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ARTICLES

Behavioural syndromes in brook charr, *Salvelinus fontinalis*: prey-search in the field corresponds with space use in novel laboratory situations

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Recently emerged brook charr foraging in still-water pools along the sides of streams tend to be either sedentary, feeding from the lower portion of the water column (a sit-and-wait tactic) near the stream bank, or very active, feeding from the upper portion of the water column (an active search tactic) away from the bank. We tested whether the search tactics used by charr in the field represent behavioural syndromes related to activity and space use. After quantifying the behaviour of fish in the field, focal individuals were captured and their behaviour quantified in novel environment experiments in the laboratory. In an aquarium, individuals that used an active search tactic in the field spent a higher proportion of time moving, spent less time near the aquarium bottom, and took less time to find their way out of an erect glass jar, on average, than did individuals that used a sit-and-wait tactic in the field. When presented with near-bank and open-water conditions over 6 days in the laboratory, individuals that used an active search tactic in the field remained active and altered their activity less, on average, than individuals that used a sit-and-wait tactic in the field. Immediate responses to a pebble dropped in the aquarium (simulated risk from above) were not correlated with field behaviour. The search tactics used by brook charr in the field reflect part of a behavioural syndrome related to general activity and space use, but not to startle responses. These initial, individual differences in behaviour provide important raw material for the initial stages of resource polymorphism.

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Key words: activity; brook charr; brook trout; foraging tactic; individual difference; personality; resource polymorphism; *Salvelinus fontinalis*; space use; startle response

Over the past decade, several prominent reviews have emphasized that individuals within a population can differ markedly in their behaviour (e.g. Boissy 1995; Bolnick et al. 2003; Sih et al. 2004). These behavioural differences can reflect diversity beyond that expected based on differences in body size or sex. Understanding the proximate mechanisms and ecological and evolutionary consequences of such differences represents an important research need. The individual differences challenge widely encountered notions that

behaviour is infinitely flexible, that individual differences in behaviour represent nonadaptive variation around a single optimal phenotype, and that individuals can be treated as ecologically equivalent in models of population dynamics and food webs (Bolnick et al. 2003; Dall et al. 2004; Sih et al. 2004). Individual differences in behaviour can reflect underlying genetic differences (Dingemanse et al. 2002, 2003) and provide the raw material upon which natural selection can act (Réale & Festa-Bianchet 2003). Such variation in behaviour may facilitate divergence in other phenotypic characters, such as morphology (Robinson & Wilson 1994; Imre et al. 2002), and even be involved in rapid speciation (Bolnick et al. 2003).

The emerging framework of behavioural syndromes provides a formal, integrative method for characterizing

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individual variation in behaviour, as well as uncovering processes responsible for that variation. Behavioural syndromes are suites of correlated behaviours reflecting among-individual consistency across different environmental situations (Sih et al. 2004). They are also referred to as personalities or coping styles (Dingemanse & Reale 2005). Examples have been studied extensively from a psychological perspective in humans and psychological and physiological perspectives in a restricted set of laboratory and domesticated animals (Koolhaas et al. 1999; Gosling 2001; Sih et al. 2004 and references therein). One example receiving attention in fish is the distinction between bold and shy individuals (Wilson et al. 1993; Sneddon 2003; Wilson & Stevens 2005). Bold individuals act normally or become actively exploratory when confronted with a novel object or environment whereas shy individuals retreat or become vigilant when confronted with the same situation (Wilson et al. 1993). Boldness may also be linked to other ecologically relevant aspects of behaviour including learning (Dugatkin & Alfieri 2003), aggression (Sundström et al. 2004), activity (Sneddon 2003), dispersal (Fraser et al. 2001), foraging, and propensity to take risks (Wilson & Stevens 2005). Broader examination of wild animals and broader application of behavioural syndromes in other disciplinary contexts are needed to rigorously assess whether the framework of behavioural syndromes is valuable and meaningful from ecological and evolutionary perspectives (Sih et al. 2004).

In this study, we apply the framework of behavioural syndromes in a novel way to help understand the role of behaviour during the initial stages of resource polymorphisms. Resource polymorphism refers to the tendency for populations to diverge into distinct subpopulations differing in foraging behaviour, morphology, and life history (Skúlason & Smith 1995). Examples of resource polymorphisms have been reported from every class of vertebrate, but they are relatively common in populations of fish, including brook charr, occupying lakes with poor species diversity and well-defined benthic and limnetic niches (Robinson & Wilson 1994; Dynes et al. 1999). Resource polymorphisms are providing excellent opportunities to examine the roles that ecological and behavioural processes have in the divergence of phenotypes within populations and, possibly, the evolution of new species (Skúlason & Smith 1995). Earlier studies emphasized the diversifying roles of alternative, spatially separated prey or habitat types and intraspecific competition (Robinson et al. 1993; Schluter 1996; Bolnick 2004). However, whether any initial individual differences in behaviour might predispose individuals to encounter and exploit a specific prey or habitat type, and whether these predispositions can be reinforced by behavioural or ecological circumstances, has not been examined satisfactorily. Often, initial selection of prey or habitats is attributed to chance (Hutchings 1996; Price et al. 2003; Stamps 2003), or simply not considered, despite increasing recognition that early social and learning processes can influence later habitat preferences and life history trajectories (Metcalf et al. 1989; Metcalf 1993; Stamps 2001). In addition, earlier studies of resource polymorphism typically focused on populations showing well-defined morphotypes. Studies examining behavioural

differences in the absence of morphological differences are needed to improve our understanding of the mechanisms and conditions promoting behavioural specialization before its reinforcement by morphological differences (McLaughlin et al. 1999; Bolnick et al. 2003; Bolnick 2004).

This study tests whether behavioural differences showed by young brook charr foraging in still-water pools along the sides of streams reflect part of behavioural syndromes related to individual differences in space use and activity. At this life stage, the charr have just recently emerged from their gravel redds (nests) and begun feeding exogenously. This study system is being recognized as a model for testing preconceptions regarding the role of behaviour during early stages of resource polymorphism in fish (Skúlason et al. 1999; Rogers et al. 2002; Sacotte & Magnan 2006). The charr show broad variation in foraging behaviour that parallels the distinction made between benthic (near-shore) and limnetic (open-water) morphs in polymorphic lake populations of fish. Some charr tend to be sedentary, feeding on crustacean prey from the lower portion of the water column at the edges of pools near the bank (a sit-and-wait tactic). Other charr tend to be active, feeding on insect prey from the upper portion of the water column away from the stream bank (an active search tactic) (Grant & Noakes 1987a; McLaughlin et al. 1999). The frequencies of sedentary and active charr across pools suggest the tactics reflect adaptive responses to local environmental conditions (McLaughlin et al. 1994; McLaughlin 2001). The differences in foraging behaviour are independent of differences in body size or shape (McLaughlin et al. 1994), but prolonged differences in activity can induce developmental differences in the size and shape of the caudal (tail) fin (Imre et al. 2002). Field observations and experiments suggest that differences between sedentary and active individuals arise because of perceptual challenges associated with detecting and capturing the different prey types, because individuals switching tactics also switch where they focus their attention within the water column (McLaughlin & Grant 2001). The differences between individuals are not correlated with differences in swimming endurance (McLaughlin & Grant 2001).

