Understanding phenotypic and genetic variation in behaviours linked to migration in Lake Superior Brook Trout

by

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ABSTRACT

UNDERSTANDING PHENOTYPIC AND GENETIC VARIATION IN BEHAVIOURS LINKED TO MIGRATION IN LAKE SUPERIOR BROOK TROUT (Salvelinus fontinalis)

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I investigated the relationship between personality and migration in Lake Superior Brook Trout (Salvelinus fontinalis) known to display migratory polymorphisms: a small bodied stream resident, and a larger bodied migrant. Resident and migrant Brook Trout were captured and crossed to create 26 families. Five personality metrics were quantified for offspring and tested for (i) repeatability and heritability, (ii) phenotypic and genetic correlations, and (iii) relationships with the migratory behaviour of their parents. Assays of risk-taking, general activity, social behaviour, and propensity to disperse were conducted for the 0+, 1+, and 2+ age classes. Personality metrics were repeatable and heritable across age classes. I found evidence for a behaviour syndrome involving risk-taking, activity, and propensity to disperse. However, the personality of the offspring was not related to the migratory status of their parents at any age, suggesting that personality and migratory behaviour are not controlled by a simple, proximate mechanism.
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# TABLE OF CONTENTS

Acknowledgements.............................................................................................................iii

Table of contents.................................................................................................................iv

List of tables........................................................................................................................v

List of figures.........................................................................................................................vi

Introduction..........................................................................................................................1

Methods...............................................................................................................................7

  Adult sampling......................................................................................................................7

  Genetic crosses...................................................................................................................8

Rearing Conditions................................................................................................................9

Behavioural experiments......................................................................................................10

Experimental setup.............................................................................................................12

Experiment 1: Time to emerge from an enclosure (risk-taking).........................................14

Experiment 2: Proportion of time spent moving (general activity).......................................15

Experiment 3: Proportion of time spent near a mirror (sociability)......................................15

Experiment 4: Movement in an artificial stream (propensity to disperse)............................17

Statistical Analysis ............................................................................................................17

Results..................................................................................................................................24

  Assessments of assignments of migrant and resident.........................................................24

  Characterizing variation in behaviour..............................................................................24

  Quantifying phenotypic and genetic correlations between behavioural measures...........25

  Relationship between behaviour in the laboratory and behaviour in the field.................26

  Comparison of genetic variation across juvenile ontogeny..............................................28

Discussion............................................................................................................................29

Bibliography.........................................................................................................................40

Appendices...........................................................................................................................65
Table 1: Repeatability, heritability, variance components, and additive genetic variance relative to the mean behavioural score for each personality metric for 0+, 1+ and 2+ age class Brook Trout

Table 2: Estimates of genetic and raw phenotypic correlations between personality metrics for 0+, 1+ and 2+ age class Brook Trout

Table 3: Estimates of between-individual and within-individual phenotypic correlations between personality metrics for 0+, 1+ and 2+ age class Brook Trout

Table 4: Summary of the relationship between the behaviour of the offspring and the migratory cross type of the parents for 0+, 1+ and 2+ age class Brook Trout

Table 5: Meta-analyses output for repeatability, between-individual, and within-individual phenotypic correlations for personality metrics across the juvenile life stage (0+, 1+, 2+ age class) for Brook Trout

Table 6: Meta-analyses output for heritability, genetic, and raw phenotypic correlations for personality metrics across the juvenile life stage (0+, 1+, 2+ age class) for Brook Trout
LIST OF FIGURES

Figure 1: Location of Lake Superior and Nipigon Bay streams where adult migrant and resident Brook Trout used to create the study crosses were sampled..........................58

Figure 2: $\delta^{13}$C and $\delta^{15}$N signatures for adipose fin tissue of adult Brook Trout used to make genetic crosses..........................................................................................................................59

Figure 3: Schematic top view of the dispersal channels used to assess propensity to disperse in 0+, 1+, and 2+ age class Brook Trout..........................................................................................................................60

Figure 4: Variation in personality metrics for 0+, 1+ and 2+ age class Brook Trout used in repeatability trials..........................................................................................................................61

Figure 5: Box plots summarizing behavioural variation between cross types sharing the same dam but different sires for behavioural metrics for 0+, 1+, and 2+ age class Brook Trout..........................................................................................................................63
INTRODUCTION

There is broad interest in understanding the ecological and evolutionary significance of personality in wild animals. The past several decades have provided rich literature demonstrating that individual animals from wild populations can differ consistently in behaviour, beyond that expected based on differences in size, age, or sex (consistent individual differences in behaviour; Bolnick et al. 2003). This variation is often measured using standardized tests assessing an individual’s willingness to take risks in unfamiliar environments (avoidance-exploration) and familiar environments (shyness-boldness), activity in a benign environment (inactive-active), agonistic reactions towards conspecifics (unaggressive-aggressive), and nonaggressive affinity for conspecifics (asocial-social), and is termed personality or temperament (Réale et al. 2007). Variation in these behaviours may also be correlated, and is often referred to as a behavioural syndrome (Sih, A. Bell, et al. 2004; Conrad et al. 2011). These forms of individual differences in behaviour challenge earlier notions that there are one or a small number of optimal phenotypes within a population (Wilson 1998) and that behaviour is infinitely flexible (Sih, A. Bell, et al. 2004). Individual differences in behaviour also raise questions about the importance of ecological and evolutionary processes, such as population and food web dynamics (Wilson and McLaughlin 2007; Bassar et al. 2010; Bolnick et al. 2011), evolvability (Wagner and Altenberg 1996; Réale et al. 2007) and natural selection in the wild (Barrett and Schluter 2008; McNamara and Leimar 2010). While prominent papers have proposed ways in which individual differences in behaviour could be relevant to ecological and evolutionary processes (Sih et al. 2004; Wolf and Weissing 2012), rigorous assessments of
these proposals are required, given the breadth of taxa, behaviours, and environmental situations over which individual differences in behaviour have been observed.

Investigating the ecological and evolutionary implications of personality in wild animals entails at least three steps. The first step involves characterizing the variation in behaviour displayed within a population (Réale et al. 2007). Variation among individuals is commonly characterized by estimating repeatability (r) and heritability (h²) of behaviour. Repeatability quantifies the proportion of phenotypic variation in behaviour that can be attributed to differences between individuals (Bell et al. 2009). When individuals differ in behaviour, repeatability characterizes how strong individual consistency in behaviour is within a population. Heritability quantifies the proportion of phenotypic variation that can be explained by the additive genetic variance of a trait (Boake 1989). Estimates of heritability are important because heritability characterizes the potential for a trait to evolve in response to selection (Falconer and Mackay 1996). Measuring heritability is also important because repeatability in behaviour can be influenced by factors other than genetic differences, including maternal effects, environmental effects and developmental histories (Boake 1989; Falconer and Mackay 1996; Lynch and Walsh 1998; Dohm 2002). The second step in characterizing personality involves quantifying phenotypic and genetic correlations between behavioural measures (Réale et al. 2007). Phenotypic correlations provide evidence of behavioural syndromes and initial evidence of the potential for ecological and evolutionary trade-offs (Bell 2005; Réale et al. 2007). Genetic correlations quantify the degree to which the covariance between behavioural measures is governed by a common set of genes (Wilson et al. 2010). Genetic correlations can provide evidence that seemingly different aspects of behaviour are influenced by a common
underlying mechanism (Crusio 2001; Sih et al. 2004a,b) and provide insight into the evolvability of the behaviours (Réale et al. 2007; Hansen and Houle 2008). The third step involves testing whether the personality differences measured in standardized laboratory or field conditions are related to ecologically interesting behaviours in the field.

I investigated the relationship between personality and migration behaviour in Brook Trout (Salvelinus fontinalis), which commonly display polymorphisms in their life history (partial migration; Dutil and Power 1980). Partial migration refers to the phenomenon where some individuals from a population remain resident in their natal habitat, while others migrate to a new habitat for part of their life cycle, but return to their natal habitat to reproduce (Jonsson and Jonsson 1993; Chapman et al. 2012a,b). I focused on partial migration because it occurs across broad taxonomic and geographic ranges, and there is growing interest in its origin and ecological implications (Chapman et al. 2011b; Chapman et al. 2012a). Partial migration is common in fishes, particularly salmonids, that spawn in streams and rivers with access to coastlines of lakes or oceans (Chapman et al. 2012b). Partial migration is interesting ecologically because it influences spatial and temporal variation in the density of animals (Fryxell and Sinclair 1988) and the resources they compete for (Olsson et al. 2006; Chapman et al. 2012a). In addition, residents and migrants contribute to population dynamics (Vélez-Espino et al. 2013) because of differences in life history traits, such as growth rate, body size, age at maturity, life span, fecundity (Chapman et al. 2012a), and possibly Darwinian fitness (Hendry et al. 2004).

My study focused on the relationship between personality and partial migration because the mechanisms involved in partial migration are potentially complex, remain poorly understood, and could involve individual differences in behaviour (Dingle & Drake 2007;
Chapman et al. 2011b). Whether individuals remain residents or become migrants may be determined by the complex interplay between genetic factors (e.g. heritability and genetic correlations), ecology (e.g. competition between and within cohorts), and physiology (e.g. metabolic rate) (Dodson et al. 2013). The relative roles of genes, ecology, and physiology are unknown for polymorphic Brook Trout in Lake Superior (Huckins et al. 2008; Wilson et al. 2008), and remain a key subject of investigation in other populations of Brook Trout (Thériault et al. 2007) and salmonid fishes (Adams et al. 2014; Mittelbach et al. 2014; Závorka et al. 2015). The role of personality in these mechanisms remains unclear; however, there is empirical evidence suggesting personality could be important. Preliminary studies of fishes have successfully related migratory status (resident or migrant) and age at migration to boldness and aggression, respectively (Metcalfe 1998; Chapman et al. 2011a,b). A small set of studies has also related other forms of space use, including dispersal and activity while foraging, to measures of risk-taking (Wilson and McLaughlin 2007; Edelsparre et al. 2013), exploratory (Rasmussen and Belk 2012) and aggressive behaviours (Duckworth and Badyaev 2007). There is also literature proposing that variation in migratory behaviour could be attributed to relationships between metabolic rate, behaviour and life histories (Forseth et al. 1999; Morinville and Rasmussen 2003).

