



# Diverse Movement Patterns of North America's Eastern Box Turtle (*Terrapene carolina* L.). Part 3: Shifts in Residency Fidelity

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Photographs by the authors. All habitat photos taken during May and June 2014

Two decades of radio tracking translocated Eastern Box Turtles (*Terrapene carolina*; taxon revision per Martina et al. 2013) revealed unanticipated individuality of movement patterns. The variety of ambulatory behaviors we have observed exceeded the expectations fostered by earlier studies (e.g., Stickel 1950, 1989; Dodd 2001) on this species. Some of our turtles exhibited the high site fidelity for small parcels of habitat reported for box turtles in seminal studies like Stickel's (1950, 1989), but others periodically shifted their home ranges or displayed almost no site fidelity after release (Seibert and Belzer 2013, 2014). Although our study population consists of translocated and headstarted turtles, movements by native Eastern Box Turtles (unpublished data from Jim Basinger cited in Seibert and Belzer 2013, 2014) residing in Virginia, part of our same (mid-Atlantic) region of North America, resemble what we see in our Pennsylvania study. Long-term travel maps from this native Virginia box turtle population were recently updated and can be viewed at: <http://home.ntelos.net/~jbasi/2014%20Summer.html>.

In order to reveal the behavioral individuality that can be obscured by pooling data, we began a series of papers that would detail the heterogeneity among excursions made by individual turtles across many years. This is the third paper in the series. Our inaugural paper (Seibert and Belzer 2013) contrasted individuals that had exhibited (to date) high site fidelity during the entirety (4–9 yrs) of their residence, with turtles that promptly exited the sanctuary. Part 2 (Seibert and Belzer 2014) focused on individuals that ranged well outside sanctuary boundaries, but occasionally returned to the interior to revisit previous areas of occupancy. This third installment examines individuals who showed remarkable fidelity to very small areas (ca. 0.3–4.5 ha) of habitat for extended periods, but then abruptly moved to settle into a new, confined sector and faithfully remained there for the next series of years.

At the start of our field studies, our expectation was that if a released turtle displayed high site fidelity for a few consecutive years, we could take that behavior as evidence that the turtle had established a home range in which it would indefinitely center its future activity. The long-term behavior of the turtles presented in this paper undercut that expectation.

## Study Site, Population, and Project Particulars

Buttermilk Hill Nature Sanctuary (BHNS) is the northwestern Pennsylvania (USA) habitat for our primary study population. Its 200-ha holdings, surrounded by extensive, unfragmented buffer habitat, combine to provide over 500 ha through which turtles can travel before encountering paved roads on its western, northern, and eastern borders or railroad tracks skirting a waterway (French Creek) on its southern boundary. All turtles in this population had been moved into the BHNS site. The adults (displaced individuals from eradicated or unrecoverable native Pennsylvania habitats) were donated to our study by licensed Pennsylvania animal rehabilitation and veterinary centers. The headstarted turtles were reared from our population's salvaged eggs (Seibert and Belzer 2013) and released as half-grown subadults (~250 g body WT; ~24 months of age). When we began our work, a resident box turtle population was absent at this sanctuary (part of which had sustained early-twentieth-century sand quarrying that was discontinued over 40 years ago).

Our methodologies (including headstarting, telemetry, geospatial mapping, population composition, and study site details) have been described previously in Belzer and Seibert (2007, 2009a, 2009b) and Seibert and Belzer (2013, 2014).

## Movement Histories

**D1.**—This headstarted female (Fig. 1) was released in late August 2002 (body WT 234 g) after 22 months of indoor rearing. Figure 2 shows the movement history (224 way-

