

Can invasive Burmese pythons inhabit temperate regions of the southeastern United States?

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Received: 14 June 2010 / Accepted: 4 September 2010
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Abstract Understanding potential for range expansion is critical when evaluating the risk posed by invasive species. Burmese pythons (*Python molurus bivittatus*) are established in southern Florida and pose a significant threat to native ecosystems. Recent studies indicate that climate suitable for the species *P. molurus* exists throughout much of the southern United States. We examined survivorship, thermal biology, and behavior of Burmese pythons from South Florida in a semi-natural enclosure in South Carolina, where winters are appreciably cooler than in Florida, but within the predicted region of suitable climate. All pythons acclimated to the enclosure, but most died after failing to seek appropriate refugia during sub-freezing weather. The remaining snakes used refugia but died during an unusually cold period in January 2010. Although all snakes died during the study, most survived extended periods at temperatures below those typical of southern Florida and none exhibited obvious signs of disease. Our study represents a first step in evaluating the results of climate matching models and we address factors that may affect range expansion in this invasive species.

Keywords Everglades National Park · Invasive alien species · *Python molurus bivittatus* · Range expansion · Risk assessment · Thermal biology

Introduction

Invasive species are one of the greatest threats to biodiversity worldwide (Pimentel et al. 2000). Control of invasive species requires timely and appropriate action to minimize spread and impact (Sakai et al. 2001). Unfortunately, in many instances, control efforts are initiated too late to prevent spread of invasive species (Kraus 2009), and preemptive control measures are often not taken or even considered. Preemptive measures to minimize chance of successful invasion are particularly important for secretive species, such as snakes, which can become firmly established well before evidence of a problem becomes apparent. Risk assessment models provide information valuable for predicting potential invasive risk and allow for actions to be taken before invasions occur or during incipient invasive stages when the possibility of control is most feasible (Stohlgren and Jarnevich 2009). However, explicit testing of risk assessment models is necessary to ensure that effort and resources are allocated to most effectively minimize spread or prevent additional introductions of invasive species.

The Burmese python (*Python molurus bivittatus*), a native to Southeast Asia, has been established in

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southern Florida, including Everglades National Park (ENP), since at least the mid 1990's and currently inhabits over 5,180 square km of largely inaccessible habitat (Snow et al. 2007). Burmese pythons can reach lengths exceeding 5.5 m and have been documented in ENP to consume American alligators (*Alligator mississippiensis*) and a wide variety of avian and mammalian prey including wading birds, bobcats (*Lynx rufus*), and white-tailed deer (*Odocoileus virginianus*; Reed and Rodda 2009). Pythons may have already substantially reduced populations of some mammal species in ENP (Holbrook and Chesnes 2010) and threaten several federally endangered species such as woodstorks (*Mycteria americana*) and Key Largo woodrats (*Neotoma floridana smalli*).

Although large constricting snakes generally live in tropical climates, the native range of *P. molurus bivittatus* extends into temperate regions (Groombridge and Luxmoore 1991; Whitaker and Captain 2004; Zhao and Adler 1993) and recent climate-matching studies indicate that climate suitable for *P. molurus* exists throughout much of the southern United States (Reed and Rodda 2009; Rodda et al. 2009). These studies have prompted extensive media attention and opposition by reptile hobbyists (Barker and Barker 2010). Another study conducted by Pylon et al. (2008) using ecological niche modeling predicted a much more restrictive range confined primarily to southern Florida and southern Texas. The exact origin and genetic makeup of pythons in ENP is unknown, as is their ability to survive in temperate regions. Moreover, evaluation of the true risk posed by Burmese pythons requires understanding factors that interact with climate to limit distributions (e.g., physiological tolerance, thermoregulatory behavior, habitat suitability, prey availability, and barriers to dispersal; Mazzotti et al. 2010). A recent study found that even during an unusually severe cold spell in northern Florida, two of nine captive pythons survived when kept in outdoor pens with heated refuge boxes, but with no underground retreats (Avery et al. 2010).

We assessed the Burmese python's ability to persist in more temperate regions of the southeastern United States by examining survivorship, thermal biology, and behavior of pythons in a semi-natural enclosure in the Upper Coastal Plain of South Carolina, an area with winter temperatures that are appreciably cooler than in southern Florida, but

within the area that appears to have mean monthly rainfall and temperature similar to part of the occupied native range as portrayed by Rodda et al. (2009). Our study is the first designed to test the ability of Burmese pythons currently inhabiting ENP to survive in more temperate regions within the United States, while monitoring their thermal biology and behavior. Although the climate-matching model developed by Rodda et al. (2009) included data for the species as a whole (i.e., *P. m. molurus* and *P. m. bivittatus*), we conducted this study using only *P. m. bivittatus* (Burmese Python) from South Florida. Both subspecies occur in tropical and temperate locales in their native range, but we conducted our study using only Burmese pythons because it is the form currently established in South Florida and the form most likely to pose a risk, either by range expansion or establishment of additional populations. Subspecific designation of *P. molurus* is based on scale and color pattern characteristics. Physiological tolerances and thermoregulatory behavior likely vary more within subspecies from temperate versus tropical locales than between the subspecies. In our study, we found that although all pythons died during unusually cold periods in December and January, they were able to survive for extended periods of time at temperatures typical of winter conditions well north of ENP.

