

Occupancy and Detection of Eastern Massasauga Rattlesnakes (*Sistrurus catenatus*): Implications for Evaluating Population Recovery Efforts

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ABSTRACT: Standardized estimates of a species' distribution before and after translocation can inform whether a reintroduction project was effective at population establishment. Occupancy modeling has grown in popularity to estimate the distribution of cryptic animals, including viperid snakes, because it can account for variations in detection probability (P) generated by site-, survey-, and population-specific factors. We estimated occupancy and P in an endangered subpopulation of the cryptic North American pit-vipers (Eastern Massasaugas, *Sistrurus catenatus*; hereafter Massasauga[s]) in preparation for future conservation translocations. During a 6-yr period at the Ojibway Prairie Complex and Greater Park Ecosystem, in Ontario, Canada, we conducted more than 1740 repeated standardized surveys at 40 plots (each ca. 2.4 ha) by using two methods (visual encounter and artificial cover object), across three seasons (spring, summer, and fall), and with different types of search effort (single vs. team surveys) and analyzed a suite of detection histories by using occupancy modeling. Massasaugas were detected at only 10% of survey sites ($n = 4/40$), and the species was presumed undetected at one additional site after accounting for P (estimated occupancy, 13%). The P for Massasaugas ranged from 0.01 to 0.73 and was most strongly influenced by search effort, season, and trap response (i.e., "trap-happy" individuals repeatedly found in the same locations). The detection probability was significantly inflated during surveys when there was at least one trap-happy snake present. Across top ranking models (based on Akaike's Information Criterion scores), team visual encounter surveys in spring and summer, and conducting at least two surveys per week, generated an average $P \geq 0.15$ after accounting for a trap response. Conversely, fall surveys and artificial cover object surveys generated a $P < 0.15$. Our study provides direction to other conservation practitioners working with small populations of cryptic snakes and will inform monitoring regimes for future conservation translocations.

Key words: Occupancy modeling; Program Presence; Repatriation; Reptile; *Sistrurus catenatus*; Survey protocol; Urban herpetology; Viperidae

THERE is a need to improve conservation translocation techniques for reptiles (Choquette et al. 2023), including evaluating appropriate monitoring methods to gauge translocation success (Germano et al. 2014). Effective posttranslocation monitoring, although challenging (Berger-Tal et al. 2020), can provide valuable information on population trajectories (Nicoll et al. 2021). Standardized estimates of a species' distribution or abundance before and after translocations are essential, because these can inform whether a project was effective at long-term population establishment and persistence (IUCN/SSC 2013), assuming evaluations are made a sufficient amount of time after translocations (Seddon et al. 2012). Although reintroduced populations can grow initially through increasing density or increasing range (Armstrong and Seddon 2008), monitoring changes in abundance of certain taxa is inhibited by low detection rates (Steen 2010; Durso et al. 2011). For populations of cryptic species, monitoring changes in distribution (e.g., Bailey et al. 2004; Sewell et al. 2012) may be a more appropriate method for evaluating long-term translocation outcomes. Occupancy modeling is one approach that could provide distribution estimates both before and after translocations, to demonstrate whether a statistically significant increase in occupancy has occurred.

Occupancy modeling has grown in popularity as a robust and effective means to estimate the distribution (i.e., occupancy) of cryptic animals at the landscape scale, including snakes, because it accounts for imperfect detection (Durso et al. 2011; MacKenzie et al. 2017). Repeated standardized surveys at replicate sites allow practitioners to assign a

probability of occupancy for each site based on the number of surveys conducted and the average detection probability (P) of the target species. To ensure unbiased occupancy estimates, five main model assumptions must be met: sites are closed to changes in occupancy, detections are independent, species are correctly identified, and there is no unmodeled heterogeneity in either occupancy probability (ψ) or P (MacKenzie et al. 2017). Furthermore, the probability of detection should be ≥ 0.15 to avoid biased occupancy estimates generated when sites with low P are indistinguishable from sites where the species is truly absent (Bailey et al. 2004). Probability of detection in squamate reptiles may be influenced by many factors, including population density (Kéry 2002; Durso et al. 2011), survey year (Seddon et al. 2011), temperature (Harvey 2005), survey effort or method (Bartman et al. 2016; Bradke et al. 2018; Lardner et al. 2019), and time of year (Kéry 2002; Sewell et al. 2012). These factors complicate the development of an appropriate monitoring regime, particularly when a species is difficult to find.

Eastern Massasaugas (*Sistrurus catenatus*) are globally imperiled (G3; NatureServe 2022), small and cryptic pit-vipers that can be difficult to detect relative to sympatric snake species (Perelman et al. 2022). In an effort to increase survey efficiency, past protocols provided recommendations on the most suitable survey conditions, time frames, methods, and vegetation communities for detection and provided minimum survey effort targets (Casper et al. 2001; OMNRF 2016a). These protocols did not, however, stipulate an ideal number of searchers during surveys, describe seasonal variations in detection rate, or agree on whether visual encounter surveys ought to be supplemented with artificial cover object surveys (e.g., Bartman et al. 2016).

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Recent studies of Massasauga *P* and occupancy in Illinois and Michigan complemented prior survey protocols by identifying variables affecting Massasauga *P* (e.g., Julian date, search effort, and substrate and air temperature; Shaffer et al. 2019; Crawford et al. 2020; Thacker 2020; Thacker et al. 2023); however, knowledge gaps remain. For example, Massasauga detection probabilities have not been estimated using data from the entire active season (spring, summer, and fall), or after accounting for a trap response. Snakes that are repeatedly found by surveyors in the same locations (i.e., “trap happy”; Bradke et al. 2018) may result in violating the independence assumption of occupancy modeling (MacKenzie et al. 2017) and inflating *P* estimates. Also, Massasauga detection probabilities estimated in “medium” or “large” subpopulations (e.g., Faust et al. 2011; Crawford et al. 2020; Thacker 2020), or in quasi-controlled settings with telemetered snakes (Shaffer et al. 2019), may not be transferable to small subpopulations at low densities (Kéry 2002; Royle and Nichols 2003). Experts have estimated that more than half of known Massasauga subpopulations are “small” (≤ 25 –50 females; Faust et al. 2011), and a small subpopulation is presumably more consistent with a posttranslocation scenario. A comparison of results from standardized surveys conducted across all seasons, with a variable number of surveyors, and using different survey methods, while accounting for the effect of a trap response, would provide quantitative evidence to support the refinement of current rattlesnake monitoring protocols. Valuable conservation dollars could thus be directed toward the most efficient search techniques, potentially reducing material and human resource costs, increasing confidence in survey results for sites without detection, and shortening the time required to evaluate snake translocations.

Our goal was to estimate *P* and occupancy with a high level of accuracy and precision, in a small and endangered subpopulation of Eastern Massasaugas before experimenting with conservation translocations as a recovery tool, to determine the most appropriate monitoring regime. Because of a high risk of local extinction and low viability (COSEWIC 2012), recovery strategies urged further research into the effectiveness of conservation translocations as a management tool for increasing abundance, distribution and viability of small subpopulations of Massasaugas (Parks Canada Agency 2015; OMNRF 2016b). Our research questions were (1) which survey season (spring, summer, or fall), survey method (visual encounter or artificial cover object), and number of surveyors per survey (single or team) offer the highest *P*, while accounting for the effect of trap response; and (2) would the current sampling regime be adequate for monitoring changes in occupancy of this species after translocation?

MATERIALS AND METHODS

Study Area and Survey Sites

Over 6 yr, we conducted repeated standardized surveys at 40 sites by using two methods, in three seasons, and with different numbers of surveyors, and we analyzed detection data using occupancy modeling. Surveys targeted Massasaugas within the Ojibway Prairie Complex and Greater Park Ecosystem, in Ontario, Canada (42.26°N, 83.07°W; datum = WGS84; Fig. 1), which represents the southernmost Canadian subpopulation. The federally and provincially endangered

Ojibway Prairie Massasauga subpopulation is ecologically, genetically, and geographically distinct in Canada, yet before our study, the range of this small subpopulation had declined by 82% in three decades, and abundance was critically low (≤ 40 mature snakes; Faust et al. 2011; COSEWIC 2012; COSSARO 2013). Conservation translocations were conducted in the 1990s and 2000s in an effort to augment the local population, but were presumed unsuccessful (19 snakes released between 1990 and 1994 [Pither 2003]; 27 snakes released in 2006 [Harvey et al. 2014]). More recently, Lincoln–Petersen estimates generated an average abundance of only 10 (95% confidence interval; [CI] = 6–80) remaining adults and subadults across ca. 20 ha in any given 2-yr period during a long-term study (J.D. Choquette and C. Fournier, personal observations).

