

1 **TITLE:** Shifting thresholds: rapid evolution of migratory life histories in

2 steelhead/rainbow trout, *Oncorhynchus mykiss*.

3 **RUNNING HEAD:** Rapid evolution of migratory life histories

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16 **SUMMARY**

17 Expression of phenotypic plasticity depends on reaction norms adapted to historic
18 selective regimes; anthropogenic changes in these selection regimes necessitate
19 contemporary evolution or extirpation. Adaptation of conditional strategies following a
20 change in the selection regime requires evolution of either the environmentally
21 influenced cue (e.g. growth rate) or the state (e.g. size threshold) at which an individual
22 switches between conditional strategies. Using a population of steelhead (*Oncorhynchus*
23 *mykiss*) introduced above a barrier waterfall in 1910, we evaluate how the conditional
24 strategy to migrate evolves in response to selection against migration. Common garden-
25 raised offspring of parents from the above-barrier population were 11% smaller and
26 31% lighter than offspring of parents from the below-barrier source population. Using a
27 novel analytical approach we estimate that the mean size at which above-barrier fish
28 switch between the resident and migrant strategy is 43% larger than below-barrier fish.
29 As a result, above-barrier fish were 30% less likely to express the migratory strategy. Our
30 results demonstrate how rapid and opposing changes in growth rate and threshold size
31 contribute to the contemporary evolution of a conditional strategy and indicate that
32 migratory barriers may elicit rapid evolution towards the resident life-history on
33 timescales relevant for conservation and management of conditionally migratory
34 species.

35

36 **KEYWORDS:** anadromy, contemporary evolution, local adaptation, partial migration,
37 threshold traits

38

39 INTRODUCTION

40 Given on-going environmental changes, it is increasingly important to quantify
41 contemporary evolution (Gienapp *et al.* 2008; Hansen *et al.* 2012), which may allow
42 populations to adapt to novel selective pressures (Gonzalez *et al.* 2012). For example,
43 species that invade novel environments often exhibit rapid phenotypic changes in
44 response to their newly invaded environment (Westley 2011). Indeed, it is now clear
45 that evolution can occur on ecologically relevant timescales (Thompson 1998),
46 particularly due to human-induced selection (Darimont *et al.* 2009) and in turn may
47 affect population dynamics (Ezard, Côté & Pelletier 2009) and other ecological and
48 ecosystem processes (Schoener 2011).

49 Phenotypic plasticity also influences how organisms respond to novel
50 environments. When environmental cues reliably predict future selective regimes,
51 organisms may maximize fitness by matching their phenotype with a trait optimum
52 (Tufto 2000). Thus, phenotypic plasticity can contribute to population persistence in
53 variable environments, so long as the cue-optimum relationship (reaction norm) is
54 maintained (Reed *et al.* 2010). However, reaction norms reflect historic selective
55 regimes; changes in the environment, either gradual (e.g. climate change) or abrupt
56 (e.g. habitat alteration), can decouple cues and trait optima, producing maladaptive
57 phenotypes (Mills *et al.* 2013) with the potential for population extirpation (Schlaepfer,
58 Runge & Sherman 2002).

59 Understanding how conditional strategies respond to selection is particularly
60 important and challenging. Conditional strategies, also called “threshold traits” (Roff
61 1996) or “polyphenisms” (Stearns 1989), are a type of phenotypic plasticity in which
62 expression of discrete traits depends on an organism’s condition relative to some
63 threshold value (Hazel & Smock 1990; Gross 1996). If heritable genetic variation
64 underlies the threshold of a conditional strategy, novel selective pressures may elicit an
65 evolutionary response, altering frequencies of ecologically important traits. For
66 example, size-selective harvest may drive declining size at maturation in fish populations
67 (Sharpe & Hendry 2009), influencing sustainable harvest levels and recovery plans
68 (Enberg *et al.* 2009). However, determining the genetic basis of conditional strategies is
69 challenging in nature because an observed shift in phenotypes can be manifested by
70 both plasticity and evolutionary responses of a given trait.

71 Migration in fishes provides an excellent system for examining the components
72 of conditional strategies and their potential for rapid evolution (Hutchings 2011; Dodson
73 *et al.* 2013). For example, the salmonid *Oncorhynchus mykiss* can exhibit divergent
74 migratory strategies, including anadromous ‘steelhead’ that migrate to and from the
75 ocean, and resident ‘rainbow trout’ which stay in freshwater. When juvenile salmonids
76 migrate from freshwater to saltwater they undergo a physiological and morphological
77 transformation referred to as “smolting”. Larger smolts are more likely to survive in the
78 marine habitat (Bond *et al.* 2008). Individuals that grow faster and achieve larger sizes in
79 freshwater habitat are more likely to undergo the anadromous migration (Beakes *et al.*
80 2010). However, this size threshold for migration can vary across populations based on

81 the local freshwater rearing conditions (Satterthwaite *et al.* 2010; 2012). There is
82 evidence of heritable genetic variation in both the switch point size at which an
83 individual smolts (Thrower, Hard & Joyce 2004; Paez *et al.* 2010; Buoro, Gimenez &
84 Prévost 2012) and individual growth rate (Carlson & Seamons 2008). Indeed, recent
85 evidence documents a genetic basis for a number of traits associated with smolting,
86 including development rate (Nichols *et al.* 2006; Haidle *et al.* 2008; Easton *et al.* 2011;
87 Miller *et al.* 2011) and smoltification (Nichols *et al.* 2008; Martínez, Garza & Pearse
88 2011). Therefore, the frequency of the smolt phenotype in a population may be
89 influenced by a combination of phenotypic plasticity and selection on the genotypes
90 underlying life history variation.

