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Marsh rabbit mortalities tie pythons to the precipitous decline of mammals in the Everglades

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To address the ongoing debate over the impact of invasive species on native terrestrial wildlife, we conducted a large-scale experiment to test the hypothesis that invasive Burmese pythons (*Python molurus bivittatus*) were a cause of the precipitous decline of mammals in Everglades National Park (ENP). Evidence linking pythons to mammal declines has been indirect and there are reasons to question whether pythons, or any predator, could have caused the precipitous declines seen across a range of mammalian functional groups. Experimentally manipulating marsh rabbits, we found that pythons accounted for 77% of rabbit mortalities within 11 months of their translocation to ENP and that python predation appeared to preclude the persistence of rabbit populations in ENP. On control sites, outside of the park, no rabbits were killed by pythons and 71% of attributable marsh rabbit mortalities were classified as mammal predations. Burmese pythons pose a serious threat to the faunal communities and ecological functioning of the Greater Everglades Ecosystem, which will probably spread as python populations expand their range.

1. Background

As non-native invasive animals spread across the planet, the importance of their impact on native terrestrial wildlife remains controversial [1] in part because of a remarkable lack of large-scale experiments. One particularly contentious debate is over the role of the invasive Burmese python (*Python molurus bivittatus* or *Python bivittatus*) in the drastic declines of mammal populations in Everglades National Park (ENP) over the last several decades [2]. ENP, globally recognized for its unique biotic communities, sits at the southern end of the Greater Everglades Ecosystem (GEE), a vast freshwater wetland ($\approx 10\,000\text{ km}^2$) encompassing most of the southern Florida peninsula [3]. The ecological processes, functionality and restoration efforts within this distinct ecosystem are probably being substantially impaired by the disappearance of once common mammalian predators and herbivores [4–6]. Declines in mammal populations in ENP appear to coincide temporally and spatially with the arrival and spread of invasive Burmese pythons [2], a large-bodied snake native to southeast Asia that preys on vertebrates. Pythons were probably introduced into ENP several decades ago via releases or escapes from private ownership [7]. Sightings and removals of pythons in ENP were sporadic in the 1980s and 1990s, increasing sharply in the early 2000s [2]. During this time, gut content analysis of invasive pythons in ENP indicated that mammals accounted for about 75% of their diet [8].

Nonetheless, previous evidence linking pythons to mammal declines has been indirect [2], and there are reasons to question whether pythons or any predator could have caused the precipitous declines seen across a range of mammalian

