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Predation and disease limit population recovery following 15 years of headstarting an endangered freshwater turtle

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ABSTRACT

Recovery strategies for endangered species vary in scope and scale, and uncertainties regarding their effectiveness make it necessary to implement evidence-based methods to ensure best management practices and the most efficient use of limited conservation dollars. Assessing recovery actions for species with slow life histories requires decades of study. We quantitatively assessed the putative recovery of two populations (PopA, PopB) of globally endangered Wood Turtles (*Glyptemys insculpta*) after 30 years of mark-recapture study and 15 years of headstarting implemented in response to a 57% reduction in population size attributed to poaching. We modeled population-specific demographic parameters to evaluate recovery efforts to date, and determine the next phase of management. Both populations showed limited recovery despite the release of 490 headstarted turtles. Recovery has been hindered by lower than expected 1-year post-release survivorship of headstarts (36%, 52% in each population, respectively), and only moderate (for turtles) adult survivorship (89%, 93%). Six headstarted turtles have, however, reproduced suggesting both populations may eventually become self-sustaining. From 2015 to 2018, subsidized predators killed 11 adult turtles, and we detected three diseases (mycotic shell disease, ranavirus, *Glyptemys* herpesvirus 2) in the headstarts. Our population viability analysis projected that both populations would recover if a predator-management strategy were implemented. Headstarting alone is not enough to save at-risk populations from local extinction when they face multi-faceted problems, including the cascading effects of landscape-scale habitat modification, for which management is challenging.

1. Introduction

Recovery programs for endangered species vary in scope and scale, and there is much debate about the most efficient use of conservation funds (Martin et al., 2018). Recovery strategies featuring intervention ecology in which humans actively manage ecological systems are growing in popularity (Hobbs et al., 2011), but there is well-deserved skepticism about using invasive recovery strategies given the uncertainties regarding their effectiveness (Fischer and Lindenmayer, 2000). Using limited conservation funds on ineffective management strategies is not a sustainable solution for protecting global biodiversity. Conservations programs must be well informed by evidence-based methods to ensure best management practices are established (IUCN/SSC, 2013; Bennett et al., 2017).

Turtles are one of the most endangered groups of animals on the planet with 61% of species listed as threatened with extinction (Lovich et al., 2018). Turtle recovery strategies vary widely (Bennett et al., 2017), and increasingly integrate aspects of intervention ecology, including headstarting. Headstarting typically involves collecting and incubating eggs, then rearing the hatchlings in protected ex-situ environments to a larger body size, followed by release into their natural habitat where their survivorship is assumed to increase compared to their smaller same-aged wild counterparts (Heppell et al., 1996; Haskell et al., 1996; Seigel and Dodd, 2000; Vander Haegen et al., 2009; Eiby and Booth, 2011; Bona et al., 2012; Mullin, 2019). Given that headstarting is often perceived as the last resort in saving populations of

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critically endangered species (Milinkovitch et al., 2013; Burke, 2015), a poorly executed headstarting project could further endanger imperilled species. Effective conservation programs must consider a species' life history (Frazer, 1992) which for turtles includes long lifespans, delayed sexual maturity, iteroparity, high survivorship of adults, and generally low but stochastic survivorship of eggs, hatchlings and younger juveniles (Brooks et al., 1991; Congdon et al., 1993; Keevil et al., 2018; Spencer, 2018). Mathematical models coupled with long-term data have shown that because of this life history, turtle populations cannot sustain even minimal chronic increases in adult mortality (Heppell et al., 1996; Gibbs and Shriver, 2002; Enneson and Litzgus, 2008; Mitrus, 2008; Spencer et al., 2017). Maintaining high adult survivorship should hence be the primary focus for turtle conservation projects. However, even with high adult survivorship, turtles are ill-adapted to recover from catastrophic declines (Brooks et al., 1991). For example, a population of Snapping Turtles (*Chelydra serpentina*) that experienced an acute mass-mortality event from predation showed no signs of recovery after 23 years (Keevil et al., 2018). Hence, increasing population size by increasing population growth rate via headstarting is an attractive tool for wildlife managers. Headstarting is, however, considered an experimental conservation strategy given uncertainties regarding its long-term effectiveness (Seigel and Dodd, 2000; Buhlmann et al., 2015; Bennett et al., 2017).

Although there is some evidence of long-term population recovery via headstarting (Milinkovitch et al., 2013; Shaver and Caillouet, 2015; Spencer et al., 2017), some longer-term studies have reported populations which, despite headstarting, have not recovered, or recovery has been hindered by unexpected problems such as disease and increased predation rates (Smeenk, 2010; Hallock et al., 2017; Dreslik et al., 2017; Daly et al., 2019). The long lifespans of turtles (Brooks et al., 1991; Congdon et al., 1993) means that having a stable population of sexually reproductive headstarted adult turtles could require several decades of effort, preventing wildlife managers from evaluating the long-term effects of headstarting on individual and population health, which has generated criticisms of headstarting (Woody, 1990; Frazer, 1992; Heppell et al., 1996; Seigel and Dodd, 2000). Long-term studies investigating the possible impacts of these management practices are thus critical to address concerns over the possible negative impacts of headstarting.

