Animal Biotelemetry

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Accelerometry to study fine-scale activity of invasive Burmese pythons (*Python bivittatus*) in the wild

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Abstract

Background: The establishment of Burmese pythons (*Python bivittatus)* in Everglades National Park, Florida, USA, has been connected to a > 90% decline in the mesomammal population in the park and is a major threat to native reptile and bird populations. Efforts to control this population are underway, but are hampered by a lack of information about fine-scale activity cycles and ecology of these cryptic animals in the wild. We aimed to establish a technique for monitoring the activity of Burmese pythons in the wild using acceleration data loggers (ADLs), while attempting to identify any behavioral patterns that could be used to help manage this invasive species in the Greater Everglades and South Florida.

Results: We obtained continuous acceleration and temperature data from four wild snakes over periods of 19 to 95 days (mean 54 ± 33 days). Snakes spent 86% of their time at rest and 14% of their time active, including transiting between locations. All snakes showed at least one period of continuous transiting lasting 10 h or more, with one animal transiting continuously for a period of 58.5 h. Acceleration data logger-derived transiting bout duration was significantly correlated with the distance snakes traveled per hour for two snakes that also carried GPS loggers. Snakes were most active in midday or early-night depending on individual and time of year, but all snakes were least likely to be active in the early mornings (0400–0700 h local time). Very little movement took place at temperatures below 14 °C or above 24 °C, with most movement taking place between 15° and 20 °C. One animal showed a highly unusual rolling event that may be indicative of a predation attempt, but this could not be confirmed.

Conclusions: Fine-scale activity and some behaviors were apparent from ADL data, making ADLs a potentially valuable, unbiased tool for monitoring large-bodied snakes in the wild. Snakes spent the majority of their time resting, but also moved continuously for several hours at a time during bouts of transiting. Results suggest that individuals may shift their diel activity pattern based on season. Understanding seasonal differences in activity levels can improve the accuracy of population estimates, help detect range expansion, and improve managers' ability to find and capture individuals.

Keywords: Accelerometer, Activity levels, Behavior, Burmese python, Invasive species, *Python bivittatus*

Background

Invasive reptiles are a growing problem in tropical to sub-tropical climates around the world, as they often exhibit strong direct interactions with prey species and encounter few predators in their introduced habitats [1]. Invasive snakes have been particularly problematic

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due to their ability to avoid detection, thereby inhibiting capture and eradication [2–4]. In South Florida, the Burmese python (*Python bivittatus*) is estimated to have been established for at least 30 years, and the population has now spread out of Everglades National Park and achieved high densities in the Greater Everglades Ecosystem in the past decade [5, 6]. Within their invasive range, pythons are associated with a large decrease in mesomammal populations and an overall decline in mammalian diversity [5, 7–9], leading to cascading effects throughout the ecosystem [10, 11].

Although individual pythons can grow to large sizes (> 5 m), they are difficult to find in the wild as they are cryptic and able to conceal themselves in small patches of vegetation [4]. Managers have employed numerous techniques to identify and control pythons in Everglades National Park, including detection dogs, traps, visual surveys and Judas python tracking. While Judas (or "scout") python tracking, using a tagged snake to reveal the location of other snakes, can be a useful tool for finding other pythons during the breeding season (Nov–Apr; see Smith et al. [12]), the primary removal tool remains human visual searching. However, these efforts are hampered by a lack of knowledge of how these animals behave in the wild, including when they are most likely to be active and the duration of activity. This information is directly relevant to optimizing human search efforts as snakes on the move are easier to detect. Other information, such as predation frequency, is also important for quantifying the direct impact of these snakes on prey species, which otherwise must be inferred from intensive surveys and population estimates [5, 7–9].

The same cryptic characteristics that make pythons difficult to eradicate also make them challenging to study in the wild. They are usually well-camouflaged, and they select habitat consisting of thick vegetation or subterranean refuges that prohibit direct observation and often attenuate the signal of VHF transmitters used for tracking. There is thus a strong need for fine-scale, remote monitoring of animal activity and behavior in large-bodied snakes. Radio- and GPS-telemetry have been used to obtain location information [13, 14], but many snake body movements and behaviors do not produce a change in location or occur too quickly to be detected when sampling is over a scale of hours. Additionally, vegetation density, underground refuges, and standing water attenuate radio signals and reduce temporal resolution of collected data, leading to potentially sparse datasets biased by an animal's habitat selection [14]. Even in best of circumstances, due to battery constraints, GPS loggers usually only provide positions on the scale of hours, resulting in relatively coarse temporal resolution.

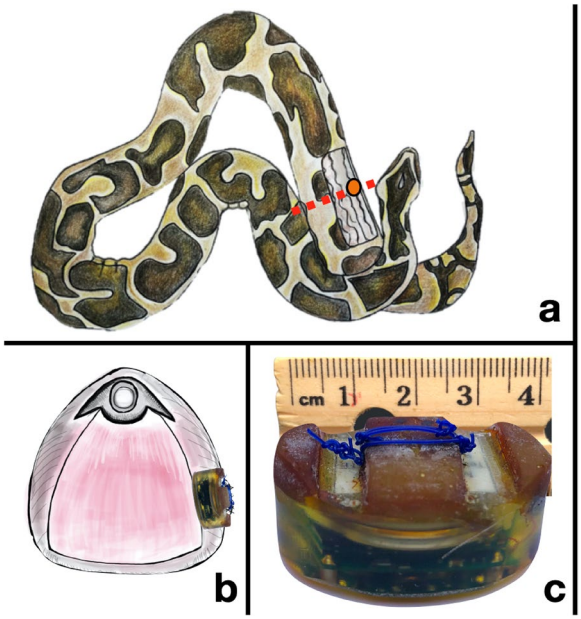

Fig. 1 Graphic representation of a Burmese python (**a**) showing ADL placement (orange circle) relative to the length of the snake's body. Red dotted line indicates a transverse section that is graphically represented in **b** showing the ADL's location relative to the body wall and vertebrate. A photograph of the ADL (G6a + Cefas Technology Inc., Lowestoft, UK) showing extra epoxy (brown sections) added to the top of the tag is shown in **c**. An aluminum crimp sleeve is embedded in the central section of epoxy, allowing suture material (blue) to be threaded through the sleeve and the snake's skin, holding the ADL in place inside the snake throughout the experiment

Acceleration data loggers (ADLs) have been increasingly incorporated into wildlife tags to measure activity, behavior, and energy expenditure in various species [e.g., 15, 16, 17, 18, 19]. With logged acceleration data, researchers can measure fine-scale body movements (e.g., flipper beats, tailbeats; [23]) as well as body posture (i.e., pitch, roll; [24]). These devices thus represent a powerful tool for quantifying activity and behavior in animals that are difficult to observe directly for long periods. Although they have been used to study the swimming dynamics of captive sea snakes [20–22], ADLs have not previously been used to study the movements of large-bodied snakes or those in terrestrial or semi-aquatic environments. The goal of this study was to establish a technique for monitoring the activity of large-bodied snakes in the wild using Burmese pythons as a model, while also attempting to identify any behavioral patterns that could be used to help manage this invasive species in the Greater Everglades and South Florida.

