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COVER: Studies on Canadian Amphibians and Reptiles in Honour of Dr. Francis Cook. Centre: Dr. Francis Cook (photo: Brian Coad). See The Publications of Francis Cook on pages 99–102. The inset photos (clockwise from top right) are: Red-bellied Snake (*Storeria occipitomaculata*; photo: Nick Cairns; see article on pages 150–166), Western Chorus Frog (*Pseudacris triseriata*; photo: Jonathan Choquette; see article on pages 176–190), Western Painted Turtle (*Chrysemys picta belli*; photo: Kelsey Marchand; see article on pages 108–119), Long-toed Salamander (*Ambystoma macrodactylum*; photo: Cynthia Paszkowski; see article on pages 168–175), Spiny Softshell (*Apalone spinifera*; photo: Christina Davy; see article on pages 120–121).

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The publications of Francis Cook

The introduction to the first part of this two-part special issue, which is dedicated to Dr. Francis Cook, provided an overview of Francis's lengthy career as a herpetologist and Editor of *The Canadian Field-Naturalist* (Halliday and Seburn 2018). Here, we outline the published contributions Francis has made over many decades.

Francis has been an active researcher and science communicator for more than 50 years. His first two papers, co-authored with Sherman Bleakeney, were published in 1957 (Bleakney and Cook 1957a,b). Major publications include results from his master's thesis on the herpetofauna of Prince Edward Island (Cook 1967), results from his doctoral dissertation on the contact zone of American Toads (*Anaxyrus americanus*) and Canadian Toads (*Anaxyrus hemiophrys*) in Manitoba (Cook 1983), and the first book-length introduction to the amphibians and reptiles of Canada (Cook 1984a,b). Francis also wrote one of the earliest summaries of rare and endangered amphibians and reptiles in Canada (Cook 1970a). More recently, he wrote a detailed history of herpetology in Canada (Cook 2007a).

The following is a list of Francis's peer-reviewed publications, his non-peer reviewed herpetological publications, and selected other publications. We have excluded book reviews (almost 100 published since 1962), tributes, and various editorial material from his lengthy tenure editing *The Canadian Field-Naturalist*. This list includes an impressive 101 publications: a clearly significant contribution to the field of herpetology in Canada.

Literature Cited

(Not Including Those in the Collection of Publications)

Halliday W.D., and D.C. Seburn. 2018. Introduction to the special issue on herpetology in Canada. Canadian Field-Naturalist 132: 1–3. https://doi.org/10.22621/cfn.v132i1.2113

Collection of Publications

Bleakney, S., and F.R. Cook. 1957a. Additional records of the Four-toed Salamander, *Hemidactylium scutatum*, from Nova Scotia. Copeia 1957: 142–143.

Bleakney, S., and F.R. Cook. 1957b. Two erythristic *Plethodon cinereus* from Nova Scotia. Copeia 1957: 143.

Cook, F.R. 1959. Amphibians seen at Moose Mountain Park, Saskatchewan, June 12–16, 1959. The Blue Jay 17: 126.

Cook, F.R. 1960. New localities for the Plains Spadefoot Toad, Tiger Salamander, and the Great Plains Toad in the Canadian prairies. Copeia 1960: 363–364.

Cook, F.R., and J.S. Bleakney. 1960. Additional records of stream salamanders in New Brunswick. Copeia 1960: 362–363.

Cook, F.R. 1961. Further records of the Eastern Blacknose Dace in Nova Scotia. Canadian Field-Naturalist 75: 51–52. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28025575.

Cook, F.R., and J.S. Bleakney. 1961. Red phase of the Red-backed Salamander from New Brunswick. Canadian Field-Naturalist 75: 53. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28025577.

Cook, F.R., and R.W. Nero. 1961. The Green Snake and the Red-bellied Snake in Saskatchewan. The Blue Jay 19: 134–135.

Cook, F.R. 1963a. Proposed rejection of the neotype and type locality of *Thamnophis sirtalis* (Linnaeus), 1758 (Reptilia). Z.N.(S.) 1600. Bulletin of Zoological Nomenclature 20: 397–400.

Cook, F.R. 1963b. The rediscovery of the Mink Frog in Manitoba. Canadian Field-Naturalist 77: 129–130. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28098902.

Cook, F.R. 1963c. Herpetology at the National Museum of Canada 1918–1963. Canadian Amphibian and Reptile Conservation Society Bulletin March 1963: 1–2.

Cook, F.R., and A.M. Rick. 1963. First record of the Blue-spotted Salamander from Cape Breton Island, Nova Scotia. Canadian Field-Naturalist 77: 175–176. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28098952.

Cook, F.R. 1964a. A northern range extension for *Bufo americanus* with notes on *B. americanus* and *Rana sylvatica*. Canadian Field-Naturalist 78: 65–66. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28020361.

Cook, F.R. 1964b. Additional records and a correction of the type locality for the Boreal Chorus Frog in northwestern Ontario. Canadian Field-Naturalist 78: 186–192. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28020490.

Cook, F.R. 1964c. Additional specimens of the Small-mouthed Salamander from Pelee Island, Ontario. Canadian Field-Naturalist 78: 201–202. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28020505.

Cook, F.R. 1964d. The rusty colour phase of the Canadian Toad, *Bufo hemiophrys*. Canadian Field-Naturalist 78: 263–267. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28020571.

Cook, F.R. 1964e. Further comments on the proposed rejection of the neotype and type-locality of *Thamnophis sirtalis* (Linnaeus, 1758) (Reptilia) Z.N.(S.) 1600. Bulletin of Zoological Nomenclature 21: 327–328.

Cook, F.R. 1964f. Communal egg laying in the Smooth Green Snake. Herpetologica 20: 206.

Cook, F.R. 1964g. The Northern Prairie Skink in Manitoba: a possible relic population. National Museum of Canada Natural History Papers Number 24: 1–11.

Cook, F.R. 1964h. The status of the Western Spotted Frog, *Rana pretiosa*, in Saskatchewan. Copeia 1964: 219.

Cook, F.R. 1964i. Endangered Canadian Amphibians and Reptiles. Canadian Amphibian and Reptile Conservation Society Bulletin February 1964: 1–3.

Cook, F.R. 1964j. Corrections and further comments on endangered Canadian amphibians and reptiles. Canadian Amphibian and Reptile Conservation Society Bulletin April 1964: 3.

Cook, F.R., and D.R.M. Hatch. 1964. A spadefoot toad from Manitoba. Canadian Field-Naturalist 78: 60–61. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28020356.

Nero, R.W., and F.R. Cook. 1964. A range extension for the Wood Frog in northeastern Saskatchewan. Canadian Field-Naturalist 78: 268–269. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28020576.

Cook, F.R. 1965a. Additions to the known range of some amphibians and reptiles in Saskatchewan. Canadian Field-Naturalist 79: 112–120. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28033600.

Cook, F.R. 1965b. Collecting and preserving amphibians and reptiles. Pages 129–141 *in* Methods of Collecting and Preserving Vertebrate Animals. *Edited by* R.M. Anderson. National Museum of Canada Bulletin 69. Revised Fourth Edition. National Museum of Canada, Ottawa, Ontario, Canada.

Cook, F.R. 1966. A guide to the amphibians and reptiles of Saskatchewan. Saskatchewan Museum of Natural History Popular Series Number 13. Saskatchewan Museum of Natural History, Regina, Saskatchewan, Canada.

Cook, F.R. 1967. An analysis of the herpetofauna of Prince Edward Island. National Museum of Canada Bulletin 212. National Museum of Canada, Ottawa, Ontario, Canada.

Cook, F.R. 1968a. Amphibians and reptiles in Canada. Pages 51–52 *in* Canada Year Book 1968. Dominion Bureau of Statistics, Canada Yearbook Division, Queens Printer, Ottawa, Ontario, Canada.

Cook, F.R. 1968b. Reptiles and amphibians. Pages 436–442 *in* Science, History and Hudson Bay. *Edited by* C.S. Beals. Volume 1. Department of Energy, Mines and Resources, Ottawa, Ontario, Canada.

Cook, F.R. 1968c. Salamanders of the Ottawa District. Trail & Landscape 2: 18–22.

Cook, F.R. 1968d. Toad, treefrogs and frogs of the Ottawa District. Trail & Landscape 2: 50–56.

Cook, F.R. 1968e. Turtles of the Ottawa District. Trail & Landscape 2: 82–87.

Cook, F.R. 1968f. Lizards and snakes of the Ottawa District. Trail & Landscape 2: 99–106.

Cook, F.R. 1968g. Amphibians and Reptiles. *In* Resource Reader. Conservation Information Branch, Saskatchewan Department of Natural Resources, Regina, Saskatchewan, Canada.

Cook, F.R. 1968h. Amphibians and reptiles of the Rideau Region. Pages 250–253 *in* The Fauna of the Rideau Region. Rideau Valley Conservation Authority Report, Ottawa, Ontario, Canada.

Cook, F.R. 1968i. On name changes. Canadian Amphibian and Reptile Conservation Society Bulletin 6(4): 1–2.

Cook, F.R. 1968j. A herpetologist in the Canadian prairies. Canadian Amphibian and Reptile Conservation Society Bulletin 7(2): 1–3.

Cook, F.R. 1969a. What should an Ottawa field-naturalist observe? I. Amphibians and reptiles. Trail & Landscape 3: 45–49.

Cook, F.R. 1969b. A herpetologist's sojourn in Jamaica. Canadian Amphibian and Reptile Conservation Society Bulletin 8(2): 1–3.

Cook, F.R. 1970a. Rare or endangered Canadian amphibians and reptiles. Canadian Field-Naturalist 84: 9–16. Accessed 6 October 2018. https://biodiversitylibrary.org/page/29553251.

Cook, F.R. 1970b. Endangered wildlife—Amphibians and reptiles. Pages 10–11 *in* Endangered Wildlife in Canada. Canadian Wildlife Federation, Ottawa, Ontario, Canada.

Cook, F.R. 1971. The National Museum of Natural Sciences research program in herpetology: where are we and can the amateur play a part? Canadian Herpetologists Society Quarterly 1(3): 3–5.

Cook, F.R., and J. Folinsbee. 1975. Second record of the Blue-spotted Salamander from Labrador. Canadian Field-Naturalist 89: 314–315. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28033044.

van Zyll de Jong, C.G., and F.R. Cook. 1975. Eastern Yellow-bellied Racer in central Saskatchewan. Canadian Field-Naturalist 89: 174–175. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28032900.

Woods, J.G., and F.R. Cook. 1976. Range extension of the Ribbon Snake in eastern Ontario. Canadian Field-Naturalist 90: 69–70. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28045546.

Cook, F.R. 1977a. Review of the Canadian herpetological scene. Pages 117–121 *in* Canada's Threatened Species and Habitats. *Edited by* T. Mosquin and C. Suchal. Proceedings of Symposium on Canada's Threatened Species and Habitats cosponsored by the Canadian Nature Federation and the World Wildlife Fund (Canada) in Ottawa 20–24 May, 1976. Canadian Nature Federation Special Publication 6. Canadian Nature Federation, Ottawa, Ontario, Canada.

Cook, F.R. 1977b. Records of the Boreal Toad from the Yukon and northern British Columbia. Canadian Field-Naturalist 91: 185–186. Accessed 6 October 2018. https://biodiversitylibrary.org/page/28061392.

Cook, F.R. 1978a. Amphibians and reptiles (Amphibiens et reptiles). Neotoma 1: 1–5.

Cook, F.R. 1978b. Salamanders (Les urodeles). Neotoma 2: 1–4.

Cook, F.R. 1978c. Canadian status of reptiles and amphibians on appendices I and II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES): *Dermochelys coriacea* Leatherback Turtle; *Caretta caretta* Loggerhead Turtle; *Lepidochelys kempi* Atlantic Ridley; *Chelonia mydas* Green Turtle; *Clemmys mulenburgi* Mulhenburg's Turtle; *Carina bottae* Rubber Boa. CITES manuscript reports, Canadian Wildlife Service, Ottawa, Ontario, Canada.

Cook, F.R. 1979a. The Two-lined Salamander, *Eurycea bislineata*, in Labrador. Canadian Field-Naturalist 93: 178–179. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28063495.

Cook, F.R. 1979b. Frogs, toads and treefrogs (Les anoures: grenouilles, crapauds et rainettes). Neotoma 3: 1–6.

Cook, F.R. 1979c. Turtles (Les tortues). Neotoma 4: 1–4.

Cook, F.R. 1979d. Snakes and lizards (Les serpentes et les lezards). Neotoma 5: 1–7.

Cook, F.R. 1979e. Field study of Canadian amphibians and reptiles (Etude sur le terrain des amphibiens et reptiles au Canada). Neotoma 6: 1–4.

Cook, F.R., and S.W. Gorham. 1979. Occurrence of the triploid form in populations of the Blue-spotted Salamander, *Ambystoma laterale*, in New Brunswick. Journal of the New Brunswick Museum 1979: 154–161.

Ussher, R.D., and F.R. Cook. 1979. The eastern limit of the Five-lined Skink in Ontario. Canadian Field-Naturalist 93: 321–323. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28063644.

Cook, F.R. 1980. Checklist of amphibians and reptiles of Canada. Canadian Amphibian and Reptile Conservation Society Bulletin 18(2): 1–6.

Cook, F.R., J.D. Lafontaine, S. Black, L. Luciuk, and R.V. Lindsay. 1980. Spotted Turtles (*Clemmys guttata*) in eastern Ontario and adjacent Quebec. Canadian Field-Naturalist 94: 411–415. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28089308.

Gordon, D.M., and F.R. Cook. 1980a. An aggregation of gravid snakes in the Quebec Laurentides. Canadian Field-Naturalist 94: 456–457. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28089353.

Gordon, D.M., and F.R. Cook. 1980b. Range extensions for the Yellow spotted Salamander, *Ambystoma maculatum*, in Quebec. Canadian Field-Naturalist 94: 460. Accessed 8 October 2018. https://biodiversitylibrary.org/page/28089357.

Schueler, F.W., and F.R. Cook. 1980. Distribution of the middorsal stripe dimorphism in the Wood Frog, *Rana sylvatica*, in eastern North America. Canadian Journal of Zoology 58: 1643–1651. https://doi.org/10.1139/z80-226

Cook, F.R. 1981a. Status report on the Leatherback Turtle in Canada. Committee on the Status of Endangered Wildlife in Canada (COSEWIC), Ottawa, Ontario, Canada.

Cook, F.R. 1981b. The snakes of Canada (for those who care). Canadian Geographic 101(3): 62–67.

Cook, F.R. 1981c. Amphibians and reptiles of the Ottawa district. Revised edition. Trail & Landscape 15: 75–109.

Cook, F.R., and J.C. Cook. 1981. Attempted avian predation by the Canadian Toad, *Bufo americanus hemiophrys*. Canadian Field-Naturalist 95: 346–347. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28062049.

Ouellet, H., et F.R. Cook. 1981. Les noms français des amphibiens et reptiles du Canada: une liste provisoire. Syllogeous 32: 1–7.

Cook, F.R. 1983. An Analysis of Toads of the *Bufo americanus* Group in a Contact Zone in Central Northern North America. National Museums of Canada Publications in Natural Sciences 3, Ottawa, Ontario, Canada.

Cook, F.R. 1984a. An Introduction to Canadian Amphibians and Reptiles. National Museum of Natural Sciences, Ottawa, Ontario, Canada.

Cook, F.R. 1984b. Introduction aux amphibiens et reptiles du Canada. Musee national des sciences naturelles, Ottawa, Ontario, Canada.

Cook, F.R., and D. Muir. 1984. The committee on the status of endangered wildlife in Canada (COSEWIC): history and progress. Canadian Field-Naturalist 98: 63–70. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28063890.

Cook, F.R. 1985a. Amphibian. Pages 53–54 *in* The Canadian Encyclopedia. Volume 1. Hurtig Publishers, Edmonton, Alberta, Canada.

Cook, F.R. 1985b. Reptile. Pages 1571–1572 *in* The Canadian Encyclopedia. Volume 3. Hurtig Publishers, Edmonton, Alberta, Canada.

Cook, F.R. 1986a. The "one hundredth" volume of the Canadian Field-Naturalist. Canadian Field-Naturalist 100: 140–142. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28072215.

Cook, F.R. 1986b. Amphibians and reptiles of eastern Ontario. The Blue Bill 33: 130–142.

Cook, F.R. 1987a. Formation of Canadian lower vertebrate societies. Canadian Field-Naturalist 101: 625. Accessed 5 October 2018. https://biodiversitylibrary.org/page/28090058.

Cook, F.R. 1987b. Report from the herpetology section of the National Museum of Natural Sciences. Canadian Association of Herpetologists Bulletin 1(2): 3–5.

Cook, F.R. 1989a. Annual display: the amphibians of Ontario. Pages 171–175 *in* Legacy: The Natural History of Ontario. *Edited by* J. Theberge. McClelland & Stewart, Inc., Toronto, Ontario, Canada.

Cook, F.R. 1989b. Once they ruled: the reptiles of Ontario. Pages 176–187 *in* Legacy: The Natural History of Ontario. *Edited by* J. Theberge. McClelland & Stewart, Inc., Toronto, Ontario, Canada.

Cook, F.R. 1991a. Workshop on declines in Canadian amphibian populations: a design for national monitoring. Canadian Field-Naturalist 105: 421–422. Accessed 5 October 2018. https://biodiversitylibrary.org/page/34348935.

Cook, F.R. 1991b. COSEWIC and the Status of the Massasauga. Rattlesnake Tales 3(2): 4–6.

Cook, F.R. 1991c. Amphibians and reptiles and the COSEWIC process. Canadian Association of Herpetologists Bulletin 5(1): 5–8.

Cook, F.R. 1992a. Pitfalls in quantifying amphibian populations in Canada. Pages 83–86 *in* Declines in Canadian Amphibian Populations: Designing a National Monitoring Strategy. *Edited by* C.A. Bishop and K.E. Pettit. Occasional Paper Number 76. Canadian Wildlife Service, Ottawa, Ontario, Canada.

Cook, F.R. 1992b. The once and future national research collection in herpetology. Canadian Association of Herpetologists Bulletin 6(1): 2–9.

Cook, F.R. 1992c. A national task force for frog declines in Canada. Canadian Biodiversity 1(4): 15–18.

Cook, F.R. 1993. After an ice age: zoogeography of the Massasauga from a Canadian perspective. Pages 19–25 *in* International Symposium and Workshop on the Conservation of the Eastern Massasauga, *Sistrurus catenatus catenatus*. *Edited by* B. Johnson and V. Menzies. Metropolitan Toronto Zoo, Toronto, Ontario, Canada.

Cook, F.R. 1994a. Comment (11) on the use of the plenary powers to validate current usage of the genus *Hydromantus* Gistel, 1848 (Case 2868). Bulletin of Zoological Nomenclature 51: 152–153.

Cook, F.R. 1994b. Comment (7) on the use of the plenary powers to validate current usage of the tribe Hemidactyliini Howell, 1856 (Case 2869). Bulletin of Zoological Nomenclature 51: 155.

Cook, F.R. 1995a. Bullfrog life history. Pages 2–3 *in* Bullfrog Management in Ontario, Workshop Proceedings. *Edited by* K. Coleman and R. Cholmondeley. Southern Region Science & Technology Transfer Unit, Workshop Proceedings WP-005, Ontario Ministry of Natural Resources, Brockville, Ontario, Canada.

Cook, F.R. 1995b. Amphibian. *In* The Canadian Encyclopedia. Revised for second edition on CD.

Cook, F.R. 1995c. Reptile. *In* The Canadian Encyclopedia. Revised for second edition on CD.

Cook, F.R. 1995d. *The Canadian Field-Naturalist*: 114 years of publication on northern North American Biodiversity. Global Biodiversity 5(1): 16–17.

Cook, F.R. 1995e. The herpetology collection: a treasure of documentation on amphibians and reptiles. Voice of Nature 1(5): 6.

Cook, F.R. 1995f. *The Canadian Field-Naturalist*: 115 years of publication on northern North American biodiversity—1880–1994. Amphipacifica 1(3): 75.

Cook, F., F. Schueler, and M. Rankin. 1998. Rideau River Biodiversity Project: an initial report on the Rideau River Biodiversity Project. Canadian Association of Herpetologists Bulletin 12(2): 22–23.

Cook, F.R., R.W. Campbell, and G.R. Ryder. 2005. Origin and current status of the Pacific Pond Turtle (*Actinemys marmorata*) in British Columbia. Wildlife Afield 2: 58–63.

Cook, F.R. 2007a. Early Canadian reptile studies: anecdote to inventory. Pages 5–22 *in* Ecology, Conservation and Status of Reptiles in Canada. *Edited by* C.N.L. Seburn and C.A. Bishop. Herpetological Conservation Number Two. Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.

Cook, F.R. 2007b. Amphibian. *In* The Canadian Encyclopedia [edited 2015]. Accessed 16 September 2018. https://www.thecanadianencyclopedia.ca/en/article/amphibian.

Cook, F.R. 2007c. Reptile. *In* The Canadian Encyclopedia [edited 2015]. Accessed 16 September 2018. https://www.thecanadianencyclopedia.ca/en/article/reptile.

Cook, F.R. 2010. Recipe for a herpetologist: an autobiography. Canadian Association of Herpetologists Bulletin 18(1): 4–11.

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Oviposition and subsequent depredation of Snapping Turtle (*Chelydra serpentina*) nests in fresh asphalt

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Abstract

On 28 June 2009, three Snapping Turtle (*Chelydra serpentina*) nests were found oviposited in fresh asphalt beside a bridge in Algonquin Provincial Park, Ontario. One nest was excavated immediately; the other two were left untouched. The two nests left *in situ* were revisited on 28 July when it was discovered that one nest had been depredated by an unknown predator. Evidence of the third nest was obliterated by tracks of large mammals crossing the bridge. These observations suggest that predators find turtle nests despite the strong odour of asphalt. To examine potential negative impacts of asphalt on turtle eggs, five clean Snapping Turtle eggs, collected elsewhere in Algonquin Provincial Park, were buried in asphalt on 28 July. After eight days, the translocated eggs had obvious staining and contained 0.081–0.376 µg/g (wet weight) polycyclic aromatic hydrocarbons (PAHs), presumably resulting from asphalt exposure. The risk of exposure to PAHs or other chemicals associated with asphalt is unknown, but the levels of PAHs in these eggs appeared lower than those associated with acute toxicity.

Key words: Snapping Turtle; *Chelydra serpentina*; asphalt; polycyclic aromatic hydrocarbons; oviposition; predation; Algonquin Provincial Park; Ontario

Introduction

In landscapes with substantial human activity, Snapping Turtles (*Chelydra serpentina*) and other freshwater turtle species oviposit in a variety of artificial substrates, such as dams, railway and road embankments, roadsides, vegetable gardens, compost, coal ash, and sand or gravel pits (Loncke and Obbard 1977; de Solla *et al.* 2001; Nagle *et al.* 2001; de Solla and Fernie 2004; Aresco 2005). In many parts of their range, most female Snapping Turtles nest in artificial substrates, because natural areas might not be available, and turtles may travel considerable distances to nest on embankments or dams (Obbard and Brooks 1980).

The use of artificial or anthropogenically modified substrates by turtles can have consequences for the developing embryo (e.g., Nagle *et al.* 2001; de Solla and Martin 2007), and possibly for egg predators and the nesting female turtles. Here we report oviposition by three Snapping Turtles in asphalt, depredation of one of those nests by an unknown predator, and the absorption of polycyclic aromatic hydrocarbons (PAHs) in turtle eggs.

Methods

Field-site observations

A search was conducted for Snapping Turtle nests in Algonquin Provincial Park, Ontario, to collect eggs for a toxicological study (internal Animal Care protocol 0902 by Environment Canada) examining their absorption of polycyclic aromatic hydrocarbons (PAHs). Algonquin Provincial Park has previously been used as a source of eggs for experiments to examine toxicity of soil-borne contaminants (e.g., de Solla and Martin 2007). Roadsides were searched for turtle nests, which were excavated and the eggs removed.

During the afternoon of 28 June 2009 on the road along Costello Creek south of Lake Opeongo (45.616815°N, 78.344354°W), three Snapping Turtle nests in fresh asphalt were observed (Figure 1). The nests were presumed to be about two weeks old, given the normal period of oviposition of Snapping Turtles in Algonquin Provincial Park. The nests were found by S.R.de S. beside a temporary bridge, newly installed as an emergency repair to keep the road open after damage to a culvert from spring runoff. "Cold patch" was used along the sides of the road to stabilize the bridge and reduce erosion from the damaged culvert (B. Steinberg pers. comm. 15 November 2010). Cold patch is a combination of asphalt and stone or gravel, which is mixed with a solvent (e.g., kerosene, diesel, or gasoline of varying composition) to make the asphalt pliable at low temperatures (Speight 2015). The asphalt along the sides of the bridge was not compacted and, thus, was loose to the touch. The smell of petroleum product was obvious. One nest was on the west side and two were on the east side of the bridge, on 45° slopes within ~60 cm of the road surface; consequently, there was no risk of tires running over the nests. All three nests had the classic mound and trough characteristics of Snapping Turtle nests (Figure 1) and were easy to

FIGURE 1. Snapping Turtle (*Chelydra serpentina*) nest deposited in "cold patch" asphalt mixture, beside a bridge in Algonquin Provincial Park, Ontario, 28 June 2009. Photo: Shane de Solla.

spot. This bridge was a known nesting area and Snapping Turtle nests in gravel and sand at this culvert were often depredated in previous years (S.R.de S. pers. obs.).

One nest was excavated immediately, whereas the other two were left untouched. Because the asphalt along the side of the bridge embankment was soft, there was little difficulty digging with a hand shovel. The excavated clutch was beneath the asphalt layer in the sand foundation of the embankment, although a considerable amount of asphalt was mixed with the sand substrate, such that the eggs were directly exposed to asphalt. All excavated eggs displayed black speckled stains (Figure 2), presumably resulting from direct exposure to the asphalt. The asphalt was very sticky and left a thick oily residue on the nitrile gloves used during nest excavation. The excavated eggs were removed from the site, but were unavailable for testing for logistic reasons.

On 28 July 2009, the site was revisited to remove eggs from the two remaining nests for artificial incubation to determine hatching success. One of the nests had been depredated and egg shells were found in the excavated cavity. Furthermore, numerous holes in the asphalt in the general area were observed, consistent with mammalian depredation attempts on turtle nests. The third clutch was no longer visible, largely because of surficial disturbance by numerous animals, probably Moose (*Alces americanus*), walking over the bridge embankment. Attempts to find the missing clutch were ceased to minimize further disturbance to the asphalt. Unlike the nest that was excavated just after oviposition on 28 June, the depredated nest cavity was completely within the asphalt with little sand visible and, in the area of the lost nest, the asphalt was deeper than a typical Snapping Turtle nest cavity (i.e., deeper than 10–15 cm; Congdon *et al.* 2008). Consequently, those eggs would have had greater exposure to asphalt than the previously excavated nest.

Control eggs for an unrelated project from a separate Algonquin site were used to measure PAHs. Five eggs were buried on 28 July in fresh asphalt at a depth of about 12 cm, which is within the typical depth of a Snapping Turtle nest cavity (Congdon *et al.* 2008). On 5 August, the eggs were removed and sealed in a clear plastic sandwich bag. The eggs that were excavated had obvious staining, substantial black speckling, and an odour of asphalt (Figure 2). Samples of asphalt and sand under the asphalt were also collected and sealed in a plastic bag. They were brought to the Canada Centre

Figure 2. Snapping Turtle (*Chelydra serpentina*) egg showing black stains after eight days incubation in “cold patch” asphalt in Algonquin Provincial Park, Ontario. Photo: Shane de Solla.

for Inland Waters in Burlington the same day and the eggs, asphalt, and soil were placed in a −80°C freezer.

PAH analysis

The five eggs and soil and asphalt samples were sent to Maxxam Analytical (Mississauga, Ontario, Canada) for measurement of PAH concentrations using gas chromatography in selective ion monitoring mode, based on United States Environmental Protection Agency (EPA) method 8270. Eighteen PAHs (Table 1), including the 16 that are considered priority PAHs by the EPA, were measured in all samples. Reportable detection limits (RDLs) ranged from 0.005 to 0.02 µg/g in turtle eggs and sand and from 0.1 to 0.4 µg/g in asphalt.

Results and Discussion

The concentrations of six PAHs were found to be above RDLs and that of 1- and 2-methylnaphthalene was highest relative to the other PAHs in the eggs (Table 1). The concentration of all PAHs in eggs ranged from 0.081 to 0.376 µg/g (wet weight). These findings support those of de Solla and Martin (2011) that Snapping Turtle embryos can directly absorb potentially harmful contaminants from material around the nest cavity. The turtles were only exposed to PAHs from the substrate for eight days and, thus, the amount of PAHs absorbed may have been appreciably larger after the full incubation period and may have resulted in more toxicity than what was observed.

Three observations reported here are of note. First, Snapping Turtles will select nesting substrates, including asphalt, where there is some risk of exposure of eggs to toxic chemicals. Second, predators, presumably mammals (e.g., skunks, Raccoons [*Procyon lotor*], foxes, etc.) are capable of detecting turtle eggs that are buried under a substrate that is pungent to a human nose. Third, turtle eggs may absorb chemicals from asphalt.

We speculate that the asphalt was attractive to the turtles likely because of its high temperature at the time the females were selecting their oviposition site or because of the lack of covering vegetation. At northern latitudes, female Snapping Turtles select exposed locations with relatively warmer substrate temperatures to oviposit than turtles at more equatorial latitudes that select shadier, cooler substrates (Ewert *et al.* 2005), and they also prefer landscapes with short or little vegetation (Kolbe and Janzen 2002). Soil composition may not be as important in the choice of oviposition site (Hughes and Brooks 2006); Snapping Turtles are known to oviposit in sand, clay, wood chips, beaver lodges and

TABLE 1. Concentrations of polycyclic aromatic hydrocarbons (PAHs) in Snapping Turtle (*Chelydra serpentina*) eggs buried in asphalt from 28 July to 5 August 2009. PAHs in asphalt and in sand immediately below asphalt are also reported.

Type of PAH	Concentration of PAHs, µg/g wet weight						
	Eggs						
	1	2	3	4	5	Sand (RDL)	Asphalt (RDL)
Acenaphthene	ND	ND	ND	ND	ND	ND (0.01)	0.6 (0.2)
Acenaphthylene	ND	ND	ND	ND	ND	ND (0.005)	ND (0.1)
Anthracene	ND	ND	ND	ND	ND	ND (0.005)	0.5 (0.1)
Benzo(a)anthracene	ND	ND	ND	ND	ND	ND (0.01)	ND (0.2)
Benzo(a)pyrene	ND	ND	ND	ND	ND	ND (0.005)	0.1 (0.1)
Benzo(b/j)fluoranthene	ND	ND	ND	ND	ND	ND (0.01)	ND (0.2)
Benzo(g,h,i)perylene	ND	ND	ND	ND	ND	ND (0.02)	0.5 (0.4)
Benzo(k)fluoranthene	ND	ND	ND	ND	ND	ND (0.01)	ND (0.2)
Chrysene	ND	ND	ND	ND	ND	ND (0.01)	ND (0.2)
Dibenz(a,h)anthracene	ND	ND	ND	ND	ND	ND (0.02)	ND (0.4)
Fluoranthene	ND	ND	ND	ND	ND	0.006 (0.005)	0.2 (0.1)
Fluorene	0.007	0.008	0.006	ND	ND	ND (0.005)	1.5 (0.1)
Indeno(1,2,3-cd)pyrene	ND	ND	ND	ND	ND	ND (0.02)	ND (0.4)
1-methylnaphthalene	0.110	0.130	0.081	0.034	0.037	— (0.005)	—
2-methylnaphthalene	0.140	0.170	0.097	0.037	0.044	— (0.005)	—
Naphthalene	0.051	0.061	0.036	0.010	0.020	ND (0.005)	1.5 (0.1)
Phenanthrene	0.006	0.007	0.005	ND	ND	ND (0.005)	3.2 (0.1)
Pyrene	ND	ND	ND	ND	ND	0.009 (0.005)	0.7 (0.1)

Note: — = no data, ND = not detected, RDL = reportable detection limit.

dams, gravel, vegetable gardens, grass fields, and other substrates (Robinson and Bider 1988; de Solla *et al.* 2001; Congdon *et al.* 2008).

Road and habitat types may influence predation patterns. Although some believe that mammalian predators find turtle nests primarily through visual cues (e.g., Strickland *et al.* 2010), they are more generally assumed to use olfactory cues (Spencer 2002; Burke *et al.* 2005). Regardless of the mechanism(s) predators use, it is evident from our observations that they are capable of finding turtle nests in substrates containing chemicals that can interfere with olfactory senses and substrates with non-typical physical structure that can interfere with visual senses. Predators may even prefer unnatural habitats, such as roadsides, for hunting (Mata *et al.* 2017).

Snapping Turtles can spend substantial time selecting oviposition sites and appear to select substrate and environmental conditions that are suitable for egg development, but they clearly sometimes select substrates or conditions that may result in exposure to contaminants or other stressors. For example, female Snapping Turtles have been observed laying eggs in compost that was sufficiently hot to kill both the eggs and nesting turtles (de Solla *et al.* 2001). Reptiles sometimes oviposit in agricultural fields (Rauschenberger *et al.* 2004; de Solla and Martin 2007), in substrates that have been exposed to oil (Van Meter *et al.* 2006), or coal-ash-contaminated soils (Nagle *et al.* 2001).

Although Snapping Turtle eggs from a site contaminated with heavy metals and PAHs had lower hatching success and increased deformities relative to controls (Bell *et al.* 2006), the effect of PAHs and oil on turtle egg development is less clear. Exposure to both oil and PAHs (through topical application to the eggshell) increased deformity rates in turtle eggs from Algonquin Provincial Park (Van Meter *et al.* 2006). Although turtle eggs are capable of absorbing PAHs from soil contaminated with Arabian light crude oil (after exposure of up to 1 L of 10 g oil/L water in soil, eggs contained up to 0.56 µg/g of total PAHs), PAH exposure did not affect either hatching success or deformity rate (Rowe *et al.* 2009). Incidents of oviposition in asphalt as described here are presumably not common, but turtles frequently use roadsides for oviposition.

Reptiles may be exposed to PAHs through avenues other than contaminated soil. Studies have discovered the presence of PAHs in wild reptiles, but there are few studies that illustrate how PAHs affect health and development. PAHs were found in wild Loggerhead Sea Turtle (*Caretta caretta*) plasma samples and correlated with electrolyte levels as well as blood enzymes (Camacho *et al.* 2013). In addition, total proteins, albumin, globulins, and creatinine were positively correlated with PAHs. The authors suggested that these correlations could reflect altered kidney function. In a separate study, significant levels of PAHs were found in various tissues, predominantly in skin and kidney samples of two species of sea snakes (Sereshk and Bakhtiari 2014). Partial life cycle PAH exposure studies would be beneficial in determining deleterious effects in reptiles.

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Literature Cited

Aresco, M.J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123: 37–44.

Bell, B., J.R. Spotila, and J.D. Congdon. 2006. High incidence of deformity in aquatic turtles in John Heinz National Wildlife Refuge. Environmental Pollution: 142: 457–465. https://doi.org/10.1016/j.envpol.2005.10.020

Burke, R.L., C.M. Schneider, and M.T. Dolinger. 2005. Cues used by raccoons to find turtle nests: effects of flags, human scent, and Diamond-backed Terrapin sign. Journal of Herpetology 39: 312–315. https://doi.org/10.1670/199-03N

Camacho, M., L.B. Octavio, L.D. Boada, L.F.L. Jurado, M. Medina, M. Zumbado, and J. Orós. 2013. Potential adverse health effects of persistent organic pollutants on sea turtles: evidences from a cross-sectional study on Cape Verde loggerhead sea turtles. Science of the Total Environment 458–460: 283–289. https://doi.org/10.1016/j.scitotenv.2013.04.043

Congdon, J.D., J.L. Greene, and R.J. Brooks. 2008. Reproductive and nesting ecology of female Snapping Turtles. Pages 123–134 *in* The Biology of the Snapping Turtle. *Edited by* A.C. Steyermark, M.S. Finkler, and R.J. Brooks. Johns Hopkins University Press, Baltimore, Maryland, USA.

de Solla, S.R., D.G. Campbell, and C.A. Bishop. 2001. Hyperthermia induced mortality of gravid Snapping Turtles, *Chelydra serpentina*, and eggs in a wood chip pile. Canadian Field-Naturalist 115: 510–512. Accessed 27 October 2018. https://biodiversitylibrary.org/page/35014673.

de Solla, S.R., and K.J. Fernie. 2004. Is cost of locomotion the reason for prolonged nesting forays of Snapping Turtles (*Chelydra serpentina*)? Canadian Field-Naturalist 118: 610–612. https://doi.org/10.22621/cfn.v118i4.67

de Solla, S.R., and P.A. Martin. 2007. Toxicity of nitrogenous fertilizers to eggs of Snapping Turtles (*Chelydra serpentina*) in field and laboratory exposures. Environmental Toxicology and Chemistry 26: 1890–1895. https://doi.org/10.1897/06-500R1.1

de Solla, S.R., and P.A. Martin. 2011. Absorption of current use pesticides by snapping turtle (*Chelydra serpentina*) eggs in treated soil. Chemosphere 85: 820–825. https://doi.org/10.1016/j.chemosphere.2011.06.080

Ewert, M.A., J.W. Lang, and C.E. Nelson. 2005. Geographic variation in the pattern of temperature-dependent sex determination in the American Snapping Turtle (*Chelydra serpentina*). Journal of Zoology 265: 81–95. https://doi.org/10.1017/S0952836904006120

Hughes, E., and R.J. Brooks. 2006. The good mother: does nest site selection constitute parental investment in turtles? Canadian Journal of Zoology 84: 1545–1554. https://doi.org/10.1139/z06-148

Kolbe, J.J., and F.J. Janzen. 2002. Spatial and temporal dynamics of turtle nest predation: edge effects. Oikos 99: 538–544. https://doi.org/10.1034/j.1600-0706.2002.11853.x

Loncke, D.J., and M.E. Obbard. 1977. Tag success, dimensions, clutch size and nesting site fidelity for the Snapping Turtle, *Chelydra serpentina*, (Reptilia, Testudines, Chelydridae) in Algonquin Park, Ontario, Canada. Journal of Herpetology 11: 243–244. https://doi.org/10.2307/1563158

Mata, C., P. Ruiz-Capillas, and J.E. Malo. 2017. Small-scale alterations in carnivore activity patterns close to motorways. European Journal of Wildlife Research 63: 64. https://doi.org/10.1007/s10344-017-1118-1

Nagle, R.D., C.L. Rowe, and J.D. Congdon. 2001. Accumulation and selective maternal transfer of contaminants in the turtle *Trachemys scripta* associated with coal ash deposition. Archives of Environmental Contamination and Toxicology 40: 531–536. https://doi.org/10.1007/s002440010206

Obbard, M.E., and R.J. Brooks. 1980. Nesting migrations of the Snapping Turtle (*Chelydra serpentina*). Herpetologica 36: 158–162.

Rauschenberger, R.H, J.J. Wiebe, M.S. Sepulveda, J.E. Buckland, and T.S. Gross. 2004. Predicting maternal body burdens of organo-chlorine pesticides from eggs and evidence of maternal transfer in *Alligator mississippiensis*. Environmental Toxicology and Chemistry 23: 2906–2915. https://doi.org/10.1897/03-584.1

Robinson, C., and J.R. Bider. 1988. Nesting synchrony — a strategy to decrease predation of snapping turtle (*Chelydra serpentina*) nests. Journal of Herpetology 22: 470–473. https://doi.org/10.2307/1564342

Rowe, C.L., C.L. Mitchelmore, and **J.E. Baker.** 2009. Lack of biological effects of water accommodated fractions of chemically- and physically-dispersed oil on molecular, physiological, and behavioral traits of juvenile Snapping Turtles following embryonic exposure. Science of the Total Environment 407: 5344–5355. https://doi.org/10.1016/j.scitotenv.2009.06.036

Sereshk, Z.H., and A.R. Bakhtiari. 2014. Distribution patterns of PAHs in different tissues of annulated sea snake (*Hydrophis cyanocinctus*) and short sea snake (*Lapemis curtus*) from the Hara Protected Area on the North Coast of the Persian Gulf, Iran. Ecotoxicology and Environmental Safety 109: 116–123. https://doi.org/10.1016/j.ecoenv.2014.06.004

Speight, J.G. 2016. Nomenclature and terminology. Pages 3–43 *in* Asphalt Materials Science and Technology. Butterworth-Heinemann, Oxford, United Kingdom. https://doi.org/10.1016/C2013-0-15469-4

Spencer, R.J. 2002. Experimentally testing nest site selection: fitness trade-offs and predation risk in turtles. Ecology 83: 2136–2144. https://doi.org/10.1890/0012-9658(2002)083[2136:ETNSSF]2.0.CO;2

Strickland, J., P. Colbert, and F.J. Janzen. 2010. Experimental analysis of effects of markers and habitat structure on predation of turtle nests. Journal of Herpetology 44: 467–470. https://doi.org/10.1670/08-323.1

Van Meter, R.J., J.R. Spotila, and H.W. Avery. 2006. Polycyclic aromatic hydrocarbons affect survival and development of common Snapping Turtle (*Chelydra serpentina*) embryos and hatchlings. Environmental Pollution 142: 466–475. https://doi.org/10.1016/j.envpol.2005.10.018

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Spatial ecology and multi-scale habitat selection by Western Painted Turtles (*Chrysemys picta bellii*) in an urban area

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Abstract

As urban centres expand, knowledge on the habitat and space use of native wildlife, particularly long-lived species, is required for proper management. Our objective was to understand space requirements and key habitat features necessary for long-term persistence of Western Painted Turtles (*Chrysemys picta bellii*) living in a Canadian urban park. Using radio telemetry, we examined seasonal habitat selection and space use over two years, 2015–2016 (n = 23), and 2016–2017 (n = 29) in Regina, Saskatchewan. Daily movements and home ranges of males and females were smaller during emergence than during nesting or post-nesting phases of the active season. Turtles inhabiting marsh sites had 2- and 4-times larger daily movements and home ranges compared to turtles inhabiting the creek. Turtles selected the shoreline habitat over urban/parkland and open water. Turtles used marsh-shoreline habitats non-randomly, selecting accessible shoreline with large trees in the active season. In contrast, turtles used creek-shoreline habitat according to availability. Overwintering sites selected by turtles were warmer and deeper than random available sites, with no difference in dissolved oxygen level. However, water was hypoxic for most overwintering sites. Our results show that turtles range widely, requiring 20–60 ha throughout the year. Urban park areas should be managed to provide accessible shorelines with a combination of cover and open basking areas. Critically, careful attention needs to be paid to managing water depth so that over-wintering sites remain viable.

Key words: *Chrysemys picta bellii*; Western Painted Turtle; habitat selection; urban ecology; radio telemetry

Introduction

Currently, more than 80% of Canadians reside in urban centres (Statistics Canada 2011). As a result, urban habitats are becoming increasingly fragmented and urban planners are challenged with designing and maintaining urban parks that can sustain healthy, native wildlife populations. Turtles have long life histories, characterized by slow somatic growth rates and late age at maturity, leading to slow population growth (Brooks *et al.* 1990). Small changes to the aquatic and terrestrial habitats of turtles, such as draining, dredging, and shoreline development, can affect their survival. Increases in adult mortality by even 2–3% per year can lead to drastic population declines and possible local extinction (Congdon *et al.* 1993; Gibbs and Shriver 2002). Urbanization impacts turtle populations by decreasing genetic diversity (Rubin *et al.* 2001), restricting aquatic mobility (Bennett *et al.* 2010), increasing adult mortality (Marchand and Litvaitis 2004; Aresco 2005; Gibbs and Steen 2005; Steen *et al.* 2006), increasing human disturbance (Pittfield and Burger 2017), and increasing rates of nest predation (Baldwin *et al.* 2004; Marchand and Litvaitis 2004). All of these factors are exacerbated at northern latitudes where climate may be an additional factor affecting turtle population parameters (i.e., shorter growing season, slowed annual somatic growth rate, further delayed age at maturity).

Previous studies have focussed on the detrimental impacts of urbanization for turtle population persistence; however, few studies examine critical features influencing persistence in urban environments (e.g., Spinks *et al.* 2003; Plummer and Mills 2008; Winchell and Gibbs 2016; Pittfield and Burger 2017). Urban systems are highly dynamic, creating continual changes to the surrounding environment. Knowledge of turtle resource requirements in response to external anthropogenic pressures is necessary as these requirements can vary temporally and spatially. Biologically relevant time periods and multiple spatial scales therefore need to be considered (Johnson 1980). Turtles are ectotherms, so their movement and habitat use are dictated by their thermal, metabolic, and reproductive needs. As such, their active season can be divided into three relevant time periods (emergence, nesting, and post-nesting), to better understand habitat selection and space use variation based on different phases of the seasonal cycle (Litzgus and Mousseau 2004; Rasmussen and Litzgus 2010). Knowledge of the core habitats and space required throughout the three phases of the active season is required to manage turtle habitat in urban systems.

Suitable overwintering habitat for adult turtles is a critical factor for northern populations over the long-term. At the extreme, turtles can spend four to six months under the ice, meaning that nearly half of their lifetime is spent in overwintering habitat (Ultsch 2006; Jackson and Ultsch 2010). Overwintering habitats are chosen in the fall, and must be adequate to ensure survival until the ice recedes in the spring. A thermally stable aquatic habitat enables reduced metabolism; however, overwintering locations can prove to be physiologically stressful or lethal by exposing individuals to severe risks such as freezing, predation, anoxia, and metabolic acidosis (Ultsch 2006). In urban environments, the risk of overwintering site selection can increase because water levels are often artificially controlled. Water level reduction during the winter can result in mortality (Bodie and Semlitsch 2000). To effectively manage populations, we need a thorough understanding of habitat requirements not only during the active season, but also during the winter. Within Canada, most studies focus on populations inhabiting relatively pristine environments (e.g., Edge *et al.* 2009; Rasmussen and Litzgus 2010; Millar and Blouin-Demers 2011; Paterson *et al.* 2012). Few studies have examined overwintering habitat use in highly urban areas at northern latitudes.

Painted Turtles (*Chrysemys picta*) are one of the most widely distributed freshwater turtles in North America, reaching their northern limit throughout southern Canada. Painted Turtles typically inhabit shallow ponds, lakes, and slow-moving creek and river systems (Ernst and Lovich 2009; COSEWIC 2017). They are habitat generalists, able to adapt to their surrounding environment (Browne and Hecnar 2007) and are fairly tolerant of polluted waters (Ernst and Lovich 2009). Due to their wide range, and typically large population sizes in comparison to other freshwater turtles, Painted Turtles have become one of the most studied freshwater turtles in North America (Ernst and Lovich 2009; Lovich and Ennen 2013). Within Canada, many studies focus on Midland Painted Turtle (*C. p. marginata*) and examine aspects of their ecology and life history (e.g., Taylor and Nol 1989; Edwards and Blouin-Demers 2007; Rollinson and Brooks 2007; Carrière *et al.* 2008; Rollinson *et al.* 2008). Western Painted Turtle (*C. p. bellii*) has received little attention in regards to habitat and space use (e.g., MacCulloch and Secoy 1983a; St. Clair and Gregory 1990; Basaraba 2014), and therefore habitat requirements are derived from studies on the other subspecies (COSEWIC 2017). Western Painted Turtles attain larger body sizes, and reach higher latitudes than the other subspecies (Ernst and Lovich 2009), therefore their habitat and space use may differ from the smaller subspecies.

Here we examine year-round habitat selection and space use by an urban population of Western Painted Turtles in Regina, Saskatchewan. This population is in a major urban centre near the northern range limit for all turtle species on the Great Plains. Little is known about Western Painted Turtle habitat selection and space use in the Saskatchewan prairie environment where populations face climatic and anthropogenic extremes. We hypothesized that turtle movements and home range sizes of males and females would vary across the active season based upon the reproductive-strategies hypothesis (Morreale *et al.* 1984). Correspondingly, we predicted that males would make the largest movements during emergence to find mates, and females would make the largest movements during nesting to find suitable nesting habitat. For habitat selection, we hypothesized that certain habitat features are necessary for turtle survival and reproduction in an urban environment. We predicted that turtles would select for particular habitats that facilitate foraging, thermoregulation, mating, and nesting. We predicted that turtles would select overwintering sites with deeper water, higher temperature, and more dissolved oxygen, compared to those available.

Study Area

Our study occurred in the City of Regina, Saskatchewan (50.417°N, 104.583°W), the provincial capital with over 214 000 residents (Statistics Canada 2017). The regional climate is characterized by short, warm summers and long, cold winters, an average of 115 frost-free days, and average daily maximum temperatures of 25.8°C (extreme: 43°C) in July and average daily minimum temperatures of −20.1°C (extreme: −50°C) in January (Environment Canada 2010). The harsh climate on the northern Great Plains results in only a small number of turtle species. In Saskatchewan, Snapping Turtle (*Chelydra serpentina*) and Western Painted Turtle reach the northern limit of their ranges; however, Western Painted Turtles are more widespread with populations throughout much of southern Saskatchewan.

Our study site was in the Wascana Creek watershed that begins southeast of Regina and flows west before entering the Qu'Appelle River. The study area was approximately 1000 ha, and consisted of two major habitat areas: a human-made lake (between Albert St. and Broad St.) and marsh (between Broad St. and Ring Rd.), and a creek flowing into the marsh on the east and flowing out of the lake on the west (Figure 1). The depth of the lake was artificially increased twice by draining and dredging in 1931 (average depth 2 m) and again during the winter of 2003–2004 (average depth 8 m) to improve water quality (Hughes 2005). The area surrounding the study site is primarily large green spaces such as urban parks and golf courses, as well as residential and commercial development; four major roads cross the study area. Most of the surrounding vegetation was originally planted in the early 1900s (Hughes 2005), with the current terrestrial shoreline dominated by large willow trees (*Salix* spp.) and emergent aquatic vegetation, largely consisting of Broad-leaved Cattail (*Typha latifolia* L.).

We defined two main habitat areas for turtles within the study site, marsh (which included the lake) and creek, separated by a large-scale water control dam under the Albert Street bridge (Figure 1) that appeared to be a complete barrier to turtle movement (K.A.M.

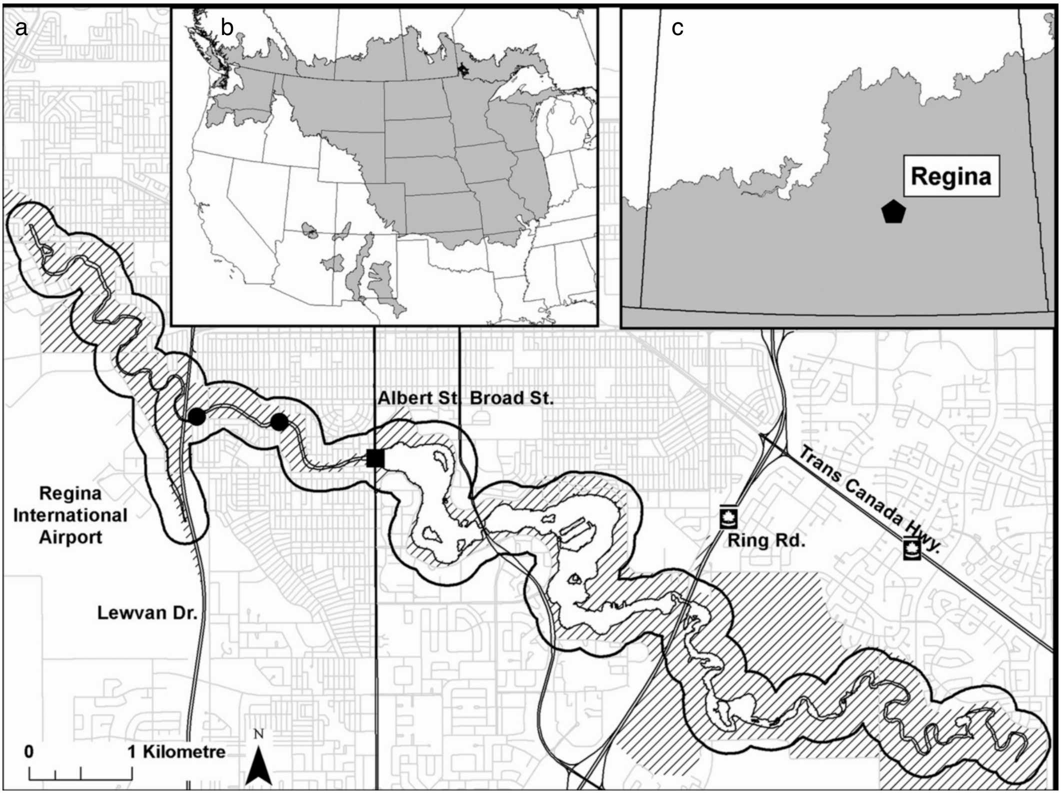

FIGURE 1. a. Study site in Regina, Saskatchewan showing the overall study area (1000 ha; black outline) indicating the barrier between the creek (West) and marsh/lake (East) habitat areas at Albert St. (square) and the two water control dams (circle) within the creek habitat. Hatched area indicates urban parkland. Insets display b. the North American range of Western Painted Turtle (*Chrysemys picta bellii*); and c. the location of the study area within Saskatchewan.

unpubl. data). Turtles caught west of the Albert Street bridge were deemed to be in creek habitat, and those caught east of the bridge were deemed to be in marsh habitat. The available habitat associated with the marsh and lake (water, shoreline, and 200 m urban buffer zone) was ~677 ha and ~270 m wide. The marsh area is designated a Federal Migratory Bird Sanctuary, and is not open to the public but the lake is open to recreational users, primarily canoes and kayaks. The creek habitat was ~325 ha and ~25 m wide with two water control dams. Few recreationists use the aquatic habitat but the surrounding parkland is used extensively.

Methods

Turtle capture and tracking

We captured turtles using a combination of hand capture, dip nets, and hoop traps baited with sardines, from April to September 2015 and 2016. Each individual was given a unique notch code that was filed into the marginal scutes of their carapace (Cagle 1939). Sex was determined using secondary sex characteristics (e.g., foreclaw length, pre-cloacal tail length, body size; Ernst and Lovich 2009). Individuals that did not display secondary sex characteristics were classified as sub-adults or juveniles (<115 cm carapace length). Body measurements were recorded, including body size (mid-line carapace length ± 1 mm), and mass (± 1 g). We attached radio transmitters (RI-2B, 14 g [*n* = 25] and 6 g [*n* = 4]; Holohil Systems Ltd., Ontario, Canada) to the rear marginal scutes using epoxy putty (Waterweld Epoxy Putty; J-B Weld, Texas, USA). The total mass of the unit (transmitter + epoxy) was <15 g and represented <5% of turtle body mass. In 2015 and 2016, 23 turtles (marsh: 12 females, four males; creek: four females, three males) and 29 turtles (marsh: 14 females, eight males; creek: four females, three males), respectively, were outfitted with radio transmitters. Twenty-two turtles (17 females, five males) were tracked in both the 2015 and 2016 field seasons. All turtles were released at the point of capture within 30 minutes.

We tracked turtles from a canoe in the open water season, and on foot (on the ice) during winter, using a portable receiver (R1000; Communications Specialists, Inc., Orange, California, USA) and hand-held three-element antenna. We relocated turtles throughout the year, separating the active season (May to September) into three biologically relevant time periods during which we examined temporal variation (Table 1). During the active season, turtles were relocated roughly every other day. For each turtle relocation, the date, time, universal transverse mercator (UTM) coordinates, and the dominant broad- and fine-scale habitat types were recorded (Table 2). We recorded locations using a handheld global positioning system unit (Garmin eTrex 20; Garmin Ltd., Olathe, Kansas, USA) uploaded to ArcGIS version 10.3.1 (ESRI, Redlands, California, USA). Individuals monitored for less than three consecutive months during either the 2015 or 2016 active season, or with less than six relocations per activity period, were excluded from the yearly and seasonal analyses, respectively.

Population size estimate

To estimate total population size encompassing both the marsh and creek habitat areas across the 2015 and 2016 field seasons we used a modified version of the Lincoln-Petersen method (Lincoln 1930; Chapman 1951; Lancia *et al.* 2005). To meet assumptions of this approach, data on hatchlings were omitted from the calculation. Additionally, multiple methods of capture (hand capture and hoop traps) were used to reduce capture bias of individuals within the population.

Movement and home range size

We calculated distance moved using the *movement.pathmetrics* function in Geospatial Modelling Environment version 0.7.4.0 (GME; Beyer 2015) which allowed us to estimate step length measurements between successive relocations for each individual during the active season. The step length measurements were divided by the number of days between relocations to provide a relative minimum daily distance moved (DDM) for each tracked individual (Rasmussen and Litzgus 2010). During winter 2017, we examined

TABLE 1. Date ranges and descriptions for the four biologically relevant seasons used to describe home-range size and assess habitat selection of Western Painted Turtles (*Chrysemys picta bellii*) in Regina, Saskatchewan during 2015 and 2016.

Season	Year	No. turtles tracked	Relocation frequency (days ± SE)	Duration	Description
Emergence	2015	11	2 ± 0	11 May–28 May	Emergence from overwintering sites until the first gravid female was found (determined by palpation of the rear leg pocket)
	2016	28	4 ± 0	9 April–19 May	
Nesting	2015	22	2 ± 0	29 May–8 July	Continues until females are no longer found gravid
	2016	28	2 ± 0	20 May–5 July	
Post-nesting	2015	23	3 ± 0	9 July–3 September	Following nesting until return to overwintering areas
	2016	23	3 ± 0	6 July–10 September	
Fall (F)/ Winter (W)	2015	18	F: 7 ± 0 W: 30 ± 0	4 September–8 April	Movements within overwintering sites
	2016	15	F: 14 ± 0 W: 30 ± 0	10 September–7 April	

TABLE 2. Definitions for large-scale and fine-scale habitat features used in the compositional analysis of Western Painted Turtle (*Chrysemys picta bellii*) habitat in Regina, Saskatchewan. Broad-scale habitat was examined at second-order habitat selection, and fine scale habitat was examined at third-order habitat selection (Johnson 1980). Note: M = marsh, C = creek.

Feature type	Habitat type	Description	Percent of habitat (%)
Broad-scale	Shoreline	15 m zone on either side of the delineated shoreline	15.0
	Urban/Parkland	200 m zone around the study area (Steen *et al.* 2012; COSEWIC 2017)	74.0
	Open water	Open water remaining between shoreline buffer areas	17.0
Fine-scale	Barrier	Human-made vertical barrier preventing shoreline access for turtles	M: 6.0 C: 3.5
	Cattails	Shoreline dominated by cattail vegetation	M: 60.3 C: 28.6
	No vegetation	Shoreline consists of open beach area; either cobblestones, soil, or sand	M: 7.4 C: 0.5
	Shrubs	Shoreline dominated by short, dense shrub vegetation; no visible bank	M: 11.0 C: 31.5
	Trees	Shoreline dominated by large overhanging trees (typically willow); bank always visible	M: 15.3 C: 35.9

turtle movement under the ice by measuring the straight-line distance between successive relocations in ArcGIS. We deployed a reference transmitter attached to a rock in the overwintering area to use as a control to confirm turtle movement.

We determined the home range of individuals by calculating the 100% minimum convex polygon (MCP) using the *genmcp* function in GME, which provides the smallest possible convex polygon that encompasses all relocations for a particular individual or group of individuals (Row and Blouin-Demers 2006). We chose MCPs over other home range metrics (e.g., kernel density) because they eliminate the effect of autocorrelation, reduce the number of arbitrary choices required in the analysis (e.g., smoothing factor), and encompass areas that may be used as movement corridors and, thus, are excluded when using kernel density estimates (Row and Blouin-Demers 2006; Rasmussen and Litzgus 2010; Markle and Chow-Fraser 2014).

All active season movement and home range data were analyzed to determine effects of season, sex, habitat area, and year on movement rates and home range size using two separate generalized linear mixed models (GLMM; Gamma distribution). The fixed effects included season, sex, habitat area, and year. The random effect was turtle ID to account for repeated measures of each individual. A χ^2 test was completed to examine the effect of the interaction between season and sex. Analyses were conducted using the lme4 package (Bates *et al.* 2015) in R version 3.3.1 (R Core Team 2016) and assumed a significance level of $P < 0.05$. We report the mean ± SE where appropriate.

Habitat selection

We examined habitat selection using compositional analysis at two spatial scales representing two categories in Johnson's (1980) hierarchy to determine whether the turtles select particular habitats disproportionately compared to what was available (Aebischer *et al.* 1993): broad-scale representing second-order selection and fine-scale representing third-order selection (Table 2). Second-order habitat selection was assessed by comparing the proportion of relocations of each individual turtle to the proportion of broad-scale habitat features available within the MCP for the entire population. Third-order habitat selection was assessed by comparing the proportion of relocations of each individual turtle within each section of the active season to the proportion of habitat features available within individual active season MCPs. Compositional analyses were completed using the *compana* function in the adehabitatHS package in R (Calenge 2006). In cases where habitat types were available but not used, we replaced the zero value with a value one order of magnitude smaller than the smallest non-zero number in the dataset (Aebischer *et al.* 1993).

Overwintering site selection

During the winter of 2015–2016 and 2016–2017, we determined overwintering locations for 19 turtles (15 marsh, four creek), and 18 turtles (14 marsh, four creek), respectively. Due to ice safety concerns, only turtles located within the marsh habitat between Broad Street and Ring Road were monitored throughout the winter months. We measured environmental variables at used and available overwintering sites from January to March by drilling holes through the ice using an auger. We chose representative used sites that were centrally located near groups of turtles with transmitters, and at least 15 m apart from other sites used for overwintering. We designated representative sites used in this way to avoid drilling through the ice directly above each turtle, potentially causing disturbance. At each site, a hole was augured into the ice and environmental variables were recorded including distance from shore (m), water depth (cm), ice thickness (cm), water temperature (°C), and dissolved oxygen level (mg/L). Both water temperature and dissolved oxygen level were measured using a YSI probe (YSI Pro Plus; YSI Inc., Yellow Springs, Ohio, USA). To examine differences in the sites used for overwintering compared to areas within the known overwintering habitat, we sampled available sites 10 m in each cardinal direction from the selected sites, as well as 30 m and 50 m west from the selected sites. To examine why the turtles selected their overwintering location versus another location available to them in the marsh habitat, we compared the sites used for overwintering to 12 randomly selected available sites. The randomly selected available sites were generated in ArcGIS using the *Random Points* function in the Data Management Toolbox.

To examine overwintering habitat selection, two separate GLMMs were constructed to examine the relationship between measured environmental variables and several fixed variables: within the known overwintering habitat and across the marsh habitat. Fixed variables included sample month, sample year, and location type (used or available). Environmental variables were recorded monthly during the winter of 2016 and 2017, so site ID was used as a random effect to account for repeated measures. This approach enabled testing the hypothesis that environmental variables differed between used and available overwintering sites. Analyses were conducted using the lme4 package in R assuming a significance of $P < 0.05$. We report the mean ± SE where appropriate.

