

Repeatability of Foraging Tactics in Young Brook Trout, *Salvelinus fontinalis*

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In this study, we repeatedly observed individually marked Brook Trout in a field setting to determine if the bimodal variation in foraging tactics previously observed in young salmonid populations (without distinct morphological differences) is generated by individuals specializing at different foraging tactics. We found significant but low repeatability in several foraging movement parameters. This indicated that while individuals did have tendencies to be sedentary versus highly active, there was considerable variation in foraging activity within individuals. These results suggest that relatively consistent differences among individuals may facilitate selection for specialized morphology and that there may be a heritable component to activity.

Key Words: Brook Trout, *Salvelinus fontinalis*, juveniles, behaviour, foraging, activity.

Recent reviews suggest that between-individual variation in behaviour, and behavioural specialization of individuals, may play an important role in the evolution of resource polymorphisms (divergent specialization on food resources) and ecological speciation (Skúlason and Smith 1995; Schluter 1996; Wilson 1998; Bolnick et al. 2003; Sih et al. 2004). Many good examples of divergent foraging behaviour and morphologies exist, particularly among fish populations (Robinson and Wilson 1994; Bolnick et al. 2003). However, most studies focus on fish species where morphological differences exist and so it is difficult to assess whether behavioural diversification preceded or followed morphological differences (Futuyma and Moreno 1988; McLaughlin et al. 1999). Behavioural diversification is believed to be an important initial step in the development and evolution of resource polymorphisms prior to their reinforcement by morphological differences (McLaughlin and Grant 1994; Wimberger 1994; Skúlason and Smith 1995; McLaughlin et al. 1999). Indeed, habitat-specific competition for food has been shown to promote divergent foraging behaviour in young charr [trout] without morphological differences, resulting in two foraging tactics with similar growth potential (McLaughlin et al. 1999). Similar growth potential may stem from differences in growth efficiencies and prey profitability of Brook Trout, *Salvelinus fontinalis*, occupying different habitats (Morinville and Rasmussen 2003). Now, if morphology is plastic, then behavioural specialization (repeatable differences among individuals) may promote specialized morphologies that increase foraging efficiency. If behavioural specialization precedes morphological differentiation, then it should be possible to find examples of repeatable

differences in foraging tactics in natural populations without distinct morphotypes. However, few studies have quantified the degree to which individuals are specialized relative to their population (Bolnick et al. 2003). To our knowledge, no study has directly quantified repeatability in foraging behaviour in a species where distinct foraging tactics exist in the absence of corresponding morphological differences, nor have any of the studies of behavioural variation in salmonid fishes quantified repeatability in behaviour.

This study fills this gap in our understanding of the existence and extent of behavioural specialization by examining the repeatability of foraging behaviour in a lake-dwelling population of young Brook Trout. Previous work in lakes has revealed bimodal variation in foraging activity of young Brook Trout, with most individuals adopting either sedentary (ambush) or highly active (pursuit) foraging tactics (Biro and Ridgway 1995; Biro 1996; Biro et al. 1997). These differences in foraging activity affect the type and rate of prey encounter by young Brook Trout and their foraging success (Biro and Ridgway 1995; Biro et al. 1996). Therefore, the aim of this study is to determine whether behavioural specialization of divergent foraging tactics exists as a potential mechanism for promoting morphological divergence in a system where no known morphological differences exist.

Methods

Study site

Scott Lake is a small lake (surface area 27 ha) with good visibility (secchi disc depth 6 m) located in Algonquin Provincial Park, Ontario, Canada. We constructed two field enclosures along a portion of the

TABLE 1. Body size and mass of young Brook Trout at time of stocking into each enclosure at Scott Lake.

