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Research Article

Is there an impact of behaviour on trapping migratory invasive sea lamprey (*Petromyzon marinus*)?

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Abstract

Trapping is used to control a variety of invasive species; however, trap encounter and entrance can vary between- and within-species depending on consistent individual differences in behaviour. We develop a framework for testing how consistent differences in behaviour might be related to trapping a migratory species. We tested whether adult migrating sea lamprey display consistent individual differences in two behaviours, boldness (measured as exit time from an enclosure) and activity (measured as the proportion of time spent moving), and whether these differences were related to trap entrance or timing. We predicted that bolder and more active individuals would migrate sooner and be more likely to be caught in a trap. We also predicted that early in the migration phenology, trapped individuals would not differ in behaviour from untrapped individuals, but later in the migration phenology, trapped individuals would be bolder and more active. We determined that sea lamprey exhibit consistent individual differences in boldness and activity but found no evidence that these differences were related to migratory timing or trap capture A greater understanding of how individual differences in behaviour influence trapping could help improve the management of invasive species by allowing for a better estimation of population size and provide insight into how to target different behavioural types.

Key words: boldness, activity, entrance, timing

Introduction

Invasive species threaten native biodiversity (Rahel et al. 2008). They establish and become abundant in novel environments, causing ecological and economic damage (Brown and Sax 2004). In many ecosystems, invasive species are predominant drivers of changes in native species abundance and in habitat alteration (Clavero and García-Berthou 2005). These changes create the need for effective management strategies. Early detection and prevention is considered the most cost-effective management approach (Vander Zanden et al. 2010). However, invasions are unlikely and detecting newly established invasive populations can be

difficult, decreasing the incentive to implement preventative measures. After establishment, the goal of eradication would be ideal, but difficult and costly to achieve. A more practical option when eradication or containment are not possible is controlling population size, thereby limiting adverse environmental and economic effects (Simberloff 2009).

Trapping can be successful in controlling and even eradicating invasive species, depending on the species' life history and population size, and ecological conditions (Gurnell et al. 2004; Howald et al. 2005; Orueta et al. 2005; Soroker et al. 2005; Hein et al. 2007). Trapping can also be cost-effective and have minimal impact on native environments or biota. Effective implementation of trapping programs requires detailed knowledge of how the behaviour of the target species can affect trapping efficiency (Bogich et al. 2008; Bravener and McLaughlin 2013). Consistent individual differences in behaviours such as activity and boldness could influence an individual's encounter with, entrance into, and overall susceptibility to traps. For example, the likelihood of being trapped was higher in individual rodents that were more exploratory (Balph 1968), red squirrels (*Tamiasciurus hudsonicus* Erxleben, 1777*)* that were more active (Boon et al. 2007), and pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus, 1758) that were less likely to respond to a threat (Wilson et al. 1993). A significant portion of the target population could remain untrapped if the trapping process is targeting individuals that are easier to trap (Harper et al. 2018). Further, if the behavioural differences are heritable (Dingemanse et al. 2002; van Oers et al. 2005) trapping could select for individuals that are less vulnerable to trapping.

We tested whether consistent individual differences in the behaviour of migrating adult sea lamprey (*Petromyzon marinus* Linnaeus, 1758) affect their vulnerability to traps. The sea lamprey is a parasitic fish that invaded the Laurentian Great Lakes in the 1920s, contributing to dramatic declines in populations of large native fishes (hosts) and alterations to food webs (Smith and Tibbles 1980). It has been the target of a basin-wide, binational control program since the late 1950s (Marsden and Siefkes, *in press*; Smith and Tibbles 1980) The two main methods of control are in-stream barriers that deny migrating adult sea lamprey access to spawning habitat in tributaries and periodic application of pesticides which kill larval sea lamprey in tributaries where they live for the first 3–4 years of life (Haeseker et al. 2007). Barriers to movement restrict the spatial extent of pesticide treatments by limiting the availability of spawning and larval rearing habitat. Trapping migrating adult lamprey prior to spawning could provide a third method of control if the proportion of the sea lamprey trapped (trapping efficiency) is high enough to overcome compensatory mechanisms of recruitment (Jones et al. 2003). Trapping would be particularly useful in large tributaries where barriers are impractical, due to shipping traffic and native fish passage, and where pesticide treatments are

challenging and costly. Decision analyses of sea lamprey management in the St. Marys river connecting lakes Huron and Superior have suggested that increasing the population captured in traps from 40% (current trapping success) to 70% may be the most beneficial control strategy (Haeseker et al. 2007). Simulation modeling has further suggested that trapping efficiency could be compromised if consistent individual differences in behaviour influence an individual's vulnerability to trapping (Harper et al. 2018).

Migratory species may not follow existing frameworks for testing how behaviour influences trap success. Biro and Dingemanse (2009) posed that for non-migratory species risk taking and activity will influence an individual's probability of encountering and entering a trap. However, individual differences in risk taking and activity could be masked in migratory species due to migratory restlessness, a phenomenon where an individual's physiology is altered to prepare for migration (Farner 1955), or change during migration (e.g. as an animal matures sexually). Further, our understanding of how individual differences in behaviour affect the vulnerability of migratory fishes to engineered river structures designed to remove invasive fishes, such as sea lamprey, from the population (traps) or to pass native fishes by in-stream barriers to movement (fishways) remains limited (Hirsch et al. 2017; Rahel and McLaughlin 2018). Both types of structure require the animals' encounter and entrance to the structure but differ in the fate of the animals that enter. Kirk and Caudill (2017) found that individual Pacific lamprey (*Entosphenus tridentatus* Richardson, 1836) that successfully used a multi-fishway complex at a hydroelectric facility displayed a wider range of movements than individuals that did not pass successfully. Individual differences were proposed as one of several possible mechanisms for the differences in passage success. Conversely, Landsman et al. (2017) demonstrated behavioural types in rainbow smelt (*Osmerus mordax* Mitchill, 1814), but no relationship was detected between behavioural type and passage success.

