Herpetological Conservation and Biology 5(2):166-173.
Submitted: 17 February 2010; Accepted: 30 June 2010.

QUANTITATIVE ASSESSMENT OF INTERGRADATION BETWEEN TWO SUBSPECIES OF PAINTED TURTLES, *CHRYSEMYS PICTA BELLII* AND *C. P. MARGINATA*, IN THE ALGOMA DISTRICT OF WEST CENTRAL ONTARIO, CANADA

***WAYNE F. WELLER*[1], *STEPHEN J. HECNAR*[2], *DARLENE R. HECNAR*[2], *GARY S. CASPER*[3], *AND F. NEIL DAWSON*[4]**

[1]*7038 Kelly Drive, Niagara Falls, Ontario L2H 3J9, Canada*
[2]*Department of Biology, Lakehead University, 955 Oliver Road, Thunder Bay, Ontario P7B 5E1, Canada*
[3]*University of Wisconsin-Milwaukee Field Station, 3095 Goose Road, Saukville, Wisconsin 53080, USA*
[4]*Northwest Science and Information, Ontario Ministry of Natural Resources, R.R.# 1, 25th Side Road, Thunder Bay, Ontario P7C 4E9, Canada*

Abstract.**—Adaptation to local environments after geographical isolation often results in development of distinct physical characteristics in organisms and recognition of subspecies, races or varieties. When barriers are removed secondary contact can result in interbreeding with progeny showing characteristics intermediate between subspecies. Four distinct subspecies of the Painted Turtle, *Chrysemys picta*, exist and likely resulted from isolation in southern refugia during the last glacial advance. Plastral patterns differ among subspecies of *C. picta* and turtles from the Algoma District of Ontario, Canada show plastral figure patterns that appear intermediate between the western (*C. p. bellii*) and midland (*C. p. marginata*) subspecies. Because former accounts of plastral patterns in painted turtles in this region are largely qualitative, we quantified and compared pattern area, length, width, perimeter/area ratio and geometric shape for Algoma District turtles with known western, midland, and intergrade populations. Plastral patterns in Algoma turtles were very similar to known intergrades from the adjacent Upper Peninsula of Michigan and differed from both western and midland turtles. We found that pattern length and geometric shape, both simple and inexpensive to measure, were useful variables to distinguish intergrades from both western and midland subspecies. Comparisons of measurements from west to east suggest that *C. p. bellii* characteristics entered into the Algoma District of Ontario from the Upper Peninsula of Michigan during post Pleistocene dispersal. Future genetic analyses may be useful to test our dispersal hypothesis and to determine how far western influence extends eastward into central Ontario.**

Key Words.—Algoma District; *Chrysemys picta*; dispersal; intergradation; Ontario; Painted Turtle

INTRODUCTION

Understanding the variation within and among species is a fundamental goal of biology. Adaptation to local or regional environments within a species often results in development of distinct physical characteristics and recognition of subspecies, races, or varieties. The evolution of subspecies is considered to result primarily through geographic isolation. When barriers are subsequently removed, and secondary contact results in interbreeding of subspecies, individuals having physical characteristics intermediate between those of the subspecies can be produced.

The Painted Turtle, *Chrysemys picta*, has a wide distribution in eastern North America and four distinct subspecies are recognized (Crother 2008): *C. p. bellii* (western); *C. p. marginata* (midland); *C. p. dorsalis* (southern); and, *C. p. picta* (eastern). Recently Starkey et al. (2003) suggested elevating *C. p. dorsalis* to a full species, a conclusion rejected by Ernst and Lovich (2009) but accepted by Crother (2008). These subspecies are thought to have recolonized the northeastern United States and southeastern Canada from southern glacial refugia where they evolved in isolation (Bleakney 1958). These subspecies are well-described and can be clearly identified, with the exception of *C. p. dorsalis* and *C. p. picta*, by distinct patterns or blotches on the plastron. Intergradation has been studied in southeastern Wisconsin, and north and western Illinois (Bishop and Schmidt 1931). We report in this paper suspected intergradation between *C. p. bellii* (Western Painted Turtle) and *C. p. marginata* (Midland Painted Turtle) in the Algoma District of west central Ontario, Canada.

