*Invasive Burmese pythons (*Python bivittatus*) are novel nest predators in wading bird colonies of the Florida Everglades*

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ORIGINAL PAPER

Invasive Burmese pythons (*Python bivittatus*) are novel nest predators in wading bird colonies of the Florida Everglades

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Abstract Invasive Burmese pythons have been shown to have population-level effects on native mammals in southern Florida. Tens of thousands of long-legged wading birds (of multiple species in Ciconiiformes, Pelecaniformes) breed in aggregations, known as colonies, on tree islands in the Everglades. Burmese pythons may pose a threat to these colonies because pythons are semi-aquatic and commonly use tree islands and arboreal habitat. However, python predation on nests of wading birds has not previously been documented or quantified. We used trail cameras to monitor nests at colonies in Everglades National Park and Water Conservation Area 3 in 2014, and 2016–2017. We did not detect Burmese python predation at monitored nests in 2014 (23 nests in 2 colonies) or 2016 (59 nests in 4 colonies). In 2017 (125 nests in 7 colonies), we detected three individual pythons consuming nestlings, fledglings, and eggs in a minimum of 7.9% (5 nests, n = 63) of monitored nests at a colony in Everglades National Park. In 2017, the overall predation rate of Burmese pythons at all monitored nests (5 of 125 nests, or 4%), was five times the native predator rate (1 of 125 nests, or 0.8%). Our study confirms that Burmese pythons are acting as predators in wading bird colonies at nontrivial rates and provides a baseline to which future studies can refer.

Keywords Predation · Invasive · Wading bird · Colony · Reproductive success · Python

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Introduction

Invasive predators have caused dramatic declines and extinctions in wildlife populations across the world (Doherty et al. 2016; Salo et al. 2007) especially in insular systems (Fritts and Rodda 1998), in ecosystems where other biotic and abiotic stressors already exist (Doherty et al. 2015), and where prey species are particularly vulnerable because of natural history traits (Bodey et al. 2011; Moore et al. 2003). Prey species may also exhibit different levels of naïveté if they have not co-evolved with a predator, ranging from inability to recognize the predator as a threat to ineffectual anti-predator responses (Banks and Dickman 2007; Carthey and Banks 2014). Mammalian invasive predators (e.g. cats, dogs, foxes) have collectively caused the greatest amount of native defaunation worldwide, often involving naïve prey species on islands (Doherty et al. 2016). As global biotic homogenization continues, reptiles constitute a growing class of invasive predator. Their energetic efficiency, as ectotherms, allows them to persist at higher densities compared to mammalian predators, even when prey abundance fluctuates. This trait coupled with others like rapid maturation and wide diet breadth means they can exert strong impacts on native fauna (Pough 1980; Reed et al. 2012; Willson 2017). On the island of Guam, for example, brown tree snakes (*Boiga irregularis*) have caused drastic declines or extinctions of native avifauna (Savidge 1987) and in the peninsular mainland of south Florida, Burmese pythons (*Python bivittatus*) are directly and indirectly negatively impacting multiple trophic levels (Hoyer et al. 2017; McCleery et al. 2015; Miller et al. 2017; Reeves et al. 2018; Sovie et al. 2016; Willson 2017).

