Generally specialized or especially general? Habitat selection by Snapping Turtles (*Chelydra serpentina*) in central Ontario

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Abstract: Habitat selection is the disproportionate use of habitat compared with availability. Many studies have focused on specialists, but few have considered habitat selection in populations that are generalists, which can be composed of generalist individuals or individuals that specialize on different habitats. We tested habitat selection and individual specialization in a northern population of a supposed generalist, the Snapping Turtle (*Chelydra serpentina* (L., 1758)), during the active season and winter using telemetry. Habitat selection was tested at two spatial scales by comparing random points to home ranges and turtle locations using Euclidean distances. Turtles selected home ranges from the habitats available in the population range. However, at the population level, all aquatic habitats were equally preferred, and the population behaved as a generalist owing to individuals specialized on different habitats. Over half of the individuals showed evidence of individual specialization on different habitat types. Turtles did not select habitat within home ranges during the active season, but overwintering turtles chose locations that were colder than haphazard stations in the same habitats, likely to reduce metabolic costs and the risk of acidosis. These findings have implications for the management of this species at risk and for understanding the evolution of resource generalization.

Résumé : La sélection d'habitat est une utilisation disproportionnée d'un habitat par rapport à sa disponibilité. Plusieurs études se sont intéressées aux spécialistes, mais peu ont considéré la sélection d'habitat dans des populations généralistes, qui peuvent être composées d'individus généralistes ou alors d'individus qui se spécialisent pour des habitats différents. Nous avons évalué la sélection d'habitat et la spécialisation individuelle dans une population nordique d'un généraliste présumé, la tortue serpentine (*Chelydra serpentina* (L., 1758)), durant la saison active et durant l'hiver à l'aide de la télémétrie. Nous avons évalué la sélection d'habitat à deux échelles spatiales en comparant des sites aléatoires aux domaines vitaux et aux positions individuelles des tortues par des distances euclidiennes. Les tortues choisissent leurs domaine vital parmi les habitats disponibles dans l'aire de répartition de la population. Cependant, au niveau de la population, les habitats aquatiques sont sélectionnés sans discrimination et la population se comporte en généraliste parce que les individus se spécialisent pour des habitats différents. Plus de la moitié des individus présentent des signes de spécialisation individuelle sur des types différents d'habitat. Les tortues ne choisissent pas d'habitat dans leur aire vitale durant la saison d'activité, mais les tortues qui hibernent choisissent des sites qui sont plus froids que les stations aléatoires dans ces mêmes habitats, qui sont susceptibles de réduire les coûts métaboliques et le risque d'acidose. Ces résultats ont des conséquences sur la gestion de cette espèce menacée et sur la compréhension de l'évolution de la généralisation des ressources.

[Traduit par la Rédaction]

Introduction

Understanding the spatial distribution of organisms in their environment is central to ecology (Krebs 1972). Typically, habitats are heterogeneously distributed through space and time, and individuals that can minimize costs and maximize the quality of resources will have a fitness advantage (Thomas and Taylor 2006). Habitat selection occurs when resources are used disproportionately to their availability (Johnson 1980) and should reflect choices made by the organism (Huey 1991). Many habitat selection studies have used common widespread species to test theoretical predictions (Gilliam and Fraser 1987; Morris 1989; Fontaine and Martin 2006), but there has been a recent shift in research to focus on habitat selection studies in species that are of conservation concern, and these species tend to be habitat specialists (Edge et al. 2010; Rasmussen and Litzgus 2010). Less recognized is the effect individual specialization has on population resource selection. Although specialization of different phenotypes on different habitat types has been demonstrated in some birds (Ebenman and Nilsson 1982), and evidence for individual diet specialization has been found in lizards (Lister 1976) and in some snails (West 1986), there are still large knowledge gaps regarding individual specialization and its effects on resource selection. Variation in behaviour between populations (Ligon and Peterson 2002; Rees et al. 2009) and within populations (Roe and Georges 2008) has been shown to be important in some turtle species and may represent

physiological constraints, heritable traits, and (or) behavioural plasticity in response to environmental factors. Resource selection may also undergo ontogenetic shifts (Stamps 1983; Lind and Welsh 1994) or differ between the sexes (Ardia and Bildstein 1997; Bull 2006). The niche width of a population is narrow for specialists and wide for generalists, and is composed of a within-individual component (WIC) and a between-individual component (BIC) (Roughgarden 1972). Generalist species that have large niche widths can be composed of either individuals that are generalists in resource use (WIC high, BIC low), or individuals that specialize on different resources (WIC low, BIC high) (Bolnick et al. 2003). Whether a generalist population is composed of individual specialists on different resources can have significant implications for its distribution, resource requirements, management, and evolution.

Comparing habitat use to availability is required to demonstrate selection, but explicitly defining what is available to an individual or population is difficult because researchers impose their own bias of "availability" to a system (Johnson et al. 2006). Using a hierarchical approach to studying habitat selection allows researchers to examine selection choices at defined and biologically relevant spatial scales, and to thereby test relevant hypotheses regarding resource use. Johnson's (1980) orders of selection explicitly define hierarchical levels: first-order selection of the population range from the geographic range; second-order selection of home ranges from the population range; and third-order selection of locations within the home range. These classifications are useful because they allow inference about the scale at which an organism selects habitat. Studying habitat selection in this framework is useful for managing and protecting wildlife that are threatened by habitat destruction and fragmentation because it identifies important resources at relevant scales.

