IRCF REPTILES & AMPHIBIANS
CONSERVATION AND NATURAL HISTORY

Diverse Movement Patterns of North America's Eastern Box Turtle (*Terrapene carolina* L.). Part 2: Circuits Across Expansive Habitat

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Photographs by the authors.

Our first two decades of radio-tracking translocated Eastern Box Turtles (*Terrapene carolina*) impressed us with the individuality of their movements. Following release into a sanctuary, we were unable to predict how any particu-

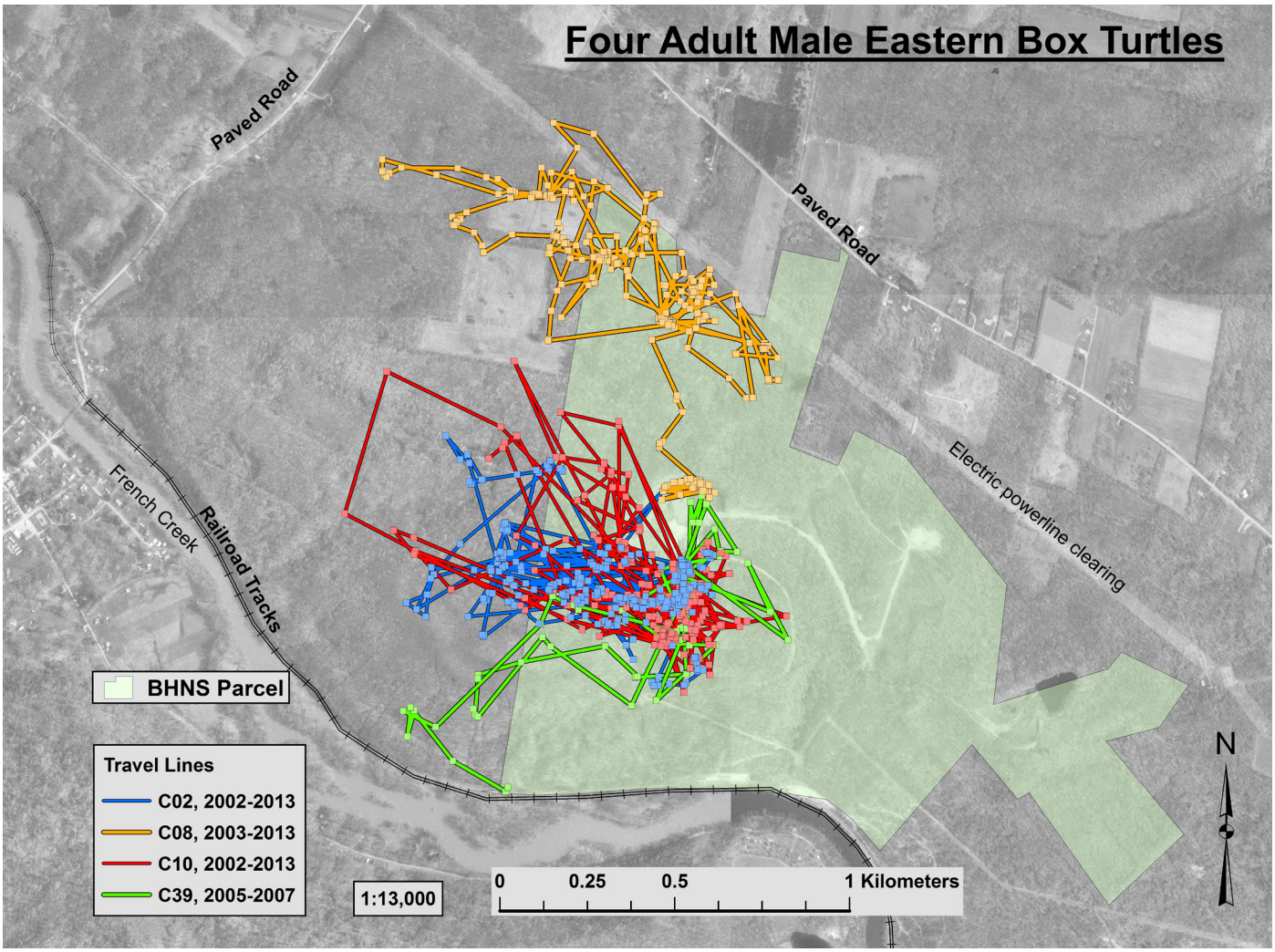

Fig. 1. Overview of multi-year movements by four adult Eastern Box Turtles (C02, C08, C10, C39) that regularly travel outside and inside the sanctuary. Green-shading = extent of sanctuary. 12-year data set for C02 (blue line)= 324 waypoints. 11-year data set for C08 (gold line) = 233 waypoints. 12-year data set for C10 (red line) = 337 waypoints. Three-year data set for C39 (green line) = 63 waypoints. Detailed maps and descriptions for each turtle provided later.

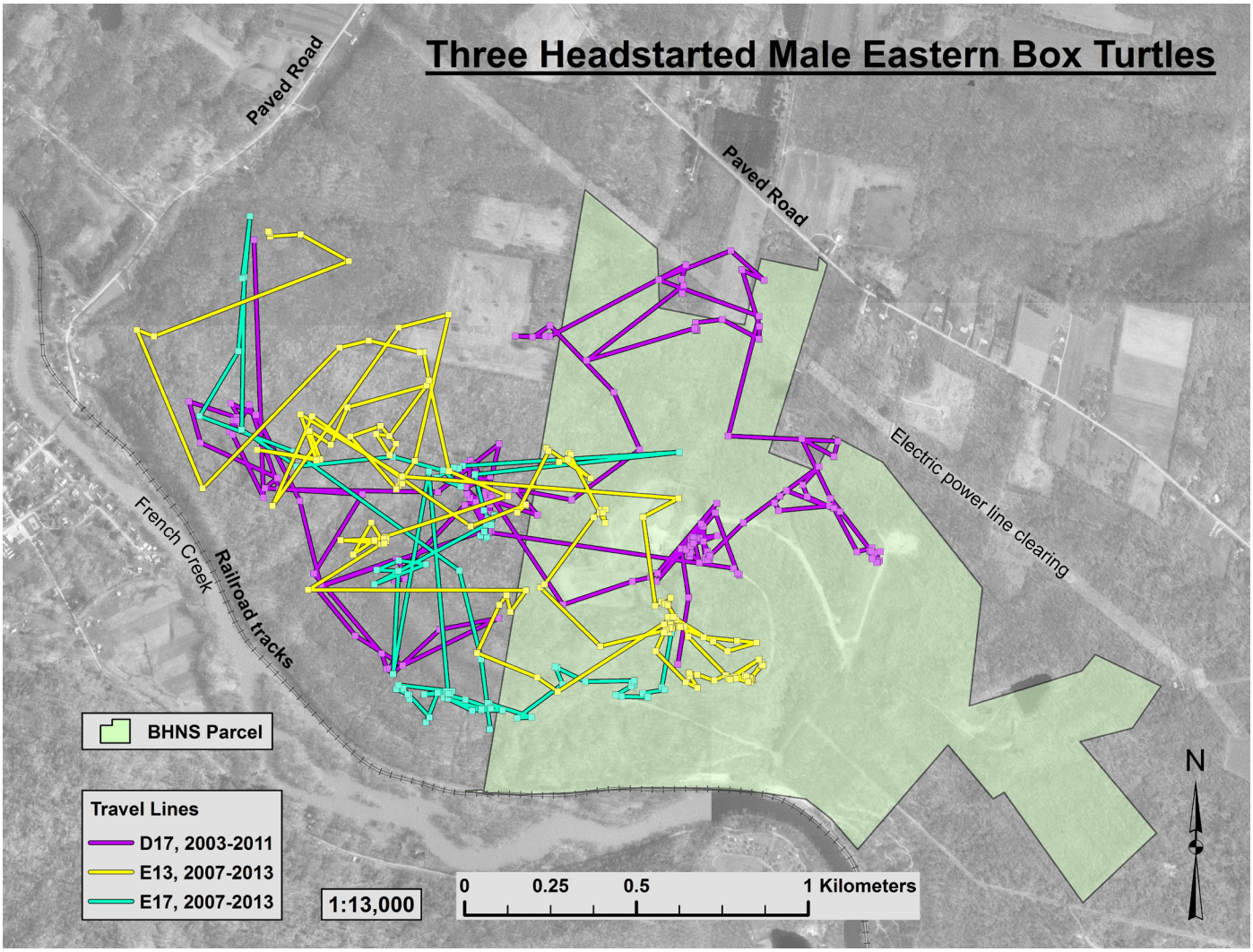

Fig. 2. Overview of multi-year movements by three headstarted Eastern Box Turtles (D17, E13, E17) that regularly travel outside and inside the sanctuary. Green-shading = extent of sanctuary. Nine-year data set for D17 (purple line) = 188 waypoints. Seven-year data set for E13 (yellow line) = 151 waypoints. Five-year data set for E17 (aqua line) = 92 waypoints. Detailed maps and descriptions for each turtle provided later.

lar turtle would use the habitat across time. Literature on *T. carolina* (e.g., Stickel 1989, Dodd 2001), noted in our prior paper on Box Turtle movement (Seibert and Belzer 2013) led us to expect that they would develop rather confined and stable home ranges. We did not anticipate the high variation in movement patterns that unfolded as fieldwork progressed. Some turtles exhibited very high site fidelity for small parcels of habitat, some periodically shifted their home ranges, and others evinced little site fidelity after release. As with movement patterns, habitat preferences also varied. Although our study population consists of translocated and headstarted turtles, unpublished data (cf. Seibert and Belzer 2013) on native Box Turtle populations in other areas manifest similar variations in behavior.

To disclose the heterogeneous movement behavior of *Terrapene carolina*, we began a series of papers to present maps of individual's excursions. This is the second in the series. The inaugural paper (Seibert and Belzer 2013) contrasted turtles that had exhibited (to date) high site fidelity during the entirety (4–9 yrs) of their residence with others that promptly exited the sanctuary. This installment focuses on individuals that range well outside the sanctuary and sporadically re-enter its confines to visit previous areas of transit. An overview of their travels is presented in Figures 1 and 2.

Study Site, Population, and Project Particulars

Buttermilk Hill Nature Sanctuary (BHNS) is the northwestern Pennsylvania (USA) habitat for our primary study population. This Mid-Atlantic site was described (including habitat photographs) in Belzer and Seibert (2009a) and Seibert and Belzer (2013). Briefly, BHNS is a 200-ha sanctuary surrounded by extensive, unfragmented buffer habitat, which combine to provide over 500 ha through which turtles can travel before encountering paved roads on its western, northern, and eastern borders, and railroad tracks skirting a waterway (French Creek) to the south. All turtles in this population had been

Fig. 3. Headstarted male D17 at end of its headstarting phase, age 27 months, 187 g body WT (left); same individual at age 11 years, 410 g body WT (right). Notice the color and pattern changes evident in these photographs; our examination of ontogenetic color-change (*Photo-dependent localized color development in the Eastern Box Turtle carapace*) is available online as a special publication of the Philadelphia Herpetological Society (http://herpetology.com/belzer2/colorintro.htm). Habitat use for D17 plotted in Fig 4. Assembly and procedure for the transmitter mounting seen on this turtle are detailed in Belzer and Seibert 2009b.

