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Home range, habitat use, and movement patterns of non-native Burmese pythons in Everglades National Park, Florida, USA

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Abstract

Background: Studies on the spatial ecology of invasive species provide critical information for conservation managers such as habitat preferences and identification of native species at risk of predation. To understand the spatial ecology of non-native Burmese pythons (*Python molurus bivittatus*), now well-established in Everglades National Park and much of South Florida USA, we radio-tracked 19 wild-caught adult pythons, 16 with VHF tags during 2006 through 2009 and 3 by GPS tags between 2010 and 2011. Our goal was to identify individual core-use areas and quantify home ranges, as well as to explore correlations of python movements with environmental parameters such as the presence of surface water.

Results: Radio-tracking periods ranged from 87 to 697 days for snakes with VHF tags, with a total of 5,119 tracking days (mean ± 1 SD = 319.9 ± 184.3 days); GPS tracking periods ranged from 12 to 93 days, with a total of 146 tracking days (mean ± 1 SD = 48.7 ± 40.7 days). We observed mean individual radio-tracked python home ranges of 22.5 km^2 (2250 ha) with overall low site fidelity; all home ranges were within the park boundary. Python core-use areas included slough and coastal habitat types, and we delineated 18 common-use areas (that is, areas where individual core-use areas spatially overlapped). Tree islands were a principal feature of common-use areas, even if they were not the predominant habitat type. Multiple common-use areas were in proximity to roads. The longest movements of individual pythons correlated well with presence of surface water, and occurred during both wet and dry seasons.
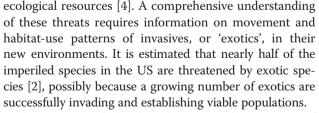
Conclusions: High-use areas determined from python habitat-use and movement data may be optimal locations for targeted control efforts and further studies on impacts to native fauna.

Keywords: Python, Minimum convex polygon, Radiotelemetry, Everglades, Invasive species, Core-use area

Background

Understanding habitat-use patterns is a fundamental aspect of animal ecology. Discerning the scope of these patterns can aid in designing appropriately timed and scaled management strategies for habitats of concern, including threatened, endangered, and invasive species. Competition with and predation by invasive species are continuing threats to native biodiversity worldwide [1-3], and invasive species can also cause harm to other

ecological resources [4]. A comprehensive understanding of these threats requires information on movement and habitat-use patterns of invasives, or 'exotics', in their new environments. It is estimated that nearly half of the imperiled species in the US are threatened by exotic species [2], possibly because a growing number of exotics are successfully invading and establishing viable populations.

The US state of Florida is home to a large variety of endangered species taxa [5] and more exotic animals than any other state. Snakes in particular have been shown to pose particularly high risks as potentially invasive species [6,7], and the recent establishment of Burmese pythons (*Python molurus bivittatus*) in south Florida poses

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a major threat to both the sensitive Everglades ecosystem and native species of conservation concern [8]. Dorcas *et al.* [9] recently described severe declines in mammal populations within the Everglades; the temporal and spatial patterns of python proliferation indicate that Burmese pythons may be one major cause of these declines.

Burmese pythons are long-lived, large-bodied constricting snakes native to Southeast Asia. Habitat and dietary generalists, these ambush predators can reach lengths greater than 6 m [10,11] and produce large clutches of eggs (8 to 107 eggs [12,13]). Despite considerable upkeep requirements to maintain and sustain giant snakes in captivity, Burmese pythons are often imported into the US where they are bred and sold as exotic pets. Although the route of entry into the wild is unclear, pythons were first observed in South Florida's Everglades National Park (ENP) in 1979, and although not recognized as established until the year 2000 [14], the snakes were likely established by at least the mid 1980s [15]. Pythons have spread throughout ENP [16,17], and impacts from pythons on some populations of native fauna in South Florida appear to be significant [9].

Despite likely being established in ENP for several decades [18], their impacts are not well understood. A single report of a translocated, radio-tagged python from their native range is available [19]; results from that study indicated a home range of 12.3 ha over a 24-day period. However, previous ecological studies on other species of snakes, including pythons, have shown that movements and habitat use can vary in relation to a number of factors such as season [20-24], sex [25,26], body size [24,27], and prey [28]. Additionally, studies focusing on large constrictors have found seasonal shifts in habitat use [29-31] and movements related to changes in weather [32]; the home range size of pythons may therefore differ in new versus native habitats. Research on large constrictors in Australia has also shown that radio-tagged snakes displayed high site fidelity, even after translocation [33]. Thus, it is reasonable to expect that pythons may display site fidelity to particularly suitable habitats, yet it is not known what those habitats may be in South Florida.

In recent years, increases in the numbers of pythons removed from ENP [34] have prompted investigations into the impacts of pythons on native prey populations [9,35], possible establishment scenarios [15], risk assessments [36], and projections of potential habitat invasion in the southeastern US. [37-40]. Additionally, because little was known about the biology of this non-native species, researchers have tested the tolerance of wild-caught *P. m. bivittatus* to cold winter temperatures outside of Florida, where none of the snakes survived [18] and to estuarine and marine salinities in a laboratory setting, where hatchling pythons were able to sustain prolonged periods in saline water [41]. A severe winter cold snap in south Florida showed that adult pythons had limited ability to withstand exposure to prolonged cold, wet weather [42]. However, despite progress in understanding the biology of this invasive species in the Everglades, python movements, home range, and general habitat-use patterns are largely unknown.

