Canadian Journal of Fisheries and Aquatic Sciences

A management-scale investigation of consistent individual differences in behaviour and trapping bias in Sea Lamprey (*Petromyzon marinus*)

Journal:	<i>Canadian Journal of Fisheries and Aquatic Sciences</i>
Manuscript ID	cjfas-2019-0448.R2
Manuscript Type:	Article
Date Submitted by the Author:	02-May-2021
Complete List of Authors:	Holub, Rachel; University of Guelph, Integrative Biology Bravener, Gale; Fisheries and Oceans Canada Central and Arctic Region, Sault Ste. Marie (Sea Lamprey Control Centre) McLaughlin, Robert; University of Guelph, Integrative Biology
Keyword:	BEHAVIOR < General, INVASIVE SPECIES < Organisms, MANAGEMENT < General
Is the invited manuscript for consideration in a Special Issue? :	Not applicable (regular submission)

SCHOLARONE™
Manuscripts

A management-scale investigation of consistent individual differences in behaviour and trapping bias in Sea Lamprey (*Petromyzon marinus*)

Rachel Holub, Gale Bravener, and Robert McLaughlin

Rachel Holub, Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, ON, Canada, N1G 2W1. Rachel.holub@gmail.com
Gale Bravener, Sea Lamprey Control Centre, Fisheries and Oceans Canada, 1219 Queen Street East, Sault Ste. Marie, ON, Canada, P6A 2E5. Gale.Bravener@dfo-mpo.gc.ca
Robert McLaughlin, Department of Integrative Biology, University of Guelph, 50 Stone Road East, Guelph, ON, Canada, N1G 2W1. rlmclaug@uoguelph.ca

* Corresponding author: Rachel Holub, 9 Upper Gullies Elementary Rd., Conception Bay South, NL, Canada, A1X 6M3, 519 362 7630, rachel.holub@gmail.com

April 2021

Abstract: The Sea Lamprey (*Petromyzon marinus*) is invasive in the Laurentian Great Lakes. Trapping in large rivers could suppress Sea Lamprey recruitment by removing migrating adults prior to spawning. Currently, the proportion of Sea Lamprey trapped (efficiency) is too low for control purposes, possibly because trapping is biased toward certain behavioural types. We tested if individual differences in time to enter a novel environment (risk-taking) and proportion of time moving (activity) under standardized laboratory conditions were correlated with time to encounter and enter a trap in the field. 638 Sea Lamprey were tagged, assessed for risk-taking and activity in sequential trials, and released in the river to be trapped. In the laboratory, individuals differed consistently in risk-taking and activity behaviours, and more active individuals entered a simulated trap sooner than less active individuals. In the field, however, the times to first trap encounter, and capture in a trap, were not correlated with risk-taking or activity. Our study provides a novel demonstration of how patterns from small-scale behavioural studies may not extend to management-scale applications.

52 **Introduction**

53 The value of integrating advances in animal behaviour into management and
54 conservation practices is the subject of ongoing discussion (Caro 2007, Berger-Tal et al. 2016,
55 Merrick and Koprowski 2017). Management and conservation plans often take a population
56 perspective, assuming individuals from the same population behave similarly (Réale et al. 2007,
57 Morales et al. 2013, Merrick and Koprowski 2017). At the same time, behavioural ecologists are
58 demonstrating that individuals from the same population can differ consistently in their
59 behaviour (Sih et al. 2004, Réale et al. 2007, Bell et al. 2009). Consistent individual differences
60 in behaviours such as responses to novelty and predators, general activity level, aggression, and
61 sociability have been demonstrated widely (Réale et al. 2007, Bell et al. 2009, Conrad et al.
62 2011). These individual differences in behaviour can influence ecological processes important to
63 management and conservation practices, such as habitat use (Sutherland 1998), dispersal
64 (Sutherland 1998, Beauchamp 2000), invasion biology (Phillips et al. 2010, Blackburn et al.
65 2011), and the creation of biological hotspots (Hastie et al. 2004).

66 Trapping to control invasive species is one practice where greater consideration of
67 consistent individual differences in behaviour could be beneficial. Trapping can be an attractive
68 control option when traps are selective for the species targeted, the proportion of the target
69 population trapped (trapping efficiency) is high, recruitment is suppressed, and the costs of
70 operating traps are low relative to other control options (Morman et al. 1980, El-Sayed et al.
71 2006, Haeseker et al. 2007). However, consistent differences in behaviour can potentially result
72 in a subset of individuals that are difficult to trap (Biro and Dingemanse 2009, Carter et al.
73 2012), reduced trapping efficiency (Carter et al. 2012, Harper et al. 2018), and a need for
74 additional trap designs or control methods targeting those remaining individuals (Bravener and

McLaughlin 2013). Maximizing trapping efficiency can be crucial for population control. Trapping is effective when the removal of individuals is high enough to suppress reproduction, recruitment, and the unwanted effects of recruits. Trapping can be a waste of resources if trapping efficiency is too low to overcome density-dependent processes that maintain population production.

Successful trapping involves at least three probabilistic events (Fig. 1). First, the target animal has to come close to the trap opening (encounter). Second, the target animal has to move from outside to inside the trap (entrance). Third, any target animal has to be killed or retained in the trap until the trap is emptied (retention) (Bravener and McLaughlin 2013). The success of each of these trapping events depends on how the target animals move in their environment and interact with traps, and the spatial and temporal placement and operation of traps to exploit the target animal's behaviour. For example, the probability of trap encounter can be influenced by placing traps where the target animals are likely to occur, by using physical or chemical stimuli to push or pull target animals to where the traps are placed, or both (Hume et al. 2015). Similarly, at a trap opening, stimuli could be used to lure an individual inside and retain them (Corkum and Belanger 2007, Johnson et al. 2013). A modest number of studies have shown that consistent individual differences in behaviour can influence vulnerability to trapping (Biro and Dingemanse 2009, Carter et al. 2012, Harper et al. 2018), but explicit tests for taxa and spatial scales relevant to resource management remain rare.

This study tested if the vulnerability of upstream migrating, adult Sea Lamprey (*Petromyzon marinus*; lamprey hereafter) to traps is influenced by consistent individual differences in behaviour. Lamprey are an invasive parasitic fish in the Laurentian Great Lakes. How this species colonized Lake Ontario remains debated (Eshenroder 2009), but it clearly

invaded the upper Laurentian Great Lakes following construction of the Welland Canal in the 1920s (Smith and Tibbles 1980, Christie and Goddard 2003). Soon after, populations of large native host (prey) fishes declined, including Lake Trout (*Salvelinus namaycush*), Walleye (*Sander vitreus*), and Lake Whitefish (*Coregonus clupeaformis*) (Smith et al. 1974, Smith and Tibbles 1980). In response to these ecological changes, the Governments of Canada and the USA created the Great Lakes Fishery Commission to oversee a binational control program for lamprey that has been underway since 1955 (Smith et al. 1974, Smith and Tibbles 1980, Christie and Goddard 2003). Two methods are used to control lamprey: in-river barriers that spatially restrict and suppress reproduction by preventing adult lamprey from accessing upstream spawning grounds and suppression of larval survival through periodic application of chemical lampricides in stretches of tributaries where larval lamprey develop for the first 4-5 years of life (Lawrie 1970, Smith and Tibbles 1980, Haeseker et al. 2007). Trapping adult lamprey before they spawn could be a valuable control method in large rivers, where barriers are impractical due to cost and the obstruction of boat and ship traffic (Haeseker et al. 2007), and where effective lampricide treatments can be challenging to carry out in the deeper, faster flowing water and costly due to the extent of habitat requiring treatment. To be a useful control tool in large rivers, trapping efficiency will need to be high enough that the removal of reproductively mature animals reduces the production of recruits (Jones et al. 2015).

Our study was conducted in the St. Marys River, a large river connecting Lakes Superior and Huron where improved trapping of lamprey would benefit the control program. Juvenile lamprey from this river are a major source of mortality for prey fishes in Lake Huron (Schleen et al. 2003). Trapping has been conducted in the St. Marys River since 1975 (Morse et al. 2003). Simulation results have suggested that the current trapping efficiency (40% on average over 10

years) is too low for control purposes (Jones et al. 2015). Research testing if trapping efficiency can be improved by manipulating lamprey behaviour using water (attraction) flow or by provisioning pheromone have shown limited promise (Johnson et al. 2013, Dawson et al. 2017, Rous et al. 2017). Alternatively, trapping efficiency could be constrained if lamprey display consistent individual differences in behavior that affect their vulnerability to trapping (Harper et al. 2018). Whether individual sea lamprey differ in their rate of upstream migration remains unknown, but individual differences in migration rate have been described in Pacific lamprey (*Entosphenus tridentatus*) (Moser et al. 2013) and individual sea and Pacific lamprey also differ markedly in their behaviour near traps and in fishways (Bravener and McLaughlin 2013, Kirk et al. 2017). Pilot laboratory studies also demonstrated that sea lamprey differ consistently in risk-taking behaviour and activity, and suggested individuals sampled from traps may differ in activity from individuals that were not trapped (McLean and McLaughlin 2018, but see Myles-Gonzalez et al. 2019).

Our study focused on two behaviours hypothesized to influence trap vulnerability: risk-taking and activity (Biro and Dingemanse 2009). The Risk-Taking Hypothesis assumes that an animal's vulnerability to trapping is influenced by its willingness to explore novel environmental situations and objects. The spawning tributaries used by lamprey are often novel locations, because lamprey are semelparous and do not home to their natal stream (Bergstedt and Seelye 1995). The metal structures used as lamprey traps can be considered novel objects, because they are not designed to mimic natural environmental features. The Activity Hypothesis assumes that more active animals will cover space quicker than less active individuals, resulting in higher encounter with, and entrance into, a trap, based on encounter rate theory (Gerritsen and Strickler 1977, De Vita et al. 1982). The two hypotheses are not mutually exclusive. Each hypothesis

144 makes four predictions (Table 1). The Risk-Taking Hypothesis predicts that lamprey will differ
145 consistently in their willingness to take risks (P1) and individuals more apt to take risks will
146 encounter (P2), enter (P3), and be trapped (P4) sooner than individuals less apt to take risks. The
147 Activity Hypothesis predicts that individual lamprey will differ consistently in their level of
148 activity (P5) and more active individuals will encounter (P6), enter (P7), and be trapped (P8)
149 sooner than less active individuals. We tested predictions 1-2, 4-6, and 8 in a two-year study
150 combining laboratory trials with releases and recaptures of PIT-tagged lamprey in the field
151 (Table 1). Prediction's P3 or P7 were not tested because the environmental conditions near the
152 trap openings made it impractical to measure trap entrance accurately.

153

154 **Materials and methods**

155 **Ethical Note**

156 All experimental protocols were assessed and approved by the University of Guelph
157 Animal Care Committee and Animal Use Protocol Number 1940.