91 Here we examine a rapid evolutionary shift in life-history expression in a
92 population of *Oncorhynchus mykiss* translocated above a waterfall barrier (Pearse *et al.*
93 2009). This presents an opportunity to illuminate the evolutionary processes that drive
94 rapid phenological shifts and the response of migratory salmonids to novel barriers
95 (Waples *et al.* 2008). In a common garden experiment, we compare the expression of
96 the migratory life-history strategy in two populations: an above-barrier population
97 transplanted above a waterfall approximately 100 years ago and a below-barrier source
98 population which maintains migratory access to and from the ocean (Pearse *et al.* 2009).
99 We use a novel model-based approach to ask two related questions: 1. Is there adaptive
100 phenotypic evolution to the novel above-barrier environment? 2. Does evolution of
101 growth rate and/or switch point size contribute to the contemporary evolution of
102 alternative migratory strategies? We find evidence for adaptive life history evolution,

103 driven by evolution of both growth rate and switch point size. Thus, the phenotypic
104 expression and genetic basis of migratory life history in *O. mykiss* can evolve on
105 timescales relevant for conservation and management.

106

107 **METHODS**

108 *A Historical Transplant Experiment*

109 Scott Creek is a 70 km² coastal watershed located in central California
110 approximately 100 km south of San Francisco. A waterfall on Big Creek, one of its
111 prominent tributaries, presents a natural barrier to anadromy approximately six river
112 km from the creek mouth. Ongoing (Hayes *et al.* 2004; 2008; Bond *et al.* 2008) and
113 historic studies (Shapovalov & Taft 1954) in the watershed indicate the below-barrier
114 source population of *O. mykiss* is dominated by the anadromous life history. Above the
115 barrier waterfall a resident population of *O. mykiss* exists, and the landowners' journals
116 document the transfer of below-barrier *O. mykiss* above the barrier 1910. Genetic data
117 from *O. mykiss* throughout the Scott Creek watershed indicate a recent genetic
118 divergence of the above-barrier population (Pearse *et al.* 2009), consistent with a 1910
119 transplantation origin (Anderson & Slatkin 2007).

120

121 *Fish Breeding and Data Collection*

122 In November 2007, juveniles were collected via backpack electrofishing above
123 and below the Big Creek barrier falls, and brought to a small hatchery facility below the
124 falls for rearing. Based on their size (above-barrier mean=68.9mm, range 51-90mm;

125 below-barrier mean=60.3, range=43-90mm), all individuals were presumed to be less
126 than one year old. In March 2010, 17 mature individuals total were crossed to create
127 over 900 individuals in 9 total pure above- and below-barrier full-sibling families.
128 Number of eggs for each female was enumerated and 20 haphazardly chosen eggs were
129 selected to estimate mean egg diameter. Offspring were reared in common garden
130 conditions for one year. The large number of related offspring allow for precise
131 estimates of population differences provided the sampled parents are representative of
132 their population of origin.

133 During peak outmigration timing in the Scott Creek watershed (March; Hayes *et*
134 *al.* 2011), all fish were lightly anesthetized using MS222, implanted with a uniquely
135 identifiable passive integrated transponder (PIT) tag (11.5 mm FDX-B Glass Transponder,
136 Allflex, Boulder, Colorado) by intraperitoneal injection with a 12 gauge needle, and small
137 ($\approx 0.3 \text{ cm}^2$) caudal fin clips collected for genetic parentage and gender analysis
138 (electronic supplementary material). We recorded fork length (mm), mass (g), and
139 “smolt condition” of each fish, after which individuals were allowed to recover for at
140 least one week prior to further manipulation. We defined “smolt condition” as a binary
141 trait based on physical appearance (Thrower *et al.* 2004; Nichols *et al.* 2008). “Non-
142 smolts” retained parr marks, cryptic stream coloration, and a rounded caudal fin,
143 including mature male parr. “Smolts” had silvery and countershaded appearance, faint
144 or complete loss of parr marks, streamlined body, and sharp pointed caudal fin typical of
145 juvenile salmonids undergoing an ocean migration. Scoring was done without
146 knowledge of cross-type. We used a seawater challenge experiment and tracked

147 movement of individuals released into Big Creek approximately 0.5 km downstream of
148 the barrier waterfall and 5.5 km upstream of the ocean to evaluate the correspondence
149 of our visual “smolt condition” scoring with the physiological (i.e. capacity to
150 osmoregulate in saltwater) and behavioral (i.e. downstream migration) characteristics of
151 smoltification (electronic supplementary material).

152

153 *Ethics Statement*

154 The study presented here was carried out in accordance with the University of
155 California, Santa Cruz IACUC and is covered under a permit issued to SAH (Permit
156 Number: Hayes1304-vers2). Handling of ESA species is covered under NMFS Section 10
157 (Permit Number: 1112 to SAH).

