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Author for correspondence:
Shannon E. Pittman
e-mail: shpittman@davidson.edu

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Conservation biology

Homing of invasive Burmese pythons in South Florida: evidence for map and compass senses in snakes

Shannon E. Pittman[1], Kristen M. Hart[2], Michael S. Cherkiss[2,3], Ray W. Snow[4], Ikuko Fujisaki[3], Brian J. Smith[2], Frank J. Mazzotti[3] and Michael E. Dorcas[1]

[1]Department of Biology, Davidson College, Davidson, NC, USA
[2]US Geological Survey, Southeast Ecological Science Center, Davie, FL, USA
[3]Ft. Lauderdale Research and Education Center, University of Florida, Davie, FL, USA
[4]US National Park Service, Homestead, FL, USA

Navigational ability is a critical component of an animal's spatial ecology and may influence the invasive potential of species. Burmese pythons (*Python molurus bivittatus*) are apex predators invasive to South Florida. We tracked the movements of 12 adult Burmese pythons in Everglades National Park, six of which were translocated 21–36 km from their capture locations. Translocated snakes oriented movement homeward relative to the capture location, and five of six snakes returned to within 5 km of the original capture location. Translocated snakes moved straighter and faster than control snakes and displayed movement path structure indicative of oriented movement. This study provides evidence that Burmese pythons have navigational map and compass senses and has implications for predictions of spatial spread and impacts as well as our understanding of reptile cognitive abilities.

1. Introduction

Navigation is the process by which animals decide when and where to move and plays an important role in species' spatial dynamics [1]. The navigational capacity of an animal is often quantified using translocation experiments that measure the ability of animals released in an unfamiliar location to orient home. The ability to home after translocation involves two senses: a map sense (determination of position in relation to a goal) and the compass sense (access to a reliable compass to maintain orientation towards the goal) [2]. This process has been studied extensively in a number of species, notably in pigeons and sea turtles [2], but has not been documented extensively in snakes.

Few studies have explicitly tested the navigational capacity of snakes [3–5], despite recent evidence that squamates have sophisticated spatial memory [6,7]. Translocation experiments have shown that many snake species display a lack of ability to home and often exhibit suboptimal movement behaviour typified by high movement rates and circular search behaviour that increase the likelihood of crossing a previously visited path [8,9]. These translocation studies have focused primarily on terrestrial species of conservation concern (e.g. rattlesnakes, hognose snakes), and few have investigated the homing abilities of large constrictors.

Understanding navigational capacity is necessary to develop a mechanistic understanding of species' spatial dynamics [10] and is critical in the context of range expansion by invasive species [11]. Navigational capacity may allow animals to exploit resources that are widely spaced or seasonally varying and reduces risk associated with searching potentially hostile or unfamiliar areas. Few studies have investigated navigation in invasive species, despite implications for movement behaviour and resource use. Invasive snakes have the ability to

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severely disrupt native ecosystems. Several large snakes have become established outside their native ranges, including Burmese pythons (*Python molurus bivittatus*), African pythons (*Python sebae*) and boa constrictors (*Boa constrictor*), and knowledge of their movement abilities could greatly inform management and control efforts [12].

The Burmese python is native to southern Asia and is one of the world's largest snakes [12]. This species is established over several 1000 km^2 of southern Florida, including most of Everglades National Park (ENP) and Big Cypress National Preserve [12]. The number of pythons found has increased substantially since the year 2000, and the population appears to have spread northward from ENP and southward into the Florida Keys. Severe declines of several once-common mammal species appear to be the result of python predation and are a testament to their ability to impact food chains [13].

To understand the spatial ecology of invasive Burmese pythons, we used radiotelemetry in 2006–2007 to study the movements and activity patterns of pythons in South Florida. As part of that study, we translocated six individuals from their original capture locations. Herein, we report and discuss the implications of the movement and homing capabilities of these translocated pythons.