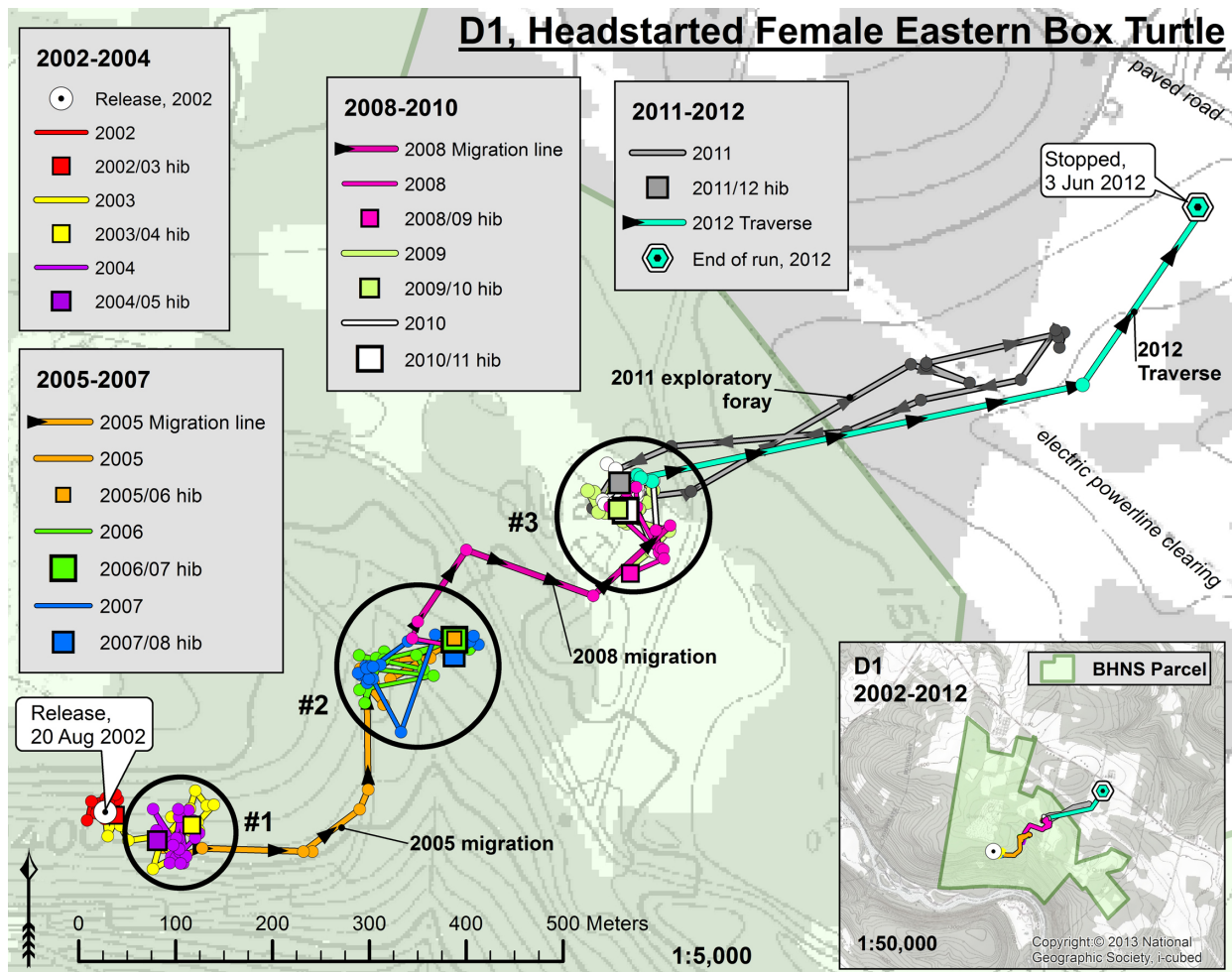


**Fig. 1.** Headstarted female Eastern Box Turtle (*Terrapene carolina*) D1 in 2006, four years after her release.

points) for her first 11 seasons. Note that GPS waypoints are seen as circles on each color-coded travel line. In this (and all other) maps, waypoints that are close to each other may overlap and appear as single circles.

The arrival of cool weather, two months after her release in 2002, prompted D1 to remain (red tracks in Fig. 2) and begin burrowing for brumation (red square in Fig. 2) in the immediate vicinity of her release point (circumpunct in Fig. 2). Upon emerging from hibernation (metonym commonly used for turtle brumation) in 2003, she made a slight (ca. 50 m) easterly move (yellow line in Fig. 2) along a shady hillside trail and then established a confined (ca. 1.5 ha) activity center (Fig. 3). During the next two-and-a-half seasons, our weekly location-determinations never found D1 outside that compact, trail-side area (circle #1 in Fig. 2). Her hibernacula for winters 2003–04 and 2004–05 (yellow and purple squares in Fig. 2) were located within 30 m of each other.

Despite such prolonged site fidelity, D1 vacated the area at the start of summer 2005 and migrated northeasterly (gold



**Fig. 2.** Eleven-season (2002–2012) movement history for headstarted female D1. Total data set = 224 waypoints. Green shading = BHNS sanctuary. Large, numbered circles enclose protracted activity-centers. ○ = release site. □ = hibernation site. Red = 2002 travel (13 waypoints); yellow = 2003 travel (28 waypoints); purple = 2004 travel (25 waypoints); gold = 2005 travel (28 waypoints); green = 2006 travel (17 waypoints); blue = 2007 travel (22 waypoints); pink = 2008 travel (17 waypoints); pale lime = 2009 travel (19 waypoints); white = 2010 travel (23 waypoints); gray = 2011 travel (26 waypoints); aqua = 2012 travel (6 waypoints).



**Fig. 3.** This section of woodland trail on a steep southern slope is the first activity center (circle #1 in Fig. 2) where D1 settled after her release. Dominant trees on the hillside are Sweet Birch (*Betula lenta*), various oaks (*Quercus* spp.), and Red Maple (*Acer rubrum*). D1 periodically moved off the trail to bask on sunny sections along the rim of a precipice out of view to the right.



**Fig. 4.** This roadside/woodland ecotone was the second activity center (circle #2 in Fig. 2) used by D1. The disturbed road swath is dominated by the invasive weed *Artemisia vulgaris*. We consistently found D1 along the eastern edge of the road during spring and summer months throughout her three years at this site. Every fall, she moved into the eastern woodland (upper center), where she dug each winter's hibernaculum at or in close proximity to the same location.

line in Fig. 2). A month later she had settled into a new, sunnier activity center approximately 300 m northeast of her initial abode. This second residence (circle #2 in Fig. 2), like her first, was small (ca. 2 ha). It encompassed an ecotone involving a dirt road with woodland on its eastern edge (Fig. 4). She spent most of her late-spring and summer months near the dry, sunny, eastern edge of the road and her fall, winter, and early-spring months deeper in the eastern woods. D1 restricted her movements (gold, green, and blue tracks in Fig. 2) and hibernacula (gold, green, and blue squares in Fig. 2)



**Fig. 5.** The third activity center used by D1 (circle #3 in Fig. 2) was along this shaded seasonal swamp. The heavy shade was created by a canopy of (in order of abundance) Black Walnut (*Juglans nigra*), Red Maple (*Acer rubrum*), Black Cherry (*Prunus serotina*), and Hazel Alder (*Alnus serrulata*).

to this second site during the three seasons of July 2005–July 2008. She actually used the identical hibernaculum for two of those winters (overlapping gold and green squares).

Then, in summer 2008, she abruptly began another short (ca. 300 m) northeasterly migration (pink line in Fig. 2). By