Both *C. p. bellii* and *C. p. marginata* occur in Ontario (Cook 1984; Conant and Collins 1998). *Chrysemys p. bellii* occurs in northwestern Ontario and extends eastward along the north shore of Lake Superior to

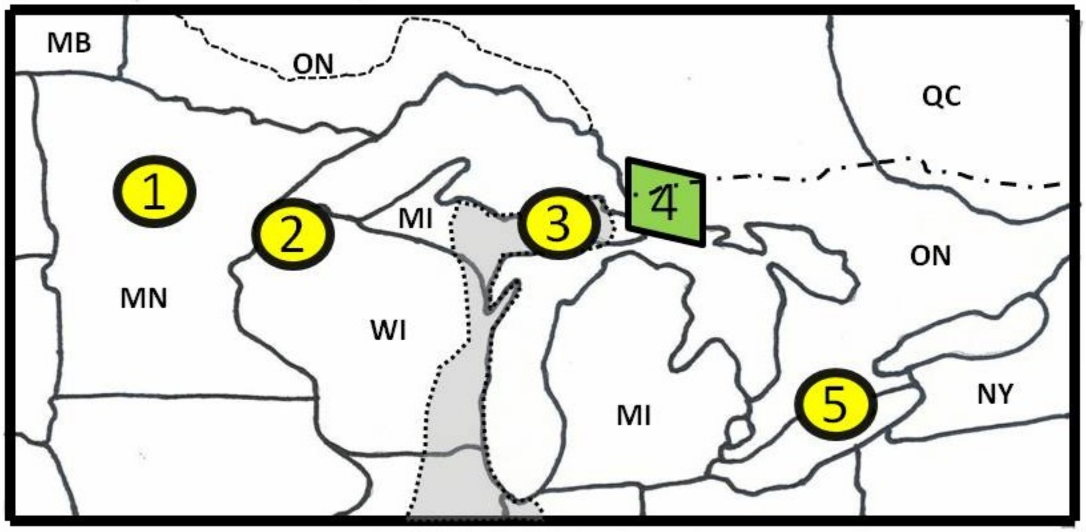

FIGURE 1. Localities of Chrysemys picta used in a study of intergradations of subspecies. Dashed line and dashed/dot line represent the northern range limit of *C. p. bellii* and *C. p. marginata*, respectively, according to Conant and Collins (1998). Shaded area represents zone of intergradation based upon Conant and Collins (1998) and Casper (unpubl. report). From west to east, 1 = *C. p. bellii* from northcentral Minnesota (MINN), 2 = *C. p. bellii* from Wisconsin (MOBA), 3 = intergrade from Michigan (PIRO), 4 = suspected intergrades from Algoma District, Ontario (ALGO), and 5 = *C. p. marginata* from southern Ontario (LOPT).

Pukaskwa National Park. *Chrysemys p. marginata* occurs throughout southern and central Ontario and extends into the Algoma District north of Sault Ste. Marie (Oldham and Weller 2000). There is an apparent 130 km gap in the range between *C. p. bellii* and *C. p. marginata* along the east shore of Lake Superior (Oldham and Weller 2000), although surveys in this area are incomplete.

The most diagnostic physical characteristic used to distinguish *C. p. bellii* and *C. p. marginata* is the extent of the dark pattern on the plastron (Logier 1939; Carr 1952). Carr (1952), and Conant and Collins (1998) describe the dark plastral figure of *C. p. bellii* as having marked transverse extensions that fill most of the plastron surface. Logier (1939) described the central dark blotch on the plastron as being very large extending outward along the sutures. The plastral figure is described by Ernst (1971) as being large and branching, and by Ditmars (1936) as having angular extensions. Bishop and Schmidt (1931) determined that the width of the dark plastral figure across the abdominal plates extends 56–86% of the plastron width. The plastral pattern of *C. p. marginata* has been described as small (Smith and Brodie 1982), non-branching (Ernst 1971), and without angular (Ditmars 1936) or transverse extensions (Carr 1952; Conant and Collins 1998) along the sutures (Logier 1939). Bishop and Schmidt (1931) determined that the width of the dark plastral figure across the abdominal plates in *C. p. marginata* extends only 13–57% of the plastron width.