Methods

We used a previously constructed enclosure (Lee and Mills 2000) at the Savannah River Ecology Laboratory on the Savannah River Site, Aiken County, South Carolina, to examine the ability of pythons to survive, while we monitored their body temperatures (T_b 's), behavior, and habitat use. The snake-proof enclosure (31 × 25 m) was surrounded by a 2.5-m high, smooth-walled fence set 0.5 m deep in concrete. We added a 0.5 m inwardly-angled hardware cloth extension at the top of the fence to prevent large pythons from scaling the fence. A 12 × 10 m pond in the center of the enclosure varied in depth between a shallow end (ca. 0.5 m deep) and a deep end (ca. 2 m deep). One corner of the shallow end contained several areas of emergent aquatic vegetation. Numerous trees (mostly *Pinus* sp.) were present in the enclosure. We constructed four large brushpiles, including two that extended into the water. We built

4 artificial underground refugia buried approximately 1 m below the surface. Each underground refuge consisted of a $1 \times 0.5 \times 0.5$ m plastic chamber (ActionPacker; Rubbermaid, Fairlawn, OH, USA) partially filled with dried sphagnum moss and accessed via 1.5 m long $\times$ 15 cm diameter corrugated plastic pipe. Microdataloggers (iButton Thermochrons, Dallas Semiconductor, Dallas, TX, USA) programmed to record hourly temperatures were used to measure water (2 deep and 2 shallow), air (2), and underground refuge temperatures (2). Additionally, two biophysical models with dataloggers were constructed to mimic the physical properties of an adult python and were used to obtain operative environmental temperatures for areas exposed to solar radiation (Peterson et al. 1993).

We released ten wild-captured male pythons from ENP (2–3.5 m total length) into the enclosure in June 2009. To monitor snake locations and T_b 's, we surgically implanted radiotransmitters (model AI-2; Holohil Ltd., Carp, Ontario, Canada) and microdataloggers (iButton Thermochrons), set to record T_b 's hourly, into each snake following the basic procedures of Reinert and Cundall (1982). Dataloggers were calibrated in a circulating water bath and all were within 0.5°C of the actual temperatures. We offered pythons pre-killed prey (primarily rodents) approximately weekly during warm weather ending in mid-October. Pythons were located via radiotelemetry approximately three times per week and their location, behavior, and habitat use were recorded. Specifically, each time a snake was located we recorded whether the snake was in aquatic, terrestrial, arboreal, or refugia habitats and the percent of each snake that was exposed (i.e., visible without disturbance). Necropsies were performed by veterinarians at the University of Georgia's College of Veterinary Medicine on snakes that died during the study and included gross examination of external snake features and all internal organs, paying particular attention to indicators of potential respiratory infection (e.g., congestion in lungs).

Long-term climate data were obtained for Homestead, Florida (Univ. of Florida—Florida Automated Weather Network) and the Savannah River Site (Kabela 2009) and daily minimum, maximum, and average air temperatures were calculated from 1998 to 2008 for comparison with 2009–2010 data from the enclosure. We compared daily maximum,

minimum and mean snake T_b 's to available environmental temperatures to evaluate thermoregulatory behavior and reaction to changing environmental temperatures. We evaluated seasonal changes in habitat use and used a linear regression (i.e., % exposure vs. day of year) to examine changes in the exposure of the snakes to potential solar radiation as environmental conditions changed during the study.

Results

Although South Carolina experienced substantially colder winter temperatures than southern Florida from 1998 to 2008, average temperatures in the summer months were similar and daily maximum temperatures were warmer in South Carolina than in Florida (Fig. 1a). The winter of 2009–2010 was appreciably colder than typical winters in South Carolina (Fig. 1b). When snakes were introduced to the outdoor enclosure in June 2009, they appeared to habituate rapidly (i.e., they were never observed attempting to escape the enclosure, retreated to appropriate habitats such as brush piles and shallow water, and most accepted pre-killed prey soon after

