly killed adult female found on the grate of a sewer. No visible external injuries were apparent on the snake.

Squamata: Typhlopidae

**Brahminy Blindsnake** (*Indotyphlops braminus*)— The Brahminy Blindsnake is represented by one record obtained during a systematic search of Bismarck Palm, *Bismarckia nobilis*, boots in 2006 (Meshaka et al. 2008). The strong fossorial habits of this snake precluded it from inclusion in walking surveys.

Squamata: Crotalidae

Florida Cottonmouth (*Agkistrodon piscivorus*)— The Florida Cottonmouth comprised 0.03% of all amphibians and reptiles and 12.00% of snakes, with three standardized records. The first detection of this species was in a survey on 6 January 2008. An adult was seen basking near the shore of the of the water body near the Miramar entrance. Individuals were active at

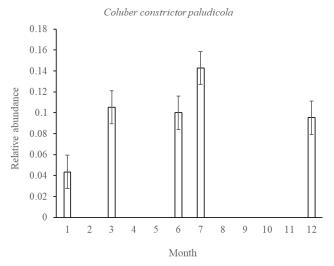


Figure 23. Relative abundance of the Everglades Racer, *Coluber constrictor paludicola*, expressed per no. survey days per month from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

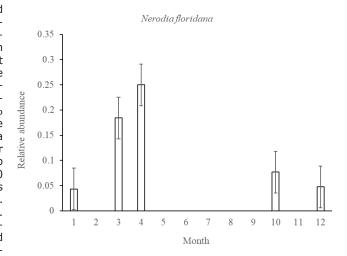


Figure 24. Relative abundance of the Florida Watersnake, *Nerodia floridana*, expressed per no. survey days per month from 165 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 25 March 2006–10 June 2021. Standard error bars accompany relative abundance values.

0948–1057 hrs, in ambient air temperatures ranging 24.4–30.6  $^{\circ}$ C, under cloud cover of 25, 50, and 100%, and with wind speeds ranging from 5.6–18.4 km/hr. On 18 May 2012, an adult near the east side of the Miramar Parkway entrance gate was found to have been freshly killed with a blow to the head. On 5 June 2015, a ca. 50–55 cm TL individual had just left the water near a culvert near the location of the previous record.

Accipitriformes: Accipitridae

Florida Red-shouldered Hawk (*Buteo lineatus extimus*)—A single, Red-shouldered Hawk was observed on 10 June 2021. Between 1435 and 1534 hrs, an adult in a West Indian Mahogany on the east side of the Mira-

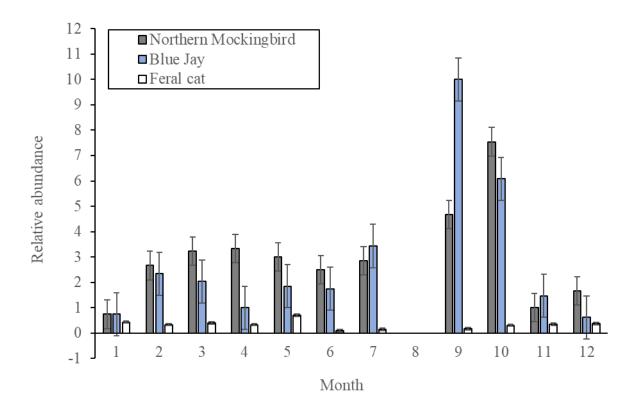


Figure 25. Relative abundance of the Northern Mockingbird, Blue Jay, and feral cat, expressed per no. survey days per month from 156 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 14 June 2007–10 June 2021. Standard error bars accompany relative abundance values.

mar Parkway entrance was being mobbed by a Northern Mockingbird. The hawk flew directly across the street and perched in the canopy of a tree.

Passeriformes: Corvidae

Blue Jay (Cyanocitta cristata)—The first detection of this species was in a survey on 3 January 2008. Inclusion of predators, such as the Blue Jay, in surveys did not begin until 14 June 2007. With 348 standardized records, the Blue Jay was the second most commonly encountered predator monitored in this study. Individuals were seen in every month of the study, with the highest numbers in September (Figure 25). Activity occurred across a wide range of times (Figure 26a) and air temperatures, especially in the range of 30.0-33.9 °C (Figure 26b). Most activity occurred in somewhat cloudy conditions (Figure 26c) and quickly declined in wind speeds > 27.4 km/hr. (Figure 26d). Twenty-two was the maximum number of individuals encountered in a survey. Multiple families of Blue Jays were seen on 16 July 2017. A single dead individual was seen on the ground on 8 January 2014.