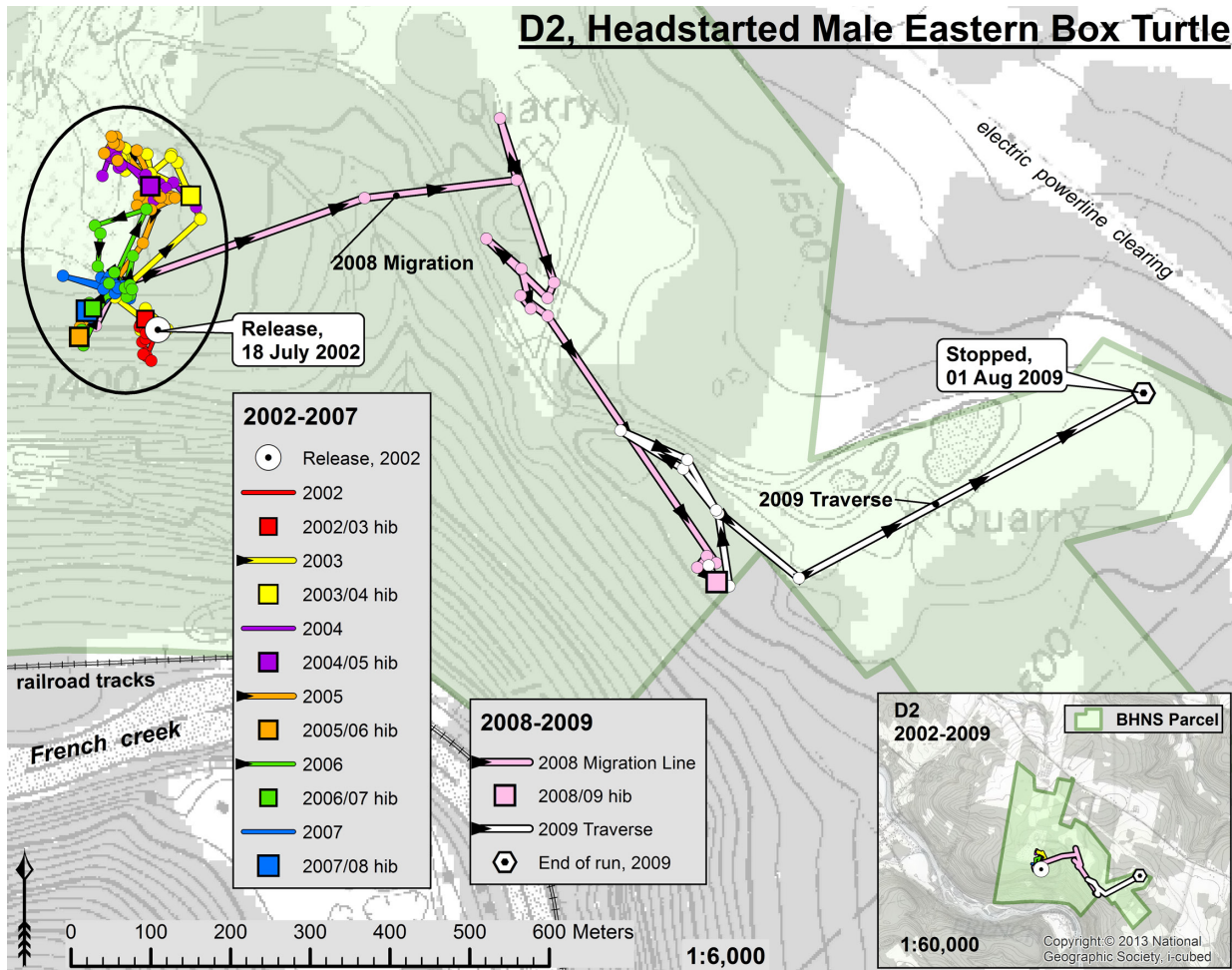
**Fig. 6.** Headstarted male Eastern Box Turtle (*Terrapene carolina*) D2 and sibling of D1 in 2009 when we terminated his outbound movement (hexagon in Fig. 7).

August 2008, she had settled into a third dedicated residence (circle #3 in Fig. 2). This one was a swampy, shaded area (Fig. 5). Like the first two, her third high-fidelity habitation was small (ca. 2.5 ha). She remained at this swampy site for 3.5 seasons (pink, pale lime, white, gray, and aqua tracks in Fig. 2). During May 2011, she initiated a three-month exploratory foray (gray line in Fig. 2) that took her about 600 m to the northeast from her swamp habitat, but she returned by late-August 2011 and brumated near her previous three hibernacula. Note that the 2009 and 2010 hibernacula (overlapping pale-lime and white squares in Fig. 2) are less than 0.5 m apart.

In late May 2012, D1 went back to her 2011 exploration zone, passed through it, and moved still farther to the northeast. This move, through alternating sunny and shaded habitats, lasted longer and was much farther than her 2005 and 2008 location-changes. By June 2012, she was about 900 m northeast of her 2011 hibernaculum, beyond the sanctuary boundary, and closing on a paved road. We interrupted that outbound traverse (aqua hexagon in Fig. 2) and confined her to a 1.6-ha pen (pen materials and construction method

described in Belzer and Seibert 2009a) inside the sanctuary in order to preclude further progress toward paved-road hazards. Consequently, we do not know if she would have established yet a fourth dedicated activity center. However, the 11 seasons of data that we do have reveal a remarkable pattern of sequential high-fidelity small-site occupations, each followed by abandonment and adoption of a new, circumscribed activity center. Notice that each time D1 abandoned a long-occupied residence, we never found her back in the abandoned area again, despite its close proximity to her newly-adopted dwelling.

**D2.**—We released a male sibling (Fig. 6) of D1 from the same (2000) clutch at the end of a 22-month headstart term at body WT 291 g. Figure 7 shows our eight seasons (2002–2009) of movement data for this headstarted male. He spent his first six-and-a-half seasons near his release site (circumpunct in Fig. 7) moving between the southern and northern ends of a circumscribed activity center (enclosed by the ellipse in Fig. 7). The expanse encompassed an area of ca. 4.25 ha, the southern end of which is a shaded hilltop (Figs. 8 and 9)



**Fig. 7.** Eight season (2002–2009) movement history for headstarted male D2. Total data set = 158 waypoints. Green shading = BHNS sanctuary. ⊙ = release site. □ = hibernation site. Red = 2002 travel (14 waypoints); yellow = 2003 travel (25 waypoints); purple = 2004 travel (25 waypoints); gold = 2005 travel (21 waypoints); green = 2006 travel (18 waypoints); blue = 2007 travel (19 waypoints); pink = 2008 travel (16 waypoints); white = 2009 travel (10 waypoints).



**Fig. 8.** This shady, flat-topped knoll is the southern portion of the first activity center (indicated by the ellipse in Fig. 7) for D2. The canopy is almost completely Red Maple (*Acer rubrum*).



**Fig. 9.** Northern aspect of the southern knoll illustrated in Fig. 8 viewed from the northern hollow pictured in Fig. 10.



**Fig. 10.** This is the more northern portion of the first activity center for D2 (indicated by the ellipse in Fig. 7). It is a small, open hollow, featuring numerous windfalls.

and the northern end a sun-exposed windfall valley (Fig. 10). He hibernated in one or the other end of this center all six winters (red, yellow, purple, gold, green, and blue squares in Fig. 7) during his protracted residency.