We assessed whether the search tactics used by recently emerged brook charr in the field represent behavioural syndromes by quantifying the activity of individuals in the field, capturing them, transporting them to the laboratory, and measuring their activity, water column use, and response to simulated risk from above in novel environment situations. We first tested whether charr that were active while searching for prey in the field would take less time to escape from an erect glass jar placed in an aquarium (experiment 1), and spend more time moving and more time in the upper part of the water column in a novel aquarium environment (experiment 2), relative to charr that were sedentary while searching for prey in the field. We then tested whether charr that were active in the field would show more active escape behaviours in response to a simulated risk from above than would charr that were sedentary in the field (experiment 3). Lastly, we tested whether the behavioural differences among charr reflected inflexible differences in activity, flexible individual predispositions in activity, or flexible behaviour in the absence of predispositions in activity by quantifying the activity of sedentary and

active charr held in near-bank and open-water type conditions intended to discourage and encourage movement, respectively.

METHODS

Field Observations

Between 5 April and 16 May 2004, we observed and captured 89 young-of-the-year (YOY) brook charr (fork length: 2.0–3.0 cm; weight: 0.050–0.300 g) from the west branch of the Credit River (mean water temperature: $\sim 10^{\circ}\text{C}$) in Erin Township, Ontario. Observations were made from seven still-water pools (surface area: ~ 1.0 – 1.5 m^2) along a 1-km stretch of river and took place between 0900 and 1200 hours (Eastern Standard Time).

For a given observation period, an observer arrived at a pool and, while sitting at the edge of the stream, watched the fish for 5–10 min while allowing them to resume their normal activity. Following this, a focal individual was arbitrarily selected for further observation. Behaviour of the focal individual was quantified at 5-s intervals for an additional 10 min. The individual was considered to be moving during a 5-s interval if, by the end of the interval, it had moved one body length or more from its location at the end of the previous 5-s interval. Counts involving movement associated with search for prey, but not attempts to capture a detected food item, were tallied on a hand counter. Search behaviour was measured because this was the behaviour quantified in earlier studies of brook charr at these study sites (McLaughlin et al. 1992, 1994, 1999). At the end of the 10-min observation period, we captured each fish using two aquarium dip nets ($18 \times 25\text{ cm}$). We captured 89 of 99 focal individuals. The remaining 10 were lost when the individual passed behind an obstruction (e.g. rock, submerged branch) or swam outside of our field of vision. Captured individuals were placed singly into 1-litre glass jars with mesh tops and held in the stream for up to 3 h before transport back to the Hagen Aqualab, University of Guelph. Up to 10 fish were collected and transported to the laboratory on any given day.

Experimental Holding Conditions

Upon arrival at Hagen Aqualab, each jar containing a captured fish was placed in a separate aerated, 38-litre rectangular ($80 \times 19\text{ cm}$ and 25 cm high) glass aquarium housed in a walk-in environmental chamber. Room and water temperature were maintained on a 12:12 h light:dark cycle at 12°C . Aquaria were opaquely painted on the bottom and sides to prevent social interactions between individual fish. Jars were assigned randomly to aquaria and placed in the middle of an aquarium, provided with a $15 \times 20\text{ cm}$ sheet of opaque PVC leaned up against the side of the jar to provide cover, and left overnight to allow the fish to acclimatize to the aquarium before the onset of experimentation. Individual fish were then randomly assigned identification numbers to minimize observer bias based on field observations.

Behavioural Experiments

Experiment 1: latency to exit a jar

Approximately 24 h later, lids were removed from the holding jars and each fish was given up to 1 h to exit its jar and enter the aquarium. All lids were removed at approximately 1300 hours (Eastern Standard Time) for all individuals during this experiment. The duration (s) from lid removal until exit or the end of the experiment, whichever came first, was recorded. Durations were related to the number of 5-s search intervals spent moving in the field using an exponential time-to-event regression (Hosmer & Lemeshow 1999). Durations for individuals that failed to exit the jar were treated as censored observations. Our prediction that fish that were more active in the field would take less time to exit the jar than fish that were less active in the field was tested using a likelihood ratio test with an alpha of 0.05. The analysis was carried out using the statistical software JMP IN (v. 4.0.4; SAS Institute, NC, U.S.A.).

Experiment 2: activity and water column use in a novel environment

This experiment followed immediately after experiment 1 and entailed quantifying the activity level and water column use of each fish within the aquarium. Activity and water column use were quantified at 5, 10, 15, 25, 35, 45, and 60 min after the onset of the experiment. The activity score of the fish was 0 if it was either at rest at the bottom or holding position anywhere in the water column and 1 if it was moving. Its location in the water column was scored as 0 if it was in the lower third of the water column, 0.5 if it was in the middle third of the water column, or 1 if it was in the upper third of the water column. Our prediction of fish that were more active in the field being more likely to move in the laboratory than fish that were less active in the field was tested using a logistic regression relating activity in the laboratory tank (1 = active, 0 = sedentary) with the number of 5-s search intervals an individual spent moving in the field. Logistic regression models how $\log_e [P/(1 - P)]$, where P is the probability of moving, changes in relation to an explanatory variable (Hosmer & Lemeshow 2000). Observations made for the same fish over time were treated as repeated measures. Statistical tests were made using generalized estimating equations in the GENMOD procedure in SAS v. 8.2 (SAS Institute, NC, U.S.A.). Our prediction of active fish from the field showing greater use of the upper portion of the water column, on average, relative to fish that were sedentary in the field was tested using a distribution-free regression (Hollander & Wolfe 1999). In addition, multiple time-to-event regression was used to determine if mean activity and mean position in the water column measured during this experiment were predictors of the time to exit the jar in experiment 1.