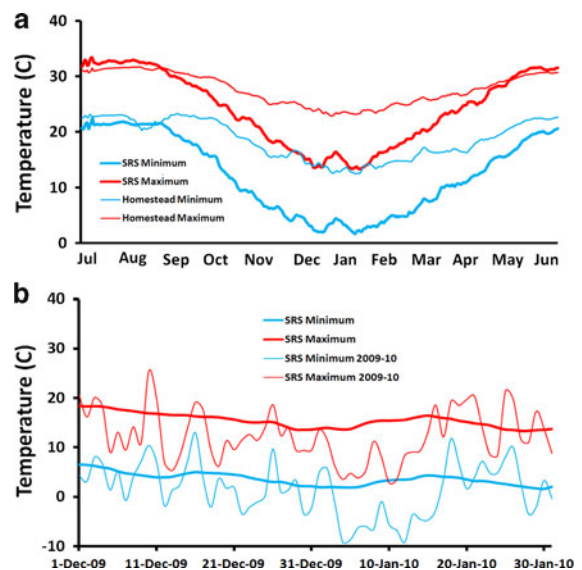


Fig. 1 **a** Mean minimum and maximum daily air temperatures (10-day moving averages) from near Everglades National Park (Homestead, Florida) and the Savannah River Site (SRS), South Carolina from 1998–2008. **b** Comparison between typical (1998–2008, 10-day moving averages) winter air temperatures on the SRS and SRS temperatures in 2009–2010

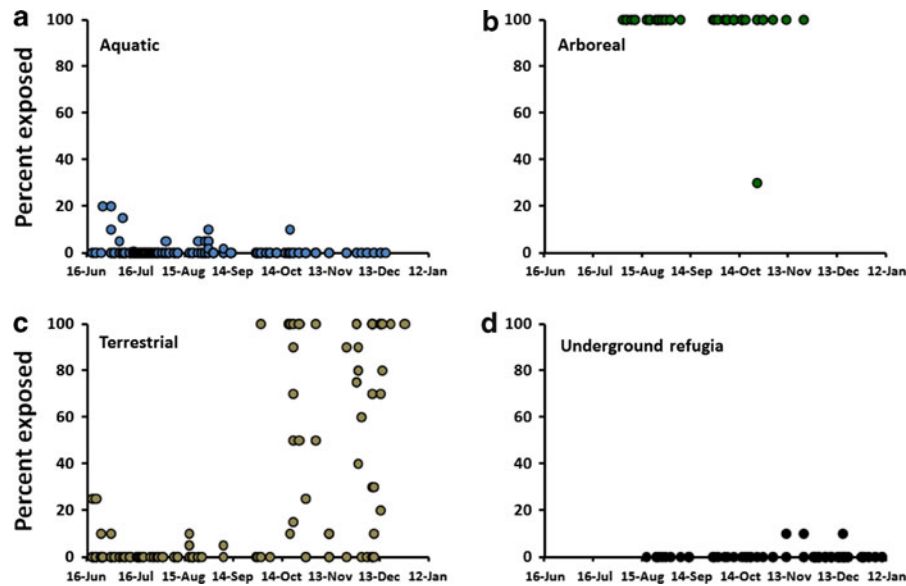


Fig. 2 Seasonal shifts in habitat use and basking behavior of 10 male Burmese pythons (*Python molurus bivittatus*) housed in a semi-natural enclosure in South Carolina from June 2009 to January 2010. Graphs depict microhabitat use and snake visibility in relation to season. Percent exposed represents the extent to which each snake was visible when located by radio-telemetry and snakes that were visible were most often basking

release). None of the pythons escaped from the enclosure. During June and July pythons were seldom visible, and used exclusively aquatic habitats (79% of relocations) and terrestrial brush piles (21% of relocations; Fig. 2). Snakes in terrestrial habitats during June and July were nearly always located under cover and were often deep within brush piles, where they were seldom visible. During June and July, snakes maintained T_b 's between 19 and 36°C, with limited daily variation resulting from thermal buffering of aquatic habitats and brush piles (Figs. 3, 4). In August some snakes began using arboreal habitats, at times climbing more than 20 m into the crowns of tall pine trees (Fig. 4). Arboreal habitat use continued through the onset of cold nights ($<5^\circ\text{C}$) in mid October and all but the two largest snakes climbed trees on at least one occasion. While in arboreal habitats, snakes were usually visible (Fig. 2) and experienced more variable T_b 's than snakes in other habitats (Figs. 3, 4). Most snakes not in trees remained in the water and were seldom visible between August and late-October (Fig. 2).

In mid-October environmental temperatures cooled appreciably, reaching a low air temperature of 3.6°C

in direct exposure to sunlight. Note that snakes shifted from predominantly aquatic habitat use and zero visibility in the summer to frequent use of terrestrial habitats and underground refugia in the fall and winter when they were frequently visible (i.e., basking). Each symbol may represent multiple snakes using the same habitat on the same date