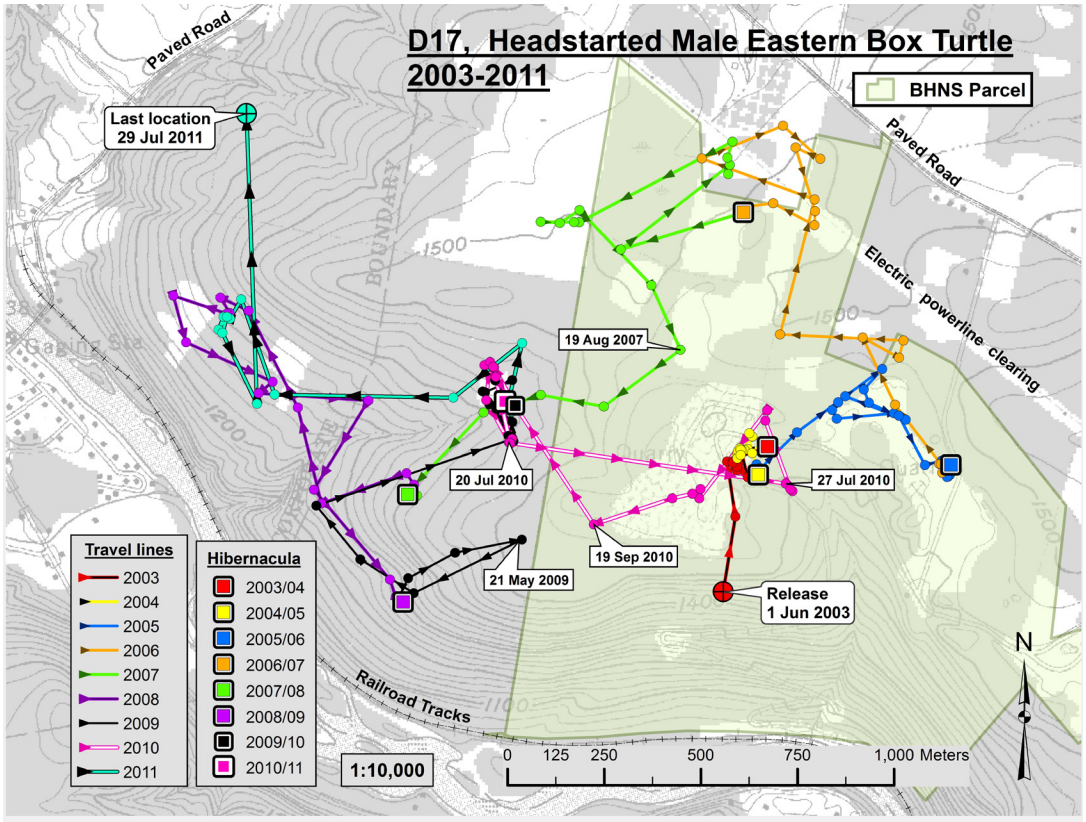

Fig. 4. Nine-year travel history for headstarted male D17. 2003 data set (red line) = 13 waypoints. 2004 data set (yellow line) = 24 waypoints. 2005 data set (blue line) = 23 waypoints. 2006 data set (gold line) = 23 waypoints. 2007 data set (green line) = 22 waypoints. 2008 data set (purple line) = 20 waypoints. 2009 data set (black line) = 24 waypoints. 2010 data set (pink line) = 26 waypoints. 2011 data set, last data before death from *Ranavirus* infection, (aqua line) = 13 waypoints. Green-shading = BHNS parcel.

moved into the BHNS site. Adults are displaced individuals from eradicated or unrecoverable native Pennsylvania habitats. They were donated to our study by licensed Pennsylvania animal rehabilitation and veterinary centers. Headstarted turtles (raised from our population's salvaged eggs; Seibert and Belzer 2013) were released as juveniles (~ 24 months old) that had attained sub-adult size (~250 g). When we began our work, a resident box turtle population was absent at the sanctuary (part of which had sustained early-twentieth-century sand quarrying that was discontinued over 40 years ago). Our headstarting methods, telemetry techniques (AR8000 receiver and Holohil transmitters), geospatial mapping (ArcGIS® software), and turtles are described in Belzer and Seibert (2007, 2009b), and Seibert and Belzer (2013).

Movement Histories

Headstarted turtles.—Figure 4 shows nine years of movement data (188 waypoints) collected for a headstarted male

(D17; Fig. 3) before he died from a *Ranavirus* infection (Belzer and Seibert 2011). During his first two years (2003, 2004) following release at age 27 months (body WT 184 g), D17 confined his habitat use to a small (~ 0.5 ha) area of the sanctuary's interior, only 375 m north of his release site. However, in the third year (2005), his behavior abruptly changed to a pattern in which, almost annually, he made long moves to explore new, far-off areas in disparate directions (see blue track in Fig. 4 for start of these excursions), such that his habitat coverage by the end of nine years had expanded 100 fold compared to his first two years. His travels outside BHNS boundaries were interspersed with returns to the edge or interior of the sanctuary (see green 2007, black 2009, and pink 2010 tracks in Fig. 4).

Fig. 5. Headstarted male E13 at end of headstart stage, age 24 months, 377 g body WT; habitat use for E13 plotted in Fig. 6.

Resembling the travels of D17 are those of two other headstarted males (E13 and E17). Movements for E13 (Fig. 5), starting from his release in 2007 at age 24 months (body WT 373 g), are shown in Fig. 6. Movements for E17 (Fig. 7), shown in Fig. 8, include five and a half seasons of data collected after his release in 2007 at age 24 months (body WT 303 g). Both E13 and E17 explored expansive habitat, but they (like D17) periodically made long treks back into the sanctuary interior to visit areas that they had frequented in previous years. For example, after his return in 2011, E13 spent the next 11 months, September 2011 (end of green track) through August 2012 (start of purple track), near the middle of the sanctuary but then resumed explorations of outlying habitat.

Because the transmitter on E17 detached in June 2010, we have no locations for him for two and a half seasons following the detachment. However, we found him by chance in May 2013, approximately 450 m northeast of his June 2007 release site. Notice how much farther afield he traveled during 2013 (green track, Fig. 8) than during his first four years, corresponding to the tendency exhibited by D17 and E13 for chronological range expansion.

Adults.—C39 (Fig. 9) is an adult male for which we have three continuous seasons (2005–2007) of data. His revisit-

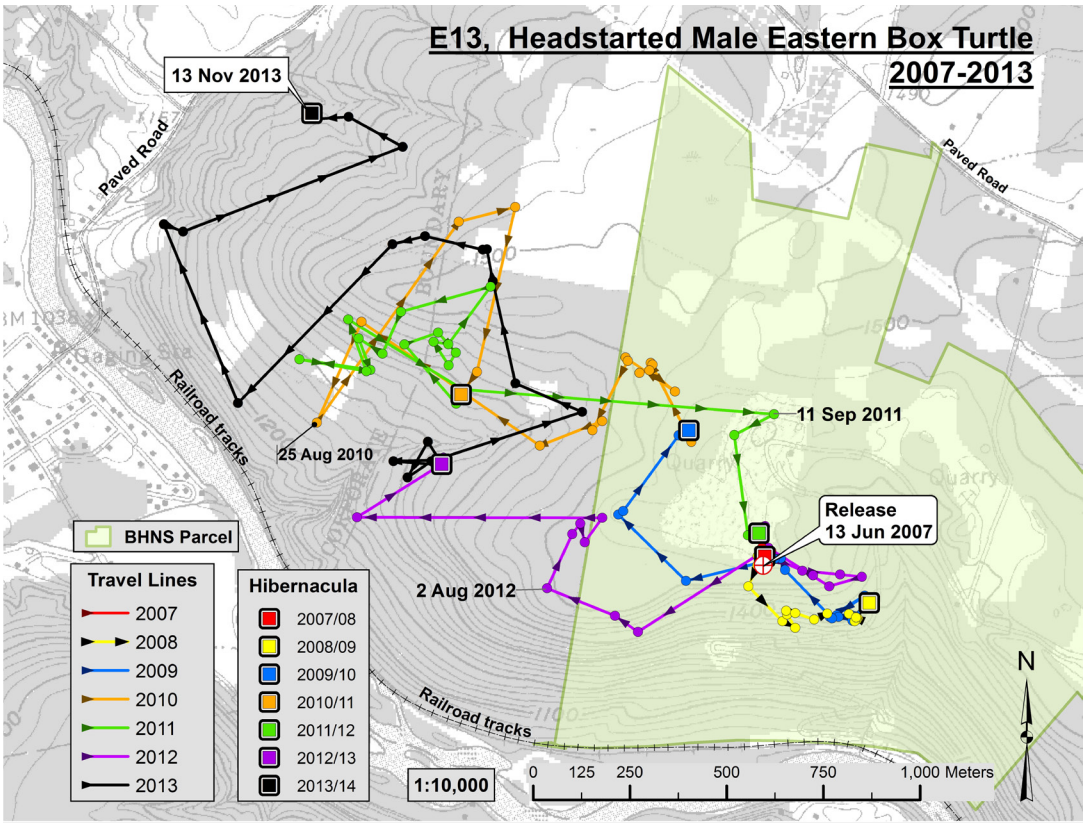

Fig. 6. Seven-year travel history for headstarted male E13. 2007 data set (red line) = 18 waypoints. 2008 data set (yellow line) = 22 waypoints. 2009 data set (blue line) = 20 waypoints. 2010 data set (gold line) = 21 waypoints. 2011 data set (green line) = 24 waypoints. 2012 data set (purple line) = 22 waypoints. 2013 data set (black line) = 24 waypoints. Green-shading = BHNS parcel.

ing the sanctuary interior after periods spent in remote habitat resembles the behavior of the previously described three headstarted turtles. However, in contrast to those three turtles, C39 moved in recurrent circuits. Both of his outbound routes (black and red tracks in Fig. 10) had a southwesterly trajectory before he veered to the south and then turned back toward the sanctuary. On his second (2007) inbound trek, he ventured farther down the southern hillside than during his 2005 return and reached railroad tracks on the floodplain. We therefore moved him into a 1.6-ha holding pen at the sanctuary to preclude his return to that hazard.

