

Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates

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Summary

1. The importance of body size and growth rate in ecological interactions is widely recognized, and both are frequently used as surrogates for fitness. However, if there are significant costs associated with rapid growth rates then its fitness benefits may be questioned.
2. In replicated whole-lake experiments, we show that a domestic strain of rainbow trout (artificially selected for maximum intrinsic growth rate) use productive but risky habitats more than wild trout. Consequently, domestic trout grow faster in all situations, experience greater survival in the absence of predators, but have lower survival in the presence of predators. Therefore, rapid growth rates are selected against due to increased foraging effort (or conversely, lower antipredator behaviour) that increases vulnerability to predators. In other words, there is a behaviourally mediated trade-off between growth and mortality rates.
3. Whereas rapid growth is beneficial in many ecological interactions, our results show the mortality costs of achieving it are large in the presence of predators, which can help explain the absence of an average phenotype with maximized growth rates in nature.

Key-words: activity, antipredator, genotype, habitat use, trout.

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Introduction

The importance of body size and growth rate in ecological interactions is widely recognized. The empirical literature is replete with evidence showing that juvenile and adult survival rates, fecundity and reproductive/competitive ability are frequently positively related to body size. Indeed, given a positive relationship between size and fitness, theory suggests that selection should favour those individuals that maximize net energy acquisition and growth (Stearns & Koella 1986; Perrin & Rubin 1990; Stearns 1992). In fact, given the difficulty of measuring reproductive success directly, this view is often reversed so that growth rate is used as a surrogate for fitness (Stearns 1992; Schlüter 1995; Lima

1998; Lind & Cresswell 2005). However, substantial genetic variation in growth rates within and among species has been documented, demonstrating that organisms rarely grow at their physiological maximum (Case 1978; Calow 1982; reviewed by Arendt 1997) and theory suggests that maximization of growth is unlikely (e.g. Calow 1982; Sibly, Calow & Nichols 1985; Abrams *et al.* 1996). None the less, rapid growth continues to be widely accepted as universally advantageous, but is it? If there are costs to rapid growth, then the idea that growth rate should always be maximized and the fitness benefits of large size (achieved through rapid growth) may be called into question.

Recent research highlights limitations in the view that faster growth is always better, indicating that various trade-offs may limit the benefit of rapid growth (Arendt 1997; Post and Parkinson 2001; Munch & Conover 2003; Biro *et al.* 2005; Stoks *et al.* 2005). In particular, we suggest that behaviourally mediated trade-offs between growth and predation mortality are especially likely to shape the evolution of intrinsic growth rate for

two reasons. First, virtually all animals are prey and therefore affected by predation risk. Second, ingestion rates and susceptibility to predation tend to increase with activity levels and use of productive habitats (reviewed in Lima 1998). Therefore, greater growth is usually achieved by increased foraging effort that leads directly to greater predation rates (e.g. Werner & Gilliam 1984; Werner & Anholt 1993; Anholt & Werner 1995; Gotthard 2000; Biro, Post & Parkinson 2003a,b; Stoks *et al.* 2005). These observations lead naturally to the prediction that predation selects against maximal growth rates in nature by removing individuals that display increased foraging effort.

Trade-offs associated with rapid growth are in general poorly known (reviewed by Arendt 1997). However, recent studies with invertebrates have shown that more rapid growth is usually associated with greater predation mortality due to greater foraging effort (e.g. Brodin & Johansson 2004; Stoks *et al.* 2005; but see McPeek 2004 and Stoks *et al.* 2005 for examples showing how increased growth efficiency can reduce behavioural effects). Similar studies with fish have shown decreased escape performance (Lankford, Billerbeck & Conover 2001; Munch & Conover 2003) and greater predation mortality (Biro *et al.* 2004a; Sundstrom *et al.* 2004) with increases in growth rate. However, Sundstrom *et al.* (2004) did not quantify behaviour to test whether the trade-off was behaviourally mediated. Whereas Biro *et al.* (2004a) showed that increased use of a risky habitat by fast-growing age-1 domestic trout (relative to a wild strain) resulted in greater growth but lower survival in the presence of predators, the 'fast growing' type did not grow more quickly in lakes without predators. Therefore, their results are equivocal in terms of understanding evolution of growth rate.