Results

Surgical implantation of ADLs near the posterior end of the snake (Fig. 1) was found to produce a signal in all three acceleration axes that could by amplified by calculating rotational magnitude (Fig. 2). Field trials ($N = 5$, total body length = 457.4 ± 63.1 cm) lasted from 13 to 95 days (mean = 46; Table 1, Fig. 3). Snake P42 was tagged twice (non-consecutively), but was found dead from unknown causes 13 days after its second deployment. Excluding this dataset, we collected acceleration and temperature data from four snakes totaling 216 days, between September and April (Fig. 3). Three of these snakes had GPS data-loggers; however, one individual's (P51) logger failed shortly after release, collecting only 16 positions. P41 collected 423 positions, averaging one position every 5.3 h, while P52 collected 240 positions, averaging one position every 3.3 h. Pressure data from the ADLs were also available for all snakes except P42, but these data were variable and showed no signs of the snakes inhabiting water deep enough to provide a clear increase in pressure.

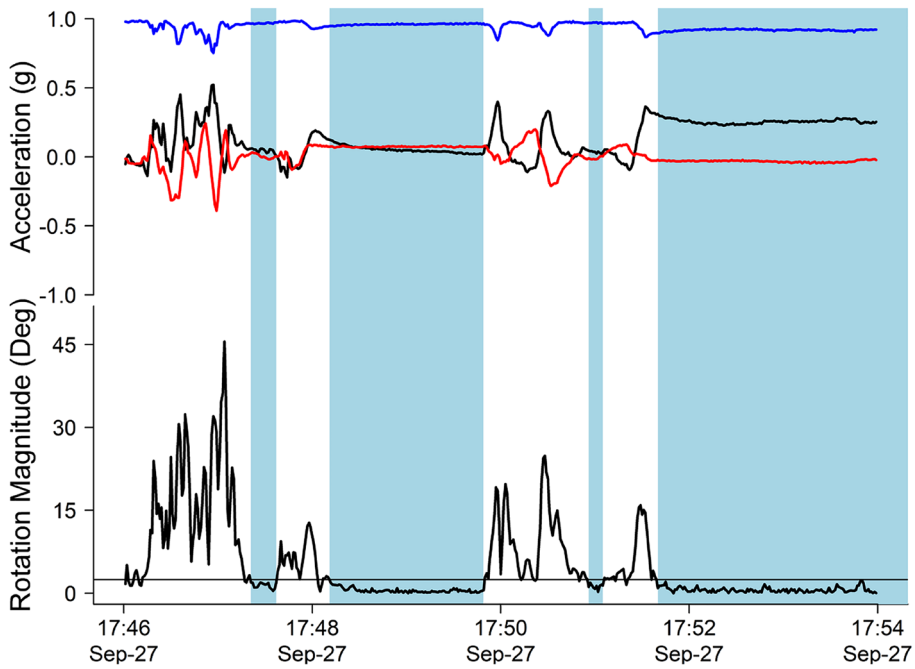

Fig. 2 Raw three-axis acceleration (top panel) and calculated vector angle rotation (bottom panel) from a tagged Burmese python (*Python bivittatus*) in Everglades National Park, South Florida, USA. Top panel: black line is the anterior–posterior axis (X), the red line is the medial lateral axis (Y) and the blue line is the dorsal ventral axis (Z). Blue shaded periods were classified as stationary, whereas un-shaded periods were classified as movement. Bottom panel: horizontal black line on rotation magnitude axis shows the threshold value separating resting from moving

Table 1 Summary information for free-living Burmese pythons, deployment times, and tag types

Python ID	Total length (cm)	Sex	Mass (kg)	Observation period	Number of days at large	Acceleration data logger tag type	Mean body temp. (C)
P42	407	F	22.1	9/27/10–10/16/10	19	Vemco (12-bit)	28.68**
P42*	"	"	21.8	12/17/10–12/30/10	13	Cefas (8-bit)	16.20
P41	466	F	51	12/17/10–3/22/11	95	Cefas (8-bit)	23.36
P51	508	F	63.6	2/17/12–4/22/12	65	Cefas (8-bit)	26.08
P52	537	F	74.6	3/12/12–4/19–12	38	Cefas (8-bit)	27.16

Summary biological and observation period data for each Burmese python (*Python bivittatus*) tagged with acceleration data loggers (ADL) in Everglades National Park, South Florida, USA

* Python P42 died 13 days after being tagged for the second time; data from this deployment not used in other analyses unless noted recorded by ADL

** Body temperature data from this deployment measured by an implanted iButton Temperature logger

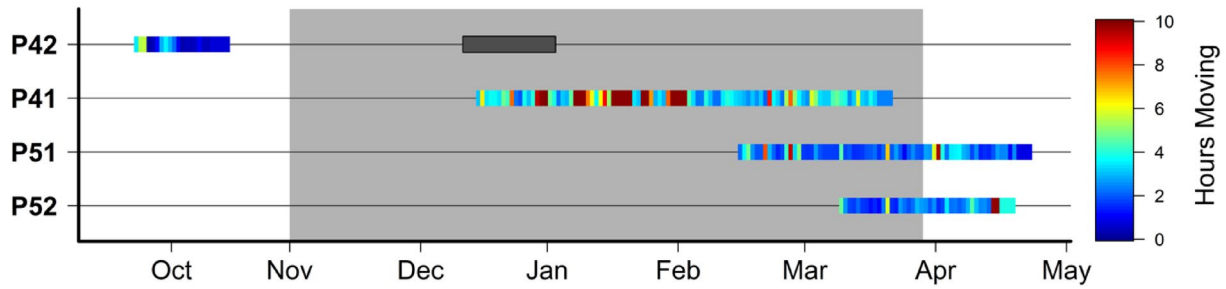

Fig. 3 Abacus plot showing the activity of Burmese pythons (*Python bivittatus*) in Everglades National Park, South Florida, USA. Each day is color coded by the number of hours spent moving. November through April (gray shaded background) is the presumed python breeding season. Some snakes were tagged in different years, but placed onto one calendar year to show seasonality. The dark grey bar for P42 shows its second deployment during which it died

Internal snake body temperatures averaged 2.6 °C above soil temperatures, varying between 6.0 °C cooler to 12.7 °C warmer than soil temperature at any given point in time. Snake temperatures varied significantly within a day compared to soil temperatures ($F_{23,5202} = 50$, $p < 0.001$), with individuals displaying the coldest average body temperatures at 10:00 h and the greatest body temperature difference above soil temperature at 16:00 h. Additionally, as the environmental temperature increased, the difference between body and soil temperatures decreased ($F_{1,5202} = 940$, $p < 0.001$), with a one degree increase in environmental temperature resulting in only a 0.43 ± 0.01 °C, increase in snake body temperature.