The movements by C10 (Figs. 11 & 12) and C02 (Fig. 17 & 18) are somewhat like those of C39, with visits to the sanctuary interior after periods spent in outlying regions. However, as time passed, both C10 and C02 increasingly constrained their movements to habitat nearer to and within the sanctuary. Compare the earlier years for C10 (Figs. 13 & 14) with later years shown in Figs. 15 and 16. For C02, compare his 2002 through 2010 tracks, detailed in Figs. 19, 20, and 21, with his 2012 and 2013 tracks, detailed in Fig. 22. Perhaps C39 also would have consolidated his habitat use had he remained at large for more years.

Our 10 years of data for turtle C08 (Figs. 23 & 24) depict a series of episodic moves from one activity center to another. He spent about a year in each (be aware that a cluster of nearby waypoints show up as one mark in our figures) before moving to the next. During his first three years (2004–2006), the annual shifts to new residence centers took him ever farther outward toward the northwest (Fig. 25, red, yellow, blue lines). In his fourth year (2007), C08 abruptly reversed direction (Fig. 25, gold line) and proceeded back to the region of his 2005 hibernaculum. He occupied various localities scattered across a ~600 m span of that general area (Fig. 26) during the next three years (2007–2009). His final three years (2011–2013) trended southeasterly (Fig. 27), and in June 2013 he reached, for the first time in nine years, a sector less than 350 m from his original release site (cf. marks in Fig. 27 for 18 June 2013 and his 1 August 2004 release).

Fig. 7. Headstarted male E17 at end of headstart stage, age 24 months, 303 g body WT; habitat use for E17 plotted in Fig. 8. E17 is a sibling of E13 from the same July 2005 clutch.

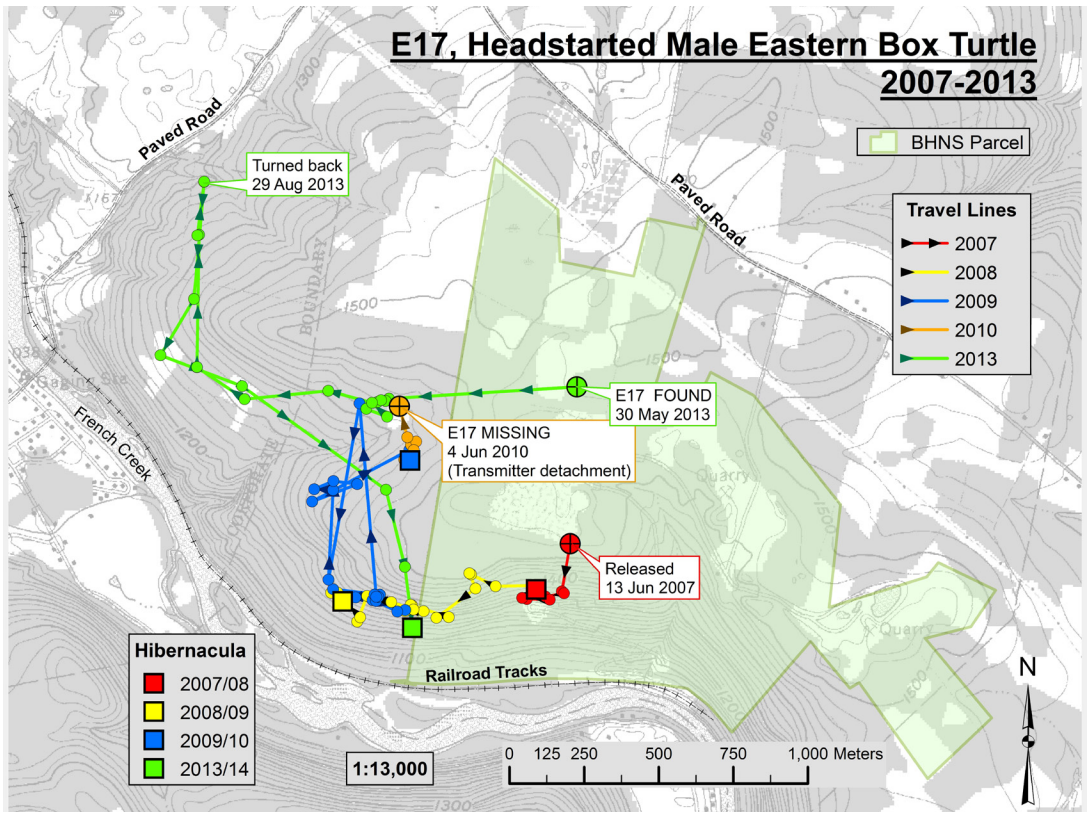

Fig. 8. Five-year travel history for headstarted male E17. 2007 data set (red line) = 9 waypoints. 2008 data set (yellow line) = 22 waypoints. 2009 data set (blue line) = 30 waypoints. 2010 data set (gold line) = 8 waypoints. 2013 data set (green line) = 23 waypoints. Green-shading = BHNS parcel.

The history for C08 differs from those of the other turtles in this paper in its absence, during his explorations of outlying areas, of intermittent returns to the sanctuary core — but by the end of this decade-long circuit, C08 did finally return to an interior site close to where we originally released him.

Discussion

Discrepancies among studies.—Whereas part I of this series (Seibert and Belzer 2013) featured individuals that either settled into a small, stable home range or else straightaway exited our sanctuary, the turtles in this installment illustrate some of the other behavioral variations to which the introductory paper (Seibert and Belzer 2013) alluded. In pondering why earlier literature on the home ranges of Box Turtles (cf. literature survey in Dodd 2001, pp. 64–74) failed to forecast our findings of highly variable behavior, we wondered if those studies had missed some of the excursive conduct we observe because turtle locations had not been determined sufficiently frequently across lengthy time spans. That speculation might be credible. For example, had our methodology not used intensive telemetry but instead employed periodic censuses such as the decennial cycle used for over fifty years at the Patuxent Research Refuge in Maryland (Stickle 1978, 1989; Hall et al. 1999), then some of the late 2004 or early 2005 locations for C08 north of his release site, if selectively compared to his southernmost June 2013 locations (Fig. 27), could have suggested that this turtle had spent the intervening years in a rather small span of habitat near the center of BHNS. When, in fact, examination of all 233 waypoints collected across 10 years shows a very different pattern.

Similarly, locations that we recorded for E17 in 2007 or 2010, if selectively compared with many of his 2013 waypoints, could have suggested a pattern of rather localized habitat use. The complete data set, however, shows his long-term activity to be quite different. Other misleading inferences could be derived with selections of intermittent data for the movements of the other turtles described in this paper.

Fig. 9. Adult male C39 (2007 body WT, 600 g). Habitat use for C39 plotted in Fig. 10. Assembly and procedure for the transmitter mounting seen on this turtle are detailed in Belzer and Seibert 2009b.

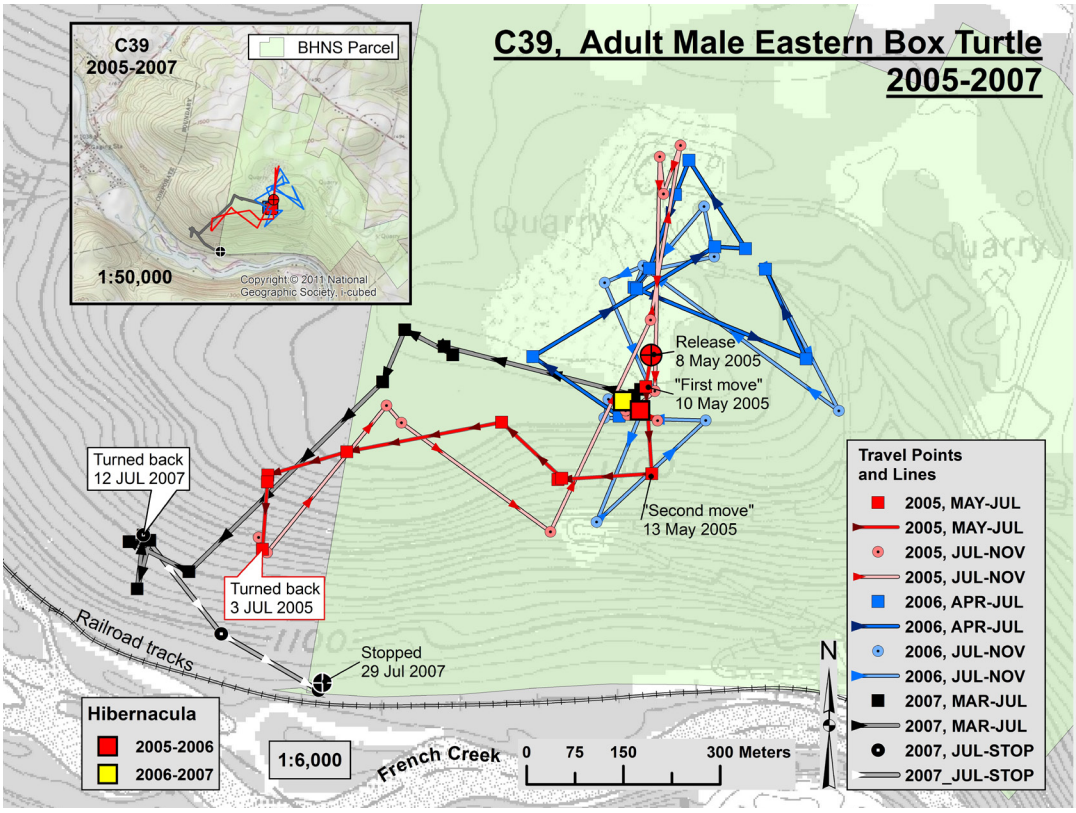

Fig. 10. Three-year travel history for adult male C39. 2005 data set (red line) = 24 waypoints. 2006 data set (blue line) = 24 waypoints. 2007 data set (gray line) = 15 waypoints. Green shading = BHNS parcel; = 2005 release location.

Intermittent or shorter-term data may miss a lot of what a turtle is actually doing. Also, we now know that, even after many years of intensively tracking a turtle, the accumulated data set can fail to predict how that turtle (let alone other turtles) might use available habitat in the future; activity centers may change gradually or abruptly.

Jim Basinger has conducted field studies like ours since 2008. Using intensive tracking techniques to chart the movements of native *T. carolina* in the Blue Ridge Bioregion of Virginia, he is compiling long-term travel histories for individual turtles and posts updated maps along with many other types of data at http://home.ntelos.net/~jbasi/boxturtle.html. Examination of his accumulating array of movement maps reveals much of the same individualistic behavior that we observe in our population of translocated turtles. For example, the travels by turtles M13 and M21 (found by scrolling through Basinger's pages of movement maps) are protracted loops with long axes of more than 2,000 m, surpassing any of the loops we have yet recorded. Such remarkably long circuits cause us to wonder if some of our turtles (discussed in Seibert and Belzer 2013) that exited the sanctuary and its buffer might have eventually returned from their distant excursions had we permitted their travels to continue for more years.