158

159 Laboratory experiments and field observations were completed from 18 June to 23 July
160 2016 and from 5 June to 21 July 2017. These dates encompassed the periods of adult lamprey
161 migration each year. The laboratory experiments were conducted at the Department of Fisheries
162 and Oceans' (DFO) aquatic facility in Sault Sainte Marie, ON, Canada (46.51° N, -84.34° W; see
163 Quantifying Behaviour in the Laboratory below). The field observations were conducted in a 300
164 m long x 70 m wide x 5-14 m deep channel downstream of the Clergue Generating Station; a
165 hydroelectric dam on the St. Marys River (Fig. 2; 46.51° N, -84.35° W). Two permanent lamprey

traps were attached to the downstream wall of the Clergue Generating Station (see Fig. 1 in McLean et al. 2015). Water is expelled through the trap entrances with the expectation that flow attracts lamprey to the traps (Almeida et al. 2002, Bravener and McLaughlin 2013). These attractant water traps are located on the north (north attractant water trap; NAWT) and the south (south attractant water trap; SAWT) sides of the river. Both traps have entrances on the two sides of the trap perpendicular to the direction of water flow. The SAWT has two additional entrances on the downstream face of the trap. During the period of adult lamprey migration, three portable traps were sited in locations with high discharge between the attractant water traps. Each of these traps has a funnel entrance on each side of a holding chamber. The traps were submerged 1-3 m below the water surface. Water at the face of the dam is roughly 15 m deep. The study channel is part of the larger river and traps are also operated at four locations on the USA side of the river, approximately 0.9 to 2.1 km away from the study site.

Sea Lamprey Collection and Holding

In 2016, subjects were collected from traps on the USA side of the St. Marys River near Sault Sainte Marie, Michigan, USA. The test subjects were assumed to have no previous experience with the study area. Subjects were held separately by sex (N = 127 males, 131 females) in two flow-through tanks (3.4 m x 0.8 m x 1.5 m) supplied with water from the St. Marys River (temperature range = 7.8 – 17.4 °C, daily mean = 13.2 °C). The holding tanks were covered to minimize light exposure. Migratory lamprey are nocturnal and seek refuge during the day (Binder and McDonald 2007). Each holding tank contained an enclosure the subjects could explore and use for cover (Fig. 3). The enclosure consisted of two halves of PVC pipe (0.10 m diameter, 0.40 m length), cut longitudinally with the outside of the pipe facing upward and glued

to a flat sheet of PVC to create semi-cylindrical chambers that were closed on one end using perforated PVC sheets. The enclosure was provided to allow the test subjects to become familiar with the enclosure design ahead of the behavioural laboratory trials. Subjects were not fed. Lamprey do not feed during their spawning migration (Sower et al. 1985).

In 2017, subjects were captured from four locations using three capture methods. The change in collection method was made to minimize any bias in the range of behavioural variation that could arise from using previously trapped animals, especially if traps are selective. The subjects used in 2017 were collected from: (i) Bridgland Creek near Thessalon, Ontario (46.30° N, -83.55° W; 105 individuals), (ii) the Cheboygan and Ocqueoc Rivers near Cheboygan, Michigan (45.65° N, -84.47° W and 45.49° N, -84.07° W respectively; 89 individuals), and (iii) the USA side of the St. Marys River near Sault Sainte Marie, MI (46.50° N, -84.33° W to 46.51° N, -84.35° W; 186 individuals) for a total of 207 males and 173 females. Subjects from Bridgland Creek were collected by electrofishing and by hand capture of individuals under and between rocks at the side of the river. Subjects from the Cheboygan and Ocqueoc Rivers were captured using eel ladder traps, requiring lamprey to climb a wetted inclined ramp (Reinhardt and Hrodey 2014). Subjects from the south side of the St. Marys River were captured in traps, as in 2016. In 2017, subjects were held in 3.4 m x 0.8 m x 1.5 m flow-through holding tanks; one holding tank for subjects from Bridgland Creek, one tank for subjects from the Cheboygan and Ocqueoc Rivers, one tank for male subjects from the St. Marys River and one tank for female subjects from the St. Marys River. Each holding tank contained an enclosure as in 2016. Water was supplied from the St. Marys River (temperature range = 7.4 – 17.0 °C, daily mean = 12.0 °C). Subjects collected from Bridgland Creek, and the Cheboygan and Ocqueoc Rivers, were not

211 separated by sex because their numbers were lower than for the St. Marys River sample and the
212 availability of holding tanks was limited.

213 Test subjects were tagged individually with 23 mm passive integrative transponder (PIT)
214 tags (RFID 3.65 mm x 23 mm HDX, 0.6 g in air) 1-3 days after arriving at the test facility.
215 Tagging involved six steps. First, each subject was placed in a 20 L container of 50 mg/L
216 solution of MS-222 (anesthetic). A subject was considered anaesthetized when its movement
217 ceased and it no longer attached to the container wall using its oral disc. Second, the individual
218 was sexed, weighed (± 1 g), and measured for total length (± 1 mm), then placed ventral side up
219 on a damp foam pad. Third, the incision site, near the ventral midline, was disinfected with a 1
220 g/L Virkon solution and rinsed with a 9 g/L saline solution. Fourth, a 5 mm incision was made
221 using a scalpel and a 23 mm PIT tag was inserted into the body cavity. The scalpel blade and PIT
222 tag had been disinfected in a 1 g/L Virkon solution and rinsed with a 9 g/L saline solution prior
223 to the incision. Suturing the incision was not necessary. Fifth, the tagged individual was placed
224 into an oxygenated recovery tank (0.65 m x 0.42 m, depth = 0.20 m) for approximately 30
225 minutes, until the individual regained mobility. Lastly, tagged subjects were returned to their
226 respective holding tanks. Scalpel blades were changed after 10 surgeries to maintain sharpness.
227

228 **Quantifying Behaviour in the Laboratory**

229 Behavioural laboratory trials used to assess individual differences in behaviour (P's 1-2,
230 4-6, and 8) began 3-17 days after tagging (mean = 7.1 days in 2016, 9.6 days in 2017). The trials
231 were conducted between 2000 – 0400 h from 18 June to 15 July 2016 and from 5 June to 20 July
232 2017. The trials were conducted at night, because lamprey are nocturnal during the spawning
233 migration (Applegate and Smith 1950). Individual trials were completed in 100% high density
234 polyethylene cattle (test) tanks (Hasting plastic round end stock tank; Fig. 3; 0.6 m x 0.6 m x 1.8

235 m) filled with standing water (depth = 0.30 m) sourced from the St. Marys River. Five separate
236 trials were run simultaneously in 5 test tanks in 2016 and 10 trials in 10 test tanks in 2017. In
237 2016, the test tanks were arranged lengthwise ~ 0.50 m apart. In 2017, the test tanks were
238 arranged lengthwise ~ 0.50 m apart in two rows of five. In both years, each test tank contained
239 an enclosure of the same design as those provided in the holding tanks. In 2017, but not 2016,
240 the test tanks were partitioned into two compartments using a solid piece of PVC with a 0.05 m
241 diameter hole in the center (0.15 m from the tank bottom) placed 0.95 m away from the exit of
242 the enclosure. The larger compartment was 1.4 m x 0.6 m x 0.6 m and contained the enclosure to
243 provide the test animal sufficient space to exit the enclosure and explore. The smaller
244 compartment was 0.5 m x 0.6 m x 0.6 m. A water pump (Lifegard Aquatics Quiet One 1200
245 aquarium pump, 317 GPH) was also placed in each test tank with an output into the smaller
246 compartment and intake at the opposite (far) end of the larger compartment behind the enclosure.
247 This configuration created a low flow through the opening between the smaller compartment and
248 the larger compartment to assist the subjects in finding the compartment entrance, like the
249 attraction flow provided in the field. The configuration changes in 2017 were made to test if
250 entrance into the smaller compartment (a potential trap) was correlated to an individual's risk-
251 taking and activity (P's 4 and 8) under smaller-scale laboratory conditions.

252 The behaviour of subjects was video-recorded during each laboratory trial. Video-
253 recordings were made using a 960H security digital video recorder (Night Owl, Walpole,
254 Massachusetts) connected to an 8 channel DVR with CAM-650 security bullet cameras. A single
255 camera was positioned over each test tank ~ 3 m above the ground and ~ 1 m away from a test
256 tank (near the smaller compartment). Red floodlights were placed next to each camera directed at

the test tanks to provide lighting, as done in earlier studies of lamprey behaviour (Hárosi and Kleinschmidt 1993, Binder and McDonald 2007, McLean and McLaughlin 2018).

Six sets of five behavioural laboratory trials were conducted per night in 2016. Before each trial, a subject was netted haphazardly from a holding tank containing lamprey that had not been tested previously. The subject was then placed singly in the enclosure within an unoccupied test tank. A clear acrylic sheet (0.24 m x 0.30 m) blocked the open exits of the enclosures and the test subjects were given five minutes to acclimate to the enclosure. Five minutes of acclimation time was provided to allow the subjects to recover from the stress of handling, while maximizing the amount of samples completed in a single night (Tix et al. 2017). The date, tank number, PIT tag number of the test subject, and time of night when the trial started were recorded prior to the start of each trial. Measurements of dissolved oxygen concentration during preliminary trials (YSI 550A dissolved oxygen meter) showed that oxygen concentrations did not change within a trial. A trial commenced when the acrylic sheet blocking the opening of the enclosure was removed. The behaviour of each test subject was video-recorded for 30 minutes during which an individual could freely leave the enclosure (a measure of risk-taking) and move about the test tank (a measure of activity). At the end of each trial, the test subject was netted from the enclosure, if it had not exited, or from the open arena, if it had exited, and returned to a holding tank. The test tank was emptied, rinsed with freshwater from the St. Marys River, and refilled (depth = 0.30 m) for the next trial. Video-recordings were made for 258 individuals. Measuring the consistency of behaviour required repeated measurements of the same individual (P's 1 and 5). In 2016, 60 test subjects were randomly selected for a second trial. For 27 test subjects, the second trial was completed the night following the first trial. For 33 test subjects, the second trial

279 was completed after the test subject had been released into the St. Marys River and recaptured by
280 the trap operators 0 - 25 days later (mean = 14 days).

281 Four sets of ten behavioural laboratory trials were conducted per night in 2017. Selection
282 of subjects, assignment to test tanks, and acclimation were conducted according to the 2016
283 methods. A perforated PVC sheet (0.24 m x 0.30 m) was used to block the enclosure entrance
284 and, once removed, each test subject was given 30 minutes to exit (a measure of risk-taking). At
285 the end of the 30 minutes, the enclosure was removed from each test tank. Any subject that had
286 not exited the enclosure after 30 minutes was gently coaxed from the enclosure by tipping and
287 removing the enclosure from the water or by gently touching the side of the subjects tail. The
288 subjects were given 30 minutes additional time to move about the large and small compartments
289 of the test tank, to ensure every subject has a measurement of activity. The trial stopped 60
290 minutes after the removal of the PVC sheet. Trials were completed for 380 individuals (males =
291 207, females = 173). To test the consistency of behaviour (P's 1 and 5) in 2017, two trials were
292 completed for 324 individuals. The second trial of the same individual was completed 1-15 days
293 (mean = 5.1 days) after the first trial.

294

295 **Quantifying Time to Encounter and Vulnerability to Trapping in the Field**

296 The times for a subject to encounter a trap and be captured in the field were measured to
297 test the relationships between risk-taking and activity, and the times to encounter a trap and be
298 captured (P2 and P4, and P6 and P8, respectively). Subjects were released from 19 June to 9 July
299 2016 and from 13 June to 15 July 2017. These dates overlapped the early, mid, and late parts of
300 the lamprey migration period each year. The encounter and capture data were collected from 19
301 June to 23 July 2016 and from 13 June to 21 July 2017.

