Research Article

Effects of European Common Reed on Blanding's Turtle Spatial Ecology

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ABSTRACT European common reed (*Phragmites australis*; common reed) is an aggressive invader of North American wetlands that forms homogenous patches and replaces native flora. Dense patches of common reed generally provide poor habitat for many species, although specific effects on at-risk turtles are largely unknown. We created 3 predictive scenarios to relate the amount of common reed in the landscape to amount of effective habitat for Blanding's turtles (*Emydoidea blandingii*) and investigated the spatial ecology of 46 adult Blanding's turtles using Euclidean distance analysis within 2 wetland complexes in southern Ontario, Canada. At the home-range scale, we identified a positive association between turtle home ranges and common reed. At the individual scale, turtle radio-locations were significantly farther from common reed patches than from random points, consistent with the hypothesis that they avoided common reed patches locally. When we analyzed habitat selection by sex, results were similar to population-level results except for nesting females. During nesting migrations, females did not avoid common reed patches at the individual scale but instead interacted with common reed, potentially placing themselves at risk of being stranded within dense patches. Our results are consistent with our dynamic home range plus saturation hypothesis that invasion of common reed reduces the amount of effective habitat for at-risk turtles in wetlands because Blanding's turtles significantly avoided common reed patches at individual scales. Management of common reed is an important step to restore habitat for Blanding's turtles and future research is needed to determine best restoration practices. © 2018 The Wildlife Society.

KEY WORDS *Emydoidea blandingii*, European common reed, great lakes, habitat selection, home range, invasive species, *Phragmites australis*, reptile, wetland.

European common reed (*Phragmites australis*; common reed) is a perennial grass that has aggressively invaded freshwater wetlands, watercourses, and beaches in North America (Chambers et al. 1999, Saltonstall 2002). European common reed first establishes in high marsh or recently disturbed areas and grows clonally from underground rhizomes to invade low marshes (Amsberry et al. 2000). Common reed patches become tall and dense (Haslam 1972), crowding out native flora by reducing solar radiation to the ground (Meyerson et al. 2000, Rice et al. 2000). Once established, common reed forms dense, homogenous stands that result in altered structure (Rice et al. 2000) and reduced plant diversity (Silliman and Bertness 2004).

The expansion of common reed and subsequent alteration to habitat structure has affected many wetland-dependent animal species including birds, amphibians, and reptiles (Meyerson et al. 2000). The effect of common reed on marsh birds is mixed (Gagnon Lupien et al. 2015); although some ecologically sensitive species (e.g., ducks, herons, egrets, and sandpipers) have been unable to use monotypic patches (Benoit and Askins 1999), more robust species (e.g., marsh wren [*Cistothorus palustris*] and red-winged blackbird [*Agelaius phoeniceus*]) have been able to do so. Where herpetofauna are concerned, however, sites dominated by common reed supported significantly fewer species of reptiles and amphibians compared to sites with little to no common reed (Mifsud 2014). Loss of shallow aquatic habitat due to aggressive colonization of common reed has been linked to long-term declines of the Fowler's toad (*Anaxyrus fowleri*; Greenberg and Green 2013). Shading on beaches from tall stands of common reed have lowered the temperature of the surrounding micro-environment and reduced hatching success of freshwater turtles (Bolton and Brooks 2010). Therefore, presence of invasive common reed is particularly detrimental to sensitive species in wetlands (Catling 2005, Gilbert et al. 2014).

The Blanding's turtle (*Emydoidea blandingii*) is a semi-aquatic turtle that relies on wetlands for feeding, mating, and overwintering, and often makes extensive over-land movements (Innes et al. 2008, Newton and Herman 2009, Edge et al. 2010). In Ontario, Canada, the Blanding's turtle is listed as threatened under the Endangered Species Act (Ontario Government 2007) and the Canadian Great

Lakes-St. Lawrence population is designated as endangered (Committee on the Status of Endangered Wildlife in Canada [COSEWIC] 2016). Although studies have reported the negative effects of common reed stands on turtle nests (Bolton and Brooks 2010, Cook et al. 2017) and others have focused on mapping and understanding the distribution and spread of common reed in the landscape (Catling and Mitrow 2011, Bourgeau-Chavez et al. 2013, Samiappan et al. 2016), no study has been completed to understand how common reed affects habitat selection by at-risk turtles.