Burmese pythons (hereafter "pythons") are apex predators native to Southeast Asia. They were introduced to south Florida through the pet trade and have been established and spreading in the greater Everglades since the 1980s (Willson et al. 2011). These constrictors have been linked to sharp population declines and local extinctions in several mammal species in Everglades National Park (Dorcas et al. 2012; McCleery et al. 2015) and they are negatively impacting both species richness and the distribution of mammals throughout the greater Everglades (Reichert et al. 2017; Sovie et al. 2016). During the 2000s, mammals constituted approximately 70% of prey species consumed by pythons, while birds and crocodilians made up the remaining 30% (Snow et al. 2007). Many adult long-legged wading birds (orders Ciconiiformes, Pelicaniformes) and rails (order Gruiformes) have been identified in python gut contents, in particular (Dove et al. 2011). Durophagy of Limpkin (*Aramus guarauna*) and Guineafowl (*Numida meleagris domesticus*) eggs has also been documented in pythons of south Florida (Dove et al. 2012). Pythons are opportunistic, generalist predators with a large isotopic niche width (Smith 2016) and may shift diets to new sources as existing ones become over-exploited in south Florida. Given the sharp declines and local extinctions that have occurred in mammal populations, it is prudent to hypothesize that pythons are shifting diets to include more birds. Current research is unclear on this subject, in part because of spatiotemporally biased diet samples from captured pythons, which makes it difficult to compare diets before and after the reduction in mammals in parts of the system. In addition to being opportunistic and having a wide diet, pythons are preadapted to aquatic habitats (Dorcas and Willson 2011; Hart et al. 2015), use arboreal habitats (Dorcas and Willson 2011; Dorcas et al. 2011), and may engage in wide-ranging foraging (Greene 1997; Reed et al. 2012). Collectively, these factors suggest that pythons could pose a substantial threat to colonially-breeding wading birds (families Ardeidae, Ciconiidae, and Threskiornithidae). Wading bird colonies in the Everglades range from dozens to thousands of nesting pairs and persist for 3–4 months during the dry season (January–May). Pythons may be attracted to colonies by the sheer number and high density of potential avian prey items. Wading birds in the Everglades typically breed on isolated islands composed of trees in open-water or herbaceous marsh. The presence of a native apex predator at these islands, the American alligator (*Alligator mississippiensis*), may facilitate wading bird reproductive success by conferring protection against many nest predators (Burtner and Frederick 2017). A water barrier can deter mammalian predators from accessing islands in the marsh (Frederick and Collopy 1989; Rodgers 1987). The aquatic isolation of these colonies does not preclude python occupancy, however, since tree islands are common-use areas and open-water marsh is a core-use habitat for pythons (Hart et al. 2015). In view of a multidimensional threat involving predator ability (terrestrial and arboreal, semi-aquatic, potentially wide-ranging foragers), potential predator motivation (altered mammalian prey densities), and prey vulnerability (potential wading bird naïveté, increasing python population), we predicted that pythons are directly impacting wading bird reproductive success through nest predation. Since pythons are highly cryptic and difficult to detect using traditional visual survey or trapping methods (< 1% detection probability; Dorcas and Willson 2013; Reed et al. 2011; Willson 2017), we tested this prediction by using trail cameras aimed at nests from multiple colonies throughout the Everglades in 2014, and 2016–2017.

Methods

Site selection and study design

We monitored nests of colonially nesting birds at sites representing a range of habitat types where wading birds breed in the Everglades (Table 1); our study area encompassed a gradient of python density increasing from north to south (Bonneau et al. 2016). The southern sites were in Everglades National Park, located within the epicenter of reported python sightings, while sites in Conservation Area 3 were closer to the northern invasion front (Fig. 1). We selected the three colonies in Everglades National Park because pythons had previously been sighted in or near them. There was no prior information regarding python occupancy in the five colonies we selected in Water Conservation Area 3, though the invasion front extends well north of those locations.

We chose to monitor colonies with $\geq$ 60 breeding pairs (including all species) because we assumed that larger aggregations would be particularly attractive to pythons due to stronger odor cues from nest contents (guano, dropped prey items, nestlings). Using their tongues, snakes can detect and localize airborne odor molecules, even potentially at long range (Greene 1997). We primarily monitored nests of Great Egrets (*Ardea alba*) and White Ibises (*Eudocimus albus*), and also a handful of small day-heron (*Egretta* spp.) nests. Great Egrets breed at many tree islands and nest in the mid-to-upper canopy while White Ibises concentrate in large numbers in only a handful of tree islands and nest in the mid-to-low canopy. We monitored White Ibises because they presented different predation opportunities (higher densities, lower nest heights) and because they are numerically dominant as nesting birds in the Everglades (Frederick et al. 2009; Kushlan et al. 1985). In most cases, White Ibises were monitored on the same transects as Great Egrets.

At each site, we deployed cameras aimed at nests along a transect, and visited weekly to check camera placement, change batteries, or switch cameras to other nests once a monitored nest failed or finished. We created transects where nesting density within a colony was highest, as determined from aerial surveys. Except for the species, we had no a priori selection

Table 1 Information on sites monitored with trail cameras in 2014, and 2016–2017

Colony	Habitat type	Area (m^2)	Previous python sightings	Year	Max breeding pairs	Nest cams	Ground cams	Proximity cams
Cuthbert Lake	Estuarine mangrove island (ENP)	1955	June 2014—python observed in empty Wood Stork nest (L. Oberhofer)	2016	60	12	1	1
				2017	55	13	5	0
Paurotis Pond	Mangrove island in borrow pit for ENP main park road	12,105	Telemetered pythons occupied island Mar 21–May 30 2008 and Apr 28–Aug 5 2010 (B. Smith)	2016	815	15	0	2
Tamiami West	Pond apple/willow relictual island bisected by canal (ENP)	584,688	Fairly frequent road kill pythons on Tamiami Trail (Rt. 41)	2014	1200	11	0	0
				2017	3138	27	9	1
Henry	Cypress dome island (WCA-3A)	10,245	–	2016	134	16	1	1
				2017	94	17	4	0
6th Bridge	Willow strand island (WCA-3A)	121,758	–	2016	788	12	0	5
				2017	11,352	4	4	2
Diana	Hardwood island (WCA-3B)	7378	–	2017	81	8	1	0
Vacation	Willow strand island (WCA-3A)	44,182	–	2017	77	9	4	0
Joule	Willow strand island (WCA-3A)	62,384	–	2014	97	12	3	0
				2017	114	10	2	0

