BARTOSZEK, I. A., HENGSTEBECK, K. C., EASTERLING, I., BASSIS, M., & ROMAGOSA, C. M. (n.d.). Subterranean Refuge Use by Burmese Pythons (*Python bivittatus*) in Southwestern Florida. *Journal of Herpetology*. https://doi.org/10.1670/21-064

Subterranean Refuge Use by Burmese Pythons (*Python bivittatus*) in Southwestern Florida

IAN A. BARTOSZEK[1A], KODIAK C. HENGSTEBECK[2], IAN EASTERLING[1], MICHELLE BASSIS[1], CHRISTINA M. ROMAGOSA[2]

[1] Conservancy of Southwest Florida,
[2] Department of Wildlife Ecology and Conservation, University of Florida

https://doi.org/10.1670/21-064

Abstract

Access to subterranean refugia, such as animal burrows, can affect the ecology and life history of wildlife in an array of habitat types. Subterranean refugia are commonly used for thermal refuge, for shelter from predators, or as suitable locations for nesting and/or brooding offspring; because of this, refugia can potentially impact rates of survivorship and recruitment. In southwestern Florida, Burmese pythons (*Python bivittatus*), an established and highly impactful invasive species, have been observed using subterranean refugia on numerous occasions. Because python management is an utmost priority in Florida, understanding the potential implications of this behavior is key to mitigating python impacts on native wildlife. We used 29 radio-telemetered Burmese pythons to investigate the extent to which pythons used subterranean refugia in the southwestern portion of their Florida range. We explored spatiotemporal patterns of refuge use and quantitatively assessed how python sex, reproductive season, and habitat type affected the probability of using different types of refugia. We observed pythons using four types of refugia, including Gopher Tortoise burrows, Nine-banded Armadillo burrows, and natural and anthropogenic ground-based cavities. Pythons used these refugia for seeking thermal refuge, aggregating, breeding, and nest brooding, and they were most likely to use refugia during their breeding and nesting seasons. Nine python nests, representing 71% of those discovered during the study, were oviposited and brooded in Gopher Tortoise or Nine-banded Armadillo burrows. Implications of this behavior warrant further assessment and incorporation into management strategies as they may affect Burmese python recruitment, survival, and dispersal.

An understanding of life history, ecology, and habitat use is critical for managing both native and invasive species (Gibbons, 1986; Rodgers, 2016). The use of specific landscape features by a species may reflect the arrangement of important resources including refuges, food, and mates (Hyslop et al., 2009; Macartney et al., 1988). Thermally stable sources of refuge are especially important for many wildlife species as they are often used for reproduction and protection from environmental conditions and predators (Kinlaw, 1999). Thus, measuring the use of features such as refugia can be used to better understand a species' resource requirements and produce more effective management strategies.

One species that requires management concerns in the United States is the invasive Burmese python (*Python bivittatus*), which is well established throughout southern Florida (Bartoszek et al., 2021; Engeman et al., 2011; Guzy et al., 2023; Hart et al., 2015). Introduced to the Florida Everglades in the 1980s via the pet trade (Willson et al., 2011), this large, long-lived, and fecund constrictor species (Currylow et al., 2022; Guzy et al., 2023) has exhibited rapid population growth throughout their invaded range at the expense of Florida's native ecosystems (Krysko et al., 2008; Snow et al., 2007). Burmese pythons are implicated in the decline of native meso-mammal populations in the Florida Everglades and surrounding areas (Dorcas et al., 2012; McCleery et al., 2015) and are known vectors for lung parasites that are now infecting native species (Farrell et al., 2019; Miller et al., 2018). To mitigate their deleterious impacts and prevent further population growth, minimizing the spread of pythons into new areas is a priority.

Since their initial introduction, pythons have spread into much of southern Florida and are now firmly established as far west as Collier County, located on the southwestern coast of Florida (Andreadis, 2011; Guzy et al., 2023). In addition to the lowland habitats, mangrove forests, and agricultural matrixes that are found throughout much of their invaded area range, pythons in Collier County have access to upland habitats such as scrub, scrubby flatwoods, and pine uplands. The dry, xeric environment that defines upland habitats makes them conducive for burrowing species, such as Nine-banded Armadillos (*Dasypus novemcinctus*) and Gopher Tortoises (*Gopherus polyphemus*). Burrows are important features within upland habitats and are commonly used as refugia by numerous commensal species (Catano & Stout, 2015; Jackson & Milstrey, 1989; Pike & Mitchell, 2013; Witz et al., 1991). Bartoszek et al. (2021) found that Burmese pythons in Collier County actively select upland habitats, possibly due to their high prevalence of animal burrows. Indeed, pythons in this region have been observed using Gopher Tortoise burrows as sources of refuge (Bartoszek et al., 2018; Metzger, 2013). This behavior may be of concern for Burmese python management as access to refugia improves survivability and recruitment in some species, subsequently leading to increased population

A Corresponding author. E-mail: ianb@conservancy.org

densities (Madsen & Shine, 1999; Roznik & Johnson, 2009; Souter et al., 2004).