Logier (1939) described two specimens from the southern area of Algoma District and western Sudbury District of central Ontario as having very large plastral blotching, and stated that the plastral patterning was more like that of *C. p. bellii* than of *C. p. marginata*. Until now the extent of this zone of suspected intergradation has not been determined quantitatively due to the paucity of samples from the area. In examining 46 specimens from this area of Ontario, we had two goals. Our first was to examine quantitatively the extent and degree of the plastral patterning in painted turtles in the Algoma District of Ontario to determine if this region can be considered a zone of intergradation between *C. p. bellii* and *C. p. marginata*. Secondly, if the Algoma turtles are determined to be intergrades, to determine which parameters best distinguish intergrades from pure *C. p. bellii* and *C. p. marginata*. To address our goals, we compared the extent and degree of plastral patterning of turtles from Algoma District with that of turtles from locations representing *C. p. bellii*, *C. p. marginata*, and from a location of known intergrades based on a quantitative assessment.

METHODS

Sample locations.—We examined plastral patterns in preserved museum specimens and live painted turtles from five regions. Extending from west to east across the Lake Superior Basin into Ontario (Fig. 1), the five

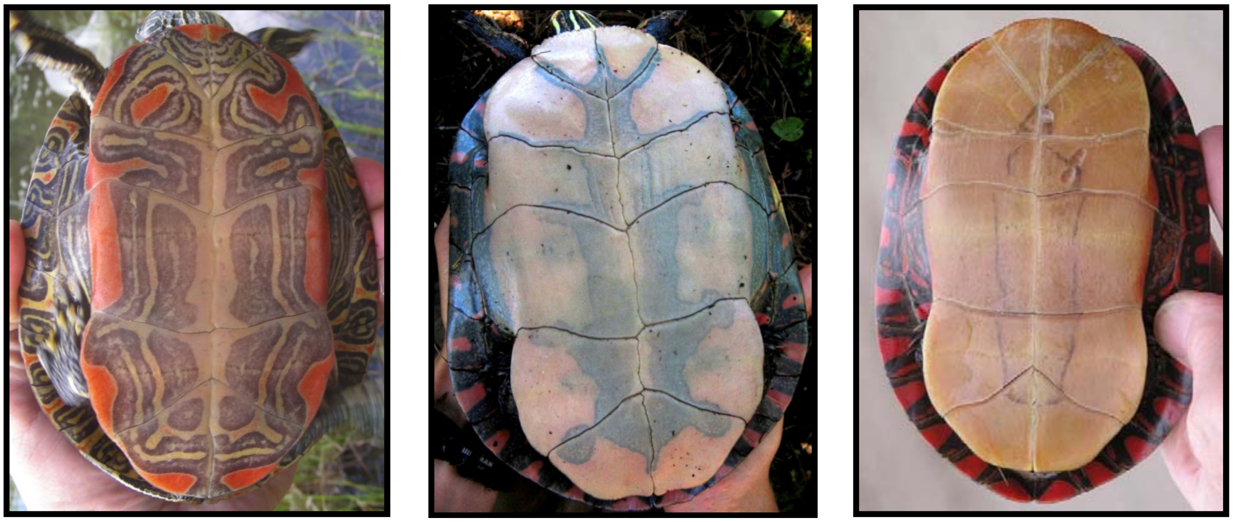

FIGURE 2. Typical plastron patterns of *C. p. bellii* (left) from Moquah Barrens (MOBA), typical intergrade (centre) from Algoma District (ALGO), and *C. p. marginata* (right) from Long Point (LOPT). Photographed by Gary Casper (left, MOBA), Alexis McEwan (centre, ALGO), and Wayne Weller (right, LOPT).

regions are as follows: representing *C. p. bellii*, Itasca County in north-central Minnesota (hereafter MINN); also representing *C. p. bellii*, Moquah Barrens in northern Wisconsin (MOBA); representing intergrades, Pictured Rocks National Lakeshore in the Upper Peninsula of Michigan (PIRO); undetermined but suspected intergrades, various localities in the Algoma District of Ontario (ALGO); and, representing *C. p. marginata*, Long Point in southern Ontario (LOPT).