In June 2008, D2 abandoned this established abode, gradually migrating 750 m southeast where he hibernated in October 2008 (pink square in Fig. 7). In spring 2009, he briefly returned toward his former residence but then reversed course and resumed an outbound trajectory, migrating to the northeast (white traverse in Fig. 7). As he approached a field under cultivation, we collected him and confined him to the sanctuary's 1.6-ha pen (noted above) for safekeeping.

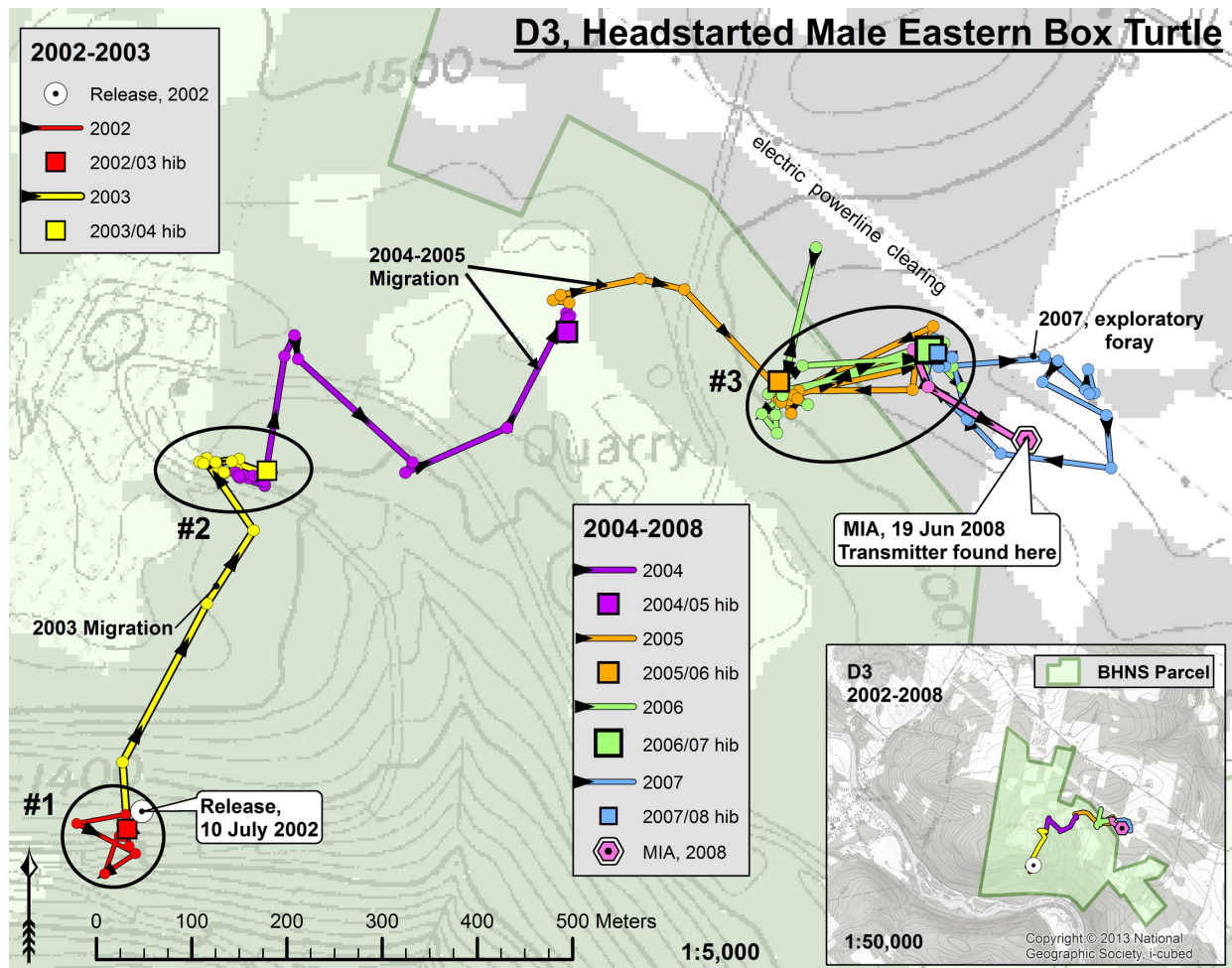
Like D1, D2 displayed high site fidelity for multiple years and then abandoned his steadfast residence. Because we terminated his travels in 2009, we do not know if he would have mirrored the rest of the pattern of D1 and settled into a new, confined, activity center for another extended period.



**Fig. 11.** Headstarted male Eastern Box Turtle (*Terrapene carolina*) D3 in 2002 when we released him following his 22-month headstart term. Compare the paucity of carapace color in this newly released juvenile with the colorful carapaces of older juveniles seen in Figs. 6, 16, and 20. Our study of this color-change phenomenon is accessible at <http://herpetology.com/belzer2/colorintro.htm>.

**D3.**—A headstarted male (Fig. 11) was hatched in 2000. Figure 12 shows his first 6.5 seasons of habitat use (121 waypoints). Following release in July 2002 (body WT 325 g, age 22 months), D3 spent his first year (red track in Fig. 12) and hibernated (red square in Fig. 12) within a small (ca. 0.75 ha) parcel adjacent to his release site (circumpunct in Fig. 12) along the shaded hillside path previously pictured in Fig. 3.

After emerging from hibernation in 2003, D3 abandoned that first abode (area enclosed by circle #1 in Fig. 12) and moved approximately 375 m to the north-northeast (yellow track in Fig. 12) where, for the next 13 months, he inhabited a small (ca. 0.4 ha) portion of sun-exposed meadow (Fig. 13). He departed that second activity center (area enclosed by ellipse #2 in Fig. 12) at the end of July 2004 and began a



**Fig. 12.** Six-and-a-half season (2002–2008) movement history for headstarted male D3. Total data set = 121 waypoints. Green shading = BHNS sanctuary. ○ = release site. □ = hibernation site. Large, numbered circle or ellipse encloses a protracted activity-center. Red = 2002 travel (12 waypoints); yellow = 2003 travel (16 waypoints); purple = 2004 travel (24 waypoints); gold = 2005 travel (21 waypoints); green = 2006 travel (21 waypoints); blue = 2007 travel (22 waypoints); pink = 2008 travel (5 waypoints).

gradual migration to the east-northeast (purple track in Fig. 12) that continued through the 2004 season. He paused in the fall, about 450 m from his 2003–04 hibernaculum, to hibernate (purple square in Fig. 12) in a dappled understory (Fig. 14) for the 2004–05 winter.