In this study, we test three hypotheses for how consistent individual differences in boldness and activity could influence when and how an individual from a migratory species would encounter and enter a trap. Boldness and activity were considered because they are expected to influence encounter with, and entrance into, traps (Biro and Dingemanse 2009; Bravener and McLaughlin 2013). Our test first assessed if individual sea lamprey collected from traps and by electrofishing downstream of traps in two Great Lake tributaries demonstrated consistent individual differences in exit time from an enclosure (a measure of boldness) and proportion of time spent moving (a measure of activity) in the laboratory. Consistent individual differences in behaviour is a prediction common to all three hypotheses. Our test then assessed predictions from each hypothesis for how trapped and untrapped sea lamprey were expected to differ in behaviour across the migration phenology.

Hypotheses Linking Behaviour and Trap Vulnerability in Migrating Species

The first hypothesis tested assumes that boldness and activity influence encounter with a trap by influencing when individuals arrive at a trap location (Arrival Time Hypothesis). The spawning river can be considered a new habitat because sea lamprey do not home to their natal stream (Waldman et al. 2008) and reside in lakes during their juvenile life-stage (Beamish 1980). Bolder individuals would be more likely to enter the river, and to move into new areas upstream, than shyer individuals. Activity differences could also influence how quickly and directly an individual migrates to, and up, the spawning tributary to the trap. Previous research has shown that Pacific lamprey exhibit consistent individual differences in upstream migration speed (Moser et al. 2013), making it plausible that sea lamprey could show differences in activity that would affect vulnerability to trapping. This hypothesis predicts that sea lamprey caught earlier in the migration phenology will display faster exit times and spend more time moving in standardized laboratory tests than sea lamprey captured later in the migration phenology, regardless of capture method (electrofished or trapped) (Figure 1).

The second hypothesis assumes that new groups of lamprey arrive at the traps nightly and that boldness and activity will influence whether they enter the trap (Nightly Separation Hypothesis). Our study traps were located at in-stream barrier dams, so individuals not entering the trap on that night might therefore spawn downstream or leave the river (Kelso and Gardner 2000; Lower 2011). Boldness is expected to influence trap entrance because a trap could be considered an unfamiliar and potentially risky space to enter. Activity is expected influence trap entrance because finding the entrance and entering the trap will depend on movement. This hypothesis predicts that, for any night in the migration phenology, trapped individuals will display faster times to exit an enclosure and a higher proportion of time spent moving than untrapped individuals electrofished downstream (Figure 1).

The third hypothesis assumes that trap sorting could take longer than one night, and that individuals collected downstream of a trap include those that will be trapped later in the season and individuals that will never be trapped (Seasonal Separation Hypothesis). Some sea lamprey will approach a trap and then retreat back to a refuge downstream over several nights during the migration period (Lower 2011). This hypothesis predicts that early in the migration phenology, trapped individuals will not differ in behaviour from untrapped individuals, because many lamprey vulnerable to trapping remain downstream of trap sites. Later in the migration phenology, trapped individuals will exit the enclosure faster and spend more time moving than untrapped individuals, because the individuals