***Measurement Variables*.—**To quantify the degree to which the dark patterning covered the plastron, we measured five variables on adult turtles (> 100 mm carapace length): pattern width; pattern length; pattern area; perimeter to area ratio of the pattern; and pattern shape. Pattern width was determined to be the maximum width of the patterning across the suture between the abdominal and femoral scutes expressed as a percentage of the width of the plastron across the same suture. Pattern length was the maximum length of the patterning along the plastron midline expressed as a percentage of the total length of the plastron. We took measurements on enlarged high resolution digital photographs or scale drawings with vernier calipers to the nearest 0.1 mm. We calculated percentage area, perimeter to area ratio, and geometric shape of the plastral patterning using SigmaScan Pro 5 (Systat Software Inc., Chicago, Illinois, USA) image analysis software. By quantifying the plastral figure coverage, we improved on the technique used by Rhodin and Butler (1997) to identify intergrades. The quantitative measure of shape is an index that measures the compactness of geometric shapes. The shape "factor" numerically ranges from a maximum of 1 for a circle, through $\pi/4$ for a square, to a minimum of 0 for an infinitely long thin line.

***Statistical analysis*.—**To determine if pattern variables differed among locations, we used one-way ANOVA. Prior to analysis, we tested for normality and homogeneity using Lilliefor's and Levene's tests, respectively. When assumptions for parametric tests were not met, we used arcsine transformation or logarithmic transformations as appropriate (Sokal and Rohlf 1995). When transformation failed to homogenize variance, we conducted Kruskal-Wallis tests. Raw data for area met the assumption of equal variance. Transformation of the other variables could not completely homogenize variance. Because our Kruskal-Wallis results were qualitatively the same as ANOVA results, we analyzed transformed variables using parametric tests. For pairwise comparisons among locations, we used Tukey's HSD (equal variance) test for area, and Games-Howell tests (unequal variance) for all other variables. All statistical analyses were conducted using Systat 12 software (Systat Software Inc., Chicago, Illinois, USA). We used $\alpha = 0.05$ to assign significance.

RESULTS

It is visually quite apparent that the plastral pattern features of typical *C. p. bellii*, suspected intergrades, and *C. p. marginata* are quite different (Fig. 2). Although there are differences among locations (Table 1), some general relationships can be seen (Fig. 3).

TABLE 1. Mean ± 1 SE (range in parenthesis) and ANOVA results (*F* values) for plastral pattern parameters among localities. See Methods for locality acronyms. Each ANOVA had (4, 205) degrees of freedom, and was highly significant ($P << 0.001$).

Parameter	**Locality**				
	MINN (n = 40)	**MOBA (n = 43)**	**PIRO (n = 40)**	**ALGO (n = 46)**	**LOPT (n = 41)**
Pattern width (%)	87.4 ± 0.85	90.8 ± 0.74	57.7 ± 1.73	51.6 ± 1.80	55.2 ± 1.33
(F = 198.3)	(77.0 – 100.0)	(79.7 – 100.0)	(37.9 – 82.6)	(26.3 – 79.6)	(35.7 – 69.2)
Pattern length (%)	94.0 ± 0.51	94.7 ± 0.44	75.92 ± 0.69	80.7 ± 0.75	71.0 ± 1.15
(F = 236.4)	(84.7 – 100.0)	(86.8 – 98.5)	(69.1 – 85.5)	(72.1 – 92.5)	(55.9 – 83.4)
Pattern area (%)	63.1 ± 1.18	66.4 ± 1.21	31.5 ± 1.10	29.8 ± 1.18	28.9 ± 1.00
(F = 277.1)	(47.9 – 80.8)	(49.5 – 84.1)	(20.5 – 48.3)	(12.9 – 53.7)	(16.1 – 40.5)
Perimeter/area ratio	2.23 ± 0.056	2.09 ± 0.064	2.53 ± 0.076	3.45 ± 0.163	2.23 ± 0.115
(F = 26.0)	(1.58 – 3.23)	(1.39 – 3.02)	(1.74 – 3.71)	(1.35 – 6.29)	(1.22 – 4.25)
Geometric Shape	0.24 ± 0.009	0.25 ± 0.011	0.37 ± 0.013	0.31 ± 0.013	0.44 ± 0.016
(F = 43.2)	(0.11 – 0.37)	(0.12 – 0.46)	(0.23 – 0.52)	(0.10 – 0.50)	(0.23 – 0.67)