Survey sites ($n = 40$) were identified as areas or discrete patches of open-canopy or semiopen-canopy vegetation that were 2.0–2.5 ha (average, 2.4 ha) and found within the recent historical subpopulation range of Massasaugas at the study area (Fig. 1). A habitat suitability model (Choquette et al. 2020), a Massasauga Critical Habitat map (Parks Canada Agency 2015), aerial photos (LIO 2006), and ground-truthing were used in combination to guide the site selection process. Most survey sites (83%; $n = 33$) were within or directly adjacent to Critical Habitat and we assumed these sites were representative of all Critical Habitat because we selected the majority of available sites therein and followed a probabilistic sampling scheme (MacKenzie and Royle 2005; Supplemental Methods S1, available online). Open and semiopen vegetation communities were targeted (e.g., meadows, prairies, thickets, and savannahs) because Massasaugas preferentially use vegetation types with relatively low canopy cover during the active season (COSEWIC 2012). Size of selected sites approximated the average size of the remaining patches of open or semiopen vegetation in the study area and was similar to the mean annual Massasauga home range size in nearby southern Michigan, USA (e.g., 2.5 ha; Bissel 2006). A geographic information system was used to map boundaries and estimate area of each survey site (ArcGIS 9.2, ESRI, Redlands, CA, USA). Site boundaries were generally discrete (e.g., edges of roads, trails, or forests), except where the presence of relatively extensive patches of open-canopy vegetation at one of the Critical Habitat blocks necessitated the delineation of arbitrary site boundaries (Supplemental Methods S1). All sites were similar in size (within 0.5 ha) to reduce impacts of survey area on occupancy or *P* (Thacker 2020).

Survey Time Frame and Protocol

Surveys occurred over a 6-yr period, and a subset of all sites was repeatedly surveyed in any given year. Site 9, for example, was surveyed 30 times overall, including 9 times in 2014, 14 times in 2015, and 7 times in 2016. We aimed to complete 19–29 surveys at each site over the 6 yr, of which 4–6 surveys were to be completed in each of two summers to account for the biennial reproductive cycle of Massasaugas (COSEWIC 2012; Supplemental Methods S2, available online). Relatively greater survey effort was invested at three specific sites across all 6 yr to produce repeat Massasauga captures for demographic estimates and to determine factors associated with increased *P*. These three sites were chosen

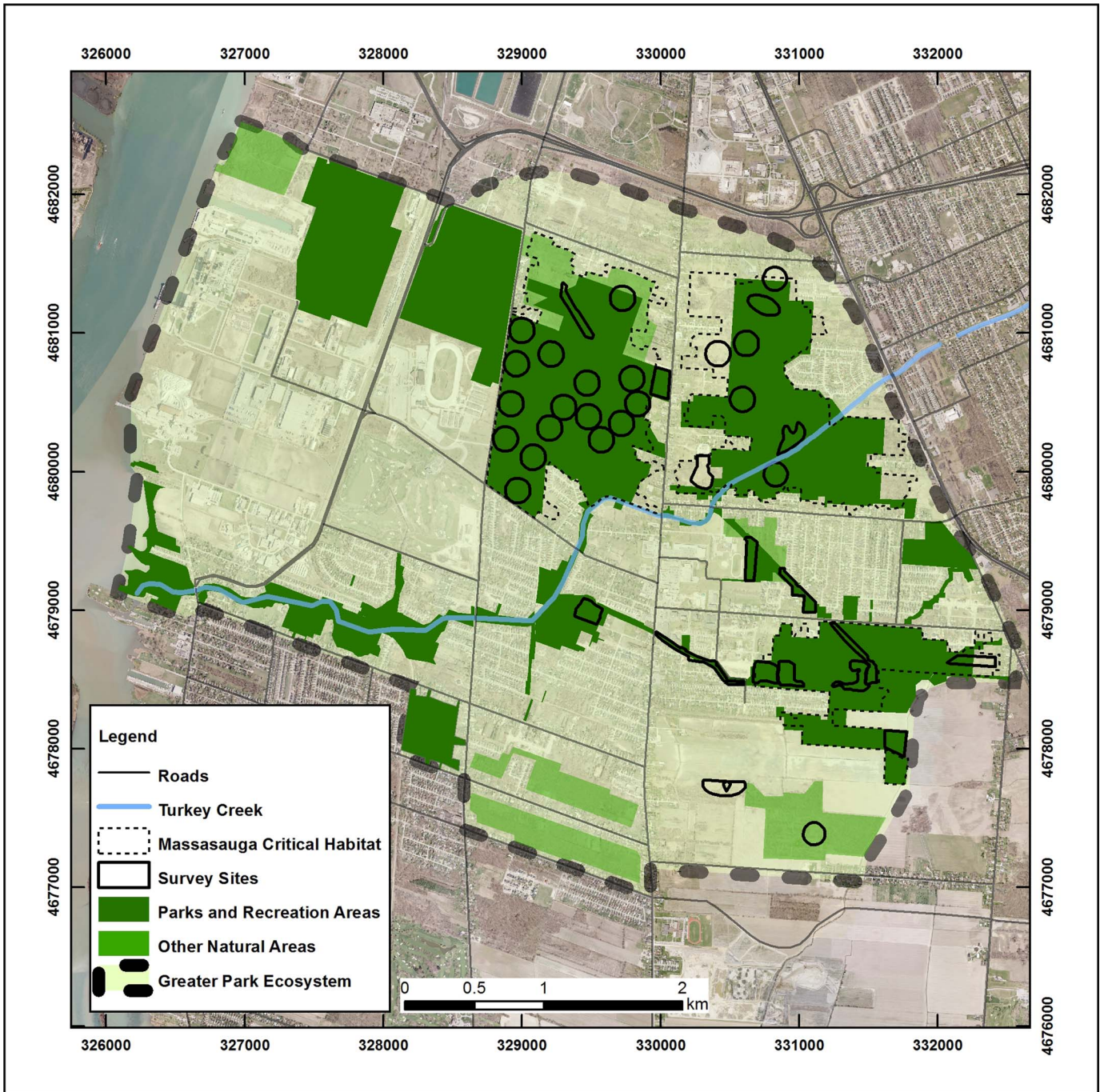


FIG. 1.—Sites where occupancy surveys were conducted targeting the Eastern Massasauga (*Sistrurus catenatus*) at the Ojibway Prairie Complex and Greater Park Ecosystem, Ontario, Canada, from 2013 to 2018. The 23.5-km² study area occurs in the city of Windsor (north) and the town of LaSalle (south), and is bordered by the Detroit River (West; Hecnar 2016); North is facing up. Two survey sites ~2 km outside of the study area boundary were also surveyed due to their proximity to historical observation records (not shown). Slight boundary adjustments occurred at four survey sites early in the study to equalize search areas. Boundaries of the three Massasauga Critical Habitat blocks follow Parks Canada Agency (2015) and include a combined area of 413 ha. Parks and Recreation Area boundaries follow Natural Heritage Area zoning (City of Windsor 2022), Natural Environment zoning and Recreation zoning (Town of LaSalle 2021), and proposed park boundary (Ontario Parks 2015). Other Natural Area boundaries based on candidate natural heritage sites (City of Windsor 1992, 2008; Town of LaSalle 1996, 2010). Air photos are from LIO (2006). Map projection is NAD 1983, UTM Zone 17N. All boundaries are approximate.

based on their proximity to the most recently confirmed observations, and surveys were conducted therein during the spring egress, summer gestation, and fall ingress periods (Supplemental Methods S3, available online). At all other sites, surveys occurred mostly during the summer gestation period because (1) gravid females would have dispersed to

gestation sites and have a relatively higher detection rate than other age classes (Hileman et al. 2018) and (2) any snakes that had been hibernating in closed-canopy vegetation outside of survey sites would have had time to migrate into patches of open-canopy vegetation. It was assumed that no colonizations or extirpations occurred at the site level

during the 6 yr due to the strong site fidelity demonstrated in this species (COSEWIC 2012) and because the occupancy status of the three sites with greater survey effort remained constant during that period (note that an incorrect closure assumption may result in an overestimation of psi ; MacKenzie et al. 2017).

Survey start and end dates in each calendar year varied due to staffing logistics and arrival of favorable weather conditions: they generally began in April and ended in September (median start and end date, 21 April and 22 September, respectively; start range, 9 April–2 May; end range, 23 August–5 October). All surveys took place within the documented activity period for the Massasauga in southeastern Michigan and southwestern Ontario (Pratt et al. 1993; Bissell 2006; Moore and Gillingham 2006; Bailey 2010). Thus, we presumed snakes were available for detection at occupied sites from the start to end of each survey period in any given year. In all years, regardless of season, each survey was generally conducted by a single surveyor on an infrequent basis (i.e., one to three surveys per site per week). From 2015 to 2018, however, spring surveys were generally conducted by a team of two or more surveyors at the same three sites more frequently (i.e., three to five surveys per site per week). Survey team composition varied annually, and at least one individual trained in our protocols was present on 100% of surveys across the study period.

Survey methods included time-constrained standardized visual encounter surveys and artificial cover object surveys. Visual encounter surveys were 1.5–2.0 h in duration and were conducted following recommended survey protocols (Supplemental Methods S4, available online). Artificial cover object surveys were conducted during visual encounter surveys in all years except 2013 (Supplemental Methods S5, available online). Survey sites were covered as evenly and thoroughly as possible, although portions with suitable microhabitats such as basking features and animal burrows were given relatively greater attention. Survey start times (AM vs. PM), surveyor(s), and start/end points were rotated to reduce heterogeneity in P arising from time of day, surveyor, and direction of travel. We attempted to meet occupancy modeling assumptions by standardizing our study design and addressed the remainder of assumptions using model covariates (Supplemental Methods S6, available online).