Subjects were released 1 - 12 days following their last behavioural trial (mean = 1.3 days in 2016, 3.6 days in 2017). Release sites were located near the north side, center, and south side of the channel, approximately 300 m downstream of the Clergue Generating Station (Fig. 2). These locations were selected to provide the subjects with ample distance to move horizontally within the channel as they proceeded upstream and to minimize the likelihood of individuals straying to other locations in the river. For each release, the subjects were divided randomly and placed in one of three aerated containers, one container for each release site. Each container held roughly equal numbers of male and female lamprey. The containers were transported by boat to the release sites. The releases were made between 2000 and 2030 h to minimize predation of the released lamprey by diurnal predators.

Encounters with traps were measured using PIT tag antennas positioned at the openings of the NAWT and SAWT. Placing PIT tag antennas on the portable traps was impractical, because trap operators lifted these traps from the water and emptied them each day and unlike the NAWT and SAWT, there was no permanent structure for attachment. PIT tag antennas on these traps pose a safety risk to the operators and are prone to physical damage. The PIT tag antennas were made with 8 gauge multi-stranded, oxygen-free, high-conductivity wire, passed through garden hose for protection from abrasion. The antennas were attached to a 1.0 m x 0.5 m metal frame and held in place with airline cable. At each trap, the antenna was connected to a tuner box (Standard Remote Tuner Box, Oregon RFID, Portland, OR) fastened to the side of the deck where the traps were secured using cable ties. The tuner box was wired using twin axial cable to a multiplexer (Multi-Antenna HDX Reader Oregon RFID, Portland, OR) located in a Fiberglass box positioned on the deck of the trap. This antenna system was powered using an AC power outlet, located on the dam. The current was converted to DC using an AC to DC power

converter (MW® model MW126A 12.5 Volt DC power supply). Each antenna was tuned to detect a PIT tag up to 0.5 m from the trap. On each morning of the data collection period, data from the previous night were downloaded and the detection ranges of the antennas were checked and adjusted.

Capture in traps was quantified by removal of subjects from all five traps with the assistance of the DFO trap operators. Traps were lifted and emptied Monday to Friday of each week. The trap operators screened the subjects removed from each trap in a coded wire tag detector with a PIT antenna placed around it. Normally, subjects collected from the traps are euthanized immediately. In 2016, 33 trapped subjects, and in 2017, all trapped subjects were given an additional behavioural trial, identical to the behavioural trials described above, prior to euthanasia.

Data Analyses

Testing Consistency of Behaviour (Laboratory; P's 1 and 5)

The time to exit the enclosure (2016 and 2017), proportion of time spent moving in the open test tank (2016 and 2017), and time to pass through the hole from the larger compartment to the smaller compartment (2017) were quantified from the video-recordings. Time to exit the enclosure provides a measure of the subject's perceived risk of staying in the enclosure versus exiting into the open compartment. This measure was quantified as the time from the start of the trial until an individual completely exited the enclosure. If a subject did not exit after 30-min, exit time was set to 1800 s. Time to exit the enclosure was measured using JWatcher Version 1.0 (Blumstein et al. 2006) in 2016 and measured manually in 2017. Proportion of time spent moving provides a measure of a test subject's baseline activity in a benign environment. In 2016,

proportion of time spent moving was quantified from when an individual exited the enclosure until the end of the 30-minute trial. In 2017, proportion of time spent moving was quantified when an individual exited the enclosure or was coaxed from the enclosure (after 30 min), until the end of the 60-minute trial. Proportion of time spent moving was measured using JWatcher in 2016 and automated using Ethovision Version 8.5 (EthoVision XT; Noldus et al. 2001) in 2017. The switch from JWatcher to Ethovision in 2017 was made because of the larger number of video recordings to process in 2017. A subject was considered not moving when it used its oral disc to attach to the side or bottom of the experimental tank, or its full body was not moving. Time to pass through the hole from the large compartment to the small compartment was used to simulate trap capture in the laboratory, admittedly at a much smaller spatial scale than in the field. We interpret an individual's passage through the hole as the outcome of searching for a way by the confining walls to move from a current, less desirable location to a potentially more desirable, but unknown location. In the field, traps are often associated with barriers to upstream movement and placed near, or provided with, attraction flows believed to signal a potential path past the barrier. Lamprey are thought to enter the traps in an effort to move past the barrier from a less desirable location (downstream) to a more desirable location (upstream). Time to pass through the hole was quantified as the time from when a subject exited the enclosure, or was coaxed from the enclosure when the enclosure was removed, until the time the subject completely entered the smaller compartment. This time measurement was quantified manually from the video recordings.

The predictions that individual lamprey differ consistently in time to exit the enclosure (P1) and proportion of time spent moving (P5) were tested following Nakagawa and Schielzeth (2010) by estimating the intraclass correlation coefficient (r) for each behavioural measure:

371
372
373
374
375
376
377
378
379
380
381
382
383
384
385
386
387
388
389

390
391
392

$$r = \frac{\sigma_a^2}{(\sigma_a^2 + \sigma_w^2)}$$

where σ_a^2 is the variance component for among individual variation and σ_w^2 is the variance component for within individual variation. The variance components were estimated from univariate generalized linear mixed models with the behavioural measures as the dependent variable and the PIT tag number (individual), water temperature, sex, $\log_{10}$ length (body size), test tank number (2016: 1-5, 2017: 1-10), and individual trial number (1st or 2nd) as independent variables. Tag number and test tank number were modeled as random effects. Water temperature, sex, length, and individual trial number were modeled as fixed effects. Tag number (Individual) was included in the model to accommodate the repeated measures made for individuals and to estimate the variance components used to calculate r . Test tank number was included to account for any variation due to spatial differences in lighting and camera orientation. All other covariates were added because they are known to influence lamprey behaviour (Binder and McDonald 2008, Bals and Wagner 2012). Day of the year was not included as a covariate because it was highly correlated with water temperature (see also McLean et al 2015, Rous et al 2017). For each behaviour, an additional model to assess repeatability was completed without the phenotypic covariates (length and sex) that could contribute to consistent individual differences. Prior to analysis, the time to exit the enclosure was $\log_{10}$ transformed and the proportion of time spent moving was arcsine square-root transformed. These transformations were completed to normalize the distributions of data as closely as possible.

Testing Time to Encounter and Capture in Relation to Behaviour (Field; P's 2, 4, 6, and 8)
A multi-model approach based on Akaike Information Criterion (AIC; Burnham and Anderson 2002) was used to determine if time (days) from release to first encounter and to

capture in the field were related to individual behaviour measured in the behavioural trials (P's 2, 4, 6, and 8). The approach involved 16 rounds of model comparisons: 4 predictions, tested in each of 2 years (2016 and 2017), with 2 model comparisons for each yearly test (1 model comparison to test for important covariates and a second to test the prediction) ($4 \times 2 \times 2 = 16$ rounds).

The individual models considered in each round of model comparison were mixed effect Cox models (Therneau 2018) relating either time to encounter or time to capture with the behavioural predictors, either time to exit an enclosure or proportion of time spent moving, and additional covariates that earlier studies have suggested could influence encounter and capture in the field, including sex, $\log_{10}$ length, and source of subjects (2017 only) (Bravener and McLaughlin 2013, Dawson et al. 2017, Rous et al. 2017). We used mixed effect Cox models because they are (i) designed for time-to-event data, (ii) use the information from both individuals that encountered a trap and those that did not, or individuals that were captured and those that were not, depending on the prediction, and (iii) can accommodate multiple measurements per individual by including individual tag number as a random effect. Time to encounter was the number of days from the date of release until the day a trap was encountered (for lamprey detected at the traps with PIT antennas), the number of days from the date of release until capture (for lamprey captured at traps without PIT antennas), and the number of days from the date of release until the end of the trapping period (for individuals that did not encounter a trap and were not captured). Similarly, time to capture was the number of days from the date of release until the day of capture in a trap, for individuals that were trapped, and the number of days from the date of release until the end of the trapping period, for individuals that were not captured. For tests of predictions regarding encounter (P2 and P6), times for individuals that

416 never encountered the monitored traps and were either captured at other traps or not captured by
417 the end of the trapping season were treated as right-censored in the Cox analyses because we had
418 incomplete information on the true time to encounter for these individuals (Hosmer and
419 Lemeshow 1999). Similarly, for tests of predictions regarding time from release to capture (P4
420 and P8), times for individuals that were not captured were also treated as right-censored in the
421 Cox analyses because we had incomplete information on the true time to capture. Our analyses
422 also assumed that all released individuals were available to encounter the traps and to be
423 captured. This assumption was made for three related reasons. First, earlier studies at this site
424 demonstrated that 75% or more of acoustic tagged sea lamprey proceed from the release sites
425 upstream into the section of the tailrace immediately downstream of the traps (Rous et al 2017).
426 Second, an independent study tracking acoustic tagged sea lamprey throughout the river showed
427 that sea lamprey moved extensively, generally in an upstream direction to the trap sites near
428 Sault Ste. Marie, but with infrequent reversals downstream that were often followed by return to
429 the trap sites (Holbrook 2015; Chapter 3). Third, it was impractical to determine when released
430 individuals might be unavailable for trapping in our study, because PIT tag technology is
431 inefficient for this level of tracking in such a large system and, given the information above, it is
432 unclear if any individual that reverses course is truly unavailable to be trapped.

433 For a given prediction, the first model set compared within a year (covariate models) was
434 used to identify the best approximating model from a model set relating time to encounter or
435 time to capture, depending on the prediction, with the fixed effects sex, $\log_{10}$ length, and source
436 of subjects (2017 only). The second model set compared within the same year (prediction
437 models) was used to assess the prediction of interest, after statistically accounting for the
438 important covariates identified in the first model set. In addition, all models included as random

effects (i) the test tank number where behavioural measurements were made, to account for any tank effects, (ii) tag number (individual), to account for repeated measurements made per individual in the laboratory, and (iii) release date (day of the year), to account for any differences in the performance of the lamprey released at different times during the migration period. This process of comparing covariate models followed by prediction models was repeated for all four predictions (P's 2, 4, 6, and 8). In each model comparison conducted, the best approximating model from a model set was determined by comparing values of delta AIC and Akaike weights. We did not conduct any additional analyses combining time to exit an enclosure and proportion of time spent moving. Pearson correlation coefficients indicated that any relationship between time to exit an enclosure and proportion of time spent moving across individual lamprey was weak (2016: $r = -0.05$, $p = 0.57$, $n = 150$ individuals; 2017: $r = -0.12$, $p = 0.02$, $n = 380$ individuals), nor was any statistically significant correlation observed in a previous study (McLean and McLaughlin 2018).

Testing Time to Encounter and Capture in Relation to Behaviour (Laboratory; P's 4 and 8)

For the 2017 data, mixed-effects Cox models were used to test the predictions relating the time a lamprey took to enter the smaller compartment (simulated laboratory trap) with the time to exit the enclosure (P4) and the proportion of time moving (P8) (Table 1). Two models were created, one relating time to enter the smaller compartment (s) as the response variable with time to exit the enclosure as the independent variable and another relating time to enter the smaller compartment with proportion of time spent moving as the independent variable. Time to exit the enclosure and proportion of time spent moving, as well as the covariates water temperature, sex, $\log_{10}$ length, and capture method/source were modeled as fixed effects. The covariates were included because there was justification to believe they could influence trap encounter and

entrance in the field (McLean et al. 2015, Dawson et al. 2017, Rous et al. 2017) and they were found to be important predictors in the AIC selection for previous models (Table 3-6). Tag number and test tank number were modeled as random effects, because multiple trials were conducted per individual and there was a possibility for tank effects. Time to exit the enclosure and proportion of time spent moving were transformed as described above.

