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# Adaptive peaks and alternative foraging tactics in brook charr: evidence of short-term divergent selection for sitting-and-waiting and actively searching

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**Abstract** Some recently emerged brook charr (*Salvelinus fontinalis*) inhabiting still-water pools along the sides of streams are sedentary and eat crustaceans from the lower portion of the water column. Others are more active and eat insects from the upper portion of the water column. We provide evidence that this divergent foraging behavior reflects short-term divergent selection brought about by intraspecific competition in the presence of alternative food sources. Rates of encounters and interactions between individuals were density dependent, and encounter and interaction events were closely timed with prey capture attempts. In addition, aggressive fish made more foraging attempts per minute than nonaggressive fish. Aggressive fish were also either inactive or very active, while nonaggressive fish exhibited intermediate levels of activity. Growth rate potential, an important component of fitness during the early life stages of brook charr, was assessed using tissue concentrations of RNA and found to be highest for sedentary fish and for active fish making frequent foraging attempts, and lower for fish exhibiting intermediate levels of activity. Our findings support contentions that individual behavior plays an important role during initial steps in the evolution of resource polymorphisms.

**Key words** Charr · Divergent selection · Fish growth
Foraging tactics · Resource polymorphism

## Introduction

In many vertebrate populations there is considerable, and sometimes apparently discrete, variation in feeding morphology and behavior (Robinson and Wilson 1994 Wimberger 1994; Skúlason and Smith 1995; Smith and Skúlason 1996). These resource or trophic polymorphisms are often accompanied by corresponding differences in growth rate, age at maturity, and mating strategies (Skúlason and Smith 1995; Smith and Skúlason 1996). Resource polymorphisms are currently attracting much interest because they offer an unparalleled opportunity to examine the roles that ecological and behavioral processes (e.g., competition and resource partitioning) play in evolutionary processes (e.g., population divergence, sympatric speciation, and adaptive radiation). Resource polymorphisms occur in every class of vertebrate (Wimberger 1994), and recent reviews suggest they are more common than originally appreciated (Robinson and Wilson 1994; Skúlason and Smith 1995; Smith and Skúlason 1996). They are particularly common in fishes inhabiting species-poor lakes with well-defined benthic and limnetic niches (Robinson and Wilson 1994).

Behavior is thought to be a crucial aspect of the evolution of resource polymorphisms (Wimberger 1994 Skúlason and Smith 1995). In species-poor environments with two or more available niches, morphological divergence and has been proposed to occur in three steps (Wimberger 1994; Skúlason and Smith 1995). First, the presence of stable, alternative food sources requiring different techniques for exploitation is expected to favor specialization in the foraging behavior exhibited by behaviorally flexible individuals. The specialization may be enhanced by biological interactions, and comparative evidence suggests competition is the most likely form of interaction promoting the diversification (Robinson and Wilson 1994; Schluter 1996; but see Brönmark and Miner 1992). Second, specialization in foraging behavior facilitates the evolution of specializations in feeding morphology, as well as differences in patterns of growth and maturity. Third, the differences in feeding morphology alter the efficiencies that morphs experience while finding and capturing the alternative prey types, thereby reinforcing the behavioral differences. The morphs may even evolve differences in habitat preference,

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timing of breeding, and mate choice, possibly leading to reproductive isolation. Resource polymorphisms may be the outcome of a genetic polymorphism or adaptive phenotypic plasticity (Robinson and Wilson 1994, 1996). In the latter case, behavior can influence which developmental trajectory a plastic genotype undertakes in a sequence similar to that outlined in the steps above (e.g., Meyer 1987; Metcalfe et al. 1989; Wimberger 1992; Metcalfe 1993).

If behavioral diversification precedes morphological diversification, it should be possible to find ecological situations where divergent foraging tactics occur among individuals exhibiting no or only subtle morphological differences. Investigations of these are important for understanding the mechanisms and conditions promoting the prerequisite specializations in behavior, prior to their reinforcement by morphological differences (step 1 vs step 3). Young brook charr (*Salvelinus fontinalis*) occupying still-water pools along the side of streams promises to be a model study system in this regard (e.g., Skúlason et al., in press). This fish exhibits conspicuous, short-term variation in foraging behavior which closely parallels the benthic/limnetic distinction reported frequently for lacustrine fishes (see Robinson and Wilson 1994). Some charr tend to be sedentary (a sit-and-wait tactic), feeding on mobile crustacean prey from the lower portion of the water column, while others tend to be very active (an active search tactic), feeding on sedentary insect prey from the upper portion of the water column (McLaughlin et al. 1992, 1994). Individuals exhibiting intermediate levels of activity are also observed. The variation in foraging behavior is not correlated with differences in body size or shape, but is it related to local environmental conditions within the pools (McLaughlin et al. 1994). In addition, similar variation in foraging behavior has been reported for young-of-the-year brook charr in much larger lakes (Biro and Ridgway 1995). This model system therefore presents an excellent opportunity to test whether the divergent foraging behavior observed in the field reflects the diversifying effects of intraspecific competition in the presence of alternative food resources. Further, the test can be carried out in a species where resource polymorphisms have been reported in other populations (e.g., Bourke et al. 1997), and a genus where resource polymorphisms occur commonly (Robinson and Wilson 1994).