Experiment 3: simulated risk from above

This experiment commenced 3 h after experiment 2. The experiment was intended to simulate an overhead predation threat. This type of experiment has been used in earlier studies examining responses to simulated

predation risk in fish (e.g. Johnsson 2003; Ward et al. 2004; Wilson & Stevens 2005). The experiment entailed dropping a pebble ($\sim 1.5 \text{ cm}^3$) from 25 cm above the middle of the tank and quantifying how the fish responded to the ensuing splash and turbulence. To standardize for the focal fish's horizontal position within the tank, the pebble was dropped when the fish was within 15 cm of the drop point. Standardizing for vertical location within the tank was not feasible because of the individual variation in water column use. For each fish, we recorded activity (see experiment 2) over a 5-s interval immediately before dropping the pebble. The immediate response of the fish to the pebble drop was quantified as (1) no detectable change in behaviour (no change), (2) cessation of activity or slow sinking to the bottom (froze), or (3) bursts of multidirectional swimming (erratic swimming). Our prediction that fish that were active in the field would show a more active startle response than fish that were sedentary in the field was tested using a logistic regression relating the behavioural response to the pebble drop to the number of 5-s search intervals that individuals spent moving in the field. We also examined whether responses of charr were related to activity immediately before the pebble drop. Analyses were performed using JMP IN (v. 4.0.4; SAS Institute, NC, U.S.A.). Only 78 of 89 fish were considered in this experiment because of limitations on the number of individuals that could be tested on the same day.

Experiment 4: consistency of activity

Set-up for this experiment commenced immediately after experiment 3. The experiment was conducted in a general holding room of Hagen Aqualab and involved exposing the fish to one of two experimental treatments: near-bank or open-water holding conditions. The near-bank treatment consisted of 20 small ($40 \times 30 \text{ cm}$ and 21 cm deep, approximately 25 litre) tanks each containing a 12-cm PVC pipe (5 cm diameter) for cover and two sides covered with 5 cm of shredded plastic 'grass'. The open-water treatment consisted of 20 large ($107 \times 53 \text{ cm}$ and 42 cm deep, approximately 238 litre) tanks containing a 38-cm piece of PVC pipe (18 cm diameter) for cover and 15-cm shredded plastic strips on one side. In the open-water treatment, the pipe and grass cover were moved to the opposite side of the tank every other day to encourage the fish to move about the tank and because our field experience with brook charr has suggested that fish showing an active search tactic are more likely to encounter new environmental situations and because responses to disturbance in the field are short-lived at this life stage (Grant & Noakes 1987b). Water depths were 12 cm in the near-bank treatment and 15 cm in the open-water treatment. These depths were roughly consistent with those where active and sedentary fish were observed in the field (A. D. M. Wilson & R. L. McLaughlin, unpublished data). Water temperature was maintained at $\sim 12^\circ\text{C}$ and ambient photoperiod at LD 12:12 h. Fish were hand fed ad libitum twice daily (Silvercup Starter, Martin Mills Ltd., Elmira, Ontario).

For this experiment, we selected individuals such that over the period of field observations we randomly chose

20 charr that were active in the field and 20 that were sedentary from the total sample of captured fish. Details of how activity was designated as active or sedentary are provided below. Ten of the active fish were assigned randomly and individually to a tank from the near-bank treatment and 10 were assigned randomly and individually to a tank from the open-water treatment. Similarly, 10 of the sedentary fish were assigned randomly and individually to a tank from the near-bank treatment and 10 were assigned randomly and individually to a tank from the open-water treatment. Our aim in this experiment was to place fish in environmental conditions (near-bank and open-water treatments) that paralleled the conditions encountered by fish using sit-and-wait and active search tactics in the field, based on our experience with the study system, in a manner analogous to a reciprocal transplant experiment. It was not to identify the specific factor(s) influencing movement per se, because the treatments differed in many features including water volume, size and density of refuges, amount of simulated vegetation, and rearrangement of the refuges and vegetation.

Individuals were designated as active or sedentary based on the number of moves made in the field. McLaughlin (2001) showed that qualitative assignments of individuals as active or sedentary generally provides a good prediction of how individuals will behave during a subsequent period of observation (Fig. 4). Qualitative observations made early in the field season during this study suggested that individuals considered to be active in the field had a cumulative movement score of 10 or more moves after 10 min of observation whereas individuals considered to be sedentary in the field had a cumulative movement score of less than 10 moves. Therefore, the value of 10 moves was used to distinguish between active and sedentary fish and to guide the assignment of fish to the treatments. Post hoc analysis of the distribution of individual movement scores revealed visually that a value of 10 was reasonable (Fig. 1). Distributions of movement scores and fork (body) lengths of experimental subjects did not differ between treatments (Wilcoxon two-sample tests: movement score: $Z = -0.51$, $P = 0.61$; fork length: $Z = 1.39$, $P = 0.17$).

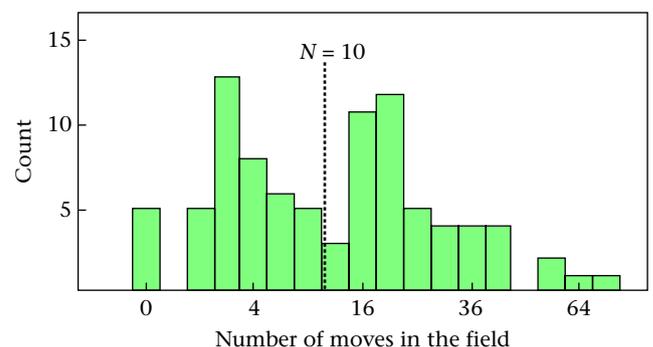


Figure 1. Frequency distribution summarizing the number of individual, recently emerged brook charr showing a given number of moves made while searching for prey during 10-min field observations. The vertical dashed line represents the value used to classify individuals as active (≥ 10) or sedentary (< 10) during assignment of individuals to treatments in experiment 4.

Activity of each fish under each treatment was scored as active or sedentary every other day at approximately 1200 hours for 6 days with day 1 being the day after set up of the experiment. Observations were made systematically beginning with lower larger tanks and progressing to smaller tanks positioned above so as not to influence the behaviour of individual fish before observation. A fish was assigned a score of 1 if it was moving at the time of observation and 0 if it was at rest or holding position in the water column. We tested whether individual differences in activity in the laboratory tank (1 = active, 0 = sedentary) were related with the number of 5-s search intervals spent moving in the field and with holding condition (near-bank/open-water) using multiple logistic regression. Observations made for the same fish across days were treated as repeated measures. Statistical tests were made using generalized estimating equations in the GENMOD procedure in SAS v. 8.2 (SAS Institute, NC, U.S.A.). Results only of the main effects model are presented here. The statistical interaction between field activity and holding condition was not significant ($G_1 = 0.11, P = 0.74$), indicating that how $\log_e [P/(1 - P)]$ scaled with field activity did not differ between the near-bank and open-water treatments. Figures present observed and predicted values for probability of moving (P), rather than $\log_e [P/(1 - P)]$, because the former is easier to interpret than the latter.