The main objective of our study was to determine if invasive European common reed affects the spatial ecology of Blanding's turtles. First, we hypothesized that Blanding's turtles can have 3 different responses to common reed: the fixed home range (FHR) hypothesis (scenario A; Fig. 1A), the dynamic home range (DHR) hypothesis (scenario B; Fig. 1B), and the dynamic home range plus saturation (DHR+S) hypothesis (scenario C; Fig. 1C). Second, we used habitat selection data to provide insight into how the Blanding's turtle is affected by dense and prolific patches of invasive common reed. In scenario A, we hypothesized that interannual distribution of turtle home ranges will have a high degree of consistency (i.e., fixed) regardless of common reed invasion. Therefore, the centroid of interannual home ranges will not move from year to year and home range overlap between years will be high. This hypothesis predicted that at the home-range scale, turtles will not avoid common reed and may even appear to select for it when the amount of common reed increases in the landscape. At the individual scale, however, turtles will avoid patches of common reed because they are difficult to move through and do not provide optimal basking or foraging opportunities (Haslam 1972, Meyerson et al. 2000, Rice et al. 2000). Overall, as the areal extent of common reed increases across the landscape, the amount of effective, or useable habitat will decrease because common reed will take over potentially suitable habitat that would subsequently be avoided by turtles (Fig. 2A).

In scenario B, we hypothesized that home ranges can, to some degree, vary spatially each year (i.e., dynamic). Therefore, the centroid of interannual home ranges will move from year to year and home range overlap between years will be low. The dynamic home range hypothesis predicted that turtles would alter habitat selection at the home-range scale, by changing the location of their home range, to avoid common reed. In this scenario, turtles would use areas of the population range that do not contain common reed or contain a low areal extent of common reed. With comparatively less area of common reed in a turtle's home range relative to the population range, avoidance of common reed at the individual selection scale would not be detected. Therefore, as the amount of common reed increases across the landscape, the amount of effective or usable habitat would remain constant (Fig. 2B).

In scenario C, we hypothesized that home ranges can vary spatially each year (analogous to scenario B); however, common reed invasion will proceed until patches within the population range could no longer be avoided. The DHR+S hypothesis includes a saturation component that predicts turtles altering selection at the home-range scale to avoid common reed until patches become so ubiquitous within the landscape that turtles can no longer avoid common reed and may even appear to select for patches. Nevertheless, at the individual scale, we predicted that turtles would avoid
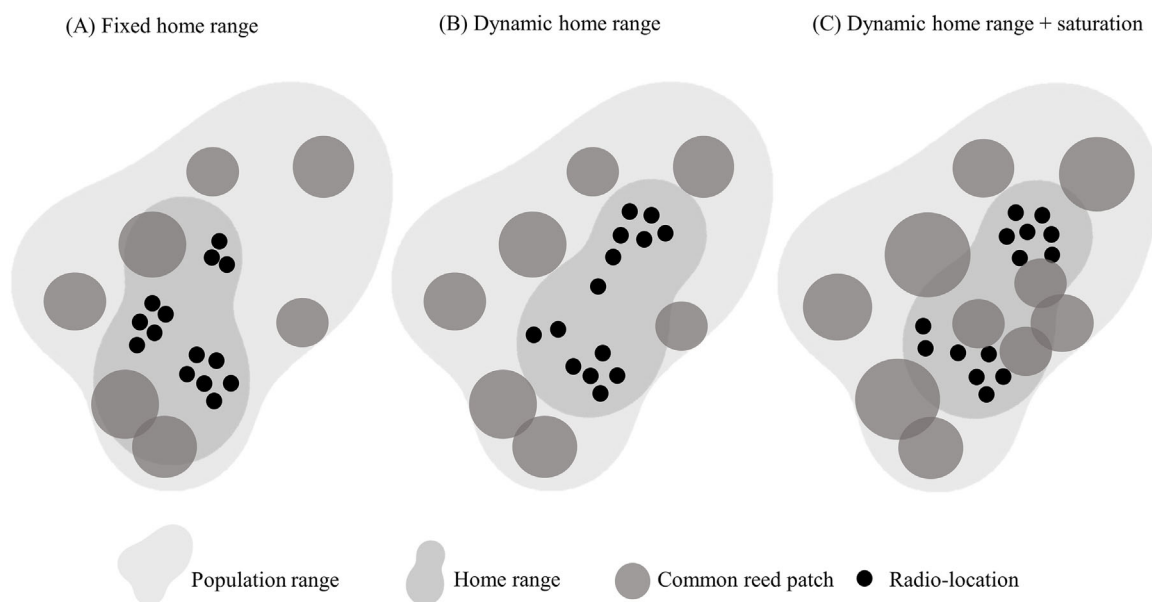