For all of the model comparisons, the estimated regression coefficients (β 's) from the best approximating models were used to determine if time to encounter, capture, or enter the smaller compartment (event), as appropriate, changed as predicted when time to exit the enclosure or proportion of time spent moving increased. The regression coefficient indicates the change in relative risk (ratio of the probability of event occurring) for encounter, being captured in the field, or being captured in the laboratory in relation to time to exit the enclosure and proportion of time moving. A regression coefficient less than 0 indicates that the time to event increased as time to exit the enclosure or proportion of time spent moving increased. A regression coefficient greater than 0 indicates that the time to event decreased as time to exit the enclosure or proportion of time spent moving increased.

All statistical analyses were conducted in R version 3.3.2 (R Core Team 2016) including the R packages lme4 (Bates et al. 2015), rptR (Stoffel et al. 2017), and coxme (Therneau 2018). A detailed list of sample sizes and individuals used for each test is available in the Supplementary Table 1.

Results

Consistency of Behaviour (Laboratory; P's 1 and 5)

The behaviour of lamprey varied considerably in the laboratory experiments. Subjects exited the enclosure in 1 to 1800 s (median = 841 s) in 2016 and 1 to 1800 s (median = 131 s) in 2017. During an exit, the subjects moved directly into the open test tank without signs of hesitation. The proportion of time spent moving varied from 0.03 to 1.00 (median = 0.60) among subjects in 2016 and from 0.08 to 1.00 (median = 0.63) among subjects in 2017. Movement in the open test tank varied between slow, gradual movements along the compartment wall to infrequent, rapid movements throughout the test tank. When not moving, subjects attached to the sides of the test tank using their oral disc. In 2017, subjects took 5 to 3667 s (median = 612 s) to find and enter the small compartment from the large compartment.

Consistent with the Risk-Taking and Activity Hypotheses, the time to exit the enclosure and the proportion of time spent moving in the test tank differed repeatably among subjects in each study year (P's 1 and 5) (Table 2). For the time to exit the enclosure, the intraclass correlation coefficients were statistically significant and similar in magnitude across years, regardless of whether the models used to estimate the variance components included sex, length, and capture method/source (2017) as covariates (Table 2). In both years, time to exit the enclosure in the first trial did not differ significantly from those in the second trial: $F_{1, 56.8} = 1.51$, $p = 0.22$ for 2016 and $F_{1, 350.2} = 0.02$, $p = 0.89$). For the proportion of time spent moving, the intraclass correlation coefficients were also statistically significant, but lower in magnitude in 2017 than in 2016 (Table 2). Within each year, similar values for the intraclass correlation were obtained regardless of whether the models used to estimate the variance components included sex, length, and source (2017) as covariates. In both years, the proportion of time spent moving in the first trial tended to be higher than the proportion of time spent moving in the second trial ($F_{1, 15.2} = 8.1$, $p = 0.01$ for 2016 and $F_{1, 355.6} = 22.9$, $p = 0.0001$). In 2016, the decline in the

507 proportion of time spend moving was 0.08 on average for the 27 subjects tested twice before
508 release in the field and 0.19 on average for the 33 subjects tested prior to release in the field and
509 after being trapped. In 2017, when all subjects were tested twice before release in the field, the
510 decline in the proportion of time spent moving between trials was 0.05 on average.

511 *Time to Encounter and Capture in Relation to Behaviour (Field; P's 2, 4, 6, and 8)*

512 Proportions of PIT-tagged subjects encountering traps in the field, and trapped over the
513 migration period, were similar for 2016 and 2017. In 2016, 60 of the 258 PIT-tagged subjects
514 (23%) were detected at the traps, 43 of the 60 (72%) at the NAWT and 17 of 60 (28%) at the
515 SAWT. Forty-six of the 258 tagged subjects (18%) were captured, 13 of the 46 (28%) in the
516 NAWT, 12 of 46 (26%) in the SAWT, and 16 of 46 (35%) in the portable traps. Five of 46
517 (11%) were captured at other trap sites in the St. Marys River. In 2017, 59 of the 380 tagged
518 subjects (16%) were detected at the traps, 27 of the 59 (46%) at the NAWT and 32 of 59 (54%)
519 at the SAWT. Sixty-two of the 380 tagged subjects (16%) were captured, 21 of the 62 (34%) in
520 the NAWT, 14 of 62 (23%) in the SAWT, and 23 of 62 (37%) in the portable traps. Four of 62
521 (6%) were captured at other trap sites in the St. Marys River.

522 Contrary to the predictions for the Risk-Taking Hypothesis (P's 2 and 4), lamprey that
523 exited an enclosure more quickly in the laboratory trials did not encounter a trap or get captured
524 sooner in the field than lamprey that exited an enclosure less quickly in the laboratory trials (Fig.
525 4). The best approximating models from the sets of candidate models for time to encounter a trap
526 (Table 3) and for time to be trapped (Table 4) did not include time to exit the enclosure as a
527 predictor for the 2016 and 2017 field trials. The best approximating model for time to be trapped
528 did include time to exit the enclosure as a predictor for the 2017 field trials, but the simpler
529 models without time to exit the enclosure had nearly equal model weights indicating that the

addition of time to exit the enclosure did not improve predictive ability (Burnham and Anderson 2002). Across both years, the estimated regression coefficients (β 's) relating time to encounter and be captured in a trap in the field with time to exit an enclosure in the laboratory were small in magnitude (-0.04 – 0.21) with 95% confidence intervals encompassing 0 in every case.

Contrary to the predictions generated from the Activity Hypothesis (P6 and P8), lamprey that spent a greater proportion of time moving in the laboratory trials did not encounter a trap or get captured sooner in the field than lamprey that spent a lesser proportion of time moving in the laboratory trials (Fig. 5). For the 2016 and 2017 field trials, the best approximating model from the set of candidate models for time to encounter a trap (Table 5) and for time to be trapped (Table 6) did not include proportion of time spent moving as a predictor. Across both years, the estimated regression coefficients (β 's) relating time to encounter and be captured in a trap in the field with proportion of time spent moving in the laboratory varied from -0.43 to 0.59, but again the 95% confidence intervals encompassed 0 in every case. The value of $\beta = 0.59$ for the relationship between time to encounter a trap and proportion of time spent moving in 2016 was the largest estimate consistent with either of the predictions, with a confidence interval of -0.66 to 1.83.

Summary distributions of time to exit and the proportion of time spent moving by trial number (1,2), encounter (no, yes), capture (no, yes) and year (2016, 2017) are provided in online Supplementary Figures S1-S2.

Time to Encounter and Capture in Relation to Behaviour (Laboratory; P's 4 and 8)

The tests of predictions from the Risk-Taking and Activity Hypotheses conducted in the laboratory experiments provided mixed results. Contrary to the predictions for the Risk-Taking Hypothesis (P4), lamprey that exited an enclosure more quickly in the laboratory trials did not

enter the smaller compartment (simulated trap) in the test tank faster than lamprey that exited an enclosure less quickly (Fig. 6). The regression coefficient relating time to enter the smaller compartment with time to exit the enclosure was positive, which was inconsistent with P4. However, the behaviour of the lamprey was consistent with the prediction of the Activity Hypothesis (P8). Lamprey that spent a higher proportion of time moving in the laboratory trials entered the smaller compartment faster than lamprey that spent a lower proportion of time moving (Fig. 6). The regression coefficient relating time to enter the smaller compartment with proportion of time spent moving was positive ($\beta = 2.56$), consistent with P8, and the 95% confidence limits of the regression coefficient were greater than 0 (2.02 to 3.10).

Discussion

Our findings provide no compelling evidence that the vulnerability of Sea Lamprey to trapping is influenced by consistent individual differences in behaviour, at least as predicted by the Risk-Taking and Activity Hypotheses. Consistent with the hypotheses, individuals differed consistently in the time to exit an enclosure into a novel area and the proportion of time spent moving in the open arena. Contrary to the hypotheses, however, the differences in time to exit an enclosure and proportion of time spent moving were not correlated with the time required to encounter a trap, or time to trap capture, when the lamprey were released in the field. Further, in the laboratory trials, time to exit an enclosure was not correlated with the time taken to enter a small compartment (simulated trap), contrary to the Risk-Taking Hypothesis. However, in the laboratory, lamprey that spent a higher proportion of time moving entered the small compartment sooner than lamprey that spent a lower proportion of time moving, suggesting the Activity Hypothesis could have merit under more confined spatial circumstances. Together these findings provide no evidence that the trapping efficiency for lamprey in the St. Marys River is constrained

by consistent individual differences in risk-taking or activity that affect individual vulnerability to traps.

These findings complement earlier studies of consistent individual differences in behaviour and trapping in lamprey. McLean and McLaughlin (2018) and Myles-Gonzalez et al. (2019) also demonstrated that lamprey from Lake Ontario tributaries display consistent individual differences in time to exit an enclosure and proportion of time spent moving in an open arena. The magnitudes of repeatability estimates obtained from this study, for lamprey from the St. Marys River, were similar to those obtained by McLean and McLaughlin (2018) and Myles-Gonzalez et al. (2019) for lamprey from smaller Lake Ontario tributaries, suggesting that repeatable differences in behaviour extend to lamprey across multiple locations. Moser et al. (2013) also observed consistent individual differences in the upstream rates of migration by Pacific Lamprey, although their study measured behaviour in the field and controlled for environmental variation statistically, whereas McLean and McLaughlin (2018), Myles-Gonzalez et al. (2019), and this study quantified consistent individual differences under standardized laboratory conditions. By controlling environmental effects in a laboratory setting, we were able to observe consistent individual differences in lamprey behaviour, an approach that has been successful in other studies assessing the ecological consequences of personalities in fishes (Wilson et al. 1993, Wilson and McLaughlin 2007, Wilson and Godin 2010, Kobler et al. 2011). As observed here, McLean and McLaughlin (2018) and Myles-Gonzalez et al. (2019) also found little and inconsistent evidence that the individual differences in behaviour quantified in the laboratory experiments were correlated with vulnerability to traps in the field. Their study design differed from this study, however. McLean and McLaughlin (2018) and Myles-Gonzalez et al. (2019) compared the behaviour of trapped lamprey with that of lamprey captured downstream of

traps, whereas this study characterized the behaviour of lamprey, released them, and compared the behaviour of individuals that were trapped sooner with that of lamprey trapped later. A potential limitation with comparing trapped lamprey with individuals downstream of a trap is that individuals downstream could be lamprey that had recently arrived and would shortly be trapped. The design of our study circumvented this limitation.