RESULTS

Experiment 1: Latency to Exit a Jar

Fish that were more active in the field took less time to escape from the glass jar than those that were less active in the field ($G_1 = 5.77, P < 0.02$). The time-to-event (jar exit) regression predicted that the most active individuals from the field would have exit times that were 30% lower, on average, than those of the least active fish from the field (Fig. 2). When

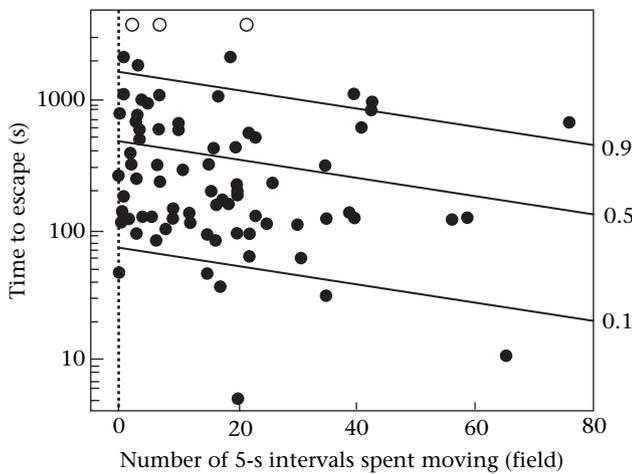


Figure 2. The time that individual, recently emerged brook charr took to exit an erect glass jar placed in a laboratory aquarium in relation to the number of moves the individuals made while searching for prey during 10-min field observations. Each point represents the duration for an individual fish. Open circles represent individuals that had not exited the jar after 1 h. Lines represent 0.1, 0.5, and 0.9 quantiles of the predicted distribution of exit times from an exponential time-to-event regression.

individual fish moved, the nature of the movement was consistent with that shown by active, foraging fish in the field. No fish showed fast or multidirectional bursts of swimming that could be interpreted as an escape response.

Experiment 2: Activity and Water Column Use in a Novel Environment

Individuals that were more active in the field also tended to be more active in an aquarium (logistic regression: $G_1 = 7.88, df = 1, P < 0.005$; Fig. 3a). Overall, the individuals tended to be more active in the aquarium than in the field and this was most noteworthy for fish that moved little in the field (five moves or less), which moved 70% of the time on average in the aquarium. When individual fish moved, the nature of the movement was again consistent with that shown by active, foraging fish in the field. No fish showed fast or multidirectional

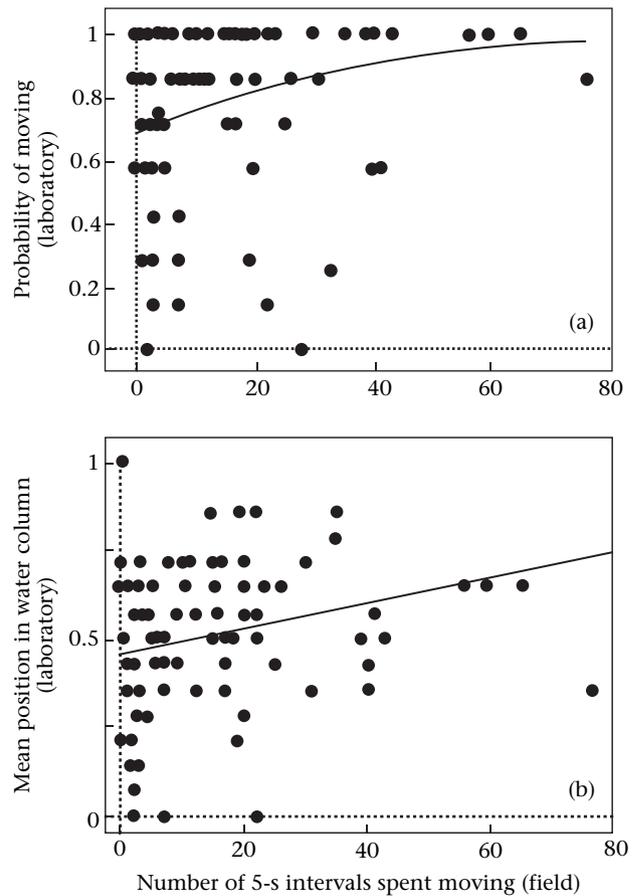


Figure 3. Activity and water column use by individual, recently emerged brook charr in a novel laboratory environment (aquarium) in relation to the number of moves that the individual made while searching for prey during a 10-min field observation. Each point represents an individual. (a) The proportion of time spent moving. The solid line depicts the predicted probability of moving obtained from a logistic regression. (b) Mean height in the water column, where 0 indicates the bottom, 0.5 the mid depth, and 1 the water surface. The solid line represents the predicted depth obtained from a distribution-free regression.

bursts of swimming that could be interpreted as an escape response. Moreover, individuals that were active in the field were also more likely to be higher in the water column than individuals that were sedentary in the field, although this relationship was not strong (Kendall rank correlation: $\tau = 0.17$, $P < 0.04$; Fig. 3b). In addition, mean activity and mean water column position following jar escape were statistically significant predictors of the time required to exit the jar in experiment 1 (multiple time-to-event regression: mean activity: $G_1 = 14.3$, $P < 0.0002$; mean position: $G_1 = 7.94$, $P < 0.005$).

Experiment 3: Simulated Risk From Above

Immediate responses to the pebble drop were variable (Table 1). Fifty-four per cent of the fish froze, 19% swam erratically and 27% showed no change in behaviour. Which of these an individual showed in response to the pebble drop was not significantly related to differences in the number of 5-s search intervals that the individual spent moving in the field (logistic regression: whole model test: $G_2 = 2.71$, $P = 0.26$). For those fish that froze or showed erratic swimming, the response showed was again unrelated to the number of 5-s search intervals that the individuals spent moving in the field (logistic regression: whole model test: $G_1 = 0.65$, $P = 0.42$). Alternatively, whether individuals showed a freeze, erratic swimming, or no change in behaviour was related to the individual's activity during the 5 s before the pebble drop (Table 1; logistic regression: $G_2 = 8.46$, $P < 0.02$). Individuals that were active before the pebble drop were more likely to show an erratic swimming response and less likely to show no response, whereas individuals that were sedentary before the pebble drop were more likely to show no response and less likely to swim erratically. In addition, individuals that were active before the pebble drop were as likely to freeze as those that were inactive. A logistic regression model considering the number of 5-s search intervals that an individual spent moving in the field, as well as the activity immediately before the pebble drop, did not contribute any statistically significant predictive power beyond that provided by a model considering only activity immediately before the pebble drop ($G_2 = 1.93$, $P = 0.38$).