Body size measures	Enclosure	Mean	Range	S.E.	<i>n</i>
Total length (mm)	1	29.6	28.0 – 32.0	0.75	5
	2	29.4	28.0 – 31.0	0.51	5
Weight (g)	1	0.17	0.13 – 0.24	0.019	5
	2	0.15	0.13 – 0.18	0.008	5

shoreline that had a combination of inundated shoreline vegetation, woody debris, and relatively open areas which are typical of areas inhabited by Brook Trout (Biro et al. 1997). Enclosures were built using beach seine mesh (6 mm openings) and supported with steel rods such that it enclosed a 5 m length of shoreline and extended from 2 to 3 m offshore. The mesh extended 20 cm above the surface of the water. This design allowed a single observer (PAB) to enter at one end of the enclosure to perform snorkelling observations, at distances that did not appear to disturb the fish; maximum depth of the enclosures was 1 m. The enclosure design also allowed fish to access natural benthic organisms, nearshore terrestrial insects and Collembola (springtails) common in their diet (unpublished data); mesh size was a compromise between minimizing the exclusion of zooplankton from the enclosure while also containing these small fish. A pilot study the previous year indicated that an enclosure of this size did not restrict the movements of fish and was not so large as to create difficulties in finding individuals within and among shoreline vegetation and debris.

Selection and marking fish

Twenty YOY (Young-of-the-Year) Brook Trout were sampled using large aquarium dipnets from nearshore habitats while snorkelling in Scott Lake and brought back to the laboratory where they were anaesthetized using tricane-methane sulfonate (MS-222), weighed (± 0.01 g), measured (total length ± 1 mm), individually marked for identification and kept overnight in aerated lake water. Marks were given by cauterizing tiny (<0.5 mm) holes in their fins using different fins and locations within a fin to achieve unique identification for each individual (McNicol and Noakes 1979). Our method differed only in that we placed and branded each fish on a flat sheet of Teflon which prevented the fin from burning onto the branding surface. Two fish which were in poor condition and several which had torn fins were discarded. Subsequently, we stocked five fish of similar size and in good condition in each enclosure (Table 1). There was no indication that the marks affected their swimming performance. Neither body length ($t = 0.22$, $P < 0.83$) nor weight ($t = 0.95$, $P < 0.36$) of fish differed significantly between the enclosures. Fish were allowed to acclimatize for one more full day before behavioural observations began.

Behavioural observations

We observed Brook Trout between 0945 and 1530 hours from 14 to 21 May, three weeks after swim-up

from spawning redds. The experiment was terminated on 22 May [after eight days] because water levels rose more than 35 cm and flooded the enclosures and fish escaped. We attempted to observe each uniquely marked individual twice each day, once between 0945 and 1130 and again between 1300 and 1530. All of the marked fish (some outside of the enclosures) were recovered on the morning of 22 May to obtain body weight (wet weight ± 0.01 g), and length (total length ± 0.5 mm).

Observations were made using mask and snorkel and recorded by a second observer floating nearby. Fish were observed at a distance of about 1 m away, and the magnifying effect of the mask underwater made individual fish marks clearly visible. A fish that was near one end of the enclosure was chosen first for observations. The observer then moved across the enclosure selecting as many new individuals to observe as possible along the way. The observer lay motionless for several minutes to ensure the fish was not disturbed and was feeding. The number of body lengths traveled by each fish and behavioural events were then called out through the snorkel during alternating 5 sec intervals according to established methods (Biro and Ridgway 1995; Biro et al. 1996, 1997). Intervals that did not include forages or agonistic behaviour were considered intervals of search, while intervals including forages were called pursuits (McLaughlin et al. 1992; Biro and Ridgway 1995). Forages were defined as the capture of a potential prey item (Biro et al. 1996). The proportion of search time spent moving was calculated as the proportion of observation intervals where the focal fish moved one body length or more (McLaughlin et al. 1992; Biro and Ridgway 1995). Although agonistic behaviour was recorded, it is a rare occurrence for this species in small lakes (Biro and Ridgway 1995; Biro et al. 1997) and was not considered further. In general, fish that spend a greater proportion of search time moving also move faster and pursue prey further than fish that are less active (McLaughlin et al. 1992; Biro and Ridgway 1995). We did not quantify actual foraging rates or success in this study because the positive relationship between feeding rates and activity is very well established in this lake and another lake with large sample sizes (Biro and Ridgway 1995; Biro 1996; Biro et al. 1996).

Statistical analyses

Univariate statistics are presented using raw data unless otherwise indicated. To meet the required assumptions for parametric statistical tests, the proportion of

TABLE 2. Back-transformed mean and range in the proportion of search time spent moving for each individual Brook Trout in the two enclosures at Scott Lake. The number of repeated observations on each fish (*n*) and number of days over which the observations took place are given.