Herein we present the results of a 30-year Wood Turtle (*Glyptemys insculpta*, IUCN Endangered, van Dijk and Harding, 2011) mark-recapture study, which has featured a headstarting component for the past 15 years. We combined historical and contemporary data to elucidate population demography. We then used population-specific demographic data in models to quantitatively assess the effectiveness of headstarting as a recovery strategy for this population to date, and to make recommendations to enhance the future success of the program. The number of species recovery projects is increasing, and the results of our long-term study provide a rare opportunity to broadly inform and guide more effective management interventions.

2. Methods

2.1. Study site and history

Detailed information about the study site is not included given that collection for the pet trade is a major threat to Wood Turtles, and poachers may obtain location data from technical reports and publications (Lindenmayer and Scheele, 2017). The two populations (PopA, PopB) of Wood Turtles are located approximately 6 km apart within a watershed in Ontario, Canada. Migration between populations is limited, as only 5 individuals have been recaptured at both sites across the 30 years of our study. Most of the sites are on private land and the area is characterized by agriculture, which has shifted from pasture to cash crop (soy, corn, and wheat) over time. Watercourses are mostly small meandering creeks with cobble bottoms, and slow to moderate flow rates, which vary with seasons. Forested riparian buffers between watercourses and agricultural land range from 2 to 300 m and vary between and within sites. Most watercourses have naturalized floodplains, which partially aid in managing seasonal flooding.

The two adjacent populations (PopA, PopB) of Wood Turtles have been studied since 1988. PopA's size declined from 162 (95% CI = 151–173) in 1993 to 57 (95% CI = 41–80) turtles (including adults and juveniles) in 1997 (65% decline) and PopB's size declined from 107 (95% CI = 98–116) in 1993 to 59 (95% CI = 46–76) turtles in 1997 (45% decline), likely as a result of illegal poaching (Figure 1). A population viability analysis (PVA) conducted in 2001 projected combined population extirpation within 100 years (Cameron and Brooks, unpubl. data). The PVA also predicted that headstarting would provide the best chance of recovery (Cameron and Brooks, unpubl. data). Thus, a headstarting program began with the collection of eggs in 2003, and the first release of headstarts to their maternal streams in 2005.

2.2. Mark-recapture study

We located turtles using various surveys including spring emergence, nesting, canine, and VHF radio-telemetry. Survey effort has varied throughout the project, as is common in long-term studies. We marked turtles using triangular notches in the marginal scutes (Cagle, 1939) and Passive Integrated Transponder (PIT) tags (Buhlmann and Tuberville, 1998). PIT tags were inserted into the hind leg pocket parallel to the bridge of the shell. Upon capture, we collected standard morphological measurements (maximum carapace length (MaxCL), midline carapace length (MidCL), maximum plastron length (MaxPL), midline plastron length (MidPL), carapace width (CW), carapace height (CH), body mass), spatial data, habitat data, and noted behaviour and health. Adults were sexed using secondary sexual characteristics (Harding and Bloomer, 1979). We examined dead turtles to determine possible cause of death.

2.3. Headstarting protocol

We collected eggs from nests of wild females in our study populations. We incubated eggs ex-situ following standardized protocols (available upon request). After hatching, we marked hatchlings using marginal scute notches and collected morphological measurements. Hatchlings were headstarted at the Ontario Turtle Conservation Centre (formerly Kawartha Turtle Trauma Centre) from 2003 to 2009, and at the Toronto Zoo from 2010-present. Most turtles were headstarted for 2 years, although headstarting time has varied from 1 to 4 years over the 15-year study. Headstarted turtles received PIT tags before release. Timing of annual release has varied, although most headstarted turtles were released in June or July. Exact release locations have also varied, but most turtles were released back into their maternal streams.

2.4. Population demographics of wild turtles

We used RMark (Laake, 2013) in R (R Core Team, 2017) to create binary capture histories, and a Jolly-Seber POPAN model (Schwarz and Arnason, 1996) in Program MARK (White and Burnham, 1999) to estimate adult population size and apparent survival of adults in PopA and PopB in 1991–2017. We then added the number of juveniles recaptured each year to create our overall population size estimates. To minimize the impact of the variability resulting from the large population decline in 1994–1996, we grouped the data in 1991–1993 and 1997–2017 and then remodelled the same parameters for both populations. The 1991–1993 population sizes were estimated using CAPTURE (White et al., 1982), which only returns a population size estimate after 3 years of mark-recapture data collection, thus only an estimate for 1993 is presented (Cameron and Brooks, unpubl. data). We then calculated annual sex ratios for both populations in 1997–2017 by blocking PopA and PopB by sex while only including captures between