Results

Population size assessment

We captured 85 turtles (26 males, 43 females, eight juveniles, and eight neonates) and recaptured 47 turtles (16 males, 31 females) in 2016 within the creek and marsh habitat. The majority of the individuals captured (88%) were from the marsh habitat, with only 10 individuals (six females, four males) found in the creek habitat. Most individuals were sexually mature adults with carapace length over 150 mm. Using the Lincoln-Petersen method, we estimated the total population size to be 82 individuals (± 8; 95% CI), resulting in a density of 0.3 turtles/ha within available shoreline and open water habitat with the marsh and the creek areas combined.

Movements and home range

Across the 2015 and 2016 field seasons, the average daily distance moved was 96 ± 8 m and 172 ± 6 m for the creek and marsh areas, respectively. The average distance that female turtles moved into upland habitat was 36 ± 10 m. The upland movements primarily occurred during nesting season. The maximum distance travelled into upland habitat was a female who moved 265 m in late July to reach a water retention pond near a golf course where she remained until fall. One male moved into upland habitat (200 m), but returned to the aquatic habitat by the next relocation. It is unclear what caused the upland movement; however, based on relocation frequency he may have spent a maximum of three days outside the creek habitat. Daily movement rates did not differ between the 2015 (162 ± 7 m) and 2016 (153 ± 7 m) active seasons ($t_1 = 0.14$, $P = 0.9$). There was no significant difference in the DDM between males and females ($t_1 = 1.7$, $P = 0.09$; Figure 2a). Marsh turtles moved longer distances compared to creek turtles ($t_1 = 11.5$, $P < 0.01$), with mean marsh turtle movements being two times longer compared to those in the creek (Figure 2b). Turtles moved longer distances during nesting ($t_2 = 7.6$, $P < 0.01$) and post-nesting ($t_2 = 4.6$, $P < 0.01$) seasons compared to during emergence (Figure 2c); however, there was no significant interaction between sex and season on DDM ($\chi^2_2 = 4.1$, $P = 0.1$; Figure 2d). During winter 2017, under ice movements were recorded. In February, turtles were found 4 ± 0.8 m (control = 0 m) from their January location. In March, turtles were found 20 ± 5 m (control = 1 m) from their February location.

Home ranges did not differ between 2015 and 2016 ($t_1 = 1.2$, $P = 0.2$). There was no significant difference between male and female home ranges ($t_1 = 0.35$, $P = 0.7$). The home ranges were significantly larger for the marsh turtles (59 ± 5 ha) than the creek turtles (19 ± 4 ha; $t_1 = 5.9$, $P < 0.01$). Across the active season, turtles had significantly larger home ranges during the nesting ($t_2 = 5.7$, $P < 0.01$) and post-nesting seasons ($t_2 = 7.2$, $P < 0.01$) compared to emergence, corresponding with increased DDM values. The interaction between sex and season did not affect turtle home range size ($\chi^2_2 = 2.8$, $P = 0.3$).

Active season habitat selection

Second-order habitat use was significantly non-random (Wilk's $\lambda_2 = 0.06$, $P = 0.002$). Shoreline habitat was used six times more than expected, accounting for 93% of the turtle relocations, and open water and urban/parkland were both used less than expected based on availability. At third-order, creek turtles used shoreline with no-vegetation 33–54 times more than expected based on availability during all three sections of the active season (Figure 3). Compositional analysis did not identify habitat use as significant (emergence: Wilk's

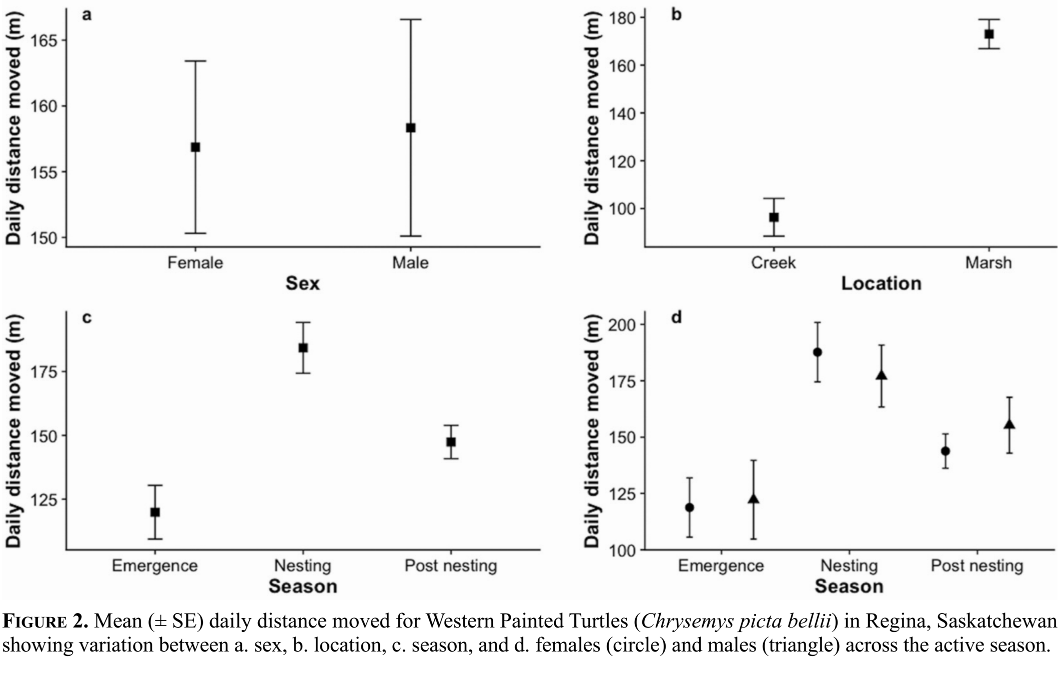

Figure 2. Mean (± SE) daily distance moved for Western Painted Turtles (*Chrysemys picta bellii*) in Regina, Saskatchewan showing variation between a. sex, b. location, c. season, and d. females (circle) and males (triangle) across the active season.

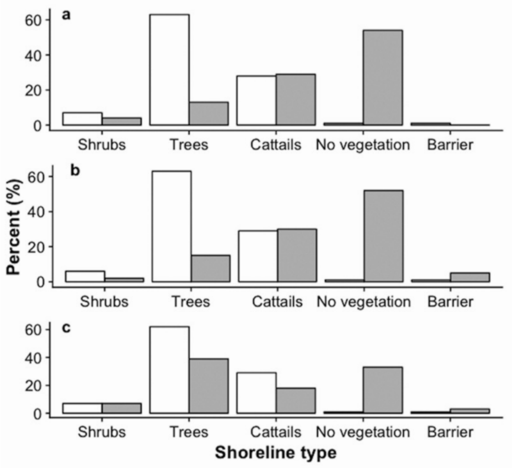

FIGURE 3. Proportion of used (grey) and available (white) shoreline habitat types within the creek habitat area during a. emergence, b. nesting, and c. post-nesting seasons.

$\lambda_4 = 0$, $P = 1$; nesting: Wilk's $\lambda_4 = 0.02$, $P = 0.09$; post-nesting: Wilk's $\lambda_4 = 0.1$, $P = 0.2$), which could be a result of a small sample size (Aebischer *et al.* 1993). In contrast, marsh turtles exhibited significant non-random habitat use across all three periods of the active season (emergence: Wilk's $\lambda_4 = 0.02$, $P = 0.002$; nesting: Wilk's $\lambda_4 = 0.14$, $P = 0.002$; post-nesting: Wilk's $\lambda_4 = 0.1$, $P = 0.002$), with shorelines consisting of trees, shrubs, and cattails being used more than expected, and no-vegetation and barrier shorelines being used less than expected based on availability. Treed shoreline accounted for on average 51% of the relocations within each period of the active season, and was selected for 1.3 times more than expected during emergence and two times more than expected during nesting and post-nesting based on availability. Within the emergence period, shrub shoreline accounted for 36% of the relocations and during both nesting and post-nesting periods, cattail shoreline accounted for 32% and 22% of relocations, respectively.

Overwintering site selection

During 2016 and 2017, the marsh habitat had approximately 142 and 136 days of ice cover, respectively. Turtles ($n = 13$) overwintered between a pair of islands along the east shore, 7 ± 0.5 m from the shoreline in 2016 and 9 ± 0.4 m from the shoreline in 2017. On average across the two years, the sites used for overwintering experienced dissolved oxygen levels of 3.8 ± 0.97 mg/L (minimum: 0.6 mg/L), water temperature of 1.6 ± 0.22°C (minimum: 0.1°C), and water depths of 148 ± 14 cm (minimum: 53 cm). Within the immediate overwintering habitat there were no significant differences in water temperature ($t_1 = -0.98$, $P = 0.3$), dissolved oxygen level ($t_1 = 0.74$, $P = 0.5$), or water depth ($t_1 = -1.4$, $P = 0.2$) between the sites used for overwintering and the randomly selected available sites. All sites within the immediate overwintering area exhibited temporal variation. In 2017, the dissolved oxygen levels were significantly higher (4 ± 4 mg/L; $t_1 = 5.7$, $P < 0.01$), the water temperatures were significantly lower (1.5 ± 0.6°C; $t_1 = -11.3$, $P < 0.01$), and the water depths were significantly shallower (195 ± 82 cm; $t_1 = -1.4$, $P < 0.01$) compared to 2016. Across both years, the dissolved oxygen levels were significantly higher ($t_2 = 12.4$, $P < 0.01$), the water temperatures significantly higher ($t_2 = 11.8$, $P < 0.01$), and the water depth significantly lower ($t_2 = -3.5$, $P < 0.01$) in March compared to January and February.

Sites used for overwintering were significantly warmer ($t_1 = 2.4$, $P = 0.02$) and deeper ($t_1 = 2.3$, $P = 0.02$) than randomly selected available sites; but there was no significant difference in the dissolved oxygen levels ($t_1 = -0.34$, $P = 0.7$; Figure 4). Over the course of the winter, multiple available sites froze to the bottom (2016: $n = 3$; 2017: $n = 9$); however, sites used for overwintering did not freeze to the bottom. Water temperatures were significantly lower ($t_1 = -3.5$, $P < 0.01$), and water depths significantly shallower ($t_1 = -6.5$, $P < 0.01$) in 2017 compared to 2016. Across both years, dissolved oxygen levels were significantly higher in March ($t_2 = 4.1$, $P < 0.01$) compared to January and February, and water depths were significantly deeper in January ($t_2 = 3.7$, $P < 0.01$) compared to February and March.

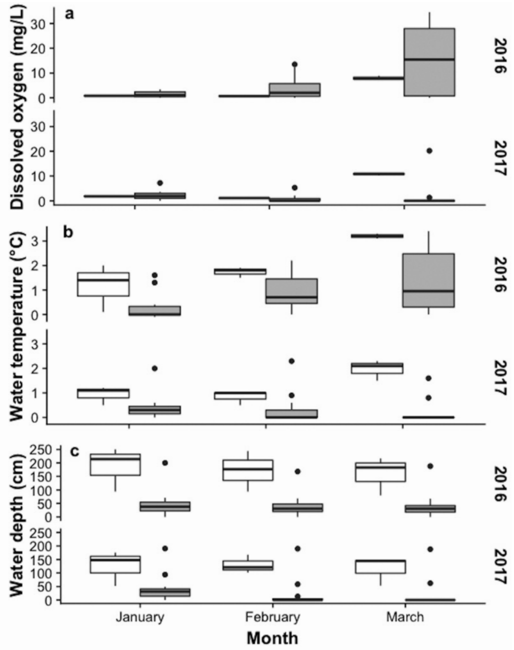

FIGURE 4. Boxplots of a. dissolved oxygen, b. water temperature, and c. water depth recorded at used (white; $n = 3$) and available (random: grey; $n = 12$) sites during the winter of 2016 and 2017. The median is depicted as the horizontal black line, boxes represent the 25th and 75th percentiles, whiskers depict the highest and lowest values, and the black circles represent outliers.

Discussion

Population size assessment

We estimated the population to be 82 (± 8) individuals, at a density of 0.3 turtles/ha, which was lower than typically recorded for this species. Painted Turtles are one of the most abundant freshwater turtle species within their range (Ernst and Lovich 2009), with some populations attaining sizes of over 3000 individuals (828 turtles/ha; Frazer *et al.* 1991). At the northern range limit in Canada, reported population sizes for Western Painted Turtles are sparse. However, a population inhabiting a water reservoir in Revelstoke, British Columbia was estimated to be approximately 242 individuals (2 turtles/ha; Basaraba 2014), and a population inhabiting the Qu'Appelle River north of Regina was estimated to be 167 individuals (11 turtles/ha; MacCulloch and Secoy 1983b). Both of these estimates are two- to three-times larger than the estimate for our study population, indicating that our study site has a lower population density than reported populations.

The majority of turtles captured during the study were sexually mature individuals over 150 mm carapace length. We captured few juveniles and subadults. Within the total study population, female turtles occurred more commonly than males by approximately a 2:1 ratio (43 females: 26 males). The high capture rate of sexually mature individuals may be the result of sampling bias, as juveniles are cryptic and difficult to capture in the traps we deployed, or an indication of low productivity and recruitment. An age shift towards adults has been previously observed in freshwater turtle populations that have been affected by anthropogenic changes (Garber and Burger 1995; Saumure and Bider 1998; Browne and Hecnar 2007). Over the two years, we only observed one successful nest (eight hatchlings), and many were found predated, mostly by Richardson's Ground Squirrels (*Urocitellus richardsonii*). This was the first assessment of population size for this study area, so temporal comparisons are not possible. However, the information gathered in the current study can be used as a baseline for future population monitoring.

Turtle movements and home range

Western Painted Turtles in this study did not conform to predictions about seasonal movements based upon the reproductive strategies hypothesis. We found that turtle movements and space use did not differ between sexes and that variation was more attributable to the season in which the movements occurred, with both sexes exhibiting decreased movement and space use during emergence in comparison to nesting and post-nesting phases of the active season. This pattern may reflect metabolic requirements as well as a response to environmental temperatures, as activity does not begin until water levels reach approximately 10°C (Ernst 1971). During emergence, Painted Turtles spend increased time basking allowing them to conserve energy, increase their body temperature following emergence, and overcome acidosis experienced during overwintering (Congdon 1989; Edwards and Blouin-Demers 2007; Carrière *et al.* 2008; Millar and Blouin-Demers 2011). Freshwater turtles such as Spotted Turtle (*Clemmys guttata*; Litzgus and Mousseau 2004) and Blanding's Turtle (*Emydoidea blandingii*; Millar and Blouin-Demers 2011) communally aggregate following hibernation, which reduces the requirement of males to actively seek females throughout the habitat. Therefore, the mixed-sex basking aggregations observed in our study population could explain the limited movements of males in contrast to the reproductive strategies hypothesis. Movements and space use increased during nesting and post-nesting phases. In addition to coinciding with warmer seasonal temperatures, this increased activity is likely related to increased efforts in searching for desired nesting habitat, food resources, or potential mates.

Movements into upland habitat were only documented during the nesting season. In contrast to previous studies (e.g., McAuliffe 1978; Bowne 2008), we did not document turtles making large overland movements to reach alternate habitat, as the majority of relocations were confined to shoreline and open water. During the nesting season, females moved into upland habitat on average <50 m from the shoreline. However, despite this very limited upland movement, females still came into contact with roads. Three females (7% of captured females) were hit by vehicles, two of which were found to be gravid, a mortality rate which, if continued, exceeds a sustainable annual loss to our study population (Brooks *et al.* 1990; Congdon *et al.* 1993; Gibbs and Shriver 2002). One additional female was documented nesting in a gravel back alley roadway ~25 m from the creek, an area bordered by residential houses and small parkland. Steen *et al.* (2012) found that Painted Turtles typically nest within 200 m of the shoreline. However, the distance travelled decreases in disturbed habitat, with females opting to nest in close proximity to the shoreline (Baldwin *et al.* 2004; Foley *et al.* 2012), which is consistent with findings in our study.

The average home range size and daily distance moved for Western Painted Turtles in our study were typical for that of the species in other parts of its range. The average home range size for turtles in both the marsh and the creek habitat areas are comparable to those reported in British Columbia, Tennessee, Ohio, and Pennsylvania (Saba and Spotila 2003; Tran *et al.* 2007; Jaeger and Cobb 2012; Basaraba 2014). In contrast, our home range estimates are 4–12 times larger than that reported for the Qu'Appelle River population north of Regina (MacCulloch and Secoy 1983a). This comparison should be interpreted with caution given the different survey methods used in the two studies. Marsh turtles had significantly larger movement rates and space use in comparison to the creek turtles. Previous studies have found a link between animal space use and the amount of habitat available (Schubauer *et al.*

1990; Plummer *et al.* 1997; Jaeger and Cobb 2012). Animals with less available habitat by necessity have smaller home ranges compared to those with more available habitat. Therefore, the observed variation in our system may not be attributed to activity level differences, but rather the space available to the individuals within them.

Active season habitat selection

Turtles across our study area selected strongly for shoreline areas; however, the features of the shoreline selected varied between marsh and creek. For example, at the level of third order habitat selection, turtles in the marsh were found to select for treed shorelines, whereas turtles in the creek preferred shorelines with no vegetation. The habitat preferences turtles exhibited were consistent with studies on other Painted Turtle subspecies; they are commonly associated with shoreline habitats (Rowe and Dalgarn 2010) and they are most commonly found on shorelines with partial cover and suitable basking areas (Pittfield and Burger 2017). In contrast to other freshwater turtles (e.g., Litzgus and Mousseau 2004; Markle and Chow-Fraser 2014), Western Painted Turtles did not shift habitat selection throughout the active season. Within the Regina urban environment, turtles may prefer to use habitat with increased protection from human disturbance, while at the same time meeting their needs as ectotherms (i.e., basking). Additionally, suitable habitat may be limited in our system, as most natural shoreline features are represented in low proportions.

Overwintering site selection

Individuals displayed high site fidelity to one overwintering area, indicating that this overwintering location may be particularly important for our study population. The area used for overwintering was the single protected area that was not drained for the large-scale dredging event through the winter of 2004. In the winters of 2015–2016 and 2016–2017, all monitored turtles returned to the same 90 m section of shoreline, after being dispersed throughout the habitat during the active season. The high site fidelity to overwintering sites and the aggregation of turtles is consistent to what is observed in Spotted Turtles (Rasmussen and Litzgus 2010) and Snapping Turtles (Brown and Brooks 1994) at their northern range limits, where suitable overwintering habitat may be limited. We found that turtles selected sites close to shore, which would allow them to be exposed to warmer water earlier in the spring than deeper areas (Ultsch 1989). Overwintering movements were negligible through the winter, but by March some turtles began to move, perhaps to seek areas with increased dissolved oxygen levels produced by incoming melt water (Ultsch 1989).

The ranges of environmental conditions at the sites used for overwintering were similar to those documented for Western Painted Turtles in British Columbia (St. Clair and Gregory 1990; Wood and Hawkes 2014) as well as for other subspecies across the range (Crawford 1991; Crocker *et al.* 2000; Rollinson *et al.* 2008). Contrary to what we expected, there was no support for the hypothesis that turtles selected sites based on dissolved oxygen levels in the water, as all used and available sites became hypoxic. However, they did select sites that were warmer and deeper compared to those randomly available to them. Lab data suggest that Painted Turtles can survive 118–150 days in anoxic conditions at 3°C (Reese *et al.* 2004; Jackson and Ultsch 2010), with Western Painted Turtles from northern populations better able to cope with the physiological effects of anoxia by accumulating less lactate than southern conspecifics and other subspecies (Reese *et al.* 2004). Therefore, similar to what was found in Blanding's Turtles in Ontario (Edge *et al.* 2009), choosing an overwintering location that will not freeze because of increased water depth and temperature may outweigh the risk of metabolic acidosis due to anoxia.

Management implications

Our data provide baseline information on population demographics and identify space use and habitat requirements of an urban population of Western Painted Turtles near the northern limit of the species range. The data we obtained from our study can serve as a baseline to document temporal changes in population size and habitat use. Through our study, we identified that overwintering habitat is critical to the persistence of this urban population. Turtles in our study population were found to move towards overwintering habitat by the beginning of September. A minimum of 2 m of water is required within 7–10 m of the shoreline in the core overwintering habitat, to ensure viable water temperatures over the winter. To ensure winter survival, water levels should not be dropped by more than 0.5 m through the winter, as this would cause overwintering sites to be compromised. Draining of Wascana Creek should be avoided. However, if depth management of Wascana Creek via dredging over the winter is found to be necessary, the core overwintering habitat should be protected so that it does not freeze solid or become drained of water.

The aquatic and terrestrial areas of the park should be managed to ensure a mosaic of shoreline habitats, which includes overhanging trees and submerged logs, to provide a protective buffer between the turtles and recreationists, and provide suitable basking areas to meet their thermal requirements. Shorelines dominated by concrete barriers and areas without vegetation cover should not be created as they will restrict shoreline access; however, they may be beneficial in high-risk areas (i.e., roadsides) to minimize risk of mortality. Finally, the majority of the population inhabits the eastern portion of the marsh, the Federal Migratory Bird Sanctuary. Public access to this section should continue to be restricted to minimize human disturbance.

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Literature Cited

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1325. https://doi.org/10.2307/1940062

Aresco, M.J. 2005. The effect of sex-specific terrestrial movements and roads on the sex ratio of freshwater turtles. Biological Conservation 123: 37–44. https://doi.org/10.1016/j.biocon.2004.10.006

Baldwin, E.A., M.N. Marchand, and J.A. Litvaitis. 2004. Terrestrial habitat use by nesting painted turtles in landscapes with different levels of fragmentation. Northeastern Naturalist 11: 41–48. https://doi.org/10.1656/1092-6194(2004)011[0041:THUBNP]2.0.CO;2

Basaraba, N.R.C. 2014. The ecology of western painted turtles (*Chrysemys picta bellii*) in a northern Canadian reservoir. M.Sc. thesis, Thompson Rivers University, Kamloops, British Columbia, Canada.

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48. https://doi.org/10.18637/jss.v067.i01

Bennett, A.M., M. Keevil, and J.D. Litzgus. 2010. Spatial ecology and population genetics of Northern Map Turtles (*Graptemys geographica*) in fragmented and continuous habitats in Canada. Chelonian Conservation and Biology 9: 185–195. https://doi.org/10.2744/CCB-0824.1

Beyer, H.L. 2015. Geospatial Modelling Environment (v. 0.7.4.0). Accessed January 2016. http://www.spatialecology.com/gme.

Bodie, J.R., and R.D. Semlitsch. 2000. Spatial and temporal use of floodplain habitats by lentic and lotic species of aquatic turtles. Oecologia 122: 138–146. https://doi.org/10.1007/PL00008830

Bowne, D.R. 2008. Terrestrial activity of *Chrysemys picta* in northern Virginia. Copeia 2008: 306–310. https://doi.org/10.1643/CE-06-224

Brooks, R.J., G.P. Brown, and D.A. Galbraith. 1990. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69: 1314–1320. https://doi.org/10.1139/z91-185

Brown, G.P., and R.J. Brooks. 1994. Characteristics of and fidelity to hibernacula in a northern population of snapping turtles, *Chelydra serpentina*. Copeia 1994: 222–226. https://doi.org/10.2307/1446689

Browne, C.L., and S.J. Hecnar. 2007. Species loss and shifting population structure of freshwater turtles despite habitat protection. Biological Conservation 138: 421–429. https://doi.org/10.1016/j.biocon.2007.05.008

Cagle, F.R. 1939. A system of marking turtles for future identification. Copeia 1939: 170–173. https://doi.org/10.2307/1436818

Calenge, C. 2006. The package "adehabitat" for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Carrière, M., N. Rollinson, A.N. Suley, and R.J. Brooks. 2008. Thermoregulation when the growing season is short: sex-biased basking patterns in a northern population of Painted Turtles (*Chrysemys picta*). Journal of Herpetology 42: 206–209. https://doi.org/10.1670/07-070R1.1

Chapman, D.G. 1951. Some properties of the hypergeometric distribution with applications to zoological censuses. University of California Publications in Statistics 1: 131–159.

Congdon, J.D. 1989. Proximate and evolutionary constraints on energy relations of reptiles. Physiological Zoology 62: 356–373. https://doi.org/10.1086/physzool.62.2.30156175

Congdon, J.D., A.E. Dunham, and R.C. Van Loben Sels. 1993. Delayed sexual maturity and demographics of Blanding's turtles (*Emydoidea blandingii*): implications for conservation and management of long-lived organisms. Conservation Biology 7: 826–833. https://doi.org/10.1046/j.1523-1739.1993.740826.x

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2017. COSEWIC assessment and status report on the Western Painted Turtle *Chrysemys picta bellii* (Pacific Coast population, Intermountain-Rocky Mountain population and Prairie/Western Boreal-Canadian Shield population) in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 17 May 2018. http://sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Western Painted Turtle_2016_e.pdf.

Crawford, K.M. 1991. The winter environment of painted turtles, *Chrysemys picta*: temperature, dissolved oxygen, and potential cues for emergence. Canadian Journal of Zoology 69: 2493–2498. https://doi.org/10.1139/z91-352

Crocker, C.E., R.A. Feldman, G.R. Ultsch, and D.C. Jackson. 2000. Overwintering behavior and physiology of eastern painted turtles (*Chrysemys picta picta*) in Rhode Island. Canadian Journal of Zoology 78: 936–942. https://doi.org/10.1139/z00-032

Edge, C.B., B.D. Steinberg, R.J. Brooks, and J.D. Litzgus. 2009. Temperature and site selection by Blanding's Turtles (*Emydoidea blandingii*) during hibernation near the species' northern range limit. Canadian Journal of Zoology 87: 825–834. https://doi.org/10.1139/Z09-073

Edwards, A.L., and G. Blouin-Demers. 2007. Thermoregulation as a function of thermal quality in a northern population of painted turtles, *Chrysemys picta*. Canadian Journal of Zoology 85: 526–535. https://doi.org/10.1139/Z07-037

Environment Canada. 2010. Canadian climate normals 1981–2010 station data: Regina international airport. Accessed 5 June 2017. https://tinyurl.com/yctz83pk.

Ernst, C.H. 1971. Population dynamics and activity cycles of *Chrysemys picta* in southeastern Pennsylvania. Journal of Herpetology 5: 151–160. https://doi.org/10.2307/1562736

Ernst, C.H., and J.E. Lovich. 2009. *Chrysemys picta*, Painted Turtles. Pages 183–211 *in* Turtles of the United States and Canada. *Edited by* C.H. Ernst and J.E. Lovich. Second Edition. The Johns Hopkins University Press, Baltimore, Maryland, USA.

Foley, S.M., S.J. Price, and M.E. Dorcas. 2012. Nest-site selection and nest depredation of semi-aquatic turtles on golf courses. Urban Ecosystems 15: 489–497. https://doi.org/10.1007/s11252-012-0229-4

Frazer, N.B., J.W. Gibbons, and J.L. Greene. 1991. Growth, survivorship and longevity of painted turtles *Chrysemys picta* in a southwestern Michigan marsh. American Midland Naturalist 25: 245–258. https://doi.org/10.2307/2426229

Garber, S.D., and J. Burger. 1995. A 20-year study documenting the relationship between turtle decline and human recreation. Ecological Applications 5: 1151–1162. https://doi.org/10.2307/2269362

Gibbs, J.P., and W.G. Shriver. 2002. Estimating the effects of road mortality on turtle populations. Conservation Biology 16: 1647–1652. https://doi.org/10.1046/j.1523-1739.2002.01215.x

Gibbs, J.P., and D.A. Steen. 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. Conservation Biology 19: 552–556. https://doi.org/10.1111/j.1523-1739.2005.000155.x

Hughes, B. 2005. The Big Dig: The Miracle of Wascana Centre. Centax Books, Regina, Saskatchewan, Canada.

Jackson, D.C., and G.R. Ultsch. 2010. Physiology of hibernation under the ice by turtles and frogs. Journal of Experimental Zoology 313A: 311–327. https://doi.org/10.1002/jez.603

Jaeger, C.P., and V.A. Cobb. 2012. Comparative spatial ecologies of female painted turtles (*Chrysemys picta*) and red-eared sliders (*Trachemys scripta*) at Reelfoot Lake, Tennessee. Chelonian Conservation and Biology 11: 59–67. https://doi.org/10.2744/CCB-0949.1

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71. https://doi.org/10.2307/1937156

Lancia, R.A., W.L. Kendall, K.H. Pollock, and J.D. Nichols. 2005. Estimating the number of animals in wildlife populations. Pages 106–153 *in* Techniques for Wildlife Investigation and Management. *Edited by* C.E. Braun. Sixth Edition. The Wildlife Society, Bethesda, Maryland, USA.

Lincoln, F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. U.S. Department of Agriculture, Circular Number 118, Washington, DC, USA.

Litzgus, J.D., and T.A. Mousseau. 2004. Home range and seasonal activity of Southern Spotted Turtles (*Clemmys guttata*): implications for management. Copeia 2004: 804–817. https://doi.org/10.1643/CH-04024R1

Lovich, J.E., and J.R. Ennen. 2013. A quantitative analysis of the state of knowledge of turtles of the United States and Canada. Amphibia-Reptilia 34: 11–23. https://doi.org/10.1163/15685381-00002860

MacCulloch, R.D., and D.M. Secoy. 1983a. Movement in a river population of *Chrysemys picta bellii* in southern Saskatchewan. Journal of Herpetology 17: 283–285. https://doi.org/10.2307/1563834

MacCulloch, R.D., and D.M. Secoy. 1983b. Demography, growth, and food of western painted turtles, *Chrysemys picta bellii* (Gray), from southern Saskatchewan. Canadian Journal of Zoology 61: 1499–1509. https://doi.org/10.1139/z83-202

Marchand, M.N., and J.A. Litvaitis. 2004. Effects of landscape composition, habitat features, and nest distribution on predation rates of simulated turtle nests. Biological Conservation 117: 243–251. https://doi.org/10.1016/j.biocon.2003.07.003

Markle, C.E., and P. Chow-Fraser. 2014. Habitat selection by the Blanding's turtle (*Emydoidea blandingii*) on a protected island in Georgian Bay, Lake Huron. Chelonian Conservation and Biology 13: 216–226. https://doi.org/10.2744/CCB-1075.1

McAuliffe, J.R. 1978. Seasonal migrational movements of a population of the western painted turtle, *Chrysemys picta bellii* (Reptilia, Testudines, Testudinidae). Journal of Herpetology 12: 143–149. https://doi.org/10.2307/1563400

Millar, C.S., and G. Blouin-Demers. 2011. Spatial ecology and seasonal activity of Blanding's Turtles (*Emydoidea blandingii*) in Ontario, Canada. Journal of Herpetology 45: 370–378. https://doi.org/10.1670/10-172.1

Morreale, S.J., J.W. Gibbons, and J.D. Congdon. 1984. Significance of activity and movement in the yellow-bellied slider turtle (*Pseudemys scripta*). Canadian Journal of Zoology 62: 1038–1042. https://doi.org/10.1139/z84-148

Paterson, J.E., B.D. Steinberg, and J.D. Litzgus. 2012. Generally specialized or especially general? Habitat selection by Snapping Turtles (*Chelydra serpentina*) in central Ontario. Canadian Journal of Zoology 90: 139–149. https://doi.org/10.1139/z11-118

Pittfield, T., and J. Burger. 2017. Basking habitat use and response of freshwater turtles to human presence in an urban canal of central New Jersey. Urban Ecosystems 20: 449–461. https://doi.org/10.1007/s11252-016-0606-5

Plummer, M.V., and N.E. Mills. 2008. Structure of an urban population of softshell turtles (*Apalone spinifera*) before and after severe stream alteration. Pages 95–105 *in* Urban Herpetology. *Edited by* R.E. Jung and J.C. Mitchell. Volume 3. Society for the Study of Amphibians and Reptiles, Salt Lake City, Utah, USA.

Plummer, M.V., N.E. Mills, and S.L. Allen. 1997. Activity, habitat, and movement patterns of Softshell Turtles (*Trionyx spiniferus*) in a small stream. Chelonian Conservation and Biology 2: 514–520.

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rasmussen, M.L., and J.D. Litzgus. 2010. Habitat selection and movement patterns of Spotted Turtles (*Clemmys guttata*): effects of spatial and temporal scales of analyses. Copeia 2010: 86–96. https://doi.org/10.1643/CE-09-141

Reese, S.A., E.R. Stewart, C.E. Crocker, D.C. Jackson, and G.R. Ultsch. 2004. Geographic variation of the physiological response to overwintering in the painted turtle (*Chrysemys picta*). Physiological and Biochemical Zoology 77: 619–630. https://doi.org/10.1086/383514

Rollinson, N., and R.J. Brooks. 2007. Proximate constraints on reproductive output in a northern population of painted turtles: an empirical test of the bet-hedging paradigm. Canadian Journal of Zoology 85: 177–184. https://doi.org/10.1139/Z07-002

Rollinson, N., G.J. Tattersall, and R.J. Brooks. 2008. Overwintering habitats of a northern population of Painted Turtles (*Chrysemys picta*): winter temperature selection and dissolved oxygen concentrations. Journal of Herpetology 42: 312–321. https://doi.org/10.1670/07-1422.1

Row, J.R., and G. Blouin-Demers. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia 2006: 797–802. https://doi.org/10.1643/0045-8511(2006)6[797:KANAEO]2.0.CO;2

Rowe, J.W., and S.F. Dalgarn. 2010. Home range size and daily movements of Midland Painted Turtles (*Chrysemys picta marginata*) in relation to body size, sex, and weather patterns. Herpetological Conservation and Biology 5: 461–473.

Rubin, C.S., R.E. Warner, J.L. Bouzat, and K.N. Paige. 2001. Population genetic structure of Blanding's turtles (*Emydoidea blandingii*) in an urban landscape. Biological Conservation 99: 323–330. https://doi.org/10.1016/S0006-3207(00)00198-1

Saba, V.S., and J.R Spotila. 2003. Survival and behavior of freshwater turtles after rehabilitation from an oil spill. Environmental Pollution 126: 213–223. https://doi.org/10.1016/S0269-7491(03)00192-1

Saumure, R.A., and J.R. Bider. 1998. Impact of agriculture development on a population of wood turtles (*Clemmys insculpta*) in southern Quebec, Canada. Chelonian Conservation and Biology 3: 37–45.

Schubauer, J.P., J.W. Gibbons, and J.R. Spotila. 1990. Home range and movement patterns of slider turtles inhabiting Par Pond. Pages 223–232 *in* Life History and Ecology of the Slider Turtle. *Edited by* J.W. Gibbons. Smithsonian Institution Press, Washington, DC, USA.

Spinks, P.Q., G.B. Pauly, J.J. Crayon, and H.B. Shaffer. 2003. Survival of the western pond turtle (*Emys marmorata*) in an urban California environment. Biological Conservation 113: 257–267. https://doi.org/10.1016/S0006-3207(02)00392-0

Statistics Canada. 2011. 2011 Census of population: population, urban and rural, by province and territory (Canada). Accessed 5 June 2017. http://www.statcan.gc.ca/tables-tableaux/sum-som/l01/cst01/demo62a-eng.htm.

Statistics Canada. 2017. 2016 Census profile: Regina (population centre), Saskatchewan and Saskatchewan (province). Accessed 5 June 2017. http://www12.statcan.gc.ca/census-recensement/2016/dp-pd/prof/index.cfm?Lang=E.

St. Clair, R.C., and P.T. Gregory. 1990. Factors affecting the northern range limit of painted turtles (*Chrysemys picta*): winter acidosis or freezing? Copeia 1990: 1083–1089. https://doi.org/10.2307/1446492

Steen, D.A., M.J. Aresco, S.G. Beilke, B.W. Compton, E.P. Condon, C. Kenneth Dodd, Jr., H. Forrester, J.W. Gibbons, J.L. Greene, G. Johnson, T.A. Langen, M.J. Oldham, D.N. Oxier, R.A. Saumure, F.W. Schueler, J.M. Sleeman, L.L. Smith, J.K. Tucker, and J.P. Gibbs. 2006. Relative vulnerability of female turtles to road mortality. Animal Conservation 9: 269–273. https://doi.org/10.1111/j.1469-1795.2006.00032.x

Steen, D.A., J.P. Gibbs, K.A. Buhlmann, J.L. Carr, B.W. Compton, J.D. Congdon, J.S. Doody, J.C. Godwin, K.L. Holcomb, D.R. Jackson, F.J. Janzen, G. Johnson, M.T. Jones, J.T. Lamer, T.A. Langen, M.V. Plummer, J.W. Rowe, R.A. Saumure, J.K. Tucker, and D.S. Wilson. 2012. Terrestrial habitat requirements of nesting freshwater turtles. Biological Conservation 150: 121–128. https://doi.org/10.1016/j.biocon.2012.03.012

Taylor, G.M., and E. Nol. 1989. Movements and hibernation sites of overwintering painted turtles in southern Ontario. Canadian Journal of Zoology 67: 1877–1881. https://doi.org/10.1139/z89-268

Tran, S.L., D.L. Moorhead, and K.C. McKenna. 2007. Habitat selection by native turtles in a Lake Erie wetland, USA. American Midland Naturalist 158: 16–28. https://doi.org/10.1674/0003-0031(2007)158[16:HSBNTI]2.0.CO;2

Ultsch, G.R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biological Reviews 64: 435–516. https://doi.org/10.1111/j.1469-185X.1989.tb00683.x

Ultsch, G.R. 2006. The ecology of overwintering among turtles: where turtles overwinter and its consequences. Biological Reviews 81: 339–367. https://doi.org/10.1017/S1464793106007032

Winchell, K.M., and J.P. Gibbs. 2016. Golf courses as habitat for aquatic turtles in urbanized landscapes. Landscape and Urban Planning 147: 59–70. https://doi.org/10.1016/j.landurbplan.2015.11.001

Wood, C.M., and V.C. Hawkes. 2014. CLBMON-11B3 Revelstoke Reach painted turtle monitoring program: annual report — 2013. Okanagan Nation Alliance and LGL Limited Environmental Research Associates, Sidney, British Columbia, Canada.

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Note

Spiny Softshell (*Apalone spinifera*) turtles exhibit scarring consistent with attempted lamprey bites

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Abstract

We captured 46 Spiny Softshells (*Apalone spinifera*) during a mark–recapture study on Lake Erie (2012–2015). Six (13%) exhibited circular scars consistent with the bites of small parasitic lampreys. Two species of parasitic lampreys occur in Lake Erie: the invasive Sea Lamprey (*Petromyzon marinus*) and the native Silver Lamprey (*Ichthyostomyzon unicuspis*). The scars showed only the marks of the putative teeth surrounding the suctorial mouth, preventing identification based on the position of the supraoral teeth and suggesting that lampreys are rapidly dislodged from the turtles. To our knowledge, this is the first evidence of lampreys biting freshwater turtles.

Key words: Spiny Softshell turtle; *Apalone spinifera*; *Ichthyostomyzon unicuspis;* parasitic lamprey; *Petromyzon marinus;* Sea Lamprey; Silver Lamprey; turtle; Lake Erie

Sea Lamprey (*Petromyzon marinus*) was inadvertently introduced into the Great Lakes in 1921, where it has had a devastating impact on the Great Lakes fisheries of Canada and the United States (Shetter 1949; Lawrie 1970). Sea Lamprey wounds are most commonly recorded on Lake Trout (*Salvelinus namaycush*; Shetter 1949; Lawrie 1970; Christie and Goddard 2003); however, a range of other teleosts also exhibit lamprey wounds (Shetter 1949). Sea Lampreys primarily feed on the blood and muscle tissue of the host species (Farmer 1980). Scars from these encounters are oval and occasionally show circular rings of tooth marks, which confirm that they were made by Sea Lampreys (Pike 1951). Parasite–prey dynamics and interactions between teleosts and lampreys in the Great Lakes have been well documented (Sullivan *et al*. 2003; Stapanian and Madenjian 2007), but little is known about other prey and feeding strategies.

From 2012 to 2015, we captured, marked, and released 46 Spiny Softshell (*Apalone spinifera*) turtles (45 females, one male; 64 captures in total) in and around Rondeau Provincial Park, on the north shore of Lake Erie, Chatham-Kent County, Ontario, Canada (42.286634°N, 81.896193°W). Spiny Softshells often exhibit a variety of marks on the carapace consistent with abrasion or infection, although we have not quantified the frequency of these during our surveys.

In 2014, we observed that five adult females and one male (13% of all individuals captured) exhibited different, distinctive scarring on their carapace that was potentially consistent with lamprey (Family Petromyzontidae) bites. Unlike typical small lesions from abrasions or infections, these scars consisted of a circle of regularly spaced punctures into the epidermis, approximately 1 cm in diameter, hypothetically consistent with the ring of teeth surrounding a lamprey's suctorial mouth (Figure 1). The depressions formed by these punctures caused the undamaged skin in the centre of the ring to appear slightly raised (~5 mm) above the surface of the surrounding carapace. Lamprey-like scarring on Spiny Softshells was observed only on the carapace, and, in

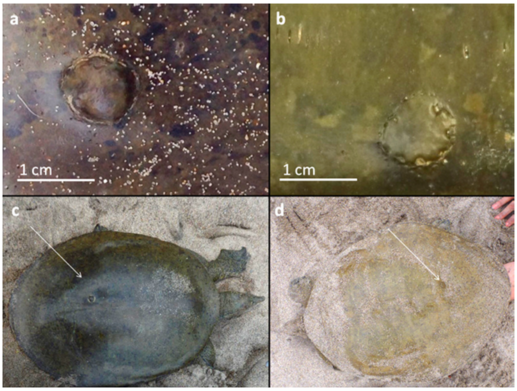

FIGURE 1. Two examples of observed scarring, potentially consistent with lamprey bites, on the carapace of female Spiny Softshells (*Apalone spinifera*) captured at Rondeau Provincial Park, Chatham-Kent County, Ontario. Panels a and b show the characteristic ring of punctures surrounding unbroken epidermis, which differs from the lesions associated with infections or abrasions. Panels c and d show the locations of these marks (white arrows) on the carapaces of two turtles. Photos: A.K. Whitear (a, c) and Juliana Skuza (b, d).

all instances, the scarring was located in the central (bony) portion of the carapace. The scars appeared fully healed, and, in one scarred turtle that was originally captured in 2014 and then recaptured in 2015, the scar retained its appearance between captures. All scarred turtles were mature (mean female carapace length = 439 mm, range = 385–473 mm; male carapace length = 184 mm).

The introduced *P. marinus* shares Lake Erie with a native parasitic lamprey, Silver Lamprey (*Ichthyomyzon unicuspis*). The Great Lakes–St. Lawrence population of *I. unicuspis* was assessed as a species of Special Concern by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2011). Bites of *P. marinus* and *I. unicuspis* may be distinguished based on the pattern of the supraorbital teeth (Pike 1951; Scott and Crossman 1998). However, the observed scars only contained marks consistent with the teeth surrounding the suctorial mouth. None included potential scarring from the supraoral teeth or rasping tongue. This is unsurprising, as softshell turtles have a strong bite. We suspect that any lamprey trying to attach to the carapace of a Spiny Softshell would be rapidly discouraged by the turtle's strong jaws, if it attached at a point that the turtle could reach. Alternatively, it may be difficult for lamprey to fasten securely onto the bony, smooth carapace of a Spiny Softshell.

To the best of our knowledge, this is the first reported evidence of lamprey attachment on freshwater turtles in Canada. It would be ideal to confirm our hypothesis with observations of lampreys attaching or attached to turtles, but this is unlikely in the wild. Still, we are unable to find a convincing competing hypothesis for the observed scarring. All Spiny Softshells with potential lamprey scars behaved normally, and the sites of the scars appeared to be fully healed. Any open wound can provide an avenue for infection, but turtles at our study site often sustain minor or even surprisingly severe injuries that do not impact their survival. If lampreys are indeed the cause of the observed marks, we consider it unlikely that this interaction would cause mortality or even have a significant sublethal impact on Spiny Softshells.

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Literature Cited

Christie, G.C., and C.I. Goddard. 2003. Sea Lamprey International Symposium (SLIS II): advances in the integrated management of sea lamprey in the Great Lakes. Journal of Great Lakes Research 29 (Supplement 1): 1–14. https://doi.org/10.1016/S0380-1330(03)70474-2

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2011. COSEWIC assessment and status report on the Silver Lamprey, Great Lakes - Upper St. Lawrence populations and Saskatchewan - Nelson Rivers populations *Ichthyomyzon unicuspis* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 17 May 2018. http://sararegistry.gc.ca/virtual_sara/files/cosewic/sr_silver_lamprey_0911_eng.pdf.

Farmer, G.J. 1980. Biology and physiology of feeding in adult lampreys. Canadian Journal of Fisheries and Aquatic Sciences 37: 1751–1761. https://doi.org/10.1139/f80-220

Lawrie, A.H. 1970. The sea lamprey in the Great Lakes. Transactions of the American Fisheries Society 99: 766–775. https://doi.org/10.1577/1548-8659(1970)99<766:TSLITG>2.0.CO;2

Pike, G.C. 1951. Lamprey marks on whales. Journal of the Fisheries Research Board of Canada 8b: 275–280. https://doi.org/10.1139/f50-017

Scott, W.B., and E.J. Crossman. 1998. Freshwater Fishes of Canada. Galt House Publications, Oakville, Ontario, Canada.

Shetter, D.S. 1949. A brief history of the sea lamprey problem in Michigan waters. Transactions of the American Fisheries Society 76: 160–176. https://doi.org/10.1577/1548-8659(1946)76[160:ABHOTS]2.0.CO;2

Stapanian, M.A., and C.P. Madenjian. 2007. Evidence that lake trout served as a buffer against sea lamprey predation on burbot in Lake Erie. North American Journal of Fisheries Management 27: 238–245. https://doi.org/10.1577/M05-156.1

Sullivan, W.P., G.C. Christie, F.C. Cornelius, M.F. Fodale, D.A. Johnson, J.F. Koonce, G.L. Larson, R.B. McDonald, K.M. Mullett, C.K. Murray, and P.A. Ryan. 2003. The sea lamprey in Lake Erie: a case history. Journal of Great Lakes Research 29 (suppl. 1): 615–636. https://doi.org/10.1016/S0380-1330(03)70520-6

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Depredation of gravid freshwater turtles by Raccoons (*Procyon lotor*)

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Abstract

During summer 2017, we found 19 dead or fatally wounded adult female turtles belonging to three at-risk species at a nesting site on the north shore of Lake Erie, Ontario. Individuals were found flipped onto their carapace, had similar holes in their body cavities, and were eviscerated. Their eggs had also been consumed. Although turtle nest depredation by Raccoons (*Procyon lotor*) is common, it is unusual for them to target large numbers of gravid turtles within a season. Depredated species included Snapping Turtle (*Chelydra serpentina*), Northern Map Turtle (*Graptemys geographica*), and Blanding's Turtle (*Emydoidea blandingii*). Our observation represents a spike in additive mortality for these populations, which could have long-term demographic consequences.

Key words: Additive mortality; depredation; predator; Raccoon; *Procyon lotor*; Blanding's Turtle; *Emydoidea blandingii;* Northern Map Turtle; *Graptemys geographica;* Snapping Turtle; *Chelydra serpentina*; Ontario

Introduction

Freshwater turtles typically exhibit high life expectancy and mortality rates that are inversely related to age (Iverson 1991). High depredation of eggs and hatchlings in the wild results in low recruitment of early life stages (Iverson 1991). Some North American freshwater turtle populations experience nest predation rates approaching 100% (63%: Congdon *et al.* 1983; 70%: Congdon *et al.* 1987; 84.2%: Burke *et al.* 1998). Elasticity (the proportional contribution of stage-specific demographic parameters to population growth) is low for turtle hatchlings relative to mature females. Populations with high adult survivorship can tolerate relatively high nest depredation as long as some recruitment is still occurring. In contrast, removing even a few mature individuals from a population may result in a disproportionally large decrease in population growth (Heppell 1998). Thus, additive mortality of adults can limit the growth of turtle populations, particularly those that are already in decline (Brooks *et al.* 1991; Stacy *et al.* 2014).

In North America, mammalian mesopredators are frequently observed depredating turtle nests. Common nest predators include Raccoon (*Procyon lotor*), Fisher (*Martes pennanti*), Gray Fox (*Urocyon cinereoargenteus*), Red Fox (*Vulpes vulpes*), River Otter (*Lutra canadensis*), American Mink (*Neovison vison*), Striped Skunk (*Mephitis mephitis*), Virginia Opossum (*Didelphis virginiana*), Eastern Wolf (*Canis lycaon*), and Coyote (*Canis latrans*; Wilhoft *et al.* 1979; Marchand *et al.* 2002; Geller 2012; Riley and Litzgus 2014). Adult turtles are more rarely targetted by predators because many species can retract into their shells for protection. Snapping Turtle (*Chelydra serpentina*) cannot fully retract, but instead displays intimidating snapping behaviour when threatened (Ernst and Lovich 2009). Nevertheless, predation of adult turtles does occur (Brooks *et al.* 1991; Baxter-Gilbert *et al.* 2013).

Erickson and Scudder (1947) suspected Raccoons as the cause of death of 26 nesting Yellow-bellied Sliders (*Trachemys scripta scripta*) and four Eastern Mud Turtles (*Kinosternon subrubrum*). They reported that these turtles shared similar injuries to the neck, intestines, and oviducts, with some carcasses adjacent to egg shells and Raccoon tracks. Similar injuries were reported on 28 depredated adult Diamond-backed Terrapins (*Malaclemys terrapin*) found during the nesting season in Gateway National Recreation Area, New York, in 1998–1999 (Feinberg and Burke 2003) and on 24 Diamond-backed Terrapins found in Merritt Island, Florida, in 1977–1978 (Seigel 1980). These authors also considered Raccoons as the most likely predator.

In 2004–2005, 35 Wood Turtle (*Glyptemys insculpta*) deaths at a site in Quebec were attributed to depredation by Raccoons (Pouliot *et al.* 2013). In some cases, Raccoons were observed attacking nesting Wood Turtles, and some dead individuals had sustained injuries that suggested they were being targetted for the unlaid eggs in their oviducts (Pouliot *et al.* 2013). Mustelids, such as American Mink and River Otter, may also depredate hibernating turtles during the winter (Brooks *et al.* 1991; Lanszki *et al.* 2006), when cold temperatures and potential hypoxia during hibernation reduce the turtle's ability to move quickly (Ultsch 1989). River Otters were recently implicated in a mass mortality of Blanding's Turtles (*Emydoidea blandingii*) on Manitoulin Island, Ontario, which increased the likelihood of extirpation for that population (Gasbarrini 2016).

Methods

In summer 2017, we conducted turtle nesting surveys at Rondeau Provincial Park (42.2808°N, 81.8525°W; Chatham-Kent County, Ontario, Canada) during an ongoing turtle conservation and research program. We monitored a nesting site (3.5 km long) daily from 5 June to 30 July 2017, with surveys typically running from 0900 to 1900. During this time, we observed semi-regular depredation of gravid or nesting females. In each case, we recorded specific injuries, measured the turtle's size (curved carapace length), and noted any evidence identifying potential predators. Following our first few observations of depredation, we also deployed Hyperfire trail cameras (Reconyx, Holmen, Wisconsin, USA) along the nesting site, in an effort to document potential predators.

Results

We observed 19 cases of depredation on gravid or post-nesting turtles: 10 Snapping Turtles, eight Northern Map Turtles (*Graptemys geographica*), and one Blanding's Turtle. All were mature females (mean curved carapace length ± SD for Snapping Turtles: 242.89 ± 13.50 mm; Northern Map Turtles: 313.13 ± 16.13 mm; Blanding's Turtle: 218 mm). The pattern of attacks was consistent among incidents. Each turtle was found flipped onto its carapace and with similar wounds (Figure 1). Snapping Turtles sustained a single hole approximately 5–8 cm in diameter above the right, hind leg, which provided access to the internal organs. Northern Map Turtles and the Blanding's Turtle exhibited multiple entry wounds around the legs and cloaca and sustained lacerations to their necks and heads. The turtles' internal organs (oviduct, intestines, and sometimes liver) were removed. If the turtles had recently nested, the nests were also depredated. If the turtles had not yet nested, the eggs were pulled from the oviduct and eaten. In both cases, eggshells were left scattered around the carcasses. Not all carcasses were found immediately post mortem because some were concealed in vegetation and were found only after the carcass had already undergone some degree of autolysis.

We observed Raccoon tracks adjacent to several carcasses, and our wildlife cameras detected Raccoons patrolling the nesting site during the day and at night.

FIGURE 1. Six depredated Snapping Turtles (*Chelydra serpentina*) exhibiting entry wounds (5–8 cm diameter) characteristic of Raccoons (*Procyon lotor*), some with eggshells adjacent. Upper left example (a) shows Raccoon tracks adjacent to the carcass (white dotted circle). Photos: Christina Davy and Alyson Karsons.

During nesting surveys, we also made several observations of a Raccoon approaching, biting, or dragging gravid Northern Map Turtles. We suspect that a single Raccoon may have been responsible for all the observed mortalities, because the cluster of depredation events and the consistent locations of the entry wounds suggests a single individual and because the locations of the observed mortalities fall within a typical Raccoon home range (~200–400 ha; Šálek *et al.* 2015). The greatest distance between two depredated turtles was 3.25 km between a Northern Map Turtle and a Blanding's Turtle, which were depredated on 11 July and 12 July, respectively.

Discussion

The injuries we observed are consistent with those described for other depredation events in which Raccoons have been implicated (e.g., Seigel 1980; Pouliot *et al.* 2013). Gravid reptiles may be more susceptible to predation during extended overland movements toward nesting sites (Schwarzkopf and Shine 1992; Cox and Calsbeek 2009), but this is the first predator-related mortality of gravid or nesting females recorded at our study site in seven years of monitoring. It is unclear what prompted this Raccoon to expand its repertoire from nest depredation (>90% at our study site) to also preying on adult turtles. To our knowledge, this depredation event specifically targetted reproductive females, which are critical to population persistence (Brooks *et al.* 1991).

Nest depredation can be high even in relatively unimpacted, "natural" areas, and predation rates may increase in anthropogenically impacted habitats where mesopredators experience increased food supply (e.g., Raccoon or Coyotes scavenging from waste bins or agricultural fields). Subsidized mesopredators can live at higher densities, because the excess food increases the carrying capacity of those habitats (Smith and Engeman 2002). This in turn puts greater pressure on prey populations, and high nest predation rates resulting from subsidized predation can severely reduce recruitment into freshwater turtle populations (Marchand *et al.* 2002). If adult survivorship is high, the population may tolerate low recruitment rates (Heppell 1998). However, the addition of additive mortality in the form of depredation of adults would increase the probability of the population's eventual extirpation (Heppell 1998).

Our observations suggest that the additive mortality we describe here may have been caused by a single Raccoon, rather than an overabundance of Raccoons at Rondeau Park. A general overall reduction (i.e., culling) of this Raccoon population is unlikely to decrease rates of turtle or turtle nest predation. Experimental removal of Raccoons from areas adjacent to a sea turtle nesting beach did not decrease rates of nest predation because of rapid dispersal into the target site by individuals from nearby areas, coupled with rapid recruitment of juveniles to the surviving Raccoon population (Barton and Roth 2007). Even a cull of 50% of the Raccoons present at a sea turtle nesting site failed to reduce nest depredation (Ratnaswamy *et al.* 1997). However, targetted removal of specific, predatory Raccoons and Armadillos (*Dasypus novemcinctus*) from another sea turtle nesting site managed to reduce nest loss from 95% to 9.4% (Engeman *et al.* 2005), suggesting that in some cases, ongoing adaptive predator control may be a useful tool for protecting turtle nests. As our observations appear likely to be caused by only one or a few Raccoons, targetting these specific individuals might alleviate future predation pressures on vulnerable females. However, although there is undoubtedly a relationship between subsidized mesopredator abundance and nest predation, we caution that Raccoons quickly learn new skills from one another and that the intense, targetted efforts required to effectively protect nesting females and their eggs would be costly to maintain.

The observed Snapping Turtle depredation ($n = 10$) represents ~1% of the estimated 800 females that nest at this site (C.M.D. unpubl. data), and our observations likely underestimate mortality because we may not have found all depredated individuals. Recurring predation events like this one could have rapid, cumulative effects on population viability, because turtle populations recover slowly or not at all from mass mortality events (Brooks *et al.* 1991). Mature females have the highest value in terms of population growth in freshwater turtles. Thus, the most critical conservation efforts may be those aimed at saving as many individual nesting turtles as possible (Heppell 1998), provided recruitment is also occurring (Bennett *et al.* 2017). Nevertheless, predation is an inevitable part of functioning ecosystems, and there is no way to eliminate this pressure completely. Considering rapid increases in additive mortality is essential to evaluating population viability, and pulses in depredation of adult turtles can have long-term effects on a population (Brooks *et al.* 1991). However, from the perspective of recovering threatened turtle populations, it is likely more effective to focus on the mitigation of the most consistent, significant sources of mortality, such as road mortality, or ongoing harvest in jurisdictions where turtles are still managed as game species.

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Literature Cited

Barton, B.T., and J.D. Roth. 2007. Raccoon removal on sea turtle nesting beaches. Journal of Wildlife Management 71: 1234–1237. https://doi.org/10.2193/2006-014

Baxter-Gilbert, J., J.L. Riley, and J.D. Litzgus. 2013. *Chrysemys picta marginata* (midland painted turtle) avian predation. Herpetological Review 44: 302–303.

Bennett, A.M., J. Steiner, S. Carstairs, A. Gielens, and C.M. Davy. 2017. A question of scale: replication and the effective evaluation of conservation interventions. FACETS 2: 892–909. https://doi.org/10.1139/facets-2017-0010

Brooks, R.J., G.P. Brown, and D.A. Galbraith. 1991. Effects of a sudden increase in natural mortality of adults on a population of the common snapping turtle (*Chelydra serpentina*). Canadian Journal of Zoology 69: 1314–1320. https://doi.org/10.1139/z91-185

Burke, V.J., S.L. Rathbun, J.R. Bodie, and J.W. Gibbons. 1998. Effect of density on predation rate for turtle nests in a complex landscape. Oikos 83: 3–11. https://doi.org/10.2307/3546540

Congdon, J.D., D.W. Tinkle, G.L. Breitenbach, and R.C. van Loben Sels. 1983. Nesting ecology and hatchling success in the turtle *Emydoidea blandingii.* Herpetologica 39: 417–429.

Congdon, J.D., D.W. Tinkle, G.L. Breitenbach, and R.C. van Loben Sels. 1987. Reproduction and nesting ecology of Snapping Turtles (*Chelydra serpentina*) in southern Michigan. Herpetologica 43: 39–54.

Cox, R.M., and R. Calsbeek. 2009. Severe costs of reproduction persist in Anolis Lizards despite the evolution of a single-egg clutch. Evolution 64: 1321–1330. https://doi.org/10.1111/j.1558-5646.2009.00906.x

Engeman, R.M., R.E. Martin, H.T. Smith, J. Woolard, C.K. Crady, S.A. Shwiff, B. Constantin, M. Stahl, and J. Griner. 2005. Dramatic reduction in predation on marine turtle nests through improved predator monitoring and management. Oryx 39: 318–326.

Erickson, A.B., and H.I. Scudder. 1947. The raccoon as a predator on turtles. Journal of Mammalogy 28: 406–407. https://doi.org/10.1093/jmammal/28.4.406

Ernst, C.H., and J.E. Lovich. 2009. Turtles of the United States and Canada. Second Edition. Johns Hopkins University Press, Baltimore, Maryland, USA.

Feinberg, J.A., and R.L. Burke. 2003. Nesting ecology and predation of Diamondback Terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. Journal of Herpetology 37: 517–526. https://doi.org/10.1670/207-02A

Gasbarrini, D.M. 2016. Investigation into the cause(s) of a mass mortality of a long-lived species in a Provincial Park and an evaluation of recovery strategies. M.Sc. thesis, Laurentian University, Sudbury, Ontario, Canada.

Geller, G.A. 2012. Notes on the nest predation dynamics of *Graptemys* at two Wisconsin sites using trail camera monitoring. Chelonian Conservation and Biology 11: 197–205. https://doi.org/10.2744/CCB-0992.1

Heppell, S.S. 1998. Application of life-history theory and population model analysis to turtle conservation. Copeia 2: 367–375. https://doi.org/10.2307/1447430

Iverson, J.B. 1991. Patterns of survivorship in turtles (order Testudines). Canadian Journal of Zoology 69: 385–391. https://doi.org/10.1139/z91-060

Lanszki, J., M. Molnár, and T. Molnár. 2006. Factors affecting the predation of otter (*Lutra lutra*) on European pond turtle (*Emys orbicularis*). Journal of Zoology 270: 219–226. https://doi.org/10.1111/j.1469-7998.2006.00132.x

Marchand, M.N., J.A. Lavaitis, T.J. Maier, and R.M. DeGraaf. 2002. Use of artificial nests to investigate predation on freshwater turtle nests. Wildlife Society Bulletin 30: 1092–1098.

Pouliot, D., D. Masse, and Y. Robitaille. 2013. Raccoon predation induced a short-term decline in a nesting population of wood turtle (*Glyptemys insculpta*). Presented at the Conference of the Canadian Amphibian and Reptile Conservation Network and Canadian Association of Herpetologists, 12–16 September 2013, Orford, Quebec, Canada.

Ratnaswamy, M.J., R.J. Warren, M.T. Kramer, and M.D. Adam. 1997. Comparisons of lethal and nonlethal techniques to reduce raccoon depredation of sea turtle nests. Journal of Wildlife Management 61: 368–376. https://doi.org/10.2307/3802593

Riley, J.L., and J.D. Litzgus. 2014. Cues used by predators to detect freshwater turtle nests may persist late into incubation. Canadian Field-Naturalist 128: 179–188. https://doi.org/10.22621/cfn.v128i2.1583

Šálek, M., L. Drahníková, and E. Tkadlec. 2015. Changes in home range sizes and population densities of carnivore species along the natural to urban habitat gradient. Mammal Review 45: 1–14. https://doi.org/10.1111/mam.12027

Schwarzkopf, L., and R. Shine. 1992. Costs of reproduction in lizards: escape tactics and susceptibility to predation. Behavioral Ecology and Sociobiology 31: 17–25. https://doi.org/10.1007/BF00167812

Seigel, R.A. 1980. Predation by Raccoons on Diamondback Terrapins, *Malaclemys terrapin tequesta*. Journal of Herpetology 14: 87–89. https://doi.org/10.2307/1563885

Smith, H.T., and R.M. Engeman. 2002. An extraordinary Raccoon, *Procyon lotor*; density at an urban park. Canadian Field-Naturalist 116: 636–639. Accessed 29 September 2018. https://biodiversitylibrary.org/page/35151882.