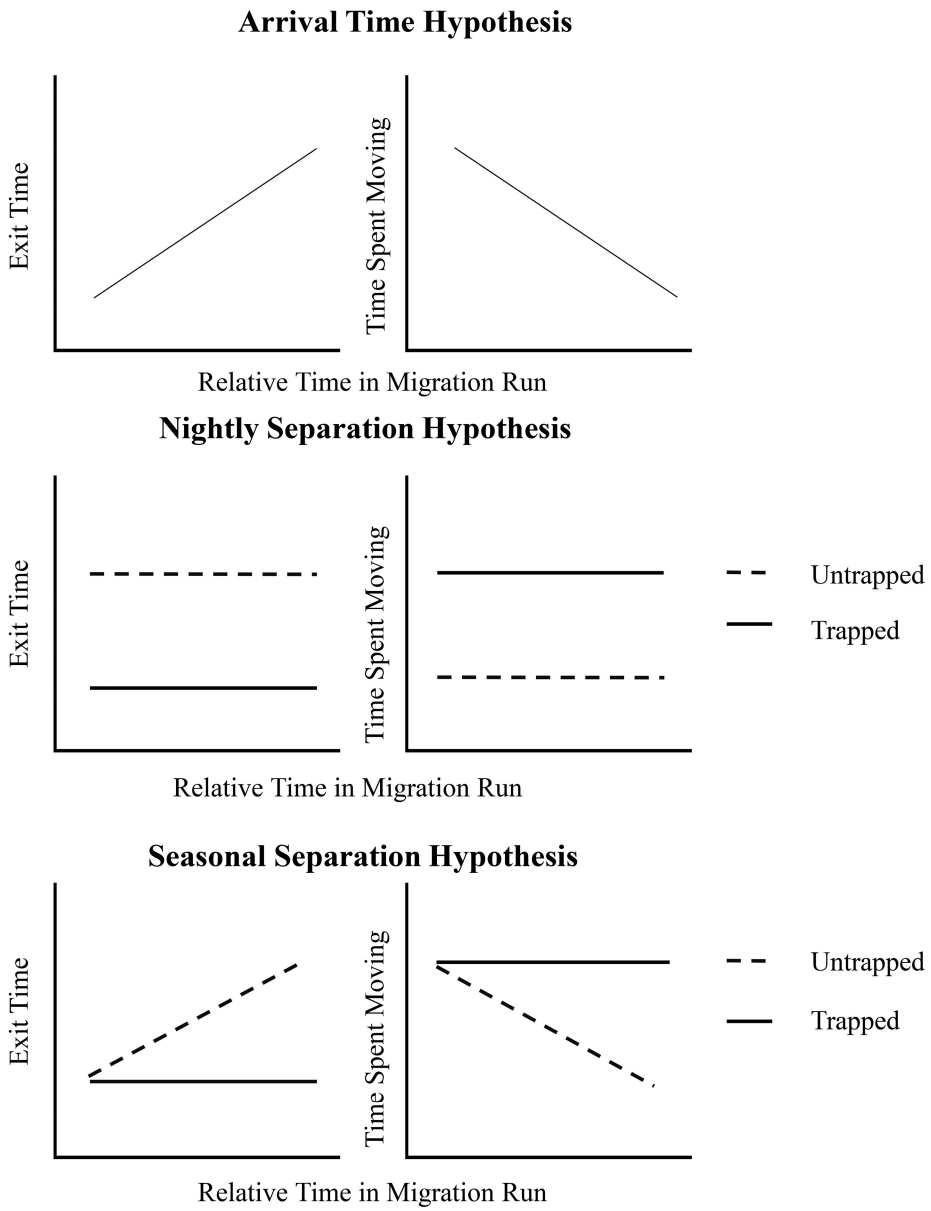

Figure 1. Predictions associated with the Arrival Time Hypothesis, the Nightly Separation Hypothesis and the Seasonal Separation Hypothesis showing the expected differences in boldness, measured as exit time, and activity, measured as the proportion of time spent moving, relative to the time that lamprey are migrating in the season (time in migration run). The predictions for the first hypothesis are independent of collection method, whereas the predictions for the second and third hypotheses depend on whether an individual is collected from a trap (Trapped; black line), or via electrofishing (Untrapped; dashed line).

remaining untrapped near the end of the migration season are those that display behaviours that make them least likely to be trapped (Figure 1).

These hypotheses represent a novel and structured framework for exploring the different ways trapped and untrapped individuals from a migratory species are expected to differ in behaviour between and within nights of trap operation. The Arrival Time Hypothesis and the Seasonal Separation Hypothesis have not been considered in previous studies. The hypotheses are not mutually exclusive, so we tested them simultaneously in a single analysis.

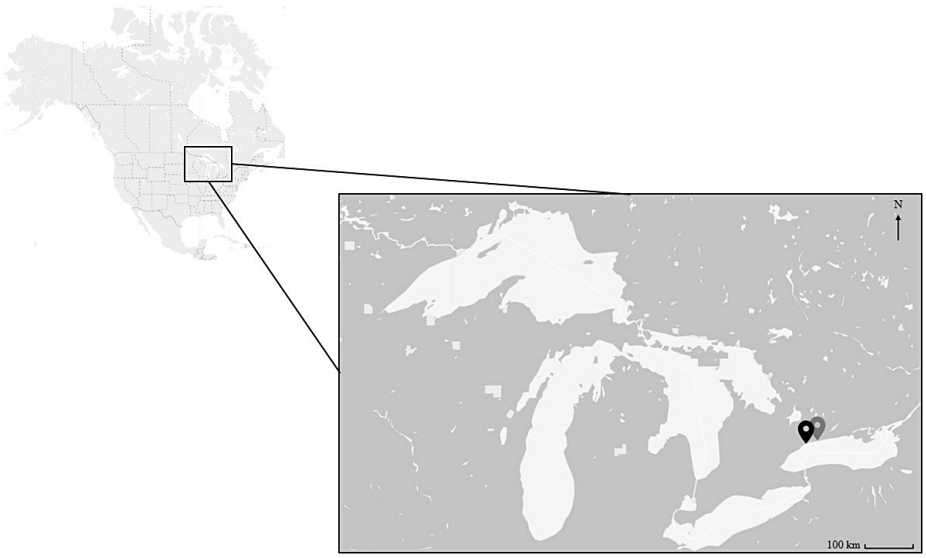

Figure 2. A map of North America showing the location of the Laurentian Great Lakes and where on Lake Ontario the sampling sites were located. Duffin's Creek is indicated by the black sampling point, and Bowmanville Creek by the grey point.

Materials and methods

Sea lamprey collection

Our research was conducted in accordance with the Canadian Council on Animal Care guidelines on the care and use of fish in research, teaching, and testing and was approved by the University of Guelph Animal Care Committee (Animal Utilization Protocol no. 1940).

Sea lamprey were collected from Duffin's Creek near Ajax, ON in 2013 and 2014, and from Bowmanville Creek in Bowmanville, ON in 2014 (Figure 2). In both years, sea lamprey were sampled prior, during, and following the peak in migration. Sampling dates in 2013 were 4, 9, 18, and 27 May. Sampling dates in 2014 were 28 and 30 May, and 2 and 6 June. The dates of the peak lamprey run varied between 2013 and 2014 because sea lamprey migratory timing is dictated by water temperature, which varies yearly. Sampling in 2013 was led by Adrienne McLean (McLean and McLaughlin 2018) and sampling in 2014 by Emelia Myles-Gonzalez. Sampling occurred between 0900 h and 1800 h. Data for 2013 and 2014 were combined to increase sample sizes and the statistical power of our tests.

Our study tested for differences in behaviour between sea lamprey collected from traps and sea lamprey collected by electrofishing downstream of traps. The traps were permanently integrated within low-head barrier dams blocking sea lamprey movement upstream at both locations. Both traps were roughly 2.5 m^3 (1.5 × 1 × 1 m) concrete boxes with two openings; one to allow water in and one to allow water out. Water is pumped through the trap from upstream. The fish enter through a small opening at the end of a mesh funnel, which they are attracted to by flow. During each sampling day, traps were emptied, and individuals were held in a flow-through

container placed in the stream. Untrapped individuals at-large downstream were sampled by electrofishing, beginning 1.5 km downstream and extending to the barrier dam. One crew member operated a Smith-Root LR24 back-pack electrofisher while the other crew member netted sea lamprey that were shocked. Electrofishing passes were made twice each sampling day to maximize the probability of capturing sea lamprey downstream, because lamprey tend to hide in refuges during the day and, upon being drawn out of their refuge by electrofishing, they can be challenging to see against the substrate and net in fast flowing water. Netted lamprey were held in a separate flow-through container within the stream. At the end of the sampling day, the trapped lamprey were electroshocked (3 pulses of 3–5 s) in their holding container to standardize shocking between the collection groups.