Concerns for Lake Superior Brook Trout provide an opportunity to examine the relationship between personality and migration. Two different migratory ecotypes of Brook Trout exist in Lake Superior: a small-bodied resident form that carries out its life cycle in stream tributaries and a large migrant form that migrates between lake habitat and stream tributaries (Huckins et al. 2008; Mucha and Mackereth 2008; Robillard et al. 2011a). The large migrant
form has declined in distribution and abundance since the mid-1800s and early 1900s (Schreiner et al. 2008; Newman et al. 2003). In the United States, there was an unsuccessful petition to list the migrant form under the U.S. Endangered Species Act (petitioners [all in Michigan] were the Sierra Club Mackinac Chapter, Lansing; Huron Mountain Club, Big Bay; and M. J. Robinson, Ann Arbor). In Canada, conservation efforts were established in the 1970s and many of the same concerns are recognized, including habitat degradation and overharvest (Schreiner et al. 2008). Understanding the genetic and environmental processes affecting migration is important for the successful conservation of Lake Superior Brook Trout after several failed attempts at rehabilitating the migrant form (Newman and Dubois 1996).

I used the offspring from genetic crosses made between wild-caught migrant and resident Brook Trout to test five hypotheses regarding how measures of personality could be related to migratory behaviour. Each hypothesis is based on the fact that migratory individuals must leave their natal habitat for a new habitat (juvenile outmigration). First, migration will require individuals to enter an unfamiliar habitat. If individuals differ in their willingness to explore unfamiliar environments, and that willingness to explore unfamiliar environments makes them more likely to enter new habitats (Risk-taking Hypothesis), then offspring of migratory parents would be expected to display greater willingness to explore novel environments than offspring of resident parents. I used time to exit an enclosure into an unfamiliar environment as a measure of risk taking, following Fraser et al. (2001) and Edelsparre et al. (2013). Second, outmigration requires movement from one habitat to another. If individuals differ in their level of activity or displacement, and increased activity or displacement makes them more likely to encounter new habitats (Activity Hypothesis), then
offspring of migratory parents would be expected to display greater activity or greater
displacement, then offspring of resident parents. I used the proportion of time spent moving in
a benign environment, displacement after 1 h in a dispersal channel, and transition rates
between compartments in a dispersal channel as measures of activity and displacement,
following Bradford and Taylor (1997) and Edelsparre et al. (2013). Third, migration involves
moving from a natal habitat where conspecific densities are high to a new habitat where
conspecific densities are low. If individuals differ in their affinity for conspecifics, and individuals
with high affinity for conspecifics are less likely to move into habitats where conspecifics are
rarer (Sociability Hypothesis), then offspring from migratory parents will be expected to display
a lower affinity for conspecifics than offspring from resident parents. I used an individual’s
proximity to its mirror image as a measure of social behaviour, following Cote and Clobert
(2007) and Cote et al. (2010). Fourth, it has been hypothesized that one or more of these
personality measures could share a common underlying mechanism, resulting in correlations
between the measures of personality (Behavioural Syndrome Hypothesis). If so, I expected that
willingness to take risks would be positively correlated with activity, and willingness to take
risks and activity would be negatively correlated with affinity for conspecifics. Fifth, it is possible
that the strength of any relationship between personality and migration is age specific
(Developmental Timing Hypothesis). Fish commonly out-migrate at predictable ages and that
outmigration can involve preparatory changes in behaviour and physiology, and underlying
changes in gene expression (Dodson et al. 2013).

I tested the predictions of these hypotheses by completing the three steps outlined by
Reale et al. (2007). My tests were completed for each of the three age classes comprising the
juvenile life stage. I first tested whether each of the five behaviours was repeatable and heritable (step 1). I then quantified the phenotypic and genetic correlations between the behaviours at each age class, to determine if there were behavioural syndromes (step 2). Next, I tested if the migratory status of the parents predicted offspring behaviour (step 3). Lastly, I tested whether the magnitudes of repeatabilities, heritabilities, and phenotypic and genetic correlations differed across the age classes (step 4).

METHODS

Adult Collection

Adult Brook Trout for mating crosses were captured in three tributaries of Nipigon Bay, Lake Superior between 24 – 27 October 2011 (Cypress River, Dublin Creek, and Maclnnnes Creek; Fig. 1). This area is one of the few locations in Lake Superior where the migratory ecotype of Brook Trout is still observed (Wilson et al. 2008). Nipigon Bay is bordered on the west by the Black Bay Peninsula and to the south by a chain of islands (Mucha and Mackereth 2008). Maximum water depth is approximately 140 m, however much of the western end of Nipigon Bay is less than 10 m deep. The surficial geology of the sample tributaries’ catchments is primarily bedrock, morainal deposits, and glacier outwash (Gartner 1979), with catchment areas ranging from 10.1 - 166.2 km² (Mucha and Mackereth 2008).

Ontario Ministry of Natural Resources and Forestry (OMNRF) staff captured adult Brook Trout from sample tributaries by electrofishing. Following capture, fish were held at the collection sites for 2-3 hours until electrofishing was complete. Fish were anesthetised in a bath of 40 mg*L⁻¹ Tricaine methane sulfonate (MS-222, TMS®, Syndel Laboratories) until they
reached a loss of equilibrium, and then were assessed for sex, spawning condition, and size. Mature females were identified by the release of eggs when gentle pressure was applied to the abdomen. Mature males were identified by pronounced colouration and release of milt. Each individual's length from the most anterior part of the head to the deepest point of the notch in the caudal fin (fork length) was measured to the nearest millimeter using a measuring board. Wet weight was measured to the nearest gram. Next, a sample of adipose fin tissue was collected using forceps, air dried, and stored in a bleach-free scale envelope. Adults were provisionally classified as a larger migrant (>250 mm fork length) or a smaller resident (<250 mm fork length) based on body size and body colouration.

Accuracy of the field assignments as migrant and resident was assessed post hoc using δ¹³C and δ¹⁵N signatures from the adipose fin samples (Fig. 2). Previous work by Robillard et al. (2011b) has established that lake-caught fish (migrants) and stream-caught fish (residents) can be distinguished with 90-94% accuracy using δ¹³C and δ¹⁵N values throughout the summer. Measurements of δ¹³C and δ¹⁵N for resident and migrant Brook Trout used for genetic crossings were quantified from adipose fin samples by the Stable Isotopes in Nature Laboratory (University of New Brunswick, Fredericton, NB).

Genetic Crosses

Twenty-six family crosses were created using gametes from 10 females (all migrant) and 18 males (10 migrant, 8 resident). Sperm from each male was crossed with eggs from 1-3 females and eggs from each female were crossed with the sperm of 2-4 males, resulting in 14 migrant x migrant crosses (MxM) and 12 migrant x resident crosses (MxR) (Appendix 1).
Offspring from different crosses either shared a father (half siblings) or were unrelated. The original intent was to set up crosses between male and female residents and migrants using a partial factorial design, but although female resident Brook Trout are known to reside in the sample tributaries (Robillard et al. 2014a), none were captured for the use of this experiment. The lack of female residents could reduce the range of possible variation observed in the offspring population.

**Rearing Conditions**

Fertilized eggs were transported from the field to the OMNRF Dorion Fish Culture Station (Dorion, Ontario) within the first 6 hours of fertilization, and held in an isolation room for 2.5 months in Heath stack egg incubators with ambient water temperatures ranging between 5-8 °C. In January 2012, the embryos were transported to the OMNRF Codrington Fisheries Research Facility (Codrington, Ontario). The embryos were hatched and offspring were reared in the OMNRF Codrington Fisheries Research Facility. Following hatch, fish were fed a daily portion of high protein commercial trout feed (Ewos Canada Limited) at a rate of 2-3 % bulk weight, and maintained under natural photoperiods and ambient temperature. Water was supplied to the facility onsite from the headwaters of March Creek. Following exogenous feeding, the families were culled to equal number of individuals, beginning at 120 fry per family and reduced numbers to 48 per family as the fish grew. In 2012, the families were housed individually in separate 25 L compartments. The compartments were created within 50 L flow-through tanks by inserting a plexiglass divider. In 2013, one of the two families in a 25 L compartment was selected at random, offspring from that family had their adipose fin clipped for identification purposes, and the tank divider was removed so that the pairs of families were
housed together in the 50 L tanks. Offspring were used in behavioural experiments during 2012 and 2013, with 24 families remaining after 2012 and 22 families remaining after 2013 (Appendix 1). In February 2014, 30 individuals from each family were selected randomly, anesthetized, measured for fork length and wet weight, and tagged with 15 mm passive integrated transponder (PIT) tags in a small incision below the dorsal fin for individual identification. Following recovery, the tagged individuals were housed in one of four circular flow-through fibreglass tanks (diameter 1.5 m and water depth 0.76 m). Each circular tank held offspring from up to six families. In June 2014, ten fish from each family were selected randomly and moved into a fifth 1.5 m diameter circular tank. At this time, individuals were anesthetized and measured for fork length and weight. One individual from each family was randomly selected from the circular tank and moved into one of five 50 L tanks at the beginning of each week during behavioural testing in 2014. At this time individuals were anesthetized and measured for fork length and weight, then given a minimum of three days to recover before behavioural experiments started.

**Behavioural Experiments**

Behavioural experiments were conducted from 13 June to 30 July 2012 with age 0+ fish (young of year; YOY; mean fork length: 56.2 mm, SE: 0.39 cm), 28 May to 26 June 2013 with age 1+ fish (mean fork length: 112.3 mm, SE: 0.67 cm) and 9 July to 21 August 2014 with age 2+ fish (mean fork length: 240.6 mm, SE: 1.42 cm). Behaviour of individuals at these age classes was examined because the age at which migrant fish leave their natal stream in these populations is unknown and analyses of age and growth histories have suggested that migrant individuals are larger (fork length) than stream resident individuals by age 1 (Robillard et al. 2011a).
Behavioural experiments were conducted by L. Sicoly in 2012 and 2013 (Sicoly 2015), and by myself in 2014. All raw behavioural data collected by L. Sicoly in 2012 and 2013 was reanalyzed by myself in 2015 to account for mislabelled family assignments (Appendix 1).