In this paper, we provide field evidence of local competition for food among the charr. For a sample of individuals collected after our observations, we then demonstrate that growth rate potential, an important component of fitness during the early life stages of brook charr, is linked to foraging behavior in a manner suggesting the presence of diversifying selection on foraging behavior.

Growth rate potential was assessed using tissue concentrations of ribonucleic acid (RNA), a biochemical index of short-term growth rate in fishes (Ferron and Leggett 1994). This index was developed to reliably predict rates of growth and mortality for wild fish (Ferron and Leggett 1994). Because production of new tissue requires protein synthesis, and therefore ribosomes, the tissue concentration of RNA, which is predominantly ribosomal RNA, provides an index of the number of ribosomes per gram of tissue. Investigations of fishes in general, and salmonids in particular, have demonstrated positive correlations between short-term growth rates and either tissue concentrations of RNA or the ratio of RNA to DNA (Wilder and Stanley 1983; Miglavs and Jobling 1989; Ferguson and Danzmann 1990; Bastrop et al. 1992; Mathers et al. 1993; Arndt et al. 1994). Unfortunately, the strength and form of the relationship varies among species and even life stages within species (Bulow 1987; Ferron and Leggett 1994). We therefore conducted a laboratory experiment to verify the relationship between specific growth rate and RNA concentration in young brook charr.

## Methods

### Behavior and growth rate potential in the field

Data were collected from 5 to 25 April 1991 and 5 April to 7 May 1992 at three sites along the Credit River: the North Branch at Highway 24 near Caledon, Ontario (43°52′ N, 80°00′ W); the West Branch approximately 1 km northeast of Erin, Ontario (43°45′ N, 80°07′ W); and Black Creek near Limehouse, Ontario (43°38′ N, 79°59′ W). The Black Creek site was used only in 1991 because a beaver dam constructed in the summer of 1991 altered stream flow substantially thereafter. Brook charr at these locations are from resident, headwater populations. Although these drainages were stocked in the 1960s and early 1970s (Ontario Ministry of Natural Resources, personal communication), studies of mitochondrial DNA revealed no evidence of hatchery stock remaining at the sites (R. McLaughlin and R. Danzmann, unpublished data). Our study sites encompassed 50- to 200-m segments of these streams containing areas of flowing water and still, backwater pools along the edges.

Observations of foraging activity were made daily between 0900 and 1700 hours unless prevented by rain or snow. The fish were too small (20–30 mm) and delicate for us to mark and reobserve individuals effectively. We therefore spread our sampling effort among sites and among the pools at each site to minimize the probability of reobserving the same fish. After arriving at a pool, the observer waited 10 min for the fish to return to the area and resume feeding. This wait minimized any bias toward bold or hungry fish because recently emerged brook charr return to their foraging location within 2 min of a disturbance, on average (Grant and Noakes 1987a). At the end of the 10 min, we usually counted all fish in the pool or within an area of approximately 1 $m^2$, whichever was smaller, and categorized the behavior of each fish as sedentary or mobile based on whether it was moving at the time it was counted. A focal fish was then selected and its fork length estimated visually to the nearest 0.1 cm.

We quantified the behavior of the focal fish using the method described by McLaughlin et al. (1992, 1994). At 5-s intervals, the observer recorded on microcassette tape (1) the distance, to the nearest body length, traversed by the focal individual, (2) whether the movement entailed an attempt to capture prey (a foraging attempt), a social interaction, or flight to cover, and (3) whether foraging attempts were directed at the substrate, the middle of the water column, or the water surface (benthic, midwater, and surface foraging attempts, respectively). Intervals not involving a foraging attempt, social interaction, or flight to cover were considered search for prey, a definition commonly used for search (Stephens and

Krebs 1986). We also noted incidences where a conspecific came within five body lengths of the focal fish (an encounter), even when there was no obvious aggressive interaction. During agonistic interactions, the focal individual was categorized as aggressive if it chased a conspecific and nonaggressive if it was chased by a conspecific. The intended duration of observation varied from 5 min under poor viewing conditions (e.g., low light, intermittent wind) to 10 min under good viewing conditions (e.g., bright light, little wind). The duration was varied in an attempt to balance the value of obtaining longer periods of observation with the need to capture the focal individuals in numbers large enough for the analysis of growth rate potential.