We designed a multi-year radio-tracking study of 16 wild-caught Burmese pythons to quantify their home ranges, characterize movement patterns across the landscape, and classify habitat use by area over time. We tested the hypothesis that pythons displayed site fidelity to the location of their initial capture. Over a shorter time period, we also tested the ability of custom GPS tags to provide multiple high-quality daily locations for an additional three pythons. Our results have implications for designing appropriately-scaled management strategies to control pythons and for understanding the potential impact of this exotic reptile on native species, many of which are of high conservation concern.

Results
Radio- and GPS tracking
We successfully radio-tracked 16 pythons (12 female, 4 male); individuals ranged in size from 263.0 to 472.0 cm total length (TL), with a mean size of 352.7 cm (SD 65.4 cm; Table 1). Radio-tracking periods ranged from 87 to 697 days, with a total of 5,119 python days across all pythons and a mean of 319.9 days (SD = 184.3 days; Table 1). For those days on which we obtained locations for radio-tracked pythons from both aerial and ground-based telemetry (n = 33 days), the straight-line distance between aerial and walk-in locations was on average 160.9 m (SD = 158.1 m); this distance is representative for eight pythons (11, 12, 14, 17, 18, 23, 25, and 27) and was calculated to estimate accuracy of aerial locations, not for use in analysis.

Three additional female pythons were also GPS-tracked; these individuals ranged in size from 466.0 to 537.0 cm TL, with a mean size of 503.7 cm (SD 35.7 cm; Table 1). GPS tracking periods ranged from 13 to 93 days, with a total of 146 days and a mean of 48.7 days (SD = 40.7 days). We recorded a total of 679 GPS locations for all three snakes, with the number of locations/day ranging from 0 to 21, with a mean of 4.7/day (SD 3.9/day; Table 1). Python locations were recorded during both daytime (391 points; 58%) and nighttime (288 points; 42%) periods.

Radio-tracked python movements
On average, pythons moved a mean of 31.2 km from the initial capture location to the final locations recorded, with a range of 6.8 to 80.1 km; average daily distances moved were 0.04 to 0.18 km (Table 1). Maximum values

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Table 1 Summary of size, sex, observed period, number of daily locations, and movements (total distance traveled, maximum and average mean daily distance, and date for maximum mean daily distance occurred) of Burmese pythons radio-tracked in Everglades National Park, South Florida, USA

Python ID	Total length (TL, cm) at capture	Sex	Observation period (number of days at large)	Number of daily observations (total Obs)	Total distance traveled (km)	Maximum of mean daily distance traveled (km)	Date for max mean daily distance traveled	Average mean daily distance traveled (km)
7	428.0	F	9/24/06 to 7/3/07 (282)	68	33.82	1.0	11/8/06 to 11/9/06	0.16
11	303.0	F	7/18/07 to 10/19/07 (93)	12	7.02	0.49	8/1/07 to 8/8/07	0.08
12	362.0	F	7/16/07 to 1/9/09 (543)	76	48.06	0.49	7/2/08 to 7/9/08	0.08
13	380.0	F	10/10/07 to 9/6/09 (697)	93	50.68	0.69	6/24/09 to 6/29/09	0.08
14	263.0	M	10/29/07 to 4/19/08 (173)	23	13.85	0.43	12/7/07 to 12/12/07	0.10
15	330.5	M	12/20/07 to 1/15/09 (392)	29	19.84	0.40	6/18/08 to 6/25/08	0.10
17	296.0	M	2/1/08 to 8/7/09 (553)	72	67.09	0.57	12/31/08 to 1/5/09	0.12
18	366.0	F	6/23/08 to 12/23/09 (548)	60	80.08	0.82	10/14/09 to 10/21/09	0.15
22	267.0	F	1/13/09 to 12/28/09 (349)	41	27.56	0.58	9/1/09 to 9/2/09	0.08
23	472.0	F	2/9/09 to 12/21/09 (315)	43	40.64	0.69	6/10/09 to 6/12/09	0.16
25	353.0	F	2/24/09 to 12/23/09 (302)	42	41.19	1.40	5/28/09 to 5/29/09	0.15
27	312.0	M	4/20/09 to 12/21/09 (245)	33	21.79	0.26	12/2/09 to 12/21/09	0.08
28	281.0	F	4/20/09 to 12/21/09 (245)	20	6.82	0.17	5/20/09 to 5/29/09	0.04
29	462.0	F	6/4/09 to 12/21/09 (200)	30	9.84	0.11	10/21/09 to 10/28/09	0.05
30	406.0	F	9/25/09 to 12/21/09 (87)	12	16.20	0.75	12/2/09 to 12/10/09	0.18
31	361.0	F	9/25/09 to 12/28/09 (95)	9	14.45	0.30	10/14/09 to 11/4/09	0.16
41[a]	466.0	F	12/17/10 to 3/20/11 (93)	84 (423)	18.39	2.43	2/1/11 to 2/3/11	0.16
51[a]	508.0	F	2/17/12 to 2/29/12 (12)	8 (16)	0.99	0.20	2/20/12 to 2/23/12	0.06
52[a]	537.0	F	3/12/12 to 4/18/12 (37)	32 (240)	2.14	1.02	4/16/12 to 4/17/12	0.06

[a]GPS-tracked pythons.

for mean daily distances traveled ranged from 0.11 to 1.40 km (Table 1), and these movements occurred during both wet and dry seasons. Four pythons moved their greatest mean daily distances in December, three in October, three in June, and two in May; other pythons moved their greatest mean daily distance in July, August, September, and November (Table 1).

