Consistent individual differences in behaviour are not predicted by metabolic phenotype of offspring from migrant and resident Brook Trout

by

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ABSTRACT

Consistent individual differences in behaviour are not predicted by metabolic phenotype of offspring from migrant and resident Brook Trout

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I tested the hypothesis that consistent individual differences (CIDs) in behaviour arise from CIDs in metabolic performance using offspring from polymorphic Brook Trout (*Salvelinus fontinalis*) from Lake Superior and its tributaries. Large, fast-growing migrants move between tributaries and the lake. Small, slow-growing residents remain in the tributaries. Four measures of behaviour: risk-taking, general activity, association with a conspecific, and propensity to disperse; as well as three measures metabolic performance: standard and maximum metabolic rate, and aerobic scope, was quantified for 60 individuals (age 2+) from migrant-migrant and migrant-resident families. Three of four behavioural measures and all of the metabolic measures were repeatable. CIDs in behaviour were not related to CIDs in metabolic performance. Further, the nature of correlations between behaviour and metabolic performance did not differ between migrant-migrant and migrant-resident offspring. The mechanisms underlying relationships between CIDs in behaviour and metabolism are likely more complex than hypothesized in current models.

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INTRODUCTION

There is broad interest in understanding the proximate basis for consistent individual differences in behaviour (Dall et al. 2004, McElreath & Strimling 2006, Wolf et al. 2007, Biro & Stamps 2008). In many populations of wild animals, individuals differ consistently in their behaviour, across time and space, and beyond what is expected based on age, body size, and life stage (Bolnick et al. 2003). Such consistent individual differences (CIDs) in behaviour have been documented in insects (Krams et al. 2013), fishes (Conrad et al. 2011, Mittelbach et al. 2014), amphibians (Wilson & Krause 2012, Sih et al. 2003), reptiles (Cote & Clobert 2007, LeGalliard et al. 2013), birds (Groothuis & Carere 2005), and mammals (Koolhaas et al. 1999, Reale et al. 2000). CIDs are attracting interest because the differences are detectable in spite of behavioural flexibility in response to variability in an animal's external environment and its internal state. This has led some authors to posit that CIDs are a consequence of differences in underlying physiological mechanisms that influence behaviour. For example, early distinctions between bold, active (proactive) individuals and shy, less active (reactive) individuals suggested that the differences were correlated with stress responses involving the hypothalamic-pituitary-adrenal axis and the sympathetic and parasympathetic nervous systems (Koolhaas et al. 1999). Other authors proposed that CIDs could be the outcome of differences in standard metabolic rate (Biro & Stamps 2010, Careau et al. 2008, Mathot & Dingemanse 2015), where standard metabolic rate is defined as the minimim metabolic rate of an inactive ectotherm while at rest in a post-absorptive, non-reproductive state at a specified ambient temperature (McNab 1997). In a more recent review, Metcalfe et al. (2016) recognized that an individual's metabolic phenotype also includes its short-term peak of energetic output (maximum metabolic rate) and the difference between its minimum and maximum metabolic rates (aerobic scope). Metcalfe et al. (2016)

suggested that individual differences in these metrics of metabolic performance might account for CIDs in behaviour.

Two main models have been proposed to explain how CIDs in behaviour might be related to standard metabolic rate: the performance and allocation models (Careau et al. 2008, Mathot & Dingemanse 2015). The performance model assumes that individuals differ in standard metabolic rate and have access to ample food resources. The individual differences in standard metabolic rate reflect the size of the individuals' digestive and metabolic machinery (e.g. intestines, liver, kidneys, and heart). Individuals with higher standard metabolic rates will have greater need to capture, ingest, extract, and mobilize energy than individuals with lower standard metabolic rates (Careau & Garland 2012). The performance model predicts that individuals with high standard metabolic rates will be more likely to display energetically costly behaviours, and in particular, behaviours that result in increased energy intake (e.g. activity and boldness), than individuals with low standard metabolic rates (Mathot & Dingemanse 2015). The allocation model assumes that individuals differ in standard metabolic rate, but have limited access to food resulting in a fixed energy budget. By expending more energy on resting metabolism, this results in less energy available for other processes such as behaviour. This model predicts that individuals with high standard metabolic rates will be less likely to display energetically costly behaviours, and in particular, behaviours that do not result in increased energy intake (e.g. activity and aggression), than individuals with low standard metabolic rates (Mathot & Dingemanse 2015). While these models represent a simplified representation of an animal's energy physiology, they provide an initial theoretical framework for examining how CIDs in behaviour and metabolism could be related.

Empirical support for the two models has been mixed, although the numbers of explicit tests of the models have been few. The performance model has received the greatest attention. Many studies that support the performance model have been conducted on fishes and salmonids in particular with a large focus on behaviours such as aggression (Cutts et al. 2001, Cutts et al. 1998) and dominance (Metcalfe et al. 1995, Cutts et al. 1999, Yamamoto et al. 1998, McCarthy 2001). Support for the performance model is not limited to these behaviours or salmonids as other studies have documented that higher resting or basal metabolic rates have resulted in an increased willingness to take risks (Huntingford et al. 2010, Krams et al. 2013) as well as higher activity levels (Gebczynski & Konarzewski 2009). Numerous studies have reported results that support the allocation model as well. For example, in tests measuring activity levels, more active individuals were found to have reduced basal metabolic rates (Deerenberg et al. 1998, Wikelski et al. 1999, Rezende et al. 2009). Similar trends have been documented in studies measuring risk taking (Mathot et al. 2015) and exploratory behaviours (Bouwhuis et al. 2014) as well as dominance (Hammond et al. 2000) that suggests there is an energy allocation trade-off between behaviour and metabolic costs. Not all studies that aim to link behaviour and metabolic performance report results in support of the performance and allocation models, in fact there are many studies that are finding no relationships at all. For example, studies have found no evidence of an existing relationship between resting and basal metabolic rates with behaviours such as activity (Farwell and McLaughlin 2009, Chappell et al. 2007), dominance (Radwan et al. 2004), as well as exploration (Gifford et al. 2014, LeGalliard et al. 2013) despite these behaviours being linked to metabolic performance in other studies.

The lack of consistent relationship between CIDs in behaviour and standard metabolic rate suggests that the current models could be over simplistic. There are at least five possible reasons that are not necessarily mutually exclusive. First, individual differences in metabolic rate, although real, may not be large enough to affect behaviour dramatically, or vice versa. Second, the complexity of metabolic processes could offer ways other than differences in behaviour to compensate for differences in standard metabolic rate, such as individual differences in the efficiency of oxygen uptake or the assimilation of energy from food (Daan et al. 1990, Konarzewsk & Ksiazek 2013). Third, variation in other aspects of an individual's metabolic phenotype, such as aerobic scope or maximum metabolic rate, could be more important in influencing an individual's behaviour than standard metabolic rate (Metcalfe et al. 2016), especially if standard metabolic rate makes up a small fraction of an individual's energy budget. Fourth, differences in standard metabolic rate could influence certain behaviours more than others, thereby resulting in support for a correlation between standard metabolic rate and behaviour when one form of behaviour is examined, but not when another form of behaviour is examined (Mathot & Dingemanse 2015). Lastly, individuals could differ in whether the performance or allocation model is most appropriate for them, which could confound tests that examine correlations across individuals. For example, individuals with greater access to energy resources (e.g. dominants) may have energy budgets consistent with a performance model, while individuals denied access to resources (e.g. subordinates) may have energy budgets consistent with the allocation model.

I tested the hypothesis that CIDs in behaviour of polymorphic Brook Trout (*Salvelinus fontinalis*) were related to CIDs in a metabolic phenotype that includes standard metabolic rate,

maximum metabolic rate, and aerobic scope. My study population offers an interesting test case because it consists of two morphs that differ in migratory behaviour, ecology, and life history (Huckins et al. 2008, Robillard et al. 2011a, Robillard et al. 2011b). One morph is migratory; it originates in tributaries to Lake Superior, Canada, migrates into the lake where it grows to a large size, matures at a late age, and returns to a tributary to spawn. The other morph remains resident in the tributary, reaches a smaller size, and matures earlier in life. Ridgway (2008) hypothesized that the two morphs could arise from behavioural and metabolic differences arising early in life, whereby migrants develop an energetic budget consistent with the performance model that requires they leave the low productivity tributaries for the more productive lake habitat; while residents adopt an energetic budget more similar to the allocation model and remain in the unproductive tributary habitat. Studies of polymorphic Brook Trout populations in Quebec have demonstrated that prior to migration migrant individuals have higher metabolic costs, consume more food per unit time, and likely live in habitats with faster currents than resident individuals (Morinville and Rasmussen 2003, 2006). Similarly, several studies examining Brook Trout shortly after emergence from their gravel nests have found that individuals differ in their foraging tactics, with some individuals displaying an active foraging tactic while others demonstrate a sit-and-wait tactic (McLaughlin et al. 1992, 1994, Biro and Ridgway 1995, Wilson and McLaughlin 2007). These differences in foraging behaviour are related to differences in early dispersal, CIDs in measures of activity and willingness to take risks (Wilson and McLaughlin 2007, Farwell & McLaughlin 2009), brain morphology (Wilson & McLaughlin 2010), and levels of the stress hormone cortisol (Farwell et al. 2014).

My investigation of the relationship between CIDs in behaviour and metabolic performance was conducted using offspring of crosses between migrant and resident Brook Trout from Lake Superior. My investigation consisted of three steps. First, I obtained data on four measures of behaviour from a companion study conducted simultaneously using offspring from the same crosses. The behavioural measures included time to exit a refuge into a novel environment (a measure of risk taking), proportion of time spent moving in an open aquarium (a measure of general activity), proportion of time an individual spent in close proximity to its reflection in a mirror (a measure of an individual's willingness to associate with a conspecific), and transition rate between compartments within a dispersal channel (a measure of the propensity to disperse). These measures have been correlated with the foraging behaviour and dispersal of individual Brook Trout in the field (Wilson and McLaughlin 2007, Farwell & McLaughlin 2009, Edelsparre et al. 2013). In addition, I tested for CIDs in three measures of metabolic performance: standard metabolic rate, maximum metabolic rate, and aerobic scope. These measures are widely used to quantify an individual's metabolic phenotype (Metcalfe et al. 2016). Second, I then tested whether CIDs in the behavioural measures were related to CIDs in the measures of metabolic performance. Relationships with specific growth rate were also examined, because growth rate is commonly related to metabolic phenotype, differs between migrants and resident Brook Trout in the field (Robillard et al. 2011b), and is a common measure of Darwinian fitness in juvenile fishes (Forseth et al. 1994, Hendry et al. 2004). Third, I tested whether the relationships between CIDs in the behavioural measures and the measures of metabolic performance differed among offspring from crosses involving migrant parents and offspring from crosses involving migrant and resident parents. Differences in correlation structure could arise between the two types of offspring if the energy budgets of migrant and

resident parents differ in a way that parallels the performance and allocation models, respectively, and those differences are heritable.

METHODS

HISTORY AND REARING OF STUDY ANIMALS

This study was conducted between May and August 2014 using 2+ year old fish from crosses made using migrant and resident adult Brook Trout. Adults were sampled in October of 2011 from three tributaries to Nipigon Bay, Lake Superior, Ontario: Cypress River, Dublin Creek, and MacInnes Creek (Sicoly 2014, Wajmer 2016; Figure 1). Nipigon Bay is one of the few areas where large migratory Brook Trout are still found in Lake Superior (Mucha & Mackereth, 2008). Three offspring from each of 20 families (60 individuals) were used in the study; 39 individuals from migrant-migrant crosses (12 families) and 21 individuals from migrant-resident crosses (7 families). No resident-resident crosses were possible because no resident adult females were captured in 2011, although resident females occur in these tributaries (Robillard et al. 2014). Assignment of the migratory phenotype of parent fish was initially made based on body size and colouration, and later confirmed using stable isotope analysis of adipose fin clips (Sicoly 2015). Embryos from the crosses were held separately, transported to the Ontario Ministry of Natural Resources and Forestry (OMNRF) Dorian Fish Culture Station (Dorian, ON), incubated until the deposition of eye pigment, and then transported to the Codrington Fish Research Facility (Codrington, Ontario) in January 2012 where the eggs were hatched and offspring reared. Fish were reared in a windowed building providing a natural light:dark regime and fed to satiation daily using a high protein commercial trout feed (Ewos

Canada Limited). Rearing water was supplied from an unnamed stream adjacent to the facility. Families were initially reared in separate tanks (2012), and then in mixtures of two families, where the adipose fins of individuals from one of the two families clipped for identification purposes (2013 and 2014). Details of the family assignments are provided in Wajmer (2016).