Immediately following each observation, we attempted to capture the focal individual using aquarium dip nets. Afterward, the site was marked. We captured 42 of 74 individuals in 1991 and 42 of 69 individuals in 1992. Each captured fish was killed immediately with a blow to the head, its fork length measured to the nearest millimeter, and the carcass placed in a labelled plastic tube and put on wet ice. Water temperature at the observation site was then recorded. At the end of the sampling day, we also measured the pool surface area and the current speed at each observation site. For active fish we took the mean of several current speed measurements made over the area traversed by that individual. Upon return to the laboratory in the evening, the captured fish were frozen at −70 °C. Placing specimens on wet ice for less than 24 h before freezing does not affect the measurement of tissue concentrations of nucleic acids (Ferguson and Drahushchak 1989).

### Concentration of RNA and growth rate in the laboratory

In January 1992, we obtained approximately 1000 brook charr embryos (hatchery stock) from the Ontario Ministry of Natural Resources' Fish Culture Section. The embryos were reared in hatchery trays in recirculated, aerated well water at 8 °C, with 10–20% of the water replaced daily.

The fish were moved into 54 × 50 × 31 cm stock tanks prior to first feeding. Mean water temperature was maintained at 8–9 °C to match the mean temperature encountered by recently emerged, wild brook charr at our field sites near Guelph (McLaughlin et al. 1992).

After the fish began feeding exogenously on commercial trout food (BioDiet), we selected haphazardly 20 fish from the stock tanks. The fish were deprived of food for 1 day; then each fish was anesthetized, measured for fork length (to the nearest millimeter) and wet weight (to the nearest 0.1 mg), placed singly into an experimental tank (39 × 25 × 31 cm), and provided with food. Experimental tanks were filled randomly to minimize any location effects. The 20 fish were then ranked by wet weight and assigned to five groups containing 4 fish of similar weight. Within each size group, one fish was assigned at random to one of the following treatments: 0.5, 1.0, 2.0, or 4.0 times the daily ration (food allotment) recommended for a fish of that weight, following Bardach et al. (1972). Thereafter, the fish were fed BioDiet at their assigned ration for 20 days. The fish were then deprived of food for 1 day, killed with a blow to the head, measured for fork length and wet weight, placed in a small labelled plastic tube, and put on wet ice. The samples were frozen at −70 °C within 2 h. Throughout the experiment, the fish were housed in water at 8–9 °C, with flow rates of 29–35 ml $s^{-1}$ through the experimental tanks. Photoperiod was altered to correspond with the natural photoperiod at this time of year (approximately 13 h light:11 h dark).

### Measurement of tissue concentrations of RNA

Each fish was weighed (mg wet tissue) and gutted prior to its preparation for measurements of nucleic acid concentrations. RNA and DNA concentrations were measured for the remaining, primarily muscle tissue according to the fluorometric technique of Karsten and Wollenberger (1972, 1977), as described in Ferguson and Drahushchak (1989). The individual who measured the tissue concentrations of RNA had no knowledge of the behavior each fish had exhibited in the field.

### Statistical analysis

Our behavioral observations were used to estimate for each individual the proportion of search time spent moving, the foraging attempts made per minute, and the proportion of foraging attempts directed at the water surface. We also estimated each focal individual's rate of encounter and rate of interaction with conspecifics. Some of these variables were transformed before analysis to normalize their distributions as much as possible. The proportion of time spent moving and the proportion of foraging attempts directed at the water surface were arcsine-square-root transformed. Foraging attempts per minute was square-root transformed. Fork length was $\log_{10}$-transformed. In analyses considering all of the fish we observed, we used our visual estimates of fork length for those fish not captured after the observation period. Measured values of fork length were used for fish that were captured. Analyses for captured fish showed that our visual estimates of fork length (EFL) were good predictors of measured fork lengths (MFL). In each year, EFL and MFL were significantly and positively correlated ($r = 0.74$ and 0.84, respectively, both $P < 0.001$). In addition, for regressions of EFL versus MFL, the regression coefficients (slopes) were not significantly different from 1 ($P > 0.10$) and the intercepts were not significantly different from 0 ($P > 0.10$).

All individuals considered in our analyses were observed foraging in still-water habitats and not resting on the stream bottom. Our observation periods lasted from 4.1 to 21.3 min (mean = 8.1 min). On 12 occasions, we quantified the behavior of an individual, waited 10 min, and requantified the behavior of that individual. Correlation coefficients between estimates made in the first and second observation periods were 0.99, 0.75, and 0.91 for the proportion of time spent moving, the proportion of foraging attempts directed at the water surface, and foraging attempts per minute, respectively.