Use of subterranean refugia by Burmese pythons is not strictly unique to upland habitats or even to Florida. In Everglades National Park, pythons use anthropogenic refugia, such as culvert pipes, to nest and brood eggs (Hanslowe et al., 2016). Additionally, throughout their native habitat of Southeast Asia, Burmese pythons take refuge in termite mounds, hollow trees, and burrows dug by Indian porcupines (*Hystrix indica*; Bhupathy & Vijayan, 1989; Sharma & Kandel, 2015; Stuart et al., 2012). Both Burmese pythons and Indian Pythons (*Python molurus*), which are close relatives, have also been observed nesting and brooding in animal burrows (Ramesh & Bhupathy, 2010; S. N. Smith et al., 2021). Regardless, little is known about the extent of subterranean refuge use by Burmese pythons in their invaded habitat or the influence that these refugia have on python habitat selection and life history.

This article investigates the extent to which invasive Burmese pythons use subterranean refugia in Collier County, Florida. We describe four different types of subterranean refugia used by Burmese pythons: Gopher Tortoise burrows, Nine-banded Armadillo burrows, and natural and anthropogenic ground-based cavities. We use tracking data from 29 very-high frequency (VHF) radio-telemetered pythons from varying time periods between January 2013 and June 2018 to explore spatiotemporal patterns of refuge use. We quantitatively assess biological and environmental variables that may influence these patterns and discuss the implications of our findings for python ecology and management.

Materials and Methods

Study Sites.—We conducted this study in Collier County, Florida, USA, which is located on the southwestern coast of Florida north of Everglades National Park. Sites of interest for the investigation included public conservation lands in Rookery Bay National Estuarine Research Reserve (44,520 ha), Collier Seminole State Park (2,600 ha), and Picayune Strand State Forest (29,540 ha), as well as adjacent private lands (Fig. 1). These sites are within the Big Cypress Basin Watershed, a western component of the Greater Everglades Ecosystem (Duever, 2005). Unlike the freshwater Everglades system that is characterized by vast expanses of herbaceous communities, the Big Cypress bioregion consists primarily of forested areas that form a mosaic of habitat types (Duever, 2005). These include natural areas such as marshes, prairies, and swamps, as well as disturbed, agricultural, and urbanized areas. Also found in this bioregion are a variety of dry upland ecosystems such as upland pine flatwoods, xeric oak habitats, and relict dune ridges (Barry et al., 2013).

Python Capture and Transmitter Implantation.—We captured Burmese pythons through active searching and aggregatory python breeding events during radio-tracking (i.e., Bartoszek et al., 2021; B. J. Smith et al., 2016). During active searches, two- or three-person teams drove or walked along canal banks, agricultural levees, or roadsides looking for pythons basking or hiding in vegetation. Captured pythons that were >2.5 m in total length and were not visibly injured or malnourished were selected and subsequently implanted with VHF radio-telemetry equipment. During transmitter implantation, we anesthetized the pythons with isoflurane and surgically implanted each python with a Holohil AI-2 radio transmitter (25 g; 158–170 MHz; Holohil Systems, Ltd., Ontario, Canada) using standard surgical procedures (Reinert & Cundall, 1982). After implantation, we provided the pythons at least 24 h of recovery before releasing them at the original capture location.

Radio-telemetry.—We tracked individual pythons for varying time periods between 18 January 2013 and 14 June 2018, using both ground-based and aerial tracking methods. We used a RA-23K VHF two-element antenna (Telonics, Mesa, Arizona 85204, USA), a Yagi three-element antenna (Titley Scientific, Columbia, Missouri 65202, USA), and a truck-mounted omnidirectional antenna (Laird Technologies, Chesterfield, Missouri 63017, USA) attached to a R-1000 telemetry receiver (Communication Specialists, Inc., Orange, California 92865, USA) for ground-based radio-telemetry, and a Cessna Skyhawk 172 with wing-mounted RA-2AHS antennae (Telonics, Mesa, Arizona 85204, USA) for aerial tracking. We located radio-tagged pythons on foot approximately once per week from December through April, which coincided with the breeding season for Burmese Pythons in Florida (Currylow et al., 2022; B. J. Smith et al., 2016), and twice per month during the remainder of the year. We conducted aerial surveys to monitor long-range movements twice per month during the entire study.

After visually locating each python, we recorded the animal's UTM coordinates (NAD83), general habitat, and the time of day. If a visual observation was not possible, we obtained an approximate location of the python within 5 m. Unless a physical measurement was required or a python nest needed to be removed, we refrained from touching or disrupting behaviors to minimize disturbances to animals. We included individual pythons in the study until natural mortality occurred.

Subterranean Refuge Use.—When tracked to subterranean refugia, we used an adult tortoise burrow camera system (Environmental Management Systems, Canton, Georgia 30114, USA) to visually confirm python presence. We classified the type of refuge that the pythons used as a Gopher Tortoise burrow, Nine-banded Armadillo burrow, natural ground-based cavity, or anthropogenic ground-based cavity. We identified Gopher Tortoise burrows by their characteristic half-moon shaped entrance and the soil mound outside the entrance (i.e., the apron) or by the presence of a tortoise if the burrow was scoped with a burrow camera system. Armadillo burrows were generally shorter (<1.5 m), were oval-shaped, and lacked an apron outside the entrance (Fig. 2; L. S. Smith et al., 2009). Because the burrow type was identified predominantly via its external appearance, it is possible that some burrows were incorrectly classified or used by both tortoises and armadillos. Finally, we categorized natural cavities as those not formed by animal or human activity (e.g., root cavities) and anthropogenic cavities as those created by human activity (e.g., culvert pipes and debris piles). While refugia such as debris piles may not be subterranean, they similarly provide buffers from environmental conditions and were included in this study.

