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Nesting Ecology and Habitat Use of *Chelydra serpentina* in an Area Modified by Agricultural and Industrial Activity

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***Abstract*.—Habitat loss and pollution have been linked to declines of numerous freshwater turtle species, which are among the most endangered vertebrates in the world. We examined characteristics of nest sites of Common Snapping Turtles (*Chelydra serpentina*) located in a system modified by agricultural and industrial land use. We compared characteristics of 150 turtle nests and patterns of nest depredation in mercury (Hg) polluted and reference sites. Of the nests found in this study, 90% were located in human disturbed soils: 79% in agricultural fields and 11% in commercial nurseries. In both Hg and reference sites, we found that 52% of all nests were located in high density nesting areas in agricultural fields bordered by a river on three sides, providing novel evidence that river geomorphology could be useful for identifying important nesting areas. We did not observe predation in the reference sites but 66% of nests were destroyed at the Hg polluted sites. We provide a predictive model demonstrating that the same characteristics influence nest-site selection in this modified system as in more intact systems, and are related to solar exposure at the time of nesting. We provide evidence that Common Snapping Turtles are attracted to agricultural areas for nesting, which could influence the fate of nests and/or development of embryos. We also suggest that research is needed to verify the importance of river geomorphology on nesting. Additionally, the high depredation rate of turtle nests containing eggs with Hg contamination suggests that the impacts of dietary Hg on predators of turtle nests merits investigation.**

Key Words.—agriculture; habitat modification; mercury; nest-site selection; predation; turtle

Introduction

Habitat loss and pollution have been directly linked to declines of many aquatic turtle species in the United States (Gibbons et al. 2000). For example, anthropogenic land use has been shown to increase mesopredator population densities, including Northern Raccoons (*Procyon lotor*), which are major predators of turtle nests (Congdon et al. 1983, 1987; Ratnaswamy et al. 1997; Garmestani and Percival 2005). In addition to increasing rates of turtle nest depredation, industrial forms of anthropogenic land use can produce environmental pollutants, such as mercury (Hg), which have adverse effects on both adults and offspring in many vertebrate species (Sakamoto et al. 2001; Crump and Trudeau 2009; Tan et al. 2009). In turtles and other oviparous species, females can maternally transfer high concentrations of Hg to their eggs, which results in increased rates of unfertilized eggs and embryonic mortalities among clutches (Bergeron et al. 2011; Todd et al. 2012; Hopkins et al. 2013a, b). Additionally, Hg is a neurotoxin and high Hg levels can impact animal reproductive behavior and fecundity (Wolfe et al. 1998), but the impacts of high Hg levels on nest site selection by turtles is not understood (Hopkins et al. 2013a, b).

Low reproductive success among aquatic turtles in polluted and modified environments can be mitigated, to some extent, by efforts to increase the amount of suitable nesting habitat or decrease depredation of nests. However, a better understanding of how these factors operate to influence nesting success across different spatial contexts is needed to inform mitigation strategies. In this study, we used riparian habitat surveys along a river upstream and downstream of an historic point source of Hg to: (1) investigate the effects of long-term exposure to Hg on the nesting ecology of the Common Snapping Turtle (*Chelydra serpentina*); (2) describe patterns of nest depredation in different habitat types; and (3) develop a predictive model for nest site selection in a system dominated by agricultural and industrial land use. The model can be used by land managers to identify habitat with a high likelihood of use by Common Snapping Turtles for nesting, and to inform mitigation efforts aimed at expanding suitable nesting habitat for the species in highly modified landscapes.

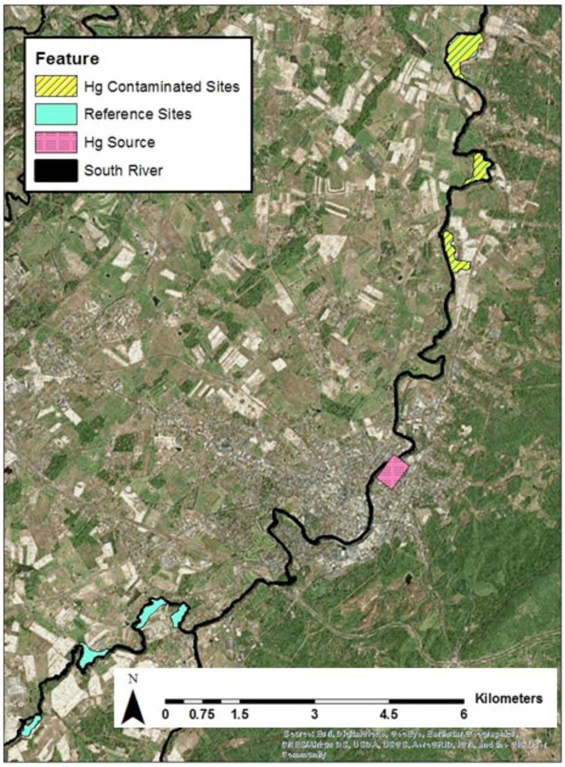

Figure 1. Visual of the study areas along the South River, Virginia, USA, monitored for Common Snapping Turtle (*Chelydra serpentina*) nests during 2013 and 2014. The historical point source of Hg is shown in pink with dots, the Hg contaminated nesting sites in yellow with stripes, and the references sites are shown with blue.

Materials and Methods

Study organism.—Common Snapping Turtles are susceptible to Hg accumulation (and maternal transfer of Hg) because they are long-lived, exhibit delayed reproductive maturity, feed in the benthos and/or at high trophic levels, and have small home ranges (Obbard at al. 1981; Congdon et al. 1994). The onset of Common Snapping Turtle nesting typically occurs during the months of May and June; nesting activity primarily occurs diurnally but some nests are constructed at night (Congdon et al. 1987; Iverson et al. 1997). Females dig nest chambers in areas with high solar exposure and normally deposit a range of 26–55 eggs. Predation rates on turtle nests are highly variable but generally range from 30–100% among years (Congdon et al. 1987) and have been linked to nest site characteristics including nest density, the distance from nests to ecological edges (i.e., river banks, forest edges, field edges, etc.), and the timing of nesting (Robinson and Bider 1988; Kolbe and Janzen 2002b; Bowen and Janzen 2005; Leighton et al. 2008; but see Congdon et al. 1983,1987).