Figure 1. Conceptual landscape schematic representing the fixed home range hypothesis (FHR; A), dynamic home range hypothesis (DHR; B), and dynamic home range plus saturation hypothesis (DHR+S; C). Each schematic depicts the hypothetical radio-locations of a Blanding's turtle, the individual's home range, and the population range in relation to the distribution of invasive European common reed.
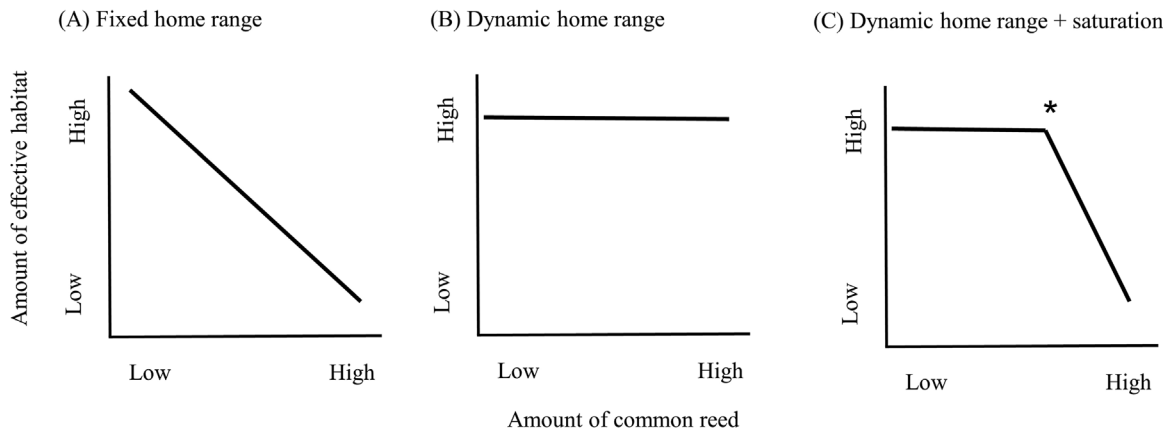
Figure 2. Simplified prediction curves corresponding to the (A) fixed home range hypothesis (FHR), (B) dynamic home range hypothesis (DHR), and (C) dynamic home range plus saturation hypothesis (DHR+S). Each curve relates the amount (areal extent) of effective Blanding's turtle habitat to the amount (areal extent) of invasive European common reed in the landscape. The asterisk in C denotes that the inflection point may occur elsewhere along the x-axis.

common reed because dense patches do not provide optimal basking or foraging opportunities and are difficult to move through (Haslam 1972, Meyerson et al. 2000, Rice et al. 2000). Therefore, availability of effective habitat would be constant at the beginning of the common reed invasion and eventually become reduced when a threshold of expansion is reached (Fig. 2C).

STUDY AREA

We conducted our study in 2 separate wetland complexes (i.e., study sites A and B) in southern Ontario, Canada located 125 km apart. Both wetlands were large (>12 km²) cattail-dominated marshes and supported a variety of species at risk, including the Blanding's turtle. At both study sites, land cover types included aquatic marsh, cattail marsh, meadow marsh, mixed organic marsh, open water, European common reed, treated European common reed, upland, and other (Table 1). Average daily temperatures at study site A ranged from −3.6°C in January to 22.6°C in July and annual precipitation was 882 mm. Similarly, at study site B, average

daily temperatures ranged from −5.4°C in January to 21.1°C in July and annual precipitation was 1,036 mm.

Our study sites were located in agriculture-dominated watersheds and were first colonized by invasive European common reed 45–70 years ago (Wilcox et al. 2003, Catling and Mitrow 2011). Portions in both study sites had been treated to control invasive common reed. At study site A, some patches of common reed were sprayed with herbicide, rolled, or both sprayed and rolled during fall 2008–2012 (we excluded treatments after 2012 because they occurred after we obtained radio-tracking data). At study site B, some patches were sprayed with herbicide and then cut down during fall 2014.

METHODS

Turtle Movements

We captured adult Blanding's turtles opportunistically by hand, dip net, or in baited hoop nets. We identified the sex of each turtle using secondary sex characteristics and weighed each turtle (Pesola Scales, Switzerland). We attached AI-2F

Table 1. Land cover types classified within delineated Blanding's turtle population ranges in 2 study areas in southern Ontario, Canada. We classified land cover types in 2011 and 2013 for site A and in 2014 and 2015 for site B.