158

159 *Statistical Analysis*

160 Cross-specific estimates of sex ratio, proportion of smolts, and growth rate (fork
161 length and mass) were generated using generalized linear mixed models implemented
162 in the Bayesian mixed model R package *MCMCglmm* (Hadfield 2010; R Core Team). The
163 variables ‘sex’ and ‘smolt’ were both modeled as binomial responses with ‘cross’ as a
164 categorical fixed effect (above-barrier or below-barrier). Family affiliation was included
165 as a random effect to account for maternal effects and initial differences in rearing
166 conditions. Models were run with priors for the family variance set to 1 with a degree of
167 belief of 0.02; the prior on residual variance was fixed at 1. Alternative priors did not

168 influence model estimates. Both models were run for 550,000 iterations, discarding the
169 first 50,000, sampling every remaining 250th iterations to reduce autocorrelation.

170 A bivariate 'animal model' (Wilson *et al.* 2010), was used to generate cross-
171 specific estimates for the growth rate parameters 'fork length' and 'mass' and the
172 covariance between the traits (r_G). The model used the phenotype of related individuals
173 as a random effect to partition phenotypic variance (V_P) into additive genetic (V_A) and
174 residual (V_R) components. However, estimates of V_A may be upwardly biased by factors
175 (e.g. maternal effects) that could not be separated from the additive genetic effects.
176 Weakly informative priors for the model were generated by equally partitioning the
177 observed V_P in fork length and mass between the V_A and V_R components, with the prior
178 belief parameter set to two. The model was run for 1,020,000 iterations, discarding the
179 first 20,000, and then sampling every 250th iteration. We calculate both trait heritability
180 ($h^2 = V_A/V_P$) and trait evolvability ($I_A = V_A/X^2$; where X is the mean phenotype), the latter
181 of which is the expected proportional change in the trait under a unit strength of
182 selection (Houle 1992; Hansen, Pélabon & Houle 2011). We also report the genetic
183 correlation between fork length and mass.

184 We examined the effects of sex, growth rate, and cross-type on incidence of
185 smolting with a generalized linear (logistic regression) model, including all variables and
186 two-way interactions. To include the effects of both continuous variables (fork length
187 and mass) in model predictions, we estimated the length-mass relationship of the
188 population, as $mass = a*FL^b$. We determined nonlinear least-squares estimates of a and
189 b using the nls function in R ($a = 3.73 \times 10^{-5}$, SE = 3.46×10^{-6} ; $b = 2.75$, SE = 1.89×10^{-2} ; $df =$

190 915). We used coefficient estimates from this model to illustrate the divergence
191 between cross types in the size dependent process of smolting (Fig. 1d). However, the
192 underlying mechanisms that trigger the expression of the alternative strategies are not
193 observable.

194

195 *The Latent Environmental Threshold Model*

196 To further investigate the evolution of the underlying threshold trait we utilized
197 the Latent Environmental Threshold Model (LETM; Buoro *et al.* 2012). The
198 environmental threshold model (ETM; Hazel & Smock 1990; Roff 1994; Tomkins & Hazel
199 2007) enables assessment of selection on conditional strategies under a single
200 framework that accommodates both phenotypic plasticity and threshold evolution. In
201 the ETM, switch points are heritable and vary among individuals within a population.
202 The ETM provides a mathematical framework to estimate the switch point; however,
203 quantifying the necessary components is not straightforward, as the proximate cue and
204 switch point are often not observable. Recently, Buoro *et al.* (2012) addressed this by
205 decomposing the ETM into “observable” and “non-observable” components; the former
206 being the expressed phenotype and an observable environmental cue (e.g. body size),
207 the latter being the switch point and the proximate environmental cue or liability trait
208 (e.g. physiological state). The resulting LETM allows the estimation of genetic variance of
209 the switch point and heritability of the conditional strategy from observations of the
210 phenotypes and the related observable cue.

211 An additional assumption of the LETM relative to the ETM is that it assumes that
212 the proximate cue (η_i) varies among individuals as a function of the environment, but is
213 unobservable. Little biological knowledge is often available regarding the proximate
214 mechanisms influencing the expression of the phenotype (Tomkins & Hazel 2007).
215 Although η_i is not observable, an observable proxy X_i , which is correlated with η_i , can be
216 measured. For example, growth rate and/or size at a given age in fish are known to be
217 strongly influenced by the environment and are thus considered as integrating various
218 environmental factors (Dieckmann & Heino 2007). The distribution of η_i can be
219 expressed conditional on X_i with some residual error ε_i (normally distributed with mean
220 0 and standard deviation σ_η). In their review of alternative migratory strategies in
221 salmonid fishes, Dodson *et al.* (2013) argue that body size is the most commonly (and
222 adequately) reported proxy of the liability trait in salmonids. We use fork length as the
223 observable proxy in the LETM.

224 Another constraint of the LETM is that there can be a unique threshold for each
225 genotype and thus the threshold of individual i (θ_i) is a polygenic quantitative trait which
226 is normally distributed with mean μ_θ and standard deviation σ_θ , as typically assumed in
227 quantitative genetics, following Hazel *et al.* (1990) and Roff (1994). Thus, the standard
228 deviation of switch point σ_θ is a measure of genetic variability. In the LETM, we assume
229 that the individual thresholds θ_i covary according to the individual relatedness; i.e., they
230 are sampling thresholds in a multivariate normal distribution depending on the additive
231 genetic relationship matrix and the additive genetic variance.

232 We apply the LETM framework to compare the switch point for migration between
233 the two populations of *O. mykiss* from above and below the barrier waterfall. We
234 extended this approach combining the analysis for the two populations and introducing
235 three additional modeling constraints:

236 (1) Both populations experienced the same environment (shared proximate cue η_i),
237 given that this was a common garden experiment.