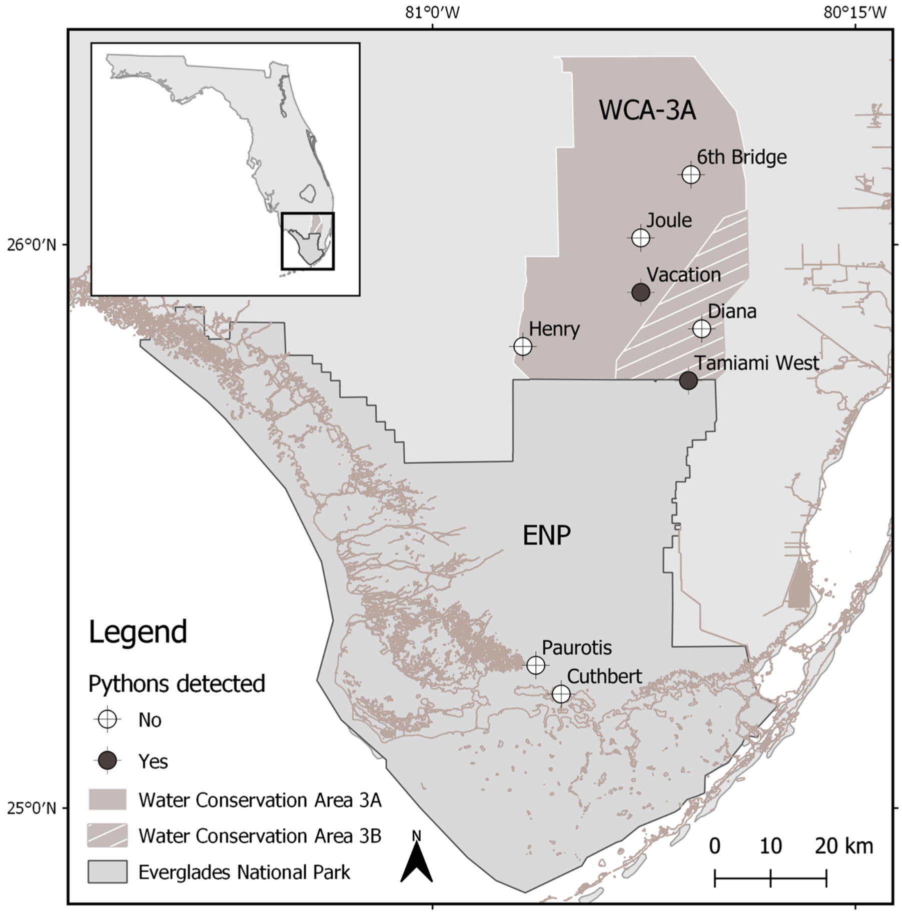

Fig. 1 Monitored colony locations. Burmese python nest predation was detected in Tamiami West (2017) at the northern edge of Everglades National Park (ENP). Python nestling predation was also incidentally detected in Vacation within Water Conservation Area-3A (WCA-3A) in 2018. Vacation was a colony we had monitored in 2017

criteria for which nests to monitor, and opportunistically selected nests at variable intervals along each transect. Inter-camera distance was between 1.5 and 10 m. In transects where White Ibis were nesting, a single camera could monitor 3–5 White Ibis nests simultaneously due to higher nest densities compared to Great Egrets or small day-heron spp., which required a camera per nest.

We sequentially installed 4–6 cameras each week on transects, with 8–18 cameras per transect. We minimized investigator disturbance to reduce potential nest abandonment by limiting each colony visit to an hour and not entering colonies until the majority of birds were incubating. Continuous monitoring began in the mid-incubation or early chick-rearing stage for most nests, and continued for an average of 38 d. We sometimes removed vegetation obscuring the view of the camera; in some colonies, we had to do this on a regular basis because vines grew quickly. In addition to cameras aimed at nests, we purposely set up cameras (0–3 in 2014 and 2016 and 1–5 in 2017, per transect) in open areas within the colonies, aimed at the ground. Some nest cameras shifted away from the nest or were aimed at vegetation or the ground adjacent to the nest. These cameras were characterized as proximity cameras and excluded from the nest dataset but still analyzed for potential python detections.

Camera pole design and setup

We mounted trail cameras on camouflage-painted telescoping metal poles (2.4–4.8 or 6.4 m) with a stabilizing foot (Online Resource 1, Fig. S11). The camera mount angled the camera downward at 20°–35° from vertical. The pole was shoved $\sim$ 0.5 m into the ground/peat within 1–3 m of the nest, until the stabilizing foot disappeared. We further stabilized each pole using parachute cord attached to nearby trees and branches.