2. Material and methods

We conducted radiotracking between August 2006 and September 2007 within and around ENP (figure 1; [14]). Python capture and radiotransmitter implantation followed Mazzotti *et al*. [14]. We released six pythons in the translocated treatment 21–36 km from capture locations to areas with suitable habitat (evidenced by the presence of pythons). We released six pythons at the location where they were originally captured (control). The translocated and control individuals were treated equally in terms of handling and holding time. All animals were placed in sealed, opaque plastic containers and were transported by vehicle to release locations (paths taken by researchers were not direct—figure 1). Snakes were anaesthetized during implantation surgeries, which occurred at the Daniel Beard Center. We radiotracked each python one to three times per week and recorded locations using a GPS from a fixed-wing aircraft (Cessna 182), flying 100–140 km h^{-1} (altitudes 152–610 m) and periodically performed walk-ins to their locations.

We compared overall speed (total distance moved/number of days tracked) and maximum speed (maximum net distance moved/day) of translocated and control snakes using Wilcoxon rank sum tests. We used Rayleigh's test to determine whether translocated pythons significantly oriented movement according to the bearing of capture locations [15]. Net orientations were calculated after 170 ($\pm$2) days for snakes released during May and after 253 ($\pm$2) days for snakes released in November. We standardized net orientations so that 0° corresponded to the bearing of the capture location, and we considered the net bearing of each translocated python as a replicate.

For each python movement path, we determined the orientation efficiency to the capture location following Bodin *et al*. [16], where positive values of orientation efficiency indicate oriented movement. We calculated the fractal dimension (FD) of all movement paths (smaller FD values signify straighter movement) using FRACTAL 5.0 (V. O. Nams, Nova Scotia Agricultural College, Truro, Nova Scotia, Canada). We compared orientation efficiencies and FDs of translocated and control snakes using Wilcoxon rank sum tests.

To test movement path structure for oriented movement, we used the scaling test for orientation following Nams [17], which tests paths for deviations from correlated random walks (CRWs) at different spatial scales. If $CRW_{diff} > 0$, the animal moved straighter than predicted by a CRW and therefore employed oriented movement, whereas if $CRW_{diff} < 0$, the animal moved more tortuously than a CRW. We performed the scaling test for orientation at the group level (translocated or control) where errors are based on among-path variation. We investigated spatial scales ranging from 1 to 5000 m.

3. Results

All translocated pythons oriented movement bearings homeward relative to their release point, and snake bearings were within $\pm 22°$ of the homeward bearing (figure 1; $n = 6$, Rayleigh's test, $p < 0.001$). Five of the six translocated pythons returned to within 5 km of their capture location; the sixth moved in the direction of the capture location (electronic supplementary material, table S1). Translocated pythons differed in orientation efficiency to capture locations compared with control pythons (table 1, Wilcoxon rank sum test, $p = 0.002$). Translocated pythons also displayed lower FDs of movement paths than control pythons (table 1, Wilcoxon rank sum test, $p = 0.002$). Translocated pythons had higher mean movement rates (table 1, Wilcoxon rank sum test, $p = 0.002$) and maximum speeds (table 1, Wilcoxon rank sum test, $p = 0.004$) than control pythons. The scaling test for orientation showed that translocated pythons moved distances greater than predicted by CRW at scales approximately 10–3000 m (electronic supplementary material, figure S1), whereas control pythons showed no difference from CRW at any spatial scale (electronic supplementary material, figure S2).

4. Discussion

This study provides evidence that Burmese pythons are capable of homing after displacement at a scale previously undocumented for any snake species. Contrary to our expectation that pythons would exhibit random wandering movement similar to other snake species displaced similar distances, the pythons in this study oriented towards their capture locations. Because snakes successfully determined the bearing towards their capture locations and maintained those bearings, this study provides evidence that Burmese pythons have navigational map and compass senses. In addition, snakes maintained oriented movement over relatively long time scales (94–296 days), demonstrating the maintenance of long-term movement goals and high motivation to reach home locations. These factors have important consequences for the spatial dynamics of the species, with implications for management.