Stacy, B.A., D.A. Wolf, and J.F.X. Wellehan, Jr. 2014. Large-scale predation by River Otters (*Lontra canadensis*) on Florida Cooter (*Pseudemys floridana*) and Florida Softshell Turtles (*Apalone ferox*). Journal of Wildlife Diseases 50: 906–910. https://doi.org/10.7589/2013-10-271

Ultsch, G.R. 1989. Ecology and physiology of hibernation and overwintering among freshwater fishes, turtles, and snakes. Biological Reviews 64: 435–515. https://doi.org/10.1111/j.1469-185X.1989.tb00683.x

Wilhoft, D.C., M.G. Del Baglivo, and M.D. Del Baglivo. 1979. Observations on mammalian predation of Snapping Turtle nests (Reptilia, Testudines, Chelydridae). Journal of Herpetology 13: 435–438. https://doi.org/10.2307/1563478

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Variable habitat selection and movement patterns among Bullsnake (*Pituophis catenifer sayi*) populations in Saskatchewan

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Abstract

Pituophis catenifer sayi (Bullsnake) is a sparsely studied subspecies of conservation concern in Canada. Basic ecological information is lacking for *P. c. sayi*, which reaches its northern range limit in western Canada. To address this gap, we used radio-telemetry to examine space use and habitat selection in three populations of Bullsnakes in disjunct river valley systems (Frenchman, Big Muddy, and South Saskatchewan River Valleys) across their Saskatchewan range. Bullsnakes in two valleys used up to three times more space, travelled 2.5-times farther from overwintering sites, and had lower home range overlap than the third population. Landscape-level habitat selection was flexible, with snakes in all populations using both natural and human-modified habitats most frequently. Fine-scale habitat selection was also similar among populations, with Bullsnakes selecting sites within 1 m of refuges, regardless of whether they were natural or anthropogenic. Based on these results, Bullsnakes are flexible in their broad scale habitat use, as long as they are provided with fine scale refuge sites. The distribution of key seasonal resources appears to ultimately determine space use and habitat selection by Bullsnakes, regardless of the geographic location of the population.

Key words: Bullsnake; *Pituophis catenifer sayi*; grassland snakes; habitat selection; home range; space use; ecology

Introduction

Pituophis catenifer sayi (Bullsnake) is widespread throughout North America, but is of conservation concern in Canada where it reaches its northern range limit. The Committee on the Status of Endangered Wildlife in Canada assessed this subspecies of Gophersnake (*Pituophis catenifer*) as Special Concern (COSEWIC 2017), and there is a corresponding need for basic ecological and population studies. Information from more southerly populations in the USA shows that space requirements (home range size) are highly variable for Bullsnakes (Moriarty and Linck 1997; Fitch 1999; Rodriguez-Robles 2003; Kapfer *et al.* 2008, 2010). Kapfer *et al.* (2010) found that habitat quality was the most important factor affecting home range: Bullsnakes in high quality areas used less space. Bullsnake habitat selection also varies across their range, with some populations selecting south facing bluffs (Kapfer *et al.* 2008), while others primarily select open grassland habitats (Moriarty and Linck 1997; Rodriguez-Robles 2003). Space and habitat use have been examined for the closely related Great Basin Gophersnake (*Pituophis catenifer deserticola*) in Canada (Williams *et al.* 2012, 2014, 2015), though only two studies have addressed space use and habitat selection by Bullsnakes specifically. Both of these studies focussed on the same Bullsnake population in the Frenchman River Valley of southwestern Saskatchewan (Martino *et al.* 2012; Gardiner *et al.* 2013). These Bullsnakes made long distance migrations between summer and winter habitats (up to 4 km), selected for lowland pasture, slopes, and roads, and relied heavily on mammal burrows as refuge sites (Martino *et al.* 2012; Gardiner *et al.* 2013). Bullsnake home ranges in the Frenchman River Valley were substantially larger than more southerly populations in the United States (up to 99 fold difference; Martino *et al.* 2012). However, it is currently unknown whether the space use and habitat selection by snakes in this one area are broadly reflective of other populations occupying various landscapes across their Canadian range.

Snake space use and habitat selection are primarily based on the spatial distribution of key resources in the environment, and thus vary within and among populations (Carfagno and Weatherhead 2006; Bauder *et al.* 2015; Gomez *et al.* 2015). For example, Prairie Rattlesnakes (*Crotalus viridis viridis*) demonstrate variation in space use throughout their geographic range (displacement from overwintering site: 2.76 to 40 km; home range: 18 to 109 ha; Bauder *et al.* 2015), with variation in prey availability being the suggested driver for these differences. Occupancy has also been linked to thermal requirements, with snakes selecting habitats conducive to optimizing thermoregulation (Burger and Zappalorti 1992; Blouin-Demers and Weatherhead 2001; Carfagno and Weatherhead 2006; Blouin-Demers and Weatherhead 2008; Cross *et al.* 2015). Retreat sites can be particularly critical as they provide suitable habitat for thermoregulation, refuge from predators, and increased foraging opportunities (Charland and Gregory 1995; Rodriguez-Robles 2003; Himes *et al.* 2006; Croak *et al.* 2013). The presence of refuges is especially important for snakes at northern latitudes, where the distribution and abundance of overwintering den sites often limits space use; snakes must move to and from suitable overwintering sites each year (Burger *et al.* 1988; Jorgensen *et al.* 2008; Bauder *et al.* 2015). As a result, the proximity of den sites relative to other key resources may be a primary determinant of space requirements in northern populations (Martino *et al.* 2012; Williams *et al.* 2012; Gardiner *et al.* 2013).

Space and habitat use by snakes may also be affected in various ways by human modification of the landscape or specific resources. The removal of native habitats can have negative impacts on abundance, activity patterns, and behaviours (Burger 2001; Kjoss and Litvaitis 2001; Beale *et al.* 2016). However, in many cases, responses vary depending on the ability of snakes to tolerate habitat changes and the quality of available resources (Driscoll 2004; Corey and Doody 2010). Ultimately, individuals may demonstrate increases, decreases, or no difference in the frequency of movements or extent of space use in human modified landscapes compared to natural landscapes (Corey and Doody 2010; Anguiano and Diffendorfer 2015; Smith *et al.* 2015; Ettling *et al.* 2016). Species may even be positively associated with modified habitats (Carfagno and Weatherhead 2006; Knoot and Best 2011). Snake response to habitat modification remains to be addressed thoroughly in areas with variation in human land use type and intensity.

Here, we quantify Bullsnake space use and habitat selection in populations from three different major river valley systems (Frenchman, Big Muddy, and South Saskatchewan River Valleys) in Saskatchewan, Canada. Our hypothesis was that habitat availability and landscape configuration, specifically the distance between overwintering dens sites and summer habitat, affect the space use and habitat selection of snakes. Consequently, we predicted that Bullsnake space use and habitat selection would vary among populations in the different river valleys, as these areas differ substantially in their available habitat types, landscape configurations, and intensity of human modification. Bullsnake spatial ecology has only been examined previously for one population in Canada, so our study aims to increase understanding of how these snakes use landscapes in various circumstances.

Methods

Study species

Bullsnakes are the largest snakes in Canada, reaching lengths of up to 2.5 m (Ernst and Ernst 2003). Bullsnakes are non-venomous constrictors that prey on small mammals, such as mice and ground squirrels, as well as birds, bird eggs, and reptiles. These snakes are diurnal during the majority of the summer, but may become more active during crepuscular periods when conditions are exceedingly hot and dry (July and August). Bullsnakes are widespread throughout the United States, with their range extending northward into Canada, across southeast Alberta to southwest and south-central Saskatchewan (Ernst and Ernst 2003). Bullsnakes nest communally or individually under rocks, logs, and within self-excavated or mammal-created burrows (Ernst and Ernst 2003; Wright 2008). Bullsnakes overwinter in extensive mammal burrows or rock crevices (Ernst and Ernst 2003; Kapfer *et al.* 2008). In 2017 Bullsnakes were assessed as a species of Special Concern in Canada mainly due to threats of habitat loss and road mortality. Life history, behavioural, and population characteristics are thought to exacerbate the effects of these threats on Bullsnakes (COSEWIC 2017). As Bullsnakes den communally and may return to the same den each year, protection of these limited den sites is important for this subspecies.

Study areas

We studied Bullsnake space and habitat use in three major river valley systems across southern Saskatchewan, Canada: the Frenchman River Valley (FRV; in 2008 and 2009; data collected by Martino *et al.* 2012), the Big Muddy Valley (BMV; in 2015), and the South Saskatchewan River Valley (SSRV; in 2016; Figure 1). Bullsnakes rely on hibernacula in valley walls; the area between valleys likely does not contain suitable overwintering sites, and much of the habitat has been converted to agriculture. Bullsnakes in the three valleys are genetically differentiated, and no movement among populations is likely (Somers *et al.* 2017).

The study area in the FRV (49°10'37"N, 107°25'33"W) is located within a community pasture. This area is composed of large tracts of native grass pasture, surrounded by cropland and roads (paved and gravel). We tracked snakes from two communal overwintering den sites within the native grassland pasture; both were located in valley hillsides with significant hill slumping and large burrow systems (Martino *et al.* 2012; Gardiner *et al.* 2013). Overwintering sites in the FRV are separated from the riparian zone in the centre of the valley by ~3–4 km. To use habitat other than the hills and slopes associated with valley walls, Bullsnakes in the FRV need to travel long distances, and almost always move downslope toward the valley centre (Martino *et al.* 2012; Gardiner *et al.* 2013).

The BMV (49°12'55"N, 105°12'09"W) site is dominated by native grass pasture in the main valley and adjacent ravines. Cattle and horse ranches are located in the valley lowlands while the surrounding uplands have been converted for crop production. Bullsnakes are found on private land in this area. Ranchers in the BMV tend to protect Bullsnakes occupying their land due to the perceived rodent control benefits the snakes provide. We tracked snakes from den sites located in crevice and burrow systems within rock formations and valley hillsides. Communal den sites in the BMV

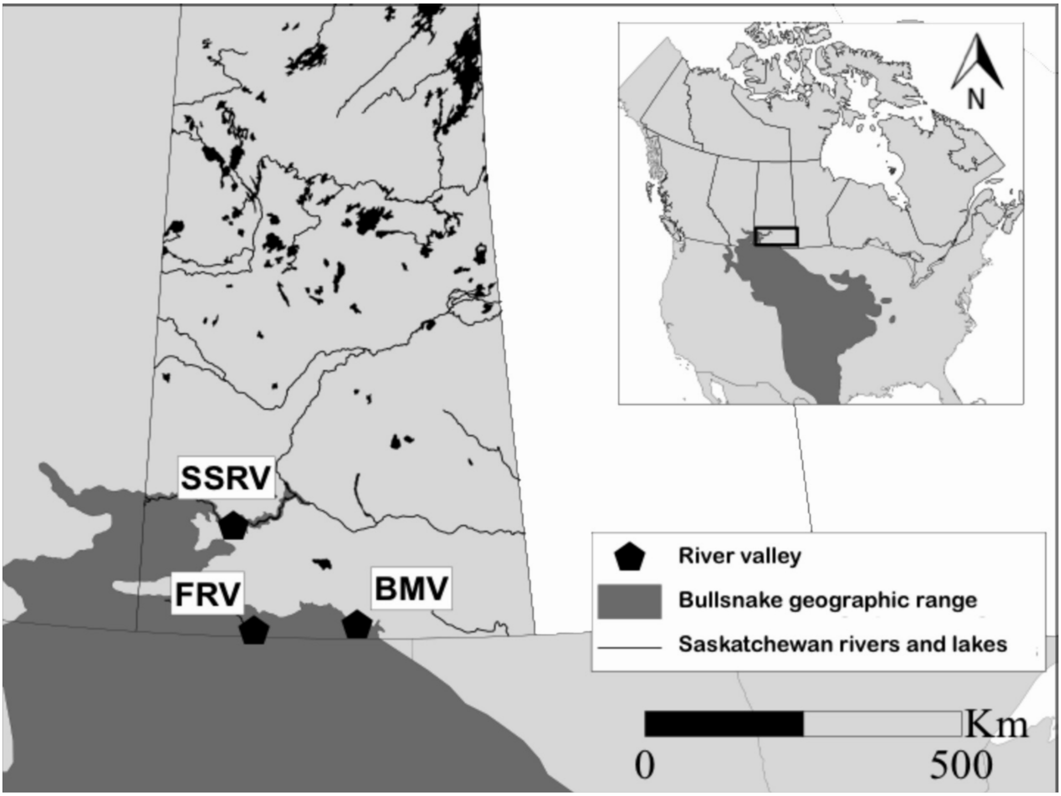

FIGURE 1. Location of study sites where Bullsnakes (*Pituophis catenifer sayi*) were tracked using radio-telemetry in southern Saskatchewan: Frenchman River Valley (FRV, 2008–2009, data collected by Martino *et al.* 2012), Big Muddy Valley (BMV, 2015), and South Saskatchewan River Valley (SSRV, 2016), indicated by the black pentagons. The North American Bullsnake range is highlighted in dark grey. Inset: the geographic range of Bullsnakes in Canada and the United States (dark grey).

were <500 m from the valley base and in ranch farmyards. Contrary to the SSRV and FRV, no large river runs through the BMV.

The study area in the SSRV (50°38'16"N, 107°59'28"W) is located in Saskatchewan Landing Provincial Park. The South Saskatchewan River has been converted into a large reservoir (Lake Diefenbaker) and this reservoir comprises the centre of Saskatchewan Landing Provincial Park, making it a popular area for summer recreational activities. The Provincial Park has ~250 000 visitors per year (D. Silversides pers. comm. 8 November 2016). Native prairie dominates the main valley and adjacent coulees. Visitor areas (including campgrounds, a golf course, and cottages) are also found throughout the base of the valley. The uplands surrounding the park are used for cattle ranching and crop production. Den sites throughout the park are found within burrow systems (this study; Royal Saskatchewan Museum unpubl. data). Den sites are found in a wide range of locations, some of which are relatively close to the valley base (~100–600 m from Lake Diefenbaker) and in various topographies, from hillsides to flat, native grass fields (this study; Royal Saskatchewan Museum unpubl. data).

Snake capture and transmitter implantation

We located Bullsnakes during their active season (April to October) using foot searches and road surveys in the FRV from 2008 to 2009 (Martino *et al.* 2012), the BMV in 2015, and the SSRV in 2016. Upon capture, snakes were measured, weighed, sexed (after Schaefer 1934), and implanted with Passive Integrated Transponder (PIT) tags. Snakes were transported to a veterinary clinic and surgically implanted with Holohil model SI-2 (Carp, Ontario, Canada), 13-g radio-transmitters (similar to Lentini *et al.* 2011) by veterinary surgeons. In 2016, implantation protocols were modified, such that the transmitter wire was implanted within the body cavity of the snake instead of under the integument. This modification was made because subcutaneous implantation of the transmitter wire may lead to wire penetration of the skin and subsequent infection (Lentini *et al.* 2011). Snakes were only implanted if the diameter of the transmitter was <50% of the body diameter at the implantation site, and the mass of the transmitter was <5% of body mass. Snakes were allowed a minimum of 24 h recovery, upon which they were released at their original capture location.

Space use and movement patterns

Following release, we relocated Bullsnakes every 48 h (when possible) for the duration of their summer active season. After snakes had returned to den sites in the fall (late August to early October), tracking was reduced to once every 1 to 2 weeks. Upon each relocation of a snake, we recorded universal transverse mercator (UTM) coordinates on a Garmin Legend HCx (Lenexa, Kansas, USA) handheld global positioning system (GPS) unit (± 2 m). We quantified Bullsnake movement patterns using ArcGIS 10.3.1 (ESRI 2015). Maximum displacement by individual snakes from their respective den sites was calculated using the Point Distance Tool. The Geospatial Modelling Environment (GME; Beyer 2015) was used to estimate 100% minimum convex polygons (MCP), as well as 50% and 95% kernel density estimates (KDE). MCP was calculated for individuals with at least 10 relocations (Himes *et al.* 2006; Parker and Anderson 2007; Kapfer *et al.* 2008, 2010; Martino *et al.* 2012) and KDE for individuals with at least 15 relocations (as in Gardiner *et al.* 2013). We defined relocations as any location to which a snake was tracked. We performed regression analysis to determine if the number of relocations per snake affected home range size (Kapfer *et al.* 2008). There was no significant positive relationship between home range size and the number of observations per snake (data not shown).

For the KDE, smoothing factors for each snake were estimated using the Plugin algorithm, which calculates the X and Y variances as well as the X/Y covariance among relocation UTM coordinates. We used this method to calculate smoothing factors, as the commonly used least squared cross-validation (LSCV) algorithm tends to oversmooth and is not recommended for individuals with multiple relocations at the same site (Row and Blouin-Demers 2006). Using the Plugin algorithm to calculate a smoothing factor also produced 95% KDE areas that were most similar to MCP areas, compared to the LSCV.

We calculated home range overlap for all river valleys using two different methods. The distances between Bullsnake MCP centroids were calculated using the Point Distance Tool, and the proportion of MCP shared was calculated using the Intersect Tool in ArcGIS. Distance between centroids and proportion of home range overlap was calculated for Bullsnakes occupying the same den sites. We constructed generalized linear models (GLM, with a gamma distribution) to estimate which variables influence snake home range size (MCP; 95% KDE; 50% KDE) and maximum displacement of snakes from den sites. Fixed effects were snake sex, snout-to-vent length, distance to nearest anthropogenic structure (i.e., farmyards, campgrounds, parking lots, cottages), and river valley. Distance to nearest anthropogenic structure was calculated as the distance between the centroid of an individual snake's MCP and the nearest anthropogenic structure point feature using the Point Distance Tool. After running the global model, we used Akaike's Information Criterion corrected for small samples size (AICc) for model selection. Competing models with ΔAIC <10 were model averaged and the 95% CI calculated (Burnham *et al.* 2011). We also performed gamma and beta regression analyses, respectively, to estimate which variables influence centroid distance and proportion of home range overlap.

Third order habitat selection: compositional analysis

Third order selection is defined as selection of habitats distinguishable by larger scale features, such as topography and vegetation type (Johnson 1980). Habitat selection at this scale was examined using compositional analysis; comparing the number of observations in each habitat type to the proportion of each habitat type available to Bullsnakes (Aebischer *et al.* 1993). Available habitat types were defined and distinguished prior to snake tracking using aerial imagery and confirmed in the field. Habitats were considered to be available to a snake if they were contained within a circular buffer zone centred on the den site that was calculated to be the maximum displacement by snakes in the corresponding population (5 km radius buffer in the FRV; 1.3 km buffer in the BMV; 2.4 km buffer in the SSRV; Gomez *et al.* 2015). Third order habitat selection by Bullsnakes in the FRV was measured by Gardiner *et al.* (2013), where available habitats included riparian areas, hills/slopes, native lowland grass pasture, mudflats, roads, irrigation areas, native upland fields, crop fields, Prairie Dog (*Cynomys ludovicianus*) towns, and open water. Habitats available to snakes in the BMV included native grass pasture, crop fields, roads/road areas, hills/slopes/rock formations, trees/tall shrubs, and farmyards. SSRV habitats included native prairie, tame grass fields, mowed areas, human-developed areas (such as parking lots, buildings, and campgrounds), crop fields, roads/road areas, beach area, trees/tall shrubs, marshes/streams, and open water

Polygons encompassing available habitats within buffer zones were traced on a high-resolution satellite image (downloaded from https://www.flysask2.ca; accessed 10 September 2016) in ArcGIS. The proportion of each habitat within the buffer zone was calculated (defined as proportion available), as well as the proportion of total observations for each individual snake within each habitat type (defined as proportion used). We used the adehabitatHS package in R (Calenge 2006) to perform compositional analysis to test for non-random habitat use (selection) and rank habitats based on their selection by Bullsnakes.

Fourth order habitat selection

Fourth order habitat selection is defined as the selection of the immediate and local habitat, comprised of physical and ecological features that distinguish it from the surrounding environment (Johnson 1980). A used versus available study design was followed to quantify fourth order habitat selection (Aebischer *et al.* 1993; Thomas and Taylor 2006). Habitat characteristics were measured at sites that were used by snakes. Habitat measurements were only taken when a snake was tracked to a new location, defined as ≥20 m from the previous location. Habitat characteristics were measured within a 50 × 50 cm quadrat at the used location and the percent grass, forb, shrub, and bare ground cover was estimated (to the nearest 5%) within the quadrat. Maximum vegetation height, distance to nearest burrow, and distance to nearest shrub were also measured. Robel pole measurements of vegetation density were taken in each cardinal direction within the quadrat and averaged (Robel *et al.* 1970). These habitat variables have been used previously to assess snake habitat selection at a fine scale (Harvey and Weatherhead 2006; Moore and Gillingham 2006; Martino *et al.* 2012; Gardiner *et al.* 2015). The same habitat characteristics were also measured at available sites. Available sites were characterized as the halfway point along a straight line between a snake's previous location and new relocation (≥20 m away from previous location; Martino *et al.* 2012; similar to Gardiner *et al.* 2015), as this habitat would be 'available' to snakes during their travel to a new location. This was done to examine whether snakes were selecting habitat at a local scale (fourth order habitat selection) within their home range. To model habitat selection, we built generalized linear mixed models (GLMMs) with a binomial distribution in the package lme4 in R (Bates *et al.* 2015; R Core Team 2016). Habitat variables were fixed effects and individual snake ID was a random effect. We developed separate models for the BMV and SSRV. Martino *et al.* (2012) previously measured fourth order habitat selection by Bullsnakes in the FRV and we used those data.

Prior to running each model, a non-parametric Spearman's test was used to examine correlations between variables. We eliminated all variables that were correlated greater than $r_s = 0.70$. As a result, percent bare ground was removed from all models, as it was negatively correlated with percent grass cover ($r_s = -0.70$ to -0.92). After eliminating the correlated variable and running the global GLMM, we used model selection based on AICc to compare all possible combinations of predictor variables. Competing models, with ΔAICc <10, were model averaged to provide parameter estimates, importance values, and SE for all variables (Burnham *et al.* 2011). The 95% CI were also calculated for all parameters.

Results

Radio-telemetry

Fourteen Bullsnakes (five females, nine males) were radio-tracked over the course of the active season in 2008 and 2009 in the FRV, with the total number of relocations per individual ranging from 10 to 50 (Table 1). In the BMV, seven Bullsnakes (four females, three males) were radio-tracked over the active season, with

TABLE 1. Summary telemetry data (means ± SD), including number of relocations, maximum displacement, home range overlap, and home range area values for Bullsnakes (*Pituophis catenifer sayi*) from three different river valleys in southern Saskatchewan: the Big Muddy Valley (BMV), South Saskatchewan River Valley (SSRV), and the Frenchman River Valley (FRV). *n* = the number of snakes tracked.

	Telemetry data		Mean maximum displacement	Home range overlap		Home range area		
River Valley	Tracking period (days)	No. relocations	From overwintering den site (m)	Distance between centroids (m)	Proportion of home range shared	Minimum convex polygon (ha)	95% kernel density estimate (ha)	50% kernel density estimate (ha)
FRV (*n* = 14)	62 ± 32.9	25 ± 13.8	1709 ± 959.2	994 ± 502.6	0.14 ± 0.2	62 ± 52.2	67 ± 55.4	12 ± 10.5
BMV (*n* = 7)	102 ± 7.0	51 ± 3.8	638 ± 380.7	195 ± 123.7	0.49 ± 0.3	17 ± 15.6	15 ± 20.3	3 ± 4.6
SSRV (*n* = 14)	72 ± 26.7	32 ± 11.6	1440 ± 568.0	736 ± 523.6	0.21 ± 0.3	50 ± 41.6	60 ± 60.3	12 ± 11.9

total relocations per individual ranging from 43 to 55 (Table 1). In the SSRV, 14 Bullsnakes (six females, eight males) were implanted with radio-transmitters. The number of relocations per snake ranged from 12 to 48 (Table 1). The maximum time between tracking events was 19 days in the FRV, seven days in the BMV, and six days in the SSRV.

Space use and movement patterns

The GLM indicated the largest factor affecting displacement from den sites by Bullsnakes was the river valley they occupied (Table 2). Bullsnakes in the FRV (493 to 3946 m) and SSRV (661 to 2427 m) had similar and relatively long maximum displacements from overwintering den sites, moving up to 2.7 times farther from dens than Bullsnakes in the BMV (Figure 2).

Fourteen snakes in the FRV, seven snakes in the BMV, and 14 snakes in the SSRV were relocated often enough to estimate MCPs, while 10 FRV, seven BMV, and 13 SSRV snakes had enough relocations to estimate the 50% and 95% KDEs. Generalized Linear Models examining differences in home range size among Bullsnakes, regardless of home range estimator, were consistent with analyses of den site displacement, indicating river valley as the only fixed effect (Table 3; Tables S1 and S2). On average, Bullsnakes in the FRV and SSRV had MCP home ranges up to 3.7 times larger, 95% KDEs up to 4.5 times larger, and 50% KDEs up to 4.4 times larger than those in the BMV (Table 1; Figure 2).

Home range overlap was greater on average in the BMV, compared to the FRV and SSRV (Table 1; Figure 2). This was supported by generalized linear regression analyses, which demonstrated that the distance between centroids increased (FRV Estimate = 799.08, $P < 0.001$; SSRV Estimate = 540.89, $P < 0.001$) and the proportion of home range overlap decreased (FRV Estimate = −1.66, $P < 0.001$; SSRV Estimate = −1.39, $P < 0.001$) in the FRV and SSRV compared to the BMV.

Third order habitat selection

Native lowland grass pasture, hills/slopes, and roads were used most frequently by Bullsnakes in the FRV (Figure 3a; Martino *et al.* 2012; Gardiner *et al.* 2013). Bullsnakes in the BMV also exhibited non-random habitat use ($\lambda = 0.002$, $P = 0.04$); the most frequently used habitat types were farmyards and native grass pasture. On average, farmyards were selected 11 times more than expected; native grass pasture, roads, and hills/slopes were used in proportion to availability; and crop fields and treed areas were not used at all (Figure 3b). Similarly, Bullsnakes in the SSRV also exhibited non-random habitat use ($\lambda = 0.014$, $P = 0.01$); the most frequently used habitats were beach area, native prairie, tame grass fields, human-developed areas (including buildings, parking lots, and campgrounds), mowed areas, and roads. Bullsnakes used beaches 91.6 times, tame grass fields 8.7 times, buildings 2.1 times, mowed areas 2.9 times, and roads 2.3 times more than expected based on availability (Figure 3c). Native prairie and marshes were used in proportion to availability; while treed areas and crop fields were used 8.7 times and two times less than expected (Figure 3c). Snakes were not observed in open water; however, they did make use of this habitat to travel from one side of Lake Diefenbaker to the other.

Fourth order habitat selection

The top model explaining differences between used and available sites in the BMV and SSRV included percent grass cover, vegetation density, and distance to the nearest burrow (Tables 4 and 5). The probability of occupancy increased with decreasing grass cover, increasing vegetation density, and decreasing distance to the

TABLE 2. Top generalized linear model, null model, and all models with ΔAIC ≤ 2 evaluating the best predictor of maximum displacement from overwintering den sites by Saskatchewan Bullsnakes (*Pituophis catenifer sayi*). Fixed effects included river valley (BMV is reference valley), distance to nearest anthropogenic structure (dist. a), snout-to-vent length (svl), and snake sex (M = male). Number of model parameters (K), AICc, difference in AICc from top model (ΔAIC), Akaike weights, parameter estimates, SE, upper and lower 95% CI, and importance values are presented. Factors with largest effect in bold.

	Model	K	AICc	ΔAIC	Weights
AIC model selection	Intercept only	1	501.50	9.57	0.00
	valley + dist. a	2	491.92	0.00	0.37
	valley	1	492.95	1.03	0.22
	valley + dist. a + svl	3	494.07	2.15	0.13

Model averaging	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	Importance values
	(Intercept)	6.34	0.42	5.62	7.05	NA
	FRV	**1.21**	**0.34**	**0.64**	**1.78**	**0.99**
	SSRV	**0.88**	**0.27**	**0.43**	**1.34**	**0.99**
	dist. a	0.00	0.00	0.00	0.00	0.61
	svl	0.00	0.00	0.00	0.01	0.26
	sexM	0.00	0.09	−0.16	0.16	0.19

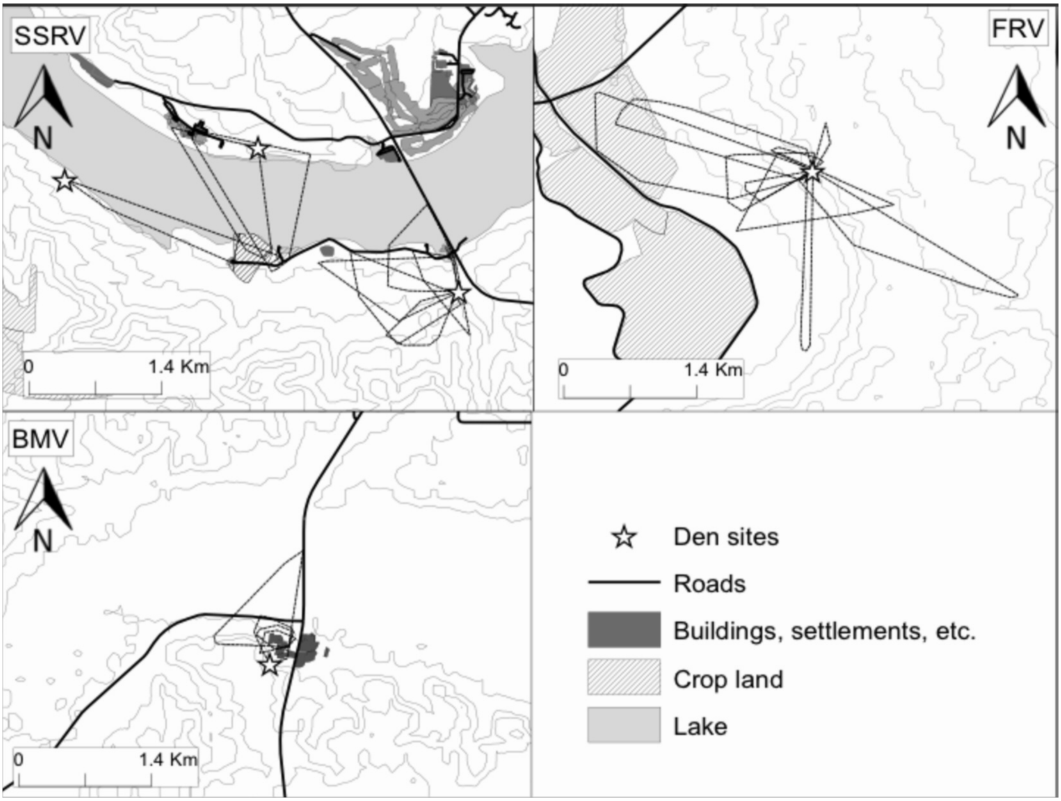

FIGURE 2. Minimum convex polygons (MCPs) for Bullsnakes (*Pituophis catenifer sayi*) in the Frenchman River (FRV), South Saskatchewan River (SSRV), and Big Muddy (BMV) Valleys. MCPs are shown for nine FRV, eight SSRV, and four BMV Bullsnakes to depict variation in home ranges observed. Den sites are indicated by stars, roads by thick black lines, human developed areas by dark grey polygons, crop fields by crosshatched polygons, lakes by light grey polygons, and contours lines by light grey lines.

TABLE 3. Top generalized linear model, null model, and all models with ΔAIC ≤ 2 evaluating the best predictor of Saskatchewan Bullsnake (*Pituophis catenifer sayi*) 95% kernel density home range estimate. Fixed effects included river valley (BMV is reference valley), distance to nearest anthropogenic structure (dist. a), snout-to-vent length (svl), and snake sex (M = male). Number of model parameters (K), AICc, difference in AICc from top model (ΔAIC), Akaike weights, parameter estimates, SE, upper and lower 95% CI, and importance values are presented. Factors with largest effect in bold.

	Model	K	AICc	ΔAIC		Weights
AIC model selection	Intercept only	1	266.50	7.24		0.01
	valley + svl	2	259.42	0.00		0.39
	valley	1	261.43	2.16		0.13
	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	Importance values
Model averaging	(Intercept)	4.00	1.18	2.03	5.97	NA
	FRV	**1.71**	**0.53**	**0.81**	**2.60**	**0.97**
	SSRV	**1.32**	**0.44**	**0.57**	**2.07**	**0.97**
	svl	−0.01	0.01	-0.03	0.01	0.63
	dist. a	0.00	0.00	0.00	0.00	0.28
	sexM	−0.09	0.24	−0.49	0.31	0.25

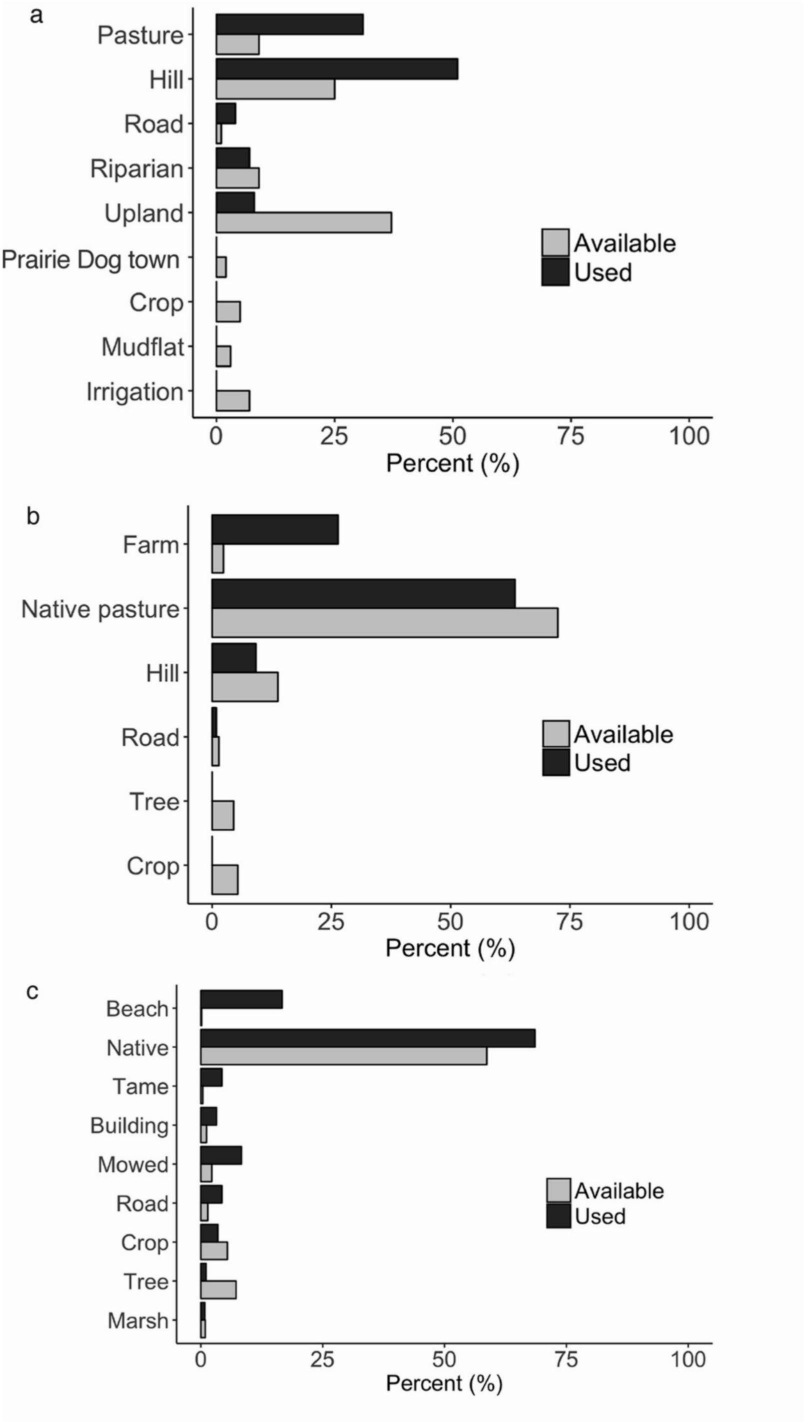

FIGURE 3. Third order habitat selection by Bullsnakes (*Pituophis catenifer sayi*) in three Saskatchewan river valleys. a. Percent of different habitats used and available within a 5 km buffer surrounding den sites in the Frenchman River Valley. b. Percent of different habitats used and available within a 1.3 km buffer surrounding den sites in the Big Muddy Valley. c. Percent of different habitat types used and available within a 2.4 km buffer surrounding den sites in the South Saskatchewan River Valley within Saskatchewan Landing Provincial Park.

TABLE 4. Top generalized linear mixed model, null model, and all models with ΔAIC ≤ 2 evaluating Bullsnake (*Pituophis catenifer sayi*) habitat selection in the Big Muddy Valley. Fixed effects included % grass cover, % shrub cover, % forb cover, distance to nearest burrow, distance to nearest shrub, maximum vegetation height, and Robel pole vegetation density. Random effect was individual snake ID (|ind|). Number of model parameters (K), AICc, difference in AICc from top model (ΔAIC), Akaike weights, parameter estimates, SE, upper and lower 95% CI, and importance values are presented. Factors with largest effect in bold.

	Model	K	AICc	ΔAIC	Weights
AIC model selection	Intercept + |ind|	2	373.88	108.72	0.00
	density + % grass + burrow + |ind|	4	265.17	0.00	0.24
	dist. shrub + density + % grass + burrow + |ind|	5	266.58	1.42	0.12
	max veg + density + % grass + burrow + |ind|	5	266.89	1.72	0.10
	% forb + density + % grass + burrow + |ind|	5	267.01	1.84	0.10
	% shrub + density + % grass + burrow + |ind|	5	267.25	2.09	0.08

Model averaging	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	Importance values
	(Intercept)	1.60	0.35	1.02	2.18	NA
	burrow	**−0.51**	**0.09**	**-0.66**	**−0.37**	**0.99**
	grass	**−0.02**	**0.01**	**-0.03**	**−0.01**	**0.99**
	density	**3.83**	**1.89**	**0.71**	**6.95**	**0.98**
	dist.shrub	0.01	0.01	−0.02	0.03	0.33
	max.veg	0.00	0.01	−0.01	0.02	0.30
	forb	0.00	0.01	−0.02	0.02	0.27
	shrub	0.00	0.01	−0.02	0.02	0.26

TABLE 5. Top generalized linear mixed model, null model, and all models with ΔAIC ≤ 2 evaluating Bullsnake (*Pituophis catenifer sayi*) habitat selection in the South Saskatchewan River Valley. Fixed effects included % grass cover, % shrub cover, % forb cover, distance to nearest burrow, distance to nearest shrub, maximum vegetation height, and Robel pole vegetation density. Random effect was individual snake ID (|ind|). Number of model parameters (K), AICc, difference in AICc from the top model (ΔAIC), Akaike weights, parameter estimates, SE, upper and lower 95% CI, and importance values are presented. Factors with largest effect in bold.

	Model	K	AICc	ΔAIC	Weights
AIC model selection	intercept + |ind|	2	539.07	123.86	0.00
	burrow + % forb + % grass + max veg + density + |ind|	6	415.24	0.00	0.11
	burrow + % grass + max veg + density + |ind|	5	415.31	0.07	0.11
	burrow + % forb + %grass + density + |ind|	5	415.44	0.20	0.10
	burrow + % grass + max veg + density + % shrub + |ind|	6	415.78	0.54	0.09
	burrow + % forb + % grass + max veg + density + % shrub + |ind|	7	416.23	0.99	0.07
	burrow + % forb + % grass + density + % shrub + |ind|	6	416.53	1.30	0.06
	burrow + % grass + density + |ind|	4	416.81	1.57	0.05
	burrow + dist. shrub + % grass + max veg + density + |ind|	6	417.16	1.92	0.04
	burrow + dist. shrub + % forb + % grass + max veg +density +|ind|	7	417.18	1.95	0.04

Model averaging	Parameter	Estimate	SE	Lower 95% CI	Upper 95% CI	Importance values
	(Intercept)	0.98	0.35	0.41	1.55	NA
	burrow	**−0.16**	**0.02**	**−0.19**	**-0.13**	**0.99**
	grass	**−0.01**	**0.01**	**−0.02**	**0.00**	**0.89**
	density	**0.81**	**0.29**	**0.33**	**1.29**	**0.98**
	max.veg	0.01	0.01	0.00	0.02	0.58
	forb	0.02	0.02	−0.02	0.05	0.56
	shrub	0.00	0.01	−0.01	0.01	0.38
	dist.shrub	0.00	0.01	−0.01	0.01	0.27

nearest burrow. The model-averaged 95% CI for distance to nearest burrow, percent grass cover, and vegetation density did not pass through zero for both river valleys and the importance values for these three variables were greater than 0.8 (Tables 4 and 5). Bullsnakes were most likely to be found within 1 m of a burrow or other refuge site (76% of the time in BMV, 73% of the time in SSRV).

Discussion

Bullsnake space use and movement patterns vary across their geographic range. Two populations in our study used more space than Bullsnakes in more southerly areas (Moriarty and Linck 1997; Fitch 1999; Rodriguez-Robles 2003; Kapfer *et al.* 2008; mean MCP: 34.43 ± 27 ha, mean 95% KDE: 71.81 ± 62 ha), while the third population used less or similar space compared to southern populations. As such, northern populations do not appear to consistently tend towards larger home ranges, as originally suggested (Martino *et al.* 2012; Gardiner *et al.* 2013). We also found individual variation in snake space use patterns within and among sites even over a small geographic scale, similar to what has been previously observed (Bauder *et al*. 2015; Gomez *et al.* 2015). Some snakes used very little space, similar to southern populations (Rodriguez-Robles 2003; Kapfer *et al.* 2008), while others required much larger home ranges (MCP up to 175 ha). Williams *et al.* (2012) found similar variation in space use among neighbouring populations of the closely related Great Basin Gophersnake. In the case of our study and Williams *et al.* (2012), variation in home range size was strongly associated with study site, and appears to be the result of corresponding variation in distance between overwintering and summer habitats/resources.

Multiple factors may be driving this variation in Bullsnake space use, including den/nest site connectivity and prey availability. Previously, prey was identified as a driver of snake space use, with smaller home ranges in areas of higher prey availability (Brown *et al.* 2005; Wisler *et al.* 2008; Baxley and Qualls 2009; Ettling *et al.* 2016). Though no formal surveys were conducted, we observed abundant prey in the den-adjacent farmyards occupied by Bullsnakes in the BMV. We also observed mating and gravid Bullsnakes in this area. This suggests that the smaller home ranges of Bullsnakes in the BMV may be due to a tighter spatial connection between seasonal resources (i.e., overwintering dens and prey/nest sites). Higher resource availability in a small area near den sites in the BMV also corresponds with our home range overlap data (Figure 2). Bullsnakes in the BMV had higher home range overlap, in addition to smaller home ranges, suggesting a sufficient availability of resources capable of supporting individuals in close proximity to dens. In contrast, summer and overwintering activity centres (in terms of the 95% KDE) were separate in the FRV and SSRV, resulting in seasonal migrations (as described in Gardiner *et al.* 2013). Home range overlap was also lower, with snakes using different areas during the active season. Snakes have been observed to migrate seasonally to locate prey in areas of low prey density (Duvall *et al.* 1990), similar to what we observed in the FRV and SSRV. Williams *et al.* (2012) also suggested that Great Basin Gophersnake movements differed among sites due to differences in food availability and predation pressures. In addition, Kapfer *et al.* (2010) suggested that Bullsnake space use may be driven by thermoregulatory and refuge needs. Regardless of driving factor, the placement of den sites in relation to active season resources appears to be a primary determinant of Bullsnake space use.

Bullsnakes are flexible in their broad scale habitat use. Here, we found various human-modified habitats to be selected for by snakes in the BMV and SSRV, in addition to habitats dominated by native vegetation that were the most frequently used, though not necessarily selected because they were typically used according to their availability (Figure 3b and c). Comparably, Bullsnakes in the FRV selected primarily for native habitats, in addition to roads (Figure 3a; Gardiner *et al.* 2013). Similarly, in Canada, Great Basin Gophersnakes use primarily native grassland habitat, in addition to slopes (Williams *et al.* 2014, 2015). Previous studies in southern range areas have also found Bullsnakes to use primarily native grassland habitats (Moriarty and Linck 1997; Rodriguez-Robles 2003; Kapfer *et al.* 2008). Slopes with native vegetation in particular appear to provide important overwintering habitat for Bullsnakes (Kapfer *et al.* 2008; Martino *et al.* 2012; Gardiner *et al.* 2013; our study). As such, native grassland habitat appears to be universally important for Bullsnakes across their range.

Retreat sites are an important habitat feature for Bullsnakes. Snakes in the BMV and SSRV selected for sites in close proximity to retreat sites, regardless of other habitat features or whether the refuge itself was natural (mammal burrow) or anthropogenic (under walkways, cement pads, stacked rocks). Bullsnakes in the FRV also demonstrated a dependence on retreat sites, as did Eastern Yellow-bellied Racers (*Coluber constrictor flaviventris*) and Prairie Rattlesnakes in the same areas (Martino *et al.* 2012; Gardiner *et al.* 2015). Suitable retreat sites are an important habitat feature for snakes, as they provide refuge from extreme temperatures and benefit thermoregulation (Huey *et al.* 1989; Webb and Shine 1998; Himes *et al*. 2006; Blouin-Demers and Weatherhead 2008; Croak *et al.* 2013). In our study, Bullsnakes remained near retreat sites (within 1 m), even when snakes were not located directly within the retreat site itself. This would be beneficial for thermoregulation, as it would allow snakes to move in and out of refuges, depending on their physiological and thermoregulatory needs (Blouin-Demers and Weatherhead 2001). Remaining close to retreat sites, particularly burrows, would also benefit Bullsnakes by allowing them to avoid predators and hunt rodent prey that occupy the burrows (Moriarty and Linck 1997; Rodriguez-Robles 2002; Heard *et al.* 2004; Himes *et al.* 2006). Of the retreat sites used by Bullsnakes, many were created via excavation by mammals. Large burrow networks may also be used as overwintering sites (Moriarty and Linck 1997; Williams *et al.* 2015). As a result, snake reliance on mammal-created refuge sites supports the importance of burrowing mammals, such as the Richardson's Ground Squirrel (*Urocitellus richardsonii*), Nuttall's Cottontail (*Sylvilagus nuttallii nuttallii*), and American Badger (*Taxidea taxus*), for Bullsnake survival.

Vegetation density and grass cover also appear to affect fine scale habitat selection by Bullsnakes. Decreased grass cover at selected sites in the BMV and SSRV is most likely a consequence of Bullsnake retreat site selection. The majority of retreat sites are typically grass free; bare ground surrounds excavated burrow entrances and anthropogenic retreat sites are constructed of cement and other materials, with little vegetation. Increased vegetation density on selected sites in our study likely reflects shrub cover, particularly the dense sagebrush common in our study areas. Snakes have previously been observed to select for sites within close proximity to shrubs as well as retreat sites (Harvey and Weatherhead 2006; Martino *et al.* 2012; Gardiner *et al.* 2015) and many of the excavated burrows used by Bullsnakes in the BMV and SSRV were located at the base of shrubs, suggesting their potential benefit. One such benefit may be thermoregulation; as sun penetrates the shrubs and warms the snake, the shrub itself provides additional cover from predators (Huey *et al.* 1989). Burrows located beneath shrubs may also receive structural support from roots, which may be important for snakes in areas of high cattle density, such as the BMV.

The introduction of human-modified habitats and anthropogenic features is potentially beneficial to snakes. For example, snakes in the SSRV were found under walkways, in parking lots under cement blocks, and under buildings. Snakes using these retreat sites occupied them over relatively long periods of time (weeks), potentially indicating that they were suitable for thermoregulation and for meeting other needs. Previous research has found that snakes use artificial structures on the landscape, such as buildings and wells, as overwintering den sites (Woodbury and Parker 1956; Costanzo 1986; Burger *et al.* 1988). Modified habitats may also yield increased prey densities, which in turn attract and benefit snakes (Corey and Doody 2010). However, use of these habitats may also be costly for snakes. The use of anthropogenic habitat features in areas of high human activity could potentially increase risk of mortality via snake-vehicle collisions or human persecution. The consumption of rodent prey (e.g., ground squirrels) in agricultural areas may also be detrimental, as snakes may be exposed to rodenticide poison through prey consumption (Bishop *et al.* 2016). When assessing how the introduction of modified habitats will affect snake populations, researchers should consider the potential threats to snakes making use of these introduced habitat features.

Conclusions

Bullsnake space requirements vary among populations as well as across their geographic range. Much of the time, data pertaining to space use by a species are based on one population or study site (Croak *et al.* 2013). Here, we highlight the importance of understanding the spatial ecology of different populations of the same species, as resource distribution may differ greatly among populations. These findings are also relevant to other snake species that demonstrate similar variability in space use (Jorgensen *et al.* 2008; Bauder *et al.* 2015; Gomez *et al.* 2015). As a result, conservation and management strategies developed for one population of a species or subspecies may not be applicable to others. Williams *et al.* (2012) found similar results, examining the effectiveness of wildlife habitat areas encompassing Great Basin Gophersnake den sites. Though the majority of gophersnakes were protected within these areas, certain individuals travelled outside of the allocated area (Williams *et al.* 2012). How to consider variance in habitat and space use among populations when developing conservation strategies remains to be addressed. A possible approach for implementing a more inclusive strategy would be to create protected buffers around den sites, based on the largest measured space use requirements for a species, to encompass both wide and narrow-ranging individuals and populations.

Bullsnakes are quite generalist in their habitat requirements, making use of a range of native and modified habitats as shown in the current and previous studies (Moriarty and Linck 1997; Rodriguez-Robles 2003; Kapfer *et al.* 2008; Martino *et al.* 2012; Gardiner *et al.* 2013). The spatial association among seasonal habitats appears to be an important determinant of Bullsnake space use. However, the specific active season resource requirements driving the seasonal migrations of Bullsnakes, or lack thereof, remain to be addressed. Measuring how active season resource availability varies among populations may be useful in uncovering the drivers of Bullsnake space and habitat use during the active season. At the local scale, retreat sites were a universally important habitat feature, regardless of refuge type (i.e., natural or anthropogenic). We recommend considering fossorial mammal populations when developing management strategies for Bullsnakes, as they are important for providing food and refuges. We also recommend considering the consequences of Bullsnakes potentially making use of anthropogenic habitat features and refuge sites. Overall, habitat features at the fine spatial scale appear to be an important determinant of Bullsnake habitat use, compared to habitat features at the landscape scale.

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Literature Cited

Aebischer, N.J., P.A. Robertson, and R.E. Kenward. 1993. Compositional analysis of habitat use from animal radio-tracking data. Ecology 74: 1313–1325. https://doi.org/10.2307/1940062

Anguiano, M.O., and J.E. Diffendorfer. 2015. Effects of fragmentation on the spatial ecology of the California kingsnake (*Lampropeltis californiae*). Journal of Herpetology 49: 420–427. https://doi.org/10.1670/13-014

Bates, D., M. Maechler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67: 1–48.

Bauder, J.M., H. Akenson, and C.R. Peterson. 2015. Movement patterns of prairie rattlesnakes (*Crotalus v. viridis*) across a mountainous landscape in a designated wilderness area. Journal of Herpetology 49: 377–387. https://doi.org/10.1670/13-153

Baxley, D.L., and C.P. Qualls. 2009. Black pine snake (*Pituophis melanoleucus lodingi*): spatial ecology and associations between habitat use and prey dynamics. Journal of Herpetology 43: 284–293. https://doi.org/10.1670/08-074R1.1

Beale, M., S. Poulin, C. Ivanyi, and G. Blouin-Demers. 2016. Anthropogenic disturbance affects movement and increases concealment in western diamondback rattlesnakes (*Crotalus atrox*). Journal of Herpetology 50: 216–221. https://doi.org/10.1670/14-112

Beyer, H.L. 2015. Geospatial Modelling Environment (Version 0.7.4.0). Accessed 2 October 2016. http://www.spatialecology.com/gme.

Bishop, C.A., K.E. Williams, D.A. Kirk, P. Nantel, E. Reed, and J.E. Elliott. 2016. A population model of the impact of rodenticide containing strychnine on great basin gophersnakes (*Pituophis catenifer deserticola*). Ecotoxicology 25: 1390–1405. https://doi.org/10.1007/s10646-016-1690-2

Blouin-Demers, G., and P.J. Weatherhead. 2001. An experimental test of the link between foraging, habitat selection, and thermoregulation in black rat snakes *Elaphe obsoleta obsoleta*. Journal of Animal Ecology 70: 1006–1013. https://doi.org/10.1046/j.0021-8790.2001.00554.x

Blouin-Demers, G., and P.J. Weatherhead. 2008. Habitat use is linked to components of fitness through the temperature-dependence of performance in ratsnakes (*Elaphe obsoleta*). Israel Journal of Ecology and Evolution 54: 361–372. https://doi.org/10.1560/IJEE.54.3-4.361

Brown, G.P., R. Shine, and T. Madsen. 2005. Spatial ecology of slatey-grey snakes (*Stegonotus cucullatus*, Colubridae) on a tropical Australian floodplain. Journal of Tropical Ecology 21: 605–612. https://doi.org/10.1017/S0266467405002671

Burger, J. 2001. The behavioral response of basking northern water (*Nerodia sipedon*) and eastern garter (*Thamnophis sirtalis*) snakes to pedestrians in a New Jersey park. Urban Ecosystems 5: 199–129. https://doi.org/10.1023/A:1022339704784

Burger, J., and R.T. Zappalorti. 1992. Philopatry and nesting phenology of pine snakes *Pituophis melanoleucus* in the New Jersey pine barrens. Behavioral Ecology and Sociobiology 30: 331–336. https://doi.org/10.1007/BF00170599

Burger, J., R.T. Zappalorti, M. Gochfeld, W.I. Boarman, M. Caffrey, V. Doig, S.D. Garber, B. Lauro, M. Mikovsky, C. Safina, and J. Saliva. 1988. Hibernacula and summer den sites of pine snakes (*Pituophis melanoleucus*) in the New Jersey pine barrens. Journal of Herpetology 22: 425–433. https://doi.org/10.2307/1564337

Burnham, K.P., D.R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. Behavioral Ecology and Sociobiology 65: 23–25. https://doi.org/10.1007/s00265-010-1029-6

Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling 197: 516–519. https://doi.org/10.1016/j.ecolmodel.2006.03.017

Carfagno, G.L.F., and P.J. Weatherhead. 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. Canadian Journal of Zoology 84: 1440–1452. https://doi.org/10.1139/z06-124

Charland, M.B., and P.T. Gregory. 1995. Movements and habitat use in gravid and nongravid female garter snakes (Colubridae: *Thamnophis*). Journal of Zoology 236: 543–561. https://doi.org/10.1111/j.1469-7998.1995.tb02731.x

Corey, B., and J.S. Doody. 2010. Anthropogenic influences on the spatial ecology of a semi-arid python. Journal of Zoology 281: 293–302. https://doi.org/10.1111/j.1469-7998.2010.00705.x

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2017. COSEWIC assessment and status report on the Bullsnake *Pituophis catenifer sayi* in Canada. COSEWIC. Ottawa, Canada. Accessed 6 December 2017. http://www.sararegistry.gc.ca/document/default_e.cfm?documentID=3280.

Costanzo, J.P. 1986. Influences of hibernaculum microenvironment on the winter life history of the garter snake (*Thamnophis sirtalis*). Ohio Journal of Science 86: 199–204.

Croak, B.M., M.S. Crowther, J.K. Webb, and R. Shine. 2013. Movements and habitat use of an endangered snake, *Hoplocephalus bungaroides* (Elapidae): implications for conservation. PLoS ONE 8(4): e61711. https://doi.org/10.1371/journal.pone.0061711

Cross, M.D., K.V. Root, C.J. Mehne, J. McGowan-Stinski, and D. Pearsall. 2015. Multi-scale response of eastern massasauga rattlesnakes (*Sistrurus catenatus*) to prescribed fire. American Midland Naturalist 173: 346–362. https://doi.org/10.1674/amid-173-02-346-362.1

Driscoll, D.A. 2004. Extinction and outbreaks accompany fragmentation of a reptile community. Ecological Applications 14: 220–240. https://doi.org/10.1890/02-5248

Duvall, D., M.J. Goode, W.K. Hayes, J.K. Leonhardt, and D.G. Brown. 1990. Prairie rattlesnake vernal migration: field experimental analyses and survival value. Natural Geographic Research 6: 457–469.

Ernst, C.H., and E.M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Books, Washington, DC, USA.

ESRI (Environmental Systems Research Institute). 2015. ArcGIS Desktop. Redlands, California, USA.

Ettling, J.A., L.A. Aghasyan, A.L. Aghaysan, and P.G. Parker. 2016. Spatial ecology of Armenian vipers, *Montivipera raddei*, in two different landscapes: human-modified and recovered-natural. Russian Journal of Herpetology 23: 93–102.

Fitch, H.S. 1999. A Kansas Snake Community: Composition and Changes over 50 Years. Krieger Publishing Co., Malabar, Florida, USA.

Gardiner, L.E., C.M. Somers, J.A. Martino, D.L. Parker, and R.G. Poulin. 2013. Balancing the dumbbell: summer habitats need protection in addition to winter dens for northern snake communities. Journal of Wildlife Management 77: 975–982. https://doi.org/10.1002/jwmg.555

Gardiner, L.E., C.M. Somers, D.L. Parker, and R.G. Poulin. 2015. Microhabitat selection by prairie rattlesnakes (*Crotalus viridis*) at the northern extreme of their geographic range. Journal of Herpetology 49: 131–137. https://doi.org/10.1670/12-266

Gomez, L., K.W. Larsen, and P.T. Gregory. 2015. Contrasting patterns of migration and habitat use in neighboring rattlesnake populations. Journal of Herpetology 49: 371–376. https://doi.org/10.1670/13-138

Harvey, D.S., and P.J. Weatherhead. 2006. A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*). Biological Conservation 130: 206–216. https://doi.org/10.1016/j.biocon.2005.12.015

Heard, G.W., D. Black, and P. Robertson. 2004. Habitat use by the inland carpet python (*Morelia spilota metcalfei*: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. Austral Ecology 29: 446–460. https://doi.org/10.1111/j.1442-9993.2004.01383.x

Himes, J.G., L.M. Hardy, D.C. Rudolph, and S.J. Burgdorf. 2006. Movement patterns and habitat selection by native and repatriated Louisiana pine snakes (*Pituophis ruthveni*): implications for conservation. Herpetological Natural History 9: 103–116.

Huey, R.B., C.R. Peterson, S.J. Arnold, and W.P. Porter. 1989. Hot rocks and not-so-hot rocks: retreat-site selection by garter snakes and its thermal consequences. Ecology 70: 931–944. https://doi.org/10.2307/1941360

Johnson, D.H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61: 65–71. https://doi.org/10.2307/1937156

Jorgensen, D., C.C. Gates, and D.P. Whiteside. 2008. Movements, migrations, and mechanisms: a review of radiotelemetry studies of prairie (*Crotalus v. viridis*) and western (*Crotalus oreganus*) rattlesnakes. Pages 303–316 *in* The Biology of Rattlesnakes. *Edited by* W.K. Hayes, K.R. Beaman, M.D. Cardwell, and S.P. Bush. Loma Linda University Press, Loma Linda, California, USA.

Kapfer, J.M., J.R. Coggins, and R. Hay. 2008. Spatial ecology and habitat selection of bullsnakes (*Pituophis catenifer sayi*) at the northern periphery of their geographic range. Copeia 2008: 815–826. https://doi.org/10.1643/CE-07-104

Kapfer, J.M., C.W. Pekar, D.M. Reineke, J.R. Coggins, and R. Hay. 2010. Modeling the relationship between habitat preferences and home-range size: a case study on a large mobile Colubrid snake from North America. Journal of Zoology 282: 13–20. https://doi.org/10.1111/j.1469-7998.2010.00706.x

Kjoss, V.A., and J.A. Litvaitis. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation 98: 285–292. https://doi.org/10.1016/S0006-3207(00)00167-1

Knoot, T.G., and L.B. Best. 2011. A multiscale approach to understanding snake use of conservation buffer strips in an agricultural landscape. Herpetological Conservation and Biology 6: 191–201.

Lentini, A.M., G.J. Crawshaw, L.E. Licht, and D.J. McLelland. 2011. Pathologic and hematologic responses to surgically implanted transmitters in eastern massasauga rattlesnakes (*Sistrurus catenatus catenatus*). Journal of Wildlife Disease 47: 107–125. https://doi.org/10.7589/0090-3558-47.1.107

Martino, J.A., R.G. Poulin, D.L. Parker, and C.M. Somers. 2012. Habitat selection by grassland snakes at northern range limits: implications for conservation. Journal of Wildlife Management 76: 756–767. https://doi.org/10.1002/jwmg.313

Moore, J.A., and J.C. Gillingham. 2006. Spatial ecology and multi-scale habitat selection by a threatened rattlesnake: the eastern massasauga (*Sistrurus catenatus catenatus*). Copeia 2006: 742–751. https://doi.org/10.1643/0045-8511(2006)6[742:SEAMHS]2.0.CO;2

Moriarty, J.J., and M. Linck. 1997. Reintroduction of bullsnakes into a recreated prairie. Pages 43–54 *in* Minnesota's Amphibians and Reptiles: Their Conservation and Status. *Edited by* J.J. Moriarty and D. Jones. Serpent's Tale Natural History Book Distributors, Lanesboro, Minnesota, USA.