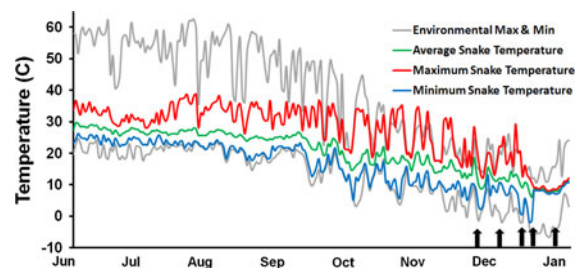
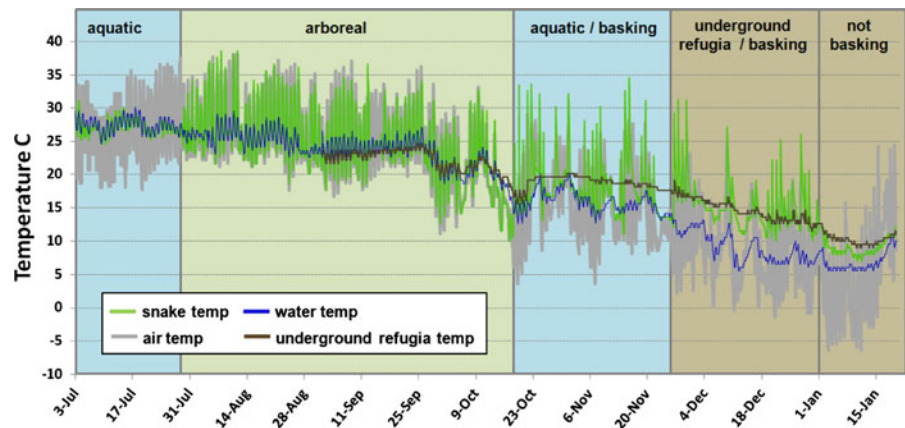


Fig. 3 Hourly minimum and maximum environmental temperatures and hourly minimum, maximum, and mean T_b 's for 10 male Burmese pythons (*Python molurus bivittatus*) kept in a semi-natural enclosure on the Savannah River Site, Aiken, South Carolina from June 2009–January 2010. Black arrows indicate dates when pythons died

during a cold spell on 16 October and water temperatures cooled to $<15^\circ\text{C}$ by the end of October (Fig. 4). At this time pythons showed a pronounced shift in habitat use, with many snakes leaving the water for terrestrial habitats and some using artificial underground refugia (Fig. 2). Moreover, snakes located in terrestrial habitats were often partially or fully exposed, reflecting basking behavior (Fig. 2). During

Fig. 4 Body temperature variation in relation to season and habitat use by one Burmese python (*Python molurus bivittatus*; Python 1244; Table 1) in a semi-natural enclosure in South Carolina. Note the pronounced effect of changes in habitat use on T_b variation and the ability of the snake to maintain T_b 's well above ambient air and water temperatures in November–January



October and November snakes generally exhibited lower and more variable T_b 's than during previous months (Fig. 3), with pronounced temperature spikes reflecting basking behavior (Fig. 4). In November, environmental temperatures continued to fall and most snakes used terrestrial habitats or underground refugia and were frequently visible while basking (Fig. 2). Consequently, we detected a weak but significant correlation between day of year and snake exposure (linear regression; $r^2 = 0.08$, $P < 0.001$) reflecting the pattern of increased basking as environmental temperatures decreased. However, through November, two individual pythons continued to retreat to aquatic habitats at night (Fig. 2), despite water temperatures dropping to 12–13°C at the end of the month (Fig. 4). In general, the pattern of increasing terrestrial habitat use and basking continued until the onset of extremely cold weather in late December and January when unusually cold weather set in (Fig. 1b). From 1 December 2009 until 14 January 2010, 33 of 44 days (75%) were below average minimum air temperature and the average low during this time period was 3.3°C below average. Between 1 January and 14 January 2010, 13 of 14 days were below the average minimum daily temperature and the average low was 7.7°C below average with only 1 day where the low recorded air temperature was above 0°C. The lowest air temperature recorded during this time period was −9.2°C on 12 January. Until this unusually cold weather, snakes were often exposed during cold weather, but nonetheless appeared healthy and active. No snakes exhibited any obvious signs of distress or disease (e.g., mouth gaping, wheezing, or nasal discharge characteristic of respiratory infections) during any part of the study.

Despite 12 nights when air temperatures dropped below 5°C, no mortality occurred until 11 December, when air temperatures dropped to −0.4°C (Fig. 3). On this date, 5 of the 10 study animals died (Table 1). Four of the five surviving snakes used underground refugia at night during this time. Of those that died, two of the snakes died while using the water as a nocturnal refuge and both were found with their heads out of the water resting on protruding branches (Table 1). Shallow water temperature on that night reached a low of 6°C. The other three snakes that died used terrestrial habitats with little or no cover. Three additional snakes died between 17 December and 4 January. Although these snakes all regularly used underground refugia at night, each snake died when it failed to return to an underground refuge on a night when air temperatures dropped to or below 0°C. The two remaining snakes used underground refugia as nocturnal refugia exclusively and ceased emerging to bask at onset of frigid weather in late December (Figs. 3, 4). Both of these snakes were found dead when underground refugia were checked in mid-January (Table 1). Overall, snakes did not necessarily die when their core T_b 's reached the lowest recorded temperature of the study and many snakes experienced prolonged periods with T_b 's below 15°C (Table 1). Necropsies showed no obvious signs of disease. Veterinarians found nothing grossly wrong with the respiratory tract (e.g., no excessive mucus or other problems suggestive of respiratory disease) and suggested the most likely cause of death as acute hypothermia rather than chronic diseases typically associated with cold stress in captive tropical reptiles.