Fish	Mean	Range	<i>n</i>	Days observed
1	0.36	0.03 – 1.0	9	6
2	0.44	0.0 – 1.0	9	6
3	0.52	0.14 – 0.95	5	4
4	0.65	0.38 – 0.88	9	5
5	0.66	0.21 – 1.0	9	4
6	0.73	0.0 – 1.0	6	5
7	0.82	0.33 – 1.0	10	6
8	0.91	0.17 – 1.0	9	5
9	0.91	0.50 – 1.0	9	6
10	0.92	0.64 – 1.0	4	3

TABLE 3. Repeatability (*R*) and corresponding one-way ANOVA results on the foraging movement parameters based on repeated measurements on known individuals. Degrees of freedom (*df*) are given in parentheses.

Movement parameter	<i>R</i>	<i>MS</i> _{among}	<i>MS</i> _{within}	<i>F</i> -ratio	<i>P</i>
Proportion of time spent moving	0.168	0.393 (9)	0.151 (70)	2.6	0.012
Average search speed	0.143	0.634 (9)	0.275 (70)	2.3	0.025
Speed while moving during search	0.161	0.271 (9)	0.109 (68)	2.5	0.017
Pursuit distance	0.308	0.522 (6)	0.116 (67)	4.5	0.0001

time spent moving was arcsine-square-root transformed, speed while moving was square-root transformed and average search speed was log (*x* +1) transformed. The repeatability of measures of foraging activity were assessed by calculating the coefficient of intraclass correlation (or simply, repeatability (*R*)). Repeatability is the proportion of variance that occurs among, rather than within individuals, calculated from a simple single-factor ANOVA for unequal sample sizes (Lessells and Boag 1987). As the proportion of among individual variance (*R*) increases in magnitude, the relative within individual variance declines. Examination of repeatability is informative because it combines both heritable and environmental components and therefore sets an upper limit for heritability (Falconer 1981).

Results

Young trout activity ranged from quite sedentary to highly active among individuals, with mean individual time spent moving ranging from 0.36 to 0.92 (Table 2). There was wide variation in activity within individuals whereby even the most sedentary individuals were on rare occasion moving continuously (Table 2). Nonetheless, there was significant repeatability in all measures of foraging activity (Table 3). The proportion of search time spent moving, speed while moving during search, and average search, speed had significant but relatively low repeatability. In contrast, distance moved in pursuit of prey had moderate repeat-

ability (Table 3). Estimates of repeatability, while generally low, indicate some degree of specialization whereby active individuals tended to remain active and sedentary individuals tended to remain sedentary (Table 2).

Substantial growth was observed during the course of the experiment confirming successful foraging and presence of natural food in the enclosures. Brook Trout increased significantly in terms of total body length (mean difference = 5 mm, paired *t* = 11.9, *P* < 0.000001, *n* = 10) and mass (mean diff. = 0.20 g, paired *t* = 18.8, *P* < 0.00001, *n* = 10), thus doubling their mass on average. However, fish that spent a greater proportion of time moving did not grow any faster or slower than more sedentary fish, either in terms of gain in length (*P* > 0.20) or weight (*P* > 0.20).

Discussion

We found evidence of significant repeatability in several measures of foraging movements for young Brook Trout. However, repeatability was low indicating that while individual fish can be characterized by their relative level of foraging activity, there was considerable variance in activity levels within individuals. In other words, the majority of the observed variance in foraging activity was accounted for by within-individual variability in activity. Therefore, the bimodal variation in the proportion of time spent moving observed previously in lake-dwelling populations of Brook Trout (Biro and Ridgway 1995; Biro 1996)

appears to be generated by individuals with highly variable, but repeatable differences in foraging activity. For example, when all observations from the present experiment are pooled, the frequency distribution of the proportion of time spent moving does not differ from a large survey of different individuals in Scott Lake in 1994 (Biro 1996; Kolmogorov-Smirnov test, $D_{\max} = 0.07$, $P < 0.0001$, $n_{\text{enclos}} = 79$, $n_{\text{survey}} = 111$). The significant repeatability of foraging tactics observed within this young Brook Trout population exhibiting behavioural divergence (without morphological divergence) supports the hypothesis that behavioural divergence precedes morphological divergence in the evolution of resource polymorphisms and ecological speciation (Wimberger 1994; Skúlason and Smith 1995; McLaughlin et al. 1999).