Trapped and electrofished lamprey were transported to the Hagen Aqualab, University of Guelph, in separate 95 L coolers equipped with aerators to supply oxygen. Upon arrival at the Hagen Aqualab, every individual was weighed (nearest gram), measured for total length (nearest millimetre) and tagged with a passive integrated transponder (PIT) tag following the methods of McLean and McLaughlin (2018). Individuals from the two groups of sea lamprey (trapped, electrofished) were held in 800 L holding tanks in 2013, and 2000 L holding tanks in 2014, and provided with untreated well water maintained at 8 °C and light cycle of 12:12 light/dark. Seven days prior to the start of behavioural trials the test animals were clock shifted so that the dark started at 1500 h. These holding conditions were used to slow the maturation process so that the replicate trials necessary for assessing repeatability of behaviour could be completed. Lamprey are nocturnal, but we clock shifted the night cycle to be able to safely access the building. Kleerekoper et al. (1961) reported that clock-shifted sea lamprey re-establish their diurnal activity pattern within two to three days. As well, Barnett et al. (2016) found that clock-shifted sea lamprey did not differ in an alarm response compared to sea lamprey that were tested at night.

Quantifying repeatability of behaviour

Fifty-one sea lamprey were tested in 2013: 15 females and 27 males sampled by trapping and 4 females and 5 males sampled by electrofishing, all from Duffin's Creek. Fifty-six sea lamprey were tested in 2014. At Duffin's Creek 10 females and 22 males were sampled from the trap, and 2 females and 1 male sampled by electrofishing. In Bowmanville Creek, 3 males were sampled from the trap, and 5 females and 3 males were sampled by electrofishing.

The behavioural tests used to quantify behaviour were conducted in five artificial streams measuring 215 × 60 × 55 cm (Figure 3). Each stream had an inflow at one end and an outflow at the opposite end that maintained

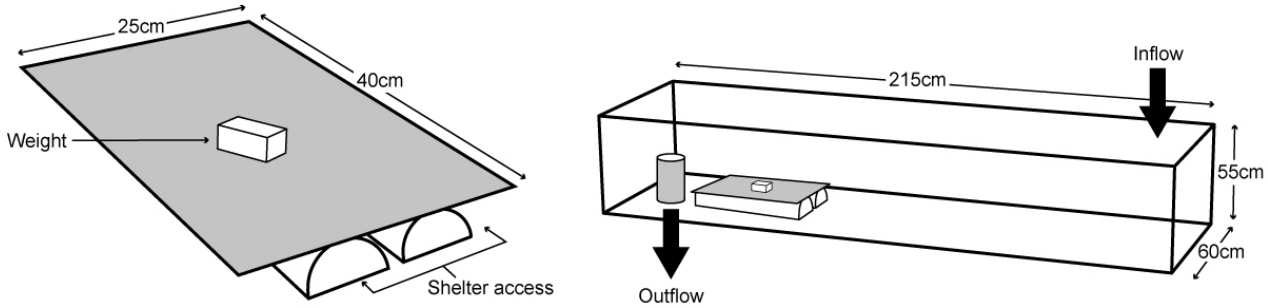

Figure 3. The enclosure used in the experimental streams (left) and the experimental stream used in the behavioural trials (right). The inflow came from a tap above the stream at one end, and an outflow draining from a standing pipe at the other. The enclosure was constructed out of a grey PVC pipe cut in half with a 40 × 25 cm sheet of PVC bolted on top. A house brick was used to weight down the enclosure. The end of the enclosure closes to the outflow was blocked with perforated PVC so that sea lamprey could only enter and exit from one end.

the water depth at ~ 30 cm. Near the outflow of each stream there was an enclosure created by two half-cylinder pieces of grey PVC pipe 40 cm in length. The downstream end of the enclosure was closed by a perforated piece of grey PVC. A grey PVC sheet (40 × 25 cm) was fastened on top and the enclosure was weighed down with a common house brick placed on top of it. Lamprey were exposed to a similar enclosure in their holding tanks prior to behavioural tests to ensure familiarity with the enclosure. Five CCTV cameras (Speco Technologies, Amityville, New York) were mounted above each experimental stream to record the behaviour of the lamprey. Each experimental stream was lit using one overhead mounted red floodlight following Binder and McDonald (2007, 2008).

A behavioural trial consisted of an acclimation period, an enclosure exit experiment, and an activity experiment. Individuals were selected haphazardly from their holding tank and placed inside an enclosure in one of the five experimental streams. A piece of perforated PVC was used to block the opening of the enclosure to the experimental stream. The lamprey was left in the enclosure for 10 min to acclimate. A trial commenced when the piece of perforated PVC was remotely removed, allowing the individual to explore the experimental stream. Boldness was measured as the length of time, in seconds, for the lamprey to fully exit the enclosure after the piece of PVC was removed. A lamprey was considered to have exited when its entire body had left the enclosure. In 2013, if the lamprey had not exited the enclosure in 1800 s, then it was given a maximum score of 1800 s. Due to the large number of individuals that did not exit (64 out of 156 trials), the exit time was lengthened to 3600 s in 2014. The proportion of time spent moving in an 1800 s period was used to assess activity in both years. However, in 2013 only individuals who exited the enclosure within 1800 s were scored for activity measurements. Also in that year, behavioural tests were run sequentially and immediately after one another until all individuals were tested. The process was repeated three times. In 2014 a separate trial was conducted for activity where, after the acclimation period, both the enclosure and barrier were removed, leaving the lamprey in an open arena.