Two hundred and sixty individuals (26 families x 10 individuals per family) were sampled at the 0+ age class, 240 individuals (24 families x 10 individuals per family) were sampled at the 1+ age class, 220 individuals (22 families x 10 individuals per family) were sampled at the 2+ age class. The value of 10 individuals per family was selected based on Monte Carlo simulations assessing the expected power of heritability estimates, given the crossing design. The sampling sequence within each year consisted of 10 strata of 26 (in 2012), 24 (in 2013) or 22 (in 2014) fish (one individual per family per stratum). The order of sampling individuals within a stratum was randomized with respect to family to minimize temporal clumping of sampling in terms of family and cross type.

Individuals from each age class were used in four behavioural experiments (Experiments 1-4). Twelve individuals were assessed per day in 2012 and 2013, and eight to 16 individuals were assessed per day in 2014; eight fish on six of 25 sampling days, 12 fish on six of the 25 sampling days, and 16 fish on 13 of the 25 sampling days. Trials were conducted over a day in either the morning, early afternoon, late afternoon, or evening. Thirteen groups of randomly selected fish were retested to assess the repeatability of the behavioural measurements. At the end of 2012, one group of 12 randomly selected fish was run through behavioural trials each day for seven days. In 2013, five groups of eight randomly selected fish were run through the behavioural trials each day for three days. The trials were run for groups at the end of the 2nd, 4th, 6th, 8th, and 10th strata. In 2014, seven groups of eight randomly selected fish were run
through the behavioural trials each day for 3 days. The trials were run for groups at the end of the 1st, 2nd, 5th, 6th, 8th, 9th and 10th strata.

**Experimental Setup**

Four sequential experiments were completed to assess an individual’s behaviour. In 2012 and 2013, the setup for Experiments 1-3 consisted of four aquaria (60.96 x 30.48 x 43.18 cm) with open tops. In 2014, the setup for experiments 1-3 consisted of four plexiglass (107 x 43 x 44 cm) with closed tops to prevent fish from jumping out. The front (long) side of each aquarium was transparent so that the test fish could be observed. The remaining sides of each aquarium were opaque so that fish in adjacent tanks could not observe each other. Behavioural observations were made from behind an opaque curtain with small openings at eye level for observing the test fish. Lighting level was dim, but adequate for the fish to be observed. In 2014, behavioural observations for Experiments 1-3 were recorded using Jwatcher 1.0 (Blumstein et al. 2000). Water was drained and subsequently rinsed at the end of each day to remove possible traces of conspecific chemical cues.

The setup for Experiment 4 consisted of four, compartmentalized, flow-through dispersal channels similar to that used previously on Chinook Salmon (Oncorhynchus tshawytscha), Killifish (Rivulus hartii), and Brook Trout (Salvelinus fontinalis) (Hiscock and Brown 2000; Brown and Brown 1992; Quinn and Busack 1985; Edelsparre et al. 2013). In 2012 and 2013, each dispersal channel consisted of a 4 m length of opaque PVC pipe (46 cm diameter) cut in half along its length. The channels were subdivided into 15 compartments of 26 cm using opaque plexiglass dividers extending perpendicular from the channel wall and spanning two thirds of the channel.
width. Openings from one compartment to the next alternated from side to side so that a test fish could not move straight down the channel (Fig. 3a). The system was flow-through, with water added at 0.24 L*s⁻¹. Two sets of 4 CCTV cameras (Speco Technologies, Amityville, New York) were mounted directly over top of the channels (one set per two dispersal channels) and wired to a four-channel quad processor and VCR video recording system (Panasonic model PV-4624S-K). Each camera spanned a 1-m section of two dispersal channels. Black semi-transparent cloth covered the channels and cameras to minimize disturbance from observers. The setup was changed for 2014 due to the increased size of the fish. Each of the four dispersal channels were grey fibreglass rectangulars (503 x 61 x 61 cm). At the ends of each chamber, grey plastic barriers spanning the width of the chamber were used to separate the water inflow valve and outflow drain from the main portion of the tank, resulting in a functional length of 420 cm for each chamber. The main area of each chamber was divided into fifteen 28 cm long compartments using opaque plastic dividers spanning from the chamber bottom to 8 cm above the water surface and extending perpendicularly from the sidewall of the chamber to a point half way across the width of the chamber. The dividers were positioned to alternate from side to side along the chamber walls so that the test fish could move between compartments but could not swim up or down the chamber in a straight line (Fig. 3b). Eight PRO-642 cameras (Swann Communications, Melbourne, Victoria) connected to a monitor and a 9 channel 960H digital video recorder (DVR; Swann Communications, Melbourne, Victoria) were mounted 112 cm above the middle of each chamber on a frame constructed of PVC pipe. Video files were stored on a 1TB HDD internal hard drive on the DVR. Black semi-transparent cloth was hung over the camera frames and dispersal channels to reduce lighting and minimize disturbances. Windows in the hatchery building were blacked out to
ensure that the only light source was the interior hatchery lights. Water temperature during
behavioural experiments ranged from 8.4-13.5 °C in 2012, 7.4-14.3°C in 2013 and 9.3-14.8 °C in
2014.

**Experiment 1: Time to Emerge from an Enclosure (Risk-Taking)**

Risk-taking behaviour was measured using an enclosure-exit experiment (Brown et al.
2005; Farwell and McLaughlin 2009; Edelsparre et al. 2013). In this experiment, the aquarium
was considered a novel environment and the time to exit a dark tube (enclosure) was
considered to represent the fish’s assessment of the relative risk of remaining in the tube
versus entering the open aquarium. The design of the enclosure was changed across years to
accommodate changes in the body sizes of test fish (fork length: \( \bar{x} = 56.0 \) mm, \( \bar{x} = 112.1 \) mm,
and \( \bar{x} = 240.6 \) mm in 2012, 2013, and 2014, respectively). In 2012 and 2013, a vertical,
freestanding, dark grey polyvinyl chloride (PVC) tube (enclosure) was positioned at a narrow
end of the aquarium (Appendix B; Fig. 1). In year 2012, the tube was 38.1 cm high and 8.9 cm in
diameter. In year 2013, it was 38.1 cm high and 15.2 cm in diameter. Each tube had a vertical
opening with a sliding door that could be pulled up from the top of the aquarium. The tube
opening was 2 cm wide in 2012 and 4 cm wide in year 2013. In year 2014, the enclosure was a
33 cm piece of PVC pipe (33 cm long X 11 cm diameter) affixed horizontally to a piece of 0.64
cm thick PVC sheeting (41 X 41 cm) that spanned the width of the tank and prevented the
enclosure from moving. Two 0.32 cm thick PVC sheets (56 X 25 cm) were used as removable
doors to block each end of the pipe and keep the fish from escaping (Appendix B; Fig. 2). An 18
x 8 cm mesh covered a hole along the top of the pipe allowed light into the enclosure.
Each test fish was placed into each tube from the top, the top was covered, and the individual was given 30 minutes to acclimate to the tube in 2012 and 2013 (Chapman et al. 2011a). In 2014, a test fish was placed into the enclosure head first through the opening in the PVC pipe, removable doors were closed, and the enclosure was positioned to the side wall. Individuals were given 30 minutes to acclimate (Chapman et al. 2011a). In all years, the experiment commenced with the door of the enclosure being opened and individuals being allowed up to 1800 s to exit the tube. The time when the test fish exited entirely from the tube was recorded to the nearest second. Fish that had not exited the enclosure after 1800 s were assigned times of 1800 s in 2012 (n = 26), 2013 (n = 22), and 2014 (n = 85).

Experiment 2: Proportion of Time Spent Moving (General Activity)

General activity was measured as the proportion of time the individual spent moving in the aquarium. In 2012, fish were not included in Experiment 2 if they did not exit the enclosure. In 2013 and 2014, fish that had not exited the enclosure before 1800 s were forced from the enclosure into the open aquarium by gently tipping the tube. The instantaneous activity of each fish was categorized as moving or not moving at 60 s intervals for the full 1800 s after the fish emerged from the enclosure (instantaneous sampling; Altmann 1974; Leger 1977). The focal individual was categorized as moving at each interval if it was beating its caudal fin and changing its location. It was categorized as not moving if it was hovering in the water column or resting on the aquarium bottom. Proportion of time spent moving was calculated as the number of intervals where the test fish was moving divided by 30 intervals.
**Experiment 3: Proportion of Time Spent Near a Mirror (Sociability)**

The proportion of time spent near a mirror in a mirror image stimulation (MIS) experiment was used as a measure of social behaviour. This experiment was conducted immediately after the completion of Experiment 2. The PVC enclosure was gently removed from the test aquarium and the test fish was confined to one end of the aquarium using a piece of plexiglass spanning the aquarium width. A mirror spanning the aquarium width and height was then inserted against the opposite end of the aquarium. After 5 minutes, the plexiglass divider was removed and the test fish was allowed to interact with the mirror and its reflection. The test fish’s location relative to the mirror was assessed every 30 s for 10 min. Location relative to the mirror was recorded as being in the third of the aquarium closest to mirror, the middle third of the aquarium, or the third of the aquarium farthest from the mirror. The dimensions of the aquarium used in 2012 and 2013 was 60.96 x 30.48 x 43.18 cm while age 0+ fish which had an average fork length of 5.6 cm, and age 1+ fish that had an average fork length of 11.2 cm. The dimensions of the aquarium used in 2014 was 107 x 43 x 44 cm while age 2+ fish that had an average fork length of 24.1 cm. I also recorded instances of the test fish charging its reflection, but these instances were infrequent (e.g. 7% of trials in 2014). The proportion of time the test fish spent near the mirror was calculated by dividing the number of intervals when the test fish was in third of the aquarium closest to the mirror by 20 intervals.

While MIS tests can be used as a measure of aggressive behaviour, I found that Brook Trout did not engage with the mirror aggressively (e.g. charging and bolting behaviour was only observed in 7% of tested fish in 2014). Fish swimming alongside their image (e.g. 47% of tested fish in 2014) was not considered an aggressive behaviour because these encounters did not
include lateral displays, stiffened fins, flexed bodies, or physical contact such as biting or swiping with their tail (Archard and Braithwaite 2011). Similar trends were observed in 2012 and 2013. MIS tests have also been criticized for their inability to show the full range of behaviour responses and for poor replication of social interactions and hierarchies (Swain and Riddell 1990; Metcalfe 1986). However, MIS tests are useful tools as they provide a standardized way of measuring behaviour between offspring from different families, and remove confounding variables such as relative size or motivational state (Svendsen and Armitage 1973; Taylor and Larkin 1986; Swain and Holtby 1989; Swain and Riddell 1990).