In this study, we directly test for and show for the first time to our knowledge that behaviourally mediated trade-offs between growth and mortality rates is a mechanism contributing to the evolution of submaximal growth rates in animal populations in the field. To do this, we contrasted the behaviour, growth and survival between domestic and wild strains of age-0 rainbow trout *Oncorhynchus mykiss* (Mitchell) as a function of predation risk in a replicated whole-lake experiment. Realistic field experiments, which allow the full suite of predator and antipredator behaviours to manifest themselves, do not restrict the expression of compensatory behaviours by prey that could affect the apparent strength of the growth/mortality trade-offs (Lind & Cresswell 2005). This work also extends our previous work with small adult-sized trout (Biro *et al.* 2004a) by considering selection against rapid growth in age-0 trout that are vulnerable to a much wider array of predators and experience very high mortality rates (e.g. Post, Parkinson & Johnston 1999; Biro *et al.* 2003a,b). Therefore, selection against rapid growth in domestic trout may be more severe for age-0 than age-1 fish. We predicted and show that the domestic strain (artificially selected for maximum intrinsic growth rate) forage

more actively, and use productive but risky habitats more than wild trout. As a consequence, domestic trout grow more quickly in all situations, experience greater survival in the absence of predators, but have lower survival in the presence of predators.

STUDY SYSTEM AND SPECIES

High phenotypic variability and heritability ($h^2 > 0.50$) in salmonid growth rate makes trout an ideal species for growth rate manipulation and study (Gjedrem 2000). Artificial selection for maximum growth rates in salmonid fishes (trout and salmon) has demonstrated that domestic salmonids have a much greater capacity for growth than wild strains (Gross 1998; Devlin *et al.* 2001). Given that greater growth in domestic salmonids is linked to higher growth-hormone levels that stimulate appetite (Johnsson *et al.* 1996; Fleming *et al.* 2002), it seems reasonable to suggest that increased hormonal motivation to feed drives the elevated activity rates, increased aggression and lower antipredator behaviour observed in domestic and growth-hormone manipulated salmonids. The converse then, is that evolution has selected for physiology that suppresses appetite and therefore average growth rates in wild strains.

Our lakes provide distinct spatial and temporal habitats for trout that differ in the abundance of food and exposure to predators, allowing us to test for the predicted behavioural changes in response to variation in food and predation. The primary predator of age-0 trout in our lakes are cannibalistic adult rainbow trout (Post, Parkinson & Johnston 1998; Biro *et al.* 2003b). Larger (older) trout are primarily preyed upon by piscivorous birds, namely common loons *Gavia immer* (unpublished data; Biro *et al.* 2004a). Nearshore and bottom habitats provide physical structure as a refuge from predation but little plankton food, whereas deep and openwater (pelagic) habitats provide abundant plankton food but lack physical structure and are risky (Post *et al.* 1998, 1999; Biro *et al.* 2003a,b,c; 2004a). Adult trout and loons are visual predators making the risk of predation lower during low-light periods at dusk (Post *et al.* 1998; Biro *et al.* 2004a). Therefore, we predicted that the elevated appetite of domestic relative to wild trout would result in an increased willingness to accept risk by foraging more in food-rich, but risky deep and pelagic (open-water) habitats during the day.

Methods

Trout were stocked 6 August 2004 into seven small experimental lakes (1.4–4 ha) located in British Columbia, Canada. Characteristics of several of the lakes used previously (K1, K2, B2, B3 and CP1) are described in detail in Biro *et al.* (2003a); the remaining lakes, RPH2 and PPH, are similar in size and trophic status to B3 and CP1, respectively. Lakes B2, B3 and RPH2 represent our predator-free treatment as they were free of all fish prior to stocking due to winterkill and have never

had loons present (Biro *et al.* 2003b). The remaining lakes (CP1, K1, K2 and PPH) all had populations of large rainbow trout (> 300 mm) and frequently have loons present and so represent our predator treatment.