The tests were not run sequentially in this year, rather all trials for boldness were completed, following all trials for activity. The entire process was repeated three times. Our statistical analyses provided no evidence that the experimental differences between 2013 and 2014 influenced the tests of our predictions and are not considered further here. Once the behavioural trials were complete, individuals were euthanized and body weight and total length were re-measured. Maturity status and sex were determined by visual inspection of gonads. Mature males were classified based on the presence of milt. Females were considered mature if they had loose eggs in the peritoneal cavity, and immature if the eggs were still connected to the ovaries by connective tissue.

Trials were conducted between 29 May and 18 June in 2013, and 26 June and 31 July in 2014. Five trials were run simultaneously (one individual in each experimental stream). Three groups of five individuals were tested each night. Repeatability of an individual in both behavioural trials was attempted for a maximum of 3 times at least 4 days apart. Due to mortality, most likely senescence (sea lamprey cease feeding once spawning migration occurs), not every individual could be measured 3 times for each behaviour.

Data analysis

Repeatability of exit time and proportion of time spent moving was estimated to test whether sea lamprey caught by trapping and electrofishing demonstrate consistent individual differences in behaviour. The repeatability of each behaviour was estimated using the intraclass correlation coefficient, $r = \sigma_a^2 / (\sigma_a^2 + \sigma_w^2)$, where σ_a^2 is the estimated among-individual variance component and σ_w^2 is the estimated within-individual variance component. The intraclass correlation can take values from 0 to 1. Values of r near 0 indicate that behaviour is not repeatable. Values of r near 1 indicate that the behaviour is highly repeatable. A meta-analysis on behavioural data by Bell et al. (2009) showed that the interquartile values of r measured for a variety of behaviours ranged from 0.2 to 0.6.

The variance components for exit time and activity were estimated separately using generalized linear mixed models. Both models had individual identity as a random effect and sex (male or female), total length, maturity status (mature or immature), and trial number (1, 2 or 3) as fixed effects. These covariates were included to control statistically for any among- and within-individual differences in behaviour arising from phenotypic attributes (size and sex; Bals and Wagner 2012) or from habituation or changes in maturity status over the trials (trial number for the same individual). Among- and within-individual variance components were estimated using a Bayesian approach in the MCMCglmm package in R (Hadfield 2010). A non-informative inverse-Wishart distribution was used as a prior, with a degree of belief of 0.2. We used 60,000 iterations, a burn-in

of 10,000 iterations, and a thinning interval to 25 (Hadfield 2010). Convergence of 3 chains was assessed by visual inspection of trace and density plots and using Gelman-Rubin and Geweke convergence diagnostic tests. Prior to analysis, exit time was $\log_{10}$ transformed and proportion of time spent moving was arcsine square-root transformed to normalize their distributions as closely as possible. Estimates of r were considered statistically significant if their 95% credible intervals did not encompass zero. Unlike confidence internals in frequentist methods, credible internals encompass the true parameter value with a probability of 0.95.

To test our predictions of how trapped and untrapped individuals would differ in behaviour across the migration phenology we used multi-model inference to identify the best approximating model from a set of approximating models (Burnham and Anderson 2002). Two rounds of model comparisons were completed to reduce the number of models compared simultaneously. The first round involved only confounding factors known to influence sea lamprey behaviour, but not of primary interest in our study. This set considered total length, trial number, and location and year effects (Duffin's 2013, Duffin's 2014, Bowmanville 2014). The best approximating model from the first round was carried forward to the second round that tested the predictions about how trapped and untrapped individuals would differ with collection method and time of season, after accounting for the effects of the factors identified as important from the first model comparison. Priors, model specifications, and transformations were kept the same as those used in the repeatability analysis. All models were bivariate MCMC mixed-models with individual identity as the random effect. The ability of the models to account for variation in the behaviours measured was assessed using the deviance information criterion (DIC; Spiegelhalter et al. 2002) values generated from the model comparison. DIC is analogous to Akaike's Information Criterion (AIC), so model weights were calculated and compared as suggested by Burnham and Anderson (2002) to find the most parsimonious model within a model set.

The variation in boldness and activity due to collection method and timing was depicted using boxplots to visually differentiate the behavioural scores. Values include those from both locations and both years. To account for variation in length and trial number, we regressed each behaviour against length and trial number, and used the equation from this regression to obtain predicted values as if all the observations were from one trial, and all the fish were the same length (geometric mean length). The residuals were separated by capture method and plotted against relative time in the migration run. Relative time in the migration run is expressed as a Z-score centred on the peak of the migration run, to remove annual differences in migration timing dates and collection dates.