It should not be too surprising that repeatability for foraging movement parameters are low when observation duration is but a small portion of total time spent foraging and behavioural flexibility is so well documented. One would expect that even the most sedentary individuals must spend time being active to find foraging locations that lend themselves to an ambush type of foraging tactic. The observed moderate repeatability in pursuit distance may reflect specialization of active individuals towards prey items located on the surface. Individuals spending more time active, and pursuing prey further have higher surface foraging rates than less active individuals (Biro and Ridgway 1995; Biro 1996; Biro et al. 1996). Individuals with moderate specialization in pursuing prey over greater distances are likely chasing down relatively large prey items that have fallen to the surface or are emerging from the surface as shown for young Brook Trout in Scott Lake (Biro 1996) and another lake (Biro and Ridgway 1995; Biro et al. 1996). By contrast, those individuals adopting a more sedentary foraging tactic tend to feed on plankton and benthic invertebrates emerging from the bottom (Biro 1996; Biro et al. 1996).

Observing repeatable differences in foraging behaviours suggests that there is a heritable component to them (e.g., Falconer 1981). If so, then behavioural specialization, in combination with morphology that can change adaptively according to activity levels (Imre et al. 2002) and prey types (Skúlason and Smith 1995; Smith and Skúlason 1996) can provide the basis for further specialization possibly leading to the evolution of resource polymorphisms as suggested for other charr species (Skúlason and Smith 1995). Genetically based differences in activity among individuals in this population should be expected given that intrinsic growth rates (IGR), activity levels and aggressiveness are all positively correlated in salmonid fishes, and growth rate has high variance and heritability (e.g., Gross 1998; Gjedrem 2000). In addition, there has been a recent increase in our appreciation of the extent of repeatable differences in behaviour in a variety of animals, termed behavioural "syndromes" and "person-

ality" (Sih et al. 2004). As Sih's review points out, more field studies are needed to uncover the extent to which repeatable differences in behaviour exist, and their stability over time and across situations. A comparison of bioenergetics between resident and anadromous stream Brook Trout revealed a much higher metabolic rate for the anadromous form and therefore a greater likelihood of habitat switching (i.e., anadromy) for the anadromous form (Morinville and Rasmussen 2003). Fundamental differences in quantitative traits such as metabolic rate may be important factors contributing to bimodal variation in foraging activity.

Bimodal variation in activity, whereby relatively few individuals have intermediate levels of activity, suggests specialization on distinct prey fields that favours alternate foraging tactics. Recent work on Brook Trout in stillwater pools in streams suggests that this is the case, and results in two foraging tactics with similar growth rates for individuals specializing on benthic versus pelagic prey items (McLaughlin et al. 1999; McLaughlin 2001). The present study supports this hypothesis given the equal short-term growth rates among individuals with different activity tendencies. However, there was considerable variability in activity within individuals that were observed over a relatively short time span, and this coupled with small sample sizes reduces considerably the power to detect any relation between foraging tactics and growth rates.

A speculative alternative hypothesis suggests that, like Rainbow Trout (*Oncorhynchus mykiss*), young Brook Trout have a genetic basis to IGR and activity levels such that those with higher IGR are more active in search of food and experience higher growth rates, but have elevated predation mortality (Werner and Anholt 1993; Biro et al. 2004). If so, then perhaps the tradeoff between growth and mortality rates favours individuals with low activity (low growth, high survival) and individuals with high activity (high growth and mortality) if frequency-dependent selection against intermediates is high. Indeed, there are good reasons to expect that there is a cost to switching between prey types, and for generalist feeding strategies (discussed in McLaughlin et al. 1999). At a minimum, greater consideration of the role of predation risk in the evolution of resource polymorphisms and ecological speciation will further our understanding of the extent and ecological implications of behavioural variation that has traditionally focused exclusively on competition for resources (but see Vamosi and Schluter 2002). Finally, it seems that further study of the mechanism(s) responsible for widespread behavioural variation within and among populations will greatly aid our understanding of important ecological processes.