Study sites.—We conducted our study near Waynesboro, Virginia, USA, where an historical Hg point source and land conversion for agriculture have produced a heavily modified and polluted landscape. In the center of Waynesboro, a manufacturing plant used a mercuric sulfate catalyst to produce acetate fiber from 1929–1950. The plant released high levels of Hg into the South River until 1976 (Carter 1977). Mercury concentrations in the river sediments and in aquatic organisms are still extremely high for more than 32 km (20 mi) downstream from the initial point source (Bergeron et al. 2010; Wada et al. 2010; Hopkins et al. 2013a). At our study sites, tissue Hg concentrations in adult female Common Snapping Turtles exceed concentrations known to cause sublethal and lethal effects in other aquatic species and waterfowl (Wolfe et al. 1998) and reduce hatching success through increased rates of egg infertility and embryonic mortality (Hopkins et al. 2013b).

In 2013 and 2014, during early May (prior to the reproductive season), we searched the study area, to 200 m on either side of the South River, for suitable nesting habitat. We defined suitable habitat as areas exposed to the sun with relatively loose substrate and sparse vegetation that would facilitate digging (Kolbe and Janzen 2002a; Beaudry et al. 2010; Paterson et al. 2013). We used aerial photography, kayaking surveys, and scouting on foot to locate sites with suitable nesting habitat. The Reference sites were four stretches of the river (ranging in length from 1.1–2.2 km) located from 10–14 km upstream of the manufacturing plant where females and eggs were not exposed to excessive Hg. The Hg sites were three stretches of the river (ranging in length from 1.5–2.5 km) located from 7–16 km downstream of the plant (Fig. 1). The Hg sites have been well characterized in relation to Hg accumulation and effects on Common Snapping Turtles and other species (Bergeron et al. 2010; Wada et al. 2010; Bouland et al. 2012; Hopkins et al. 2013b). However, to verify Hg levels at our sites, during the 2014 nesting season, we sub-sampled blood from nesting females and tissue from turtle eggs for Hg analysis. Both the reference and Hg sites along the South River are dominated by farmland: reference sites were 61% farmland, 23% forest, 10% residential, and 5% water (i.e., the South River and its tributaries); Hg sites were 68% farmland, 20% forest, 8% residential, and 4% water. We characterized land cover using the National Land Cover Database (NLCD 2011 dataset; Homer et al. 2015).

Nesting surveys.—We visited areas where we identified suitable habitat daily throughout the nesting season. In 2013, we conducted morning and evening surveys. However, because we found only 2.3% of all

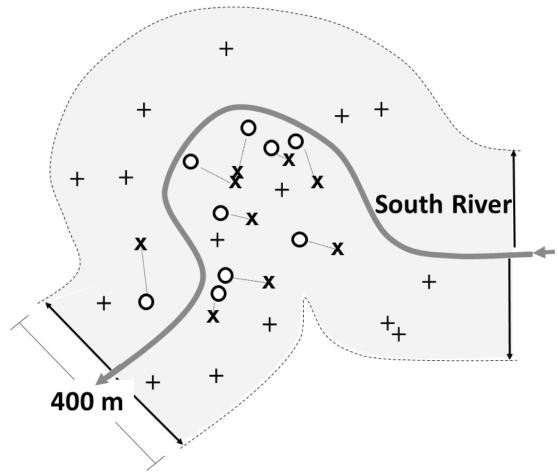

Figure 2. Sampling design used in 2014 for Common Snapping Turtle (*Chelydra serpentina*) nests, random points, and paired random point habitat surveys along the South River, Virginia, USA. Turtle nests (O), paired random points (X), and random habitat surveys (+) were conducted in the areas where nesting was detected (the reference site had four nesting areas, Hg site had three nesting areas), within 100–200 m on either side of the South River throughout the nesting season.

nests in the evening (although we discovered 12% of nests in morning surveys freshly depredated, making their oviposition time unknown), we conducted surveys exclusively in the morning in the latter part of the 2013 nesting season and during the entire 2014 season. To find nests, we searched for signs of recent nesting activity and for migrating or nesting females. Common Snapping Turtles create a mark where nests have been made that can be easily recognized by trained surveyors (Steyermark et al. 2008). When females were spotted nesting, we left them undisturbed until the nests were completed.

We assigned a unique identification number to each nest and recorded the geospatial coordinates of the nest site. To mark the precise locations of nests, we also placed a ground stake 1 m away from each nest, which was flush with the ground and unlikely to attract predators (Strickland et al. 2010). We used ArcGIS (Esri, Redlands, California, USA) to determine the distance to the South River or to the nearest water. Additionally, we categorized the soil type in which we located nests using the soil survey database of the Natural Resource Conservation Service (2010). When appropriate, we used range finders to ascertain the distance from nest sites to forest and/or agricultural field edges. Lastly, we recorded nest site characteristics of the area around the nest using a 1 m^2 sampling plot. Specifically, we measured soil water content and estimated the percentage composition of canopy cover, bare ground, forb, grass, crop, coarse woody debris, leafy detritus, other detritus, tree, shrub, and rock (Table 1), at the nest site using Daubenmire classes (Daubenmire 1959). We estimated soil water content from soil cores taken to a depth of 20 cm soil, collected at two random points within the 1 m^2 sampling plot surrounding the nest. We combined and homogenized the cores to yeild one soil sample per nest and determined the water content gravimetrically through weighing soil samples and then drying them to a constant mass in an Isotemp drying oven (Fisher Scientific, Ottawa, Ontario, Canada) using the following equation:

$$\text{Water Content (\%)} = \left(\frac{\text{Sample Mass}_{\text{Wet}} - \text{Sample Mass}_{\text{Dry}}}{\text{Sample Mass}_{\text{Dry}}} \right) \text{x } 100$$

In 2013, we re-visited nests (n = 87) daily during the nesting season and bi-weekly once the nesting season ended. We noted threats to hatching success such as predation, flooding, or tilling of agricultural fields that occurred during the first month of incubation. We considered nests depredated on day zero if the nest was never witnessed intact, because we conducted surveys every 24 h during the nesting season. In 2014, we did not use nests to evaluate predation because we collected nests to be used in subsequent experimental studies (Molly Thompson et al., unpubl. data).

Surveys.—To compare characteristics of used nest sites to available habitat, we collected habitat data associated with nests (Table 1) at randomly selected points. We randomly selected 15 sets of coordinates that were both within 100 m (in 2013) or 200 m (in 2014) of either side of the South River and along portions of the river that were within 200 m of areas used for nesting the same season (Fig. 2). We increased our sampling area in 2014 because turtles were found nesting greater than 100 m from the South River in 2013.