The absence of a relationship between consistent individual differences in behaviour and vulnerability to trapping in lamprey runs counter to the theoretical justification and empirical support for this relationship in other situations and taxa. The logic of the Risk-Taking and Activity Hypotheses is compelling (Fig. 1). Differences in risk-taking and activity are commonly hypothesized to influence vulnerability to trapping and to other capture methods (Réale et al. 2007, Biro and Dingemanse 2009, Carter et al. 2012). Further, empirical tests with other taxa showing that activity and risk-taking can influence susceptibility to trapping (Biro and Dingemanse 2009), angling (Cooke et al. 2007, Wilson et al. 2011), and netting (Biro and Post 2008) have provided reason to believe that susceptibility to trapping in lamprey could also be affected by individual differences in activity and risk-taking. Conversely, studies reporting no relationship between vulnerability and consistent individual differences in behaviour have been rare (eg. Michelangeli et al. 2016). For lamprey trapping in the St. Marys River, consistent individual differences in behaviour was a lead explanation for low trapping success, because such differences can result in a portion of the population that is not vulnerable to trapping (Harper et al. 2018), and because previous tests trying to exploit or manipulate behavioural flexibility by placing traps near high flows or adding pheromones did not consistently increase trapping efficiency (Johnson et al. 2013, Dawson et al. 2017, Rous et al. 2017). Further, any relationship between the probability of trap capture and consistent individual differences in

behaviour could be important, because trapping efficiency is relatively low (40%) for lamprey in the St. Marys River, and many lamprey remain untrapped. Any relationship between the probability of trap capture and consistent individual differences in behaviour would be less important as trapping efficiency approaches 100%, because most or all of the lamprey are being trapped irrespective of their behavioural differences. Finally, simulation models have also suggested that reasonable distributions of consistent individual differences in behaviour, based on earlier empirical studies, could create strong trapping bias and reduced trapping efficiency (Harper et al. 2018). Despite these reasons for expecting that consistent individual differences in behaviour could limit trapping efficiency, this study provided little empirical support for the key predictions that increased risk-taking and activity would lead to faster trap encounter and capture. These field tests are strong because there was wide and repeatable inter-individual variability in behaviour, steps were taken to maximize the potential variation in behavioural types used in the field releases, similar field results were observed across two trapping seasons, and the sample sizes (258 individuals in 2016 and 380 individuals in 2017) were substantially larger than the sample sizes tested in earlier field studies where vulnerability to trapping or capture was related to behaviour ($N = 28$ to 104; Réale et al. 2000, Cooke et al. 2007, McLean and McLaughlin 2018).

The contrary nature of our findings raises the perplexing question of why we did not observe a relationship between the consistent individual differences in lamprey behaviour and vulnerability to trapping. One possible explanation could be that the differences in behaviour detected in the laboratory experiments are not manifested under more complex field conditions. For example, responses of lamprey to chemical attractants in the field have been more complicated than responses observed in laboratory trials, especially when there is a background

signal of the attractant (Johnson et al. 2009, Luehring et al. 2011). For our study, a change in lamprey behaviour in field conditions could occur in two ways relevant to lamprey trapping. First, the nature of individual differences in behaviour can vary with environmental context. Biro (2012), for example, recognized that differences in behaviour measured in rapid laboratory assays could differ from those that exist in the field, because the former are measured under unfamiliar, contrived circumstances. For example, under normal field conditions the drive to migrate upstream could dampen individual differences in risk-taking and activity that are observed in laboratory flumes where cues used for migration are missing. Testing if consistent individual differences in the behaviour of lamprey in the laboratory trials correlate with their behaviour in the field would be useful, but past experience suggests such a test will be challenging and expensive to carry out (Rous et al. 2017). Second, during migration the physiology of lamprey changes in ways that affect behaviour and possibly erode the stability of individual differences in behaviour. Lamprey cease feeding prior to upstream migration so their energy reserves are declining as the migration progresses (Sower et al. 1985). At the same time they are maturing, which could also alter their movement behaviour as the time remaining to reproduce declines (Applegate and Moffett 1955). McLean and McLaughlin (2018) provide evidence showing that activity for individual lamprey can decline during the migration period. A study investigating if the repeatability of the behavioural differences changes between release in the field and recapture in traps is underway.

It also remains possible that vulnerability of lamprey to traps is related to consistent individual differences in behaviour, but we failed to observe the relationship. This possibility could have happened if there was inadequate time for the individual differences in behaviour to be revealed in the encounters and captures in this large management-level scale study. Studies

668 where a relationship between consistent individual differences in behaviour and vulnerability to
669 capture has been detected were carried out on smaller spatial scales (e.g., capture within a home
670 range or in a small pond) where the probability that a target individual would encounter a trap,
671 net, or lure during a given period of time was high (Cooke et al. 2007, Boon et al. 2008, McLean
672 and McLaughlin 2018). Conversely, the St. Marys River is relatively large (~100 km long and 1
673 km wide; Schleen et al. 2003), the lamprey can be highly mobile throughout the river (Holbrook
674 et al. 2016), the density of traps is quite low and concentrated at a small number of barriers to
675 upstream movement (Bravener and McLaughlin 2013), and the period of peak upstream
676 migration is relatively short (30-50 days; Vélez-Espino et al. 2011, Rous et al. 2017). Under
677 these conditions, there may be inadequate time for individual differences in behaviour to
678 manifest themselves into trap encounters and captures, even if the Risk-Taking and Activity
679 Hypotheses were true. Consistent with this idea, trapping efficiencies in smaller tributaries tend
680 to be higher than in the St. Marys River (Haeseker et al. 2007, Bravener and McLaughlin 2013,
681 Myles-Gonzalez et al. 2019). An alternative possibility is that vulnerability of lamprey is related
682 to consistent individual differences in behaviour, but involves behaviours other than risk-taking
683 and activity. For example, vulnerability to trapping could involve social behaviours. Cote and
684 Clobert (2007) and Cote et al. (2010) hypothesized that asocial individuals may colonize new
685 habitats first with social individuals following them. This hypothesis could extend to trapping,
686 whereby the traps are treated as empty habitat patches, such as a refuge, or a possible
687 passageway to new habitat upstream, because the traps emit flows as an attractant near barriers to
688 upstream movement. We consider this hypothesis to be unlikely. Using video observations,
689 McLean et al. (2015) found no evidence that the occurrence of other lamprey at a trap opening
690 interfered with or increased the probability of another lamprey entering the traps in the St. Marys

River. Still, investigations of hypotheses involving other behaviours remain needed. For example, whether trap entrance is influenced by the density of lamprey already in a trap remains uncertain. In addition, a recent study has suggested that individual lamprey could differ in their preference for different trap designs, including the design examined in this study and a design involving a wetted, inclined ramp (Reinhardt and Hrodey 2014, 2019).

Our study has three potential limitations that are important for interpreting the results and could be examined more rigorously in future studies. First, 34% of measurements for time to exit the enclosure in 2016 and 27% in 2017 were censored. The subjects remained in the enclosure for the entire 30 minutes of the laboratory trials so the true time until exit remains unknown and the distributions of exit times were biased toward shorter durations. This missing information could reduce the estimate of repeatability for the exit times, although values of repeatability estimated in this study were very similar to those estimated by Myles-Gonzalez et al. (2019) for lamprey tested in trials lasting 1 h. Second, the measurement of activity only considered horizontal movements. Water depth was shallow in the test tanks, but vertical use of the water column is important to trapping in large rivers where the water is much deeper (~15 m near the traps). Rous et al. (2017) determined that trap catch at our study site is limited, in part, by a spatial mismatch between the traps near the water surface and the lamprey that spend much of their time near the river bottom. Third, the fates of individual lamprey released, but not captured by the end of the migration period were not determined. Some of these undetected animals could have been trapped elsewhere in the St. Marys River or its tributaries. We consider this idea unlikely. Only, 2% of lamprey released were captured in the 15 traps operated on the USA side of the river and this low percentage is consistent with earlier studies of acoustic tagged lamprey at this same field site (Bravener and McLaughlin 2013, Rous et al. 2017).

This study highlights the importance of not assuming the findings from simple laboratory or field experiments relating behaviour with trapping extend seamlessly to larger, management-scale trapping operations, even when consistent individual differences in behaviour are observed. The lack of support for the Risk-Taking and Activity Hypotheses questions the idea that lower than desired trapping efficiency observed in the St. Marys River is due to consistent individual differences in behaviour affecting vulnerability to trapping. In the absence of such evidence, this study cannot support recommendations in favour of developing new trap designs targeting behavioural phenotypes that are not trapped effectively using current designs. However, this assessment could change as additional aspects of individual variation in behaviour are explored, or if environmental conditions or specific trap designs are found where consistent individual differences in behaviour are shown to matter. The insights from this study, and previous studies investigating the efficiency of trapping lamprey, reveal that the factors influencing trapping success are complex. Further, while the consistent individual differences in behaviour were not related to vulnerability to trapping, they also should not be ignored. Such inter-individual differences in behaviour could be important in other contexts relevant to the lamprey control program, such as the evolution of resistance to chemical lampricides (Dunlop et al. 2018).

Acknowledgements

We thank K. Cottenie and S. Crawford for comments on earlier drafts of the manuscript; J. Wolf, M. Brunet, and B. Bennett for their assistance in the field; personnel from the Department of Fisheries and Oceans and US Fish and Wildlife Service, in particular T. Voigt, D. Smith, K. Letson, and P. Hrodey for help obtaining, housing, and releasing Sea Lamprey; M. Cornish and M. Davis for contributing to the construction of the behaviour setup; N. Dingemanse

for encouraging us to conduct lab tests of the hypotheses; and a team of volunteers that helped process the video. This research was funded by grant 2014_McL_54025 from the Great Lakes Fishery Commission's Sea Lamprey Research Program.

References

Almeida, P.R., Quintella, B.R., Dias, N.M., and Andrade, N. 2002. The anadromous sea lamprey in Portugal: biology and conservation perspectives. *In* Proceedings of the International Congress on the Biology of Fish: the Biology of Lampreys. Vancouver. pp. 49–58.

Applegate, V., and Smith, B. 1950. Sea Lamprey spawning runs in the Great Lakes. *In* Species Scientific Report: Fisheries.

Applegate, V.C., and Moffett, J.W. 1955. The Sea Lamprey. *Sci. Am.* **192**(4): 36–41.

Bals, J.D., and Wagner, C.M. 2012. Behavioral responses of sea lamprey (*Petromyzon marinus*) to a putative alarm cue derived from conspecific and heterospecific sources. *Behaviour* **149**(9): 901–923.

Bates, D., Mächler, M., Bolker, B.M., and Walker, S.C. 2015. Fitting linear mixed-effects models using lme4. *J. Stat. Softw.* **67**(1): 1–48. doi:10.18637/jss.v067.i01.

Beauchamp, G. 2000. Individual differences in activity and exploration influence leadership in pairs of foraging zebra finches. *Behaviour* **137**(3): 301–314.

- 757 Bell, A.M., Hankison, S.J., and Laskowski, K.L. 2009. The repeatability of behaviour: a
758 meta-analysis. *Anim. Behav.* **77**: 771–783. doi:10.1016/j.anbehav.2008.12.022.
- 759 Berger-Tal, O., Blumstein, D.T., Carroll, S., Fisher, R.N., Mesnick, S.L., Owen, M.A.,
760 Saltz, D., St Claire, C.C., and Swaisgood, R.R. 2016. A systematic survey of the
761 integration of animal behavior into conservation. *Conserv. Biol.* **30**: 744–753.
762 doi:10.1111/cobi.12654.
- 763 Bergstedt, R.A., and Seelye, J.G. 1995. Evidence for lack of homing by Sea Lamprey.
764 *Trans. Am. Fish. Soc.* **124**(2): 235–239.
- 765 Binder, T.R., and McDonald, D.G. 2007. Is there a role for vision in the behaviour of sea
766 lampreys (*Petromyzon marinus*) during their upstream spawning migration? *Can. J.*
767 *Fish. Aquat. Sci.* **64**: 1403–1412. doi:10.1139/f07-102.
- 768 Binder, T.R., and McDonald, D.G. 2008. The role of temperature in controlling diel activity
769 in upstream migrant sea lampreys (*Petromyzon marinus*). *Can. J. Fish. Aquat. Sci.*
770 **65**(6): 1113–1121. doi:10.1139/f08-070.
- 771 Biro, P.A. 2012. Do rapid assays predict repeatability in labile (behavioural) traits? *Anim.*
772 *Behav.* **83**: 1295–1300. Elsevier Ltd. doi:10.1016/j.anbehav.2012.01.036.
- 773 Biro, P.A., and Dingemanse, N.J. 2009. Sampling bias resulting from animal personality.
774 *Trends Ecol. Evol.* **24**(2): 66–67. doi:10.1016/j.tree.2008.10.004.