Preparation for my study began in February of 2014, when each family was culled to 30 individuals, each individual was tagged with a 12 mm passive integrated transponder (PIT) tag, and individuals were thereafter housed in mixed family groups in 4 large 1500L circular holding tanks. Prior to tagging, a fish was placed in a 40mg/mL solution of tricaine methane sulfonate (MS-222) and anesthetised. Anaesthesia was determined by loss of equilibrium. Fork length (to the nearest mm) and weight (to the nearest g) were recorded. The number of the fish's tag was then recorded and loaded into the PIT tag injector. A small incision was made on the left side of the fish below the dorsal fin, the needle of the injector was inserted under the skin, and the tag deployed in the area above the pectoral fin. Each tag, injector, and scalpel was sterilized using 95% ethanol and rinsed with fresh water prior to each surgery. Immediately following surgery, tagged individuals were placed in a pool of fresh ambient water to recover. Once equilibrium was re-established, each fish was placed in its appropriate circular holding tank. In June 2014 ten fish from each family were randomly selected and placed in a fifth 1500L circular tank. All test fish used for the behavioural and metabolic performance trials were later selected from this tank. At the time of time of transfer, individuals were anesthetised and measured for fork length and weight.

QUANTIFICATION OF BEHAVIOUR

Behavioural measurements used in my study were obtained from a larger investigation of CIDs in the behaviour of the offspring over the juvenile period (ages 0+ to 2+ years) (Sicoly 2015, Wajmer 2016) that included measurements for 220 individuals from 22 families. Individuals for the behavioural measurements were selected using a stratified random sampling protocol consisting of 10 sequential time strata of 22 randomly selected individuals (one individual per family per stratum) (Wajmer 2015). At the beginning of each week of data collection, one individual per family was removed from the large 1500L circular tank that housed all 2014 test fish and transported to a smaller 50L oval tank where they were housed for the period of behavioural and metabolic measurements. Five subsets of eight individuals were selected every two weeks in July through August 2014 and the behaviour of these individuals was measured three times over three consecutive days to quantify the consistency (repeatability) of behavioural performance.

Four sequential experiments were used to quantify CIDs in behaviour. The first three experiments were conducted in four test aquaria (107 x 43 x 44 cm). A piece of opaque corrugated plastic was placed over each aquarium to standardize the background above. The sides and backs of the aquarium were also opaque to ensure that fish in adjacent aquaria would not observe each other, while the front (long) side of each aquarium remained transparent so that each test fish could be observed. The aquaria were arranged so that one observer could observe two aquaria at a time and a second observer could observe the remaining two aquaria. An opaque curtain was hung from ceiling to floor between the observer and the aquaria to prevent any disturbances caused by movements from the observer. Behavioural observations were made

though small, eye level openings in the curtain. Lighting in the room was dim, but adequate for observation.

Experiment 4 was conducted in four compartmentalized dispersal channels similar to those used by Northcote & Kelso (1981), Bradford & Taylor (1997), and Edelsparre et al. (2013). Each dispersal channel was a fiberglass, rectangular flume (503 X 61 X 61 cm). Grey plastic barriers spanning the width of the chamber near the ends of each flume were used to separate the water inflow valve and outflow drain from the main portion of the channel resulting in a functional test length of 420 cm for each channel. The test area was divided into 15 equal sized partial compartments by attaching opaque plastic dividers extending perpendicular from the side of the channel for 2/3 of the width of the channel at locations every 28 cm along the inner wall of the flume. The placement of the dividers alternated from side to side, preventing individuals from swimming straight down the dispersal channel. An apparatus constructed of PVC pipe was placed over top of the flume and outfitted with overhanging video cameras (PRO-642, Swann Communications, Melbourne, Victoria) wired to a 9 channel 960H digital video recording system (DVR; Swann Communications, Melbourne, Victoria) to record the behaviour of the test fish. Black semi-transparent cloth was hung over the apparatus covering both sides and ends of the dispersal channel to reduce lighting and minimize disturbances from observers. The behaviour in four test fish was quantified simultaneously using these setups.

Time spent to exit an enclosure into a novel environment (experiment 1) was used as a measure of an individual's willingness to take risks, following Brown et al. (2005), Farwell &

McLaughlin (2009), and Edelsparre et al. (2013). Time to exit is considered to reflect a test fish's assessment of the relative risk of moving from a familiar environment to a new environment. Within each aquarium, a dark-grey piece of opaque PVC tube (enclosure) was placed horizontally on the bottom at the left most end of the aquarium. The tube was 33 cm in length with an inside diameter of 11 cm. Each tube had a rectangular area (144 cm^2) on top where a hole had been cut and covered with mesh to allow light into the enclosure. One end of the tube closest to the side of the aquarium was covered with a flat piece of opaque PVC to prevent a test fish from exiting that end. The other end of the tube was covered temporarily with a flat piece of opaque PVC that served as a sliding door that could be pulled upwards from the top of the aquarium allowing the test fish to exit. Prior to the start of experiment 1, the test fish were placed singly into each tube from the back and blocked off. Each fish was given 30 minutes to adjust to the tube. The experiment commenced when the sliding door was removed. Each individual was given 1800 s to exit the refuge. The time to exit the tube (to the nearest s) was the duration from when the door was removed until the fish's entire body was outside of the tube. If the fish had not exited by 1800 s, it was assigned an exit time of 1800 s and was forced into the open aquarium by gently lifting the tube.

Experiment 2 began immediately upon exiting the enclosure in experiment 1. Proportion of time spent moving was assessed using event sampling (Altman 1974, Martin & Bateson 1986). Each test fish's activity level was scored as moving or not moving at 60 s intervals for a period of 1800 s. The fish's activity at the time of each 60 s interval was assigned as moving if it was actively beating its caudal (tail) fin to propel itself around the aquarium or as not moving if the test fish was hovering in the water column without beating its caudal fin or lying on the

bottom of the aquarium. The proportion of time spent moving during the experiment was estimated as the number of times an individual was scored as moving divided by 30.

Experiment 3 began after a 5 minute acclimation period following the completion of experiment 2. A mirror image stimulation (MIS) test was used to assess a test fish's response to a potential conspecific. Following experiment 2, the test fish was confined to the right side of the tank using a piece of opaque Plexiglas while the PVC tube was removed and replaced with a mirror positioned along the left side of the aquarium and spanning the entre height and width of the aquarium. After 5 minutes the Plexiglas barrier was removed allowing the fish access to the mirror and its reflection. Proportion of time spent near reflection in a mirror was assessed using event sampling. The horizontal location of the test fish relative to the mirror was quantified at 30 s intervals for 600 s. At each interval, the fish's location was scored as being in the third of the aquarium closest to reflection, middle third of the aquarium, or the third of the aquarium farthest from the mirror. The proportion of time spent near the mirror was quantified as the number of intervals in the third of the aquarium closest to the mirror divided by 20. Instances of the test fish charging the mirror, or swimming parallel with their reflection along the mirror, were also recorded, but were too infrequent to analyze.

MIS tests have been criticized because they may not elicit the full diversity of behavioural responses or represent normal social interactions relative to tests involving a real conspecific (Ruzzante 1992, Holtby 1992, Balzarini et al. 2014). MIS tests were used here because they (i) were more feasible given the number of fish being tested, (ii) offer greater

control over differences in body size, condition, and sex (Swain & Riddell, 1990), and (iii) have been used successfully to quantify social behaviour in other studies of salmonid fishes (Svendsen & Armitage 1973, Taylor & Larkin 1986, Swain & Holtby 1989, Swain & Riddell 1990).

Experiment 4 was conducted immediately following experiments 1-3. Each test fish was placed singly into the center compartment of one of four dispersal chambers. Two pieces of opaque plastic, one at each end of the compartment, were used to contain the fish within the center compartment for 30 minutes and allow it adjust to the new environment. Following this, the barriers blocking the exits were removed and each test fish's movement within the channel was recorded on the DVR for two hours. Durations of times spent within and movements between compartments were used to estimate an instantaneous transition rate between compartments for each individual, a measure of the propensity to disperse. For each individual, I used the video recordings to measure the duration an individual spent within a compartment, before moving to an adjacent compartment, until the individual reached one end of the dispersal channel or, in the case of individuals that moved very little, until 60 minutes had transpired. I stopped once an individual reached the end of the channel because the individual was then forced to reverse course. I continued longer for individuals that did not reach the end of the compartment to acquire multiple transitions per individual and to minimize the truncation of durations occurring because individuals spent a long time in one compartment.

QUANTIFICATION OF METABOLIC PERFORMANCE

Metabolic performance was measured for 60 individuals from 20 of the 22 families. Two families were not sampled due to time constraints. Individuals used for the metabolic trials were selected at random from the test fish sampled at the beginning of the week for the behavioural trials. Three sampling blocks of 20 test fish (1 individual per family) for a total of 60 individuals were used for the metabolic trials; each sampling block was completed before moving on to the next. The behavioural and metabolic experiments were conducted by different experimenters. This ensured that the measurements of behaviour and metabolic performance were collected in a double blind manner that should minimize experimenter bias.

The oxygen consumption rates of test fish were measured using four custom-built 1.1 L (3.5 cm internal diameter, 29.5 cm in length) cylindrical glass respirometers. Each respirometer was connected to its own flow-through respirometry system with independent flow controls. The respirometry systems were submerged in one of two 50 L tanks (two systems per tank) at a water temperature of 8.7 °C (+/- 0.3). Water temperature was controlled using two chilling systems that cooled ambient water within a 75 L basin before it flowed into the tanks containing the respirometry systems. An individual respirometry system consisted of a glass chamber connected to two water pumps (Marineland MaxiJet-400, Blacksburg, VA, USA) using gas-proof tubing. One pump supplied the glass chamber with fresh, oxygenated water at a rate of 4.51 min/L and returned the flushed water back to the chilling basin (flush pump). The second pump circulated water from the glass chamber past a dissolved oxygen probe (Vernier Technologies S120, Beaverton, OR, USA) and back.

To quantify the rate of oxygen consumption during a trial, the flush pump to each glass chamber was deactivated and the decline in oxygen concentration in the water over 5 minutes was measured using a Vernier Technologies Lab Pro (Vernier Software and Technology, Beaverton, OR, USA) connected to the dissolved oxygen probes. During this time, dissolved oxygen concentrations never fell below 6 mg/L. Data from the Lab Pro was transferred into Logger Pro software (version 3.8.6; Vernier Software and Technology). The rate at which O_2 concentration of the water declined with time ($R[O_2]$; milligrams of oxygen per litre per minute) was quantified using a linear regression. A test fish's rate of oxygen consumption ($M[O_2]$; milligrams O_2 per hour) was quantified as:

$$M[O_2] = R[O_2] \times (V-V_m) \times 60 \quad (1)$$

where V is the respirometer volume (in litres) and V_m is the volume of the fish (in litres). The oxygen probes were calibrated daily over the duration of the experiment using fully aerated water from the experimental tank and an anoxic solution of sodium sulphite.

The experimental setup allowed for the simultaneous measurement of four individual fish per day with the standard metabolic rate trials being completed before the maximum metabolic rate trials. The four test fish for a set of trials were selected the evening prior to measurement, placed singly into a respirometer, and allowed to recover from handling and adjust to the respirometer for 14 – 16 h. After being placed in the respirometer, the fish remained motionless on the bottom of the chamber. Each chamber was covered in black cloth to provide a dark environment to reduce outside disturbances.

Measurements of oxygen consumption commenced the following morning at 09 00h each day following the overnight acclimation period. Three trials were run per fish. At the beginning of a trial, the flush pump was deactivated and the oxygen concentration in the respirometer was recorded for 5 minutes. The flush pump was then reactivated and fresh oxygenated water was pumped through the respirometer over a 5 minute recovery period. This process was repeated for two more trials. An individual's mean rate of oxygen consumption was estimated as the mean of the slopes from three linear regressions relating oxygen concentration over time. This average was used as an estimate of the minimum rate of oxygen consumption R_{min} $[O_2]$.

Maximum metabolic rate was quantified approximately 30 minutes after the conclusion of the trials quantifying standard metabolic rate. It was quantified using a "chase protocol" (Cutts et al. 2002, Norin & Malte 2011, Healey & Schulte 2012) for providing measurements representative of biochemically and physiologically exhaustive exercise (Reidy et al. 1995). Maximum metabolic rate was estimated through the use of chase protocols and used to calculate aerobic scope by subtracting standard metabolic rate (Clark et al. 2013) and has been used in many physiological studies (e.g. Norin & Malte 2011; Healey & Schulte 2012; Roche et al. 2013). During the chase protocol, a test fish was removed from a respirometer and placed singly into a 50 L tank containing oxygenated water at a temperature of 8.7 °C (+/- 0.3). A combination of hand chasing and gentle tail pinching was used to chase the fish until it reached exhaustion (~4.5-5 minutes). In these trials, the test fish typically displayed burst swimming for the first 1-1.5 minutes, followed by slower swimming with infrequent swimming bursts (2-3 minutes), and then concluding with 1-2 minutes of slow swimming until exhaustion. The test fish was considered to have reached exhaustion when it became unresponsive to physical stimulation.