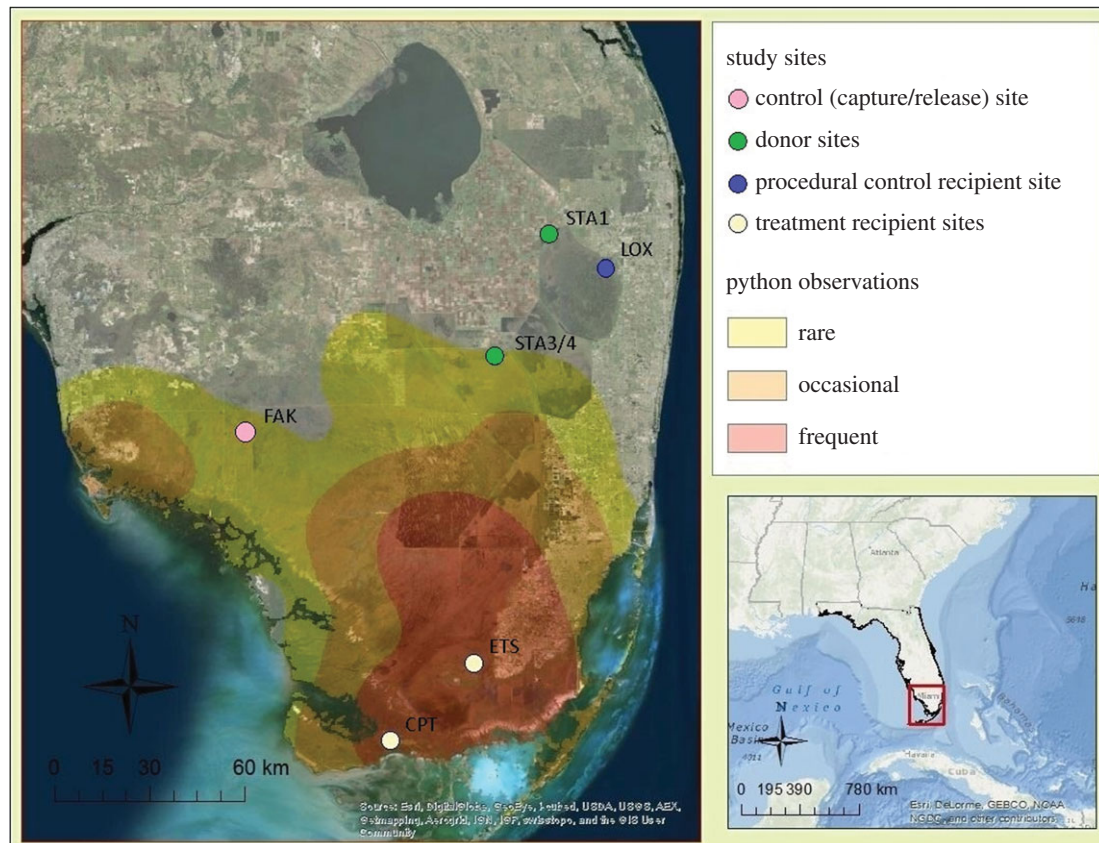


Figure 1. Location of study sites in south Florida, United States. Relative frequency of Burmese python observations were based on 2008–2013 records in the Early Detection and Distribution Mapping System [18]. ETS, East Taylor Slough; CPT, Coastal Prairie Trail; FAK, Fakahatchee Strand Preserve State Park; LOX, Arthur R. Marshall Loxahatchee National Wildlife Refuge; STA, Storm Water Treatment Area.

functional groups. Introduced predators, including snakes, have reduced or eliminated fauna on islands [9–11], yet there are no accounts of a lone introduced apex predator (apart from humans) removing a functionally diverse, continental mammal community. Additionally, ecological theory provides little support for the hypothesis that an apex predator could extirpate small, broadly dispersed, fecund, generalist herbivores [12–14]. To test the hypothesis that pythons are driving the decline of mammal populations, we experimentally manipulated marsh rabbit (*Sylvilagus palustris*) populations in ENP.

Marsh rabbits are small (≈ 1 kg) lagomorphs found near fresh and brackish water throughout the southeastern USA [15]. Sexually active throughout the year, marsh rabbits can produce up to six litters of three to five young annually [15]. Through the 1980s, this species was one of the most commonly seen mammals in ENP [2,3]. Despite having a wide variety of natural predators, marsh rabbits are still common in areas of the GEE outside of ENP. For these reasons, and because rabbit populations are generally resilient and capable of persisting under considerable predation pressure [16,17], we chose marsh rabbits as a model to understand the impacts of pythons on mammals in ENP. If pythons caused the declines of marsh rabbits in ENP, we predicted that (i) pythons would be the dominant cause of marsh rabbit mortality in ENP, (ii) mammals would cause more marsh rabbit mortalities in areas of the GEE where pythons were rare or absent, (iii) marsh rabbit populations introduced in ENP would not persist, and (iv) unlike endothermic predators (i.e. mammals), the timing of python-caused mortality would vary with seasonal climate conditions.

2. Material and methods

(a) Study design

Using marsh rabbits as a model, we experimentally manipulated their populations to determine the role of pythons in driving mammal declines within ENP. We compared the risk of mortality from different causative agents in areas with established Burmese python populations to similar areas where pythons were rare or absent (figure 1). We also evaluated the influence of environmental factors on temporal variation in mortality rates from the dominant predators of marsh rabbits (e.g. pythons and mammals) in the GEE.