Experiment 4: Consistency of Activity

Individuals in this experiment differed in the level of activity they showed over the 6 days, and an individual's

Table 1. Startle responses of individual, recently emerged brook charr to a pebble dropped on the water surface in relation to an individual's activity in the 5 s before the pebble drop

Activity	Response		
	Froze	Erratic swimming	No change
Sedentary	29	6	18
Active	13	9	3

probability of moving was related both to the behaviour they showed previously in the field and to the holding conditions in the laboratory (Fig. 4). After adjusting statistically for differences between near-bank and open-water holding treatments, individuals that had been active in the field also tended to be more active during the experiment than individuals that had been less active in the field ($G_1 = 5.43$, $P < 0.02$; Fig. 4). After adjusting statistically for the activity level of individuals in the field, individuals in near-bank conditions showed significantly higher levels of activity than individuals in open-water conditions (multiple logistic regression: $G_1 = 4.71$, $P < 0.03$; Fig. 4). Furthermore, predicted probabilities of movement indicated that individuals that were active in the field reduced their probability of moving less in response to the open-water treatment than did individuals that were less active in the field (Fig. 4). This last finding may seem contradictory, given that no statistically significant interaction between activity and holding condition was detected (see Methods). The apparent contradiction is a consequence of the logistic regression modelling $\log_e [P/(1 - P)]$ and the figures depicting the probability of movement (P). For any given level of activity, predicted values of $\log_e [P/(1 - P)]$ can differ by a constant amount between near-bank and open-water treatments, while back-transformed values of P do not.

DISCUSSION

Our study supports three main conclusions. First, the sit-and-wait and active search tactics used by brook charr in the field reflect part of a behavioural syndrome

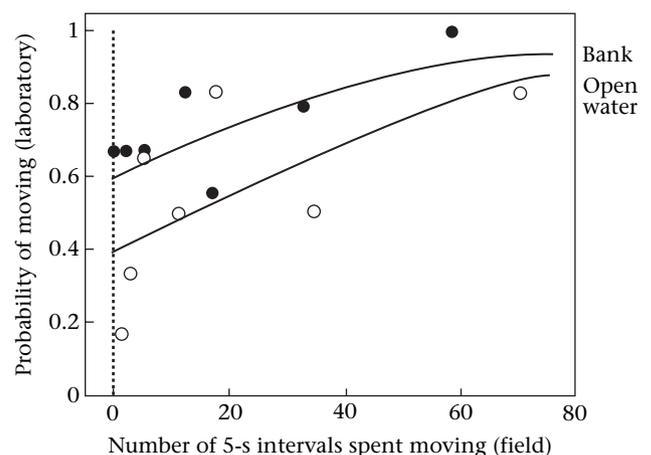


Figure 4. The proportion of time recently emerged brook charr were observed moving under near-bank and open-water holding conditions (treatments) in relation to the number of moves made while searching for prey during a 10-min field observation. For presentation purposes, values of the number of moves made in the field were divided into classes containing two to three individuals from each treatment. Each point represents the mean proportion of time spent moving by individuals for a class in the near-bank (●) and open-water (○) treatments. The lines represent the predicted probabilities of observing an individual moving in the near-bank and open-water treatments and were obtained from a multiple logistic regression fitted to the data prior to any classification.

encompassing general activity and space use (experiments 1, 2 and 4), but not startle responses (experiment 3). Second, activity of charr in the laboratory was shaped both by flexible responses to environmental conditions and by underlying predispositions to be active (experiments 2 and 4) and the predispositions were repeatable for up to 6 days (experiment 4). Third, charr that were least active in the field showed the greatest change in activity, on average, and greater variability in their responses to different laboratory conditions (experiments 2 and 4).

Our study has applied the framework of behavioural syndromes in a unique way to a topic, resource polymorphism, that is currently the focus of much ecological and evolutionary interest. The nature of phenotype–environment interactions fostering phenotypic diversification, and the important behavioural processes, in particular, remain poorly understood (Rogers et al. 2002; Sacotte & Magnan 2006). Our findings suggest that recently emerged brook charr either differ in their propensity to move and use the water column at the time of emergence in ways that predispose them to adopt a sit-and-wait or active search tactic, or that very early experience, within a few weeks of emergence, quickly promotes and reinforces variation in the propensity to move and use the water column. Further investigation is required to delineate between these possibilities; however, showing the tactics as part of a behavioural syndrome represents an important first step. Observing predispositions at such an early life stage suggests that processes beyond chance could be shaping the early variation in foraging behaviour. Predispositions in space use early in life can enhance the opportunity for behavioural processes, such as prey or habitat cueing and training, and habitat imprinting and fidelity (Stamps 2001; McCairns & Fox 2004), possibly in concert with resource competition (Metcalf et al. 1989; Bolnick 2004), to reinforce initial individual differences in foraging behaviour. Such predispositions have not been considered thoroughly in theoretical models of habitat selection in general, such as ideal-free distribution theory and its variants (Stamps 2001), or in game-theoretic and bioenergetic models of the early stages of resource polymorphisms (e.g. McLaughlin 2001; De Kerckhove et al. 2006).

Our demonstration of a space use syndrome in brook charr is useful in another, related context. Individual specializations in diet and water column use lasting up to several months have been observed repeatedly in stream-dwelling salmonid fish (Bryan & Larkin 1972; Ringler 1985; Nielsen 1992) and activity and water column use can influence the numbers and kinds of prey encountered. Bryan (1973) conducted laboratory trials with juvenile rainbow trout, *Oncorhynchus mykiss*, to examine whether repeated experience with a prey type led to preferences for that type when alternative prey were also presented (training bias). Bryan concluded that training biases were too weak to account for the individual specializations observed for rainbow trout and brook charr in the field. However, Bryan did not consider the possibility of predispositions in activity and water column use or the potential reinforcing effects of social interactions. A complementary experiment revealed that individuals introduced into outdoor ponds developed differences in

diet and water column use and interacted aggressively but were nonterritorial (Bryan & Larkin 1972).