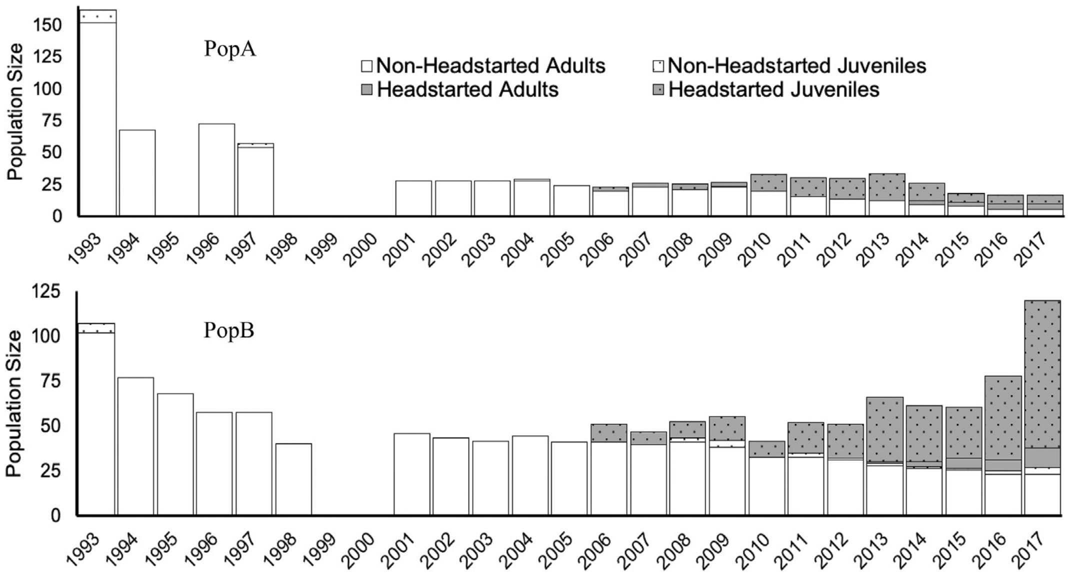

Fig. 1. Population size and demographics of two populations (PopA, top and PopB, bottom) of Wood Turtles (*Glyptemys insculpta*) between 1993 and 2017. A suspected poaching event in 1994–1996 caused a population decline. The headstarting program began with the collection of eggs in 2003, with the first release of headstarted turtles in 2005. Headstarted turtles were not included in the population until 1-year post-release. Note the differences in the scales on the y-axes.

emergence (1 April) and pre-nesting (15 May) in an attempt to maintain homogeneity in capture probability between sexes (McKnight and Ligon, 2017). We fitted 3 parameter variations per model where probability of entry (pent) was held constant while apparent survival (phi) and capture probability (p) were either constant (.) or time-dependent (t). We chose models based on QAIC$_c$ (quasi-Akaike's information criterion) then QDeviance. We also scrutinized all models to ensure they were biologically valid and reflected the known declines in population size (time-dependent apparent survival) and known yearly variation in survey effort (time-dependent variation in capture probability).

2.5. Population demographics of headstarted turtles

Juvenile turtles are often omitted from demographic analyses because the assumption of capture homogeneity may be violated, partly due to their stochastic survivorship and catchability (Congdon and Gibbons, 1996; Koper and Brooks, 1998; Hasler et al., 2015). It is not possible to exclude juveniles when evaluating a headstarted turtle population which likely has a juvenile-biased age structure given the large number of young turtles released. However, we intensively survey our populations each year, and most individuals are captured every year, which provides an extensive mark-recapture dataset similar to census data, thus mitigating violation of this equal catchability assumption. We used the last capture date for each individual to infer conservative estimates of population size and apparent survival for headstarted turtles post-release. Our method assumes that a headstarted turtle has not survived past their year of last capture. We did not include release year or within 1-year post-release captures when estimating population size. We did, however, include all turtles released when calculating post-release apparent survivorship. This method, when complemented with known-fate radio-telemetry data (Mullin, 2019), provides a good understanding of post-release survival of headstarted turtles.

2.6. Reproductive biology of headstarted turtles

We used our extensive mark-capture dataset to estimate size and age at maturity of headstarted Wood Turtles. We confirmed reproductive status in males based on observed mating attempts and in females through gravidity. We compared these values to those of wild non-headstarted Wood Turtles reported in the literature and to historical data from our population (Brooks et al., unpubl. data).

2.7. Individual turtle health

We assessed the general health (e.g., new injuries, shell and skin discoloration, activity level) of all turtles upon capture, and those with potentially serious health complications were brought into captivity for further assessment. We sent turtles to either the Ontario Turtle Conservation Centre (Peterborough, Canada) or the Toronto Zoo Wildlife Health Centre (Toronto, Canada). Dead turtles were sent to the Canadian Wildlife Health Cooperative (University of Guelph, Guelph, Canada) for necropsies.