Activity levels

Fine-scale movements were typically brief, with periods of continuous movement lasting 30.5 ± 21.2 s on average, and the longest period of continuous movement averaging 3.2 ± 2.3 h across all snakes. Periods of continuous rest lasted 281 ± 326 s on average, and the longest period of continuous rest averaged 1.6 ± 2.0 h across all snakes. Overall, snakes spent $86.1\% \pm 7.2\%$ of their time resting with comparatively little time spent active (Table 2). Snakes generally spent more time active during the day except for P42, which was significantly more active at night. All snakes spent < 6% of their time transiting except for P41, which spent 14.3% of its time transiting and was recaptured 15 km from its release site while other snakes were recaptured within 2.1 km or their release (Table 2).

Transiting bouts were significantly shorter than non-transiting periods, lasting an average of 2.7 h (Table 3), and the dominant locomotory period (or gait frequency; the time between body movements) during transiting was between 4 and 10 s (Fig. 4). However, all individuals exhibited at least one transiting bout that lasted over 10 h, with one individual (P41) transiting for up to 58.5 h consecutively (Table 3). While transiting, snakes spent $70.6 \pm 5.7\%$ of their time moving with the average movement lasting 2.3 ± 0.6 min, followed by 0.9 ± 0.18 min of rest. During non-transiting periods, individuals spent 7.9% ($\pm 4.2\%$) of their time exhibiting small-scale movements (Table 3), which were short in duration (15.1 ± 7.1 s) and followed by 6.5 ± 8.9 min of rest. No movement ever exceeded 12.5 min in duration unless it was part of a transiting bout. Intervals between transiting

Table 2 Recapture distance and activity levels for free-living Burmese pythons

	Recapture distance (km)	% time resting	% time active	% time active (day)	% time active (night)	% time transiting	% time transiting (day)	% time transiting (night)
P42	0.8	92.5	7.5	3.7	11.3	5.4	1.4	9.5
P41	15	75.5	24.5	32.2	16.7	14.3	21.9	6.7
P51	2.1	88.4	11.6	13.2	10	3.5	3.7	3.5
P52	1.8	87.9	12.1	15.1	9.1	4.2	5.8	2.7
Mean ±SD	4.9 ±6.7	86.1 ±7.2	13.9 ±7.3	16.1 ±11.9	11.7 ±3.4	6.9 ±5.0	8.2 ±9.3	5.6 ±3.1

Time spent resting, active, and transiting during day and night for each Burmese python (*Python bivittatus*) tagged with an acceleration data logger (ADL) during field trials in Everglades National Park, South Florida, USA. Recapture distance is the displacement distance between the snake's initial release location and its recapture location at the end of the monitoring period

Table 3 Duration of transiting bouts and intervals between bouts for free-living Burmese pythons

	Mean transiting bout duration (h)	Maximum transiting bout duration (h)	% time moving when transiting	Mean interval between bouts (h)	Max interval between bouts (h)	% time moving when not transiting
P42	2.1	10.1	67.6	25.9	137.3	2.3
P41	3.7	58.5	78.8	16.8	94.7	12.3
P51	2.4	11.4	66.7	43.9	232.6	8.5
P52	2.3	16.4	69.7	37.4	165.8	8.3
Mean ± SD	2.7 ± 0.7	24 ± 23	70.6 ± 5.7	31 ± 12	157 ± 57	7.9 ± 4.2

Mean and maximum duration of transiting bouts (hours) and percent time moving when transiting, as well as mean interval between transiting bouts and percent time moving when not transiting for each Burmese python (*Python bivittatus*) during field trials in Everglades National Park, South Florida, USA