Detailed observation and weather data were recorded in the field generally following recommendations in a 2001 survey protocol (Casper et al. 2001). Surveys were conducted during a predefined range of recommended weather conditions (Supplemental Methods S4) to reduce the impact of associated variables on detection as much as possible. Shaded air temperature was recorded at waist height to the nearest degree Celsius with a digital thermometer (model 317C, Test Products International Inc.; accuracy, $\pm 1^\circ\text{C}$; model 9835, Taylor Precision Products Inc.; accuracy, $\pm 0.6^\circ\text{C}$), wind speed was coded using the Beaufort scale, and cloud cover was recorded via subjective assignment of a weather category (e.g., sunny, overcast, etc.) and by estimating cloud cover to the nearest 10%. All weather data were recorded immediately before and after each survey. Any missing air temperature or weather condition data were retrieved using Environment Canada's historical hourly weather data for Windsor International Airport (~ 7.5 km from study site) for

the hour nearest the time of snake observation or survey start/end.

Occupancy Modeling

Occupancy modeling analyses were completed in program Presence (v2.13.18, released December 2021; USGS Patuxent Wildlife Research Center, Blacksburg, VA, USA). Only results from standardized visual encounter surveys were included in analyses. Results from 237 nonstandardized surveys and site visits were excluded from analyses, even if the target species was detected, because they did not adhere to our standardized survey protocol. For example, we excluded surveys that were conducted with air temperatures or wind speeds outside of the protocol based on the average of start and end measurements, repeat surveys at the same site on the same day, site visits as part of related conservation projects, and surveys that were < 1.5 h long. Any surveys that were > 2.0 h long were included in analyses based on results from the first 2.0 h only. Massasauga observations that did not occur during standardized visual encounter surveys (including those reported to us by park users) were labeled “incidental.” Six surveys ended early after a Massasauga was detected (i.e., before 1.5 survey hours), but these were so few that their inclusion had a negligible impact on P estimates ($n = 6$; 0.3% of standardized surveys; increase in P of 0.006).

The detection probabilities were first estimated separately for each calendar year of study by using a single season analysis, 1000 bootstraps, no covariates on occupancy or detection (i.e., a null model), and a detection history (DH) wherein sampling occasions were based on calendar day. Estimates for single years were generated to determine the optimum number of repeat surveys (Supplemental Methods S2) and served as null models against which we compared covariate-fitted models. Regardless of year, 1–11 (mean, 3) sites were surveyed during any given sampling occasion (i.e., calendar day) and results for sites not surveyed during a sampling occasion were considered “missing” observations. Yearly variations occurred in the total number of sites surveyed (mean, 19; range, 9–31), sampling occasions (mean, 102; range, 79–114), and missing observations (mean, 1616; range, 785–2675). The daily DHs from each year were combined to create a complete 6-yr dataset that was then reformatted such that each sampling occasion represented the first to the n th survey at each site following the chronological sequence of surveys (Supplemental Methods S7, available online). In other words, the first survey at each site was considered sampling occasion 1, the second survey was sampling occasion 2, and so on, regardless of the calendar day when the surveys were conducted.

For the combined 6-yr dataset, we conducted separate single season analyses using three different DHs (daily, weekly and monthly; Table 1), but all were based on the same underlying detection data. The daily DH is as described above, whereas the weekly and monthly DHs were coded based on the pooled weekly or monthly results of all surveys at each site. This allowed for a comparison of results at different temporal scales, each providing a unique tradeoff between the number of missing observations and the temporal precision of the data (Table 1). One site covariate and six survey covariates were selected a priori based on

TABLE 1.—Example daily, weekly, and monthly DHs for Eastern Massasauga (*Sistrurus catenatus*) surveys completed at one survey site at the Ojibway Prairie Complex and Greater Park Ecosystem, Ontario, Canada, in May 2013. In total, 12 daily surveys were completed during this example period. At least one Massasauga was detected (1) during 6 of the 12 surveys, and none were detected (0) during the other 6 surveys. Dashed boxes in the “daily” row are used to distinguish surveys completed in each of the five calendar weeks in that month. Blacked out cells show how the DH was condensed from 12 survey periods (daily), to 5 (weekly), and finally to 1 (monthly). The column on the right shows the number of survey periods and missing observations for the entire 2013–2018 dataset and for each DH. A missing observation occurred when a site was not surveyed during a survey period. For a given DH, all models were constructed and compared using an equal number of survey periods.

DH	Survey period (May 2013)												Total no. of survey periods and missing observations (2013–2018)
	1	2	3	4	5	6	7	8	9	10	11	12	
Daily	1	0	0	0	1	1	1	0	1	1	0	0	255, 8468
Weekly	1	1	1	1	0	[Blacked out]						129, 3863	
Monthly	1	[Blacked out]											34, 974

their suspected influence on *psi* or *P*, and all or a subset of these were included in relevant model sets (Supplemental Methods S3). For the site covariate, general location, each site was assigned to one of four categories based on its proximity to a distinct Critical Habitat block (Critical Habitat Block 1, 2, 3, and other). The survey covariates were generally categorical and as follows: season (meteorological spring, summer, or fall), survey frequency (daily DH only, <5 or ≥5 d since prior survey of a site), calendar year, cloud cover (daily DH only, sunny or cloudy), and search effort (daily DH, single or team surveys; weekly DH, one or two or more surveys per week; monthly DH, continuous based on number of surveys per month). We also included a covariate on trap response, based on whether a trap-happy snake was present or absent at a site during a survey. Trap-happy snakes were individuals found within 10 m of the same location on at least three successive occasions (Supplemental Methods S3). Additive models using logical combinations of these base covariates were also used in model sets. To avoid model overparameterization, and because we followed a standardized survey protocol regarding weather conditions (Supplemental Methods S4), and surveyed sites of similar size and with suitable open-canopy vegetation, we excluded time of day, air temperature, wind speed, site size, and vegetation community type as model parameters. A unique global or subglobal model was used in each analysis to assess model fit using 1000 bootstraps (Lamothe et al. 2021), and from this, *c-hat* was adjusted to account for model overdispersion. The Quasi-Akaike’s Information Criterion (QAIC) was used to evaluate models.

A preliminary step was taken before running the daily, weekly, and monthly analyses to identify relative importance of the six survey covariates and eliminate those with low support. This reduced the eventual number of parameters being estimated, thereby avoiding model overparameterization (MacKenzie 2006; MacKenzie et al. 2017). Using a general model for occupancy *psi*(location), a suite of models was run using all relevant combinations of single and paired

covariates on detection (i.e., for the daily DH each of the six covariates on detection were represented in six models). Model weights were summed for the group of models represented by each covariate, and covariates with relatively low support (e.g., summed model weight ≤0.001) were excluded from the next step in the analyses. The final daily, weekly and monthly analyses included one site covariate and combinations of three or four survey covariates, as well as the null models. The most general (global) model was included in all analyses. Overparameterized models were removed from each model set, which occurred when the number of significant digits was less than six (the default in Presence), or when negative SEs appeared in the variance–covariance matrix. The result was a set of 11, 9, and 22 models in the daily, weekly, and monthly analyses, respectively. Results were presented for all models with substantial support ($\Delta AIC = 0-2$), the next highest model ($\Delta AIC > 2$, if applicable), and the null model. A critical appraisal was conducted to further explore the influence of survey covariates on *P* (Supplemental Results S8, available online). Models with no support ($AIC > 10$) were not presented (Supplemental Results S9, available online).

RESULTS

Visual Encounter Surveys

In total, 1742 standardized visual encounter surveys were completed across 40 sites, representing 3822 person-hours (Table 2). The median number of surveys per site overall was 29 (range, 5–255); however, this value was higher for the seven sites at Critical Habitat Block 1 (118; range, 30–255) and lower for the eight sites at Critical Habitat Block 2 (10; range, 5–29). Most sites (80%; *n* = 32) received the target of 19–29 standardized surveys overall, and the majority of sites (90%; *n* = 36) received the target of four to six summer surveys in at least two different calendar years (Supplemental Methods S2).

At least one Massasauga was detected during 150 out of the 1,742 standardized visual encounter surveys (8.6% of

TABLE 2.—Annual Eastern Massasauga (*Sistrurus catenatus*) observations and detection probabilities from 2013 to 2018 at the Ojibway Prairie Complex and Greater Park Ecosystem, Ontario, Canada. INC = incidental observations (i.e., those not recorded during standardized surveys) that were included in the total number of observations; Trap response is defined in Supplemental Methods S3.