Trail camera programming

In 2016, we deployed 41 new Reconyx Hyperfire 500 and 19 previously used Bushnell Trophy Cam HD trail cameras, powered with Energizer Ultimate Lithium AA batteries. Cameras were set on a continuous (day and night) time lapse of 5 min intervals (Online Resource 1, Table S1) with motion detection disabled. In 2017, we added 30 new Bushnell Trophy Cam HD Essential trail cameras. A portion of nests in 2017 (32) were set to 1 min time lapse intervals to test whether predator detection was improved but we found interval length made no difference. We used 32 GB SDHC class 4 SanDisk cards to store camera images. Night vision was set on 'balanced' in Reconyx and 'high' in Bushnell cameras.

Image analysis

We analyzed nest images in an accelerated slideshow setting with XnView software. We set a 150–250 ms (ms) delay between each picture. Most images were analyzed at 150–200 ms delay. In 2017, we increased the delay to 250 ms when the frame included extensive background, to ensure that we did not miss potential pythons on the ground. To analyze images, we softly focused central vision on the nest(s) and engaged peripheral vision to detect changes in light and movement in the background from frame to frame. Whenever something shifted, or an unidentified object appeared, we toggled the images back and forth to determine what had entered the frame. To analyze ground and proximity cameras, we looked for sudden changes in the frame with paracentral and peripheral vision. We examined all images from beginning to end of camera deployment, except for cases where the nest failed and the camera continued recording images at an empty nest. We scanned generally not more than 20,000–30,000 images per day to mitigate eye strain and ensure consistent mental focus. In 2014, images were analyzed by a student technician; in 2016 and 2017, 85% of images were analyzed by SCMO and 15% by a volunteer technician.

Scoring nest fates

In all nests we noted whether partial or complete egg or chick loss occurred. Loss categories were predation, dead/abandoned, scavenged, unhatched, and unknown. In some cases, Great Egret chicks were pushed out of the nest due to sibling competition. Nests were considered fledged if at least one chick reached fledging age (21 days for Great Egrets and Black-crowned Night-Herons, 14 days for White Ibises and small herons). We scored nest fate as follows: "unsuccessful" if all eggs or chicks died in the nest or were abandoned prior to fledging date, "scavenged" if a vulture or other bird consumed the nest contents after all eggs or chicks died, were abandoned, or were poorly attended by parents, and "depredated" if we witnessed a predator consuming or removing the contents of an active nest.

Estimating daily detection probability in Tamiami West

Since cameras were spatially correlated within transects, we used a null occupancy model with correlated detections (MacKenzie et al. 2002) to estimate the daily Burmese python detection probability across trail cameras in the site 'Tamiami West' with positive detections. The model was run using PRESENCE 12.7 in the R software interface (Hines 2006).

Calculating confidence intervals for observed predation rates

We used Wilson confidence intervals because the Wilson method performs well when sample size is small and the observed rate is an extreme value, i.e. close to zero or one (Brown et al. 2001). For the transects in Tamiami West where the observed python predation rate was greater than zero, we calculated two-sided 95% confidence intervals. For all other sites where the observed predation rate was zero, we calculated upper one-sided 95% confidence intervals. We used the 'prevalence' package in R to calculate the Wilson intervals (Devleesschauwer et al. 2014).

Results

Python detections

In 15,336 monitoring hours at 23 nests in two colonies and 58,824 monitoring hours at 59 nests in four colonies, we did not detect pythons in 2014 or 2016. In 114,834 monitoring hours at 125 nests in seven colonies in 2017, we detected pythons at one colony (Table 2). The colony with positive detections, Tamiami West, was located within the northern boundary of Everglades National Park adjacent to Water Conservation Area 3A (Fig. 1). We detected pythons on nine different occasions between 2 April and 16 May across two transects designated "GREG" for Great Egret and "WHIB" for White Ibis, which were approximately 475 m apart. We distinguished individual pythons based on markings and size (see Online Resource 1) and detected one python, P1, in the northern GREG transect, where we monitored 21 nests, mostly belonging to Great Egrets. We detected two pythons, P2 and P3, on eight different occasions in the WHIB transect, where we monitored 42 White Ibis nests. The daily probability of python detection calculated in the null occupancy model with correlated detections was 0.18 (0.02–0.67 95% CI) across all cameras in Tamiami West in 2017 (mean 21.2 ± 4.3 [SD] daily active cameras across the 63 d monitoring period).

