



# Direct manipulation of behaviour reveals a mechanism for variation in growth and mortality among prey populations

PETER A. BIRO\*, MARK V. ABRAHAMS† & JOHN R. POST‡

\*Department of Environmental Science, University of Technology

†Department of Zoology, University of Manitoba

‡Department of Biological Sciences, University of Calgary

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Understanding the relation between behavioural processes and their population- or community-level consequences is fundamental to developing a mechanistic understanding of ecosystems. Rarely are such links made, particularly outside the laboratory, and rarely is behaviour manipulated directly through genetic or hormonal manipulation. The area that provides the greatest promise is the relation between foraging behaviour and its subsequent growth and survival consequences. In whole-lake experiments, we used domestic and wild strains of rainbow trout, *Oncorhynchus mykiss*, differing in intrinsic activity and anti-predator behaviours in the laboratory, to determine whether differences in activity and habitat use between strains exist in the field and could provide a behavioural mechanism for previous studies showing a trade-off between growth and survival. Domestic trout made up the majority of gill net catches (greater overall activity), particularly in deep and pelagic habitats that had abundant food but offered little or no physical habitat structure to escape from predation. Thus, greater activity rates (inferred) and use of risky habitats (directly observed) by domestic trout provides a behaviourally mediated mechanism for previous large-scale studies showing trade-offs between growth and mortality.

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The behaviour of individuals at risk of predation may be key to understanding within- and among-population variation in growth and survival of prey populations, although few empirical studies exist that have made convincing connections between behaviour and variation in growth or survival at a population or community level (Lima 1998; but see Schmitz 1998; Biro et al. 2003a, b). Reasons why convincing links have not been made include the use of indirect manipulations of behaviour (Anholt 1997), short-term/small-scale experiments that are likely to overestimate the importance of behavioural

variation (Sutherland 1996; Lima 1998; Schmitz 2001), and experiments that do not have sufficient realism to allow results to be extrapolated to natural situations (e.g. Lima & Zollner 1996; Sutherland 1996; Fryxell & Lundberg 1997; Lima 1998) or allow expression of compensatory behaviours that could mitigate effects of predation risk (Lind & Cresswell 2005).

Large-scale field experiments suggest that the trade-off between growth and mortality rates, mediated by behaviour, may be a key mechanism generating variation in growth and particularly survival among prey populations (Biro et al. 2003a, b, c, 2005). However, those studies indirectly manipulated behaviour by altering predator presence, changing food levels and varying conspecific density to create variation in behaviours affecting growth and predation. Therefore, the direct contribution of behavioural variation to survival may have been overestimated. To overcome such limitations, one must directly manipulate behaviour within a species using daylength,

*Correspondence:* P. A. Biro, Department of Environmental Science, University of Technology Sydney (UTS), Box 123, Broadway NSW, Australia (email: [peter.biro@uts.edu.au](mailto:peter.biro@uts.edu.au)). M. V. Abrahams is at the Department of Zoology, University of Manitoba, Winnipeg MB R3T 2N2, Canada. J. R. Post is at the Department of Biological Sciences, University of Calgary, 2500 University Drive NW, Calgary AB T2N 1N4, Canada.

hormonal or genetic manipulations (Anholt 1997). For instance, domestication and increases in growth hormone (GH) in trout and salmon (salmonids) have resulted in genotypes and phenotypes that are behaviourally distinct, displaying greater activity rates and increased willingness to feed when at risk of predation, elevated appetite and greater growth (e.g. Johnsson et al. 1996; Gross 1998; Abrahams & Sutterlin 1999). Sundstrom et al. (2004) and Biro et al. (2004) took advantage of these manipulations to show a trade-off between growth and mortality rates (greater growth at a high mortality cost) for GH-transgenic and domestic types, relative to wild types, in seminatural stream channels and whole-lake experiments, respectively. Whether the growth–mortality trade-off was mediated by behaviour was unclear, however, because Sundstrom et al. (2004) did not quantify behaviour and Biro et al. (2004) assumed that greater use of the open-water pelagic habitat was the principal cause of the trade-off. Although numerous studies have reported trade-offs between growth and mortality, with some identifying behaviour as the mechanism (reviewed in Lima 1998), no direct manipulation of behaviour conducted at large scales under realistic conditions yet exists.