Year ^a	No. of observations	No. of unique individuals	Survey effort (person-hours); no. of standardized surveys; no. of sites surveyed	P (null model; <i>psi</i> (.) <i>P</i> (.))	No. of sites affected by trap response
2013	45 (1 INC)	19	397; 160; 9	0.35 (0.26–0.46)	3
2014	13 (2 INC)	6	347; 190; 14	0.10 (0.05–0.18)	0
2015*	21 (13 INC)	14	651; 359; 31	0.05 (0.02–0.12)	0
2016*	32 (4 INC)	15	729; 316; 18	0.12 (0.07–0.18)	0
2017*	78 (17 INC)	11	951; 426; 29	0.25 (0.19–0.31)	3
2018*	36 (3 INC)	5	747; 291; 13	0.19 (0.13–0.26)	2

^a Asterisk (*) indicates year when spring surveys were generally conducted by a team of two or more surveyors at the same three sites three to five times per week (see Materials and Methods).

surveys), and all detections during visual encounter surveys occurred entirely within four sites, all within Critical Habitat Block 1 (naïve occupancy = 0.10; 4/40 sites). Detection rate at the four occupied sites was 18% (150/842 surveys). Overall, surveys were conducted most often by a single surveyor (74%), on an infrequent basis (63%), or in the summer (61%; Supplemental Results S10, available online). At the four occupied sites, a comparable proportion of surveys were conducted in spring (48%) and summer (45%), at the expense of fall surveys (7%), and single surveyors completed a similar proportion of surveys (49%) as team surveyors (51%; Supplemental Results S10). A trap-happy snake was only present during 15% of surveys at occupied sites (Table 2; Supplemental Results S10). No Massasaugas were detected within Critical Habitat Block 3, where conservation translocations were previously conducted (Pither 2003; Harvey et al. 2014).

Massasauga Observations

We recorded 225 Massasauga observations, representing at least 39 unique individuals; 185 of these observations occurred during standardized visual encounter surveys, and >1 snake was found during some surveys. Forty of the observations were incidental (i.e., they did not occur during standardized surveys), but all occurred within, or very close to, the four occupied sites. No incidental observations were included in occupancy modeling analyses. In each year, and excluding neonates, more than half of observations were of individuals already marked in that year (range, 54–89%). Included in the grand total are two observations of dead adult Massasaugas (2013, 2018), two adult skin sheds (both in 2018), and five litters of neonates (2013, 2015, 2016, and 2017; representing 34 observations). Zero to two occupied sites were used annually by Massasaugas for reproduction, which was determined based on the detection of neonates near a postpartum female, and all four occupied sites were used for reproduction during the study.

Survey conditions were summarized below using data from 196 Massasauga observation records. For clarity, all 225 Massasauga observations were reduced to 196 after combining observations of multiple neonates found together into a single observation record for each litter. Observations occurred from 10 April to 12 September, with a median date of 1 June (i.e., 151st calendar day) and litters of neonates were observed from 16 to 30 August. A large proportion of observations occurred in May (40%), June (19%) and August (17%), compared with April (9%) and September (2%). Observations were made equally in the spring (49%) and

summer (49%), whereas very few occurred in the fall (2%). Excluding neonates, a similar number of unique individuals were observed in the spring of each year (mean, 5) compared with the summer (mean, 4). Mean shaded air temperature for all Massasauga observations was 21°C (SD, 4.2; range, 10–33°C; Supplemental Methods S4), and the peak number of observations occurred between 22 and 25°C (*n* = 73; 38%). Median time of day for all observations was 1335 h (range, 0903–1940 h), with the peak between 1100 and 1159 h (*n* = 39, 20%). Mean cloud cover for all observations was 54% (SD, 33%; range, 0–100%), with the peak when cloud cover was 100% (*n* = 38; 20%). Time of day and/or date was not recorded for two incidental Massasauga observations.

The vast majority of Massasaugas were detected by sight (91%), with very few detected by sound (8%) or found under existing wood and metal rubbish (2%). During surveys, Massasaugas were only detected using visual encounter search methods, and none were found under our standardized artificial cover objects. We conducted 1343 cover object surveys, 615 of which occurred at sites occupied by Massasaugas, and these generated detections of five other snake species: *Pantherophis vulpinus*, *Storeria dekayi*, *Storeria occipitomaculata*, *Thamnophis butleri*, and *Thamnophis sirtalis*.

Detection Probability

Annual estimates of *P* using a null model ranged from 0.05 to 0.35 and were above 0.15 in 2013, 2017, and 2018

TABLE 3.—Relative covariate importance based on combined model weights when using a general model for occupancy *psi*(location) and all possible combinations of single and paired covariates on detection for each of 3 DHs, by using Eastern Massasauga (*Sistrurus catenatus*) detection data collected at the Ojibway Prairie Complex and Greater Park Ecosystem, Ontario, Canada, from 2013 to 2018. Model weights based on QAIC were summed for the group of models represented by each covariate. Covariates with relatively low support in any given DH category (e.g., summed model weight ≤0.001) were excluded from further analyses using that DH.

Covariate ^a	QAIC		
	Daily DH	Weekly DH	Monthly DH
Trap response	0.9999	0.9956	0.4272
Search effort*	0.9913	1.0000	0.8144
Season	0.0055	0.0005	0.7088
Cloud cover	0.0014	NA ^b	NA
Survey frequency	0.0008	NA	NA
Calendar year	0.0000	0.0040	0.0160

^a Asterisk (*) indicates search effort was coded differently for daily, weekly, and monthly DHs (Supplemental Methods S3).

^b NA = not applicable.

TABLE 4.—Model selection summary of the top and null occupancy models fit to Eastern Massasauga (*Sistrurus catenatus*) survey data from the Ojibway Prairie Complex and Greater Park Ecosystem, Ontario, Canada, from 2013 to 2018. P for all “trap” models is for surveys not influenced by trap-happy snakes). $\Delta QAIC$ = relative difference in QAIC values compared with the top ranked model; w = Akaike’s weight for each model (model weights do not sum to 1 because of the model results that have not been presented); N_{par} = number of parameters; $-2l$ = twice the negative log-likelihood values; loc = general location; CH = Critical Habitat; su/wk = surveys per week; su/mo = surveys per month.

Model ^a	$\Delta QAIC$	w	N_{par}	$-2l$	ψ_i (95% CI)	P (95% CI)
Daily DH						
$\psi_i(\cdot) P(\text{season}+\text{effort}+\text{trap})^{**}$	0.00	0.45	6	692.72	0.13 (0.05–0.30)	0.15 (0.12–0.20): Spring, Team 0.26 (0.18–0.36): Summer, Team 0.17 (0.14–0.21): Team
$\psi_i(\text{loc}) P(\text{effort}+\text{trap})^{**}$	0.01	0.45	7	689.36	0.61 (0.23–0.89): CH Block 1 0.00 (0.00–1.00): Other sites	
$\psi_i(\cdot) P(\text{effort}+\text{trap})$	2.95	0.10	4	704.44	0.13 (0.05–0.30)	
Weekly DH						
$\psi_i(\cdot) P(\text{trap}+\text{effort})^{**}$	0.00	0.64	4	401.64	0.12 (0.05–0.29)	0.35 (0.28–0.43): ≥ 2 su/wk ≥ 2 su/wk;
$\psi_i(\cdot) P(\text{year}+\text{trap}+\text{effort})^{**}$	1.20	0.35	9	389.68	0.12 (0.05–0.29)	0.56 (0.37–0.74): 2013* 0.38 (0.22–0.57): 2014 0.24 (0.13–0.41): 2015 0.37 (0.24–0.52): 2016 0.43 (0.28–0.58): 2017* 0.24 (0.14–0.38): 2018*
Monthly DH						
$\psi_i(\cdot) P(\cdot)$	65.15	0.00	2	495.62	0.10 (0.04–0.24)	0.23 (0.20–0.28)
$\psi_i(\text{loc}) P(\text{year}+\text{season}+\text{effort})^{**}$	0.00	0.45	13	131.38	0.57 (0.23–0.86): CH Block 1 0.00 (0.00–1.00): Other sites	Summer, 4 su/mo (for comparison): 0.68 (0.38–0.88): 2013* 0.41 (0.16–0.72): 2014 0.38 (0.16–0.67): 2015 0.36 (0.17–0.61): 2016 0.36 (0.16–0.62): 2017* 0.19 (0.07–0.42): 2018*
$\psi_i(\text{loc}) P(\text{season}+\text{trap})^{**}$	0.26	0.39	8	141.64	0.57 (0.23–0.86): CH Block 1 0.00 (0.00–1.00): Other sites	0.59 (0.42–0.75): Spring 0.39 (0.27–0.53): Summer 4 su/mo (for comparison): 0.40 (0.21–0.62): Spring 0.31 (0.19–0.46): Summer
$\psi_i(\cdot) P(\text{season}+\text{trap}+\text{effort})$	3.53	0.08	6	148.91	0.12 (0.04–0.28)	0.44 (0.36–0.53)
$\psi_i(\cdot) P(\cdot)$	38.60	0.00	2	191.98	0.10 (0.04–0.25)	

^a Single asterisk (*) indicates year with trap-happy snakes; double asterisk (**) indicates models with considerable support based on relative difference in QAIC values compared with the top ranked model ($\Delta QAIC$).

