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Conservation Genetics of Wood Turtle (*Glyptemys insculpta*) Populations in Ontario, Canada

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***Abstract.*—Isolated and peripheral populations of declining species are increasingly a focus of conservation action. Using five polymorphic microsatellite loci, we investigated the age specific and spatial genetic structure of Wood Turtles (*Glyptemys insculpta*) in Ontario. We found genetic structure was significant between all populations (F_{ST} 0.12–0.22; D 0.204–0.392). Bayesian clustering resolved two genetic clusters that separated the population in the north from all other samples. We found high levels of genetic diversity and low inbreeding coefficients in three of our populations (H_E = 0.65; F_{IS} = 0.062); however, the southern population that had experienced the largest declines in the past had the lowest levels of heterozygosity and highest levels of inbreeding (H_O = 0.460; F_{IS} = 0.328). Our preliminary comparison of data among age cohorts in the central population found generally lower, but not significant ($P > 0.3$), levels of genetic diversity in the youngest age group. Genetic diversity in these younger cohorts was comparable to levels in the southern population. Our results illustrate the potential effect of population isolation on genetic variability and structure of Wood Turtles; as well as, suggest the importance of investigations at different age-scales in the future to reveal such patterns in species with long generation times.**

Key Words.—conservation genetics; genetics; *Glyptemys insculpta*; peripheral; Wood Turtle

Introduction

Investigations of the effect of isolation on population genetic diversity are increasingly used to inform management and conservation practices (Lönn and Prentice 2003; Fritz et al. 2006). Knowledge of these effects can reveal the effects of fragmentation on the species as a whole (Lesica and Allendorf 1995); however, it is also necessary to account for differing temporal scales in genetic studies. In the case of population isolation, ecological effects such as decreased movements or extinction can be almost immediate, while the more subtle effects on genetic diversity and population fitness only accumulate over generations. Such investigations across temporal scales are particularly important for species with long generation times and are essential for the effective management and conservation of species at risk (Frankham and Brook 2004).

The Wood Turtle, *Glyptemys insculpta,* is a widespread species occupying a range from Minnesota in the USA to Nova Scotia in eastern Canada. Throughout this range the species is in decline, primarily due to human induced habitat fragmentation and the corresponding spread of predators (Brooks et al. 1992; Arvisais et al. 2002). Declines are further confounded by the life history of the species as Wood Turtles have delayed sexual maturity up to 17 years (Brooks et al. 1992); therefore, high survivorship is necessary to maintain population viability. Within Ontario, declines are widespread (Ontario Wood Turtle Recovery Team 2010) and Wood Turtle populations are now extirpated from 21 known localities, with remaining populations occupying three disjunct ranges (Fig. 1). The wood turtle is listed as 'threatened' under COSEWIC (2008) and endangered under Ontario's Endangered Species Act; therefore, knowledge of the extant population, including genetic diversity, is necessary and the lack of such data on the Ontario population has been noted (Ontario Wood Turtle Recovery Team 2010).

Studies elsewhere have revealed some evidence of reduced genetic diversity in isolated populations of the species (Castellano et al. 2009; Spradling et al. 2010), although in Québec