We manipulated behaviour directly by using two genotypes of rainbow trout, *Oncorhynchus mykiss* (domestic and wild), known to differ in their foraging and anti-predator behaviour, and introduced these genotypes into five small lakes differing in predator presence. The aim was to determine whether the genotype-specific patterns of growth and mortality identified by Biro et al. (2004) were linked to corresponding differences in spatial and temporal risk-taking behaviour in terms of overall swimming activity and habitat use not presented in that study. We predicted that domestic trout would display higher overall activity rates than wild trout in the presence of predators, as shown in previous laboratory studies (e.g. Johnsson & Abrahams 1991). This greater activity in search of food should increase encounter rates and susceptibility to predators and lead directly to greater predation mortality (Werner & Anholt 1993; Anholt & Werner 1998; Biro et al. 2003b, c), particularly during daylight hours when fish are most vulnerable to visual predators. In addition, we predicted that domestic trout would use deep and pelagic habitats more than wild trout to access more abundant food there. Habitats used by trout are ranked in terms of plankton food abundance (their primary food item): pelagic > deep > shallow (Post et al. 1999; Biro et al. 2003a). However, pelagic habitats provide no habitat complexity from which to escape predation, deep habitats provide some, and shallow habitats provide abundant macrophytes and woody debris (Post et al. 1998, 1999; Biro et al. 2003a, b). Therefore, greater growth and higher predation mortality previously observed for the domestic trout strain (Biro et al. 2004; Sundstrom et al. 2004) should result from greater activity rates in combination with the use of productive but risky habitats by the domestic phenotype. If so, then this direct manipulation of behaviour would provide compelling evidence that the trade-off between growth and mortality is mediated by behaviour, and that this mechanism can

explain variation in growth and mortality among prey populations.

## METHODS

Trout were stocked on 6 June 2003 into five small experimental lakes (1.5–4 ha) located in British Columbia, Canada. Characteristics of the lakes used (K1, K2, B2, B3 and CP1) are described in detail in Biro et al. (2003a). The lakes contained no natural fish populations and were closed to fishing. Although small, these lakes have all the features of much larger lakes, and fish display normal feeding and antipredator behaviours (Post et al. 1998; Biro et al. 2003a). Domestic and wild strains of rainbow trout were obtained from the Fraser Valley Trout Hatchery, FVTH (Abbotsford, British Columbia), reared to a common average length (mean length = 15 cm) under identical conditions. The wild strain was reared from eggs and milt collected from a nearby wild trout population. The domestic strain resided entirely within the hatchery system and originated from a stock in California, U.S.A., that was widely distributed across North America (K. Scheer, FVTH, personal communication). Because the two strains were reared identically, variation in growth and survival rates should be driven primarily by genetic variation between the two strains (Johnsson & Abrahams 1991). The adipose fin (a vestigial fin) was clipped on wild fish to distinguish between strains. Each strain was stocked at a rate of 165 trout/ha into each lake. The only significant predator of small adult-sized trout in the lakes is the common loon, *Gavia immer*, a visual predator that frequently consumes about 50% of the trout population (Beckmann et al. 2006). Lakes B2 and B3 have never had loons present and so represented our zero risk treatment. Loons are absent from these lakes because the lakes are small and densely forested to the water's edge, making take-off and landing by loons impossible (Beckmann et al. 2006). The remaining lakes had frequent loon visits throughout the summer with one to two loons present (more details in Biro et al. 2004).