- 775 Biro, P.A., and Post, J.R. 2008. Rapid depletion of genotypes with fast growth and bold
776 personality traits from harvested fish populations. *Proc. Natl. Acad. Sci.* **105**(8): 2919–
777 2922. doi:10.1073/pnas.0708159105.
- 778 Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošík, V., Wilson,
779 J.R.U., and Richardson, D.M. 2011. A proposed unified framework for biological
780 invasions. *Trends Ecol. Evol.* **26**(7): 333–339. doi:10.1016/j.tree.2011.03.023.
- 781 Blumstein, D.T., Evans, C., and Daniel, J.C. 2006. JWatcher 1.0.
- 782 Boon, A.K., Réale, D., and Boutin, S. 2008. Personality, habitat use, and their consequences
783 for survival in North American red squirrels *Tamiasciurus hudsonicus*. *Oikos* **117**:
784 1321–1328. doi:10.1111/j.2008.0030-1299.16567.x.
- 785 Bravener, G.A., and McLaughlin, R.L. 2013. A behavioural framework for trapping success
786 and its application to invasive sea lamprey. *Can. J. Fish. Aquat. Sci.* **70**(10): 1438–
787 1446. doi:10.1139/cjfas-2012-0473.
- 788 Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference: A
789 practical information-theoretic approach (2nd ed). *In Ecological Modelling*.
790 doi:10.1016/j.ecolmodel.2003.11.004.
- 791 Caro, T. 2007. Behavior and conservation: a bridge too far? *Trends Ecol. Evol.* **22**(8): 394–
792 400. doi:10.1016/j.tree.2007.06.003.

- 793 Carter, A.J., Heinsohn, R., Goldizen, A.W., and Biro, P.A. 2012. Boldness, trappability and
794 sampling bias in wild lizards. *Anim. Behav.* **83**(4): 1051–1058. Elsevier.
795 doi:10.1016/j.anbehav.2012.01.033.
- 796 Christie, G.C., and Goddard, C.I. 2003. Sea Lamprey International Symposium (SLIS II):
797 Advances in the integrated management of Sea Lamprey in the Great Lakes. *J. Great*
798 *Lakes Res.* **29**(Suppl. 1): 1–14. doi:10.1016/S0380-1330(03)70474-2.
- 799 Conrad, J.L., Weinersmith, K.L., Brodin, T., Saltz, J.B., and Sih, A. 2011. Behavioural
800 syndromes in fishes: A review with implications for ecology and fisheries
801 management. *J. Fish Biol.* **78**: 395–435. doi:10.1111/j.1095-8649.2010.02874.x.
- 802 Cooke, S.J., Suski, C.D., Ostrand, K.G., Wahl, D.H., and Philipp, D.P. 2007. Physiological
803 and behavioral consequences of long-term artificial selection for vulnerability to
804 recreational angling in a teleost fish. *Physiol. Biochem. Zool.* **80**(5): 480–490.
805 doi:10.1086/520618.
- 806 Corkum, L.D., and Belanger, R.M. 2007. Use of chemical communication in the
807 management of freshwater aquatic species that are vectors of human diseases or are
808 invasive. *Gen. Comp. Endocrinol.* **153**: 401–417. doi:10.1016/j.ygcen.2007.01.037.
- 809 Cote, J., and Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proc.*
810 *R. Soc. B Biol. Sci.* **274**(1608): 383–390. doi:10.1098/rspb.2006.3734.
- 811 Cote, J., Fogarty, S., Weinersmith, K., Brodin, T., and Sih, A. 2010. Personality traits and
812 dispersal tendency in the invasive mosquitofish (*Gambusia affinis*). *Proc. R. Soc. B*
813 *Biol. Sci.* **277**: 1571–1579. doi:10.1098/rspb.2009.2128.

- 814 Dawson, H.A., Bravener, G., Beaulaurier, J., Johnson, N.S., Twohey, M., McLaughlin,
815 R.L., and Brenden, T.O. 2017. Contribution of manipulable and non-manipulable
816 environmental factors to trapping efficiency of invasive sea lamprey. *J. Great Lakes*
817 *Res.* **43**: 172–181. doi:10.1016/j.jglr.2016.10.009.
- 818 De Vita, J., Kelly, D., and Payne, S. 1982. Arthropod encounter rate : A null model based
819 on random motion. *Am. Nat.* **119**(4): 499–510.
- 820 Dunlop, E.S., McLaughlin, R., Adams, J. V., Jones, M., Birceanu, O., Christie, M.R.,
821 Criger, L.A., Hinderer, J.L.M., Hollingworth, R.M., Johnson, N.S., Lantz, S.R., Li, W.,
822 Miller, J., Morrison, B.J., Mota-Sanchez, D., Muir, A., Sepúlveda, M.S., Steeves, T.,
823 Walter, L., Westman, E., Wirgin, I., and Wilkie, M.P. 2018. Rapid evolution meets
824 invasive species control: the potential for pesticide resistance in sea lamprey. *Can. J.*
825 *Fish. Aquat. Sci.* **75**: 152–168. doi:10.1139/cjfas-2017-0015.
- 826 El-Sayed, A.M., Suckling, D.M., Wearing, C.H., and Byers, J.A. 2006. Potential of mass
827 trapping for long-term pest management and eradication of invasive species. *J. Econ.*
828 *Entomol.* **99**(5): 1550–1564. doi:10.1603/0022-0493-99.5.1550.
- 829 Eshenroder, R.L. 2009. Comment: Mitochondrial DNA analysis indicates Sea Lampreys are
830 indigenous to Lake Ontario. *Trans. Am. Fish. Soc.* **138**(5): 1178–1189.
831 doi:0.1577/T08-035.1.
- 832 Gerritsen, J., and Strickler, J.R. 1977. Encounter probabilities and community structure in
833 zooplankton: a Mathematical Model. *J. Fish. Res. Board Canada* **34**: 73–82.

- 834 Haeseker, S.L., Jones, M.L., Peterman, R.M., Bence, J.R., Dai, W., and Christie, G.C. 2007.
835 Explicit consideration of uncertainty in Great Lakes fisheries management: decision
836 analysis of sea lamprey (*Petromyzon marinus*) control in the St. Marys River. Can. J.
837 Fish. Aquat. Sci. **64**: 1456–1468. doi:10.1139/F07-114.
- 838 Hárosi, F.I., and Kleinschmidt, J. 1993. Visual pigments in the sea lamprey, *Petromyzon*
839 *marinus*. Vis. Neurosci. **10**(4): 711–715. doi:10.1017/S0952523800005411.
- 840 Harper, D., Horrocks, J., Barber, J., Bravener, G., Schwarz, C., and McLaughlin, R.L. 2018.
841 An evaluation of statistical methods for estimating abundances of adult sea lamprey. J.
842 Great Lakes Res. **44**: 1362–1372. doi:10.1016/j.jglr.2018.08.004.
- 843 Hastie, G.D., Wilson, B., Wilson, L.J., Parsons, K.M., and Thompson, P.M. 2004.
844 Functional mechanisms underlying cetacean distribution patterns: Hotspots for
845 bottlenose dolphins are linked to foraging. Mar. Biol. **144**: 397–403.
846 doi:10.1007/s00227-003-1195-4.
- 847 Holbrook, C.M. 2015. Dynamics of Sea Lamprey, *Petromyzon marinus*, spawning
848 migrations in large rivers, with application to population assessment and control in
849 the Great Lakes. PhD, Department of Fisheries and Wildlife, Michigan State
850 University, East Lansing, MI.
- 851 Holbrook, C.M., Bergstedt, R.A., Barber, J., Bravener, G.A., Jones, M.L., and Krueger,
852 C.C. 2016. Evaluating harvest-based control of invasive fish with telemetry:
853 Performance of sea lamprey traps in the Great Lakes. Ecol. Appl. **26**(6): 1595–1609.
854 doi:10.1890/15-2251.1.

- 855 Hosmer, D. W. and Lemeshow, S. 1999. Applied Survival Analysis: Regression
856 modeling of time-to-event data. New York: John Wiley. pp. 386.
- 857 Hume, J.B., Meckley, T.D., Johnson, N.S., Luhning, T.M., Siefkes, M.J., and Wagner, C.M.
858 2015. Application of a putative alarm cue hastens the arrival of invasive sea lamprey
859 (*Petromyzon marinus*) at a trapping location. Can. J. Fish. Aquat. Sci. **72**: 1799–1806.
860 doi:10.1139/cjfas-2014-0535.
- 861 Johnson, N.S., Yun, S.S., Thompson, H.T., Brant, C.O., and Li, W. 2009. A synthesized
862 pheromone induces upstream movement in female sea lamprey and summons them
863 into traps. Proc Natl Acad Sci U S A **106**(4): 1021-1026.
- 864 Johnson, N.S., Siefkes, M.J., Wagner, C.M., Dawson, H., Wang, H., Steeves, T., Twohey,
865 M., and Li, W. 2013. A synthesized mating pheromone component increases adult sea
866 lamprey (*Petromyzon marinus*) trap capture in management scenarios. Can. J. Fish.
867 Aquat. Sci. **70**: 1101–1108. doi:10.1139/cjfas-2013-0080.
- 868 Jones, M.L., Brenden, T.O., and Irwin, B.J. 2015. Re-examination of sea lamprey control
869 policies for the St. Marys River: completion of an adaptive management cycle. Can. J.
870 Fish. Aquat. Sci. **72**: 1538–1551.
- 871 Kirk, M.A., Caudill, C.C., and Heino, J. 2017. Network analyses reveal intra- and
872 interspecific differences in behaviour when passing a complex migration obstacle. J.
873 Appl. Ecol. **54**(3): 836-845.

- 874 Kobler , A., Maes, G. E., Humblet, Y., Volckaert, F. A. M., and Eens, M. 2011.
875 Temperament traits and microhabitat use in bullhead, *Cottus perifretum*: fish
876 associated with complex habitats are less aggressive. Behaviour. **148**(5/6): 603-625.
- 877 Lawrie, A.H. 1970. The Sea Lamprey in the Great Lakes. Trans. Am. Fish. Soc. **99**(4): 766–
878 775. doi:10.1577/1548-8659(1970)99<766:TSLITG>2.0.CO;2.
- 879 Luehring, M.A., Wagner, C.M., and Li, W. 2011. The efficacy of two synthesized sea
880 lamprey sex pheromone components as a trap lure when placed in direct competition
881 with natural male odors. Biol. Invasions **13**(7): 1589-1597.
- 882 McLean, A.R., Barber, J., Bravener, G., Rous, A.M., and McLaughlin, R.L. 2015.
883 Understanding low success trapping invasive sea lampreys : an entry-level analysis.
884 Can. J. Fish. Aquat. Sci. **72**: 1876–1885.
- 885 McLean, A.R., and McLaughlin, R.L. 2018. Consistent individual differences in sea
886 lamprey (*Petromyzon marinus*) behaviour: Implications for control via trapping. J.
887 Great Lakes Res. **44**: 482–490. doi:10.1016/j.jglr.2018.03.002.
- 888 Merrick, M.J., and Koprowski, J.L. 2017. Should we consider individual behavior
889 differences in applied wildlife conservation studies? Biol. Conserv. **209**: 34–44.
890 Elsevier Ltd. doi:10.1016/j.biocon.2017.01.021.
- 891 Michelangeli, M., Wong, B.B.M., and Chapple, D.G. 2016. It's a trap: Sampling bias due to
892 animal personality is not always inevitable. Behav. Ecol. **27**(1): 62–67.
893 doi:10.1093/beheco/arv123.