2.8. Population modelling

We compiled population-specific demographic parameter estimates to perform population viability analyses (PVA) in VORTEX (Lacy et al., 2005) to calculate r (intrinsic rate of population increase) for both PopA and PopB. We used data available in the peer-reviewed literature to augment our model if data were not available from our long-term dataset. We modeled and compared 4 management scenarios which included: (1) continue incubating eggs and headstarting hatchlings, (2) incubate eggs and direct-release non-headstarted hatchlings, (3) protect nests and incubate eggs in-situ then release hatchlings, and (4) no management. We performed elasticity analyses on management scenarios (1) and (4) in VORTEX (Lacy et al., 2005). We chose scenario (1) because the headstarting project likely will continue, thus further evaluating parameters to inform best management practices. We also chose scenario (4) to evaluate parameter sensitivity if management ceased. We then recommended a management strategy based on our elasticity analyses and re-ran all 4 models incorporating this recommended strategy using theoretical parameter changes to establish clear goals for the headstarting program.

3. Results

3.1. Population demographics

We released 126 headstarted turtles into PopA, and 364 headstarted

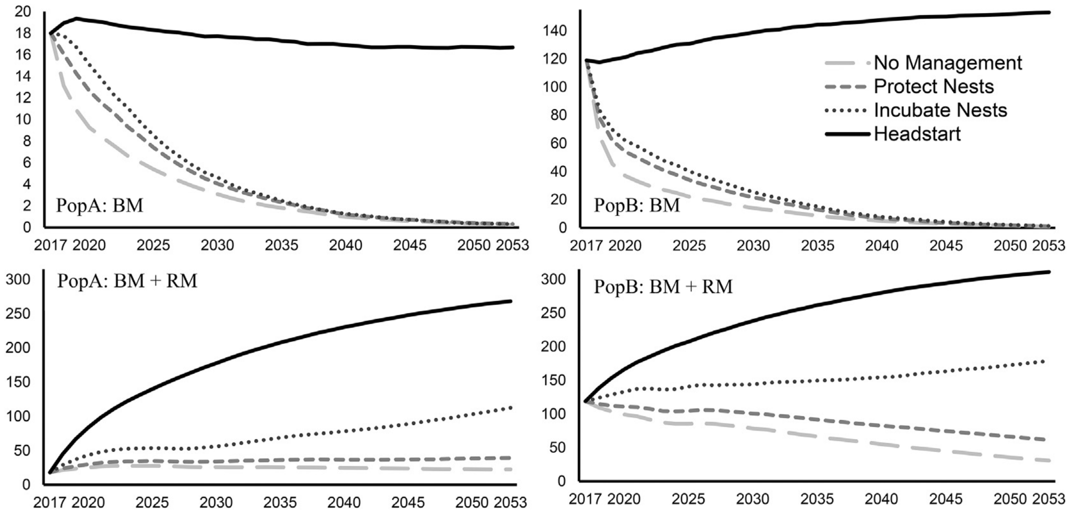

Fig. 2. Population viability analysis models of projected Wood Turtle (*Glyptemys insculpta*) population sizes (y-axis) for PopA (left) and PopB (right) using a variety of management scenarios (No Management, Protect Nests, Incubate Nests (and direct release hatchlings), and Headstart) projected 36 years from 2017, thus 50 years after the headstarting program began (2003–2053). All models presented are slight alterations to a base model (BM) created from a combination of population-specific life-history data complemented by data from the literature; however, the bottom models for PopA and PopB have the Recommended Management Strategy (RM) incorporated. Note the differences in the scales on the y-axes.

turtles into PopB during 2005–2017. Mean MaxCL of measured headstarts was 107 mm (n = 462, range = 76–145, SD = 65), and mean mass was 191 g (n = 451, range = 63–458, SD = 12). PopA has experienced limited recovery, as we estimated the population size to be 17 turtles (6 wild adults [95% CI = 4–10], plus known juveniles) in 2017, which is lower than both the pre-decline (162 turtles in 1993) and post-decline (57 turtles in 1997) population sizes. PopB has partially recovered, as we estimated the population size to be 117 (23 wild adults [95% CI = 15–32], plus known juveniles) in 2017, which is above both the pre-decline (107 turtles in 1993) and post-decline (59 turtles in 1997) population sizes. Both PopA (39% juveniles) and PopB (74% juveniles) currently have juvenile-biased population structures (reflecting the large numbers of headstarts released) relative to pre-decline in 1993 (9% in PopA, 6% in PopB).

PopA's 1-year post-release apparent survival of headstarted turtles was 36.7%, which gradually increased from 61.9% 2-years post release to 100% 7-years post release. PopB's 1-year post-release apparent survival of headstarted turtles was 52.6%, which gradually increased from 60.6% 2-years post release to 100% 6-years post release. We have observed recruitment of headstarted turtles to adulthood: PopB currently has 4 headstarted adults (1♂, 3 ♀) and PopB has 9 headstarted adults (3 ♂, 6 ♀).