238 (2) Both populations are characterized by similar genetic variance and heritability of
239 the conditional strategy, so that they are characterized by the same propensity
240 to respond to selection (shared θ_i). Analyses of the two populations separately
241 confirmed that estimates of heritability are similar (results not shown).

242 (3) The means of the threshold (μ_θ) may vary between the two populations.

243

244 *MCMC Conditions and Diagnostics*

245 Bayesian Markov chain Monte Carlo (MCMC) algorithms provide a flexible
246 framework for analyzing latent variable models and their conditional structure (Clark
247 2004). We used this approach to fit the LETM to data. Joint posterior distributions of
248 model parameters of interest were obtained by MCMC sampling implemented for the
249 LETM in the R package *rjags* (Plummer 2003). Convergence of MCMC sampling was
250 assessed by Brooks-Gelman-Rubin diagnostics (Brooks & Gelman 1998).

251 Bayesian analyses require specifying prior probability distributions for model
252 parameters. Here all priors were non informative or weakly informative to ensure that
253 all information comes from data. More details are available in Buoro *et al.* (2012).

254 Results reported from models are posterior medians and 95% posterior probability
255 intervals. Support for differences between crosses is reported as the percent of the
256 posterior distributions in agreement with the direction of the difference observed.

257

258 **RESULTS**

259 Nine families were produced: five pure above-barrier (three females crossed to
260 four males) and four pure below-barrier (three females crossed to four males). Number
261 of eggs per female varied considerably (range: 301 – 832) but egg diameters were
262 similar (range: 4.5 – 5.0 mm); there were no significant differences between above- and
263 below-barrier females, suggesting that maternal effects were minimal, perhaps not
264 surprising given parents were raised from young-of-year to maturity in the same
265 hatchery environment.

266 Parentage was determined for 917 offspring that survived the duration of the
267 experiment, and genetic sex was assigned to 853. As there was no apparent bias in
268 which fish could not be assigned sex, we use the reduced dataset only in models where
269 sex is included as a variable. Offspring sex ratio was estimated as 50% male in above-
270 barrier crosses (43% - 57%; Fig. 1a), and 43% male in below-barrier crosses (37% - 49%;
271 Fig. 1a), with 93% of the posterior distribution supporting the lower incidence of males
272 in the below-barrier crosses. Incidence of maturity among males differed significantly
273 between crosses (chi-squared = 36.6, df = 1, $p < 0.001$): mature males accounted for
274 27.8% of all above-barrier males (14.0% of all fish), but only 5.4% of below-barrier males
275 (2.3% of all fish).

276 Expression of the migratory life-history was substantially reduced in the above-
277 barrier population. Frequency of smolts in above-barrier offspring was 54% (40% - 68%;
278 Table 1; Fig. 1b), compared to 75% (64% - 83%; Table 1; Fig. 1b) in below-barrier
279 offspring. Support for the lower incidence of smolts in above-barrier offspring was 98%
280 of the posterior distribution. A greater proportion of fish scored as 'smolts' survived the
281 seawater challenge (58 of 71 smolts, 57 of 127 non-smolts, chi-squared = 23.9, df = 1, p
282 < 0.001; Fig. 2a), but survival of fish scored 'smolts' did not differ between the crosses
283 (chi-squared = 0.27, df = 1, p = 0.60). A higher proportion of smolts were detected
284 migrating downstream than non-smolts (361 of 1038 smolts released, 50 of 541 non-
285 smolts released; chi-squared = 136.9, df = 1, p < 0.001; Fig. 2b) and significantly more
286 below-barrier smolts were detected moving downstream than above-barrier smolts
287 (43% to 24%; chi-squared = 41.5, df = 1, p < 0.001). Fork length (FL) positively influenced
288 these elements of smoltification (GLM, survival: FL = 0.032, 0.007 SE, p < 0.001;
289 detection: FL = 0.014, 0.006 SE, p = 0.023). However, size and smolt state are strongly
290 positively correlated (Fig. 1d), making it difficult to isolate their individual effects.

291 Fish from above-barrier crosses grew slower than fish from below-barrier
292 crosses; above-barrier fish had smaller mean fork length (137mm; 116 - 158mm) and
293 mass (28.9; 14.7 - 42.1g) than below-barrier fish (FL: 154mm; 132 - 173mm; mass:
294 43.5g; 28.4 - 54.7g) (Table 1; Fig. 1c). Probabilities that above-barrier fish were smaller
295 in length and mass were 86.8% and 90.9%, respectively. For both metrics of growth, V_A
296 accounted for a majority of the total V_P (h^2 FL = 0.73; 0.41 - 0.96; h^2 mass = 0.74; 0.42 -
297 0.96; Table 1). Expected proportional changes in fork length and mass under a unit

298 strength of selection were 2.9% (1.0 – 5.0%) and 15.7% (4.1 – 36.9%), respectively.
299 There was strong statistical support for a positive genetic correlation between the two
300 measures of growth rate ($r_G = 0.97$; 0.94 – 0.99). Logistic regression supported migration
301 as a size-dependent process that is also influenced by cross and sex (Fig. 1d).