- 894 Morales, J.A., Cardoso, D.G., Della Lucia, T.M.C., and Guedes, R.N.C. 2013. Weevil x
895 Insecticide: Does “Personality” Matter? PLoS One **8**(6): e67283.
896 doi:10.1371/journal.pone.0067283.
- 897 Morman, R.H., Cuddy, D.W., and Rugen, P.C. 1980. Factors influencing the distribution of
898 sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can. J. Fish. Aquat. Sci.
899 **37**(11): 1811–1826. doi:10.1139/f80-224.
- 900 Morse, T.J., Ebener, M.P., Koon, E.M., Morkert, S.B., Johnson, D.A., Cuddy, D.W.,
901 Weisser, J.W., Mullet, K.M., and Genovese, J.H. 2003. A case history of sea lamprey
902 control in Lake Huron: 1979 to 1999. J. Great Lakes Res. **29**(Suppl. 1): 599–614.
- 903 Moser, M., Keefer, M.L., Caudill, C.C., and Burke, B.J. 2013. Migratory behavior of adult
904 pacific lamprey and evidence for effects of individual temperament on migration rate.
905 *In* Physiology and Ecology of Fish Migration. pp. 132–151.
- 906 Myles-Gonzalez, E., McLean, A., and McLaughlin, R. 2019. Is there an impact of
907 behaviour on trapping migratory invasive sea lamprey (*Petromyzon marinus*)? Aquat.
908 Invasions **14**(3): 531–550.
- 909 Nakagawa, S., and Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data:
910 a practical guide for biologists. Biological Reviews **85**: 935–956.
- 911 Noldus, L.P.J.J., Spink, A.J., and Tegelenbosch, R.A.J. 2001. EthoVision: A versatile video
912 tracking system for automation of behavioral experiments. Behav. Res. Methods,
913 Instruments, Comput. **33**(3): 398–414.

- 914 Phillips, B.L., Brown, G.P., and Shine, R. 2010. Evolutionarily accelerated invasions: The
915 rate of dispersal evolves upwards during the range advance of cane toads. *J. Evol. Biol.*
916 **23**: 2595–2601. doi:10.1111/j.1420-9101.2010.02118.x.
- 917 Réale, D., Gallant, B.Y., Leblanc, M., and Festa-Bianchet, M. 2000. Consistency of
918 temperament in bighorn ewes and correlates with behaviour and life history. *Anim.*
919 *Behav.* **60**: 589–597. doi:10.1006/anbe.2000.1530.
- 920 Réale, D., Reader, S.M., Sol, D., McDougall, P.T., and Dingemanse, N.J. 2007. Integrating
921 animal temperament within ecology and evolution. *Biol. Rev.* **82**: 291–318.
922 doi:10.1111/j.1469-185X.2007.00010.x.
- 923 Reinhardt, U.G., and Hrodey, P.J. 2014. Field comparison of eel-ladder-style and traditional
924 sea lamprey traps. Project completion report to the Great Lakes Fisheries Commission.
925 Available from <http://www.glfc.org/research/scr.php#ac>.
- 926 Reinhardt, U.G., and Hrodey, P.J. 2019. Trap happiness and catch bias in sea lamprey traps.
927 *Fishes* **4**(2): 1–11. doi:10.3390/fishes4020034.
- 928 Rous, A.M., Mclean, A.R., Barber, J., Bravener, G., Castro-Santos, T., Holbrook, C.M.,
929 Imre, I., Pratt, T.C., and McLaughlin, R.L. 2017. Spatial mismatch between sea
930 lamprey behaviour and trap location explains low success at trapping for control. *Can.*
931 *J. Fish. Aquat. Sci.* **74**: 2085–2097. doi:10.1093/icesjms/fsr174.
- 932 Schleen, L.P., Christie, G.C., Heinrich, J.W., Bergstedt, R.A., Young, R.J., Morse, T.J.,
933 Lavis, D.S., Bills, T.D., Johnson, J.E., and Ebener, M.P. 2003. Development and
934 implementation of an integrated program for control of sea lampreys in the St. Marys

- 935 River. J. Great Lakes Res. **29**(Suppl. 1): 677–693. doi:10.1016/S0380-1330(03)70523-
936 1.
- 937 Sih, A., Bell, A.M., Johnson, J.C., and Ziemba, R.E. 2004. Behavioral syndromes: An
938 integrative overview. Q. Rev. Biol. **79**(3): 241–277. doi:10.1086/422893.
- 939 Smith, B.R., and Tibbles, J.J. 1980. Sea Lamprey (*Petromyzon marinus*) in Lakes Huron,
940 Michigan, and Superior: History of invasion and control, 1936-78. Can. J. Fish. Aquat.
941 Sci. **37**: 1780–1801.
- 942 Smith, B.R., Tibbles, J.J., and Johnson, B.G.H. 1974. Control of the sea lamprey
943 (*Petromyzon marinus*) in Lake Superior, 1953-70. Gt. Lakes Fish. Comm. Technical
944 Rep. 26. doi:10.1111/tra.12141.
- 945 Sower, S.A., Plisetskaya, E., and Gorbman, A. 1985. Changes in plasma steroid and thyroid
946 hormones and insulin during final maturation and spawning of the sea lamprey,
947 *Petromyzon marinus*. Gen. Comp. Endocrinol. **58**: 259–269. doi:10.1016/0016-
948 6480(85)90342-9.
- 949 Stoffel, M. A., Nakagawa, S., and Schielzeth, H. 2017. rptR: Repeatability estimation and
950 variance decomposition by generalized linear mixed-effects models. Methods Ecol.
951 Evol. **8**: 1639-1644 doi:10.1111/2041-210X.12797.
- 952 Sutherland, W.J. 1998. The importance of behavioural studies in conservation biology.
953 Anim. Behav. **56**: 801–809. doi:10.1111/j.1474-919X.1995.tb08439.x.

- 954 Team, R.C. 2016. R: A language and environment for statistical computing. R Foundation
955 for Statistical Computing, Vienna, Austria.
- 956 Therneau, T.M. 2018. coxme: Mixed effects Cox models. Available from [https://cran.r-](https://cran.r-project.org/package=coxme)
957 [project.org/package=coxme](https://cran.r-project.org/package=coxme).
- 958 Tix, J.A., Hasler, C.T., Sullivan, C., Jeffrey, J.D., and Suski, C.D. 2017. Elevated carbon
959 dioxide has limited acute effects on *Lepomis macrochirus* behaviour. J. Fish Biol. **90**:
960 751–772. doi:10.1111/jfb.13188.
- 961 Vélez-Espino, L.A., McLaughlin, R.L., Jones, M.L., and Pratt, T.C. 2011. Demographic
962 analysis of trade-offs with deliberate fragmentation of streams: Control of invasive
963 species versus protection of native species. Biol. Conserv. **144**(3): 1068–1080.
964 doi:10.1016/j.biocon.2010.12.026.
- 965 Wilson, A.D.M., Binder, T.R., McGrath, K.P., Cooke, S.J., and Godin, J.-G.J. 2011.
966 Capture technique and fish personality: angling targets timid bluegill sunfish, *Lepomis*
967 *macrochirus*. Can. J. Fish. Aquat. Sci. **68**: 749–757. doi:10.1139/f2011-019.
- 968 Wilson, A.D.M., and Godin, J.-G.J. 2010. Boldness and intermittent locomotion in the
969 bluegill sunfish, *Lepomis macrochirus*. Behav. Ecol. **21**(1): 57–62.
970 doi:10.1093/beheco/arp157.
- 971 Wilson, A.D.M., and McLaughlin, R.L. 2007. Behavioral syndromes in brook charr,
972 *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel
973 laboratory situations. Anim. Behav. **74**(4): 689–698.
974 doi:10.1016/j.anbehav.2007.01.009.

- 975 Wilson, D.S., Coleman, K., Clark, A.B., and Biederman, L. 1993. Shy bold continuum in
976 pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait.
977 J. Comp. Psychol. **107**(3): 250–260. doi:10.1037/0735-7036.107.3.250.

Draft

977 **Table 1.** A summary of the hypotheses and predictions tested, whether the test was conducted in the laboratory or field, and whether the prediction
 978 was supported (Yes/No).

Hypothesis	Predictions	Where the test was conducted		Support	
		Lab	Field	2016	2017
Risk-Taking	Repeatability (P1)	X		Yes	Yes
	Higher risk-taking decreased time to encounter (P2)		X	No	No
	Higher risk-taking decreased time to be captured (P4)	X (2017 only)	X	No	No
Activity	Repeatability (P5)	X		Yes	Yes
	Higher activity decreased time to encounter (P6)		X	No	No
	Higher activity decreased time to be captured (P8)	X (2017 only)	X	No	Yes (lab) No (field)

979

980 **Table 2.** Intraclass correlation coefficients and lower and upper confidence limits quantifying individual repeatability in the time to exit an
981 enclosure and the proportion of time spent moving during behavioural trials in 2016 and 2017. Models with adjustments for covariates included
982 individual ID, water temperature, sex, log₁₀ length, test tank number, and trial number. Models without adjustments for covariates only included
983 water temperature, individual ID, tank number, and trial number. Analyses for 2016 are based on 120 trials conducted on 60 individuals for exit
984 time and 38 trials for 19 individuals for proportion of time spent moving. Analyses for 2017 are based on 648 trials conducted on 324 individuals
985 for exit time and 646 trials for 323 individuals for proportion of time spent moving.
986

Behaviour	Intraclass correlation (r)	
	2016	2017
Exit time		
With adjustment for covariates	0.26 (0.06, 0.50)	0.25 (0.16, 0.35)
Without adjustment for covariates	0.26 (0.04, 0.50)	0.26 (0.16, 0.36)
Proportion of time moving		
With adjustment for covariates	0.68 (0.42, 0.89)	0.20 (0.12, 0.31)
Without adjustment for covariates	0.66 (0.35, 0.87)	0.20 (0.12, 0.31)

987
988
989

Table 3. The models and their ranks used to test the prediction for time to exit an enclosure in the laboratory and time to encounter a trap in the field. Negative log-likelihood, Akaike Information Criterion (AIC), difference in AIC between each model and the best approximating model (ΔAIC), degrees of freedom (df), and the model weights (w_i) are provided for each model. Model set 1 assessed covariates expected to influence time to encounter a trap, model set 2 assessed the risk-taking predictions using the best model carried forward from model set 1. Every model included individual ID, test tank number, and date of release (day of year) as random effects. 2016 and 2017 were modeled separately.