American Crow (*Corvus brachyrhynchos*)—The first detection and only record of the American Crow was that of a pair in a tree by the southwest pond during a survey on 12 March 2019 between 1120 and 1226 hrs. They were vocal, and one of the pair held sticks between its mandibles.

Passeriformes: Laniidae

**Loggerhead Shrike** (*Lanius Iudovicianus*)—The first detection of this species was in a survey on 16 June 2007.

Three of the four individuals seen appeared to comprise a family. Inclusion of predators, such as the Loggerhead Shrike, in surveys did not begin until 14 June 2007. With 10 records, the Loggerhead Shrike was ephemeral in its colonization of Nautica. A single individual was seen on each day: 17 June 2007, 30 April 2008, 1 May 2008, 1 July 2008, 16 June 2009, and 25 March 2011. Its presence was associated with the open habitat of the recent construction and plantings and was enforced by hurricanes in 2004 and 2005, especially Hurricane Katrina in 2005. Hurricane Irma in 2017 and Hurricane Dorian in 2019 were damaging but not sufficiently so as to open the maturing canopy of large trees, such as Royal Poincianas.

Passeriformes: Mimidae

Northern Mockingbird (Mimus polyglottos)-The first detection of this species was opportunistic in 2002. Inclusion of predators, such as the Northern Mockingbird, in surveys did not begin until 14 June 2007. One individual was seen during two surveys that day. With 419 standardized records, the Northern Mockingbird was the most commonly encountered predator monitored in this study. Individuals were seen in every month of the study, with the highest numbers in October (Figure 25). Activity occurred across a wide range of times (Figure 26a) and air temperatures, especially in the range of 28.9-33.9 °C (Figure 26b). Most activity occurred in somewhat cloudy conditions (Figure 26c), and nearly all individuals were seen in wind speeds < 27.7 km/hr. (Figure 26d). Thirteen was the maximum number of individuals encountered in a survey.

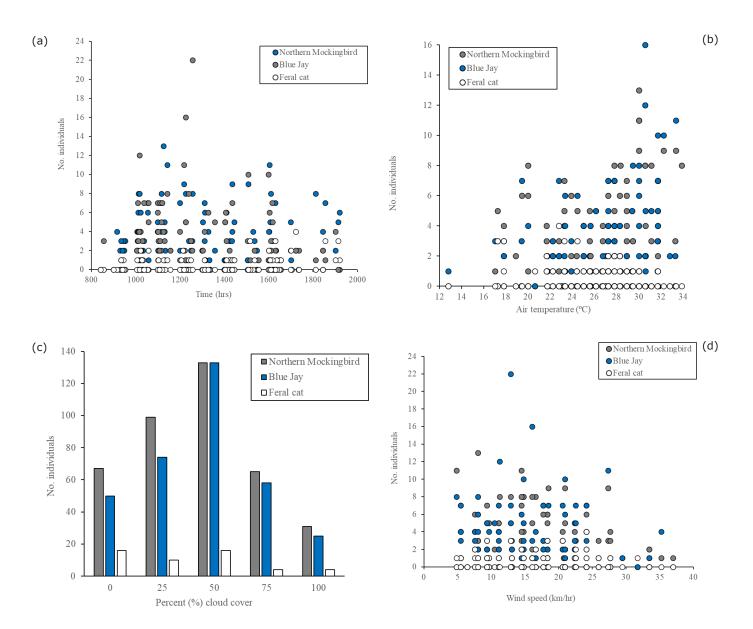


Figure 26. Activity of the Northern Mockingbird, Blue Jay, and feral cat from 156 standardized surveys along a 3.22 km. roundtrip walk in the Nautica residential community, Miramar, Florida, during 14 June 2007–10 June 2021. (a) Time of day; (b) ambient air temperature; (c) percent cloud cover; (d) wind speed.

#### Carnivora: Felidae

Cat (Felis catus)—The first detection of this species was in a survey on 4 January 2008. Inclusion of predators, such as the feral cat, in surveys did not begin until 14 June 2007. With 55 standardized records, the feral cat was ubiquitous in the study site. Individuals were seen in every month of the study, with the highest numbers in May (Figure 25). Activity occurred across a wide range of times (Figure 26a) and in air temperatures ranging 17.2–31.8 °C, especially 17.2–24.5 °C (Figure 26b). Most activity occurred in lightly cloudy conditions (Figure 26c), and quickly declined in wind speeds > 24.1 km/hr. (Figure 26d). Four was the maximum number of individuals encountered on a survey.