Minimum convex polygon (MCP) home ranges for radio-tracked pythons varied in size from 1.7 to 87.4 km², with a mean of 22.5 km² (SD = 21.3 km²) or 2,250 ha (Table 2). The size of MCPs was not influenced by tracking duration or gender ($t = 0.49$, $P = 0.630$). The mean size of MCPs for females ($n = 12$) was 24.1 km² (SD = 23.9 km²), whereas the mean size for males ($n = 4$) was 17.8 km² (SD = 12.1 km²).

After overlaying all python MCPs to determine common-use areas, we identified 18 individual polygons of areas that were used by multiple radio- and GPS-tracked pythons

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Table 2 Size of MCP (minimum convex polygon) home range in km for each python radio- and GPS-tracked in Everglades National Park, South Florida, USA, with associated habitat types

| Python | Habitat type | | | | | | | | Total area (km²) |
	Upland forest pineland	Slough	Tree islands	Coastal	Lowland forest	Disturbed	Marsh prairie	Other	
7	0.2 (1.2)	**18.3 (96.8)**	0.4 (2.0)	0	0	0	0	0	18.9
11	0	0.5 (13.8)	0	**3.3 (86.2)**	0	0	0	0	3.8
12	0	**41.6 (91.7)**	0.4 (0.9 0)	0.6 (1.3)	0.01 (0.02)	0	0	0.07 (0.16)	45.3
13	0	0.4 (3.8)	0	**11.1 (96.2)**	0	0	0	0	11.5
14		0.2 (2.7)		**5.8 (97.2)**	0	0	0	0	6.0
15	0.04 (0.2)	**23.1 (93.5)**	1.1 (4.4)	0.5 (2.0)	0	0	0	0	24.8
17	7.3 (23.5)	**22.3 (71.8)**	0.8 (2.6)	0.6 (2.0)	0	0.04 (0.14)	0	0	31.1
18	7.7 (8.8)	**77.8 (89.0)**	1.4 (1.6)	0.5 (0.6)	0	0.04 (0.05)	0	0	87.4
22	0	2.2 (9.6)	0	**19.6 (85.4)**	0	0	0	1.2 (5.0)	23.0
23	0.06 (0.2)	**33.8 (97.4)**	0.8 (2.4)	0	0	0	0	0	34.6
25	0.3 (1.4)	**19.2 (94.1)**	0.7 (3.4)	0.2 (1.1)	0	0	0	0	20.4
27	0.05 (0.6)	4.5 (48.7)	0.03 (0.3)	1.2 (13.4)	2.2 (23.9)	0.2 (1.6)	1.1 (11.5)	0	9.3
28	0	0.2 (10.5)	0	**1.6 (89.5)**	0	0	0	0	1.7
29	0	**2.8 (100.0)**	0	0	0	0	0	0	2.8
30	1.5 (5.7)	**17.5 (66.3)**	0.1 (0.2)	7.3 (27.7)	0	0.02 (0.08)	0	0	26.4
31	0.1 (0.7)	0.5 (4.0)	0	**11.7 (95.3)**	0	0	0	0	12.2
41[a]	0.3 (1.1)	**20.9 (90.3)**	0.6 (2.4)	1.4 (5.9)	0 (0)	0 (0.2)	0 (0)	0 (0.1)	23.1
51[a]	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	**0.2 (100)**	0 (0)	0.2
52[a]	0 (0)	0.1 (25)	0 (0)	0 (0)	0 (0.3)	0 (0.6)	**0.3 (74.1)**	0 (0)	0.5

Values in parentheses are % of total home range area, and those in bold are >50.0% of the total home range. [a]GPS-tracked pythons.
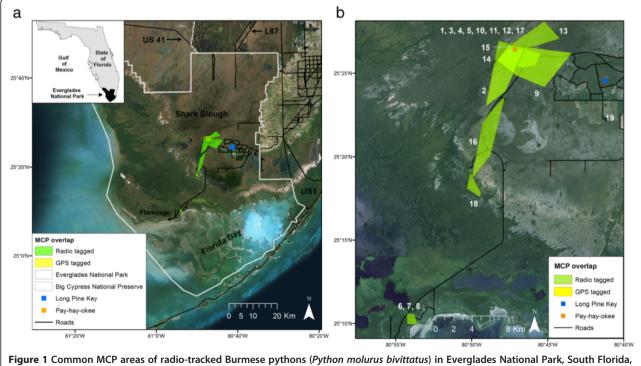

Figure 1 Common MCP areas of radio-tracked Burmese pythons (*Python molurus bivittatus*) in Everglades National Park, South Florida, USA (a) and zoom-in map of python common-use areas (b).

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(Figure 1, Table 3). A given common-use area was used by between two and five pythons, and most commonly (that is, mode) by two pythons. The mean size of common-use areas was 4.8 km^2 (SD = 6.1 km^2) and up to 22.4 km^2.