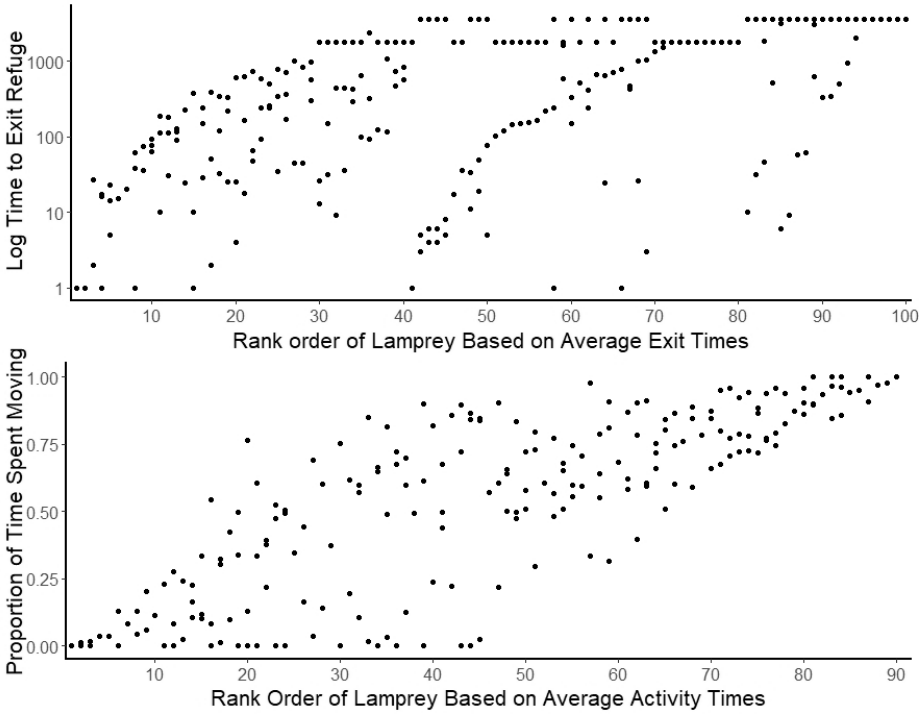

Figure 4. Individuals differed in exit time (top) and activity (bottom) in both 2013 and 2014. For each figure, individuals are ranked from lowest to highest based on the mean of three repeated measures of a given behavioural trait: exit time (top) and, activity time (bottom). Each closed circle represents the value measured for a trait in a single trial. Vertical closed circles at the same location on the x-axis depict multiple measurements for the same individual.

All statistical analysis were completed in R version 3.2.4 (R Development Core Team 2016), including the MCMCglmm (Hadfield 2010) and ggplot2 packages (Wickham 2010).

Results

The differences in exit time and proportion of time spent moving were repeatable. The estimated intraclass correlation was moderate but statistically significant for time to exit the enclosure (boldness; exit time: r = 0.18, 95% credible intervals: 0.06 to 0.29) and high and statistically significant for activity (proportion of time spent moving: r = 0.46, 95% credible intervals: 0.33 to 0.59). There was large inter-individual variation in both exit time and proportion of time spent moving (Figure 4). In the model estimating repeatability of exit time, exit times were higher for larger individuals (posterior mean = 0.006, 95% credible intervals: 0.0026 to 0.0091). Mean behavioural scores changed marginally when controlling for location and year effects (exit time: r = 0.18, 95% credible intervals: 0.07 to 0.30; proportion of time spent moving: r = 0.45, 95% credible intervals: 0.32 to 0.58), suggesting that combining the data from two years and across sites did not influence the repeatability estimates.

We found no strong support for the Arrival Time, the Nightly Separation or the Seasonal Separation Hypotheses (Table 1). The model including total body length and trial number was the best approximating

Table 1. Assessment of model sets for sea lamprey boldness and activity. Sea lamprey were collected from tributaries to Lake Ontario (Duffin's Creek and Bowmanville Creek) by trapping and electrofishing. Models were compared using the deviance information criterion (DIC).

Model number	Candidate model	DIC	ΔDIC	K	w_i
Model Set 1 (assessment of covariates)					
1.5	Length + Trial	948.7	0.00	5	0.283
1.8	Length + Trial + Location and Year	949.2	0.45	6	0.226
1.7	Trial + Location and Year	949.5	0.80	5	0.190
1.3	Trial	949.9	1.15	4	0.159
1.2	Length	952.4	3.64	4	0.046
1.4	Location and Year	952.7	4.02	4	0.038
1.6	Length + Location and Year	953.1	4.40	5	0.031
1.1	Intercept	952.5	4.78	3	0.026
Model Set 2 (assessment of predictors)					
1	Length + Trial	948.7	0.00	5	0.346
2	Length + Trial + Collection Method	949.1	0.38	6	0.286
5	Length + Trial + Collection Method + Collection Date	950.6	1.87	7	0.135
3	Length + Trial + Collection Date	950.8	2.08	6	0.122
4	Length + Trial + Collection Method x Collection Date	951.0	2.28	8	0.110

Note: Model set 1 considered covariates known to influence sea lamprey behaviour. Model set 2 tests predictions for collection method and collection date (from the Arrival Time, the Nightly Separation, and the Seasonal Separation hypotheses) after considering the covariates. The best approximating model from model set 1 was taken as the baseline model for model set 2. K is the number of parameters in the model and w_i is model weights.

model in the first model set which considered the possible confounding factors. Lamprey had a shorter exit time and spent less time moving in the third trial compared to the first two trials (posterior mean = −0.12, 95% credible intervals: −0.22 to −0.021). In the second model comparison, the model including length and trial continued to be the best approximating model (Table 1) and models considering collection method and time in the migratory run were ranked much lower in terms of probability of being the best model in the model set.

The model representing the Arrival Time Hypothesis had moderate support. It predicts a difference in behaviours depending on collection date and had a low probability of being the best approximating model with a ΔDIC slightly greater than 2 (Table 1). Contrary to what was predicted, individuals that arrived earlier in the migration run, regardless of collection method, were not quicker to exit an enclosure nor were they more active than individuals that arrived later in the migration run (posterior mean = −0.004, 95% credible intervals: −0.0090 to 0.0019; Figure 5). The model representing the Nightly Separation Hypothesis had the second most support with a ΔDIC less than 2 but is not considered competitive because it was essentially the best approximating model after being penalized for the addition of one parameter (Burnham and Anderson 2002). Sea lamprey did not differ in activity or exit time between the trapped and electrofished group (posterior mean = 0.14, 95% credible intervals: −0.16 to 0.30; Figure 5). The model representing the Seasonal Separation Hypothesis received the least support. It predicts a statistical interaction between collection method and collection date and had the lowest probability of being the best approximating model (Table 1). As the migratory season progressed, there were no differences in