We captured marsh rabbits from donor populations and randomly assigned them to one of three sites: two sites in ENP and a procedural control site in the GEE, where pythons had not been observed (figure 1). The purpose of the procedural control was to account for the influence of translocation on mortality events. We also established a control site where pythons were rare or absent to compare causes of mortality in ENP with an established population of marsh rabbits that was not manipulated. At the control site, we captured and released rabbits without translocating them.

(b) Study sites

ENP is a large (600 000 ha) federally protected wetland listed as an International Biosphere Reserve, a World Heritage Site and a Wetland of International Importance in the Ramsar Convention. The park has a diversity of vegetative communities that once supported a varied mammalian community, including a large population of marsh rabbits. However, recent reports suggest that there are few, if any, self-sustaining marsh rabbit populations in ENP [2]. ENP also hosts a well-established population of

invasive Burmese pythons [18]. To capture some of the variations in natural communities within the park, we translocated marsh rabbits to two locations (figure 1; electronic supplementary material, Study Sites): a coastal marsh wetland (Coastal Prairie Trail; CPT) and a freshwater wetland (East Taylor Slough; ETS).

We used approximately 2000 python presence records from the Early Detection and Distribution Mapping System [19] to select control sites in areas where pythons were rarely or never detected. We used presence records because low detection and capture probabilities of cryptic pythons over the vast Everglades landscape have hindered the development of rigorous population estimates for these snakes [20]. We selected Arthur R. Marshall Loxahatchee National Wildlife Refuge (LOX) as our procedural control site. Loxahatchee National Wildlife Refuge is approximately 60 000 ha of protected wild land located about 100 km northeast of ENP (figure 1). At the initiation of our study, no Burmese pythons had been detected within 10 km of the refuge. For our control site, we selected Fakahatchee Strand Preserve State Park (FAK; figure 1), an approximately 30 000 ha protected area at the westernmost edge of the GEE. Marsh rabbits were commonly seen on this site during the study, and only two Burmese pythons had been detected and removed within 10 km of the study site since 2003.

Our sites with donor marsh rabbit populations were located in the northern section of the GEE, and included Storm Water Treatment Areas (STAs) and the adjacent Holey Lands Wildlife Management Area (figure 1). Within these areas, we captured rabbits on levees that provide an elevated platform where the rabbits congregated. We also captured rabbits from the shoulders of roads where the dominant vegetation was brush broom grass (*Andropogon* spp.) and Brazilian pepper trees (*Shinus terebinthifolius*).

(c) Trapping, handling and tracking

To capture rabbits, we identified areas with extensive rabbit activity and saturated those areas with Tomahawk live traps (model no. 107, Tomahawk, WI, USA), reinforced to protect captured marsh rabbits. We placed traps near rabbit runs, pellet piles and in dense vegetation, and baited them with apples and apple cider. We opened traps in the evening, and checked and closed them in the morning.

We placed trapped rabbits in a handling bag and manually restrained them. We recorded mass (g), sex, right ear length (mm), right hind foot length (mm), total body length (mm) and unique markings, and classified rabbits as adult (more than 700 g) or juvenile (less than 700 g) [21]. We excluded rabbits with a body mass index (calculated as the ratio between foot size and mass) less than 80% of average from the study and released them at the capture site because of their potentially poor condition. We fitted adult rabbits in good condition with a Sirtrack (Havelock North, New Zealand) V5C 161 (28 g) radio transmitter in the 166 MHz range with a mortality sensor.

We immediately released rabbits captured at the control site (FAK) and transported marsh rabbits captured from donor sites (STA) in individual 58 × 37 × 29 cm plastic pet carriers. Given the successful implementation of hard release (directly into the environment) protocols for other marsh rabbit translocations [22], we released translocated marsh rabbits within 6 h of processing. We maintained a balanced sex ratio at each site and released members of the same sex at least 60 m apart [22].