Land cover type	Description	Site A (ha)	Site B (ha)
Aquatic marsh	>25% cover of floating species (e.g., fragrant water lily [*Nymphaea odorata*], yellow water lily [*Nuphar lutea*], water shield [*Brasenia schreberi*]), >25% submerged species, and <25% emergent species (e.g., bulrush [*Schoenoplectus* spp.]).	15.0	102.0
Cattail marsh	>75% cover of cattails (*Typha* spp.) with homogenous appearance.	278.0	415.0
Meadow marsh	Seasonally flooded meadow marsh dominated by grass and sedge hummocks.	30.0	88.0
Mixed organic marsh	Graminoid or forb dominated shallow marsh with >25% vegetation cover.	8.0	19.0
Open water	Water deeper than 2 m with <25% vegetation cover.	310.0	238.0
European common reed	Dense invasive common reed typically growing in circular shapes throughout the marsh.	73.0	103.0
Treated European common reed	Invasive common reed that has undergone treatment.	11.0	2.0
Upland	Any terrestrial area dominated by coniferous or deciduous trees or shrubs, including open or shrubby sand beach. Also includes anthropogenic land uses such as agricultural fields, campgrounds, open fields, roads, road shoulders, or trails.	420.0	214.0
Other	Land cover types unique to either population and excluded from analyses (e.g., treed swamp, thicket).	148.0	2.0

radio transmitters (Holohil Systems, Carp, Ontario, Canada; 19 g) with quick dry and plumber's epoxy to rear marginal scutes. The transmitter did not exceed 5% of the turtle's body mass. We released turtles at their original capture site immediately after tagging. In study site A, we radio-tracked 8 females and 9 males. During the active season of 2011 (12 Apr–23 Aug 2011) we tracked 4 males and 2 females, and in 2013 (27 Apr–22 Sep 2013) we tracked 5 males and 6 females. In study site B, we radio-tracked 15 females and 14 males during the active seasons of 2014 (21 Apr–27 Aug 2014) and 2015 (12 Apr–20 Aug 2015). Overall, we collected data for 46 adult Blanding's turtles (23 males, 23 females). We used a 3-element Yagi antenna (Wildlife Materials International, Murphysboro, IL, USA) and a Lotek Biotracker Receiver (Lotek Wireless, Newmarket, Ontario, Canada) to track each turtle, and we recorded global positioning system (GPS) location (Garmin Handheld, Olathe, KS, USA) and vegetation type at each tracked location. We radio-tracked turtles 1–2 times/week during the active season and 1–2 times during the overwintering season. All work was carried out under approved animal use protocols from McMaster University (numbers 11-02-05 and 14-09-35) and site-specific permits (Wildlife Scientific Collectors Authorization 1076122/1073523/1062330, Species at Risk Act-0R-2014-0260, Endangered Species Act M-102-6326447130, AY-B-005-13, AY-B-004-11).

Home Range Analyses

We estimated individual turtle home ranges and the population range in Geospatial Modeling Environment 0.7.2.1 (Spatial Ecology, www.spatialecology.com, accessed 9 Aug 2016) and ArcGIS 10.3 (ESRI, Redlands, CA, USA). To calculate individual turtle home ranges, we selected a kernel density bandwidth (smoothing factor, h) that resulted in the 95% contour area equaling the area of the 100% minimum convex polygon (Row and Blouin-Demers 2006). This modified approach has been used to study habitat selection in turtles (Edge et al. 2010, Paterson et al. 2012) and delineates home range based on the distribution of radio-locations while allowing for a more standardized application when matched to the area of the corresponding minimum convex polygon. For individual turtles that were tracked in multiple years, we pooled data for home range estimation. We estimated population range as the 100% minimum convex polygon surrounding all turtle radio-locations and subsequently buffered this estimate (452 m for site A; 315 m for site B) to encompass home ranges of individual turtles (Edge et al. 2010, Paterson et al. 2012).

We estimated the change in home range location and orientation between years for 20 (11 males, 9 females) individual turtles in study site B that had a complete tracking dataset in 2 consecutive years. We excluded 4 females where we did not capture the nesting migration in both years because this could artificially alter the home range location and orientation between years. For each individual turtle, we estimated annual home range using a 100% minimum convex polygon. We used ArcGIS 10.3 to determine the centroid of the home range and measured the distance between the 2014

home range centroid and the 2015 home range centroid. The calculated distance provides an estimate of how far a turtle home range shifted between years. For the same subset of turtles, we also calculated the percent of the 2015 home range that overlapped with the 2014 home range. Although the centroid shift provides context to the overall location of the home range within the landscape, the percent overlap determines the amount of area that was used in both years or if the orientation of the home range changed.