We also conducted paired random habitat surveys to assess nest site characteristics described above but at a finer scale. Nests encountered were paired with a random point located between 5 and 30 m from the actual nest site on the same day that the nest was discovered (30 m was the average distance female Common Snapping Turtles traveled from the South River to nest sites in 2013). We used a list of random azimuths and distances to locate the paired random point for each nest (Fig. 2).

Statistical methods.—We performed all statistical tests in JMP Pro version 11.2.0 (SAS Institute Inc., Cary, North Carolina, USA) or Microsoft Excel 2013 with significance assessed at $\alpha = 0.05$. In all analyses involving eggs or habitat characteristics, we use nests (or random points) as the sampling unit. We used logistic regression to examine patterns of predation in relationship to key habitat characteristics (Marchand and Litvaitis 2004a; Fisher and Wiebe 2006). Nest fate was

Table 1. Habitat characteristics sampled at Common Snapping Turtle (*Chelydra serpentina*) nest sites, random points, and paired random points along the South River, Virginia, USA, from 2013–2014. Habitat variables were used to investigate predation and nest site characteristics and are expressed as the percentage of each variable in the 1 m^2 area around the nest site or random point.

Variable	Description
CANOPY	percentage of canopy closure, estimated as the percent of ground obscured by vegetation
BG	percentage of bare ground/dirt
FORB	percentage of broad leafed (non-crop) vegetation
GRASS	percentage of grasses
CROP	percentage of crops (corn or soy)
WOOD	percentage of coarse woody debris, downed trees, or woody tree roots
LEAF	percentage of leafy detritus
DETRITUS	percentage of detritus other than leafy or woody (such as compost in agricultural fields)
TREE	percentage of tree
SHRUB	percentage of shrubs
ROCK	percentage of rocks, including pebbles to roughly 3 cm
RIVER	shortest distance (in m) to the South River
WATER	shortest distance (in m) to the nearest water source (river, tributary, or pond)
FOREST	shortest distance (in m) to forest bordering open habitat in the direction of the South River
FIELD	shortest distance (in m) to the edge of an open area in the direction of the South River
SOIL	type of soil classified using SSURGO database, categorical, 13 types of soils were present within the study area
WATER	percentage of water in soil cores taken from within 1 m of nest sites (to 20 cm in depth)

the dichotomous dependent variable and the following continuous predictor variables were used to model probability of nest success: (1) percentage canopy cover over the nest site; (2) distance to the nearest water body; (3) shortest distance to the South River; and (4) the distance to field and forest edges (Wilhoft et al. 1979; Marchand and Litvaitis 2004a). In 2014, we collected eggs from nests and in 2013 we did not find nests after being destroyed by predators in reference sites. Because of this, we restricted our logistic regression tests on predation patterns to Hg sites during the 2013 nesting season (Appendix A).

To accomplish our objective of developing a predictive model for nest site selection in a system dominated by anthropogenic land use, we evaluated relationships between characteristics of nest sites and random points using univariate logistic regression analyses for each habitat variable measured (Keating and Cherry 2004; Hughes and Brooks 2006) except for soil type, which was tested using a Fisher's exact test. Initially, we compared nest sites to random points separately within reference and Hg sites (using univariate logistic regressions), and directly compared characteristics of nest sites in reference and Hg sites (using *t*-tests for each variable), but found little variation between sites in both analyses. Because trends between habitat characteristics at nest sites and random points were highly similar between reference and Hg sites for most variables tested (n = 10/14, Appendix B), and only a few characteristics differed in availability (percentage grass and crops) or use (percentage bare ground and distance to the South River), we elected to present pooled data between sites and discuss trends in habitat use compared to random habitat availability along the South River both up and downstream of the Hg source.

At a finer resolution, we compared characteristics of nest sites to paired random points using paired *t*-tests and Wilcoxon signed-rank tests. We tested differences in soil types between nest sites and paired points using Fisher's exact tests. Initially, we investigated differences between nest site characteristics and paired points separately within reference and Hg sites and between sites (Appendix C), as we did for analyses at the larger spatial scale. Because we found little variation in habitat use and availability between reference and Hg sites, we elected to present paired analyses with data pooled between sites.

We chose to use the habitat characteristics of Common Snapping Turtle nest-sites and random points to develop our predictive model, rather than paired habitat data, because differences in selection were very minor at the paired resolution. We used a correlation matrix to identify correlated features (from all listed in Table 1) and we retained one feature from each highly correlated pair ($|r| \geq 0.7$) to include in multivariate regression models (Hosmer and Lemeshow 2004; Marchand and Litvaitis 2004b). We also removed habitat characteristics that had very low frequencies of occurrence at both random points and nest sites (i.e., rocks, coarse woody debris, etc.). Using the resulting

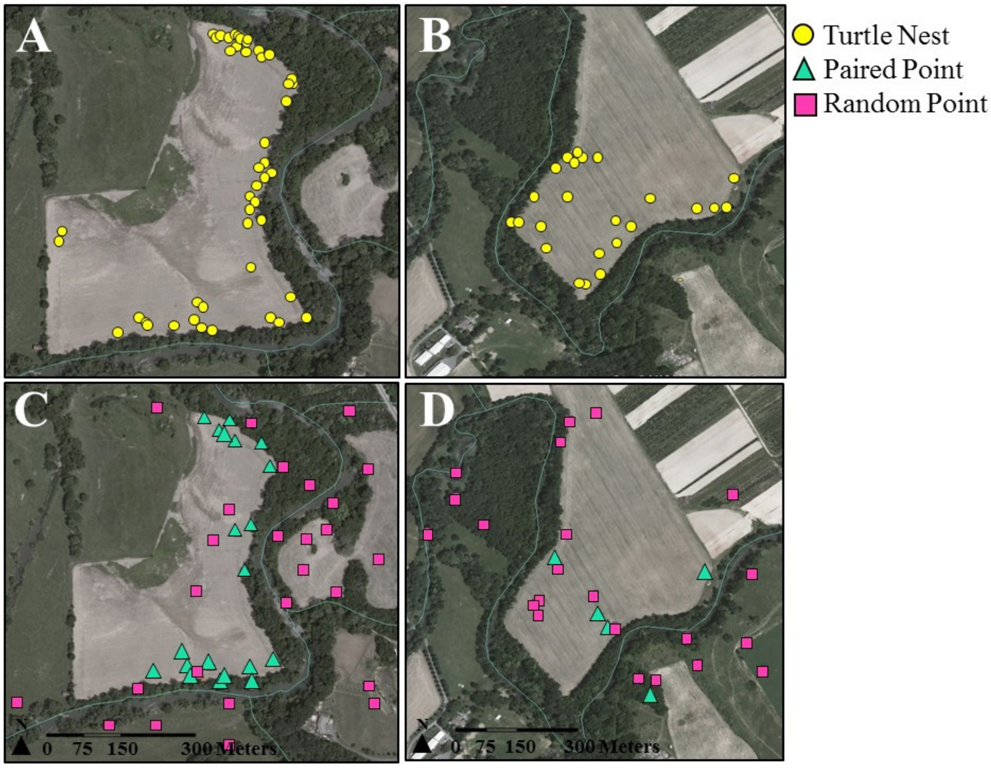

Figure 3. Two high density Common Snapping Turtle (*Chelydra serpentina*) nesting areas (turtle nest sites are shown with yellow circles), one in a Hg site (A) and one in a reference site (B) along the South River, Virginia, USA, used by Common Snapping Turtles during 2013 and 2014. The paired habitat points corresponding to turtle nests are shown with blue triangles, and locations where random habitat points were sampled are shown with pink squares for the Hg site (C) and the reference site (D).