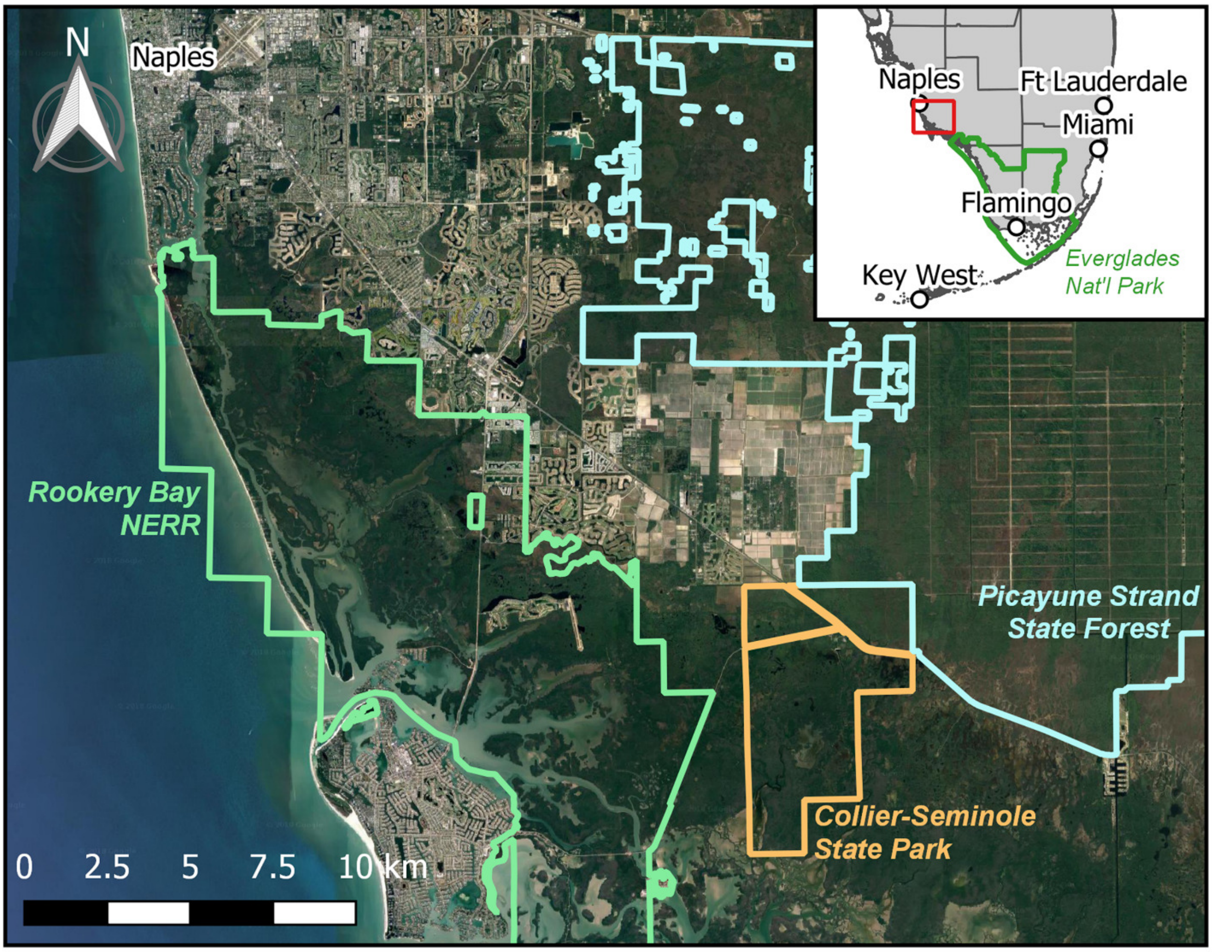

FIG. 1. The study area for radio-tracking 45 invasive Burmese pythons to assess their use of subterranean refugia in Florida, USA (highlighted in red on the inset map). The study area is primarily within Collier County, located on the southwestern coast of Florida north of Everglades National Park. It includes Rookery Bay National Estuarine Research Reserve, Collier Seminole State Park, and Picayune Strand State Forest.

We classified refuge use by pythons into three categories: seeking refuge, aggregating, and nest brooding. Instances of pythons seeking refuge were characterized by relatively short periods of refuge occupancy (<1 wk) and involved only one python to the best of our knowledge. Aggregating was characterized by multiple pythons being present in the same refuge or on the surface within 10 m of python-occupied refugia. Suspected aggregations were verified via burrow excavation and python capture. Finally, nest brooding was characterized by female pythons visibly brooding eggs within refugia. Python nests were also verified via burrow excavation, followed by egg collection and removal.