Not all pattern parameters we examined clearly identify that the turtles from the Upper Peninsula of Michigan (PIRO), or from the Algoma District of Ontario (ALGO) showed characteristics intermediate between *C. p. bellii* from MINN and MOBA, and *C. p. marginata* from LOPT. Although all parameters differed significantly among the five locations (Table 1), some clearly indicated intermediates. Pattern width for both PIRO and ALGO turtles was significantly narrower than for *C. p. bellii*, but was not different from *C. p. marginata* (Fig. 3a). Pattern length was intermediate between the longer patterns of *C. p. bellii* and the shorter patterns of *C. p. marginata* (Fig. 3b). Pattern area for PIRO and ALGO turtles did not differ from each other or from *C. p. marginata* from LOPT, but was significantly less than pattern area from *C. p. bellii* from both locations (Fig. 3c). ALGO turtles had the greatest perimeter/area ratio of all locations (Fig. 3d). PIRO turtles had ratios higher than those for *C. p. bellii* but not *C. p. marginata* (Fig. 3d). The ratio for PIRO turtles was also significantly lower than that for ALGO turtles. Shape of the plastral pattern for both PIRO and ALGO turtles was intermediate between *C. p. bellii* and *C. p. marginata* (Fig. 3e).

DISCUSSION

The fact that the plastron patterns of ALGO painted turtles were more similar to those of PIRO intergrades than to those of either *C. p. bellii* or *C. p. marginata* suggests that the Algoma District turtles are *bellii-marginata* intergrades. Painted turtles from these two intergrade populations (PIRO, ALGO) had two pattern characteristics (pattern length and shape) that were clearly intermediate between the *C. p. bellii* and *C. p. marginata* populations. Pattern length for intergrades was shorter than in *C. p. bellii* but longer than *C. p. marginata*. Shape for PIRO and ALGO turtles indicated that the pattern was not as rectangular as in *C. p. bellii*, nor as square as in *C. p. marginata*. Also of note is that the perimeter/area ratio distinguished ALGO turtles from both *C. p. bellii*, the PIRO intergrade population, and *C. p. marginata*. Perimeter/area ratio was higher for intergrades than for *C. p. bellii* or *C. p. marginata* because the pattern tends to move outward along the plastral seams in intergrades (Fig. 2). This resulted in a more convoluted pattern having greater edge than in *C. p. marginata* where the pattern remains closer to the central transverse seam, and in *C. p. bellii* where the pattern tends to fill nearly the entire plastron.

Intergrades could not be distinguished from *C. p. marginata* using either pattern area or pattern width. This result could be interpreted as an indication that there is more *C. p. marginata* than *C. p. bellii* influence in the two intergrade populations that we examined. This suggests that these variables are not useful characters in identifying intergrades. In a general sense, pattern length for the intergrade populations also seems to show greater similarity with *C. p. marginata* than *C. p. bellii*.

Our results suggest that pattern length and shape are the best and most useful variables to identify intergrades between *C. p. bellii* and *C. p. marginata*. Clearly, genetic analyses would be the most logical next step to identify and quantify the degree of *bellii-marginata* intergradation of PIRO and ALGO painted turtles. Notwithstanding this, the usefulness of simple and inexpensive morphological measurements to identify intergradation has been demonstrated.

Both *C. p. bellii* and *C. p. marginata* are cold-adapted subspecies (Holman and Andrews 1994) that are considered primary post-glacial invaders of the Great Lakes region (Holman 1992a). Based on geological, paleontological, and physiological evidence, Holman (1992a) suggested that painted turtles were near to the retreating ice sheet and rapidly entered into Michigan by two major routes: from Indiana and Ohio into southern Michigan and from Wisconsin into the Upper Peninsula.