characteristics, we fit several logistic models based on knowledge of the species and indications of importance from univariate analyses ($P < 0.200$). Models were then fitted and reduced using Wald tests and Likelihood Ratio Statistics (Hosmer and Lemeshow 2004). We present four final models that we rank using deviance and receiver operating curve (ROC) indices (Pearce and Ferrier 2000). Results of egg contamination with Hg are given as Egg total Hg (THg) in parts per million (ppm) dry weight (dwt). We present values as means ± one standard error (SE).

Results

In the two seasons (spring-summer, 2013–2014) of this study, we located 150 Common Snapping Turtle nests in the reference (n = 62) and Hg sites (n = 88). The average date of nesting was 2 June ± 1.3 d (SE), and among turtles that nested in the morning (the time of day most surveys were conducted), the average time that we observed turtles finish nesting was 0840 ± 0.2 h (SE). The average egg THg in clutches collected downstream of the Hg source was nearly 10 × higher than concentrations in clutches collected upstream (Hg sites = 2.6 ± 0.2 ppm, n = 10; reference sites = 0.3 ± 0.3 ppm, n = 8). We found no elevated concentrations of THg (above 0.5 ppm) among samples from the reference sites, supporting our longer term mark recapture efforts that indicate Common Snapping Turtles do not move between our reference and contaminated sites.

We primarily found nests in: (1) agricultural fields (n = 119, 79%); (2) commercial nursery properties with open patches of bare ground or grassy areas (n = 17, 11%); and (3) within 5 m of rivers or tributaries that offered banks with exposed soils (i.e., sparsely vegetated soil; n = 7, 5%). We found no depredated nests in the reference sites in 2013 and we did not evaluate depredation patterns in 2014. Of the 45 nests we found in 2013 at the Hg sites, depredation was high among nests in agricultural fields (n = 23/32, 72%), and in nursery properties (n = 7/9, 78%), but did not occur among nests found located near rivers or tributaries (n = 0/4, 0%).

Of the 150 total nests found, 52% were found in just two of the seven total nesting areas that we identified (Fig. 3). The two nesting areas used at high rates were in agricultural fields bordered by the South River on three sides (horseshoe bend nesting areas; Fig. 2 and Fig. 3). A *post-hoc* Fisher's exact test, with nest density as the binary response, showed that soil types differed between low and high density areas ($P < 0.001$, Fig. 4). The two high density nesting areas in our study represented two

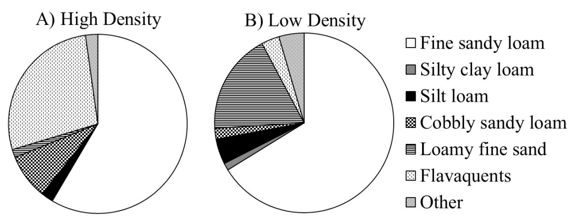

Figure 4. Percentage of soil categories (categories from the Natural Resource Conservation Service 2010) at high density Common Snapping Turtle (*Chelydra serpentina*) nesting areas (A) and low density nesting areas (B) along the South River, Virginia, USA, 2013–2014.

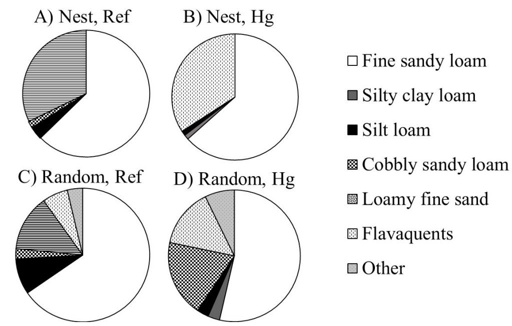

Figure 5. The percentage composition of soils (categories from the Natural Resource Conservation Service 2010) at Common Snapping Turtle (*Chelydra serpentina*) nest sites (A and B) and random points (C and D) sampled along the South River near Waynesboro, Virginia, USA, 2013–2014.

extremes of predation probability in 2013; the reference site experienced 0% predation (n = 0/20 nests); whereas, the Hg site experienced 83% predation (n = 24/29 nests).

During the 2013 nesting season, we found that 66% of nests were depredated at the Hg sites; whereas, none were depredated at the reference sites (Table 2). Logistic regression relating predation to habitat characteristics (in 2013 at the Hg site) showed that increasing distances of nests to forest edges decreased the likelihood of predation (χ^2 = -2.00, df = 32, P = 0.046), but that the distance of nests to the nearest water source, the South River, and field edges were not useful predictors of predation (in all cases P > 0.160; Table 2). Other potential sources of nest destruction that we identified include the tilling of agricultural fields and flooding. We found one nest destroyed by tilling in July; however, it is unknown if more nests were destroyed during crop harvesting in the fall. We found one nest partially washed away by flooding and nine nests to be under a pool of water for over one week (all in Hg sites).

Of the 14 habitat characteristics we examined, 11 were useful in distinguishing between nest sites and random points; percentage canopy cover, forbs, grass, crops, and leafy detritus, other detritus, bare ground, and distance to forest and field edges (in all cases $P \leq$ 0.009; Table 3). We found that soil composition differed between reference and Hg sites but that nests at both sites were associated with less variation in soil type than random points (Fisher's exact: P < 0.001). Nest sites were in loamy soils with sand more than random points and in loamy soils with cobble, clay, and silt less than random points (Fig. 5).