Of 16 radio-tracked pythons, we had sufficient number of daily locations for 13 pythons to create kernel density estimates (KDEs), of which least squares cross-validation (LSCV) was minimized only for five pythons, likely due to mostly linear movements of pythons. Thus, since LSCV was not minimized, we only attempted KDEs for these five pythons. The KDE home ranges of these five pythons are widely spaced, and there was no common area (Figure 2). Mean home ranges (95% KDE) and core areas (50% KDEs) across all five pythons were 7.3 km^2 (SD = 5.8 km^2) and 1.5 km^2 (SD = 1.4 km^2), respectively, smaller than the MCP estimates.

MCP home ranges for pythons occurred primarily within slough habitat for 9/16 (56%) radio-tracked pythons and within coastal habitat for 6/16 (38%) pythons (Table 2). Mean distance of the centroid to the nearest road for each MCP common-use areas (n = 18) was 0.5 km (SD = 0.7 km; Table 3). Further, mean elevation of the common-use areas ranged from 17.0 to 50.3 cm (Table 3), and habitat types for common-use areas were predominantly slough and coastal, included tree islands,

with some variation across the landscape (Table 4). Up to 12 tree islands were present in one common-use area, with individual tree island areas up to 0.4 km^2 in size (Table 4). Radio-tracked pythons that crossed a road (n = 11) did so a 2 to 23 times, with a mean of 6.9 crossings (SD = 7.2 crossings) throughout their tracking periods.
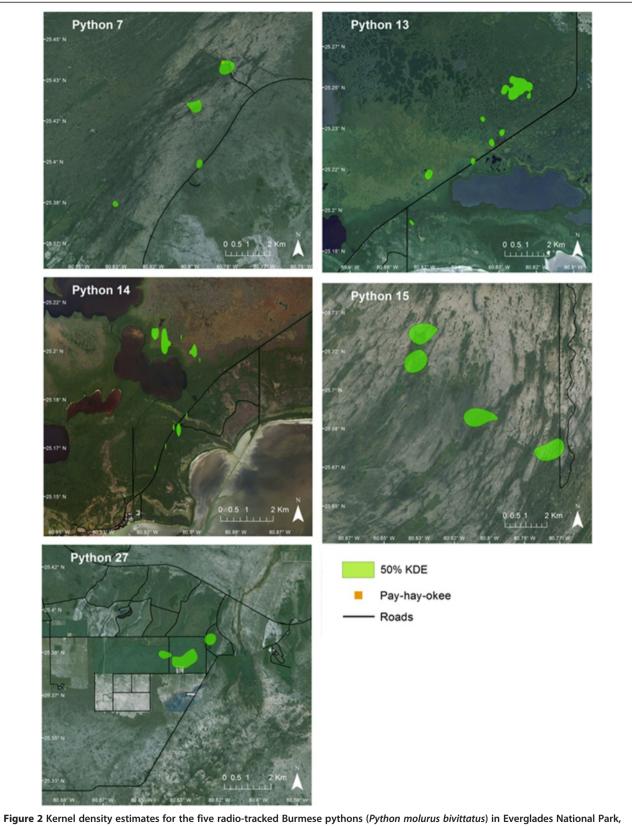
Movements of some radio-tracked pythons were correlated to air temperature: movements of python 14 were significantly correlated with mean and min daily air temperature; python 23 movements were significantly correlated with min and max daily air temperatures; and movements of python 27 were significantly (negatively) correlated with all three factors (mean, min, and max daily air temperatures; Table 5). Moreover, for all radio-tracked pythons, mean daily distances moved were lower when water was present (75.4 m, n = 451, SD = 116.0 m) versus absent (143.6 m, n = 260, SD = 220.2 m; Satterthwaite two-tailed t-test; $P < 0.0001$, $t = -5.74$).

Site fidelity was tested across the entire tracking periods for all radio-tracked pythons, and only one male (python 15) showed site fidelity throughout the tracking duration (that is, movements were more constrained than a random path). However, we observed seasonal site fidelity: pythons 15, 16, and 17 displayed site fidelity

Table 3 Area, elevation, and distance by National Elevation Dataset (NED) and distance to roads for MCP common-use area from pythons radio-tracked in Everglades National Park, South Florida, USA

Common-use polygon ID	Python ID	Area km^2	Mean (SD) EDEN elevation (cm)	Mean (SD) NED elevation (m)	Centroid distance to roads (km)	Number of tree islands	Mean area (SD) of tree island (s) km^2
1	7, 17	4.90	22.3 (4.6)	0.22 (0.10)	1.10	2	0.2 (0.2)
2	7, 18	12.50	17.0 (7.3)	0.17 (0.10)	1.50	6	0.1 (0.1)
3	7, 23	0.50	27.9 (4.1)	0.06 (0.16)	0.00	1	0.4 (0.0)
4	7, 25	4.10	22.0 (4.8)	0.21 (0.11)	0.90	2	0.2 (0.2)
5	7, 17, 18, 23, 25	0.50	27.9 (4.1)	0.06 (0.16)	0.01	1	0.4 (0.0)
6	11, 14	0.03	NA	−0.44 (0.04)	0.10	0	-
7	11, 28	1.10	NA	−0.13 (0.15)	0.20	0	-
8	11, 14, 28	0.02	NA	−0.42 (0.03)	0.04	0	-
9	17, 18	22.40	46.7 (20.3)	0.49 (0.23)	0.70	12	0.1 (0.1)
10	17, 23	0.90	27.9 (4.1)	0.13 (0.16)	0.30	2	0.2 (0.1)
11	17, 25	8.02	28.5 (9.8)	0.30 (0.14)	0.20	6	0.1 (0.1)
12	17, 18, 23, 25	0.80	27.9 (4.1)	0.11 (0.17)	0.04	1	0.4 (0.0)
13	18, 23	8.40	50.3 (13.8)	0.49 (0.19)	2.20	3	0.2 (0.1)
14	18, 25	9.60	26.2 (10.3)	0.27 (0.15)	0.20	6	0.1 (0.1)
15	18, 23, 25	10.9	NA	0.09 (0.15)	0.60	1	0.4 (0.0)
16	18, 30	0.80	27.9 (4.1)	0.13 (0.18)	0.04	4	0.02 (0.01)
17	18, 30, 31	0.02	NA	−0.19 (0.01)	1.04	0	-
18	30, 31	1.90	NA	−0.25 (0.06)	2.10	0	-
19[a]	51, 52	0.0004	64.3 (−)	0.62 (−)	0.19	0	-