**Experiment 4: Movement in an artificial stream (Propensity to Disperse)**

Net displacement (for 0+, 1+ and 2+) and an estimation of transition rate between compartments in an artificial stream (for 1+ and 2+) were used as measures of propensity to disperse. This experiment followed Experiments 1-3. Individual fish were placed into the middle compartment of a dispersal channel and temporally prevented from leaving the compartment by perforated PVC barrier allowing water flow. Each fish was given 30 minutes to acclimate (Edelsparre et al. 2013) before the barriers were removed, allowing each fish to move throughout the channel. Fish were placed in the center compartment so they could move with or against the flow. Fish movements were recorded for one hour using overhead cameras. Net displacement (distance from the starting compartment to the end compartment one hour post start) and an estimation of transition rate (see below) were used as measures of propensity to disperse. Net displacement was chosen as a measure of propensity to disperse because it is a simple measure of the outcome of the dispersal process at a specific time. Transition rate was
chosen as a measure of propensity to disperse because it characterizes the entire dispersal process and can predict the likelihood of future movements (Edelsparre et al. 2013).

At the completion of behavioural experiments fish were either euthanized or returned to their family tanks. In 2012 and 2013 fish were euthanized with a lethal dose of MS-222 and measured for fork length (nearest mm) and body weight (nearest g). At this time, their brains were extracted so they could be used by another researcher for genetic testing. At the end of behavioural testing in 2014, fish were returned to the circular tanks housing their families. In the fall of 2014, the maturity of remaining fish was assessed. Mature females were identified by the release of eggs when gentle pressure was applied to the abdomen. Mature males were identified by pronounced colouration and release of milt. With the exception of three males, all individuals were classified as mature.

Statistical Analysis

Experiments 1-3 provided estimates of the time to exit the enclosure, proportion of time spent moving, and proportion of time spent near the mirror. The movements recorded in Experiment 4 provided a measure of net displacement, but required further analysis to obtain an estimate of transition rate in a dispersal channel. To estimate transition rate between compartments, I quantified the time each individual spent in each compartment in the dispersal channel for the first 5 and 12 minutes of observation time for 1+ and 2+ age class individuals, respectively. Durations of 5 and 12 minutes were selected because preliminary examinations of the video demonstrated that the most mobile test fish started to reach the end of the dispersal chamber by these times. In 2013, transition rates for each individual were then estimated using the conditional modes obtained for a mixed effects Cox model relating the times spent in a
compartment to fork length and water temperature (fixed effects) while accounting for individual identity (a random effect). Transition rates were estimated the same way in 2014 with the addition of time of day as a fixed effect (factor with four levels; morning, early afternoon, late afternoon, and evening). Additional fixed effects included water temperature and fork length because fish behaviour can vary with temperature (Biro et al. 2010) and body size (Thériault et al. 2007). Trial number for the day was included because fish can alter their behaviour based on the time of day (Helfman 1986). I was not able to estimate transition rates for some of the test fish due to errors with the recording system, where some video was corrupted making it impossible to analyze movements of the fish. This analysis was completed once to obtain estimates for 226 of 240 fish sampled in 2013, and 209 of the 220 fish sampled in 2014.

This process was completed a second time for the subset of fish used in the repeatability trials to obtain estimates for each individual in 2014. For these estimates, trial number for the repeated measures (factor with three levels; 1, 2 or 3) was included as a fixed effect to account for potential habituation (Nakagawa and Schielzeth 2010). This model was used to obtain estimates of 49 of the 56 fish sampled in 2014. Models were run using the coxme package in R 3.1.1 (R Development Core Team 2014).

Characterizing the Repeatability and Heritability of Behaviour (Step 1)

Repeatability was estimated for each behavioural measure using data for the subset of fish that were measured multiple times for 0+ (N = 12), 1+ (N = 40) and age 2+ (N = 56) individuals. The interclass correlation, \( r = \sigma_a^2 / (\sigma_e^2 + \sigma_a^2) \), was used to quantify repeatability,
where $\sigma^2_A$ is the variance estimated between individuals and $\sigma^2_E$ is the variance estimated within individuals (Lessells et al. 2009). The variance components were estimated using a mixed effects animal model (Kruuk 2004) relating values of the behaviour to individual identity as a random effect and water temperature, fork length, and trial number as fixed effects for models conducted in 2012, 2013 and 2014. Time of day was also included in 2014. Each model was run using R 3.1.1 (R Core Team, 2014) using Markov chain Monte Carlo Generalized Linear Mixed Modelling (MCMCglmm) methods (Hadfield 2010). Separate models for each age class used an inverse-Wishart prior distribution, 80 000 iterations, a burn-in of 20 000 iterations, and a thinning interval of 25. Time demands required for video analysis prevented me from acquiring the data needed to calculate transition rate for repeated measures in 2012 and 2013. Mixing and convergence for all of the Bayesian models were confirmed using trace and density plots, as well as Geweke and Gelman-Rubin diagnostic tests. Geweke diagnostic tests compare an early section of the Markov chain after the burn-in period to a section much later in the chain to confirm convergence (Geweke 1991). Gelman-Rubin diagnostic tests were run to confirm convergence by running three parallel models that were each independently required to reach the same posterior distribution (Gelman and Rubin 1992). All Bayesian analysis significance testing was done by assessing credible intervals: if 95% credible intervals did not overlap with zero, then the effect was considered significant (Wilson et al. 2010). To meet assumptions of normality in all analyses, time to exit the enclosure was $\log_{10}$ transformed, both proportion of time spent moving and proportion of time spent close the mirror were arcsine square-root transformed, and net displacement was square root transformed.
Narrow sense heritabilities ($h^2$) were calculated for each behavioural measure using univariate animal models in the MCMCglmm package. Heritability estimates were calculated as $V_A / V_P$, where $V_A$ is the additive genetic variance and $V_P$ is the phenotypic variance. Each model considers how a behavioural trait is predicted by a given matrix of additive genetic effects and includes water temperature and fork length as fixed effects in 2012, 2013 and 2014. Time of day was also included as a fixed effect in 2014. Separate models were run for each age class using an inverse-Wishart prior distribution, 120 000 iterations, a burn-in of 30 000 iterations, and a thinning interval of 50 (Hadfield 2010).

Quantifying Phenotypic and Genetic Correlations between Behavioural Measures (Step 2)

Phenotypic correlations between behavioural measures were assessed in two ways. First, raw phenotypic correlations were calculated between pairs of behavioural measurements using Pearson's correlation coefficient ($r$) for all individuals in 2012, 2013 and 2014 ($N=260$, $N=240$, and $N=220$, respectively). Second, between-individual ($r_{\text{ind}_y, \text{ind}_z}$) and within-individual ($r_{\text{e}_y, \text{e}_z}$) correlation coefficients were calculated in MCMCglmm for the subset of fish measured multiple times for each age class ($N=84$, $N=40$, and $N=56$, respectively) as:

\[
\begin{align*}
    r_{\text{ind}_y, \text{ind}_z} &= \frac{\text{COV}_{\text{ind}_y, \text{ind}_z}}{\sqrt{V_{\text{ind}_y} V_{\text{ind}_z}}} \\
    r_{\text{e}_y, \text{e}_z} &= \frac{\text{COV}_{\text{e}_y, \text{e}_z}}{\sqrt{V_{\text{e}_y} V_{\text{e}_z}}}
\end{align*}
\]

where $\text{COV}_{y,z}$ represents the covariance between behavioural measure ($y$) and behavioural measure ($z$), and $V_y$ and $V_z$ are the corresponding phenotypic variances for each behavioural measure (Dingemanse and Dochtermann 2013). The variances and covariances were estimated using a multivariate mixed effects model (i.e., a single model with multiple dependent variables) in MCMCglmm (Dingemanse and Dochtermann 2013). Separate models were
conducted for each age class relating behavioural measures to random and fixed effects. Individual identity was modelled as a random effect, and fork length, temperature and trial number were modelled as fixed effects at all age classes. Time of day was also included as a fixed effect in 2014. Separate models were run for each age class using an inverse-Wishart prior distribution, with 150,000 iterations, a burn-in of 50,000, and a thinning interval of 50 (Hadfield 2010). Convergence and significance was assessed as described above.

Genetic correlations ($r_G$) between behavioural measures were calculated using a multivariate model in MCMCglmm to estimate the additive genetic variances for the traits and genetic covariances between the traits. The random effect of individual identity was linked to additive genetic values through the inclusion of a pedigree. Water temperature and fork length were included as fixed effects in 2012, 2013 and 2014. Time of day was also included as a fixed effect in 2014. Separate models were run for each age class using an inverse-Wishart prior distribution, with 200,000 iterations, a burn-in of 75,000 and a thinning interval of 50 (Wilson et al. 2010). Genetic correlations were considered significant if 95% credible intervals of the estimates did not overlap with zero (Wilson et al. 2010).

**Relationship between Behaviour in the Laboratory and Behaviour in the Field (Step 3)**

The relationship between the behaviour of offspring and the migratory life history of their parents was tested using univariate animal models in MCMCglmm relating each behaviour measure to cross type (MxM or MxR). Each model used a given matrix of additive genetic effects as a random effect and water temperature, fork length, and cross type as fixed effects in 2012, 2013 and 2014. Time of day was also included as a fixed effect in 2014. Separate models were run for each age class using an inverse-Wishart prior distribution, with 110,000 iterations,
a burn-in of 25,000 and a thinning interval of 50 (Wilson et al. 2010). Posterior means and credible intervals were used to assess the statistical significance of the relationships between each offspring behaviour and cross type.

A multivariate analysis of variance (MANOVA) was used to test for differences in behavioural measures between families at each age class. Separate models were conducted for behavioural measures in 2012, 2013, and 2014. Each model related the dependent variables [time to exit the enclosure, proportion of time spent moving, proportion of time spent near a mirror, net displacement, and transition rate (when applicable)] to family, the independent variable. In all years, water temperature, length, and family were included in the model as fixed effects. Time of day was also included in 2014. An analysis of variance (ANOVA) was used to test for differences in individual behavioural measures between families at each age class. Each model used an individual behavioural measure as the dependent variable, and family as the independent variable. Water temperature, length and family were included in the models as fixed effect at all age classes. Time of day was also included as a fixed effect in 2014.