Parker, J.M., and S.H. Anderson. 2007. Ecology and behavior of the midget faded rattlesnake (*Crotalus oreganus concolor*) in Wyoming. Journal of Herpetology 41: 41–51. https://doi.org/10.1670/0022-1511(2007)41[41:EABOTM]2.0.CO;2

R Core Team. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Robel, R.J., J.N. Briggs, A.D. Dayton, and L.C. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. Journal of Rangeland Management 23: 295–297. https://doi.org/10.2307/3896225

Rodriguez-Robles, J.A. 2003. Home ranges of gopher snakes (*Pituophis catenifer*, Colubridae) in central California. Copeia 2003: 391–396. https://doi.org/10.1643/0045-8511(2003)003[0391:HROGSP]2.0.CO;2

Row, J.R., and G. Blouin-Demers. 2006. Kernels are not accurate estimators of home-range size for herpetofauna. Copeia 2006: 797–802. https://doi.org/10.1643/0045-8511(2006)6[797:KANAEO]2.0.CO;2

Schaefer, W.H. 1934. Diagnosis of sex in snakes. Copeia 1934: 181. https://doi.org/10.2307/1435852

Smith, R.M., J.R. Spotila, and W.F. Bien. 2015. Spatial ecology of northern pinesnakes (*Pituophis m. melanoleucus*) in disturbed and undisturbed habitats in the New Jersey pine barrens. Herpetologica 71: 19–25. https://doi.org/10.1655/HERPETOLOGICA-D-13-00028

Somers, C.M., C.F. Graham, J.A. Martino, T.R. Frasier, S.L. Lance, L.E. Gardiner, and R.G. Poulin. 2017. Conservation genetics of the eastern yellow-bellied racer (*Coluber constrictor flaviventris*) and bullsnake (*Pituophis catenifer sayi*): river valleys are critical features for snakes at northern range limits. PLoS ONE 12(11): e0187322. https://doi.org/10.1371/journal.pone.0187322

Thomas, D.L., and E.J. Taylor. 2006. Study designs and tests for comparing resource use and availability II. Journal of Wildlife Management 70: 324–336. https://doi.org/10.2193/0022-541X(2006)70[324:SDATFC]2.0.CO;2

Webb, J.K., and R. Shine. 1998. Using thermal ecology to predict retreat-site selection by an endangered snake species. Biological Conservation 86: 233–242. https://doi.org/10.1016/S0006-3207(97)00180-8

Williams, K.E., K.E. Hodges, and C.A. Bishop. 2012. Small reserves around hibernation sites may not adequately protect mobile snakes: the example of great basin gophersnakes (*Pituophis catenifer deserticola*) in British Columbia. Canadian Journal of Zoology 90: 304–312. https://doi.org/10.1139/Z11-136

Williams, K.E., K.E. Hodges, and C.A. Bishop. 2014. Phenology and demography of great basin gophersnakes (*Pituophis catenifer deserticola*) at the northern edge of their range. Herpetological Conservation and Biology 9: 246–256.

Williams, K.E., K.E. Hodges, and C.A. Bishop. 2015. Hibernation and oviposition sites of great basin gophersnakes (*Pituophis catenifer deserticola*) near their northern range limit. Journal of Herpetology 49: 207–216. https://doi.org/10.1670/13-162

Wisler, C., U. Hofer, and R. Arlettaz. 2008. Snakes and monocultures: habitat selection and movements of female grass snakes (*Natrix natrix l.*) in an agricultural landscape. Journal of Herpetology 42: 337–346. https://doi.org/10.1670/07-027.1

Woodbury, A.M., and D.D. Parker. 1956. A snake den in cedar mountains and notes on snakes and parasitic mites. Herpetologica 12: 261–268.

Wright, J.D. 2008. Bullsnake, *Pituophis catenifer sayi*, nesting biology in Alberta. Canadian Field-Naturalist 122: 138–141. https://doi.org/10.22621/cfn.v122i2.572

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SUPPLEMENTARY MATERIAL:

TABLE S1. Top generalized linear model, null model, and all models with ΔAIC ≤ 3 evaluating the best predictor of Saskatchewan Bullsnake (*Pituophis catenifer sayi*) 50% kernel density core area size.

TABLE S2. Top generalized linear model, null model, and all models with ΔAIC ≤ 2 evaluating the best predictor of Saskatchewan Bullsnake (*Pituophis catenifer sayi*) minimum convex polygon home range size.

Incidentally gathered natural history information on Bullsnakes (*Pituophis catenifer sayi*) in southeastern Alberta

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Abstract

We present observations on Bullsnakes (*Pituophis catenifer sayi*) gathered during a study of Prairie Rattlesnakes (*Crotalus viridis*) in a multiple-use, mixed grass landscape adjacent to the South Saskatchewan River, ~30 km northeast of Medicine Hat, Alberta, in May–October 1997. Hibernacula shared with rattlesnakes were located close to the river. We captured 31 Bullsnakes, either in a drift fence array around a hibernaculum or by hand; three were recaptured once. Emergence from the hibernaculum ended in mid-May, and return to it began in early September. A gap in capture events occurred between early July and late August, possibly attributable to fossorial activity during the height of the summer. The sex ratio of captured adult snakes was 0.64 in favour of males. Males attained the greatest maximum body sizes, but there was no significant size dimorphism by sex. Bullsnakes were assignable to juvenile, subadult, and adult classes by body size. Most captures were made on slopes in the immediate vicinity of the river, in areas classed as "thin breaks", but four captures, about 7 km east of the river, provide evidence of long-distance movements from hibernacula. Captures were seldom made in the vicinity of anthropogenic features. Gas field development has increased greatly in the years since these data were collected. Our findings provide a baseline for Bullsnake population responses to such changes.

Key words: Bullsnake; *Pituophis catenifer sayi*; habitat; size distribution; hibernacula; landscape use; human interactions; Alberta

Introduction

Gophersnake (*Pituophis catenifer*) is a large oviparous constrictor occupying a variety of habitats across much of western North America (Ernst and Ernst 2003). Populations are divided geographically among several subspecies (Ernst and Ernst 2003). In Alberta, populations of Bullsnakes (*P. c. sayi*) are found scattered throughout the dry mixed grass and mixed grass subregions of the Grassland Natural Region, clustering around the vicinities of badlands terrain and major and minor river valleys (Russell and Bauer 2000; Kissner and Nicholson 2003; COSEWIC 2017). Summaries of what is known of Bullsnake ecology in Alberta are provided by Kissner and Nicholson (2003), Wright (2008), and COSEWIC (2017). Fortney *et al*. (2012), Martino *et al*. (2012), Gardiner *et al*. (2013), and Somers *et al*. (2017) have examined various aspects of Bullsnake habitat use and movement in southeastern Saskatchewan.

Bullsnake is currently considered to be a species of special concern (COSEWIC 2017). There is evidence of recent range contraction in Alberta (Russell and Bauer 2000; Kissner and Nicholson 2003) and reason for concern over the continuing impact of human activities. Oil and gas field development in the habitat of Bullsnakes, with concomitant mortality from increased road traffic, is seen as the principal threat (Didiuk 2003; Kissner and Nicholson 2003; Alberta Wild Species General Status Listing 2015; COSEWIC 2017). In Alberta, Bullsnake has held "sensitive" status since 2006 (Alberta Wild Species General Status Listing 2015).

In this contribution, we report observations (size and sex distributions, activity over the season, thermal biology, habitat use, and distribution across the landscape) of the Bullsnake population collected incidentally in 1997, during a study of Prairie Rattlesnake (*Crotalus viridis*) in southeastern Alberta (Powell *et al*. 1998). We include additional data and analyses as Supplemental Materials: patterns in morphology (sections S1 and S2), capture situation (section S3), environmental temperatures (section S4), and the characteristics of various sites and the number of Bullsnakes caught in those sites (section S5). These additional data go beyond the main goal of this manuscript, but may be useful to others studying Bullsnakes.

Study Area

The study area was about 30 km northeast of Medicine Hat, Alberta, in a region of rolling mixed range and cropland, bounded on the west by the South Saskatchewan River (Figure 1); latitude and longitude for the centre of the mapped area: 50.21°N, 110.56°W. This area has large coulees running to the east and northeast from the river channel, where the South Sas-

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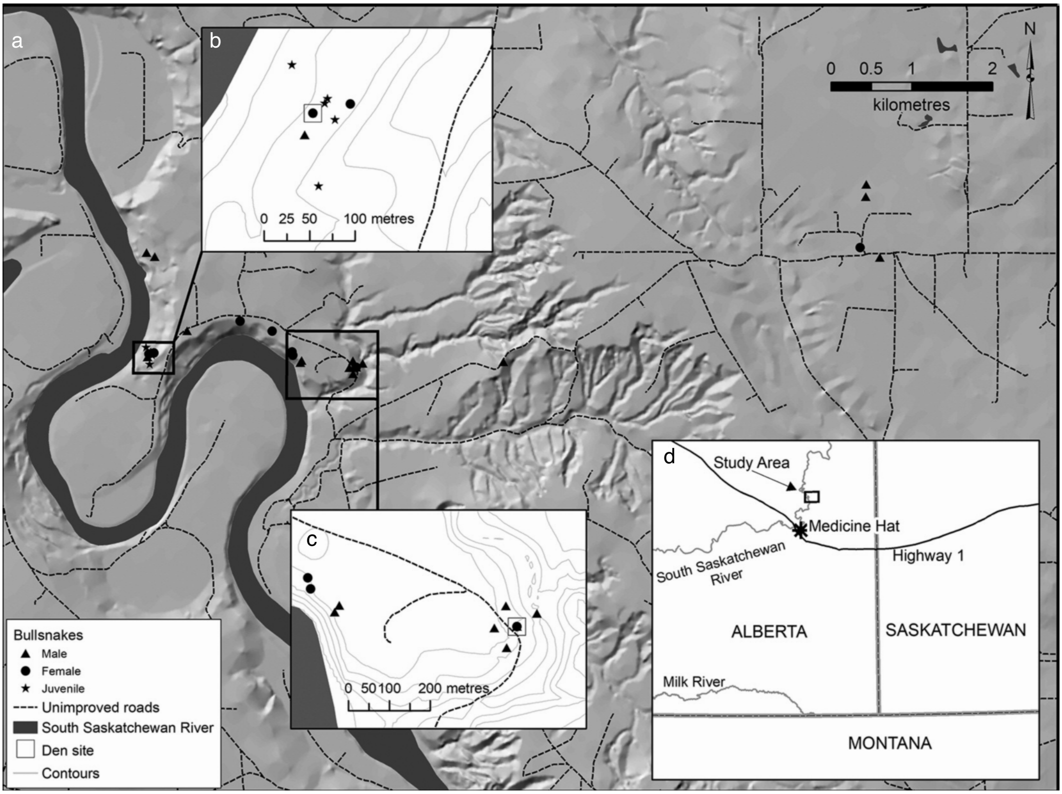

FIGURE 1. a. Relief map of study area and distribution of the 31 Bullsnakes (*Pituophis catenifer sayi*) captured during this study. Some points represent multiple captures. One capture several kilometres to the south is not included. b–c. Framed areas on main map at higher scale. d. Location of the study area.

katchewan River meanders between large alluvial flats and high steep eroding bluffs with abundant slump blocks. The river bank has a mean elevation of 630 m above sea level; elevation to the east reaches 770 m.

The rattlesnake radiotelemetry study covered the territory extending ~15 km to the east of the river, where radio-implanted rattlesnakes were collected and monitored. Tracking the movements of rattlesnakes also took us ~5 km to the south of the fenced hibernacula, which were the geographic central focuses of the study (Figure 1). Most of this area is rangeland, dotted with gas wells and laced by their access roads and pipelines, with limited areas of cultivation immediately to the east of the fenced hibernacula and at the eastern extremity of monitored rattlesnake movement. Although the study area was not pristine at the time of our study, much of it was unmodified and covered with native vegetation.

Within this general area, Bullsnake captures were restricted to a smaller zone at the west end, bounded to the west by the South Saskatchewan River (Figure 1). The general land cover type within this area is mixed grassland, with small patches of agricultural land predominantly to the northeast (Alberta Biodiversity Monitoring Institute 2010).

Methods

Hibernaculum study

Fieldwork was initiated in September 1996. Two hibernacula were identified in the study area. Drift fences and funnel traps were installed in early May 1997 around one of these, which consisted of a series of old Coyote (*Canis latrans*) dens on the upper slopes of a coulee extending east from the river (Figure 1c). All snakes (including Prairie Rattlesnakes and Wandering Garter Snakes [*Thamnophis elegans vagrans*]) that emerged after the fences and traps were set up were captured, processed (see below), and released outside the fences. In the spring and fall of 1997, the immediate area of this hibernaculum (henceforth referred to as the fenced dens) was regularly searched for denning activity and snakes of all species, to a distance of ~1 km north along the east bank of the South Saskatchewan River. All snakes captured in this area (and elsewhere, throughout the study) were processed, and the universal transverse mercator (UTM) locations of the capture points were recorded using a handheld global positioning system receiver: GPS 12 XL (Garmin Ltd., Olathe, Kansas, USA). The traps were reversed in early September 1997, and all captured snakes were released inside the fences. The fences and traps were removed on 14 October 1997, terminating the 1997 field season.

Snake capture, measurements, and marking

Bullsnakes were captured incidentally while we searched for rattlesnake dens, surveyed our fence and traps, searched for free-roaming rattlesnakes, and radio-tracked eight rattlesnakes. A large amount of terrain was covered on foot, and activities were carried out daily over the entire study period. We captured, or attempted to capture, all Bullsnakes encountered.

All captured snakes were weighed to the nearest gram with a Light Line spring balance (Model No. 10010 – 50 g; and Model No. 42500 – 2500 g; PESOLA Präzisionswaagen AG, Schindellegi, Switzerland). Snout-to-vent length (SVL) and tail length were measured by stretching out the snake against a tape measure laid on the ground. Sex was determined by cloacal probing, although not always with certainty for very young snakes (which were categorized as juveniles and not included in sex-ratio calculations). All snakes of sufficient size (≥40 cm SVL) were individually marked with Passive Integrated Transponder (PIT) tags (Anitech TX 1412L, Anitech Enterprises, Inc., Markham, Ontario, Canada), injected dorsally on the left side of the vertebral column ~4 cm ahead of the tail base. Smaller snakes were marked using individual subcaudal scute clip patterns. Recaptures at intervals of more than three weeks were remeasured, as described above. Recaptures of shorter duration were subjected only to PIT tag reading and the collecting of associated environmental data.

At the time of all hand captures, we recorded the temperature (shaded) of the ground, as near as possible to the spot where the snake was resting, UTM coordinates, brief descriptions of weather conditions (including the temperature of the air at 1 m), and the capture situation (activities, if any, and posture) of the snake.

To determine whether adult and juvenile Bullsnakes select different environmental temperatures, we compared mean ground temperatures and mean air temperatures at 1 m for male, female, and juvenile hand captures by means of analysis of variance (ANOVA). To test for possible relations between insolation and surface activity, we cross-tabulated our insolation categories (overcast, sunny, or mixed sun and cloud) and snake capture situation and performed a χ^2 test for random association on the resultant table. All statistical tests were carried out using PAST (Hammer *et al.* 2001). Results of these analyses are provided in Supplemental Material sections S3 and S5.

Mapping

Our GPS data for each hand capture allowed us to examine the distribution of Bullsnakes across the landscape relative to biotic and abiotic characteristics. We used ArcGIS software (version 10.5; Esri, Redlands, California, USA) for visualization and spatial analysis. A shapefile layer of the Bullsnake captures was created from the recorded GPS coordinates, which were in a UTM zone 12N projection. This layer was overlain on various thematic layers (in shapefile, geodatabase, and Esri grid formats) to determine the following characteristics of the Bullsnake capture locations: topography, generalized land cover, vegetation, and human impact.

Topography was represented by hill shading generated from a digital 10-m resolution elevation model (AltaLIS 2010). Generalized land cover classifications were determined using the Alberta Biodiversity Monitoring Institute's (ABMI 2010) Land Cover Inventory dataset. Site types (landforms/landscape categorization) were determined from the grassland vegetation inventory (Alberta Sustainable Resource Development 2010a,b) and native vegetation from the native prairie vegetation inventory (Alberta Sustainable Resource Development 2004). Human impact factors came from the following sources: agricultural uses from ABMI's (2014) Wall-to-Wall Human Footprint Inventory; roads from the 2016 AltaLIS roads layer; and pipelines and wells from the Alberta Energy Regulator (2017a,b). We superimposed our 1997 Bullsnake distribution data onto two maps (1997 and 2017) depicting gas wells and gas line emplacements, to examine the relationship of Bullsnake habitat use to such features and demonstrate changes in human use of the landscape over this period.

Results

Capture numbers and seasonal distribution

Over the study period, we captured 31 Bullsnakes. Three were recaptured once, and the capture–recapture interval for two was sufficient to require re-measurement. One Bullsnake was recovered from a trap at the fenced dens in the spring (13 May) and six in the fall (6 September to 10 October). Four Bullsnakes were hand captured in the vicinity of dens in the spring and early summer and 10 in the fall (1 September to 3 October). The remaining 10 were encountered while searching for rattlesnakes across the study area. Our adult Bullsnake sample consisted of 16 males and nine females (Table S1), and thus exhibited a proportion of males (males/[males + females]) of 0.64.

Our first capture occurred on 11 May (several Bullsnakes were encountered in the area of the river before this, but were not captured) and our last on 10 October (Figures S1, S2). A gap is evident between 12 June and 19 August (days 163–231) in which only one capture was made, although one dead adult Bullsnake was found on a gas field access road on 2 August.

Hibernacula

Two hibernacula were identified in the study area. The first, the fenced dens, is described above (Figure 1b). The second was located high in an area of slumped terrain immediately above the South Saskatchewan River, facing northeast (Figure 1c). Although other concentrations of Bullsnake captures in similar situations along the course of the river may represent additional overwintering sites, we cannot confidently state that snakes congregating at them were associating with hibernacula.

Taking the presence of snakes in funnel traps to indicate timing of hibernacula use, egress ended on 13 May and ingress began on 6 September, continuing until 10 October.

Lengths and masses of the snakes

We divided all captured snakes into males, females, and juveniles, i.e., young-of-the-year, sex undetermined (Table S1). The distributions of male and female SVLs overlapped broadly and were discontinuous for both sexes (Figure S3). Males fell into two SVL classes: a small number ranging between 59 and 74 cm and the remainder between 104 and 134 cm. A small number of females were distributed over the 40–60 cm and the 80–90 cm intervals, but most lay within the 110–130 cm interval. Hatchlings were mostly within the 30–40 cm interval of the SVL distribution, although one exceeded 50 cm. The SVL distributions of both males and females overlapped that of hatchlings at their lower ends.

The distributions of male and female masses likewise overlapped broadly (Figure S4). Male masses fell into three groups: 50–150 g, 250–450 g, and 500–750 g. The groups into which female masses fell were more tightly defined: 48–200 g, 400–450 g, and 600–650 g. Juveniles comprised a single mass class, <50 g, which overlapped the lower end of the female mass distribution.

These SVL and mass distributions suggest that Bullsnakes at this location fall into clearly defined size categories. Given the small sample size, further division of snake size distributions is unwarranted.

Growth data are available for only two individuals that were captured twice (Table S2), both adult males that fell into the adult male SVL division at first capture. The smaller snake's increase in mass moved it from the subadult mass class to the adult mass class over the capture-recapture period.

Movement

Movement data are available for the two males that were recaptured. The larger of these was captured on 9 June, and recaptured on 2 July (Table S2), moving 96 m nearly due north over this 22-day period. Both capture and recapture were on flat uplands, among the furthest of our captures from the river. The smaller one was captured on 13 May and recaptured on 20 September, moving 375.5 m in a southwest direction over this 130-day interval, from grassland immediately adjacent to a promontory delimited by the river to a slump on the northwest-facing side of this promontory

Capture situation and insolation

The greatest numbers of hand captures, in the widest range of situations, were made on sunny days or days with mixed sun and cloud. These data are tabulated and the results of a χ^2 analysis for association are given in Table S3.

Environmental temperatures

The distributions of the air and ground temperatures experienced by males, females, and juveniles overlapped broadly (Figure S5).

Distribution over landscape

The great majority of Bullsnakes were captured in the immediate vicinity of the South Saskatchewan River, on the bluffs overlooking the channel (Figure 1). One of the two dens identified was near the top of a steep slope forming the upper reaches of the river channel; the other (the fenced dens) lay on the upper reaches of a seasonal channel in close proximity to the river. Only six Bullsnakes were captured at any distance from the South Saskatchewan River, two of which were associated with coulees formed by temporary watercourses draining into the South Saskatchewan. Four were located on relatively flat uplands ~7 km from the South Saskatchewan; the distance was calculated from the easternmost meander of the river, as we could not be certain of the den in which these snakes overwintered. Juveniles were restricted to the immediate vicinity of the river. Bullsnakes captured at the greatest distance from the river (three males, one female) were all in the adult SVL class.

The area immediately adjacent to the South Saskatchewan River, where most captures were made and both dens were located (Figure 1), is divided between "thin breaks", "limy", and "overflow" site types (Alberta Sustainable Resource Development 2010a,b), covering the steeper slopes of the river channel. Adjacent inland terrain is classified as sand—likely Aeolian or glaciofluvial in this area (Alberta Sustainable Resource Development 2010a,b). Descriptions of these pertinent site types (Alberta Sustainable Resource Development 2010a,b) and numbers of Bullsnake captures made in each are provided in Table S4. Bullsnakes captured at upland locations were found on margins of tame pasture (two captures), and crop site types (two captures).

Shrub coverage over the study area ranged between the 0–2% and 31–60% class intervals (Alberta Sustainable Resource Development 2004). All Bullsnake captures were made in areas of 0–10% shrub coverage, the majority being within the 3–6% category.

Nesting

We found one Bullsnake nest (1 September) in our study area, located low on the slope of an area of choppy sandhills site type (duned surface of loamy sand and sand soils, with thin vegetation cover; Alberta Sustainable Resource Development 2010a,b), ~2.2 km north by northeast of the northernmost Bullsnake hand capture. The nest had evidently been excavated by a predator of undetermined identity. Some of the eggs had been consumed, leaving only the shells, but, as a single hatchling shed skin was found next to the nest, others had evidently hatched.

Interactions with human landscape modifications

Bullsnakes were generally not associated with human-built structures. Although an unimproved road and a gas pipeline ran along the top of slopes defining the river channel in the area with the greatest density of captures (Figures 1, 2a), snake captures here were almost entirely confined to the slopes themselves. The four captures made away from the river were associated with unimproved roads or areas of modified prairie and were the only ones made in the vicinity of agricultural artifacts. Our two mapped hibernacula were closely associated with buried gas lines, but no Bullsnakes were captured in the vicinity of gas wells (Figure 2a). One Bullsnake was found run over, evidently by a gas field maintenance vehicle, on a gas field access road (not mapped), on 2 August. Two of our hand captures were made on unimproved roads (Table S3).

A marked increase in the density of gas wells and gas lines in the study area has occurred between 1997 and 2017 (Figure 2). The majority of Bullsnake captures in 1997 occurred in areas still untouched in 2017 by gas field development, but much of the terrain east of the South Saskatchewan River has been dissected by such development in the intervening 20 years.

Discussion

The bias in favour of male snakes in our capture sample is similar to that reported elsewhere. For example, the proportion of male adult and juvenile Bullsnakes captured in drift fences during one active season in the adjacent Canadian Forces Base (CFB) Suffield and Suffield National Wildlife Area (Table S2 in Didiuk 2003) was 0.57, which does not differ significantly from our data ($\chi^2_1 = 0.97$, $P = 0.32$). A male bias in Bullsnake captures, and at hatching, has been noted in Nebraska (Gutzke *et al.* 1985; but see Kapfer *et al.* 2008a, for Wisconsin), indicating that the skewed sex ratio in our sample was not a result of intersexual differences in mortality or catchability (Gutzke *et al.* 1985). Also, the lack of significant sexual size dimorphism in our sample (Table S1) has been noted in other parts of the range of this species (Diller and Wallace 1996; Kapfer 2009), although the largest individuals in many populations are males (Kapfer 2009).

The mass and SVL of our juvenile, subadult, and adult Bullsnakes correspond roughly to those of Didiuk (2003). Iverson *et al.* (2008) distinguished a first-year class in their Nebraska Bullsnake sample, but, in that study, body size distribution did not otherwise fall into obvious age or size classes. Bullsnakes in a Wisconsin population were divided among four age-size categories (Kapfer *et al.* 2008a).

The number of Bullsnakes (31) captured over the five months of our study was small compared with the number of Prairie Rattlesnakes (333) captured in the same area over the same period. We recaptured only three Bullsnakes over this period, although 129 of our marked Prairie Rattlesnakes were recaptured at least once (Powell *et al.* 1998), suggesting that the Bullsnake population is much smaller than the syntopic rattlesnake one. This discrepancy is not reflective of a lack of active sampling effort; suitable habitat for both species was searched frequently over most of the study period, even though rattlesnakes were the desired target of these efforts. The number of Bullsnakes captured in the fenced dens in the fall (11) was also much smaller than the number of rattlesnakes taken at these dens (62). Bullsnakes were observed climbing the fences surrounding these dens, whereas rattlesnakes were not; thus, this capture method may have been unreliable for the former species, although the traps and fence were set up for the greater portion of the period in which snakes were returning to the dens. However, if we assume that the relative numbers of Bullsnakes and Prairie Rattlesnakes captured by passive methods in the fall roughly represent relative population sizes, Bullsnakes are still present in much smaller numbers.

A study of snake movements and numbers in the nearby CFB Suffield and Suffield National Wildlife Area used drift fence arrays set at successively greater distances from the South Saskatchewan River and close to hibernacula in the vicinity of the river (Didiuk 2003). The numbers of Bullsnakes and Prairie Rattlesnakes captured in drift fences over a time span comparable to our study period (395 rattlesnakes, 307 Bullsnakes; Didiuk 2003) did not show the same relative abundance as shown by our data. The habitat in Didiuk's (2003) study area was similar to that in ours. Human presence in the Suffield National Wildlife Area and CFB Suffield is greatly restricted, but gas field activities are conducted in the National Wildlife Area and grazing has been permitted in adjacent areas of the military reserve. Thus, it is unlikely that environmental differences are responsible for the differences in relative numbers of Bullsnakes and Prairie Rattlesnakes between Didiuk's (2003) study and ours.

If Bullsnakes spend the majority of the active season underground (Brown and Parker 1982; Ernst and Ernst 2003; Rodríguez-Robles 2003), walking surveys are likely to miss their presence, whereas the drift fence arrays used by Didiuk (2003) would catch snakes active on the surface, if they were moving significant distances. Our primary method for capturing Bullsnakes away from the vicinities of hibernacula may, thus, have been unsuitable for accruing a representative sample in our study area.

Bullsnake densities appear to be low elsewhere in its range (Fitch 1982; Kapfer *et al.* 2008a). Our findings are consistent with this. Smaller numbers and lower densities in Alberta Bullsnake populations, which are the northernmost of the species' geographical distribution (Russell and Bauer 2000; Ernst and Ernst 2003; Kissner and Nicholson 2003), are to be expected relative to populations further south. Bullsnakes are oviparous (Russell and Bauer 2000; Ernst and Ernst 2003; Kissner and Nicholson 2003; Wright 2008), and the

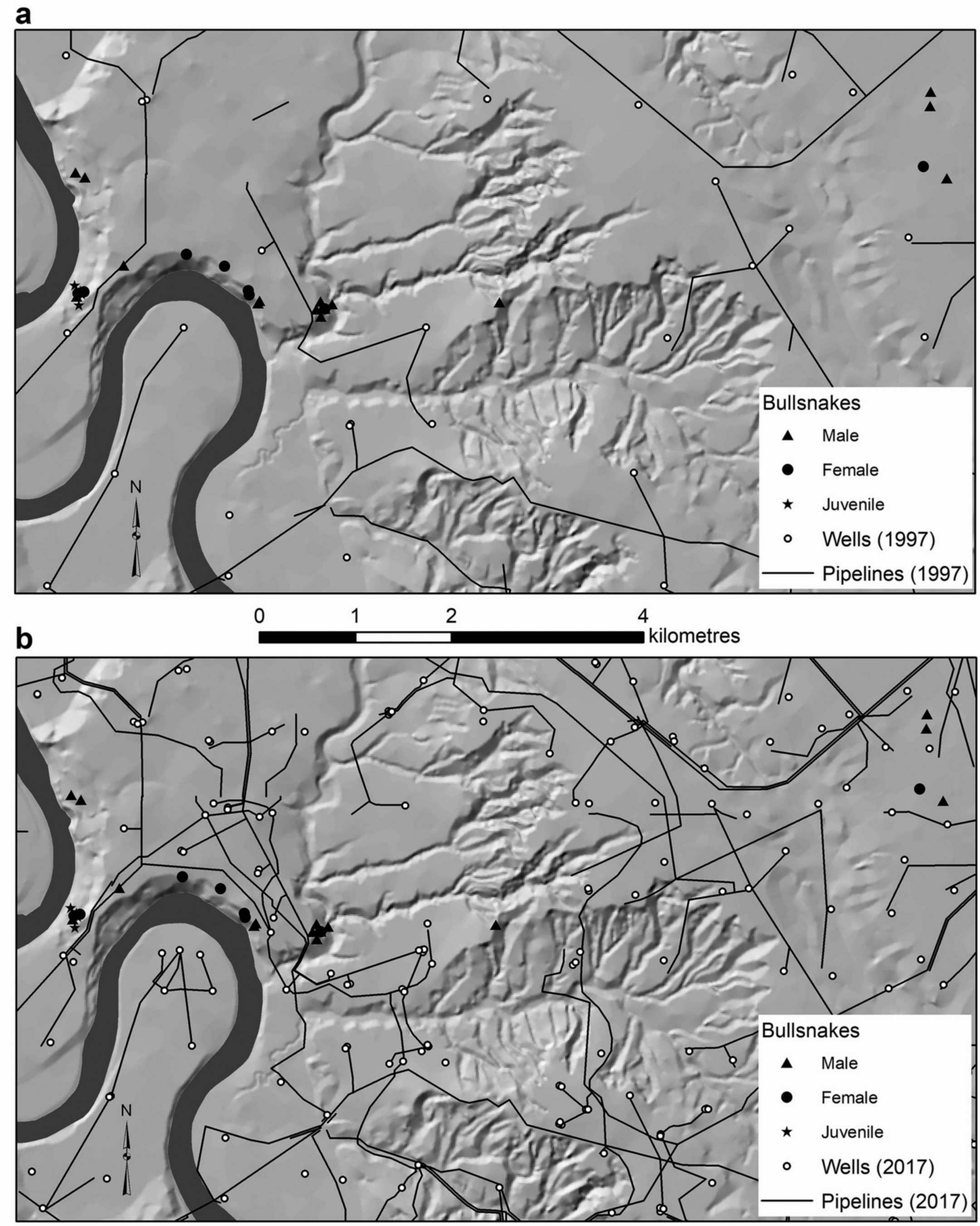

FIGURE 2. a. Study area displaying Bullsnake (*Pituophis catenifer sayi*) captures in relation to gas wells (open circles) and gas pipelines (black lines) in place in 1997. b. Bullsnake captures of 1997 superimposed on map of gas wells and gas pipelines in place in 2017.

success or failure of incubation will depend on seasonal weather conditions and, thus, will potentially vary greatly from year to year at this latitude (Wright 2008). Wright (2008) found that Bullsnake nests in the vicinity of Drumheller, Alberta, were restricted to the microclimatic conditions found in coulees and canyons, a factor that imposes limitations on recruitment.

The seasonal pattern of activity exhibited by Bullsnakes in our study (Figures S1 and S2) is consistent with that reported elsewhere (Brown and Parker 1982; Didiuk 2003; Kapfer *et al.* 2008b; Gardiner *et al.* 2013). Our fieldwork did not begin until early May, and our encounters with several individuals before the commencement of data collection indicated that we missed that portion of the Bullsnake population that emerged prior to this (Didiuk 2003; Kissner and Nicholson 2003; Gardiner *et al.* 2013). However, the fencing and open traps around the fenced dens were maintained sufficiently late in the fall that we are confident that our data are indicative of activity during this period. No Bullsnakes emerged after mid-May, and return to the fenced dens began on 6 September. Didiuk (2003), at his South Saskatchewan River hibernacula, recorded protracted emergence in spring and dispersal from hibernaculum areas by May, and Bullsnakes began appearing in the vicinities of hibernacula in September (Didiuk 2003). For a Utah population of Great Basin Gophersnake (*Pituophis catenifer deserticola*) the timing of spring emergence was more tightly constrained by environmental temperature than that of fall return (Vetas 1951). We have no information on seasonal environmental temperature cues for Alberta Bullsnake populations, but a similar relationship appears likely, as fall returns to the fenced dens took place over a 6-week period, while spring emergence was apparently largely complete early in the active season.

We have posited that the prolonged lacuna in Bullsnake captures in mid- to late-summer (Figures S1 and S2) may be due to a strong tendency toward fossorial activity. Bullsnakes have been noted to spend the greater proportion of the active season in burrows (Brown and Parker 1982; Rodríguez-Robles 2002, 2003; Ernst and Ernst 2003). Over their range, they feed preferentially on rodents and other small mammals (Hisaw and Gloyd 1926; Brown and Parker 1982; Fitch 1982; Reynolds and Scott 1982; Cook 1984; Diller and Johnson 1988; Diller and Wallace 1996; Rodríguez-Robles 1998, 2002; Russell and Bauer 2000; Ernst and Ernst 2003; Kissner and Nicholson 2003; COSEWIC 2017). They are accomplished diggers (Carpenter 1982; Sterner *et al.* 2002); Fitch (1982) considered Bullsnakes to be specialized for hunting pocket gophers (*Thomomys* spp.) in their tunnels. It is thus possible that many of the Bullsnakes in our study area that had dispersed away from the vicinity of the South Saskatchewan River from 12 June to 19 August were actively hunting or lying quiescent underground and were only active on the surface for short periods. Capture situations (Table S3), whether adjacent to the river or elsewhere, would thus represent surface activity of individuals that had emerged temporarily from their fossorial pursuits. Martino *et al.* (2012) found that the presence of burrows was the best predictor of Bullsnake activity in Grasslands National Park; a minority of our hand captures were made adjacent to burrows or holes (Table S3), but we surveyed only the area in the immediate vicinity of the capture. Thus, this relationship may hold true for our hand captures as well. If summer fossoriality is the rule for Bullsnakes, the difference in relative numbers between them and Prairie Rattlesnakes may be more apparent than real. Our data do not allow us to test this hypothesis.

Most of our Bullsnake hand captures were made in the vicinity of the river (Figure 1), early and late in the active season (Figures S1 and S2). If our assumption is correct that activity further from the river takes place largely underground, Bullsnakes must have moved away from the area adjacent to the river after their period of activity there early in the summer, and moved back late in the summer. Didiuk (2003) recorded most adult Bullsnake captures within 0.2–1 km of the South Saskatchewan River valley rim, but small numbers of captures were made as far as 13.5 km from the river. Bullsnakes exhibited strong directionality in spring dispersal away from the river and fall return to it (Didiuk 2003), and individual movements between capture and recapture points could be quite rapid (Didiuk 2003). However, Didiuk (2003) reported Bullsnake captures within 1 km of the river over the entire summer, in contrast to our data (Figures S1 and S2). Gardiner *et al.* (2013) reported that home ranges of Bullsnakes in Grasslands National Park, Saskatchewan, exhibited a dumbbell shape—two activity areas (around the hibernaculum and the area of summer activity) separated by a transit corridor, which was traversed quickly in the spring and fall. Our few captures in upland habitat, some 7 km from the easternmost point along the course of the river, are likely of adult snakes that moved this distance (or some fraction thereof). These snakes could represent a portion of the population that moved comparable distances from the river to those of some of Didiuk's (2003) widely-ranging adult Bullsnakes, but it does not appear to be a large portion. However, again, the propensity of Bullsnakes to spend a great deal of time underground could result in underestimation.

Elsewhere in its distribution, Gophersnake has been shown to overwinter individually, instead of in communal dens shared with other species (Williams *et al.* 2012). This has not been recorded in Alberta, but if some of the Bullsnakes from our study did overwinter individually in dens located away from the South Saskatchewan River, they would not be required to make long seasonal dispersals to upland habitat. Further data on Bullsnake movement in Alberta is required to test this possibility.

Martino *et al.* (2012), examining Bullsnake movement in Grasslands National Park, Saskatchewan, found that they travelled 493–3946 m (mean 1709 ± 256 m) during the active season, with a mean daily movement of 52 ± 7 m. The distances moved by Bullsnakes in Grasslands National Park were much smaller than those recorded for Bullsnakes denning along the South Saskatchewan River (Didiuk 2003; Martino *et al.* 2012). Evidently Bullsnakes exhibit annual movement patterns that accord with local topography, the locations of hibernacula within it, and, presumably, resource availability across it. Studies of Gophersnake home range area and movement elsewhere in the species' geographical distribution (Fitch and Shirer 1971; Rodríguez-Robles 2003; Kapfer *et al.* 2008b) indicate much shorter movements and smaller home ranges than those described for Bullsnakes in Alberta (Didiuk 2003) and Saskatchewan (Martino *et al.* 2012; Gardiner *et al.* 2013).

Bullsnake hand captures were generally made close to unimproved roads (Figure 1) and to gas field lines, but never around gas well installations (Figure 2a). Few captures were made in the vicinity of agricultural modifications: installations, equipment, or modified land. Road mortality, particularly resulting from oil and gas field activity, is seen as one of the more pressing threats to Bullsnake populations in Alberta (Didiuk 2003; Kissner and Nicholson 2003; COSEWIC 2017). In the area of Grasslands National Park, Saskatchewan, Bullsnakes were found in the vicinity of roads at four times the expected rate for the area occupied by roads (Martino *et al.* 2012). Fortney *et al.* (2012) also found that Bullsnakes in Grassland National Park tended to be found on, and close to, roads, this tendency being a function of the proximity of roads to hibernacula and of the type of road (paved, gravel, trail). The area over which our Bullsnake population occurred did not feature any paved roads, and the roads present at that time experienced low levels of traffic. Even so, we recorded one road fatality during our study period, which suggests that road mortality is a constant possibility even here.

Our data were collected in 1997. At that time, gas field installations were relatively few and widely scattered across the area of Bullsnake activity (Figure 2a). In the intervening 21 years, a marked increase in the number of wells and gas lines is evident, both in the vicinity of the hibernacula and across the presumed summer foraging range of the snakes (Figure 2b). This will inevitably have been accompanied by an increase in vehicular traffic and its associated likelihood of Bullsnake road mortality.

The data presented here provide a baseline for numbers and activity of this species across a landscape for which human activity is well-documented, both at present and over two decades ago. This may be useful for future studies of the impact of increased human activity on a Bullsnake population at the northern extremities of its geographic distribution.

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We are pleased to be able to contribute to this tribute to Francis Cook, who has played such a fundamental role in furthering our understanding of the amphibians and reptiles of Canada and in inspiring others to explore the biology of these underappreciated components of this nation's vertebrate fauna. In his iconic book, *Introduction to Canadian Amphibians and Reptiles* (1984, page 175), he states: "Any interested naturalist has an opportunity to make a useful contribution to our knowledge through detailed observations of local habitats… for all species". Our contribution is made in this spirit.

Literature Cited

ABMI (Alberta Biodiversity Monitoring Institute). 2010. Wall-to-wall land cover inventory [geodatabase]. ABMI, Edmonton, Alberta, Canada. Accessed 6 December 2017. http://www.abmi.ca/home/data-analytics/da-top/da-product-overview/GIS-Land-Surface/Land-Cover.html.

ABMI (Alberta Biodiversity Monitoring Institute). 2014. Wall-to-wall human footprint inventory [geodatabase]. ABMI, Edmonton, Alberta, Canada. Accessed 6 December 2017. http://www.abmi.ca/home/data-analytics/da-top/da-product-overview/GIS-Land-Surface/HF-inventory.html.

Alberta Energy Regulator. 2017a. Pipelines [shapefile]. Alberta Energy Regulator, Calgary, Alberta, Canada. Accessed 27 November 2017. https://www.aer.ca/providing-information/data-and-reports/maps-mapviewers-and-shapefiles.

Alberta Energy Regulator. 2017b. List of wells in Alberta [shapefile]. Alberta Energy Regulator, Calgary, Alberta, Canada. Accessed 27 November 2017. https://www.aer.ca/providing-information/data-and-reports/statistical-reports/st37.

Alberta Sustainable Resource Development. 2004. Native prairie vegetation inventory [shapefile]. Spatial & Numeric Data Services, University of Calgary (distributor), Calgary, Alberta, Canada.

Alberta Sustainable Resource Development. 2010a. Grassland vegetation inventory [shapefile]. Spatial & Numeric

Data Services, University of Calgary (distributor), Calgary, Alberta, Canada.

Alberta Sustainable Resource Development. 2010b. Grassland vegetation inventory (GVI) specifications. 5th edition. Government of Alberta, Edmonton, Alberta, Canada.

Alberta Wild Species General Status Listing. 2015. Wild species status search. Accessed 3 February 2018. http://aep.alberta.ca/fish-wildlife/species-at-risk/wild-species-status-search.aspx.

AltaLIS. 2010. Alberta province-wide digital elevation model grid format [raster]. Spatial & Numeric Data Services, University of Calgary (distributor), Calgary, Alberta, Canada.

Brown, W.S., and W.S. Parker. 1982. Niche dimensions and resource partitioning in a Great Basin Desert snake community. Pages 59–81 *in* Herpetological Communities: A Symposium of the Society of the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977. *Edited by* N.J. Scott, Jr. Wildlife research report 13. United States Fish and Wildlife Service, Washington, DC, USA.

Carpenter, C.C. 1982. The Bullsnake as an excavator. Journal of Herpetology 16: 394–401. https://doi.org/10.2307/1563570

Cook, F.R. 1984. Introduction to Canadian Amphibians and Reptiles. National Museums of Canada, Ottawa, Ontario, Canada.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2017. COSEWIC assessment and status report on the Bullsnake *Pituophis catenifer sayi* in Canada. COSEWIC. Ottawa, Ontario, Canada. Accessed 27 January 2018. http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Bullsnake_2017_e.pdf.

Didiuk, A.B. 2003. CFB Suffield and Suffield National Wildlife Area. Cooperative reptile and amphibian studies. Snake conservation research and management 2002. Canadian Wildlife Service, Prairie and Northern Region, Edmonton, Alberta, Canada. Accessed 17 November 2017. http://www.ceaa-acee.gc.ca/050/documents/29548/29548E.pdf.

Diller, L.V., and D.R. Johnson. 1988. Food habits, consumption rates, and predation rates of western rattlesnakes and gopher snakes in southwestern Idaho. Herpetologica 52: 228–233.

Diller, L.V., and R.L. Wallace. 1996. Comparative ecology of two snake species (*Crotalus viridis* and *Pituophis melanoleucus*) in southwestern Idaho. Herpetologica 52: 343–360.

Ernst, C.H., and E.M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Books, Washington, DC, USA.

Fitch, H.S. 1982. Resources of a snake community in prairie-woodland habitat of northeastern Kansas. Pages 83–97 *in* Herpetological Communities: A Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977. *Edited by* N.J. Scott, Jr. Wildlife research report 13. United States Fish and Wildlife Service, Washington, DC, USA.

Fitch, H.S., and H.W. Shirer. 1971. A radio telemetric study of spatial relationships in some common snakes. Copeia 1971: 118–128. https://doi.org/10.2307/1441605

Fortney, A.N., R.G. Poulin, J.A. Martino, D.L. Parker, and C.M. Somers. 2012. Proximity to hibernacula and road type influence potential road mortality of snakes in southwestern Saskatchewan. Canadian Field-Naturalist 126: 194–203. https://doi.org/10.22621/cfn.v126i3.1360

Gardiner, L.E., C.M. Somers, J.A. Martino, D.L. Parker, and R.G. Poulin. 2013. Balancing the dumbbell: summer habitats need protection in addition to winter dens for northern snake communities. Journal of Wildlife Management 77: 975–982. https://doi.org/10.1002/jwmg.555

Gutzke, W.H.N., G.L. Paukstis, and L.L. McDaniel. 1985. Skewed sex ratios for adult and hatchling Bullsnakes, *Pituophis melanoleucus*, in Nebraska. Copeia 1985: 649–652. https://doi.org/10.2307/1444757

Hammer, Ø., D.A.T. Harper, and P.D. Ryan. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4: 1–9.

Hisaw, F.L., and H.K. Gloyd. 1926. The bull snake as a natural enemy of injurious rodents. Journal of Mammalogy 7: 200–205. https://doi.org/10.2307/1373511

Iverson, J.B., C.A. Young, and T.S. Akre. 2008. Body size and growth in the Bullsnake (*Pituophis catenifer sayi*) in the Nebraska Sandhills. Journal of Herpetology 42: 501–507. https://doi.org/10.1670/07-030.1

Kapfer, J.M. 2009. Body size and sexual size dimorphism of Bullsnakes (*Pituophis catenifer sayi*) in Wisconsin, USA. Herpetological Conservation and Biology 4: 353–357.

Kapfer, J.M., J.R. Coggins, and R. Hay. 2008a. Estimates of population size, measurements of sex ratios, and reported mortality rates for Bullsnakes (*Pituophis catenifer sayi*) at a site in the upper midwestern United States. Journal of Herpetology 42: 265–269. https://doi.org/10.1670/07-2021.1

Kapfer, J.M., J.R. Coggins, and R. Hay. 2008b. Spatial ecology and habitat selection of Bullsnakes (*Pituophis catenifer sayi*) at the northern periphery of their geographic range. Copeia 2008: 815–826. https://doi.org/10.1643/CE-07-104

Kissner, K.J., and J. Nicholson. 2003. Bullsnakes (*Pituophis catenifer sayi*) in Alberta: literature review and data compilation. Species at risk report 62. Alberta Sustainable Resource Development, Fish and Wildlife Division, Edmonton, Alberta, Canada.

Martino, J.A., R.G. Poulin, D.L. Parker, and C.M. Somers. 2012. Habitat selection by grassland snakes at northern range limits: implications for conservation. Journal of Wildlife Management 76: 759–767. https://doi.org/10.1002/jwmg.313

Powell, G.L., A.P. Russell, M.M.A. Hill, N.E. O'Brien, and J.L. Skilnick. 1998. A preliminary investigation of movements, habitat use, and population trends in the prairie rattlesnake (*Crotalus viridis*) in a multiple-use rural landscape in southeastern Alberta. The 1997 field season. Alberta Conservation Association, Edmonton, Alberta, Canada.

Reynolds, R.P., and N.J. Scott, Jr. 1982. Use of a mammalian resource by a Chihuahuan snake community. Pages 99–118 *in* Herpetological Communities: A Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977. *Edited by* N.J. Scott, Jr. Wildlife research report 13. United States Fish and Wildlife Service, Washington, DC, USA.

Rodríguez-Robles, J.A. 1998. Alternative perspectives on the diet of Gopher Snakes (*Pituophis catenifer*, Colubridae): literature records versus stomach contents of wild and museum specimens. Copeia 1998: 463–466. https://doi.org/10.2307/1447442

Rodríguez-Robles, J.A. 2002. Feeding ecology of North American gopher snakes (*Pituophis catenifer*, Colubridae). Biological Journal of the Linnean Society 77: 165–183. https://doi.org/10.1046/j.1095-8312.2002.00098.x

Rodríguez-Robles, J.A. 2003. Home ranges of Gopher Snakes (*Pituophis catenifer*, Colubridae) in Central California. Copeia 2003: 391–396. https://doi.org/10.1643/0045-8511(2003)003[0391:HROGSP]2.0.CO;2

Russell, A.P., and A.M. Bauer. 2000. The Reptiles and Amphibians of Alberta. 2nd Edition. University of Calgary Press, Calgary, Alberta, Canada.

Somers, C.M., C.F. Graham, J.A. Martino, T.R. Frasier, S.L. Lance, L.E. Gardiner, and R.G. Poulin. 2017. Conservation genetics of the eastern yellow-bellied racer (*Coluber constrictor flaviventris*) and bullsnake (*Pituophis catenifer sayi)*: river valleys are critical features for snakes at northern range limits. PLoS ONE 12: e0187322. https://doi.org/10.1371/journal.pone.0187322

Sterner, R.T., B.E. Petersen, S.A. Shumake, S.E. Gaddis, J.B. Bourassa, T.A. Felix, G.R. McCann, K.A. Crane, and A.D. Ames. 2002. Movements of a Bullsnake (*Pituophis catenifer*) following predation of a radio-collared northern pocket gopher (*Thomomys talpoides*). Western North American Naturalist 62: 240–242.

Vetas, B. 1951. Symposium: a snake den in Tooele County, Utah: temperatures of entrance and emergence. Herpetologica 7: 15–20.

Williams, K.E., K.E. Hodges, and C.A. Bishop. 2012. Small reserves around hibernation sites may not adequately protect mobile snakes: the example of Great Basin Gophersnakes (*Pituophis catenifer deserticola*) in British Columbia. Canadian Journal of Zoology 90: 304–312. https://doi.org/10.1139/z11-136

Wright, J.D. 2008. Bullsnake, *Pituophis catenifer sayi,* nesting biology in Alberta. Canadian Field-Naturalist 122: 138–141. https://doi.org/10.22621/cfn.v122i2.572

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SUPPLEMENTARY MATERIAL:

SECTION S1. Size of Bullsnakes (*Pituophis catenifer sayi*).

SECTION S2. Snout-to-vent length and mass of recaptured Bullsnakes (*Pituophis catenifer sayi*).

SECTION S3. Capture situation and insolation during capture of Bullsnakes (*Pituophis catenifer sayi*).

SECTION S4. Environmental temperature measured during hand capture of Bullsnakes (*Pituophis catenifer sayi*).

SECTION S5. Site types of hand captures of Bullsnakes (*Pituophis catenifer sayi*).

TABLE S1. Summary of the lengths and masses of all captured Bullsnakes (*Pituophis catenifer sayi*).

TABLE S2. Growth and movement data for the two Bullsnakes (*Pituophis catenifer sayi*) recaptured after an interval >3 weeks.

TABLE S3. Cross-tabulation of situation at capture with insolation for all hand-captured Bullsnakes (*Pituophis catenifer sayi*).

TABLE S4. Numbers of Bullsnakes (*Pituophis catenifer sayi*) hand captured in each site type in the 1997 field season.

FIGURE S1. Distribution of snout-to-vent lengths (SVL) of Bullsnakes (*Pituophis catenifer sayi*) captured over the study period, 11 May (day 131) to 10 October (day 283) 1997.

FIGURE S2. Mass of Bullsnakes (*Pituophis catenifer sayi*) captured over the study period, 11 May (day 131) to 10 October (day 283) 1997.

FIGURE S3. Distribution of snout-to-vent lengths (SVL) of all Bullsnakes (*Pituophis catenifer sayi*) captured over the study period, 11 May to 10 October 1997.

FIGURE S4. Distribution of mass of all Bullsnakes (*Pituophis catenifer sayi*) captured over the study period, 11 May to 10 October 1997.

FIGURE S5. Ground (a) and air (b) temperatures for all hand captures of Bullsnakes (*Pituophis catenifer sayi*).

Morphology, reproduction, habitat use, and hibernation of Red-bellied Snake (*Storeria occipitomaculata*) near its northern range limit

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Abstract

Northern regions limit ectotherms to relatively short periods of feeding and breeding interrupted by long periods of inactivity. This may force cool-climate ectotherms into different ecological or demographic trade-offs than their southern conspecifics. Our aim is to examine demography, morphology, reproduction, habitat use, and hibernation by populations of Red-bellied Snake (*Storeria occipitomaculata*) near their northern range limit. This research was conducted in southwestern Manitoba and data on summer activity were collected from April to September 2007–2009 using coverboard and pedestrian surveys. Hibernation sites were monitored over three winters (2007–2008, 2008–2009, and 2009–2010), and thermal profiles of *Formica* ant mounds were collected in 2008–2009 and 2009–2010. Females reached sexual maturity at a smaller size than most other populations that have been reported but appear to have similar clutch sizes to the rest of the range. The majority of adult females captured at our summer sites were gravid (96%) suggesting annual reproduction, and activity patterns suggest fall breeding. Near its northern range maxima, this species appears to use relatively warm habitat, have rapid reproduction, and co-opt ant mounds to survive in a difficult climatic environment. Much remains unknown and future studies should further examine the variation in size at maturity and the relationship between body size and clutch size. In addition, little is known about diet, benefits of fall mating, use of open prairie habitats, and late-season migration by *S. occipitomaculata*.

Key words: Red-bellied Snake; *Storeria occipitomaculata*; cool-climate; temperate; Manitoba; thermoregulation; brumation

Introduction

Regions with extended cold seasons present challenges for many ectothermic species, which is reflected by the limited species diversity of snakes and other squamates at higher latitudes (Kiester 1971). These regions have short summers and long, cold winters that limit individuals to relatively short periods of feeding and breeding interrupted by long periods of forced inactivity (Gregory 2009). Because short active seasons can limit the time available to allocate resources, cold-climate individuals may have different ecological tradeoffs than their lower latitude conspecifics (Gregory 2009). As such, aspects of growth (Blouin-Demers *et al.* 2002), reproduction (Gregory 2009), and habitat use (Weatherhead *et al.* 2012) can differ within species across a range, reflecting local selective pressures (Fitch 1981).

Sexual size dimorphism (SSD) has been examined in numerous snake species (reviewed in Shine 1994). Sexual size dimorphism is common but can vary geographically with northern populations. They are often less dimorphic than southern populations which is often attributed to phylogenetic conservatism (Shine 1994; Cox *et al.* 2007). Size at maturity can be conserved across the range of most species, but the age at which an individual reaches mature size may be more plastic (Blouin-Demers *et al.* 2002). Cold-climate reptiles are expected to grow more slowly and have delayed maturity (Atkinson 1994; Berrigan and Charnov 1994). This is not the case for all species; some populations are able to compensate for shorter growing seasons and have similar or higher reproductive rates compared to southern conspecifics (Tuttle and Gregory 2012, 2014).

The ability of a female to successfully reproduce in any given year is typically dependent on body condition. Most northern reptiles are viviparous with lecithotrophic embryos requiring provisioning predevelopment. The time required to replenish energy stores may delay subsequent reproduction and lead to less than annual reproduction. In some species, yolk is supplemented by limited placental nourishment, allowing gravid snakes some control of provisioning during development (King 1993). In these cases, prolonged gestation would allow for larger or more neonates. This has a cost, as prolonged gestation limits the ability of the mother to feed that, in an already short season, may lead to tradeoffs in energy expenditure not required in less stressful environments.

In high-latitude regions many snakes are not always able to maintain ideal body temperatures, even during the active season (Blouin-Demers and Weatherhead 2001). Reproductive requirements of females also contribute to differences in habitat use and temperature selection between sexes. Thermal requirements to grow developing embryos may cause females to select different habitats than males and alter their thermoregulatory behaviour (Shine *et al.* 2006). The cold-climate hypothesis predicts that warmer temperatures will be selected by gravid female squamates in cold climates to ensure rapid embryo development (Tinkle and Gibbons 1977). This may lead to increased use of more thermally attractive open or edge habitat than in other parts of a species' range.

Cold-climate reptiles can avoid inclement conditions and limit energy expenditures through hibernation (Gregory 2009). Failure to select appropriate hibernacula leads to death but selecting purely for overwinter survival also has associated costs (Gienger and Beck 2011). Time spent in hibernation subtracts from time spent foraging, therefore hibernacula are often chosen to extend the length of the active season (Gienger and Beck 2011). Features often associated with successful hibernation sites allow for access to soil below the frost line, stability in humidity and temperature, and access to the water table (Harvey and Weatherhead 2006a). The availability of suitable hibernacula is likely the most important form of habitat selection for snakes at high latitudes and may limit the distribution of some species (Harvey and Weatherhead 2006b).

Red-bellied Snake (*Storeria occipitomaculata*) occupies most of eastern North America and is widely distributed in Canada, reaching the northwestern edge of its range in eastern Saskatchewan (Ernst and Ernst 2003). Across its range there have been a number of studies of this species (e.g., Blanchard 1937; Lang 1969; Semlitsch and Moran 1984; Willson and Dorcas 2004; Brown and Phillips 2012) but there has been little research at its northern range limit, with the exception of two natural history observations (Criddle 1937; Gregory 1977). *Storeria occipitomaculata* is a small-bodied, cryptic snake that comes in several ground-shaded dorsal colour morphs and has a bright, reddish-orange ventral surface. They are viviparous, likely with some limited placental provisioning (Blackburn *et al.* 2009). This species, like other members of the genus *Storeria*, feeds primarily on molluscs (Trapido 1944; Brown 1979; Semlitsch and Moran 1984; Pisani and Busby 2011) although not exclusively (Ernst and Ernst 2003). With few species of slugs and snails native to the northwestern edge of its range, local diet remains unknown. This species is considered uncommon to rare throughout much of its range (Ernst and Ernst 2003) but it can be abundant in suitable habitat (Lang 1971). Little is known about population densities for this species, although most studies have recorded low recapture rates (Blanchard 1937; Gregory 1977; Semlitsch and Moran 1984). Typically, *S. occipitomaculata* inhabit thick grassy, herbaceous, and shrubby vegetation, and also can be found in wetlands, riparian areas, and along forest edges and in old field and prairie habitats (Wright and Wright 1957; Cook 1984; Pisani and Busby 2011) as well as drier grasslands habitats (Lang 1969; Brown and Phillips 2012). Criddle (1937) and Lang (1969) both found this species to use abandoned (or nearly so) ant mounds of species of the genus *Formica* as overwintering sites, with the snakes often found hibernating at high densities.

The objective of this study is to examine demography, morphology, reproduction, habitat use, and hibernation in populations of *S. occipitomaculata* near their northern range limit. The stressful environment at high latitudes may force these populations to make trade-offs in their growth, reproduction, and habitat use. We asked the following questions: 1) What are the demographics, morphology, and reproductive traits of this population of *S. occipitomaculata*? and 2) Under what conditions do they hibernate?

Methods

Study sites

Field work in summer habitat use took place in southwestern Manitoba, Canada at the following locations (Figure 1a): Spruce Woods Provincial Park (SWPP; 49.7108°N, 99.2528°W), Assiniboine Corridor Wildlife Management Area (ACWMA; 49.6675°N, 99.5614°W), Oak Lake (49.6644°N, 100.7133°W), and Canadian Forces Base Shilo (CFB Shilo; 49.7381°N, 99.5183°W). A wide variety of habitats were investigated, including agricultural areas, beaver ponds, mixed forest, and mixed-grass prairie. Most sites included water and/or mixed grass prairie. Investigation into hibernation was conducted at the Souris River Bend Wildlife Management Area (SRBWMA; 49.4883°N, 99.8775°W; Figure 1b). Habitat at this area includes mixed forest and grassland, bordered by marsh, agricultural fields, and gravel roads. Details on the habitat types are provided below.

Demography and morphometrics

We recorded the following measurements for all snakes: date, time, snout-vent length (SVL in mm), tail length (mm), head width (mm), head length (mm), mass (g), sex, age, and reproductive condition. We classified all individuals into three age classes: young-of-year (YOY), juvenile, and adult. *Storeria occipitomaculata* were classified into age classes based on their SVL, natal scars, and the minimum breeding SVL of females: YOY (<110mm), juvenile (100–154 mm), and adult (>154 mm). For the age-class analysis we only included the first capture for individuals that were recaptured multiple times within the same season.

To determine reproductive condition, two researchers independently counted enlarged ovarian follicles by palpation (Fitch 1987) and the average of their counts was recorded. All captured individuals were scale-clipped for identification and released at their capture site within 15 minutes of capture. The activity period (27 April to 8 September) was classified by two-week periods numbered 1 through 10. No snakes in this study received more than three clipped ventral scales.

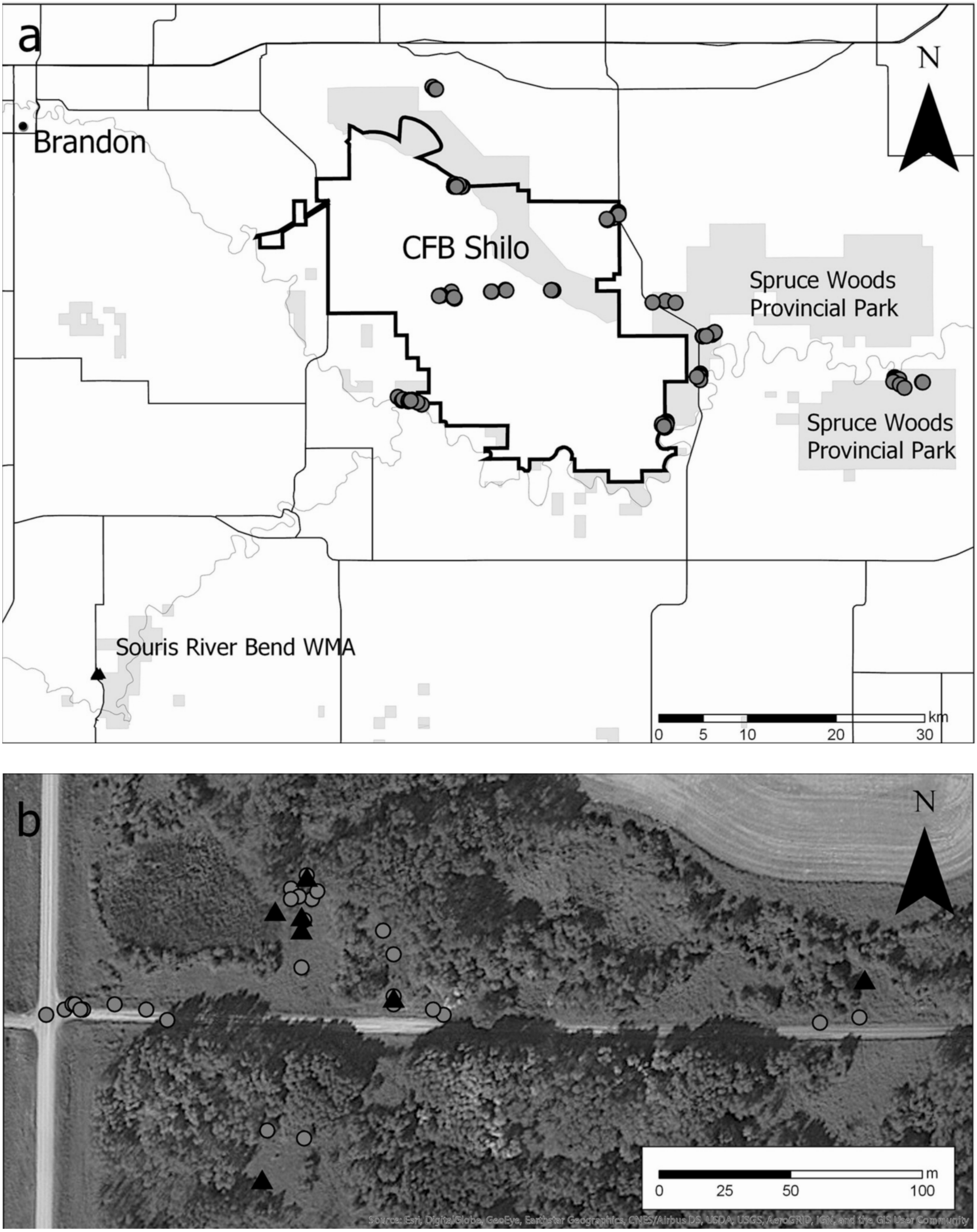

FIGURE 1. a. Map of summer sites (grey circle) and hibernation sites (black triangle) surveyed for Red-bellied Snake (*Storeria occipitomaculata*) 2007–2010 in southwestern Manitoba. b. Map of hibernation study site at Souris River Bend Wildlife Management Area surveyed 2007–2010 showing den sites (black triangle) where traps were set and locations of individual captures (grey circle) outside of the traps. Base map from World Imagery. Accessed 7 October 2018. https://support.esri.com/en/technical-article/000012040.