After reaching exhaustion, the fish was transferred back to its respirometry chamber (~10-15 seconds), the flush pump was deactivated, the decline in oxygen concentration was recorded for 5 minutes, and the flush pump was reactivated for a 5 minute recovery period, as done in trials quantifying standard metabolic rate. Eight trials, per each test fish, were conducted over 75 minutes providing eight measurements of the decline in oxygen concentration $R[O_2]$. For each fish, the values of $R[O_2]$ were regressed against time where a logarithmic curve was fitted to back calculate an intercept providing an estimate for the maximum rate of oxygen consumption $R_{max}[O_2]$.

The experimental protocols for quantifying $R_{min}[O_2]$ and $R_{max}[O_2]$ were conducted twice for each individual with 42 hours of rest between the end of the first and the start of the second test day. During the interim, test fish were housed in a 50 L tank in and fed the evening following their metabolic performance trials. This was the only time test fish were fed between the first and second test days.

STATISTICAL ANALYSIS

My behavioural experiments provided measures of the time to exit an enclosure (a measure of risk taking), the proportion of time an individual spent moving in an open aquarium (a measure of general activity), and the proportion of time an individual spent near their reflection (a measure of responsiveness to a potential conspecific). Transition rates between compartments in the dispersal channel were quantified to estimate an individual's propensity to disperse. An individual's transition rate between compartments ($seconds^{-1}$) was estimated using

the conditional modes obtained from a mixed effects Cox model relating the durations to individual identity, water temperature, and compartment location (Inner, Middle, Outer). There were 7 compartments to each side of the starting (center) compartment. Inner compartments were classified as compartments 0–2 where compartment 0 was the starting (center) compartment, middle as compartments 3–6, and outer as compartment 7 signifying that the end of the channel had been reached. Individual identity was modeled as a random effect. Water temperature and compartment location were modeled as fixed effects. The Cox models were calculated using the Coxme package in R (Therneau 2015). My metabolic experiments provided measurements of each individual's minimum rate of oxygen consumption (R_{min} $[O_2]$), maximum rate of oxygen consumption (R_{max} $[O_2]$), and aerobic scope (R_{max} $[O_2]$ - R_{min} $[O_2]$). Specific growth rate ($\ln[W_2-W_1]/[t_2-t_1]$) for each individual was calculated using weight (W_1) measured in February 2014 (t_1) and weight (W_2) measured throughout the summer at the time of the metabolic experiments (t_2)

Water temperature varied between the behavioural and metabolic experiments (mean: 11.6°C; 95% confidence limits: 11.31 – 11.88°C for the behavioural experiments and mean: 8.7°C; 95% confidence limits: 8.64 – 8.75°C for the metabolic experiments) and, for individuals, between the two days of measurement. Body mass also varied among individuals (geometric mean = 157.8 g; 95% confidence limits: 148.4 – 167.2 g). Adjustments to account for the influence of water temperature and body mass on the behavioural and metabolic measures was addressed in three ways. First, for the tests of repeatability, unadjusted values of Rmin $[O_2]$ and Rmax $[O_2]$ as well as the behavioural measures were used in general linear mixed models that included body mass and water temperature as fixed effects. Second, when testing for relationships between metabolic performance and behaviour, linear regressions relating each

behavioural measure to water temperature were used to statistically adjust the value measured for each individual to the value expected at a mean water temperature of 11.6°C. Identical adjustments were made for R_{min} $[O_2]$ and R_{max} $[O_2]$ using the appropriate mean temperature of 8.7°C. As I had two metabolic measures for each individual (measured on separate days), the temperature adjusted values for each individual were then averaged across the two measurement days. And third, when addressing individual variation in metabolic performance as well as graphical depiction of individual differences (Figure 3), multiple regressions were used to regress the values for R_{min} $[O_2]$ and R_{max} $[O_2]$ against water temperature and body mass to statistically adjust the value measured for each individual to the value expected at the mean water temperature during the metabolic experiments (8.7°C) and mean body mass (157.8 g) of the individuals sampled. Aerobic scope was calculated as the difference between the averaged values of R_{min} $[O_2]$ and R_{max} $[O_2]$ over the two measurement days after making the appropriate adjustments for water temperature and body mass depending on the test. In each case the values of the metabolic measures (R_{min} $[O_2]$ and R_{max} $[O_2]$), body mass, and water temperature were $\log_{10}$ transformed prior to analysis. Measures of metabolic performance that have been corrected for body mass and water temperature whether the adjustments were made prior or during a test will be used as proxies for standard metabolic rate, maximum metabolic rate, and aerobic scope. Cross type (migrant-migrant and migrant-resident) was not included as a predictor in each adjustment because preliminary analyses of covariance indicated that any relationships with temperature and body mass did not differ between the cross types.

Repeatability of the metabolic and behavioural measures was tested using the intraclass correlation coefficient ($r = \sigma_A^2/\sigma^2 + \sigma_A^2$), where σ_A^2 is the variance component estimated

between individuals and σ^2 is the variance component estimated across repeated observations. These variance components were estimated using generalized linear mixed-effects models with restricted maximum likelihood (Nakagawa & Schielzeth 2010). Intraclass correlation coefficients for the behavioural measures could not be calculated for fish measured for meteabolic performance specifically because their behaviour was measured only once. Instead, intraclass correlation coefficients for the behavioural measures were calculated using behavioural data obtained from Wajmer (2016) who repeated the behavioural measures three times for a subset of 56 fish. In all of the models, unadjusted values of the behavioural and metabolic performance measurements were used and individual identity was treated as a random effect. Water temperature, body mass, and trial number included as fixed effects. Water temperature and body mass were included because they are known to affect fish metabolism (Clarke & Johnston 1999) and behaviour **(**Theriault et al. 2007, Biro et al. 2009**)**. Trial number was included to control for potential habituation or fatigue between trials. All generalized linear mixed-effect models were fit using the R package lme4 (Bates et al. 2014). Likelihood ratio tests were used to test for statistical significance by comparing models including individual identity as a random effect with models excluding individual identity as a random effect. The R package RLRsim was used to run all likelihood ratio tests (Scheipl et al. 2008).

I used generalized linear models and generalized linear mixed models to test my predictions of how individual differences in the behavioural measures were expected to be related to differences in the metabolic measures. The general model structure included one of the four behavioural measures as a dependent variable with one of the three measures of metabolic performance as the independent variable. In the generalized mixed models, family identification

was included as a random effect to account for the possibility that offspring from the same family resembled each other more than offspring from different families. Body mass was included as a fixed covariate in each model because metabolism and behaviour can vary with size. For these analyses, temperature adjusted values of Rmin [O_2] and Rmax [O_2], aerobic scope (R_{max} [O_2] -R_{min} [O_2]), and body mass were log10 transformed and proportion of time spent moving, proportion of time spent near reflection, and transition rate were arcsine square-root transformed. Partial correlation coefficients were used to assess the magnitude of relationships among the variables characterizing behaviour and metabolic performance, after adjusting statistically for body mass and, as appropriate, family identification. My tests were initially made using all of the individuals irrespective of parental cross type. To test for whether the relationships between the behavioural measures and metabolic measures differed between individuals from the different cross types, I redid the tests above including cross type and the interaction between the metabolic predictor and cross type. A statistically significant interaction between the metabolic measure and cross type would indicate individuals from each cross type are utilizing energy in different ways and potentially follow different allocation strategies.

RESULTS

Individuals differed considerably in their measures of behavioural and metabolic performance. The measures used to characterize behaviour were similarly variable across individuals (Figure 2). Time to exit an enclosure ranged from 1 to 1800 seconds, proportion of time an individual spent moving ranged from 0 to 0.93, the proportion of time an individual spent near its reflection ranged from 0 to 1, and rates of transition between compartments in the dispersal channel ranged from 0 to 0.312 s^{-1}. The individual with the highest standard metabolic

rate had a value 2.1 times greater than the individual with the lowest standard metabolic rate (329.8 vs. 160.2 μmol O_2/g/h) (Figure 3). Individuals displaying the highest and lowest estimates of maximum metabolic rate, respectively, differed by a factor of 1.71 (2366.1 vs. 1377.5 μmol O_2/g/h), while the highest and lowest estimates of aerobic scope differed by a factor of 1.75 (2036.2 vs. 1159.6 μmol O_2/g/h) (Figure 3).

The intraclass correlations for the metrics of behaviour for multiple sets of individuals sampled during the same study period demonstrated that intraclass correlation coefficients were low to moderate in magnitude, ranging from 0.09 for proportion of time spent near reflection to 0.52 for time to exit an enclosure. The coefficients were statistically significant for all of the behavioural metrics except the proportion of time an individual spent near its reflection in the mirror (likelihood ratio tests: G's > 3.8, df = 1, p's < 0.021 for time to exit a refuge, proportion of time spent moving, and transition rate, respectively and G = 2.1, df = 1, p > 0.06 for proportion of time an individual spent near its reflection in the mirror). The individual differences in metabolic performance were repeatable. Intraclass correlations coefficients estimated for the metrics of metabolic performance were all relatively high, ranging from 0.66 for standard metabolic rate to 0.74 for aerobic scope. All of the coefficients were statistically significant (likelihood ratio tests: All G's > 31.7, df = 1, all p <0.0001).

I found no evidence that individual differences in the metrics of behavioural performance were predicted by individual differences in metabolic performance. After statistically controlling for body mass, partial correlation coefficients for the relationships between individual

behavioural metrics and individual metabolic metrics were all small and not statistically significant (Table 1; Figures 4-6). This result was consistent regardless of whether family effects were considered (Table 1).

Conversely, I did detect significant correlations between some of the measures of behavioural performance (Table 1) and between the different measures of metabolic performance. For the behavioural measures, individuals that took longer on average to exit the enclosure spent a lower proportion of time moving in the open aquarium, on average, than did individuals that took less time to exit the enclosure. However, neither time to exit the enclosure nor proportion of time moving in the aquarium was significantly related with the proportion of time an individual spent near its reflection or the rate at which individuals moved between compartments (Table 1). For the metabolic measures, individuals with higher standard metabolic rates had higher maximum metabolic rates and higher aerobic scope, than individuals with lower standard metabolic rates (Table 1). The magnitudes of the individual partial correlation coefficients were similar regardless of whether family effects were considered in the analysis.

The individual differences in behaviour were not significantly correlated with specific growth rate (Table 1). Conversely, individuals with higher standard metabolic rate, maximum metabolic rate, and aerobic scope grew faster than individuals with lower standard metabolic rate, maximum metabolic rate, and aerobic scope (Table 1, Figure 7).

There was no evidence that the relationships between the behavioural and metabolic measures differed with cross type in a manner expected if individuals from different cross types were using different energy allocation strategies. The statistical interaction between each metabolic measure and cross type was not statistically significant for any of the behavioural measures (all F's < 2.35, all $p > 0.13$) (Figures 4, 5, and 6 for standard metabolic rate, maximum metabolic rate, and aerobic scope respectively) As well, the intercepts of the relationships between the metabolic and behavioural measures did not differ significantly with respect for cross type (ANCOVAs: F's < 2.32, all $p > 0.14$), with the exception of proportion of time spent near reflection; standard metabolic rate ($F = 9.44$, $p = 0.003$) (Figure 4), maximum metabolic rate ($F = 11.7$, $p = 0.001$) (Figure 5), and aerobic scope ($F = 11.7$, $p = 0.001$) (Figure 6). Growth rates and body sizes did not differ between offspring from the two different cross types. The statistical interaction between each metabolic measure and cross type was not statistically significant when each of the three metabolic measures were considered (all F's < 0.69, all $p > 0.41$) (Figure 7). The intercepts of the relationships between the measures of metabolic performance and growth rate also did not differ significantly with respect to cross type (ANCOVAs: all F's < 2.91, all $p > 0.09$) (Figure 7).

DISCUSSION

Three main findings emerged from my study. First, Brook Trout displayed CIDs in three of four measures of behaviour, with proximity to the mirror being the only measure that was not repeatable and in all three measures of metabolic performance. Second, no statistically significant relationship between the CIDs in behaviour and in metabolic performance was observed. Third, there was also no evidence suggesting that relationships between CIDs in

behaviour and metabolic performance differed between offspring from the two cross types, which could arise if the two types of offspring were expressing different strategies of energy allocation.