[a]Common-use area of GPS-tracked pythons.

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Figure 2 Kernel density estimates for the five radio-tracked Burmese pythons (*Python molurus bivittatus*) in Everglades National Park, South Florida, USA.

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Table 4 Habitat types within 18 common-use areas for Burmese pythons radio-tracked in Everglades National Park, South Florida, USA

Common-use polygon ID	Habitat type						
	Upland forest pineland	Slough	Tree islands	Coastal	Disturbed	Marsh prairie	Total area (km^2)
1	0.2 (4.7)	**4.3 (88.8)**	0.3 (6.6)	0	0	0	4.9
2	0.2 (1.9)	**11.9 (95.4)**	0.4 (2.8)	0	0	0	12.5
3	0.04 (8.9)	**0.3 (51.9)**	0.2 (39.2)	0	0	0	0.5
4	0.2 (5.5)	**3.5 (86.6)**	0.3 (7.9)	0	0	0	4.1
5	0.04 (9.0)	**0.3 (51.2)**	0.2 (39.8)	0	0	0	0.5
6	0	0.0003 (0.8)	0	**0.03 (99.2)**	0	0	0.0
7	0	0.08 (7.3)	0	**1.0 (92.7)**	0	0	1.1
8	0	0	0	**0.02 (100.0)**	0	0	0.0
9	1.6 (7.0)	**20.0 (89.3)**	0.8 (3.6)	0.04 (0.2)	0	0	22.4
10	0.06 (6.9)	**0.6 (68.9)**	0.2 (24.2)	0	0	0	0.9
11	0.3 (3.5)	**7.2 (89.1)**	0.6 (7.4)	0	0	0	8.0
12	0.06 (8.3)	**0.5 (62.7)**	0.2 (29.0)	0	0	0	0.8
13	0.06 (0.8)	**8.0 (96.0)**	0.3 (3.2)	0	0	0	8.4
14	0.3 (2.9)	**8.7 (90.7)**	0.6 (6.4)	0	0	0	9.6
15	0.1 (7.8)	**0.5 (65.0)**	0.2 (27.2)	0	0	0	0.8
16	1.0 (8.8)	**9.8 (90.0)**	0.03 (0.3)	0.1 (0.6)	0.02 (0.2)	0	10.9
17	0.001 (9.4)	**0.02 (90.6)**	0	0	0	0	0.020
18	0.08 (4.4)	0.2 (12.6)	0	**1.6 (83.0)**	0	0	1.9
19[a]	0	0	0	**0**	0	**0.0004 (100.0)**	0.0004

Percentage of habitat by common-use area is in parentheses, and values in bold are >50%. [a]Denotes common-use area of GPS-tracked pythons. See Figure 1 for spatial locations.

during the dry season, whereas pythons 15, 17, and 22 displayed site fidelity during the wet season. There were too few observations for pythons 11 and 28 in the dry season and for pythons 14 and 31 during the wet season to assess seasonal site fidelity.

GPS-tracked python movements

On average, GPS-tracked pythons moved a mean of 7.2 km from initial capture location to final location, with a range of 1.0 to 18.4 km; average daily distances moved were 0.1 to 0.2 km (Table 1). Maximum values for mean daily distances traveled ranged from 0.2 to 2.4 km (Table 1). Pythons moved on average 32.2 m during daytime and 18.0 m during night time hours, with a range of (0 to 621.0 m) and (0 to 566.0 m), respectively. MCP home ranges varied in size from 0.1 to 23.1 km^2, with a mean of 7.9 km^2 (SD = 13.0 km^2). Two pythons shared a common area with size of 372 m^2. LSCV was minimized only for one python; the resulting KDE home range was 0.02 km^2 (95% KDE) with a core area of 0.002 km^2 (50% KDE).

GPS-tracked pythons were found in a mosaic of habitats during their tracking time, including upland forest pineland, slough, tree islands, coastal, lowland forest, disturbed, and marsh prairie habitats (Table 2). Within their home ranges, pythons were detected in slough and marsh prairie habitat types most frequently, although there was some use of coastal habitat, tree islands, and upland forest pinelands. Our MCP analysis showed that 1/3 (33%) of GPS-tracked pythons had >50% of their home ranges within slough habitat, whereas 2/3 (67%) of GPS-tracked pythons had >50% of their home range within marsh prairie habitat (Table 2). None of the GPS-tracked pythons crossed a road during their time in the field.