Summer activity

Field sites were surveyed every 2–3 weeks in 2007–2009, from April to September of each year. Surveys were done at various times of day to compare daily habitat usage as the season progressed. We used the same search corridor each time a site was visited to standardize search effort. These routes travelled around or through potentially suitable habitat, often following barriers such as creeks, park paths, or tree lines. Animals were captured by hand as they moved in the open, or when located under cover objects, both natural and artificial (e.g., plywood, sheet metal).

We recorded the following environmental and location data at each capture site: universal transverse mercator coordinates, capture location (in the open or under cover, cover type, and cover thickness), and aspect (0–360°). Collection localities were recorded using a Garmin® GPS60 handheld global positioning system (GPS) receiver (Olathe, Kansas, USA; WAAS enabled accuracy: <3 m, 95% typical). GPS data were used to classify the capture locations according to land cover classes defined by the Manitoba Land Initiative (2012). The following seven classes were used: agriculture, bogs, coniferous forest, deciduous forest, mixedwood forest, grassland, and roads (including trails). Assignments were made using ArcGIS version 10 (ESRI 2011).

Hibernation field data collection

This study took place from September 2007 to June 2010, targetting spring and fall (from 12 April to 5 June in 2008; from 6 May to 2 June in 2009; from 4 April to 20 May in 2010; from 15 September to 4 October in 2007; from 6 September to 25 October in 2008, and 20 September to 4 October in 2009). No traps were used in 2009 (see below for a further description of trapping).

Five abandoned ant mounds were monitored throughout the study (Figure 1b). We replaced two of the mounds that were monitored in 2007 and 2008 with two new mounds in 2008, 2009, and 2010 because the mounds monitored in 2007 and 2008 were destroyed. All ant mounds were ringed with 40 cm tall aluminum flashing. Three openings were cut in the aluminum flashing and a mesh funnel trap made of hardware cloth was placed in each. In fall, two traps were placed on the inside of the flashing at every mound to capture individuals entering the mounds, and one trap was placed on the outside to capture individuals exiting the mounds; the reverse occurred in the spring trapping sessions. Traps were checked every 24–48 h and all individuals were removed from traps. Visual searches were also conducted around the trap sites when traps were checked. All captured individuals were measured (as described above), given a unique scale-clip, and released at the capture site. Individuals caught in traps were released in their direction of travel.

Temperature profiles of the ant mounds were created using iButton® thermal probes (San Jose, California, USA) attached to plastic landscaping rods. iButtons® were placed in Ziploc® bags and attached to the poles using duct tape. They were deployed over two winters, from 27 September 2007 to 29 May 2008 and 20 September 2008 to 3 June 2009. The iButtons® were set at four distances from the surface: 40, 80, 120, 160 cm in the 2007–2008 hibernation period; and at 0, 40, 80, 120 cm in the 2008–2009 hibernation period. Temperatures were recorded every 3 h. In 2007–2008 all iButtons® deployed at 160 cm below the surface failed because they were below the water table. We did not deploy any iButtons® at this depth in 2008–2009. In 2008–2009, air temperature (1.5 m above the surface) was also recorded.

Statistical analysis

All data analyses were done in R 3.2.1 (R Development Core Team 2017) with $\alpha = 0.05$. We report means, SE, and ranges. Data were log-transformed or nonparametric tests were used, when assumptions of parametric tests were not satisfied. Unless otherwise indicated, adult females include both gravid and non-gravid individuals. Unpaired t-tests (package stats; function t.test) were used to compare SVLs within and between sexes, and those captured in the summer versus at the hibernation site (spring and fall). Chi-square analyses (package stats; function chisq.test) were used to compare among categorical variables (see Table 1 for all comparisons). Linear models (package stats; function lm) were used to test for morphological and reproductive relationships (see Table 2 for detailed models). For P values between 0.05 and 0.1 power analyses were conducted (package pwr) with reference power = 0.80.

We calculated the mean temperature at each depth for all five dens for each 3 h period within each year. In some cases, we did not have temperatures for all depths at all den sites due to failure of some of the iButtons®. In 2007–2008, one iButton® failed at a den site at both the 80 cm and 120 cm depths. In 2008–2009, one iButton® failed at the 80 cm depth, and three iButtons® failed at the 120 cm depth. Air temperature and surface temperature (0 cm) were only recorded in 2008–2009.

Results

Summer demography, morphometrics, and habitat use

Over the three years we captured 88 individuals (Table S1). Most individuals were adults ($n = 81$; 92%), with only five juveniles and two YOY captured. There was no significant difference in the numbers of captures in each age class (YOY, juvenile, adult) among the three years (Table 1) and no significant difference in the numbers of adult males and females captured among years (Table 1). Adult sex ratios varied during the active season (Table 1; Figure 2) with more males captured in late summer (after 3 August).

Adult female *S. occipitomaculata* tended to be longer (female: 184.2 ± 2.2 mm; male: 175.3 ± 4.0; male: female body size = 0.95; $t_{31.3} = 1.94$, $P = 0.06$). Samples were unequal (female: $n = 53$; male: $n = 21$) and power was low (0.50; package pwr; function pwr.t2n.test).

TABLE 1. Chi-square test statistics for comparisons among categories for: summer sites and hibernation sites for Red-bellied Snake (*Storeria occipitomaculata*).

Category	Comparison	χ^2	*df*	*P*
SUMMER				
age class (YOY, J, AD)*	year	4.04	4	0.400
adult sex	year	4.02	2	0.130
adult sex	activity (10 periods)	18.44	9	0.030
activity (10 periods)	land-cover use	62.35	27	< 0.001
adult sex	land-cover use	1.34	3	0.720
HIBERNATION				
age class (YOY, J, AD)*	spring versus fall	86.28	2	< 0.001
adult sex	spring versus fall	0.17	1	0.680
species	capture location (trap, mound, road, and grassland)	28.33	9	< 0.001
direction of movement (entering versus exiting)	spring versus fall	0.40	1	0.530

*YOY = young-of-year; J = juvenile; AD = adult.

TABLE 2. Linear models to test for the effects of snout-vent length (SVL) and sex of Red-bellied Snake (*Storeria occipitomaculata*) on tail length, head width, head length, natural log-transformed mass, and number of follicles. Models were done separately for summer sites (S) and the hibernation site (H). The final linear model tests for the effect of year and SVL on the number of follicles in adult females captured at summer sites.

Model		Site type	*F*	*df*	*P*	Adjusted r^2
tail length =	sex + SVL + sex × SVL	S	3.95	3,69	0.010	0.11
		H	51.34	3,39	< 0.001	0.78
	sex	S	6.83	1,69	0.010	
		H	38.54	1,39	< 0.001	
	SVL	S	3.76	1,69	0.060	
		H	115.28	1,39	< 0.001	
	sex × SVL	S	1.26	1,69	0.260	
		H	0.20	1,39	0.660	
head width =	sex + SVL + sex × SVL	S	4.25	3,69	0.008	0.12
		H	16.18	3,39	< 0.001	0.52
	sex	S	3.19	1,69	0.080	
		H	1.16	1,39	0.290	
	SVL	S	8.29	1,69	0.005	
		H	47.35	1,39	< 0.001	
	sex × SVL	S	1.28	1,69	0.260	
		H	0.01	1,39	0.910	
head length =	sex + SVL + sex × SVL	S	9.18	3,62	< 0.001	0.27
		H	16.43	3,26	<0.001	0.61
	sex	S	3.02	1,62	0.090	
		H	1.15	1,26	0.290	
	SVL	S	23.30	1,62	< 0.001	
		H	43.95	1,26	< 0.001	
	sex × SVL	S	1.21	1,62	0.270	
		H	4.19	1,26	0.050	
log(mass) =	sex + SVL + sex × SVL	S	60.12	3,69	< 0.001	0.71
		H	119.20	3,39	<0.001	0.89
	sex	S	39.76	1,69	< 0.001	
		H	2.25	1,39	0.140	
	SVL	S	140.16	1,69	< 0.001	
		H	350.32	1,39	< 0.001	
	sex × SVL	S	0.45	1,69	0.500	
		H	5.15	1,39	0.030	
no. follicles =	year + SVL + year × SVL	S	9.53	5,68	< 0.001	0.38
	year	S	11.80	2,33	< 0.001	
	SVL	S	22.61	1,33	0.040	
	year × SVL	S	0.12	2,33	0.890	

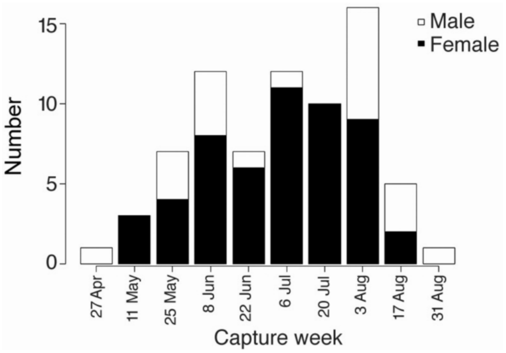

FIGURE 2. Numbers of adult male and female Red-bellied Snake (*Storeria occipitomaculata*) captured during summer surveys 2007–2009 at Spruce Woods Provincial Park (SWPP), Assiniboine Corridor Wildlife Management Area (ACWMA), Oak Lake, and Canadian Forces Base Shilo (CFB Shilo). The season was divided into ten, two-week periods and the capture week indicates the start of the two-week period.

Sample sizes of 60 in each group would have detected a significant difference ($\alpha < 0.05$) with power = 0.80. Males had significantly longer tails than females (Table 2; Figure 3a). Males tended to have wider and longer heads (Table 2). Females were significantly heavier than males (Table 2; Figure 3b).

The majority of adult females captured were gravid (*n* = 46; 96%). Enlarged follicles were detected from 14 May to 11 August. Gravid females had 4–12 follicles (modes = 5, 6, 7, and 10, median = 7). The number of follicles increased with SVL (Table 2; Figure 4) and was significantly different among the three years (2007: modes = 0, 4, and 7, median = 6; 2008: mode = 6, median = 6; 2009: mode = 10, median = 9; Table 2; Figure 4).

Individuals were most commonly found in grassland habitat (*n* = 51; 59%), followed by deciduous forest (*n* = 22; 25%), roads (*n* = 9; 10%), and mixedwood forest (*n* = 5; 6%). Land-cover use differed across the 10, two week periods (Table 1; Figure 5). Mixedwood forest

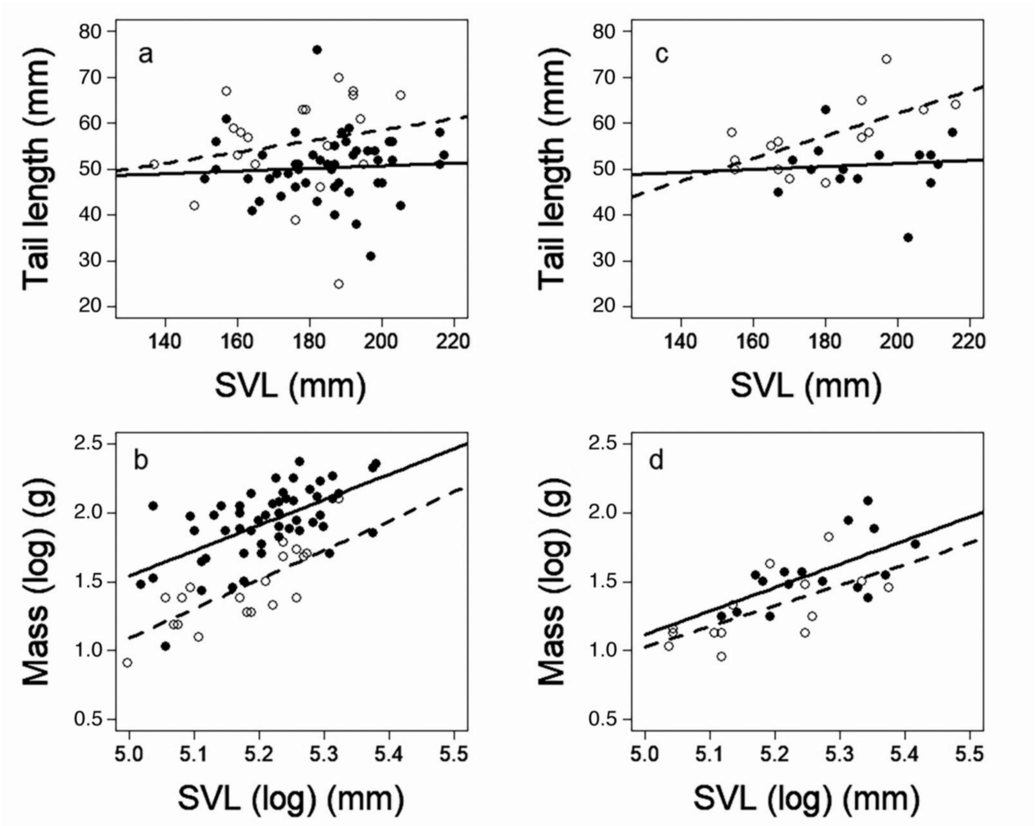

FIGURE 3. a. Snout-vent length (SVL) versus tail length, and b. natural log-transformed SVL versus natural log-transformed mass for adult male (open circle, dashed line) and female (filled circle, solid line) Red-bellied Snake (*Storeria occipitomaculata*) captured during summer surveys 2007–2009 at Spruce Woods Provincial Park (SWPP), Assiniboine Corridor Wildlife Management Area (ACWMA), Oak Lake, and Canadian Forces Base Shilo (CFB Shilo). c. SVL versus tail length, and d. natural log-transformed SVL versus natural log-transformed mass for adult male (open circle, dashed line) and female (filled circle, solid line) *S. occipitomaculata* captured during spring and fall surveys 2007–2010 at the hibernation site (Souris River Bend Wildlife Management Area).

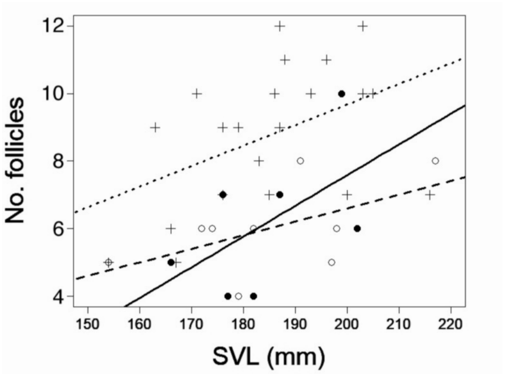

FIGURE 4. Snout-vent length (SVL) versus number of follicles for adult gravid female Red-bellied Snake (*Storeria occipitomaculata*) captured during summer surveys 2007–2009 at Spruce Woods Provincial Park (SWPP), Assiniboine Corridor Wildlife Management Area (ACWMA), Oak Lake, and Canadian Forces Base Shilo (CFB Shilo). Linear regressions are shown separately for each year: 2007 (open circle, dashed line), 2008 (filled circle, solid line), and 2009 (cross, dotted line).

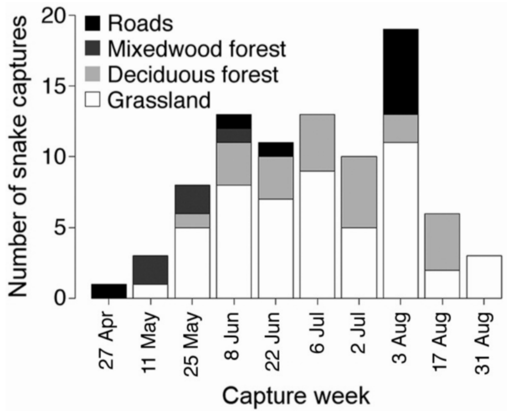

FIGURE 5. Habitat use of Red-bellied Snake (*Storeria occipitomaculata*) captured during summer surveys 2007–2009 at Spruce Woods Provincial Park (SWPP), Assiniboine Corridor Wildlife Management Area (ACWMA), Oak Lake, and Canadian Forces Base Shilo (CFB Shilo). The season was divided into ten two-week periods and the capture week indicates the start of the two-week period.

was used in spring (11 May to 15 June), while roads and grassland were most commonly used in late summer (3–10 August). There was no difference in landcover use of males and females (Table 1).

Approximately a third of captures were on flat ground (*n* = 23; 30%). Individuals that were captured on slopes were captured on slopes with a mean aspect of 18.2 ± 1.04° (south facing). Most captures were under cover (*n* = 73; 87%). Preferred cover types were: plywood (*n* = 41; 56%), natural log (*n* = 9; 12%), railway tie (*n* = 8; 11%), plank (*n* = 6; 8%), and other (*n* = 9; 13%). Mean cover thickness was 36.5 ± 5.2 mm (range = 1–220 mm, median = 19 mm). Sampling effort for slope and cover types was not quantified. Therefore, the above values do not necessarily reflect habitat selection, and may simply reflect a bias in availability.

Hibernation demography, morphometrics, and habitat use

At the hibernation site (SRBWMA) we found 57 individuals representing all three age classes for *S. occipitomaculata*. Adults were the most common (*n* = 35; 61%), followed by similar percentages of juveniles (*n* = 12; 21%) and YOY (*n* = 10; 18%). There was a significant difference in the numbers caught by age class (YOY, juvenile, adult) between spring and fall (Table 1). In the fall there were more adults (*n* = 25; 71% of all adults) and YOY (*n* = 10; 100% of all YOY) captured, and more juveniles captured in the spring (*n* = 11; 89% of all juveniles). There was no significant difference in the numbers of males and females captured in the spring versus the fall (Table 1). Adult female *S. occipitomaculata* captured at the hibernation site were significantly larger than males (193.9 ± 4.4 mm and 178.9 ± 5.4 mm respectively; $t_{26.1} = 2.17$, $P = 0.04$). Males had significantly longer tails than females (Table 2; Figure 3c). There was no difference between head widths (Table 2) or head lengths of males and females (Table 2). There was no difference in mass between males and females (Table 2; Figure 3d).

Storeria occipitomaculata shared the hibernation site with three other species of snakes: Plains Garter Snake (*Thamnophis radix)*, Red-sided Garter Snake (*T. sirtalis parietalis*)*,* and Smooth Greensnake (*Opheodrys vernalis*) that used both the surrounding area and den sites. Over three years we captured 166 individuals (Table 3). Most were found during fall surveys (*n* = 114; 69%). Trapping percentages were highest in *O. vernalis* and *T. radix* (Table 4). Individuals were first captured in traps on 16 September 2007, 13 September 2008, and 23 September 2009. Timing of the first spring captures in traps was more variable: 7 May 2009 and 9 April 2010. More individuals were captured during our visual searches, either in the grassland (*n* = 50; 30%), on the road (*n* = 28; 17%), or inside aluminum flashing on ant mounds (*n* = 13; 8%). The remaining individuals (*n* = 75; 45%) were captured inside traps. There were significant differences among the four species in capture sites (Table 1). *Storeria occipitomaculata* and *O. vernalis* were captured significantly more often on roads than *Thamnophis* spp. Most snakes found in the grassland were *T. sirtalis parietalis*, and there were no *O. vernalis* found in this habitat. Most snakes found on ant mounds were *Thamnophis* spp.

There was no significant difference in direction of movement (entering or exiting the ant mound) in fall as compared to spring (Table 1). Few *S. occipitomaculata*, *T. radix*, and *T. sirtalis parietalis* were recaptured within the same season (11% in total; Table S2). There were only three individuals (2%; all *Thamnophis* spp.) recaptured between seasons; one of these individuals had

TABLE 3. Numbers of each species captured in different capture locations (trap, ant mound, road, or grassland) at the Souris River Bend Wildlife Management Area study site 2007–2010. Percentages within each category are indicated in brackets. Species are: Smooth Greensnake (*Opheodrys vernalis*), Northern Red-bellied Snake (*Storeria occipitomaculata*), Plains Garter Snake (*Thamnophis radix*), and Red-sided Garter Snake (*Thamnophis sirtalis parietalis*). Only visual searches were conducted in fall 2009.

Year, season	Capture location	Smooth Greensnake	Northern Red-bellied Snake	Plains Garter Snake	Red-sided Garter Snake	Total
2007, fall	Trap	0	16	4	2	22 (71)
	Mound	0	0	1	4	5 (16)
	Road	1	1	0	0	2 (6)
	Grassland	0	1	1	0	2 (6)
	Total	1	18	6	6	31
2008, spring	Trap	1	0	1	0	2 (50)
	Mound	0	0	0	0	0
	Road	0	0	0	0	0
	Grassland	0	0	1	1	2 (50)
	Total	1	0	2	1	4
2008, fall	Trap	4	4	5	24	37 (46)
	Mound	1	1	0	5	7 (9)
	Road	1	16	1	3	21 (27)
	Grassland	0	1	1	12	14 (18)
	Total	6	22	7	44	79
2009, spring	Trap	0	3	0	0	3 (13)
	Mound	0	0	0	0	0
	Road	0	2	1	0	3 (13)
	Grassland	0	4	1	13	18 (75)
	Total	0	9	2	13	24
2009, fall	Road	1	1	0	0	2 (50)
	Grassland	0	2	0	0	2 (50)
	Total	1	3	0	0	4
2010, spring	Trap	2	4	2	3	11 (46)
	Mound	0	0	1	0	1 (4)
	Road	0	0	0	0	0
	Grassland	0	8	1	3	12 (50)
	Total	2	12	4	6	24
Total	Trap	7 (64)	27 (42)	12 (57)	29 (41)	75 (45)
	Mound	1 (9)	1 (2)	2 (10)	9 (13)	13 (8)
	Road	3 (27)	20 (31)	2 (10)	3 (4)	28 (17)
	Grassland	0	16 (25)	5 (24)	29 (41)	50 (30)
	Total	11 (7)	64 (39)	21 (13)	70 (42)	166

also been recaptured within a season. No *O. vernalis* were recaptured. Few individuals were found dead on the road (3%) or dead in a trap or within the aluminum flashing (3%). When individuals were recaptured within the season, they were most frequently first captured in a trap entering the ant mound and secondly captured in a trap exiting the ant mound ($n = 11$; 61%). All other recaptures (first capture/second capture) were grassland/road (*T. sirtalis parietalis*; $n = 2$), grassland/grassland (*T. sirtalis parietalis*; $n = 2$), road/road (*S. occipitomaculata*; $n = 1$), mound/grassland (*T. sirtalis parietalis*; $n = 1$), and mound/mound (*T. sirtalis parietalis*, $n = 1$). A single *T. sirtalis parietalis* was recaptured, both times in a trap that exited the mound.

Thermal profiles of den sites

Air temperature and surface temperature (0 cm) were highly variable, and both stayed below freezing from 1 November to 1 March (Figure 6). Temperatures at a depth of 40 cm were more stable but were below freezing from 1 December to 1 April. Temperatures at a depth of 80 cm and 120 cm below the surface were also stable but largely stayed above freezing. In 2007–2008, the temperature at the 80 cm depth dipped to minus 0.1°C in February but stayed above freezing in 2008–2009.

Summer versus hibernation morphometrics

Adult females tended to be larger at the hibernation site than at summer sites (hibernation: 193.9 ± 4.4 mm; summer: 184.2 ± 2.2 mm; $t_{23.3} = 1.99$, $P = 0.06$). Sample sizes were unequal (summer: $n = 53$; hibernation: $n = 17$), and power was low (0.54; package pwr; function pwr.t2n.test). Sample sizes of 47 in each group would have detected a significant difference ($\alpha < 0.05$) with power = 0.80. There was no significant difference in SVL of adult males captured at the hibernation site compared to the summer sites (hibernation: 178.9 ± 5.4 mm; summer: 175.3 ± 4.0 mm respectively; $t_{26.2} = 0.55$, $P = 0.59$). For adult females, there was no sig-

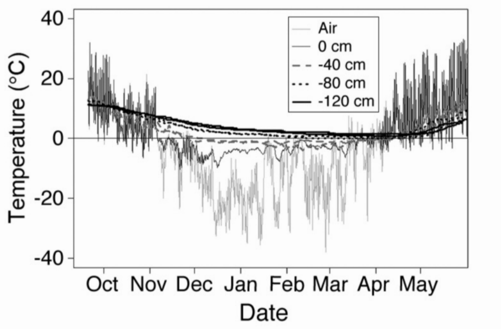

FIGURE 6. Mean temperatures from iButtons® placed at five den sites at Souris River Bend Wildlife Management Area over winter (20 September–22 May) in 2007–2008 and 2008–2009. Separate lines are shown for each winter; air temperature and surface temperature (0 cm) were only recorded in 2008–2009.

nificant difference in tail or head length (Table 4) for individuals captured at the hibernation site compared to those captured at summer sites. Adult females at the hibernation site had wider heads than those from summer sites (Table 4). For adult males, there was no significant difference in tail length, head width, or head length (Table 4) for individuals captured at the hibernation site compared to those captured at summer sites. Both adult females (Table 4; Figure 3b) and adult males (Table 4; Figure 3d) were significantly heavier for their body size at summer sites compared to the hibernation site.

Discussion

Our study examined demography, morphology, reproduction, habitat use, and hibernation in populations of *S. occipitomaculata* in southwestern Manitoba. This area is relatively arid and has an average daily temperature across the year of only 2.2°C (Environment Canada 2016). This is a stressful environment, but the explosive productivity of summer may be enough to compensate (Tuttle and Gregory 2014). Variation between populations we observed and other parts of this species' range may indicate how they make up for this stress.

The demographics of *S. occipitomaculata* were similar to the findings of Blanchard (1937) with adults accounting for the vast majority of observations. We suspect this may simply reflect the difficulty of finding juveniles using walking surveys. When using funnel traps at hibernation sites we collected more YOY and juveniles. However, Semlitsch and Moran (1984) also observed adult biased demographics using passive trapping.

Although we observed female biased SSD in this population, differences were not large. Male to female body size ratios were similar to populations from Michigan, Minnesota, and interestingly South Carolina, but less dimorphic than populations in Virginia, Indiana, or Pennsylvania (reviewed in Meshaka and Klippel 2011). Body sizes at our study sites were smaller than most other locales, including other northern populations (Criddle 1937; Meshaka and Klippel 2011). The minimum size of gravid snakes in our study was 154 mm,

TABLE 4. Linear models comparing tail length, head width, head length, and natural log-transformed mass of Red-bellied Snake (*Storeria occipitomaculata*) between summer and hibernation sites (site variable). Models were done separately for each sex. SVL = snout-vent length.

Model		Sex	*F*	*df*	*P*	Adjusted r^2
tail length =	site + SVL	F	0.24	2,64	0.790	0.02
	site		0.15	1,64	0.700	
	SVL		0.58	1,64	0.570	
	site + SVL	M	2.13	2,31	0.140	0.06
	site		0.19	1,31	0.670	
	SVL		4.08	1,31	0.050	
head width =	site + SVL	F	2.49	2,64	0.090	0.04
	site		4.61	1,64	0.040	
	SVL		0.37	1,64	0.550	
	site + SVL	M	7.12	2,31	0.003	0.27
	site		0.51	1,31	0.480	
	SVL		13.72	1,31	< 0.001	
head length =	site + SVL	F	5.80	2,54	0.005	0.15
	site		0.08	1,54	0.780	
	SVL		11.52	1,54	0.001	
	site + SVL	M	3.78	2,25	0.040	0.17
	site		0.04	1,25	0.840	
	SVL		7.5	1,25	0.010	
log(mass) =	site + SVL	F	36.61	2,64	< 0.001	0.52
	site		36.77	1,64	< 0.001	
	SVL		36.46	1,64	< 0.001	
	site + SVL	M	21.58	2,31	< 0.001	0.56
	site		4.50	1,31	0.040	
	SVL		38.66	1,31	< 0.001	

larger than those in South Carolina (Semlitsch and Moran 1984) and similar to Virginia (Mitchell 1994), but smaller than most of the rest of the range (Meshaka and Klippel 2011). The literature suggests, while body size in *S. occipitomaculata* varies, average clutch sizes are similar across its range. In our study, gravid females had similar clutch sizes to other populations (7–9 young; Meshaka and Klippel 2011). Northern reptiles are often thought to be constrained, having slower growth and delayed maturity relative to southern populations (Atkinson 1994) but this is not always the case (Angilletta *et al.* 2004; Tuttle and Gregory 2012, 2014). Early maturity is usually accomplished by increased growth to similar minimum size (Tuttle and Gregory 2012, 2014). *Storeria occipitomaculata* appears to mature at a smaller size in the southeast and northwest portions of its range while maintaining similar clutch sizes to physically larger populations elsewhere.

Although spring breeding has been widely reported in this species (Semlitsch and Moran 1984; Ernst and Ernst 2003; Meshaka and Klippel 2011) the abundance of males in late summer suggests August breeding activity (Blanchard 1937; Trapido 1940; Willson and Dorcas 2004). Although we did not directly observe any fall mating, it has been reported previously in Manitoba (Gregory 1977). Also, we found evidence of primary vitellogenesis pre-hibernation in two road-killed specimens collected in October 2007 and captured gravid females as early as 14 May. In our study, the majority of adult females captured during the summer were gravid (96%) suggesting annual reproduction similar to populations in the south (Semlitsch and Moran 1984). Reproduction should be limited by available resources (Aldridge 1979) and biennial reproduction appears to be common in northern snakes (Larsen *et al.* 1993; Gregory 2009). Mating in late summer/fall would provide females with a longer foraging and gestation period that would allow for greater provisioning of offspring *in utero* and may explain this population's ability to reproduce annually despite the short season. This is likely an important life history trait for a short lived species like *S. occipitomaculata* (Snider and Bowler 1992).

The habitat use by *S. occipitomaculata* we observed in Manitoba was similar to that found in Minnesota (Lang 1971) and Illinois (Brown and Phillips 2012) but differed from findings in Kansas (Pisani and Busby 2011). We found disproportionate use of grassland habitat on flat land or with south facing aspects. Pisani and Busby (2011) found the majority of their sample associated with moister habitats avoiding open habitats on north, west, and east slopes, and usually associated with water. These differences may reflect local availability, local adaptation, or perhaps a trade-off made by northern *S. occipitomaculata*, sacrificing osmotic preferences for thermal ones. This may be compensated for by microhabitat selection. In our study, most captures were under cover (87%) and more than half were found under plywood. This pattern may reflect our sampling methods rather than true preferences, although a preference for cover objects is common in small snakes (Halliday and Blouin-Demers 2015; Gregory and Tuttle 2016).

Land-cover use differed across the 10, two week periods of our study. Use of mixedwood forest by *S. occipitomaculata* occurred in spring, while they used roads and grassland most commonly in late summer and fall (at the hibernation site). Semlitsch and Moran (1984) suggested that moisture gradients and food availability drove activity pulses and habitat choice in this species in South Carolina. Alternatively, use of grasslands in late summer may reflect habitat preferences of gravid females, because grasslands are warmer than forest habitats in keeping with the cold climate hypothesis (Tinkle and Gibbons 1977) although we did not observe a sex bias in habitat choice.

Over the course of three years, the first arrival of *S. occipitomaculata* at hibernation sites was later than other species and was consistently associated with the first frost or nighttime temperatures below freezing similar to Lang (1971). In cold regions such as Minnesota or Manitoba, it is difficult to understand why a small snake would arrive at a hibernaculum so late in the season when hard frosts are likely. Although *S. occipitomaculata* appears to be able to cope with several days of cold weather, a prolonged or particularly hard frost may cause mortality (Lang 1971). Critical thermal minimum (CT_{min}) has not been determined in *S. occipitomaculata* but ranges from 2.5 to 11.5°C in other snake species with body size, species, and latitudinal effects (reviewed in Cox *et al.* 2018) so it likely above 0°C. In the smaller Ring-necked Snake (*Diadophis punctatus*) CT_{min} was 11.5°C and decreased with increasing body size, suggesting that small individuals require higher CT_{min} (Cox *et al.* 2018).

The use of ant mounds by *S. occipitomaculata, O. vernalis, and T. sirtalis parietalis* has been previously reported by Criddle (1937), Carpenter (1953), Lang (1971), and Pisani (2009). These mounds do not offer a thermal advantage over the winter compared to surrounding soil (Scherba 1962). However, due to their insulation and ability to collect solar radiation, these sites are warmer and more stable during the active season (Scherba 1962; Duff *et al.* 2016), thereby potentially increasing season length. The thermal profiles we generated at the hibernation site indicated stability increases with soil depth but, even at 80 cm, temperatures dipped below freezing. This is similar to the temperature profile generated by Lang (1971), although the frost lines at most of the ant mounds he investigated were slightly deeper, likely due to the shallow water table at our hibernation site. The temperature profile of the mounds suggests that these snakes would have to hibernate near or below the water table (Costanzo 1989) which was ~120 cm in our study. Criddle (1937) found this to be the case when he excavated a mound near Treesbank, Manitoba and found many of the snakes at ~144 cm depth, in contact with the water table. Without these abandoned ant mounds *S. occipitomaculata,* poorly suited to true burrowing with its kinetic skull and large eyes, would be unable to access such thermally stable and humid refuges (Pisani 2009). These sites, or other similar fossorial retreats, are likely critical for the persistence of this species at such northern climates.

Caution must be taken when comparing snapshots of populations' life histories (Seigel and Fitch 1985). There is a great deal of variation reported across the species' range and among individuals, and like Meshaka and Klippel (2011), we found a limited effect of latitude between the population we observed and the rest of the range. This observation adds to our understanding of how this species can survive in an area that is climatically unsuitable for terrestrial activity for much of the year. In this area, this species appears to use relatively warm habitats, rapid reproduction, and abandoned ant nests to persist and thrive. Productive habitats, such as the northern Great Plains, may allow this species to adopt a "fast" lifestyle that favours early maturity and higher than expected annual fecundity, with most females reproducing annually (Tuttle and Gregory 2014). Much remains unknown and future studies should confirm the genetic or environmental underpinning of body size at maturity and clutch size along with local diet, timing of breeding, and the drivers and risks associated with late-season migration for this species.

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Literature Cited

Aldridge, R.D. 1979. Female reproductive cycles of the snakes *Arizona elegans* and *Crotalus viridis*. Herpetologica 35: 256–261.

Angilletta, M.J., Jr., T.D. Steury, and M.W. Sears. 2004. Temperature, growth rate, and body size in ectotherms: fitting pieces of a life-history puzzle. Integrative and Comparative Biology 44: 498–509. https://doi.org/10.1093/icb/44.6.498

Atkinson, D. 1994. Temperature and organism size: a biological law for ectotherms? Advances in Ecological Research 25: 1–58. https://doi.org/10.1016/S0065-2504(08)60212-3

Berrigan, D., and E.L. Charnov. 1994. Reaction norms for age and size at maturity in response to temperature: a puzzle for life historians. Oikos 70: 474–478. https://doi.org/10.2307/3545787

Blackburn, D.G., K.E. Anderson, A.R. Johnson, S.R. Knight, and G.S. Gavelis. 2009. Histology and ultrastructure of the placental membranes of the viviparous brown snake, *Storeria Dekayi* (Colubridae: Natricinae). Journal of Morphology 270: 1137–1154. https://doi.org/10.1002/jmor.10650

Blanchard, F.N. 1937. Data on the natural history of the red-bellied snake, *Storeria occipitomaculata* (Storer), in Northern Michigan. Copeia 1937: 151–162. https://doi.org/10.2307/1436135

Blouin-Demers, G., K.A. Prior, and P.J. Weatherhead. 2002. Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland. Journal of Zoology 256: 1–10. https://doi.org/10.1017/S0952836902000018

Blouin-Demers, G., and P.J. Weatherhead. 2001. Thermal ecology of black rat snakes (*Elaphe obsoleta*) in a thermally challenging environment. Ecology 82: 3025–3043. https://doi.org/10.1890/0012-9658(2001)082[3025:TEOBRS]2.0.CO;2

Brown, E.E. 1979. Stray food records from New York and Michigan snakes. American Midland Naturalist 102: 200–203. https://doi.org/10.2307/2425088

Brown, L.E., and C.A. Phillips. 2012. Distribution, habitat, and zoogeography of the semifossorial red-bellied snake *Storeria occipitomaculata* (Storer) in Illinois. Illinois Natural History Survey Bulletin 39: 297–322.

Carpenter, C.C. 1953. A study of hibernacula and hibernating associations of snakes and amphibians in Michigan. Ecology 34: 74–80. https://doi.org/10.2307/1930310

Cook, F.R. 1984. Introduction to Canadian Amphibians and Reptiles. National Museum of Natural Sciences, National Museums of Canada, Ottawa, Ontario, Canada.

Costanzo, J.P. 1989. Effects of humidity, temperature, and submergence behavior on survivorship and energy use in hibernating garter snakes, *Thamnophis sirtalis*. Canadian Journal of Zoology 67: 2486–2492. https://doi.org/10.1139/z89-351

Cox, R.M., M.A. Butler, and H.B. John-Alder. 2007. The evolution of sexual size dimorphism in reptiles. Pages 38–49 *in* Sex, Size and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. *Edited by* D.J. Fairbairn, W.U. Blanckenhorn, and T. Székely. Oxford University Press, New York, New York, USA. https://doi.org/10.1093/acprof:oso/9780199208784.003.0005

Cox, C.L., M.L. Logan, O. Bryan, D. Kaur, E. Leung, J. McCormack, J. McGinn, L. Miller, C. Robinson, J. Salem, J. Scheid, T. Warzinski, and A.K. Chung. 2018. Do ring-necked snakes choose retreat sites based upon thermal preferences? Journal of Thermal Biology 71: 232–236. https://doi.org/10.1016/j.jtherbio.2017.11.020

Criddle, S. 1937. Snakes from an ant hill. Copeia 1937: 142. https://doi.org/10.2307/1436960

Duff, L.B., T.M. Urichuk, L.N. Hodgins, J.R. Young, and W.A. Untereiner. 2016. Diversity of fungi from the mound nests of *Formica ulkei* and adjacent non-nest soils. Canadian Journal of Microbiology 62: 562–571. https://doi.org/10.1139/cjm-2015-0628

Environment Canada. 2016. National Climate Data and Information Archive, Environment Canada. Accessed 18 May 2018. https://tinyurl.com/ya5pe4cl.

Ernst, C.H., and E.M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Books, Washington, DC, USA.

ESRI. 2011. ArcGIS Desktop. Redlands, California, USA.

Fitch, H.S. 1981. Sexual size differences in reptiles. University of Kansas Museum of Natural History Miscellaneous Publications 70: 1–72.

Fitch, H.S. 1987. Collecting and life-history techniques. Pages 143–164 *in* Snakes: Ecology and Evolutionary Biology. *Edited by* R.A. Seigel, J.T. Collins, and S.S. Novak. Macmillan, New York, New York, USA.

Gienger, C.M., and D.D. Beck. 2011. Northern Pacific Rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula. Canadian Journal of Zoology 89: 1084–1090. https://doi.org/10.1139/z11-086

Gregory, P.T. 1977. Life history observations of three species of snakes in Manitoba. Canadian Field-Naturalist 91: 19–27. Accessed 11 November 2018. https://biodiversitylibrary.org/page/28061222.

Gregory, P.T. 2009. Northern lights and seasonal sex: the reproductive ecology of cool-climate snakes. Herpetologica 65: 1–13. https://doi.org/10.1655/0018-0831-65.1.1

Gregory, P.T., and K.N. Tuttle. 2016. Effects of body size and reproductive state on cover use of five species of temperate-zone Natricine snakes. Herpetologica 72: 64–72. https://doi.org/10.1655/HERPETOLOGICA-D-15-00021

Halliday, W.D., and G. Blouin-Demers. 2015. Efficacy of coverboards for sampling small northern snakes. Herpetology Notes 8: 309–314.

Harvey, D.S., and P.J. Weatherhead. 2006a. Hibernation site selection by Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) near their northern range limit. Journal of Herpetology 40: 66–73. https://doi.org/10.1670/89-05A.1

Harvey, D., and P.J. Weatherhead. 2006b. A test of the hierarchical model of habitat selection using eastern massasauga rattlesnakes (*Sistrurus c. catenatus*). Biological Conservation 130: 206–216. https://doi.org/10.1016/j.biocon.2005.12.015

Kiester, A.R. 1971. Species density of North American amphibians and reptiles. Systematic Biology 20: 127–137. https://doi.org/10.2307/2412053

King, R.B. 1993. Determinants of offspring number and size in the brown snake, *Storeria dekayi*. Journal of Herpetology 27: 175–185. https://doi.org/10.2307/1564934

Lang, J.W. 1969. Hibernation and movements of *Storeria occipitomaculata* in northern Minnesota. Journal of Herpetology 3: 196–197.

Lang, J.W. 1971. Overwintering of three species of snakes in northwestern Minnesota. M.Sc. thesis, University of North Dakota, Grand Forks, North Dakota, USA.

Larsen, K.W., P.T. Gregory, and R. Antoniak. 1993. Reproductive ecology of the common garter snake *Thamnophis sirtalis* at the northern limit of its range. American Midland Naturalist 129: 336–345. https://doi.org/10.2307/2426514

Manitoba Land Initiative. 2012. Manitoba Conservation and Water Stewardship. Accessed 5 February 2012. https://mli2.gov.mb.ca.

Meshaka, W.E., and A.N. Klippel. 2011. Seasonal activity, reproduction, and growth of the Northern Redbelly Snake, *Storeria occipitomaculata occipitomaculata* (Storer, 1839), from Pennsylvania. Journal of Kansas Herpetology 37: 16–20.

Mitchell, J.C. 1994. The Reptiles of Virginia. Smithsonian Institution Press, Washington, DC, USA.

Pisani, G. 2009. Use of an active ant nest as a hibernaculum by small snake species. Transactions of the Kansas Academy of Science. Kansas Academy of Science 112: 113–118. https://doi.org/10.1660/062.112.0215

Pisani, G.R., and W.H. Busby. 2011. Ecology of the Smooth Earth Snake (*Virginia valeriae*) and Redbelly Snake (*Storeria occipitomaculata*) in Northeastern Kansas. Kansas Biological Survey, Lawrence, Kansas, USA.

R Development Core Team. 2017. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Scherba, G. 1962. Mound temperatures of the ant *Formica ulkei* Emery. American Midland Naturalist 67: 373–385. https://doi.org/10.2307/2422715

Seigel, R.A., and H.S. Fitch. 1985. Annual variation in reproduction in snakes in a fluctuating environment. Journal of Animal Ecology 54: 497–505. https://doi.org/10.2307/4494

Semlitsch, R.D., and G.B. Moran. 1984. Ecology of the redbelly snake (*Storeria occipitomaculata*) using mesic habitats in South Carolina. American Midland Naturalist 111: 33–40. https://doi.org/10.2307/2425539

Shine, R. 1994. Sexual size dimorphism in snakes revisited. Copeia 1994: 326–346. https://doi.org/10.2307/1446982

Shine, R., J. Webb, A. Lane, and R. Mason. 2006. Flexible mate choice: a male snake's preference for larger females is modified by the sizes of females encountered. Animal Behaviour 71: 203–209. https://doi.org/10.1016/j.anbehav.2005.04.005

Snider, A.T., and J.K. Bowler. 1992. Longevity of reptiles and amphibians in North American collections. Herpetological Circulars No. 21. Society for the Study of Amphibians and Reptiles Publications, Lawrence, Kansas, USA.

Tinkle, D.W., and J.W. Gibbons. 1977. The distribution and evolution of viviparity in reptiles. Miscellaneous Publications, Museum of Zoology, University of Michigan 154: 1–55.

Trapido, H. 1940. Mating time and sperm viability in *Storeria*. Copeia 1940: 107–109. https://doi.org/10.2307/1439051

Trapido, H. 1944. The snakes of the genus *Storeria*. American Midland Naturalist 31: 1–84. https://doi.org/10.2307/2421382

Tuttle, K.N., and P.T. Gregory. 2012. Growth and maturity of a terrestrial ectotherm near its northern distributional limit: does latitude matter? Canadian Journal of Zoology 90: 758–765. https://doi.org/10.1139/z2012-044

Tuttle, K.N., and P.T. Gregory. 2014. Reproduction of the Plains Garter Snake, *Thamnophis radix*, near its northern range limit: more evidence for a "fast" life history. Copeia 2014: 130–135. https://doi.org/10.1643/CH-13-119

Weatherhead, P.J., J.H. Sperry, G.L.F. Carfagno, and G. Blouin-Demers. 2012. Latitudinal variation in thermal ecology of North American ratsnakes and its implications for the effect of climate warming on snakes. Journal of Thermal Biology 37: 273–281. https://doi.org/10.1016/j.jtherbio.2011.03.008

Willson, J.D., and M.E. Dorcas. 2004. Aspects of the ecology of small fossorial snakes in the western Piedmont of North Carolina. Southeastern Naturalist 3: 1–12. https://doi.org/10.1656/1528-7092(2004)003[0001:AOTEOS]2.0.CO;2

Wright, A.H., and A.A. Wright. 1957. Handbook of Snakes of the United States and Canada. Cornell University Press, Ithaca, New York, USA.

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SUPPLEMENTARY MATERIAL:

TABLE S1. Numbers of Red-bellied Snake (*Storeria occipitomaculata*) in three age classes (young-of-year [YOY], juvenile, adult) for each sex that were captured during summer surveys 2007–2009 at Spruce Woods Provincial Park (SWPP), Assiniboine Corridor Wildlife Management Area (ACWMA), Oak Lake, and Canadian Forces Base (CFB) Shilo.

TABLE S2. Number of captures, recaptures, and dead animals for individuals captured at the hibernation site (Souris River Bend Wildlife Management Area) during spring and fall surveys 2007–2010.

Spring Peeper (*Pseudacris crucifer*) in Labrador, Canada: an update

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Abstract

Spring Peeper (*Pseudacris crucifer*) was first confirmed in Labrador in 1998, when vocalizations were recorded near Happy Valley-Goose Bay. Prior to this, only unsubstantiated reports of Spring Peepers in Labrador existed. In 2006, we visually documented nine Spring Peepers at six locations west of Happy Valley-Goose Bay, in the lower Churchill River valley. In 2014, using auditory surveys, we further documented 1–10 Spring Peepers calling at 13 additional locations in the same general area. These new records support earlier findings and provide additional information on the species at the extreme northeastern edge of its range.

Key words: Amphibian; Spring Peeper; *Pseudacris crucifer*; range; Labrador

Introduction

Bleakney (1954) reported that a student described watching "tiny tree frogs with suction disc finger tips and huge vocal sacs" in a ditch near Menihek Lake Camp in western Labrador, suggesting that the frogs in question were Spring Peepers (*Pseudacris crucifer*). Maunder (1983) subsequently reported that two environmental personnel working in Labrador heard what they believed to be at least one Spring Peeper calling on the evening of 11 July 1980 near Thomas Brook (53.17°N, 60.93°W) in the lower Churchill River Valley.

However, the first tangible evidence for Spring Peepers in Labrador was provided by Bergman (1999). In her account, Bergman described hearing infrequent calls of single Spring Peepers throughout the day on 14 June 1998 while canoeing on the Peters and Goose Rivers (between 53.33°N, 60.78°W and 53.40°N, 60.43°W), as well as a large chorus of Spring Peepers that same evening adjacent to the Goose River (53.38°N, 60.48°W). The following evening, she made an audio recording of two Spring Peepers calling in a small marsh on the south bank of the Goose River (53.37°N, 60.50°W). This recording is vouchered in the natural history collection of The Rooms Provincial Museum in St. John's, Newfoundland (NFM HE-122). In an addendum to her publication, Bergman indicated that she had been informed that school children had observed "weensy tree frogs" with "sticky feet" that were consistent in colour with Spring Peepers, in the trees and bushes near Gosling and Alexander Lakes, near Happy Valley-Goose Bay.

Since Bergman's (1999) publication, there have been no additional peer-reviewed, published records of the species in Labrador. However, in 2006, a series of field-based studies was initiated in support of an environmental assessment of the Lower Churchill Hydroelectric Generation Project. As part of these studies, we documented Spring Peepers and other amphibians along the north and south sides of the lower Churchill River Valley in central Labrador.

Methods

Our study area focussed on the segment of the lower Churchill River Valley between Horse Island Rapids (52.9965°N, 61.5323°W) and Muskrat Falls (53.2247°N, 60.8640°W; Figure 1), in the vicinity of the abovementioned hydroelectric project. Specifically, we surveyed natural habitats within 2 km of the river and its tributaries, primarily in road accessible areas. Note: on completion of the hydroelectric project, the projected reservoir-related flooding will not inundate much of the area we surveyed (see Figure 2-1 and Figure A-1 in Stassinu Stantec 2014).

Ground surveys to locate and identify amphibians occurred 13–15 July 2006 in 27 locations in our study area, as well as in areas along the Goose River and Lake Winokapau (Minaskuat Inc. 2008a). To supplement these efforts, observations of amphibians were collected during five other field programs targetting other components (e.g., wetland and rare plant surveys), but inclusive of suitable habitat for amphibians. Combined, these surveys spanned a period from 24 June to 14 September 2006 and involved visits to >400 locations over 75 field days (Minaskuat Inc. 2008b,c,d,e,f). All surveys were conducted by groups of 2–4 people (with at least one wildlife biologist per group) operating per field day. Groups walked through wetlands and forested habitats as they were encountered and documented all amphibians heard or observed.

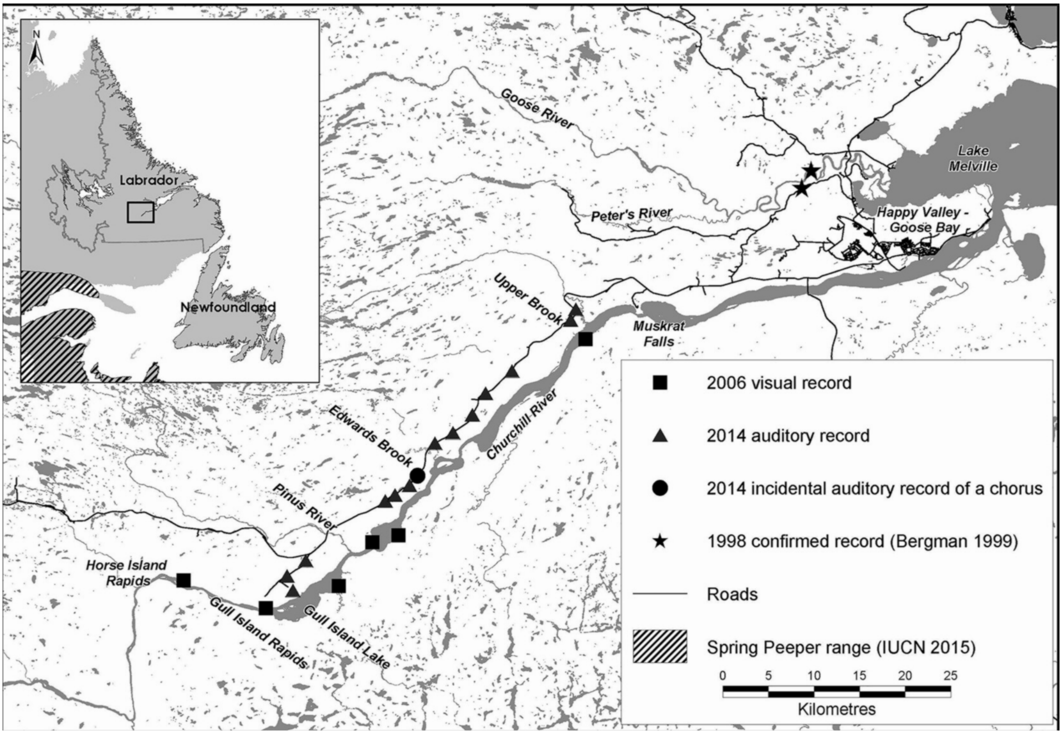

FIGURE 1. Spring Peeper (*Pseudacris crucifer*) records in Labrador, Canada.

To gain a more complete understanding of the extent of Spring Peeper distribution within our study area, we conducted systematic auditory surveys in 2014. Twenty-three locations along the lower Churchill River Valley were surveyed over three evenings, 16–18 June, coinciding with the expected breeding period for Spring Peeper (based on calling activity) in the region. Auditory survey locations were spaced a minimum of 0.8 km apart (based on standard operating procedures: nocturnal amphibian survey [unpubl.]; Stantec, Corner Brook, Newfoundland and Labrador; March 2014) along road-accessible areas between Gull Island Lake (52.9845°N, 61.3543°W) and Muskrat Falls.

Surveys started ~0.5 h after sunset (between 2110 and 2130) and were conducted only when winds were <20 km/h, there was little or no precipitation, and air temperatures were >10°C. At each stop, a two-person team listened for calling Spring Peepers for 5 minutes. If the number of Spring Peepers calling could not be distinguished (because of call overlap), we estimated a range for the total number of Spring Peepers in the area (e.g., 6–10 individuals).

Results

During the 2006 ground surveys, we found nine Spring Peepers at six locations (Table 1). On 24 July, three recently transformed froglets (Figure 2a) and one adult (Figure 2b) were found in a wetland complex made up of bog, swamp, and shallow water, located at 53.2247°N, 60.8640°W (Figure 2c). Between 23 and 27 July, five adults were found at five other locations between Horse Island Rapids and Pinus River (53.0363°N, 61.1796°W; Table 1). We did not capture and preserve any of the frogs encountered but took representative images (Figures 2a and 2b) that have been deposited in the natural history collections of The Rooms Provincial Museum (NFM HE-121).

During the 2014 auditory surveys, we documented Spring Peepers calling at an additional 13 locations (Table 1). We documented 6–10 individuals at three locations, 2–5 individuals at another three locations, two individuals at two separate locations, and a single individual at the remaining five locations. We did not make any audio recordings of the calls. All Spring Peeper observations in 2014 were from locations different from those identified in 2006. We did not hear any choruses during the surveys; however, K.R.R. previously heard a Spring Peeper chorus within the study area (53.0942°N, 61.1457°W) while conducting avifauna surveys in late May of the same year. This location, a shallow water wetland along the Trans Labrador Highway, was visited again during auditory sampling on 14 June, but no Spring Peepers were calling at that time.

TABLE 1. Visual and auditory records of Spring Peepers (*Pseudacris crucifer*) in the lower Churchill River Valley, Labrador, Canada, in 2006 and 2014. For the auditory records, the general location and coordinates indicate the position of the biologist during the survey.

General location and habitat	No. peepers	Year	Date	Survey type	Location
Alder (*Alnus* sp.) shrub habitat on the banks of a tributary inflow to the Churchill River (southside) near Gull Island Lake	1 adult	2006	July 23	Visual	52.9880°N 61.2794°W
Open fen/bog along the northside of the Churchill River near Horse Island Rapids	1 adult	2006	July 23	Visual	52.9965°N 61.5323°W
Wetland along the southside of the Churchill River near Pinus River	1 adult	2006	July 23	Visual	53.0363°N 61.1796°W
Bog/swamp/shallow water wetland complex along the southside of the Churchill River near Lower Brook.	1 adult 3 juveniles	2006	July 24	Visual	53.2247°N 60.8640°W
Open bog along the northside of the Churchill River near Gull Island rapids	1 adult	2006	July 25	Visual	52.9675°N 61.3989°W
Mixed deciduous forest along the northside of the Churchill River near Pinus River	1 adult	2006	July 29	Visual	53.0302°N 61.2225°W
Gull Island road	6–10	2014	June 16	Auditory	52.9988°N 61.3633°W
Gull Island road	2–5	2014	June 16	Auditory	52.9988°N 61.3633°W
Gull Island road	1	2014	June 16	Auditory	53.0137°N 61.3322°W
TLH* between Pinus River and Edwards Brook	1	2014	June 16	Auditory	53.0703°N 61.1996°W
TLH between Pinus River and Edwards Brook	2–5	2014	June 16	Auditory	53.0762°N 61.1836°W
TLH near Edwards Brook	1	2014	June 16	Auditory	53.1261°N 61.1158°W
TLH between Pinus River and Edwards Brook	2	2014	June 17	Auditory	53.0852°N 61.1594°W
TLH between Edwards Brook and Lower Brook	2	2014	June 17	Auditory	53.1360°N 61.0857°W
Along the TLH	6–10	2014	June 17	Auditory	53.1529°N 61.0531°W
Along the TLH	1	2014	June 17	Auditory	53.1739°N 61.0308°W
TLH between Edwards Brook and Lower Brook	6–10	2014	June 17	Auditory	53.1952°N 60.9862°W
TLH between Edwards Brook and Lower Brook	1	2014	June 18	Auditory	53.2439°N 60.8875°W
TLH between Edwards Brook and Lower Brook	2–5	2014	June 18	Auditory	53.2543°N 60.8785°W

*TLH = Trans Labrador Highway.

FIGURE 2. Spring Peepers (*Pseudacris crucifer*) captured in a small wetland complex adjacent to the main stem of the lower Churchill River, Labrador, on 24 July 2006 (53.2247°N, 60.8640°W). a. Recently transformed Spring Peeper captured in a dip net. b. Adult Spring Peeper found in a peat moss (*Sphagnum* sp.) dominant carpet punctuated by patches of low shrubs, graminoids, and forbs. c. Aerial view of the location of Spring Peeper captures. Photos: M.D. MacDonald.

Discussion

To date, all tangible records of Spring Peepers in Labrador have been from within the High Boreal Forest (Lake Melville) Ecoregion (Meades 1990). This ecoregion is considered unique in Labrador in that summers are warmer and shorter and winters less severe than in the adjacent ecoregions (Meades 1990; Way *et al.* 2016). The ecoregion itself has been described as a "thermal oasis" because it supports several species, including Leopard Frog (*Lithobates pipiens*), that are typically only found further south (Maunder 2016). The occurrence of more "southern" species in the ecoregion has been attributed to a historical northward shift in warm temperatures and, consequently, warmer-area species, followed by a southward shift and subsequent cooling that left some of those species trapped in the area (Maunder 2016; see also Vilks and Mudie 1983; Way *et al.* 2016).

Relative to our study area in the lower Churchill River, the nearest records of Spring Peepers are from >400 km away, near Sept-Îles, Quebec (Bleakney 1954; Bider and Matte 1996) and, possibly, western Labrador near Menihek Lake Camp (Bleakney 1954). As such, Spring Peeper populations near Happy Valley-Goose

Bay and along the lower Churchill River Valley appear to be functionally isolated from neighbouring populations to the south and west and are considered "disjunct". However, as we did not survey any areas outside of the lower Churchill River Valley and given the limited amphibian-related research in Labrador in general, it remains possible that Spring Peepers, like Wood Frogs (*Rana sylvatica*; Chubbs and Phillips 1998), occur in isolated populations elsewhere in Labrador. Whether the populations of Spring Peepers documented here and by Bergman (1999) are disjunct from populations in neighbouring Quebec requires further study.

Before our study, the only confirmed record of Spring Peepers in Labrador was Bergman's (1999) account of this species near Happy Valley-Goose Bay. Here, we documented the presence of Spring Peeper over a larger geographic area in central Labrador, including 19 areas south and west of Bergman's observations. Bergman indicated that the closest confirmed record of Spring Peeper was 500 km to the southwest of her observation, near Sept-Îles, Quebec. Our study has narrowed this gap by approximately 80 km and has provided additional information on this species at the extreme northeastern edge of its range.

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Literature Cited

Bergman, C.M. 1999. Range extension of Spring Peepers, *Pseudacris crucifer*, in Labrador. Canadian Field-Naturalist 113: 309–310. Accessed 2 October 2017. https://biodiversitylibrary.org/page/34235171.

Bider, J.R., and S. Matte. 1996. The Atlas of Amphibians and Reptiles of Québec. St. Lawrence Valley Natural History Society, Sainte-Anne-de-Bellevue, Quebec, and Ministère de l'Environment et de la Faune, Direction de la faune et des habitats, Québec, Quebec, Canada.

Bleakney, J.S. 1954. Range extensions of amphibians in eastern Canada. Canadian Field-Naturalist 68: 165–171. Accessed 2 October 2017. https://biodiversitylibrary.org/page/28111797.

Chubbs, T.E., and F.R. Phillips. 1998. Distribution of the wood frog, *Rana sylvatica*, in Labrador: an update. Canadian Field-Naturalist 112: 329–331. Accessed 2 October 2017. https://biodiversitylibrary.org/page/34257677.

IUCN (International Union for Conservation of Nature). 2015. P*seudacris crucifer*. The IUCN red list of threatened species, version 2017-2. IUCN, Cambridge, United Kingdom. Accessed 6 November 2017. http://maps.iucnredlist.org/map.html?id=55892.

Maunder, J.E. 1983. Amphibians of the Province of Newfoundland. Canadian Field-Naturalist 97: 33–46. Accessed 29 November 2017. https://biodiversitylibrary.org/page/28008727.

Maunder, J.E. 2016. Labrador's "warm oasis": who knows what mushrooms lurk there? Omphalina 7: 4–5. Accessed 29 November 2017. https://issuu.com/nlmushrooms/docs/o-vii-5.

Meades, S.J. 1990. Natural regions of Newfoundland and Labrador — Part 4. Technical report. Protected Areas Association, St. John's, Newfoundland and Labrador, Canada. https://doi.org/10.13140/RG.2.1.2704.2165

Minaskuat Inc. 2008a. Herpetile surveys in the lower Churchill River Valley. Environmental baseline report LCP-535746. Newfoundland and Labrador Hydro, St. John's, Newfoundland and Labrador, Canada.

Minaskuat Inc. 2008b. Forest songbird surveys. Environmental baseline report LCP535750. Newfoundland and Labrador Hydro, St. John's, Newfoundland and Labrador, Canada.

Minaskuat Inc. 2008c. Project area ecological land classification. Environmental baseline report LCP535722. Newfoundland and Labrador Hydro, St. John's, Newfoundland and Labrador, Canada.

Minaskuat Inc. 2008d. Rare plant survey in the lower Churchill River Valley. Environmental baseline report LCP535725. Newfoundland and Labrador Hydro, St. John's, Newfoundland and Labrador, Canada.

Minaskuat Inc. 2008e. Wetland assessment and evaluation. Environmental baseline report LCP535750. Newfoundland and Labrador Hydro, St. John's, Newfoundland and Labrador, Canada.

Minaskuat Inc. 2008f. Wildlife habitat associations in the lower Churchill River Valley. Environmental baseline report LCP535740. Newfoundland and Labrador Hydro, St. John's, Newfoundland and Labrador, Canada.

Stassinu Stantec Ltd. 2014. Nalcor Energy Lower Churchill Project environmental effects monitoring program – 2014 herptile: field surveys for Spring Peeper, Blue-spotted Salamander and Northern Two-lined Salamander (interim report). Nalcor Energy, St. John's, Newfoundland and Labrador, Canada. Accessed 2 October 2017. https://muskratfalls.nalcorenergy.com/wp-content/uploads/2014/08/2014-Herptile-Environmental-Effects-Monitoring-Program.pdf.