Taken together, these findings support neither the performance or allocation models developed to relate CIDs in behaviour with CIDs in standard metabolic rate. If the differences between migrant and resident parental types are the outcome of phenotypic plasticity (Dodson et al. 2013), then the performance model would probably be the most appropriate of the two models for my study animals. The offspring were reared under similar conditions, fed a ration (ad libitum) encouraging positive growth, and positive growth rates were observed for all individuals over the approximately 5 months (February to July) prior testing. The positive relationships observed between standard metabolic rate, maximum metabolic rate, aerobic scope, and specific growth rate were also consistent with the performance model, and not the allocation model. However, the key relationship between behaviour and standard metabolic rate was not detected. If the differences in parental phenotypes were heritable, and access to food varied among individuals, then offspring from the different crosses could exhibit different patterns of covariation between behaviour and standard metabolic rate, with offspring of the migrant-migrant crosses being consistent with the performance model and offspring of migrant-resident crosses being more consistent with the allocation model (Ridgway 2008). This possibility was not supported here and, while the differences in behavioural measures are heritable across the juvenile life stage (Wajmer 2016, Sicoly 2015), they are unrelated to the migratory behaviour of parents. Instead, my findings suggest that the relationship between CIDs in behaviour and CIDs in metabolic measures of performance may be more complicated than suggested by the simple

models, a conclusion that is also supported by a number of other studies that have also not detected a relationship between CIDs in behaviour and CIDs in measures of baseline metabolic rates (Chappell et al. 2007, Radwan et al. 2004, LeGalliard et al. 2013), including the earlier evaluation by Farwell and McLaughlin (2009) for young-of-the-year Brook Trout.

My study further offers some insight into possible explanations for why no relationship was observed between CIDs in behaviour and metabolic phenotype. I suspect the differences in metabolic performance observed for Brook Trout are large enough to affect behaviour because mass-adjusted differences in standard metabolic rate, aerobic scope and maximal metabolic rate varied by a factor of two; similar variation in measures of metabolic performance were observed in studies on other fishes in the literature (Norin et al. 2016, Norin & Malte 2011). The behavioural differences were also large. The possibility that CIDs in other aspects of an individual's metabolic phenotype might be more important in shaping behaviour, or vice versa (Metcalfe et al. 2016), can be ruled out, because no relationship was observed between behaviour and either aerobic scope or maximum metabolic rate. In addition, both standard metabolic rate and aerobic scope are potentially important based on their relative contribution to energy expenditures. For example, standard metabolic rate and aerobic scope make up 13.8 and 86.2% of the maximal metabolic rate, respectively. The possibility that the nature of relationships between behaviour and metabolic measures might differ for offspring from the different cross types was also not supported. Given these outcomes, future studies should focus on whether differences in metabolic performance are more tightly correlated with specific types of behaviours. For example, Methot and Dingemanse (2015) recently posited that there are two types of behaviours, gain, and expenditure. Where "gain" behaviours are those that bring in net

energy (e.g. foraging) and "expenditure" behaviours are those that are energetically costly and only expend energy (e.g. activity, aggression). They hypothesized that gain and expenditure behaviours would be influenced by standard metabolic rate differently; however, distinction between these two types of behaviours can be difficult. Future studies should also consider whether animals can compensate for CIDs in standard metabolic rates by adjusting other aspects of their physiology that are not necessarily reflected in behaviour, given that standard metabolic rate is a summation of many underlying physiological processes (Hochachka et al. 2003).

My findings also offer some insight into the development of the migrant and resident morphs of Brook Trout. In the field, migrant and resident Brook Trout display clear differences in growth rate, energy metabolism, and life history (Robillard et al. 2011b, Morinville & Rasmussen 2003, Ridgway 2008). Under hatchery conditions, such differences were not observed, particularly among offspring with migrant vs resident sires, suggesting the variation in life history is a consequence of phenotypic plasticity (Dodson et al. 2013), possibly related to habitat heterogeneity and competition for the best feeding habitats (Dodson et al. 2013, Morinville & Rasmussen 2006). The behavioural measurements for offspring reared under hatchery conditions were also repeatable and heritable, but unrelated to the migratory phenotype of the parents at each age class of the juvenile life stage (Wajmer 2016). Although my findings do not represent an explicit test of phenotypic plasticity, they do contribute to our understanding of the roles that differences in genotype and phenotypic plasticity could have in shaping the behavioural and metabolic variation in polymorphic Brook Trout from Lake Superior, and for this species more broadly. This understanding is valuable for determining the degree to which

migratory polymorphisms evolve via a common mechanism or unique, site specific adaptations (Van Dyck & Baguette 2005, Fausch et al. 2002).

My study has some potential limitations that are important to consider because of how they could influence my conclusions. The first is that my sample size of fish, 60 individuals, was moderate in size, which could have limited the statistical power of my tests relating behaviour with metabolic performance. I consider this unlikely. My analyses were able to detect statistically significant relationships between the different metabolic measures and between two behavioural measures, time to exit the enclosure and proportion of time spent moving, that were found to be correlated in earlier research with these fish (Sicoly 2015, Wajmer 2016). For studies that have reported evidence of a correlation between behaviour and metabolic performance, the correlation coefficients have averaged 0.61 (Table 2). With my sample size, the power of my tests for detecting a correlation coefficient of that magnitude would be 0.99. Another potential limitation is that my study design did not include offspring from resident x resident crosses. This raises the possibility that my sample of fish did not include the full suite of genotypes, and possibly phenotypes, available in the wild population. Despite this, I still observed wide variation in all of the behavioural and metabolic measures. A third potential limitation is that my standardized tests of behaviour may have excluded an aspect of behaviour important to this study system and the adoption of resident versus migratory tactics, such as aggression, feeding behaviour, or habitat selection. The behaviours selected for my tests have been related previously to significant aspects of the space use behaviour of juvenile Brook Trout in the field, including the use of sit-and-wait and active foraging tactics, vertical use of the water column, and juvenile dispersal (Wilson & McLaughlin 2007, Farwell & McLaughlin 2009, Edelsparre et al. 2013).

Overt aggression was rare in the mirror image tests (Sicoly 2015, Wajmer 2016) and tends to be rare in the field (McLaughlin et al. 1999). Lastly, it remains possible that behavioural measures, such as proportion of time spent moving, missed subtle variation among individuals that could compensate for differences in metabolic performance, such as differing reliance on steady versus intermittent forms location (Kramer and McLaughlin 2001).

Despite these limitations, my study also had some key strengths. Several lines of evidence suggest my measurements of behaviour and metabolic performance were precise and accurate. Measurements of oxygen consumption, uncorrected for body size and temperature, were highly repeatable across trials for the same individual (standard metabolic rate: 0.78; maximum metabolic rate: 0.92; aerobic scope: 0.9). Measurements of standard metabolic rate were also consistent with values reported in the literature for salmonid fishes of similar size (Brett & Glass 1973, Rao 1967, Kelly et al. 2014), suggesting the estimates were accurate. Although there are fewer data available for measurements of maximum metabolic rate and aerobic scope, the magnitude of variation found in the literature were similar to the values reported in this study (Norin & Malte 2011, Killen et al. 2012, Norin et al. 2016). Further, the intraclass correlation coefficients summarizing the repeatability of behaviour and the metabolic rates were comparable in magnitude to values reported in recent meta-analyses of the repeatability of behaviour (Bell et al. 2009) and baseline and maximal metabolic rates in vertebrates (Nespolo & Franco 2007). The repeatability of aerobic scope, while not included in the meta-analyses, was also comparable in magnitude to values reported in the literature (Norin & Malte 2011, Norin et al. 2016). My consideration of maximum metabolic rate and aerobic scope, in addition to standard metabolic rate was also unique and was recently recommended as

an avenue for additional research (Metcalfe et al. 2016). Lastly, my study uniquely sought to exploit the potential contrast in behaviour and metabolic performance that a polymorphic population might provide, although the differences in behaviour and life history observed for the parent Brook Trout in the field were not observed in their offspring in the lab.

Delineating the proximate mechanisms for CIDs in behaviour is likely to remain an ongoing challenge. On the one hand, CIDs in behaviour have to be related to underlying energetic and neuro-endocrine mechanisms (Koolhaas et al. 1999). Simple conceptual frameworks such as the performance and allocation models developed around CIDs in standard metabolic rate (Careau et al. 2008, Mathot & Dingemanse 2015), and the distinction between proactive and reactive individuals developed around differences in stress responses (Koolhaas et al. 1999), have provided useful entry points for studying the proximate mechanisms for CIDs in behaviour. However, findings inconsistent with the energetic models, such as mine, and with the proactive-reactive distinction, such as Schjolden et al. (2005), have encouraged recent revisions to the models (e.g. Methot and Dingimanse 2015, Koolhaas et al. 2010). Our understanding of the proximate basis for CIDs in behaviour is still missing important aspects of the underlying mechanisms.

REFERENCES

Altmann, J. 1974. Observational study of behaviour: sampling methods. Behaviour, **49**, 227-267.

Balzarini, V., Taborsky, M., Wanner, S., Koch, F., & Frommen, J.G. 2014. Mirror, mirror on the wall: the predictive value of mirror tests for measuring aggression in fish. *Behavioural Ecology and Sociobiology*, **68**, 871-878.

Bates, D., Maechler, M., Bolker, B., & Walker, S. 2014. lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-6. http://CRAN.R-project.org/package=lme4.

Bell, A.M., Hankison, S.J., & Laskowski, K.L. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour*, **77**, 771–783.

Biro, P.A. & Ridgway, M.S. 1995. Individual variation in foraging movements in a lake population of young-of-the-year brook charr (*Salvelinus fontinalis*). *Behaviour*, **132**, 57–74.

Biro, P.A. & Stamps, J.A. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution*, **23**, 361–368.

Biro, P.A., Beckmann, C., & Stamps, J.A. 2009. Small within-day increases in temperature affects boldness and alters personality in coral reef fish. *Proceedings of the Royal Society*, **277**, 71-77.

Biro, P.A., & Stamps, J.A. 2010. Do consistent individual differences in metabolic rate promote consistent individual differences in behaviour? *Trends in Ecology & Evolution*, **25**, 653-659.

Bolnick, D.I., Svanback, R., Fordyce, J.A., Yang, L.H., Davis, J.M., Hulsey, C.D., & Forister, M.L. 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist*, **161**, 1-28.

Bouwhuis, S., Quinn, J.L., Sheldon, B.C., &Verhulst, S. 2014. Personality and basal metabolic rate in a wild bird population. *Oikos*,**123**, 56–62.

Bradford, M.J. &Taylor, G.C. 1997. Individual variation in dispersal behaviour of newly emerged chinook salmon (*Oncorhynchus tshawytscha*) from the Upper Fraser River, British Columbia. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 1585-1592.

Brett, J.R., & Glass, N.R. 1973. Metabolic rates and critical swimming speeds of sockeye salmon *(Oncorhynchus nerka)* in relation to size and temperature. *Journal of Fish Research Board of Canada*, **30**, 379-387.

Brown, C., Jones, F., & Braithwaite, V. 2005. In situ examination of boldness-shyness traits in the tropical poecilid, *Brachyraphis episcopi*. *Animal Behaviour*, **70**, 1003-1009.

Bryant, D.M. and Newton, A.V. 1994. Metabolic costs of dominance in dippers, Cinclus cinclus. *Animal Behavior*, **48**, 447–455.

Careau, V., Thomas, D., Humphries, M.M., & Reale, D. 2008. Energy metabolism and animal personality. **Oikos**, **117**, 641-653.

Careau, V., Thomas, D., Pelletier, F., Turki, L., Landry, F., Garant, D., & Reale, D. 2011. Genetic correlation between resting metabolic rate and exploratory behaviour in deer mice (Peromyscus maniculatus). *Journal of Evolutionary Biology*, **24**, 2153–2163.

Careau, V. & Garland, T. 2012. Performance, personality, and energetics: correlation, causation and mechanism. *Physiological and Biochemical Zoology*, **85**, 543-571.

Chappell, M.A., Garland, T., Rezende, E.L., & Gomes, F.R. 2004. Voluntary running in deer mice: speed, distance, energy costs and temperature effects. *Journal of Experimental Biology*, **207**, 3839– 3854.

Chappell, M.A., Garland, T., Robertson, G.F., & Saltzman, W. 2007. Relationships among running performance, aerobic physiology and organ mass in male Mongolian gerbils. *Journal of Experimental Biology*, **210**, 4179–4197.

Clark, T.D., Sandblom, E., & Jutfelt, F. 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *Journal of Experimental Biology*, **216**, 2771–2782.

Clarke, A. & Johnston, N.M. 1999. Scaling of metabolic rate with body mass and temperature in teleost fish. *Journal of Animal Ecology*, **68**, 893-905.