We tracked rabbits via triangulation at least once every 48 h using a hand held receiver (TRX-2000, Wildlife Materials Murphysboro, IL, USA; or R-1000, Communication Specialists, Orange, CA, USA) and a three-element Yagi antenna (Wildlife Materials, Murphysboro, IL, USA). If we detected a mortality signal or if a rabbit was in the same location for consecutive tracking sessions, we homed in on the rabbit to obtain a visual observation. We recorded mortality locations using a Garmin

(Olathe, KS, USA) eTrex 20 handheld global position system unit at the physical location of the animal.

(d) Cause-specific mortality

We examined mortality sites to determine the likely cause of death, and classified mortalities as predations by python, avian, mammalian, reptilian (non-python) and unknown endothermic predators. We classified rabbit mortalities as from an avian predator based on bird faecal sprays, presence of feathers, removal of eyes, fur and internal organs spread around the carcass in a 20–50 cm diameter circle and/or beak impressions on the collar [23,24]. We classified rabbit mortalities as from a mammalian predator based on the presence of mammal scats and tracks, opening of the body and removal of organs, skin 'pulled over the legs', bite marks to the head, the breaking of one or more long bones and/or the burial of the carcass [24]. Predation by pythons and other reptiles was unique because reptiles consumed the entire rabbit, allowing visual confirmation that the transmitter was inside a snake or alligator. We identified reptilian predators to species and recorded the weight, length and sex of animals when it was safe and reasonable to do so.

We stored carcasses of rabbits not obviously killed by a predator at –20°C for 1–12 months and performed complete necropsies on them at the Wildlife Research Laboratory (Florida Fish and Wildlife Conservation Commission, Gainesville, FL, USA). We examined fixed tissue samples embedded in paraffin, sectioned at 5–6 µm and stained with haematoxylin and eosin. Following necropsy, we classified rabbits that died within 10 days of release with signs of pulmonary edema, severe autolysis, and cuts and laceration consistent with trap injuries as trapping-related mortalities.

We used molecular techniques to further investigate rabbits that showed signs of snake predation (anterior of body exhibiting signs of partial ingestion). Specifically, we used quantitative PCR (qPCR) to test for Burmese python DNA on the fur of two predated rabbits. We isolated DNA for all samples following Qiagen's DNeasy Blood and Tissue kit (Valencia, CA, USA). We used species-specific Burmese python qPCR primers with TaqMan probes and TaqMan Fast Advanced Master Mix (Applied Biosystems, Foster City, CA, USA) on the ABI StepOne-Plus Real-Time system using the Fast qPCR profile. To avoid cross-contamination of reagents and equipment, we included negative controls and positive controls (rabbit and python tissue DNA samples) in each qPCR. We conducted qPCR assays using three technical replicates and sequenced traditional PCR products to confirm species identification in positive samples. After necropsies, we ruled out the possibility of predation by non-Burmese python ectotherms. We categorized the remaining marsh rabbit mortalities with signs of predation as caused by unknown endothermic predators (mammals and birds).

(e) Predation risk analysis

We estimated cause-specific mortality risks among causative agents using a non-parametric cumulative incidence function estimator that is an extension of the Cox proportional hazards model. We used animals in the study from 24 September 2012 until they died or were censored on 19 August 2013. We examined difference among sites and sex for the most common causes of mortality by comparing cumulative incidence of competing risk using a K-sample test [25]. To control for stress and increased susceptibility to predators after translocation, we excluded animals that had died within 10 days of their release from the analysis (electronic supplementary material, table S1). Similar to other studies [26,27], we observed that most rabbits established stable home ranges and ceased extreme exploratory behaviour after 10 days. We conducted our analysis using the *cmprsk* package (v. 2.2–7) for R.