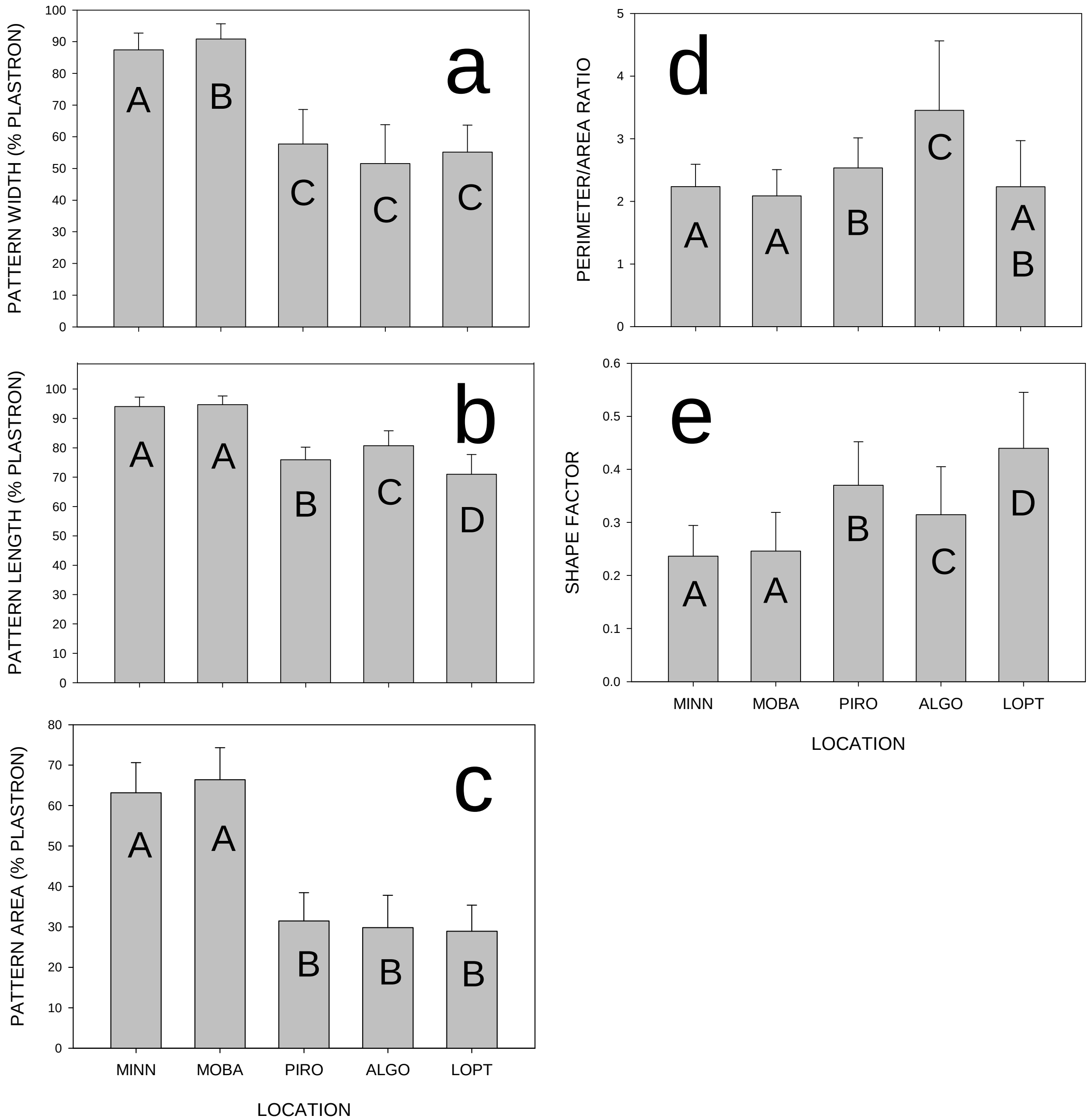

FIGURE 3. Mean (+ 1 SD) value of plastron pattern width (a), pattern length (b), pattern area (c), perimeter/area ratio (d), and shape (e) for *Chrysemys picta* subspecies from each location (acronyms as in Fig. 1). Capital letters within shaded bars represent results of Games-Howell paired comparison tests (panels a, b, d, and e) or Tukey's paired comparison tests (c). Bars that share the same letter are not significantly different ($P > 0.05$).

He considered that the Straits of Mackinaw acted as a barrier to dispersal but suggested that movement of turtles from Ontario into northern Michigan was possible in the Sault Ste. Marie area. Ernst and Fowler (1977) and others (e.g., Harding and Holman 1990; Conant and Collins 1998) considered that painted turtles in the eastern portion of Michigan's Upper Peninsula are intergrades with the *C. p. bellii* influence coming from Wisconsin via the western portion of the Upper Peninsula. Presumably, this reflects post Pleistocene dispersal routes. The similarity of the ALGO and PIRO intergrades suggests that the Upper Peninsula of Michigan acted as a post-Pleistocene dispersal route for *C. p. bellii* characteristics to enter central Ontario. There is no evidence based on the current geographic distributions of Painted Turtles in this area of Ontario that the range of *C. p. bellii* ever came in contact with, or overlapped that of Painted Turtles from the areas in Algoma District we sampled. Although *C. p. bellii* does occur in northwestern Ontario, it extends eastward along the north shore of Lake Superior and then southward only to the Pukaskwa National Park area. It is presumed that cold climate establishes the range boundary for this species (St. Clair and Gregory 1990) in northern Ontario. It is interesting to note that the 130 km gap in range between *C. p. bellii* in northern Ontario and the Algoma District locations closely coincides with the area of the harshest climate along Lake Superior's north shore. Michigan's Upper Peninsula is separated from the Algoma area by the relatively narrow, shallow St. Mary's River, and it is unlikely that the river would be a barrier for an aquatic, cold-adapted turtle. In fact, it might provide suitable habitat. Considering that post-glacial dispersal came from southern refugia, it seems unlikely that the *C. p. bellii* influence came from northwestern Ontario turtles migrating southeastward along the north shore of Lake Superior.