Table 1 Demographic attributes and fate of ten Burmese pythons from southern Florida kept in a semi-natural outdoor enclosure in South Carolina from June 2009 to January 2010

Snake ID	Introduction date	Sex	SVL (cm)	Δ Mass (%) [*]	Min T _B (°C) survived (date) [†]	Date of death (Min T _B [°C]) ^{††}	Behavior leading to death
1051	6/18/2009	♂	212	7%	8.2 (21 November)	11 December (6.7)	Often used underground refugia as refuge but stayed coiled in a terrestrial brush pile during a cold spell
1175	6/18/2009	♂	219	−14%	7.2 (4 December)	11 December (4.6)	Used underground refugia as refuge; moved to water during a warm spell; found dead in water with head propped on emergent branch
1176	6/18/2009	♂	237	−9%	8.2 (6 December)	11 December (2.6)	Used a terrestrial brush pile exclusively as refuge; stayed coiled at edge of brush pile during a cold spell
1245	6/18/2009	♂	180	9%	5.1 (11 December)	11 December (5.6)	Used terrestrial coverboard (plywood) as refuge, found dead coiled under board during a cold spell
1254	6/27/2009	♂	181	27%	9.6 (25 October)	11 December (7.1)	Used water exclusively as refuge; found dead with body in water and head propped on a emergent branch
1243	6/18/2009	♂	148	2%	7.6 (7 November)	17 December (7.6)	Used underground refugia as refuge but moved to water during a warm spell; found dead with body half in water, half on emergent brush
1132	6/18/2009	♂	191	−15%	5.7 (7 November)	28 December (5.7)	Used underground refugia as refuge, found dead coiled at the entrance to the underground refugia tunnel
1252	6/27/2009	♂	275	5%	9.7 (6 December)	4 January (0.6)	Used underground refugia as refuge but emerged on one of the coldest days and died just outside entrance
1213	6/27/2009	♂	190	−10%	5.1 (18 October)	25 December–7 January (7.1)	Used underground refugia exclusively as refuge; last seen basking 25 December; found dead in underground refugia on 14 January; had been dead >1 week
1244	6/18/2009	♂	227	−12%	10.1 (17 October)	7–14 January (7.1)	Used underground refugia exclusively as refuge; last seen basking 1 January; found freshly dead in underground refugia on 14 January

* Change in snake body mass over the course of the study, expressed relative to initial mass

[†] Minimum body temperature experienced by each snake, prior to the date of its death

^{††} Minimum body temperature experienced by each snake on the date of its death. Although the snake may have died before this temperature was reached, this temperature represents the minimum temperature that may have been responsible for each snake's death

Discussion

Our results suggest that Burmese pythons from the population currently established in Florida are capable of withstanding conditions substantially cooler than those typically experienced in southern Florida, but may not be able to survive severe winters in regions as temperate as central South Carolina. Although pythons quickly habituated to the enclosure and South Carolina environmental conditions, at the onset of sub-freezing temperatures, several of the pythons exhibited inappropriate thermoregulatory behaviors that likely resulted in their death (i.e., failing to seek appropriate refugia). Others died during an unusually severe and prolonged cold spell, despite the fact that they used subterranean refugia. Our study helps to address the potential for range expansion in pythons, but many questions remain that must be addressed to fully evaluate the ability of this species to inhabit regions outside of southern Florida.

Understanding proximate factors that contributed to the pythons' deaths is important for evaluating factors that may limit their potential distribution within the United States. Husbandry manuals for Burmese pythons indicate that they often succumb to respiratory disease in captivity if kept below 18.3°C (De Vosjoli and Klingenberg 2005). We found no evidence of respiratory disease, despite the fact that all of the snakes experienced prolonged temperatures below 15°C. Necropsy and the fact that all pythons' deaths were correlated with periods of low environmental temperatures indicate that the snakes died as the result of acute hypothermia. Additionally, all snakes appeared healthy and active up until the times of their deaths, there were no obvious demographic correlates with time of death, and no evidence that inadequate food contributed to any of the snakes' deaths (Table 1). In fact, the smallest, largest, and thinnest snakes were all among the last snakes to die (Table 1). Thus, we conclude that snakes died as a result of acute or prolonged exposure to temperatures below their thermal tolerance limits.