#### DISCUSSION

Nautica provided a 19-year view of how an urban south Florida herpetofaunal community can respond over time from one kind of human-mediated disturbed habitat that has been converted into another kind of disturbed habitat consisting of human dwellings in an exotic-species-rich subtropical clime. A first of its kind for south Florida, this case study uncovered temporal patterns in relative abundance, colonization patterns, and inter- and intra-specific associations. The indigenous species' biodiversity remained diminished. Aquatic turtles were the most diverse segment of the native herpetofauna; however, their abundance and the extent of their juvenile recruitment were unknown to us. The composition of the

exotic herpetofauna at Nautica mirrored that of Florida and the United States generally (Meshaka et al. 2022), having been dominated by lizards. The detection rate of all species was the fastest during 2002–2008, by which time 17 species were detected. Only the Florida Brownsnake was detected outside of the original survey loop. It was included in the species list for Nautica because the Fantasy Isle segment was subsequently incorporated into the study and had been walked numerous times opportunistically during the duration of the study.

Colonization dynamics varied greatly among species. As discussed in an earlier study of Nautica (Meshaka et al. 2008), the development was built on highly disturbed land with a depauperate native herpetofauna and an established exotic herpetofauna not needing dispersal to colonize the new development. Subsequent dispersal events resulted in unsuccessful colonization of one species, the Bark Anole, seen only once during this study in 2008. Another species, the Giant Ameiva, was first seen in the north-central part of Nautica in 2006, and not again until 2008, at which time multiple sightings were made. No individuals were seen after 2008, until 2021, when an individual was detected near the west entrance. We do not know if it was established elsewhere in less-shaded areas of Nautica or if these records represent unsuccessful colonization events. Successful colonization was documented in two species: the Green Iguana and the Northern Curly-tailed Lizard. A single opportunistic observation was made of an adult Green Iguana in 2004 and a young adult Northern Curly-tailed Lizard in 2010; however, neither species was seen again until 2017 in standardized surveys.

Three species were reported between one and three times, but not seen again. The Southeastern Five-lined Skink was seen only in 2006, 2007, and 2009. In light of its habits being amenable to visual detection, we believe that this species is gone, at least from our route. We are unsure of the status of the Southern Ring-necked Snake, a fossorial species seen only once, in 2009, and the Florida Cottonmouth, a semi-aquatic species seen once in each of 2008, 2012, and 2015. The generally nocturnal habitats of anurans and geckos limited our ability to measure the relative abundance of those groups. The aquatic habits of turtles and the dearth of basking sites at Nautica likewise limited our ability to assess this group. Aquatic trapping, having proven fruitful in other urban settings in south Florida (Witzell 1999, Johnston et al. 2008), could provide much-needed information on the responses of aquatic turtles to this urban setting.

Diurnally active lizard species provided the best numbers to assess interactions with and effects of abiotic and biotic factors at Nautica. The Brown Basilisk was the only species to have increased in abundance during this study. This increase in its numbers was reflected in the increase in the number of locations along the survey associated with observations of it. Among the anoles, both the Knight Anole and Brown Anole declined over time, while the North American Green Anole did not change in its abundance over the course of the study. The role of cats was equivocal as a factor in the herpetofaunal activity. Cats may have had a negative impact on Knight Anole and Brown Basilisk activity, but too few data were available to be certain. We wonder if the generally clumped distribution of the Brown Basilisk precluded an accurate assessment of an effect of its predator. Conversely, the numbers of the Brown Anole were higher when more cats were active. We attribute this relationship to the greater efficacy of hunting by cats when prey was more active.

The North American Green Anole was more commonly encountered when fewer cats were seen. The same negative relationship was found with the Northern Mockingbird and Brown Basilisk, both known predators, and the Brown Anole, a competitor (Culbertson and Hermann 2019) and predator (Gerber and Echternacht 2000). On the other hand, the activity of this native species was positively associated with that of the Blue Jay and Wood Slave.