Several Monte Carlo simulations were used to assess the suitability of our sampling in relation to the activity and size of the fish. First, our selection of sedentary and mobile fish over each field season was not significantly different from that expected for random sampling of the sedentary and mobile fish available at the time of each selection, based on our visual counts ($P > 0.30$ and $P > 0.50$ for 1991 and 1992, respectively). Second, for the 42 fish captured in 1991 and for the 42 captured in 1992, the means and variances for the proportion of time spent moving and for fork length did not differ significantly from those expected for 1000 random samples of 42 fish selected from the 74 and 69 fish observed in 1991 and 1992, respectively.

Data were aggregated across sampling sites because earlier work has failed to reveal any significant differences among them (McLaughlin et al. 1992, 1994; McLaughlin and Grant 1994). It was also necessary to aggregate data on social behavior for 1991 and 1992 because of the low number of aggressive interactions observed.

For fish observed in the field, bimodality in frequency distribution for the proportion of search time spent moving was assessed using the saddle test in the MODECLUS procedure of SAS (1997). Fitness surfaces can be complex (e.g., have more than one peak) and difficult to characterize, particularly with small sample sizes (see Schluter and Nychka 1994). For fish collected from the field, we assessed how tissue concentration of RNA, our index of growth rate potential and short-term fitness, changed in relation to the proportion of time spent moving and the foraging attempts made per minute in four steps. First, we constructed contour plots characterizing the surface of this relationship. Second, we approximated the surface statistically by fitting the following polynomial equation:

$$Y = B_0 + (B_1 \times x_1) + (B_2 \times x_2) + (B_{11} \times x_1^2) + (B_{22} \times x_2^2) + (B_{12} \times x_1x_2) + (B_{111} \times x_1^3) + (B_{222} \times x_2^3) + (B_{122} \times x_1x_2^2) + (B_{112} \times x_1^2x_2) + (B_{1112} \times x_1^3x_2) + (B_{2221} \times x_1x_2^3)$$

where $Y$ was the tissue concentration of RNA, $x_1$ was the proportion of time spent moving, $x_2$ was foraging attempts made per minute, and $B$s represent the regression coefficients. This equation was selected because inspection of the contour plots suggested a simple second-order polynomial would not be adequate, particularly for our 1992 dataset, and preliminary analyses confirmed this. Third, we determined whether the overall, fitted equation was significant statistically and whether it described a saddle (minimax) system. A saddle system would indicate the existence of two distinct maxima (peaks) in growth rate potential (Khuri and Cornell 1996). Fourth, we constructed contour plots using the predicted values from the fitted equations and compared these visually with the surfaces obtained in the first step. The contour plots obtained from the fitted equations are provided here. For the analysis, tissue concentration of RNA was expressed on a relative scale, like relative fitness, by dividing each value by the sample mean.

For fish collected in our laboratory experiment, the relationship between tissue concentration of RNA and specific growth rate was analyzed using analysis of covariance, with food ration as a nominal, fixed effect and tissue concentration of RNA as a continuous effect.

## Results

### Behavior and growth rate potential in the field

In 1991 and in 1992, frequency distributions of the proportion of search time spent moving were somewhat U-shaped indicating that, during our observation periods, most individuals tended to spend little of their search time moving or much of their search time moving, and relatively fewer individuals tended to spend intermediate proportions of their search time moving (Fig. 1). For both distributions, the hypothesis of a single mode was rejected in favor of the hypothesis of two modes (clusters) (saddle test: $z = 2.3$, $P < 0.03$ and $z = 2.6$, $P < 0.03$, for 1991 and 1992, respectively).

Individuals that spent a large proportion of time moving directed more foraging attempts toward the water surface than did individuals that spent a small proportion of time moving ($r_s = 0.60$, $P < 0.0001$, $n = 74$ and $r_s = 0.56$, $P < 0.0001$, $n = 69$ for 1991 and 1992, respectively; Fig. 2a). They also made more foraging attempts per min (Fig. 2b). Overall, the variation in foraging behavior was very similar between years, although in 1992, the rate at which foraging attempts per minute increased with the proportion of time spent moving was significantly higher than in 1991 (regression coefficients: 0.016 vs 0.009, respectively; comparison of slopes: $F = 5.55$, $P < 0.02$, $df = 1{,}139$). The individuals spending most of their time moving in 1992 made more foraging attempts per minute than those spending most of the time moving in 1991, but there was little difference between years for fish that spent little time moving.