It is interesting to note that plastral length (Fig. 3b) and geometric shape (Fig. 3e) of the plastral pattern of PIRO turtles confounds an apparent west to east trend because PIRO turtles are more *C. p. marginata*-like than the ALGO turtles. This result is not surprising considering that *C. p. marginata* occurs both to the south and the east of PIRO. Although Holman (1992a) suggested that the Straights of Mackinaw may have acted as a barrier, we note that the present width is < 6 km and that it may only have been 1.6 km wide in post-glacial times in some areas (Hough 1958). Recent genetic analyses from garter snakes on islands between upper and lower Michigan suggest that the area is a secondary contact zone for herpetofauna (Placyk et al. 2007). Both the Straits of Mackinaw and the St. Mary's River are only narrow, shallow, cold-water (draining Lake Superior) waterways, and would not likely be formidable barriers for a cold-tolerant (Holman and Clouthier 1995) aquatic turtle. Painted Turtles frequently occur in larger rivers and shallow nearshore areas throughout the Laurentian Great Lakes. Furthermore, Painted Turtles occur on Isle Royale, which is an 'oceanic' island in Lake Superior that is about 22 km from the Canadian mainland.

This unexpected trend of ALGO turtles being more '*C. p. bellii*-like' in length and shape than PIRO turtles could be explained simply in terms of geography and sequence of post-glacial invasions. First, *C. p. bellii* moved eastward across the Upper Peninsula of Michigan into ALGO and came into contact with *C. p. marginata* turtles moving westward from central Ontario. Secondly, ALGO turtles moved westward into the Upper Peninsula of Michigan and came into contact with *C. p. marginata* moving northward from southern Michigan. The position of the maximal extent of the Laurentide Ice Sheet and patterns of its retreat (Holman 1992a, b) suggest that the western *C. p. belli* invasion into the Upper Peninsula and into Algoma would have preceded invasion by *C. p. marginata* from the south. Examination of variation in plastral characteristics of intergrades across the Upper Peninsula led Ernst and Fowler (1977) to suspect multiple invasion routes as well. Ernst and Fowler (1977) suggested *C. p. belli* invaded from the west while *C. p. marginata* entered by three routes: along the east coast of Wisconsin; island hopping from southern Michigan across the Straits of Mackinaw; and, from west central Ontario in the east. Upper Peninsula intergrades would have thus received three sources of *C. p. marginata* characteristics while Algoma intergrades received only the one source from Central Ontario. Because few specimens are available to examine, it is not known to what extent the *C. p. bellii* influence seen in painted turtles from the Algoma District of Ontario extends eastward towards the Sudbury area in central Ontario. Nuclear or mitochondrial DNA analyses may help confirm whether the *C. p. bellii* characteristics identified in this study entered central Ontario via the dispersal route south of Lake Superior through the Upper Peninsula of Michigan, or via a route north of Lake Superior through northwestern Ontario. These same analyses could also be used to determine how far *C. p. bellii* characteristics extend eastward from the Algoma District towards the Sudbury District. Our sampling locations fall into two separate clades identified by mitochondrial DNA analyses (Starkey et al. 2003), with MINN and MOBA samples falling within a clade corresponding to *C. p. belli*, and PIRO, ALGO and LOPT within a clade corresponding to *C. p. marginata*. This supports our contention that PIRO and ALGO populations are more strongly influenced by the *C. p. marginata* genome from the east. However, Starkey et al. (2003) did not include Canadian samples, and reported mixed results in the eastern Upper Peninsula of Michigan where secondary contact between clades appears to be operating. Our results extend this conclusion into the northern Lake Superior region. Both Ernst and Fowler (1977) and Holman (1992a) suggested that *C. p. marginata* entered the Upper Peninsula of Michigan from the Algoma District of Ontario. Our results suggest that this area served as a two-way corridor and also permitted *C. p. belli* to enter central Ontario from Michigan.