In this study, negative relationships were not detected between two potential intraguild predators, the Knight Anole and Brown Basilisk, and their common prey, the Brown Anole. The overlap of peak monthly activity with that of the Brown Anole was non-existent in the Knight Anole and weakly so in the Brown Basilisk. Consequently, the seasonal flush of YOY of the Brown Anole did not coincide with activity at a time in the year that could have been most impactful. The activity of the two predators was also greatest at ambient temperatures that scarcely overlapped those of the Brown Anole, whose maximum numbers of observations occurred at cooler temperatures (range = 24-30 °C) than of the Knight Anole (range = 30-35 °C) and Brown Basilisk (range = 29-32 °C). The preferred range of times of activity during the day in the Brown Anole (range = 1000-1600 hrs) subsumed that of both the Knight Anole (range = 1130-1430 hrs) and nearly that of the Brown Basilisk (range = 1230-1630 hrs). A 2006-2009 subset of data from Miramar (Meshaka 2010) corroborated differences in seasonal activity and thermal associations between the Knight Anole and the Brown Anole.

At this site (Meshaka et al. 2008) and elsewhere in southern Florida (Meshaka 1999b, 1999c, 2020, Meshaka et al. 2020), the Brown Anole was most often found on the ground or close to it, especially females and juveniles (Meshaka 1999b, 1999c, Meshaka et al. 2020). The Knight Anole at this site (Meshaka et al. 2008) and elsewhere (Meshaka 1999a, 1999b, 1999c, Meshaka and Rice 2005) in southern Florida was most often, but certainly not exclusively, found higher above the ground than the Brown Anole; its presence was possibly enforcing structural niche separation, as seen in Cuba (Meshaka 1999a). At our study site, most adults and subadults of the Brown Basilisk were seen on the ground or within 1 m above it. Of these two predators at Miramar, the Brown Basilisk may have had the greater opportunity to negatively impact the Brown Anole, an evolutionary stranger.

Numbers of the North American Green Anole at Nautica, although much lower than the other two Anolis species, did not change during the course of this study. At another south Florida urban and residential site, where the Knight Anole was abundant (Meshaka and Rice 2005, Meshaka et al. 2020), the North American Green Anole and the Brown Anole were uncommon (Meshaka 1999a). Even males of the Brown Anole were not found at tree heights exceeding 2 m, whereas the North American Green Anole was found at heights ranging from ground level to at least 3 m (Meshaka 1999a). It was hypothesized that the presence of the Knight Anole suppressed negative impacts by the Brown Anole on the North American Green Anole, perhaps through differential predation on the Brown Anole (Meshaka 1999a). Behavioral mechanisms by the North American Green Anole to avoid contact with the Knight Anole was thought to be an interesting and testable hypothesis (Meshaka 1999a). To that end, the presence of the predatory Cuban Treefrogs on buildings was associated with the persistence of two otherwise ecologically incompatible Hemidactylus geckos

(Meshaka et al. 2020). At Nautica, perch heights of the North American Green Anole and the Knight Anole most often exceeded 180 cm (Meshaka et al. 2008); however, the peak month of activity of the North American Green Anole in our study was February, one of two months when no Knight Anole was encountered. As found in our study, considerable overlap in weather conditions is associated with activity of the North American Green Anole and the Knight Anole, the latter of which having preferred higher ambient temperatures for its activity. Thus, the North American Green Anole could avoid its predator in part by both month and daily temperatures. Greater overlap occurred between the North American Green Anole and the Brown Anole, especially in diel pattern and ambient temperature, with the former species including higher temperatures in its preferred range. These two species differed in perch height preference and in peak month of sightings, with February being a waning month of the late-summer surge in numbers of the Brown Anole. Perhaps, the Knight Anole enforces structural niche partitioning in the Brown Anole, which in turn alleviates the potential for competition and predation between the North American Green Anole and Brown Anole.

**Future**—Our case study demonstrated one way in which ecological processes can operate within and among native and exotic species of amphibians and reptiles in an increasingly common urban subtropical setting in southern Florida. In this regard, it is important to note that in the nearly two decades since the construction of Nautica, the native terrestrial herpetofauna remained depauperate, exotic counterparts experienced accelerated colonization patterns, and one exotic lizard species possibly contributed to the persistence of a native lizard. Repeated visits to Nautica can serve to test and provide explanations for the observed trends in the community's dynamics. The initiation of similar studies, even if shorter in duration, can in turn provide an understanding of the variation in responses given different circumstances.

We recognize, however, that the extent to which, if even at all, this phenomenon is a conservation-related priority is a decision made by humans, and it is *Homo sapiens* that ultimately determines the design of growing kinds of artificial habitats under the category of urban ecosystems.

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