Discussion

Our study presents the first home range estimates for wild Burmese pythons in their introduced range. Home range size for Burmese pythons in ENP (MCP 22.5 km^2 or 2,250 ha) were far greater than those reported in their native range, albeit for a single report from the Lantau Island, Hong Kong, showing a home range size of 12.3 ha over 24 days [19]. Our home range estimate was also much greater than that estimated for most other ambush snake predators that have previously been radio-tracked [43]. Large-bodied carpet pythons (*Morelia spilota*) had home ranges of 17.6 ha [30] and 22.5 ha [33], and diamond pythons (*Morelia spilota spilota*) had home ranges

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Table 5 Correlations of Burmese python movements with air temperatures in South Florida

Python	Correlation, mean daily air temperature (C°) vs. mean daily distance traveled (m)	Min daily air temperature (C°) vs. mean daily distance traveled (m)	Max daily air temperature (C°) vs. mean daily distance traveled (m)
7	0.149	0.143	0.161
11	0.555	0.525	−0.117
12	0.183	0.195	0.146
13	0.128	0.106	0.166
14	**0.44***	**0.454***	0.214
15	0.045	0.009	0.034
17	−0.021	−0.06	0.031
18	0.123	0.12	0.139
22	0.181	0.181	0.225
23	0.459	**0.43***	**0.447***
25	0.226	0.163	0.275
27	**−0.512***	**−0.478***	**−0.525***
28	−0.079	−0.231	−0.082
29	−0.265	−0.236	−0.288
30	−0.203	−0.218	−0.244
31	0.261	0.233	0.353

Bolded and *values denote $P < 0.05$.

of 52 ha for males and 27 ha for females [29]. Further, daily movements of Burmese pythons in ENP (range 0.11 to 1.40 km) were larger than that reported for diamond pythons (100 m per week; [33]), and we observed only seasonal site fidelity patterns, indicating that most pythons did not consistently stay in a limited home range area throughout the year. ENP pythons have the ability to move relatively large distances and occupy relatively large home ranges, a capability that must be considered when population-spread scenarios are examined and risk assessments are performed. Further, [44] provided evidence that Burmese pythons are capable of homing long distances (21 to 36 km), in a relatively short period of time (94 to 296 days), after displacement at a scale previously undocumented for any snake species.

In addition to our python geo-referenced presence and absence data, this new home range information can help further our understanding of which prey species are at risk in ENP, including those that may be threatened, endangered, or rare. For example, in ENP, wood storks (*Mycteria americana*), Florida panthers (*Puma concolor coryi*), and Cape Sable seaside sparrows (*Ammodramus maritimus mirabilis*) are species of conservation concern that have home ranges proximal to the common-use areas of radio-tracked pythons [45-47]. Because pythons eat a variety of prey in ENP [48-50], it is possible that these species of conservation concern may be at risk of predation. Therefore, a logical

next step is to determine the impact of pythons on native species near these core and common-use areas in the Everglades. Whether pythons can slow the pace of native population restoration for other top predators in ENP such as alligators and iconic wading birds is already a serious management concern, but empirical evidence is lacking.

Pythons displayed significant movements when surface water was absent, indicating dispersal may occur under locally 'dry' conditions. Perhaps Everglades' pythons need to move greater distances from one relatively wet habitat patch to another to maintain access to adequate prey resources. Our evidence of site fidelity by season for some individuals during wet and dry seasons may support this hypothesis. Future fine-scale tracking coupled with very fine-scale activity loggers could complement and refine these initial radio-tracking results to illuminate dispersal strategies used by pythons in ENP.

Roads can serve as either a barrier or a corridor for wildlife [51], we found that 67% of radio-tracked pythons crossed a road with no record of road-caused mortality during the study period. Although home ranges for many snakes included roads, this may be biased because road-cruising was a capture method used in this study. Regardless, the ability of pythons to utilize roads with possibly relatively lower rates of mortality than other species (see [51]) further highlights the inconspicuous and cryptic nature of pythons in ENP, where overall detectability is low.

We found an overlap in MCP home ranges for individuals; however, it should be noted that based on how we acquired our study animals (that is, sometimes opportunistically obtaining pythons that were co-located with other radio-tagged pythons or close to roads), one might expect an overlap in some habitat-use areas. Overlapping home ranges may offer adult pythons increased encounter rates with other adults during the springtime mating period. Moreover, common-use areas may contain especially suitable habitat patches where factors such as prey availability and environmental conditions are favorable. In our study, the predominant habitat class within python home ranges was slough, and many pythons frequented areas with tree islands; tree islands are patches of woody vegetation within a freshwater wetland matrix dominated by non-woody species [52]. Thus, in addition to providing a hospitable shaded, structured habitat, tree islands are also utilized by many small mammals and birds. Some tree islands consist of rough terrain with nearly impenetrable vegetation, making surveys for secretive animals in such habitat extremely difficult. To date, no organized searches for pythons on tree islands in ENP have been initiated, but resource managers may need to give consideration to python search efforts in these habitats as data from radio-tagged pythons indicates that they spend long periods of time there. Our results

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suggest that evaluation of python habitat use on tree islands occurring in close proximity to python home range polygons is warranted.