Both PopA (10 adults) and PopB (31 adults) currently have fewer sexually mature adults than when the headstarting program began in 2003 (28 adults in PopA, 41 adults in PopB; Figure 1). Annual apparent adult survivorship was 88.8% in PopA and 92.8% in PopB during 1997–2017. A total of 34 turtles in PopA, and 71 turtles in PopB were confirmed dead during 2005–2017. Included is one dead headstarted turtle from PopB that was found 40 km downstream from its release point 11-months post-release; presumably it drowned during spring flooding. We also observed an acute period of elevated mortality during 2016–2018 when we found 4 dead adults in PopA and 7 dead adults in PopB. We suspect predation is the cause of mortality for 47.1% and 64.4% of mortalities observed in PopA and PopB, respectively. Raccoons (*Procyon lotor*) tracks were observed near many of the dead turtles, and raccoon hairs were found on a dead adult female in PopB (Mullin et al., 2018).

The sex ratios (2014–2017) in both PopA and PopB for both headstarted and wild adults are female biased. Only 2 of the remaining 6 wild adults in PopA are male, and one of these males is missing both front limbs and may be unable to copulate. Female reproductive frequency was 47% at PopA and 64% at PopB during 2014–2017. Both populations have been intensively surveyed and we have encountered only 2 unmarked adults (one male in each population) during 2010–2018. Of 51 non-headstarted hatchlings released in 2009, only 1 has ever been recaptured, and this turtle has not been seen since 2016 despite intensive targeted search effort. We observed evidence of natural recruitment despite collecting eggs from nests for headstarting; we captured 2 wild juveniles in PopA and 9 wild juveniles in PopB during 2008–2017.

3.2. Reproductive biology of headstarted turtles

Female headstarted turtles matured at 10 years (known age) and 166 mm MaxCL, and headstarted males matured at 10 years and 172 mm MaxCL. Observations in the early 1990s at our site suggested that wild females matured at 10 years (growth line estimated age) and 158 mm MaxCL, and wild males matured at 12 years and 173 mm MaxCL (Brooks et al. unpubl. data). Headstarted females matured at larger body sizes but similar ages to wild females, whereas headstarted males matured younger but at similar body sizes to wild males, but note that these comparisons are based on low samples sizes (4 confirmed reproductive headstarted females, 2 confirmed reproductive headstarted males). A headstarted female from PopB (Age = 15, MaxCL = 163 mm) was observed mating on three occasions in 2015–2018, but she apparently did not nest. An adult female headstarted turtle from PopA (Age = 15, MaxCL = 184 mm) is above the estimated threshold for sexual maturity, but she apparently has never nested.

3.3. Population modelling

Our population models projected that PopA would decline regardless of management scenario, while PopB would recover only if headstarting was used (Fig. 2). Our elasticity analysis predicted that decreasing adult and/or juvenile survivorship would cause the largest decreases in population growth rate, whereas increasing adult and/or juvenile survival caused the greatest increases in population growth rate (Table 1). Based on our elasticity analysis, we recommended a management strategy that incorporates predator reduction and a split-release scenario (equal number of headstarts released in each population). Our recommended management strategy assumes that predator

Table 1

Elasticity analyses to evaluate deviations in the intrinsic rate of Wood Turtle (*Glyptemys insculpta*) population increase (r) of the "Headstarting Program" and "No Management Program" base models resulting from a variety of parameter changes, as noted. Given that PopA is the closest to extirpation, parameters within this table are sorted by largest population growth rate to the smallest population growth rate for the PopA Headstarting Program.

Parameter change	Headstarting program population growth rate		No management program population growth rate	
	PopA (r)	PopB (r)	PopA (r)	PopB (r)
All juvenile mortality rates decreased by 25%[a,b]	0.0352	0.0339	−0.0287	−0.0724
Split release scenario[c]	0.0234	−0.0069	NA	NA
All juvenile mortality rates decreased by 10%[a,b]	0.0157	0.0200	−0.0577	−0.1077
Adult mortality rates decreased to 5%	0.0029	0.0104	−0.0515	−0.1007
Age at sexual maturity decreased by 2 years	−0.0009	0.0090	−0.1074	−0.1163
Stable age distribution[d]	−0.0016	0.0065	−0.1976	−0.1844
Proportion of adult females breeding annually increased to 70%	−0.0018	0.0069	−0.1068	−0.1326
Lifespan increased to 90 years	−0.0018	0.0093	−0.1258	−0.1299
Fertilized eggs/clutch decreased by 25%	−0.0020	0.0069	−0.1442	−0.1389
Adult mortality rates are 10%	−0.0021	−0.0044	−0.1250	−0.1754
Lifespan decreased to 50 years	−0.0021	0.0090	−0.1466	−0.186
Proportion of adult females breeding annually decreased to 30%	−0.0022	0.0069	−0.1527	−0.1496
Fertilized eggs/clutch increased by 25%	−0.0022	0.0071	−0.1120	−0.1295
Base model	−0.0023	0.0069	−0.1276	−0.1337
Age at sexual maturity increased by 2 years	−0.0025	0.0055	−0.1482	−0.1410
Adult mortality rates increase to 15%	−0.0032	0.0012	−0.2012	−0.2537
All juvenile mortality rates increased by 10%[a,b]	−0.0191	−0.0122	−0.1436	−0.1420
All juvenile mortality rates increased by 25%[a,b]	−0.0850	−0.3820	−0.1568	−0.1451