Estimated predation rates

The overall python predation rate of monitored nests in the Tamiami West colony was an estimated 7.9% (5 nests, n = 63). The rate of nest predation was 4.76% (1 nest, n = 21) in the GREG transect, and 9.5% (4 nests, n = 42) in the WHIB transect (Fig. 2) of Tamiami West. At the colonies where the observed rate was zero, the upper 95% Wilson confidence intervals bounded 14.4–25.2% (Fig. 2) and the sites with the highest upper confidence limits contained the fewest nests monitored. In the WHIB transect of Tamiami West, we detected additional python predation events on three separate occasions across the span of 5 days. On those occasions, python P3 suddenly appeared on camera with chick(s) in its coils, which likely came from three different nests outside the camera frame. In all cases, the chicks were small, with minimal feather development, and appeared not more than 10 days old, which means that they were not yet mobile and still nest-bound (De Santo et al. 1990). We did not include these predation events in the overall rate, however, because the chicks originated from nests we were not monitoring. These additional detections of chicks that were constricted and consumed on camera confirm that python P3 was depredating additional nests within the transect. The overall colony python predation rate in 2017 was 1 in 7, or 14.2% of monitored colonies. A Great Horned Owl (*Bubo virginianus*) was the only native predator we documented depredating a Great Egret nest from the colony Henry in 2017 on the western edge of WCA-3A (1 nest, n = 16, or 6.25%). We detected a raccoon (*Procyon lotor*), on a ground camera in the WHIB transect of Tamiami West on 7 May 2017, 15 May 2017, and 19 May 2017, but never witnessed any predation events involving raccoons. The overall predation rate at all camera-monitored nests in all colonies (pythons plus native predators) was 4.8% (6 nests, n = 125) in 2017 and 0% in 2014 and 2016. The overall python predation rate (4%, 5 of 125 nests) was five times the overall native predator rate (0.8%, 1 of 125 nests) in 2017.

Table 2 Burmese python detections in Tamiami West (2017)

Date	Cam ID	Transect	Python ID	Behavior	Species	Loss	Entered frame	Hours observed
2 April 2017	Recon27	GREG	P1	Predation	GREG	2 chicks	19:55	0.67
3 April 2017	Bush61	WHIB	P2	Predation	WHIB	2 eggs	03:49	0.57
21 April 2017	Bush16	WHIB	P3	Predation	WHIB	4 + chicks	00:10	4.33
21 April 2017	Bush20	WHIB	P3	Predation, climbing	WHIB	2 + chicks	11:21	2.10
24 April 2017	Bush20	WHIB	P3	Predation, climbing	WHIB	2 chicks	02:22	2.12
25 April 2017	Bush20	WHIB	P3	Predation, eating	WHIB	2 chicks	18:01	2.25
7 May 2017	Bush50	WHIB	P2[a]	Climbing	NA	NA	20:20	1.42
16 May 2017	Recon20	WHIB	P3	Predation	WHIB	1 juvenile	19:20	1.0
16 May 2017	Bush19	WHIB	P3	Climbing	NA	NA	20:25	0.50

[a]Unconfirmed detection but presumed P2 based on size and similar location

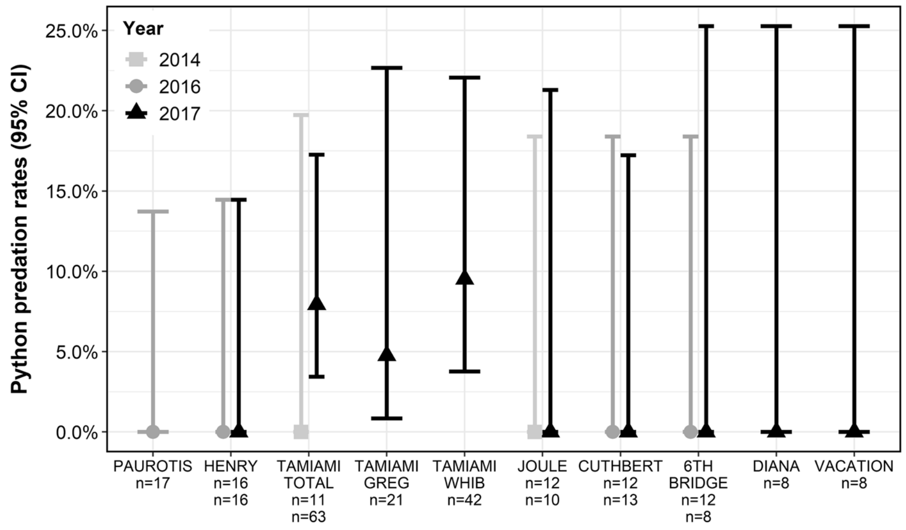

Fig. 2 Estimates of nest predation rates with 95% Wilson confidence intervals. Sample size of nests on the x-axis for each year monitored. For Tamiami West, the site with detections in 2017, the overall estimated predation rate is reported for both years monitored (Tamiami Total), as well as the rate in each of the two separate transects in 2017 (Tamiami GREG and Tamiami WHIB). This was the only occasion where there were two transects to report