Conrad, J.L, Weinersmith, K.L., Brodin, T., Saltz, J.B., & Sih, A. 2011. Behavioural syndromes in fishes: a review with implications for ecology and fisheries management. *Journal of Fish Biology*, **78**, 395-435.

Cote, J. & Clobert, J. 2007. Social personalities influence natal dispersal in a lizard. *Proceedings of the Royal Society B-Biological Sciences*, **274**, 383–390.

Cutts, C.J., Metcalfe, N.B., & Caylor, A.C. 1998. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology*, **52**, 1026–1037.

Cutts, C.J., Metcalfe, N.B., & Caylor, A.C. 1999. Competitive asymmetries in territorial juvenile Atlantic salmon, Salmo salar. *Oikos*, **86**, 479–486.

Cutts, C.J., Adams, C.E., & Campbell, A. 2001. Stability of physiological and behavioural determinants of performance in Arctic char (*Salvelinus alpinus*). *Canadian Journal of Fisheries and Aquatic Sciences*. **58**, 961-968.

Cutts, C.J., Metcalfe N.B., & Taylor A.C. 2002. Juvenile Atlantic salmon (*Salmo salar*) with relatively high standard metabolic rates have small metabolic scopes. *Functional Ecology*, **16**, 73–78.

Daan, S., Masman, D., & Groenewold, A. 1990. Avian basal metabolic rates: their association with body composition and energy expenditure in nature. *American Journal of Physiology – Regulatory, Integrative and Comparative Physiology*, **259**, 333–340.

Dall, S.R.X., Houston, A.I., & McNamara, J.M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.

Deerenberg, C., Overkamp, G. J. F., Visser, G.H., & Daan, S. 1998. Compensation in resting metabolism for experimentally increased activity. *Journal of Comparative Physiology B*, **168**, 507-512.

Dodson, J. J., Aubin-Horth, N., Thériault, V., & Páez, D. J. 2013. The evolutionary ecology of alternative migratory tactics in salmonid fishes. *Biological Reviews*, **88**, 602–625.

Van Dyck, H. & Baguette, M. 2005. Dispersal behaviour in fragmented landscapes: routine or special movements? *Basic and Applied Ecology*, **6**, 535–545.

Edelsparre, A.H., McLaughlin, R.L., & Rodriguez, M.A. 2013. Risk taking not foraging behaviour predicts dispersal of recently emerged stream brook charr (*Salvelinus fotninalis*). *Ecosphere,* **4**, 1-19.

Farwell, M., Fuzzen, M.L.M., Bernier, N.J, & McLaughlin, R.L. 2014. Individual differences in foraging behavior and cortisol levels in recently emerged brook charr (*Salvelinus fontinalis*). *Behavioural Ecology and Sociobility*, **68**, 781-790.

Farwell, M., & McLaughlin, R.L. 2009. Alternative foraging tactics and risk taking in brook charr (*Salvelinus fontinalis*). *Behavioural Ecology*, **20**, 913-921.

Fausch, K. D., Torgersen, C. E., Baxter, C. V., & Li, H. W. 2002. Landscapes to riverscapes: Bridging the gap between research and conservation of stream fishes. *BioScience*, **52**, 483–498.

Forseth, T., Ugedal, O., & Jonsson, B. 1994. The energy budget, niche shift, reproduction and growth in a population of Arctic Charr, Salvelinus alpinus. *Journal of Animal Ecology*, **63**, 116-126.

Gebczynski, A.K. & Konarzewski, M. 2009. Locomotor activity of mice divergently selected for basal metabolic rate: a test of hypotheses on the evolution of endothermy. Journal of *Evolutionary Biology*, **22**, 1212–1220.

Gifford, M.E., Clay, T.A., & Careau, V. 2014. Individual (co)variation in standard metabolic rate, feeding rate, and exploratory behvior in wild-caught semiaquatic salamanders. *Physiological and Biochemical Zoology*, **87**, 384–396.

Groothuis, T. G. G. & Carere, C. 2005. Avian personalities: characterization and epigenesis. *Neuroscience and Biobehavioral Reviews*, **29**, 137–150.

Hammond, K.A., Chappell, M.A., Cardullo, R.A., Lin, R.-S., & Johnson, T.S. 2000. The mechanistic basis of aerobic performance variation in red junglefowl. *Journal of Experimental Biology*, **203**, 2053–2064.

Healey, T.M., & Schulte, P.M. 2012. Thermal acclimation is not necessary to maintain a wide thermal breadth of aerobic scope in the common killifish (*Fundulus heteroclitus*). *Physiological and Biochemical Zoology,* **85**, 107–119.

Hendry, A.P., Bohlin, T., Jonsson, B., & Berg, O.K., 2004. To sea or not to sea? anadromy versus non-anadromy in salmonids. *Evolution Illuminated: Salmon and their Relatives*. Oxford University Press, New York, NY, 93–125.

Hochachka, P.W., Darveau, C.A., Andrews, R.D., & Suarez, R.K. 2003. Allometric cascade: a model resolving body mass effects on metabolism. *Comparative Biochemistry and Physiology Part A*, **134**, 675-691.

Holtby, L.B. 1992. Through a glass, darkly: A response to Ruzzante's reappraisal of mirror image stimulations studies. *Canadian Journal of Fisheries and Aquatic Sciences,* **49**, 1968-1969.

Huckins, C. J., Baker, E. A., Fausch, K. D., & Leonard, J. B. 2008. Ecology and life history of coaster brook trout and potential bottlenecks in their rehabilitation. *North American Journal of Fisheries Management*, **28**, 1321–1342.

Huntingford, F.A., Andrew G., Mackenzie, S., Morera, D., Coyle, S.M., Pilarczyk, M., &Kadri, S. 2010. Coping strategies in a strongly schooling fish, the common carp *Cyprinus carpio, Journal of Fish Biology*, **76**, 1576-1591.

Kelly, N.I, Burness, G., McDermid, J.L., & Wilson, C. 2014. Ice age fish in a warming world: minimal variation in thermal acclimation capacity among trout (*Salvelinus namaycush*) populations. *Conservation Physiology*, **2**, 1-14.

Killen, S.S., Marras, S., Steffensen, J.F. McKenzie, D.J. 2012a. Aerobic capacity influences the spatial position of individuals within fish schools. *Proceedings of the Royal Society B*, **279**, 357–364.

Killen, S.S., Mitchell, M.D., Rummer, J.L., Chivers, D.P., Ferrari, M.C.O., Meekan, M.G. & McCormick, M.I. 2014. Aerobic scope predicts dominance during early life in a tropical damselfish. *Functional Ecology* **28,** 1367–1376.

Konarzewski, M. & Ksiazek, A. 2013. Determinants of intra-specific variation in basal metabolic rate. *Journal of Comparative Physiology B: Biochemical, Systemic, and Environmental Physiology*, **183**, 27–41.

Koolhaas, J.M, de Boer, S.F., Coppens, C.M., & Buwalda, B. 2010. Neuroendocrinology of coping styles: towards understand the biology of individual variation. *Frontiers in Neuroendocrinology*, **31**, 307-321.

Koolhaas, J.M., Korte, S.M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W. & Blokhuis, H. J. 1999. Coping styles in animals: current status in behaviour and stress-physiology. *Neuroscience and Biobehavioral Reviews,* **23**, 925–935.

Kramer, D.L. & McLaughlin, R.L. 2001. The behavioural ecology of intermittent locomotion. *American Zoologist*, **41**, 137-153.

Krams, I., Kivleniece, I., Kuusic, A., Krama, T., Freeberg, T.M., Mand, R., Sivacova, L., Rantala, M.J., & Mand, M. 2013. High repeatability of anti-predator responses and resting metabolic rate in a beetle. *Journal of Insect Biology*, **27**, 57-66.

Lahti, K., Laurila, A., Enberg, K., & Piironen, J. 2001. Variation in aggressive behaviour and growth rate between populations and migratory forms in the brown trout, *Salmo trutta*. *Animal Behaviour*, **62**, 935-944.

Le Galliard, J-F., Paquet, M., Cisel, M., & Montes-Poloni, L. 2013. Personality and the pace-of-life syndrome: variation and selection on exploration, metabolism and locomotor performances. *Functional Ecology*, **27**, 136–144.

Martin, P., & Bateson, P. 1986. Measuring behaviour: an introductory guide. Cambridge University Press.

Mathot, K.J, & Dingemanse, N.J. 2015. Energetics and behaviour: unrequited needs and new directions. *Trends in Ecology & Evolution*, **30**, 199-206.

Mathot, K.J., Nicolaus, M., Araya-Ajoy, Y.G., Dingemanse, N.J., & Kempenaers, B. 2015. Does metabolic rate predict risk-taking behaviour? A field experiment in a wild passerine bird. *Functional Ecology*. **29**, 239–249.

McCarthy, I.D. 2001. Competitive ability is related to metabolic asymmetry in juvenile rainbow trout. *Journal of Fish Biology*, **59**, 1002–1014.

McElreath, R. & Strimling, P. 2006. How noisy information and individual asymmetries can make 'personality' an adaptation: a simple model. *Animal Behaviour*, **72**, 1135–1139.

McLaughlin, R.L., Grant, J.W.A., & Kramer, D.L. 1992. Individual variation and alternative patterns of foraging movements in recently-emerged brook char (*Salvelinus fontinalis*). *Behaviour*, **120**, 286-301.

McLaughlin, R.L. & Grant, J.W.A. 1994. Morphological and behavioural differences among recently-emerged brook charr, *Salvelinus fontinalis*, foraging in slow vs. fast-running water. *Environmental Biology of Fishes*, **39**, 289–300.

McLaughlin, R.L., Ferguson, M.M. & Noakes, D.L.G. 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. *Behavioral Ecology and Sociobiology*, **45**, 386–395.

McNab, B.K. 1997. On the utility of uniformity in the definition of basal metabolic rate of metabolism, *Physiological Zoology*, **70**, 718-720.

Metcalfe, N.B., Taylor, A.C., and Thorpe, J.E. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behaviour*, **49**, 431–436.

Metcalfe, N.B., Leeuwen, T.E., & Killen, S.S. 2016. Does individual variation in metabolic phenotype predict fish behaviour and performance?, Journal of Fish Biology, **88**, 298-321.

Mittelbach, G.G., Ballew, N.G., & Kjelvik, M.K. 2014. Fish behavioral types and their ecological consequences. *Canadian Journal of Fisheries and Aquatic Sciences*, **18**, 1–18.

Morinville, G.R., & Rasmussen, J.B. 2003. Early juvenile bioenergetics differences between anadromous and resident brook trout (Salvelinus fontinalis), *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 401-410.

Morinville, G.R & Rasmussen J., B. 2006. Does life-history variability in salmonids affect habitat use by juveniles? A comparison among streams open and closed to anadromy. *Journal of Animal Ecology*, **75**, 693-704.

Mucha, J.M., & Mackereth, R.W. 2008. Habitat use and movement patterns of brook trout in Nipigon Bay, Lake Superior. *Transactions of the American Fisheries Society*, **137**, 1203-1212.

Nakagawa, S., & Schielzeth, H. 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. *Biological reviews of the Cambridge Philosophical Society*, **85**, 935–56.

Nespolo, R.F., & Franco, M. 2007. Whole-animal metabolic rate is a repeatable trait: a meta-analysis. *The Journal of Experimental Biology*, **210**, 2000-2005.

Norin, T., & Malte, H. 2011. Repeatability of standard metabolic rate, active metabolic rate and aerobic scope in young brown trout during a period of moderate food availability. *Journal of Experimental Biology*, **214**, 1668–1675.

Norin, T., Malte, H., & Clark, T.D. 2016. Differential plasticity of metabolic rate phenotypes in a tropical fish facing environmental change. *Functional Ecology*, **30**, 369-378.

Northcote, T.G., & Kelso, B.W. 1981. Differential response to water current by two homozygous LDH phenotypes of young rainbow trout (*Salmo gairdneri*). *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 48-352.

Radwan, J., Kruczek, M., Labocha, M.K., Grabiec, K., & Koteja, P. 2004. Contest winning and metabolic competence in male bank voles Clethrionomys glareolus. *Behaviour*, **141**, 343–354.

Rao, G.M.M. 1967. Oxygen consumption of rainbow trout *(Salmo gairdneri)* in relation to activity, salinity and temperature. Doctoral dissertation. University of Toronto, Toronto, Ontario.

Reidy, S.P., Nelson, J.A., Tang, Y., & Kerr, S.R. 1995. Post-exercise metabolic rate in Atlantic cod and its dependence upon the method of exhaustion. *Journal of Fish Biology*, **47**, 377–386.