Habitat Selection

In each wetland complex, we delineated and classified land cover using ArcGIS 10.3. We classified land cover into 9 classes: aquatic marsh, cattail marsh, meadow marsh, mixed organic marsh, open water, common reed, treated common reed, upland, and other (Table 1). We selected image data that aligned temporally with turtle radio-tracking data to minimize temporal discrepancies and used field-collected data to ground-truth the land cover delineations. For study site A, we classified 2010 orthophotos (Southwestern Ontario Orthophotography Project) to complement 2011 and 2013 radio-tracking data. For study site B, we classified 2015 orthophotos (Southwestern Ontario Orthophotography Project) and 2015 image data collected by an unmanned aerial vehicle to complement 2014–2015 radio tracking data.

We used Euclidean distance analysis (EDA) to analyze habitat selection (non-random habitat use) at the second-order and third-order scale (Johnson 1980). We chose to use EDA, a distance-based analysis, over compositional analysis, a classification-based analysis (Aebischer et al. 1993), because it is more tolerant of radio-tracking and GPS locational errors, can be applied at multiple spatial scales, avoids the unit sum constraint (Conner and Plowman 2001), and has been used to investigate habitat selection by turtles (Edge et al. 2010, Paterson et al. 2012). Euclidean distance analysis provides a method to compare observed habitat use to random habitat use by calculating distance ratios (d_{ij}) as $d_{ij} = (u_{ij}/r_{ij})$, where u_{ij} represents used distances and r_{ij} represents random distances. To determine if land cover types are being used non-randomly at the second-order scale, we compared habitat use in individual turtle's home ranges to habitat availability in the population range (Johnson 1980). Therefore, u_{ij} is the mean distance from random locations within an individual's (i) home range to the nearest edge of each land cover type (j; represents use) and r_{ij} is the mean distance from random locations within the population range to the nearest edge of each land cover type (represents availability). We also tested for non-random habitat use at the third-order scale by comparing habitat use by turtles to what was generally available within their home range (Johnson 1980). At this selection scale, u_{ij} was the mean distance from individual radio-locations to the nearest edge of each land cover type and r_{ij} was the mean distance from random locations within an individual's home range to each land cover type. If habitat use is random at either scale, we would expect the mean ratio of used distances (u_{ij}) to random distances (r_{ij}) to equal 1.0. If the turtle is closer to a particular land cover type than is expected by random, the distance ratio

(d_{ij}) would be <1.0 (selection). Conversely, if the turtle is farther from a particular land cover type than is expected by random, the distance ratio (d_{ij}) would be >1.0 (avoidance).

We tested for evidence of non-random habitat use using a permutational multivariate analysis of variance (perMANOVA; 10,000 permutations) to identify any distance ratios that significantly differed from 1.0. We then used Wilcoxon signed rank tests to determine the land cover types turtles selected (d_{ij} < 1.0) or avoided (d_{ij} > 1.0). We used Holm's sequential correction when making multiple comparisons (Holm 1979). We tested for non-random habitat use by all tracked Blanding's turtles, males, females, and females when nesting migrations were excluded. We identified a nesting migration as the movements from a resident wetland area to the nest site and back to a resident wetland area. We completed all spatial analyses in ArcGIS 10.3 and statistical tests in R 3.3.1 (R Version 3.3.1, www.r-project.org, accessed 21 Jun 2016) and JMP 13 (SAS Institute, Cary, NC, USA).

RESULTS

We radio-tracked 46 adult Blanding's turtles (23 males, 23 females) and collected 1,105 radio-locations across 4 years. We collected an average of 20 ± 4 (SE) radio-locations/turtle (17 turtles) in study site A, and an average of 25 ± 2 locations in study site B (29 turtles). When we pooled data for both populations, mean home range area was 32.8 ± 6.4 ha, ranging from 0.62 ha to 260 ha. Although female home range (46 ± 11.9 ha) compared to male (20 ± 3 ha) was not significantly different ($Z = -1.8$, $P = 0.07$) and varied among individual females, average female home range size was double the area of males. In addition, female home ranges were 0.67 km longer than males (1.6 ± 0.2 km vs. 0.93 ± 0.1 km, respectively; $Z = -2.5$, $P = 0.01$). Even when home range area is held constant, the approximate length of the home range shape can vary. In general, male ranges were rounded and covered a shorter linear distance (Figs. S1A,B, available online in Supporting Information) compared to female ranges, which were more elongated and covered a greater linear distance (Figs. S1C,D, available online in Supporting Information).