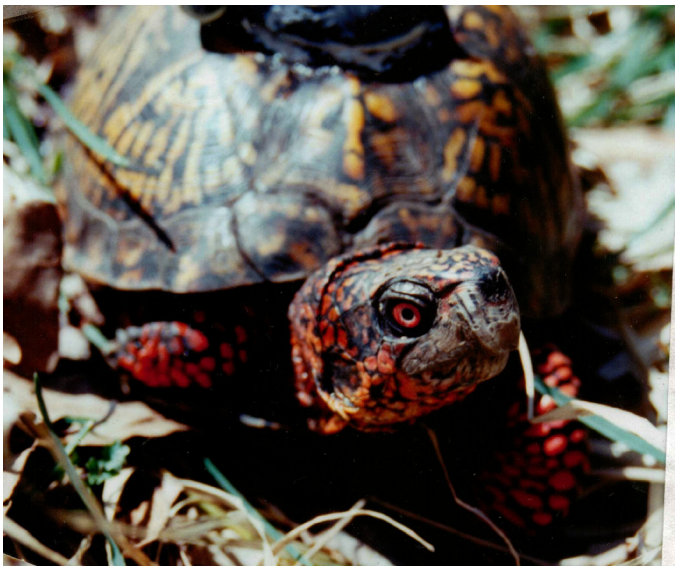

Fig. 11. Adult male C10 (2009 body WT, 650 g). Habitat use for C10 plotted in Fig. 12.

In the observations section (http://home.ntelos.net/~jbasi/Observations.html) of his webpage, Basinger noted that the summaries of box turtle movements available in the published literature do not reflect the variety of travel histories revealed by his telemetry tracking and thread trailing. The diversified patterns of habitat use that Basinger has recorded for native *T. carolina* in Virginia correlate nicely with the unexpected array of travels that we have observed among our translocated box turtles in Pennsylvania. The fact that both of these studies employ intensive tracking across spans of many years probably accounts for the correspondence between our respective findings.

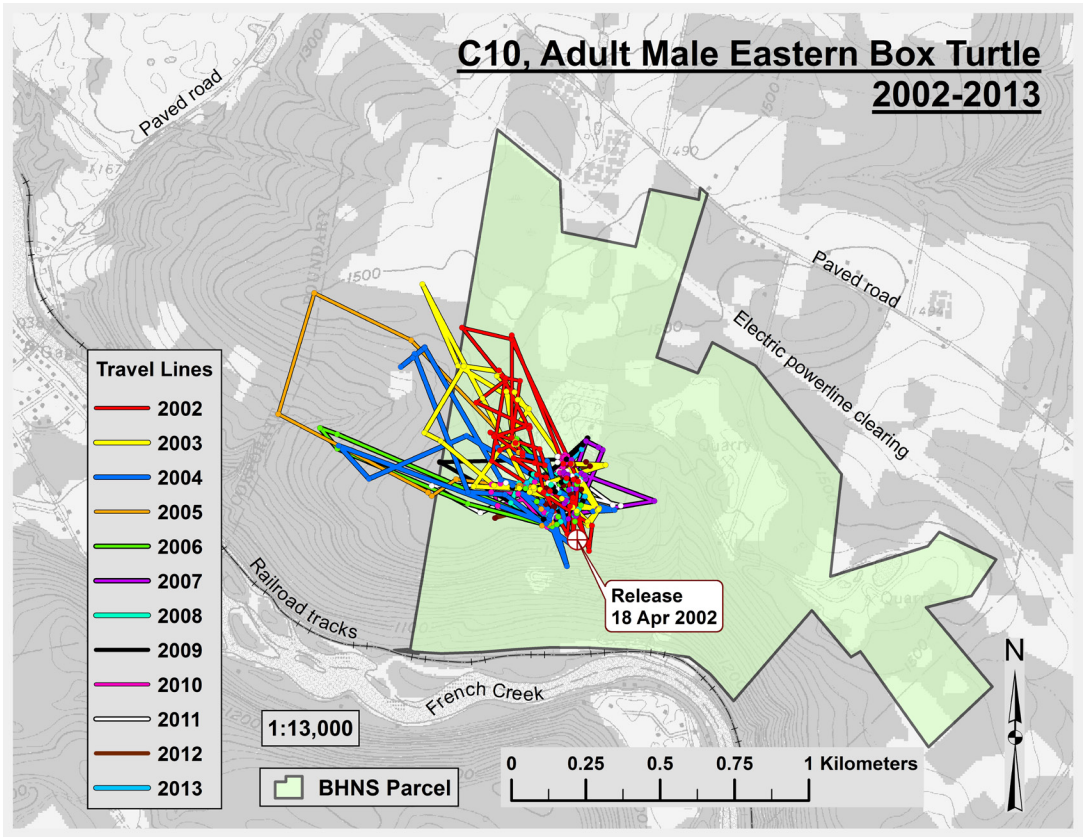

Fig. 12. Twelve-year travel history for adult male C10. Total data set = 337 waypoints. Details found in the enlarged, three-year-increment maps of Figs. 13, 14, 15, and 16. Green-shading = BHNS parcel.

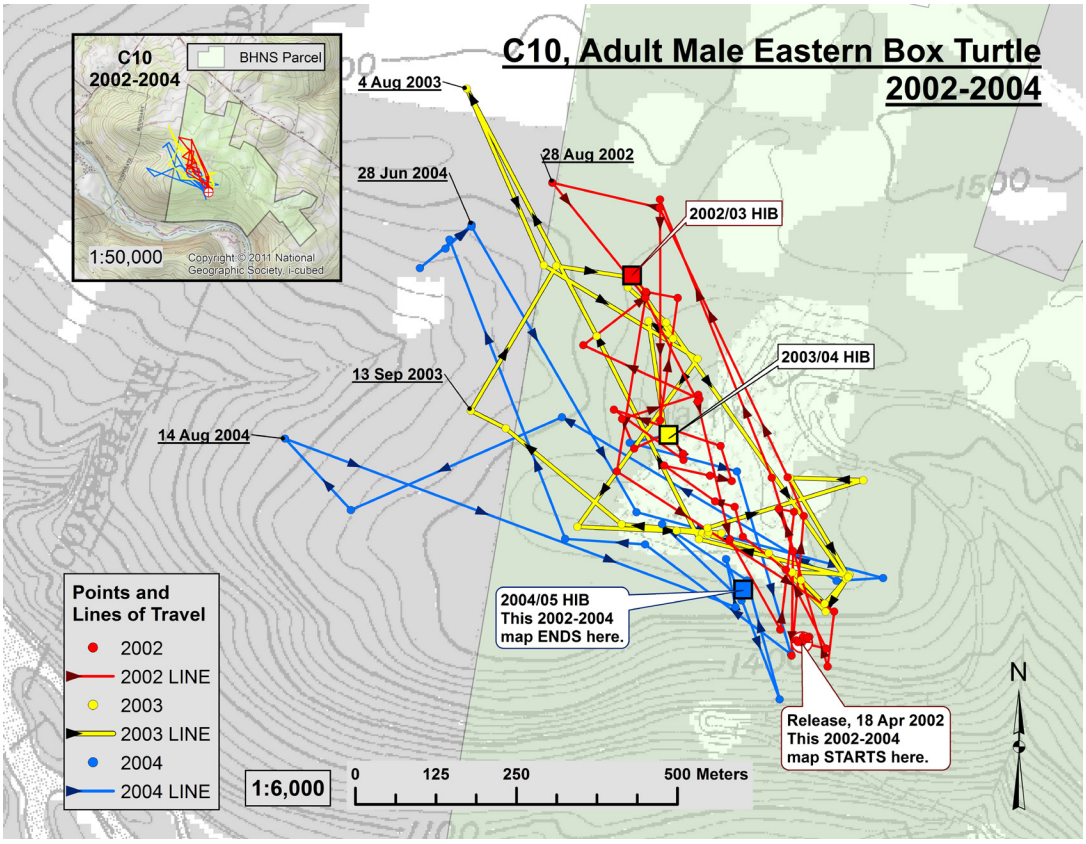

Fig. 13. 2002–2004 travel history for adult male C10. 2002 data set (red line) = 46 waypoints. 2003 data set (yellow line) = 34 waypoints. 2004 data set (blue line) = 25 waypoints. Note annual transits beyond sanctuary boundary. Green shading = BHNS parcel; = 2002 release location.

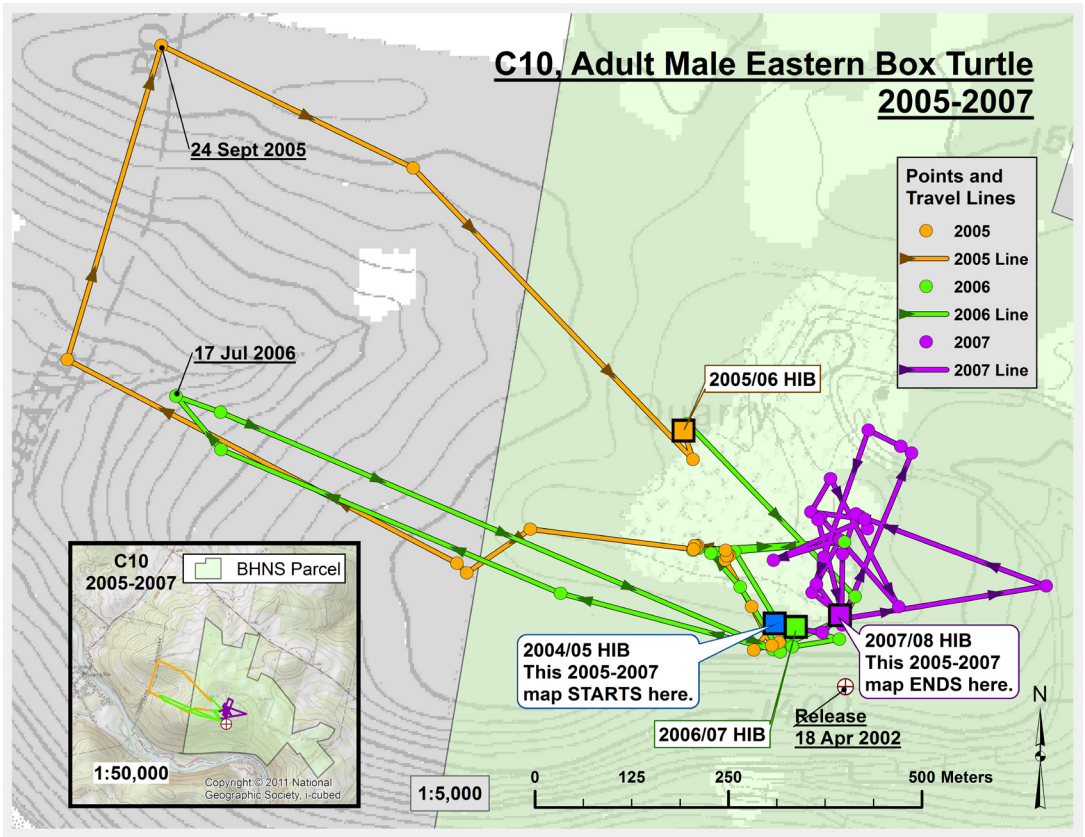

Fig. 14. 2005–2007 travel history for adult male C10. 2005 data set (gold line) = 23 waypoints. 2006 data set (green line) = 20 waypoints. 2007 data set (purple line) = 29 waypoints. Note 2005 and 2006 transits beyond sanctuary boundary. Green shading = BHNS parcel; = 2002 release location.