Acknowledgments.—We thank the staff of Lake Superior Provincial Park (Ontario Parks, Ministry of Natural Resources), Chequamegon-Nicolet National Forest (U.S. Forest Service), and Pictured Rocks National Lakeshore (U.S. National Parks Service) for logistical assistance and permission to trap turtles. Digital photographs were kindly provided by James Trottier, Ontario Ministry of Natural Resources, Blind River, Ontario, Canada. We also thank Ashley Spenceley, Alexis McEwan, Jenny L. Anderson, Brian Heeringa, Lora M. Loope, Priya Nanjappa Mitchell, and Ryne D. Rutherford for field assistance, and Dr. Les Buck, University of Toronto, for permission to examine turtles from central Minnesota, USA. Funding was provided by a U.S. EPA GLNPO grant, and an Ontario Ministry of Natural Resources grant (Canada Ontario Agreement funds) to SJH and GSC, and an NSERC Discovery grant to SJH.

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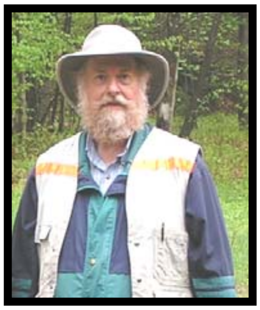

WAYNE WELLER is an Environmental Scientist with Ontario Power Generation, the largest producer of electricity in the province of Ontario. He received his Bachelors of Science from University of Toronto, and completed graduate courses and conducted a long-term population study of Jefferson Salamanders (*Ambystoma jeffersonianum*) in southern Ontario for his Masters of Science program at University of Toronto. His current research focuses on distribution of amphibians and reptiles in Ontario, and on geographic variation in Painted Turtles in Ontario and Québec. Wayne is pictured in Cameron County, Pennsylvania on 14 May 2009. (Photographed by Andrew L. Johnson)

STEPHEN J. HECNAR is a Professor of Biology at Lakehead University in Thunder Bay, Ontario, Canada where he teaches ecology, biogeography, and herpetology. He received a B.Sc. from Lakehead University and an M.Sc. and Ph.D. from the University of Windsor, Windsor, Ontario, Canada. He is a field-based empirical ecologist who's interests include spatial and temporal trends of populations and communities, biogeography, macroecology, and conservation of amphibians and reptiles. He advises several species and ecosystem recovery teams and government agencies and has provided invited reviews for over 50 journals and funding agencies. Steve is also a long-standing member of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) Amphibian and Reptile Species Subcommittee. Details of his laboratory and work can be found at http://flash.lakeheadu.ca/~shecnar/. (Photographed by Darlene R. Hecnar)

DARLENE R. HECNAR is a Research Assistant and part-time Animal Care Technician in the Biology Department at Lakehead University in Thunder Bay, Ontario, Canada where she maintains the amphibian and reptile collection and is a lab instructor in the herpetology course. She has taken many courses in fine arts, environmental studies, and various sciences among several institutions and completed a B.Sc. in Biology at Lakehead University. Her interests include herpetological field methodologies, photography, image analysis, and behavior and husbandry of amphibians and reptiles. Darlene is also an accomplished artist who teaches fiber arts to the community in her spare time. (Photographed by Stephen J. Hecnar)

GARY S. CASPER is a research scientist at the University of Wisconsin-Milwaukee Field Station, where he performed his Ph.D. work on biogeography. He previously served on the curatorial staff at the Milwaukee Public Museum. He has had a lifelong interest in herpetology and conservation, with a recent emphasis on herp. inventory and monitoring in the western Great Lakes, and taxonomy and conservation of the Butler's Gartersnake (*Thamnophis butleri*). (Photographed by Gary S. Casper)

F. NEIL DAWSON is Wildlife Assessment Program Leader with the Ontario Ministry of Natural Resources, Northwest Science & Information Section in Thunder Bay, Ontario, Canada. He received a B.Sc. from the University of Guelph in Ontario, Canada. He is currently involved in developing a large scale population monitoring program for terrestrial vertebrates (including reptiles and amphibians) that may be impacted by forest management activities in Ontario. He has had a lifelong interest in Ontario's herpetofauna, particularly turtles. (Photographed by Chris Mills)