302 Threshold fork length also differed substantially between the divergent
303 populations. The above-barrier threshold was larger than the below-barrier threshold
304 (difference estimated of 0.60; 0.28 - 0.91 with > 99% of support). The mean threshold
305 for the above-barrier population is 43% (25% - 61%) larger than the below-barrier
306 population. In the LETM, the scale of the proximate cue is arbitrary and the link between
307 proximate and observable cues is an undefined function (eq. 3 in Buoro *et al.* 2012). For
308 the sake of illustration, we scale the proximate cue to the observable cue such that the
309 two cues share a 1:1 relationship (i.e., a one millimeter increase in fork length
310 corresponds to a one unit increase in the proximate cue). On this scale the median
311 posterior difference in thresholds would be 17 mm (8 - 25 mm). In below-barrier
312 offspring, the mean threshold fork length is 42 mm less than the mean fork length. In
313 contrast, this difference in mean threshold and mean fork length in above-barrier
314 offspring is only 9 mm. Thus, a much larger proportion of the fork length and threshold
315 size distributions overlap in the above-barrier population (Fig. 3), reducing expression of
316 the migratory behavior.

317

318 **DISCUSSION**

319 Human activities increasingly threaten migratory species by presenting barriers
320 to movement (Wilcove & Wikelski 2008). Dams in particular have been responsible for
321 large declines in the distribution and diversity (Gustafson *et al.* 2007) of migratory
322 salmonids in the United States. We investigated the response to selection against
323 migration in a population of *Oncorhynchus mykiss* isolated above a barrier waterfall for
324 ~100 years. The migratory phenotype at age-1 was reduced by 30% (18 – 40%) in the
325 above-barrier families, consistent with evolutionary adaptation to selection for the non-
326 migratory strategy. This rapid evolution was driven by changes in growth rate as well as
327 evolution of the underlying size threshold. These changes in fish length represent a
328 rapid evolutionary rate of change of 1,156 ‘Darwins’ (Haldane 1949). The estimated fork
329 length threshold value changed at a rate of 1,381 Darwins. Both rates are similar to
330 those observed for populations introduced to novel habitats (Hendry, Farrugia &
331 Kinnison 2008). More generally, our results indicate that migratory behavior has a
332 heritable genetic basis that can evolve rapidly.

333 The rapid evolutionary change in the frequency of the migratory life history
334 strategy is mediated by a shift in the distribution of the switch point relative to the cues
335 that trigger migration (Fig. 3), consistent with the view of migration as a threshold trait
336 (Pulido 2011; Dodson *et al.* 2013). Previous theoretical models of threshold traits
337 assumed that the expression of the discrete states are under polygenic control, either
338 by genetic variation in the proximate cue (Wright 1934; Falconer 1965) or the switch
339 point (Hazel & Smock 1990; Roff 1994; Hazel, Smock & Lively 2004), but could not
340 examine the potential for both (Roff 2011). The LETM (Buoro *et al.* 2012) allowed us to

341 separately estimate the switch point and proximate cue (body size) to identify
342 evolutionary shifts in their distributions (Fig. 3). Simultaneous evolution of these two
343 aspects enabled shifts in migratory behavior (Fig. 1b).

344 This study represents a relatively rare example of the evolution of switch points
345 (Roff 2011). Genetic variation has been reported in the switch point underlying the
346 expression of many threshold traits, including male morphologies (Moczek 2003;
347 Buzatto, Simmons & Tomkins 2012), reproductive strategies (Piche, Hutchings &
348 Blanchard 2008), and migratory tactics (Beakes *et al.* 2010; Paez *et al.* 2010). However,
349 there are few examples of the switch point trait actually responding to selection in a
350 natural population (but see Moczek 2003; Tomkins & Brown 2004). Perhaps the best
351 example comes from an artificial selection experiment on alternative male morphs of a
352 mite (*Rhizoglyphus echinopus*). By increasing the hiding places available to (and
353 presumably the fitness of) a non-fighter morph, Tomkins *et al.* (2011) were able to
354 induce an evolutionary increase in the mean size at which males express the alternative
355 fighter morph. Thus, switch points can evolve over a few generations when faced with
356 strong directional selection.

357 Body size of salmonid fishes is a key trait that is heritable and that selection acts
358 upon. Carlson and Seamons (2008) found the median estimates for length-at-age and
359 mass-at-age heritability to be 0.29 (range -0.10 to 0.73) and 0.32 (range 0 to 1),
360 respectively. In the present study, above-barrier offspring reared in a common-garden
361 environment were 11% and 31% smaller than below-barrier offspring in fork length and
362 mass, respectively, and heritability was high for both traits (Table 1). In the below-

363 barrier source population, selection favors larger fish due to the strong size-selective
364 mortality migrants experience at sea (Bond *et al.* 2008). Following transplantation above
365 the barrier waterfall, genetic variants conferring faster growth would be quickly lost due
366 to the relationship between size and smolting (Fig. 1d). Thus, above the barrier
367 waterfall, high-risk foraging behaviors that increase growth opportunities could
368 decrease relative fitness by increasing both predation risk (Biro *et al.* 2006) and the
369 likelihood of exceeding the environmentally cued threshold to migrate over the
370 waterfall. However, while our results suggest the frequency of the migratory phenotype
371 is significantly reduced in the above-barrier population, the incidence of migrants
372 (54.2%) is still quite high. Why would the migrant phenotype remain so common? One
373 possibility is that the short time since the transplantation occurred has not given
374 selection sufficient opportunity to remove the migratory phenotype. This is consistent
375 with the results of Pearse *et al.* (2014), who found significantly lower frequency of
376 alleles associated with anadromy in long-established resident populations compared
377 with recently established above-barrier populations. However, the high growth rate of
378 our experimental fish, which is typical for salmonid hatcheries intent on maximizing the
379 number of fish that migrate upon release (Hayes *et al.* 2004), likely also contributed. In
380 fact, *in situ* incidence of smolts in the above-barrier population is likely much lower; 95%
381 of fish rearing in the upper watershed are <100 mm in length after one year of growth
382 (Hayes *et al.* 2008), well below the mean threshold size estimated here.