The types of resources that are selected or preferred depend on the spatial distribution and availability of each resource in the environment and the requirements of different species (e.g., physical barriers, physiological constraints). Freshwater turtles may select habitats based on a number of resources, including food (Compton et al. 2002), mates (Morreale et al. 1984; Gibbons 1986), oviposition sites (Schwarzkopf and Brooks 1987; Wilson 1998; Standing et al. 1999), refuges (Huey 1991), and overwintering sites safe from freezing, acidosis, and predators (Brooks et al. 1991; Greaves and Litzgus 2007, 2008; Edge et al. 2009; Rasmussen and Litzgus 2010). During the active season in Ontario (April–October), turtles move through the environment searching for resources to meet growth, maintenance, and reproductive needs. The home-range size of individual turtles depends on these resource requirements and resource availability in their habitats. Because female turtles invest more energy in reproduction than males (Congdon et al. 1983; Marlen and Fischer 1999), they often have larger home ranges (Litzgus and Mousseau 2004). However, males of some species exhibit larger home ranges than females owing to mate-searching behaviour (Morreale et al. 1984; O'Connor et al. 1994; Bernstein and Richtsmeier 2007).

Turtles spend the other half of the year (November–March) inactive at overwintering sites (Ultsch 2006). The long and cold winters of temperate North America have significant consequences for the ecology and life history of turtles (St.

Clair and Gregory 1990; Brown and Brooks 1994; Edge et al. 2009) and the selection of an appropriate overwintering site may be the difference between survival and death. A number of stressors can affect overwintering turtles, including predators, parasites, fungal and bacterial infections, temperature, and dissolved oxygen content (Brooks et al. 1991; Brown and Brooks 1994; Ultsch 2006). However, the most common two external stressors that affect survival are freezing temperatures and low oxygen. Extremely cold temperatures increase the risk of freezing to death, and low oxygen levels in the water and the inability to breathe owing to ice cover may lead to metabolic and respiratory acidosis in hibernating aquatic turtles (Ultsch and Jackson 1982; Reese et al. 2002, 2004). Physiological adaptations to these stressors determine overwintering strategies used by different species and therefore affect required resources during that time period. Measuring physical characteristics at turtle hibernacula can help managers identify and protect appropriate hibernacula, which are considered critical habitat. Water depth can affect both the temperature and dissolved oxygen content that individuals experience over the winter because areas that freeze to the substrate increase the risk of freezing mortality and create anoxic environments, but areas that contain deep water may pose more risk for predation by river otters (*Lontra canadensis* (Schreber, 1777)) (Brooks et al. 1991).

The Snapping Turtle (*Chelydra serpentina* (L., 1758)) is a large freshwater turtle that reaches its northern range limit in Ontario (Conant and Collins 1998; Ernst and Lovich 2009). Snapping Turtles are regarded as habitat generalists and are found in a wide variety of aquatic habitats including lakes, ponds, rivers, and various wetlands, but also make extensive overland trips through forested habitat (Obbard and Brooks 1981; Brown et al. 1994; Ernst and Lovich 2009). Although there have been a number of descriptive habitat studies published on this species, none have investigated habitat selection (comparing use with availability) in the wild. Although this species is widespread (Conant and Collins 1998; Ernst and Lovich 2009) and relatively abundant, it has been listed as Special Concern in Canada because some of its life-history traits (e.g., delayed maturity, low recruitment) make populations especially vulnerable to human threats (COSEWIC 2008). Understanding habitat selection by this generalist species can inform recovery actions that include identification of critical habitat, and this information has implications for developing management strategies to prevent extirpation of populations.

We examined habitat selection by adult Snapping Turtles near their northern limit during the active season at two different spatial scales (second-order selection of home range from the population range and third-order selection of locations within the home range; Johnson 1980) and during the winter when turtles are inactive at low temperatures. After a preliminary field season tracking this population, we observed individuals spending large amounts of time in specific habitats and that different turtles appeared to be using different habitat types. These observations led us to test the hypothesis that, during the active season, Snapping Turtles are aquatic habitat generalists at the population level because of individual specialization on different habitats. We predicted that at the population level, selection of all aquatic habitats over upland would be evident, but that there would be no

preference among aquatic habitats. In addition, we predicted that the BIC of the population's niche width would be high and that individual habitat niche widths would differ from the niche width of the population. We hypothesized that home-range size would vary between the sexes and among seasons to accommodate high resource requirements for reproductive females and temporal variation in food availability. We predicted females would have larger home ranges than males and that home ranges would be largest in the summer when females are reacquiring resources invested in that year's reproduction. We also tested the hypothesis that turtles select overwintering sites based on cold temperatures to minimize acidosis because colder water holds more dissolved oxygen and would further depress metabolic rates of individuals, which would lower energetic and oxygen demands. We predicted that turtle body temperatures during winter would be colder than haphazard stations in the same habitats, and that dissolved oxygen levels would not differ between turtles and haphazard stations in the same habitat.
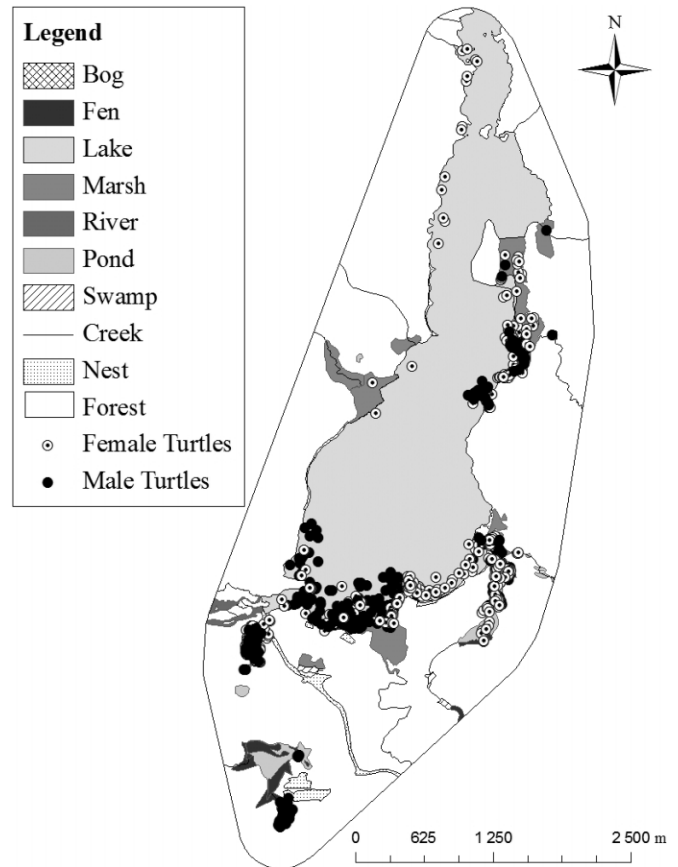
Materials and methods