Réale, D., Gallant, B.Y., Leblanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, **60**, 589–597.

Rezende, E.L., Gomes, F.R., Chappell, M.A., & Garland Jr., T. 2009. Running behavior and its energy cost in mice selectively bred for high voluntary locomotor activity. *Physiological and Biochemical Zoology*, **82**, 662–679.

Ridgeway, M.S. 2008. A roadmap for coasters: landscapes, life histories, and the conservation of brook trout. *Transactions of the American Fisheries Society*, **137**, 1179-1191.

Robillard M.M., McLaughlin, R.L., & Mackereth, R.W. 2011a. Diversity in habitat use and trophic ecology of brook trout in Lake Superior and tributary streams revealed through stable isotopes. *Transactions of the American Fisheries Society*, **140**, 943-953.

Robillard, M.M., Casselman, J.M., McLaughlin, R.L., & Mackereth, R.W. 2011b. Alternative growth histories in populations of Lake Superior brook trout: Critical support for partial migration. *Biological Conservation*, **144**, 1931-1939.

Robillard, M.M., McLaughlin, R.L., & Mackereth, R.W. 2014. Sexual maturation in stream residents from migratory populations of brook trout inhabiting Lake Superior tributaries. *Journal of Great Lakes Research*, **40**, 1016-1021.

Roche, D.G., Binning, S.A., Bosiger, Y., Johansen, J.L., & Rummer, J.L. 2013. Finding the best estimates of metabolic rates in a coral reef fish. *Journal of Experimental Biology*, **216**, 2103–2110.

Ros, A.F.H., Becker, K. & Oliveira, R.F. 2006. Aggressive behaviour and energy metabolism in a cichlid fish, *Oreochromis mossambicus*. *Physiology and Behavior* **89,** 164–170.

Ruzzante, D.E. 1992. Mirror image stimulation, social hierarchies, and population differences in agonistic behaviour: A reappraisal. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 1966-1968.

Scheipl, F., Greven, S. & Kuechenhoff, H. 2008. Size and power of tests for a zero random effect variance or polynomial regression in additive and linear mixed models. *Computational Statistics & Data Analysis*, **52**, 3283-3299.

Schjolden, J., Stoskhus, A., & Winberg, S. 2005. Does individual variation in stress responses and agonistic behaviour reflect divergent stress coping strategies in juvenile rainbow trout? *Physiological and Biochemical Zoology*, **78**, 715-723.

Sicoly, L. 2015. Understanding behavioural diversity and its link to migration in Lake Superior brook trout. M.Sc. Thesis, University of Guelph, Guelph, ON.

Sih, A., Kats, L. B. & Maurer, E. F. 2003. Behavioural correlations across situations and the evolution of antipredator behaviour in a sunfish-salamander system. *Animal Behaviour,* **65**, 29–44.

Svendsen, G.E. & Armitage, K.B. 1973. Mirror-image stimulations applied to field behavioral studies. *Ecology*, **54**, 623-627.

Swain, D.P., & Holtby, L.B.1989. Differences in morphology and behaviour between juvenile coho salmon (*Oncorhynchus kisutch*) rearing in a lake and in its tributary stream. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1406-1414.

Swain, D.P., & Riddell, B.E. 1990. Variation in agonistic behaviour between newly emerged juveniles from hatchery and wild population of coho salmon, *Oncorhynchus kisutch*. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 566-571.

Taylor, E.B., & Larkin, P.A. 1986. Current response and agonistic behaviour in newly emerged fry of chinook salmon, *Oncorhynchus tshawytscha*, from ocean- and stream-type populations. *Canadian Journal of Fisheries and Aquatic Sciences*, **43**, 565-573.

Thériault, V., Garant, D., Bernatchez, L., & Dodson, J. J. 2007. Heritability of life-history tactics and genetic correlation with body size in a natural population of brook charr (*Salvelinus fontinalis*). *Journal of Evolutionary Biology*, **20**, 2266–77.

Therneau, T. 2015. Mixed Effects Cox Models. *Reference Manual*, 1–14.

Wajmer, N. 2016. Understanding phenotypic and genetic variation in behaviours linked to migration in Lake Superior Brook Trout. M.Sc. Thesis, University of Guelph, Guelph, ON.

Wikelski, M., Lynn, S., Breuner, C., Wingfield, J.C., and Kenagy, G.J. 1999. Energy metabolism, testosterone and corticosterone in white-crowned sparrows. *Journal of Comparative Physiology A*, **185**, 463-470.

Wilson, A.D.M, & Krause, J. 2012. Personality and metamorphosis: is behavioral variation consistent across ontogenetic niche shifts? *Behavioural Ecology*, **23**, 1316-1323.

Wilson, A.D.M., & McLaughlin, R.L. 2007. Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations. *Animal Behaviour*, **74**, 689-698.

Wilson, A.D.M. & McLaughlin, R.L. 2010. Foraging behaviour and brain morphology in recently emerged brook charr, *Salvelinus fontinalis*. *Behavioral Ecology and Sociobiology*, **64**, 1905–1914.

Wolf, M., van Doorn, S., Leimar, O., & Weissing, F.J. 2007. Life-history trade-offs favour the evolution of animal personalities. *Nature*, **447**, 581–584.

Yamamoto, T., Ueda, H., & Higashi, S. 1998. Correlation among dominance status, metabolic rate and otolith size in masu salmon. *Journal of Fish Biology*, **52**, 281–290.

Table 1: Correlations between the behavioural and metabolic measurements. Partial correlations after adjusting for family identity as a random effect are provided above the diagonal. Correlations when family identity is not considered are provided below the diagonal. Correlations having p-values < 0.05 are bolded.

	Behavioural Measures				Metabolic Measures			
Measurement	Time to Exit a Refuge	Proportion of Time Spent Moving	Proportion of Time Spent Near Reflection	Transition Rate	Standard Metabolic Rate	Maximum Metabolic Rate	Aerobic Scope	Specific Growth Rate
Time to Exit a Refuge (s)	-	**-0.59**	-0.01	0.08	-0.24	-0.09	-0.08	-0.04
Proportion of Time Spent Moving	**-0.48**	-	0.04	-0.09	0.08	-0.04	-0.06	0.09
Proportion of Time Spent Near Reflection	-0.02	-0.02	-	-0.05	-0.2	-0.17	-0.13	0.07
Transition Rate (s^{-1})	0.08	-0.07	-0.04	-	0.09	-0.01	-0.03	-0.01
Standard Metabolic Rate (µmol O_2/g/h)	-0.15	0.09	-0.2	0.13	-	**0.45**	**0.29**	**0.52**
Maximum Metabolic Rate (µmol O_2/g/h)	-0.09	0.02	-0.18	-0.02	**0.43**	-	**0.98**	**0.58**
Aerobic Scope (µmol O_2/g/h)	-0.07	0.01	-0.15	-0.05	**0.27**	**0.98**	-	**0.57**
Specific Growth Rate (g g^{-1} d^{-1})	-0.06	0.07	0.03	-0.11	**0.53**	**0.59**	**0.57**	-

Table 2: Correlation coefficients of significant relationships between behaviour and metabolic performance reported in the literature.

Behaviour	Metabolic Measure	Correlation Coefficient	Species	Source
Dominance	Basal metabolic rate	0.48	Dipper (*Cinclus cinclus*)	Bryant & Newton 1994
Aggression	Standard metabolic rate	0.56	Arctic Char (*Salvelinuues arcticus*)	Cutts et al. 2001
Dominance	Resting metabolic rate	0.62	Rainbow Trout (*Oncohynchus mykiss*)	McCarthy 2001
Aggression	Standard metabolic rate	0.99	Brown Trout (*Salmo trutta*)	Lahti et al. 2002
Aggression	Routine metabolic rate	0.76	Mozambique tilapia (*Oreochromis mossambicus*)	Ros et al. 2006
Dominance	Aerobic scope	0.51	Ambron Damsel (*Pomacentrus amboinensis*)	Killen et al. 2014
Activity	Resting metabolic rate	0.46	Deer Mouse (*Peromyscus maniculatus*)	Chappell et al. 2004
Exploration	Resting metabolic rate	0.78	Deer Mouse (*Peromyscus maniculatus*)	Careau et al. 2011
Activity	Resting metabolic rate	0.46	House Mouse (*Mus musculus*)	Rezende et al. 2009
Risk taking	Resting metabolic rate	0.48	Mealworm Beetle (*Tenebrio molitor*)	Krams et al. 2013

FIGURES

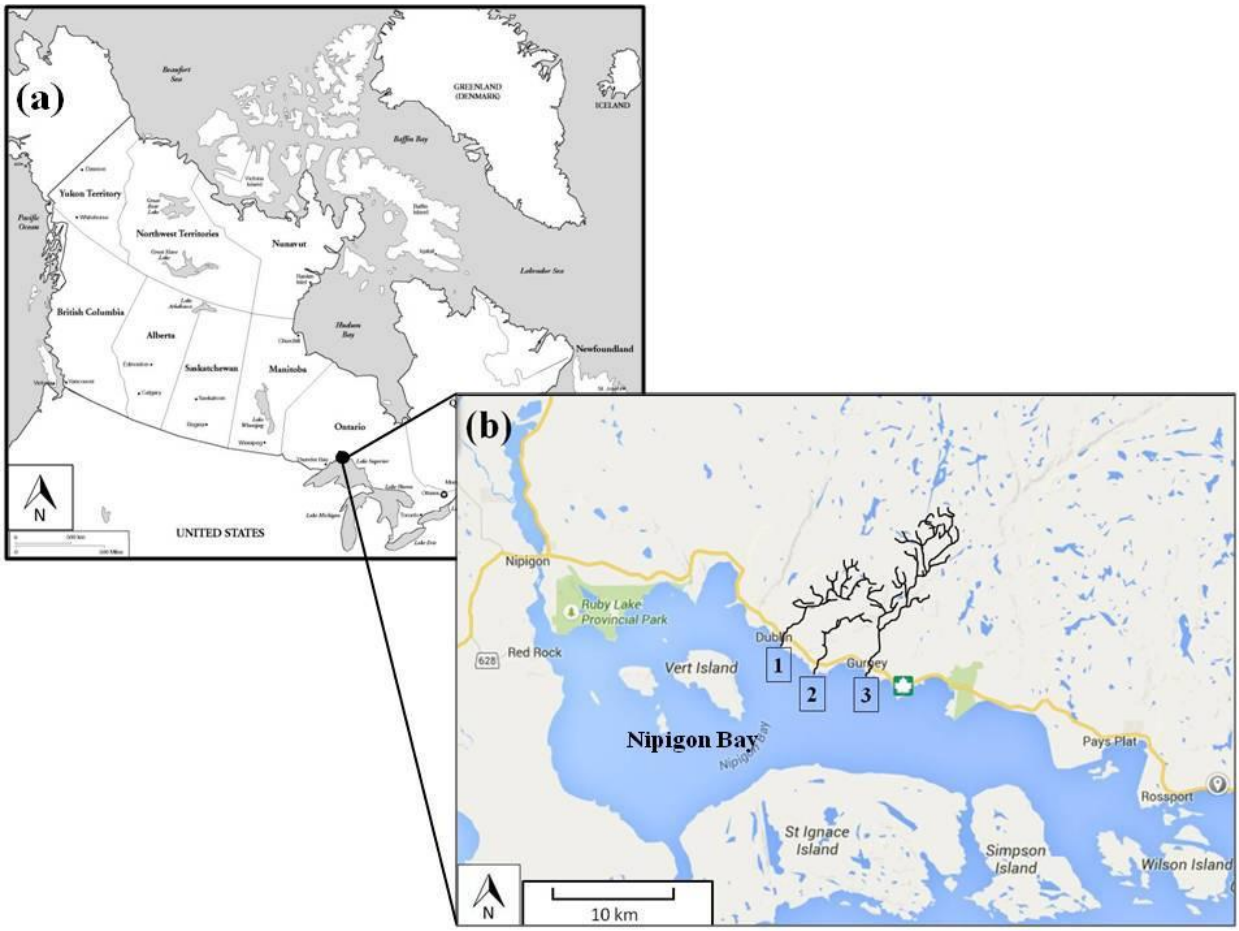

Figure 1: Sample locations for the migrant and resident adult Brook Trout used to create the crosses for this study (from Wajmer 2016). (a) The location of Nipigon Bay in Lake Superior. (b) The tributaries sampled in Nipigon Bay: Dublin Creek (1), MacInnes Creek (2), and Cypress River (3).