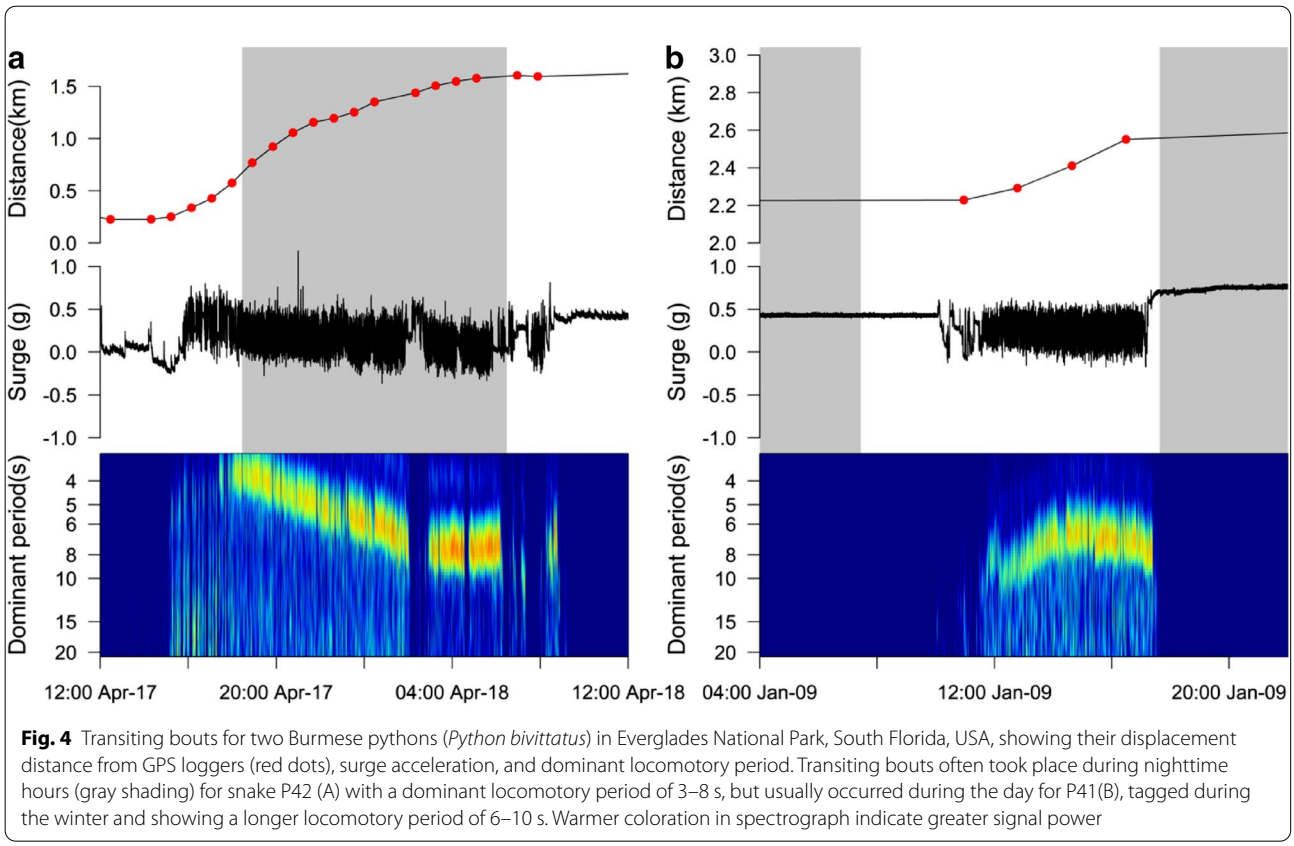

Fig. 4 Transiting bouts for two Burmese pythons (*Python bivittatus*) in Everglades National Park, South Florida, USA, showing their displacement distance from GPS loggers (red dots), surge acceleration, and dominant locomotory period. Transiting bouts often took place during nighttime hours (gray shading) for snake P42 (A) with a dominant locomotory period of 3–8 s, but usually occurred during the day for P41(B), tagged during the winter and showing a longer locomotory period of 6–10 s. Warmer coloration in spectrograph indicate greater signal power

bouts lasted an average of 31 ± 12 h (Table 3), but could continue for up to 232 h (snake P51).

Diel activity patterns

Snakes displayed transiting behavior and other movements during all hours of the day, although early morning (0400–0700 h) was the period with least movement for all individuals. Movements were not uniformly distributed throughout the day and patterns varied between individuals (Table 2, Fig. 3). Snake P42, released in September, spent the majority of its time moving during the early hours of the night (1900–0100 h), and moved little during the day. Conversely, snake P41, tagged in December, was most likely to move during daylight hours (0900–1700 h). The remaining snakes (P51 and P52) were tagged in the spring and each showed low levels of activity during both day and nighttime hours.

The difference in diel activity patterns between P42 and P41 was almost entirely driven by the timing of concentrated transiting bouts (Fig. 4). Snake P42 spent much more time transiting at night (9.5% of night time spent transiting) than during the day (1.4% transiting; Table 2.), and was especially likely to show transiting behavior in the evenings (2000–2200 h) when it

spent > 20% of its time transiting. Snake P41 was far more likely to exhibit transiting behavior during the day, when it spent > 21% of its time transiting, but only spent 6.7% of its time transiting at night.

Environmental temperature ($F_{1,5182} = 60.5$, $p < 0.001$), hour of the day ($F_{23,5182} = 13.3$, $p < 0.001$, and the interaction between these variables ($F_{23,5182} = 8.9$, $p < 0.001$) were important predictors of percent time transiting (Fig. 5). At cooler temperatures (< 14 °C), snakes displayed little transiting behavior, but transiting became more likely during the mid-morning when temperatures reached 14° to 20 °C. Once daytime temperatures exceeded 24 °C, transiting movements became less common. However, as temperatures increased further there was an increase in activity during nighttime hours.

GPS accelerometer calibration

The two individuals with complete GPS tracks showed different patterns of movement and habitat use. Throughout its 95-day deployment, P41 traveled over 15 km from its release location, including the longest transiting bout (58.5 h) measured in this study, as well as a 48-h period of rapid (2.4 km/day) displacement during which the snake was believed to be transiting through water based on its inferred movement path and the lack of GPS fixes during this period (Fig. 6). In contrast, P52 stayed within 300 m of its release location for over 35 days before moving 1.8 km over the next 3 days until it was recaptured. Snakes did not have an equal probability of logging a GPS position across hour of the day (GLMM: $F_{1,23} = 4.71$, $p = 0.039$, Fig. 6). Both P41 and P52 were more likely to log a GPS position during daylight hours than at night,

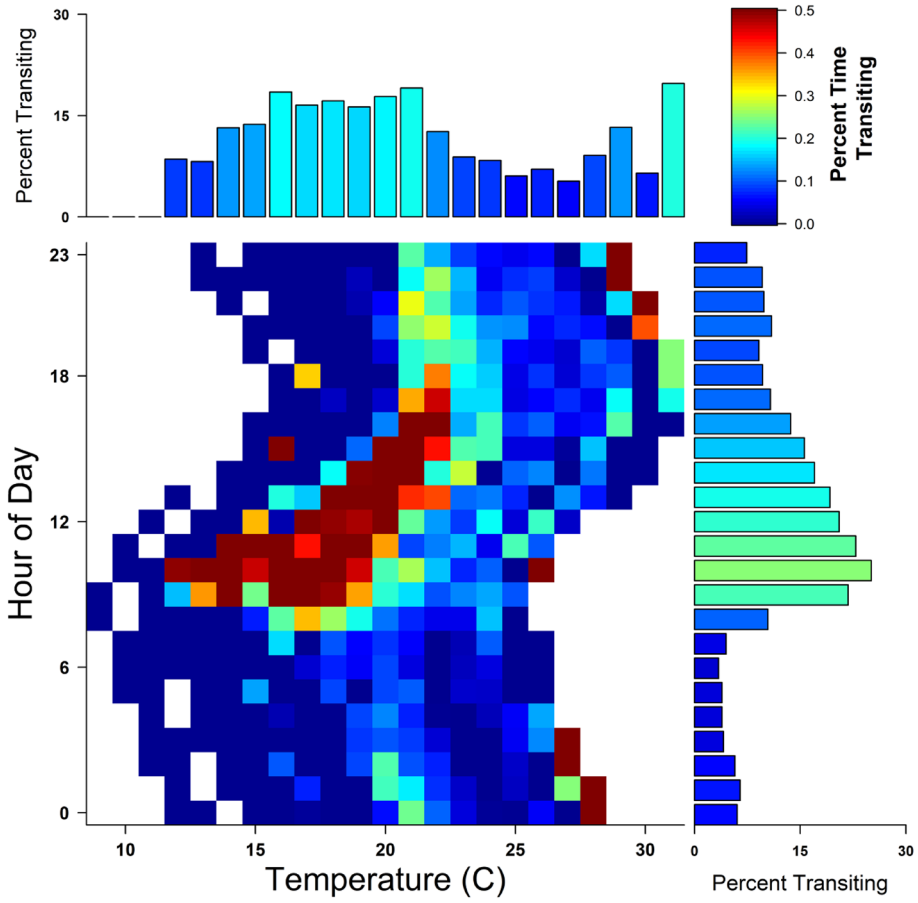

Fig. 5 Percent of time spent transiting according to time of day and environmental temperature for all tagged Burmese pythons (*Python bivittatus*) in Everglades National Park, South Florida, USA. Percent time transiting is represented by color across hour of the day on the *Y* axis and environmental temperature on the *X*-axis. All colors in this figure correspond to the percent time transiting legend in the upper right corner. The top barplot represents the percent time transiting across the environmental temperature range observed and right bar plot represents the percent time transiting across hour of the day