We obtained a domestic strain of rainbow trout from a local hatchery. The wild strain came from Tunkwa Lake, BC. Fish from both strains were raised to a common length (mean = 37 mm) and mass (mean = 0.58 g; both $F_{1,398} < 0.95$, $P_s > 0.3$). The adipose fin of the domestic strain was clipped for identification. Each strain was stocked at a density of 2000 trout ha^{-1} into each lake. Because both strains are reared identically, variation in growth and survival rates in the field should be driven primarily by genetic variation between these strains (Johnsson & Abrahams 1991). To establish differences in intrinsic growth rates and the potential for behavioural variation between strains, we held 200 of each strain in separate 800 L circular tanks in the hatchery at 10 °C and fed them to excess several times a day from 6 August until 27 October.

We assessed relative activity rates and use of food-rich but risky deep and pelagic habitats by trout, 1–8 September, using multifine-mesh sinking and floating experimental gillnets that capture trout 45 mm in length and larger (see Biro *et al.* 2003a). We timed this netting to ensure that fish were larger than 45 mm in length; the smallest fish we captured, in the lake with lowest growth (a predator lake), was 49 mm in length. We set 1.5 m deep nets along the 1.5 m depth contour, 2.5 m deep nets along the 2.5 m contour, and 5 m deep nets floating at the surface in the pelagic habitat. Two nets of each type were simultaneously set for 1 h in haphazardly selected locations; we allowed nets to fish longer and set additional nets in lakes with low catch rates. Gillnet catch rates represent a combination of fish activity rates and density; however, given equal stocking densities of each strain then the relative proportion of each should represent differential activity rates, at least within a habitat.

We estimated autumn population size and mean mass from 13 to 24 October by lethal gillnet sampling in all habitats for five consecutive nights with a standardized effort (Post *et al.* 1999; Biro *et al.* 2003a). One week prior to autumn netting, we stocked marked domestic and wild trout (mean length = 84 mm and 72 mm, respectively) into each lake to estimate the proportion of each group recaptured over the five nights of netting. Up to 750 of each strain were stocked into the largest lakes, 300–500 in the smaller lakes. Domestic trout were considerably more vulnerable to the nets than wild trout in all lakes. To estimate the number of survivors, we used an established equation that relates the proportion of the population of wild strain trout captured by gillnets over five nights of netting as a function of fish size (Biro *et al.* 2003a). We then used the size- and strain-specific probability of recapture from the October marked fish to modify the existing vulnerability equation by forcing it through the data point for each strain yielding a unique equation for each strain

and in each lake. To do this, we modified the exponent that controls the rate at which gillnet vulnerability reaches an asymptote (see Biro *et al.* 2003a). It is possible to obtain survivorship values greater than unity when applying such correction factors to the total catch (Post *et al.* 1999), but this bias will not affect conclusions drawn from estimates among experimental treatments. Growth rate was expressed as the vulnerability corrected autumn mean mass.

All analyses were conducted with general linear models using type III sums of squares tests of significance. Analyses of catch rates of all trout, and proportions of domestic trout caught, were done as repeated measures (day and dusk samples for a given lake) on log (standardized catch rate +1) and arcsine-square root transformed data ($n = 7$ lakes total), respectively. Each lake represented a single datum in the analyses of growth and survival, which was expressed as the percentage difference relative to the domestic strain within each lake ($n = 6$ lakes total; BP3 experienced a ‘summerkill’ in late September killing nearly all fish and was therefore omitted from this analysis). Analyses of differences in growth and survival between strains in each lake were on the raw data assuming normal errors as they varied both positive and negative. By examining differences in performance between the two phenotypes within a single lake, we were able to control for biotic and abiotic variation among lakes and conduct a more powerful experiment.