Fifty percent (71/143) of the individuals encountered another conspecific during an observation period. Of

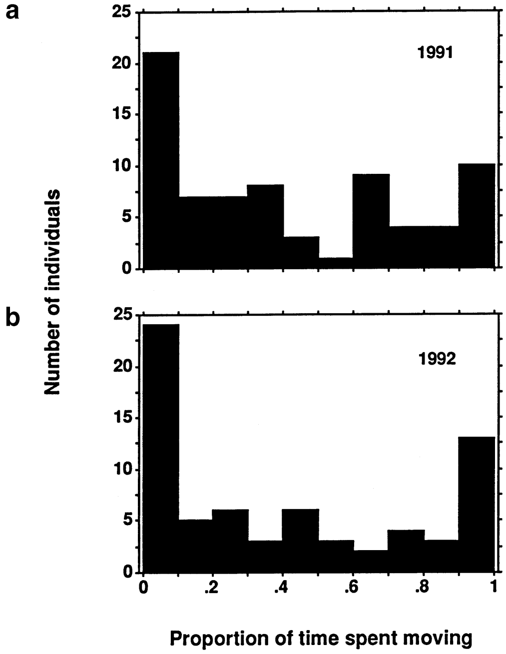

**Fig. 1** Frequency distributions of individual variation in the proportion of search time spent moving by recently emerged brook charr in still-water pools [$n = 74$ individuals in 1991 (**a**) and $n = 69$ in 1992 (**b**)]

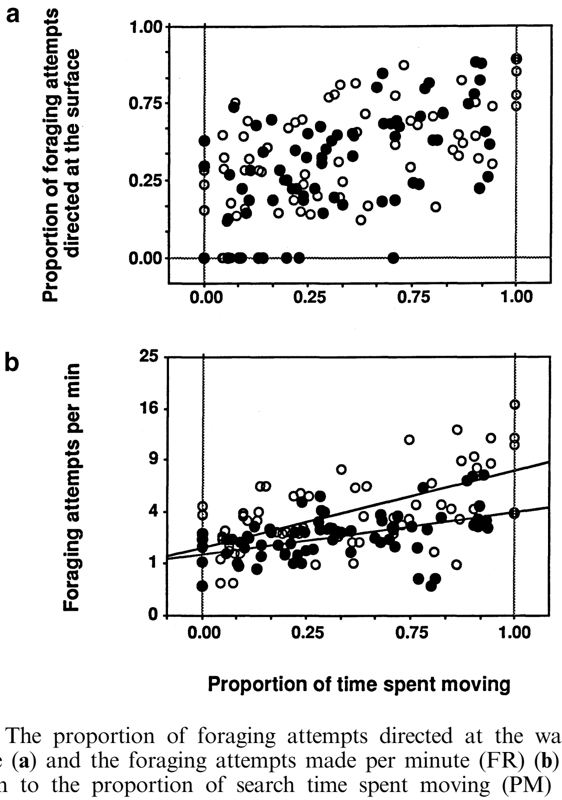

**Fig. 2** The proportion of foraging attempts directed at the water surface (**a**) and the foraging attempts made per minute (FR) (**b**) in relation to the proportion of search time spent moving (PM) by recently emerged brook charr. Each point represents an individual fish observed in 1991 (*closed circles*) or 1992 (*open circles*). Proportions are presented on an arcsine-square-root scale and foraging attempts per minute on a square-root scale. **b** Equations for regression lines are $FR^{1/2} = 1.18 + 0.009 \times \arcsin(PM^{1/2})$ ($r = 0.50$, $P < 0.0001$, $df = 72$) and $FR^{1/2} = 1.32 + 0.016 \times \arcsin(PM^{1/2})$ ($r = 0.63$, $P < 0.0001$, $df = 67$) for 1991 and 1992, respectively

these, 45% (32/71) were involved in at least one aggressive interaction and the probability of an individual becoming involved in an aggressive interaction upon encountering another fish was 0.33 (SE = 0.03). The rate of encounters with conspecifics and the rate of interactions were higher, on average, when local density was higher ($r_s = 0.30$, $P < 0.025$ and $r_s = 0.43$, $P < 0.005$, $df = 55$, respectively).

Of the 32 fish involved in aggressive interactions, 17 were categorized as aggressive and 13 as nonaggressive. Two could not be categorized. Frequency distributions for the proportion of time spent moving differed significantly between aggressive and nonaggressive fish (Kolmogorov-Smirnov two-sample test: $P < 0.025$; Fig. 3). Aggressive fish tended to exhibit either a low or high proportion of time spent moving (Fig. 3a), while nonaggressive fish tended to exhibit intermediate proportions of time moving (Fig. 3b). These intermediate levels of activity for nonaggressive fish were not a consequence of marked changes in activity before and after an aggressive interaction. The proportion of time nonaggressive individuals spent moving after an aggressive interaction was positively correlated with the proportion of time they spent moving prior to the interaction ($r = 0.63$, $P < 0.02$). There was also no consistent change in the proportion of time spent moving following an aggressive interaction (Wilcoxon matched-pair sign-rank test: $P > 0.60$).