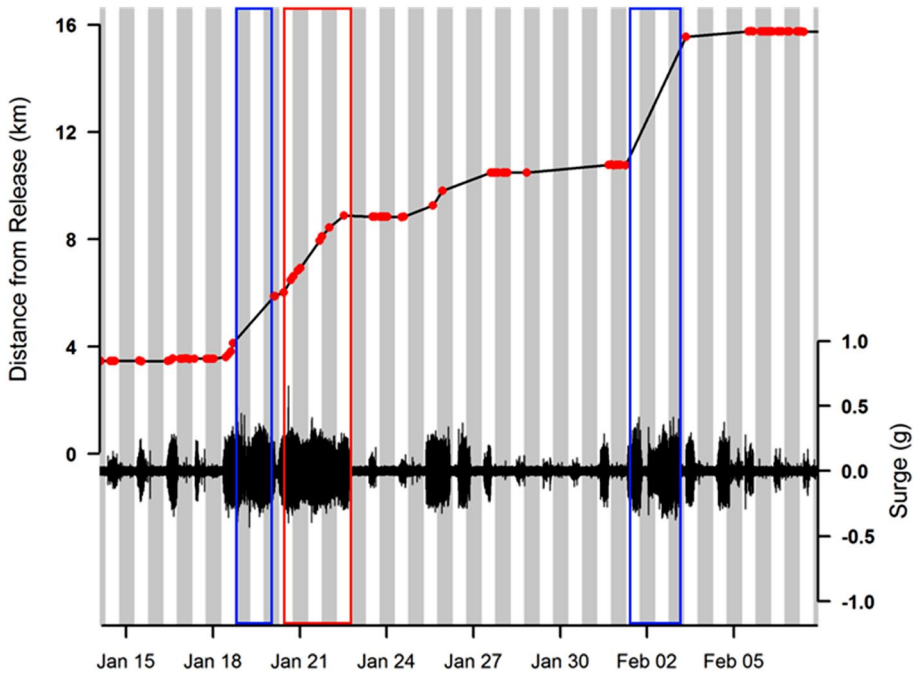

Fig. 6 Displacement distance and surge acceleration during January for snake P41, a Burmese python (*Python bivittatus*) in Everglades National Park, South Florida, USA. During this period, the individual had high activity levels and displayed most of its movement during the day. This period included a 58-h transiting bout (Jan. 20th–22nd; red box) as well as two periods of rapid displacement at a rate of 2.4 km/day (Jan. 19th–20th and Feb. 1st–3rd; blue boxes) during which the snake was likely in an aquatic environment based on habitat from its inferred movement path and the lack of GPS fixes (indicated by red dots) during transiting. Gray shaded bars indicate nighttime hours

and both individuals had a significantly higher probability of logging a position between 1000 and 1400 h ($Z > 2.58$, $p < 0.009$) than at other times of day.

GPS distance (hourly) traveled for P41 and P52 was positively correlated with both the percent of each hour spent moving ($T = 51.9$, $p < 0.001$) and with the percent of each hour transiting ($T = 54.2$, $p < 0.001$). However, the percent of each hour transiting was better than percent time moving ($\Delta AIC = 58$) at predicting the GPS distance traveled ($R^2 = 0.58$).

Unique behavioral events

Even after correcting for attachment angle, tag orientation was highly variable throughout all deployments, likely due to variations in habitat type used (i.e., brush, arboreal, aquatic, or subterranean) and snake body position. However, across all individuals, pitch and roll values rarely (< 0.05%) exceeded ± 80 degrees from horizontal. Incidents ($N = 105$) in which roll angle exceeded 90 degrees were typically short in duration (34 ± 111 s), but a subset of these lasted for extended periods and may indicate unique behavioral events.

One event began with snake P42 in a resting (non-transiting) state when it began a 2-h period of highly atypical rolling behavior, including rolling over completely two times (Fig. 7). The snake started by rolling laterally 220 degrees and ultimately rolled completely, 360 degrees from its original position, over a period of 15 s. Approximately 1.5 h later, during which time it displayed a moderate amount of activity, the snake again commenced atypical rolling behavior and completed another full lateral roll (360 degrees) in the opposite direction from the first roll over a period of ~ 1 min. After this, the snake continued atypical rolling behavior (> 90 degrees) for an additional 15 min. The subsequent night (15 h later), the snake displayed transiting behavior for 50 min, after which it did not engage in transiting behavior for a period of 5.7 days. These were the only instances of complete lateral rolling (180–360 degrees) detected throughout our 216 d of monitoring. The only similar event to this occurred when snake P41 rolled ~ 200 degrees for a period of ~ 20 s before rolling back into its original position.

Discussion

Acceleration data loggers effectively differentiated between patterns of rest vs. activity over several weeks in free-living Burmese pythons. The use of ADLs and other inertial sensors is rapidly expanding in wildlife research [18, 19, 25], where they are most often applied