At the paired, fine scale resolution, only three of the 11 variables that we examined differed between nest sites and paired random points. Nest sites had lower canopy cover and forbs, and higher levels of bare ground than paired random points (in all cases P ≤ 0.033; Table 4). Compared to nests in the reference sites, turtle nests in the Hg sites had less bare ground (20.1% ± 5.7 less bare ground) than in reference sites, despite no difference in bare ground availability between the reference and Hg sites (χ^2 = -1.92, df = 45, P = 0.129; Appendix B). We also found that nests in the Hg sites had wetter soil (20.4% ± 0.5 higher soil water content) despite no difference in water availability compared to the reference sites ($t_{1, 45}$ = -1.10, P = 0.164; Appendix C).

Of the four competing models discriminating between turtle nest sites and randomly select points, we recommend the model that had one of the highest AUC values (0.904), the highest number of true positives (Accuracy = 0.708), and the largest percentage decrease in deviance compared to the deviance of the null model (48.3% compared to the next highest at 42.02%; Table 5). The selected model predicts the probability of habitat use by Common Snapping Turtles for nesting

Table 2. Comparison of Common Snapping Turtle (*Chelydra serpentina*) nest predation rates in reference (REF) and Hg sites along the South River, Virginia, USA, and relationships between predation rates (during the first month of incubation) and habitat characteristics (linear distance in m between nests and habitat characteristics) during the 2013 season. The number of nests is shown as n, rate is the percent of nests depredated at each site. For each habitat characteristics (mean ± SE), P-values represent results from univariate logistic regression analysis.

	REF Sites		Hg Sites						
	n	Rate	n	Rate	CANOPY	FIELD	FOREST	WATER	RIVER
Depredated	0	–	31	65.6%	0	12.4 ± 1.5	12.6 ± 1.4	31.4 ± 2.7	31.4 ± 2.7
Not Depred.	39	100%	17	35.4%	6.7 ± 6.7	18.4 ± 4.7	25.3 ± 5.9	32.9 ± 6.3	38.4 ± 5.5
B	–	–	–	–	–	-0.0640	-0.1056	-0.0049	-0.0298
X^2	–	–	–	–	–	$X^2_{1,33}$ = -1.41	$X^2_{1,32}$ = -2.00	$X^2_{1,42}$ = 1.2	$X^2_{1,37}$ = -1.2
P-value						0.160	**0.046**	0.281	0.227

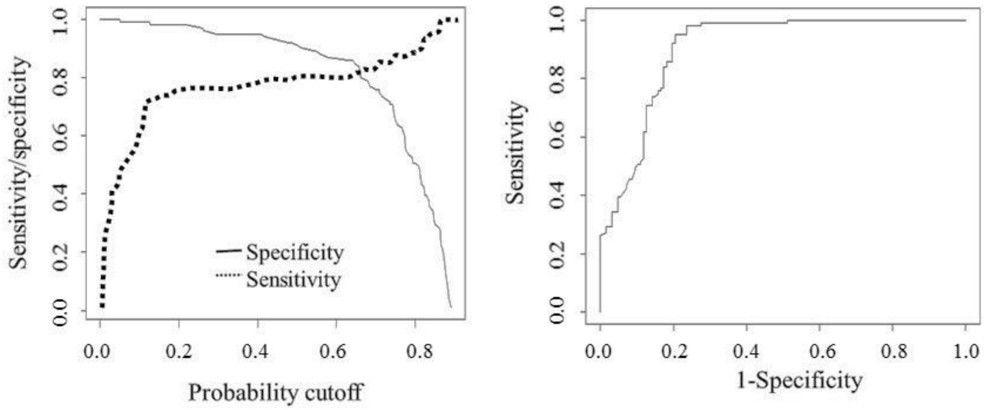

Figure 6. Performance of our highest ranked predictive model developed to identify nesting habitats of Common Snapping Turtle (*Chelydra serpentina*) along the South River, Virginia, USA, 2013–2014. Model specificity versus possible probability cutpoints and sensitivity (Left) showed that the optimal cut point for classification for our models is 0.658; the sensitivity versus 1-specificity (the ROC Curve: see Methods) of our highest ranked model showed an AUC of 0.904 (Right).

using the negative influence of canopy cover, the negative influence of ground cover by forbs, the positive influence of bare ground, and the positive influence of detritus (Table 6). The probability of a site being suitable for nesting can be estimated as:

$$P = \frac{EXP(-2.152+(0.042*BG)+(-0.045*FORBS)+(-0.045*CANOPY)+(0.028*DETRITUS))}{1+EXP(-2.152+(0.042*BG)+(-0.045*FORBS)+(-0.045*CANOPY)+(0.028*DETRITUS))}$$

Discussion

We found strong similarities in the nesting ecology of Common Snapping Turtles in Hg contaminated and reference sites; in both areas turtles favored disturbed areas for nesting and seemed to choose sites primarily based on high solar exposure. However, turtle nests in the Hg sites were located in sites with wetter soil and less bare ground than in reference sites, despite no difference in water content or bare ground availability between the reference and Hg sites. Moreover, 66% of nests in the contaminated sites were depredated compared to 0% in the reference sites.

The differences in soil water content that we observed between sites may be biologically significant; turtles selected nest sites with higher soil water content in the Hg sites than in the reference sites and nest flooding was only observed in the Hg sites (n = 10 nests). Consequently, Hg may impact turtle reproductive success through both maternal behavior (e.g., increased selection of nest sites in floodplains) and maternal transfer of Hg to eggs that causes increased rates of unfertilized eggs and embryonic mortalities (Hopkins et al. 2013a, b). While Hg has been shown to alter neural function and behavior in vertebrates (Wolfe et al. 1998), ours is one of the first studies to suggest that Hg may impact nest site selection in turtles. Yet, the impact of Hg on nest site selection was restricted to soil water content and bare ground; the other 12 nest site characteristics examined showed similar trends in both areas.

The striking difference in depredation rates between our reference and Hg sites may have been related to predator community structure, which is not necessarily related to Hg pollution. The property owner of two of our four reference sites actively hunted mesopredators on his land while tenants at the Hg sites reported that Ground Hogs (*Marmota monax*) and White-tailed Deer (*Odocoileus virginianus*) are the only animals hunted on their property (Kevin Freed, pers comm, Larry Shifflett, pers comm.). However, we cannot rule out the possibility that Hg, which readily biomagnifies in predators, directly influences predator populations, community structure, or predator feeding ecology.