Our findings for brook charr have some resemblance to the distinction drawn between proactive and reactive individuals in other taxa (e.g. Koolhaas et al. 1999). Proactive individuals tend to be more active and tend to explore their environment and form routines more quickly than reactive individuals, but they also take more time to adjust to environmental change (Koolhaas et al. 1999; Sih et al. 2004). Correspondingly, the charr most active in the field showed the least change in activity when tested in the laboratory (experiment 2) and when tested in near-bank and open-water holding conditions (experiment 4). Proactive individuals can also show greater dispersal in the field than reactive individuals (e.g. Fraser et al. 2001; Dingemans et al. 2003). Correspondingly, diffusion analyses of the dispersal movements made by other populations of brook charr suggest that populations can consist of slow- and fast-dispersers (Rodríguez 2002; Coombs 2004), although it remains to be determined whether this dispersal behaviour is linked to the foraging behaviour adopted early in life. Brook charr in our study pools differ from the general proactive–reactive distinction in one noteworthy way, however. Proactive individuals tend to be more aggressive than reactive individuals (e.g. Koolhaas et al. 1999). While we have not tested aggressiveness here, earlier field observations indicated that the most active and the most sedentary fish were aggressive in social interactions (McLaughlin et al. 1999). Individuals showing intermediate levels of activity tended to be nonaggressive.

There were instances where the charr behaved differently than we expected. One instance was their tendency to be less active under open-water conditions than under near-bank conditions, contrary to our expectation. Our qualitative impression, developed during the observations, was that the fish were more wary in the former condition. A specific explanation to account for this finding is not possible because the holding conditions differed in more than one feature that might affect cautiousness (see Methods). Regardless, this unexpected result and lack of explanation for it does not detract from our findings that the activity of sedentary and active fish from the field differed between the near-bank and open-water treatments and that the magnitude of this difference was higher for sedentary fish than for active fish. Another instance was the absence of a positive correlation between the startle behaviour of charr in response to a simulated risk from above and their activity while foraging in the field. Instead, startle responses were highly variable and the expression of the less commonly performed responses, erratic swimming and no response, depended on an individual's activity immediately before the pebble was dropped in the tank. Three aspects of the findings regarding startle response are notable. First, we have qualitatively observed the startle responses of brook charr during almost two decades of research at these field sites and the variability in responses of charr in the laboratory experiment is consistent with that in the field (R. L. McLaughlin, personal observation). Second, our findings are difficult to interpret in a broader context because very few studies of

animal personalities or behavioural syndromes have considered the responses of individuals at the moment of attack or impending risk (Quinn & Cresswell 2005). Authors of earlier studies typically focused on antipredator (inspection) behaviour before an attack or cautiousness following an attack (Quinn & Cresswell 2005). These latter attributes were not examined here; however, Wilson & Stevens (2005) demonstrated that juvenile rainbow trout show positive correlations between latency to forage in the presence and absence of an aquatic predator and in the presence and absence of a simulated risk from above (pebble drop), although they did not measure the immediate responses of the trout to the risk from above. Third, given the complexity of predator–prey relationships in terms of the diversity of predators and their behaviour, resultant antipredator responses of prey and environmental conditions may favour context specificity in startle responses (Quinn & Cresswell 2005).

The potential genetic and physiological bases of the behavioural variation observed in recently emerged brook charr present interesting directions for future investigation. From a genetic perspective, heritable differences in activity and boldness have been demonstrated in a variety of taxa including mammals (*Ovis canadensis*, Réale et al. 2000), birds (*Parus major*, Dingemanse et al. 2003), and fish (*Poecilia reticulata*, Godin & Dugatkin 1996; *Salmo trutta*, Sundström et al. 2004). Behavioural differences between domesticated and wild strains of salmonids further suggest the presence of genetic variation for exploratory behaviour, risk taking, and aggression (Huntingford & Adams 2005). In addition, a genetic basis for intermorph differences in water column use and activity has been found in polymorphic populations of Arctic charr (*Salvelinus alpinus*, Skúlason et al. 1993) and lake whitefish (*Coregonus clupeaformis*, Rogers et al. 2002), and for intermorph differences in prey capture and rejection in a polymorphic population of brook charr (Sacotte & Magnan 2006). From a physiological perspective, the variation in search tactics and activity of brook charr are not linked to differences in swimming ability, given that, regardless of the search tactic employed, individuals are capable of swimming for prolonged periods at speeds five or more times higher than the speed commonly used by individuals using the active search tactic (McLaughlin & Grant 2001). Alternatively, the predispositions in search tactics and activity are not related to standard metabolic rate (M. Farwell, unpublished data), in the same way that routine activity and basal metabolic rate are correlated in some birds and mammals (e.g. Birt-Friesen et al. 1989; Ricklefs et al. 1996 and references therein), and as found in the early- and late-migrating Atlantic salmon (*Salmo salar*, Metcalfe et al. 1995; Cutts et al. 1998) and as recently proposed for migrant and stream-resident brook charr from the same population (Morinville & Rasmussen 2003, 2006). Our interpretation is that the differences in foraging behaviour observed in the field and in activity and space use in the laboratory reflect variability in how individual brook charr perceive similar environmental conditions in terms of potential opportunity and risk. There is growing recognition that individuals within populations differ in how they cope

with new environmental situations (Koolhaas et al. 1999; Øverli et al. 2005). Moreover, strains of rainbow trout that show low and high physiological (cortisol) responses to stress also show different levels of activity in a variety of social and nonsocial situations (Øverli et al. 2005; Schjolden et al. 2005a, b, 2006).

The relationships we have demonstrated between the activity of recently emerged brook charr foraging in the field and their activity and space use in the laboratory are subtle, but they are comparable in magnitude to the correlations observed between different measures of activity and space use in the field (McLaughlin et al. 1992, 1994, 1999). We would expect evidence for behavioural syndromes to be subtle during the initial developmental and evolutionary stages of resource polymorphism and before the action of behavioural, physiological, morphological and ecological processes that might reinforce the correlations. What we have uniquely demonstrated is that the raw material for such processes exists at a very early life stage in a population lacking distinct morphotypes. This suggests that initial, individual differences in behaviour could have a more complex and important role in facilitating resource polymorphism than is currently recognized by hypotheses of diversification emphasizing the roles of chance, and of ecological conditions, such as the presence of alternative prey sources and resource competition (Robinson & Wilson 1994; Schluter 1996).