Results

INTRINSIC GROWTH RATE DIFFERENCES IN THE LABORATORY

Domestic trout consumed more food due to elevated appetite and consequently had significantly greater growth than wild trout when raised in the laboratory and fed to excess. Domestic trout consumed 4.32 kg of feed and gained a total of 4.60 kg of biomass (conversion rate = 1.06), whereas the wild trout only consumed 1.81 kg of feed and gained a total of 1.48 kg of biomass (CR = 0.81). Domestic trout were substantially longer (122 vs. 92 mm: $F_{1,276} = 412$, $P < 0.0001$) and more than three-times as heavy as wild trout by the end of October (26.0 vs. 8.5 g: $P < 0.0001$).

PATTERNS OF ACTIVITY AND HABITAT USE IN THE FIELD

Catch rates for all trout (domestic and wild) were substantially higher in lakes without predators than in lakes with predators (predator effect: $F_{1,30} = 10.9$, $P < 0.003$; Fig. 1a). Trout were also more frequently caught at dusk than during daytime (time effect: $F_{1,30} = 4.6$, $P < 0.05$; Fig. 1b). Catch rates of trout were similar among habitats in lakes without predators, with greatest catch rates in the pelagic habitat, whereas trout in lakes with predators avoided deep and pelagic habitats

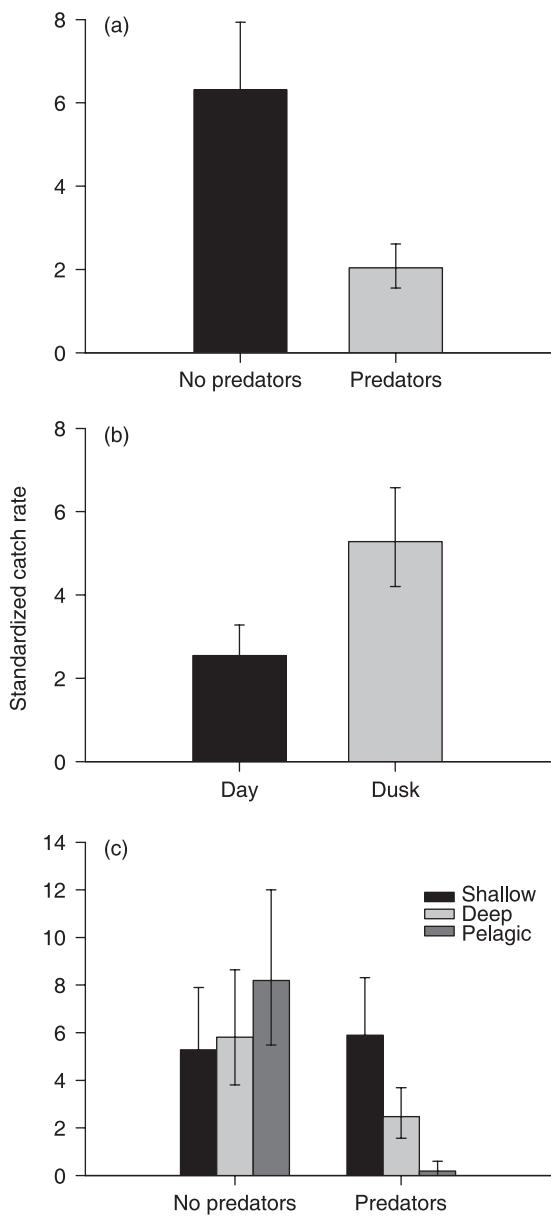


Fig. 1. Standardized catch rate ($\text{no fish net}^{-1} \text{ha}^{-1} \text{h}^{-1}$) of all trout in relation to (a) the presence or absence of predators, (b) time of day, and (c) habitat and predator presence (i.e. habitat \times predation interaction). Least-squares means ($\pm \text{SE}$) are shown for back-transformed data.

(predator \times habitat interaction: $F_{2,30} = 5.6$, $P < 0.01$; Fig. 1c). In fact, there was no daytime use of the pelagic habitat by trout in any lake with predators, and only a few fish were caught at dusk in two lakes (Fig. 1c). Remaining main and interaction effects had no effect on trout catch rates (all $P > 0.1$).