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Literature Cited

- Biro, P. A.** 1996. Space-use by juvenile brook charr (*Salvelinus fontinalis*) in lakes: the central-place territorial model does not apply. MSc thesis. University of Guelph, Guelph, Ontario, Canada.
- Biro, P. A., M. V. Abrahams, J. R. Post, and E. A. Parkinson.** 2004. Predators select against high growth rates and risk-taking behaviour in domestic trout populations. *Proceedings of the Royal Society of London B* 271: 2233-2237.
- Biro, P. A., and M. S. Ridgway.** 1995. Individual variation in foraging movements in a lake population of young-of-the-year brook charr (*Salvelinus fontinalis*). *Behaviour* 120: 1-12.
- Biro, P. A., M. S. Ridgway, and R. L. McLaughlin.** 1996. Does the rate of foraging attempts predict ingestion rate for young-of-the-year brook trout (*Salvelinus fontinalis*) in the field? *Canadian Journal of Fisheries and Aquatic Sciences* 53: 1814-1820.
- Biro, P. A., M. S. Ridgway, and D. L. G. Noakes.** 1997. The central-place territorial model does not apply to space-use by juvenile brook charr (*Salvelinus fontinalis*) in lakes. *Journal of Animal Ecology* 66: 837-845.
- Bolnick, D. I., R. Svanback, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister.** 2003. The ecology of individuals: incidence and implications of individual specialization. *The American Naturalist* 161: 1-28.
- Falconer, D. S.** 1981. *Introduction to quantitative genetics*, 2nd edition. Longman, London.
- Futuyma, D. J., and G. Moreno.** 1988. The evolution of specialization. *Annual Review of Ecology and Systematics* 19: 207-233.
- Gjedrem, T.** 2000. Genetic improvement of cold-water fish species. *Aquaculture Research* 31: 25-33.
- Gross, M. R.** 1998. One species with two biologies: Atlantic salmon (*Salmo salar*) in the wild and in aquaculture. *Canadian Journal of Fisheries and Aquatic Sciences* 55: 131-144.
- Imre, I., R. L. McLaughlin, and D. L. G. Noakes.** 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. *Journal of Fish Biology* 61: 1171-1181.
- Lessells, C. M., and P. T. Boag.** 1987. Unrepeatable repeatabilities: a common mistake. *The Auk* 104: 116-121.
- McLaughlin, R. L.** 2001. Behavioural diversification in brook charr: adaptive responses to local conditions. *Journal of Animal Ecology* 70: 325-337.
- McLaughlin, R. L., M. M. Ferguson, and D. L. G. Noakes.** 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.
- McLaughlin, R. L., and J. W. A. Grant.** 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., J. W. A. Grant, and D. L. Kramer.** 1992. Individual variation and alternative patterns of foraging movements in recently-emerged brook charr (*Salvelinus fontinalis*). *Behaviour* 120: 286-301.
- McNicol, R. E., and D. L. G. Noakes.** 1979. Caudal fin branding fish for individual recognition in behavior studies. *Behavior Research Methods and Instrumentation* 11: 95-97.
- Morinville, G. R., and J. B. Rasmussen.** 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences* 60: 401-410.
- Robinson, B. W., and D. S. Wilson.** 1994. Character release and displacement in fishes: a neglected literature. *The American Naturalist* 144: 598-627.
- Schluter, D.** 1996. Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society of London B* 351: 807-814.
- Sih, A., A. Bell, and J. Chadwich.** 2004. Behavioral syndromes: an ecological and evolutionary overview. *Trends in Ecology and Evolution* 19: 372-378.
- Skúlason, S., and T. B. Smith.** 1995. Resource polymorphisms in vertebrates. *Trends in Ecology and Evolution* 10: 366-370.
- Smith, T. B., and S. Skúlason.** 1996. Evolutionary significance of resource polymorphisms in fishes, amphibians, and birds. *Annual Review of Ecology and Systematics* 27: 111-133.
- Vamosi, S. M., and D. Schluter.** 2002. Impacts of trout predation on fitness of sympatric sticklebacks and their hybrids. *Proceedings of the Royal Society of London B* 269: 923-930.
- Werner, E. E., and B. R. Anholt.** 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *The American Naturalist* 142: 242-272.
- Wilson, D. S.** 1998. Adaptive individual differences within single populations. *Philosophical Transactions of the Royal Society London B* 353: 199-205.
- Wimberger, P. H.** 1994. Trophic polymorphisms, plasticity, and speciation in vertebrates. *In Advances in Fish Foraging Theory and Ecology*. Edited by D. J. Stouder, and K. Fresh. Belle Baruch Press, Columbia, South Carolina.

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