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References

- Birt-Friesen, V. L., Montevecchi, W. A., Cairns, D. K. & Macko, S. A. 1989. The activity-specific metabolic rates of free-living northern gannets and other seabirds. *Ecology*, **70**, 357–367.
- Boissy, A. 1995. Fear and fearfulness in animals. *Quarterly Review of Biology*, **70**, 165–191.
- Bolnick, D. I. 2004. Can intraspecific variation competition drive disruptive selection? An experimental test in natural populations of sticklebacks. *Evolution*, **58**, 608–618.
- Bolnick, D. I., Svanbäck, R., Fordyce, J. A., Yang, L. H., Davis, J. M., Hulsey, C. D. & Forister, M. L. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist*, **161**, 1–28.
- Bryan, J. E. 1973. Feeding history, parental stock, and food selection in rainbow trout. *Behaviour*, **45**, 123–153.
- Bryan, J. E. & Larkin, P. A. 1972. Food specialization by individual trout. *Journal of the Fisheries Research Board of Canada*, **29**, 1615–1624.
- Coombs, M. 2004. Juvenile brook charr (*Salvelinus fontinalis* Mitchell) dispersal is compatible with simple diffusion and predictable

- using simple mathematical dispersal models. M.Sc. thesis, Trent University.
- Cutts, C. J., Metcalfe, N. B. & Taylor, A. C. 1998. Aggression and growth depression in juvenile Atlantic salmon: the consequences of individual variation in standard metabolic rate. *Journal of Fish Biology*, **52**, 1026–1037.
- Dall, S. R. X., Houston, A. I. & McNamara, J. M. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. *Ecology Letters*, **7**, 734–739.
- De Kerckhove, D., McLaughlin, R. L. & Noakes, D. L. G. 2006. Ecological mechanisms favouring behavioural diversification in the absence of morphological diversification: a theoretical examination using brook charr (*Salvelinus fontinalis*). *Journal of Animal Ecology*, **75**, 506–517.
- Dingemans, N. J. & Reale, D. 2005. Natural selection and animal personality. *Behaviour*, **142**, 1159–1184.
- Dingemans, N. J., Both, C., Drent, P. J., van Oers, K. & Noordwijk, A. J. 2002. Repeatability and heritability of exploratory behaviour in great tits from the wild. *Animal Behaviour*, **64**, 929–938.
- Dingemans, N. J., Both, C., van Noordwijk, A. J., Rutten, A. L. & Drent, P. J. 2003. Natal dispersal and personalities in great tits (*Parus major*). *Proceedings of the Royal Society of London, Series B*, **270**, 741–747.
- Dugatkin, L. A. & Alfieri, M. S. 2003. Boldness, behavioral inhibition and learning. *Ethology, Ecology and Evolution*, **15**, 43–49.
- Dynes, J., Magnan, P., Bernatchez, L. & Rodríguez, M. A. 1999. Genetic and morphological variation between two forms of lacustrine brook charr. *Journal of Fish Biology*, **54**, 955–972.
- Fraser, D. F., Gilliam, J. F., Daley, M. J., Le, A. N. & Skalski, G. T. 2001. Explaining leptokurtic movement distributions: intrapopulation variation in boldness and exploration. *American Naturalist*, **158**, 124–135.
- Godin, J. G. J. & Dugatkin, L. A. 1996. Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Sciences, U.S.A.* **93**, 10262–10267.
- Gosling, S. D. 2001. From mice to men: what can we learn about personality from animal research. *Psychological Bulletin*, **127**, 45–86.
- Grant, J. W. A. & Noakes, D. L. G. 1987a. Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology*, **56**, 1001–1013.
- Grant, J. W. A. & Noakes, D. L. G. 1987b. Escape behaviour and use of cover by young-of-the-year brook trout, *Salvelinus fontinalis*. *Canadian Journal of Fisheries and Aquatic Sciences*, **44**, 1390–1396.
- Hollander, M. & Wolfe, D. A. 1999. *Nonparametric Statistical Methods*. 2nd edn. New York: J. Wiley.
- Hosmer, D. W., Jr & Lemeshow, S. 1999. *Applied Survival Analysis: Regression Modeling of Time to Event Data*. New York: J. Wiley.
- Hosmer, D. W. & Lemeshow, S. 2000. *Applied Logistic Regression*. 2nd edn. New York: J. Wiley.
- Huntingford, F. & Adams, C. 2005. Behavioural syndromes in farmed fish: implications for production and welfare. *Behaviour*, **142**, 1207–1221.
- Hutchings, J. A. 1996. Adaptive phenotypic plasticity in brook trout, *Salvelinus fontinalis*, life histories. *Ecoscience*, **3**, 25–32.
- Imre, I., McLaughlin, R. L. & Noakes, D. L. G. 2002. Phenotypic plasticity in brook charr: changes in caudal fin induced by water flow. *Journal of Fish Biology*, **61**, 1171–1181.
- Johnsson, J. I. 2003. Group size influences foraging effort independent of predation risk: an experimental study on rainbow trout. *Journal of Fish Biology*, **63**, 863–870.
- Koolhaas, J. M., Korte, S. M., De Boer, S. F., Van Der Vegt, B. J., Van Reenen, C. G., Hopster, H., De Jong, I. C., Ruis, M. A. W. & Blokhuis, H. J. 1999. Coping styles in animals: current status in behaviour and stress-physiology. *Neuroscience and Biobehavioral Reviews*, **23**, 925–935.
- McCairns, R. J. S. & Fox, M. G. 2004. Habitat and home range fidelity in a trophically dimorphic pumpkinseed sunfish (*Lepomis gibbosus*) population. *Oecologia*, **140**, 271–279.
- McLaughlin, R. L. 2001. Behavioural diversification in brook charr: adaptive responses to local conditions. *Journal of Animal Ecology*, **70**, 325–337.
- McLaughlin, R. L. & Grant, J. W. A. 2001. Field examination of perceptual and energetic bases for intermittent locomotion by recently-emerged brook charr in still-water pools. *Behaviour*, **138**, 559–574.
- McLaughlin, R. L., Grant, J. W. A. & Kramer, D. L. 1992. Individual variation and alternative patterns of foraging movements in recently-emerged brook charr (*Salvelinus fontinalis*). *Behaviour*, **120**, 286–301.
- McLaughlin, R. L., Grant, J. W. A. & Kramer, D. L. 1994. Foraging movements in relation to morphology, water column use, and diet for recently emerged brook trout (*Salvelinus fontinalis*) in still-water pools. *Canadian Journal of Fisheries and Aquatic Sciences*, **51**, 268–279.
- McLaughlin, R. L., Ferguson, M. M. & Noakes, D. L. G. 1999. Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching. *Behavioral Ecology and Sociobiology*, **45**, 386–395.
- Metcalfe, N. B. 1993. Behavioural causes and consequences of life history variation in fish. *Marine and Freshwater Behaviour and Physiology*, **23**, 205–217.
- Metcalfe, N. B., Huntingford, F. A., Graham, W. D. & Thorpe, J. E. 1989. Early social status and the development of life-history strategies in Atlantic salmon. *Proceedings of the Royal Society of London, Series B*, **236**, 7–19.
- Metcalfe, N. B., Taylor, A. C. & Thorpe, J. E. 1995. Metabolic rate, social status and life-history strategies in Atlantic salmon. *Animal Behaviour*, **49**, 431–436.
- Morinville, G. R. & Rasmussen, J. B. 2003. Early juvenile bioenergetic differences between anadromous and resident brook trout (*Salvelinus fontinalis*). *Canadian Journal of Fisheries and Aquatic Sciences*, **60**, 401–410.
- Morinville, G. R. & Rasmussen, J. B. 2006. Does life-history variability in salmonids affect habitat use by juveniles? A comparison among streams open and closed to anadromy. *Journal of Animal Ecology*, **75**, 693–704.
- Nielsen, J. L. 1992. Microhabitat-specific foraging behavior, diet, and growth of juvenile coho salmon. *Transactions of the American Fisheries Society*, **121**, 617–634.
- Øverli, Ø., Winberg, S. & Pottinger, T. G. 2005. Behavioral and neuroendocrine correlates of selection for stress responsiveness in rainbow trout: a review. *Integrative and Comparative Biology*, **45**, 463–474.
- Price, T. D., Qvarnström, A. & Irwin, D. E. 2003. The role of phenotypic plasticity in driving genetic evolution. *Proceedings of the Royal Society of London, Series B*, **270**, 1433–1440.
- Quinn, J. L. & Cresswell, W. 2005. Personality, anti-predation behaviour and behavioural plasticity in the chaffinch *Fringilla coelebs*. *Behaviour*, **142**, 1377–1402.
- Réale, D. & Festa-Bianchet, M. 2003. Predator-induced natural selection on temperament in bighorn ewes. *Animal Behaviour*, **65**, 463–470.
- Réale, D., Gallant, B. Y., LeBlanc, M. & Festa-Bianchet, M. 2000. Consistency of temperament in bighorn ewes and correlates with behaviour and life history. *Animal Behaviour*, **60**, 589–597.
- Ricklefs, R. E., Konarzewski, M. & Daan, S. 1996. The relationship between basal metabolic rate and daily expenditure in birds and mammals. *American Naturalist*, **147**, 1047–1071.