[a] Not including age 0 to age 1 for Headstarting Program because eggs are collected for ex-situ incubation.

[b] Juvenile mortality rates were capped at a lower limit of 15%, and an upper limit of 95% to replicate natural stochasticity within the model.

[c] Splitting the number of headstarts released at PopA and PopB, thus 36 headstarted turtles released each to PopA and PopB.

[d] Stable age distribution as calculated in VORTEX (Lacy et al., 2005).

reduction will increase juvenile and adult survivorship, as predation was the suspected cause of most mortalities (see Mullin, 2019).

The model for our recommended management strategy projected recovery of PopA and PopB for (1) continued incubation of eggs and headstarting, (2) incubating eggs and direct-release of hatchlings, but predicted limited population growth or declines with (3) protecting nests, and (4) no management (Fig. 2). Limited population growth of PopB for scenarios 3 and 4 is likely due to eggs being removed from PopB to supplement PopA given the split-release scenario. To confirm this, we revised the management strategy and removed the supplementation aspect and remodelled PopB. After incorporating this change, we predicted recovery of PopB using all management scenarios.

3.4. Diseases in headstarts

Most headstarted turtles from the 2015–2018 release cohorts have mycotic shell disease, which worsened as turtles emerged from overwintering. Two turtles with extensive infections were sampled and analyzed in January 2018; one turtle had an infection consistent with *Nannizziopsiaceae* spp. and the other turtle had an infection consistent with *Pureocillium lilacinum*. Lab diagnostics (through cultures, histopathology, and computerized tomography scans) revealed only superficial growth of fungal agents in the outer keratinized layer of the carapace, which did not extend into deeper tissues. There was no dermal inflammation or evidence of systemic infection. One headstarted juvenile from PopA was found dead during its first winter post-release and sent for a necropsy in February 2018; it was emaciated, had pulmonary mineralization, hepatic necrosis, and tested positive for ranavirus, though future study is needed to reconfirm this diagnosis and the extent of infection within the population. One adult female headstarted turtle from PopA was found in spring 2018 with clinical symptoms of ranavirus; diagnostic testing revealed that she did not have ranavirus but instead had *Glyptemys* herpesvirus 2 (GlyHV-2); this turtle was sexually mature and had previously nested.

4. Discussion

4.1. Population demography and modelling

Both PopA and PopB have benefited from headstarting, although their long-term viability requires continuation of management intervention. PopA has continued to decline despite headstarting efforts and is projected to continue declining if not actively managed. Recovery of PopA has been limited by several factors including small founder population size, low number of released headstarts, low post-release survival of headstarted turtles, low adult survival, and low female reproductive frequency. In contrast, PopB has partially recovered, likely due to the larger founder population size, greater number of released headstarts, their higher post-release survival, slightly higher adult survival, and higher female reproductive frequency.

High adult survival is the most important demographic parameter for turtle population persistence, as it helps offset naturally stochastic survivorship of eggs and juveniles (Iverson, 1991; Congdon et al., 1993; Heppell et al., 1996; Enneson and Litzgus, 2008; Spencer et al., 2017). Schneider et al. (2018) reported 97% adult survival in a growing population of Wood Turtles. Our reported adult survival values for PopA (89%) and PopB (93%) are lower, suggesting that the recovery of our study populations will require an increase in adult survival. Additionally, our estimates of overall adult survivorship may be overestimates because stable survivorship across most years may mask infrequent acute increases in adult mortality such as that observed in 2016–2018. Given the established importance of adult survivorship to population growth and persistence, increasing adult survivorship should be a primary goal for this Wood Turtle recovery program.