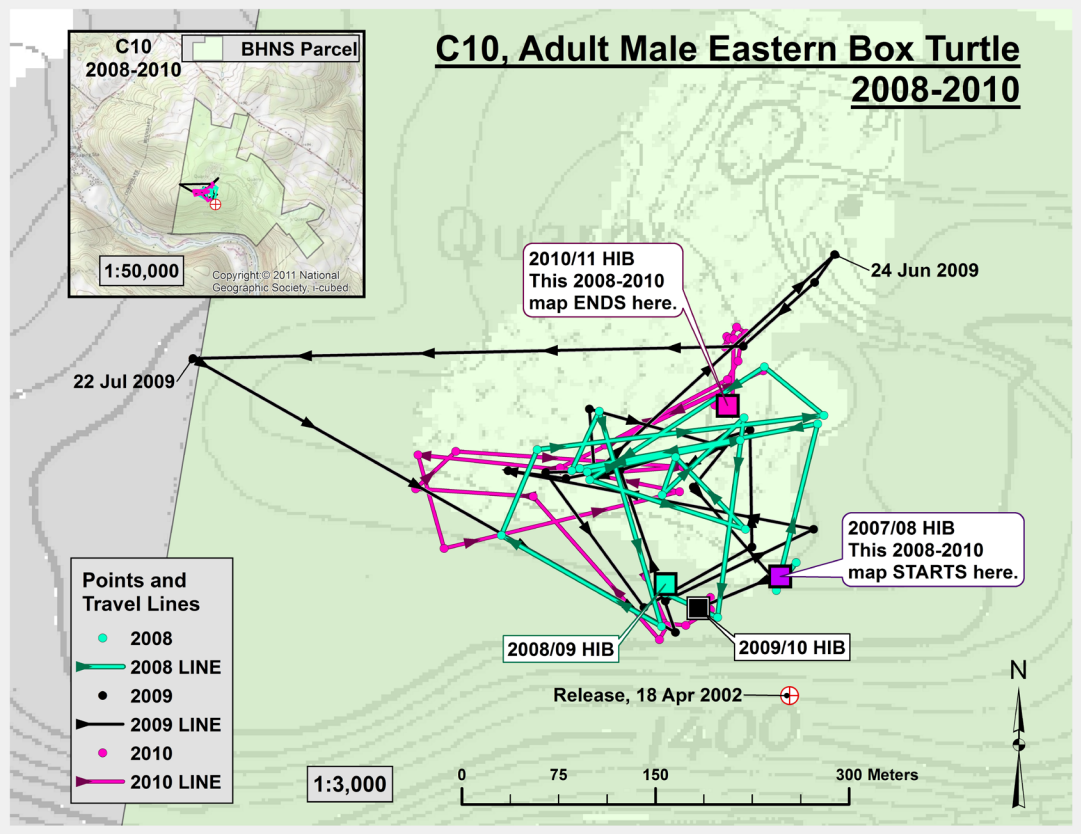

Fig. 15. 2008–2010 travel history for adult male C10. 2008 data set (aqua line) = 24 waypoints. 2009 data set (black line) = 25 waypoints. 2010 data set (pink line) = 30 waypoints. Note preponderance of habitat use confined to sanctuary interior. Green shading = BHNS parcel; = 2002 release location.

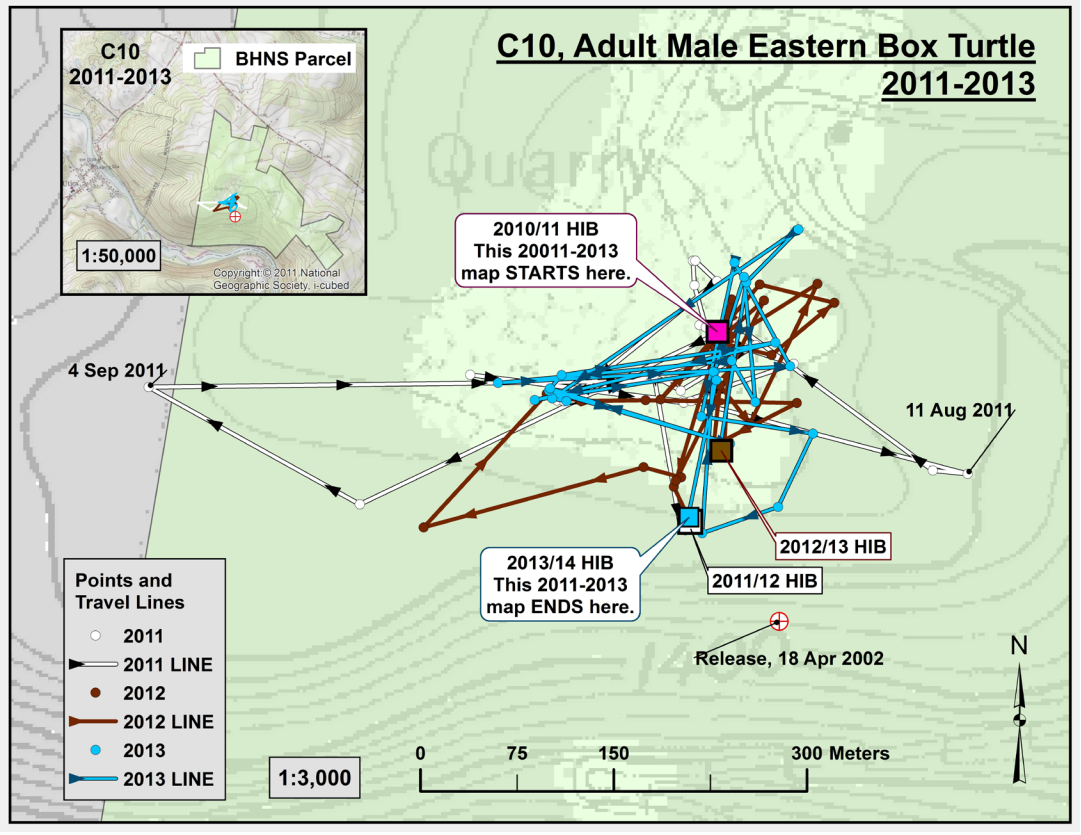

Fig. 16. 2011–2013 travel history for adult male C10. 2011 data set (white line) = 28 waypoints. 2012 data set (brown line) = 26 waypoints. 2013 data set (blue line) = 27 waypoints. Note preponderance of habitat use confined to sanctuary interior. Green shading = BHNS parcel; = 2002 release location.

Winter versus summer site fidelity.—After a 36-month lapse in tracking for E17, the 2013 resumption in his telemetry revealed a sizeable range expansion for this turtle during the lapse. He did return, however, from his most distant recorded 2013 location to spend the winter near the hibernation (metonym often used in turtle literature for brumation) site that he used in 2008 (cf. 2013 green square and 2008 yellow square in Fig. 8). Such a long trek to re-use that southern area suggests some degree of site fidelity. Whether he will use that wintering area again remains to be seen. In a future installment of this series, we will examine hibernation-site fidelity.

Fig. 17. Adult male C02 (2002 body WT, 475 g). Habitat use for C02 plotted in Fig. 18.

That examination will show that, as with summer movement behavior, Box Turtles exhibit considerable variation in hibernacula. Some individuals consistently return to the same site to spend their winters, others re-use several different favored sites, others almost never re-use a former hibernation site, and the pattern for any one turtle might change over time.

Inherent behavioral tendencies?—Speculation on whether an individual Box Turtle has an inherent, idiosyncratic tendency for how it uses accessible habitat is unsound with the current paucity of suitable long-term data. However, we can share our observations on the behavior of a small number of turtles that had been released at two different sanctuaries (Seibert and Belzer 2013). C02, C08, and C10 (along with four other turtles not included in this paper) had previously resided as translocated turtles at a smaller sanctuary, McKeever Environmental Learning Center (McK), located 19 km southwest of BHNS (Seibert and Belzer 2013) for approximately seven years. As noted in Seibert and Belzer (2013), they were evacuated from the McK site because that sanctuary's small size could not accommodate their movements, and were subsequently re-released at the larger BHNS. At both sanctuaries, C02 made longer excursions during his earlier years, generally toward the west. Also, at both sites, as years passed, the range of his excursions decreased, with his movements becoming concentrated nearer the two sanctuaries' cores. Similarly, at both sanctuaries, C10 made more distant excursions during

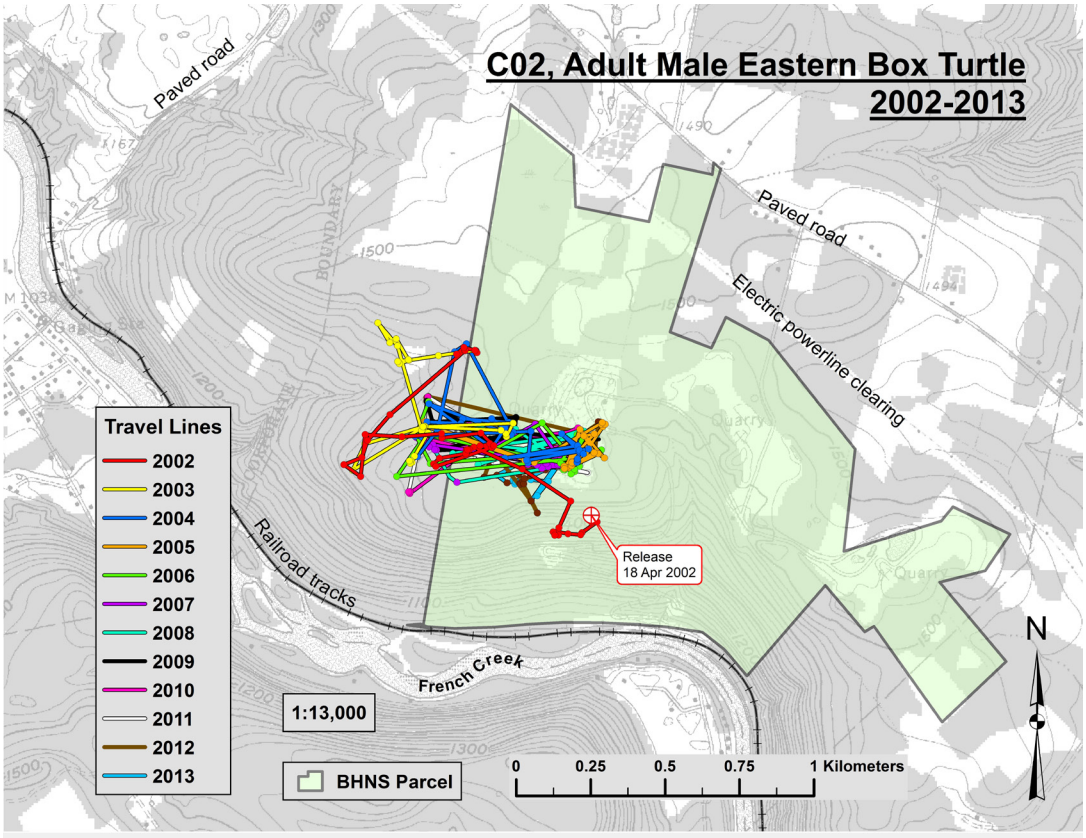

Fig. 18. Twelve-year travel history for adult male C02. Total data set = 324 waypoints. Details found in the enlarged, three-year-increment maps of Figs. 19, 20, 21, and 22. Green shading = BHNS parcel.