Data Analysis.—We used generalized linear models in R version 3.5.3 to assess how selected biological and environmental variables affected the probability of pythons using subterranean refugia. Our response variable was binary and categorized by whether a python was in refugia at the time of radio-tracking (1 = python located within refugia, 0 = python not located within refugia). Our predictor variables included snout-vent length, sex, reproductive season, and habitat type. Python reproductive season was categorized as breeding season (December–March), nesting season (April–July), or nonbreeding season (August–November; Currylow et al., 2022; B. J. Smith et al., 2016). We used the Florida Cooperative Land Cover Map (CLC) version 3.3 provided by the Florida Fish and Wildlife Conservation Commission and Florida Natural Areas Inventory, along with ArcGIS version 10.5 (Environmental Systems Research Institute, Inc., Redlands, California 92373, USA) to assign each geographic location a specific habitat type. We verified habitat types assigned by the CLC in Google Earth Pro (Google LLC, Mountain View, California 94043, USA). To minimize model parameters, we recategorized specific habitat categories assigned by the CLC into the following broad categories: marsh/prairie, swamp, flatwoods, scrub, mangrove, disturbed habitat, agricultural area, or urban area. We ranked models using the Akaike information criterion (*AICc*) and corrected for small sample sizes (*AICc*; Hurvich & Tsai, 1993) and *AICc* weight (ω; Wagenmakers & Farrell, 2004). The weight of any particular model depends on the set of candidate models and varies from 0 (no support) to 1 (complete support). We considered any models within 2.0 *AICc* units of the best model to be competing models.

FIG. 2. Various animal burrows used by invasive Burmese pythons in southwestern Florida, USA. These include both active (A) and inactive (B) Gopher Tortoise burrows, as well as Nine-banded Armadillo burrows (C, D). Panel A also shows a snake track where a python has entered the burrow.

RESULTS

We tagged and tracked 45 mature adult Burmese pythons (male: n = 30, female: n = 15). We excluded any pythons tracked for <1 yr, resulting in 29 pythons (male: n = 21, female: n = 8) being used for analysis (Table 1). We tracked pythons for an average of 803 d (range: 358–1,969 d) to 2,285 locations (male: n = 1,637, female: n = 648, mean = 79). Pythons were in subterranean refugia 409 times (male: n = 273, female: n = 136, mean = 14). We found individual pythons in refugia during 18% of their locations on average (range: 0–55% of locations). Four pythons were never observed using refugia (Table 1).

Gopher Tortoise burrows were the refugia used by pythons most often (n = 225; Fig. 3), followed by Nine-banded Armadillo burrows (n = 108), then natural ground-based cavities (n = 40), and anthropogenic ground-based cavities (n = 36). At least 23 Gopher Tortoise burrows used by pythons during the study were co-occupied by both a Burmese python and a Gopher Tortoise concurrently, as recorded on our burrow camera. Natural ground-based cavities used by pythons were most commonly root cavities from uprooted trees or networks of limestone cavities beneath the ground surface. Anthropogenic ground-based cavities were metal or concrete culvert pipes or horticultural or limestone debris piles.

Radio-tagged pythons used subterranean refugia for three general purposes: seeking refuge, aggregating, and nest brooding. We categorized most instances of pythons using refugia as seeking refuge, which occurred in all refuge types. Aggregations involved 2-7 pythons and occurred on eight separate occasions in all refuge types. Aggregations occurred either entirely within refugia (i.e., all pythons involved were underground) or partially within refugia (i.e., one or more pythons were underground, and one or more pythons were above ground within 10 m). Finally, nest brooding occurred on nine occasions (Fig. 3A). These nesting events occurred either in Gopher Tortoise burrows (n = 5) or armadillo burrows (n = 4) and made up 71% of all nesting attempts by radio-tagged female pythons. All other nests located during this study were found above ground. Clutches laid in refugia ranged in size from 21–63 eggs (mean = 47).

We saw considerable variation in subterranean refuge use by pythons depending on sex, season, and habitat type; these were significant predictor variables in our best fitting model of python refuge use (McFadden's R^2 = 0.33; Table 2). The next closest model was 4.27 $\Delta AICc$ from the top model, indicating fairly strong support for our top model.

TABLE 1. Tracking data for radio-tagged Burmese Pythons used to study subterranean refuge use by invasive pythons in southwestern Florida. Locations represent the total number of times each python was radio-tracked. Refugia represent Gopher Tortoise burrows, Nine-banded Armadillo burrows, and natural and anthropogenic ground-based cavities. The % represents the number of locations in refugia in proportion to the total number of locations for that specific python.