We used experimental gill nets set in different habitats to directly assess habitat use by trout in each lake, and we inferred trout activity rates from gill net catch rates (see below). Each gill net had seven panels of graded, stretched-mesh monofilament, ranging from 2.5 to 8.75 cm, creating a 105-m-long gang of gill net. Sinking gill nets (2.3 m deep) were set along the 2-m and 4-m depth contours to assess the use of shallow and deep habitats by trout. A single floating gill net (6 m deep) was set along the centre of the lake, at the surface, to assess the use of the open-water pelagic habitat. All three nets were set within 5 min of each other and in parallel. Netting duration ranged from 0.5 h in predator-free lakes, where catch rates were high and lake size was small, to 2 h in the largest predator lakes, where catch rates were low during daytime. Daytime gillnetting was conducted between 1000 and 1500 hours, and dusk nets were set 0.5 h before sunset for a total duration of 1 h. We conducted a single netting trial to minimize killing fish that were needed to assess relative growth survival of each strain (Biro et al.

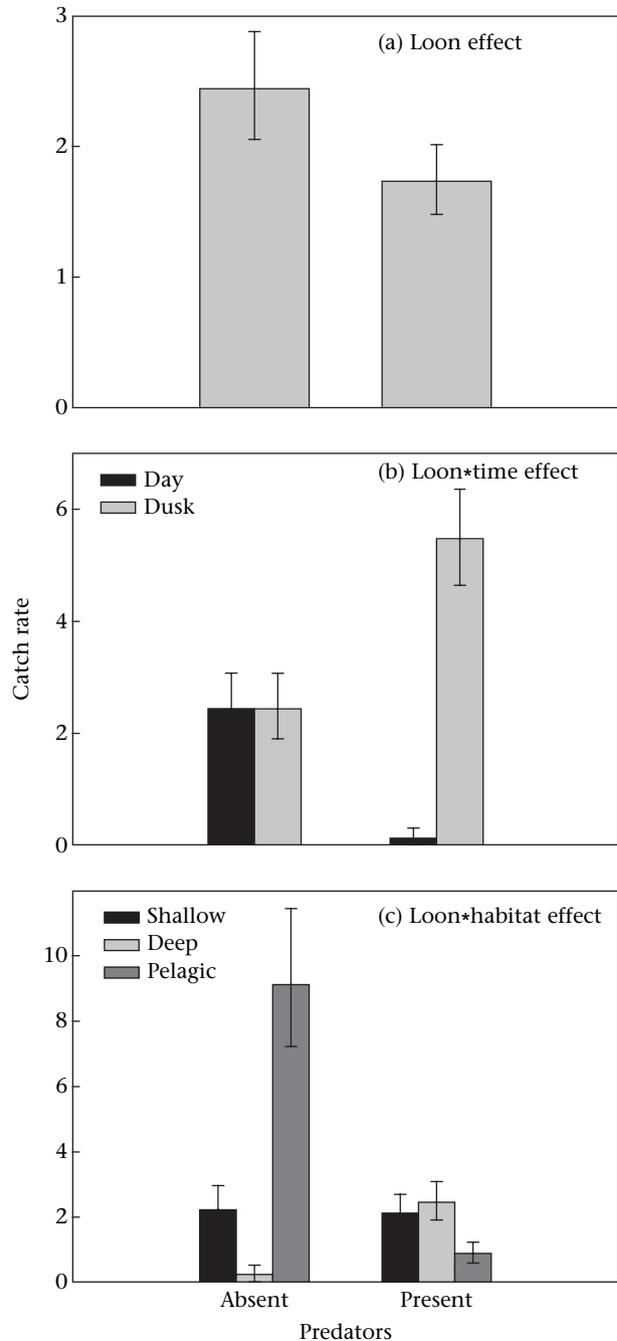
2004). Following removal from the nets, fish were placed in a large aerated recovery container to ensure that injured fish were not returned to the lake. Those that were bleeding or did not recover (i.e. not swimming and breathing normally) were euthanized with an overdose of the anaesthetic MS-222. Catch rates were standardized according to the area of gill net set per unit lake area and netting duration. Netting was done within 2 weeks of stocking, allowing fish enough time to acclimate, but making it unlikely that significant differences in density were due to predation. If significant mortality did occur within this period, it would be biased towards the domestic strain (Biro et al. 2004) and reduce catch rates of domestic trout, making our results conservative. Therefore, differences in catch rates should represent differential activity rates, given the equal stocking densities of each strain and the mathematical fact that fish encounter rate or catch rate is likely to be proportional to activity rate when using stationary sampling gear such as gill nets.