Climate is typically considered a major factor limiting the distributions of ectotherms (Andrewartha and Birch 1954; Ayrinhac et al. 2004). Body temperatures of ectotherms are typically maintained within thermal tolerance limits through behavioral decisions (i.e., thermoregulatory behavior; Huey 1982). Many temperate reptiles are capable of

withstanding prolonged periods with T_b 's below 5°C and some are even tolerant of freezing (Storey and Storey 1992). Although individual pythons in our study survived short-duration drops in core T_b as low as 4°C, most deaths were associated with T_b 's between 5 and 10°C. Thus, it appears that the lower limits of physiological tolerance for Florida pythons are higher than those of many temperate North American reptiles (Avery 1982). It is important to note, however, that some snakes, including boids, can exhibit substantial thermal heterogeneity among various regions of their bodies (Peterson et al. 1993). We only measured snake core T_b and thus cannot rule out the possibility that snakes' heads experienced temperatures lower than the temperatures we measured. Artificial underground refugia remained relatively warm compared to other environmental temperatures (Fig. 4) but many of the snakes failed to remain underground, presumably resulting in their deaths. Thus, poor thermoregulatory decisions appeared to result in the death of most of the snakes tested. Such inappropriate behavior was noted during the same extreme cold spell in captive pythons in Gainesville, Florida (Avery et al. 2010) and in free-ranging pythons in South Florida (Mazzotti et al. 2010). However, in both Florida cases, some snakes also adopted behaviors that allowed them to survive the unusually cold temperatures; in Gainesville, two pythons remained in heated artificial refuges, and in South Florida many surviving snakes were captured after the cold spell. If such variation in behavior is heritable, natural selection could result a python population better adapted to cold weather.

The two pythons that survived the longest remained within underground refugia until their deaths during the prolonged, extreme cold spell in early January 2010. During this time, underground refugia temperatures stayed above 5°C, but this was apparently too cold for those snakes to withstand for an extended period of time. We do not know if thermal conditions within the underground refugia were similar to many refugia available in the Upper Coastal Plain of South Carolina (e.g., stump holes, animal burrows). However, refugia temperatures only dropped below 10°C for 5 days during the unusual cold spell, and some refugia that would be available to hibernating pythons in South Carolina may be much deeper than the refugia we provided, thus providing better protection from lethal temperatures.

Thus, it is likely that some of the snakes from Florida could survive typical winters in South Carolina, provided they are able to locate suitable refugia and do not adopt inappropriate thermoregulatory behavior. In their native range, Burmese pythons are found in a variety of climates including the foothills of the Tibetan Plateau and Himalaya Mountains (Groombridge and Luxmoore 1991; Reed and Rodda 2009; Whitaker and Captain 2004; Zhao and Adler 1993). Indian pythons (*P. m. molurus*) are known to retreat from below-freezing temperatures to burrows created by mammals (Bhupathy and Vijayan 1989), and presumably Burmese pythons inhabiting temperate regions exhibit similar behaviors.

The pythons we studied apparently lacked the physiological tolerances and/or behaviors that allow Burmese pythons to inhabit temperate regions in their native range. Although little is known regarding geographic variation in cold tolerance and thermoregulatory behavior in pythons within their native range, it is likely that like other reptiles (Wilson and Echternacht 1987), Burmese pythons exhibit geographic variation in thermoregulatory behavior and/or cold tolerances and that such characteristics are heritable (Hoffmann et al. 2002). It is possible that pythons present in Florida are derived from warm-locality genetic stock and lack these traits (Avery et al. 2010; Mazzotti et al. 2010). Little is known about the genetics of Florida pythons or their origins, but the species has been imported in large numbers from tropical regions of southeast Asia in the past (Reed 2005). Recent experiments on Australian Tiger Snakes (*Notechis scutatus*) demonstrated that snakes raised in one thermal environment adopt inappropriate thermoregulatory behaviors and fail to maintain preferred T_b 's after an environmental shift (Aubret and Shine 2010). Thus, alternatively, the pythons we tested, which were all from southern Florida and at least 1.5 years old, may have been acclimatized to the warmer environmental conditions they experienced when young, prompting them to behave inappropriately when confronted with colder conditions in South Carolina. Testing naïve snakes and/or snakes from known localities within their native range is therefore necessary to evaluate competing effects of genetics, plasticity, and acclimatization on cold-tolerance in Burmese pythons. Such tests are necessary to develop a complete understanding of how these affect population-level processes and thus the

potential for this species to inhabit temperate portions of the southeastern United States.

Our study revealed that both physiological tolerance and thermoregulatory behavior likely play important roles in the ability of invasive pythons to persist in temperate regions of the United States (Mazzotti et al. 2010). Studies have documented evolution of physiological cold tolerance in invasive species (e.g., Hoffmann and Weeks 2007; Bertoli et al. 2010). However, when compared to physiology, thermoregulatory behavior can evolve relatively rapidly, provided it is a product of heritable behavioral traits (Angiletta et al. 2002). Because the consequences of inappropriate thermoregulatory behavior are severe (i.e., death), selection for appropriate thermoregulatory behavior will be strong as pythons expand their range northward through the Florida peninsula. Consequently, future generations of pythons may be better equipped to invade temperate regions than those currently inhabiting southern Florida.