**Comparison of Genetic Variation Across Juvenile Ontogeny**

I used meta-analyses to evaluate the consistency of estimates for repeatability and heritability estimates, as well as raw phenotypic, between-individual, within-individual and genetic correlations across the 0+, 1+, and 2+ age classes. To ensure standardized measures, repeatability and heritability estimates, and correlation coefficients were converted into effect sizes using Fisher's $r$ to $z$ transformation (Polderman et al. 2015). To test the homogeneity of the variation around the effect sizes, the homogeneity statistic ($Q_t$) was calculated using a
random-effects model in the metafor package in R 3.2.1 (R Core Team 2015). The models testing homogeneity included the effect sizes and corresponding variances for each behaviour or correlation at each age class. Variance was calculated for repeatability and heritability estimates using the formula $V = 1/(n-3)$, where $n$ is sample size (Borenstein et al. 2009). To attain the variance for correlations, the credible intervals reported for each correlation were standardized using Fisher's $r$ to $z$ transformation. The range between the upper and lower interval was then divided by four to attain the standard error. The standard error was then squared to attain the variance. The average heritabilites and correlation coefficients across years reported by the models were back transformed and assessed for significance using back transformed confidence intervals reported by the models. If 95% confidence intervals did not overlap with zero, then the effect was considered significant. Significant homogeneity between age classes was reported if the homogeneity statistic ($Q_t$) had a p-value of less than 0.05.

RESULTS

Assessment of assignments as migrant and resident

Adults classified as migrants were 432 mm in fork length ($CL_{0.95}$: 402-462) and 849 g wet weight ($CL_{0.95}$: 686-1013) on average. Adults classified as stream resident were 185 mm in fork length ($CL_{0.95}$: 147-223) and 85 g wet weight ($CL_{0.95}$: 17-153) on average. Analyses of $\delta^{13}C$ and $\delta^{15}N$ supported the field assignments of parent fish as migrant and resident. A biplot of $\delta^{13}C$ and $\delta^{15}N$ revealed complete separation of adults assigned as migrant and resident (Fig. 2). Adults classified as migrants had higher $\delta^{13}C$ values than adults classified as residents ($\delta^{13}C$: $\bar{x} = -19.1\pm0.23\%$ vs. $\bar{x} = -23.5\pm0.38\%$, respectively).
Characterizing Repeatability and Heritability in Behaviour (Step 1)

The behaviour displayed in the experiments differed markedly for individuals at the 0+, 1+, and 2+ age classes. Time to exit an enclosure ranged from 1 to 1800 seconds, proportion of time spent to 1 and net displacement ranged from 0 to 7 compartments at all three ages classes. Transition rates ranged from 0.46 to 5.2 1*s\(^{-1}\) at the 1+ age class and 0.48 to 10.4 1*s\(^{-1}\) at the 2+ age class. The subset of individuals measured multiple times displayed similar, wide inter-individual variation for all the behavioural measures.

Individual differences in behaviour were repeatable within each age class, although intra-class correlation coefficients varied in magnitude between behaviours and between age classes (Table 1). For age 0+, estimates of repeatability ranged from 0.42 for time to exit an enclosure to 0.83 for the proportion of time an individual spent near the mirror (Fig.4; Table 1). For age 1+, estimates of repeatability ranged from 0.57 for the net displacement in a dispersal chamber to 0.75 for proportion of time spent moving (Fig.4; Table 1). For age 2+, estimates of repeatability ranged from 0.15 for transition rate in the dispersal chamber to 0.58 for the time to exit the enclosure (Fig.4; Table 1).

Estimates of narrow-sense heritability indicate additive genetic variance for these behaviours at every age class. For age 0+, heritability estimates ranged from 0.24 for the proportion of time an individual spent near the mirror to 0.35 for the proportion of time an individual spent moving (Table 1). For age 1+, heritability estimates ranged from 0.08 for net displacement to 0.48 for the proportion of time an individual spent moving (Table 1). For age
2+, heritability estimates ranged from 0.07 for transition rate to 0.46 for the proportion of time and individual spent moving (Table 1).

Quantifying Phenotypic and Genetic Correlations between Behavioural Measures (Step 2)

There was evidence of significant raw phenotypic correlations between behavioural measurements at the 0+, 1+, and 2+ age classes (Table 2). Raw phenotypic correlations revealed individuals that took less time to exit the enclosure also spent a higher proportion of their time moving in the activity experiment at all age classes (Table 2). As well, individuals that took less time to exit the enclosure had a higher net displacement in the dispersal channel compared to individuals that took longer to exit the enclosure at the 0+ and 1+ age classes (Table 2). Individuals that spent more time moving in the activity experiment also had a higher net displacement at the 0+ age class. At the 2+ age class, individuals that spent more time moving in the activity experiment spent more time near their reflection in the sociality experiment and had a higher transition rate in the dispersal channel (Table 2). There was evidence for between and within-individual correlations between behavioural measures at the 0+, 1+, and 2+ age classes, with the exception of between-individual correlations at the 0+ age class (Table 3). Between-individual correlations revealed that individuals that took less time to exit the enclosure spent a higher proportion of their time moving in the activity experiment at the 1+ and 2+ age classes, and had a higher net displacement in the dispersal channel at the 1+ age class (Table 3). Additionally, individuals that spent a higher proportion of their time moving in the activity experiment had a higher net displacement in the dispersal channel at the 1+ age class. Within-individual correlations revealed that individuals that took less time to exit the enclosure spent a higher proportion of their time moving in the activity experiment at the 0+
and 2+ age classes (Table 3). Additionally, individuals that took less time to exit the enclosure
also a higher proportion of their time near the mirror in the sociality experiment at the 2+ age
class (Table 3). Genetic correlations varied in magnitude at all three age classes, but in all
instances the 95% credible intervals included 0 (Table 2).

*Relationship between Behaviour in the Laboratory and Behaviour in the Field (Step 3)*

There was no evidence that differences in the behavioural measures quantified for
offspring were related to the migratory behaviour of their parents (Table 4). Offspring from pure
migrant crosses did not take less time to exit a enclosure, did not spend a higher proportion of
their time moving, did not spend a lower proportion of their time near a mirror, did not have a
higher net displacement, or a higher transition rate in a dispersal channel compared to offspring
from migrant-resident crosses at any age class.

The absence of relationships between the behaviour of offspring and migratory
behaviour of parents was not due to an absence of variation among families. There was
significant between-family variation in the behavioural measures (MANOVA: Pillai_{100,824} = 0.61,
p = 0.002, MANOVA: Pillai_{115,995} = 0.78, p = 0.0001, and MANOVA: Pillai_{105,835} = 0.75, p = 0.007
for 0+, 1+, and 2+ age classes, respectively; Fig. 5). Significant family differences in proportion of
time spent moving were detected at 0+ \((F_{25, 206} = 2.10, p = 0.003)\), 1+ \((F_{23, 199} = 2.96, p =
0.00002)\) and 2+ \((F_{21,167} = 2.63, p = 0.0003)\) age classes. Significant family difference in time to
exit an enclosure, net displacement and transition rate were detected in some age classes but
not others. For time to exit a enclosure, significant family differences were detected at the 1+
\((F_{23, 199} = 1.63, p = 0.04)\) and 2+, \((F_{199} = 1.63, p = 0.04)\) age classes, but not at the 0+ \((F_{25, 206} =
0.82)\)
1.31, p = 0.16) age class. For net displacement, significant family differences were detected at
the 0+ ($F_{25, 206} = 2.10, p = 0.003$) age class, but not at the 1+ ($F_{23, 199} = 1.20, p = 0.25$) or 2+
$F_{21,167} = 0.92, p = 0.57$) age classes. For transition rate, significant family differences were
detected at the 1+ ($F_{23, 199} = 1.61, p = 0.05$) age class, but not at the 2+ ($F_{21,167} = 0.89, p = 0.61$)
age class. No family differences were detected at 0+ ($F_{25, 206} = 1.13, p = 0.32$), 1+ ($F_{23, 199} = 0.95$,
p = 0.53) and 2+ ($F_{21,167} = 1.47, p = 0.10$) age classes for proportion of time spent near a mirror.

Comparison of Genetic Variation across Juvenile Ontogeny

Repeatability and heritability estimates for measured behaviours were statistically
significant across the juvenile life stage (Table 5; Table 6). All repeatability estimates showed
significant heterogeneity for behaviours between age classes, while only the heritability estimate
for net displacement in a dispersal chamber showed significant heterogeneity between years
(Table 5; Table 6). Repeatability estimates varied little in magnitude for the juvenile life stage, and
ranged from 0.56 for net displacement in a dispersal chamber to 0.62 for proportion of time spent
moving and proportion of time spent near a mirror (Table 5). Heritability estimates for the
juvenile life stage varied more in magnitude and ranged from 0.12 for transition rate in a dispersal
chamber to 0.42 for proportion of time spent moving (Table 6). Coefficients for between-
individual correlations ranged from values near zero to values near $\pm 0.40$ (Table 5). Coefficients
for within-individual correlations ranged from values near zero to values near $\pm 0.25$ (Table 5).
Significant heterogeneity between years for within-individual correlations existed for time to exit
the enclosure and proportion of time spent moving, and time to exit the enclosure and proportion
of time spent near a mirror. Coefficients for raw phenotypic correlations ranged from values near
zero to values near $\pm 0.30$ (Table 6). Coefficients of genetic correlations ranged from near zero to
values near ± 0.40 (Table 6). Between-individual, within-individual, and genetic correlations revealed that individuals that took less time to exit the enclosure spent a higher proportion of their time moving in the activity experiment.

DISCUSSION

This study demonstrated that the personality metrics of risk-taking, general activity, sociability, and propensity to disperse for Brook Trout were repeatable and heritable across the juvenile period of ontogeny. The magnitudes of phenotypic and genetic correlations suggest the possibility of a behavioural syndrome between time to exit an enclosure, proportion of time spent moving, and possibly net displacement and transition rate in a dispersal channel. However, the statistical significance of the phenotypic correlations varied with age class and the genetic correlation coefficients for individual ages were not statistically significant, but were moderate and consistent in magnitude. In addition, there was no evidence for a relationship between the personality metrics measured for the offspring and the migratory behaviour of their parents, contrary to the predictions of the Risk-Taking, Activity, and Sociability Hypotheses.