The map sense involves either path integration using the memory of an outward path or sampling local environmental cues to determine position relative to a goal location [2]. The pythons in our study showed significant orientation towards the home locations without the memory of an outward path and therefore likely used local cues at the release site to determine their position relative to home [18]. Python homing movement paths in our study were significantly different than CRW, supporting the assertion that the snakes used compass cues to maintain bearings over long distances (compass step) [17]. Potential cues underlying the map sense in pythons

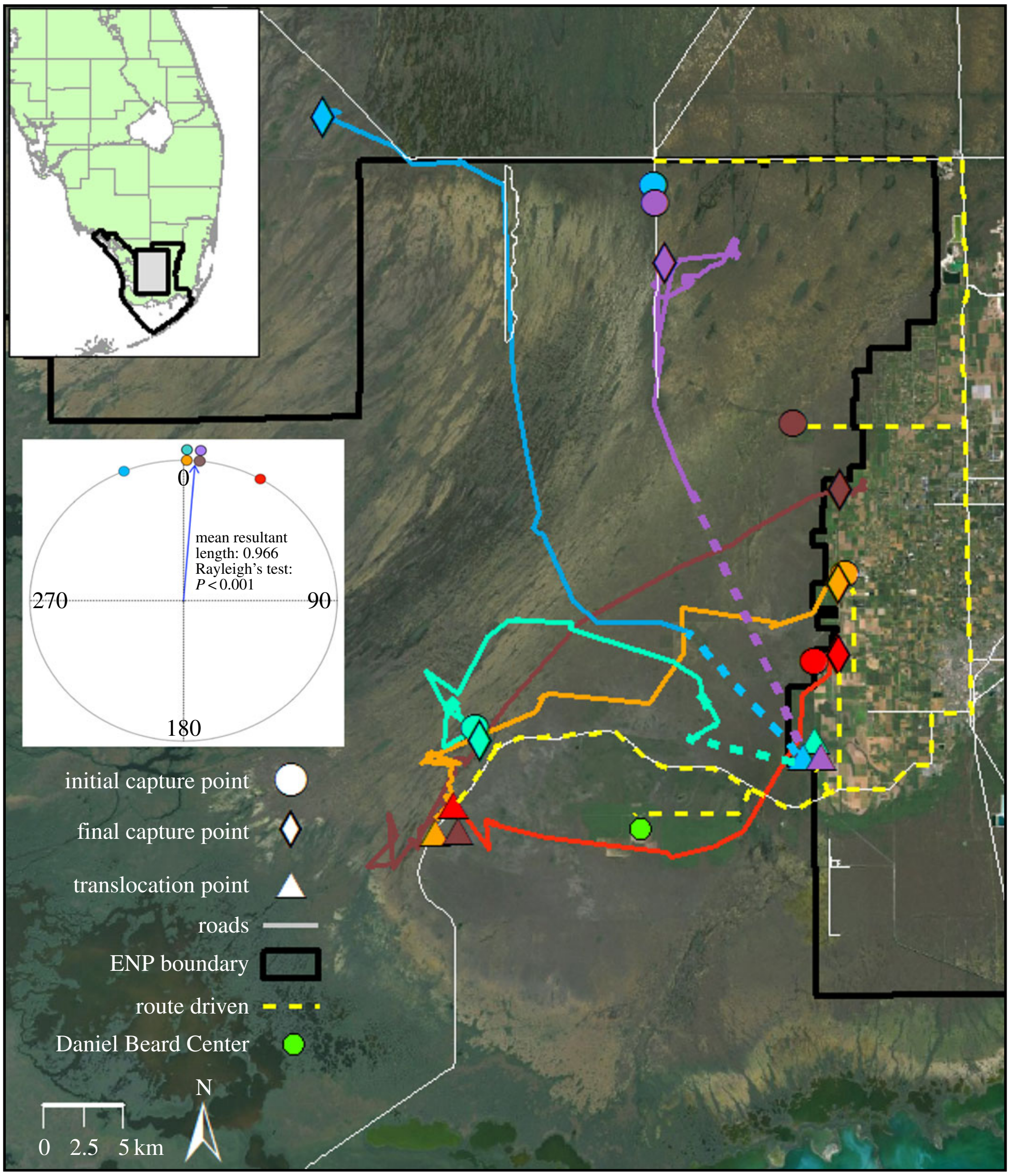

Figure 1. Circular statistics, movement paths, capture locations and final capture locations of six translocated pythons within and near ENP. Long dotted lines indicate the distance between the release location and the first relocation point. Zero degrees correspond to the bearing towards the capture location. Yellow dotted lines indicate roads travelled by researchers to translocate snakes. All snakes were taken to the Daniel Beard Center for radiotransmitter implantation.

Table 1. Summary statistics of movement data from translocated and control snakes. Numbers represent mean (s.d.).

	no. of snakes	speed (m d^{-1})	max. speed (m d^{-1})	orientation efficiency	FD
translocated	6	309 (148)	1755 (492)	0.55 (0.18)	1.09 (0.05)
control	6	108 (31)	498 (264)	−0.26 (0.16)	1.33 (0.09)

may include olfactory and magnetic cues that change predictably through space [3]. The compass step could be accomplished through the use of magnetic, celestial, olfactory or polarized light cues, all of which can generate reliable compasses in reptiles [4]. Future studies focused on determining the sensory systems underlying the map and compass steps of navigation in pythons would be valuable [19,20].

Understanding navigation in invading species improves the ability to control populations and prevent expansion. For example, dispersal behaviour significantly affects the dynamics of invasion fronts [11]. High navigational capacity effectively lowers risk to dispersing individuals (the subadult life stage in Burmese pythons) and may increase the incidence of exploratory movements and the survival of dispersers. The presence of map and compass sense in pythons therefore may influence the survival and behaviour of dispersing subadult pythons, impacting spread dynamics. Navigational ability also affects population dynamics by enabling individuals to exist at high densities even when resources are scarce [21,22]. The combination of density-dependent dispersal and high survival of dispersers may lead to fat-tailed dispersal kernels and accelerating invasion fronts [23].

Snakes have proven to be devastating invaders, and Burmese pythons are high-impact apex predators capable of disrupting food webs where invasive. This study suggests that this species has navigational map and compass senses, a novel finding for a snake species and a potentially crucial component to the invasion dynamics of Burmese pythons and similar species. Future research is warranted into the dynamics of snake invasions that place an emphasis on understanding sensory and navigational capacity to best inform conservation efforts.

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Data accessibility. Data reported are available online in the electronic supplementary material. Data deposited in dryad: http://dx.doi.org/10.5061/dryad.pm136.