- Ringler, N. H. 1985. Individual and temporal variation in prey switching by brown trout, *Salmo trutta*. *Copeia*, **1985**, 918–926.
- Robinson, B. W. & Wilson, D. S. 1994. Character release and displacement in fishes: a neglected literature. *American Naturalist*, **144**, 596–627.
- Robinson, B. W., Wilson, D. S., Margosian, A. S. & Lotito, P. T. 1993. Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. *Evolutionary Ecology*, **7**, 451–464.
- Rodríguez, M. A. 2002. Restricted movement in stream fish: the paradigm is incomplete, not lost. *Ecology*, **83**, 1–13.
- Rogers, S. M., Gagnon, V. & Bernatchez, L. 2002. Genetically based phenotype-environment association for swimming behaviour in lake whitefish ecotypes (*Coregonus clupeaformis* Mitchell). *Evolution*, **56**, 2322–2329.
- Sacotte, S. & Magnan, P. 2006. Inherited differences in foraging behaviour in the offspring of two forms of lacustrine brook charr. *Evolutionary Ecology Research*, **8**, 843–857.
- Schjolden, J., Backström, T., Pulman, K. G. T., Pottinger, T. G. & Winberg, S. 2005a. Divergence in behavioural responses to stress in two strains of rainbow trout (*Oncorhynchus mykiss*) with contrasting stress responsiveness. *Hormones and Behaviour*, **48**, 537–544.
- Schjolden, J., Stoskhus, A. & Winberg, S. 2005b. Does individual variation in stress responses and agonistic behaviour reflect divergent stress coping strategies in juvenile rainbow trout? *Physiological and Biochemical Zoology*, **78**, 715–723.
- Schjolden, J., Pulman, K. G. T., Pottinger, T. G., Metcalfe, N. B. & Winberg, S. 2006. Divergence in locomotor activity between two strains of rainbow trout *Oncorhynchus mykiss* with contrasting stress responsiveness. *Journal of Fish Biology*, **68**, 920–924.
- Schluter, D. 1996. Ecological speciation in postglacial fishes. *Philosophical Transactions of the Royal Society of London, Series B*, **351**, 807–814.
- Sih, A., Bell, A. & Johnson, J. C. 2004. Behavioural syndromes: an ecological and evolutionary overview. *Trends in Ecology & Evolution*, **19**, 372–378.
- Skúlason, S. & Smith, T. B. 1995. Resource polymorphisms in vertebrates. *Trends in Ecology & Evolution*, **10**, 366–370.
- Skúlason, S., Snorrason, S. S., Ota, D. & Noakes, D. L. G. 1993. Genetically based differences in foraging behaviour among sympatric morphs of arctic charr (Pisces: Salmonidae). *Animal Behaviour*, **45**, 1179–1192.
- Skúlason, S., Snorrason, S. S. & Jonsson, B. 1999. Sympatric morphs, populations and speciation in freshwater fish with emphasis on arctic charr. In: *Evolution of Biological Diversity* (Ed. by A. E. Magurran & R. M. May), pp. 70–92. Oxford: Oxford University Press.
- Sneddon, L. U. 2003. The bold and the shy: individual differences in rainbow trout. *Journal of Fish Biology*, **62**, 971–975.
- Stamps, J. A. 2001. Habitat selection by dispersers: integrating proximate and ultimate approaches. In: *Dispersal* (Ed. by J. Clobert, E. Danchin, A. A. Dhondt & J. D. Nichols), pp. 230–242. Oxford: Oxford University Press.
- Stamps, J. 2003. Behavioural processes affecting development: Tinbergen's fourth question comes of age. *Animal Behaviour*, **66**, 1–13.
- Sundström, L. F., Petersson, E., Höjesjö, J., Johnsson, J. I. & Järvi, T. 2004. Hatchery selection promotes boldness in newly hatched brown trout (*Salmo trutta*): implications for dominance. *Behavioural Ecology*, **15**, 192–198.
- Ward, A. J. W., Thomas, P., Hart, P. J. B. & Krause, J. 2004. Correlates of boldness in three-spined sticklebacks (*Gasterosteus aculeatus*). *Behavioral Ecology and Sociobiology*, **55**, 561–568.
- Wilson, A. D. M. & Stevens, E. D. 2005. Consistency in context-specific measures of shyness and boldness in rainbow trout, *Oncorhynchus mykiss*. *Ethology*, **111**, 849–862.
- Wilson, D. S., Coleman, K., Clark, A. B. & Biederman, L. 1993. Shy-bold continuum in pumpkinseed sunfish (*Lepomis gibbosus*): an ecological study of a psychological trait. *Journal of Comparative Psychology*, **107**, 250–260.