Other researchers have reported high post-release survival of headstarted turtles (Haskell et al., 1996; Vander Haegen et al., 2009; Bona et al., 2012; Michell and Michell, 2015; Tuberville et al., 2015). Post-release survival of headstarted turtles in our study was much lower, especially at 1-year post-release. The greatest threat to juvenile survivorship at our sites appears to be abundant predators, primarily Raccoons. We suspected 58% of the 105 confirmed turtle mortalities resulted from predation, and this is likely a conservative estimate as the causes of 40% of the 105 mortalities are unknown. Dreslik et al. (2017)

also suspected Raccoon predation as a major factor negatively impacting the success of an Alligator Snapping Turtle (*Macrochelys temminickii*) headstarting program. Our study populations are located within agricultural lands which provide food subsidies (i.e., corn and soy) for a variety of species, including Raccoons. Agriculture also fragments habitats while increasing edge habitat, providing travel corridors for predators (Gehring and Swihart, 2003). There are also regular culls of coyotes near the study sites (R.C. White, unpubl. data), which likely reduces predation pressures on meso-predators. These landscape level habitat alterations change community composition and impact predator-prey dynamics (Oro et al., 2013), which may be impairing recovery efforts. Additionally, heavy equipment is another cause of mortality to both juvenile and adult Wood Turtles within agricultural lands (Saumure et al., 2007).

We predicted with our elasticity analyses that increasing adult and juvenile survivorship will increase population growth rate (Table 1), which is a similar finding to other elasticity analyses (Enneson and Litzgus, 2008; Gasbarrini, 2016). Accordingly, we predicted that both populations could recover if a predator-reduction management strategy was implemented. Our predator-reduction model was based on estimates of increased adult and juvenile survivorship (inferred from Congdon et al., 1993; Schneider et al., 2018; and Brooks et al., unpubl. data) and not population-specific parameters. Engeman et al. (2005) and Urbanek et al. (2016) reported that predator removal increased nest survivorship of Sea Turtles and Blanding's Turtles (*Emydoidea blandingii*), respectively. Pramuk et al. (2013) also predicted that recruitment of Western Pond Turtles (*Actinemys marmorata*) could be increased by removing invasive predatory American Bullfrogs (*Lithobates catesbeianus*). Additionally, through personal communication, we know that predator removal is being used to manage other Wood Turtle populations, although none of the results are published. Predator removal appears to be effective, but there are both practical and ethical considerations for this management strategy (Smith et al., 2010). Further research on the effectiveness of predator-removal for increasing juvenile and adult turtle survivorship is needed, and should be undertaken as a collaborative effort with other researchers who use this management strategy.

Sex ratios were female-biased in both PopA and PopB. Reported sex ratios vary among studies of Wood Turtles but are predominantly reported as either female-biased (Brooks et al., 1992; Schneider et al., 2018) or equal (Harding and Bloomer, 1979; Walde et al., 2003). Lovich et al. (1990) suggest that reports of female-biased Wood Turtle populations may be an artifact of sampling effort; however, given the extensive survey effort and lack of new captures at our sites, this is likely not the case for our populations. Undetected sex-biased mortality from predators may have negative impacts on recovery projects, thus future research should investigate the potential causes of female-biased sex ratios to understand threats and develop mitigation strategies.

Our elasticity analyses predicted that the number of females breeding annually impacts population growth (Table 1). Studies that assume 100% of adult females breeding (e.g., Spencer et al., 2017) likely overestimate the parameter, which will consequently reduce the precision of PVA and may misinform management plans. Number of adult females breeding annually (female reproductive frequency) is a difficult metric to estimate; however, it is an important parameter for population modelling (Gibbons, 1982; Moll and Iverson, 2008; Keevil et al., 2018; this study). The number of adult females breeding annually in PopA (47%) and PopB (64%) are lower than previously reported for other Wood Turtle populations by Walde et al. (2007; 83%) and Jones (2009; 71%). Encounter rates between females and males at our site may be rare given the small population size and female-biased sex-ratio; thus, females in our populations may be reproducing primarily using stored sperm (Gist and Jones, 1989). A large female headstart in PopA has yet to nest despite being of reproductive size and age; this turtle may not have encountered and mated with a male given the low number of adult males in PopA. If the study populations continue to decline, then encounters between adult males and females could become more infrequent, which may result in decreases in number of adult females breeding annually.

Finally, differences in population growth rates between PopA and PopB are likely related to differences in the number of headstarted turtles released into each site (Gasbarrini, 2016; Dreslik et al., 2017; this study). The collection of eggs for headstarting at PopB has been facilitated by artificial nesting sites (similar to Buhlmann and Osborn, 2011). Similar nesting sites were built in PopA, but females seem to prefer nesting in other locations. Nonetheless, the artificial nesting sites in PopB may be important to the future of the project because they encourage turtles not to nest in the cropland, which may present an ecological sink (Mui et al., 2016).

4.2. Reproductive biology of headstarted turtles

A subset of headstarted turtles have reached sexual maturity and reproduced, which is important information supporting a trajectory towards self-sustaining populations. A lack of observed reproduction by headstarted turtles is an aspect of headstarting that has been criticized (e.g., Woody, 1990; Frazer, 1992; Heppell et al., 1996; Seigel and Dodd, 2000). However, we did not focus this study on the impacts of headstarting on reproductive development; further analyses are needed to examine maternal investment (egg size, clutch size, body size relationships) and paternal investment (sperm quality, sperm quantity) in headstarted adult turtles as compared to wild adults. It has also been suggested that increasing juvenile growth rates decreases age at maturity (Hildebrand, 1932; Congdon and Van Loben Sels, 1993); thus, headstarted turtles should mature at younger ages than their wild counterparts, and our limited data support this hypothesis. The outcomes of population manipulations in long-lived species can go undetected for many years after a management project has started. Long-term studies investigating the possible impacts of headstarting on reproductive biology are thus critical, as we do not want our mitigation measures to incur negative consequences.