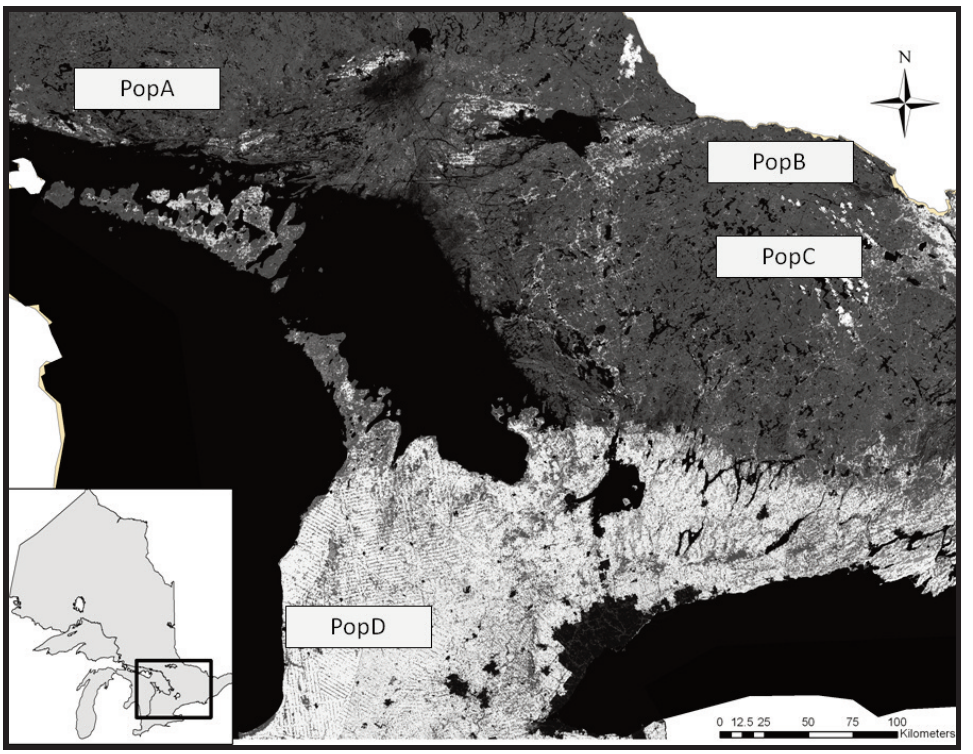


Figure 1. Map of Southern Ontario showing the approximate location of the four sites where we sampled Wood Turtles (*Glyptemys insculpta*) for genetic analysis in this study. We do not provide exact locations due to potential for illegal collection of .

there was high genetic variability (Tessier et al. 2005). However, none of these studies accounted for the effect of generation time on genetic diversity. Herein, we present a preliminary study using genetic data from Wood Turtles (N = 79) sampled across three age cohorts and three regions in Ontario. We amplified five microsatellites and used these to assess population and cohort specific genetic diversity and structure. We hypothesized that there would be significant variability across Ontario, possibly as a result of habitat fragmentation or human interference. We also hypothesized that due to the long maturation time of turtles decreased genetic diversity would be most evident in the younger individuals. As human induced population declines of Wood Turtles are relatively recent; 50 to 70% reduction in some Ontario populations in the past 20 years (Ontario Wood Turtle Recovery Team 2010), reduced genetic diversity should only be evident in the younger cohorts, while older individuals would have higher genetic diversity reflective of previously larger turtle populations. The results of our study will be important for understanding the effect of population reductions on genetic diversity of species with long generation times, and will also assist in the effective formulation of conservation strategies for Wood Turtles to maintain diversity and population connectivity both within Ontario, and in the species as a whole.

Materials and Methods

We collected blood and tissue (tail/digit clippings) samples from turtles from four sites across three regions of Ontario: (1) PopA, in central Ontario (N = 42); (2) PopB (N = 8) and PopC (N = 19) in eastern Ontario; and (3) PopD (N = 10) in south-western Ontario (Fig. 1). We cannot provide the exact locations of the sampling sites due to the potential for illegal collection. We collected all samples from adults with the exception of those from PopA. In PopA we collected samples from both adults and hatchlings. When sampling hatchlings we only sampled one sibling per clutch to avoid bias. We

divided samples from PopA into three age cohorts: <15 (N = 8), 15–25 (N = 16), > 25 (N = 18) years of age based on single counts of the number of growth rings on scutes (one annulus is assumed to represent one year [Galbraith et al. 1989]); although, we recognise that this approach may underestimate the age of older individuals (Wilson et al. 2003; Bertolero et al. 2005; Attum et al. 2011). We preserved blood samples on Whatman FTA cards and placed them in lysis buffer for a minimum of 24 hrs prior to extraction. We stored tissue samples in lysis buffer from time of collection. We treated samples twice with Proteinase K and then incubated samples at 60º C for two hours and 37º C for 12 hours. We extracted DNA using Qiagen DNeasy Kits after which we re-suspended extracted DNA in 50 µl of 0.1 M Tris-EDTA and quantified this DNA using PicoGreen dsDNA Quantification Kit (Molecular Probes).