Analyses were conducted with general linear models, using type III sums of squares tests for the significance of effects. Analyses of total catch rates (domestic and wild) and proportions of domestic trout caught were done as repeated measures (day versus dusk samples within a lake) on log-(standardized catch rate +1) and sin-/(square-root (proportion of domestic trout in catch)) transformed data. Each lake represented a single datum. We tested for all main effects (predator presence, time of day and habitat) and all possible interactions in the statistical model, but we were mainly interested in interaction effects, including predator presence. Examining the proportion of domestic trout in the raw catch in each lake, by time of day and habitat, allowed us to control for differences between lakes that might affect activity and habitat use such as food abundance.

## RESULTS

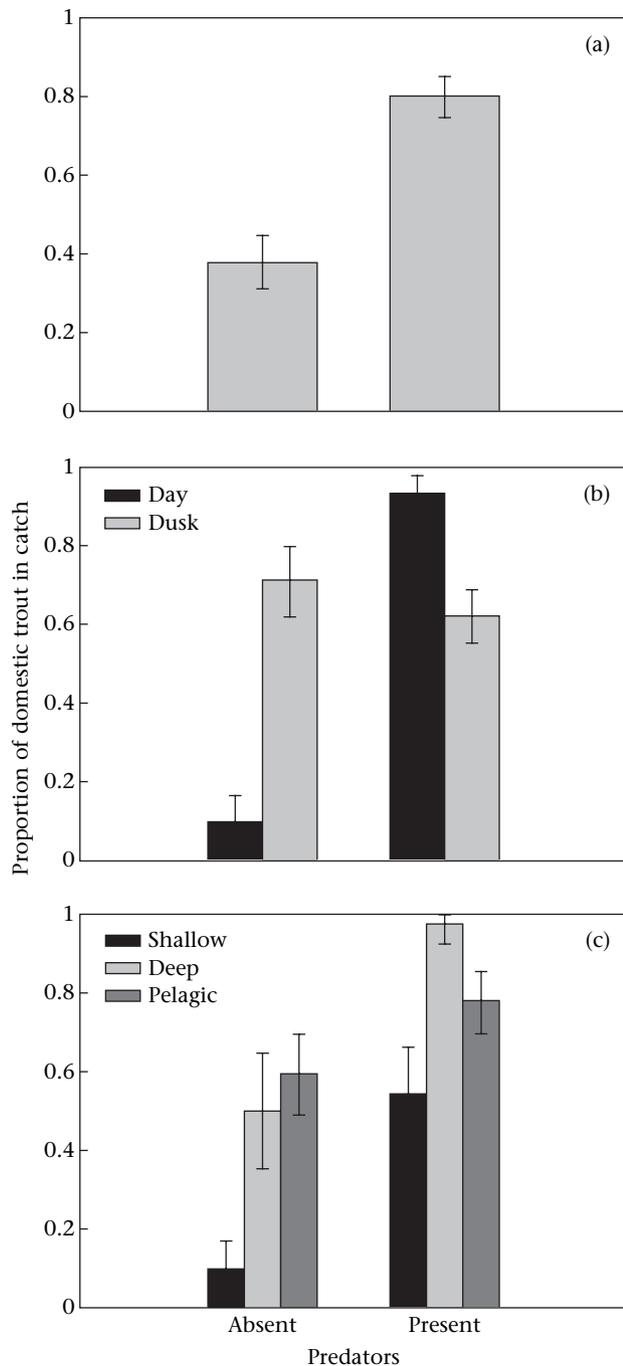
The catch rate of all trout, domestic and wild, was lower in the presence of predators than in the absence of predators, but this effect was not significant (predator effect:  $F_{1,18} = 2.2$ ,  $P = 0.1$ ; Fig. 1a). More importantly, predator presence differentially affected catch rates of trout during day and dusk (Fig. 1b). Catch rates during day and dusk did not differ in the absence of predators, but was very low during daytime and very high at dusk in the presence of predators (predator \* time interaction:  $F_{1,18} = 31$ ,  $P < 0.0001$ ; Fig. 1b). Predator presence also affected habitat use by trout (Fig. 1c). In the absence of predators, trout were caught primarily in the pelagic habitat and at high rates, whereas in the presence of predators, catch rates were lower and skewed towards shallow and deep littoral habitats (predator \* habitat interaction:  $F_{2,18} = 26$ ,  $P < 0.0001$ ; Fig. 1c). There was no three-way interaction between predator presence, time of day and habitat ( $P = 0.8$ ).