The lack of any relationship between offspring personality and parental migratory phenotype suggests that Brook Trout personality and migratory behaviour are not the outcome of a shared mechanism that results in straightforward phenotypic and genetic correlations. My findings contrast with the handful of studies that have supported the Risk-Taking Hypothesis by demonstrating that individuals with a greater willingness to enter unfamiliar environments are more likely to undertake long distance movements (Salvelinus fontinalis; Edelsparre et al.)
2013), and bolder individuals tend to migrate while less bold individuals remain resident 
(Rutilus rutilus; Chapman et al. 2011a). However, my results are consistent with Höjesjö et al. 
(2011) findings that boldness and aggression in young-of-the-year Brown Trout (Salmo trutta) 
were not related to variation in parental migratory behaviour. My findings for the Activity 
Hypothesis was consistent with Cote et al. (2011) findings that levels of general activity in 
Mosquitofish (Gambusia affinis) do not influence dispersal distance, but contrast with Závorka 
et al. (2015) findings that laboratory activity was positively correlated with field dispersal in 
Brown Trout. My findings for the Sociality Hypothesis contrast with studies demonstrating that 
individuals classified as less social are more likely to disperse greater distances compared to 
individuals classified as more social (Gambusia affinis; Cote, Clobert, et al. 2010; Cote et al. 
2011). With the exception of Metcalfe (1998) and Höjesjö et al. (2011), these studies only 
considered phenotypic correlations between personality metrics and long-distance movements, 
so the involvement of genetic mechanisms remains unclear.

The absence of a relationship between offspring personality and parental migratory 
behaviour is relevant to the broad interest in whether long-distance movements, such as 
dispersal or migration, are extensions of routine behaviour (Van Dyck and Baguette 2005) and 
personality traits (Réale et al. 2007). Such hypothesized relationships imply that the existence 
of a movement or space use syndrome involves shared proximate mechanisms for small- and 
large-scale movements. The alternative hypothesis is that long-distance movement evolves 
independently of routine behaviour, and is therefore influenced by different genetic and 
physiological mechanisms, because different kinds of movements are required to move 
between and within habitat patches (Van Dyck and Baguette 2005; Fausch et al. 2002). My
findings for Lake Superior Brook Trout are consistent with the latter hypothesis. An earlier study of recently emerged Brook Trout from a stream-resident population also found no evidence that juvenile dispersal was related to the activity that individuals displayed while foraging (foraging tactic), but was related to an individual’s performance in a refuge exit test (Edelsparre et al. 2013).

A possible reason for the lack of a relationship between offspring personality and parental migratory behaviour is that the migrant and resident life histories arise via plastic developmental responses involving competition between individuals within and among cohorts for space and food (Dodson et al. 2013). Genetic differences between migrant and resident phenotypes are observed for some populations, but less frequently (Reid et al. 2005; Nichols et al. 2008). Plasticity can involve the uncoupling of morphological mechanisms responsible for phenotypic and genetic correlations between traits to facilitate distinctly different phenotypes (West-Eberhard 1989; West-Eberhard 2005; Dodson et al. 2013). However, the phenotypic and genetic correlations quantified here were relatively consistent over the juvenile life stage (see below). I did not see evidence of correlations becoming uncoupled with increasing age, but also did not see evidence of individuals diverging into apparent migrant and resident phenotypes.

It is also possible that offspring personality is related to parental migratory behaviour, but our ability to detect the relationship was limited by features of our experimental design and analytical methods. At least four design features warrant consideration. First, my analyses could have lacked the sample size and hence statistical power needed to detect actual relationships. Effective tests of genetic correlations, in particular, can require large sample sizes (Lynch and Walsh 1998). In addition, the range in personality phenotypes may have been limited by the
absence of offspring from resident-resident crosses (i.e. reduced genotypic and phenotypic variation). The range of phenotypes could also have been limited by any genotype-rearing environment interaction arising because captive rearing conditions differed from, and were presumably much simpler, than natural conditions. Food availability and competition, in particular, were probably less variable across individuals in the lab than expected in field, and access to food can be a key driver in the expression of migratory behaviour (Nordeng 1983; Olsen et al. 2006; O’Neal and Stanford 2011; Dodson et al. 2013). The importance of these concerns remains unclear.

Second, my design and analyses did not explicitly consider several biological processes that could affect my ability to estimate the amount of additive genetic variance for the behavioural metrics I studied, including maternal effects, dominance, and epistasis (Kruuk 2004). These effects could be important because my colleagues who sampled and crossed the parent fish were unable to complete the partial factorial design. Maternal effects could be particularly relevant in my study, because they can be an important source of inter-individual variation in phenotype (Lynch and Walsh 1998), particularly during early life stages (Einum and Fleming 1999). Maternal effects arise when the mother’s phenotype influences the offspring’s phenotype in ways beyond the effects of genes passed on from the mother. They can have genetic or environmental causes (Kruuk 2004; Lynch and Walsh 1998). Examples of maternal effects are widely known for fishes, including traits such as growth rate (Einum and Fleming 1999) and boldness (Höjesjö et al. 2011). Age-specific changes in heritability can be indicative of maternal effects (Réale et al. 1999), but my analyses provided no evidence of such change. More direct analyses (Wilson et al. 2010) remain to be completed.
Third, comprehensive sensitivity analyses of the priors used in my analyses remain needed. Outcomes of Bayesian analyses can be sensitive to the form of prior selected (e.g. uniform, normal, gamma), the starting values used, and the upper and lower bounds of the starting values. It will be important to extend my analyses with different prior specifications (Kéry and Schaub 2012). Preliminary sensitivity analyses were completed by Lauren Sicoly (personal communication). She compared Bayesian estimates of genetic correlations obtained through MCMCglmm to estimates obtained using ASReml and found the estimates and their confidence/credible intervals to be highly consistent. I explored inverse-Wishart and inverse-Gamma priors when estimating phenotypic and genetic correlations. I found it much easier to achieve model convergence using the former. However, there is still a need to examine how robust the parameter estimates are to the starting values selected for the priors (Kéry and Schaub 2012).

A final feature warranting consideration is that the experimental design could have missed a behavioural dimension of personality important to migration, such as aggression. In salmonid fishes, aggression influences access to resources and ultimately ecological processes, such as habitat selection, and possibly the expression of life history traits, such as juvenile growth rate, and length and age of maturation (Cutts et al. 1998; Dodson et al. 2013). In Brook Trout, however, aggression tends to be infrequent and expressed less overtly in the lab (this study) and the field (McLaughlin et al. 1999) when compared to other stream salmonids (Cutts et al. 1998).

Other aspects of my study are relevant to behavioural ecologists’ efforts to assess the evolutionary and ecological significance of personality in different taxa and ecological
circumstances. There is interest in understanding the degree to which personality differences in wild animals are shaped by genetic, maternal, and environmental influences during development (Réale et al. 2007). The evidence for heritability of personality traits in wild animals is increasing; however, the range of taxa and study systems examined thus far remains limited (Réale et al. 2007; Van Oers and Sinn 2013). Examples are needed for fishes in particular, because there is a general lack of estimates of heritability for behavioural traits for this taxonomic group (Mittelbach et al. 2014), and because morphological and life history traits can display significant plasticity (Pigliucci 2005). Estimates of heritability and genetic correlations are also important for understanding the opportunity for, and potential direction of, short-term adaptive evolution. For example, it has been hypothesized that behavioural syndromes could constrain short-term evolution, but the genetic contributions to behavioural syndromes remain poorly examined (Dochtermann and Dingemanse 2013), and their importance in terms of constraining short-term evolution are just beginning to be assessed (Hansen and Houle 2008; Dochtermann and Dingemanse 2013). The repeatability and heritability estimates provided here suggest that genetic factors shape behavioural differences among Lake Superior Brook Trout. There is considerable potential for personality traits to evolve, perhaps with the exception of the metrics of dispersal, where heritability estimates were lower. The evidence of a syndrome involving risk taking, activity, and measures of the propensity to disperse also suggests that any short-term adaptation in personality would likely be constrained toward individuals where risk taking, activity, and propensity to disperse are low or individuals where risk taking, activity, and propensity to disperse are high. Behavioural
combinations involving high risk taking and low activity and movement, or vice versa, could be less likely to evolve because of the nature of the phenotypic and genetic correlations.

These conclusions for Lake Superior Brook Trout offer useful insights for interpreting the individual variation in behaviour observed for 0+ Brook Trout from other lake- and stream-resident populations (McLaughlin and Grant 1994; Biro and Ridgway 1995). In these systems, individuals observed in the field differ conspicuously in foraging behaviour, with some individuals remaining sedentary and searching for prey from the lower part of the water column (a sit-and-wait tactic) and others more actively searching for prey from the upper part of the water column (an active search tactic). This activity during prey search is repeatable (Biro and Ridgway 1995), or correlated with repeatable variation in activity measured in the lab (Wilson and McLaughlin 2007) and exit behaviour in the presence and absence of a novel object in the field (Farwell and McLaughlin 2009). For the stream resident study system, individuals displaying a sit-and-wait tactic also have relatively smaller telecephalon volumes (Wilson and McLaughlin 2010), the portion of the brain involved with space use, and higher titres of cortisol (Farwell and McLaughlin 2009), a hormone mediating physiological and behavioural responses to aversive stimuli. The differences in behaviour also appear to be the outcome of diversifying selection (McLaughlin et al. 1999; McLaughlin 2001). There is emerging evidence that other salmonid fishes can display similar personality differences, particularly in activity, and correlations between laboratory activity and dispersal in the wild have been observed (Závorka et al. 2015). Although I worked on a different Brook Trout population, my study provides evidence that the individual variation in behaviour observed in these studies could be heritable and potentially functionally adaptive, and that correlations observed between measures of exit
times and proportion of time spent moving in the field and laboratory could reflect a behavioural syndrome with an underlying genetic mechanism.