Rodda et al. (2009) and Pyron et al. (2008) proposed conflicting predictions of the amount of suitable climate present for Indian/Burmese pythons (*P. molurus*) in the United States. Although our results are consistent with the predictions of the Pyron et al. (2008) model, they do not necessarily refute the Rodda et al. (2009) model. Despite the fact that snakes in our study did not survive within their predicted region of suitable climate, the northern extent of the climate match predicted by Rodda et al. (2009) is determined by python populations from the latitudinal limit of the species' native range. Thus, the models presented in Rodda et al. (2009) do not indicate that all pythons can survive in areas of the predicted climate match. Moreover, the status of the species *P. molurus* remains unclear and whether the results of climate matching studies apply equally to both Indian (*P. m. molurus*) and Burmese (*P. m. bivittatus*) pythons remains unknown. Finally, it is important to remember that although the time frame considered for expansion of the pythons' range in the United States is typically short-term (i.e., decades), it may take much longer for the species to spread into all regions of suitable climate and habitat.

Some pythons in our study were able to withstand long periods of considerably colder weather than is typical for South Florida, suggesting that some snakes currently inhabiting Florida could survive typical winters in areas of the southeastern United

States more temperate than the region currently inhabited by pythons. Moreover, our results are specific to translocated pythons from southern Florida. Burmese pythons originating from more temperate localities within their native range may be more tolerant of cold temperatures and would presumably be more likely to successfully become established in temperate areas of North America. The susceptibility to cold we observed may reflect a tropical origin of the Florida pythons or acclimatization of snakes to warm southern Florida winters early in life. Future investigations are needed to assess the roles that genetics, phenotypic plasticity, and acclimatization play in determining cold-tolerance of Burmese pythons and provide a comprehensive assessment of the risk that these and other giant constricting snakes pose as invasive species.

Acknowledgments We thank R. Bauer and S. Poppy for assisting with many aspects of the study and helping to track snakes. For assistance with various project logistics and advice, we thank K. Andrews, M. Cherkiss, B. DeGregorio, J. Greene, C. Hagen, K. Hart, E. Kabela, F. Mazzotti, T. Mills, S. Pfaff, M. Pilgrim, M. Rochford, S. Snow, T. Tuberville, A. Tucker, T. Walters, and A. Wolfe. R. Snow provided and transported animals. We especially thank R. McManamon and B. Ritchie from the Univ. of Georgia School of Veterinary Medicine who conducted necropsies. E. Eskew assisted with calibrating dataloggers. S. Foley assisted with data analysis. E. Eskew, S. Price, K. Hart, R. Reed, R. Snow, and two anonymous reviewers all provided comments on the manuscript. All procedures used in the study were approved by the University of Georgia Animal Care and Use Committee (no. A2009 2-041). Pythons were collected under scientific collecting permit #EVER-2009-SCI-0001 issued by the NPS. This material is based upon work supported by the US Dept. of Energy under Award Number DE-FC-09-075R22506 to the University of Georgia's Savannah River Ecology Lab. Partial funding was provided by the Davidson College Department of Biology and Duke Power.

References

Andrewartha HG, Birch LC (1954) The distribution and abundance of animals. University of Chicago Press, Chicago

Angiletta MJ, Niewiarowski PH, Navas CA (2002) The evolution of thermal physiology in ectotherms. *J Therm Biol* 27:249–268

Aubret F, Shine R (2010) Thermal plasticity in young snakes: how will climate change affect the thermoregulatory tactics of ectotherms? *J Exp Biol* 213:242–248

Avery RA (1982) Field studies of body temperatures. In: Gans C, Pough FH (eds) *Biology of the reptilia*, vol 12. Academic Press, New York, pp 93–166

Avery ML, Engeman RM, Keacher KL, Humphrey JS, Bruce WE, Mathies TC, Mauldin RE (2010) Cold weather and the potential range of introduced Burmese pythons. *Biol Invas* (in press)

Ayrinhac A, Debat V, Gibert P, Kister A, Legout H, Moreteau B, Vergilino R, David J (2004) Cold adaptation in geographical populations of *Drosophila melanogaster*: phenotypic plasticity is more important than genetic variability. *Funct Ecol* 18:700–706

Barker DG, Barker TM (2010) Review: giant constrictors: biological and management profiles and an establishment risk for nine large species of pythons, anacondas, and the boa constrictor by Robert N. Reed and Gordon H. Rodda 2009. U.S. Geological Survey Open-File Report 2009-1202, xviii+302 pp. Bull Chicago Herp Soc 45:1–8