Python predation observations

We detected python P1 (1.5–2 m long) depredating a Great Egret nest 1.5 m off the ground in a willow (*Salix caroliniana*) on 2 April 2017 at 19:55 (Fig. 3). It constricted two 30 day old fledglings simultaneously and removed one, leaving the other (Online Resource 2), which was scavenged by a Turkey Vulture (*Cathartes aura*) on 5 April 2017. We detected python P2 (1–2 m long) depredating a White Ibis nest containing two eggs on 3 April 2017. The snake had ascended ~ 1.1 m up a Brazilian Pepper (*Schinus terebinthifolius*) trunk inclined at ~ 45°. The incubating adults left, but several came back while P2 was in the nest and perched above it, peering down at it (Online Resource 3). Once the snake exited the frame,

Fig. 3 Python P1 documented 2 April 2017 constricting two Great Egret fledglings (30 days old) in their nest just after dusk (20:20:00). This nest was monitored in the GREG transect of Tamiami West

it took several hours for all adults breeding nearby to return. Given the 5 min time lapse intervals and the fact that the nest was at the edge of the frame, we must infer that the python ate the eggs upon invading the nest. The two eggs were clearly present as the adult flushed off the nest and were clearly gone after the python left. The adult of this nest never returned to incubate. We detected python P3 (3–4 m long) first at 00:15 on 21 April 2017. The brooding adult White Ibises left their nests soon after P3 entered the frame and came back intermittently during the next several hours while the python was present. P3 depredated two nests (< 0.5 m high) containing White Ibis chicks not more than 10 days old (Online Resource 4). After the python exited the frame, it was over an hour before the breeding adults returned. We detected P3 again at 11:21 on 21 April 2017, ~ 10 m from the first camera. We observed a small White Ibis chick pinned in its coils as it moved over some low nests, scattering the chicks in those nests in all directions, though they all appeared to return later (Online Resource 5). P3 ascended 1 m to reach a nest at the top of the frame and then dropped to the ground below, constricting and then consuming at least two Ibis chicks (likely 10–14 days old) in its coils. P3 failed to consume one constricted chick; it was left on the ground and later scavenged by Turkey Vultures on 23 April 2017. A few adults returned intermittently while the python was present, and all adults returned immediately after P3 exited the frame. We detected P3 on the same camera on 24 April 2017 at 02:22. It descended ~ 1 m from a Brazilian Pepper and appeared to drop at least one chick on the ground, and then coil around it (Online Resource 6). We also detected P3 in the same spot on 25 April 2017 at 18:01, when it appeared on the ground with a White Ibis chick in its coils, which it consumed (Online Resource 7). We detected what was likely python P2 on 7 May 2017, based on size and location, although we could not confirm this sighting. The snake ascended a Brazilian Pepper branch containing empty White Ibis nests that had already fledged (Online Resource 8). We detected python P3 again on 16 May 2017 at 19:20, coiled around what appeared to be a juvenile White Ibis (Online Resource 9). P3 exited the frame at 8:25 and was detected on camera < 5 m away, where it ascended 1–3 m up a Brazilian Pepper tree (Online Resource 10). In total, we recorded 14.95 h of python activity on cameras in Tamiami West (Fig. 4). Python P3 was detected for

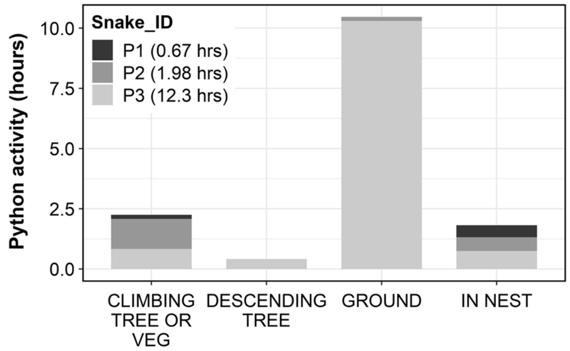

Fig. 4 Breakdown of Burmese python activity separated into four different categories: climbing trees or vegetation, descending trees, on the ground, or in a nest. For each individual, the sum of the time engaged in each activity equals the total number of hours present on trail cameras in Tamiami West

12.3 h, followed by P2 (1.98 h) and P1 (0.67 h). Python P3 spent the most time on the ground (> 80% of time on camera) and the rest of the timing climbing or descending trees, or in nests (Fig. 4). Python P1 spent > 70% of its time on camera in a nest, and python P2 spent > 60% of its time climbing (Fig. 4).