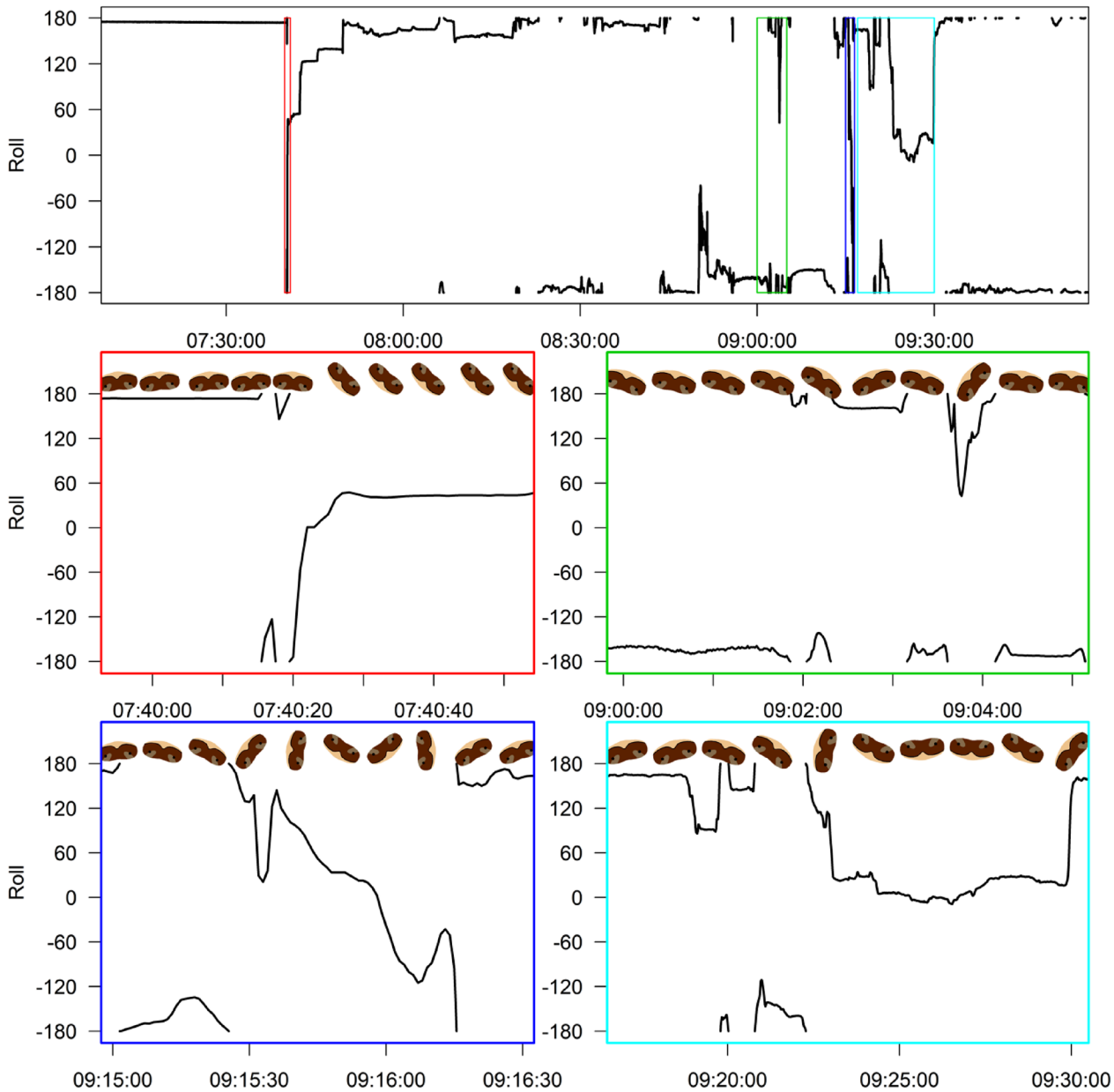

Fig. 7 Roll angle of snake P42, a Burmese python (*Python bivittatus*) in Everglades National Park, South Florida, USA, showing a unique, 2-h long behavioral event during which the snake displayed abnormal body postures, and rolled over completely at two separate times. Snake head schematics represent the approximate roll angles shown in the data trace below. Note that head schematics are used for roll visualization, but the actual roll angle was measured in the posterior third of the snake's body where the ADL was implanted. Data at the far left and right sides of the top panel represent typical body position with low variation in roll

using very high (> 10 Hz) sampling frequency in order to identify behaviors or energy expenditure based on repetitive, high-acceleration movements (e.g., running, flying, swimming, etc.) over relatively short periods of time [26–28]. In contrast, the slow, usually rectilinear, movements of large-bodied snakes [29] are intermittent and occur at low frequencies. This allowed us to accurately describe their locomotion using a much lower sampling frequency (1 Hz) which extended our monitoring time to several months before filling up ADL memory. However, the low acceleration values of snake movements complicated our effort to distinguish body movements from sensor noise in the low-resolution (8-bit) ADLs applied to three of our four wild snakes. Our use of an angular rotation metric

overcame this problem, providing clarity and consistency in comparing movements among individuals and removing artifacts that can arise from dynamic acceleration-based metrics (such as ODBA; Overall Dynamic Body Position; [17]) when using tag types of differing sensor resolution on different individuals. Additionally, while the 1 Hz sampling frequency was sufficient to detect active vs. resting behavior, it may have missed faster locomotor behaviors with a duration shorter than a few seconds.

We found that pythons spent an average of 86.1% of their time resting. This overall pattern is typical of many ambush-foraging snakes [29, 30] and has been noted in Burmese pythons [31–33], but never quantified in the wild. Although resting periods were interrupted by changes in body position and short movements lasting a few seconds to minutes, snakes typically went for over a day at a time and sometimes several days between transiting events.

During transiting, pythons often moved for several hours at a time during periods that also corresponded with longer displacement distances as revealed by GPS loggers. Previous studies have shown that these animals are capable of long-distance dispersal of several kilometers [9, 13], with one snake moving a total of 80 km over an 18-month period. Our results show that these movements are often conducted during bouts of continuous transiting lasting several hours, up to nearly 60 h in snake P41. During this extended transiting period, P41 traveled farther in a single day (2.43 km/day) than any other snake tracked by Hart et al. [13] and it moved faster than translocated snakes exhibiting homing behavior described by Pittman et al. [34]. Given the limits of python metabolism and energetics [35] this long period of continuous transiting by snake P41 appears to indicate the activity of a highly motivated individual. While the proximate motivation of this transiting is unknown, it may represent a search for suitable habitat, prey, or mates, and this was the only deployment that took place entirely during the presumed python breeding season in the Greater Everglades Ecosystem.

The differences in diel movement patterns observed here were likely driven primarily by temperature. Most species exhibit diurnal activity patterns due to evolution of particular physiological traits that are optimized at certain temperatures [36]. While we observed strong diel behaviors in two individuals, they showed opposing patterns, possibly due to the fact that P41 was tagged in winter (and moved primarily during midday) and P42 was tagged during much warmer temperatures in early fall (and moved primarily at night). Bhatt and Choudhury [37] found that pythons in India were crepuscular during the warmer months and diurnal during the cooler months. Because pythons are ectothermic, thermoregulation strategies play a large role in behavior determination [38]. By altering their movement patterns (temporally or spatially) at different temperatures, snakes may maximize physiological rates in order to minimize energetic costs or to maximize digestion or locomotion speed. Size may also play a role, as larger animals lose body heat more slowly [39], and thermal inertia may allow large pythons to move even on cool evenings.