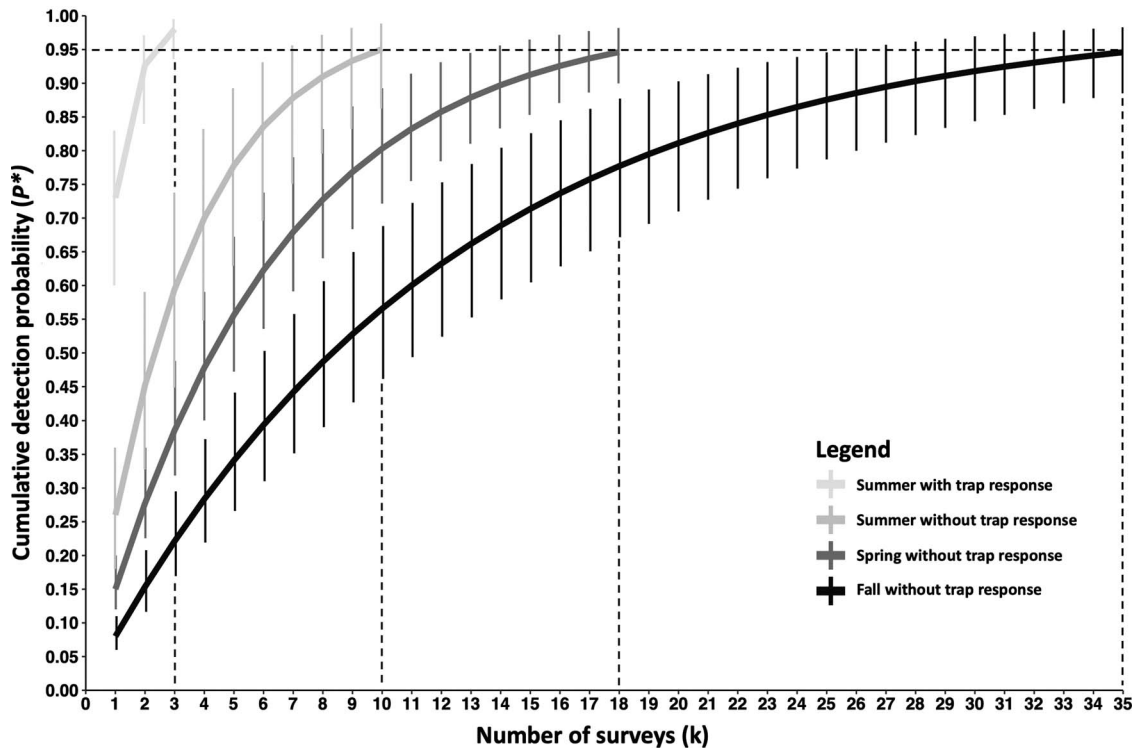


FIG. 2.—Four cumulative detection probability curves based on the results of team standardized visual encounter surveys targeting the Eastern Massasauga (*Sistrurus catenatus*) at the Ojibway Prairie Complex and Greater Park Ecosystem, Ontario, Canada, from 2013 to 2018 (see Materials and Methods for details). Cumulative detection probability (P^*) is based on the formula: $P^* = 1 - (1 - P)^k$, where k is the number of surveys and P is the estimated detection probability given a defined set of methods and conditions. Estimates of P are from the top model using the daily DH (Table 4). From left to right: team survey in summer with trap response (trap-happy snake present), team survey in summer without trap response (no trap-happy snake present), team survey in spring without trap response, and team survey in fall without trap response. Dashed vertical lines depict the number of survey occasions required to achieve 95% confidence in absence, when the target species was not detected. Vertical error bars depict the 95% CI around each estimate of P^* . Note: Although not depicted, the P estimate for surveys conducted by a single surveyor in the summer without trap response (the highest P for nonteam surveys, regardless of season) was identical to the P estimate for team survey in fall without trap response.

(Table 2). The combined 2013–2018 dataset included 34–255 survey occasions and 974–8458 missing observations (Table 1). Sample covariates on search effort and trap response were of relatively high importance regardless of the version of DH used, whereas season was of high importance only with the monthly DH (Table 3). All other covariates on detection, which included cloud cover, survey frequency, and calendar year, were of relatively low importance (summed model weight ≤ 0.001 ; Table 3).

Results from the top model using the daily DH indicated that P was influenced by season with additive effects from search effort and trap response (Table 4). Estimates of P were significantly higher for surveys influenced by trap response vs. those without, for team surveys vs. single surveys, and for summer or spring surveys vs. fall surveys (i.e., 95% CIs did not overlap; Table 4; Supplemental Results S9). Furthermore, trap response appeared to have a stronger effect on P than season or search effort (Supplemental Results S8). The highest overall P occurred during the summer, with team surveys when a trap-happy snake was present (0.73, 95% CI = 0.60–0.83). When surveys were not influenced by trap response, team surveys achieved a P at or above the 0.15 threshold in spring and summer (0.15 and 0.26, respectively), but not in fall (0.08; Fig. 2).

Regardless of whether the weekly or monthly DH was used, trap response and search effort remained important covariates on P (Table 4). An additive effect between search

effort and trap response using the weekly DH substantially improved model fit with only one additional parameter, as indicated by a decrease in the $-2\log$ -likelihood ($-2l$) value of ca. 30 or 54, compared with weekly models with only one or the other covariate (Supplemental Results S9). Based on the top weekly model, when surveys were not influenced by trap response, P was ≥ 0.15 only when two or more surveys were completed per week (Table 4). The highest P overall, using the weekly DH, occurred during weeks when two or more surveys were completed and when a trap-happy snake was present during a survey (0.76, 95% CI = 0.63–0.86). Although the inclusion of the calendar year covariate did improve model fit based on the $-2l$ value for both weekly and monthly DHs, it required five additional parameters and did not generate significantly different P estimates between years (Table 4). Using the second-best monthly model, and when surveys were not influenced by trap response, a significantly higher P occurred in the spring (0.59) and summer (0.39) than in the fall (0.04).

Occupancy Estimation

Based on the top model using the daily DH, the estimated Massasauga psi in the study area was 0.13 (95% CI = 0.05–0.30), which was very similar to psi estimates from the highest ranking models using the weekly DH (Table 4). Because we sampled a finite population of sites (MacKenzie et al.

2017), a *psi* of 0.13 estimated the proportion of our study sites that were occupied by Massasaugas (i.e., 5/40 sites). Note that the SEs estimated by program Presence, and associated confidence intervals (Table 4), are imprecise for finite populations (MacKenzie et al. 2017). Massasaugas were only detected at four sites (naïve occupancy, 0.10). Therefore, results suggest this species was present and remained undetected at a fifth site during the study period.

The site-specific probability of occupancy at sites where we did not detect Massasaugas was very low overall (mean *psi*-conditional, 0.03; range, 0.01–0.09; $n = 36$). When grouped by general location, and for sites with nondetection, site-specific probability of occupancy was highest at sites in Critical Habitat Block 2 (mean *psi*-conditional, 0.06; range, 0.02–0.16; $n = 8$). Furthermore, the four sites with the greatest probability of Massasauga occupancy (*psi*-conditional approximately, 0.09; 95% CI approximately, 0.03–0.22) were all situated in Critical Habitat Block 2 and were the sites surveyed the fewest number of times (five or six surveys each). Massasaugas were thus most likely to have escaped detection at a site in Critical Habitat Block 2. Assuming all five occupied sites were in Critical Habitat, and extrapolating to all available sites therein (Supplemental Methods S3), Massasaugas occupied an estimated 12% of Critical Habitat during our study.

An equally high-ranking model using the daily DH suggested that *psi* was not constant across the study landscape but was influenced by general location (the *psi* [loc] model; Table 4). This model differed from the top model by only one parameter and had a very similar $-2l$ value ($\Delta-2l < 4$); therefore, we deemed the general location parameter as uninformative when using the daily DH, and the second-ranking model as not competitive (Arnold 2010). The two top monthly models also included the general location covariate. Both models provided an estimated *psi* for sites in Critical Habitat Block 1 of 0.59 (95% CI = 0.23–0.86), whereas a *psi* of 0.00 (95% CI = 0.00–1.00) was generated for all other sites (Table 4). We deemed occupancy outputs from those models as uninformative given *psi* could not be estimated with any meaningful level of certainty for sites outside of Critical Habitat Block 1. Presumably, limitations were caused by the use of a categorical covariate to account for spatial correlation, as opposed to a continuous covariate (e.g., Euclidian distance; MacKenzie et al. 2017).

DISCUSSION

Our results provide support for a strong influence of trap-response on Massasauga detection probability. The presence of trap-happy snakes likely explains the relatively high *P* estimated separately for 2013, 2017, and 2018 when using the null model, because yearly differences in *P* were not apparent after accounting for trap response and using the combined 2013–2018 dataset. Although the highest estimates of *P* in our study were for surveys influenced by trap response, prior knowledge of the location of individual snakes violates occupancy modeling assumptions, so a comparison of survey techniques is only meaningful in the absence of those effects. After accounting for trap response, standardized visual encounter surveys conducted during spring and summer and by a team resulted in the highest *P* (0.15–0.26). In other words, surveyors detected the species during 2 or 3

out of every 10 surveys, on average, at sites occupied by Massasaugas and when trap-happy snakes were not present.