We screened samples at five microsatellite loci: CmuA19 (AF517227); CmuB21 (AF517231); CmuD28 (AF517237); CmuD40 (AF517238); and CmuD87 (AF51724) (King and Julian 2004). We amplified these microsatellite regions using PCR reactions carried out in 10 µl volumes: 1X PCR buffer, 1.5 mM $MgCl_2$, 0.2 mM dNTPs, 0.3 mM of each of the five fluorescently labelled primers, 0.05 Unit Taq (Invitrogen), 10 ng of template DNA. Thermocycling conditions consisted of 95º C for five minutes, followed by 29 cycles of: 94º C for one min, annealing temperature (60º C (except CmuB21(56º C) and CmuD87 (51º C)) for one min, 72º C for one min, and a final step at 60º C for 45 minutes. We ran positive and negative controls alongside all extractions and PCRs and we genotyped amplified DNA in MegaBACE 1000 using MegaBace Genetic Profiler 2.0 software (GE Healthcare Lifesciences, Québec, Canada). We confirmed genotypes manually three times.

We calculated standard diversity indices (H_O (observed heterozygosity) and H_E (expected heterozygosity)) and tested for linkage disequilibrium and Hardy-Weinberg equilibrium (HWE) in Genepop v3.4 (Raymond and Rousset 1995) using a MCMC chain of 10,000 steps, 100 batches and 1000 iterations per batch. We calculated F_{IS} (the coefficient of inbreeding; 1-H_O/H_E) and allelic richness (N_A; genetic diversity corrected for the smallest sample size) in Fstat (Goudet 1995). We compared genetic diversity (H_O and H_E) among populations using ANOVA and investigated isolation by distance using Mantel tests of F_{ST} (Weir and Cockerham 1984) and D (Jost 2008), the latter calculated in Smogd (Crawford 2010), against the natural logarithm of Euclidean genetic distance using ade4 (Chessel et al. 2004) in R 2.7.1, assessing significance after 999 permutations.

We used a Bayesian clustering in Structure 2.1 (Pritchard et al. 2000) and Principal Components analysis (PCA) implemented in ade4 (Chessel et al. 2004) and adegent (Jombart 2008) to determine population structure. We visualised PCA scores using ggplot2 (Wickham 2009). For the Structure analysis we inferred populations (K) from 1 to 10 (burn-in 100,000, MCMC 10^6, 3 independent runs) and chose the most likely number of populations based on ln Pr|K and ΔK (Evanno et al. 2005). We visualised Structure results using Distruct (Rosenberg 2004). We also carried out a preliminary investigation of age specific patterns in genetic diversity through calculation of genetic diversity indices and comparison of these indices among the three cohorts using ANOVA. In all analyses we set $\alpha = 0.05$.

Results

All of our loci except CmuA19 were polymorphic with seven to nine alleles per locus. We identified three alleles at CmuA19. H_O ranged from 0.37 to 0.73 and H_E ranged from 0.47 to 0.87 (Table 1). In our global tests there was no significant linkage disequilibrium detected between each locus pair ($P > 0.05$ in all cases); however, there were departures from HWE at four of our five loci (Table 1). We found that H_O ranged from 0.46 to 0.72 and H_E ranged from 0.59 to 0.75 (Table 2) at the population scale. At this scale we also found that PopA deviated from HWE at 3 of the 5 loci ($P < 0.01$) and PopD deviated from HWE at one locus (CmuB21; $P = 0.0018$).