After emerging from hibernation in May 2005, D3 resumed his trek (gold track in Fig. 12) and, seven weeks later, settled into a meadow ecotone about 250 m east of the previous winter's hibernaculum. This ecotone became the western border of a third, relatively expansive (ca. 3.5 ha) activity center that he occupied for the next three seasons (ellipse #3 in Fig. 12). This third residence included a sunny meadow (Fig. 15) on its western perimeter and shaded woodland through its eastern extent. D3 hibernated at the western edge of this third site during his first (2005) winter there (gold square in Fig. 12), but then used its eastern end for hibernating during the next two winters (green and blue squares in Fig. 12).

During his protracted occupation of this third habitat, D3 traveled back and forth between its eastern and western ends. In May 2007, he embarked on an exploratory foray

(blue track in Fig. 12) that extended 200 m beyond the site's eastern margin. However, during August he backtracked and in October 2007 burrowed into the same hibernaculum (blue square in Fig. 12) that he had used the previous winter (overlapping green square). In spring 2008, D3 returned to the eastern area (pink track in Fig. 12), which he had explored during the 2007 summer. Our tracking ended there when his transmitter detached (pink hexagon in Fig. 12).

The movement behavior of D3 was similar to that of D1 in its pattern of establishing serial dedicated residences, with each being a relatively short distance from the previous one. Both turtles also have in common the fact that neither was ever found in a previously used activity center after resettling a new one. However, the sojourns by D3 at his first two dwellings lasted little more than one year each (in contrast to the three-year durations exhibited by D1).

**D4.**—This male (Fig. 16) is a sibling from the same clutch as D3; although D4 and D3 were not conceived by the mother that produced D1 and D2, they (like D1 and D2) hatched



**Fig. 13.** This field-woodland ecotone was the second activity center (indicated by ellipse #2 in Fig. 12) used by D3. The tree line is almost entirely Sweet Birch (*Betula lenta*). The first activity center occupied by D3, previous to his move into this second domicile, was a hillside trail approximately 100 m to the west of the view seen in Fig. 3.



**Fig. 14.** This flatland is the dappled understory where D3 hibernated for the winter of 2004–05 (indicated by the purple square in Fig. 12). This site's thin soil is the aftermath of a sand-quarrying operation that ceased approximately 40 years ago. The sparse vegetation is Sweet Birch (*Betula lenta*) and Lowbush Blueberry (*Vaccinium angustifolium*).

in 2000. When released in Aug 2002, following a 24-month headstart term, D4 weighed 300 g. Figure 17 shows 11.5 seasons (Aug 2002–Aug 2011, plus 2013 through 2014) of available movement data (249 waypoints). Location data are missing for the 21 months of Sept 2011–June 2013 due to transmitter detachment. We resumed tracking on 6 July 2013 when we found D4 interacting with one of our telemetered turtles near the 2011 locale where his transmitter had fallen off.

D4 confined his first six-and-a-half seasons (Sept 2002–2008) of activity (ellipse #1 in Fig. 17) to a small (ca. 3 ha) shaded basin (Fig. 18) approximately 150 m north of his release site (circumpunct in Fig. 17). This site is swampy each spring and after heavy rainfall. In late June 2008, D4 initiated



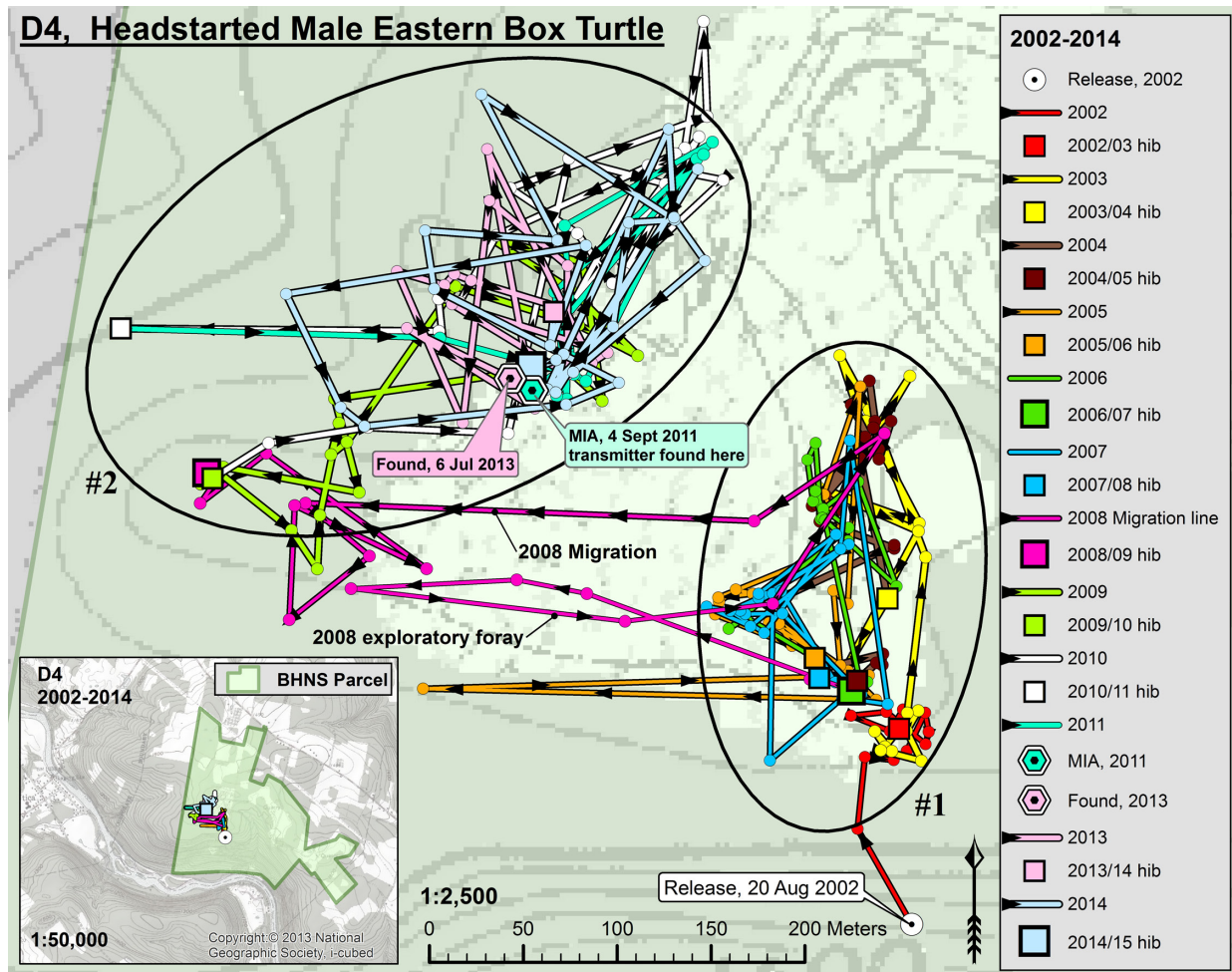
**Fig. 15.** This meadow-woodland ecotone was the third activity center (indicated by ellipse #3 in Fig. 12) used by D3. The meadow in the foreground, at the western end of the activity zone, is dominated by mixed goldenrod species (*Solidago* spp.). The tree line, at the eastern end of the zone, includes Sweet Birch (*Betula lenta*), Red Maple (*Acer rubrum*), mixed oak (*Quercus* spp.), and Black Cherry (*Prunus serotina*).

