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Genetic architecture and maternal contributions of early-life survival in lake trout *Salvelinus namaycush*

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The influences of additive, non-additive and maternal effects on early survival (uneyed embryo survival, eyed embryo survival, alevin survival and overall survival to first feeding) were quantified in lake trout *Salvelinus namaycush* using a 7 × 7 full-factorial breeding design. Maternal effects followed by non-additive genetic effects explained around one third of the phenotypic variance of the survival traits. Although the amount of additive genetic effects were low ($<1\%$), suggesting a limited potential of the traits to respond to new selection pressures, how maternal and non-additive genetic effects may respond to selection under certain circumstances are discussed.

Key words: additive genetic effects; genetic architecture; maternal effects; non-additive genetic effects.

Examining the architecture of phenotypic traits may speak to their selection history and evolutionary potential, providing valuable insights into adaptive mechanisms for coping with novel selective pressures (Lande & Shannon, 1996; Rice & Emery, 2003). Although potentially counterintuitive at first glance, traits with high non-additive genetic effects and low additive genetic effects may indicate strong historical selection (Crnokrak & Roff, 1995; Neff & Pitcher, 2005; Roff & Emerson, 2006). There is a negative relationship between the amount of additive genetic variation and the ties of associated phenotypic traits to individual fitness (Kruuk *et al.*, 2000). This relationship may arise because selection erodes additive genetic variance leaving a few beneficial alleles that contribute to non-additive genetic variance (Crnokrak & Roff, 1995; Neff & Pitcher, 2005; Roff & Emerson, 2006). In addition, traits with high additive genetic effects can have the potential to rapidly adapt to new selection pressures. There is a direct relationship between the evolutionary response to selection and the amount of additive genetic variance or narrow-sense heritability (Falconer & Mackay, 1996). Traits with high maternal genetic and non-additive genetic effects also

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§Author to whom correspondence should be addressed. Tel.: +1 519 253 3000 ext. 2710; email: tpitcher@uwindsor.ca have the potential to respond to selection pressures under certain circumstances, such as converting non-additive to additive genetic effects during a population bottleneck (Goodnight, 1988; Carson, 1990; Räsänen & Kruuk, 2007).

The amount of additive and non-additive genetic effects for traits can also speak to mate choice selection (Neff & Pitcher, 2005). Large additive genetic effects may indicate female choice for good genes in males such that females prefer the same males, whereas large non-additive genetic effects may indicate female choice for compatible genes in males such that females prefer different males. Both mechanisms are probably important for sexual selection in wild populations (Neff & Pitcher, 2005). Information on potential mate choice selection is important for broodstock management to increase offspring survival (Pitcher & Neff, 2007; Neff *et al.*, 2011), as well as increasing the understanding of mating systems in general (Neff & Pitcher, 2005).

Here, the architecture (additive genetic, non-additive genetic and maternal effects) of three early-life survival traits (uneyed embryo survival, eyed embryo survival and alevin survival, including overall survival to first feeding) was examined in lake trout *Salvelinus namaycush* (Walbaum 1792). The fish were from Kingscote Lake in southern Ontario, Canada (45° 12′ N; 78° 12′ W), a natural population with silver-gold skin pigmentation distinct from the typical phenotype (many gold spots on a dark green background) of other *S. namaycush* populations. Previous genetic analyses have also indicated strong positive selection acting on this population, such as major histocompatibility complex genes (Wilson & Mandrak, 2004; Wilson & Evans, 2010; Kuntz, 2014).

Parental individuals originated from fertilized eggs of single-pair matings produced in autumn 1999 and 2000 using wild *S. namaycush* from Kingscote Lake in southern Algonquin Park, Ontario. These fish were reared at the Ontario Ministry of Natural Resources and Forestry (OMNRF) Codrington Fisheries Research Facility, Codrington, Ontario. Families were reared separately at equal family sizes until 2 years old. Fish were then marked to family using finclips or branding and the families were pooled at equal family sizes into 1000 l tanks. Fish were periodically culled as their body size increased and then moved to 6000 l tanks. For this study, 49 families were produced on 26 October 2009 at Codrington using the mature adults from the 1999 and 2000 wild-spawn collections. Seven mature females from the year 2000 cohort (mean ± S.D. = 3628 ± 545 g) and seven mature males from the year 1999 cohort (3909 ± 494 g) were mated in all possible combinations to produce a 7 × 7 full-factorial breeding design as outlined by Lynch & Walsh (1998). Ripe females were anaesthetized, dry-spawned and eggs were segregated into 30 ml sub-samples in separate 500 ml glass jars for fertilization. The families were produced by a sub-sample of eggs from a single female with sperm from a single male, using all female × male combinations to achieve the full-factorial breeding design. For each family, the fertilized eggs were equally divided into two randomly selected sections (replicates) of vertical incubation trays (tray $n = 7$ and section $n = 16$ per tray). Eggs were supplied with water from a natural spring-fed stream (Marsh Creek) at ambient temperatures for southern Ontario streams. Three offspring survival traits were measured: uneyed embryo survival (days 0–39 post-fertilization), eyed embryo survival (days 40–77), alevin survival (days 78–123). Overall survival to first feeding (days 0–123) was also examined. Dead embryos and alevins were counted and removed every 2 days from the trays. Water temperature was 6·3° C, range ± 1·5° C across these periods.