Our Structure analysis revealed the likelihood of the combined data had a peak at K

Table 1. Genetic parameters for five microsatellite loci from Wood Turtles (*Glyptemys insculpta*) sampled across Ontario.

Locus	Number of Alleles	Ho	H_E	*P*
CmuA19	3	0.367	0.476	0.0007
CmuB21	7	0.607	0.845	< 0.0001
CmuD28	10	0.734	0.874	0.00362
CmuD40	10	0.443	0.757	< 0.0001
CmuD87	10	0.789	0.670	0.249

Abbreviations: H_O: observed heterozygosity, H_E: expected heterozygosity, *P* value indicates whether heterozygosity deviated from expectations under Hardy-Weinberg Equilibrium.

= 2 which separated the central PopA from the other three sampling sites (Fig. 2). This was supported by the PCA which separated PopA from the other populations on both the first and second principal components (Fig. 3). Our F_{ST} values were all significantly positive and values of genetic distance measured using D were all high (Table 2). We found no evidence of isolation by distance (F_{ST}: r = -0.07, P = 0.55; D: r = 0.071; P = 0.54). We also found that genetic diversity did not vary among populations (H_O: $F_{1,16}$ = 1.68, P = 0.21; H_E: $F_{1,16}$ = 0.66, P = 0.59), however, there was a general trend of higher observed heterozygosity and lower F_{IS} values in the central and eastern regions of Ontario (H_O: 0.56–0.72; and F_{IS}: 0.01–0.09) when compared to the south-western population (H_O: 0.460; and F_{IS}: 0.328).

We found no significant difference in genetic diversity among cohorts (H_O: $F_{1,12}$ = 1.7, P = 0.34; H_E: $F_{1,12}$ = 0.6235, P = 0.79). However, we did find that generally turtles < 15 years of age had lower levels of H_O, H_E, N_A and MNA than turtles 16–25 and > 25 years of age (Table 2).

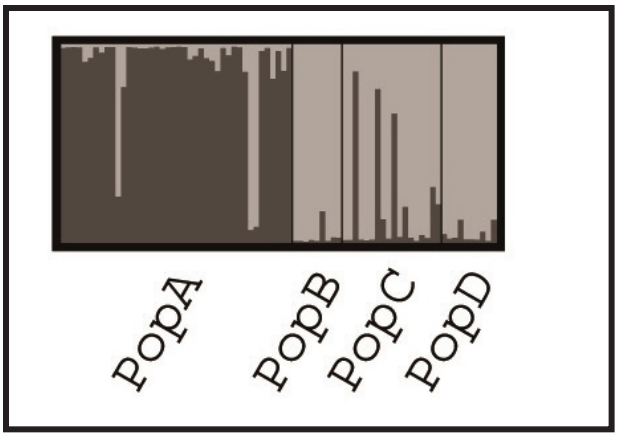
Discussion

The effects of fragmentation and population reductions on genetic diversity may be subtle, particularly in species with long generation times. Herein, we revealed the effect of such processes on Wood Turtle populations in Ontario. Our population genetic analysis found the lowest levels of diversity in the population that had the largest reduction in population size. However, comparable levels of diversity were found in the youngest age cohort of turtles in the central population. Although the differences among cohorts were not significant these results

Table 2. Genetic parameters of four populations of Wood Turtles (*Glyptemys insculpta*) sampled across Ontario. Data split into the three age cohorts in PopA are shown in italics. FST is shown below the diagonal and D above the diagonal. Significant FST values are indicated in bold.