Snake ID	Sex	Total length (cm)	Snout-vent length (cm)	Mass (kg)	Days included in study	Locations	Locations in refugia	
							(*n*)	%
PYBI_01	M	338	295	21.8	1,969	157	20	13%
PYBI_02	F	231	202	15.6	1,807	122	2	2%
PYBI_03	F	305	268	22.2	543	59	32	54%
PYBI_04	M	389	342	37.5	773	70	7	10%
PYBI_06	M	315	272	16.7	416	29	3	10%
PYBI_08	F	341	300	25.9	777	63	1	2%
PYBI_09	F	445	392	45.4	871	84	0	0%
PYBI_10	F	427	376	47.2	1,515	104	12	12%
PYBI_13	M	268	235	11.7	1,246	134	42	31%
PYBI_14	M	358	315	26.3	500	54	0	0%
PYBI_15	M	317	274	16.4	397	34	0	0%
PYBI_17	M	377	334	27.3	800	89	0	0%
PYBI_19	M	285	252	12.7	1,231	126	30	24%
PYBI_20	F	377	330	30.1	847	75	27	36%
PYBI_21	M	329	286	17.9	1,051	146	27	18%
PYBI_22	M	344	301	23.6	933	119	37	31%
PYBI_24	M	310	267	16.6	904	62	2	3%
PYBI_26	F	422	371	46.8	487	67	37	55%
PYBI_27	M	284	248	10.4	774	88	20	23%
PYBI_28	M	321	279	19.2	777	67	23	34%
PYBI_29	M	267	232	10.2	624	76	2	3%
PYBI_30	F	330	291	26.6	566	74	25	34%
PYBI_31	M	296	260	11.7	547	57	8	14%
PYBI_32	M	310	271	16.0	549	62	14	23%
PYBI_33	M	306	268	15.4	533	51	9	18%
PYBI_34	M	321	282	16.7	531	68	3	4%
PYBI_35	M	309	270	15.9	518	63	9	14%
PYBI_37	M	320	272	15.1	445	46	13	28%
PYBI_38	M	306	269	11.2	358	39	4	10%

Snout-vent length did not affect the probability of refuge use. However, it should be noted that only reproductively mature pythons were used for this study. The importance of subterranean refugia to neonate and subadult pythons remains unclear. Female pythons, with the probability of being located within refugia *(P)* = 0.37 (*P*-value < 0.01), were 1.3 times more likely to be in refugia than male pythons (*P* = 0.29, *P*-value = 0.01; Fig. 5A). The probability of pythons using subterranean refugia also varied seasonally, with pythons generally being 7.3 times more likely to use refugia during the breeding season (December–March; *P* = 0.37, *P*-value < 0.01) and 4.9 times more likely during the nesting season (April–July; *P* = 0.25, *P*-value < 0.01) than during the nonbreeding season (August–November; *P* = 0.05, *P*-value < 0.01; Fig. 4A; Fig. 5B). Male pythons used refugia most often during the breeding season (80% of instances), while female pythons used refugia most often during the nesting season (58% of instances). The nonbreeding season had the lowest amount of refuge use by both males and females (3% and 2% of instances, respectively).

Finally, the probability of refuge use by pythons significantly varied depending on different habitat types (Fig. 4B; Fig. 5C). The probability of using refugia was highest in scrub habitats, being at least 1.8 times greater than in any