Vilks, G., and P.J. Mudie. 1983. Evidence for postglacial paleoceanographic and paleoclimatic changes in Lake Melville, Labrador, Canada. Arctic and Alpine Research 15: 307–331. https://doi.org/10.2307/1550827

Way, R.G., A.G. Lewkowicz, and P.P. Bonnaventure. 2016. Development of moderate-resolution gridded monthly air temperature and degree-day maps for the Labrador-Ungava region of northern Canada. International Journal of Climatology 37: 493–508. https://doi.org/10.1002/joc.4721

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Long-toed Salamander (*Ambystoma macrodactylum*) hibernacula in Waterton Lakes National Park revealed using Passive Integrated Transponder telemetry

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Abstract

Long-toed Salamanders (*Ambystoma macrodactylum*) spend most of their lives on land; however, their fossorial nature makes studying their use of habitat difficult. Using Passive Integrated Transponder (PIT) telemetry over two years, we found and characterized nine overwintering sites of Long-toed Salamanders in the vicinity of Linnet Lake and Stable Pond in Waterton Lakes National Park, excavating five of them. These sites were typically associated with stumps and decaying root systems that gave the salamanders access to deep subterranean hibernacula. Overwintering sites were located up to 168 m from the shores of breeding ponds. Given the importance of such terrestrial sites to these populations of Long-toed Salamanders, it is vital that conservation efforts include the preservation of these features and ensure that a sufficient area surrounding breeding ponds remains undisturbed.

Key words: Long-toed Salamander; *Ambystoma macrodactylum*; amphibian; terrestrial habitat; conservation; overwintering refugia; Waterton Lakes National Park; Alberta

Introduction

Long-toed Salamander (*Ambystoma macrodactylum*) is a widespread, relatively common species of "mole salamander" (Ambystomatidae) of western North America, whose Canadian range includes portions of British Columbia and Alberta (Petranka 1998; Lee-Yaw and Irwin 2012). In Alberta, it is patchily distributed, mainly along the east slopes of the Rocky Mountains, defining the northeastern edge of the species' global range. Isolated Alberta populations occur near Fairview in the north and Stavely in the south (Russell and Bauer 2000).

Provincially, Long-toed Salamander is listed as a species of special concern (Alberta Environment and Parks 2014). Although Alberta's populations of the Long-toed Salamander currently appear stable, a number of threats have been identified. These include energy sector and forestry activity, urbanization, fish stocking, and the widespread construction of roads near breeding ponds (Graham and Powell 1999).

Long-toed Salamanders in Alberta breed mainly in shallow, productive, fish-free ponds and lakes in a variety of landscape types (Graham and Powell 1999; Pearson 2004). Adults enter breeding ponds at ice-off and leave by early summer, whereas larvae metamorphose and leave ponds in late summer and early fall (Graham and Powell 1999). Use of the terrestrial environment by juveniles and adults has been more difficult to document because of the subterranean habits of the species. During the active season, Long-toed Salamanders, like other mole salamanders, are typically found in the leaf litter and emerge on moist nights to forage for invertebrate prey. In Alberta, they occupy home ranges of 115–280 m^2 and can travel up to 900 m from breeding ponds to reach these sites (Sheppard 1977; Graham 1997).

Little is known about the species' overwintering locations. In the single study exploring this aspect of habitat use in Alberta, Sheppard (1977) employed radioactive marking to locate three Long-toed Salamander hibernacula in the Bow Valley. Information on overwintering behaviour can be critical for the conservation of northern amphibian populations, where the existence of appropriate hibernation sites, near breeding ponds and foraging habitat, may dictate the size, distribution, and persistence of populations (Browne and Paszkowski 2010).

Fine-scale patterns of terrestrial habitat use are often difficult to document for amphibians at any time of year, because of their small body size and cryptic nature. Technical limitations come into play when applying tracking devices to small-bodied vertebrates, either internally or externally, and transmitters can affect behaviour and survivorship (Weatherhead and Blouin-Demers 2004; Barron *et al.* 2010). However, radio-frequency identification (RFID) and Passive Integrated

Transponder (PIT) technologies provide a convenient method for investigating habitat use and movement patterns of small species, including amphibians (Cucherousset *et al.* 2008; Hamed *et al.* 2008; Connette and Semlitsch 2012; Ryan *et al.* 2014). PIT tags and "PIT telemetry" can liberate investigators from the size constraints and battery-life limitations of conventional radio telemetry.

We used this technology to study a population of Long-toed Salamanders in Waterton Lakes National Park in southwestern Alberta. The Long-toed Salamanders breeding in Linnet Lake and nearby Stable Pond have been the subject of research since the 1990s, in part because of mortality of migrating salamanders on the adjacent Entrance Road (Fukumoto and Herrero 1998). In 2008, four tunnels under Entrance Road were installed to reduce roadkill at Linnet Lake (Pagnucco *et al.* 2012). We captured Long-toed Salamanders at Linnet Lake (2013, 2014) and Stable Pond (2014) and PIT tagged them. At Linnet Lake our fundamental objective was to assess tunnel use with stationary RFID antennae as animals moved to and from this breeding site (Atkinson-Adams 2015). In addition, we used PIT telemetry to investigate the use of terrestrial habitat surrounding breeding sites during the summer and fall of 2013 (Linnet Lake) and 2014 (Stable Pond). One goal of these surveys was to locate Long-toed Salamander hibernation sites and characterize their above- and below-ground features. We postulated that one reason that Long-toed Salamanders crossed Entrance Road was to move between aquatic breeding sites and specific terrestrial macro- or micro-habitats required for overwintering.

Study Area

Research centred on two breeding sites in Waterton Lakes National Park, Alberta: Linnet Lake (in 2013 and 2014) and Stable Pond (in 2014; Figure 1). Linnet Lake (49.07°N, 113.9°W) is a small (3.9 ha), shallow (5 m maximum depth) lake at an elevation of ~1260 m in a bowl-like catchment basin. The vegetation around the lake is dominated by stands of Douglas Fir (*Pseudotsuga menziesii* (Mirbel) Franco) and poplar (*Populus* spp.), with an understorey of small trees and shrubs, such as Chokecherry (*Prunus virginiana* L.), Saskatoon (*Amelanchier alnifolia* (Nuttall) Nuttall ex M. Roemer), and Snowberry (*Symphoricarpos albus* (L.) S.F. Blake). The lake is surrounded by a moderately steep hillside (slope up to 15%) except on the north end, which is a flat, low-lying area adjacent to Middle Waterton Lake. The park's Entrance Road runs along the west side of the lake at a straight-line distance of 13–110 m. The stretch of this road bordering the lake is punctuated by four salamander tunnels spaced ~80–110 m apart (described in detail by Pagnucco *et al.* 2012). Linnet Lake is inhabited by three fish species: White Sucker

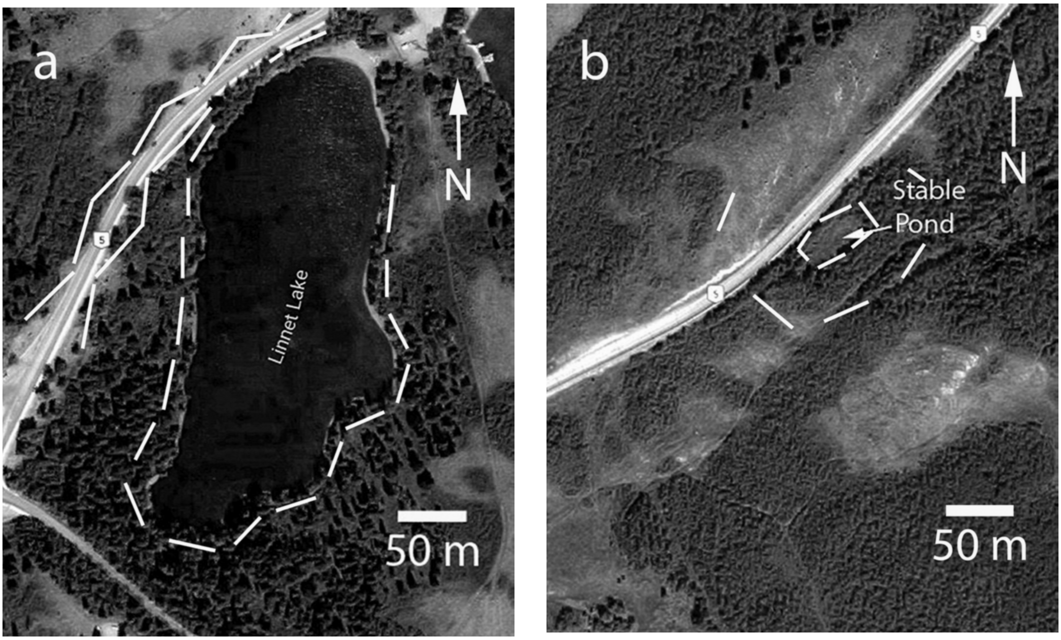

FIGURE 1. Images of the two study sites in Waterton Lakes National Park, Alberta. a. Linnet Lake. b. Stable Pond, which is 1.2 km northeast of Linnet Lake. Entrance Road (Highway 5) runs west of each water body. The approximate location of our drift fences and, in the case of Linnet Lake, permanent fencing along Entrance Road are indicated by white lines. Source: Linnet Lake, 49.07°N, 113.9°W; Stable Pond, 49.07°N, 113.88°W. Data provider: Imagery, DigitalGlobe (2017); Map data, Google Canada (2017). Date Accessed: 1 May 2018.

(*Catostomus commersonii*), Longnose Sucker (*Catostomus catostomus*), and Lake Chub (*Couesius plumbeus*). Western Toads (*Anaxyrus boreas*) and Western Tiger Salamanders (*Ambystoma mavortium*) are also found on site.

Stable Pond (49.07°N, 113.88°W) is a small (0.15 ha), fishless pond 1.2 km to the northeast of Linnet Lake, at an elevation of 1275 m. With a maximum depth of 1.6 m, it typically dries up by midsummer (22 July in 2013, 7 August in 2014) to become a grass-dominated meadow. Stable Pond is surrounded by poplar forest and flat terrain that breaks into open grass and low shrubs to the south and poplar forest with isolated stands of Douglas Fir to the east. To the west, the pond is immediately bordered by Entrance Road. Western Toads and Boreal Chorus Frogs (*Pseudacris maculata*) also breed in Stable Pond.

Methods

Salamander capture

To capture salamanders at Linnet Lake, a series of 16 (2013) or eight (2014) 30-m drift fences (silt fencing, 1 m high) were installed 10–25 m from the lake to create temporary barriers to salamander movement; no pitfall traps were employed here (Atkinson-Adams 2015). In addition, four permanent fences (corrugated plastic, 45 cm high) designed to keep salamanders off the road and to funnel them into the under-road tunnels were present on both sides of Entrance Road, each varying in length from 40 m to 123 m. Fences were walked nightly beginning on 25 April in 2013 and on 17 April in 2014; all salamanders were captured and held for identification or marking (see below). Nightly searches continued until five consecutive nights passed with no salamander encounters, which occurred in late June in both years. Searches were re-initiated on the next rainy night and continued nightly until no salamanders were encountered (8 July in 2013 and 2 July in 2014). Salamanders were also opportunistically caught around Linnet Lake and on Entrance Road.

In 2014, drift fences (silt fencing, 1 m high) were installed to capture salamanders at Stable Pond: a series of five 30-m fences, 3 m from the high waterline and five 30-m fences, 50 m from the high waterline (Atkinson-Adams 2015). Fifty pitfall traps, made from #10 food service cans (15.9 cm in diameter, 17.8 cm deep), were buried either along both sides of fences (April–June) or only along the pond side of fences (July–August) to capture young-of-the year (YOY). Ten minnow-traps (42 cm × 19 cm, 6.4-mm mesh, 2.5-cm openings) were placed in the pond, evenly spaced around the perimeter, to trap breeding adults. Traps were checked daily, usually within 1 h of sunrise. Handling of captured salamanders was the same as described above for Linnet Lake.

Salamander marking

Captured salamanders from a single fence or trap were placed individually on moist paper towelling in a site-labelled plastic container and transported to an indoor laboratory for marking and identification. Recaptured, PIT-tagged salamanders were individually identified with a hand-held half-duplex (HDX) proximity reader (Datamars, Lamone, Switzerland). Unmarked juvenile and adult salamanders were anaesthetized by immersion in 1 g/L trimethane sulfonate solution until unresponsive to prodding (typically 6–10 minutes). Salamanders with swollen vents (could be sexed) were considered mature adults, and smaller salamanders without swollen vents (could not be sexed) were considered juveniles. Juvenile salamanders captured at Stable Pond in July and, later, those bearing gill remnants behind the jaw were considered YOY. No YOY were seen at Linnet Lake.

PIT tagging involved the insertion of a 12 mm × 2.12 mm sterile HDX PIT tag (Texas Instruments, Dallas Texas, USA) weighing 0.1 g (10% of body weight maximum, typically <2%) into the body cavity via a 3-mm incision made using a fresh #11 scalpel blade just anterior to the right hind leg and slightly toward the midline. The incision was closed with Vetbond Tissue Adhesive (3M, St. Paul, Minnesota, USA), which was applied to the dried incision while holding the opposing edges of the incision together with forceps. Consistent with other studies on urodeles, PIT-tag implantation had no apparent short-term effects on salamander behaviour or survival (e.g., Ott and Scott 1999). PIT-tagged animals were also marked either by clipping the second phalangeal joint on toe three of the right hind leg or through injection of red or orange visual implant elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA) subdermally at the ventral base of the tail just posterior to the vent. After wound closure, salamanders were placed in a container of non-chlorinated water shallow enough to allow their heads to remain above water until they recovered from anaesthesia (typically 10–15 minutes). Once recovered (moving, responsive to prodding), individuals were placed in their original containers and released within 3 h near the point of capture.

Using PIT telemetry to locate overwintering salamanders

We began using PIT telemetry to search the terrestrial environment for tagged salamanders after peak migration of adults from breeding sites (4 June 2013 at Linnet Lake and 9 June 2014 at Stable Pond). Scanning was performed to document movement patterns and habitat use by adults and juveniles in summer (not reported here, see Atkinson-Adams 2015) and to identify locations to survey for hibernating salamander in fall. In both years, scanning was initiated near the shoreline, working outward to areas ~200 m from shore in a series of rectangular transects during the summer season, ending on 29 August in both years. We scanned 98 850 m^2 at Linnet Lake and 51 450 m^2 at Stable Pond following methods described in Kuhnz (2000).

Walking in straight-line transects, we brought a handmade RFID scanner as close as possible to the ground and swept side-to-side (see Atkinson-Adams *et al.* 2016). Transects were 30 m long with overlap between adjacent transects to minimize unscanned terrain. The scanner was a wand-like portable RFID antenna used in conjunction with a tuning capacitor and HDX backpack reader (Oregon RFID, Portland, Oregon, USA) set to scan five times per second. The portable RFID antenna consisted of a 61-cm diameter antenna loop encased in sturdy plastic tubing attached to a length of polyvinyl chloride tubing (length ~2 m, diameter 3.2 cm). Systematic testing indicated a maximum vertical detection depth of ~72 cm in soil or rocky substrates with the scanner placed directly on the ground (Atkinson-Adams *et al.* 2016), which is comparable to the depths at which Sheppard (1977) found overwintering Long-toed Salamanders using radioactive tracers.

We scanned for overwintering Long-toed Salamanders 3–15 October 2013 at Linnet Lake and 15–23 November 2014 at Stable Pond. Based on values reported by Sheppard (1977), we assumed that adults had summer home ranges averaging 150 m^2, and that overwintering sites would be located within or near these home ranges. Thus, we returned to the location of the most recently detected individuals from summer scanning efforts (e.g., 28 August 2013 and 26 August 2014) and scanned a 30 m × 30 m (900 m^2) plot orientated north–south and centred on the August location using the transect-scanning methods described above. In addition to scanning at known late-summer locations, we sampled a previously unscanned area across (west of) Entrance Road at Linnet Lake in 2013 and the dried bottom of Stable Pond in 2014.

Characterization of overwintering sites

When a salamander was detected during searches for overwintering sites, its location was marked and then returned to for investigation after the 30 m × 30 m plot was scanned completely. If multiple salamanders were detected in the same plot, sites were examined in the order in which they were found.

To characterize overwintering sites, aboveground features were recorded: dominant vegetation, light level, percentage cover, and number and type of aboveground objects. Then, an attempt was made to excavate the salamander to describe the underground hibernaculum and to see if other individuals were present. Light levels were measured as per cent transmittance (foot-candles) using a light meter (Model 217, General Electric, Boston Massachusetts, USA). Estimated per cent cover within a 1-m-diameter circular plot, centred on the site, were recorded: leaf litter, grass/forb, woody vegetation, small (<10 cm diameter) and large (≥10 cm diameter) woody debris, rock, moss, and bare ground. The number and type of aboveground objects—small (1.5–10 cm diameter) and large (≥10 cm diameter) trees, wood (bark, logs, or stumps), rocks ≥10 cm wide—and the presence of mammal burrows were determined within a 2-m radius of the relocation site. After it was characterized, we carefully excavated the site with a spade until either the salamander was located with a hand-held HDX proximity reader (maximum read range ~12 cm) or it was determined that alterations caused by further digging would be too extensive to repair. Excavations were then returned as nearly as possible to their original state, including returning above- and below-ground material and re-establishing tunnels and air spaces to allow the replaced salamanders to emerge in the spring.

Results

PIT telemetry yielded reasonable rates of relocation for tagged Long-toed Salamanders using our handmade RFID scanner (Atkinson-Adams *et al.* 2016) to survey terrestrial habitat. In summer, 32 of 404 tagged Linnet Lake salamanders (2013) and 82 of 629 tagged Stable Pond salamanders (2014) were detected in 81 and 83 days of scanning, respectively. The area surrounding both breeding sites was heavily vegetated and uneven, with scattered large rocks and woody debris, which limited the number of detections (Atkinson-Adams *et al.* 2016). We found little evidence that PIT tags were readily lost or were the cause of substantial mortality. Summer scanning uncovered five “naked” PIT-tags on or near the soil surface at Linnet Lake and 22 at Stable Pond, representing 2% and 9% of implanted tags, respectively. Tags may have been shed by living animals (Ott and Scott 1999) or may represent disintegrated carcasses of dead animals. At Stable Pond, we located intact carcasses of two salamanders that still contained PIT tags. Our surveys in October and November succeeded in uncovering hibernating sites. We located seven salamanders in fall 2013 (all with PIT tags) and nine salamanders in fall 2014 (seven with PIT tags, plus two additional individuals without tags co-occurring with tagged salamanders).

In October 2013, during 13 days of scanning at Linnet Lake, we sampled 14, 30 m × 30 m plots based on old locations and 12 500 m^2 of new area on the far side of Entrance Road. Seven salamanders were detected: one was 87 m west of Entrance Road, the others were east of the road (Figure 1). Three of the seven salamanders were located on the soil surface, <5 cm deep in the leaf litter, 74 m, 127 m, and 143 m from the shoreline of Linnet Lake. When revisited on 15 October, after a spell of warm weather (day-time high of 12°C), these three individuals were gone; thus, these locations were not considered to be hibernation sites and are not described in Table 1. A different individual was detected at one of these locations on 12 April 2014 (under 10–20 cm snow) and 19 April (no snow), but was absent in May, only to be detected again on 16 November 2014. Three of the salamanders had been previously relocated following PIT tagging and were 15 m, 19 m, and 134 m from the earlier locations.

TABLE 1. Characteristics of overwintering sites for Long-toed Salamanders (*Ambystoma macrodactylum*) located using Passive Integrated Transponder (PIT) telemetry in Waterton Lakes National Park, Alberta. Habitat data were collected within a 1-m diameter circular plot centred on the relocation site.

	Linnet Lake, 2013			Stable Pond, 2014					
PIT number	135912	501602/90267	135798	501702/517467	501608	522687	517363	501711	511365
Sex of salamander*	F	F/F	M	M/F	M/(M)	YOY	M/(J)	M	F
SVL, mm	71.2	71.4/71.3	66.0	57.2/66.5	61.5	35.5	58.2	61.2	71.7
Weight, g	7.7	5.6/6.7	5.8	3.3/4.4	4.6	ND	3.7	4.5	7.2
Date	8 Oct.	12 Oct.	13 Oct.	20 Nov.	20 Nov.	21 Nov.	21 Nov.	21 Nov.	23 Nov.
Refuge type	Stump	Stump	Stump/burrow	Stump	Root	Root	Root	Root	Root
Depth, cm	ND	ND	ND	ND	28	28	27	30	38
Distance from shore, m	168	85	25	3	118	52	47	49	92
Dominant vegetation†	Shrub	Grass	Conif./decid.	Decid.	Decid.	Decid.	Decid.	Decid.	Decid.
Light, %	58	50	22	38	38	47	31	46	47
Slope, %	11	4	5	6	3	6	5	6	3
Aspect, °	116	5	56	225	243	216	208	216	225
Leaf cover, %	20–29	70–79	30–39	1–9	1–9	1–9	1–9	ND	1–9
Dried grass cover, %	1–9	60–69	1–9	1–9	1–9	1–9	1–9	ND	1–9
Woody plant cover, %	1–9	10–19	1–9	10–19	10–19	10–19	1–9	ND	1–9
Grass/forbs cover, %	1–9	1–9	1–9	1–9	1–9	1–9	1–9	ND	1–9
LWD cover, %	10–19	0	1–9	10–19	0	0	0	ND	20–29
SWD cover, %	1–9	1–9	10–19	0	0	0	1–9	ND	1–9
Rock cover, %	1–9	0	0	0	0	0	0	ND	0
Bare ground, %	20–29	0	10–19	0	0	0	0	ND	0
Moss cover, %	0	1–9	10–19	0	0	0	0	ND	0
Snow cover, %	0	0	0	80–89	80–89	70–80	80–90	ND	60–70
No. trees ≥10 cm diameter	0	0	3	1	5	3	2	2	1
No. trees < 10 cm diameter	21	6	6	26	22	21	5	22	0
No. woody features	4	4	5	2	1	2	0	0	2
No. rocks	2	0	0	0	ND	0	0	0	ND
No. burrows	1	1	8	0	ND	0	1	ND	ND

Note: LWD = large woody debris, ND = not determined, SVL = snout-to-vent length, SWD = small woody debris.

*F = female adult, M = male adult, YOY = young-of-year, J = juvenile, () = untagged (found with PIT-tagged individuals 501608 and 517363). Sex and size information are available only for PIT-tagged animals and were collected at the time of tagging.

†Conif./decid. = coniferous and deciduous tree species.

For the three apparent hibernation sites at Linnet Lake, it was not possible to excavate salamanders to determine actual depth, precise refuge type, or presence of other occupants. All three locations, one of which contained two PIT tagged individuals, were within 2 m of old rotten stumps of coniferous or deciduous trees and were at estimated depths >25 cm based on adjacent excavations and combined readings from our custom-made RFID scanner and a hand-held HDX proximity reader (maximum read range ~12 cm). Three salamanders appeared to be in the matrix of decomposed roots associated with the stump itself and one appeared to be within a network of small mammal tunnels in the slope immediately below the stump, which, based on the presence of cone scales, were likely used by Red Squirrels (*Tamiasciurus hudsonicus*). Sites were 25–168 m from the shoreline of Linnet Lake. We found no pattern in vegetation cover or larger-scale characteristics of overwintering sites (Table 1). The dominant vegetation varied among sites and was deciduous trees, a mix of coniferous and deciduous trees, shrubs, or grass. Detailed characteristics of the sites are presented in Table 1.

In November 2014, during nine days of scanning at Stable Pond, we sampled eight, 30 m × 30 m plots, including the dried pond bed. The weather was cold (reaching a low of −26°C), with 12 cm of snow on the ground. We detected nine salamanders in six hibernation sites, 3–118 m from the edge of Stable Pond's high-water limit (Table 1). Detected sites were all in areas dominated by deciduous trees. As had been seen at Linnet Lake, one site was clearly associated with a stump, and two PIT-tagged individuals were detected there. The stump was not excavated, but salamanders appeared to be within the rotten wood matrix of the trunk and its roots at a depth of ~36 cm. The other five overwintering sites at Stable Pond were not obviously associated with specific aboveground objects, but logs and/or large deciduous trees were present within 2 m. These five sites were excavated, and two contained a second, untagged salamander. The seven salamanders were 28–38 cm below the ground surface within cavities left by decomposed roots 1.5–3 cm in diameter (likely *Populus* spp.). In all cases, the bark of the roots maintained their shapes even when no wood remained inside, thus creating tiny tunnels. One of the salamanders was one of 44 PIT-tagged YOY. Three of these salamanders had also been detected at Stable Pond during scanning in the summer at locations 10 m, 20 m, and 168 m from their hibernation sites. Additional characteristics of Stable Pond sites are presented in Table 1.

Discussion

Overwintering macro- and micro-habitats are critical to northern terrestrial salamanders, as they spend a good portion of the year in these locations (Petranka 1998), which are vulnerable to natural and anthropogenic disturbances year-round. Knowledge of how far away from breeding ponds anurans and salamanders hibernate can help to establish conservation buffers to prevent unintended site degradation and destruction (Semlitsch and Bodie 2003). At our study sites in Waterton Lakes National Park, hibernacula of Long-toed Salamanders located using PIT telemetry were within 3 m and 168 m of breeding sites. Overwintering sites are likely much more distant for many individuals, especially those breeding in Linnet Lake. Using RFID antennas at openings for two of the four under-road tunnels, we detected 22% of 404 PIT-tagged salamanders in 2013 and 10% of 643 PIT-tagged salamanders in 2014 moving through these structures. These individuals would have travelled at least 200 m between their breeding lake and terrestrial habitat on the other side of Entrance Road.

What terrestrial macrohabitat features Long-toed Salamanders might have been seeking in crossing the road after breeding remains unclear. Vegetation cover surrounding hibernacula, for example, simply reflected the dominant plants growing around the breeding lake and pond. At a finer scale, Long-toed Salamanders in the vicinities of Linnet Lake and Stable Pond were found to overwinter in microhabitats created by the decomposing wood of tree stumps and their root systems. They also used tunnels at the interface of the decaying wood and the soil. The origin of these tunnels was unknown, but they may have been made by mammals or invertebrates. Monitoring of the under-road tunnels at Linnet Lake with cameras documented the presence of Deer Mice (*Peromyscus maniculatus*), shrews, voles, ground squirrels (*Spermophilus* spp.), chipmunks (*Tamias* spp.), and Red Squirrels at the site (Pagnucco 2010). The use by salamanders of burrows created by small mammals is well documented, including the use by Jefferson (*Ambystoma jeffersonianum*) and Spotted Salamanders (*Ambystoma maculatum*) of vertically oriented tunnels as overwintering sites (Madison 1997; Faccio 2003). Further north in Alberta's Aspen Parkland, Western Toads hibernate in below-ground tunnel systems linked to Red Squirrel cone middens (Browne and Paszkowski 2010) and Western Tiger Salamanders use Northern Pocket Gopher (*Thomomys talpoides*) burrows (Welsh 2016).

Inspection of three stumps that contained salamanders uncovered vertical tunnels within the soft, flakey wood that created spaces for salamanders to travel through and find shelter. Seven salamanders, located at five overwintering sites within poplar stands at Stable Pond, occupied similar passageways inside isolated complexes of hollow, rotten roots at depths >25 cm that were not connected to stumps or living trunks (Table 1). Thus, various forms of standing, downed, and buried woody debris appear to offer appropriate hibernating conditions for Long-toed Salamanders at Waterton Lakes National Park, whether surrounded by grass, shrubs, or trees. Snow cover is likely very important in insulating these sites, as we estimated that the depth of the frost line at Waterton Lakes, based purely on freezing index degree-days, is ~1400 cm (Urecon Ltd.

2018). However, the park is one of the wettest areas in Alberta with an average annual total snowfall of 575 cm at the town site (Parks Canada 2017), which is 1.3 km from Linnet Lake; thus, hibernating salamanders at shallower soil depths are likely protected from freezing. We located salamanders at a narrow range of depths, 27–38 cm. Our locations may not represent the true hibernation depths typical for these Long-toed Salamander populations, but instead reflect the limitations of PIT tag telemetry or the depths of temporary, early-season refugia from which animals eventually move deeper into the soil matrix.

Our findings share some aspects with Sheppard's (1977) observations for Long-toed Salamanders at a site ~250 km northwest of Waterton in the Bow River valley. Sheppard found Long-toed Salamanders overwintering in refugia associated with the roots of trees. However, at his study site, it appeared that salamanders moved below ground through the loose gravel substrate rather than using tunnels or decomposing root systems. Ambystomatid species differ in their digging abilities, some being active excavators, while others are passive excavators that use their wedge-shaped heads to widen existing spaces in the substrata (Semlitsch 1983). It is generally assumed that Long-toed Salamander is a passive excavator, but this has not been definitively shown. At Sheppard's sites, the trees and roots associated with overwintering sites were living spruce, and he makes no mention of mammal burrows or any other possible points of entry to below-ground areas. Also, his sites were in a relatively flat area consisting of glacial deposits, which had high soil moisture levels. With one exception, the hibernacula in our study were substantially uphill from the aquatic breeding pond.

Like Sheppard, we found Long-toed Salamanders overwintering communally, as eight of the 13 salamanders (61.5%) that we located occurred with a second individual. Sheppard found three juvenile salamanders overwintering with adults, and we also found one 1–2-year-old juvenile overwintering with an adult male, indicating that different age classes will share hibernacula. Juvenile Spotted Salamanders are attracted to burrows occupied by conspecifics, possibly an adaptation permitting naïve juveniles to find higher-quality refuges (Green *et al.* 2016). Long-toed Salamanders have been shown to express territorial behaviour, such as biting and avoidance (Ducey 1989); thus, the tolerance of conspecifics at hibernation sites that we observed may underscore the importance of these refuges and possibly their limited availability.

Despite the limitations of PIT-tag technology, such as low detection rates in rugged terrain or in dense vegetation and modest depth of detection, we were able to identify several salamander hibernacula in a relatively cost-effective manner (see also Ousterhout and Burkhart 2017). Our study has expanded knowledge of this poorly known, but important, aspect of the biology of Long-toed Salamander at the northeastern edge of its distribution. Over its geographic range, the species is viewed as adaptable, occurring in habitats as varied as sage-brush and alpine elevations over 2700 m (Graham and Powell 1999; Werner *et al.* 2004). With respect to hibernation sites, we found the species to be flexible in terms of vegetation cover, but consistently occurring in microhabitats provided by decaying wood at and below the soil surface.

The persistence of populations of Long-toed Salamanders in Waterton Lakes National Park and elsewhere in Alberta requires the conservation of structurally complex terrestrial habitat around breeding ponds to provide both foraging and overwintering sites. Our results are consistent with the recent provincial recommendation for the creation of 250-m buffers, featuring forest patches with downed woody debris, around Long-toed Salamander breeding ponds (Alberta Environment and Parks 2016). We recommend the preservation of standing dead tree trunks and stumps in forested buffers, even after disturbances such as logging, insect outbreaks, and wildfire, as a management action that will provide winter microhabitat for the species.

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Literature Cited

Alberta Environment and Parks. 2014. Endangered, threatened, special concern and data deficient species in Alberta. Alberta Environment and Parks, Edmonton, Alberta, Canada. Accessed 30 October 2018. https://open.alberta.ca/dataset/d5f03916-aa1a-4c37-acee-354e69a479f0/resource/7bc9e468-740d-4f06-8805-212eb178ffa0/download/speciesatriskguide-aug27-2014.pdf.

Alberta Environment and Parks. 2016. Long-toed Salamander conservation management plan. Species at risk conservation management plan no.1. Alberta Environment and Parks, Edmonton, Alberta, Canada.

Atkinson-Adams, M.R. 2015. Movement and habitat use by long-toed salamanders (*Ambystoma macrodactylum*) in Waterton Lakes National Park, Alberta. M.Sc. thesis, University of Alberta, Edmonton, Alberta, Canada.

Atkinson-Adams, M.R., C. Paszkowski, and G. Scrimgeour. 2016. Effects of substrate on PIT tag detection with a self-made portable RFID antenna: implications for PIT telemetry. Herpetological Review 47: 198–201.

Barron, D.J., J.D. Brawn, and P.J. Weatherhead. 2010. Meta-analysis of transmitter effects on avian behavior and ecology. Methods in Ecology and Evolution 1: 180–187. https://doi.org/10.1111/j.2041-210X.2010.00013.x

Browne, C.L., and C.A. Paszkowski. 2010. Hibernation sites of western toads: characterization and management implications. Herpetological Conservation and Biology 5: 49–63.

Connette, G.M., and R.D. Semlitsch. 2012. Successful use of a passive integrated transponder (PIT) system for below-ground detection of plethodontid salamanders. Wildlife Research 39: 1–6. https://doi.org/10.1071/WR11055

Cucherousset, J., P. Marty, L. Pelozuelo, and J.-M. Roussel. 2008. Portable PIT detector as a new tool for non-disruptively locating individually tagged amphibians in the field: a case study with Pyrenean brook salamanders (*Calotriton asper*). Wildlife Research 35: 780–787. https://doi.org/10.1071/WR08074

Ducey, P.K. 1989. Agonistic behavior and biting during intraspecific encounters in Ambystoma salamanders. Herpetologica 45: 155–160.

Faccio, S.D. 2003. Postbreeding emigration and habitat use by Jefferson and Spotted salamanders in Vermont. Journal of Herpetology 37: 479–489. https://doi.org/10.1670/155-02A

Fukumoto, J., and S. Herrero. 1998. Observations of the long-toed salamander, *Ambystoma macrodactylum*, in Waterton Lakes National Park, Alberta. Accessed 2 October 2018. https://biodiversitylibrary.org/page/34257935. Canadian Field-Naturalist 112: 579–585.

Graham, K.G. 1997. Habitat use of Long-toed salamanders (*Ambystoma macrodactylum*) at three different scales. M.Sc. thesis, University of Guelph, Guelph, Ontario, Canada.

Graham, K.L., and G.L. Powell. 1999. Status of the Long-toed Salamander (*Ambystoma macrodactylum*) in Alberta. Wildlife status report 22. Alberta Environmental Protection, Fisheries and Wildlife Management Division, and Alberta Conservation Association, Edmonton, Alberta, Canada.

Greene, K.M., S.E. Pittman, and M.E. Dorcas. 2016. The effects of conspecifics on burrow selection in juvenile spotted salamanders (*Ambystoma maculatum*). Journal of Ethology 34: 309–314. https://doi.org/10.1007/s10164-016-0476-6

Hamed, M.K., D.P. Ledford, and T.F. Laughlin. 2008. Monitoring non-breeding habitat activity by subterranean detection of Ambystomatid salamanders with implanted passive integrated transponder (PIT) tags and a radio frequency identification (RFID) antenna system. Herpetological Review 39: 303–306.

Kuhnz, L.A. 2000. Microhabitats and home range of the California legless lizard using biototelemtry. M.Sc. thesis, San Jose University, San Jose, California, USA.

Lee-Yaw, J.A., and D.E. Irwin. 2012. Large geographic range size reflects a patchwork of divergent lineages in the long-toed salamander (*Ambystoma macrodactylum*). Journal of Evolutionary Biology 25: 2276–2287. https://doi.org/10.1111/j.1420-9101.2012.02604.x

Madison, D.M. 1997. The emigration of radio-implanted spotted salamanders, *Ambystoma maculatum*. Journal of Herpetology 31: 542–551. https://doi.org/10.2307/1565607

Ott, J.A., and D.E. Scott. 1999. Effects of toe-clipping and PIT-tagging on growth and survival in metamorphic *Ambystoma opacum*. Journal of Herpetology 33: 344–348.

Ousterhout, B.H., and J.J. Burkhart. 2017. Moving beyond the plane: measuring 3D home ranges of juvenile salamanders with passive integrated transponder (PIT) tags. Behavioral Ecology and Sociobiology 71: 59. https://doi.org/10.1007/s00265-017-2284-6

Pagnucco, K.S. 2010. Using under-road tunnels to protect a declining population of long-toed salamanders (*Ambystoma macrodactylum*) in Waterton Lakes National Park. M.Sc. thesis, University of Alberta, Edmonton, Alberta, Canada.

Pagnucco, K.S., C.A. Paszkowski, and G.J. Scrimgeour. 2012. Characterizing movement patterns and spatio-temporal use of under-road tunnels by long-toed salamanders in Waterton Lakes National Park, Canada. Copeia 2012: 331–340. https://doi.org/10.1643/CE-10-128

Parks Canada. 2017. Waterton Lakes National Park. Climate. Parks Canada, Ottawa, Ontario, Canada. Accessed 30 October 2018. https://www.pc.gc.ca/en/pn-np/ab/waterton/nature/environment/climat-climate.

Pearson, K.J. 2004. The effects of introduced fish on the long-toed salamander (*Ambystoma macrodactylum*) in southwestern Alberta, Canada. M.Sc. thesis, University of Lethbridge, Lethbridge, Alberta, Canada.

Petranka, J.W. 1998. Salamanders of the United States and Canada. Smithsonian Institution Press, Washington, DC, USA.

Russell, A.P., and A.M. Bauer. 2000. The Reptiles and Amphibians of Alberta. University of Calgary Press, Calgary, Alberta, Canada.

Ryan, K.J., J.D. Zydlewski, and A.J.K. Calhoun. 2014. Using passive integrated transponder (PIT) systems for terrestrial detection of blue-spotted salamanders (*Ambystoma laterale*) in situ. Herpetology Conservation and Biology 9: 97–105.

Semlitsch, R.D. 1983. Burrowing ability and behavior of salamanders of the genus *Ambystoma*. Canadian Journal of Zoology 61: 616–620. https://doi.org/10.1139/z83-082

Semlitsch, R.D., and J.R. Bodie. 2003. Biological criteria for buffer zones around wetlands and riparian habitats for amphibians and reptiles. Conservation Biology 17: 1219–1228. https://doi.org/10.1046/j.1523-1739.2003.02177.x

Sheppard, R.F. 1977. The ecology and home range movements of *Ambystoma macrodactylum krausii* (Amphibia Urodela). M.Sc. thesis, University of Calgary, Calgary, Alberta, Canada.

Trenham, P.C., and B.H. Shaffer. 2005. Amphibian upland habitat use and its consequences for population viability. Ecological Applications 15: 1158–1168. https://doi.org/10.1890/04-1150

Urecon Ltd. 2018. Ambient temperatures — below ground. Urecon Ltd., Coteau-du-Lac, Quebec, Canada. Accessed 10 May 2018. http://www.urecon.com/applications/municipal_ambient_below.html.

Weatherhead, P.J., and G. Blouin-Demers. 2004. Long-term effects of radiotelemetry on black ratsnakes. Wildlife Society Bulletin 32: 900–906.

Welsh, K.J. 2016. Occupancy, abundance, and summer ecology of the Western Tiger Salamander (*Ambystoma mavortium* Baird) in the Beaver Hills, Alberta. M.Sc. thesis, University of Alberta, Edmonton, Alberta, Canada.

Werner, J.K., B.A. Maxwell, P. Hendricks, and D.L. Flath. 2004. Amphibians and Reptiles of Montana. Mountain Press Publishing Company, Missoula, Montana, USA.

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Checklist and status of the amphibians and reptiles of Essex County, Ontario: a 35 year update

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Abstract

Essex County, Ontario, supports a diverse assemblage of Canadian herpetofauna. It is home to the only Canadian populations of three species/subspecies and contains two of Canada's 11 Important Amphibian and Reptile Areas. A checklist and status assessment of the herpetofauna of Essex County was previously compiled in 1983. Changes to natural habitats and an increase in monitoring efforts (e.g., citizen science) over the past 35 years warrant an updated assessment of herpetofaunal status. The county was subdivided using a 10 × 10 km grid overlay, and recent observations (1997–2016) submitted to provincial databases were tabulated for each grid square. We compared current status' of herpetofauna in Essex County to those of the 1983 study using a similar classification scheme of 'extirpated from Essex' (EE; no recent observations) and 'rare in Essex' (RE; distribution $\leq$5 squares). We found that 11 species declined in status. The majority of reptiles and amphibians (62%) that historically occurred in Essex County are now either EE (31%) or RE (31%) and almost half (45%) of the 29 extant species/subspecies are RE. A large proportion of salamanders and squamates are EE or RE (86% and 65%, respectively). Amount of natural area and sampling effort were important variables describing patterns of observed herpetofaunal species/subspecies richness, and observed richness was highest along the western and southern edges of the mainland (16–19 species). To prevent future extirpations, recovery efforts in Essex County should occur across multiple locations and target RE species.

Key words: Essex County; herpetofauna checklist; species status assessment; reptiles and amphibians; species richness; habitat loss; citizen science; Pelee Island; Ojibway Prairie Complex; endangered species

Introduction

Essex County is within Canada's Carolinian zone, an area with the greatest diversity of flora and fauna and one of the highest concentrations of globally rare species in all of Canada (ERCA 2002; Jalava *et al.* 2009). The county is very important to Canadian herpetofauna, in particular, as it contains the only Canadian populations of three species/subspecies (Blue Racer [*Coluber constrictor foxii*], Lake Erie Watersnake [*Nerodia sipedon insularum*], and Small-mouthed Salamander [*Ambystoma texanum*]), the only Canadian location of one extirpated species (Blanchard's Cricket Frog [*Acris blanchardi*]), and contains two of the 11 Important Amphibian and Reptile Areas in Canada (CHS 2017).

The first comprehensive checklist and status assessment of the herpetofauna of Essex County was compiled in the early 1980s as part of a detailed study of the Environmentally Significant Areas of the county (Oldham 1983, 1984a,b). This work provided a preliminary detailed account of each species/subspecies known to inhabit Essex County at that time, complete with historical observations. The work included results of herpetofaunal surveys at Point Pelee National Park (PPNP), Pelee Island, and Ojibway Prairie Complex (OPC), with supporting data derived from local naturalist's observations, museum collections, and the author's own extensive field work in the region (Oldham 1983).

Since that time, documentation of native herpetofauna has increased dramatically in Ontario and become more sophisticated. For example, in 1984 the Ontario Herpetofaunal Summary (OHS), a citizen science initiative, officially began its first year (Pulfer 2014). Annual reports detailing observation records were developed from 1984 to 1986 (Oldham and Sutherland 1986; Oldham 1988; Weller and Oldham 1988), mostly out of the Essex Region Conservation Authority (ERCA) office in Essex, Ontario. In 2009, Ontario Nature developed the Ontario Reptile and Amphibian Atlas (ORAA) by incorporating the OHS data, expanding herpetofaunal monitoring in the province, and increasing the number of observations for areas previously lacking data (Ontario Nature 2017). With continuing technological development, the submission, management, and display of observation records have advanced. For example, the ORAA has now logged over 3000 volunteer participants submitting over 350 000 observations (Ontario Nature 2015). Unfortunately, an increase in monitoring effort has been met with a decrease in availability and quality of reptile and amphibian habitat as urbanisation and agricultural activities intensify. For example, 78 ha of natural area were removed from within the Town of LaSalle for housing developments between 1986 and 1996 (Town of LaSalle 2016). At the turn of this century, 97% of wetlands and 95% of original forest cover in Essex County had been lost, leaving the natural landscape in a highly degraded and fragmented state (ERCA 2002). Drastic changes in both the landscape as well as monitoring efforts over the last three decades warrant an updated assessment of the current herpetofauna of Essex County and its collective status.

Our goal was to provide an updated checklist and report on the status of the herpetofauna of Essex County since it was last assessed 35 years ago. Our questions were: 1) What is the current occupancy and distribution of herpetofauna in Essex County? 2) What is the trend in status of herpetofauna in Essex County over the last 35 years? and 3) In which areas of Essex County have the greatest number of herpetofaunal species/subspecies been reported?

Methods

We confined our study to the geographic boundary of the County of Essex (42.167ºN, 82.783ºW), which lies within the Carolinian Zone of southwestern Ontario. We subdivided the area using the same 10 × 10 km grid overlay used by the OHS and ORAA (Figure 1). Grid squares included those that contained landmass or islands (or a portion thereof) and at least one 'recent' reptile or amphibian observation ($n = 33$). Five potential grid squares were not included in the study as they either contained a portion of landmass/islands but no recent observations, or had recent observations but consisted entirely of open water. Current occupancy and distribution of herpetofauna in Essex County, in addition to species/subspecies richness per grid square, was determined primarily from observation records that were submitted to the ORAA within the previous 20 years (1997–2016; $n = 4226$) and available online (Ontario Nature 2017; records from other provincial or national databases were not included). Data were retrieved from the ORAA in winter 2017. Observation records ($n = 9$) for two species of turtle (Eastern Spiny Softshell [*Apalone spinifera spinifera*] and Spotted Turtle [*Clemmys guttata*]) were retrieved directly from the Natural Heritage Information Centre (NHIC 2017) because records for these species are not displayed by the ORAA. Additional resources were used to support regional status assessments as required (e.g., Committee on the Status of Endangered Wildlife in Canada [COSEWIC] and Committee on the Status of Endangered Wildlife in Ontario [COSSARO] status reports, academic journal articles, and books). All observations made between 1997 and 2016 were considered 'recent' and those made prior to 1997 were considered 'historical'.

The total number of 10 × 10 km squares with at least one recent observation was tallied for each species/subspecies. We classified species/subspecies with recent observations from ≤5 squares (≤15%) as rare in Essex County (RE), similarly to Oldham (1983). In almost all cases, we classified a species as extirpated from Essex County (EE) if no verified observations were submitted in the past 20 years and if its current status was subjected to additional scrutiny from outside experts (e.g., species status reports, published accounts). A change in status from RE to EE does not necessarily imply a species became extirpated since the previous county-level status assessment. An extirpation event may have actually occurred prior to the 1980s; however, we argue that sufficient time has now passed and/or new studies have occurred to presume that a given species has become locally extirpated. Amphibians and reptiles that were not classified as RE or EE were recently reported from >5 squares (>15%) and therefore considered widespread.

The number of recent ORAA and NHIC observation records submitted from each 10 × 10 km grid square was tallied and displayed in a graduated map using natural breaks (jenks) in a geographic information system (GIS; ArcGIS 9.1, Esri, Redlands, California, USA; Figure 2). These data were used to summarize the number of herpetofauna species/subspecies reported within each 10 × 10 km grid square (i.e., observed richness). Observed richness was displayed in a graduated map using manual breaks in a GIS (Figure 3). Finally, the amount of natural area (i.e., land that has not been converted to agricultural, industrial, urban, or residential uses) present within each 10 × 10 km grid square was mapped by merging five distinct data layers (Table 1; we estimated 5.9% natural area remaining in Essex County, which is very similar to the 6.5% natural area estimated by ERCA [2002]). A Dissolve function was performed on the resultant natural area merged file to eliminate overlapping boundaries within each polygon. The Explode feature was used to separate the resultant natural area multipart feature into separate polygons. All polygons that occurred across multiple grid squares were then split along the intersecting grid line. In order to select polygons of natural areas in each individual grid square, the Select by Location feature was used. Summary statistics for the selected grid square were then obtained using the attribute table, with the sum representing hectares of natural area in the selected square. These data were then displayed in a graduated map using manual breaks in a GIS (Figure 4). We used linear regression in Microsoft Excel 2010 (version 14.0.7190.5000, Microsoft Corporation, Redmond, Washington, USA) to predict the number of herpetofauna species/subspecies reported per square (dependent variable) based on amount of natural area per square (independent variable). Due to a small sample size we did not account for the impact of spatial autocorrelation on species richness.

Results

Widespread herpetofauna of Essex County

Sixteen species (seven amphibians, nine reptiles) are widespread in Essex County based on recent observations within six or more grid squares (Table 2). Six species of anurans that were previously considered wide-

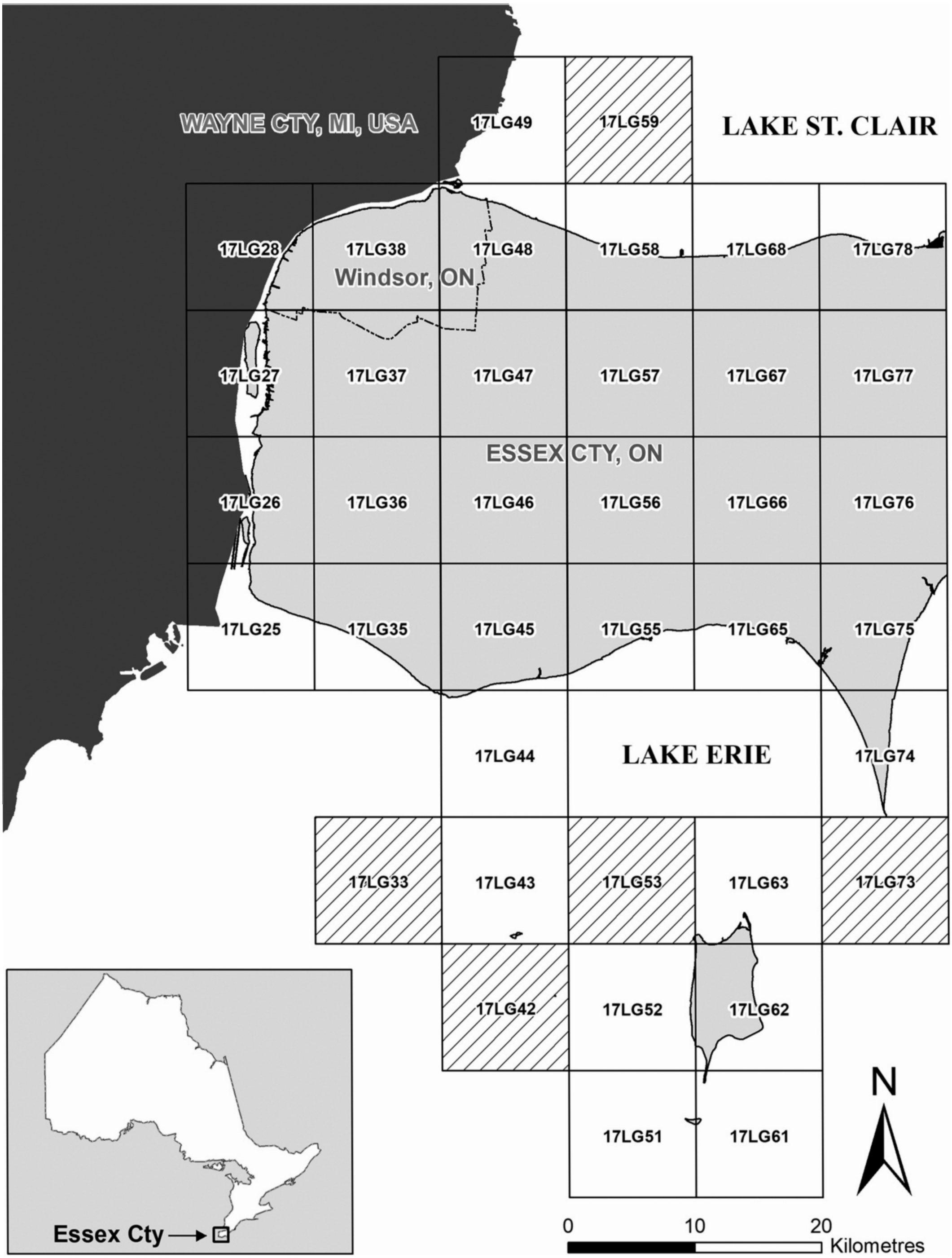

FIGURE 1. Map of Essex County, Ontario, showing 10 × 10 km grid overlay. Grid square labels correspond with those used by Ontario Nature (2018), and hatched grid squares were not included in the study.

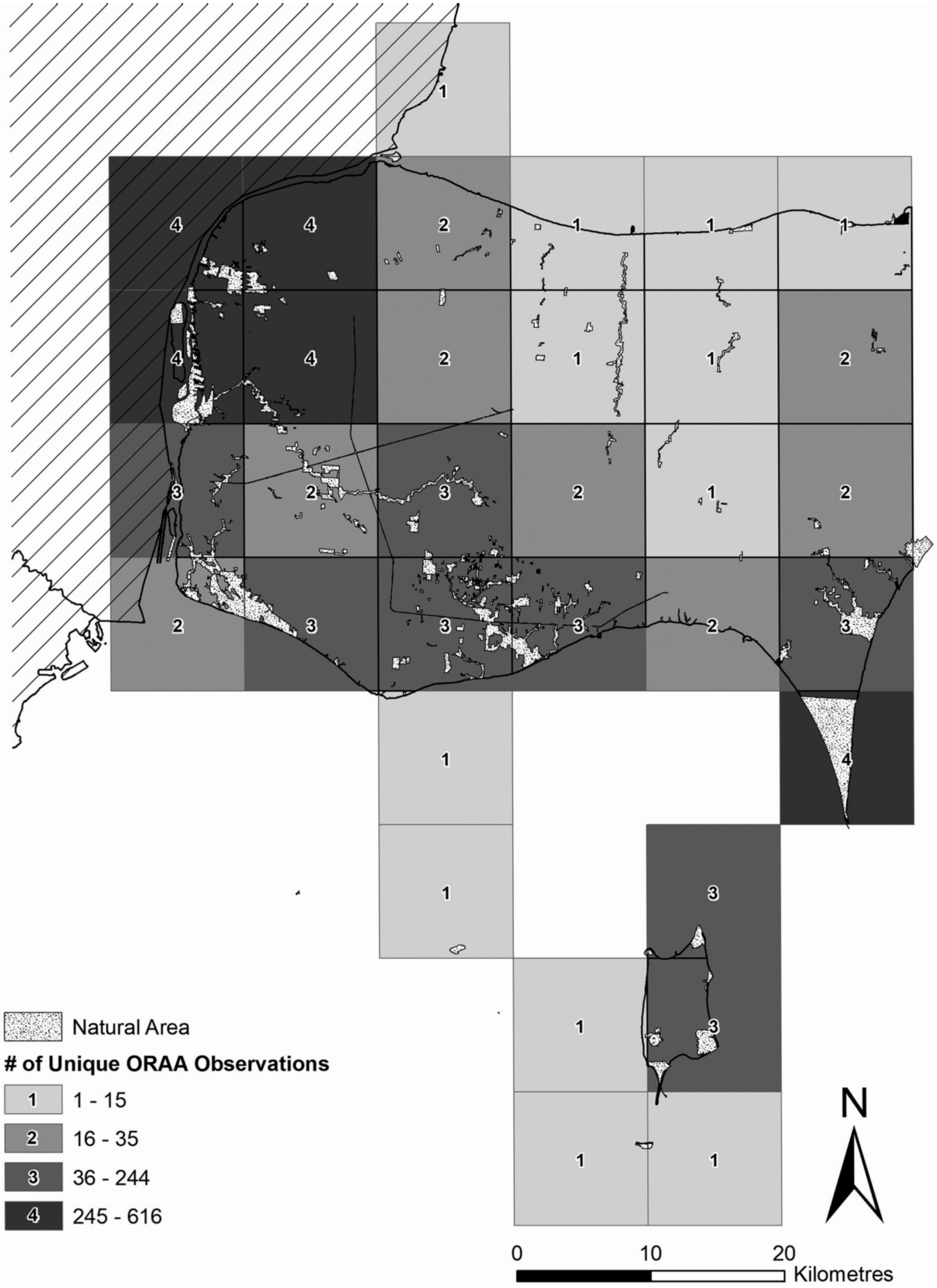

FIGURE 2. Number of recent reptile and amphibian observations submitted to the Ontario Reptile and Amphibian Atlas (ORAA) per grid square. See Table 1 for description of natural area.

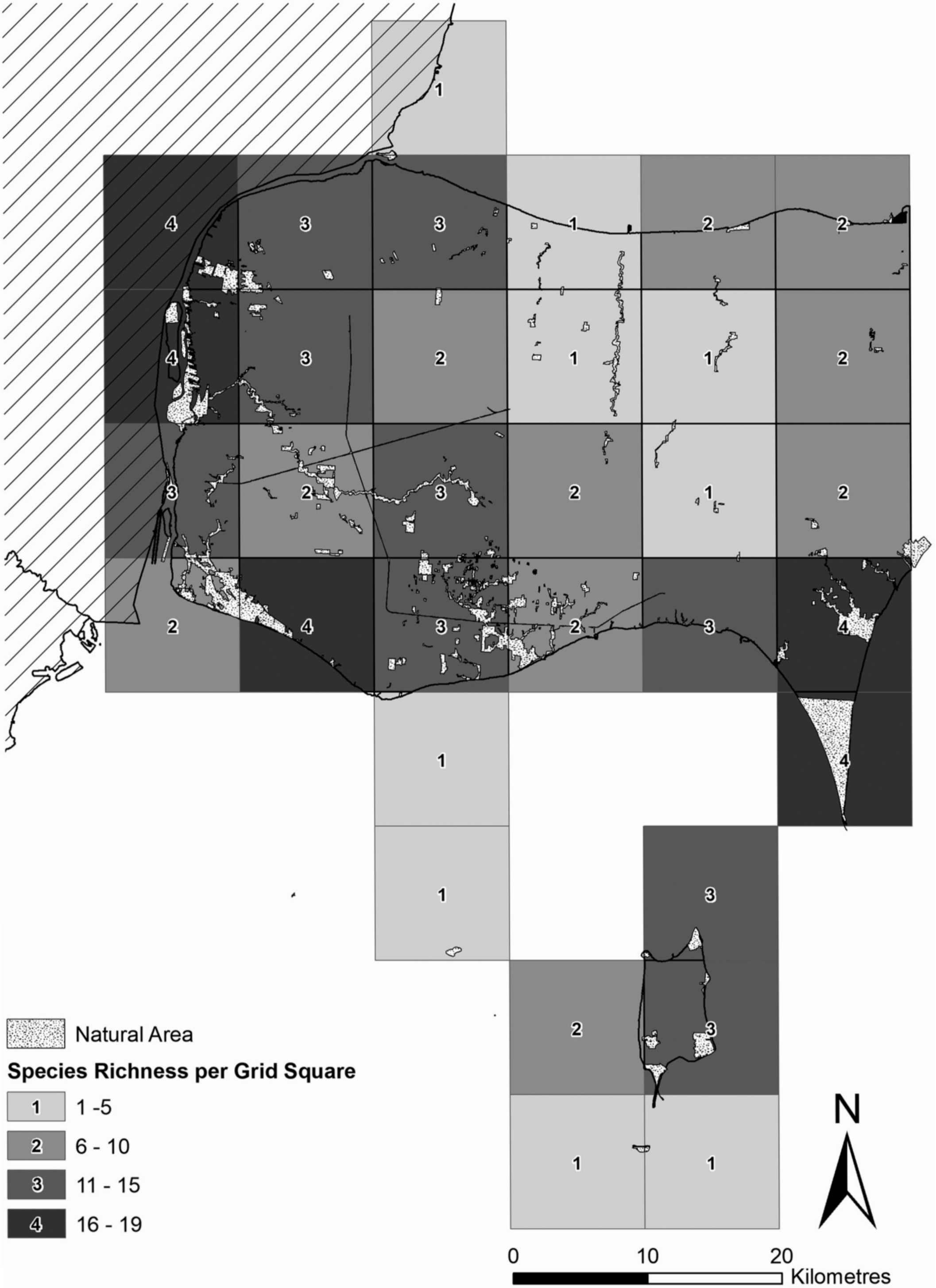

FIGURE 3. Observed herpetofaunal species/subspecies richness per grid square in Essex County, Ontario. See Table 1 for description of natural area.

TABLE 1. Data layers merged in a geographic information system to create a 'natural area' shapefile, which was subsequently used to estimate amount of 'natural area' within each 10 × 10 km grid square in Essex County, Ontario. Boundaries for all ERCA (Essex Region Conservation Authority) layers are approximate, subject to verification by ERCA and subject to change (copyrighted by ERCA: 1983, 1994, 2008, and 2016). LIO = Land Information Ontario.

Data Layer	Source	Year	Description
Environmentally Significant Areas	ERCA	1983, 1994	Refer to Oldham (1983)
Significant Valleylands	ERCA	2008	Refer to Government of Ontario (2005)
ERCA Lands	ERCA	2016	Lands that are owned or managed by ERCA
Areas of Natural and Scientific Interest	LIO	2014	Refer to Government of Ontario (2005)
Provincially Significant Wetlands	LIO	2006	Refer to Government of Ontario (2005)

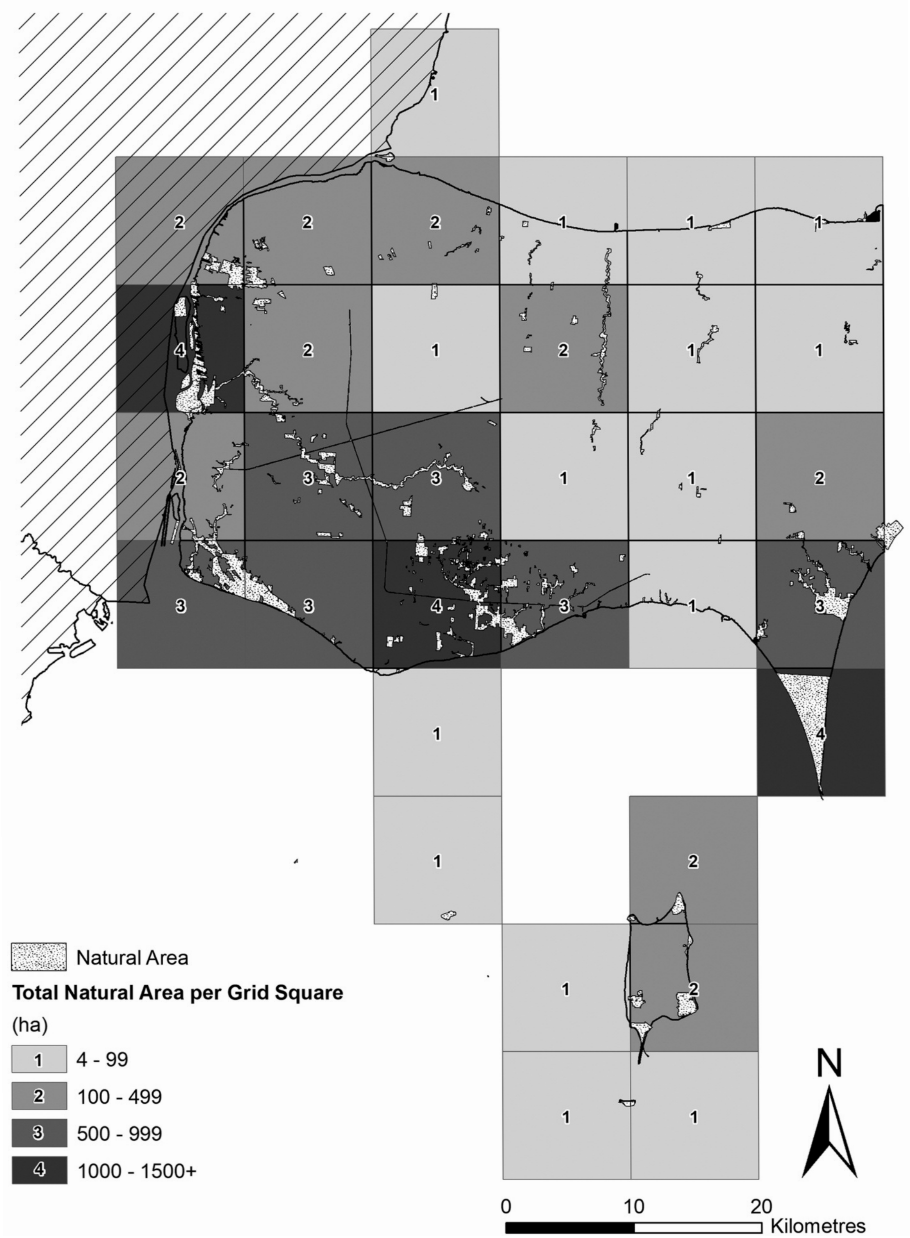

FIGURE 4. Amount of natural area (ha) per grid square in Essex County, Ontario. See Table 1 for description of natural area.