Results from the daily DH provided evidence for a significantly greater *P* during team surveys compared with single surveys, for all seasons combined and also during spring and summer seasons only (i.e., 95% CIs do not overlap). *P* also significantly increased as the number of surveys completed per week increased from one to two or more. These results are consistent with those of other studies wherein a positive relationship between Massasauga *P* and search effort was reported (Shaffer et al. 2019; Crawford et al. 2020; Thacker et al. 2023). Results from both the daily and monthly DH also provide evidence of a seasonal effect on *P*. Regardless of the DH used, surveys during the fall were significantly less productive than those in other seasons because average estimates of *P* were ≤ 0.08 in all cases and this result contradicts prior recommendations to survey during the entire Massasauga active season. Average *P* was higher during summer than spring using the daily DH, but this result was reversed when using the monthly DH, and in both cases, differences were nonsignificant. Further study may reveal calendar month to be a more informative covariate than spring or summer. For example, we recorded the greatest number of snake observations per standardized survey in one spring and one summer month (0.26 snakes/survey in each of May and June), which was higher than encounter rates in April (0.14), July (0.15), or August (0.19).

Our method for conducting artificial cover object surveys was ineffective at sampling Massasaugas. Perelman et al. (2022) also found no Massasaugas under artificial cover objects in Pennsylvania, USA, and Bartman et al. (2016) found gravid females using artificial cover objects in Michigan as basking surfaces only. Conversely, Massasaugas have been detected by other researchers under larger plywood and metal cover objects than those that we used (Amber et al. 2021; Yagi et al. 2023; T. Preney, personal observation). Further study on the most beneficial type and size of artificial cover object for sampling Massasaugas is warranted in an effort to improve *P* estimates.

We did not incorporate all variables recorded during surveys into our models as covariates to avoid overparameterization and because we standardized our site selection approach and our survey protocol. Regardless, additional insights into most suitable survey conditions can be gleaned from the summary of our Massasauga observation data, which may be used to refine survey protocols and improve *P* during future surveys: (1) the majority of observations (95% of 194 observations) were made from 0900 to 1800 h, with a peak from 1100 to 1300 h (36%). Similarly, Crawford et al. (2020) found that Massasauga *P* reached a maximum at ca. 1300 h; (2) the majority of observations were made during air temperatures ranging from 14 to 29°C (95% of 194 observations), with a peak occurring during temperatures ranging from 22 to 25°C (38%). Shaffer et al. (2019), however, found Massasauga *P* was greatest during air temperatures ranging from ca. 13 to 21°C; and (3) Massasaugas were observed in similar numbers under the full range of cloud cover scenarios (0–100% cloud cover), with a slight peak in observations during surveys with 100% cloud cover (20% of 193 observations). Similarly, in a study by Thacker et al. (2023), cloud cover was not a strong predictor of Massasauga *P* during spring and summer surveys.

Estimates of *psi*

Occupied sites were spatially clustered within Critical Habitat Block 1 only, yet our top daily model suggested no significant effect of the general location covariate on occupancy. The Massasauga *psi* estimated by that model (0.13) is less than half that estimated for Massasaugas across southern Michigan (Thacker et al. 2023) and similar to occupancy probabilities estimated for rare aquatic snakes in South Carolina, USA (Durso et al. 2011). Occupancy estimates generated by our top models using both the weekly and daily DHs were higher than those estimated by the null models; therefore, estimated occupancy would have been even lower had we not included covariates on detection. In effect, the estimated number of our study sites occupied by Massasaugas increased from four to five after accounting for detection heterogeneity.

Occupancy estimates had poor precision for the *psi*(.) model regardless of the DH used (SE [*psi*]/*psi* = 48%; see Bailey et al. 2004), and for our top daily model, the estimated CI was large relative to the proportion of sites occupied (upper 95% CI ca. 12 sites). Thus, a substantial increase in Massasauga distribution would need to be documented in a posttranslocation scenario before we could confidently demonstrate that a statistically significant increase in *psi* has occurred. Because we sampled a large proportion of the sites of interest, a finite population correction such as the delta method might improve the precision of the *psi* SEs. For example, the delta method may reduce the SE on *psi* estimates by up to 25–39% (MacKenzie et al. 2017). Additional investigations are warranted to assess the extent to which the precision of our *psi* estimate could be improved, with the aim of reducing the statistical threshold needed to detect a posttranslocation change in occupancy. Certainly, our results provide a liberal estimate of the proportion of sites occupied by Massasaugas during the study period.

Suitability of Sampling Regime

The suitability of occupancy modeling for estimating distribution and changes therein in cryptic animals can be challenged by low detectability, resulting in poor or uninformative occupancy estimates (MacKenzie et al. 2002; Guillera-Aroita et al. 2014; Durso and Seigel 2015). Therefore, at occupied sites, the survey methods should be able to detect the target species at least 15% of the time (Bailey et al. 2004). Based on our results, the 15% threshold was only met during team visual encounter surveys in spring and summer by using the daily DH, or when two or more surveys were conducted per week by using the weekly DH. The *P* may be further improved by focusing survey effort within certain months (e.g., May, June, or August); however, to avoid biased occupancy estimates, surveys should be spread across both spring and summer. For example, in 2014, Massasaugas were not observed at two sites until summer (June and July, respectively), and in 2017, Massasaugas were detected at four sites in spring (May), yet only one of those sites yielded summer detections.

Massasauga occupancy surveys should be designed to detect evidence of reproduction if results are to be used to gauge whether or not population establishment has occurred (Choquette et al. 2023). Evidence of Massasauga reproduction could include (1) spring detections of yearlings that

were born the previous summer, (2) detections of “suspected” gravid females in spring or summer, and (3) detections of neonates with a postpartum female in mid to late August (Bissell 2006). The latter would provide the strongest evidence for current year reproduction at a survey site; however, it may require intensive search effort at suspected or known gestation sites to confirm. For example, multiple surveys per week at gestation sites in August may be needed to successfully intercept postpartum females with their litters before dispersal. In this case, a removal sampling design applied in summer could help to focus resources toward a subset of sites (MacKenzie et al. 2017).

Declaring absence of cryptic vipers from a site with a high level of confidence may require substantial levels of search effort, particularly when population density is low (Kéry 2002). With a *P* ranging from 0.25 to 0.30, OMNRF (2016a) recommended conducting 10 surveys over two active seasons before concluding absence with 95% confidence, but that greater survey effort would be necessary for low density populations. Our study was focused on a small, low-density population of Massasaugas, and given an average of 25 repeat surveys at the 36 sites where the species was not detected, we report a mere 3% chance, on average, of Massasauga occupancy at any of those sites. Alternatively, and assuming a *P* of 0.21 (average of spring and summer *P* from daily DH), 14 negative visual encounter surveys conducted by a team of at least two surveyors would be required to declare absence from a site with 95% confidence (Fig. 2).

Limitations

We did not include an exhaustive list of environmental variables as covariates in our analyses because we chose to conduct our surveys during conditions already deemed suitable for Massasauga detection. Regardless, our top models may have omitted finer scale influences of certain variables on Massasauga *P* (e.g., air temperature and time of day; Shaffer et al. 2019; Crawford et al. 2020), and we obviously cannot rule out the effect of variables for which we did not explicitly account. For example, although we selected sites with open and semi-open canopies, we did not quantify canopy cover and thus did not directly account for its effect on occupancy (Thacker et al. 2023). Nor did we record substrate temperature or solar irradiance, two variables known to affect Massasauga *P* (Crawford et al. 2020; Thacker 2020). Finally, the way in which we coded the trap response covariate may have resulted in overly conservative (low) *P* estimates after accounting for trap response; we treated all surveys influenced by a trap-happy snake in the same way, ignoring whether a non-trap-happy snake was also found during a survey (two or more individuals were detected during 13 surveys, excluding litters of neonates with mother). Regardless, a monitoring protocol for an endangered species based on a conservative *P* estimate would reduce the risk of declaring false absences.

We did not cross validate our model results with a data set from another study area with similar vegetation communities and Massasauga abundance and therefore cannot fully comment on the transferability of our results (e.g., Wenger and Olden 2012). Some insights into potential transferability, however, were gained via critical analysis of model predictions using two subsets of our dataset a posteriori. Those results suggested that the effect of trap response was the most

important variable influencing P , compared with the effect of season (spring vs. summer) or search effort (single vs. team surveys in the spring). Therefore, a trap response effect on P is presumed to be the most transferable of our results to other study systems.