Table 1. Sources of mortality for marsh rabbits living more than 10 days in ENP at the Costal Prairie Trail (CPT) and East Taylor Slough (ETS) sites, and at control and procedural control sites from 14 September 2012 to 19 August 2013. Number of mortalities outside parentheses, percentage of classified mortalities per site inside brackets.^a

	endothermic			ectothermic			total
	avian	mammalian	unknown	python	reptilian (non-python)	censored/alive	
ENP (CPT)	1 (11%)	1 (11%)	1 (11%)	6 (66%)	0	3	12
ENP (ETS)	0	0	2 (15%)	11 (85%)	0	1	14
control	5 (18%)	20 (71%)	9 (24%)	0	3 ^b (8%)	8	45
procedural control	3 (38%)	3 (33%)	1 (11%)	0	2 ^c (22%)	0	9

^aThe percentages of mortalities classified as python and reptilian (non-python) were calculated using unknown endothermic mortalities values, the percentages of classified avian and mammalian mortalities excluded unknown endothermic mortalities. Unknown endothermic mortalities were probably caused by mammals and birds but not reptiles.

^bRattlesnake.

^cAmerican alligator.

For our comparative analysis, we pooled rabbits by sex after finding no difference in cumulative hazard risk between the sexes (test statistic = 1.06, $p = 0.30$). We also pooled both ENP sites upon finding no difference in the cumulative hazard risk between the sites from python (test statistic = 0.55, $p = 0.50$), mammalian (test statistic = 1.16, $p = 0.28$) or avian (test statistic = 1.27, $p = 0.28$) predators. Similarly, we pooled the control and procedural control sites upon finding no difference in the hazard risk from mammalian (test statistic = 0.002, $p = 0.97$) and avian predators (test statistic = 2.93, $p = 0.087$).

(f) Temporal variation in mortality rates

Like most ectothermic animals, python behaviour and physiology are closely linked to environmental temperatures. Many pythons feed more during warm seasons and their digestion operates most efficiently at body temperatures greater than 25°C [28,29]. Pythons are also highly aquatic and higher water levels during summer may allow for easier access to areas of congregated prey [21]. Accordingly, we predicted that, unlike that of endothermic predators, predation by pythons would vary with environmental conditions. We specifically hypothesized higher python predation rates (i) with increasing temperatures (*temperature*), (ii) when average biweekly temperatures exceeded 25°C (*more than 25°C*), (iii) with increased water levels in major sloughs (*water level*), (iv) when water levels in major sloughs exceeded 800 cm, flooding surrounding areas (*more than 800 cm*), (v) with the additive influence of increased temperatures and water levels (*water level + temperature*), (vi) under the interactive influence of increased water levels and temperatures (*water level × temperature*) and (vii) with temperature more than 25°C and water depths more than 800 cm (*>800 cm & 25°C*). To determine if these environmental factors could explain heterogeneity in marsh rabbit mortalities from pythons or other major predators, we evaluated their influence on rabbit mortality rates from pythons and mammals over the same time period, which was 12 October 2012 (first week ≥ 4 rabbits on all sites) to 25 July 2013 (end of week the last rabbit died in ENP).

We examined our hypotheses by developing two sets (python and mammal) of seven candidate models that reflected each hypothesis, as well as a constant model, and evaluated them in a known-fate survival framework using MARK v. 7.1. We pooled data from the release sites in ENP and pooled both control sites because we found no difference in the risk of predation from mammals and pythons between these paired

sites. We populated climate variables using temperatures recorded at the Homestead Air Force Base (National Climatic Data Center) and water-level readings from the Everglades Depth Estimation Network (EDEN) [30]. We identified the most parsimonious models based on changes in Akaike's information criterion corrected for small sample sizes ($\Delta AICc$) and AIC weights (ω_i).