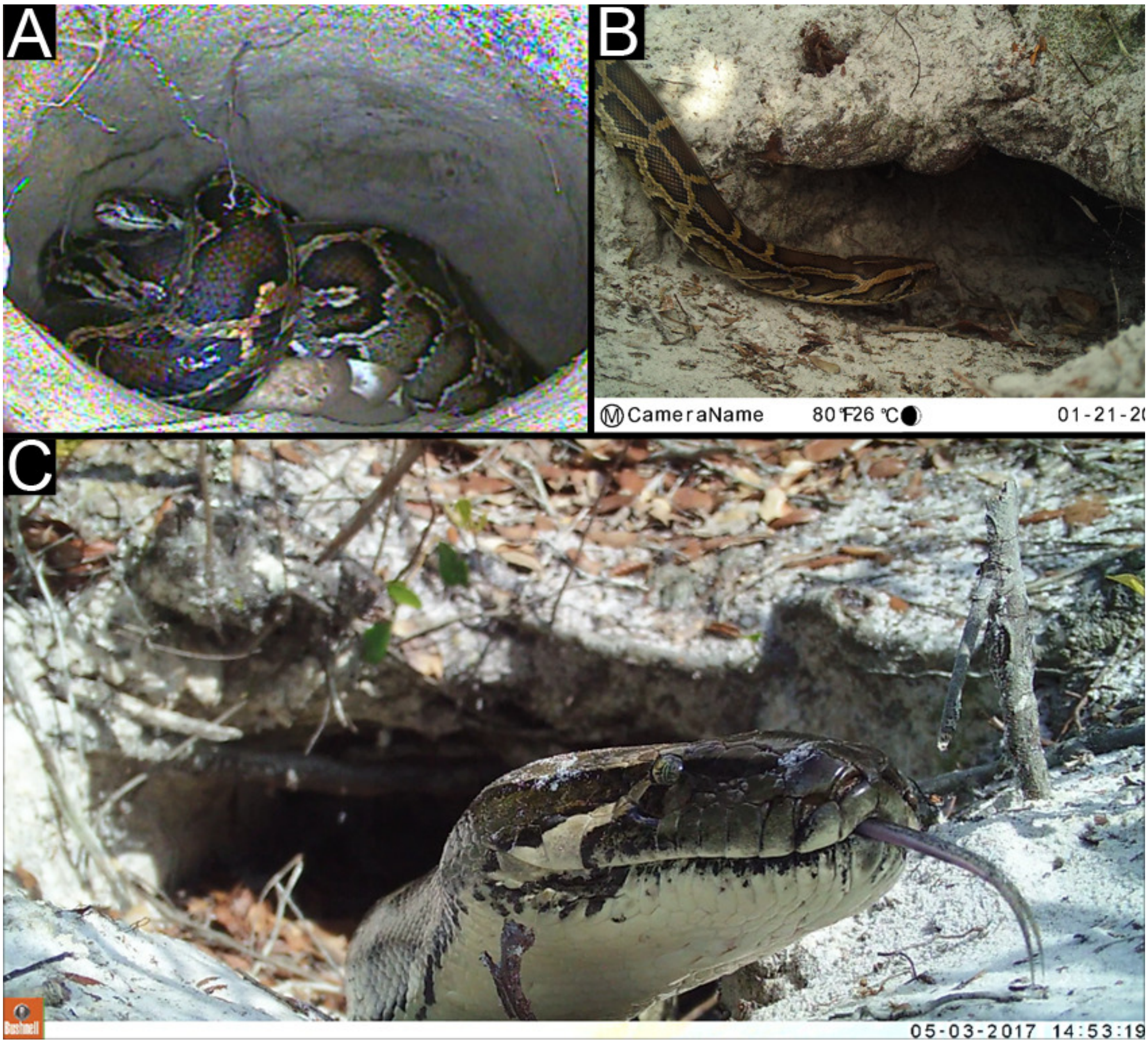

FIG. 3. Invasive Burmese pythons using Gopher Tortoise burrows in southwestern Florida, USA. Pythons were observed via burrow camera brooding eggs at the termini of Gopher Tortoise burrows (A) on numerous occasions. Pythons were also seen both entering (B) and exiting (C) Gopher Tortoise burrows, captured via trail camera.

TABLE 2. Model selection for logistic regression models of Burmese python refuge use. Fixed effects considered in the models included sex (Sex), python reproductive season (Seas) and habitat type (Hab). Reproductive season was defined according to Smith et al. (2016) and Currylow et al. (2022). Habitat types were determined using the CLC version 3.3. *AIC*, Akaike information criterion.

Model	Wald test *P*-value			*AICc*	Δ*AICc*	ω	McFadden's R^2
	Sex	Seas	Hab				
Sex + Seas + Hab	0.01	<0.001	<0.001	1,461	0.00	0.89	0.33
Seas + Hab	-	<0.001	<0.001	1,465	4.27	0.11	0.33
Sex + Hab	0.03	-	<0.001	1,565	104	0.00	0.28
Hab	-	-	<0.001	1,568	107	0.00	0.28
Sex + Seas	<0.01	<0.001	-	2,005	544	0.00	0.07
Seas	-	<0.001	-	2,010	549	0.00	0.07
Sex	0.02	-	-	2,146	685	0.00	<0.01
Null	-	-	-	2,149	688	0.00	0.00

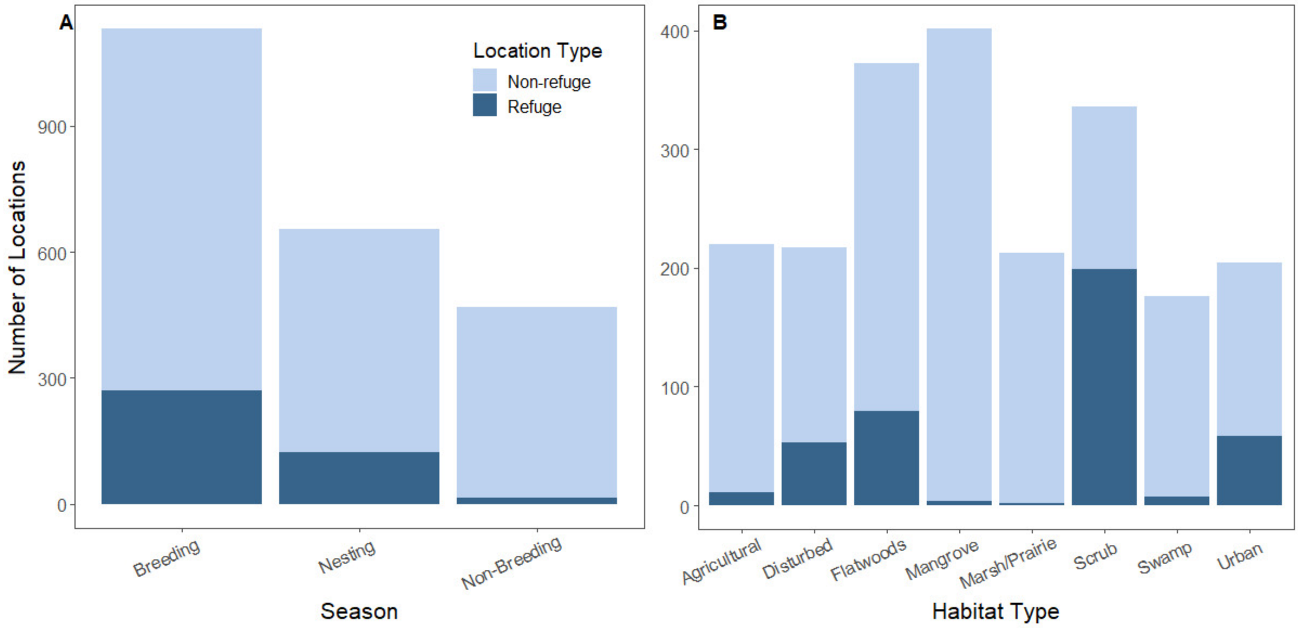

FIG. 4. Number of nonrefuge and refuge locations pythons were radio-tracked to during the study of refuge use by invasive Burmese pythons in southwestern Florida, USA. Data are organized via python reproductive season (A; Currylow et al., 2022; B. J. Smith et al., 2016) and general habitat type (B). Nonrefuge represents any location not considered subterranean refugia, including locations on the ground surface or in water.