4.3. Diseases in headstarts

We observed unexpected cases of disease in our Wood Turtle headstarting program, including mycotic shell disease, ranavirus, and GlyHV-2. Mycotic shell disease with likely fungal causative agents has been reported in freshwater turtles (Hallock et al., 2017), tortoises (Rose et al., 2001; Nardoni et al., 2011), and sea turtles (Cabañes et al., 1997). A fungal infection on the shell can be highly infectious, chronic, and debilitating and can lead to secondary infections, which can kill the infected individual, and individuals who recover retain pitted scutes (Wallach, 1975). Poor husbandry is most often the cause of fungal infections in chelonians (Hatt, 2010), and all reported cases are of turtles that had direct or indirect ties to captive-rearing. A Western Pond Turtle headstarting project which previously reported on short-term recovery (Vander Haegen et al., 2009) is now reporting on disease outbreaks, which are compromising long-term recovery goals (Hallock et al., 2017). Future headstarting projects should remain vigilant in monitoring shell diseases. The detection of ranavirus in our population is concerning, and is the second confirmed case in Ontario, along with one Snapping Turtle (Canadian Wildlife Health Cooperative, 2018). Ranavirus is reported to have caused mass mortalities in Eastern Box Turtles (*Terrapene carolina*; Kimble et al., 2017) and may be lethal to other turtles (Johnson et al., 2008; Allender et al., 2013). One turtle in our population tested positive for GlyHV-2, a novel alphaherpesvirus previously confirmed in 5/9 (56%) of tested Wood Turtles, but not found in Bog Turtles (*Glyptemys muhlenbergii*) or Spotted Turtles (*Clemmys guttata*; Ossiboff et al., 2015a). GlyHV-2 may be part of the natural disease ecology (host-pathogen evolution) of Wood Turtles, and is likely not a significant threat to healthy individuals or populations (Ossiboff et al., 2015a). Nonetheless, given the lack of evidence regarding the impact of

GlyHV-2 on populations, the precautionary principle should be applied as there are other herpesviruses that have resulted in mortalities in other turtle species, including but not limited to, Emydidae herpesvirus 1 (EmyHV-1) in Northern Map Turtles (*Graptemys geographica*; Ossiboff et al., 2015b), Testudinid herpesvirus 3 (TeHV-3) in tortoises (Origgi, 2012), and Chelonid fibropapilloma-associated turtle herpesviruses (CFPHV) in all seven species of sea turtles (Alfaro-Núñez et al., 2014).

Inadvertently introducing diseases to wild populations of endangered species through conservation management strategies can be devastating as the negative effects may be exacerbated by small population sizes and reduced genetic diversity (Flanagan, 2000; Smith, 2015). Thus, diseases in managed populations of endangered species need to be well understood and the effects mitigated. Applying the precautionary principle, we have quarantined the turtle infected with GlyHV-2. We have not quarantined the turtles with mycotic shell disease given the abundance (> 50) of turtles infected along with the lack of evidence of severe physiological impairment. We are currently completing follow-up studies examining the presence and prevalence of these diseases within the study populations. We have also established management guidelines to prevent unintentional spread via our mark-recapture study.

4.4. Conservation implications

After 15 years of headstarting, our two populations of Wood Turtles have shown some evidence of recovery; however, long-term persistence will require additional intervention, including continued headstarting, predator removal, and disease management. PopA will require greater intervention than PopB. PopB has higher adult survival, higher post-release survival of headstarted turtles, more eggs collected and hence more headstarted turtles released, and a higher proportion of females breeding annually, all of which have led to greater recovery compared to PopA. In comparison to other headstarting projects, both PopA and PopB have seen limited evidence of recruitment, although some of the earliest headstarted turtles released are now reaching sexual maturity, indicating that a pending shift in population demographics may eventually lead to self-sustainability. Importantly, headstarting alone is not enough to save both PopA and PopB from local extinction as these populations face multi-faceted complex problems for which management is challenging.

CRediT authorship contribution statement

Damien I. Mullin: Investigation, Data curation, Formal analysis, Conceptualization, Writing - original draft.**Rachel C. White:**Investigation, Data curation, Funding acquisition, Writing - review & editing.**Andrew M. Lentini:**Writing - review & editing.**Ronald J. Brooks:**Writing - review & editing.**Karine R. Bériault:**Investigation, Data curation, Writing - review & editing.**Jacqueline D. Litzgus:**Supervision, Conceptualization, Funding acquisition, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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