(g) Pellet surveys

Prior to the translocation of marsh rabbits to ENP, we surveyed the park for marsh rabbits using faecal pellet counts [31], road cruising surveys and artificial latrines [32] near the CPT and ETS study sites. To determine the persistence of the marsh rabbit population after translocation to ENP, we checked and cleared the artificial latrines at ETS once a month throughout the course of the study. Additionally, after the translocations to ENP, we searched for the presence of juvenile (less than 6 mm in diameter) and adult (greater than 6 mm) marsh rabbit pellets [21] in areas used by introduced marsh rabbits with a grid of 10 × 10 m cells. We calculated mean pellet densities (pellets m⁻²) as the average number of pellets in a 1 m² circular plot at each grid node. In February 2013 (five months post-release), we sampled a total of 5 ha of habitat; in December 2013 (15 month post-release), we resampled the same 5 ha and expanded the survey area to encompass an additional 10 ha used by radiotracked marsh rabbits.

3. Results

We captured, released and radiotracked 95 adult marsh rabbits from 14 September 2012 to 19 August 2013 (coastal ENP = 15, freshwater ENP = 16, procedural control = 15, control = 49). Eighty rabbits survived the 10-day adjustment period needed to reduce exploratory movements and acclimate to the sites. Additionally, 10 rabbits were censored after the 10-day adjustment period (e.g. lost signal from predation or equipment failure), and two rabbits were alive at the end of the study, such that we documented 68 rabbit mortalities. We classified the cause of mortality for 55 rabbits and listed the remaining 13 rabbits as mortalities from an unknown endothermic predator (table 1). Marsh rabbits in ENP faced the greatest risk of predation from pythons,

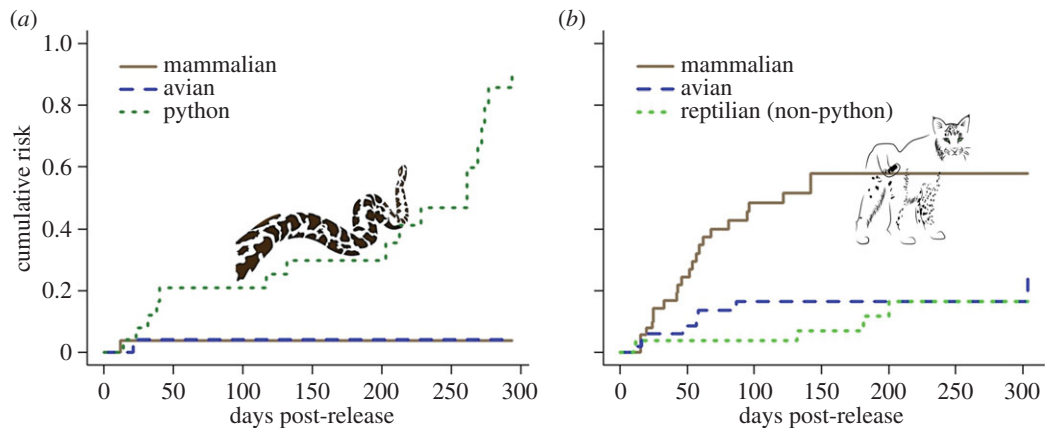


Figure 2. Cumulative cause-specific predation risk for marsh rabbits from predators (a) in ENP (where pythons are established) and (b) at control and procedural control site in regions of the GEE (where pythons have never or rarely been observed). Data were collected from 24 September 2012 to 19 August 2013.