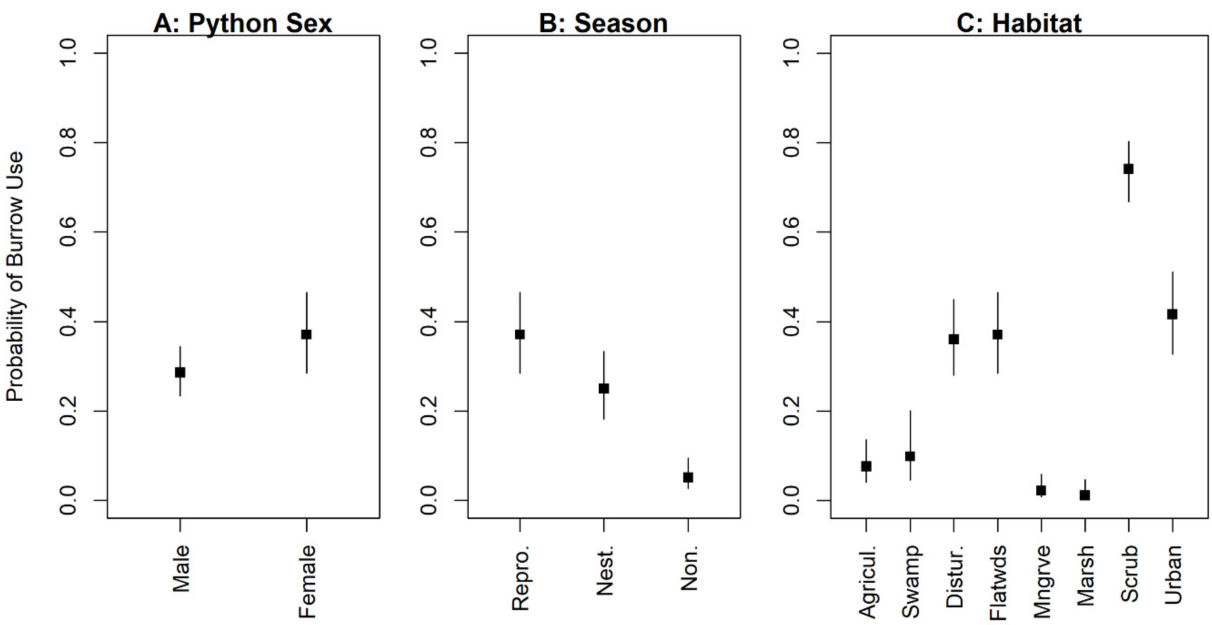

FIG. 5. Probability of burrow use by invasive Burmese pythons in southwestern Florida, USA depending on (A) python sex, (B) reproductive season, and (C) habitat type, based on results from the top logistic regression model of python burrow use. In the figure, Repro., Nest., and Non. represent the python reproductive, nesting, and nonreproductive seasons, respectively. Agricul., Swamp, Distur., Flatwds, Mngrve, Marsh, Scrub, and Urban represent agricultural areas, swamp habitats, disturbed areas, flatwood habitats, mangrove habitats, marsh/prairie habitats, scrub habitats, and urban areas, respectively. Error bars represent 95% confidence intervals.

other habitat type ($P = 0.74$, P-value < 0.01). Probability of refuge use was also high in urban areas ($P = 0.42$, P-value < 0.01), flatwoods habitats ($P = 0.37$, P-value < 0.01), and disturbed habitats ($P = 0.36$, P-value < 0.01), but the probability was lower in swamp habitats ($P = 0.10$, P-value < 0.01), agricultural areas ($P = 0.08$, P-value < 0.01), mangrove habitats ($P = 0.02$, P-value $= 0.03$), and marsh/prairie habitats ($P = 0.01$, P-value $= 0.01$).

Discussion

Burmese pythons in southwestern Florida regularly used various forms of subterranean refugia. Nearly all the radio-tagged pythons used refugia during the study, with some individuals using refugia during >50% of the instances in which we radio-tracked them. Furthermore, refuge use was most prevalent during breeding and nesting seasons, suggesting that access to refugia may benefit reproduction and possibly influence habitat selection during those periods. During the breeding season, radio-tagged pythons aggregated in refugia on numerous occasions. Aggregating for breeding purposes is a behavior that is seen often in large species of snakes (Bartoszek et al., 2018; Myers & Eells, 1968; Pope, 1961; Wall, 1921) and doing so within refugia may protect individuals involved from predators or harsh environmental conditions. Throughout the nesting season, most nesting attempts by radio-tagged female pythons occurred within animal burrows. To our knowledge, these are the first documented occurrences of pythons in Florida using Gopher Tortoise and armadillo burrows for egg brooding purposes. In addition to protection from nest predators and environmental conditions, refugia may provide stable microenvironments for egg incubation and could substantially benefit recruitment. Indeed, thermally stable sources of refuge, including burrows dug by large varanid species, have significantly benefited Water Python (*Liasis fuscus*) reproduction in Australia (Madsen & Shine, 1999). Access to animal burrows led to increased survival for both mother and hatchling Water Pythons, which may be similarly beneficial for Burmese Pythons in Florida.