In both reference and Hg sites, female Common Snapping Turtles nested largely in agricultural fields and in disturbed soils at commercial nursery properties, which may prove maladaptive. Other studies have observed that Common Snapping Turtles, and other turtle species, often nest in human-disturbed soils including earthen dams, gardens, road-shoulders, and agricultural fields (Bobyn and Brooks 1994; Castellano et al. 2008; Beaudry et al. 2010). Not surprisingly, a recent study of nest site selection by Blanding's Turtles (*Emydoidea blandingii*) in agricultural landscapes found that vegetation cover increased significantly over turtle nests in the agricultural sites but not in reference sites (Mui et al. 2015). Lower incubation temperatures in Common Snapping Turtle nests in agricultural fields and the production of male biased offspring sex ratios have been observed in Minnesota, USA (Freedberg et al. 2011). Additionally, crop canopies impair the ability of hatchlings to use environmental cues for orientation

Table 3. Average habitat characteristics (mean ± SE) of Common Snapping Turtle (*Chelydra serpentina*) nest sites and randomly selected points and results of univariate logistic regression analyses investigating the extent to which each habitat characteristic could be used to distinguish between turtle nest sites and random points along the South River, Virginia, USA. Data from reference and Hg sites are pooled; the number of each type of characteristic measured is shown as n; regression coefficients ("β"), one standard error (SE), and Wald chi-square statistic (Wald χ^2) from Wald tests for each univariate model against the intercept-only model.

Variable	n	Nest	n	Random	"β"	SE	Wald χ^2	df	*P*-value
CANOPY	150	0.9 ± 0.5	161	26.5 ± 3.2	-0.0510	0.0125	16.63	1	**< 0.001**
BG	150	71.3 ± 2.2	161	22.9 ± 2.5	0.0426	0.0043	96.05	1	**< 0.001**
FORB	150	4.9 ± 0.9	161	19.0 ± 1.8	-0.0596	0.0108	30.42	1	**< 0.001**
GRASS	150	5.2 ± 1.3	161	31.0 ± 2.9	-0.0378	0.0063	36.05	1	**< 0.001**
CROP	150	5.8 ± 0.7	161	3.2 ± 1.5	0.1385	0.0413	11.23	1	**< 0.001**
WOOD	150	< 0.01 ± < 0.01	161	1.1 ± 0.3	-1.5751	0.9780	2.58	1	0.108
LEAF	150	0.6 ± 0.2	161	5.9 ± 1.3	-0.1144	0.0436	6.90	1	**0.009**
DETRITUS	150	14.7 ± 1.5	161	8.7 ± 1.4	0.0193	0.0070	7.63	1	**0.006**
TREE	150	0.1 ± 0.07	161	1.6 ± 0.6	-0.1784	0.1087	2.69	1	0.101
SHRUB	150	< 0.01 ± < 0.01	161	5.2 ± 1.5	-0.7464	0.5246	2.02	1	0.155
ROCK	150	0.7 ± 0.2	161	0.4 ± 0.3	0.0326	0.0415	0.62	1	0.432
RIVER	132	58.8 ± 7.9	161	60.5 ± 4.5	-	-	-	-	-
WATER	138	36.2 ± 2.1	161	48.1 ± 2.9	-0.0119	0.0037	10.01	1	**0.002**
FOREST	126	23.2 ± 2.6	68	54.4 ± 4.6	-0.0282	0.0057	24.40	1	**< 0.001**
FIELD	124	22.4 ± 2.8	93	55.0 ± 6.0	-0.0240	0.0056	18.33	1	**< 0.001**

that guide them towards water (Pappas et al. 2013; Congdon et al. 2015). Consequently, agricultural land may provide attractive but unsuitable nesting habitat for aquatic turtles.

Nest density at both reference and Hg sites was related to river geomorphology and soil type. Overall, turtle nest density was highest in agricultural fields that were bordered by the South River on three sides. To our knowledge, the effect of this river geomorphology (i.e., horseshoe bends in rivers) on turtle nest site selection has not been investigated. However, recent work suggests that nesting in these areas could be advantageous because hatchlings emerging from nests in agricultural fields have impaired orientation and horseshoe bends provide three directions for the hatchlings to find water (Pappas et al. 2013; Congdon 2015). In addition, the river deposits substrate in the floodplain along its inner bank, and creates deep pools with woody debris on the outside of bends (Harrison et al. 2011), which likely provide high quality in-stream habitat for females to use before and after nesting (Braudrick and Grant 2001; Garcia et al. 2012) and may represent high quality hatchling habitat. High density nest areas were found more in flavaquents, and less in loamy fine sand, compared to low density nest areas. The tendency to avoid sandy areas for nesting has been documented in Painted Turtles (*Chrysemys picta*; Christens and Bider 1987; Ratterman and Ackerman 1989) and may be due to the low water holding capacity of sand because turtle embryos are sensitive to the hydric conditions of nest substrates (Packard et al. 1987; Deeming 2004).

Common Snapping Turtles and other aquatic turtles are known to nest both solitarily and in high densities, and their nest sites and communal nesting areas are often well defined and consistently used (Burke et al. 1998; Robinson and Bider 1988). In some cases, high density nesting has been shown to decrease predation rates, possibly by satiating nest predators with a few nests, leaving the other nests in the area less likely to be depredated (Robinson and Bider 1988; Eckrich and Owens 1995). However, evidence to support this hypothesis is lacking (Burke et al. 1998; Doody et al. 2003; Marchand and Litvaitis 2004a). The two high density nesting areas in our study represented two extremes of predation probability in 2013; the reference site experienced no predation; whereas, the Hg site experienced 83% predation. Although we did not find a relationship between nest density and nest predation, we found that increased distance of nests from forest edges was associated with a decreased likelihood of predation. This may be the result of higher mesopredator density and/or activity near forests than in open fields. Our observations are thus consistent with other studies that found that nesting farther from ecological edges decreases the probability of predation of turtle nests (Kolbe and Janzen 2002b; Leighton et al. 2008; but see Congdon et al. 1983, 1987).

The key habitat characteristics incorporated in our predictive model for Common Snapping Turtle nest site

Table 4. Habitat characteristics of Common Snapping Turtle (*Chelydra serpentina*) nest sites and paired random points (reference and Hg sites pooled) along the South River, Virginia, USA, in 2014. The number of nests measured is shown as n. Nest averages (mean ± SE) are presented and Paired Mean Difference (Paired Mean Diff.) is the percent difference between nest sites and paired random points, relative to the nest site (i.e., on average, nest sites had 12.8% less canopy cover and 13.2% more bare ground than paired random points). Differences between nest and paired random points were tested with a paired *t*-test except for FOREST, which was tested with a Wilcoxon signed-rank test.