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w_i
2016					
Model set 1 (assessment of covariates)					
Intercept	-267.210	539.6	0	4	0.428
Log_{10} length	-266.431	540.3	0.71	6	0.300
Sex	-267.208	541.6	1.98	5	0.159
Log_{10} length, sex	-266.423	542.2	2.66	7	0.113
Model set 2 (assessment of risk-taking prediction)					
Intercept	-267.210	539.6	0	4	0.687
Time to exit	-266.996	541.2	1.57	5	0.313
2017					
Model set 1 (assessment of covariates)					
Log_{10} length, sex	-362.957	894.1	0	159	0.706

Table 3 (continued)

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w _i
Sex	-363.945	896.4	2.23	160	0.231
Log ₁₀ length	-360.794	900.7	6.54	165	0.027
Source, log ₁₀ length	-360.333	901.9	7.80	166	0.014
Intercept	-362.744	903.2	9.11	164	0.007
Source	-360.877	903.3	9.16	166	0.007
Source, log ₁₀ length, sex	-369.198	903.8	9.68	159	0.006
Source, sex	-368.155	906.8	12.65	162	0.001
Model set 2 (assessment of risk-taking prediction)					
Log ₁₀ length, sex	-362.957	894.1	0	159	0.808
Log ₁₀ length, sex, time to exit	-364.562	897.0	2.88	159	0.192

Table 4. The models and their ranks used to test the prediction for time to exit an enclosure in the laboratory and time to capture in the field. Negative log-likelihood, Akaike Information Criterion (AIC), difference in AIC between each model and the best approximating model (ΔAIC), degrees of freedom (df), and the model weights (w_i) are provided for each model. Model set 1 assessed covariates expected to influence time to trap capture, model set 2 assessed the risk-taking predictions using the best model carried forward from model set 1. Every model included individual ID, test tank number, and date of release (day of year) as random effects. 2016 and 2017 were modeled separately.

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w_i
2016					
Model set 1 (assessment of covariates)					
Intercept	-221.471	450.6	0	7	0.46
Log ₁₀ length	-221.252	451.8	1.18	7	0.255
Sex	-221.363	452.4	1.83	8	0.184
Log ₁₀ length, sex	-221.161	453.6	3.03	8	0.101
Model set 2 (assessment of risk-taking prediction)					
Intercept	-220.1961	450.0	0	8	0.569
Time to exit	-221.4713	450.6	0.557	7	0.431
2017					
Model set 1 (assessment of covariates)					
Log ₁₀ length, sex	-472.172	1113.1	0	173	0.870
Sex	-474.306	1117.4	4.29	174	0.102

Table 4 (Continued)

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w _i
Source, Log ₁₀ length, sex	-475.39	1120.9	7.82	174	0.017
Source, sex	-475.937	1122.1	8.98	175	0.01
Source, log ₁₀ length	-469.991	1127.7	14.58	183	0.001
Source	-469.248	1128.3	15.18	184	0
Log ₁₀ length	-481.150	1138.0	24.89	178	0
Intercept	-481.485	1139.4	26.27	179	0
Model set 2 (assessment of risk-taking prediction)					
Log ₁₀ length, sex, time to exit	-471.849	1112.7	0	174	0.552
Log ₁₀ length, sex	-472.172	1113.1	0.41	173	0.448

1006
1007
1008
1009
1010
1011
1012

Table 5. The models and their ranks used to test the prediction for proportion of time spent moving in the laboratory and time to encounter a trap in the field. Negative log-likelihood, Akaike Information Criterion (AIC), difference in AIC between each model and the best approximating model (ΔAIC), degrees of freedom (df), and the model weights (w_i) are provided for each model. Model set 1 assessed covariates expected to influence time to encounter a trap, model set 2 assessed the activity predictions using the best model carried forward from model set 1. Every model included individual ID, test tank number, and date of release (day of year) as random effects. 2016 and 2017 were modeled separately.

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w_i
2016					
Model set 1 (assessment of covariates)					
Intercept	-156.898	318.8	0	4	0.409
Log ₁₀ length	-155.844	319.3	0.51	6	0.317
Sex	-156.896	320.8	1.96	5	0.153
Log ₁₀ length, sex	-155.836	321.3	2.44	7	0.120
Model set 2 (assessment of predictor activity)					
Intercept	-156.898	318.8	0	4	0.647
Proportion of time spent moving	-156.514	320.0	1.21	5	0.353
2017					
Model set 1 (assessment of covariates)					
Log ₁₀ length, sex	-362.976	893.9	0	159	0.715
Sex	-363.933	896.2	12.31	159	0.225

Table 5 (Continued)

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w _i
Log ₁₀ length	-360.754	900.6	6.67	165	0.025
Source, log ₁₀ length	-360.247	901.9	7.93	166	0.014
Source	-360.619	903.0	9.09	166	0.008
Intercept	-362.699	903.2	9.24	164	0.007
Source, log ₁₀ length, sex	-369.166	903.9	9.96	159	0.005
Source, sex	-368.064	906.7	12.74	162	0.001
Model set 2 (assessment of predictor activity)					
Log ₁₀ length, sex	-362.976	893.9	0	159	0.74
Log ₁₀ length, sex, proportion of time spent moving	-362.962	896.0	2.09	160	0.26

1018

1019

1020

1021

1022

1023

1024

Table 6. The models and their ranks used to test the prediction for proportion of time spent moving in the laboratory and time to trap capture in the field. Negative log-likelihood, Akaike Information Criterion (AIC), difference in AIC between each model and the best approximating model (ΔAIC), degrees of freedom (df), and the model weights (w_i) are provided for each model. Model set 1 assessed covariates expected to influence time to encounter a trap, model set 2 assessed the activity predictions using the best model carried forward from model set 1. Every model included individual ID, test tank number, and date of release (day of year) as random effects. 2016 and 2017 were modeled separately.

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w_i
2016					
Model set 1 (assessment of covariates)					
Intercept	-131.045	270.6	0	7	0.478
Sex	-130.738	272.1	1.44	8	0.233
Log ₁₀ length	-131.001	272.4	1.77	8	0.197
Log ₁₀ length, sex	-130.749	273.9	3.31	9	0.091
Model set 2 (assessment of predictor activity)					
Intercept	-131.0455	270.6	0	7	0.711
Proportion of time spent moving	-131.0729	272.4	1.80	8	0.289
2017					
Model set 1 (assessment of covariates)					
Log ₁₀ length, sex	-472.216	1113.3	0	173	0.848
Sex	-474.203	1117.0	3.70	174	0.134

Table 6 (Continued)

Models considered	Negative log-likelihood	AIC	ΔAIC	df	w _i
Source, log ₁₀ length, sex	-476.147	1121.4	8.11	174	0.015
Source, sex	-477.222	1125.2	11.91	175	0.002
Source, log ₁₀ length	-470.054	1127.7	14.42	183	0.001
Source	-469.263	1128.3	14.97	184	0
Log ₁₀ length	-481.103	1137.9	24.63	178	0
Intercept	-481.441	1139.3	26.00	179	0
Model set 2 (assessment of predictor activity)					
Log ₁₀ length, sex	-472.216	1113.3	0	173	0.995
Log ₁₀ length, sex, proportion of time spent moving	-477.365	1123.9	10.59	174	0.005

Fig.1. The process involved in trapping an individual identifying the probabilistic events ($P_{\text{encounter}}$, P_{entrance}) and the corresponding predictions for the time to each event (P's 2,3,4,6,7,8). The trapping states of an individual range from not close enough to the trap to enter (unavailable), close enough to the trap to enter (available), and entrance into a trap (trapped). The willingness to take risks, activity levels, and the repeatability of these behaviours (P1 and P5) was quantified in the laboratory. Field indicates the time to event was measured in the field. Lab indicates the time to event was measured in the lab. NT indicates the prediction was not tested in this study. (Figure modified from Bravener and McLaughlin (2013)).

Fig. 2. A map of a portion of the St. Marys River near the Clergue Generating Station and its location within the Laurentian Great Lakes. Depicted are the north (NAWT) and south (SAWT) attractant water traps, and the three portable traps between the attractant water traps, and the north (N), centre (C), and south (S) sites of Sea Lamprey releases (white circles). The St. Marys River flows from left to right. Map created using Google Maps (2021).

Fig. 3. Drawings of the enclosures (A) and the laboratory tanks (B) used for behavioural laboratory trials in 2016 and 2017. The enclosure consisted of a 40 cm long piece of grey PVC pipe (10 cm inner diameter) cut in half lengthwise to create two half tubes positioned between two sheets of grey PVC with the cut sides facing downward. The laboratory tanks were 1.83 m cattle troughs. In 2017, a barrier was placed 95 cm from the enclosure to divide the each tank into two compartments: a larger compartment with the enclosure and a smaller compartment at the opposite end. A pump (black box) was attached to a hose (black line) that ran through the back (point of intake) and along the side of the tank to the smaller compartment (point of output) where it was attached to a wooden beam (vertical black rectangle).

Fig. 4. Data used to test if individuals exiting an enclosure faster in the laboratory trials (x-axis) encountered a trap (A for 2016 and B for 2017) and were captured (C for 2016 and D for 2017) sooner after release in the field (y-axis) than individuals exiting an enclosure slower in the laboratory trials. Each dot represents a single trial. The 2016 analysis is based on 318 trials involving 258 individuals (A and C). The 2017 analysis is based on 704 trials involving 380 individuals (B and D). The lines are provided for visual purposes. Bottom, middle, and top lines represent 0.1, 0.5, and 0.9 percentiles, respectively, for the distributions of time to encounter or be captured predicted at a given time to exit the enclosure, based on a parametric time-to-event regression with a Weibull distribution. Exit time from the enclosure is presented on a log₁₀ scale.

Fig. 5. Data used to test if individuals with a higher proportion of time spent moving in the laboratory trials (x-axis) encountered a trap (A for 2016 and B for 2017) and were captured (C for 2016 and D for 2017) sooner after release in the field (y-axis) than individuals with a lower proportion of time spent moving in the laboratory trials. Each dot represents a single trial. The 2016 analysis is based on 169 trials involving 150 individuals (A and C). The 2017 analysis is based on 703 trials involving 380 individuals (B and D). The lines are provided for visual purposes. Bottom, middle, and top lines represent 0.1, 0.5, and 0.9 percentiles, respectively, for the distributions of time to encounter or be captured predicted at a given time to exit the enclosure, based on a parametric time-to-event regression with a Weibull distribution. Proportion of time spent moving is presented on an arcsine square-root scale.

1164

1165 **Fig. 6.** Data used to test the predictions that individuals exiting an enclosure faster in the

1166 laboratory trials (A; x-axis) and individuals spending a higher proportion of time moving in the

1167 laboratory trials (B; x-axis) will enter the smaller compartment (y-axis) sooner after exiting an

1168 enclosure than individuals exiting an enclosure slower in the laboratory trials and spending a

1169 lower proportion of time moving in the laboratory trials. Each dot represents a single trial. The

1170 analyses are based on 704 trials involving 380 individuals for time to exit the enclosure and 703

1171 trials involving 380 individuals for proportion of time spent moving. The lines are provided for

1172 visual purposes. Bottom, middle, and top lines represent 0.1, 0.5, and 0.9 percentiles,

1173 respectively, for the distributions of time to enter the smaller compartment predicted at a given

1174 time to exit the enclosure or proportion of time spent moving, based on a parametric time-to-

1175 event regression with a Weibull distribution. Exit time from the enclosure and entrance time into

1176 the smaller compartment is presented on a log₁₀ scale. Proportion of time spent moving is

1177 presented on an arcsine square-root scale.