We had consecutive tracking datasets in 2014 and 2015 for 20 Blanding's turtles in study site B (11 males, 9 females). We had 2 turtles (1 male, 1 female) where the home range centroid shifted by only 100–110 m and home ranges in 2014 and 2015 overlapped by 94–100%. In contrast, 8 turtles (5 males, 3 females) had home ranges that overlapped by <50% and home range centroids that shifted 55–600 m. The total range in home range overlap varied from 4% to 100%. On average, the home range centroid shifted by 209 ± 38 m and home ranges overlapped by $53 \pm 6\%$.

Blanding's turtles in study site A had a population range that was 110 ha larger than those in site B (1,293 ha vs. 1,183 ha, respectively), but the proportion of habitat invaded by common reed was comparable. Within both population ranges, 13–14% of area susceptible to invasion (i.e., wetlands and beach) was infiltrated by common reed. Although the proportion of common reed within the population range was comparable

between sites, patch distribution differed. Study site B had 5 times more individual patches of common reed than did site A (581 vs. 153 patches, respectively), resulting in patches occurring 12 m closer together in B than in A (patches were 20 m apart vs. 32 m apart, respectively; Fig. S2).

Habitat Selection

Blanding's turtles were using habitats non-randomly at the second-order or home-range scale ($F_{8,388} = 32.2$, $P \le 0.001$). The most preferred were aquatic, cattail, meadow, and mixed organic marshes (lowest mean distance ratio; Fig. 3A). Common reed patches were located closer to random locations within home ranges than to random locations within the population range ($Z = -517.5$, $P \le 0.001$; Fig. 3A), indicating apparent selection of common reed at the home-range scale.

At the third-order or individual scale, there was also evidence of non-random habitat use ($F_{8,388} = 4.7$, $P \le 0.001$), but in this case, we identified avoidance of common reed ($Z = 227.5$, $P = 0.008$; Fig. 3B). Turtles selected aquatic and mixed organic marshes. We also found turtles selecting patches of treated common reed at the individual scale, whereas uplands, open water, cattail marshes, and meadow marshes were used randomly with respect to availability (Fig. 3B).

We conducted separate analyses for males, females, and females with nesting migrations excluded. At the home-range scale, we confirmed non-random habitat use by males ($F_{8,190} = 31.4$, $P \le 0.001$), females ($F_{8,189} = 11.8$, $P \le 0.001$), and for females when nesting migrations were
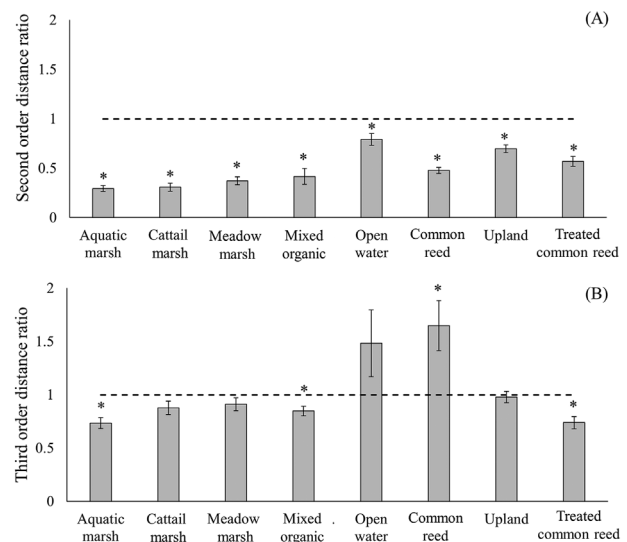

Figure 3. The second-order (A) and third-order (B) mean ($\pm$SE) distance ratios for land cover types in 2 study areas in southern Ontario, Canada. We calculated distance ratios using data collected from 46 adult Blanding's turtles in 2011, 2013, 2014, and 2015. The asterisk denotes that the distance ratio is significantly different from 1.0 (dashed line). Mean distance ratios <1.0 indicate that the land cover type was used more often than expected (selected), whereas mean distance ratios >1.0 indicate that the land cover type was used less often than expected (avoided). Lack of significant difference between distance ratios and 1.0 indicates the land cover type was neither selected nor avoided more than expected.

excluded ($F_{8,184} = 9.41$, $P \leq 0.001$). For all 3 groups, patches of common reed were closer to locations within the home range compared to the mean distance at the population range (male: $Z = -138$, $P \leq 0.001$; female: $Z = -138$, $P \leq 0.001$; females excluding nesting: $Z = -138$, $P \leq 0.001$; Fig. 4). All groups also used habitat non-randomly at the individual scale (males: $F_{8,190} = 3.0$, $P = 0.003$; females: $F_{8,189} = 4.0$, $P \leq 0.001$; females excluding nesting: $F_{8,184} = 12.5$, $P \leq 0.001$). Similar to third order results for all Blanding's turtles, males avoided common reed patches ($Z = 77$, $P = 0.01$; Fig. 4). Females, however, did not avoid common reed at the third-order scale ($Z = 31$, $P = 0.36$; Fig. 4), except when nesting migrations were excluded ($Z = 99$, $P = 0.001$; Fig. 4).