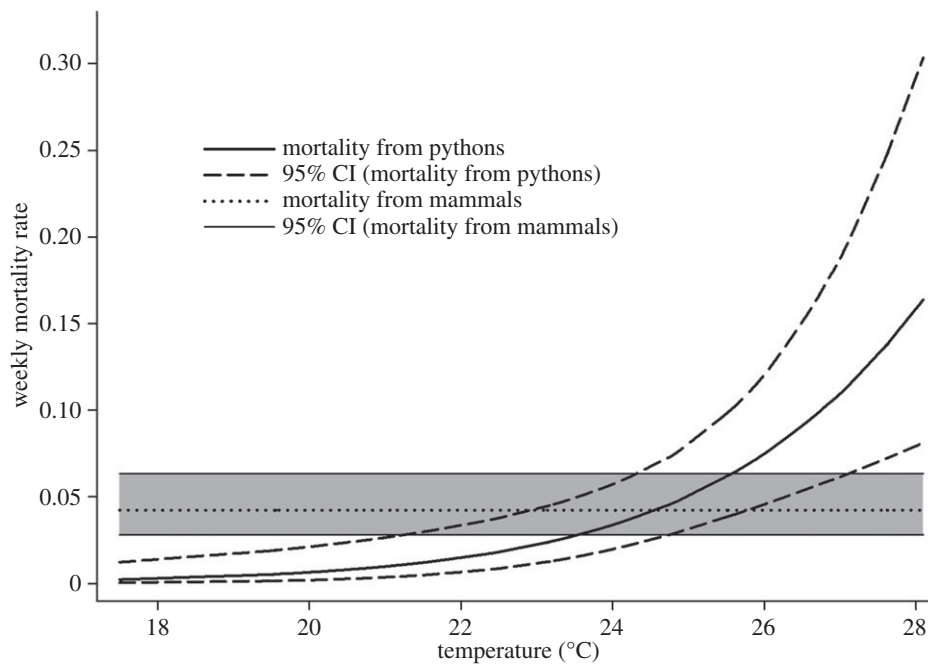


Figure 3. Estimates derived from our most parsimonious models of weekly marsh rabbit mortality from pythons and mammals as a function of temperature. Python-induced mortality rates were generated from the known fates of 26 rabbits released in ENP. Mammal-induced mortality rates were generated from the known fates of 55 rabbits in areas of the GEE with minimal invasive python activity. Models included data from 12 October 2012 to 25 July 2013.

which accounted for 77% of all mortalities (table 1). We attributed only one rabbit mortality in ENP to mammal predation. This was in stark contrast to results from control sites, where no rabbits were killed by pythons and we attributed 71% of classified mortalities to mammals (table 1). Only three rabbits (8%) at the control site were eaten by snakes, all native rattlesnakes (*Crotalus adamanteus*).

Comparing ENP and the control sites, rabbits' cumulative hazard risk was markedly higher from pythons in ENP (test statistic = 15.28, $p < 0.001$; figure 2) and from mammals on the control sites (test statistic = 17.26, $p < 0.001$; figure 2). We did not find a significant difference in the cumulative hazard risk from avian predators (test statistic = 2.00, $p = 0.157$; figure 2) between ENP and the control sites. Mortality from non-python reptiles occurred only on the control and procedural control site, and the hazard risk was significantly higher on the procedural control site (test statistic = 10.98, $p < 0.001$; table 1).

We failed to detect marsh rabbits in ENP during extensive surveys conducted prior to translocation. After translocation, the presence of pellets on artificial latrines demonstrated that marsh rabbits were present on the ENP release sites from November 2012 to June 2013. We detected juvenile and adult pellets from systematic pellet counts at the ENP release sites in February 2013, demonstrating that reproduction was occurring, but did not detect marsh rabbit pellets at either site during extensive surveys in December 2013 (electronic supplementary material, table S2). Consistent with our pellet counts, we found temporal heterogeneity in the mortality rates of rabbits eaten by pythons in ENP. Our most parsimonious model showed rabbit mortality rates from pythons increasing with rising temperatures (electronic supplementary material, table S3; figure 3). Conversely, rabbit mortality rates from the most common predators outside of ENP (mammals) were not influenced by changing environmental conditions (electronic supplementary material, table S4; figure 3).