Study site

The 1033 ha study site is on the northeast side of Algonquin Provincial Park, Ontario (17T E728000, N509400) and consists of a mosaic of wetlands in an upland softwood forest with a central lake (Fig. 1). The site is relatively undisturbed, with a number of areas designated for camping, recreational fishing, and controlled logging. Access to the site is limited to one logging road. Wetlands were classified into one of five categories based on the Canadian Wetland Classification System (Warner and Rubec 1997), and the remaining habitat was categorized, based on water source, substrate, and vegetation, into five additional habitat types not described by the classification system (Table 1). The entire site was mapped using ArcGIS version 9.2 (Environmental Systems Research Institute (ESRI), Inc., Redlands, California, USA) using a combination of existing mapping databases, orthophotographs, and ground truthing with a handheld GPS (GPSmap 76CSx; Garmin, Kansas City, Kansas, USA).

Data collection

Adult Snapping Turtles were captured using a combination of visual surveys, dip nets, and hoop traps baited with sardines from April to June 2009 and 2010. Each individual received a metal tag with a unique alphanumeric code wired to the rear marginal scutes of the carapace (Loncke and Obbard 1977). Turtles were sexed using eversion of hemipenes when possible, or the ratio of posterior plastron lobe to precloacal tail length (Mosimann and Bider 1960). Once caught, turtles were outfitted with radio transmitters (6 from Holohil Systems, Carp, Ontario, Canada, and 16 from Advanced Telemetry Systems (ATS), Isanti, Minnesota, USA). The ATS transmitters were attached to the middle of the carapace using marine epoxy (LePage, Brampton, Ontario, Canada). Holohil Systems transmitters were attached by wiring the flaps of the radio onto the rear marginals of the carapace using copper wire, then covering the wire with epoxy to strengthen the attachment and reduce drag in vegetation. The holes in the rear marginal scutes for attaching the transmitter were made with a manual drill. The entire package attached to the turtle

Fig. 1. Study site in Algonquin Provincial Park, Ontario, showing the population range (1033 ha) of Snapping Turtles (*Chelydra serpentina*) estimated using 964 radiolocations (circles) over the active seasons of 2009 ($n = 11$ turtles) and 2010 ($n = 11$ turtles).

weighed <15 g and represented <1% of each individual's body mass. All work was carried out under an approved Laurentian University Animal Care Committee protocol and was authorized by permits from the Ontario Ministry of Natural Resources.

Only turtles with at least 20 radiolocations were included in the analyses, and seasonal home ranges (see below) were only estimated for turtles with at least seven locations in each season. Eleven turtles were included for 2009, and eleven for 2010. Although nine of the turtles were tracked both years, each year of data was treated as an independent sample of home range and habitat selection ($n = 22$; 10 males and 12 females). Turtles were located every 1–3 days from April to September and every 5–7 days in October using a unidirectional three-element Yagi antenna and an R410 Scanning Receiver (ATS). Locations were recorded with a handheld GPS (GPSmap 76CSx) and uploaded to ArcGIS version 9.2.

The active season was split into three seasonal categories based on biologically relevant processes: prenesting, nesting, and postnesting (Table 2). The prenesting season began the date the turtles first left their overwintering sites and ended when the first gravid female (determined by palpation) was found. The nesting season was defined as the day the first gravid female was found until the last known female had oviposited. The postnesting season was from the end of nesting

Table 1. Classification of habitat types in the population range of radio-tagged Snapping Turtles (*Chelydra serpentina*) in Algonquin Provincial Park, Ontario.

Habitat	Substrate	Water source	Water table	Vegetation
Bog	Peat	Precipitation	At or slightly below surface	*Sphagnum* dominated
Creek*	Variable	Variable	Above the surface, flowing, breadth <3 m	Variable, confined to shoreline
Fen	Peat	Groundwater	Fluctuating	Graminoid species and brown mosses
Lake*	Variable	Variable	Above surface >2 m	Variable, but confined mainly to shorelines and bays
Marsh	Mineral	Variable	Shallow and fluctuates dramatically	Emergent aquatic macrophytes
Nest*	Sand or gravel	Precipitation	Below surface	Sparse trees and (or) forbs
River*	Mineral	Variable	Above surface, flowing, breadth >3 m	Variable, confined to shoreline
Swamp	Peatland and (or) mineral	Groundwater	At or below the surface	Woody plants often>1m high (shrubs, trees)
Pond	Mineral	Variable	Free surface water up to 2 m deep	Submerged or floating aquatic plants (<25% of area)
Forest*	Variable	Precipitation	Below surface	Dominated by trees

Note: Wetlands were classified using the Canadian Wetland Classification System (Warner and Rubec 1997), and the remaining habitats (indicated by an asterisk) were classified into five habitats.

Table 2. The dates for the three biologically relevant seasons used to describe home-range size in Snapping Turtles (*Chelydra serpentina*) in Algonquin Provincial Park, Ontario, during 2009 and 2010.