a westerly foray (lower dark-pink track in Fig. 17) into an adjacent, sunny meadow, returned to his shaded residence in early July, but then abandoned that entrenched habitation in August (upper dark-pink track in Fig. 17). About one week later, he reached the forest/meadow ecotone (Fig. 19) along a ridge located about 170 m to the west and northwest, where he hibernated during the 2008–09 winter (and all winters to date thereafter).

His occupancy of this second, more sun-exposed, site (ellipse #2 in Fig. 17) continues to the present. Since his 2008 move into this ridge-associated ecotone, D4 has never (to date) been observed back at his first abode, despite the close proximity between the two sites (Fig. 17).



**Fig. 16.** Headstarted male Eastern Box Turtle (*Terrapene carolina*) D4 and sibling of D3 in 2013 when his detached telemetry assembly was replaced.



**Fig. 17.** Eleven-and-a-half season (2002–2014, less 2012 telemetry lapse) movement history for headstarted male, D4 (sibling of D3). Total data set = 249 waypoints. Green shading = BHNS sanctuary. ○ = release site. □ = hibernation site. Large, numbered ellipses enclose protracted activity-centers. Red = 2002 travel (13 waypoints); yellow = 2003 travel (28 waypoints); brown = 2004 travel (24 waypoints); gold = 2005 travel (22 waypoints); green = 2006 travel (17 waypoints); blue = 2007 travel (22 waypoints); dark pink = 2008 travel (19 waypoints); light lime = 2009 travel (21 waypoints); white = 2010 travel (24 waypoints); aqua = 2011 travel (15 waypoints); light pink = 2013 travel (18 waypoints); powder blue = 2014 travel (18 waypoints).

The movement history for D4 resembles that of D1 and D3 in its pattern of multi-year, high site fidelity for a restricted area, followed by a shift to a new dedicated residence not far away. However, each tenancy by D4 lasted much longer than those observed for D1 and D3.

**E7.**—Our population’s fifth (to date) individual that has exhibited the distinctive serial-homesite pattern featured in this paper is E7, a headstarted female (Fig. 20). She is maternally unrelated to the previous four (D-series) headstarted turtles. E7 hatched in 2003 and was released in June 2005 at a body WT of 231 g following her 20-month headstarting term. Each of her three protracted activity centers were located along the western extent of the shady foot trail pictured in habitat Fig. 3. This western section of the trail (more so than the eastern section that D1 occupied earlier in the decade) is more prone to retain short-term puddles following rain storms. Figure 21 provides the map of her first seven-

and-a-half seasons of movement (159 waypoints) at the sanctuary.

By July 2005, three weeks after her release, E7 had settled into a small area (enclosed by circle #1 in Fig. 21) approximately 150 m southwest of her release site (circumpunct in Fig. 21). She remained within that expanse (ca. 0.3 ha) for the remaining four months of the 2005 activity season (latter portion of red track in Fig. 21), hibernated there for the winter of 2005–06, and continued to occupy it for the first half of the 2006 activity season (initial yellow track in Fig. 21).

During August of 2006, E7 moved west-southwest (yellow track in Fig. 21), following or paralleling the foot trail. By mid-September, she had settled into a new activity center (enclosed by circle #2 in Fig. 21) approximately 275 m from her first site. She occupied that second locale (ca. 1.25 ha) for the next 45 months (yellow, purple, gold, green, and first blue waypoints; Fig. 21) and hibernated within it all four winters (2006–07 through 2009–10).





**Fig. 18.** This shady basin is the first activity center (indicated by ellipse #1 in Fig. 17) used by D4. The reduced insolation of the basin floor is produced by a topographical elevation on its eastern and southern sides, and a canopy dominated by Red Maple (*Acer rubrum*) and Sweet Birch (*Betula lenta*).



**Fig. 19.** This ecotone is the second activity center (indicated by ellipse #2 in Fig. 17) occupied by D4. It consists of an intermittently swampy sedge meadow in the foreground (a closer view of the swamp is provided in Fig. 6 of Seibert and Belzer 2013), a dry slope dominated by mixed golden-rod (*Solidago* spp.), and mixed hardwoods (*Betula lenta*, *Acer* spp., *Quercus* spp., *Populus tremuloides*) along the hilltop.

In July 2010, E7 departed her second activity center and shifted farther to the west-southwest (blue track in Fig. 21), still moving along (or parallel to) the hillside foot trail. By the start of August 2010, she had adopted a third abode (enclosed by ellipse #3 in Fig. 21) and occupied this new location (ca. 0.5 ha) for the next 21 months. E7 temporarily left the area to explore habitat 150 m farther to the west-southwest during the 2011 season (pink track in Fig. 21), but returned in the fall of 2011 to hibernate about 65 m south of her 2010 hibernaculum.