Bertoli CI, Scannapieco AC, Sambucetti P, Norry FM (2010) Direct and correlated responses to chill-coma recovery selection in *Drosophila buzzatii*. *Entomologia Experimentalis Et Applicata* 134:154–159

Bhupathy S, Vijayan VS (1989) Status, distribution and general ecology of the Indian Python, *Python molurus molurus* Linn. in Keoladeo National Park, Bharatpur, Rajasthan. *J Bombay Nat Hist Soc* 86:381–387

De Vosjoli P, Klingenberg R (2005) Burmese pythons: plus reticulated pythons and related species. Advanced Vivarium Systems, Laguna Hills

Groombridge B, Luxmoore R (1991) Pythons in South-east Asia. A review of distribution, status, and trade in three selected species. Report to Cites Secretariat, Lausanne

Hoffmann AA, Weeks AR (2007) Climatic selection on genes and traits after a 100 year-old invasion: a critical look at the temperate-tropical clines in *Drosophila melanogaster* from eastern Australia. *Genetica* 129:133–147

Hoffmann AA, Anderson A, Hallas R (2002) Opposing clines for high and low temperature resistance in *Drosophila melanogaster*. *Ecol Lett* 5:614–618

Holbrook J, Chesnes T (2010) An effect of Burmese pythons (*Python molurus bivittatus*) on mammal populations in southern Florida. *Florida Sci* (in press)

Huey RB (1982) Temperature, physiology, and the ecology of reptiles. In: Gans C, Pough FH (eds) *Biology of the reptilia*, vol 12. Academic Press, New York, pp 25–91

Kabela E (2009) Savannah River Site annual meteorology report. SRNL-RP-2009-00251

Kraus F (2009) Alien reptiles and amphibians: a scientific compendium and analysis. Springer, New York

Lee JR, Mills MS (2000) Design and construction of an outdoor enclosure for the study of snake thermal ecology. *Herpetol Rev* 31:24–26

Mazzotti FJ, Cherkiss MS, Hart KM, Snow S, Rochford MR, Dorcas ME, Reed R (2010) Cold-induced mortality of invasive Burmese pythons in south Florida. *Biol Invas* (in press)

Peterson CR, Gibson AR, Dorcas ME (1993) Snake thermal ecology: the causes and consequences of body-temperature variation. In: Seigel RA, Collins JT (eds) *Snakes: ecology and behavior*. McGraw-Hill, New York, pp 241–314

Pimentel D, Zuniga R, Morrison D (2000) Environmental and economic costs of nonindigenous species in the United States. *Bioscience* 50:53–65

- Pyron RA, Burbrink FT, Guiher TJ (2008) Claims of potential expansion throughout the U.S. by invasive python species are contradicted by ecological niche models. *PLoS ONE* 3:e2931
- Reed RN (2005) An ecological risk assessment of nonnative boas and pythons as potentially invasive species in the United States. *Risk Anal* 25:753–766
- Reed RN, Rodda GH (2009) Giant constrictors: biological and management profiles and an establishment risk assessment for nine large species of pythons, anacondas, and the boa constrictor. U.S. Geological Survey Open-File Report 2009–1202
- Reinert HK, Cundall D (1982) An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982: 702–705
- Rodda GH, Jarnevich CS, Reed RN (2009) What parts of the US mainland are climatically suitable for invasive alien pythons spreading from Everglades National Park? *Biol Invas* 11:241–252
- Sakai AK, Allendorf FW, Holt JS, Lodge DM, Molofsky J, With KA, Baughman S, Cabin RJ, Cohen JE, Ellstrand NC, McCuley DE, O’Neil P, Parker IM, Thompson JN, Weller SG (2001) The population biology of invasive species. *Ann Rev Ecol Syst* 32:305–332
- Snow RW, Krysko KL, Enge KM, Oberhofer L, Warren-Bradley A, Wilkins L (2007) Introduced populations of *Boa constrictor* (Boidae) and *Python molurus bivittatus* (Pythonidae) in southern Florida. In: Henderson RW, Powell R (eds) *Biology of the boas and pythons*. Eagle Mountain Publishing, Eagle Mountain, pp 416–438
- Stohlgren TJ, Jarnevich CS (2009) Risk assessment of invasive species. In: Clout MN, Williams PA (eds) *Invasive species management: a handbook of principles and techniques*. Oxford University Press, Oxford, pp 19–46
- Storey KB, Storey JM (1992) Natural freeze tolerance in ectothermic vertebrates. *Ann Rev Physiol* 54:619–637
- Whitaker R, Captain A (2004) *Snakes of India: the field guide*. Draco Books, Chengalpattu
- Wilson M, Echternacht AC (1987) Geographic variation in the critical thermal minimum of the green anole, *Anolis carolinensis* (Sauria: Iguanidae), along a latitudinal gradient. *Comp Biochem Physiol A* 87:757–760
- Zhao E, Adler K (1993) *Herpetology of China*. Society for the Study of Amphibians and Reptiles, St. Louis