Social interactions were closely linked to prey capture events with 36% of encounters (61/170) and aggressive interactions (23/64) occurring at the time a focal individual attempted to capture a prey item (Fig. 4). After statistically adjusting for variation in the proportion of time spent moving, moreover, aggressive individuals exhibited a higher rate of foraging attempts per minute than nonaggressive individuals (analysis of covariance: adjusted means = 4.4 and 2.4 foraging attempts per minute, respectively; $F = 9.70$, $df = 1,27$, $P < 0.005$; Fig. 5).

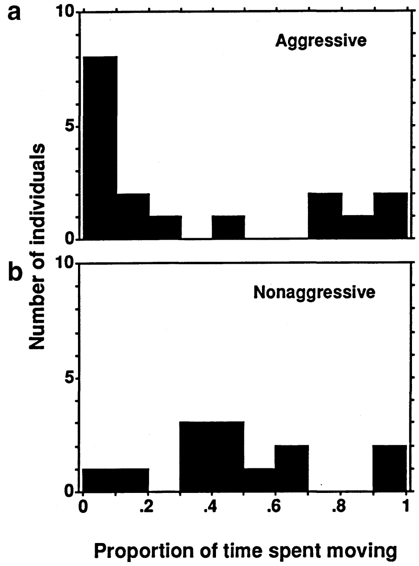

Fig. 3 The proportion of search time spent moving by recently emerged brook charr that were classified as aggressive (a) or nonaggressive (b) in social contests

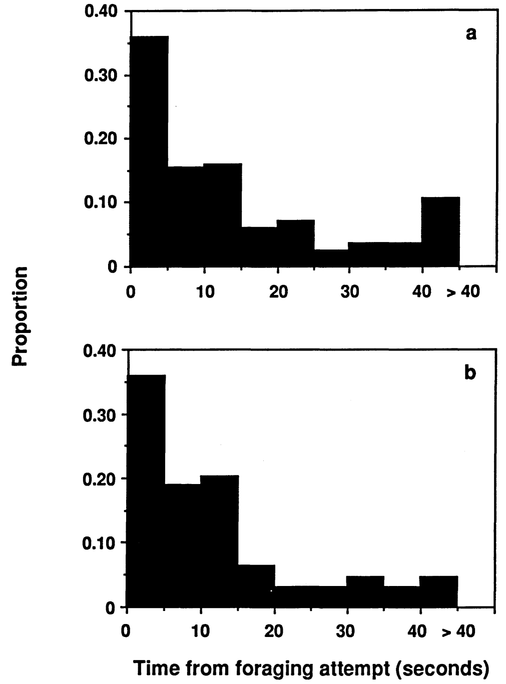

Fig. 4 The time interval between when a focal individual encountered a conspecific (a) or interacted aggressively with a conspecific (b) and the focal individual's most recent foraging attempt

For fish collected in the field, tissue concentrations of RNA ranged from 401 to 2077 μg per gram tissue (mean = 1185) in 1991 and 521–2078 μg per gram tissue (mean = 1259) in 1992. In both years, the relative concentration of RNA (growth rate potential) observed among individuals varied significantly with the propor-

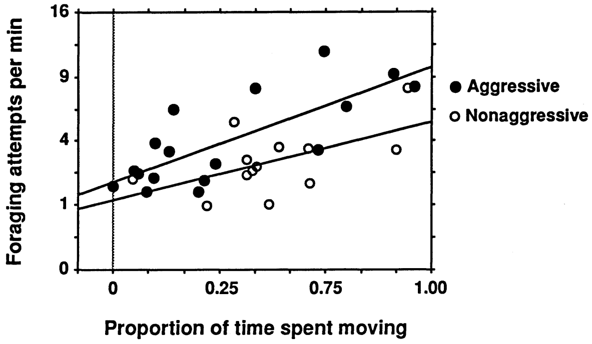

Fig. 5 Foraging attempts made per minute in relation to the proportion of search time spent moving by aggressive (*closed circles*) and nonaggressive (*open circles*) individuals. Proportion of search time spent moving is presented on an arcsine-square-root scale and foraging attempts per minute on a square-root scale

tion of time the individuals spent moving and the number of foraging attempts they made per minute ($F = 2.30$, $P < 0.04$, $df = 11{,}30$ and $F = 2.53$, $P < 0.025$, $df = 11, 29$, for 1991 and 1992, respectively). The fitted response surfaces (see Methods) accounted for 46% of the variation in growth rate potential in 1991 and 49% of the variation in 1992. In both years, growth rate potential was above average for fish exhibiting a low proportion of time spent moving and few foraging attempts per minute and for fish exhibiting a high proportion of time spent moving and many foraging attempts per minute (Fig. 6). Growth rate potential was average or below average for fish spending intermediate proportions of time moving, and for fish exhibiting a high proportion of time spent moving, but low foraging attempts per minute.