Bartoszek et al. (2021) found that upland habitats, particularly those near water features, are more strongly selected by Burmese pythons in southwestern Florida than any other land cover class included in the study, which indicates that upland habitats are an important feature of python home ranges. Pythons in our study used refugia in upland habitats such as scrub and flatwoods more often than any other type of habitat, likely due to the higher prevalence of refugia than in other habitats, although that was not measured in this study. Nonetheless, it is possible that increased access to refugia such as animal burrows may contribute to strong selection for these habitats.

Access to refugia may be particularly important to Burmese Pythons in Florida during periods where environmental temperatures fall outside their thermal tolerance. Cold spells in southern Florida, while uncommon, have previously led to high rates of mortality in radio-tagged Burmese Pythons (Mazzotti et al., 2011). However, this mortality has only been reported in the Florida Everglades, where pythons have less access to natural subterranean refugia, as much of the region floods on a seasonal basis and lacks macro-burrower species such as Gopher Tortoises and Nine-banded Armadillos. Many native species use the thermal stability of burrows to escape harsh environmental conditions, especially cold spells (Jackson & Milstrey, 1989; Pike & Mitchell, 2013). Pythons in this study regularly used burrows as sources of refuge, which may improve their survival during periods of cold weather. Additionally, though assessing range expansions by pythons in Florida is outside the scope of this study, it is nonetheless worth acknowledging that access to refugia such as burrows could potentially improve the likelihood of pythons establishing in areas north of their current range. Xeric habitats, and the burrowing species that accompany them, are uncommon in most of the Everglades, but they become much more frequent in coastal and inland regions just north of Collier County. If the distribution of Burmese pythons expands north, their access to xeric habitats and associated subterranean refugia will increase considerably and provide ample shelters for thermal refuge.

We found that Burmese pythons in southwestern Florida use Gopher Tortoise burrows more than any other type of refuge. Adult Gopher Tortoise burrows are generally wider and longer than most other types of subterranean refugia that pythons have access to in southwestern Florida, reaching widths that are >30 cm and lengths that are >6 m (Hansen, 1963). Because of this, these burrows may be more conducive for large snakes such as Burmese pythons, particularly for pythons that are aggregating. Additionally, tortoise burrows can reach depths of >2.5 m (Hansen, 1963) and maintain impressive thermal stability (Anderson, 2001; Pike & Mitchell, 2013), which could benefit python egg incubation during nest brooding.

Gopher Tortoise populations are in decline across their range, in large part due to loss of habitat (Diemer, 1986). Burmese pythons could further impact Gopher Tortoises by competing for burrow space where their ranges overlap. Bartoszek et al. (2018) reported an aggregation in which seven adult Burmese pythons were tightly packed inside a single active tortoise burrow with the tortoise trapped at the burrow terminus. The pythons in this case filled nearly the entire burrow and blocked the resident tortoise from exiting. Further, female pythons that brood eggs inside burrows occupy those burrows for the duration of incubation, which has been reported to last >60 d in captivity (Branch & Erasmus, 1984; De Vosjoli & Klingenberg, 2005; Wagner, 1976). Such aggregations and nesting events could completely displace resident tortoises from their burrows and potentially expose them to predators and harsh environmental conditions.

The findings of this study are the result of over six years of research on nearly 2,300 python locations. However, we still know little about the true importance of refugia to these snakes or how access to refugia, especially within xeric habitats, could impact their success in Florida despite this extensive research. Previously, it was suggested that pythons in Florida will not inhabit xeric highland habitats (Pyron et al., 2008) and are unlikely to use burrows to seek refuge from cold environmental temperatures (Jacobson et al., 2012). On the contrary, this study documented that pythons regularly inhabit xeric habitats in southwestern Florida, and the burrows within these habitats are features that are regularly utilized. Access to the refugia within these habitats could affect not only recruitment and survival rates of Burmese pythons, but also their distribution in Florida. Further assessment of this behavior and incorporation into management control strategies is warranted.

Acknowledgments

P. Andreadis was instrumental in the inception of this tracking project. We thank C. Prokop-Ervin, J. Kittle, M. Lasky, K. King, A. Furst, and A. Flanagan for invaluable assistance in the field. We thank staff at Rookery Bay National Estuarine Research Reserve and Collier Seminole State Park for site access and assistance. Research was permitted under animal care protocol USGS-FORT IACUC-2013-1. Radiotelemetry activities were permitted under Florida Fish and Wildlife Conservation Commission permits EXOT-15-29, EXOT-15-29a, EXOT-15-35, and EXOT-17-06. Funding and project support were provided in part by the USGS Greater Everglades Priority Ecosystem Science Program, USGS Invasive Species Program, the Naples Zoo Conservation Fund, and private philanthropy through the Conservancy of Southwest Florida. The authors have no conflict of interest.

Accepted: December 18, 2023 EDT

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