In the presence of predators, domestic trout made up the great majority of the catch; in the absence of predators, domestic trout made up a slight minority of the catch (predator effect:  $F_{1,11} = 22$ ,  $P < 0.001$ ; Fig. 2a). Predator presence also differentially affected the



**Figure 1.** Standardized catch rate of all trout combined, domestic and wild genotypes, in relation to the presence or absence of loons, time of day and habitat. Shown are significant effects of (a) predator presence, and interactions between predator presence and (b) time of day and (c) habitat. Back-transformed least-squares means ( $\pm$ SE) are shown.

proportion of domestic trout in the catch in day versus dusk samples, and across habitats (Fig. 2b, c). In the presence of predators, almost all fish caught during daytime were domestic trout, with numbers declining slightly at dusk; in the absence of predators, the pattern reversed (predator \* time interaction:  $F_{1,11} = 28$ ,  $P < 0.0005$ ; Fig. 2b). Domestic and wild trout were caught in similar numbers



**Figure 2.** Proportion of the total catch of trout that were domestic in relation to (a) the presence or absence of predators, (b) time of day and (c) habitat. Back-transformed least-squares means ( $\pm$ SE) are shown.

in deep and pelagic habitats in the absence of predators, with few domestic trout in the shallow habitat; in contrast, domestic trout made up the majority of the catch in deep and pelagic habitats, with an equal mix of both strains in the shallow habitat (predator  $\times$  habitat interaction:  $F_{2,11} = 3.9$ ,  $P = 0.05$ ; Fig. 2c). There was no three-way interaction between predator presence, time of day and habitat ( $P = 0.8$ ).

## DISCUSSION

The aim of this study was to determine, by way of a direct behaviour manipulation, whether the trade-off between growth and mortality is mediated by behaviour in realistic large-scale experiments. In a previous field study, the domestic trout genotype showed greater growth but decreased survival compared to a wild type in the presence of predators (Biro et al. 2004). The present study focused on the mechanistic basis for those growth and survival differences by examining in detail the spatial and temporal variation in activity rates and habitat use of the two trout genotypes. Several observations indicate that predation risk is a function of overall activity, habitat use and time of day, and that domestic trout accept greater risk in terms of all these behavioural measures, as predicted from smaller-scale experiments (see Introduction). First, both domestic and wild trout responded to the presence of predators by reducing activity rates to low levels during daytime, and dramatically increasing activity at dusk, as inferred from gill net catch rates. Second, trout avoided deep and pelagic habitats during the daytime in the presence of predators, but used the pelagic habitat (where food was most abundant) most in the absence of predators. Low daytime activity rates and avoidance of deep and pelagic habitats, which have little habitat complexity, are consistent with trout avoiding visual predators during daytime. Third, the low catch rates of trout in deep and pelagic habitats during daytime when predators were present were nearly all domestic trout. In fact, domestic trout made up 80% of the overall catch, and more than 50% of the catch in most combinations of habitat and time of day when in the presence of predators, suggesting that overall activity rates of domestic trout within lakes were higher than those of wild trout. It should follow, then, that greater overall activity and greater daytime use of deep and pelagic habitats by the domestic genotype should lead to greater growth (given sufficient food) but higher predation mortality. Indeed, domestic trout do experience higher growth and significantly greater mortality in the presence of predators (Biro et al. 2004). Together, these results suggest that behaviourally mediated trade-offs between growth and mortality rates, at the individual level, scale up over large spatial and temporal scales to directly contribute to variation in growth and survival at the population level.