DISCUSSION

In our study sites, where common reed patches are widespread, we found evidence that turtles avoided common reed patches at the individual scale. We also found that the average location (centroid shift) and orientation (home range overlap) of the Blanding's turtle's home range varies between years, supporting the concept of a dynamic home range. Taken together, the avoidance of common reed at the individual scale and dynamic home range provides support for our dynamic home range plus saturation (DHR+S) hypothesis. Although we identified apparent selection by Blanding's turtles of European common reed at the home-range scale, this finding may be the result of co-dependence between common reed and meadow marsh. The shallow marshes that common reed invades (Jung et al. 2017) are also selected by Blanding's turtles at the home-range scale. Regardless of whether Blanding's turtles select common reed or select areas that are subsequently invaded by common reed, the tight spatial coupling of these land cover types inevitably leads to the proliferation of common reed in Blanding's turtle home ranges.

We determined that home range centroids shifted by approximately 210 m between 2014 and 2015 for 20 Blanding's turtles, and home range area overlapped by 53% (ranging from 4–100%). A mean shift in home range centroid by 210 m and only half the home range area overlapping between the 2 years provides support that Blanding's turtle home ranges are not fixed. Additional studies have reported that home ranges of Blanding's turtles can vary on an annual basis (Grgurovic and Sievert 2005, Schuler and Thiel 2008). Although evidence indicates that home ranges are dynamic to some degree, the tendency for Blanding's turtles to exhibit fidelity to resident wetlands (Congdon et al. 2011, Markle and Chow-Fraser 2014) may limit the extent of home-range variability. Therefore, some degree of overlap in home ranges year to year may be adaptive for turtles that overwinter in the same resident wetlands. Ultimately, home ranges must include areas used for overwintering, nesting, feeding, mating, and thermoregulation (Burt 1943); however, the degree of home range variability will depend upon the availability of habitat in the landscape, a turtles' ability to access it, and a turtle's fidelity to a feature or area.

Although our data support the DHR+S hypothesis, patterns of habitat selection can only be differentiated between the FHR and DHR+S hypothesis at the start of common reed colonization when the amount or areal extent of common reed is low (Figs. 2A,C). With time-series data for a population just beginning to experience invasion, we could determine if turtles can change the location and orientation of their home range in response to common reed, at least during the early stages of invasion. Because the majority of wetlands in southern Ontario have already been invaded by common reed, future research could obtain similar data in a wetland after common reed have been successfully treated. Any new re-growth of European common reed could provide researchers an opportunity to determine the response of turtle spatial ecology to early invasion conditions.
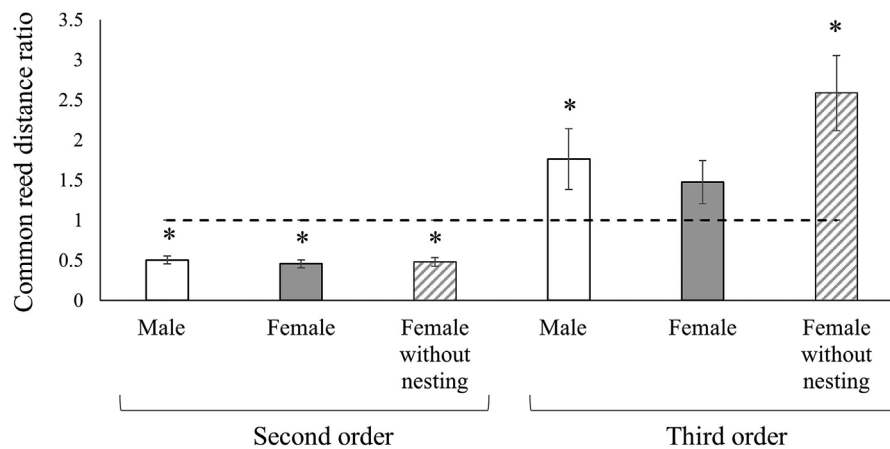

Figure 4. Mean (±SE) distance ratio for invasive European common reed at the second-order and third-order scale calculated using data from 23 adult female Blanding's turtles and 23 adult male Blanding's turtles collected in 2 study areas in southern Ontario, Canada, in 2011, 2013, 2014, and 2015. The asterisk denotes that the mean distance ratio is significantly different from 1.0 (dashed line). Mean distance ratios <1.0 indicate that the land cover type was used more often than expected (selected), whereas mean distance ratios >1.0 indicate that the land cover type was used less often than expected (avoided). Lack of a significant difference between distance ratios and 1.0 indicates that invasive European common reed was neither selected for nor avoided more than expected. We removed locations acquired during nesting migration when we calculated the distance ratio for the females without nesting category.