Nest fates

Of 125 total nests monitored in 2017, 68% fledged, 12.8% had not reached fledging age but were alive when the camera batteries ran out, 8.8% of nests failed (all chicks died in nest or eggs were abandoned), 4.8% were depredated, 4% were scavenged, 0.8% were displaced and destroyed, and 0.8% did not hatch (Online Resource 1, Table S2). Of 59 total nests monitored in 2016, 76.3% fledged, 15.2% had not reached fledging age but were alive when the batteries ran out, 3.4% failed, and 5.1% were scavenged (Online Resource 1, Table S3). Of 23 nests monitored in 2014, 65.3% fledged, 4.3% were alive when the batteries ran out, 21.7% were scavenged, and 8.7% failed (Online Resource 1, Table S4). All scavengers were birds—mainly Turkey Vultures, but also Black Vultures (*Coragyps atratus*), Boat-tailed Grackles (*Quiscalus major*), and an American Crow (*Corvus brachyrhynchos*). Scavenging occurred in Joule and Tamiami West in 2014, Paurotis Pond and 6th Bridge in 2016, Henry, Joule and Vacation in 2017. Predation by a Great Horned Owl (*Bubo virginianus*) occurred in Henry (2017) and predation by Burmese pythons occurred in Tamiami West (2017). An Anhinga

(*Anhinga anhinga*) forcibly displaced an incubating Great Egret and removed the eggs at Cuthbert in 2017.

Discussion

We documented the first confirmed instances of Burmese pythons depredating nest contents of two long-legged wading bird species. All python predation events occurred in one colony within the northern boundary of Everglades National Park in 2017 (Fig. 1). In April 2018, a python was incidentally detected on a trail camera consuming two Great Egret nestlings in a colony we had monitored in 2017, which was 20 km north of Everglades National Park (W. Gabel, pers. comm.; Figure 1; Online Resource 11). These detections provide insight on the foraging ecology of an invasive heavy-bodied constrictor and confirm that pythons are directly impacting wading bird reproduction in the Florida Everglades.

When we detected pythons in nests, they were visually obvious. The length of time pythons were present in the camera frame ranged from 0.5 to 4.33 h. We are confident we did not miss python predation occurring within a time lapse interval at any nest. We never witnessed total, unexplained nest content disappearance within a 5 min interval. Any unexplained single chick absence we attributed to sibling aggression, since larger chicks often attack the weakest nestling(s) until they climb off the edge or are pushed out of the nest (Ploger and Medeiros 2004). We attributed unexplained, single egg absence to parental removal, rather than predation. The predation and scavenging events we observed resulted in total loss, rather than partial disappearance of eggs or chicks.

We could not equate the non-detection of python predation in most colonies with the unequivocal absence of predation in those colonies because nests were strongly under-sampled relative to availability. Our interpretation of the confidence intervals in the colonies where the observed rate was zero was that predation rates exceeding 14–25% were probably not occurring (Fig. 2). We were aware of a clear tradeoff between saturation of detections at one colony, or detection of biologically-significant predation rates at multiple colonies. We chose to distribute cameras across multiple sites. Our detections in Tamiami West suggest that python predation events may be clustered, given the number of events we detected within the WHIB transect. In addition, spatial use by individual pythons may be quite localized within a colony. Python P3 apparently stayed near the WHIB transect encompassing approximately 1600 m^2 from 21 April to 16 May 2017 in a 584,688 m^2 colony; this suggests that it would be easy to miss a Burmese python in other large colonies.

Nest height may be inversely correlated with python predation risk. The vertical stratification of wading bird nests is species specific (Burger 1979). Vertical nest stratification may make low-nesting species like ibises more vulnerable than others. Python predation of a Limpkin and Guineafowl nest has also been documented in South Florida—these two species are typically ground-nesters (Dove et al. 2012). However, higher nests do not preclude accessibility: in June 2014, a python was found by an Everglades National Park biologist in an empty Wood Stork nest in a mangrove 2–4 m high (L. Oberhofer pers. comm.). We documented a python depredating a Great Egret nest 1.5 m off the ground, which indicates mid-canopy nests in willow trees are accessible as well. Nest accessibility could relate to the size of the python, although more research is necessary to determine this. Of the three snakes we detected in 2017, we found that the largest python, P3, spent the most time on the ground and was likely 3–3.5 m in length. P1, the individual that climbed the highest (1.5 m) was at most 2.5 m in length and smaller in girth (see Online Resource 1).

Burmese pythons, along with most constrictors, are primarily characterized as ambush predators, implying a passive "sit-and-wait" strategy (Ross and Winterhalder 2015). However, active versus ambush strategies fall along a continuum (Beaupre and Montgomery 2007) and intermediate modes appear to exist, while some species engage in multiple strategies. For example, both active and ambush predation has been documented in woma pythons (*Aspidites ramsayi*) in Australia (Bruton 2013). Greene (1997) calls heavy-bodied constrictors such as pythons "mobile ambushers" because they may travel considerable distances to find optimal sit-and-wait locations. The pythons we observed were climbing up to 1.5 m and actively accessing eggs and chicks in immobile nests. Active foraging is a more common tactic when rate of prey movement is reduced and energetic costs of predator movement are lowered (Beaupre and Montgomery 2007; Ross and Winterhalder 2015); these factors are consistent with python predation events in a colony of densely packed nests.