TABLE 2. Historical and current status of the amphibians and reptiles of Essex County, Ontario. IN = introduced species, RE = species considered rare in Essex County, and EE = species considered extirpated from Essex County. Previous (i.e., historical) status retrieved from Oldham (1983). Last observation date, number of recent (i.e., 1997–2016) observations, and number of recent grid squares retrieved from Ontario Nature (2017), unless otherwise specified ('?' indicates uncertain or conflicting last observation date or no. of grid squares—see Results for details). Conservation status ranks retrieved from NatureServe (2017), and Ontario ESA (*Endangered Species Act*) status retrieved from Government of Ontario (2018). CP = Carolinian population, TDP = *Ambystoma texanum* dependent population. G = global rank, T = Infraspecific taxon rank (e.g., subspecies), N = national rank. N-ranks displayed are for species or subspecies, not for distinct populations (i.e., designatable units). Conservation status ranks: 5 = Secure, 4 = Apparently Secure, 3 = Vulnerable, 2 = Imperilled, 1= Critically Imperilled, U = Unrankable, NA = Not Applicable, X = Presumed Extinct/Extirpated. Common and scientific names follow Crother (2017).

Species name	Conservation status rank	Ontario ESA status	Essex County status		Last obs. date	No. recent obs. records	No. recent grid squares (%)
			Previous	Current			
AMPHIBIANS							
FROGS AND TOADS (ANURA)							
Blanchard's Cricket Frog (*Acris blanchardi*)	G5, NX	EXT	RE	EE	1970s? (COSSARO 2011a)	0	0 (0)
Eastern American Toad (*Anaxyrus a. americanus*)	G5T5, N5	–	–	–	2016	608	26 (79)
Fowler's Toad (*Anaxyrus fowleri*)	G5, N2	END	RE	EE	1967 (Ontario Nature 2018)	0	0 (0)
Gray Treefrog (*Hyla versicolor*)	G5, N5	–	RE	EE	1992 (Ontario Nature 2018)	0	0 (0)?
American Bullfrog (*Lithobates catesbeianus*)	G5, N5	–	–	–	2015	66	13 (39)
Green Frog (*Lithobates clamitans*)	G5, N5	–	–	–	2016	198	19 (58)
Northern Leopard Frog (*Lithobates pipiens*)	G5, N5	–	–	–	2016	313	19 (58)
Wood Frog (*Lithobates sylvaticus*)	G5, N5	–	RE	EE	1979? (Oldham 1983)	0	0 (0)
Spring Peeper (*Pseudacris crucifer*)	G5, N5	–	–	–	2016	86	6 (18)
Western Chorus Frog (*Pseudacris triseriata*)	G5, N4	–	–	–	2016	389	18 (55)
SALAMANDERS (URODELA)							
Blue-spotted Salamander (*Ambystoma laterale*)	G5, N5	END (TDP)	RE	RE	2015	11	3 (9)
Spotted Salamander (*Ambystoma maculatum*)	G5, N5	–	RE	EE	1994 (Ontario Nature 2018)	0	0 (0)?
Small-mouthed Salamander (*Ambystoma texanum*)	G5, N1	END	RE	RE	2015	5	1 (3)
Eastern Tiger Salamander (*Ambystoma tigrinum*)	G5, NU	EXT	RE	EE	1915 (Ngo *et al.* 2009)	0	0 (0)
Common Mudpuppy (*Necturus m. maculosus*)	G5T5, N4	–	RE	–	2016	7	7 (21)
Red-spotted Newt (*Notopthalmus v. viridescens*)	G5T5, N5	–	RE	RE	2013	5	1 (3)
Eastern Red-backed Salamander (*Plethodon cinereus*)	G5, N5	–	RE	RE	2016	3	1 (3)
REPTILES							
SNAKES AND LIZARDS (SQUAMATA)							
Blue Racer (*Coluber constrictor foxii*)	G5T5, N1	END	RE	RE	2016	16	2 (6)
Timber Rattlesnake (*Crotalus horridus*)	G4, NX	EXT	EE	EE	1930s? (Rowell 2012)	0	0 (0)
Eastern Hog-nosed Snake (*Heterodon platirhinos*)	G5, N3	THR	RE	EE	1979? (Rowell 2012)	0	0 (0)
Eastern Milksnake (*Lampropeltis triangulum*)	G5, N3N4	–	RE	EE	1980s? (COSEWIC 2014a)	0	0 (0)
Lake Erie Watersnake (*Nerodia sipedon insularum*)	G5T2, N2	SC	RE	RE	2016	51	6 (18)?
Northern Water Snake (*Nerodia s. sipedon*)	G5T5, N5	–	–	–	2016	35	12 (36)
Smooth Greensnake (*Opheodrys vernalis*)	G5, N5	–	RE	EE	1985 (Ontario Nature 2018)	0	0 (0)
Gray Ratsnake (*Pantherophis spiloides*)	G4G5, N3	END (CP)	RE	EE	1967 (Ontario Nature 2018)	0	0 (0)
Eastern Foxsnake (*Pantherophis vulpinus*)	G5, N3	END (CP)	–	–	2016	503	24 (73)
Common Five-lined (Skink *Plestiodon fasciatus*)	G5, N3	END (CP)	RE	RE	2015	24	4 (12)

TABLE 2. (*continued*)

Species name	Conservation status rank	Ontario ESA status	Essex County status		Last obs. date	No. recent obs. records	No. recent grid squares (%)
			Previous	Current			
Queensnake (*Regina septemvittata*)	G5, N2	END	n/a	RE	2016	34	2 (6)
Eastern Massasauga (*Sistrurus catenatus*)	G3, N3	END (CP)	RE	RE	2015	70	1 (3)
Dekay's Brownsnake (*Storeria dekayi*)	G5, N5	–	–	–	2016	271	16 (49)
Red-bellied Snake (*Storeria occipitomaculata*)	G5, N5	–	RE	RE	2016	37	5 (15)
Butler's Gartersnake (*Thamnophis butleri*)	G4, N2	END	–	–	2016	346	8 (24)
Northern Ribbonsnake (*Thamnophis saurita*)	G5, N3	SC	n/a	EE	1988? (COSEWIC 2002)	0	0 (0)
Eastern Gartersnake (*Thamnophis s. sirtalis*)	G5T5, N5	–	–	–	2016	401	25 (76)
TURTLES (TESTUDINES)							
Eastern Spiny Softshell (*Apalone s. spinifera*)	G5T5, N2	END	RE	RE	2013 (NHIC 2017)	4	4 (12)?
Snapping Turtle (*Chelydra serpentina*)	G5, N5	SC	–	–	2016	215	22 (67)
Midland Painted Turtle (*Chrysemys picta marginata*)	G5T5, N4	–	–	–	2016	288	24 (73)
Spotted Turtle (*Clemmys gutatta*)	G5, N2	END	RE	RE	2013 (NHIC 2017)	5	5 (15)?
Blanding's Turtle (*Emydoidea blandingii*)	G4, N3	THR	–	–	2016	114	18 (55)
Northern Map Turtle (*Graptemys geographica*)	G5, N3	SC	–	–	2016	81	15 (46)
Eastern Musk Turtle (*Sternotherus odoratus*)	G5, N3	SC	RE	RE	2015	17	4 (12)
Woodland Box Turtle (*Terrapene c. carolina*)	G5T5, NU	EXT	RE	EE	<1900? (COSEWIC 2014c)	0	0 (0)
Eastern Box Turtle (*Terrapene carolina*)	G5, NU	–	–	IN	–	–	–
Red-eared Slider (*Trachemys scripta elegans*)	G5T5, NNA	–	–	IN	–	–	–

spread remain widespread today (reported from 6–26 squares [18–79%]; Table 2), whereas one salamander that was previously considered RE is now considered widespread based on recent observations from seven squares (21%) and new research on local abundance and distribution (Detroit River: Craig *et al.* 2015). Five species of snakes are widespread in Essex County, despite two of these being Species at Risk (SAR) in Ontario (reported from 8–25 squares [24–75%]; Table 2). None were previously considered RE. Finally, four turtle species are considered widespread locally, three of which are SAR and none of which were previously classified RE (reported from 15–23 squares [46–70%]).

Rare and extirpated herpetofauna of Essex County

We classified 13 species/subspecies as rare in Essex County (RE; four salamanders, six squamates, and three turtles; Table 2) and an additional 13 species as extirpated from Essex County (EE; four anurans, two salamanders, six squamates, and one turtle; Table 2). A relatively large proportion of salamanders (86%) and squamates (65%) are either extirpated (EE) or limited in distribution (RE), compared to turtles (50% EE/RE) or anurans (40% EE/RE; Table 2). Details regarding changes to Essex County status, questionable last observation dates, and questionable number of recent squares are provided below (in order of taxonomic group).

BLANCHARD'S CRICKET FROG (EE): Previously RE based on call records from Pelee Island and other locations. COSEWIC (2011) assessed the species as Endangered based on unconfirmed reports from Pelee Island as recently as 1997 and the "miniscule" chance that a very small population persists. Regardless, it has been considered extirpated from Ontario (Hecnar and Hecnar 2005; COSSARO 2011a; Ontario 2018) and we consider it EE.

FOWLER'S TOAD (*Anaxyrus fowleri*; EE): Previously RE based on the possibility of it persisting undetected at one or two locations in Essex County (e.g., Big Creek sub-watershed), despite being considered extirpated from PPNP and Pelee Island. We now consider it EE based on a lack of observations in 50 years and expert opinion (COSEWIC 2010a).

GRAY TREEFROG (*Hyla versicolor*; EE): Previously RE based on observations from Pelee Island. Additional historical sightings were reported from Windsor (EL 1976) and the PPNP area (Hecnar and Hecnar 2004; Ontario Nature 2017). We now consider the species EE based on expert opinion (Pelee Island: King *et al.* 1997; PPNP: Hecnar and Hecnar 2004), and a 25 year absence of records despite recent herpetofaunal surveys at historical locations (COSEWIC 2010b; Gardner-Costa *et al.* 2013) and 20 years of county-wide amphibian call surveys (Tozer 2016). We presume recent observations of single individuals from three disjunct squares (R. Jones unpubl. data) are vagrants (e.g., via nursery stock: Livo *et al.*1998) as opposed to members of resident breeding populations (following King *et al.* 1997; IUCN 2012).

WOOD FROG (*Lithobates sylvaticus*; EE): Previously RE based on unverified records from OPC and four dispersed conservation areas. Verified historical (or recent) records of this species are absent for the county (e.g., King *et al.* 1997; Hecnar and Hecnar 2004; Tozer 2016; Ontario Nature 2017). Regardless, its confirmed current or historical presence in all adjacent counties (i.e., Chatham-Kent [Ontario Nature 2017], Wayne [MIHerp Atlas 2017], and Erie/Ottawa [King *et al.* 1997]), implies a contiguous historical range that included Essex County.

SPOTTED SALAMANDER (*Ambystoma maculatum*; EE): Previously RE based on records from only two private woodlots in the Hillman Creek sub-watershed. No recent records exist, although it may have escaped detection on private lands. Regardless, we presume this species to be EE based on a high number of recently submitted observations (Figure 2) from the sub-watershed with historical records (i.e., 17LG75 in Figure 1) coupled with a lack of detection.

EASTERN TIGER SALAMANDER (*Ambystoma tigrinum*; EE): Previously RE based on presumed presence at Pelee Island and extirpation from PPNP. Authorities now suggest that the historical presence of this species in Ontario is based entirely on a single accepted specimen reportedly collected from PPNP in 1915 (Hecnar and Hecnar 2005; Ngo *et al.* 2009).

TIMBER RATTLESNAKE (*Crotalus horridus*; EE): Previously EE based on historical observations from Pelee Island (the lone 1918 sighting from PPNP was presumed to be a vagrant from the western Lake Erie Islands). Although some authors consider the historical Pelee Island records to be questionable (King *et al.* 1997) or invalid (Environment Canada 2010), others (following detailed assessments) conclude that there is sufficient evidence of its former presence on Pelee Island (COSEWIC 2001; COSSARO 2011b; Rowell 2012).

EASTERN HOG-NOSED SNAKE (*Heterodon platirhinos*; EE): Previously RE based on records from two locations (OPC and PPNP; see Dance and Campbell 1981) and its presumed extirpation from Pelee Island. We now consider it EE based on a lack of recent observations (one 2001 observation record from Pelee Island is presumed to be erroneous) and expert opinion (King *et al.* 1997; Hecnar and Hecnar 2004; COSEWIC 2007; Rowell 2012).

EASTERN MILKSNAKE (*Lampropeltis triangulum*; EE): Previously RE based on observations from the Cedar Creek and Big Creek sub-watersheds and presumed extirpations from PPNP and Pelee Island. Some historical observations, however, may represent misidentifications (Rowell 2012). We now consider it EE based on a lack of recent verified records and expert opinion (King *et al.* 1997; Hecnar and Hecnar 2004; COSEWIC 2014a).

Lake Erie Watersnake (RE): Previously RE based on observations from three Lake Erie islands, including Pelee Island. Although recent observations exist from six squares (18%; Table 2), we consider it RE because its contemporary range includes only three or four freshwater islands (COSEWIC 2015), one of which (Middle Island) straddles the boundary line between two squares otherwise dominated by open water.

Smooth Greensnake (*Opheodrys vernalis*; EE): Previously RE based on single specimens reported from two locations (PPNP, grid 17LG74 and Sandwich West Township, grid 17LG27; Figure 1). Few additional historical records exist (Ontario Nature 2017). We now consider it EE based on a lack of records in over 30 years and substantial search effort at historical locations (Figure 2).

Gray Ratsnake (*Pantherophis spiloides*; EE): Previously RE based on unconfirmed reports from PPNP and Pelee Island (but see Rowell [2012] for further evidence of historical presence in Essex County). We now consider it EE based on a lack of recent observations and expert opinion (Hecnar and Hecnar 2004; Rowell 2012).

Queensnake (*Regina septemvittata*; RE): No previous Essex County status. The first confirmed observation in Essex County did not occur until the mid-1980s (see Oldham 1986).

Northern Ribbonsnake (*Thamnophis saurita septentrionalis*; EE): No previous Essex County status and no recent records (Rowell 2012). The few historical records appear to be data deficient (e.g., King *et al.* 1997), of questionable validity (e.g., DCL 2009), or conflicting in nature (e.g., records in COSEWIC [2002, 2012] and Ontario Nature [2017]). Regardless, its current or historical presence has been confirmed in many adjacent or nearby counties (i.e., Chatham-Kent [Ontario Nature 2017], Oakland [MIHerpAtlas 2017] and Erie/Ottawa [King *et al.*1997]), implying a contiguous historical range that included Essex County.

Eastern Spiny Softshell (RE): Previously RE and “probably declining” (Oldham 1983), based on observations from PPNP and three other general areas (Pelee Island, Lake St. Clair, and Lake Erie). Still considered RE, however, additional verified reports not included in Table 2 (i.e., not in NHIC database: Hecnar and Hecnar 2004; T. Preney unpubl. data) suggest this species might be widespread.

Spotted Turtle (RE): Previously RE based on known occurrences at four locations. Spotted Turtles have declined from most of their historical Essex County range (Oldham 1983; Hecnar and Hecnar 2004; COSEWIC 2004, 2014b). Recent observations of single animals from three out of five squares (Table 2) may not represent resident populations (i.e., released animals or vagrants: T. Preney unpubl. data), suggesting actual distribution is smaller than reported.

Woodland Box Turtle (*Terrapene carolina carolina*; EE): Previously RE based on observations at four locations. While some authors maintained the possibility of a remnant native population in Essex County (Oldham 1983; King *et al.* 1997), recent studies suggest that all 20th century observations are the provenance of released pets (COSEWIC 2014c; see below). We consider it EE as per expert opinion (COSEWIC 2014c; COSSARO 2015).

Introduced herpetofauna of Essex County

Two turtle species are classified as introduced based on recent and historical observations in Essex County and evidence suggesting both can overwinter and reproduce in Ontario.

Eastern Box Turtle (*Terrapene carolina*): Based on genetic analyses, both subspecies of Eastern Box Turtle have been reported from Essex County: *T. c. carolina* (Woodland Box Turtle; historically native to Ontario, see above) and *T. c. triunguis* (Three-toed Box Turtle; native to the south-central United States; COSEWIC 2014c). Most Ontario sightings of this species since 1960 have been from Essex County, including >50 from PPNP (COSEWIC 2014c). Box turtles can overwinter and reproduce in Ontario (COSEWIC 2014c).

Red-eared Slider (*Trachemys scripta elegans*): This species has occurred at the OPC since the 1980s (Oldham 1983; Choquette and Valliant 2016) and at other Essex County locations more recently (Browne and Hecnar 2007; Seburn 2015; Ontario Nature 2017). There is circumstantial evidence that Red-eared Sliders can overwinter in Ontario and successful reproduction is suspected (although not yet established; Seburn 2015).

Herpetofaunal richness across Essex County

Herpetofaunal richness in southern Ontario (Ecoregions 6E and 7E; Armstrong and Dodge 2007) is 47 species/subspecies (excludes nine extirpated, out of range, or non-native species; Ontario Nature 2017). By comparison, contemporary herpetofaunal richness in Essex County is 29 species/subspecies (Table 3), or 62% (29/47) of the southern Ontario species diversity.

The number of recent reptile and amphibian observations submitted per grid square ranged from 1 to 616 ($\bar{x} = 128$), and the number of species/subspecies reported per grid square (i.e., observed richness) ranged from 1 to 19 ($\bar{x} = 9$). Grid squares with the lowest observed species/subspecies richness (1–10) dominate the central-eastern portion of the county and the Lake Erie Islands (outside of Pelee Island; Figure 3). Grid squares with the highest observed species/subspecies richness (11–19) occur in the western half of the county, along the north shore of Lake Erie, and on Pelee Island (Figure 3). Furthermore, the five grid squares with the greatest observed species/subspecies richness overall (16–19; Figure 3) are along the western and southern edges of Essex County (17LG28, 17LG27, 17LG35, 17LG75, and 17LG74 in Figure 1). The latter squares include some or all of the following larger natural areas: OPC, Detroit River Marshes, Turkey Creek Marshes, Canard River Marshes and Canard River Mouth Marsh, Fighting Island Marsh, Big Creek Marsh, Hillman Marsh, and PPNP (ERCA 2001).

The number of herpetofaunal species/subspecies reported per grid square was positively correlated with number of hectares of natural area per square ($r = 0.59$, $n = 31$, $P < 0.001$). Amount of natural area explained a significant, albeit moderate, proportion of variance in observed richness ($r^2 = 0.35$, $F_{1,31} = 16.77$, $P < 0.001$). Additional factors, such as uneven sampling effort (i.e., number of observations submitted) per grid square likely influenced observed richness (see Hortal *et al.* 2007; Pardo *et al.* 2013), particularly in squares with very low number of observations (e.g., 1–15 observations; Figure 2). As expected, observed richness was also positively correlated with number of recent observations submitted per square ($r = 0.68$, $n = 31$, $P < 0.001$). In order to account for effect of uneven sampling on the relationship between natural area and observed richness, we subsequently incorporated sampling effort and natural area in a multiple linear regression. Both the amount of natural area ($\beta = 0.004$, 95% CI = 0.000–0.008, $P < 0.029$) and number of observations submitted ($\beta = 0.013$, 95% CI = 0.006–0.021, $P < 0.001$) explained a greater proportion of variance in observed richness per square than natural area alone (adjusted $r^2 = 0.51$, $F_{2,30} = 17.63$, $P < 0.001$).

Status of herpetofauna in Essex County

Of the 29 species/subspecies of herpetofauna recognized in Essex County, we consider seven (two SAR) to be the most widespread in the region (i.e., recorded from >18 squares [>55%]) and six (four SAR) to be the most restricted (i.e., recorded from ≤2 squares [≤6%]; Table 2). Furthermore, almost half (13/29; 45%) of extant herpetofaunal species/subspecies in Essex County are limited in distribution (i.e., RE).

Of the 40 native species/subspecies of herpetofauna recognized from Essex County in the early 1980s, only one (3%) was considered extirpated (EE) while 24 (60%) were considered RE (Oldham 1983). The majority (70%, 28/40) of herpetofauna have not changed in local status since the early 1980s. Most surprisingly, however, more than a quarter (11/40; 28%) of reptile and amphibian species have declined in status—a decline that is entirely represented by species that went from being considered rare (RE) historically to extirpated (EE) today. Currently, we recognize 42 native species/subspecies of herpetofauna in Essex County, 13 (31%) of which are now classified EE, with another

TABLE 3. An updated checklist of the reptiles and amphibians of Essex County, Ontario. IN = introduced species, RE = species considered rare in Essex County, and EE = species considered extirpated from Essex County.

AMPHIBIANS (17 species)

FROGS AND TOADS (ANURA) — 10 species

☐ Blanchard's Cricket Frog (*Acris blanchardi*) EE
☐ Eastern American Toad (*Anaxyrus a. americanus*)
☐ Fowler's Toad (*Anaxyrus fowleri*) EE
☐ Gray Treefrog (*Hyla versicolor*) EE
☐ American Bullfrog (*Lithobates catesbeianus*)
☐ Green Frog (*Lithobates clamitans*)
☐ Northern Leopard Frog (*Lithobates pipiens*)
☐ Wood Frog (*Lithobates sylvaticus*) EE
☐ Spring Peeper (*Pseudacris crucifer*)
☐ Western Chorus Frog (*Pseudacris triseriata*)

Salamanders (Urodela) — 7 species

☐ Blue-spotted Salamander (*Ambystoma laterale*) RE
☐ Spotted Salamander (*Ambystoma maculatum*) EE
☐ Small-mouthed Salamander (*Ambystoma texanum*) RE
☐ Eastern Tiger Salamander (*Ambystoma tigrinum*) EE
☐ Common Mudpuppy (*Necturus m. maculosus*)
☐ Red-spotted Newt (*Notopthalmus v. viridescens*) RE
☐ Eastern Red-backed Salamander (*Plethodon cinereus*) RE

REPTILES (25 species)

SNAKES AND LIZARDS (SQUAMATA) — 17 species

☐ Blue Racer (*Coluber constrictor foxii*) RE
☐ Timber Rattlesnake (*Crotalus horridus*) EE
☐ Eastern Hog-nosed Snake (*Heterodon platirhinos*) EE
☐ Eastern Milksnake (*Lampropeltis triangulum*) EE
☐ Lake Erie Watersnake (*Nerodia sipedon insularum*) RE
☐ Northern Watersnake (*Nerodia s. sipedon*)
☐ Smooth Greensnake (*Opheodrys vernalis*) EE
☐ Gray Ratsnake (*Pantherophis spiloides*) EE
☐ Eastern Foxsnake (*Pantherophis vulpinus*)
☐ Common Five-lined Skink (*Plestiodon fasciatus*) RE
☐ Queensnake (*Regina septemvittata*) RE
☐ Eastern Massasauga (*Sistrurus catenatus*) RE
☐ Dekay's Brownsnake (*Storeria dekayi*)
☐ Red-bellied Snake (*Storeria occipitomaculata*) RE
☐ Butler's Gartersnake (*Thamnophis butleri*)
☐ Northern Ribbonsnake (*T. saurita septentrionalis*) EE
☐ Eastern Gartersnake (*T. s. sirtalis*)

Turtles (Testudines) — 8 species (+ 2 introduced species)

☐ Eastern Spiny Softshell (*Apalone s. spinifera*) RE
☐ Snapping Turtle (*Chelydra serpentina*)
☐ Midland Painted Turtle (*Chrysemys picta marginata*)
☐ Spotted Turtle (*Clemmys guttata*) RE
☐ Blanding's Turtle (*Emydoidea blandingii*)
☐ Northern Map Turtle (*Graptemys geographica*)
☐ Eastern Musk Turtle (*Sternotherus odoratus*) RE
☐ Woodland Box Turtle (*Terrapene c. carolina*) EE
☐ Eastern Box Turtle (*T. c. carolina/T. c. triunguis*) IN
☐ Red-eared Slider (*Trachemys scripta elegans*) IN

13 (31%) classified as RE. Only one species, Common Mudpuppy (*Necturus maculosus maculosus*), appears to have improved in status.

Discussion

With only 6.5% natural habitat remaining and 80% of the region in agriculture (ERCA 2002), Essex County provides a natural experiment on the impact of landscape-scale habitat loss on an assemblage of herpetofauna. Our results suggest that almost one third of historically occurring species/subspecies are extirpated, and almost half of those remaining are limited in distribution, impacts that have disproportionately affected salamanders and squamates. Furthermore, nine species of reptiles and amphibians that are not at risk in the province (Gray Treefrog, Wood Frog, Blue-Spotted Salamander [*Ambystoma laterale* excluding *texanum*-dependant population], Spotted Salamander, Red-spotted Newt [*Notopthalmus v. viridescens*], Eastern Red-backed Salamander [*Plethodon cinereus*], Eastern Milksnake, Smooth Greensnake, and Red-bellied Snake [*Storeria occipitomaculata*]) are either rare or absent here. In southern Ontario, herpetofaunal species richness was positively related to amount of forest cover (amphibians: Hecnar and M'Closkey 1998), and strongly influenced by proximity of nearby populations (PPNP: Hecnar and Hecnar 2005). Also, the number of endangered species found regionally in southern Canada was positively correlated with intensity of agricultural land use (Kerr and Cihlar 2004). Therefore, the large loss and severe fragmentation of amphibian and reptile habitat that has occurred in Essex County, primarily because of intensive agriculture and an extensive concession-style road network, was probably a leading factor in the landscape-scale defaunation of the region.

Grid squares with the highest herpetofaunal species/subspecies richness (i.e., 17LG27, 17LG28, 17LG35, 17LG74, and 17LG75; Figures 1 and 3) are ideal targets for broad-scale conservation efforts (e.g., habitat restoration and land acquisition), however, not all species are represented in these squares. Of 29 species/subspecies occurring in Essex County, the maximum number reported from any single square was 19 (Figure 3). Even when species/subspecies richness within the five richest squares is tabulated, only 22 species/subspecies are represented. Full representation (i.e., 29 species/subspecies) can be maintained by also targetting conservation efforts within five squares of moderately high richness (i.e., 17LG26, 17LG37, 17LG45, 17LG62, and 17LG63) which are collectively occupied by the six RE species with the smallest distributions (Table 2).

A major assumption of this study is that patterns of observed species/subspecies distributions and richness per square are reliable indicators of true patterns. Sampling effort is clearly uneven among squares, and our analysis demonstrated that observed richness was influenced by amount of natural area and number of observations submitted. So how reliable are our interpretations? While we acknowledge that observed distributions and richness do not fully represent their true counterparts, we found that the majority of squares with the lowest sampling effort were also those with the lowest amounts of natural area. Therefore additional search effort in those squares (while increasing observed distributions of locally common species and subsequently increasing observed richness therein) is unlikely to alter observed distributional patterns of RE species or relative patterns of observed species richness. The greatest changes in observed richness would be expected from increased search effort in two squares (17LG36 and 17LG25), as both are characterised by relatively high amounts of natural area, low number of submitted observations, and low observed richness, making them ideal candidates for future surveys.

A declaration of local extirpation generally requires various levels of scrutiny, including date of last observation, knowledge of search effort, generation time, etc. In this study we chose a 20-year cut-off as a minimum to classify a species as extirpated from the county. It is possible that an amphibian or reptile species could persist in spite of it not being reported in two decades (e.g., Seburn and Mallon 2017). However, in all but three cases (Gray Treefrog, Smooth Greensnake, and Spotted Salamander; none reported in 22–31 years) each EE species was subject to other levels of scrutiny (e.g., detailed species status reports) prior to being considered extirpated.

To prevent future extirpations in Essex County, recovery efforts should target both SAR and common species that are locally rare because provincial ranks alone do not reflect local status in all cases. For example, five locally widespread herpetofauna are listed as SAR provincially, while four RE species are widespread across southern Ontario (Table 2). Regarding SAR, we've identified seven provincially Endangered herpetofauna with small local distributions (i.e., RE; Table 2) and which are arguably at relatively greater risk of extirpation from Essex County (e.g., Massasauga [*Sistrurus catenatus*] and Queensnake [*Regina septemvitatta*]) and Canada as a whole (e.g., Blue Racer and Small-mouthed Salamander). Conversely, provincially widespread species such as the Eastern Red-backed Salamander and Red-spotted Newt are locally rare but not SAR in Ontario, therefore a lack of legal protection could result in further declines and extirpations. Six RE species with the most limited local distributions (three salamanders and three snakes; Table 2) are ideal candidates for targetted conservation interventions (e.g., habitat enhancement, threat mitigation, and population management), in order to prevent further biodiversity loss from this herpetologically significant region of Canada.

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Literature Cited

Armstrong, D.K., and J.E.P. Dodge. 2007. Paleozoic Geology of Southern Ontario. Miscellaneous Release – Data 219. Project Summary and Technical Document. Sedimentary Geoscience Section, Ontario Geological Survey, Sudbury, Ontario, Canada.

Browne, C.L., and S.J. Hecnar. 2007. Species loss and shifting population structure of freshwater turtles despite habitat protection. Biological Conservation 138: 421–429. https://doi.org/10.1016/j.biocon.2007.05.008

CHS (Canadian Herpetological Society). 2017. Important Reptile and Amphibian Areas. Accessed 4 October 2018. http://canadianherpetology.ca/conservation/impara.html.

Choquette, J.D., and L. Valliant. 2016. Road mortality of reptiles and other wildlife at the Ojibway Prairie Complex and Greater Park Ecosystem in Southern Ontario. Canadian Field-Naturalist 130: 64–75. https://doi.org/10.22621/cfn.v130i1.1804

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2001. COSEWIC assessment and status report on the Timber Rattlesnake *Crotalus horridus* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_timber_rattlesnake_2001_eng.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2002. COSEWIC assessment and status report on the Eastern Ribbonsnake *Thamnophis sauritus* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. https://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_eastern_ribbonsnake_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2004. COSEWIC assessment and update status report on the Spotted Turtle *Clemmys guttata* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. https://sararegistry.gc.ca/virtual_sara/files/cosewic/sr_spotted_turtle_edited_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2007. COSEWIC assessment and update status report on the Eastern Hog-nosed Snake *Heterodon platirhinos* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_eastern_hognosed_snake_0808_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2010a. COSEWIC assessment and status report on the Fowler's Toad *Anaxyrus fowleri* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr%5FFowler%27s%20Toad%5F0810%5Fe%2Epdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2010b. COSEWIC assessment and status report on the Butler's Gartersnake *Thamnophis butleri* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. https://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_butlers_gartersnake_0911_eng.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2011. COSEWIC status appraisal summary on the Blanchard's Cricket Frog *Acris blanchardi* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. https://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/blanchard_cricket_frog_sse_0911_eng.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2012. COSEWIC assessment and status report on the Eastern Ribbonsnake *Thamnophis sauritus* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. https://wildlife-species.canada.ca/species-risk-registry/virtual_sara/files/cosewic/sr_coulevre_mnc_e_ribbonsnake_1113_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2014a. COSEWIC assessment and status report on the Eastern Milksnake *Lampropeltis triangulum* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. https://sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Eastern Milksnake_2014_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2014b. COSEWIC assessment and status report on the Spotted Turtle *Clemmys guttata* in Canada. COSEWIC. Ottawa, Ontario, Canada. Accessed 4 October 2018. https://sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Spotted Turtle_2014_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2014c. COSEWIC assessment and status report on the Eastern Box Turtle *Terrapene carolina* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Eastern Box Turtle_2014_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2015. COSEWIC assessment and update status report on the Lake Erie Watersnake *Nerodia sipedon insularum* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Lake Erie Watersnake_2015_e.pdf.

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2016. COSEWIC assessment and status report on the Spiny Softshell *Apalone spinifera* in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 4 October 2018. http://www.sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Spiny Softshell_2016_e.pdf.

COSSARO (Committee on the Status of Species at Risk in Ontario). 2011a. COSSARO candidate species at risk evaluation for Blanchard's Cricket Frog (*Acris blanchardi*). Ontario Government Documents, Toronto, Ontario, Canada. Accessed 4 October 2018. http://www.ontla.on.ca/library/repository/mon/26004/316820.pdf.

COSSARO (Committee on the Status of Species at Risk in Ontario). 2011b. COSSARO candidate species at risk evaluation for Timber Rattlesnake (*Crotalus horridus*). Ontario Government Documents, Toronto, Ontario, Canada. Accessed 4 October 2018. http://www.ontla.on.ca/library/repository/mon/26004/317141.pdf.

COSSARO (Committee on the Status of Species at Risk in Ontario). 2015. COSSARO candidate species at risk evaluation for Eastern Box Turtle (*Terrapene carolina*). Ontario Government Documents, Toronto, Ontario, Canada. Accessed 4 October 2018. http://cossaroagency.ca/wp-content/uploads/2017/06/Accessible_COSSARO-evaluation-Eastern-box-turtle.pdf.

Craig, J.M., D.A. Mifsud, A.S. Briggs, J. Boase, and G. Kennedy. 2015. Mudpuppy (*Necturus maculosus maculosus*) spatial distribution, breeding water depth, and use of artificial spawning habitat in the Detroit River. Herpetological Conservation and Biology 10: 926–934.

Crother, B.I. 2017. Scientific and Standard English Names of Amphibians and Reptiles of North America North of Mexico, with Comments Regarding Confidence in our Understanding. Eighth Edition. Society for the Study of Amphibians and Reptiles Herpetological Circular 43.

Dance, K.W., and C.A. Campbell. 1981. Eastern hognose snake sighted at Point Pelee National Park, Ontario. Ontario Field Biologist 35: 40–42.

DCL (Dillon Consulting Ltd.). 2009. Wildlife investigations re. species at risk Matchette/Sprucewood commercial development site Windsor, ON. Report for Wood Bull, LLP Barristers and Solicitors, Toronto, Ontario, Canada.

EL (Ecologistics Ltd.). 1976. Windsor Airport environmental study. Report for Transport Canada, Ottawa, Ontario, Canada.

Environment Canada. 2010. Recovery strategy for the Timber Rattlesnake (*Crotalus horridus*) in Canada. *Species at Risk Act* Recovery Strategy Series. Environment Canada, Ottawa, Ontario, Canada. Accessed 5 October 2018. https://www.registrelep-sararegistry.gc.ca/virtual_sara/files/plans/rs_timber_rattlesnake_final_0310_e.pdf.

ERCA (Essex Region Conservation Authority). 2001. Natural areas map of Essex Region. Essex Region Conservation Authority, Essex, Ontario, Canada.

ERCA (Essex Region Conservation Authority). 2002. Essex Region biodiversity conservation strategy – habitat restoration and enhancement guidelines. ERCA, Essex, Ontario, Canada.

Gardner-Costa, J., T. Preney, and D. Zhao. 2014. Ojibway Prairie Bioblitz 2014: summary report for partners. Ojibway Nature Centre, Windsor, Ontario, Canada. Accessed 5 October 2018. http://www.essexcountynature.com/wp-content/uploads/2018/03/Ojibway-Prairie-BioBlitz-2014-Report_revisedv2.pdf.

Government of Ontario. 2005. Provincial policy statement. Ministry of Municipal Affairs and Housing, Toronto, Ontario, Canada.

Government of Ontario. 2018. Species at risk in Ontario. Accessed 5 October 2018. https://www.ontario.ca/environment-and-energy/species-risk-ontario-list.

Hecnar, S.J., and D.R. Hecnar. 2004. Losses of amphibians and reptiles at Point Pelee National Park. Pages 127–139 *in* Parks and Protected Areas Research in Ontario: Planning Northern Parks and Protected Areas. *Edited by* C. Rehbein, G. Nelson, T. Beechey, and R. Payne. Proceedings of the Parks Research Forum of Ontario AGM, 4–6 May 2004, Lakehead University, Parks Research Forum of Ontario, University of Waterloo, Waterloo, Ontario, Canada.

Hecnar, S.J., and D.R. Hecnar. 2005. Feasibility of repatriation of extirpated herpetofauna to Point Pelee National Park. Final Report of Memorandum of Understanding CR 02-51. Department of Biology, Lakehead University, Thunder Bay, Ontario, Canada.

Hecnar, S.J., and R.T. M'Closkey. 1998. Species richness patterns of amphibians in southwestern Ontario ponds. Journal of Biogeography 25: 763–772. https://doi.org/10.1046/j.1365-2699.1998.2540763.x

Hortal, J., J.M. Lobo, and A. Jiménez-Valverde. 2007. Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. Conservation Biology 21: 853–863. https://doi.org/10.1111/j.1523-1739.2007.00686.x

IUCN (International Union for Conservation of Nature). 2012. Guidelines for application of IUCN Red List criteria at regional and national levels: version 4.0. IUCN, Gland, Switzerland and Cambridge, United Kingdom. Accessed 5 October 2018. http://s3.amazonaws.com/iucnredlist-newcms/staging/public/attachments/3101/reg_guidelines_en.pdf.

Jalava, J.V., J.D. Ambrose, and N.S. May. 2009. National Recovery Strategy for Carolinian woodlands and associated species at risk: phase I. Draft 11. Carolinian Canada Coalition and Ontario Ministry of Natural Resources, London, Ontario, Canada.

King, R.B., M.J. Oldham, W.F. Weller, and D. Wynn. 1997. Historic and current amphibian and reptile distributions in the island region of western Lake Erie. American Midland Naturalist 138: 153–173. https://doi.org/10.2307/2426663

Livo, L.J., G.A. Hammerson, and H.M. Smith. 1998. Summary of Amphibians and Reptiles Introduced into Colorado. Northwestern Naturalist 79: 1–11. https://doi.org/10.2307/3536811

MIHerpAtlas. 2017. Michigan Herp Atlas: a statewide herpetological atlas and data hub. Accessed 5 October 2018. http://www.miherpatlas.org.

NHIC (Natural Heritage Information Centre). 2017. Provincially tracked species and observation data. ESRI File geodatabase. Data provided by Ontario Ministry of Natural Resources. Queen's Printer, Toronto, Ontario, Canada.

NatureServe. 2017. NatureServe Explorer: an online encyclopedia of life [web application]. Version 7.1. NatureServe, Arlington, Virginia, USA. Accessed 3 May 2018. http://explorer.natureserve.org.

Ngo, A., V.L. McKay, and R.W. Murphy. 2009. Recovery Strategy for Tiger Salamander (*Ambystoma tigrinum*) (Great Lakes Population) in Canada. *Species at Risk Act* Recovery Strategy Series. Parks Canada Agency, Ottawa, Ontario, Canada. Accessed 5 October 2018. https://registrelep-sararegistry.gc.ca/virtual_sara/files/plans/rs_tiger_salamander_great_lakes_0409_e.pdf.

Oldham, M.J. 1983. Environmentally significant areas of the Essex Region. A Background Report to the Essex Region Conservation Plan. Essex Region Conservation Authority, Essex, Ontario, Canada.

Oldham, M.J. 1984a. A preliminary list of the amphibians of Essex County. Canadian Amphibian and Reptile Conservation Society Bulletin 21(5): 1–6.

Oldham, M.J. 1984b. A preliminary list of the reptiles of Essex County. Canadian Amphibian and Reptile Conservation Society Bulletin 22: 1–8.

Oldham, M.J. 1986. The queen snake, a reptile new to Essex County. The Egret 3(3): 25–26.

Oldham, M.J. 1988. Ontario herpetofaunal summary 1985. World Wildlife Fund Canada, Toronto; Essex Region Conservation Authority, Essex; and Ontario Ministry of Natural Resources, Southwestern Region, London, Ontario, Canada.

Oldham, M.J., and D.A. Sutherland. 1986. 1984 Ontario herpetofaunal summary. Essex Region Conservation Authority, Essex and World Wildlife Fund, Toronto, Ontario, Canada.

Ontario Nature. 2015. ORAA infographic. Accessed 5 October 2018. https://ontarionature.org/wp-content/uploads/2017/11/ON_Nature_Spring-2015_Ontario_Reptile_and_Amphibian_Atlas_infographic.pdf.

Ontario Nature. 2017. Reptiles and amphibians of Ontario – interactive map. Accessed 5 October 2018. https://ontarionature.org/oraa/maps.

Ontario Nature. 2018. Reptiles and amphibians of Ontario – interactive map. Accessed 5 October 2018. https://ontarionature.org/oraa/maps.

Pardo, I., M.P. Pata, D. Gómez, and M.B. García. 2013. A novel method to handle the effect of uneven sampling effort in biodiversity databases. PLoS One 8: e52786. https://doi.org/10.1371/journal.pone.0052786

Planck, R.J., and J.T. Planck. 1977. Ecology and status of the Butler's garter snake*, Thamnophis butleri* (Cope), in southwestern Ontario. Department of Supply and Services, Toronto, Ontario, Canada.

Pulfer, T. 2014. Thirty years of tracking herps. ON Nature 1: 7.

Rowell, J. 2012. The Snakes of Ontario: Natural History, Distribution and Status. Art Bookbindery, Winnipeg, Manitoba, Canada.

Seburn, D.C. 2015. Distribution of the exotic Pond Slider (*Trachemys scripta*) in Ontario. Canadian Field-Naturalist 129: 342–348. https://doi.org/10.22621/cfn.v129i4.1756

Seburn, D.C., and E. Mallon. 2017. Has the Eastern Red-backed Salamander (*Plethodon cinereus*) declined in Ontario? Canadian Field-Naturalist 131: 115–119. https://doi.org/10.22621/cfn.v131i2.1981

Town of LaSalle. 2016. Town of LaSalle Official Plan. 5 January 2015 Office Consolidation. Corporation of the Town of LaSalle, LaSalle, Ontario, Canada.

Tozer, D.C. 2016. The state of marsh birds and frogs: Nottawasaga Valley-Lake Simcoe watershed report 1995–2015. Bird Studies Canada, Port Rowan, Ontario, Canada. Accessed 5 October 2018. https://www.birdscanada.org/download/GLMMPWatershedrpt.pdf.

Weller, W.F., and M.J. Oldham. 1988. Ontario herpetofaunal summary: 1986. Ontario Field Herpetologists, Cambridge, Ontario, Canada.

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Book Reviews

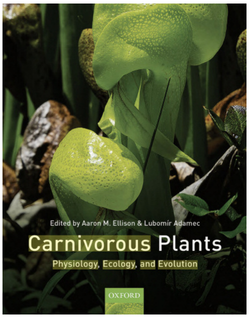
Book Review Editor's Note: *The Canadian Field-Naturalist* is a peer-reviewed scientific journal publishing papers on ecology, behaviour, taxonomy, conservation, and other topics relevant to Canadian natural history. In line with this mandate, we review books with a Canadian connection, including those on any species (native or non-native) that inhabits Canada, as well as books covering topics of global relevance, including climate change, biodiversity, species extinction, habitat loss, evolution, and field research experiences.

Currency Codes: CAD Canadian Dollars, USD US Dollars, EUR Euros, AUD Australian Dollars, GBP British Pound.

BOTANY

Carnivorous Plants: Physiology, Ecology, and Evolution

Edited by Aaron M. Elison and Lubomír Adamec. 2018. Oxford University Press. 510 pages, 125.00 CAD, Cloth. Also available as an E-book.



When *Carnivorous Plants: Physiology, Ecology, and Evolution* arrived on my doorstep, I knew by its heft that this would not be a light read. As a review of the most up to date research on carnivorous plants, this is ideal for senior undergraduate or graduate students, academics, and those with a keen interest in carnivorous plants, but it would be a difficult read if you had no background knowledge in evolutionary biology, botany, or biochemistry. There is a baseline of assumed vocabulary, so if you've never heard the words Diptera, saprophagous, or entomophily, grab a dictionary. In other words: this is a textbook, so plan accordingly.

Editors Aaron Ellison and Lubomír Adamec have done an excellent job of compiling a collection of chapters that represent a range of knowledge in the field, including an overview of the carnivorous syndrome, the evolution of each major genus of carnivorous plant, symbiotic insect and microbial communities, biotechnology and pharmaceuticals, and the mechanisms of prey attraction, retention, and digestion.

Approximately 800 known species of carnivorous plants are found around the world, with hotspots in southeast Asia, Australia, South Africa, and the southeast United States. They grow in a variety of habitats, but thrive in nutrient-poor, warm, and wet conditions. To be truly carnivorous, a plant must display all five of the following traits: capture prey in specialized traps; kill the captured prey; digest the prey; absorb nutrients from the killed prey; and use the nutrients for plant growth and development.

The mechanics of prey attraction, capture, and retention are remarkable. Robert Naczi covers the systematics and evolution of my favourite carnivorous plant—*Sarracenia purpurea* (commonly known as the Northern Pitcher Plant or Purple Pitcher Plant, and native to peatlands in eastern North America)—in Chapter 9. As discussed in Chapter 12, contrasting red and green stripes called "nectar guides" attract prey to the lip of the pitcher, along with olfactory cues. Downward facing hairs on the interior guide the prey to the water-filled bottom, where most insects die by drowning. Although the liquid is mostly collected precipitation, death comes faster in a pitcher plant than in pure water—possibly because of the addition of digestive enzymes, and other animals that live in the pitcher plant that help to breakdown prey (more on that later).

One of the interesting contradictions of carnivorous plants is that they are almost all entomophilic (pollinated by insects). These are plants that have evolved to attract and trap insects for prey, and yet they rely on insects for survival of the species. Cross *et al.* (Chapter 22) explain that pollinator-prey conflict is rare, owing perhaps to several adaptations, including physical space between the flower and the trap, temporal space between the time of pollination and the time of trap maturation, and different scents emitted by different parts of the plant, designed to attract different insects.

I am fascinated by carnivorous plants and their mutualistic relationship with certain arthropods. I first learned about the Pitcher Plant Mosquito, *Wyeomyia smithii,* while reviewing *The Secret Life of Flies* (Bocking 2017). The female lays eggs in the water of the pitcher, where the mosquitoes hatch and live their entire larval lifecycle, living off the decomposing prey and resident bacterivores and microbes. The trap of a pitcher plant is home to an entire food web that helps the plant break down prey so the plant can more easily absorb its nutrients. The life of *W. smithii* in *S. purpurea* is the most studied relationship of a carnivorous plant and its inquiline (an animal that lives in the living space of another) but, as is discussed in detail in Chapter 24, most carnivorous plants are host to several species of invertebrates, microbes, and bacteria. We may think about the complexity of the hairs on a sundew, but this is just the surface: there are entire communities of organisms living on, within, and amongst these astonishing plants.

Until recently, the conservation status of only 10% of carnivorous plants was understood. Now we have a basic understanding of about 70%, but there is still work to do. In particular, it's difficult to model how these plants will adapt to a changing climate. Their habitats are diverse and widespread, but it is likely that the availability of suitable habitat will decrease faster than new habitat will become available. Fitzpatrick and Ellison conclude in Chapter 28 that one of our best assurances against species loss is habitat protection. In Canada, we must protect our wetlands, where most carnivorous plants are found.

This is not a book of fast, easy facts, but it does reward the careful and thorough reader who is passionate about botany. The next time you walk by a sundew, bladderwort, or pitcher plant in your local wetland, you might find yourself with some questions about how these crazy organisms even exist. If you're curious, spend some time with those plants, and with this book.

Literature Cited

Emma Bocking. 2017. [Book review] The Secret Life of Flies. Canadian Field-Naturalist 131: 287–288. https://doi.org/10.22621/cfn.v131i3.2059

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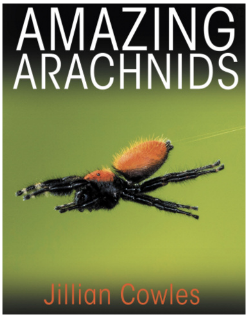
ENTOMOLOGY

Amazing Arachnids

By Jillian Cowles. 2018. Princeton University Press. 328 pages, 45.00 USD, Cloth, 35.00 USD, E-book.



Amazing Arachnids graced my desk unopened for several weeks while I assumed, based on the title and eye-popping cover, that the book would be a photographic tour of the more spectacular spiders, scorpions, and their kin. That, of course, would have been enough in itself but, when I finally dove into the book, I found it to be much, much more. *Amazing Arachnids* is a thorough treatment of the entire class Arachnida, packed with stunning photos (mostly by the author) and replete with original observations and insights, all stitched together by carefully crafted and densely packed text. I'm not an arachnid specialist, but I found her treatment of even the most obscure arachnid subgroups to be original, readable, and richly detailed.

The first chapter brought me up to speed on basic arachnid structure, biology, and classification in an extensive and exhaustively illustrated introduction, including nice summaries of such disparate subjects as reproductive strategies, fossils, hunting strategies, phylogeny, and vision. The photographic pages covering the "arachnid orders at a glance" (pp. 24–25) were especially useful as an informative snapshot of the orders to be covered in colourful detail in the following pages.

The next nine chapters deal with arachnids other than spiders. Every chapter, even those dealing with relatively obscure groups such as short-tailed whipscorpions and microwhipscorpions, reflects the same level of meticulous scholarship and photographic acumen, with excellent photographs supporting almost every one of the remarkable bits of behaviour and morphology detailed for every group. The author has clearly spent years finding and carefully photographing not only every taxon, but also the details of hunting, habitats, sexual behaviour, and even minute structures such as spermataphores. It is perhaps not surprising that the lively narrative and associated photographs bring scorpions to life and absorb the reader into the history, biology, taxonomy, and structure of these spectacularly armed arachnids. But she succeeds, impressively, in doing the same for the less familiar pseudoscorpions, vinegaroons, short-tailed whipscorpions, tailless whipscorpions, microwhipscorpions, harvestmen, wind spiders, and even ticks and mites. Each order is exposed as beautiful and full of surprises.

The remainder of the book, including somewhat more than half of its 328 pages, covers the spiders. Chapter 11 introduces the order Araneae and offers fascinating detail about sociality, silk, sex, and special behaviours. Oddly, it does not include a section on spider classification or phylogeny. I would have found a summary hierarchical classification or family tree useful to prepare me for the family-by-family coverage in the subsequent chapters. Chapter 12 begins that coverage with the tarantulas, trapdoor spiders, and other "mygalomorphs", including nine richly illustrated pages each for the tarantulas and the trapdoor spiders, and shorter sections for the less familiar families. Chapter 13 covers three families of orb weavers, while Chapter 14 includes half a dozen families of "irregular web builders". One of these families, the black widow family Theridiidae, is clearly a favourite of the author, as her treatment of this group is full of first-hand insight and especially original photos (although this does not mean short shrift for the pholcids and other families discussed in this chapter). Chapter 15 covers the variety of families considered to be crevice weavers, ground weavers, and sheet web builders, with the brown recluse family Sicariidae getting top billing and a particularly readable treatment. Chapter 16 is the most colourful of all, with a good balance of spectacular photos and clear text about everyone's favourite spiders, the Salticidae. The author says that "Jumping spiders have so many pleasing qualities that it would be difficult to decide what is most admirable about these delightful little creatures" (p. 237), but this chapter gives the reader lots on which to base such a decision. The remaining chapters cover the lynx spiders, crab spiders, sand spiders, wolf spiders, fishing spiders, spitting spiders, and the various families of "wandering hunters". As with the rest of this book, these chapters are illustrated with incredible action photos and detailed shots of taxa and structures. Most of the photos are from the spider hotspots of the American Southwest, and this book could serve as a field guide to Arizona arachnids. But this in no way detracts from its value to Canadian naturalists, because it is an exceptionally readable and authoritative review of Arachnida. I consider this an essential volume for any naturalist with any interest in arthropods.

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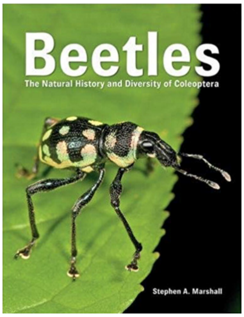
Beetles: The Natural History and Diversity of Coleoptera

By Stephen A. Marshall. 2018. Firefly Books. 784 pages, 95.00 CAD, Cloth.



A massive work like this book is rarely expected even after a lifetime of study. However, (a) this book has not come out at the end of Marshall's career and (b) this tome is not even his second one, it's his third!

One can open this book anywhere in the almost 800 pages and be met with beautiful photographs of beetles, many of them taken in the field; alone, these would make the book a centrepiece on any naturalist's coffee table. However, the huge volume of information in the text will make this a go-to reference book for even the most ardent coleopterist.

The writing is casual, occasionally humorous (with a mandatory reference to The Beatles!), with scientific jargon kept to a minimum. Having said that, the 'minimum' often includes complex names and processes, simply because no easier words exist. Some zoological background would certainly make the text more digestible to the reader. I would not, however, let this prevent me from gifting this book to an amateur entomologist, nor even a novice.

Part 1 introduces beetle biology (excluding taxonomy), including size diversity, beetle look-a-likes, life histories, and much more. This section is richly illustrated with large, excellent photographs. It is here that we find out why beetles are so successful, both in sheer numbers and diversity. Habitat and food specialists are each given a subsection, as have been defences, pests, and anatomy. There are more; suffice it to say that I can't imagine a topic which has not been addressed.

Part 2 of this book is a taxonomic look at essentially all of the 180 beetle families. As in his book *Flies* (Marshall 2012), Marshall writes about each family, richly illustrating them with a diversity of species from around the globe; there are over 250 photographs for scarab beetles (superfamily Scarabaeoidea) alone! Again, most of the thousands of shots are of live beetles *in situ*, but some are clearly taken under studio-like settings and a minority are taken of museum specimens (pinned or pointed). There are even photographs of stamps which feature beetles.

The final part of this book is "Studying Beetles". Here, Marshall describes catching, preserving, and photographing beetles. Collecting methods are described, often in detail other authors may have left out. Notes on some legal issues, with an example of those who got into trouble for not following the laws, are described. Finally, the book finishes with a key, richly illustrated, which is very nice. However, and this is literally the only downfall of the book, many of the labelled structures are not magnified enough to be useful.

A book of this quality and magnitude is rare; there should be no second thoughts about getting this for yourself or other insect enthusiast.

Literature Cited

Marshall, S.A. 2012. Flies: The Natural History and Diversity of Diptera. Firefly Books, Richmond Hill, Ontario, Canada.

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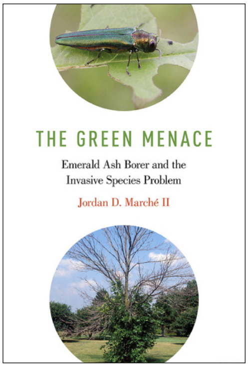
The Green Menace: Emerald Ash Borer and the Invasive Species Problem

By Jordan D. Marché II. 2017. Oxford University Press. 320 pages, 77.00 USD, Cloth.



Despite its relatively recent arrival, Emerald Ash Borer (EAB; *Agrilus planipennis*) is one of the most destructive invasive species in North America. In little over 20 years, the economic impact of this beetle is estimated in the billions, while its ecological damage is incalculable. *The Green Menace*, by Jordan Marché II, provides a thorough case-study of this invasion, from the first signs of ash (*Fraxinus* spp.) decline detected in Michigan in 1998, the belated attribution of the problem to the EAB in 2002, and through the varied, and largely futile, efforts to eradicate it since then.

For the most part, the book is arranged chronologically. The first chapter reviews what was known about EAB prior to 1998. EAB arrived in Michigan sometime before 1998, but wasn't properly identified until 2002, a period covered in Chapter Two. Chapter Three provides a brief survey of invasion ecology and integrated pest management, and the first steps in developing a government response to EAB. This is followed by two chapters on EAB biology and its social and economic impact. The later stages of the failed effort to eradicate the beetle, or at least contain it to Michigan, are presented in Chapter Seven. More recent efforts to manage EAB with chemical pesticides, biological control, and breeding resistant ash varieties are each explored in separate chapters.

The great strength of the book is the meticulous cataloguing of the historical details of the story. This includes the conventional timeline of the detection of EAB. That is, the first symptoms were detected by Michigan arborists in 1998. They didn't notify plant pathologists (at Michigan State University) until 2001. That lead to a tentative diagnosis that the problem was due to a disease called "Ash Yellows". However, the presence of an as-yet-unidentified beetle was also noted. This species, one of more than 2700 in the genus *Agrilus*, was unknown to North American entomologists, and didn't appear in any regional references. Not surprisingly, it took until the following summer before it was properly identified. With that information in hand, authorities were at last in position to initiate control efforts.

However, Marché also documents reports from 1998 documenting ash trees in the area declining as a result of infestation by one or two beetles. At the time, the beetles were suspected to be native species, but identification wasn't confirmed until 2002, as mentioned above. In effect, EAB had an extra four years to establish and spread. In retrospect, it may have been possible to control it had forceful action been taken in 1998 or 1999. By 2002, it was almost certainly too late—not that we knew it yet.

The chronological presentation of the story highlights the challenges faced by the scientists charged with eradicating EAB. Putting a name on the pest was only the first challenge: nearly nothing was known about its biology or ecology. As with so many noxious invasive species, it is largely unremarkable in its home range, such that it hadn't attracted the attention of Chinese entomologists. There were reports of EAB attacking plantings of North American ash species introduced into China, but they weren't accessible to English-speaking scientists in North America.

In the meantime, it took years to clarify the life history and dispersal potential of EAB. Unfortunately, early data suggested that females could disperse only up to a half mile (0.8 km), and control buffers were established using this figure. As it turns out, this grossly underestimated how far the beetles actually travel. Furthermore, EAB remains difficult to detect for the first two years after arriving in a new location. Consequently, when control efforts started in earnest in 2002 and 2003, EAB had already moved beyond the quarantine zone.

While the central focus of the book is the EAB program managed by the Michigan Department of Agriculture (MDA), it also includes efforts to control the pest in Ontario. Lead by the Canadian Food Inspection Agency, an ambitious plan to remove all ash trees from a firewall in southwest Ontario, the so-called "Ash Free Zone", 10 km across and 30 km long, was implemented in 2004 (pp. 111–112). This didn't keep EAB from spreading to the rest of the province, but Marché argues that it was still worthwhile. Despite the public outcry, the ash-free zone may have bought researchers crucial time to develop more robust strategies.

In sum, the first half of the book very effectively presents the challenges posed by invasive species. At a time when seemingly anything you might want to know can be learned by consulting your phone, it is humbling to realize how much about our natural world remains a mystery. Marché has harsh criticism for MDA staff, particularly the opportunities lost in the crucial period between 1998 and 2002. But even had they acted swiftly, and the government provided the requested funding, controlling or eradicating EAB would still have been a formidable challenge.

At this point EAB continues to spread largely unchecked across North America. However, the second half of the book outlines three approaches that may ultimately lead to effective long-term management. Chemical control methods are now available. While they will never be practicable on a large scale, they may nevertheless provide foresters and landscapers with tools for managing small numbers of important trees. Longer term solution will require a combination of biological control or breeding ash stock resistant to EAB attack.

Overall, *The Green Menace* provides a very insightful case study of the early invasion, establishment, and spread of a serious forest pest. The text does occasionally get bogged down in minutiae. That said, this will undoubtedly serve as an important document for the study of invasive species. I highly recommend it for anyone interested in invasive species, habitat conservation, or large-scale ecological management issues.

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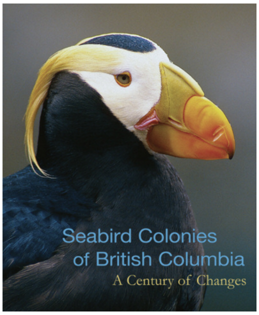
ORNITHOLOGY

Seabird Colonies of British Columbia: A Century of Changes

By Michael S. Rodway, R. Wayne Campbell, and Moira J.F. Lemon. 2017. Wildlife Afield, Volume 13, Numbers 1 & 2, January–December 2016. Biodiversity Centre for Wildlife Studies. 298 pages, 40.00 CAD, Paper.



This book provides a detailed synthesis of knowledge on the distribution and status of 16 species of colonial seabird (two species of storm-petrel, three cormorants, one shorebird, one gull, and nine alcids) that had nested in British Columbia (BC) up to 1990. One additional species has since nested in the province, that being Black-legged Kittiwake (*Rissa tridactyla*). When I began reading this book, I was disappointed to read that the cut-off date for data summaries on these colonial seabirds was 1990 (the last year of focussed surveys and associated comprehensive provincial population estimates by the Canadian Wildlife Service). However, as it turns out, even though the cut-off date for detailed data inclusion is 1990, the book actually contains substantial information for at least some species up to 2015.

The book begins with a tribute to Harry Carter, one of the important contributors to seabird monitoring and research in BC, followed by introductory chapters that provide an overview of how the species for the book were selected, important attributes of BC's coastal environments, the history of seabird monitoring and research in BC, and detailed discussions of survey methods, data presentation, and population estimation. There is some repetition between these introductory sections and the species accounts, but it is useful to have all of the survey history and methodology summarized initially, even if some of those same topics recur in later parts of the book (albeit with different levels of detail).

The heart of the book for most readers will be the species accounts. These occupy roughly a third of the book. Each species account provides general information on the species in BC, as well as sections on appearance, breeding, and conservation. Detailed tabular summaries of numbers of nests/burrows and numbers of birds observed at each colony are provided, accompanied by cartographic summaries showing the relative size of each colony and its location along the coast. One of the interesting additional attributes of each species account (and of other parts of the book) is the sidebar that provides anecdotes about the species, about incidents that occurred during the surveys, or about relevant contributions of some of the surveyors, all of which add to our understanding of these species and the challenges involved in monitoring them. Each species account also is accompanied by a line drawing and usually several black and white photographs of the bird and/or its colonies. These accounts are fascinating and provide insights into each species' biology. For example, although Brandt's Cormorant (*Phalacrocorax penicillatus* [unfortunately misspelled *pencillatus* in the book]) is rather rare and localized as a breeder in BC, numbers build in the late summer from colonies further south along the American west coast, so that the species is relatively common and more widespread on the BC coast during fall, winter, and early spring, before the southern birds return to their breeding colonies.

Following the species accounts, additional chapters cover threats to seabirds and their colonies in BC (including direct exploitation, logging and erosion, manmade obstacles, real estate-associated development, mariculture, commercial fishery interactions, oil pollution, plastics and other pollutants, parasites and diseases, natural predators, introduced species, climate change and associated oceanic changes, and natural disturbances). There is also a section dealing with conservation measures and recommendations. The final part of this book is the Literature Cited section, which is often ignored by readers unless they are searching for a reference. However, in this book, the section is sprinkled with photographs that supplement or further explain the results of some of the papers cited. I really enjoyed reading the captions of these photographs, which add value to the Literature Cited section, in my opinion (an unorthodox approach, but welcome).