After emerging from hibernation, E7 initiated a westward move (brown track in Fig. 21) during late May 2012 and



**Fig. 20.** Headstarted female Eastern Box Turtle (*Terrapene carolina*) E7 in 2012 when we terminated her outbound movements (brown hexagon in Fig. 21).

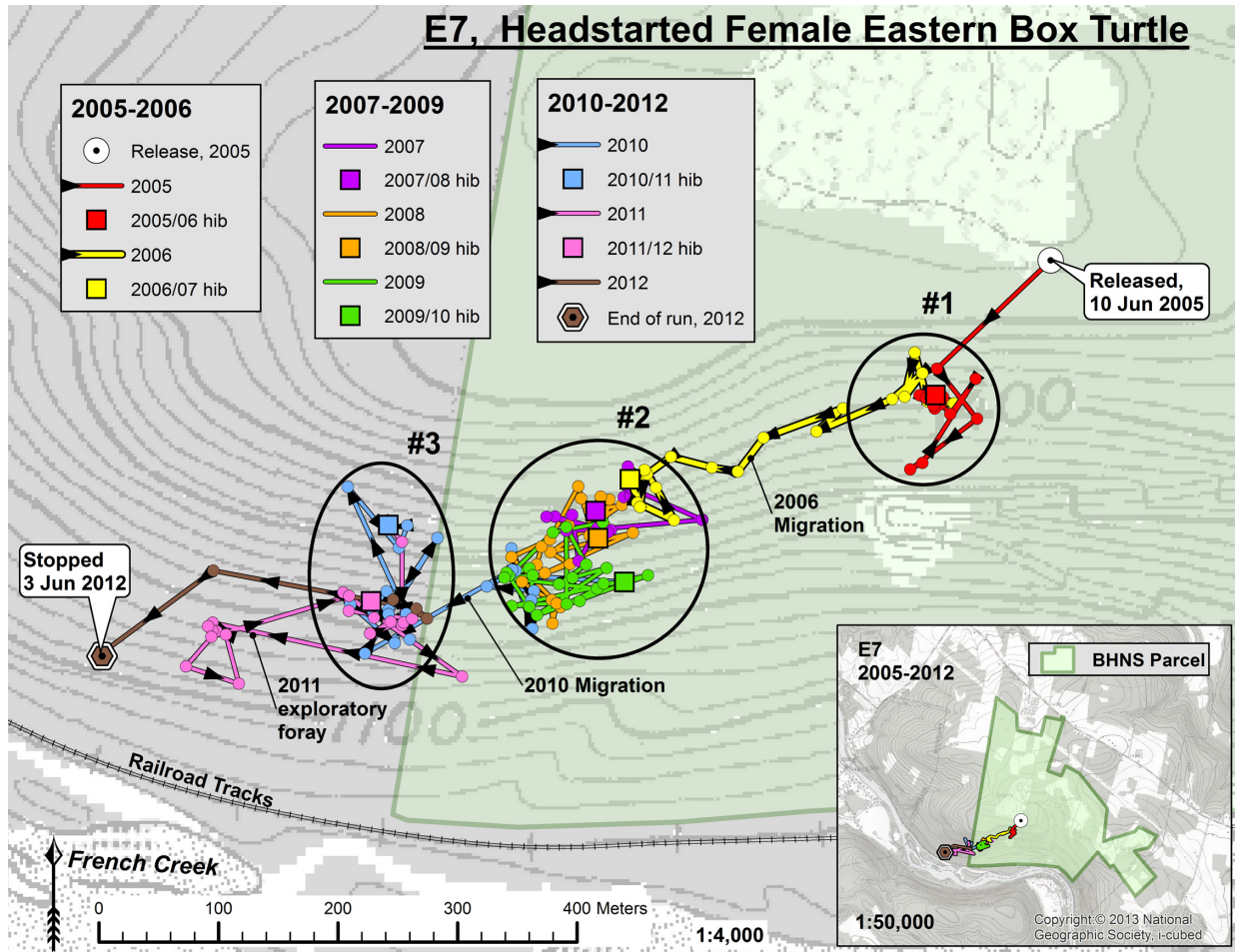
then turned south, bringing her by early June 2012 close to railroad tracks at the bottom of the hillside (Fig. 21). We carried her from that hazardous area and released her into the sanctuary's 1.6-ha pen for safekeeping.

### Discussion

**Peregrination spectrum.**—Hall et al. (1999) characterized *Terrapene carolina carolina* (recently reclassified as *Terrapene carolina*; Martina et al. 2013) as a sedentary species whose individuals occupy the same small ranges for multiple decades. That delineation is consistent with the Eastern Box Turtle's demonstrated homing aptitude (e.g., Lemkau 1970; Madden 1975; Posey 1979; DeRose and Taylor 1982) and with some home-range field studies (e.g., Stickle 1989; Dodd 2001). The initial movement history for each turtle presented in this paper also seems to corroborate that depiction. Their weekly positions, located across protracted time-spans, were always within very circumscribed parcels.

However, these particular turtles undercut the protracted site-fidelity paradigm in that, after an extended period of residency, each one eventually abandoned its established home to settle into a new dedicated abode and then occupy that new one for another extended time-span. Moreover, to date, these turtles have never been found revisiting any of their former activity centers after they abandoned them, even when the distance was small. So far, only juvenile and sub-adult turtles in our population have displayed this serial-residency behavior, but generalizations may change as a data pool grows (Seibert and Belzer 2013).

Our series on Eastern Box Turtle movements aims to highlight the variety, individuality, and unpredictability of how they travel in their environs, and the unreliability of trying to generalize that behavior. We noted (Seibert and Belzer



**Fig. 21.** Seven-and-a-half season (2005–2012) movement history for headstarted female, E7. Total data set = 159 waypoints. Green shading = BHNS sanctuary. ○ = release site. □ = hibernation site. Large, numbered circle or ellipse encloses a protracted activity center. Red = 2005 travel (19 waypoints); yellow = 2006 travel (20 waypoints); purple = 2007 travel (22 waypoints); gold = 2008 travel (24 waypoints); green = 2009 travel (21 waypoints); blue = 2010 travel (25 waypoints); pink = 2011 travel (22 waypoints); brown = 2012 travel (6 waypoints).