Management Implications

Our study generated baseline distribution data that can be used to evaluate changes in the distribution of a small sub-population of Massasaugas after population management activities such as conservation translocations. We found no evidence that Massasauga translocations previously conducted at one Critical Habitat Block 12–24 yr before our study were successful at population establishment; therefore, more intensive efforts are warranted. Results can also provide guidance on improving survey protocols to increase P for this and other cryptic species. Based on our site size and search time, spring and summer surveys conducted by at least two people, and at least twice weekly are recommended. Focusing surveys in May (spring) and June (summer) may increase detection rate, and surveys in August to detect neonates are recommended if aiming to confirm population establishment. Surveyors should avoid using the artificial cover object survey method of as presented herein and should avoid conducting visual encounter surveys during the latter part of the Massasauga active season (September and October), to avoid wasting effort when P is lowest. We stress the importance of explicitly accounting for the effect of trap response when planning occupancy studies and when modeling datasets; trap-happy snakes artificially inflate P , leading to a violation of occupancy modeling assumptions and the potential to misguide practitioners regarding the true amount of search effort required to detect small subpopulations of Massasaugas and potentially other viperids.

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RÉSUMÉ: Les estimations normalisées de la répartition d'une espèce avant et après la translocation peuvent permettre de déterminer si un projet de réintroduction a été efficace pour l'établissement de la population. La modélisation de l'occupation a gagné en popularité pour estimer la distribution des animaux cryptiques, y compris les serpents de la famille des Vipéridés, car elle peut tenir compte des variations de la probabilité de détection générées par des facteurs spécifiques au site, aux prospections et à la population. Nous avons estimé l'occupation et la probabilité de détection (P) pour une sous-population menacée d'une espèce de crotale cryptique d'Amérique du Nord (Massasauga de l'Est, *Sistrurus catenatus*), en vue de futures translocations à des fins de conservation. Au cours d'une période de 6 ans, nous avons mené plus de 1740 prospections standardisées répétées sur 40 sites (chacun d'une taille approximative de 2,4 ha) en utilisant deux méthodes (détection à vue et abris artificiels), au cours de trois saisons (printemps, été et automne), et avec différentes types de prospection (prospections individuelles ou en équipe), et nous avons analysé l'historique des détections en utilisant une modélisation de l'occupation. Les Massasaugas ont été détectés dans seulement 10% des sites d'étude ($n = 4/40$), et l'espèce a été présumée non détectée dans un site supplémentaire après prise en compte de la probabilité de détection (occupation estimée = 13%). La probabilité de détection des Massasaugas variait de 0,01 à 0,73 et était davantage influencée par l'effort de prospection, la saison et du "trap response" (c'est-à-dire les individus "positif au piège," individus trouvés de façon répétée aux mêmes endroits). La probabilité de détection a significativement été augmentée au cours des prospections lorsqu'au moins un serpent "positif au piège" était présent. Parmi les modèles les mieux classés (basés sur l'AIC), les prospections basées sur la détection à vue en équipe au printemps et en été, et aussi les prospections réalisées au moins deux fois par semaine, ont généré des P moyens $\geq 0,15$ après avoir tenu compte du "trap response." Inversement, les prospections d'automne et les prospections basées sur les abris artificiels ont généré un $P < 0,15$. Notre étude fournit des indications pour tous ceux qui travaillent dans la conservation de petites populations de serpents cryptiques et fournira des informations sur les méthodes de surveillance pour les futures translocations à des fins de conservation.

SUPPLEMENTAL MATERIAL

Supplemental material associated with this article can be found online at <https://doi.org/10.1655/Herpetologica-D-23-00055.S1>,

<https://doi.org/10.1655/Herpetologica-D-23-00055.S2>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S3>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S4>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S5>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S6>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S7>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S8>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S9>, <https://doi.org/10.1655/Herpetologica-D-23-00055.S10>.

LITERATURE CITED

- Amber, E.D., W.E. Peterman, and G.J. Lipps, Jr. 2021. Eastern Massasauga Rattlesnake: Ohio Population Survey and Survey Technique Development. Report No. FHWA/OH-2021-03. Prepared for The Ohio Department of Transportation, Office of Statewide Planning & Research. The Ohio State University, USA.
- Armstrong, D.P., and P.J. Seddon. 2008. Directions in reintroduction biology. *Trends in Ecology and Evolution* 23:20–25. DOI: <https://dx.doi.org/10.1016/j.tree.2007.10.003>
- Arnold, T.W. 2010. Uninformative parameters and model selection using Akaike's Information Criterion. *Journal of Wildlife Management* 74:1175–1178. DOI: <https://dx.doi.org/10.1111/j.1937-2817.2010.tb01236.x>
- Bailey, R.L. 2010. Modeling Habitat Suitability and Population Demographics of the Eastern Massasauga Rattlesnake in Managed Lands in Southwestern Michigan. Master's thesis, Michigan State University, USA.
- Bailey, L.L., T.R. Simons, and H. Pollock. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications* 14:692–702.
- Bartman, J.F., N. Kudla, D.R. Bradke, S. Otieno, and J.A. Moore. 2016. Work smarter, not harder: Comparison of visual and trap survey methods for the Eastern Massasauga rattlesnake (*Sistrurus catenatus*). *Herpetological Conservation and Biology* 11:451–458.
- Berger-Tal, O., D.T. Blumstein, and R.R. Swaisgood. 2020. Conservation translocations: A review of common difficulties and promising directions. *Animal Conservation* 23:121–131. DOI: <https://dx.doi.org/10.1111/acv.12534>
- Bissell, K.M. 2006. Modeling Habitat Ecology and Population Viability of the Eastern Massasauga Rattlesnake in Southwestern Lower Michigan. Master's thesis, Michigan State University, USA.
- Bradke, D., E. Hileman, J. Bartman, L. Faust, R. King, N. Kudla, and J. Moore. 2018. Implications of small population size in a threatened pit-viper species. *Journal of Herpetology* 52:387–397. DOI: <https://dx.doi.org/10.1670/18-026>
- Casper, G.S., T.G. Anton, R.W. Hay, . . . T.P. Wilson. 2001. Recommended Standard Survey Protocol for the Eastern Massasauga, *Sistrurus catenatus*. U.S. Fish and Wildlife Service, USA.
- Choquette, J.D., M.R. Macpherson, and R.C. Corry. 2020. Identifying potential connectivity for an urban population of rattlesnakes (*Sistrurus catenatus*) in a Canadian park system. *Land* 9:313. DOI: <http://dx.doi.org/10.3390/land9090313>
- Choquette, J.D., J.D. Litzgus, J.X.Y. Gui, and T.E. Pitcher. 2023. A systematic review of snake translocations to identify potential tactics for reducing post-release effects. *Conservation Biology* 37:e14016. DOI: <https://dx.doi.org/10.1111/cobi.14016>
- City of Windsor. 1992. City of Windsor Candidate Natural Heritage Site Biological Inventory. Evaluation Report. Corporation of the City of Windsor, ON, Canada.
- City of Windsor. 2008. City of Windsor Update to the CNHS Inventory. Corporation of the City of Windsor, ON, Canada.
- City of Windsor. 2022. Consolidated Zoning By-Law 8600: A By-Law to Zone Certain Lands within the Limits of the Corporation of the City of Windsor. Corporation of the City of Windsor, ON, Canada.
- COSEWIC (Committee on the Status of Endangered Wildlife in Canada). 2012. COSEWIC Assessment and Status Report on the Massasauga *Sistrurus catenatus* in Canada. Ministry of Environment and Climate Change Canada, Canada.
- COSSARO (Committee on the Status of Species at Risk in Ontario). 2013. COSSARO Candidate Species at Risk Evaluation for Massasauga (*Sistrurus catenatus*) Carolinian Population. Ministry of the Environment, Conservation and Parks, Canada.
- Crawford, J.A., M.J. Dreslik, S.J. Baker, C.A. Phillips, and W.E. Peterman. 2020. Factors affecting the detection of an imperiled and cryptic species. *Diversity* 12:177. DOI: <http://dx.doi.org/10.3390/d12050177>
- Durso, A.M., and R.A. Seigel. 2015. A snake in the hand is worth 10,000 in the bush. *Journal of Herpetology* 49:503–506. DOI: <https://dx.doi.org/10.1670/15-49-04.1>
- Durso, A.M., J.D. Willson, and C.T. Winne. 2011. Needles in haystacks: Estimating detection probability and occupancy of rare and cryptic snakes. *Biological Conservation* 144:1508–1515. DOI: <https://dx.doi.org/10.1016/j.biocon.2011.01.020>
- Faust, L., J. Szymanski, and M. Redmer. 2011. Range Wide Extinction Risk Modeling for the Eastern Massasauga Rattlesnake (*Sistrurus catenatus*). Lincoln Park Zoo and U.S. Fish and Wildlife Service, USA.
- Germano, J., J.G. Ewen, H. Mushinsky, E. McCoy, and L. Ortiz-Catedral. 2014. Moving towards greater success in translocations: Recent advances from the herpetofauna. *Animal Conservation* 17:1–3. DOI: <http://dx.doi.org/10.1111/acv.12172>
- Harvey, D.S. 2005. Detectability of a large-bodied snake (*Sistrurus c. catenatus*) by time-constrained searching. *Herpetological Review* 36:413–415.
- Harvey, D.S., A.M. Lentini, K. Cedar, and P.J. Weatherhead. 2014. Moving Massaugas: Insight into rattlesnake relocation using *Sistrurus c. catenatus*. *Herpetological Conservation and Biology* 9:67–75.
- Hecnar, S.J. 2016. IMPARA [Important Amphibian and Reptile Areas] Update—Two new locations designated. *Canadian Herpetologist* 6:18–20.
- Hileman, E.T., R.B. King, and L.J. Faust. 2018. Eastern Massasauga demography and extinction risk under prescribed-fire scenarios. *Journal of Wildlife Management* 82:977–990. DOI: <https://dx.doi.org/10.1002/jwmg.21457>
- IUCN/SSC (International Union for the Conservation of Nature/Species Survival Commission). 2013. Guidelines for Reintroductions and other Conservation Translocations, Version 1.0. International Union for the Conservation of Nature, Switzerland.
- Kéry, M. 2002. Inferring the absence of a species: A case study of snakes. *Journal of Wildlife Management* 66:330–338. DOI: <https://dx.doi.org/10.2307/3803165>
- Lamothe, K.A., K.A. McNichols-O'Rourke, and T.J. Morris. 2021. Occupancy and detection of Wavyrayed Lampmussel (*Lampsilis fasciola*) in Ontario, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 78:1305–1311. DOI: <https://dx.doi.org/10.1139/cjfas-2020-0325>
- LIO (Land Information Ontario). 2006. Southwestern Ontario Orthophotography Project 2006. Ontario Ministry of Natural Resources and Forestry, Canada.
- Lardner, B., A.A. Yackel Adams, J.A. Savidge and R.N. Reed. 2019. Optimizing walking pace to maximize snake detection rate: A visual encounter survey experiment. *Herpetologica* 75:218–223. DOI: <https://dx.doi.org/10.1655/D-18-00020>
- MacKenzie, D.I. 2006. Modeling the probability of resource use: The effect of, and dealing with, detecting a species imperfectly. *Journal of Wildlife Management* 70:367–374. DOI: [https://dx.doi.org/10.2193/0022-541X\(2006\)70\[367:MTPORU\]2.0.CO;2](https://dx.doi.org/10.2193/0022-541X(2006)70[367:MTPORU]2.0.CO;2)
- MacKenzie, D.I., and J.A. Royle. 2005. Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology* 42:1105–1114. DOI: <https://dx.doi.org/10.1111/j.1365-2664.2005.01098.x>
- MacKenzie, D.I., J.D. Nichols, G.B. Lachman, S. Droege, J.A. Royle, and C.A. Langtimm. 2002. Estimating site occupancy rates when detection probabilities are less than one. *Ecology* 83:2248–2255. DOI: [https://dx.doi.org/10.1890/0012-9658\(2002\)083\[2248:ESORWD\]2.0.CO;2](https://dx.doi.org/10.1890/0012-9658(2002)083[2248:ESORWD]2.0.CO;2)
- MacKenzie, D.I., J.D. Nichols, J.A. Royle, K.H. Pollock, L.L. Bailey, and J.E. Hines. 2017. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence*. Elsevier, USA.
- 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* 4:742–751. DOI: [https://dx.doi.org/10.1643/0045-8511\(2006\)6\[742:SEAMHS\]2.0.CO;2](https://dx.doi.org/10.1643/0045-8511(2006)6[742:SEAMHS]2.0.CO;2)
- NatureServe. 2022. NatureServe Explorer. Available at <https://explorer.natureserve.org/>. Accessed 12 October 2022. NatureServe, USA.
- Nicoll, M.A.C., C.G. Jones, J.G. Groombridge, S. Henshaw, K. Ruhomaun, V. Tatayah, N. Zuel, and K. Norris. 2021. Contrasting recovery trajectories of four reintroduced populations of the endangered Mauritius Kestrel (*Falco punctatus*). *Ibis* 163:1294–1309. DOI: <https://dx.doi.org/10.1111/ibi.12987>