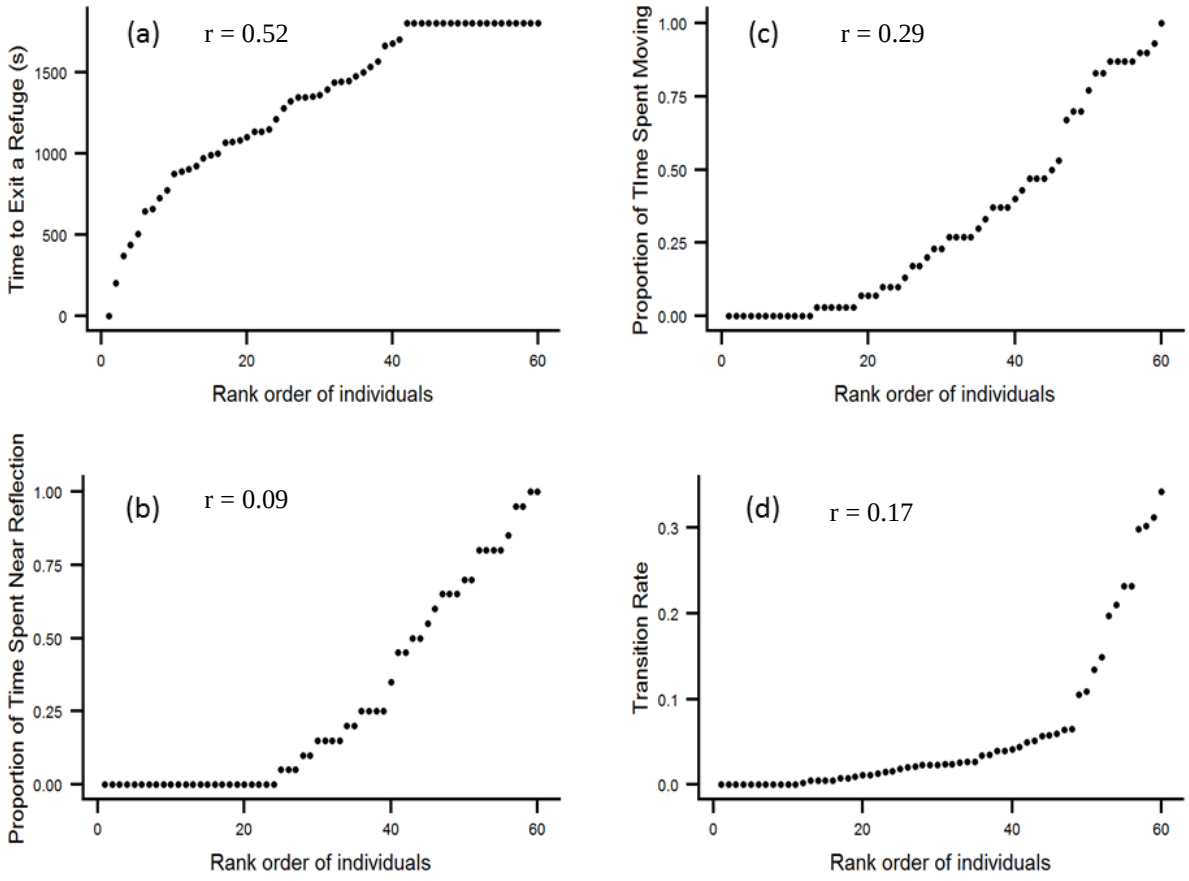

Figure 2: Individual variation in the measurements of time to exit a refuge (a), proportion of time an individual spent moving (b), proportion of time an individual spent near its reflection (c), and the transition rate between compartments of the dispersal channels. N = 60. Each closed circle represents a measurement for an individual at 11.6°C. Intraclass correlations (r) in each panel were calculated for 56 individuals using behavioural data from Wajmer (2016). Individuals were ranked from lowest to highest based on the magnitude of estimated values for the summarized behavioural measurement. An individual's rank can differ between panels.

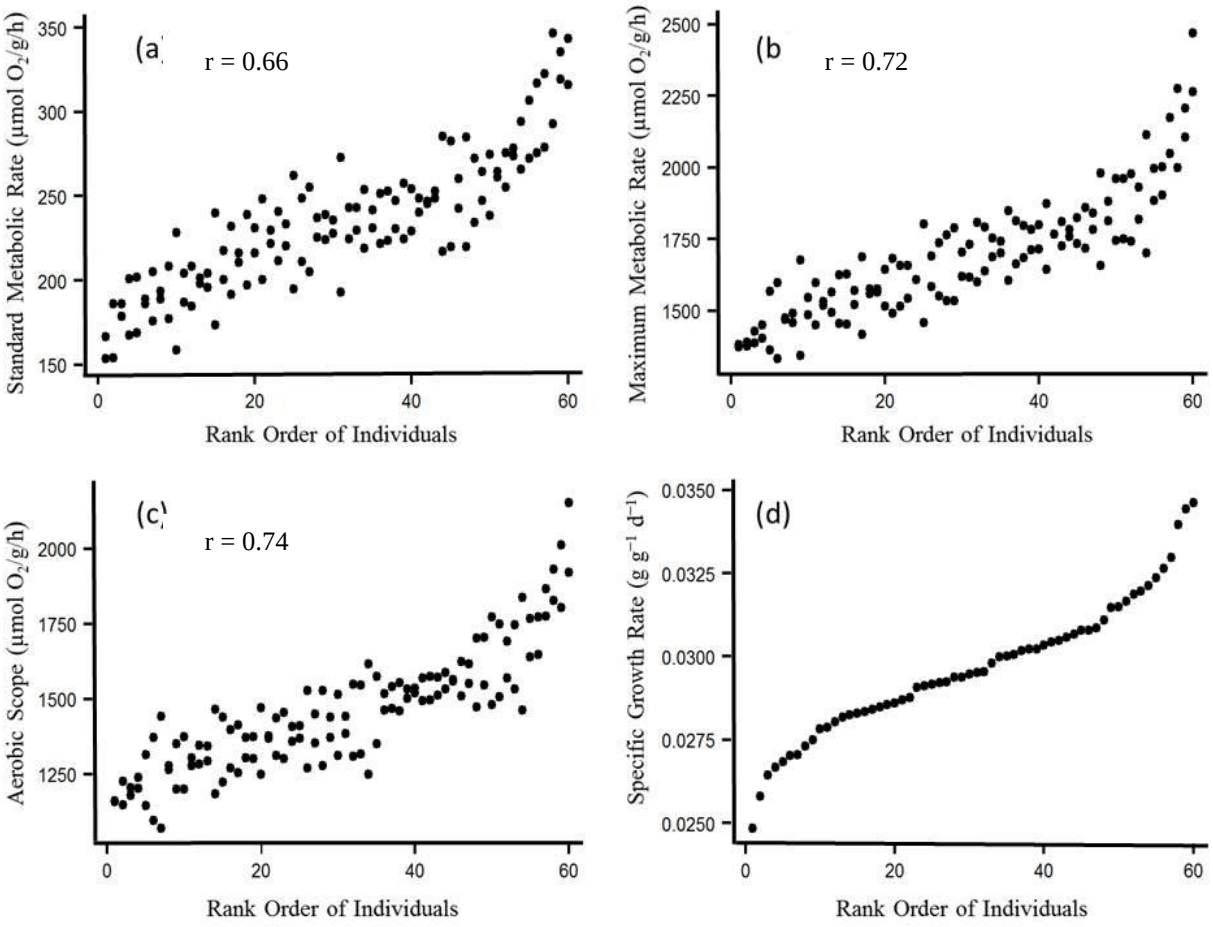

Figure 3: Individual variation in estimates of standardard metabolic rate (a), maximum metabolic rate (b), aerobic scope (c), and specific growth rate (d). N = 60. Each closed circle represents an individual measurement. For a-c, intraclass correlation coefficients (r) in each panel were calculated based on the two measurements made per individual. Values shown have been adjusted to a 157.8 g individual, the geometric mean body mass for the study sample, and to a water temperature of 8.7°C, the mean temperature over the study. Individuals in panels a-c were ranked from lowest to highest based on the mean of the two measurements per individual. An individual's rank can differ between panels.

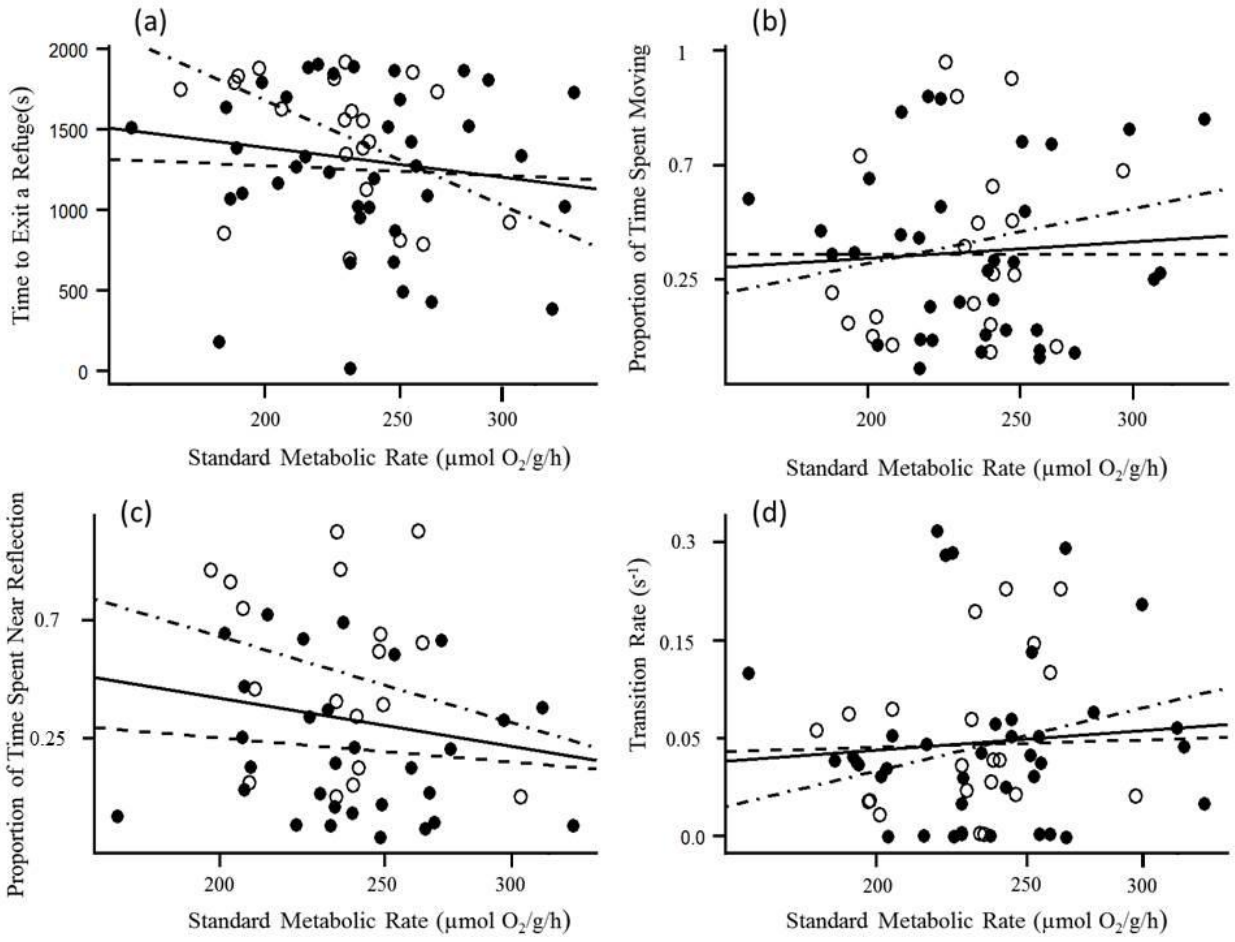

Figure 4: Partial regression plots depicting the relationships between time to exit a refuge (a), proportion of time spent moving (b), proportion of time spent near reflection (c), and transition rate (d) at 11.6°C with standard metabolic rate for a individual at 8.7°C. Each closed circle represents an individual from a migrant-migrant cross and each open circle represents an individual from a migrant-resident cross. Dashed lines indicate the partial regression line for individuals from migrant-migrant crosses and dot-dashed lines from migrant-resident crosses. Solid lines represent the partial regression lines irrespective of cross type. The partial regressions statistcally adjusted for variation in body mass and family identity.