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References

1. Nathan R, Getz WM, Revilla E, Holyoak M, Kadmon R, Saltz D, Smouse PE. 2008 A movement ecology paradigm for unifying organismal movement research. *Proc. Natl Acad. Sci. USA* **105**, 19 052–19 059. (doi:10.1073/pnas.0800375105)
2. Gould JL. 1998 Sensory bases of navigation. *Curr. Biol.* **8**, R731–R738. (doi:10.1016/S0960-9822(98)70461-0)
3. Rodda GH, Phillips JB. 1992 Navigational systems develop along similar lines in amphibians, reptiles, and birds. *Ethol. Ecol. Evol.* **4**, 43–51. (doi:10.1080/08927014.1992.9525349)
4. Southwood A, Avens L. 2009 Physiological, behavioral, and ecological aspects of migration in reptiles. *J. Comp. Physiol. B* **180**, 1–23. (doi:10.1007/s00360-009-0415-8)
5. Jacobs LF, Schenk F. 2003 Unpacking the cognitive map: the parallel map theory of hippocampal function. *Psychol. Rev.* **110**, 285–315. (doi:10.1037/0033-295X.110.2.285)
6. Ladage LD, Roth TC, Cerjanic AM, Sinervo B, Pravosudov VV. 2012 Spatial memory: are lizards really deficient? *Biol. Lett.* **8**, 939–941. (doi:10.1098/rsbl.2012.0527)
7. Holding ML, Frazier JA, Taylor EN, Strand CR. 2012 Experimentally altered navigational demands induce changes in the cortical forebrain of free-ranging northern pacific rattlesnakes (*Crotalus o. oreganus*). *Brain Behav. Evol.* **79**, 144–154. (doi:10.1159/000335034)
8. Reinert HK. 1991 Translocation as a conservation strategy for amphibians and reptiles: some comments, concerns, and observations. *Herpetologica* **47**, 357–363.
9. Reinert HK. 1999 Impacts of translocation on the behavior and survival of timber rattlesnakes, *Crotalus horridus*. *J. Herpetol.* **33**, 45–61. (doi:10.2307/1565542)
10. Putman NF, Verley P, Shay TJ, Lohmann KJ. 2012 Simulating transoceanic migrations of young loggerhead sea turtles: merging magnetic navigation behavior with an ocean circulation model. *J. Exp. Biol.* **215**, 1863–1870. (doi:10.1242/jeb.067587)
11. Holway DA, Suarez AV. 1999 Animal behavior: an essential component of invasion biology. *Trends Ecol. Evol.* **14**, 328–330. (doi:10.1016/S0169-5347(99)01636-5)
12. Dorcas ME, Willson JD. 2011 *Invasive pythons in the United States: ecology of an introduced predator*. Athens, GA: University of Georgia Press.
13. Dorcas ME *et al*. 2012 Severe mammal declines coincide with proliferation of invasive Burmese pythons in Everglades National Park. *Proc. Natl Acad. Sci. USA* **109**, 2418–2422. (doi:10.1073/pnas.1115226109)
14. Mazzotti FJ, Cherkiss MS, Hart KM, Snow RW, Rochford MR, Dorcas ME, Reed RN. 2010 Cold-induced mortality of invasive Burmese pythons in south Florida. *Biol. Invasions* **13**, 143–151. (doi:10.1007/s10530-010-9797-5)
15. Batschelet E. 1981 *Circular statistics in biology*. London, UK: Academic Press.
16. Bodin C, Benhamou S, Poulle M-L. 2006 What do European badgers (*Meles meles*) know about the spatial organisation of neighbouring groups? *Behav. Process.* **72**, 84–90. (doi:10.1016/j.beproc.2006.01.001)
17. Nams VO. 2006 Detecting oriented movement of animals. *Anim. Behav.* **72**, 1197–1203. (doi:10.1016/j.anbehav.2006.04.005)
18. Dyer F. 1998 Cognitive ecology of navigation. In *Cognitive ecology: the evolutionary ecology of information processing and decision making* (ed. R Dukas), pp. 201–254. Chicago, IL: University of Chicago Press.
19. Tsoar A, Nathan R, Bartan Y, Vyssotskib A, Dell'Omoc G, Ulanovskyd N. 2011 Large-scale navigational map in a mammal. *Proc. Natl Acad. Sci. USA* **108**, E718–E724. (doi:10.1073/pnas.1107365108)
20. Walcott C. 1996 Pigeon homing: observations, experiments and confusions. *J. Exp. Biol.* **199**, 21–27.
21. Mueller T, Fagan WF. 2008 Search and navigation in dynamic environments: from individual behaviors to population distributions. *Oikos* **117**, 654–664. (doi:10.1111/j.0030-1299.2008.16291.x)
22. Bartoń KA, Hovestadt T, Phillips BL, Travis JMJ. 2012 Risky movement increases the rate of range expansion. *Proc. R. Soc. B* **279**, 1194–1202. (doi:10.1098/rspb.2011.1254)
23. Travis JMJ, Mustin K, Benton TG, Dytham C. 2009 Accelerating invasion rates result from the evolution of density-dependent dispersal. *J. Theor. Biol.* **259**, 151–158. (doi:10.1016/j.jtbi.2009.03.008)