The increased likelihood of obtaining GPS logger fixes during daytime hours was likely related to animal behavior and habitat. Both snakes that carried GPS loggers were more active during the day than at night, increasing the probability of their antennas being exposed. Smith et al. [14] found that lower GPS fix rates in these snakes were caused not only by vegetation density but also by python microhabitat selection, since fixes cannot be obtained when the animals are underwater or underground. Additionally, individuals may be more likely to bask in the sun during the day [37], increasing the likelihood of logging a GPS position. While GPS fix rates appear to be highest during periods of transiting, we noticed several notable exceptions likely related to microhabitat. For instance, snake P41 showed two lengthy periods of transiting activity with no accompanying GPS fixes during the events (Fig. 6; Jan 19th–20th; Feb 1st–3rd). This suggests that the GPS antenna was not exposed during these transiting periods and that the animal may have been traveling through water. This inference is supported by spatial habitat data from the snake's inferred GPS track and substantiates concerns that aquatic dispersal is possible for this species [40].

Of particular interest was our detection of a unique behavioral event involving a 2-h period of atypical lateral rolling. Although it is possible that this was an attempted or successful foraging event, it may also have been an interaction with a conspecific (although it did not take place during the breeding season) or predator, or some other unknown event. Without additional corroborating evidence, we cannot assign function to this event, but its unique characteristics within our broader dataset make it noteworthy. Future work using long-duration captive experiments may help to create behavioral profiles to better identify specific behaviors in the wild.

Given our lengthy monitoring periods, the fact that we did not detect more unique acceleration events suggestive of feeding or breeding is surprising and may be due to a number of biological and technical factors. First, feeding in pythons is likely rare [30, 41–43], as these animals may go weeks or months without feeding [35]. Captive female pythons also exhibit reproductive aphagia, possibly starting at the time of copulation [44], and most of our data are from female snakes during the breeding season. It

is therefore possible that our animals did not feed during the time they were monitored, and reduced python feeding during winter months is supported by patterns of marsh rabbit predation presented by McCleery et al. [8]. Second, placement of our ADL package on the posterior third of the animal may have prevented the device from detecting movements associated with striking or feeding. Preliminary captive trials showed the posterior part of the animal to remain largely stationary during striking behavior. Although python breeding aggregations have been frequently observed in the Everglades [12, 45], copulating snakes are often found in a resting state. Any unique movements associated with recognition and courtship may be slow [29] and therefore difficult to differentiate from other movements.

We were able to identify fine-scale activity patterns from ADL data traces, illustrating the utility of this technology to provide detailed information on the movements of large-bodied snakes in the wild. This information can inform a variety of management plans, as effective control and eradication techniques often rely upon specific and predictable behaviors. For example, Smith et al. [12] found road cruising and the Judas (or "scout") technique to be complementary management approaches for catching Burmese pythons, depending on the season. Road cruising is optimally effective at times of day and seasons when pythons are most likely to be moving and crossing roads, whereas the scout technique is most effective at targeting an entirely different behavior (breeding). Both of these removal techniques are labor intensive and incur substantial cost [12], so using ADL data to optimize the timing of each could greatly improve management efficiency. Coupling movement frequencies with tracking data could also be a promising new method for estimating densities of secretive snakes [46].

Conclusions

Fine-scale activity and some behaviors were apparent from ADL data, making ADLs a potentially valuable tool for monitoring large-bodied snakes in the wild. Individuals spent 86.1% of their time resting, but often moved continuously for several hours at a time during bouts of transiting. Individuals may shift diel activity pattern based on season. Understanding seasonal differences in activity levels can improve the accuracy of population estimates, help detect range expansion, and improve managers' ability to find and capture individuals.

Methods

All animals utilized in this study were visually spotted and captured crossing a road at night or on roadsides during daytime searches within Everglades National Park. Capture and tagging were 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, EVER-2009-SCI-001, and EVER-2011-SCI-0002. After experiments were finished, snakes were euthanized in accordance with established management protocols.

Tag attachment and field trials

Three-dimensional acceleration data were recorded using either a Vemco XYZ (16 × 108 mm, 35 g weight, 12-bit resolution, range −2 −+2 units of gravity—g, 5 MB memory, Vemco, Nova Scotia, Canada) or Cefas G6a (2.8 × 1.6 cm; 18 g weight; 8-bit resolution, range −2 −+2 units of gravity—g, 56 MB memory, Cefas Technology Ltd., Lowestoft, UK) acceleration data loggers (ADL). Cefas G6a tags additionally recorded pressure and temperature, while an iButton temperature logger (8-bit resolution, range −40 to 85 ℃, Maxim Integrated, San Jose, CA) was used for animals that received a Vemco ADL. All tags were set to record tri-axial acceleration at 1 Hz and temperature every 30 min during the 2011 field season or every 30 s in the 2012 season. This sampling regime minimized memory usage and maximized record duration, allowing the tags to record for approximately 3 months before their memory would be full. Preliminary trials showed that this 1-Hz acceleration sampling rate produced highly similar results ($R^2 > 0.97$) to a 5-Hz sampling rate when comparing several metrics of acceleration in these slow-moving snakes (Additional file 1: Fig. S1.)

To ensure retention, ADLs were surgically implanted within the lateral body wall (see [13, 47]) 2/3 the distance from the head to the tail to avoid puncturing the lung in the anterior half of the body (Fig. 1). To ensure that the movements and postures recorded by the ADL accurately reflected those of the snake, loggers were held in place by suture material passed through the skin of the snake and through a single barrel aluminum crimp sleeve (8 × 1.8 mm) that was epoxied to the logger. Sutures were externally visible after surgery and were examined at the end of experiments to ensure they were still in place and had prevented tag movement inside the snake (Fig. 1). Upon release, snake movements were observed and noted for several minutes to later validate acceleration signatures, and similar observations were taken at the end of trials during recapture.

Two VHF transmitters (Model: AI-2, 25 g, Holohil Systems, Ltd., Carp, ON, Canada) were implanted into each snake, as in Hart et al. [13] to ensure snake relocation and recovery at the end of the experiment. Some individuals were also implanted with GPS data loggers, recording a position every 1–2 h (Quantem 4000E Medium

Backpack, Telemetry Solutions; see Hart et al. [13] for information of GPS loggers and attachment methods). After 20–95 days, snakes were located via their VHF transmitters, captured, and brought back to the laboratory for surgical removal of all tags.