Generalized linear mixed-effects models with binomial error distribution, logit link function and Laplace approximation were used to examine the genetic architecture and maternal contributions of survival traits using the fullfact package (Houde *et al.*, 2016) in R 3.2.2 (www.r-project.org). Statistical significance was set at $\alpha = 0{\cdot}05$. The model partitioned the phenotypic variance of the survival traits using random effects for dam identification (ID; maternal genetic and environmental variance, V_D), sire ID (paternal genetic variance, V_S) and dam ID × sire ID (non-additive genetic variance, $V_{D\times S}$). Binary values were used for individual survival (*i.e.* 1 for alive and 0 for dead) because within-family variation using the survival averages of family replicates can overestimate genetic effects (Puurtinen *et al.*, 2009; Neff *et al.*, 2011). A random effect for tray ID was also included to account for potential spatial position effects. The residual variance component was a constant of $\pi^2\, 3^{-1}$ (Nakagawa & Schielzeth, 2013). Significances of the random effects were determined by likelihood ratio tests between the full model and a reduced model without a random effect. The additive, non-additive and maternal variance components of the survival traits were calculated based on (Lynch & Walsh, 1998): $V_A = 4 \times V_S$, $V_N = 4 \times V_{D\times S}$ and $V_M = V_D - V_S$. Variance component 95% C.L. were produced using a bootstrap method modified from Houde *et al.* (2013). Binary values of the individuals were resampled with replacement within each family replicate using the original replicate size and the variance components were calculated for the resampled data, with the process repeated 1000 times. A bootstrap bias correction for the difference between the observed and mean bootstrap values was used to adjust the 95% C.L. (Efron & Tibshirani, 1993).

Across all 49 families, uneyed embryo survival was 67·8% (11 310 out of 16 675 embryos), eyed embryo survival was 92·8% (10 501 out of 11 310 embryos), alevin survival was 78·5% (8239 out of 10 501 alevins) and overall survival was 49·4% (8239 out of 16 675 embryos). Eight alevins died due to spinal deformities and were excluded from the analysis because the sample size was too small to be informative. The remaining 2254 alevins died from natural causes without spinal deformities. Spatial position (*i.e.* tray) effects were non-significant for all traits (Table I). Dam and dam × sire effects were significant for all traits, whereas sire effects were non-significant (Table I). Additive genetic effects explained very little (<1%) of the observed phenotypic variance of the traits (Table I). Maternal effects explained the most phenotypic variance for the traits, followed by non-additive genetic effects (Table I and Fig. 1). Maternal body mass explained approximately half of the maternal effects across traits and there were positive trends with offspring survival (Tables SI and SII, Supporting Information).

This study adds to the growing number of studies finding that maternal and non-additive genetic effects are important in explaining the phenotypic variance of survival and fitness-related traits at early-life stages of fishes (Wedekind *et al.*, 2001, 2008; Pitcher & Neff, 2006; Evans & Neff, 2009; Houde *et al.*, 2013, 2015). Moreover, additive genetic effects tended to be less important in explaining the phenotypic variance of those traits (Carlson & Seamons, 2008). Interestingly, in the present study, maternal body size explained about half of the maternal effects for the survival traits, with the remainder being explained by other properties of maternal identity. Larger maternal body size in particular has been frequently associated with higher offspring survival and fitness-related traits (Green, 2008).

The non-additive genetic effects for the early-life survival traits may indicate female mate choice *via* pre-spawning or post-spawning selection for compatible alleles in

TABLE I. Summary of the observed data results for the architecture of survival traits for *Salvelinus namaycush* from Kingscote Lake, Ontario, using mixed-effects models containing random effects for dam identification (ID), sire ID, dam ID × sire ID. All mixed-effects models contained a random effect tray ID. Significance of the effects was determined using likelihood ratio tests. The maternal (V_D), additive (V_A) and non-additive (V_N) variance components were calculated as: $V_A = 4 \times (V_S)$, $V_N = 4 \times (V_{D \times S})$ and $V_M = V_D - V_S$, where V_S is the paternal genetic and environmental variance. Family replicate values are presented in Table SI (Supporting Information)