Domestic trout made up the majority of the catch, ranging from 75% in the presence of predators to 90% in their absence (predator effect: $F_{2,30} = 8.9$, $P < 0.01$; Fig. 2a). Domestic trout also made up a larger proportion of the catch during daytime than at dusk, although this effect was marginally significant (time effect: $F_{1,30} = 3.7$, $P = 0.06$; Fig. 2b). The proportion of domestic trout in the catch increased as a function of depth, with domestic trout making up just under 70% of the catch

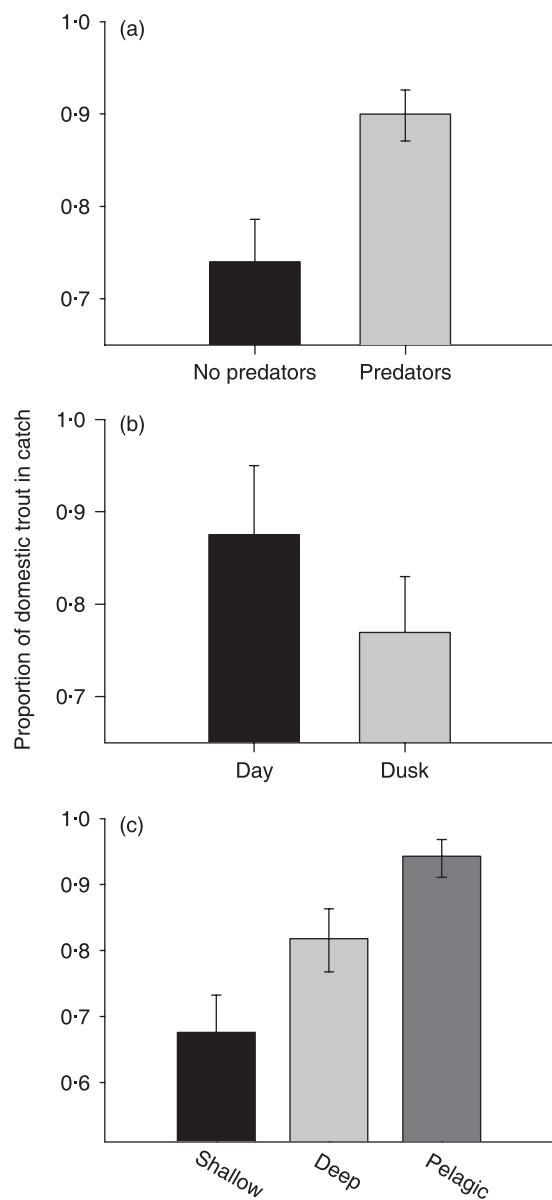


Fig. 2. Proportion of domestic trout in the catch in relation to (a) the presence or absence of predators, (b) time of day, and (c) habitat. Least-squares means ($\pm \text{SE}$) are shown for back-transformed data.

in shallow habitats and 95% in the pelagic habitat (habitat effect: $F_{2,30} = 10.2$, $P < 0.0005$; Fig. 1c). Therefore, the few fish captured in dangerous deep and pelagic habitats in the presence of predators (Fig. 1c) were overwhelmingly comprised of domestic trout (Fig. 2c). The remaining main and interaction effects had no effect on the proportion of domestic trout caught (all $P > 0.1$).

GROWTH AND SURVIVAL IN THE FIELD

Higher catch rates in deep and pelagic habitats by domestic trout was linked to faster growth than wild trout in all lakes, but this more risky foraging effort resulted in lower survival when predators were present (Fig. 3). Therefore, higher intrinsic growth rates in