Theory and laboratory studies show that food-dependent foraging behaviour by prey can determine variation in growth and survival (e.g. Werner & Anholt 1993; Anholt & Werner 1998). More recently, whole-lake experiments have similarly shown that food- and density-dependent foraging activity and habitat use leads to higher predation mortality (Biro et al. 2003a, b). However, all of these studies indirectly manipulated prey-foraging effort by altering food levels, predator density and prey density. Therefore, it is always possible that the manipulations designed to manipulate prey behaviour may themselves confound (at least in part) the apparent link between behaviour, growth and survival. For example, although augmenting food levels by fertilizing lakes reduces activity and mortality in prey fish populations (Biro et al. 2003a),

the omnivorous predators may consume fewer prey fish only because of greater overall food abundance. Therefore, the direct contribution of behavioural variation to mortality may have been overestimated. In the present study, we overcame such limitations by directly manipulating the behaviour of our study species and contrasting spatial and temporal activity and habitat use responses to predation within single lakes. As [Anholt \(1997\)](#) pointed out, the key to establishing links between behaviour and population dynamics is to make convincing manipulations of behaviour, and then to examine the effect of that behavioural variation on birth and death rates, and/or individual growth rates known to affect those rates. We also suggest that another key component to making those linkages is by conducting experiments at realistic spatial and temporal scales. Our study represents, to our knowledge, the only replicated whole-system study to document spatial and temporal variation in activity and habitat use of prey in response to predation, and to do so with direct behavioural manipulation using two behavioural genotypes. As such, it provides a valuable test of theory and confirmation of results obtained from smaller-scale and shorter experiments (see below). It also provides evidence for a behavioural mechanism that can mediate the often-observed trade-off between growth and mortality (reviewed in [Lima 1998](#)). Large-scale and long-term experiments prevent overestimation of behavioural effects that may be common to small-scale experiments, because they allow full expression of predator and prey behaviours (reviewed in [Lima 1998](#)), including those that may compensate for behaviours with negative consequences ('compensatory behaviour'; [Lind & Cresswell 2005](#)).

Our results were consistent with those from controlled laboratory studies showing greater foraging effort and decreased antipredator behaviour by domestic trout (e.g. [Johnsson & Abrahams 1991](#)). Our results also confirm the behavioural mechanism suggested by previous large-scale studies showing a mortality cost to rapid growth between different behavioural genotypes ([Sundstrom et al. 2004](#); [Biro et al. 2004](#)). Variation in the behaviour of salmonid fish by means of artificial selection or hormone manipulation appears to be similar, but less pronounced, than the variation observed naturally within and among populations in nature. Indeed, there are many examples in the literature of consistent and genetically based differences in behaviour between individuals from within and among populations, and these differences are likely to have consequences for growth and survival (reviewed in [Sih et al. 2004](#)). The proximate basis for greater activity, reduced antipredator behaviour and greater aggression in domestic trout and salmon appears to be elevated growth hormone (GH), which seems to stimulate appetite and metabolism. This in turn results in increased levels of behaviours that serve to increase food intake rate, such as greater activity and aggression, and to decrease antipredator behaviour (e.g. [Johnsson et al. 1996](#); [Fleming et al. 2002](#)). Thus, evolution of behavioural types may be linked to evolution of growth rate. If so, this relation would affect how we think about the relative roles of behaviour and life-history evolution in populations and community dynamics.

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