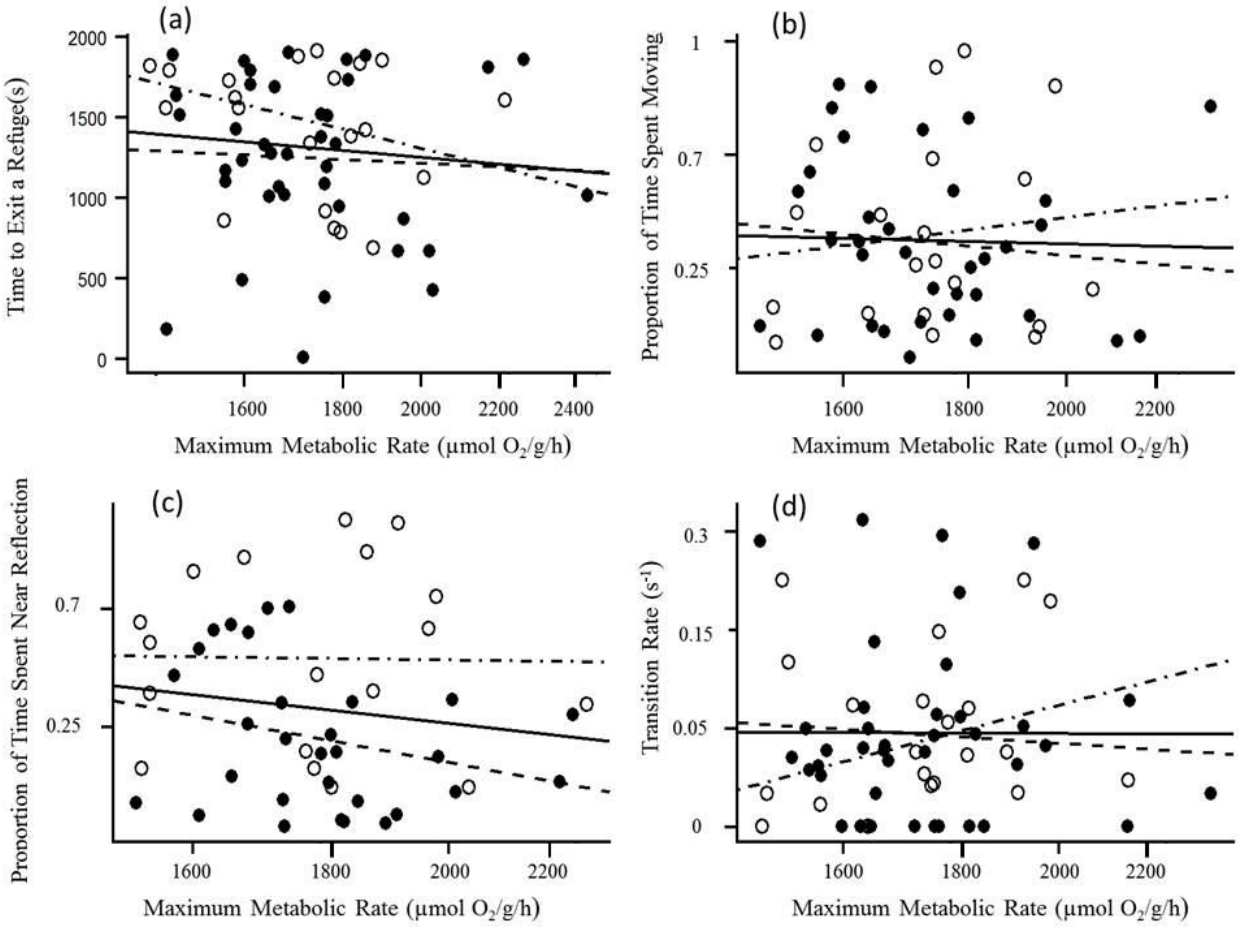

Figure 5: Partial regression plots depicting the relationships between time to exit a refuge (a), proportion of time spent moving (b), proportion of time spent near reflection (c), and transition rate (d) at 11.6°C with maximum metabolic rate for a individual at 8.7°C. Each closed circle represents an individual from a migrant-migrant cross and each open circle represents an individual from a migrant-resident cross. Dashed lines indicate the partial regression line for individuals from migrant-migrant crosses and dot-dashed lines from migrant-resident crosses. Solid lines represent the partial regression lines irrespective of cross type. The partial regressions statistcally adjusted for variation in body mass and family identity.

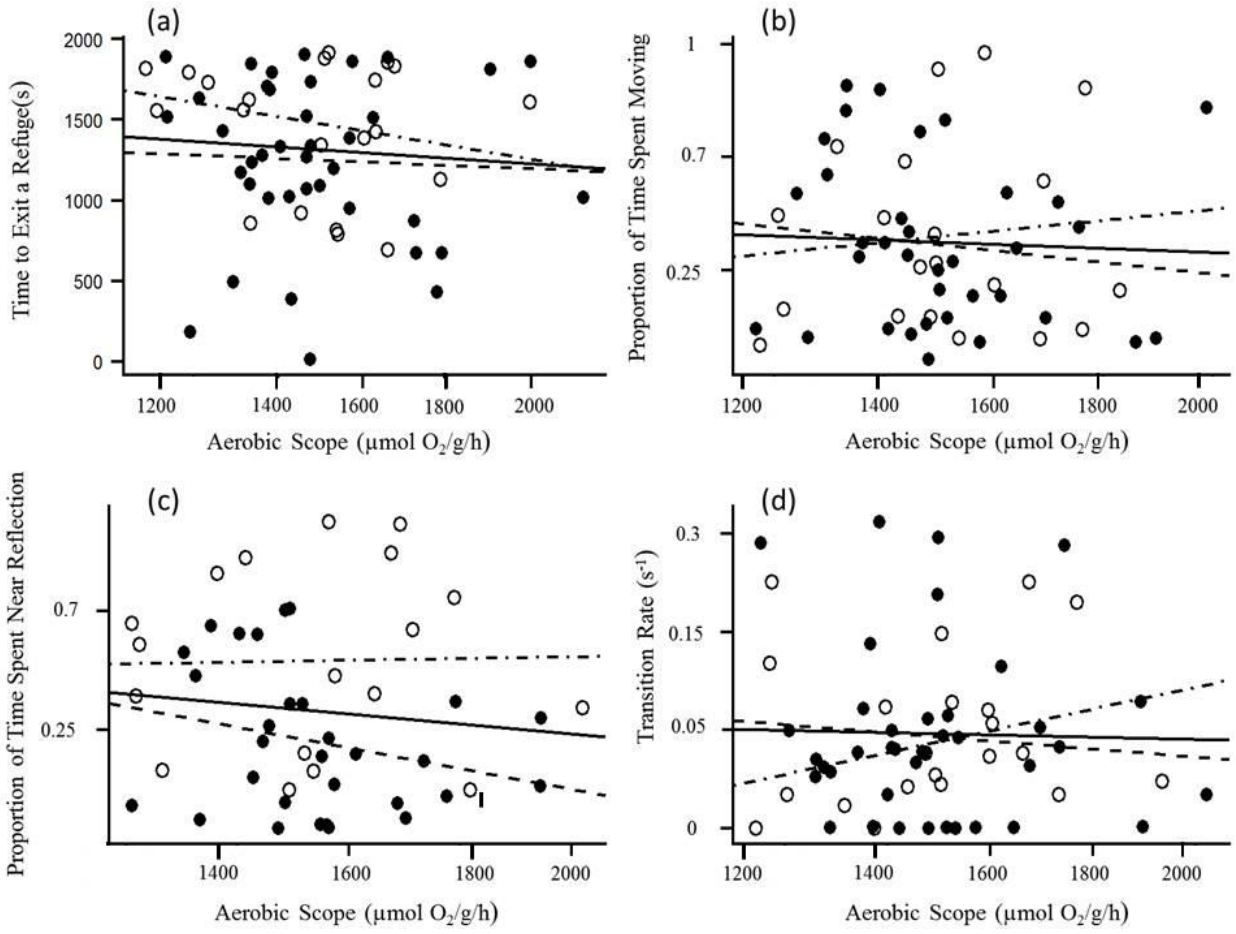

Figure 6: Partial regression plots depicting the relationships between time to exit a refuge (a), proportion of time spent moving (b), proportion of time spent near reflection (c), and transition rate (d) at 11.6°C with aerobic scope for a individual at 8.7°C. Each closed circle represents an individual from a migrant-migrant cross and each open circle represents an individual from a migrant-resident cross. Dashed lines indicate the partial regression line for individuals from migrant-migrant crosses and dot-dashed lines from migrant-resident crosses. Solid lines represent the partial regression lines irrespective of cross type. The partial regressions statistcally adjusted for variation in body mass and family identity.

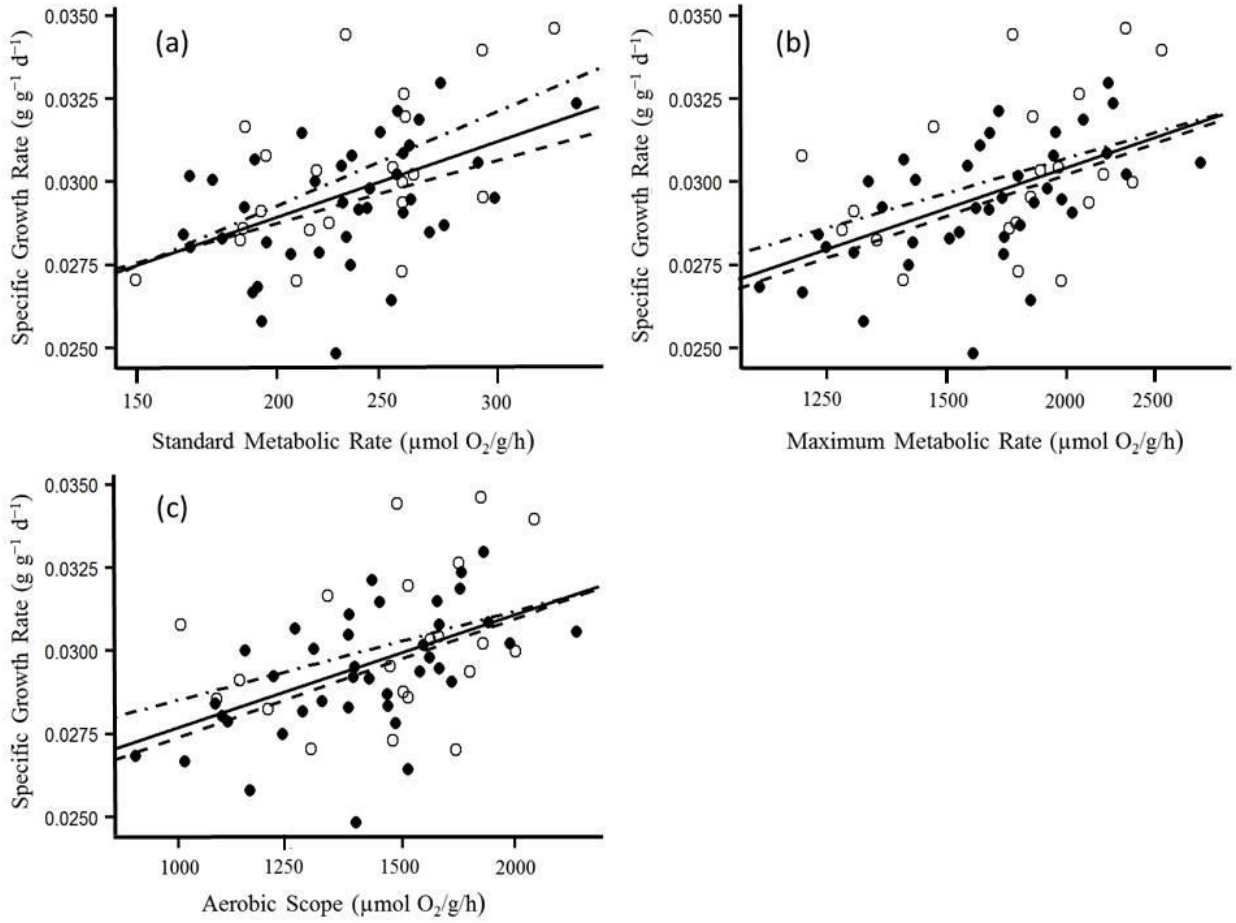

Figure 7: Partial regression plots depicting the relationships between specific growth rate and (a) standard metabolic rate, (b) maximum metabolic rate, and (c) aerobic scope for a individual at 8.7°C. Specific growth rate ($\ln[W_2-W_1]/[t_2-t_1]$) for each individual was calculated using weight (W_1) measured at tagging in February 2014 (t_1) and weight (W_2) measured at the time of the metabolic experiments (t_2). Each closed circle represents an individual from a migrant-migrant cross and each open circle represents an individual from a migrant-resident cross. Dashed lines indicate the partial regression line for individuals from migrant-migrant crosses and dot-dashed lines from migrant-resident crosses. Solid lines represent the partial regression lines irrespective of cross type. The partial regressions statistcally adjusted for variation in body mass and family identity.