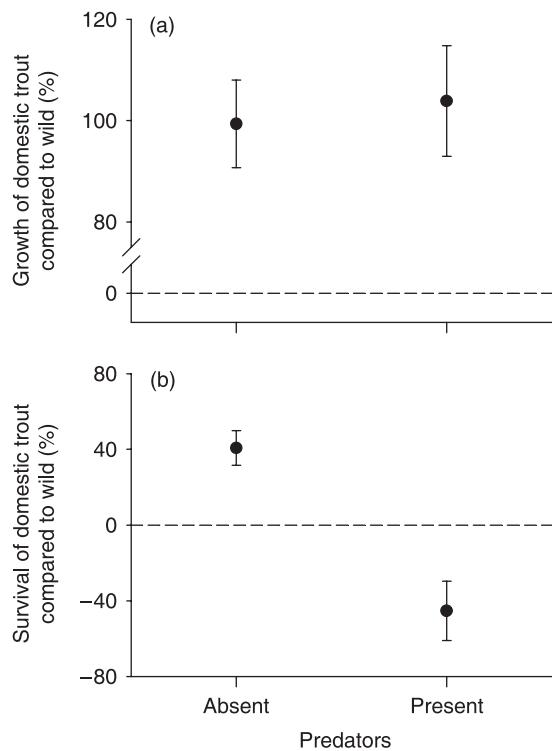


Fig. 3. Differences in (a) growth and (b) survival between domestic and wild trout. Per cent differences were calculated as $(\text{domestic} - \text{wild})/\text{wild} \times 100$. Dashed lines in each represent no difference between strains.

domestic trout was only costly in the presence of predators. The presence of predators had no effect on growth differences between domestic and wild trout ($F_{1,4} = 0.07, P > 0.8$), with domestic trout always growing faster and achieving autumn mean masses twice that of wild trout (Fig. 3a). Survival consequences for higher growth rates in domestic trout depended upon variation in predator abundance. Survival of domestic trout was significantly higher than wild trout in the absence of predators, but significantly lower in their presence ($F_{1,4} = 12.7, P < 0.025, R^2 = 0.75$; Fig. 3b).

Discussion

In the laboratory, we demonstrated genetically based differences in maximum intrinsic growth rates between the strains of trout we used. Growth rate of domestic trout (in terms of mass) was three times greater than the wild strain, and was achieved by greater appetite and consumption capability. Greater appetite should then, in turn, lead to greater use of deeper habitats (risky, but with abundant food) by domestic trout in nature when food is limiting. Indeed, domestic trout used deep and pelagic habitats more than wild trout, although both strains avoided these habitats in the presence of predators. As a consequence of greater use of food-rich habitats, domestic trout achieved growth rates about twice that of the wild strain in each lake. However, greater use of risky habitats by domestic trout to achieve high growth was associated with greater predation mortality

in the presence of predators, such that domestic survival was about half that of the wild strain. In addition, relative catch rates of domestic trout were higher in general, and if gillnet catch rates are proportional to swimming activity (see Methods), then we have indirect evidence for greater growth associated with foraging activity. Taken together, these results provide evidence that behaviourally mediated trade-offs between growth and mortality rates is a mechanism that selects against maximal growth, and contributes to the evolution of submaximal average growth rates in animal populations. It seems unlikely that domestic trout simply grew fast and had no capacity to avoid predators as they did respond in the appropriate way to predator presence by moving to safer shallow habitats, particularly during daytime when risk is highest. To our knowledge, this study is one of only three to directly examine behaviourally mediated costs of rapid growth (Biro *et al.* 2004a; Stoks *et al.* 2005), and the only to successfully demonstrate it in a vertebrate species since Biro *et al.* (2004a) did not show a growth benefit for domestic trout when in the absence of predators.

Our results call into question the fairly widespread acceptance that fast growth necessarily confers fitness advantages (see Introduction). Faster growth did provide a +40% survival advantage to the domestic trout when there were no predators. However, faster growth in the domestic strain led to a 40% survival disadvantage in the presence of predators. Therefore, if the decline in growth advantage is due entirely to enhanced risky foraging by the domestic strain then this would indicate a 80% disadvantage to faster growth in the domestic trout when predators are present. Therefore, maximal growth rates may not persist in nature where predators are normally present given the trade-offs demonstrated here. This indicates that faster growth should not be viewed as universally being better, and that ecologists might pay greater attention to the process that leads to faster growth (foraging behaviour) and its consequences under risk of predation. Our results differ from our previous work with older trout, which showed that both strains of age-1 trout grew equally well when predators were absent, but domestic trout did grow faster when predators were present (Biro *et al.* 2004a). Therefore, our previous work was equivocal in terms of understanding evolution of growth rate as domestic trout did not grow faster than wild trout in all situations as expected. We have no explanation for the disparate results between the studies.