Knowledge of the 'detectability' of an invasive species is important for planning control and eradication programs [53]. Mazzotti *et al.* [42] reported that pythons in South Florida were less detectable by humans in natural areas than in artificial habitats, potentially a result of the combination of habitat accessibility and python visibility. A field test of traps in the wild further revealed low overall capture rates and detections of pythons in surveyed areas [54]. Burmese pythons are extremely cryptic and well camouflaged in the Everglades, thus making them relatively difficult to detect for any given observer. In addition, the use of newer technology like our custom GPS tags can provide much more fine-scale location data for interpreting python habitat use and movements during day and night time hours.

Surveys and control measures such as trapping and direct, repeated visual searches in likely python habitats at specific times of the year (that is, winter) and day may increase removal rates of pythons. Currently, the extent that such removals actually reduce an apparently dense population of secretive snakes in a largely inaccessible landscape is unknown and could be low. Regardless, our results shed light on the area in which a given adult python's daily activities are focused, and as such, inform planning of searches (that is, location and areal extent) intended to detect pythons in the wild.

Conclusions

The persistence of the non-native Burmese python population in the Everglades necessitates a range of scientific tools to understand the biology of this species in its new environment. Our results provide a new understanding of python movement rates, home range size, and habitat preferences. In addition, the use of GPS tracking technology can provide detailed daily movement data which we have not had to date, information that is useful for refining estimates of the impact these invaders are having on native prey populations. Sites we have identified as common- and core-use areas may be suitable for monitoring for python presence (for example, skin sheds) and targeted for python removal efforts. Moreover, these sites may be useful as study areas for detecting changes in species composition of prey resources available to pythons.

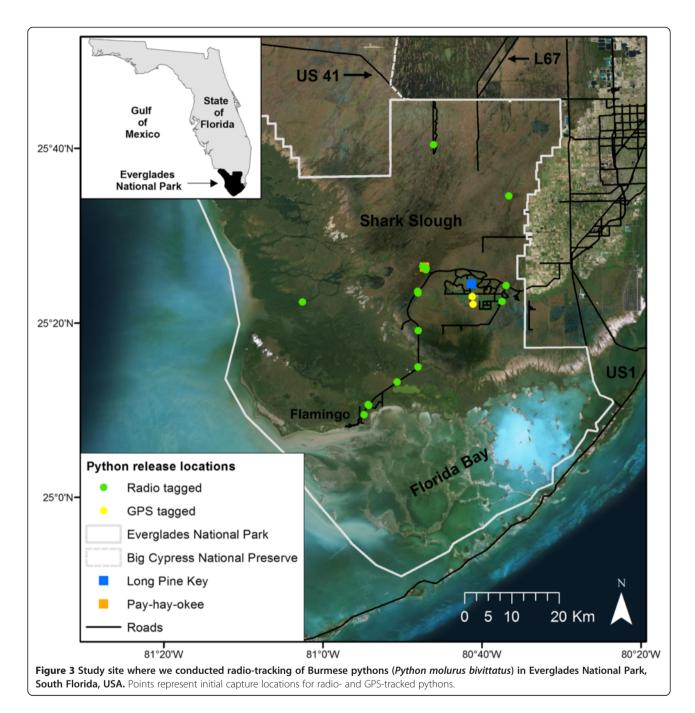## Methods

Ethics statement

All python radio-tracking was permitted under University of Florida animal care protocols F162 and 009-08-FTL, Florida Fish and Wildlife Conservation Commission permit ESC 08–02 and National Park Service (Everglades) permits EVER-2007-SCI-001 and EVER-2009-SCI-001.

Study site

We conducted python tracking from October 2007 through April 2012 within ENP (Figure 3). Everglades National Park is 0.9 million ha of wilderness bordered on the west and north by Big Cypress National Preserve and Tamiami Trail (US 41), extending into the mangrove-lined west coast of Florida and Florida Bay [12]. Habitat types in ENP are varied and include cypress swamps, hardwood hammocks, and wet prairies characterized by sawgrass (*Cladium jamaicense*). We conducted tracking in several locations throughout ENP, as well as in the remote coastal mangroves.

Python captures and implantation of radio and GPS transmitters

We caught all pythons (radio-tracked and GPS-tracked) by conducting road-cruising surveys of ENP roadways and levees during morning and evening hours. We obtained additional pythons by finding new individuals in proximity to already radio-tagged pythons. We hand-captured all pythons and temporarily restrained each individual in a snake bag within a large plastic storage container. We recorded capture locations using a hand-held GPS unit. We measured each python, taking mass in kilograms and standard lengths (snout-vent length (SVL), total length (TL), and girth, in centimeters). Each python was implanted intraperitoneally (in the body cavity) with two radio transmitters [55-59]; the second transmitter was a 'backup' in the event that the first one failed. We used two transmitter sizes, Holohil models SI-2 (11 g) and AI-2 (25 g) (Holohil Systems, Ltd., Carp, ON, Canada). Three pythons received the additional GPS tag (Quantum 4000E Medium Backpack; Telemetry Solutions, Concord, CA, USA); transmitter weights did not exceed 0.1% of each snake's body mass. The expected battery life for each VHF transmitter was between 9 and 12 months. GPS tags lasted between 2 and 5 months, depending on the frequency (number of times/day) with which the tags were programmed to attempt to acquire locations and how long each location took to complete. Tags were programmed to record locations every hour. Points from the tags were downloaded after the transmitter was recovered. We anesthetized each snake before implantation using isoflurane administered with an anesthesia machine; the surgery lasted between 30 to 60 min for each snake. After surgery, we observed each python for at least 24 h before release. Prior to release, we visually inspected each python to assess its health and alertness, as well as any problems related to implantation. None of the snakes used in our analyses showed any problems related to transmitter implantation. Snakes were tracked to the

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Figure 3 Study site where we conducted radio-tracking of Burmese pythons (*Python molurus bivittatus*) in Everglades National Park, South Florida, USA. Points represent initial capture locations for radio- and GPS-tracked pythons.

extent the battery life would allow, until they needed to be re-implanted with new transmitters or in the case of four snakes, until they were found deceased.