We can only speculate on the net effect of a python in a wading bird colony. Pythons can eat more than their body mass during a predation event—for example, a python has been documented consuming a fawn (*Odocoileus virginianus*) whose mass was 111% of the python's mass (Bartoszek et al. 2018). Since wading bird nestlings are much smaller food items than a fawn, postprandial responses would be less energetically costly for pythons (Secor and Diamond 1997), and frequent predation events in a colony would be possible. It is unclear what might constitute satiation in a wild python exposed to an unlimited supply of nests containing small prey items. Captive juvenile pythons in a feeding trial have eaten 15–35% of their mass in the form of mice or rats every 10 days for 12 weeks (Cox and Secor 2007). If an approximately 50 kg python like P3 were to eat up to 35% of its mass within 10 days, depredating 10 day old White Ibis chicks at 300 g each (Kushlan 1977), it could consume 58 individuals or 19 nests (average 3 individuals per nest) at a time. Between 21 and 25 April 2017, we detected python P3 on four occasions in the act of consuming or constricting at least 8 White Ibis chicks on camera, suggesting that it was rapidly consuming nestlings within a small area of the colony.

The pythons we detected did not appear to cause nest abandonment in nests adjoining those depredated in Tamiami West. In fact, the overall probability of nests surviving to fledge young on the WHIB transect was 86.9%, which is generally very high for White Ibises. On multiple occasions in this transect, all adults left their nests when the python appeared, but they soon came back (within 1–3 h). For example, three White Ibis adults returned to perch within 1–2 m of the snake while P2 was consuming two White Ibis eggs and all resumed incubating within 3 h after the python left. Predation frequency by python P3 appeared high in the WHIB transect, especially when compared to predation of any kind in all other transects. Clumped or universal nest abandonment, rather than predator mobbing, appears to be most common recourse for wading birds when predation pressure from native mammalian predators like raccoons is high (Frederick and Collopy 1989; Rodgers 1987). Both raccoons and pythons are capable of killing both adults and young. Wading birds could be naïve on some level since they did not react to python predation in the same way that they typically react to raccoons.

We did not detect python predation in the first 2 years of monitoring, but this could have been for multiple reasons. The sample size of monitored nests and site selection could have played a role in the lack of detections in 2014 and 2016. We monitored two sites and 23 nests in 2014, four sites and 59 nests in 2016, and nearly doubled those numbers in 2017 (seven sites, 125 nests). We did not monitor Tamiami West in 2016 (where we detected pythons in 2017) due to a reduced and scattered nesting effort there. Because it was an El Niño year, 2016 was not comparable in terms of water conditions. Unusually high water and low recession rates negatively affected breeding wading birds in multiple ways: (1) reducing foraging efficiency, (2) reducing the overall number of nests initiated, and (3) delaying nesting by approximately 4–6 weeks in some areas of the Everglades. The supranormal water conditions in 2016 may also have affected pythons in some unknown way. It is possible that colonies were less of an attractant in general in 2016 because of reduced nesting densities at some sites.

Besides the three individuals we detected on camera in Tamiami West, an additional gravid female Burmese python was detected and euthanized on 19 April 2017 at the edge of the access road abutting the west side of the colony (EddMAPS record 4885685). The snake appeared larger than P1 or P2 and could not have been P3 because we first observed P3 after 19 April 2017. This suggests that a minimum of four individual pythons had been occupying an area of 0.71 km^2 in the vicinity of the colony. Many islands in the Everglades, including this site, are occupied annually by wading bird colonies, and this predictability may make it easy for pythons to revisit colonies.

We observed all detected python individuals engage in predation at least once, which suggests that active or opportunistic nest predation may not be a rare behavioral trait in pythons. We detected python predation events in one out of eight colonies monitored (12.5%) across 3 years. This is a conservative estimate, since camera density was significantly under-representative of most colonies. Our interpretation of the absence of detected predation is only that predation in most colonies was not extremely high. This study provides an initial estimate of Burmese python predation rates in representative wading bird sites encompassing a range of habitats. Future studies should account for the fact that predation events may be clustered by creating multiple transects in large colonies to better ensure that monitored nest fates are representative of the entire colony.

Wading birds are important indicator species in the Everglades, which is home to one of the largest restoration efforts in the world (Doren et al. 2009). The Comprehensive Everglades Restoration Program uses wading birds to chart the success of efforts to restore the functionality of historical hydrological processes after massive anthropogenic alteration (Frederick et al. 2009). Wading bird reproduction in the Everglades is generally not limited by predation (Frederick and Spalding 1994); therefore, wading bird reproductive success has hitherto been a reliable indicator of prey availability and hydrologic conditions. However, the novel nest predation pressure exerted by pythons in colonies could constitute a disruption to restoration predictions and consequent practices, and therefore should be monitored in the future.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Human and animal rights statement This research was conducted in accordance with the University of Florida Animal Care and Use Committee (IACUC #201708305 and #201408305).

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