Population	Age	N	HO	HE	MNA	NA	FIS	PopA	PopB	PopC	Pop D
PopA		41	0.562	0.620	6.6	4.38	0.095				
	<15	8	0.525	0.492	3.6	3.6	-0.073				
	16-25	15	0.600	0.674	5.4	4.62	0.114				
	>25	18	0.533	0.604	5.4	4.21	0.120		0.392	0.226	0.204
PopB		8	0.589	0.596	5.8	5.40	0.040	0.212		0.273	0.210
PopC		19	0.725	0.753	5.4	4.58	0.012	0.175	0.156		0.265
PopD		10	0.460	0.673	4.8	4.53	0.328	0.212	0.121	0.214	

Abbreviations: N: sample size, HO: observed heterozygosity, HE: expected heterozygosity, MNA: mean number of alleles, NA: allelic richness (based on 8 individuals), FIS: inbreeding coefficient.



FIGUREE 2. Proportional membership of each of the individual Wood Turtle (*Glyptemys insculpta*) sampled across Ontario to one of the two genetic clusters identified using STRUCTURE. Each bar on the bar plot represents an individual and the proportion of that bar coloured light or dark grey illustrates the proportion of alleles from that individual that were assigned to cluster 1 or cluster 2 respectively.

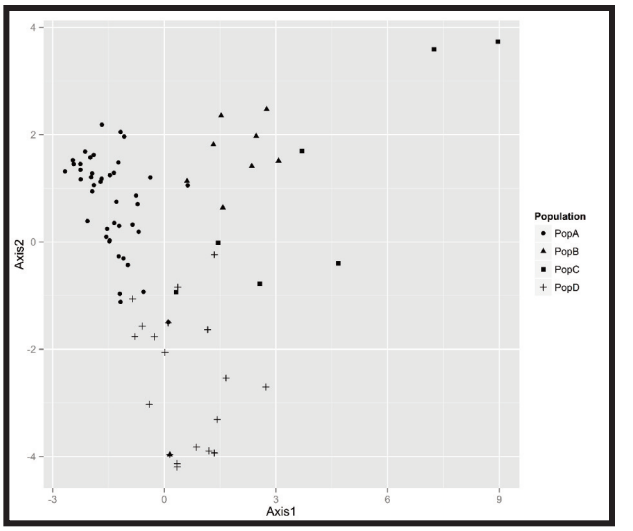


FIGURE 3. PCA scores for individual Wood Turtles (*Glyptemys insculpta*) sampled at four locations across Ontario.

may suggest low levels of diversity in all populations in the future. These data will have important management and conservation implications; our population-level analysis supports immediate directed conservation actions for the southern population, while the cohort level analysis suggests that all populations may need such actions.

We must acknowledge confounding effects that may be driving the patterns observed in our data. First our sample size was quite small. Nevertheless, this sample size is comparable to previous studies of the same species (Castellano et al. 2009; Spradling et al. 2010), both of which encompassed a considerably larger geographic spread than our study. A second issue may be the small number of microsatellite markers that we used to assess population genetic structure (N = 5). Although this is identical to a similar study in Québec (Tessier et al. 2005), it is slightly lower than other assessments (Castellano et al. 2009; Spradling et al. 2009). The optimum number of microsatellites needed to assess genetic structure is not definite, and varies with respect to the polymorphic nature of the markers, as well as the particular research question being addressed (e.g., Kalinowski 2002, 2005; reviewed by Selkoe and Toonen 2006). In the absence of a large number of loci, Kalinowski (2002) suggested that population genetic structure may be assessed using few loci that have a number of unique alleles in each. In our study there were only two alleles unique to our populations; one at CmuD28 and one at CmuD40. This could mean that our markers may have missed subtle levels of genetic structuring and so reduced the power of our analyses. This must be remembered throughout the following interpretation of our data. Finally, we cannot discount the possibility of sampling of parent-offspring pairs in some of our populations. Although only adults were sampled in Pop B, C and D, we did not carry out aging of adult turtles in these populations, and our high F_{IS} values suggest that there was sampling of close relatives in some of our populations which, may have influenced our results.