Variable	n	Nest	n	Paired Mean Diff.	Test Statistic	*P*-value
CANOPY	60	0.33 ± 0.3	60	-12.8	*t* = 2.31	0.031
BG	60	55.8 ± 3.9	60	13.2	*t* = -2.58	0.020
FORB	60	4.0 ± 1.4	60	-7.9	*t* = 1.85	0.033
GRASS	60	9.3 ± 2.6	60	-2.4	*t* = 0.97	0.336
CROP	60	5.6 ± 0.7	60	-0.2	*t* = 0.94	0.353
WOOD	60	0	60	-0.8	*t* = 1.03	0.307
LEAF	60	1.0 ± 0.4	60	-0.1	*t* = -0.35	0.725
DETRITUS	60	21.9 ± 3.1	60	1.5	*t* = 0.27	0.791
TREE	60	0.18 ± 0.17	60	-0.3	*t* = 1.00	0.323
SHRUB	60	0.02 ± 0.02	60	-2.9	*t* = 0.96	0.342
ROCK	60	0.9 ± 0.4	60	0.2	*t* = -0.73	0.467
WATER	44	44.1 ± 3.8	44	4.0	*t* = -1.46	0.151
FOREST	36	17.8 ± 2.3	36	-5.8	*z* = 96.00	0.113
FIELD	34	16.9 ± 2.8	34	-1.1	*t* = 0.26	0.799

selection were primarily related to solar exposure, which is consistent with the findings of many other studies of nest site selection by aquatic turtles (e.g., Janzen and Morjan 2001; Valenzuela 2001; Paterson et al. 2013). Our model predicts the likelihood that a particular location would be used for nesting by Common Snapping Turtles based on the positive influence of high levels of bare ground and detritus, and the negative influence of high levels of forbs and canopy cover. For example, our model would predict the likelihood of nesting use to be 0.047 for a site with the average characteristics of the randomly selected sites used in this study. The optimal probability cut point for this model is 0.658 (Fig. 6). When using our model for management decisions, if the characteristics of a site (i.e., percentage bare ground, forb, detritus, and canopy cover) equate to a probability of use higher than 0.658, then the logistic regression predicts that the site will be suitable for nesting. This model could be used to select sites to survey for nesting turtles or areas that might be prioritized for conservation actions, or to inform restoration activities that aim to increase suitable turtle nesting habitat (e.g., sites may be altered to increase the percentage bare ground and detritus while decreasing the percentage of forbs and canopy cover).

Results from our study can be used to mitigate low reproductive success among aquatic turtles due to anthropogenic activities. Because the 200 m area along both sides of the South River is dominated by agricultural land use in our reference (61%) and Hg sites (68%), measures to promote best management practices for turtles and turtle nests are needed. For example, avoiding monoculture and planting a variety of crops at varying times in areas with high turtle nesting rates may help diversify thermal effects of crops on nests and thus help to produce mixed hatchling sex ratios. Because hatchlings of some turtle species overwinter in their nests and others (such as Common Snapping Turtles) emerge in the fall when corn and soy are harvested, we support prior recommendations that the

Table 5. Comparison of ROC evaluations and deviance indices of predictive habitat models developed using logistic regression analysis of habitat data collected at Common Snapping Turtle (*Chelydra serpentina*) nest sites and random points along the South River, Virginia, USA, during 2013 and 2014. Predictive models were tested against 20% of each dataset that was not used for model fitting.

		ROC				DEVIANCE		
Rank	MODEL STRUCTURE	AUC	Accuracy	Null	df	Residual	df	Decrease
1	BG + FORB + CANOPY + DETRITUS	0.904	0.708	309.8	225	160.1	221	48.32
2	BG + FORB + CANOPY + GRASS + FOREST + WATER	0.904	0.688	216.9	156	126.5	150	41.07
3	BG + CANOPY + WATER	0.890	0.670	309.8	222	179.6	225	42.02
4	GRASS + FORB + FOREST	0.895	0.665	232.8	169	148.1	166	36.46

Table 6. Estimated Coefficients, standard errors, *Z*-scores, two-tailed *P*-values and 95% confidence intervals for the model that best predicted Common Snapping Turtle (*Chelydra serpentina*) nesting habitat use within 100–200 m of the South River, Virginia, USA. For each term in the model the estimated regression coefficient ("β") and 1 SE are shown; statistical significance (Sig.) of each regression coefficient was tested using the Wald chi-square statistic (Wald χ^2).

VARIABLE	"β"	SE	Wald χ^2	*P*-value
BG	0.0419	0.0072	5.86	< 0.001
FORB	-0.0458	0.0217	-2.11	< 0.001
CANOPY	-0.0452	0.0216	-2.09	0.035
DETRITUS	0.0282	0.0101	2.78	0.037
INTERCEPT	-2.1518	0.6216	-3.462	<0.001

cutting height of disc mowers (a traditional harvesting tool) be set to at least 100 mm above the soil surface to help to reduce nest destruction and hatchling injury or mortality likely associated with fall crop harvests (as per Saumure and Bider 1998 and Saumure et al. 2007). Of course, identifying high density nesting areas and protecting them from destructive agricultural activities and excessive predation may be the most beneficial management action in many scenarios.

In addition to highlighting the importance of best management practices for crop planting and harvesting, our work identifies key future research needs. First, because growing crops increasingly shade nests throughout incubation, experimental research is needed to understand how agriculture practices may impact turtle nest success and hatchling characteristics (Mui 2015). Additionally, our work suggests that horseshoe bends in rivers may create high quality nesting habitat, and future work should verify whether this is a general pattern in freshwater turtles that could allow land managers to prioritize protection of habitat of high conservation importance. Finally, Hg studies traditionally focus on fish and fish eating wildlife (Crump and Trudeau 2009) because Hg is methylated and becomes bioavailable in aquatic systems. The predation of Common Snapping Turtle eggs that contain high levels of Hg in eggs (which is well documented; Hopkins et al. 2013a), suggest that turtles provide dietary subsidies of Hg to terrestrial mesopredators and highlight the need for studies on the effects of excessive Hg on nest predators.

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Appendix A. Comparison of Common Snapping Turtle (*Chelydra serpentina*) nest predation rates between reference (REF) and Hg sites along the South River, Virginia, USA (2013–2014), and relationships between predation (during the first month of incubation) and habitat characteristics. *P*-values are for comparisons between reference and Hg sites, and depredated nests versus those that were not depredated (mean ± SE), using logistic regressions.