383 Gender-specific differences in maturation schedules appear to play an important
384 role in the rapid evolution of the resident life history described here. Early maturity is

385 also a threshold trait (Piche *et al.* 2008), but the decision-window occurs prior to that of
386 smoltification (Mangel & Satterthwaite 2008). Our study did not explicitly quantify the
387 maturation threshold; rather, the LETM subsumes variation produced by multiple
388 development pathways. Smaller thresholds for early maturity may achieve the same
389 outcome as larger thresholds for migration (lower probability of migration), but are
390 constrained by the minimum energetic state necessary to mature. Due to the greater
391 energetic requirements and associated fecundity advantage, rates of anadromy in
392 salmonid populations are often female biased (Ohms *et al.* 2014). Males, on the other
393 hand, can reach maturity in a single year of freshwater growth. We found males were
394 less likely to smolt at a given size, particularly in above-barrier families, and more likely
395 to mature at larger body sizes (illustrated by the decline in the male logistic curve at
396 larger fork lengths in Fig. 1d). The higher incidence of mature males in above-barrier
397 offspring is consistent with the strong negative genetic correlation between smolting
398 and early maturation documented by Thrower *et al.* (Thrower *et al.* 2004). The 2.3%
399 rate of early male maturity in below-barrier offspring is consistent with the ~3%
400 observed annually in the Big Creek Hatchery steelhead stock (S. Hayes; *pers. obs.*),
401 suggesting the phenotype was also segregating in the founding population prior to
402 introduction above the barrier waterfall. Further, alleles conferring early maturity
403 should rapidly accumulate in this population as these males have earlier, and potentially
404 more numerous, reproductive bouts. Interestingly, while males and females were found
405 in equal proportion in the above-barrier families, females significantly outnumbered
406 males in progeny of below-barrier parents (Fig 1a). The cause of this difference is

407 unclear, as an equal sex-ratio in juvenile *O. mykiss* was found in a nearby population
408 (Rundio *et al.* 2012).

409 Contrasting traits of introduced and source populations following biological
410 invasions can provide valuable insight into contemporary evolution (Westley 2011).
411 However, such studies are often opportunistic, as in the present case, and thus
412 consideration of the results must be done within the context of a possibly imperfect
413 study design. For instance, although unlikely, it is impossible to rule out the presence of
414 a previously established, genetically divergent *O. mykiss* population above the barrier
415 before the human-mediated introduction in 1910 (Pearse *et al.* 2009). Further, our
416 results from a single above- and below-barrier population pair, with a limited number of
417 parents represented in the breeding design, may not be representative of all
418 populations. However, given that *O. mykiss* have been widely introduced above barriers
419 there is a unique opportunity to test predictions from our study in independent
420 populations. Recently, Pearse *et al.* (2014) found parallel adaptive genomic evolution in
421 multiple above-barrier populations, including Big Creek, with the degree of evolution
422 consistent with time since isolation from the paired below-barrier populations. Thus, Big
423 Creek appears representative of many populations undergoing similar genomic
424 evolution following recent isolation above barriers.

425 A growing body of literature highlights the complicated interplay between
426 resident and anadromous forms of *O. mykiss* (Zimmerman & Reeves 2000; Thrower *et*
427 *al.* 2004; Pearse *et al.* 2009; Hayes *et al.* 2012; Courter *et al.* 2013), and the challenges
428 and opportunities for management and conservation of species with conditional

429 migration. However, the US Endangered Species Act (NMFS 2006) protects listed
430 steelhead populations, but protects only “naturally spawned anadromous *O. mykiss*
431 (steelhead) populations below natural and manmade impassable barriers”, while
432 excluding the resident forms that they are connected to. In addition, fragmentation of
433 aquatic migratory corridors and on-going introductions are likely causing contemporary
434 evolution throughout the range of *O. mykiss*. We found that migration is highly heritable
435 ($h^2 = 0.91$; $SD = 0.09$) and can evolve rapidly in response to selection. On the other hand,
436 *O. mykiss* isolated for many decades still produce some smolts with the capacity to
437 osmoregulate in seawater (see also Thrower *et al.* 2004). This suggests conservation of
438 physiological and behavioral components of smoltification in isolated *O. mykiss*
439 populations via cryptic genetic variation, and that isolated *O. mykiss* populations could
440 contribute to the recovery of genetically similar endangered migratory populations
441 downstream but will likely be sensitive to the strength and duration of selection
442 experienced during isolation. Thus, our study demonstrates that evolution of key life-
443 history traits can occur on timescales relevant for management and conservation and
444 provides insight into how ecological and genetic variation interact to promote rapid
445 adaptation to ongoing environmental change.