Aspects of my findings are also relevant to fishery managers’ efforts to restore the migrant ecotype of Brook Trout in Lake Superior. Genetic analyses of microsatellite markers provided evidence that resident and migrant ecotypes originate from the same populations (D’Amelio and Wilson 2008), but the ecological and potential genetic processes involved in generating the migrant and resident phenotypes remain poorly understood (Schreiner et al. 2008; Wilson et al. 2008). A recent decision not to list the migrant ecotype under the US Endangered Species Act relied on expert judgment that the two ecotypes probably arise via phenotypic plasticity (petitioners [all in Michigan] were the Sierra Club Mackinac Chapter, Lansing; Huron Mountain Club, Big Bay; and M. J. Robinson, Ann Arbor). While I have not explicitly tested for phenotypic plasticity in migratory behaviour, the lack of any relationship between the personality of offspring and migratory behaviour of parents suggests that a mechanism involving environmental contingency could operate in Brook Trout. A clearer understanding of how the migratory ecotypes arise is needed in order to guide the restoration migratory phenotype. Possible management actions include tightening of angling regulations, habitat restoration, and stocking tributaries where the migrant ecotype historically occurred (Schreiner et al. 2008). The findings of a recent demographic model parameterized for Brook Trout suggest that the survival of migrants is crucial to the stability of the polymorphism (Vélez-Espino et al. 2013). My results are consistent with a key assumption of that model: that migrants and residents are alternative phenotypes from a single genotype. The absence of a relationship between personality and migratory behaviour also suggests that any personality-
related differences in susceptibility to angling (Cooke et al. 2002) will not cause correlated selection on migratory behaviour. With the habitat restoration option, the possibility that migratory behaviour is plastic reveals the need for a better understanding of the habitat features important in determining which life history is adopted. Certain habitat alterations could have counterintuitive results. For example, changes that increase food availability in the tributaries could favour individuals to adopt a resident life history. With the stocking option, evidence that migratory behaviour is plastic minimizes any need to stock specific migratory and resident genotypes.

A noteworthy feature of my study is that heritability, and phenotypic and genetic correlations changed minimally over the juvenile life stages. Variation among age classes was observed for all repeatability estimates. Temporal changes in these estimates could have occurred because of (i) changes in fish size and ability relative to the nature of the personality tests and sizes of testing apparatuses with age, (ii) maternal effects declining with age (Sih and Bell 2008; Wilson et al. 2010), and (iii) the onset of migratory preparedness at older ages. The changes that I did observe were likely due to changes in the scaling of fish size relative to the first possibility. Differences in repeatability were most visibly obvious between ages 0+ and 2+. There was little evidence of systematic changes in heritability with age. There was also little evidence of changes the phenotypic and genetic estimates of variation at ages 1+ and 2+ years; the ages when Brook Trout commonly begin to out-migrate (Morinville and Rasmussen 2003).

The relationship between the development of migrant and resident phenotypes and personality differences is still not completely unrelated. There is the possibility that findings would differ had I been able to track the development of personality and migratory behaviour
of known individuals over time. It is also possible that personality could be related to migratory behaviour in ways I did not test. For example, maternal influences could shape offspring personality through differences in egg size and quality. Egg size can influence resting metabolic rate (Einum 2003) and hence aggression and activity (Biro et al. 2010). Such differences in personality could then affect an individual’s ability to explore new habitats, and defend space and food, in ways that ultimately influence the individual’s developmental trajectory. Similarly, consistent individual differences in behaviour observed in the field could be the outcome of reinforcement by density-, frequency-, and status-dependent selection (Gross 1996; Dall et al. 2004). In this case, it could be possible to observe a correlation between migratory behaviour and personality, but where differences in personality are a possible by-product of the mechanisms influencing migratory behaviour.

There is growing interest in the causes and consequences of animal personality in ecological and evolutionary contexts. Few studies have examined the phenotypic and genetic implications of personality over ontogeny, and related it to important behaviours in the field. Here, I have (1) used Lake Superior Brook Trout to characterize the repeatability and heritability of risk-taking, general activity, sociability and dispersal propensity at three different age classes, (2) quantified phenotypic and genetic correlations between behavioural metrics, and (3) tested whether the personality differences measured in standardized laboratory conditions of the offspring are related to the migratory behaviour of parents in the field. My study provides evidence for repeatable and heritable behavioural variation at each age class. Phenotypic and genetic correlations between time to exit a enclosure, proportion of time spent moving, net displacement and transition rate in a dispersal chamber provided evidence of a
behavioural syndrome involving risk-taking, general activity and possibly propensity to disperse, however offspring personality was unrelated to parental migratory behaviour. A simple causal relationship between personality and migration does not seem to be supported in this system, and the causes of migration may be related to developmental plastic responses to currently unknown environmental effects.


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**Hadfield, J.** 2010. MCMC methods for multi-respoinside generalized linear mixed models: The


O’Neal, S.L., & Stanford, J. A. 2011. Partial migration in a robust brown trout population of a


Sicoly, L. 2015. Understanding behavioural diversity and its link to migration in Lake Superior brook trout. *MSc thesis, University of Guelph, ON.*


Swain, D., & Riddell, B. 1990. Variation in agonistic behavior between newly emerged juveniles from hatchery and wild populations of Coho Salmon, Oncorhynchus kisutch. *Canadian Journal of Fisheries and Aquatic Sciences, 47,* 566–571.


Table 1. Estimates of repeatability ($r$), heritability ($h^2$), variance components of additive genetic variance ($V_A$) and phenotypic variance ($V_P$), and the additive genetic variance relative to the mean score of each behavioural trait ($V_A/\bar{Z}$) for Brook Trout at the 0+, 1+, and 2+ age class. Bolded values indicate statistically significant estimates based on 95% credible intervals that exclude zero.
<table>
<thead>
<tr>
<th>Trait</th>
<th>$r$</th>
<th>$h^2$</th>
<th>$V_A$</th>
<th>$V_A/\bar{z}$</th>
<th>$V_P$</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>0+</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>0.42</td>
<td>0.34</td>
<td>0.17</td>
<td>0.0004</td>
<td>0.33</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>0.65</td>
<td>0.35</td>
<td>0.05</td>
<td>0.14</td>
<td>0.09</td>
</tr>
<tr>
<td>Proportion of time spent near a mirror</td>
<td>0.83</td>
<td>0.24</td>
<td>0.07</td>
<td>0.21</td>
<td>0.20</td>
</tr>
<tr>
<td>Net displacement</td>
<td>0.80</td>
<td>0.30</td>
<td>0.25</td>
<td>0.05</td>
<td>0.61</td>
</tr>
<tr>
<td><strong>1+</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>0.71</td>
<td>0.23</td>
<td>0.14</td>
<td>0.0004</td>
<td>0.48</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>0.75</td>
<td>0.48</td>
<td>0.10</td>
<td>0.17</td>
<td>0.12</td>
</tr>
<tr>
<td>Proportion of time spent near a mirror</td>
<td>0.61</td>
<td>0.31</td>
<td>0.05</td>
<td>0.09</td>
<td>0.14</td>
</tr>
<tr>
<td>Net displacement</td>
<td>0.57</td>
<td>0.08</td>
<td>0.12</td>
<td>0.04</td>
<td>1.03</td>
</tr>
<tr>
<td>Transition rate</td>
<td>-</td>
<td>0.17</td>
<td>0.13</td>
<td>0.10</td>
<td>0.69</td>
</tr>
<tr>
<td><strong>2+</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>0.58</td>
<td>0.31</td>
<td>0.05</td>
<td>0.00004</td>
<td>0.10</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>0.42</td>
<td>0.46</td>
<td>0.10</td>
<td>0.29</td>
<td>0.10</td>
</tr>
<tr>
<td>Proportion of time spent near a mirror</td>
<td>0.27</td>
<td>0.31</td>
<td>0.08</td>
<td>0.24</td>
<td>0.17</td>
</tr>
<tr>
<td>Net displacement</td>
<td>0.16</td>
<td>0.11</td>
<td>0.10</td>
<td>0.02</td>
<td>0.60</td>
</tr>
<tr>
<td>Transition rate</td>
<td>0.15</td>
<td>0.07</td>
<td>0.09</td>
<td>0.07</td>
<td>1.04</td>
</tr>
</tbody>
</table>
Table 2. Estimates of raw phenotypic ($r_p$; above the diagonal) and genetic ($r_g$; below the diagonal) correlations between behavioural traits for Brook Trout at the 0+, 1+, and 2+ age classes. Standard errors are provided below the raw phenotypic correlations coefficients and credible intervals are found below the genetic correlation coefficients. Bolded phenotypic correlation coefficients were significant based on standard error. Bolded correlation coefficients represent significance based 95% credible intervals that exclude zero.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Age 0+</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Time to exit the enclosure(s)</td>
</tr>
<tr>
<td></td>
<td>-</td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>-0.27</td>
</tr>
<tr>
<td></td>
<td>(-0.67, 0.33)</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>-0.25</td>
</tr>
<tr>
<td></td>
<td>(-0.34, 0.60)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>-0.59</td>
</tr>
<tr>
<td></td>
<td>(-0.86, 0.17)</td>
</tr>
<tr>
<td>Trait</td>
<td>Time to exit the enclosure (s)</td>
</tr>
<tr>
<td>--------------------------------------------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td><strong>Age 1+</strong></td>
<td></td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>-</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>-0.29 (-0.67, 0.29)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>0.17 (-0.51, 0.60)</td>
</tr>
<tr>
<td>Net displacement</td>
<td><strong>-0.18</strong> (-0.81, 0.44)</td>
</tr>
<tr>
<td>Transition rate</td>
<td>0.21 (-0.55, 0.70)</td>
</tr>
<tr>
<td><strong>Age 2+</strong></td>
<td></td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>-</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>-0.31 (-0.68, 0.11)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>0.11 (-0.44, 0.51)</td>
</tr>
<tr>
<td>Net displacement</td>
<td>0.15 (-0.40, 0.65)</td>
</tr>
<tr>
<td>Transition rate</td>
<td>-0.40 (-0.66, 0.43)</td>
</tr>
</tbody>
</table>
Table 3. Estimates of phenotypic correlations at the between-individual level (above the diagonal) and at the within-individual level (below the diagonal) between behavioural traits for Brook Trout at the age 0+, 1+, and 2+ age classes. Credible intervals are found below correlation coefficients. Bolded coefficients represent significance based 95% credible intervals that exclude zero.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Age 0+</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Time to exit the enclosure(s)</td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>(-0.86, 0.32)</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>-0.26</td>
</tr>
<tr>
<td></td>
<td>(-0.54, -0.03)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>-0.03</td>
</tr>
<tr>
<td></td>
<td>(-0.25, 0.23)</td>
</tr>
<tr>
<td>Net displacement</td>
<td>0.20</td>
</tr>
<tr>
<td></td>
<td>(-0.06, 0.41)</td>
</tr>
<tr>
<td>Trait</td>
<td>Time to exit the enclosure(s)</td>
</tr>
<tr>
<td>-------</td>
<td>-------------------------------</td>
</tr>
<tr>
<td>Time to exit the enclosure(s)</td>
<td>-</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>-0.05 (-0.25, 0.18)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>0.17 (-0.02, 0.40)</td>
</tr>
<tr>
<td>Net displacement</td>
<td>-0.13 (-0.37, 0.05)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Trait</th>
<th>Time to exit the enclosure(s)</th>
<th>Proportion of time spent moving</th>
<th>Proportion of time spent near a reflection</th>
<th>Net displacement</th>
<th>Transition rate</th>
<th>Age 2+</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to exit the enclosure(s)</td>
<td>-</td>
<td>-0.43 (-0.68, -0.05)</td>
<td>-0.14 (-0.51, 0.18)</td>
<td>0.04 (-0.44, 0.41)</td>
<td>-0.35 (-0.65, 0.12)</td>
<td></td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>-0.40 (-0.55, -0.23)</td>
<td>-</td>
<td>0.20 (-0.23, 0.52)</td>
<td>0.03 (-0.41, 0.48)</td>
<td>0.28 (-0.11, 0.67)</td>
<td></td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>-0.19 (-0.35, -0.003)</td>
<td>0.16 (-0.19, 0.57)</td>
<td>-</td>
<td>-0.06 (-0.51, 0.36)</td>
<td>0.05 (-0.39, 0.46)</td>
<td></td>
</tr>
<tr>
<td>Net displacement</td>
<td>-0.02 (-0.34, 0.03)</td>
<td>0.03 (-0.21, 0.15)</td>
<td>-0.08 (-0.25, 0.11)</td>
<td>-</td>
<td>0.002 (-0.47, 0.60)</td>
<td></td>
</tr>
<tr>
<td>Transition rate</td>
<td>-0.14 (-0.34, 0.03)</td>
<td>0.10 (-0.09, 0.27)</td>
<td>0.09 (-0.11, 0.24)</td>
<td>0.15 (-0.05, 0.30)</td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>
Table 4: Summary of the relationship between the behaviour of the offspring and the migratory cross type (MxM or MxR) of the parents for 26 families of 0+, 24 families of 1+, and 22 families of 2+ age class Brook Trout. At the 0+ age class all tests included 259 individuals for each behaviour. At the 1+ age class all tests included 236 individuals, with the exception of transition rate, which included 225 individuals. At the 2+ age class all tests included 220 individuals with the exception of net displacement and transition rate, which included 210 and 205 individuals, respectively. Bolded posterior means represent significance based 95% credible intervals that exclude zero.