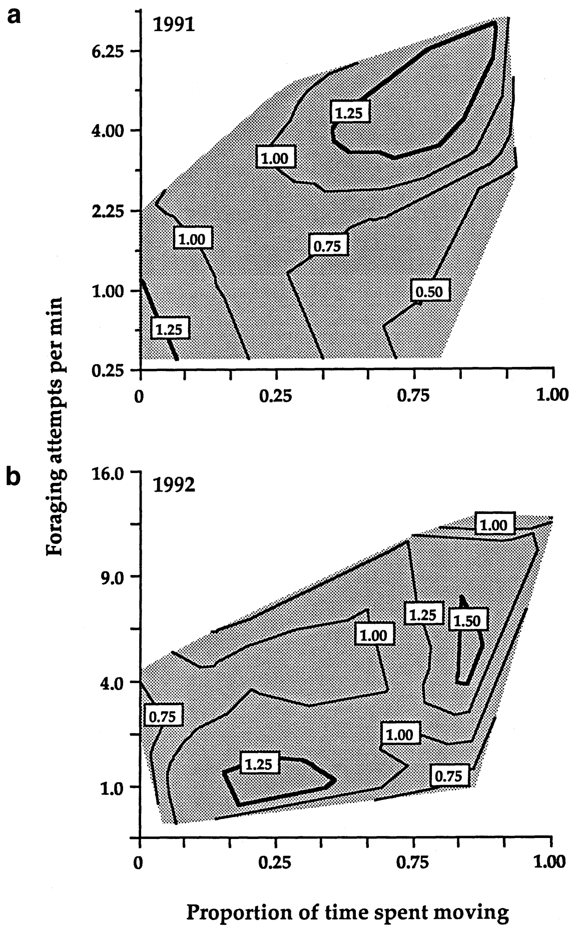

**Fig. 6** Tissue concentrations of RNA, an index of growth rate potential, in relation to proportion of search time spent moving and foraging attempts made per minute by recently emerged brook charr in 1991 (**a**) and 1992 (**b**). Like relative fitness, concentrations of RNA are expressed as multiples of the sample mean. Positions of peaks in RNA concentration are indicated by a *thicker contour line*. Proportion of search time spent moving is presented on an arcsine-square-root scale and foraging attempts per minute on a square-root scale

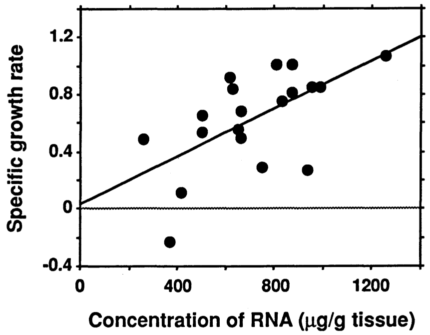

**Fig. 7** Leverage plot showing the relationship between specific growth rate and tissue concentrations of RNA after statistically controlling for daily food ration

### Concentration of RNA and growth rate in the laboratory

In our laboratory experiment, the tissue concentration of RNA and food ration explained 68% of the variance in specific growth rate. There was no significant, statistical interaction between concentration of RNA and food ration, suggesting they affected growth rate independently ($F = 1.45$, $df = 3{,}11$, $P > 0.25$). After statistically adjusting for food ration, fish with higher tissue concentrations of RNA grew faster than those with lower concentrations of RNA, as expected (partial $r = 0.60$, $F = 7.77$, $df = 1{,}14$, $P < 0.02$; Fig. 7). After statistically adjusting for the tissue concentration of RNA, fish given a higher food ration grew significantly faster than those given a lower food ration ($F = 8.55$, $df = 3{,}14$, $P < 0.002$).