There is one subsection in the "Conservation Measures and Recommendations" section dealing with legislation and conservation status listing of species that I disagreed with, particularly with regard to peripheral or range-edge taxa. There are varying opinions as to how such taxa should be dealt with. Although I agree that there may be higher priority species that should be listed before range-edge ones, I do not agree that range-edge populations are not likely to be genetically diverse. No evidence is provided for this proposition, yet, in other groups of organisms (e.g., various angiosperms), there is ample evidence that important evolutionary processes occur in range-edge populations. Furthermore, range-edge populations may become source populations for northward colonization as climate changes (not necessarily a reason for listing, but certainly a reason for certain types of conservation action).

When reading this book, it is important to remember that the context for the species accounts and discussion is BC-focussed. For example, observers on the coasts in the Maritime Provinces might be bemused by the suggestion that Double-crested Cormorant (*Phalacrocorax auritus*) could be called "Freshwater" Cormorant; certainly, it is the cormorant most likely to breed on freshwater bodies, but by no means exclusively. Another BC seabird-centric comment that would not hold true in many oceanic regions of the world is that "seabirds … are easy to … identify compared to other marine species …" (p. 220).

Overall, I found this book to be an excellent in-depth account and summary of the breeding occurrence and status of the 16 seabird species that nested in BC up to 1990. I did find a number of typographical errors and an occasional missing word but, all in all, these do not detract from the value of the book. For anyone interested in seabirds in general, or for breeding birds of BC specifically, this book is well worth reading.

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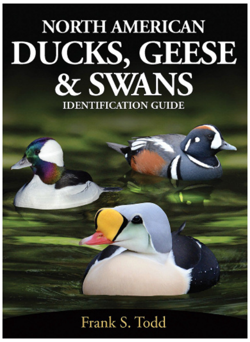
North American Ducks, Geese & Swans Identification Guide

By Frank S. Todd. 2018. Hubbs Seaworld Research Institute. Distributed in Canada by Hancock House Publishers. 203 pages, 29.95 USD, Paper.



This is a visually stunning book, with superb photographs of each species in a variety of behavioural postures and flight angles, plumages, and age classes; for example, I counted 40 images for Common Merganser (*Mergus merganser*) alone (pp. 167–170). There is very little text: a short preface, an introductory page to each section (whistling ducks, geese, swans, perching ducks, dabbling ducks, pochards, eiders, sea ducks, stiff-tailed ducks, and "urban" waterfowl, which includes escaped or released exotics), the length, wingspan, and weight of each species, along with a bulleted list of key plumage characteristics and a statement about population size. Each species account also includes a small range map at varying scales. An appendix gives the body mass, number and colour of eggs, incubation time, and number of days from hatching to fledging for each species. The author stretches the definition of North America (usually Canada, the USA, and Mexico) to include the Caribbean, Greenland, the Hawaiian Islands, and United States territories in the Pacific (the Marianas and Aguigan islands). When you include subspecies, Eurasian vagrants, and accidentals, this book covers some 125 "forms".

While the photographs are excellent, they are not consistently labelled with sex and/or age, and there is no definition of the terms that are used, such as fledgling, juvenile, immature, young, subadult, and first year juvenile, which overlap and can be confusing. And I assume that a summer male is the same as an eclipse male? The Hawaiian Duck (*Anas wyvilliana*) account (pp. 80–81) nicely shows three different age classes of ducklings (at 10, 22, and 72 days), but most other accounts only have one photo with no age indicated. More age-specific labels for other ducklings would have been useful.

There are no source references for population size estimates nor for conservation status (given as stable, increasing, or decreasing) so it is difficult to assess how accurate these numbers are. For example, the population size for "Northern" Mallard (*Anas platyrhynchos platyrhynchos*) is given as ca. 20 000 (p. 69), which must be missing a few zeros. Some statements are confusing, such as when the population size for "Greenland" Mallard (*A. p. conboschas*) is given as ca. 15 000–30 000, followed by "but recent estimates of ca. 100 000" in parentheses (p. 71)—does this mean the author believes the lower range to be more accurate? Some species accounts include both a North American and a global population estimate, while others have only one, even though those birds also breed or winter outside of North America (also the case for the range maps). Other accounts just refer to "population size" without specifying geographic extent.

There are some major errors in the range maps. Having studied Harlequin Ducks (*Histrionicus histrionicus*) for over 20 years, I naturally checked that account first, and discovered that the entire inland breeding range for western North America is missing on the range map (p. 133). And while Greenland is shown on the map, it does not indicate any presence of Harlequin Ducks there, which there are, including birds which migrate from Labrador, Quebec, and Nunavut after breeding (COSEWIC 2013). Conversely, the Tundra Swan (*Cygnus columbianus*) range map (p. 46) only shows breeding range but no wintering range. Considering that waterfowl undertake such spectacular migrations, with abundant numbers seen at stopover sites, some indication of migration routes on the range maps would have been helpful, especially for beginning birders.

There is no indication what audience the author was aiming for; perhaps he simply wanted to showcase a lifetime of waterfowl photography in a book. Todd died before the book was published, and it was completed by three friends, which may have contributed to some of the inconsistencies. While it works as an identification guide, do not buy this as a field guide, but rather as more of a coffee table book that you browse through for the truly excellent photos unlike those in any other book.

Literature Cited

COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2013. COSEWIC assessment and status report on the Harlequin Duck *Histrionicus histrionicus* eastern population in Canada. COSEWIC, Ottawa, Ontario, Canada. Accessed 12 November 2018. http://www.registrelep-sararegistry.gc.ca/virtual_sara/files/cosewic/sr_Harlequin%20Duck_2013_e.pdf.

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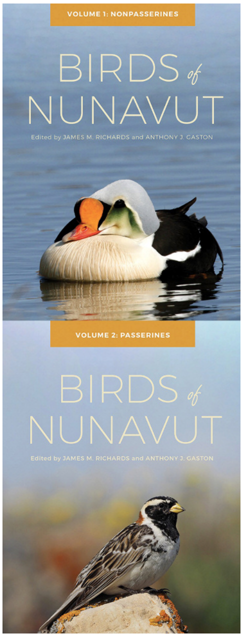
The Birds of Nunavut, Volume 1: Nonpasserines, Volume 2: Passerines

Edited by James M. Richards and Anthony J. Gaston. 2018. University of British Columbia Press. 820 pages, 805 colour photos, and 155 maps, 125.00 CAD, Cloth or PDF, 150.00 CAD, Cloth and PDF.



The Birds of Nunavut is a beautiful and comprehensive two-volume tome that documents the current and historical knowledge of birds known to occur within the territorial boundaries of Nunavut. This is a work of very considerable effort and integration involving 18 co-authors, 805 stunning colour photos, and 155 maps. The Foreword by Jason Akearok, Executive Director of the Nunavut Wildlife Management Board, grounds the effort with a holistic and interactive Inuit perspective on birds, wildlife, environment, and conservation. I have had the double opportunity of working with UBC Press when the manuscript was in production and of now reviewing the finished product.

Volume 1 overviews the territory's ecology, ornithological history, protected areas, monitoring activity, and anthropogenic and climatic threats. It also details the accounts of non-passerine species and is the larger book at 499 pages. Passerine accounts are laid out in Volume 2. For species that breed in Nunavut, each account opens with a synopsis of the species' range and general characteristics, a territorial distribution map, and sections on Appearance, Subspecies, Distribution, Where to See It, Behaviour, Habitat, Diet and Foraging, Phenology, Breeding, and Canadian Status and Threats. Photographs of species that breed in Nunavut include varied combinations of morphs, sexes, winter-plumaged birds, immatures, juveniles, nests and eggs, and young. For species that do not breed in the territory, sections on Distribution and Occurrence in Nunavut are included with photographs of breeding plumaged adults.

Massive in area, Nunavut, like so many other geographic jurisdictions, has some sharply delineated straight and rigidly angled boundaries; the western borders sever continuous ecological expanses and, hence, avian distributions. Owing to small local human aggregations and to research sites and protected areas that are ecologically distributed over most of the territory, key areas stand out as ornithological information hotspots. The hottest ones, as expected in terms of diversity and rarity occurrences, tend to be located near southern boundaries (e.g., Akimiski, Charlton, and Twin islands in James Bay). Yet, with huge uninhabited areas and with major active research sites, there is implied excitement of the bird information yet to be tapped.

The Birds of Nunavut establishes a firm benchmark from which expected changes can be gauged and periodically updated with supplemental checklists. The ongoing and incrementing flow of bird knowledge and documentation mean that geographic bird compilations, however thorough, are essentially outdated before they are published. Thus it is essential for an endeavour of this nature to offer a way forward. With this consideration in mind at the outset, the editors suggest that new observations be submitted to the Canadian Wildlife Service in Yellowknife or to www.eBird.ca. This approach will go a long way in maintaining real-time as well as long-term information about the birds in Nunavut.

While the two volumes have the dimensions and elegance of coffee table books, species accounts are presented in a compelling identification format. The *Birds of Nunavut* has all the makings of a first rate, high quality field guide—descriptions, image quality, and informative distribution maps. So considering yet another way forward, *The Birds of Nunavut* provides a natural substantial framework for a downsized pocket field guide. The existing components need only be distilled to a smaller more portable format. While it is so much easier to envision such a suggestion than to execute it, the editors and publisher might want to consider such an option. Such effort could bring the identification, occurrence, and distributional information directly into the hands of people in the field, where usage and feedback about the birds of Nunavut could be maximized.

On reviewing the prepublication version of this book for UBC Press and again here, my big disappointment with *The Birds of Nunavut* is its rather matter-of-fact attention to many conservation issues and its relative paralysis in offering constructive possibilities for robust conservation initiatives. The omission and lack of even a mention of the warm water run-offs into James Bay from the massive hydro-electric development in northern Quebec and potential synergisms with a changing ocean is totally baffling. For some time, we have been well aware of the risks and consequences of these warm freshwater outflows into James and Hudson Bays (e.g., Prinsenberg 1980; Milko 1986), leading to fresher sea water, thinner sea ice, and closing polynyas with major effects on marine birds, mammals, and fishes and resulting consequences for aboriginal people and their communities. While the authors recognize the extreme importance of a wintering aggregation of eiders in a local polynya for the residents of Sianikiluag in the Belcher Islands, they fail to mention that the warm freshwater from the hydro development is causing the polynya to freeze over (https://arcticeider.com/en/knowledge-solutions#?tab=knowledge&section=collapseOne#collapseOne). The game has changed for all of us, and the time for business as usual is over; crisis management is now essential at every step of the way. We have to recognize and address major human-induced threats to wildlife and our environment and offer constructive possibilities to act on them. Otherwise, it is just not going to happen.

I have many geographic bird books in my library—*The Birds of Nunavut* is the best one. Given the nature of the subject in our current pivotal state of changing climate, *The Birds of Nunavut* offers more than just another book about birds; it is an invitation to engage in an ongoing rapidly changing environmental process.

Literature Cited

Milko, R.. 1986. Potential ecological effects of the proposed GRAND Canal Diversion Project on Hudson and James Bays. Arctic 39: 316–326. https://doi.org/10.14430/arctic2094

Prinsenberg, S.J. 1980. Man-made changes in the freshwater input rates of Hudson and James Bays. Canadian Journal of Fisheries and Aquatic Sciences 37: 1101–1110. https://doi.org/10.1139/f80-143

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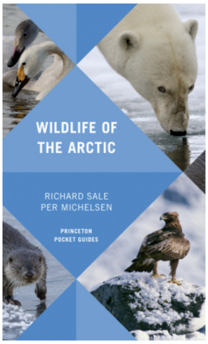
Zoology

Wildlife of the Arctic

By Richard Sale and Per Michelsen. 2018. Princeton University Press. 304 pages, 19.95 USD, Paperback.



Wildlife of the Arctic provides a good overview of the Arctic environment and many of the animals that live there. The authors are both explorers of the Arctic, with decades of combined experience in the region, which has provided them with unique perspectives on Arctic wildlife. Richard Sale has written multiple books about exploring different parts of the world, including a few about Arctic wildlife. Per Michelsen is an outdoor photographer who has focussed mostly on the Arctic and sub-Arctic.

The preface to the book offers a good glimpse into the intended audience of the book: the authors discuss early Arctic explorers and how the Arctic continues to inspire adventurers. The intended audience is for those interested in exploring the Arctic, from first-time visitors to people exploring new areas of the Arctic. This book will likely not be sufficient for ecologists and more advanced naturalists. Individual species accounts are quite general, the list of species and species accounts is not exhaustive, and no range maps are provided (species accounts typically contain a single sentence about the species range). More taxa-specific guides are recommended for people requiring detailed accounts of species in the Arctic.

The authors begin by describing the physical environment of the Arctic and how animals have adapted to living there. The authors also spend a few pages defining what they consider to be Arctic. The definition of the Arctic can be ambiguous, sometimes being defined by the Arctic Circle (66.56°N), other times by the tree line, and still other times based on average temperature. These authors decided instead to use their own definition, which they feel the average person would likely agree with. This definition of the Arctic uses the average temperature, but also includes areas that the average person would consider to be Arctic, such as Churchill, Manitoba, and the entirety of Iceland, which are not included by the standard temperature definition.

After setting the stage, the authors then spend most of the book describing Arctic wildlife with species accounts of birds and mammals, including marine mammals, illustrated by many very nice photographs, followed by a small section describing the general variety of ecosystems, invertebrates, fungi, and plants found in the Arctic. Within the species accounts, the authors typically provide nearly a page of information about each group of species (e.g., ducks, eagles, rodents, ungulates), but then vary the amount of information that they provide for individual species. Some species accounts are only a couple of sentences (e.g., Siberian Brown Lemming [*Lemmus sibiricus*]), while others span a half page (Arctic Ground Squirrel [*Urocitellus parryii*]) or more than a page (Reindeer/Caribou [*Rangifer tarandus*]). The amount of information provided for each species is not a function of what is known about the species, but more likely related to how familiar the authors are with these species or to the more "iconic" species that Arctic travellers are likely to encounter and possibly care more about. For example, raptor species (e.g., eagles, hawks, and falcons) have nearly a page devoted to each of them, whereas waterfowl have a quarter of a page. Some species of mammals didn't receive species accounts: there is a single page on shrews, but no individual species accounts, unlike with other groups.

The authors do not provide species accounts for amphibians, reptiles, and fish, although they mention amphibians and reptiles found in the Arctic in the section on how wildlife have adapted to cold environments, and they mention fish when discussing Arctic ecosystems. There is no explanation provided for why these species are excluded, but it is likely related to which species will be seen most by Arctic explorers. However, a section on fish species that are important to Arctic people, such as Arctic Char (*Salvelinus alpinus*), would have been useful for first-time visitors of the Arctic.

The common names used for species are generally European, which may be confusing for readers from North America. The authors usually list the European name first with the North American name in parentheses (e.g., "Red-throated Diver (Red-throated Loon)"). In some cases, however, they don't acknowledge the North American name this way; for example, "Common Merganser" is listed simply as "Goosander", with a statement in the description that it is "occasionally called Common Merganser". In other cases, the authors first state the North American name with the European name in parentheses (e.g., "Moose (Elk)"). More consistency in the treatment of European versus North American names is needed, and a few sentences in the introduction describing how different names are denoted would have been useful.

Overall, this book will be a useful general introduction to Arctic wildlife for travellers who have an interest in the topic. However, for details about specific groups of species, readers should look to taxa-specific guides.

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Guide to the Parasites of Fishes of Canada Part V: Nematoda

By Hisao P. Arai and John W. Smith. Edited by Michael D.B. Burt and Donald F. McAlpine. 2016. Zootaxa 4185, Magnolia Press. 274 pages, freely available (https://biotaxa.org/Zootaxa/article/view/zootaxa.4185.1.1), PDF.

Over the last four decades, the parasites impacting Canadian fish species have been described in Volumes I–IV of the *Guide to the Parasites of Fishes of Canada*, with *Part V: Nematoda* by Hisao P. Arai and John W. Smith bringing much needed attention to the parasitic nematodes affecting Canadian fishes. Nematodes occupy nearly every habitat from soil to sea and are recognized as one of the most abundant multicellular animals on earth. Parasitic nematodes of fishes can pose a threat not only to fish health but also to the organisms (including humans) that consume these infected hosts, emphasizing the urgency to study this group of organisms.

This volume is first and foremost an identification key for the nematode parasites of Canadian fishes, providing detailed information on all taxonomic levels. The taxonomy follows the broader taxonomic guides on nematodes of vertebrates while incorporating research discoveries made in recent decades. Species are described that have only just gained recognition in recent years, despite having negative economic consequences (e.g., *Huffmanela canadensis*, *Philometra rubra*, and *Anguillicola crassus*). The book is remarkably thorough, compiling information from an expansive reference list of over 800 citations, which is reflected in the level of detail in each key.

The keys and descriptions cover 88 species, spanning 47 genera expertly described by the authors. These keys provide a concise yet detailed description of each listed taxon. Each species or taxonomic rank includes a morphological description, reported hosts, host anatomical site, geographical distribution, and previous literature records. This information is coupled with over 100 detailed illustrations that present nematode anatomy in a way that cannot often be appreciated within photographic images. These illustrations provide the reader with views of organisms in their entirety, and views of specific anatomy relevant to species identification. Fish parasitologists will benefit from details provided within the introduction on the procedures and protocols used to collect, examine, and identify nematodes from fish hosts. Although these components of the book will be most relevant to experts within the field, broader information on Phylum Nematoda, nematode morphology, and the geographical distributions of nematodes can be gleaned by readers lacking familiarity with this area of research. The indices by nematode and fish species are particularly valuable for readers seeking species-specific information. These indices will be useful for fisheries biologists looking to understand which nematode species may be present in a target population, based on their potential hosts and geographical distributions.

The authors make it clear that morphology-based identification is still a major component of nematode taxonomy, and that molecular-based taxonomic information is lacking for most species. This book should serve as a call to action for further attention into nematode phylogenetics, as a greater understanding of their taxonomy may benefit fish and human health alike. Despite focussing primarily on Canadian parasitic nematodes, these nematode species affect fishes from around the world, highlighting the value of this guide to a global readership.

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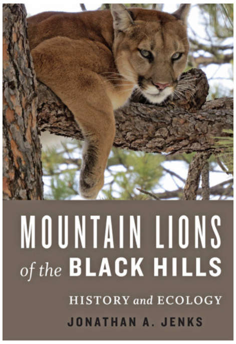
Mountain Lions of the Black Hills: History and Ecology

By Jonathan A. Jenks. 2018. Johns Hopkins University Press. 160 pages, 75.00 USD, Cloth or E-book.



I have always had a childhood fascination with Mountain Lions (*Puma concolor*) and a recent narrative I read of a lion travelling from South Dakota to Connecticut got me very interested in learning more about its origins (Way 2017). And so, it was with good fortune that I was able to find it here with *Mountain Lions of the Black Hills*. The book was an enjoyable read and is a valuable contribution to North America's predatory fauna. Mountain Lion is a cat with many names: Cougar, Puma, Catamount, Panther, and Deer Tiger, among others. Their large range once included virtually all the lower 48 United States from coast to coast, but by the 1960s they were reduced to small populations in the western United States and a token population in south Florida. In *Mountain Lions of the Black Hills*, author Jonathan Jenks describes his research team's experiences and findings from over 200 of these amazing animals, radio-tracked as they returned to a portion of the northern Great Plains in western South Dakota.

Jenks has an easy-to-read style where each chapter is written like a stand-alone scientific manuscript with a complete Literature Cited section at the end. Each bibliography cites peer-reviewed articles and graduate theses/dissertations, many from his own students. However, chapters contain simplified enough language to make it readable for the layman and each chapter smoothly flows from one to another as he reports on Mountain Lion ecology, characteristics (e.g., body size and distribution), diet, population dynamics, disease ecology, nutrition, behaviour, and genetics. I particularly liked the sections on dispersal (e.g., pages 57–59) showing how far young Mountain Lions can travel when they leave their mother's territory. Jenks provides very interesting discussion on how that population of lions is connected to others in Wyoming, Colorado, and North Dakota.

Jenks explores a population that was just recolonizing the Black Hills in the late 1990s yet quickly saturated the area within about 10 years. His research examined the impact of a changing prey base on population growth then decline as lions went from a protected species to having an established hunting season set on the cats. A theme of Jenks' prose is figuring out how to balance conserving Mountain Lions with the needs of humans.

I found the book to be useful and a great reference for the species as it slowly expands its range eastward, reclaiming territory that had been lost within the past 100–200 years. It is easy to find key information on the species, such as territory sizes for males (300+ km^2) and females (66–198 km^2), body weights of males (averaging 130–150 pounds, 59–68 kg) and females (90 pounds, 41 kg), litter sizes (averaging 3+), age of dispersal (a relatively young 15 months of age), and population size in the Black Hills (150–250). The book is only 160 pages yet has 57 black and white photos and

15 graphs/tables. I loved all the pictures and thought that it complemented the text perfectly. In fact, I wish more scientifically-oriented books were like this: simple to read, containing concise information, and well-illustrated!

Jenks also explored people's evolving perceptions of Mountain Lions and I found that chapter (8) interesting in a few respects. While I enjoyed the book and thought it was well done, I was troubled by the incessant use throughout of the euphemistic word "harvest" (Johns and Dellasalla 2017) and a total lack of discussion about the ethics of killing a sentient large carnivore (Vuchetich and Nelson 2014). Abundant research indicates carnivores are ecologically important, and are social, sentient, family-oriented animals which regulate their own numbers by defending territories (Eisenberg 2014). Sociological research has consistently demonstrated society's decreasing support of lethal control and trophy hunting, especially regarding carnivores (Jackman and Way 2018). So, it was of interest to me that the main findings from Chapter 8—that sociological research supported hunting Mountain Lions in South Dakota—are from government reports which had not apparently experienced peer review. I can't help but think that a pro-hunting stance, which all of these government agencies have, may have biased these documents. Given all of the great data presented throughout the book, Jenks' team could've designed a scientifically rigorous hunting season using similar data and methods as described in Washington State, whereby "harvest thresholds" were established in which no more than 14% of the estimated density of adult resident Mountain Lions could be killed by hunters in relatively small areas to prevent localized over-harvest (see Beausoleil *et al*. 2013). This provision allows some human recreational use of carnivores, but at a level that should not upset the natural social organization, population stability, or immigration of transient Mountain Lions, and at a level that results in low mortality of adult residents. This protection threshold is particularly important given the relatively isolated nature of the population in the Black Hills. Conversely, it appears that the state of South Dakota just willy-nilly picked "quotas" not based on science but rather on perceived public opinion starting with conservative harvests in 2005 and moving to reduce the population in a short amount of time (~ five years). While Jenks does an admiral job documenting how the population stayed genetically healthy, I couldn't help but think of how carnivore hunting generally favours biased or outdated research over the best available independent science (Artelle *et al*. 2018; Karns *et al*. 2018).

Overall, this is a valuable book. The illustrations make it a valuable reference for wildlife enthusiasts. It was well written with just a few minor errors. The only thing that perplexed me was the high price for a seemingly simple black and white hardcover book. For the life of me, I cannot fathom why it was $75 USD when it could probably be $10 USD when printed with a softcover. Otherwise, I can't read enough about Mountain Lions and other large carnivores and dream of the day when a similar type of book is written on a recovered Mountain Lion population(s) here in the northeast United States where I reside!

Literature Cited

Artelle, K.A., J.D. Reynolds, A. Treves, J.C. Walsh, P.C. Paquet, and C.T. Darimont. 2018. Hallmarks of science missing from North American wildlife management. Science Advances 4(3): eaao0167. https://doi.org/10.1126/sciadv.aao0167

Beausoleil, R.A., G.M. Koehler, B.T. Maletzke, B.N. Kertson, and R.B. Wielgus. 2013. Research to regulation: Cougar social behavior as a guide for management. Wildlife Society Bulletin 37: 680–688. https://doi.org/10.1002/wsb.299

Eisenberg, C. 2014. The Carnivore Way: Coexisting with and Conserving North America's Predators. Island Press, Washington, DC, USA.

Jackman, J.L., and J.G. Way. 2018. Once I found out: awareness of and attitudes toward coyote hunting policies in Massachusetts. Human Dimensions of Wildlife 23: 187–195. https://doi.org/10.1080/10871209.2017.1397824

Johns, D., and D.A. Dellasalla. 2017. Caring, killing, euphemism and George Orwell: how language choice undercuts our mission. Biological Conservation 211: 174–176. https://doi.org/10.1016/j.biocon.2017.03.030

Karns, G.R., A. Heeren, E.L. Toman, R.S. Wilson, H.K. Szarek, and J.T. Bruskotter. 2018. Should grizzly bears be hunted or protected? Social and organizational affiliations influence scientific judgments. Canadian Wildlife Biology & Management 7: 18–30.

Vuchetich, J., and M.P. Nelson. 2014. Wolf hunting and the ethics of predator control. Oxford Handbooks Online 1–15. https://doi.org/10.1093/oxfordhb/9780199927142.013.007

Way, J.G. 2017. [Book Review] Heart of a Lion: A Lone Cat's Walk Across America. Canadian Field Naturalist 131: 82–84. https://doi.org/10.22621/cfn.v131i1.1972

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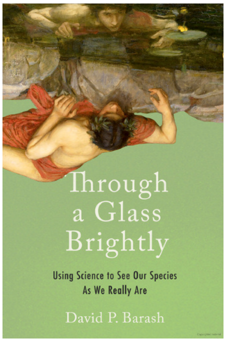
OTHER

Through a Glass Brightly: Using Science to See Our Species as We Really Are

By David B. Barash. 2018. Oxford University Press. 208 pages, 30.95 CAD, Cloth.



David Barash uses quirky humour, a sprawling compendium of references—from the Bible, to classical writers, to poets and academics new and old, to SpongeBob Squarepants (seriously!)—and succinct recaps of scientific research to put the boots to 15 paradigms that many of us take as pretty much self-evident. An evolutionary biologist, professor emeritus of psychology, and prolific author, Barash writes knowledgeably and comfortably on such topics as the meaning of life, whether we have unique and separate selves, parent/child conflict, monogamy, the nature of truth, and war and peace. His explorations and explanations of science, especially biology, provide the basis for his iconoclastic approach to the 'common knowledge' positions on these topics. As iconoclasts go, he's very good.

Divided into two sections, the book builds on several of his previous publications, as he notes in nearly every chapter. Each section begins with a prelude, and it's worth repeating their lengthy titles to get the gist of the sections and hence the book. Part I, "The Allure of Human Centrality, or, How We Persistently Try to Deny Our Place in the Natural World – And Fail", brings up to the present the long and ongoing debate, dating back centuries, over the superiority of *Homo sapiens* compared to any other species and the notion that the universe revolves around us. The latter view was held in the Ptolomeic world, and its debunking by Copernicus and Galileo took a few centuries to catch on. Similarly, the notion that we are the centre of our psychological universe, with nature—seen as 'outside' ourselves—being there for our use and disposal, more than lingers. We can see it in everything from the 'yuck' response to bugs and spiders to climate change denial/inaction that helps maintain the status quo. Thus, the first order of business in this section is a critical examination of this big-picture myth of human centrality. Barash explores our modocentrism through (among other things) the concept of a 'reverse' world map, then moves on to the question of how we determine the meaning of life in the face of biological purposelessness. He demolishes any self-satisfaction humans may find in the notion that our body plan is well-designed, rejects the notion that human consciousness is necessary for the universe to exist, and notes that, despite our tough talk, many organisms are much tougher than we are. Want to compete with extremophiles, anyone?

More radically, he boldly favours—which is different from advocating!—the cloning of humans and chimpanzees, if only to demonstrate our connectedness to everything, thereby refuting the common belief that only human life is important. The concept of connectedness is used to expose the illusion that self exists independently of everything else. Rather, we are all symbionts, as demonstrated by our bacteria-filled microbiomes.

In Part II, Barash provides "New Ways of Understanding Human Nature". He makes the argument here that human behaviour itself "is altogether natural… woven from the same biological cloth as other living things" (p. 85). The point here is neither the reduction of humans to the level of animals, nor the elevation of animals to the level of humans, but to get rid of the level itself so that we can see our inter-relatedness to all living beings. This shift in thinking, so hard for many to accept, becomes more acceptable if it's seen as "lateral", not "downwards".

The chapters in Part II explore aspects of this, putting under the lens, to provide only several examples, our beliefs in our capacity for thoughtfulness, the inevitability of a generation gap, our ability to distinguish truth and falsity, the problem of morality, and evolutionary theory. Other commonly held views receive this close scrutiny: humans are monogamous, altruism proves our higher nature, humans are natural born killers, and we have free will so are truly 'captains of our fate'. In each instance, Barash seeks to explode the old paradigms, replacing them with science-based concepts that serve us better in our understanding of ourselves and the natural world. Perhaps the most sobering is explored in Chapter 16, "The Paradox of Power". Here, Barash asserts that our cultural capacity to develop weapons outpaces our biological, evolutionary capacity to develop restraints in using them: "We are, via cultural evolution, in over our biological heads" (p. 186).

Each of the myriad topics Barash tackles in this short book could be addressed in books of their own—and often have been, as noted above, in other books of his. Here he is summarizing, it seems to me, a life's work of thinking, researching, and synthesizing. As such, the book is an excellent introduction to topics that are worthy of the reader's further exploration. While Barash's tone often disguises the serious purpose behind the book, that purpose is clearly laid out in his concluding remarks: to help us see ourselves as we really are. In other words, his purpose is to provide fresh paradigms that enhance our understanding of human behaviour and, through that, our sense of responsibility for the quality of our lives, and the world we live in.

The two introductory preludes set up each section; chapters therein are short, with brief references cited in endnotes after each chapter. The book is indexed but does not have a bibliography. Other writers have written bigger books on these topics. But for a solid, accessible, thoughtful introduction, this is an excellent place to start, recommended reading for anyone interested in these questions.

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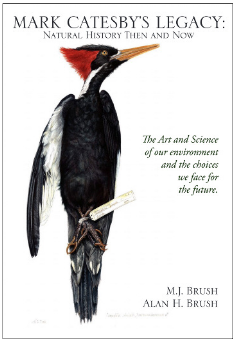
Mark Catesby's Legacy: Natural History Then and Now

By M.J. Brush and Alan H. Brush. 2018. The Catesby Commemorative Trust. 191 pages and 32 original watercolour plates, 28.95 USD, Paper.



Catesby's "watercolors … were his legacy; [they] provided a perspective on nature, history and the environment, … and an amazing tale of perseverance, exploration and art" (p. 6). They became "the benchmark for the early stage of the age of exploration and discovery in eastern North America" (p. 6). Alan and M.J. Brush have chosen the perfect time to answer for the reader the question of how much Catesby's world has changed in the centuries since his wonderful depiction of it.

Mark Catesby was born in Castle Hedingham, Essex, 24 March 1683, during the coldest winter in living memory. Mark's first transatlantic voyage to Virginia was as a chaperone for his eldest sister Elizabeth and her two children, sailing to Virginia to rejoin her husband, Dr. William Cocke, where they arrived 23 April 1712. Mark's first principal host was William Byrd II on his James River estate. Catesby travelled widely, visited Jamaica in 1714, then Bermuda, and was mentioned in the *Philosophical Transactions of the Royal Society* in 1715. He regularly sent specimens to interested people in England, then returned to England by mid-October 1719. While in England during 1721, Catesby gained support of sponsors within the Royal Society, enabling him to sail to Charles Town, South Carolina, where he arrived 3 May 1722. He collected birds and plants until he reached the Bahamas early in 1725. He returned to England in 1726. Alan and M.J. Brush were stimulated by the Catesby Commemorative Trust which in November 2012 held a symposium to mark the 300th anniversary of Catesby's first voyage in three centres: Washington, DC, Richmond, Virginia, and Charleston, South Carolina. The symposium resulted in *The Curious Mister Catesby* (Neston and Elliott 2015).

From their home in Connecticut, Alan and M.J. Brush sailed their 330 Cape Dory cutter along the Atlantic coastline, often following the Intercoastal Waterway constructed in 1919 along the North Carolina and Georgia coasts. They then explored shallower waters between the islands of the Bahamas. "The deck of a small sailboat offers an unprecedented view" (p. 15). One of their reported challenges was to explore the ways plants and animals made their living over the 300 years since Catesby's time, in light of the continually shifting, changing, and often hostile world. With Alan's life-long learning in biology, particularly ornithology, and M.J.'s artistic skills, we have the perfect combination throughout this book, chapter by chapter.

Most readers should find Alan's "brief history" of ornithology informative, but especially the page on the contributions of Linnaeus, who gave each bird and plant a genus and unique species name, which quickly became the world standard. Variations and refinements were contributed by two French scientists, Brisson and Reaumur, followed by the German Blumenbach, and then finally Charles Darwin specified natural selection working on natural variation. Next, Alan details the stories of three bird species declared extinct since Catesby's time, including Passenger Pigeon (*Ectopistes migratorius*), which was seen in aggregations of more than two million birds by Alexander Wilson in 1806, until the final aviary captive died in 1914 after 29 years in the Cincinnati Zoo. Ivory-billed Woodpecker (*Campephilus principalis*) and Bachman's Warbler (*Vermivora bachmanii*) were last seen in 1943 and 1958, respectively.

M.J. provides gorgeous paintings of the plants, the Southern Orange, Southern Magnolia, Franklinia, Catalpa, Carolina Jessamine, Longleaf Pine, Wild Olive, Mountain Laurel, Sheep Laurel, Bog Laurel, Tulip Tree, Empress Tree, Brazilian Pepper-Tree, Morrows' Honeysuckle, Smooth Cordgrass, and fish, such as the Gray Triggerfish, Silk Snapper, Black Sea Bass, Graysby, and Yellow-fin Tuna, as well as Gray Sea Turtle and Caribbean Spiny Lobster.

Alan and M.J. point out the dynamic equilibrium of a salt marsh, with its grasses, snails, and shells, and the role they play for the White Ibis, Scarlet Ibis, Great Blue Heron, Green Heron, Fish Crow, American Oystercatcher, crabs, scallops, and oysters. M.J.'s most recent exciting expedition was as a deep-sea artist in a self-propelled, titanium submersible along the floor of the Atlantic Ocean, where the fish of great depths are beyond the reach of sunlight. These organisms are visible under such conditions because some of the body appendages of colonial squid and jellyfish are transparent, with photophores that attract prey.

I recommend without reservation this delightful and informative book as a companion for any naturalist visiting the lower Atlantic coast and through the Bahama Islands. It makes a great companion too for the larger, heavier *The Curious Mister Catesby*.

Literature Cited

Neston, E.C., and D.J. Elliott. 2015. The Curious Mister Catesby. A Wormsloe Foundation Nature Book. The University of Georgia Press, Athens, Georgia, USA.

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Prepared by Barry Cottam

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BOTANY

Michigan Ferns and Lycophytes: A Guide to Species of the Great Lakes Region. By Daniel D. Palmer. 2018. University of Michigan Press. 392 pages, 29.95 USD, Paper.

Mushrooms of the Northeastern United States and Eastern Canada. A Timber Press Field Guide. By Timothy J. Baroni. 2017. Workman Publishing. 600 pages, 27.95 USD, Cloth, 14.99 USD, E-book.

The Allure of Fungi. By Alison Pouliot. 2018. CSIRO Publishing. 280 pages, 49.99 AUD, Paper.

Sex on the Kitchen Table: The Romance of Plants and Your Food. By Norman C. Ellstrand. 2018. University of Chicago Press. 208 pages, 75.00 USD, Cloth, 20.00 USD, Paper, 18.00 USD, E-book.

Floral Mimicry. By Steven D. Johnson and Florian P. Schiestl. 2016. Oxford University Press. 188 pages, 120.00 USD, Cloth, 59.95 USD, Paper.

Tree: A Life Story. Revised Edition. By David Suzuki and Wayne Grady. Foreword by Peter Wohlleben. 2018. Greystone Books. 206 pages, 19.95 CAD, Paper. Also available as an E-book.

Trees in Canada. 100th Anniversary Redesigned Edition. By James Laird Farrar. 2018. Firefly Books. 512 pages, 60.00 CAD, Cloth.

ENTOMOLOGY

Field Guide to the Flower Flies of Northeastern North America. By Jeffrey H. Skevington and Michelle M. Locke, with Andrew D. Young, Kevin Moran, William J. Crins, and Stephen A. Marshall. 2019. Princeton University Press. 536 pages, 3000 colour plates, and 414 maps, 27.95 USD, Flexibound.

Our Native Bees: North America's Endangered Pollinators and the Fight to Save Them. By Paige Embry. 2018. Timber Press. 40 pages and 104 colour images, 24.95 USD, Cloth.

Where Honeybees Thrive: Stories from the Field. Animalibus of Animals and Cultures, Volume 10. By Heather Swan. 2017. Pennsylvania State University Press. 176 pages, 29.95 USD, Paper.

Butterflies of the Pacific Northwest. By Robert Michael Pyle and Caitlin C. LaBar. Timber Press. 464 pages, 612 colour photos, and 198 maps, 27.95 USD, Flexibound.

The Bee: A Natural History. By Noah Wilson-Rich, with contributions from Kelly Allin, Norman Carreck, and Andrea Quigley. 2018. Princeton University Press. 224 pages, 17.95 USD, Paper. Cloth edition published in 2014. Also available as an E-book.

Insect Behavior: From Mechanisms to Ecological and Evolutionary Consequences. Edited by Alex Cordoba-Aguilar, Daniel Gonzalez-Tokman, and Isaac Gonzalez-Santoyo. 2018. Oxford University Press. 448 pages, 110.00 CAD, Cloth, 54.95 CAD, Paper.

HERPETOLOGY

Peterson Field Guide to Reptiles and Amphibians of Eastern and Central North America. Fourth Edition. By Bob Powell, Roger Conant, and Joseph T. Collins. 2016. Houghton Mifflin Harcourt. 512 pages, 21.99 USD, Paper.

Eye of Newt and Toe of Frog, Adder's Fork and Lizard's Leg. The Lore and Mythology of Amphibians and Reptiles. By Marty Crump. 2015. 304 pages and 155 colour plates, 35.00 USD, Cloth, 21.00 USD, E-book.

Snakes of the World: A Catalogue of Living and Extinct Species. By Van Wallach, Kenneth L. Williams, and Jeff Boundy. 2017. CRC Press (Taylor & Francis Group). 1237 pages, 168.00 USD, Cloth, 64.00 USD, Paper or E-book.

Reptiles of Victoria: A Guide to Identification and Ecology. By Peter Robertson and A. John Coventry. 2019. CSIRO Publishing. 336 pages, 45.99 AUD, Paper.

U.S. Guide to Venomous Snakes and Their Mimics. Reprint Edition. By Scott Shupe. 2019. Skyhorse Publishing. 160 pages, 14.99 USD, Paper.

Atlas of Reptile Development. By Jacqueline E. Moustakas-Verho and Raul Diaz. 2019. CRC Press (Taylor & Francis Group). 300 pages, 119.96 USD, Cloth.

The Maryland Amphibian and Reptile Atlas. By Heather R. Cunningham and Nathan H. Nazdrowicz. 2018. Johns Hopkins University Press. 312 pages, 74.95 USD, Cloth or E-book.

Dreaming in Turtle: A Journey Through the Passion, Profit, and Peril of Our Most Coveted Prehistoric Creatures. By Peter Laufer. 2018. Macmillan Publishers, St. Martin's Press. 304 pages, 28.99 USD, Cloth, 14.99 USD, E-book.

Herping Texas: The Quest for Reptiles and Amphibians. By Michael Smith and Clint King. 2018. Texas A&M University Press. 336 pages and 156 colour photographs, 30.00 USD, Flexibound. Also available as an E-book.

Status of Conservation and Decline of Amphibians: Australia, New Zealand, and Pacific Islands. Edited by Harold Heatwole and Jodi Rowley. 2018. CSIRO Publishing. 248 pages, 160.00 AUS, Cloth. Also available as an E-book.

Amphibians and Reptiles of Florida. By Kenneth L. Krysko, Kevin M. Enge, and Paul E. Moler. 2019. University Press of Florida. 816 pages, 80.00 USD, Cloth.

Reptiles and Amphibians of Australia. Seventh Edition. By Harold Cogger. 2018. CSIRO Publishing. 1096 pages, 160.00 AUS, Cloth.

Field Guide to the Amphibians and Reptiles of Britain and Europe. By Jeroen Speybroeck, Wouter Beukema, Bobby Bok, and Jan Van Der Voort. Illustrated by Ilian Velikov. 2016. Bloomsbury Publishing. 432 pages, 25.00 GBP, Paper.

Field Guide to East African Reptiles. By Steve Spawls, Kim Howell, Harald Hinkel, and Michele Menegon. 2018. Bloomsbury Publishing. 624 pages, 35.00 GBP, Paper.

The Lizards, Crocodiles, and Turtles of Honduras: Systematics, Distribution, and Conservation. Bulletin of the Museum of Comparative Zoology Special Publications Series 2. By James R. McCranie. 2018. Harvard University Press. 672 pages, 44.95 USD, Paper.

ORNITHOLOGY

Snowbird: Integrative Biology and Evolutionary Diversity in the Junco. Edited by Ellen D. Ketterson and Jonathan W. Atwell. 2016. University of Chicago Press. 416 pages, 60.00 USD, Cloth, 10.00–60.00 USD, E-book.

Golden-winged Warbler Ecology, Conservation, and Habitat Management. Studies in Avian Biology Series. By Henry M. Streby, David E. Andersen, and David Buehler. 2016. CRC Press (Taylor & Francis Group) in collaboration with the American Ornithological Society. 238 pages, 152.00 USD, Cloth, 46.36 USD, E-book.

Ecology and Conservation of North American Sea Ducks. Studies in Avian Biology Series. Edited by Jean-Pierre L. Savard, Dirk V. Derksen, Dan Esler, and John M. Eadie. 2018. CRC Press (Taylor & Francis Group) in collaboration with the American Ornithological Society. 610 pages, 148.00 USD, Cloth, 55.96 USD, Paper, 55.96 USD, E-book.

Ecology and Management of Blackbirds (Icteridae) in North America. By George M. Linz, Michael L. Avery, and Richard A. Dolbeer. 2017. CRC Press (Taylor & Francis Group). 240 pages, 95.96 USD, Cloth, 43.96 USD, E-book.

Phenological Synchrony and Bird Migration: Changing Climate and Seasonal Resources in North America. Studies in Avian Biology Series. Edited by Eric M. Wood and Jherime L. Kellermann. 2017. CRC Press (Taylor & Francis Group) in collaboration with the American Ornithological Society. 246 pages, 128.00 USD, Cloth, 47.96 USD, Paper or E-book.

Birds. By Robert Bateman. Foreword by Peter Matthiessen. 2018. Firefly Books. 176 pages and 200 paintings, 29.95 CAD, Paper.

Animal Musicalities: Birds, Beasts, and Evolutionary Listening. By Rachel Mundy. 2018. Wesleyan University Press. 264 pages, 29.95 USD, Cloth, 23.99 USD, E-book.

Bird Brains: The Intelligence of Crows, Ravens, Magpies, and Jays. Revised Edition. By Candace Savage. 2018. Greystone Books. 144 pages, 29.95 CAD, Paper.

Bird Species: How They Arise, Modify and Vanish. By Dieter Thomas Tietze. 2018. Springer. 278 pages, 109.99 USD. Also available as an E-book.

Species: The Evolution of the Idea, Second Edition. By John S. Wilkins. 2018. CRC Press (Taylor & Francis Group). 389 pages, 95.96 USD, Cloth, 43.96 USD, E-book.

Swifts in a Tower. New Edition. Edited by Andrew Lack. 2018. Unicorn Publishing Group, distributed by University of Chicago Press. 260 pages, 22.95 USD, Cloth. Original edition by David Lack, published in 1956.

Urban Ornithology: 150 Years of Birds in New York City. By P.A. Buckley, Walter Sedwitz, William J. Norse, and John Kieran. 2018. Comstock Publishing Associates. 536 pages, 75.00 USD, Cloth.

Birds New to Science: Fifty Years of Avian Discoveries. By David Brewer. 2018. Christopher Helm. 416 pages, 60.00 USD, Cloth.

The Extended Specimen: Emerging Frontiers in Collections-Based Ornithological Research. Studies in Avian Biology Series. By Michael S. Webster. 2017. CRC Press (Taylor & Francis Group) in collaboration with the American Ornithological Society. 240 pages, 111.96 USD, Cloth, 43.96 USD, E-book.

Listening in the Field: Recording and the Science of Birdsong. By Joeri Bruyninckx. 2018. MIT Press. 240 pages, 34.00 USD, Cloth.

Ecology and Conservation of Birds in Urban Environments. Edited by Enrique Murgui and Marcus Hedblom. 2017. Springer. 538 pages, 219.00 USD, Cloth or Paper, 169.00 USD, E-book.

Gulls Simplified: A Comparative Approach to Identification. By Pete Dunne and Kevin T. Karlson. 2018. Princeton University Press. 208 pages, 24.95 USD, Paper. Also available as an E-book.

Landfill. By Tim Dee. 2018. Little Toller Books. 240 pages, 16.00 GBP, Cloth.

The Genius of Birds. By Jennifer Ackerman. 2017. Penguin Random House. 352 pages, 17.00 USD, Paper.

The Empire of the Eagle: An Illustrated Natural History. By Mike Unwin and David Tipling. 2018. Yale University Press. 288 pages and 400 colour illustrations, 40.00 USD, Cloth.

Belonging on an Island: Birds, Extinction, and Evolution in Hawai‘i. By Daniel Lewis. 2018. Yale University Press. 320 pages, 45.00 USD, Cloth.

The House of Owls. By Tony Angell. Foreword by Robert Michael Pyle. 2016. Yale University Press. 224 pages, 18.00 USD, Paper.

Where Song Began: Australia's Birds and How They Changed the World. By Tim Low. 2016. Yale University Press. 424 pages, 32.50 USD, Cloth.

ZOOLOGY

Bats in the Anthropocene: Conservation of Bats in a Changing World. Edited by Christian C. Voigt and Tigga Kingston. 2016. Springer Open. 615 pages, 59.99 USD, Cloth. Free E-book available at https://link.springer.com/book/10.1007%2F978-3-319-25220-9.

And Then There Were None: The Demise of Desert Bighorn Sheep in the Pusch Ridge Wilderness. By Paul R. Krausman. Illustrated by Bethann Garramon Merkle. 2017. University of New Mexico Press. 248 pages, 65.00 USD, Cloth or E-book.

Field Guide to Carnivores of the World, 2nd Edition. By Luke Hunter. Illustrated by Priscilla Barrett. 2018. Bloomsbury Publishing. 256 pages, 25.00 GBP, Paper. Also available as an E-book.

Eager: The Surprising, Secret Life of Beavers and Why They Matter. By Ben Goldfarb. 2018. Chelsea Green Publishing. 304 pages, 24.95 USD, Cloth.

The Way of Coyote: Shared Journeys in The Urban Wilds. By Gavin Van Horn. 2018. University of Chicago Press. 224 pages, 25.00 USD, Cloth, 18.00 USD, E-book.

The Great Apes: A Short History. By Chris Herzfeld. Translated by Kevin Frey. Foreword by Jane Goodall. 2017. Yale University Press. 344 pages, 26.00 USD, Cloth.

Carnivore Minds: Who These Fearsome Animals Really Are. By G.A. Bradshaw. 2017. Yale University Press. 360 pages, 35.00 USD, Cloth.

Across the Bridge: Understanding the Origin of the Vertebrates. By Henry Gee. 2018. University of Chicago Press. 288 pages, 75.00 USD, Cloth, 25.00 USD, Paper, 10.00–25.00 USD, E-book.

Eyes to See: The Astonishing Variety of Vision in Nature. By Michael Land. 2018. Oxford University Press. 208 pages, 28.50 CAD, Cloth.

*__Keepers of the Wolves. Second Edition.__ By Richard P. Thiel. 2018. University of Wisconsin Press. 264 pages, 22.95 USD, Paper.

Biology and Ecology of Pike. Edited by Christian Skov and P. Anders Nilsson. 2018. CRC Press (Taylor & Francis Group). 402 pages, 151.96 USD, Cloth, 46.36 USD, E-book.

Octopus, Squid, and Cuttlefish: A Visual, Scientific Guide to the Oceans' Most Advanced Invertebrates. By Roger Hanlon, Mike Vecchione, and Louise Allcock. 2018. University of Chicago Press. 224 pages, 40.00 USD, Cloth, 24.00 USD, E-book.

***Muskellunge Management: Fifty Years of Cooperation Among Anglers, Scientists, and Fisheries Biologists.** Proceedings of the "Hugh C. Becker Memorial Muskie Symposium", held in Minnetonka, Minnesota, 13–15 March 2016. American Fisheries Society Symposium, Volume 85. Edited by Kevin L. Kapuscinski, Timothy D. Simonson, Derek P. Crane, Steven J. Kerr, James S. Diana, and John M. Farrell. 2017. American Fisheries Society. 675 pages, 79.00 USD, Cloth or PDF.

Cutthroat Trout: Evolutionary Biology and Taxonomy. Edited by Patrick Trotter, Peter Bisson, Luke Shultz, and Brett Roper. 2018. American Fisheries Society. 362 pages, 79.00 USD, Cloth or PDF.

Sharks: Ancient Predators in a Modern Sea. Salvador Jorgensen. 2018. Firefly Books. 256 pages, 29.95 CAD, Paper.

Big Pacific: An Incredible Journey of Exploration and Revelation. Edited by Rebecca Tansley. 2017. CSIRO Publishing. 240 pages, 49.95 AUD, Cloth.

***Eye of the Shoal: A Fishwatcher's Guide to Life, the Ocean and Everything.** By Helen Scales. 2018. Bloomsbury Sigma. 288 pages, 15.29 GBP, Cloth, 8.99 GBP, Paper, 14.26 GBP, E-book.

Spineless: The Science of Jellyfish and the Art of Growing a Backbone. By Juli Berwald. 2018. Riverhead Books. 352 pages, 16.00 USD, Paper.

Squid Empire: The Rise and Fall of the Cephalopods. By Danna Staaf. 2017. ForeEdge. 256 pages, 27.95 USD, Cloth, 22.99 USD, E-book.

Orca: How We Came to Know and Love the Ocean's Greatest Predator. By Jason M. Colby. 2018. Oxford University Press. 408 pages, 29.95 CAD, Cloth. Also available as an E-book.

Spying on Whales: The Past, Present, and Future of Earth's Most Awesome Creatures. By Nick Pyenson. 2018. Viking. 336 pages, 27.00 USD, Cloth, 17.50 USD, Audiobook, 13.99 USD, E-book.

OTHER

What Species Mean: A User's Guide to the Units of Biodiversity. By Julia D. Sigwart. 2018. CRC Press (Taylor & Francis Group). 232 pages, 79.96 USD, Cloth, 43.96 USD, E-book.

Handbook of Australasian Biogeography. CRC Biogeography Series. Edited by Malte C. Ebach. 2017. CRC Press (Taylor & Francis Group). 376 pages, 84.00 USD, Cloth, 46.36 USD, E-book.

Welcome to Subirdia: Sharing Our Neighborhoods with Wrens, Robins, Woodpeckers, and Other Wildlife. By John M. Marzluff. Illustrated by Jack DeLap. 2015. Yale University Press. 320 pages, 18.00 USD, Paper.

Birders of Africa: History of a Network. By Nancy J. Jacobs. 2016. Yale University Press. 352 pages, 60.00 USD, Cloth.

Hubbard Brook: The Story of a Forest Ecosystem. By Richard T. Holmes and Gene E. Likens. 2016. Yale University Press. 288 pages and 187 colour illustrations, 45.00 USD, Cloth.

Sustaining Lake Superior: An Extraordinary Lake in a Changing World. By Nancy Langston. 2017. Yale University Press. 312 pages, 35.00 USD, Cloth.

The Human Planet: How We Created the Anthropocene. By Simon L. Lewis and Mark A. Maslin. 2018. Yale University Press. 480 pages, 25.00 USD, Cloth.

Visual Voyages: Images of Latin American Nature from Columbus to Darwin. By Daniela Bleichmar. 2017. Yale University Press in association with the Huntington Library, Art Collections, and Botanical Gardens. 240 pages, 50.00 USD, Cloth.

The Aliens Among Us: How Invasive Species Are Transforming the Planet—and Ourselves. By Leslie Anthony. 2017. Yale University Press. 400 pages, 30.00, Cloth.

Ecology and Management of Terrestrial Vertebrate Invasive Species in the United States. Edited by William C. Pitt, James C. Beasley, and Gary W. Witmer. 2017. CRC Press (Taylor & Francis Group). 403 pages, 79.95 USD, Cloth or E-book.

Conservation Criminology. Edited by Meredith L. Gore. 2017. Wiley-Blackwell. 248 pages, 103.29 CAD, Cloth, 82.99 CAD, E-book.

Biodiversity Conservation and Phylogenetic Systematics: Preserving our Evolutionary Heritage in an Extinction Crisis. Topics in Biodiversity and Conservation, Volume 14. Edited by Roseli Pellens and Philippe Grandcolas. 2016. Springer Open. 407 pages, 51.99 EU, Cloth or E-book. Open access on Springer website.

Messages from Islands: A Global Biodiversity Tour. By Ilkka Hanski. 2016. University of Chicago Press. 272 pages, 100.00 USD, Cloth, 32.50 USD, Paper, 10.00–32.50 USD, E-book.

A Year with Nature: An Almanac. By Marty Crump. 2018. University of Chicago Press. 384 pages, 30.00 USD, Cloth, 18.00 USD, E-book.

Critical Terms for Animal Studies. Edited by Lori Gruen. 2018. University of Chicago Press. 448 pages, 97.50 USD, Cloth, 32.50 USD, Paper. Also available as an E-book.¡

Nature's Temples: The Complex World of Old-Growth Forests. By Joan Maloof. 2016. Timber Press. 200 pages, 27.95 USD, Cloth, 14.99 USD, E-book.

Seaweed Chronicles: A World at the Water's Edge. By Susan Hand Shetterly. 2018. Workman Publishing. 288 pages, 24.95 USD, Cloth, 11.99 USD, E-book.

Extreme Conservation: Life at the Edges of the World. By Joel Berger. 2018. University of Chicago Press. 368 pages, 22.89 USD, Cloth.

The Wizard and the Prophet: Two Remarkable Scientists and Their Dueling Visions to Shape Tomorrow's World. By Charles C. Mann. 2018. Knopf. 640 pages, 19.68 USD, Cloth, 13.55 USD, Paper.

A Wilder Time: Notes from a Geologist at the Edge of the Greenland Ice. By William E. Glassley. 2018. Bellevue Literary Press. 224 pages, 12.18 USD, Paper.

Improbable Destinies: Fate, Chance, and the Future of Evolution. By Jonathan B. Losos. 2018. Riverhead Books. 384 pages, 28.00 USD, Cloth, 17.00 USD, Paper, 12.99 USD, E-book.

A Fierce Green Fire: Aldo Leopold's Life and Legacy. New Edition. By Marybeth Lorbiecki. 2016. Oxford University Press. 400 pages, 32.95 CAD, Paper. Also available as an E-book.

Alien Species and Insect Conservation. By Tim R. New. 2016. Springer. 242 pages, 159.00 USD, Cloth, 119.00 USD, E-book.

Current Trends in Wildlife Research. Wildlife Research Monographs. Edited by Rafael Mateo, Beatriz Arroyo, and Jesus T. Garcia. 2016. Springer. 303 pages, 159.00 USD, Cloth, 119.00 USD, E-book.

Defending Biodiversity: Environmental Science and Ethics. By Jonathan A. Newman, Gary Varner, and Stefan Linquist. 2017. Cambridge University Press. 455 pages, 99.99 USD, Cloth, 47.99 USD, Paper.

Tropical Conservation: Perspectives on Local and Global Priorities. Edited by A. Alonso Aguirre and Raman Sukumar. 2017. Oxford University Press. 528 pages, 99.00 USD, Cloth.

Sacred Bovines: The Ironies of Misplaced Assumptions in Biology. By Douglas Allchin. 2017. Oxford University Press. 264 pages, 34.95 USD, Cloth. Also available as an E-book.

The New Ecology: Rethinking a Science for the Anthropocene. By Oswald J. Schmitz. 2016. Princeton University Press. 256 pages, 35.00 USD, Cloth, 22.95 USD, Paper. Also available as an E-book.

Coves of Departure: Field Notes from the Sea of Cortez. By John Seibert Farnsworth. 2018. Cornell University Press, Comstock Publishing Associates. 168 pages, 18.95 USD, Paper.

Nature Hikes: Near-Toronto Trails and Adventures. By Janet Eagleson. Photography by Rosemary G. Hasner. 2018. Firefly Books. 240 pages, 24.95 CAD, Paper.

Rare and Wonderful: Treasures from the Oxford University Museum of Natural History. By Kate Diston and Zoë Simmons. 2018. Bodleian Library, University of Oxford. Distributed by University of Chicago Press. 224 pages and 50 colour plates, 35.00 USD, Cloth.

This Land Is Your Land: The Story of Field Biology in America. By Michael J. Lannoo. 2018. University of Chicago Press. 304 pages, 90.00 USD, Cloth, 30.00 USD, Paper, 10.00–30.00 USD, E-book.

Vernon Bailey: Writings of a Field Naturalist on the Frontier. By David J. Schmidly. 2018. Texas A&M University Press. 472 pages, 45.00 USD, Cloth. Also available as an E-book.

Land Bridges: Ancient Environments, Plant Migrations, and New World Connections. By Alan Graham. 2018. University of Chicago Press. 288 pages, 150.00 USD, Cloth, 50.00 USD, Paper, 10.00–50.00 USD, E-book.

Eastern Alpine Guide: Natural History and Conservation of Mountain Tundra East of the Rockies. Edited by Mike Jones and Liz Willey. 2018. University Press of New England. 360 pages, 35.00 USD, Paper, 34.99 USD, E-book.

The Tangled Tree: A Radical New History of Life. By David Quammen. 2018. Simon & Schuster. 480 pages, 30.00 USD, Cloth, 18.00 USD, Paper, 14.99 USD, E-book.

Unnatural Selection. By Katrina van Grouw. 2018. Princeton University Press. 304 pages and 304 black and white illustrations, 45.00 USD, Cloth.

Invasion Dynamics. By Cang Hui and David M. Richardson. 2017. Oxford University Press. 336 pages, 115.00 CAD, Cloth, 60.00 CAD, Paper. Also available as an E-book.

Conservation Drones: Mapping and Monitoring Biodiversity. By Serge A. Wich and Lian Pin Koh. 2018. Oxford University Press. 144 pages, 55.00 CAD, Cloth, Also available as an E-book.

†**The Environment: A History of the Idea.** By Paul Warde, Libby Robin, and Sverker Sörlin. 2018. Johns Hopkins University Press. 256 pages, 29.95 USD, Cloth.

News and Comment

Upcoming Meetings and Workshops

Canadian Conference on Fisheries Research

The Canadian Conference on Fisheries Research to be held 3–6 January 2019 at the London Convention Centre, London, Ontario. The theme of the conference is: ‘Resilience, Adaptation, and Mitigation Strategies for Conserving Canada’s Aquatic Resources’. Registration is currently open. More information is available at https://www.uwo.ca/sci/ccffr_scl2019.

Society for Integrative & Comparative Biology Annual Meeting

The Society for Integrative & Comparative Biology Annual Meeting, with the American Microscopical Society, The Crustacean Society, and Animal Behavior Society, to be held 3–7 January 2019 at the Tampa Marriott Waterside and Tampa Convention Center, Tampa, Florida. Registration is currently open. More information is available at http://www.sicb.org/meetings/2019/index.php.

Science, Practice & Art of Restoring Native Ecosystems Conference

The Science, Practice & Art of Restoring Native Ecosystems Conference to be held 11–12 January 2019 at the Kellogg Center, East Lansing, Michigan. Registration is currently open. More information is available at https://conference.stewardshipnetwork.org.

Midwest Fish & Wildlife Conference

The 79th Midwest Fish & Wildlife Conference to be held 27–30 January 2019 at the Hilton Cleveland Downtown Hotel, Cleveland, Ohio. The theme of the conference is: ‘Communicating Science to Fan the Flames of Conservation’. Registration is currently open. More information is available at http://www.midwestfw.org.

Forests Ontario Annual Conference

The Forests Ontario Annual Conference to be held 8 February 2019 at the Nottawasaga Inn, Alliston, Ontario. The theme of the conference is: ‘Natural Connections’. Registration is currently open. More information is available at https://www.forestsontario.ca/community/annual-conference.

Society for Range Management Annual Meeting

The 72nd annual meeting of the Society for Range Management to be held 10–14 February 2019 at the Hilton Minneapolis, Minneapolis, Minnesota. The theme of the conference is: ‘Gateway to the Prairie’. Registration is currently open. More information is available at http://annualmeeting.rangelands.org.

Wisconsin Wetlands Association’s Wetland Science Conference

The Wetland Science Conference of the Wisconsin Wetlands Association to be held 19–21 February 2019 at the Madison Marriott West, Madison, Wisconsin. Registration is currently open. More information is available at https://conference.wisconsinwetlands.org.

Entomological Society of America – Southeastern Branch Meeting

The 93rd annual meeting of the Southeastern Branch of the Entomological Society of America to be held 3–6 March 2019 at the Renaissance Mobile Riverview Plaza Hotel, Mobile, Alabama. Registration is currently open. More information is available at https://www.entsoc.org/southeastern/2019-branch-meeting.

Entomological Society of America – Eastern Branch Meeting

The 90th annual meeting of the Eastern Branch of the Entomological Society of America to be held 9–12 March 2019 at The Inn at Virginia Tech, Blacksburg, Virginia. Registration is currently open. More information is available at https://www.entsoc.org/eastern/2019-branch-meeting.

Entomological Society of America – North Central Branch Meeting

The 74th annual meeting of the North Central Branch of the Entomological Society of America to be held 17–20 March 2019 at the Hyatt Regency Cincinnati, Cincinnati, Ohio. Registration is currently open. More information is available at https://www.entsoc.org/northcentral/2019-branch-meeting.

Alberta Chapter of The Wildlife Society Conference

The Alberta Chapter of The Wildlife Society Conference to be held 22–24 March 2019 at the Coast Canmore Hotel + Conference Centre, Canmore, Alberta. The theme of the conference is: 'Connectivity'. More information is available at https://www.actws.ca/conference.

Entomological Society of America – Pacific Branch Meeting

The 103rd annual meeting of the Pacific Branch of the Entomological Society of America to be held 31 March–3 April 2019 at the Hyatt Regency Mission Bay Spa & Marina, San Diego, California. Registration is currently open. More information is available at https://www.entsoc.org/pacific/2019-branch-meeting.

Book Reviews

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