<table>
<thead>
<tr>
<th>Trait</th>
<th>0+ (26 Families)</th>
<th>1+ (24 Families)</th>
<th>2+ (22 Families)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>-0.02 (-0.30, 0.29)</td>
<td>0.14 (-0.18, 0.46)</td>
<td>0.03 (-0.16, 0.22)</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>0.02 (-0.14, 0.16)</td>
<td>0.05 (-0.16, 0.24)</td>
<td>-0.07 (-0.29, 0.15)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>0.15 (-0.04, 0.35)</td>
<td>-0.03 (-0.21, 0.15)</td>
<td>-0.01 (-0.21, 0.21)</td>
</tr>
<tr>
<td>Net displacement</td>
<td>-0.09 (-0.46, 0.31)</td>
<td>-0.22 (-0.56, 0.16)</td>
<td>-0.16 (-0.31, 0.35)</td>
</tr>
<tr>
<td>Transition rate</td>
<td>-</td>
<td>0.22 (-0.11, 0.55)</td>
<td>0.04 (-0.52, 0.26)</td>
</tr>
</tbody>
</table>
Table 5. Summary of meta-analysis output for repeatability estimates (column left of the diagonal) and between-individual correlation coefficients (above diagonal) and within-individual coefficients (below diagonal) for combined age classes (0+, 1+ and 2+) of Brook Trout. Confidence intervals are found below correlation values. Bolded estimates are significant at 95% confidence intervals by excluding zero. Values that show significant heterogeneity between age classes are denoted by asterisks.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Combined age classes (0+, 1+ and 2+)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Repeatability $r^2$</td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>0.59* ($0.41, 0.72$)</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>0.62* ($0.39, 0.78$)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>0.62* ($0.20, 0.84$)</td>
</tr>
<tr>
<td>Net displacement</td>
<td>0.56* ($0.10, 0.82$)</td>
</tr>
</tbody>
</table>
Table 6. Summary of meta-analysis output for heritability estimates (column left of the diagonal), genetic correlation coefficients (above diagonal) and raw phenotypic correlation coefficients (below diagonal) for combined age classes (0+, 1+ and 2+) of Brook Trout. Confidence intervals are found below correlation values. Bolded estimates represent are significant at 95% confidence intervals by excluding zero. Values that show significant heterogeneity between age classes are denoted by asterisks.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Combined age classes (0+, 1+ and 2+)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Heritability ($h^2$)</td>
</tr>
<tr>
<td>Time to exit the enclosure (s)</td>
<td>0.30 (0.23, 0.36)</td>
</tr>
<tr>
<td>Proportion of time spent moving</td>
<td>0.42 (0.35, 0.49)</td>
</tr>
<tr>
<td>Proportion of time spent near a reflection</td>
<td>0.29 (0.21, 0.35)</td>
</tr>
<tr>
<td>Net displacement</td>
<td>0.16* (0.02, 0.30)</td>
</tr>
<tr>
<td>Transition rate</td>
<td>0.12 (0.02, 0.22)</td>
</tr>
</tbody>
</table>
Figure 1: Locations where adult migrant and resident Brook Trout used to create the study crosses were sampled in Lake Superior (a) and Nipigon Bay (b). Sample tributaries are bolded and numbered: Dublin Creek (1), MacInnes Creek (2), and Cyprus River (3).
Figure 2: $\delta^{13}$C and $\delta^{15}$N signatures of adult Brook Trout used to make genetic crosses. At time of capture, individuals were classified as resident (closed circle) or migrant (open circle) based on body size and colouration. Labels above figure show the ranges of $\delta^{13}$C and $\delta^{15}$N values for stream (resident) and lake (migrant) caught Brook Trout in Nipigon Bay and tributaries (Robillard et al. 2011).
Figure 3: Schematic of the top-view of dispersal channels used to assess propensity to disperse in 0+ and 1+ (a), and 2+ age class (b) Brook Trout. Channels used in 0+ and 1+ age class experiments were 4.0 m in length and 4.2 m in length in age 2+ experiments. Each channel had an area of inflow at one end and a drain for outflow at the opposite end. Opaque barriers prevented fish from entering these areas in 2014. The remainder of the channel was divided into 15 equally spaced compartments separated by opaque half barriers. During acclimation, individual fish were placed in compartment 8 and were blocked by removable barriers denoted by dotted lines.
Figure 4: Plots summarizing the individual variation for each behavioural measure at the 0+, 1+, and 2+ age classes (N=80, N=40 and N=56, respectively) for time to exit a enclosure, proportion of time spent moving, proportion of time spent near a mirror, net displacement and transition rate. Each point represents an individual measurement. For each plot, individuals were ranked from lowest to highest based on their mean value for a given behavioural measure. Rank order of individuals varies between plots.
Figure 5: Comparison of behavioural variation between MxM and MxR crosses sharing the same female (dam) but different males (sire) for time to exit a enclosure, proportion of time spent moving, proportion of time spent near a mirror, net displacement and transition rate for 0+, 1+, and 2+ age classes. The variation in each family is summarized by box plots. Shaded box plots indicate MxM crosses and open box plots indicate MxR crosses. Vertical bars represent the standard error and outliers are plotted as individual points. One outlier for transition rate was removed for graphical representation in age 2+ Brook Trout.
APPENDIX A

Figure 1: Visual summary of the crosses made between parent migrant and resident Brook Trout caught in Nipigon Bay tributaries used to generate the families studied in my experiments. Ten migrant females (F*) and ten migrant males (M*) and eight resident males (M) were sampled. Migrant individuals are denoted by using asterisks. The crossing diagrams differ from those in Sicoly (2015, Appendix C) because three corrections were made for family assignments. All analyses provided here have been re-run to accommodate these corrections. Two families were used up in both the 0+ and 1+ age classes, resulting in 24 (14 MxM and 10 MxR) and 22 (13 MxM and 9 MxR) families being used at the 1+ and 2+ age class behavioural experiments, respectively. Families excluded from experiments at the 1+ and 2+ age classes are depicted by dotted lines.
APPENDIX B:

Figure 1: Top (a) and side view (b) of enclosure used in time to emerge from a enclosure (experiment 1) in 2012 and 2013. The enclosure consisted of a vertical freestanding open top PVC tube. In year 2012, the tube was 38.1 cm high and 8.9 cm in diameter. In year 2013, it was 38.1 cm high and 15.2 cm in diameter. Each tube had a vertical opening with a sliding door that could be pulled up from the top of the aquarium. The tube opening was 2 cm wide in 2012 and 4 cm wide in year 2013.
Figure 2: Top (a) and side view (b) of enclosure used in time to emerge from a enclosure (experiment 1) in 2014. The enclosure consisted of a horizontal PVC pipe with a length of 33 cm and an internal diameter of 11 cm. The enclosure was secured to a PVC sheet base. The enclosure contains a rectangular mesh covered hole to allow light into the tube. The ends of the tube can be blocked by removable doors consisting of PVC sheeting. During the experiment, one end of the enclosure was against the aquarium wall. After acclimation, the second door was removed so fish could exit the enclosure.