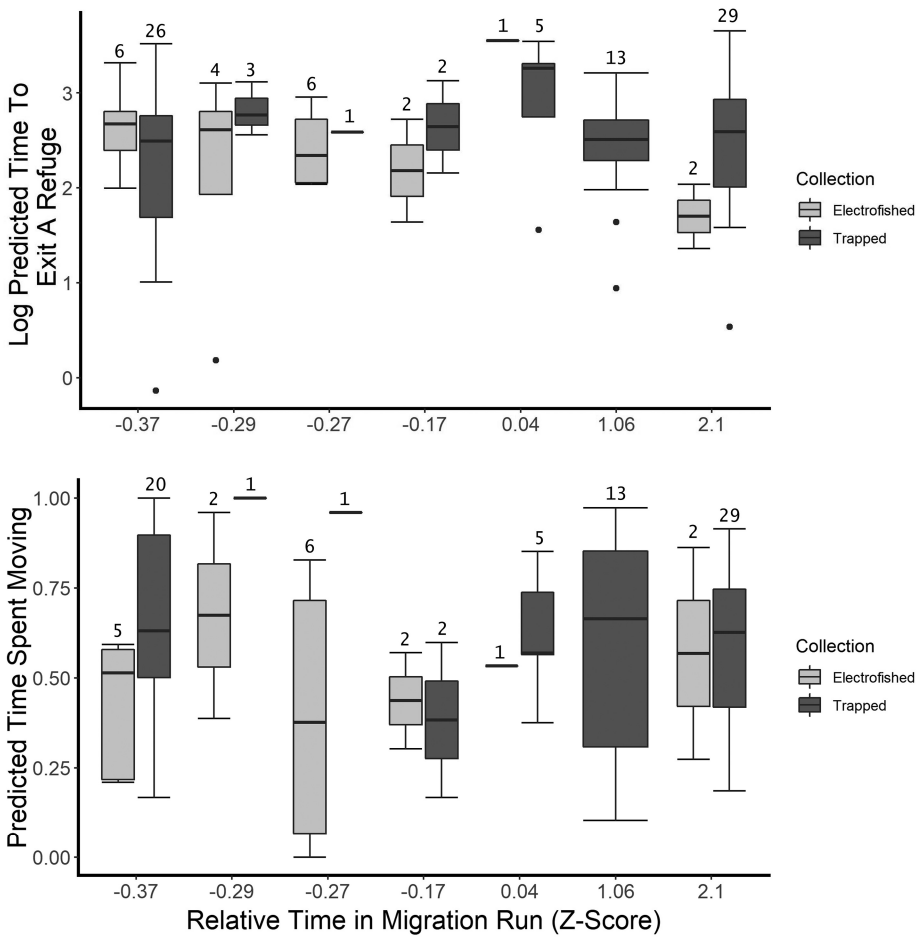

Figure 5. Boxplots summarizing the predicted values of exit time (top) and proportion of time spent moving (bottom), and their respective standard error bars, in relation to the relative time during the migration run when the sea lamprey were caught. Predicted values have been adjusted to remove variation due to trial number and total length, by adjusting the predictions statistically to correspond with the first trial and geometric mean length. Time during the migration run progresses from left to right and is expressed as a Z-score to adjust for year-to-year variation in the seasonal timing of migration. Sea lamprey caught by electrofishing are shown in light grey and those caught by trapping are shown in dark grey.

behaviour detected between the lamprey captured in traps and those captured downstream of the trap by electrofishing (posterior mean = −0.006, 95% credible intervals: −0.0097 to 0.022; Figure 5).

Discussion

Our study found no evidence that vulnerability to trapping in sea lamprey is influenced by individual differences in boldness or activity. Sea lamprey differed consistently in exit time and proportion of time spent moving under standardized laboratory conditions, as predicted by each hypothesis, which contributes to the limited research demonstrating consistent individual differences in boldness and activity in invasive species (Biro and Dingemanse 2009). Furthermore, it encourages sea lamprey managers to consider how individual differences in behaviour could be important to the control program in other ways, such as evolutionary responses to control methods (Dunlop et al. 2018). There was no relationship between the

individual differences in exit time and proportion of time spent moving and the date that the lamprey were collected, or the method by which they were collected, contrary to predictions from all three hypotheses. While simulation models suggest consistent individual differences in behaviour could dramatically affect trapping efficiency (Harper et al. 2018), our empirical findings do not support this concern.

A key strength of our study is the expanded and novel consideration of how individual differences in the behaviour of sea lamprey could influence their probability of encountering and entering a trap, and ultimately trap success. Under the Nightly Separation Hypothesis, we evaluated the widely-tested prediction that bolder more active individuals would be more likely to be trapped than shy and less active individuals. We uniquely tested how individual differences in behaviour could influence the time of arrival at traps, and potentially the time of exposure to traps, if early arriving individuals remain vulnerable for a longer time than later arriving individuals (Arrival Time Hypothesis). The Arrival Time Hypothesis is probably not relevant for trapping non-migratory fishes but is relevant for trapping migratory fishes, such as the sea lamprey. Similarly, the Seasonal Separation Hypothesis has not been considered previously in studies trapping non-migratory fishes, but again could be highly relevant to trapping migratory fishes. An expanded consideration of how individual differences in behaviour can influence the dynamics of trapping migratory species is valuable for understanding how a species' vulnerability to trapping, and similar management actions (e.g., fish passage), can be shaped by individual differences in an animal's ecology and life history. Our expanded consideration of individual differences in behaviour of sea lamprey can further be valuable for understanding why relationships between behaviour and trapping success are not always observed, as, for example, in recent work by Michelangeli et al. (2016) on the delicate skink (*Lampropholis delicate* DeVis, 1888) who suggest that that trap bias may only be associated with passive trapping techniques that involve a response to novelty. Additionally, the work by Landsman et al. (2017) indicated that boldness does not contribute to individual fish passage success in rainbow smelt. We suggest that future researchers recognize the multiple and complex ways in which individual differences in boldness and activity could affect an animal's vulnerability to trapping.