	Season		
Year	Prenesting	Nesting	Postnesting
2009	30 April – 30 May	1–25 June	25 June – 10 October
2010	27 April – 27 May	28 May – 13 June	14 June – 5 October

until approximately the second week of October, when turtles were at overwintering sites.

Home ranges

Home-range sizes were calculated using 100% minimum convex polygons (MCPs) using the HAWTHS Tools (Beyer 2004) extension in ArcGIS. For habitat selection analyses, home ranges were estimated as 95% kernels with an area that equalled the individual's 100% MCP (Row and Blouin-Demers 2006; Edge et al. 2010). Kernels were constructed using a smoothing factor that resulted in the kernel area equalling the 100% MCP. Therefore the home ranges had the same areas as the MCPs, but their kernel density determined the shapes. Home ranges were compared between the sexes and among seasons using a two-way ANOVA on log-transformed data. A Tukey HSD test was used to examine which seasons had significantly different home-range sizes. Estimates of home-range sizes from radio-tracked animals are sensitive to both sample size and sampling rate (Swihart and Slade 1985; Girard et al. 2002). Because inadequate sampling can result in underestimates of home-range size, we tested the relationships between individual home-range size and number of locations for annual and seasonal data using an ANCOVA with carapace length as a covariate to ensure that we had adequate sampling to estimate home ranges (Girard et al. 2002).

Habitat selection

We measured habitat selection during the active season in two ways. First, we used Johnson's (1980) hierarchical approach to determine at what spatial scale habitat selection may be occurring. Second, we used Petraitis' (1979) likeli-

hood approach for niche width to determine whether Snapping Turtles are habitat generalists at the population level as a result of individual specialization on different habitats. Hierarchical habitat selection was measured using the method based on Euclidian distances (Conner and Plowman 2001) at two spatial scales: second-order selection and third-order selection. Habitats at larger resolutions are considered to be available to the animal at finer resolutions; therefore, at each scale, habitats are selected from those habitats available one level up in the hierarchy (Bissonette et al. 1997). Random points ($n = 964$) were generated within the population range, defined as the MCP of radiolocations for all individuals with a 375 m buffer. The MCP for all points would not include all home ranges because individual home ranges were constructed using 95% kernels, which extend borders around outer points with high densities of locations. A 375 m buffer was the minimum distance that contained all individual kernel home ranges. The number of random points equalled the total number of turtle telemetry points ($n = 964$). For the analysis of second-order selection, habitat availability was measured as the mean distance from random points to each habitat type (r_{ij}) in the population range, for each habitat j by individual i. Habitat use was quantified as the mean distance from random points within each turtle's home range to each habitat type (u_{ij}). A matrix of ratios was calculated for each habitat for each individual ($d_{ij} = u_{ij} / r_{ij}$), and if turtles were selecting home ranges randomly, then the expected mean ratio for each habitat would be one. Values <1 represent preference for a habitat, whereas values >1 indicate avoidance of that habitat. For third-order selection, habitat availability was measured as the mean distance from random

points within home ranges to each habitat type (r_{ij}), and habitat use was quantified as the mean distance from telemetry points to each habitat type (u_{ij}). Similarly, a matrix of ratios was calculated for each habitat for each turtle. For each scale of selection, a MANOVA was used to test if the mean distance ratios (mean d) for each habitat were significantly different than one (random habitat use) using individual turtles as replicates. If there was evidence of selection at a given scale, then post hoc analyses tested which habitats were being used disproportionately to availability. To test which habitat ratios were significantly different than one, t tests with a Bonferroni correction for multiple tests ($\alpha = 0.05/10$ habitats $= 0.005$) were used. In addition, habitats were ranked using pairwise comparisons with a Tukey HSD test.

To test whether the population's generalist habitat selection strategy was due to individual habitat generalists or individual specialists on different habitats, we measured the area of each habitat type inside an individual's home range using ArcGIS. We used an approach analogous to tests of individual specialization in diet based on mass or number of items in different categories (Bolnick et al. 2002, 2003). Let **N** be a matrix where elements n_{ij} are the areas (ha) for individual i's home range containing habitat j. This matrix was transformed to p_{ij}, which are the proportions for individual i's home range containing habitat j:

$$[1] \qquad p_{ij} = n_{ij} / \sum_j n_{ij}$$

The variable q_j is the proportion of the jth habitat in the population's habitat niche:

$$[2] \qquad q_j = \sum_i n_{ij} / \left(\sum_i \sum_j n_{ij} \right)$$

We measured individual specialization for home-range habitat composition using the likelihood approach for measuring niche width (Λ) adapted for individuals (Petraitis 1979; Bolnick et al. 2002), which uses the product (Π) of likelihood ratios comparing the population's habitat niche (q_j) to each individual's habitat niche (p_{ij}):

$$[3] \qquad \Lambda_i = \Pi_j (q_j / p_{ij})^{n_{ij}}$$

The likelihood values were standardized to account for individual differences in home-range size (HR_i) using the equation (Petraitis 1979):

$$[4] \qquad W_i = (\Lambda_i)^{1/HR_i}$$

The value W estimates the degree of overlap in the habitat composition of home ranges between each individual and the population. It ranges from zero (individual specializing on only one habitat) to one (individual habitat niche the same as the population's) and the mean (mean W) represents the degree of individual specialization in the population. To determine if individual home-range compositions significantly deviated from the population's habitat composition, we used the equation:

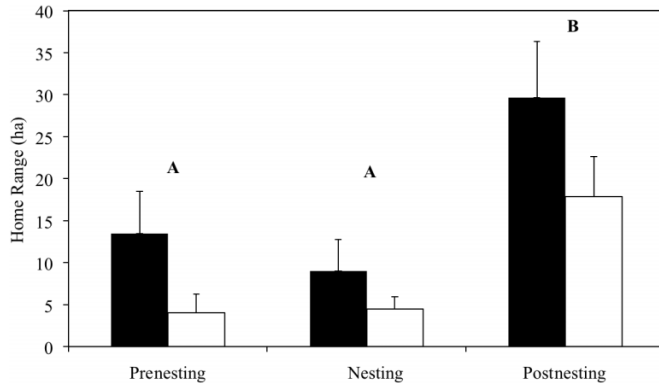$$[5] \qquad J_i = -2 \ln (\Lambda_i)$$

This equation has an approximately χ^2 distribution with ($r - 1$) degrees of freedom (Petraitis 1979), where r is the number of habitat types (10). Therefore, P values were generated for each individual using J with 9 degrees of freedom. A

χ^2 test was used to compare rates of individual specialization between males and females.

Overwintering site selection

To study selection of overwintering sites, we measured three variables important for survival during this period: temperature, dissolved oxygen, and water depth. Turtles were tracked once per month for one winter, from November 2009 to March 2010. To estimate body temperature during hibernation, temperature data loggers (iButtons; Maxim, Sunnydale, California, USA) were attached to the rear carapace of turtles in October 2009 using marine epoxy (LePage) and recorded the temperature every 120 min. To compare estimates of body temperatures of turtles to those available in the surrounding aquatic environment, 40 haphazard stations were deployed in November and December of 2009 in four different habitats (creek, lake, marsh, and pond) within the study site. Haphazard rather than purely random stations were used because of difficulty accessing the site during the winter; stations were placed in locations that could be safely sampled on the ice during winter months (after the method of Edge et al. 2009). At least three stations were placed in each water body, and if possible, more than one of each habitat type was used. Ten stations were placed in creeks: four stations were in one, and three each in two others. Three stations were placed in the one lake in the study area. Nine stations were placed in three marshes (three each), and 15 stations were placed in five ponds (three each). The temperature data loggers at the stations were synchronized with the data loggers on turtles. The data loggers were waterproofed with Plasti-Dip (Plasti-Dip International, Blaine, Minnesota, USA) and then attached with epoxy to either a brick or a pine strapping. The stations were deployed so that the temperature data loggers were buried 2–5 cm into the substrate because in the late fall the turtles were buried in mud and not resting on top of the bottom substrate. Mean monthly temperatures were compared between turtle body temperatures and haphazard stations in different habitat types using a repeated-measures ANOVA (type III). For post hoc analyses, Wald tests (Wald 1943) were used to compare linear models of turtle temperatures to linear models of haphazard station temperatures in each habitat. In November 2009, the water depth (water surface to substrate; cm) was measured at turtle and haphazard stations using a metre stick. Fall water depths were compared among the different habitat types and turtles using an ANOVA on log-transformed data. A dissolved oxygen meter (YSI 556 MPS; YSI Inc., Yellow Springs, Ohio, USA) was used to measure dissolved oxygen concentration (mg/L) at turtle and haphazard stations. A hole was drilled through the ice with a 7 cm hand auger during March, when oxygen levels below the ice would be the lowest, and the YSI probe was inserted through the hole to measure dissolved oxygen in the water column at the substrate surface. The dissolved oxygen concentrations were compared between haphazard stations and turtle locations using an ANOVA. Post hoc analyses on fall water depth and dissolved oxygen concentrations were done using Tukey HSD tests. Data are presented using means and standard errors unless stated otherwise. All statistical analyses were done using R (R Foundation for Statistical Computing, Vienna, Austria).

Fig. 2. Seasonal home-range sizes (mean + SE) of female (solid bars; $n = 10$) and male (open bars; $n = 12$) Snapping Turtles (*Chelydra serpentina*) in Algonquin Provincial Park, Ontario, during 2009 and 2010. Postnesting home ranges were larger than prenesting and nesting home ranges ($P < 0.05$), as indicated by the letters above the bars. Female home ranges were larger than male home ranges ($F_{[1,18]} = 5.6$, $P < 0.05$).

Fig. 3. Distance ratios ($d = u_j / r_j$; mean + SE) for second-order habitat selection of home ranges from the population range by Snapping Turtles (*Chelydra serpentina*) ($n = 22$) in Algonquin Provincial Park, Ontario, in 2009–2010 using 964 random points. Habitats are ranked most preferred (left) to least preferred (right), and habitats with an asterisk have a d value significantly different than 1 (corrected $\alpha = 0.005$), indicating selection for that habitat.
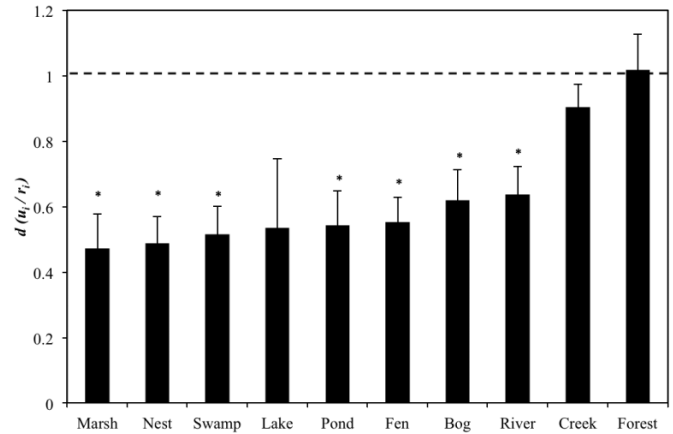