Acceleration data analysis

Recovered ADLs were downloaded and then analyzed in R (version 3.1.0) and Igor Pro 6.0 wave analysis software (Wavemetrics, Oregon, USA) using the Ethographer extension [26]. To ensure that the tag was oriented in the same frame of reference as the snake, the tag attachment angle was corrected for by rotating the acceleration data so that the average position of the tag across the entire deployment was level and horizontal (Z: dorso-ventral axis was parallel to gravity) [48]. Burmese pythons move primarily through rectilinear locomotion and thus the primary source of acceleration during movement should be along the anterior–posterior axis. To ensure the tag was oriented along the snakes' anterior–posterior axis, the acceleration data were rotated around the dorso-ventral axis (Z-axis) to maximize the dynamic acceleration along the anterior–posterior axis (X-axis). Due to the low acceleration movements exhibited by the snakes, we calculated roll (1) and pitch (2) from the raw acceleration data:

$$\text{Roll} = \text{atan}(Y_{\text{accel}}, Z_{\text{accel}}), \tag{1}$$

$$\text{Pitch} = \text{atan}(-X_{\text{accel}}, (Y_{\text{accel}} \times \sin(\text{Roll})) + (Z_{\text{accel}} \times \cos(\text{Roll}))). \tag{2}$$

We observed little dynamic acceleration during deployments with tag measurement error accounting for the majority of variation in the root mean squared acceleration. Therefore, python movements were instead characterized by a change in tag orientation. To do this, we reduced the dimensionality of the acceleration data by calculating the three-dimensional vector angle (angular rotation) between acceleration data points at a 5-s lag (3):

$$\text{VectorAngle} = \text{Acos}\frac{\sum \text{XYZ}_{\text{t}} * \text{XYZ}_{\text{t}-5}}{\sqrt{\sum \text{XYZ}_{\text{t}} * \text{XYZ}_{\text{t}}} * \sqrt{\sum \text{XYZ}_{\text{t}-5} * \text{XYZ}_{\text{t}-5}}}. \tag{3}$$

This metric provides the minimum angle that the tag moved, regardless of the axis over which the movement occurred. A 5-s lag was chosen because it increases the magnitude of movement to facilitate differentiation between movement and sensor measurement error, but it is still a sufficiently short period of time to isolate discrete periods of movement. Additionally, to examine for the possibility of cyclical movements that would be indicative of rectilinear locomotion, we did a continuous wavelet transform of the x-axis using the *biwavelet* package in R. Periodicity values between 3 and 20 s were investigated as possible periodicities of rectilinear locomotion exhibited by the snakes. At each time point, the periodicity with the greatest spectral power was deemed the "dominant" locomotion frequency.

Physical movement vs. behavioral movement

Physical movement was determined by examining the rotation of the tag from the vector angle metric (angular rotation). Because locomotion in large-bodied snakes is slow, intermittent, and includes repeated intervals of rest for a given body section even when the snake is moving continuously, we applied a filter to translate physical movement of the tag into behavioral (snake) movement or locomotion. Visual examination of the vector angle data showed that acceleration sensor noise contributed to movements less than two degrees. Thus, the snake was considered to be resting any time that the tag moved ≤ 2.5 degrees for at least 7 consecutive seconds. All other periods that were at least 3 s in duration were classified as movement (Fig. 2). Brief movements lasting 1 or 2 s were re-classified as resting.

To separate temporally brief, discrete snake movements (e.g., body repositioning and postural changes) from transiting movements (repetitive movements associated with a change in snake location), a running sum (window size = 3600 s; 1 h) of the movement state (moving = 1, stationary = 0) was used to determine the total amount of time moving within a 1-h period. Snakes were considered to be in a transiting bout when an individual maintained a high activity (> 33% moving) for at least 20 consecutive minutes. During these transiting bouts, all snake movements were considered transiting movements and typically showed a clear dominant locomotory period or gait. All movements that were not during transiting bouts were considered small-scale movements and changes of body position or posture.

Temperature analysis

Since ADLs were surgically implanted, they reported internal body temperature of the snake. To examine trends in activity and possible thermoregulatory behavior, we compared snake movement and body temperature to environmental temperature from the Florida Automated Weather Network (FAWN) Homestead station (25.5126 N, 80.5031 W), which was less than 30 km away from the snakes' release location. These data were collected every 15 min and were linearly interpolated to be at the same frequency as the summarized ADL data (1 min). We used soil temperature at 10 cm depth as a proxy for environmental temperature because it is more stable than ambient air temperature and represents

the temperature that the snakes are most exposed to through conduction; it also most closely correlated with snake body temperatures.

GPS data analysis

GPS data were filtered to only retain times when the GPS was able to log a 2- or 3-D position (excluding points without a reliable location). Depending on snake body orientation or habitat type, the GPS was not able to continuously record locations. GPS data were standardized by linearly interpolating hourly positions throughout each snake's entire deployment. The straight-line distance between each hourly position was calculated as the distance the snake traveled during that hour.

Statistical analysis

All values are reported as mean ± standard deviation unless otherwise noted. Means were calculated using each individual's mean, and thus individuals are equally weighted regardless of deployment duration. For each individual, all activity data throughout their entire deployment was aggregated by hour and compared to a uniform distribution using a Chi-squared test to examine if individuals showed diel differences in activity. Environmental temperature was also aggregated by hour and the combined effects of temperature and time of day on activity was quantified with generalized additive models (mgcv package in R). GPS accelerometer linear regressions were performed using the lme4 package in R, with p-values calculated using the lmerTest package, with snake ID as a random effect. Model comparison was performed using Akaike Information Criterion (AIC), with significance determined by a ΔAIC of 2 [49].

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s40317-020-00227-7.

Additional file 1: Figure S1. Comparison of four separate metrics of acceleration calculated from values sampled at 5 Hz versus the same metrics calculated from data that had been downsampled to 1 Hz. All comparisons produced highly similar ($R^2 > 0.97$) results between sampling rates, justifying our use of a 1 Hz sampling interval for deployments on pythons.

Abbreviations

ADL: Acceleration data logger; ODBA: Overall dynamic body acceleration; Hz: Hertz; GAMM: Generalized Additive Mixed Model; FAWN: Florida Automated Weather Network.

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Author's contributions

NW and KH conceived and designed the study. NW was responsible for ADL design and maintenance and programming. CW conducted data analyses, MC performed surgeries and, with FM and KH, supervised field trials. All authors participated in manuscript preparation. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets supporting the conclusions of this article are publicly available in Hart et al. [50]: https://doi.org/10.5066/P91MLPXJ.

Ethics approval and consent to participate

All capture and tagging were 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, and EVER-2011-SCI-0002.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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