There are three plausible biological explanations for why we did not find support for any of our hypotheses relating differences in behaviour to vulnerability to trapping sea lamprey. The first is that lamprey may exhibit context dependent differences in behaviour. Individuals may display consistent individual differences in behaviour under a constant lab environment that are not representative of their behaviour in the field (Killen et al. 2016). Complex changes in behaviour are also possible over the migratory season; sea lamprey are maturing during migration and are

expending their fixed energy reserves over time, because this species is semelparous and does not feed during migration (Applegate and Moffett 1955). Migratory restlessness could also reduce the magnitude of individual differences that might normally be observed for other life stages in the laboratory or the field. Behaviours may also be masked by environmental cues, such as conspecific alarm cues which have been shown to influence activity rates, and timing of trap encounter in sea lamprey (Hume et al. 2015; Luhring et al. 2016). A second possible explanation for why we did not have any support for our hypotheses is that vulnerability of sea lamprey to trap encounter, entrance, or retention is influenced by behaviours other than, or in addition to, boldness and activity. We focused on boldness and activity because there is theoretical justification and empirical evidence demonstrating that these two behaviours can differ between trapped and untrapped animals (Biro and Dingemanse 2009). In addition, the evidence that aggression or social behaviours might influence trapping of sea lamprey is less compelling (Johnson et al. 2013; McLean et al. 2015). A third possible explanation for why we did not observe differences between trapped and electrofished sea lamprey has to do with the lamprey's tendency to refuge in and under cover from light during the day (Kelso and Gardner 2000). It is possible that the behaviours trapped lamprey use to encounter and enter traps are the same behaviours untrapped lamprey used to encounter and enter refuges downstream of the traps, resulting in little difference in behaviour when the two groups are compared.

Despite these possible explanations, our findings are valuable for evaluating explanations for why the efficiency of trapping sea lamprey is lower than desired in large rivers such as the St. Marys River. The hypothesis that individual differences in behaviour affect vulnerability to trapping is a viable explanation for the low trapping efficiency for sea lamprey and management actions to improve trapping efficiency will depend on the importance of alternative explanations. From earlier research on sea lamprey, it is clear that trap encounter and entry in the field are not random events with fixed probability; encounter and entry vary with season, water temperature, and time of day (Bravener and McLaughlin 2013; McLean et al. 2015; Dawson et al. 2016). Trap encounter and entrance are not markedly improved by increased (attraction) flows, nor limited because strong flows make it difficult for individuals to reach or enter the traps (Rous et al. 2017). In addition, there is no evidence that the presence of conspecifics at the trap opening, or in the trap, interfere with trap entrance (McLean et al. 2015). Chemical attractants have generally increased trap success modestly, but variably across tributaries (Johnson et al. 2013, 2015). Yet, in any given tributary, many migrating animals remain untrapped. During our study, for example, estimates of trapping efficiency varied between location and year (Duffin's Creek 2013: 67.5%, Duffin's Creek 2014: 41.5%, Bowmanville Creek 2014: 21.7%) and simulation

modelling has shown that consistent individual differences in behaviour could lead to and an underestimation of population size, and overestimation of trapping efficiency, by 20–30% (Harper et al. 2018). Although additional research remains needed, our study provides initial and novel empirical evidence that sea lamprey can differ consistently in their behaviour, but these differences do not appear to affect vulnerability to trapping in the field.

Our study has four uncertainties that warrant further consideration. The first, and admittedly most limiting for our tests, was that the number of untrapped individuals caught by electrofishing was small in both years. The tributaries sampled were chosen because of the consistency in the number of lamprey that migrate into the tributary each year. Our sample sizes for electrofished lamprey were limited in part because high water levels during our study years made it difficult to electrofish all the river habitat and because reduced visibility in the streams while electrofishing made it challenging to see and net the lamprey exposed by electrofishing. We attempted to overcome this limitation by combining the data from both the 2013 and 2014 sampling years. We also note that other studies assessing behavioural differences between capture method have had small sample sizes (Garamszegi et al. 2009; Carter et al. 2012; Michelangeli et al. 2016). Secondly, it is also possible that some individuals hiding in refuges during the day were not drawn out during electrofishing. Previous studies for lamprey and for other species have also experienced difficulty in capturing at-large individuals (McLean and McLaughlin 2018; Carter et al. 2012). If individual vulnerability to electrofishing was biased toward the bolder, more active individuals downstream of traps, this could have reduced any difference between the electrofished and trapped sea lamprey and therefore the power of our statistical tests. Thirdly, the two capture groups could have been exposed to different experiences that influenced their behaviour. Individuals caught in the trap were also electroshocked in an attempt to reduce these differences, but electrofished individuals did not experience trapping. An alternative design where the sea lamprey are captured in the same way, assayed for their behaviour, released, and monitored for vulnerability to trapping could overcome this limitation and is currently underway (Rachel Holub, *personal communication*, U. Guelph). Lastly is the possibility of trap escapement by sea lamprey. It is assumed that electrofished lamprey are not lamprey who entered a trap and later escaped: this is unlikely given the small size of trap entrances (5.1 cm diameter), one trap opening per trap, and the constant flow attraction encouraging lamprey away from the trap opening.

Poor trapping efficiency is an issue that needs to be resolved for trapping to be a viable method for controlling invasive species in general (El-Sayed et al. 2006), and sea lamprey in particular (Haeseker et al. 2007; Jones et al. 2015). The reasons for the lower than desired trapping efficiency for sea lamprey in the Great Lakes remain uncertain. Understanding behavioural

influences on trapping could allow managers to better estimate population size and provide insight into whether new trap designs are needed to target different behavioural types. From a control perspective, the consequences of consistent individual differences in behaviour for trapping are most relevant in large systems where control methods other than trapping are less effective and practical, and where the assessment of management actions is more challenging. Trapping in larger systems may also be more challenging if the extra space offers greater opportunity to avoid traps. These large systems, such as the St. Marys River connecting Lake Superior and Huron, can provide spawning habitat for many sea lamprey in the Great Lakes.

More broadly, a greater understanding of how individual differences in behaviour influence trapping could improve the management of invasive species. Situations that involve the trapping of invasive species could also offer rich opportunities to assess the ecological significance of consistent individual differences in behaviour. More recently, the quality and quantity of published literature that recognizes how behaviour can influence vulnerability to trapping has increased. Yet, a recent review on the integration of behaviour into conservation and management suggests that the role of behaviour in invasive species control measures remains largely unexplored (Berger-Tal et al. 2016).

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