Results

Home ranges

The number of radiolocations was not related to seasonal home-range sizes in the prenesting season ($F_{[2,9]} = 1.36$, $P = 0.21$), nesting season ($F_{[2,14]} = 1.19$, $P = 0.25$), or postnesting season ($F_{[2,18]} = 0.07$, $P = 0.94$) based on ANOVAs using carapace length as a covariate. Similarly, there was no relationship between the number of radio locations and annual home-range size ($F_{[2,18]} = 0.11$, $P = 0.92$) based on an ANCOVA using carapace length as a covariate. Both season ($F_{[2,21]} = 8.84$, $P < 0.001$) and sex ($F_{[1,21]} = 5.25$, $P < 0.05$) affected the home-range size (log-transformed) of turtles (Fig. 2), but the interaction of season and sex on home-range size was not significant ($F_{[2,21]} = 0.60$, $P = 0.55$). Female home ranges were larger than those of males and home ranges were larger for both sexes in the postnesting season than in the nesting ($P < 0.0001$) and prenesting ($P < 0.01$) seasons. Home-range sizes did not differ between the nesting and prenesting seasons ($P = 0.94$).

Habitat selection

We found evidence of second-order habitat selection ($F_{[10,12]} = 47.63$, $P < 0.0001$). Distances to habitats in the population range from points within home ranges were significantly different than distances from random points in the population range ($\alpha = 0.005$) except for creek ($P = 0.18$), lake ($P = 0.04$), and upland forest ($P = 0.88$) habitat types (Fig. 3). Marsh, nesting, and swamp habitats were the most preferred (lowest mean d values), followed by ponds, lake, and fen. River, creek, and upland forest had the highest mean d values. Habitat ranking using pairwise comparisons (summarized in Table 3) showed few differences in habitat preference, suggesting that the Snapping Turtles in our study are habitat generalists. The only mean d values that were significantly different were between marsh, nesting, and swamp habitats compared with upland forest ($P < 0.05$; Table 3).

There was no evidence of third-order habitat selection ($F_{[10,12]} = 1.97$, $P = 0.13$) and there was no difference in distances to habitat types between random points within home ranges and actual telemetry points.

The habitat composition of the home ranges of individual turtles varied from generalized to very specialized. The W values ranged from 0.04 to 1 (mean $W = 0.66 \pm 0.08$). P values using the χ^2 distribution to assign individuals to generalists or specialists resulted in 12 of 22 turtles (55%) being classified as specialists based on the proportional areas of habitats in their home range (Table 4). There was no difference in the propensity for specialization between males and females ($\chi^2_{[1]} = 0.40$, $P > 0.05$).

Overwintering site selection

Snapping turtles hibernated in a variety of habitats including creek ($n = 2$ turtles), marsh ($n = 1$), pond ($n = 4$), and lake ($n = 4$). One temperature logger in the lake failed, and this habitat was removed from temperature analyses because variance could not be estimated for only two stations. Mean monthly temperatures differed among turtles and haphazard stations in different habitat types ($F_{[4,26]} = 3.14$, $P < 0.05$) and among months ($F_{[3,24]} = 7.04$, $P < 0.001$) (Fig. 4). The mean body temperatures of turtles (1.29 °C) were significantly lower than mean water temperatures at haphazard stations in ponds, marshes, and creeks ($P < 0.05$), and mean temperatures at haphazard stations (2.59 °C) did not differ among habitats ($P > 0.05$ for all comparisons). Fall water depths differed significantly among categories ($F_{[4,16]} = 10.19$, $P < 0.001$) (Fig. 5). However, pairwise comparisons only detected a difference in water depth between lake and creek habitats ($P < 0.001$), and creek and pond habitats ($P < 0.01$). The mean fall water depths at turtle overwintering sites were not different from depths at haphazard stations in any of the habitat types ($P > 0.05$). Dissolved oxygen levels at overwintering sites used by turtles ranged widely among individuals (0.55–15.63 mg/L). Dissolved oxygen concentration varied among categories ($F_{[4,15]} = 33.93$, $P < 0.00001$) (Fig. 6). Pairwise comparisons detected differences between the mean dissolved oxygen concentration at turtle sites and the haphazard stations in the lake ($P = 0.03$). Lake and creek habitats had higher dissolved oxygen concentra-

Table 3. Adjusted P values (significantly different comparisons are in boldface type) from pairwise comparisons (a Tukey HSD test) of mean distance ratios (mean d) for habitat selection of home ranges from the population range by Snapping Turtles (*Chelydra serpentina*) in Algonquin Provincial Park, Ontario, during 2009 and 2010.

	Mean d	Marsh	Nesting	Swamp	Lake	Pond	Fen	Bog	River	Creek
Marsh	0.472									
Nest	0.487	1.000								
Swamp	0.515	0.999	1.000							
Lake	0.534	0.999	0.999	1.000						
Pond	0.542	0.999	0.999	1.000	1.000					
Fen	0.552	0.999	0.999	1.000	1.000	1.000				
Bog	0.620	0.994	0.998	0.999	0.999	0.999	0.999			
River	0.636	0.988	0.990	0.999	0.999	0.999	0.999	1.000		
Creek	0.905	0.152	0.188	0.274	0.344	0.377	0.416	0.718	0.783	
Forest	1.017	**0.020**	**0.027**	**0.047**	0.066	0.076	0.089	0.249	0.306	0.999

Note: Habitats are ranked from most preferred (low mean d values) to least preferred (high mean d values).

Table 4. Standardized niche overlap values (W_i) for Snapping Turtles (*Chelydra serpentina*) ($n = 22$) in Algonquin Provincial Park, Ontario, for 2009 and 2010.