Regardless of which hypothesis applies (FHR or DHR+S), avoidance of common reed at the individual scale has serious implications for Blanding's turtles in an invaded wetland. Avoiding common reed at the individual scale means a reduced amount of effective or usable habitat in the turtle's home range. In our study, common reed occupied 170 ha, meaning over 14% of total wetland area was no longer available for Blanding's turtles. Blanding's turtles may be avoiding common reed patches because they are difficult to move through, provide reduced foraging opportunities, or provide inadequate thermal conditions (Haslam 1972, Meyerson et al. 2000, Rice et al. 2000). For example, exotic plant-dominated areas provide less variable and lower temperatures, resulting in avoidance by ectotherms (Hacking et al. 2013, Carter et al. 2015). Without pre-invasion data, we do not know if turtles used areas that are now occupied by common reed. However, turtles selected aquatic and mixed organic marshes at the individual scale and common reed was the only land cover type avoided. Based on these data, the invasion of European common reed and the subsequent replacement of wetland area reduces the amount of available habitat for Blanding's turtles. Blanding's turtles use aquatic and emergent marshes for feeding, mating, and over-wintering (Bury and Germano 2003, Ernst and Lovich 2009, Edge et al. 2010, Markle and Chow-Fraser 2014). Therefore, loss of aquatic and emergent marshes will have detrimental effects on the population in the long term. Even if Blanding's turtles continue to vary the location and orientation of their home range from year to year, a reduction in the total amount of effective habitat as a result of expansion of common reed would likely occur, in addition to a change in the spatial ecology of Blanding's turtles.

When we analyzed males and females separately, we did not detect avoidance of common reed at the individual scale for females until we removed nesting migrations. We attribute the lack of avoidance of common reed during nesting migrations to the need of gravid females to access nesting habitat as quickly and directly as possible, even if this means crossing through continuous barriers of common reed. Female home ranges were twice as large as males, though not significantly bigger, but the shapes of the home ranges were different (Fig. S1). Because of long-distance movements during the nesting season, the home ranges of females were 0.67 km longer compared to those of males and this led to increased interactions with common reed patches. The tendency for females to exhibit nest-site fidelity (Standing et al. 1999, Markle and Chow-Fraser 2014) and thus use the same travel corridor and nesting area every year, means that their chance of encountering common reed patches would increase as these stands continue to expand. Therefore, gravid females may be especially susceptible to common reed invasion. This does not mean that males are safe from common reed; at one of our study sites, a male Blanding's turtle was found stuck in a dense common reed patch and presumably desiccated, and other researchers have observed similar fatal situations (Gilbert et al. 2014).

Treated patches of common reed were selected at the individual scale (Fig. 3A). In study site B, common reed patches were sprayed with herbicide and stalks were cut to the ground during late summer and fall. In the following spring, we observed radio-tagged and untagged Blanding's turtles and other turtle species basking in these newly open areas. Although this evidence is only anecdotal, turtles used areas that were recently treated. In study site A, common reed patches were sprayed with herbicide in fall and dead standing biomass was rolled in the winter. Following these treatments, we located tagged Blanding's turtles crossing areas that had been rolled. In both study sites, treatment efforts were concentrated on patches that were often located near areas that had been frequently used by turtles. This may explain why we found a high positive association between radio-locations and treated patches, and why the treated patches were used so quickly. An appropriately designed study should be conducted to determine how turtles use treated patches of common reed at various stages of revegetation.

MANAGEMENT IMPLICATIONS

Considering our findings, continued control of European common reed in wetlands will be important to restore marsh habitat used by Blanding's turtles for feeding, mating, and overwintering. To avoid unintended consequences of treatment, the type and timing of treatment should be carefully considered and evaluated from a herpetological perspective. Long-term studies are required to determine treatment effects on aquatic and semi-aquatic species living in areas undergoing control of common reed. Although successful control of common reed can be challenging, it will be an important step in restoring habitat for Blanding's turtles.

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