	REF Sites		HG Sites		DEPREDATION IN HG SITES			
	n	Rate	n	Rate	Veg. Cover	Field Edge	Water Body	South River
DEPREDATED								
2013	0	–	31	65.6%	0	28.0 ± 4.8	39.9 ± 4.2	41.2 ± 7.3
2014	0	–	8	–	2.5 ± 2.5	11.9 ± 1.7	29.4 ± 6.5	26.1 ± 4.7
NOT DEPREDATED								
2013	39	100%	17	35.4%	6.7 ± 6.7	27.1±4.9	31.6 ± 6.8	157.5 ± 46.9
2014	23	–	32	–	0	20.8 ±4.5	38.8 ± 6.4	91.1 ± 29.0
P-VALUE								
2013	–	–	–	–	> 0.999	0.194	0.290	0.101
2014	–	–	–	–	0.998	0.146	0.475	0.290
POOLED					0.146	0.079	0.265	0.001

Appendix B. Comparison of habitat characteristics of Common Snapping Turtle (*Chelydra serpentina*) nest sites and randomly selected points in reference and Hg site along the South River, Virginia, USA, 2013–2014. The number of each type of characteristic measured is shown as n. Within sites, *P*-values are from univariate logistic regressions. Nest site characteristics (mean ± SE) are compared between reference and Hg sites, using either *t*-tests or Wilcoxon/Kruskal-Wallis tests.

	REFERENCE SITES					HG SITES					REF-V-HG	
	Nest		Random			Nest		Random			Nest	Random
Variable	n	Mean ± SE	n	Mean ± SE	*P*-value	n	Mean ± SE	n	Mean ± SE	*P*-value	*P*-value	*P*-value
CANOPY	62	0.7 ± 0.6	89	23.7 ± 3.9	0.012	88	1.1 ± 0.8	72	30.0 ± 5.3	0.002	0.746	0.341
BG	62	77.6 ± 3.0	89	23.4 ± 3.4	< 0.001	88	66.9 ± 3.0	72	18.5 ± 3.7	< 0.001	0.009	0.129
FORB	62	4.1 ± 0.6	89	20.1 ± 2.6	< 0.001	88	5.4 ± 1.4	72	17.7 ± 2.4	< 0.001	0.941	0.898
GRASS	62	1.3 ± 3.8	89	26.5 ± 3.8	0.005	88	8.0 ± 2.1	72	36.5 ± 4.4	< 0.001	0.001	0.016
CROP	62	8.9 ± 1.4	89	5.1 ± 2.4	0.339	88	4.1 ± 0.7	72	0.2 ± 0.2	0.002	0.004	0.035
WOOD	62	0	89	1.1 ± 0.4	0.991	88	< 0.05 ± 0	72	1.2 ± 0.4	0.128	0.399	0.905
DETRITUS	62	0.2 ± .1	89	4.5 ± 1.4	0.030	88	1.0 ± 0.3	72	7.6 ± 2.4	0.075	0.079	0.469
TREE	62	0.05 ± 0	89	1.9 ± 1.0	0.390	88	0.2 ± 0.1	72	1.2 ± 0.6	0.171	0.201	0.534
SHRUB	62	0	89	4.6 ± 2.0	0.994	88	< 0.05 ± 0	72	6.7 ± 2.5	0.224	0.399	0.312
ROCK	62	0.6 ± 0.3	89	0.6 ± 0.5	0.997	88	0.8 ± .03	72	0.2 ± 0.2	0.170	0.306	0.494
RIVER	61	37 ± 4	89	54.1 ± 5	0.010	71	71 ± 12	72	65 ± 7	0.636	0.043	0.415
WATER	61	36 ± 3	89	49 ± 4	0.023	77	37 ± 3	72	47 ± 4	0.055	0.935	0.423
FOREST	42	23 ± 3	48	49 ± 6	< 0.001	84	23 ± 4	20	60 ± 7	0.002	0.787	0.206
FIELD	41	21 ± 7	40	47 ± 7	0.001	83	23 ± 4	53	70 ± 11	0.004	0.885	0.085

Appendix C. Comparison of habitat characteristics of nest sites of Common Snapping Turtles (*Chelydra serpentina*) and randomly paired random points (mean ± SE) in reference and Hg sites along the South River, Virginia, USA, 2013–2014. The number of nests of each type is shown as n, results are from paired *t*-tests for all variables except percent water and distance to tributary which were tested using Wilcoxon signed-rank test. Mean paired difference (Diff.) is the percentage difference between nest sites and paired random points, and is relative to the nest site (i.e., nest sites in reference sites had 17.1% less canopy cover than at paired random points).

	REFERENCE SITES				HG SITES				REF-V-HG	
Variable	n	Nest mean	Diff.	*P*-value	n	Nest mean	Diff.	*P*-value	Nest *P*-value	Random *P*-value
CANOPY	17	0	-17.1	0.185	29	0.53 ± 0.53	-11.9	0.080	0.468	0.746
WATER	17	8.2 ± 0.6	-0.7	0.313	29	10.3 ± 0.4	0.2	0.639	**0.006**	0.164
BG	17	63.9 ± 6.9	11.4	0.136	29	51.1 ± 4.5	14.3	**0.040**	0.052	0.107
FORB	17	1.1 ± 0.5	-8.9	0.197	29	5.7 ± 2.1	-7.3	0.136	0.294	0.153
GRASS	17	3.1 ± 2.3	1.2	0.222	29	12.9 ± 3.7	-4.6	0.281	0.201	0.213
CROP	17	8.3 ± 1.4	1.8	0.296	29	4.0 ± 0.7	-1.3	0.282	**0.006**	**0.061**
WOOD	17	0	-1.6	> 0.15	29	0	-0.3	0.326	–	0.547
DETRITUS	17	0.14 ± 0.07	1.1	0.308	29	1.5 ± 0.6	-20.1	0.057	0.197	0.761
TREE	17	23.2 ± 6.5	5.0	0.492	29	21.2 ± 3.2	-0.4	0.471	0.341	0.107
SHRUB	17	0	0	–	29	0.3 ± 0.3	-0.5	0.326	0.278	0.468
ROCK	17	0	-7.7	–	29	0.03 ± 0.03	-17.5	0.345	0.447	0.523
RIVER	17	0.14 ± 0.07	0.04	0.580	29	1.4 ± 0.6	50.4	0.441	0.381	0.406
WATER	17	32.9 ± 4.7	.09	0.779	26	83.1 ± 27	7.7	0.217	0.489	0.287
FOREST	17	32.4 ± 4.7	0.2	0.131	26	35.3 ± 5.5	5.2	0.779	0.710	0.760
FIELD	14	19.8 ±5.2	-5.6	0.051	22	16.7 ± 2.1	-5.8	0.296	0.494	0.764