Isolated populations of turtles have been reported to have lower levels of diversity than populations elsewhere in species range. Spradling et al. (2010) reported lower genetic diversity (H_E = 0.6) in an isolated population in Iowa, USA, when compared to both a central population (H_E = 0.75), and also a central population sampled in a separate study (H_E = 0.9; Castellano et al. 2009). Tessier et al. (2005) also reported low diversity in their two most isolated populations (H_E = 0.561 and 0.673).

The levels of diversity we found in Ontario (0.66) were similar to those reported for the isolated populations in Iowa and Québec (Tessier et al. 2005, Spradling et al. 2010), and overall highlight the detrimental effect of population isolation on genetic diversity of this species.

When we compared genetic diversity between our sampling areas our most isolated population, PopD, had generally lower, but not significant, levels of diversity than populations elsewhere. When compared to other studies (Tessier et al. 2005; Castellano et al. 2009; Spradling et al. 2010) the levels of heterozygosity in PopD are the lowest reported to date (0.46). These results were not unexpected. PopD lies within a very heavily populated region within southern Ontario (see Fig. 1), while our other sampled populations are located more towards the periphery of the Wood Turtle's range. These populations are likely to have diverged more recently from larger populations within Michigan and Québec, and so retained higher levels of genetic diversity, which has been reported in previous mitochondrial analysis of the region (Amato et al. 2008).

The variable genetic diversity of Wood Turtles across Ontario was also reflected in our assessment of genetic structure which was significant and high among all sampling locations. Wood Turtles have high site fidelity (Arvisais et al. 2002), which generally results in significant genetic structure (Tessier et al. 2005; Castellano et al. 2009; Spradling et al. 2010). Although the clustering of our sampled populations into two groups, the centralcentral PopA and other populations (Fig. 2), may represent a true division of PopA from other areas within Ontario, additional samples are needed to confirm this. Therefore whether PopA represents a distinct management unit (Moritz 1994) is unclear. Regardless, the extreme geographic isolation of all of our sampled populations from each other, together with the high F_{ST} and D values among them indicating low levels of gene flow, supports separate management practices for each of our sampled populations.

Given the low genetic diversity in PopD, the focus of more controlled management and conservation measures to augment genetic diversity in this population would appear to be a priority. However, our analysis of the PopA cohorts revealed more subtle patterns. When divided into age categories the youngest turtles exhibited generally decreased heterozygosity and allelic richness. These levels were similar to those found in PopD which underwent the most drastic population declines. Although these differences were not significant these data may reflect a trend of decreasing diversity in the younger age cohorts. This may indicate low genetic diversity in these populations in the future. Further research should assess whether this pattern exists across the range of the species.

Overall, although population sizes are potentially critically low within all of the populations that we sampled, the southern PopD is a high conservation concern due to its demographic history and the isolation of that population from turtle populations elsewhere. However, our novel cohort-specific analysis suggests even populations that have not undergone drastic population declines may be experiencing reductions in genetic diversity. Additional research is needed to confirm this, particularly as the reduction in the effective population size across our populations is unknown, so it is unclear how current diversity compares to that previously found within the population. It is probable that although the long generation time of the Wood Turtle can be an advantage, buffering the effects of fragmentation and population reduction, this may only work over short temporal scales. More robust conclusions regarding Wood Turtles may be possible after further study with increased number of molecular markers, as well as further sampling from each population. We hope that this preliminary study will be built upon by additional analysis. Currently, we suggest that maintaining current levels of Wood Turtle genetic variation and population sizes through the protection and management of existing populations and habitat should be a high priority for conservation efforts for this species.

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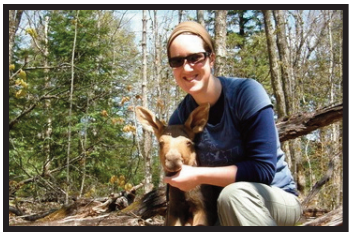

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