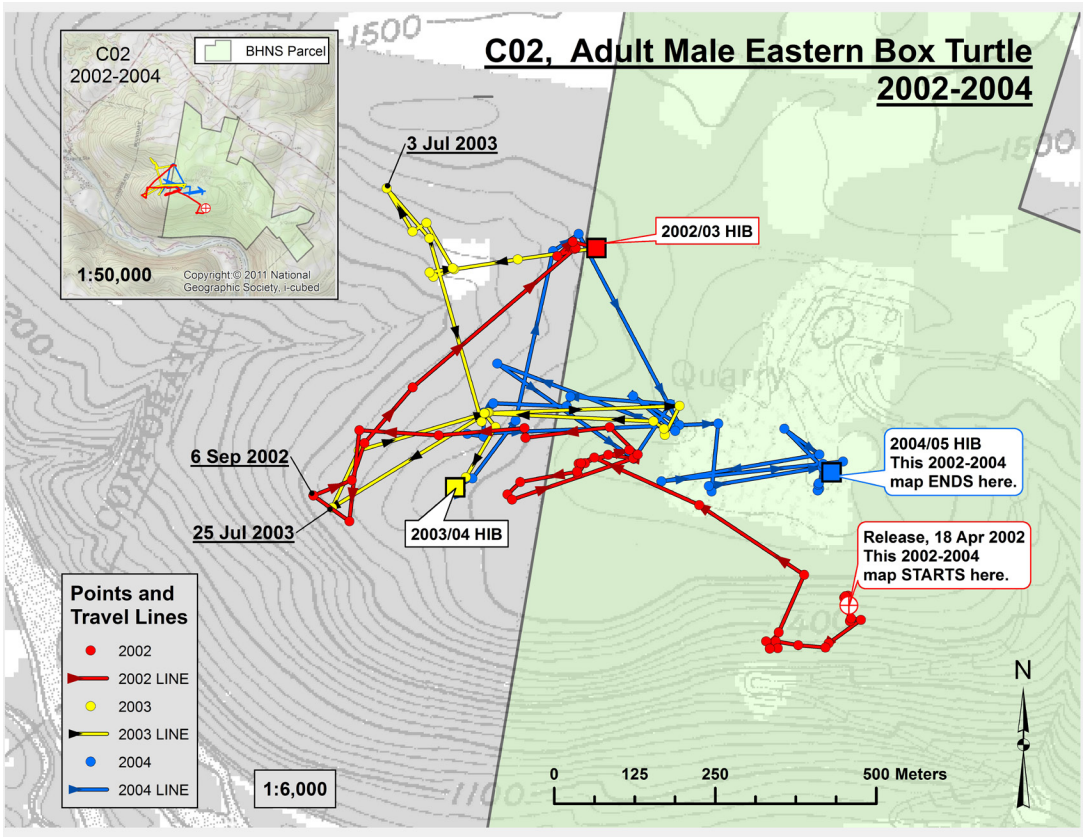

Fig. 19. 2002–2004 travel history for adult male C02. 2002 data set (red line) = 48 waypoints. 2003 data set (yellow line) = 28 waypoints. 2004 data set (blue line) = 29 waypoints. Note annual transits well beyond sanctuary boundary. Green shading = BHNS parcel; = 2002 release location.

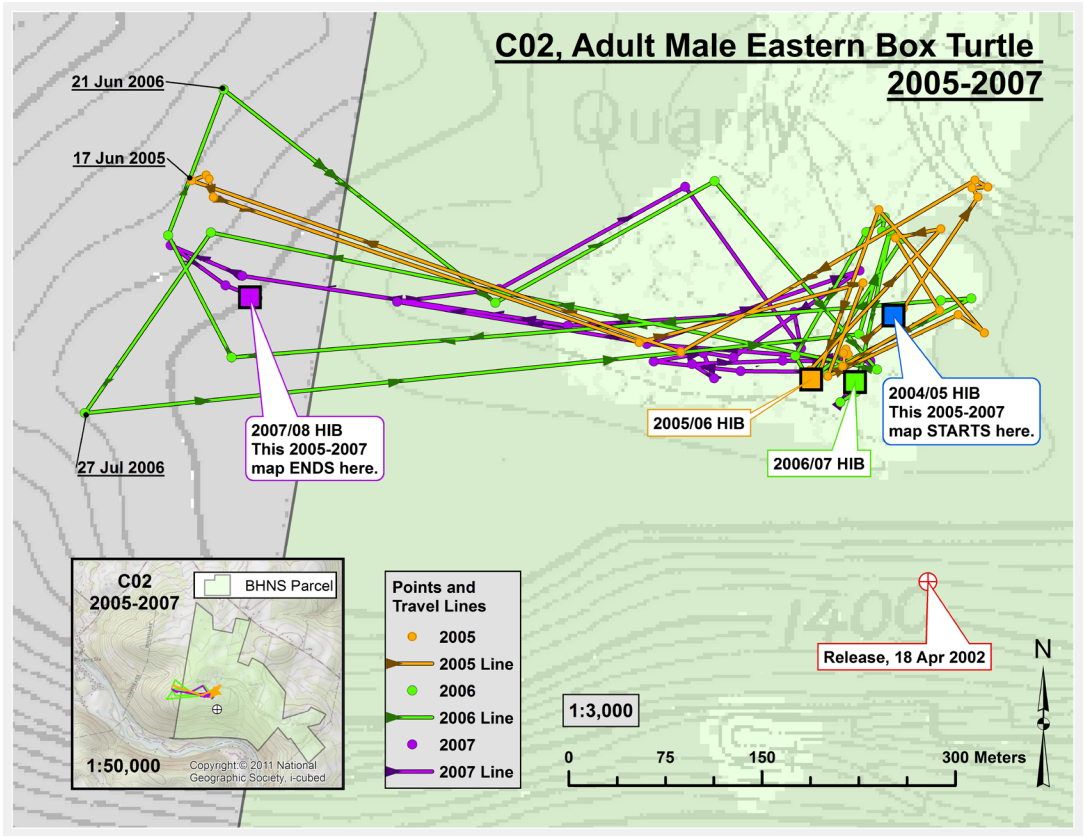

Fig. 20. 2005–2007 travel history for adult male C02. 2005 data set (gold line) = 26 waypoints. 2006 data set (green line) = 22 waypoints. 2007 data set (purple line) = 22 waypoints. Note that annual transits exceed 100 m beyond sanctuary boundary. Green shading = BHNS parcel; = 2002 release location.

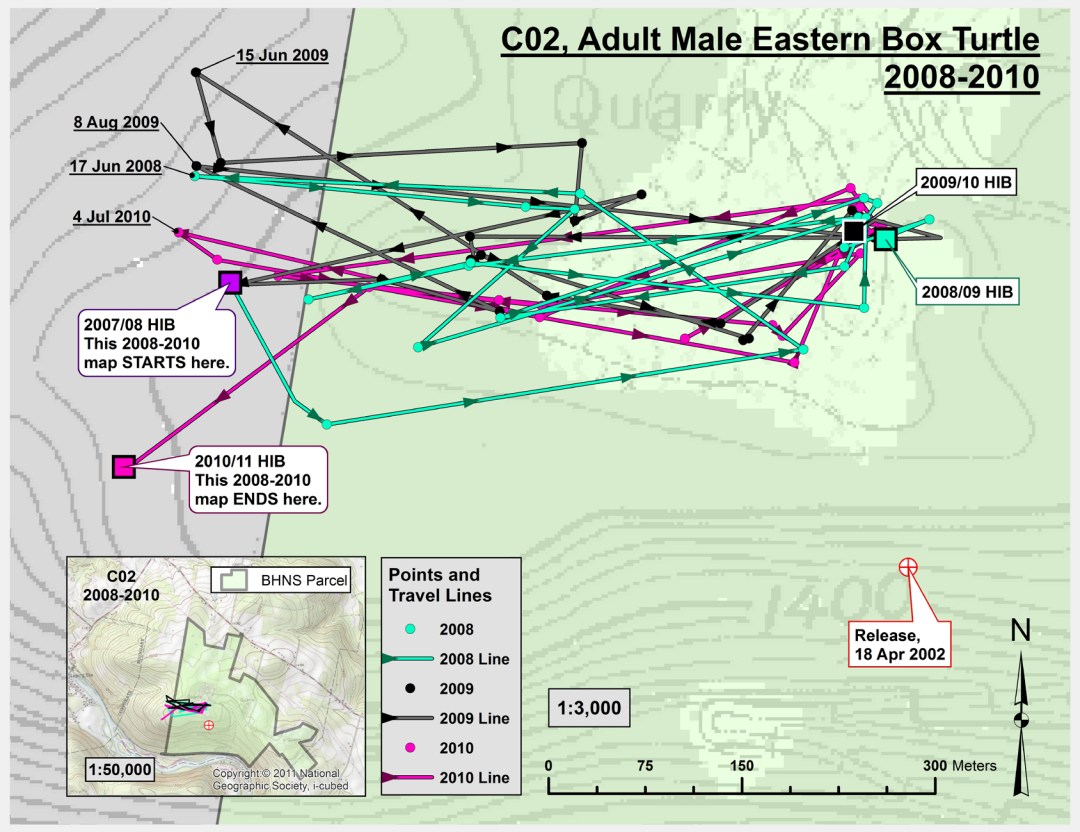

Fig. 21. 2008–2010 travel history for adult male C02. 2008 data set (aqua line) = 23 waypoints. 2009 data set (black line) = 24 waypoints. 2010 data set (pink line) = 25 waypoints. Note preponderance of habitat use shifting toward sanctuary interior. Green shading = BHNS parcel; = 2002 release location.