- OMNRF (Ontario Ministry of Natural Resources and Forestry). 2016a. Survey Protocol for Ontario's Species at Risk Snakes. Species Conservation Policy Branch, OMNRF, Canada.
- OMNRF (Ontario Ministry of Natural Resources and Forestry). 2016b. Recovery strategy for the Massasauga (*Sistrurus catenatus*) — Carolinian and Great Lakes-St. Lawrence populations in Ontario. Ontario Recovery Strategy Series. OMNRF, Canada.
- Ontario Parks. 2015. Ojibway Prairie Park Management Plan. Ontario Parks, Southwest Zone, Canada.
- Parks Canada Agency. 2015. Recovery strategy for the Massasauga (*Sistrurus catenatus*) in Canada. Species at Risk Act Recovery Strategy Series. Parks Canada Agency, Ottawa, ON, Canada.
- Perelman, Z., W. Lutterschmidt and H. Reinert. 2022. Community structure of terrestrial vertebrates in a restored meadow habitat in Pennsylvania: Assessing the potential prey base for Eastern Massasauga Rattlesnakes. *Northeastern Naturalist* 29:370–381. DOI: <https://dx.doi.org/10.1656/045.029.0308>
- Pither, R. 2003. Contingency Plan for the Management of the LaSalle Massasauga Rattlesnakes. Report to the Eastern Massasauga Rattlesnake Recovery Team, Canada.
- Pratt, P., K. Cedar, and J. Barten. 1993. A remnant population of Eastern Massasauga Rattlesnakes at Ojibway Prairie, Windsor, Ontario. Pp. 8–9 in *Proceedings of the International Symposium and Workshop on the Conservation of the Eastern Massasauga Rattlesnake (Sistrurus catenatus catenatus)* (B. Johnson and V. Menzies, eds.). Metropolitan Toronto Zoo, Canada.
- Royle, J.A., and J.D. Nichols. 2003. Estimating abundance from repeated presence-absence data or point counts. *Ecology* 84:777–790. DOI: [https://dx.doi.org/10.1890/0012-9658\(2003\)084\[0777:EAFRPA\]2.0.CO;2](https://dx.doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2)
- Seddon, P.J., C.M. Roughton, J. Reardon, and D. MacKenzie. 2011. Dynamics of an endangered New Zealand skink: Accounting for incomplete detectability in estimating patch occupancy. *New Zealand Journal of Ecology* 35:247–253.
- Seddon, P.J., W.M. Strauss, and J. Innes. 2012. Animal translocations: What are they and why do we do them? Pp. 1–32 in *Reintroduction Biology: Integrating Science and Management* (J.G. Ewen, D.P. Armstrong, K.A. Parker, and P.J. Seddon, eds.). Wiley-Blackwell, USA.
- Sewell, D., G. Guillera-Aroita, R.A. Griffiths, and T.J.C. Beebee. 2012. When is a species declining? Optimizing survey effort to detect population changes in reptiles. *PLoS One* 7:e43387. DOI: <https://dx.doi.org/10.1371/journal.pone.0043387>
- Shaffer, S.A., G.J. Roloff, and H. Campa, III. 2019. Survey methodology for detecting Eastern Massasauga Rattlesnakes in southern Michigan. *Wildlife Society Bulletin* 43:508–514. DOI: <https://dx.doi.org/10.1002/wsb.1009>
- Steen, D.A. 2010. Snakes in the grass: Secretive natural histories defy both conventional and progressive statistics. *Herpetological Conservation and Biology* 5:183–188.
- Thacker, A.J. 2020. Great Lakes Snake: Estimating the Occupancy and Detection Probabilities of the Eastern Massasauga Rattlesnake (*Sistrurus catenatus*). Master's thesis, Grand Valley State University, USA.
- Thacker, A.J., E.T. Hileman, P. Keenlance, E.M. McCluskey, A. Swinehart, J. Kovach, and J.A. Moore. 2023. Modeling occupancy and detection probabilities to update the status of threatened eastern massasauga rattlesnake populations. *Global Ecology and Conservation*, 43:e02422. DOI: <https://dx.doi.org/10.1016/j.gecco.2023.e02422>
- Town of LaSalle. 1996. Town of LaSalle Official Plan Review: Candidate Natural Heritage Area Biological Inventory and Land Use Policy Direction. Discussion Paper No. 1. Corporation of the Town of LaSalle, Canada.
- Town of LaSalle. 2010. Town of LaSalle Official Plan Review: Update to the Candidate Natural Heritage Area Inventory. Corporation of the Town of LaSalle, Canada.
- Town of LaSalle. 2021. The Town of LaSalle Comprehensive Zoning By-Law: A By-Law to Regulate the Use of Land, and the Character, Location and Use of Buildings and Structures in the Town of LaSalle. Draft. Corporation of the Town of LaSalle, Canada.
- Wenger, S.J., and J.D. Olden. 2012. Assessing transferability of ecological models: An underappreciated aspect of statistical validation. *Methods in Ecology and Evolution* 3:260–267. DOI: <https://dx.doi.org/10.1111/j.2041-210X.2011.00170.x>
- Yagi, A., K. Yagi, F. Papini, C. Blott, M. Babin, and J. de Vuyst. 2023. Adaptive Management of an Ecological Trap: Restoration of Species at Risk reptile habitat in a partially-mined peat bog. Report for Ontario Ministry of Environment Conservation and Parks. STrees Inc., Canada.

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