Year	Sex	W_i
2010	**Male**	**0.04**
2010	**Male**	**0.08**
2009	Male	0.1
2009	**Male**	**0.14**
2010	**Female**	**0.16**
2009	**Female**	**0.16**
2009	**Male**	**0.36**
2009	**Female**	**0.8**
2009	**Male**	**0.81**
2010	**Female**	**0.81**
2009	Male	0.83
2010	**Male**	**0.83**
2009	Female	0.85
2009	**Female**	**0.88**
2010	Male	0.91
2010	Female	0.92
2009	**Female**	**0.96**
2009	Male	1
2010	Female	1
2010	Female	1
2010	Male	1
2010	Male	1

Note: Values in boldface type represent individuals who had home-range habitat compositions significantly different than the niche of the population's habitat composition ($P < 0.05$).
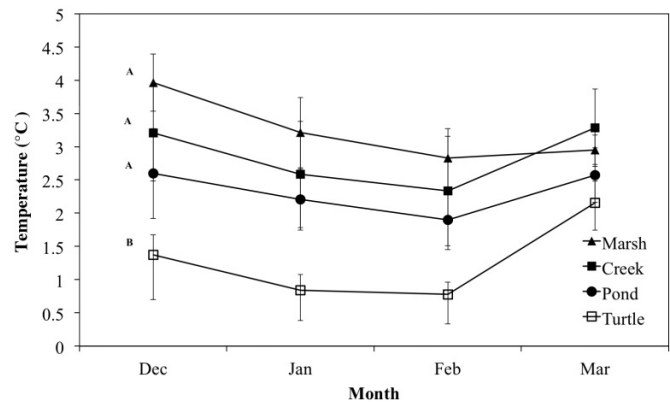
Fig. 4. Monthly body temperatures (mean ± SE) of Snapping Turtles (*Chelydra serpentina*) ($n = 9$) and monthly temperatures at haphazard stations in pond ($n = 12$), marsh ($n = 7$), and creek ($n = 9$) habitats in Algonquin Provincial Park, Ontario, during the winter of 2009–2010. A repeated-measures ANOVA showed significant differences among categories ($F_{[4,27]} = 2.94$, $P < 0.05$), and turtles were significantly colder than haphazard stations in all three habitats.

tions than marshes and ponds ($P < 0.05$). Dissolved oxygen levels were similar among turtles, marsh, pond, and creek habitats ($P > 0.05$ for all comparisons).

Discussion

Home ranges

We found support for the hypotheses that home-range size differed between the sexes because of different reproductive strategies, and that home ranges differed among seasons. Seasonal home ranges were largest in the postnesting season, and approxi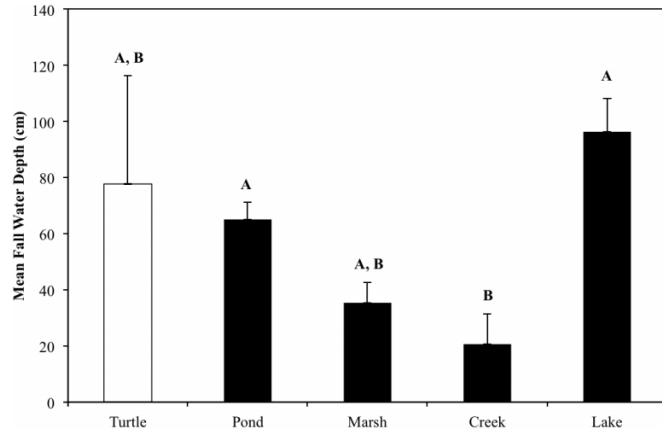mately the same size in the prenesting season and nesting season (Fig. 2). The seasonal change in home-range size may be due to increased foraging activity during the warmer months (Brown and Brooks 1993). Female home ranges were larger than those of males and may be the result of long distance movements to nesting habitat in June (Obbard and Brooks 1980). However, in our population, female home ranges were largest in the postnesting season, not in the nesting season. Although females travelled to specific nesting sites, their resulting home ranges were similar to those of males, likely because of foraging or mate searching behaviour at this time. Because female turtles invest much more energy in offspring than males (Congdon et al. 1983; Marlen and Fischer 1999), large home ranges may be required after the nesting season since females search a wider area to recoup energetic losses from the eggs just laid and to acquire energy for next years' reproductive output. The smaller home ranges of males during the nesting season may be due to individuals positioning themselves near bottlenecks for female migration or near nesting areas to intercept females for mating opportunities (Brown and Brooks 1993).

Both sexes in our population had larger home ranges than reported elsewhere for this species (Obbard and Brooks

Fig. 5. Fall water depth (mean + SE) at Snapping Turtle (*Chelydra serpentina*) overwintering locations (*n* = 9) and haphazard stations in pond (*n* = 15), marsh (*n* = 9), creek (*n* = 10), and lake (*n* = 3) habitats in November 2009. Treatment group significantly affected water depths ($F_{[4,16]}$ = 10.19, $P < 0.001$), but turtle overwintering sites were not significantly different in water depth than any of the habitat types with haphazard stations ($P > 0.05$).
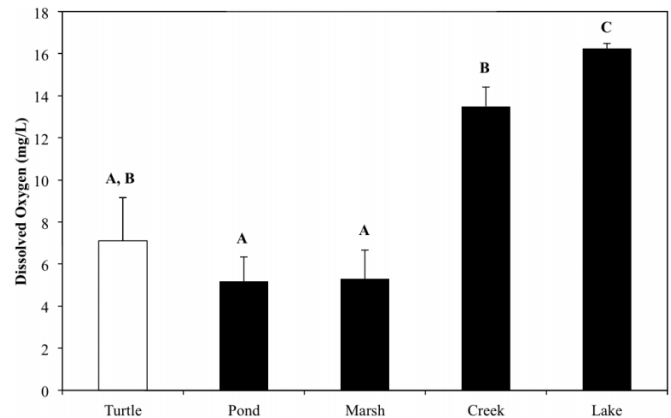

Fig. 6. Dissolved oxygen concentrations (mean + SE) in Snapping Turtle (*Chelydra serpentina*) overwintering sites (*n* = 7) and haphazard sites in pond (*n* = 12), marsh (*n* = 6), creek (*n* = 10), and lake habitats during March 2010 in Algonquin Provincial Park, Ontario. The dissolved oxygen levels differed among categories ($F_{[4,15]}$ = 33.93, $P < 0.00001$) and turtle overwintering sites had lower dissolved oxygen than haphazard stations in the lake, as indicated by the letters above the bars. Dissolved oxygen levels did not differ between turtles and stations in pond, marsh, and creek habitats ($P > 0.05$).