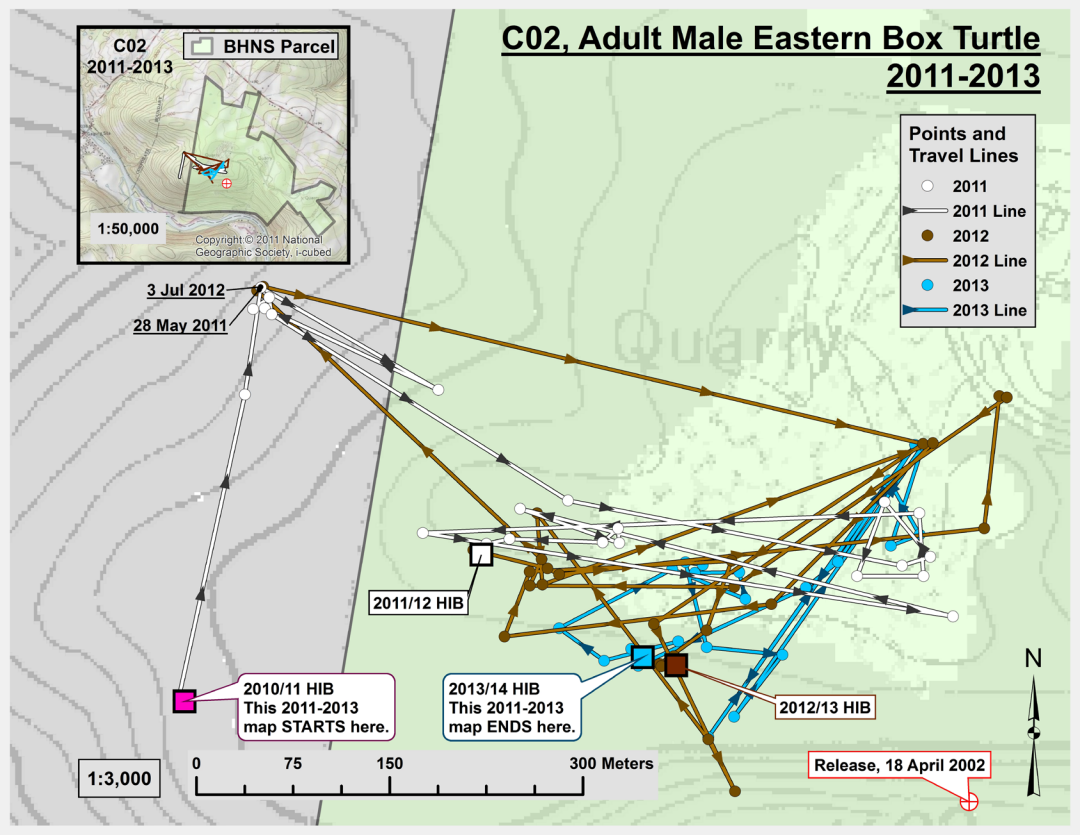

Fig. 22. 2011–2013 travel history for adult male C02. 2011 data set (white line) = 26 waypoints. 2012 data set (brown line) = 27 waypoints. 2013 data set (blue line) = 24 waypoints. Note that the increasingly consolidated habitat use was confined completely within the sanctuary boundary during 2013. Green shading = BHNS parcel; = 2002 release location.

Fig. 23. Adult male C08 (2009 body WT, 520 g). Habitat use for C08 plotted in Fig. 24.

his earlier years but increasingly confined his movements to more central sanctuary regions in later years.

The behavior of C08 displayed some similarity at both sanctuaries in so far as his pattern showed a repetition of protracted residency in a small patch of habitat followed by a long move to adopt a new concentrated activity area. However, his outbound trajectory at McK was toward the northeast and southeast, whereas at BHNS it was toward the northwest. The movements of two other re-released turtles (not included in this paper) bore partial similarities at both sanctuaries, whereas those for two other doubly-released turtles did not.

Male activity penchants?—After selecting turtles that fit the movement criterion for this paper (ranging far afield with episodic revisits to former locations in the sanctuary interior), we noticed that they were all males. Seibert and Belzer (2013) remarked that males seem more prone than females to range farther. The turtles in this paper reinforce that impression.

For those adult males (C02 and C10) that reduced their range over time and began to frequent more central areas

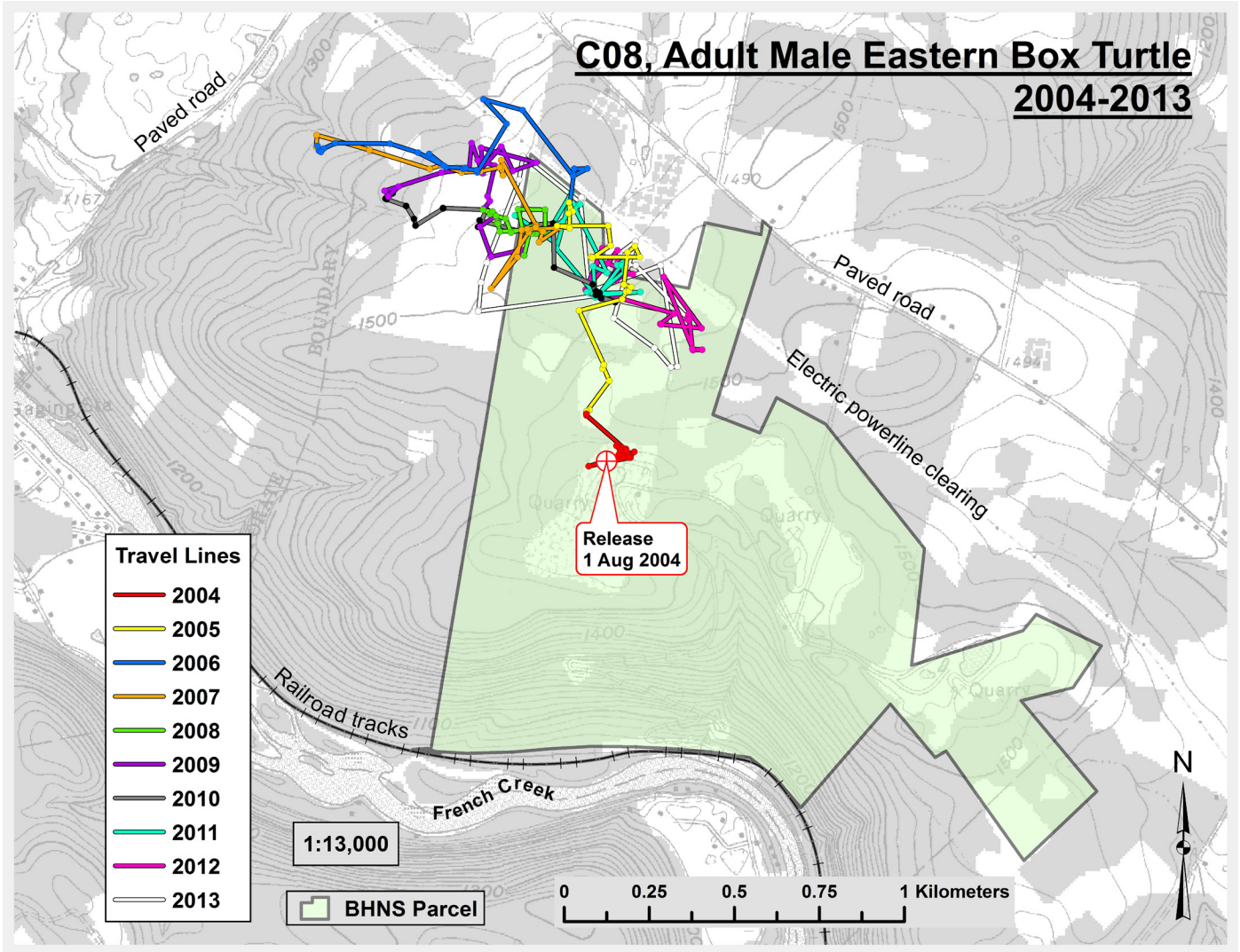

Fig. 24. Ten-year travel history for adult male C08. Total data set = 233 waypoints. Details found in the enlarged, several-year-increment maps of Figs. 25, 26, and 27. Green shading = BHNS parcel.

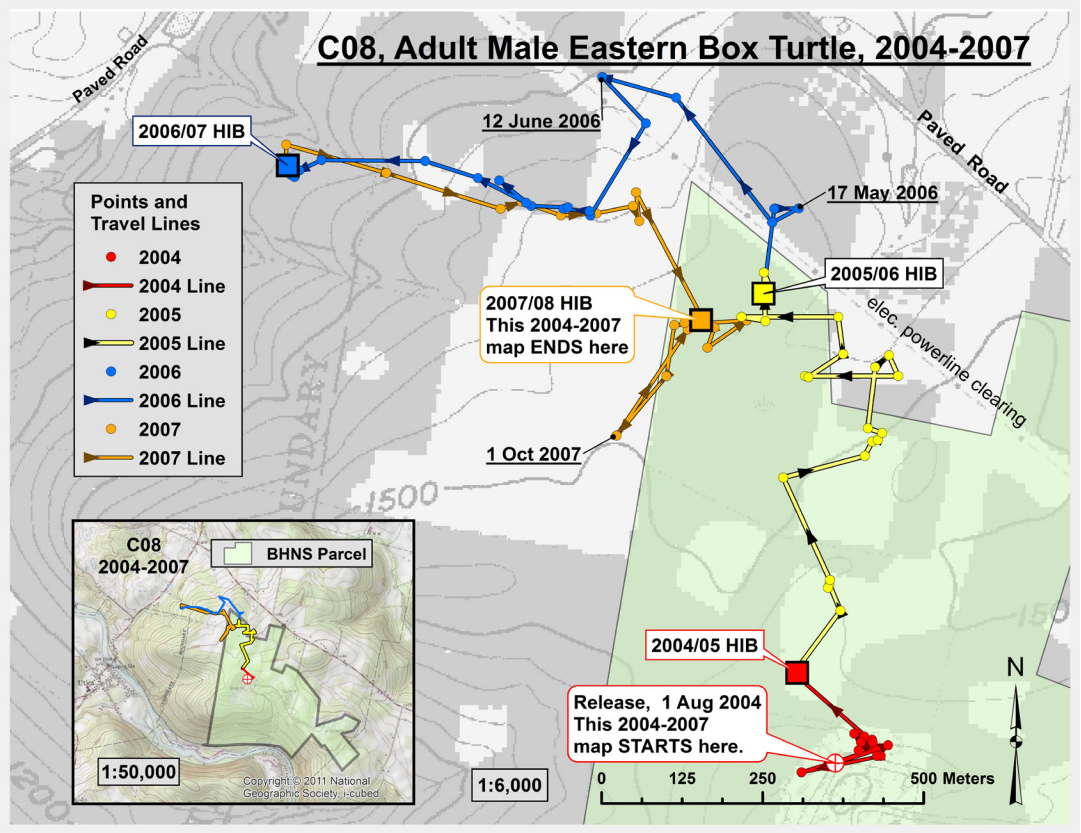

Fig. 25. 2004–2007 travel history for adult male C08. 2004 data set (red line) = 14 waypoints. 2005 data set (yellow line) = 24 waypoints. 2006 data set (blue line) = 20 waypoints. 2007 data set (gold line) = 21 waypoints. Note steady migration to northwest ended with the 2007 reversal of course. Green shading = BHNS parcel; = 2004 release location.