4. Discussion

Our findings provide strong empirical evidence that pythons caused reductions in marsh rabbit populations in ENP [2]. Not only were pythons the dominant predators of marsh rabbits in ENP, but only one mammalian predation event occurred in the park. Outside of ENP, mammals (bobcats *Lynx rufus* and coyotes *Canis latrans*) were the dominant cause of marsh rabbit mortalities. The lack of mammalian predations of marsh rabbits in ENP was consistent with the reported declines of most mammalian species in the park [2] and may be attributed to direct (predation) or indirect (e.g. depletion of prey base) impacts of pythons on populations of mammalian predators.

Five months after their release in February 2013, marsh rabbits had established reproductive populations in ENP (electronic supplementary material, table S2). However, with seasonally increasing temperatures, ectothermic pythons probably increased their foraging activity [33,34]. Marsh rabbit mortality increased above baseline rates at temperatures over $\approx 25^{\circ}\text{C}$, rising to over 11% per week when average temperatures were more than 27°C (figure 3). Average weekly temperatures in ENP are generally over 27°C for a 15-week period from mid-June to late September. Increased water levels did not appear to have a substantial influence on python's predation of marsh rabbits (electronic supplementary material, table S3). As both species are strongly associated with water, it is possible that rising water levels had little influence on how accessible marsh rabbits were to pythons.

The seasonally high rates of mortality demonstrated in this study help to explain the apparent capacity of pythons to greatly reduce or eliminate marsh rabbits from ENP. Nevertheless, attributing large reductions in rabbit populations to an apex predator appears to contradict ecological theory. Reproductive parameters, not survival rates, should most influence population growth of fecund, early-maturing species like marsh rabbits [12]. One explanation for this contradiction in theory is that marsh rabbits were naive to predation by an introduced predator such as the Burmese python. In fact, continental populations have often shown elevated population suppression from alien compared with native predators [35,36,37]. Indeed, ENP's marsh rabbits and other mammals may have been ill-adapted to avoid predation by very large snakes, last present in the eastern USA at 20.6–16.3 Ma [2].

The loss of marsh rabbits and other mammals from ENP [2] is probably causing a massive rearrangement of the ENP food web, losses in ecosystem function, and complex and unpredictable cascading effects [5,6,11]. As prey and predators at multiple trophic levels, nutrient cyclers and engineers of

vegetation, mammals are an indispensable component of the GEE [38,39]. Our research clearly establishes pythons as a causal agent of marsh rabbit declines, a species we selected because of its theoretical resilience to predation pressure [16,17]. Accordingly, pythons are a logical and likely explanation for the observed declines in less fecund mammalian python prey species found in ENP (i.e. raccoon *Procyon lotor*, round-tailed muskrat *Neofiber alleni*, bobcat) [8].

Only with the recovery of ENP's mammal populations will it be possible to restore the health and functionality of this World Heritage Site. However, it seems unlikely that marsh rabbits and other mammal populations will rebound without action to manage pythons, as pythons are capable of persisting in the environment by switching to different prey and going long periods without food [40,41]. Furthermore, as this study illustrates, reintroductions and augmentations alone show little promise for recovering the park's mammals. Without effective tools and a strategy for reducing the prevalence of these invasive snakes [20], the dire state of mammals in the Everglades will probably remain unchanged, and even spread if python populations expand northward or become established elsewhere in the USA [42].

Disclaimer. The findings of this study do not necessarily reflect the opinion of the Florida Fish and Wildlife Conservation Commission, Gainesville, Florida and all opinions expressed are those of the authors.

Ethics statement. All trapping, handling and tracking protocols were conducted under a permit from the Florida Fish and Wildlife Conservation Commission (LSSC-12-00039) and were approved by the University of Florida's Non-Regulatory Animal Research Committee (005-WEC).

Data accessibility. Data are available as electronic supplementary material.

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Author contributions. R.A.M., R.N.R. and K.M.H. conceived the study; A.S. conducted and supervised data collection; R.A.M. and A.S. analysed the data; M.E.H. conducted molecular analysis; M.W.C. and A.S. conducted necropsies; and R.A.M. and A.S. drafted the manuscript. All authors contributed to the interpretation of the results and revised the manuscript.

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