446

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456

457 **DATA ARCHIVAL LOCATION:** Dryad if accepted

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- 663

664 FIGURE 1. Comparison of above-barrier (red) and below-barrier (blue) offspring sex ratio
665 (a), smolt incidence (b), observed fork lengths and data density (c), and predicted smolt
666 incidence from logistic regression (see Methods) (d). In (a) and (b), solid and thin lines
667 represent 50% and 95% posterior probability intervals. In (c), the shaded area
668 represents data density. For (d), fish mass is estimated for a given fork length based on
669 the length-mass relationship as described in the Methods. Open circles in (d) are the
670 predicted incidence of smolts for the median posterior probability fork length of the
671 given cross and assuming the mean effect of sex. Lighter red lines indicate female (♀)
672 and male (♂) specific predictions. Sex specific predictions for below-barrier offspring are
673 indistinguishable from the mean. Logistic curves decline for above-barrier fish at larger
674 body sizes due to the incidence of early maturing males (see Results).

675

676 FIGURE 2. Relationships between different metrics of smoltification. 'Smolt score' and
677 (a) the survival of individuals in seawater and (b) the probability of being detected
678 migrating downstream. General assessment of our 'smolt' scoring criteria was
679 independent of the effect of cross type, and include offspring of additional crosses
680 (above-barrier x below-barrier and F1 backcrosses) made at the same time as the
681 crosses presented here ('All crosses', black circles; see Supplemental Material for further
682 details). Estimates for above-barrier (red circles) and below-barrier (blue circles) crosses
683 are also presented. Error bars represent 2 s.e.

684

685 FIGURE 3. A comparison of distributions of thresholds (in blue) and fork lengths (in
686 yellow) for (a) the below-barrier source population, and (b) the derived above-barrier
687 population. Dashed lines and arrows indicate the direction and magnitude of the
688 response to selection against downstream migration in the above-barrier population.

689 TABLE 1. Estimates and Bayesian 95% credible intervals from the bivariate animal model
 690 for the observable environmental cues (fork length and mass) and switch point size.

	fork length (mm)	mass (g)	switch point
Above	137 (116 - 158)	28.9 (14.7 - 42.1)	128 (121 - 135)
Below	154 (132 - 173)	43.5 (28.4 - 54.7)	112 (104 - 120)
<i>P</i>	86.8%	90.9%	> 99.9%
V_A	701 (268 - 1082)	286.1 (124.5 - 451.8)	---
V_p	954 (730 - 1174)	389.2 (293.3 - 471.1)	---
I_A	2.9% (1.0 - 5.0%)	15.7% (4.1 - 36.9%)	---
h^2	0.73 (0.41 - 0.96)	0.74 (0.42 - 0.96)	---
<i>d</i>	-1156 (-3247 - 922)	-3695 (-10552 - 1842)	1381 (674 - 2159)

P: Posterior density supporting above-barrier fall offspring are smaller than below-barrier offspring.

I_A : Evolvability, defined as the additive genetic variation divided by mean phenotype squared (here, mean of BB). See Hansen *et al.* (2011).

d: Darwins, the change in the trait by a factor of *e* per one million years.

Other abbreviations defined in text.

691

Figure 1.

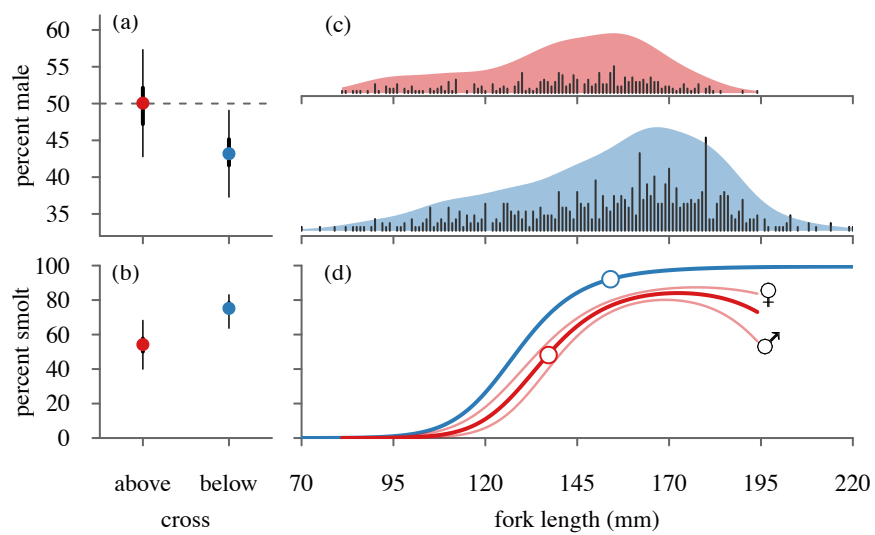


Figure 2.