1981; Brown and Brooks 1993; Pettit et al. 1995; De Solla et al. 1999). Home-range size requirements may vary greatly among populations because of differences in wetland productivity and nest-site availability. Northern locales have lower productivity (Dunn et al. 2000), which may require individuals to have larger home ranges to acquire adequate resources (Brown et al. 1994). Also, because inadequate incubation temperatures may limit the northern range limit of turtles (Bobyn and Brooks 1994), appropriate nest sites are likely limiting factors for many populations of temperate turtles. Differences in productivity, habitat distributions, and population densities may mask the effect of reproductive strategies on home-range sizes in turtles.

Habitat selection

Snapping Turtles showed evidence of selection of habitats in home ranges from those available in the population range (second-order selection). Turtles preferred home ranges that were farther from forested upland habitat than random points, and closer to wetland and nesting habitats than random points. The selection of home ranges close to nesting habitats, even by male turtles, suggests males position themselves close to these areas to increase mating opportunities, as noted above and suggested by Brown and Brooks (1993). There were no differences in preference for specific aquatic habitat types (Table 3) and, as predicted, our study population appears to be an aquatic generalist that uses a broad variety of habitat types. There was no evidence of selection of habitats at locations from those available within home ranges (third-order selection), further supporting our hypothesis that Snapping Turtles are habitat generalists. Turtle locations had similar distances to each habitat type as random points within home ranges, suggesting that habitat selection does not occur at this scale in our study population.

Individual specialization on different habitat types appears to be widespread in our study population (12 out of 22 turtles specialized). The low mean *W* (0.66) indicates significant individual specialization; however, the lack of published data

on individual habitat specialization makes comparisons difficult. The high rate of individual specialization on habitats during the active season in our population has significant implications for management. Instead of focusing on specialized wetland types, managers should protect large wetland systems that contain high densities of turtles and a variety of habitats. In addition, owing to the lack of knowledge on hatchling and juvenile habitat requirements, future work should target these age classes to fully understand resource preferences and specialization in this species because these attributes may display ontogenetic shifts (Ernst and Lovich 2009). Future work should also test whether individual specialization on different habitats is a heritable or plastic trait, as this would dictate the significance of losing individuals from specific habitat types. Our study included data from only two field seasons, but Snapping Turtles are long-lived, and it is possible that an individual could be deemed a specialist on different habitats in different years, and thus on a broader temporal scale be exhibiting generalist behaviour.

Overwintering site selection

In support of our prediction, we found evidence that radio-tagged Snapping Turtles selected overwintering sites with colder temperatures than the surrounding environment (Fig. 4). Turtles hibernated in a number of habitats (creek, pond, marsh, and lake), but chose sites with temperatures that approached freezing and were cooler than much of the rest of the available habitat. Choosing colder overwintering sites may reduce metabolic costs (because metabolic rate is directly tied to body temperature in ectotherms) during winter and help decrease metabolic acidosis (Herbert and Jackson 1985*a*, 1985*b*). Selection of cold overwintering sites has been demonstrated in the field for a number of temperate freshwater turtle species near their northern range limits, including Blanding's Turtles (*Emydoidea blandingii* (Holbrook, 1838)) (Edge et al. 2009), Spotted Turtles (*Clemmys guttata*

(Schneider, 1792)) (Litzgus et al. 1999; Rasmussen and Litzgus 2010), and Wood Turtles (*Glyptemys insculpta* (LeConte, 1830)) (Greaves and Litzgus 2007, 2008). The selection of cold overwintering sites appears to be a strategy employed by all freshwater turtle species so far tested in northern temperate climates, indicating that there must be a fitness advantage to such thermal behaviour.

In further support of our prediction, there was no evidence to suggest that Snapping Turtles selected overwintering sites based on levels of dissolved oxygen (Fig. 6). Snapping turtle overwintering sites varied greatly in their dissolved oxygen concentrations (0.55–15.63 mg/L), and these values are in the range reported at hibernacula on the west side of Algonquin Park (Brown and Brooks 1994). In laboratory studies, Snapping Turtles have been shown to be anoxia tolerant (Reese et al. 2002), and our field data support this conclusion. The large variation in dissolved oxygen levels recorded at hibernacula was because some individuals overwintered in anoxic substrates, whereas other turtles moved out of eutrophic wetlands and hibernated in creeks, where there were high levels of dissolved oxygen. The hibernacula of Snapping Turtles on the west side of Algonquin Park were categorized into three types by Brown and Brooks (1994): stream sites, shore sites, and muddy sites. Most turtles in our study also used sites that fell into one of these three categories, indicating that overwintering site selection may be similar across populations. Snapping Turtles overwintered at sites that varied widely in water depth, and water depth did not differ significantly between turtle sites and haphazard stations, suggesting that temperature is more important in site selection than the risk of predation by otters in deeper, open water. In summary, we found support for the hypothesis that Snapping Turtles select overwintering sites with lower temperatures regardless of dissolved oxygen content, likely to reduce metabolic costs and reduce metabolic acidosis.

Acknowledgements

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