Trait	*n*	*P*	σ^2 (% total variance)	Phenotypic variance	% Phenotypic variance
Uneyed embryo survival (days 0–39)					
Dam	7	<0·001	1·401 (28·9)	Maternal	28·8
Sire	7	>0·05	0·005 (0·1)	Additive	0·4
Dam × sire	49	<0·001	0·161 (3·3)	Non-additive	13·3
Tray	7	>0·05	0 (0)		
Residual			$\pi^2 3^{-1}$ (67·7)		
Eyed embryo survival (days 40–77)					
Dam	7	<0·001	1·054 (23·4)	Maternal	23·4
Sire	7	>0·05	0 (0)	Additive	0·0
Dam × sire	49	<0·001	0·164 (3·6)	Non-additive	14·6
Tray	7	>0·05	0 (0)		
Residual			$\pi^2 3^{-1}$ (73·0)		
Alevin survival (days 78–123)					
Dam	7	<0·001	0·758 (17·3)	Maternal	17·1
Sire	7	>0·05	0·007 (0·2)	Additive	0·6
Dam × sire	49	<0·001	0·167 (3·8)	Non-additive	15·2
Tray	7	>0·05	0·166 (3·8)		
Residual			$\pi^2 3^{-1}$ (75·0)		
Overall survival (days 0–123)					
Dam	7	<0·001	1·926 (36·1)	Maternal	35·8
Sire	7	>0·05	0·012 (0·2)	Additive	0·9
Dam × sire	49	<0·001	0·087 (1·6)	Non-additive	6·5
Tray	7	>0·05	0·025 (0·5)		
Residual			$\pi^2 3^{-1}$ (61·6)		

males, which can be important for maintaining beneficial gene combinations that optimize offspring survival (Pitcher & Neff, 2006, 2007). There has been no indication of the genetic introgression of historically stocked *S. namaycush* sources into the Kingscote population (Halbisen & Wilson, 2009; Wilson & Evans, 2010), supporting the possibilities of beneficial gene combinations and mate choice for the Kingscote population. In addition, Kingscote population males had higher sperm velocity when exposed to the ovarian fluid of a related female than to an unrelated female (Butts *et al.*, 2012). This presumed increase in fertilization success of genetically more similar males may be analogous to that observed with Atlantic salmon *Salmo salar* L. 1758 based on the similarity at the major histocompatibility class I locus (Yeates *et al.*, 2009). Future research is warranted on the possibility of pre or post-spawning mate choice for the compatibility of alleles for *S. namaycush*.

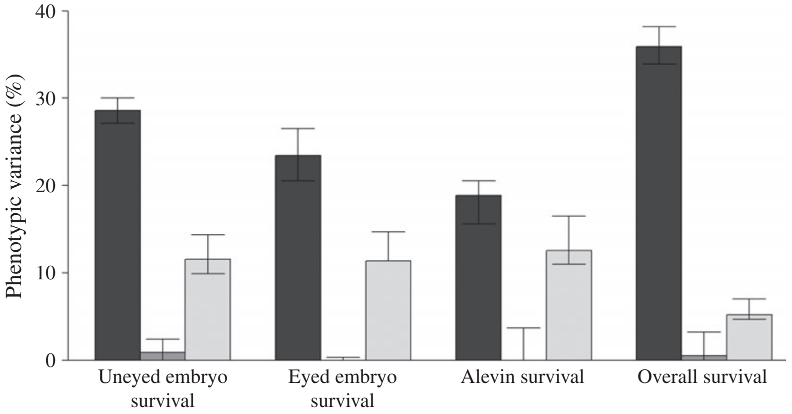

Fig. 1. The maternal, additive and non-additive effects underlying the phenotypic variance of early-life survival of *Salvelinus namaycush* from Kingscote Lake, Ontario. Displayed are the bias-corrected median and 95% C.L. for maternal, additive genetic and non-additive genetic effects (note the lower C.I. for eyed embryo survival is the same as the bias-corrected median value). ■, maternal; ▨, additive; □, non-additive.

The detection of low additive genetic effects for the early-life survival traits may speak to the finite adaptive resources within landlocked populations of *S. namaycush* (Wilson & Mandrak, 2004; Wilson & Evans, 2010; Kuntz, 2014). Low additive genetic effects can indicate strong selection pressures (Crnokrak & Roff, 1995; Roff & Emerson, 2006). Supporting evidence for natural selection and local adaptation within the Kingscote population is its unique skin pigmentation with non-dominant inheritance and lack of hatchery introgression despite decades of stocking from allopatric sources (Halbisen & Wilson, 2009; Wilson & Evans, 2010) as well as evidence for strong positive selection based on the major histocompatibility class II beta gene (Kuntz, 2014). The low amount of additive genetic effects observed in this study suggests that this *S. namaycush* population may not be able to respond rapidly to novel selection pressures relating to survival of early-life stages. The higher maternal effects, however, may contain genetic effects that may respond to selection (Räsänen & Kruuk, 2007) and this study could not separate maternal genetic and environmental effects by examining one generation (Wilson *et al.*, 2005). Quantifying the genetic component of the maternal effects by examining more generations is needed to assess the adaptive potential of these traits.

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Supporting Information

Supporting Information may be found in the online version of this paper:
Table SI. Summary of survival traits for *Salvelinus namaycush* from Kingscote Lake

Table SII. Summary of the results for the architecture of survival traits for *Salvelinus namaycush* from Kingscote Lake

Fig. S1. Relationship between maternal body size and survival traits for *Salvelinus namaycush* from Kingscote Lake

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