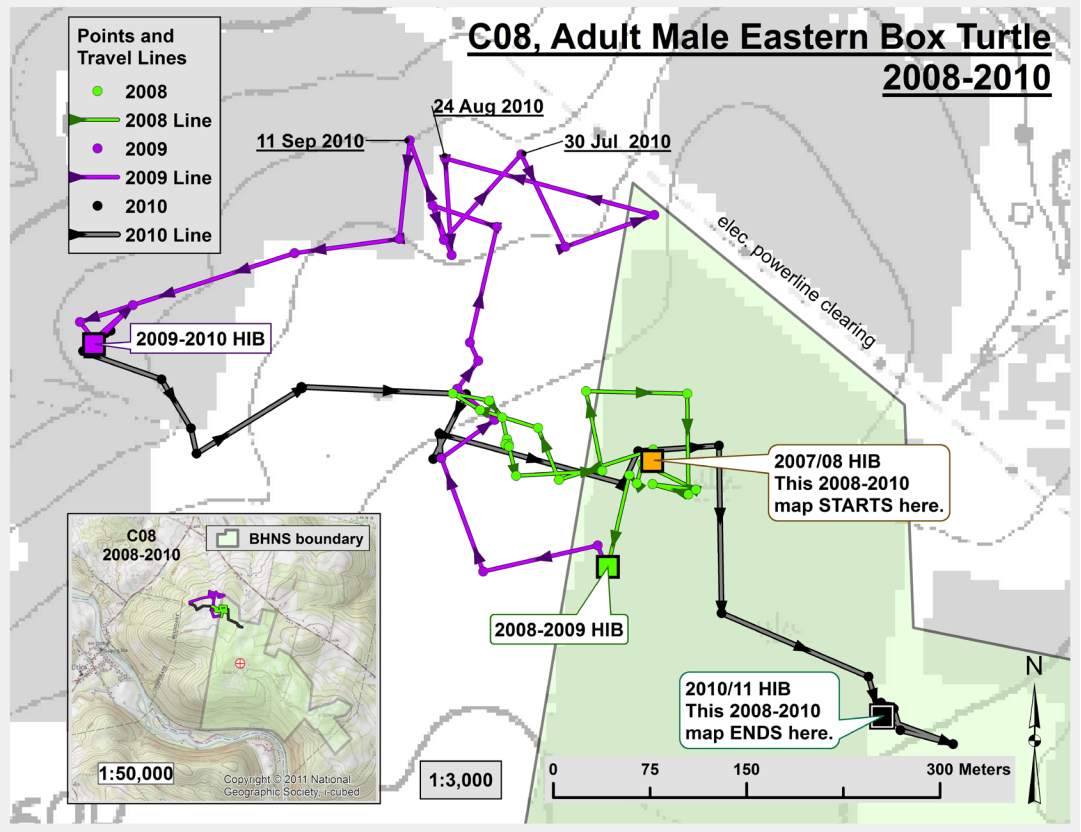

Fig. 26. 2008–2010 travel history for adult male C08. 2008 data set (green line) = 23 waypoints. 2009 data set (purple line) = 23 waypoints. 2010 data set (gray line) = 26 waypoints. Green shading = BHNS parcel; = 2004 release location.

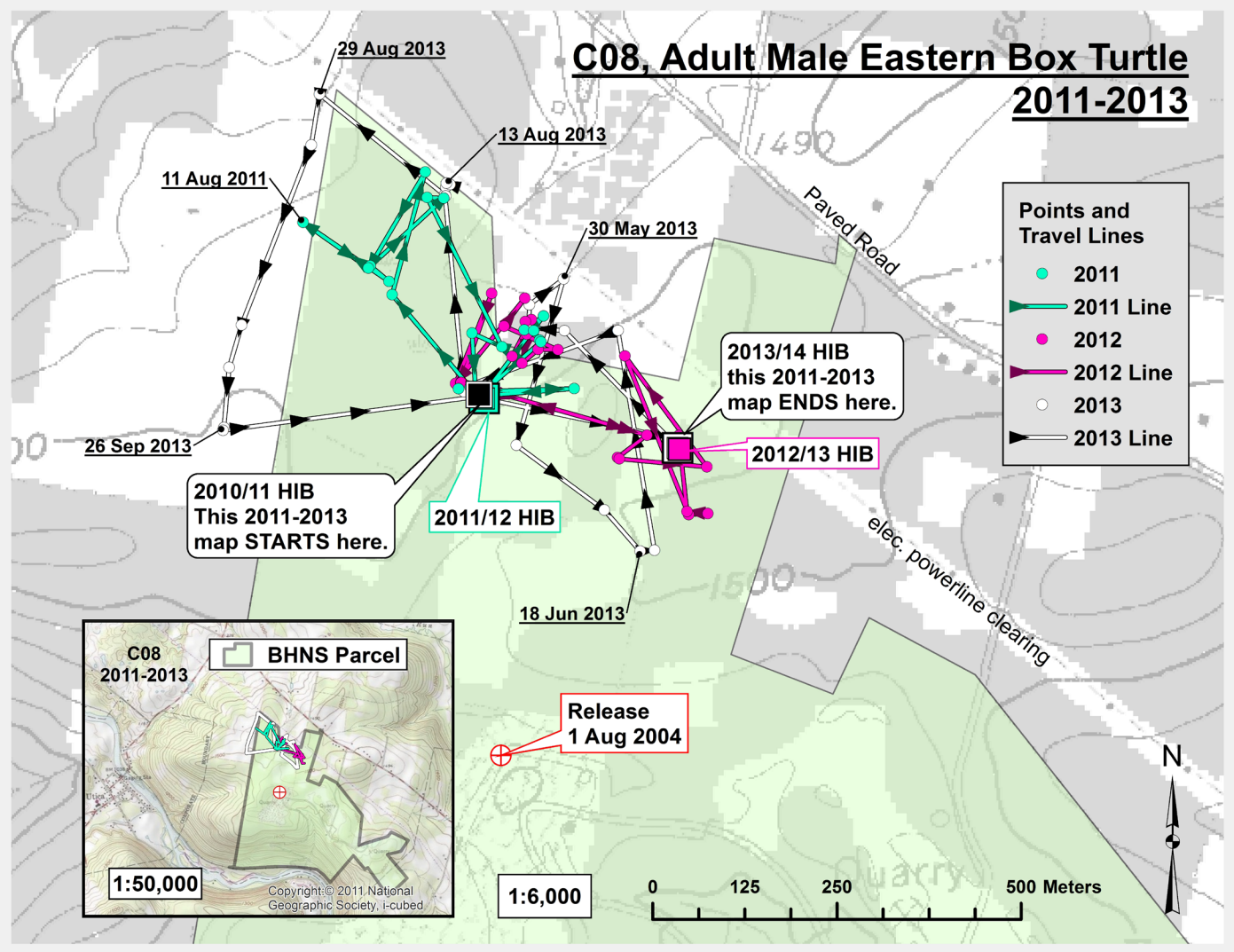

Fig. 27. 2011–2013 travel history for adult male C08. 2011 data set (aqua line) = 27 waypoints. 2012 data set (pink line) = 28 waypoints. 2010 data set (white line) = 27 waypoints. Green shading = BHNS parcel; = 2004 release location.

where encounters with females were more likely, we were tempted to speculate that they had learned where females might be found and so began to limit their movements to such areas. However, our experiments at McK (Belzer 1999), in which far-ranging males were repeatedly carried back to the sanctuary interior and provided with food and mates, failed to engender fidelity for the sanctuary interior. Although the males ate the proffered food and mated with proffered females, they quickly returned to the outlying areas that they had been exploring.

Movements of the turtles featured in this paper might suggest that headstarted male juveniles generally expand their range over time, whereas adult males consolidate theirs. Scrutiny of the turtles examined in Part I of our series (Seibert and Belzer 2013), however, reveals patterns for other adult and headstarted males that contradict such a supposition, underscoring the central contention of this series: Trying to predict or characterize behavior for any population of *Terrapene carolina* is often a misleading exercise owing to appreciable individuality among its members.

Acknowledgements

We are deeply grateful to the owners of the Buttermilk Hill Nature Sanctuary for their ongoing permission and patience during these long-term studies on their property. Without their aegis, we would never have gained the insights on habitat use that are beginning to emerge.

Our open-ended studies are enabled by a special research permit issued in 1993 by the Pennsylvania Fish and Boat Commission (FBC). We provide the FBC with annual updates on our fieldwork in compliance with the permit. We also comply with Guidelines for the Use of Live Reptiles in Field Research (ASIH, HR, and SSAR; http://www.asih.org/files/hacc-final.pdf).

In 2000, the Pennsylvania Department of Conservation and Natural Resources (DCNR) and the GIS Department at Pennsylvania State University provided us Environmental Systems Research Institute (ESRI) ArcView® version 3.1 software and instruction in its use. ArcGIS® version 10.2 software was awarded to SS by an ESRI Environmental Conservation Program grant.

The Bartramian Chapter of the Audubon Society, the Chelonian Research Foundation's EBTCT operational account, the Bebko family at the Pittsburgh Cat Clinic/Hospital, Fred Hillan, the late Jude Holdsworth, Coxsackie Antiques, Edward Pencoske, Hannah and Lisa Toombs, and a Fall 2003 release-time stipend granted to WRB by Clarion University of Pennsylvania provided financial assistance that enabled these studies.

Ben Atkinson, Chris Hammond, Ryan McGarrity, and the late Frank Weiss volunteered valuable field assistance at various times during the past two decades. We also are indebted to many other volunteers for their dedicated and intensive labor in headstarting hatchlings from our salvaged eggs. Although too many to list, we are pleased to acknowledge Erin Lenze, Jeff McFadden, and Vincent Spina, the volunteers who headstarted the three juveniles featured in this article. We thank Jim Basinger and Joseph Lombardi for suggestions that improved early drafts of our manuscript.

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