Radiotelemetry

We released each python within a few hundred meters of its original capture location (Figure 3). Once a week, we radio-located each radio-tracked python with a VHF tag from a fixed-wing aircraft (Cessna 182), flying at speeds between 100 and 140 km/h and altitudes between 152 and 610 m. We used a Habit Osprey VHF telemetry

receiver (Habit Research Ltd., Victoria, British Columbia, Canada) and H antennas mounted to the wings of the airplane or handheld from the ground to monitor telemetry signals. We recorded GPS locations for all pythons located during walk-ins; however, walk-in data was only used to confirm aerial locations and ground-based GPS locations, not in analysis of python movements or home range, as the number of visual confirmations was not consistent across all pythons. Pythons with GPS transmitters were also tracked aerially and visually located weekly. Locations were manually recorded not only on a

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handheld GPS by the observer during the flight as for all other pythons but also on-board the implanted GPS tag.

Statistical and spatial data analysis
Python movements
To visualize radio-tracked python movements over time, we plotted aerial telemetry locations for all pythons by date using a geographic information system [60] and created tracks by connecting successive points, assuming a straight-line movement. For a subset of radio-tracked pythons for which we had walk-in locations and aerial telemetry locations on the same day, we calculated the distance between aerial and ground locations to test the accuracy of aerial locations.

To calculate the mean daily and average mean daily distance traveled, we connected successive points, assuming a straight-line movement. We used aerial locations for radio-tracked pythons and chose one GPS location per day for each GPS-tracked snake. If there were multiple locations per day, we chose the point calculated using the maximum number of satellites (range 3 to 10). If there were multiple locations that shared a maximum number of satellites, we chose the point with highest maximum satellite signal strength (range 32 to 45) used to calculate the location. To separate out movements during day and night time hours, we calculated the distance between successive locations during those times. Since data collected between radio-tracked and GPS-tracked pythons were collected on different scales (weekly versus multiple per day), and with different technology, data for GPS pythons was analyzed separately.

Home ranges
For all radio-tracked pythons, we calculated the MCP ($n = 16$) estimates and, when possible (at least 20 daily locations), KDE ($n = 5$) from aerial tracking data to define home ranges. For GPS-tracked pythons, we used all GPS locations to calculate MCPs ($n = 3$) and KDEs ($n = 1$).

Home range metrics, by definition, describe the area traversed by an animal during normal daily activities, excluding migrations or erratic movements [61]. Estimates of MCP identify home ranges as the area within a polygon formed by joining outermost re-sighting positions of an animal [62-65]; MCP has been commonly applied in other snake tracking studies [28,29,31]. In addition to calculating MCPs, we assessed the overlap of individual python MCPs to determine 'hotspots' or common-use areas and calculated the centroid for each MCP. Similarly, kernel density is a non-parametric method used to identify one or more areas of disproportionately heavy use (that is, core areas) within a home-range boundary [66,67], with appropriate weighting of outlying observations. As [67] suggested, for KDEs, we used the 95% contour to represent home ranges and the 50% to depict 'core' areas for each animal following [68,69]. We used the Home Range Tools extension [70] with ArcGIS 9.3 [60] and a fixed kernel LSCV smoothing factor (h_{cv}; [68,71]) for each individual KDE; we estimated KDEs only for pythons that had ≥20 mean daily locations.

Habitat use and environmental variables
We overlaid the ENP boundary on all resulting maps of python home ranges and core-use areas. We reclassified a land cover and land use map [72], using a modified Davis classification for habitat types [73]; modifications included compiling similar habitat types into fewer, broader categories of habitat classes. The reclassified map includes upland forest/pineland, slough, tree islands, coastal, lowland forest, disturbed, marsh prairie, and other habitat types. Additionally, because many previous python observations have been logged near roads (NPS and USGS, unpublished data), which can act as barriers to other animal movements [51], we determined the number of individual python movement paths that crossed a road.

To assess how python movements differed seasonally, we calculated movement distances across seasons; we defined seasons in ENP as 'wet' during May through October and 'dry' during November through April [74]. To explore whether radio-tracked python movements were correlated with environmental variables, we assessed Pearson's correlation coefficients with mean, min, and max air temperature recorded at a local weather station (that is, JBTS owned by South Florida Water Management District), downloaded from their DBHYDRO database [75]. We also assessed movements in relation to water presence/absence and elevation using a spatially explicit daily surface water depth model developed by Everglades Depth Estimation Network [76,77]. We conducted all statistical tests in R [78] and used an α level of 0.05 for all analysis to assess statistical significance.

Site fidelity
Finally, to test the hypothesis that radio-tagged pythons displayed high site fidelity during their entire tracking periods or by season (wet and dry), we conducted Monte Carlo random walk simulations using Animal Movement Analysis Extension for ArcView 3.2 [79]; we compared observed movement paths with 1,000 randomly generated paths for all radio-tracked animal for both entire tracking periods and by season.

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