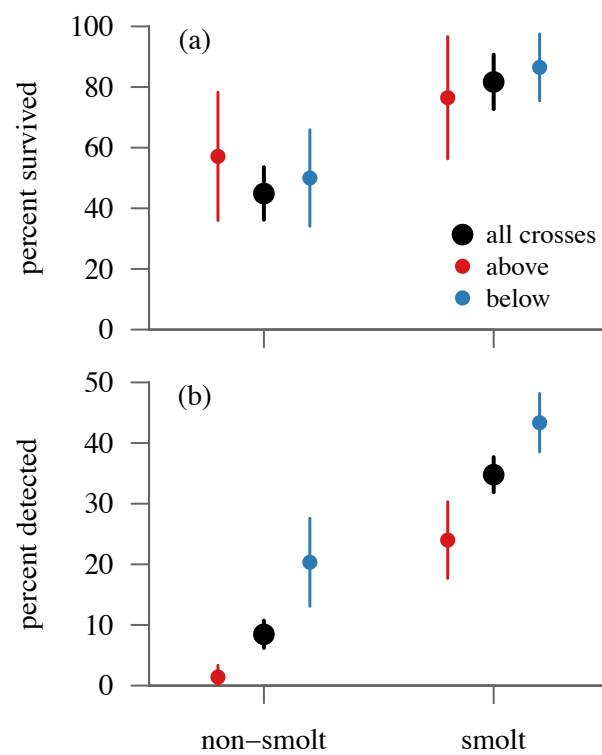
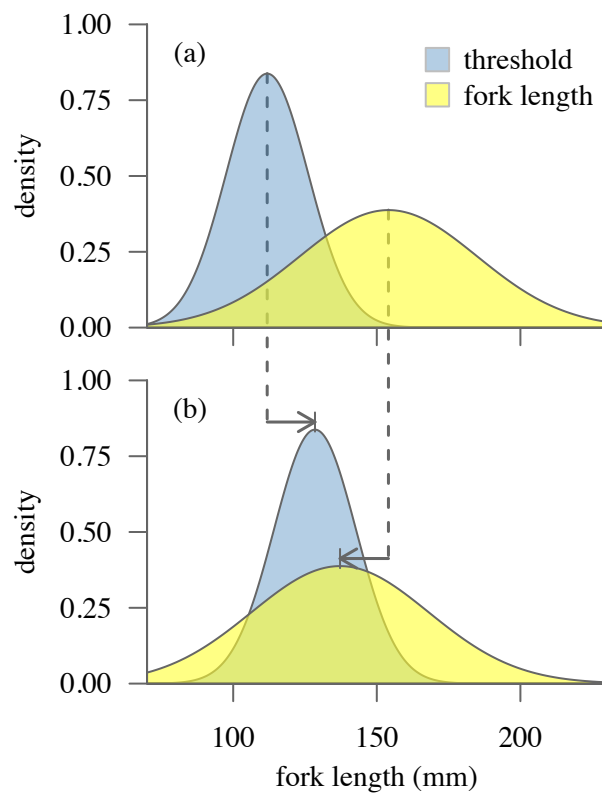


Figure 3.



1 **SUPPLEMENTAL MATERIAL**

2 **TITLE:** Shifting thresholds: rapid evolution of migratory life histories in
3 steelhead/rainbow trout, *Oncorhynchus mykiss*.

4 **RUNNING HEAD:** Rapid evolution of migratory life histories

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17 **SUPPLEMENTAL METHODS**

18 *Genotyping and Parentage Analysis*

19 Small ($\approx 0.3 \text{ cm}^2$) caudal fin clips were collected from all juveniles for genetic parentage
20 analysis. Tissue samples were digested with proteinase K, followed by DNA extraction
21 with a semi-automated filter-based system (DNeasy 96 Tissue Kit) on a BioRobot 3000
22 (QIAGEN Inc.). A panel of 95 single nucleotide polymorphisms (SNPs) was genotyped for
23 all individuals (Abadia-Cardoso *et al.* 2013), and a gender identification assay consisting
24 of an autosomal and a Y chromosome-linked (Brunelli *et al.* 2008) gene probe was used
25 to determine genetic sex of all genotyped fish . Genotyping was conducted using
26 TaqMan assays (Applied Biosystems, Inc.) on 96.96 Dynamic Genotyping Arrays with the
27 EP1 Genotyping System (Fluidigm Corporation). Two negative controls were included in
28 each array and genotypes were scored using SNP Genotyping Analysis Software v3.1.1
29 (Fluidigm). Individual SNP genotypes were used for parentage analysis with the program
30 SNPPit (Anderson), following Abadía-Cardoso *et al.* (2013), and the accuracy of the
31 inferred parentage assignments was assessed by comparing the genetic parentage
32 results with the known family crosses.

33

34 *Seawater Challenge and Instream Movement*

35 We used two experiments to evaluate whether our visual 'smolt' scoring corresponded
36 with the capacity to osmoregulate in saltwater and downstream migration
37 characteristics of smoltification. These assessments of our 'smolt' scoring criteria were
38 independent of the effect of cross type, and we therefore increased sample size by

39 including offspring of additional crosses (above-barrier x below-barrier and F1
40 backcrosses) made at the same time as the crosses presented here. First, we tested the
41 hypothesis that non-smolts and smolts would survive equally when moved from
42 freshwater to seawater. A subset of fish (127 non-smolts, 71 smolts) was haphazardly
43 selected and a seawater challenge performed following Beakes et al. (2010). Fish were
44 introduced into a large seawater-fed tank (salinity 35 ‰) at the approximate time of
45 peak downstream migration (March-April) and monitored every 6-12 hours for 12 days.
46 Second, we tested the null hypothesis that non-smolts and smolts would be detected
47 migrating downstream in equal proportions following release. All fish not included in the
48 seawater challenge were released into Big Creek approximately 0.5 km downstream of
49 the barrier waterfall and 5.5 km upstream of the ocean. Movement was monitored over
50 six weeks by three instream PIT tag readers and a smolt trap, all located downstream of
51 the release site (Bond *et al.* 2007; Hayes *et al.* 2011). All detections and recaptures were
52 interpreted as movement downstream unless the individual was detected again at the
53 same site more than 24 hours later (n = 2).

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