2013) that their habitat choices are similarly idiosyncratic, changeable, and unpredictable. Notice the inconsistency, even between siblings, that is evident in Table 1.

The field procedures, which are revealing that movement patterns are much more varied than has been broadly chronicled, employ frequent location-sightings and long time-spans (e.g., Seibert and Belzer 2013, 2014; Jim Basinger <<http://home.ntelos.net/~jbasi/Philosophy%20and%20Methodology.html#YearlyRoutes>>, <<http://home.ntelos.net/~jbasi/Mapping.html>>; and a seven-year composite for turtle M1 at <<http://home.ntelos.net/~jbasi/boxturtle.html>>). Seibert and Belzer (2014) wondered if the protocols, from which the sedentary-box-turtle characterization had emerged, failed to locate turtles frequently enough or for sufficiently long durations to recognize the full extent of their movement spectrum. Madden (1975) asserted that adequately defining a turtle’s range is difficult and requires considerable quantities of data. He posited that the relatively sparse information obtained in recapture studies falls short for assessing the

nature of box turtle movement patterns and their ecological significance. His study indicated that, although some box turtles certainly have neat and compact home ranges, other home-range patterns are by no means exceptional. Our findings concur with Madden’s view.

**Vacillating perceptions.**—Dodd’s (2001) review of box turtle-movement literature disclosed that the sex which is reported to range farther varies by study. Sex was represented equally among the four turtles in this paper that ranged beyond sanctuary boundaries by the end of their serial-home-site progression. Previous papers in our series (Seibert and Belzer 2013, 2014) described other distinctive, far-ranging-turtle progressions, including long treks that took the turtle out of the sanctuary and circumnavigations of broad terrain. When we review all of our turtles, tracked for five or more years, about half of them (n = 50) displayed one or another pattern that involves broad domains. Seventy-eight percent of this wide-ranging category is male.

**Table 1.** Movements of five Eastern Box Turtles (*Terrapene carolina*) highlighting the variety, individuality, and unpredictability of travel (s = rounded number of seasons).

<b>D1</b> (female): 3s on dry, shaded slope → 3s on dry, sunny plane → 3s on shaded, swampy flatland → 1s of sun/shade traverse
<b>D2</b> (male sibling of D1): 7s on sun/shade terrain → 1s on sun/shade traverse
<b>D3</b> (male): 1s on shaded hillside → 1s on dry, sunny plane → 1s in transit across varied habitat 1s on dappled flatland → 3s in mixed meadow/forest → 1s of sun/shade traverse
<b>D4</b> (male sibling of D3): 6s in seasonally wet, shaded basin → 6s at sunnier, elevated, meadow-forest-ecotone
<b>E7</b> (female): 1s on intermittently wet, shaded slope → 4s on intermittently wet, shaded slope → 2s on intermittently wet, shaded slope → short traverse across and down shaded, steep hill

The other half (n = 54) of our population which was tracked for five years or more can be pooled into a group characterized by high site fidelity across prolonged timespans. Although many of these turtles exploited habitat broader than the very small parcels featured in Seibert and Belzer (2013), they did reliably occupy discrete tracts. Only 39% of this more-settled category is male.

This summary of our data would endorse males as the sex that ranges over longer distances. However, we draw attention to the longitudinal-data comparisons in Seibert and Belzer (2013) that demonstrated how an evaluation prompted by available data can change as additional data accrue. This caution applies to findings about age classes as well. Williams and Parker (1987) reported that younger age classes ranged farther than adults. Our accumulated decade of data on juveniles, at least at this time, does not support that contention; juveniles and sub-adults constitute half of our total population but somewhat less (46%) of its wide-ranging subclass.

**Gene-flow strategies.**—A long-term field study using dogs (Schwartz and Schwartz 1974) to periodically detect resident *Terrapene carolina triunguis* (recently reclassified as *T. mexicana triunguis* by Martina et al. 2013 although recognizing *Terrapene triunguis*, *T. mexicana*, and *T. yucatana* as distinct species would be more consistent with current practices) in a Missouri habitat, suggested that Three-toed Box Turtles are largely sedentary, but free-roaming transients occur occasionally (Schwartz et al. 1984). Transients were conceptualized as individuals that continuously move from one habitat to another, periodically encounter new populations where they mate, and leave their genes, and then move on. Such transients were envisioned as the agent for gene flow between isolated populations (Kiestler et al. 1982; Schwartz et al. 1984). This transient concept also appears in the Eastern Box Turtle literature (e.g., Stickel 1950; Williams 1961; Williams and Parker 1987).

Madden (1975) tracked Eastern Box Turtles in New York. Although he observed disparate inclinations as they traveled through various habitats, he found no evidence for a clear-cut transient class and challenged the more dichotomized characterizations of movement patterns.

Jim Basinger, tracking Eastern Box Turtles in Virginia, demonstrated that some individuals that might easily be mistaken for transients are actually residents that circulate across very large home ranges (see <http://home.ntelos.net/~jbasi/Transient%20ID.html>). This Virginia population displays an intergradation rather than a dichotomy of movement patterns (see the maps archived at <http://home.ntelos.net/~jbasi/boxturtle.html>). Protracted histories of turtle travel at our Pennsylvania site (Seibert and Belzer 2013, 2014, this article, and unpublished data) are concordant; the diverse patterns appear to intergrade across a broad spectrum.

The wide array of movement patterns that we see suggests to us an alternative perspective on gene flow. Perhaps a distinct class of transient individuals is not the primary agent of gene flow for this species. Instead, producing a panoply of innate movement propensities among offspring may be what promotes gene flow within and among different populations. Our studies of mating behavior (Belzer 2002; Belzer and Seibert 2009a) indicated that chance encounters between the sexes as they traverse habitats constitute a critical aspect of finding mates. In such a circumstance, endowing each generation with a broad mixture of ingrained movement propensities would increase the chances that at least one or another of a population's extant perambulation patterns would promote mating encounters. This view of population interaction suggests that much larger protected habitats and corridors are needed for *Terrapene* population recovery than has generally been assumed.

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also comply with Guidelines for the Use of Live Reptiles in Field Research (HACC 2004)

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