Although selection against maximal growth rates in domestic age-0 trout provides an explanation for its absence in nature, it is one of several life stages where selection on growth occurs. For instance, those relatively few domestic trout that do survive their first year are likely to have an overwinter survival advantage owing to their large body size (Biro *et al.* 2004b), thus favouring evolution of rapid growth. However, the following growing season the faster growing domestic trout is again selected against (also 50% lower survival) when

in the presence of piscivorous bird predators (Biro *et al.* 2004a), but those surviving avian predation may subsequently have a size-based reproductive advantage. Clearly, to understand fully evolution of intrinsic growth rate requires directly estimating relative survivorship at several life stages and also quantifying reproductive success. It will also require understanding the context dependence of the processes we have quantified here, such as how rapid growth phenotypes are selected upon as a continuous function of risk, food and conspecific density. This is no easy task, but the results from this study and others that measure the various components contributing to overall success of the different strains will shed light on this issue, and also have implications for the likelihood of invasion of wild populations by domesticated salmonid fishes that escape from open net-cage aquaculture operations. For instance, natural water bodies may be susceptible to invasion where human disturbance and overfishing have dramatically reduced predator abundance, such as for many commercially exploited fish species, which are major predators but are severely depleted (Christensen *et al.* 2003).

Consideration of all the components affecting survival and ultimately reproductive fitness can also yield insight into the persistence of growth variation in wild strains. For instance, it is possible that a fairly wide range of growth rates produces similar lifetime fitness (Mangel & Stamps 2001). So, while predation may keep the average growth rate low, variation in growth rate may allow adaptive evolution of growth as predation and/or environmental conditions change. Indeed, we observed no survival cost for the fast growing phenotype in the absence of predators, and in fact they had survival rates greater than the wild phenotype. Therefore, phenotypes with a rapid growth rate in a population would be able to take advantage of times or situations where predators are few to grow rapidly to a large size. This may explain why some wild individuals grow at rates similar to a domesticated phenotype (unpublished data), and contribute to high variation in intrinsic growth rates in salmonid fishes from which domestic strains were developed (e.g. Gjedrem 2000).

Based on our results, we suggest that risk-taking behaviour may be the major determinant of predation mortality, and therefore the major mechanism for selection against maximum growth rates. Although we cannot reject the possibility that reduced escape performance is also a factor (e.g. Lankford *et al.* 2001), it seems unlikely to be a major factor for two reasons. First, we controlled for body size initially and second, previous work has shown rapid nonlinear increases in survival with increasing body size for young trout in our lakes (Parkinson, Post & Cox 2004). So, despite rapidly declining size-based vulnerability to predation, domestic trout experienced higher mortality and this was linked to more risky foraging behaviour. Previous studies have shown clear mortality costs associated with high intrinsic growth rate in the presence of predators, but none could distinguish between behaviourally

related vulnerability and escape-related vulnerability (Gotthard 2000; Lankford *et al.* 2001; Olsson & Shine 2002; Munch & Conover 2003; Sundstrom *et al.* 2004; but see Stoks *et al.* 2005).

The fact that domestic trout achieved growth rates two times greater than wild trout across all situations likely reflects greater growth hormone levels in domestic trout that stimulate appetite and physiology to allow greater consumption and growth (Johnsson *et al.* 1996; Abrahams & Sutterlin 1999; Fleming *et al.* 2002; this study). Thus, while domestic and wild trout both responded in an appropriate way to the presence of predators, domestic trout accepted greater risks while foraging to achieve higher growth rate. In other words, their behaviour was not completely flexible in the presence of predators and the elevated appetite in domestic trout encourages individuals to accept risk (see also Biro *et al.* 2004a). Perhaps selection, by removing individuals that are more active and use risky habitats, indirectly selects for appetite suppression in a population.

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