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## Discussion

Our findings are consistent with the hypothesis that the variation in foraging behavior exhibited by recently emerged brook charr in the field represents diversification brought about by intraspecific competition in the presence of alternative food sources. The support comes from four significant features of our brook charr system. First, the conspicuous, bimodal variation in the proportion of time spent moving during search for prey is correlated with diet and microhabitat (water column) use, with more sedentary individuals feeding on aquatic crustaceans from the lower portion of the water column and more active individuals feeding on insect prey from the upper portion of the water column (Grant and Noakes 1987b; McLaughlin et al. 1994; this study). Second, density-dependent rates of encounters and aggressive interactions between conspecifics, plus the temporal proximity between this social behavior and prey capture attempts, indicate that intraspecific competition (sensu Milinski and Parker 1991) is occurring on a local scale (this study). Intraspecific competition is a common feature of this system in particular (this study; Grant 1990), and stream-dwelling populations of salmonid fishes in general (Elliott 1990b; Grant and Kramer 1990; Nakano 1995; Fausch et al. 1997). Third, aggression is correlated with the variation in foraging behavior (this study). Aggressive fish tend to be either inactive or very active, while nonaggressive fish tend to exhibit intermediate levels of activity. Aggressive fish also exhibit substantially higher rates of foraging attempts, for a given level of activity, than do nonaggressive fish. Fourth, growth rate potential, an important component of fitness during this early life stage, is also correlated with the variation in foraging behavior and supports the notion of short-term diversifying selection on foraging behavior (this study).

The reason for the lower growth rate potential of individuals exhibiting intermediate levels of activity while searching for prey is not entirely clear. It appears that switching between foraging tactics entails a tradeoff, possibly due to learning (Bence 1986) or travel costs (Murdoch et al. 1975). Searching for benthic (crustacean) prey and surface (insect) prey is certainly mutually exclusive to some degree. For example, brook charr switching from hovering to moving reduce the proportion of foraging attempts they direct at the substrate and increase the proportion they direct at the water surface, and vice versa (Grant and Noakes 1987b; R. McLaughlin, unpublished data). Correlated shifts in mobility and water column use have also been reported for dolly varden charr (*S. malma*) inhabiting pools of running water (Fausch et al. 1997), although the nature of the shifts is different in running water than it is in the still-water pools we have studied. Furthermore, brook charr switching from hovering to moving also experience a reduced probability of capture upon attack for benthic prey and an increased probability of capture upon attack for midwater prey, while the probability of capture upon attack for surface prey remains unchanged (R. McLaughlin, unpublished data). Lastly, analysis of stomach contents has demonstrated the likelihood an individual has eaten an benthic prey is negatively correlated with the likelihood it has eaten a surface prey (McLaughlin et al. 1994).

The conclusion that diversifying selection on foraging behavior is occurring within our study system depends upon the adequacy of growth rate potential as an index of fitness, at least over the short term. We believe that growth rate potential is the best available field measure of fitness for recently emerged brook charr. The evidence available for stream-dwelling salmonids, including brook charr, indicates that increased growth rate improves fitness through size-dependent effects on survival during the first few weeks of high mortality following emergence from the gravel (e.g., Elliott 1989, 1990a, 1990b; Hutchings 1991). We do not know how long the growth differences we observed are maintained, but evidence from a variety of salmonid fishes indicates that behavioral differences arising early in life can have important longer-term consequences (e.g., Metcalfe et al. 1989; Nielsen 1992). For brook charr, increased growth rate over the longer term improves fitness through size-selective overwinter survival (Hunt 1969; Shuter and Post 1990) and size-dependent effects on fecundity (Hutchings 1993, 1996). Finally, faster growth is favored when mortality and competition are size dependent and when there are time constraints on reaching a minimum size (Arendt 1997).

Recent reviews of the evolution of growth rate have reiterated that there can be tradeoffs associated with increasing growth rate, although these tradeoffs are not all well understood (Arendt 1997; Conover and Schultz 1997). Predation risk is the most obvious and important fitness component which is not considered by our measure of growth rate potential, and animals will accept a lower growth rate to avoid predators (Werner and Gilliam 1984). Based on our experience with this system, predation risk, at least while the charr are foraging, is likely low and does not differentially affect one behavioral phenotype over another. This stream system is relatively free of piscivorous fishes and the individuals large enough to be potential, facultative piscivores remain in the main stream channel, away from the small, shallow pools occupied by recently emerged brook charr. Larger semi-aquatic predators, such as mink, herons, and kingfishers are seen occasionally, but at 2–3 cm in length, recently emerged brook charr are well below the minimum prey length of 5+ cm normally eaten by these predators (Alexander 1991; R. McLaughlin personal observation). Invertebrate predators, including diving beetles, water scorpions, and larvae of large odonates, are also seen occasionally and can eat small fish, but in 10 years of field research we have never seen one attempt to capture a young brook charr. Despite our observations, however, examining how individual brook charr adjust their foraging behavior in response to the presence of potential predators remains a question we need to address further.

Although we have provided evidence for two peaks in growth rate potential, the peaks sometimes did not correspond exactly with the peaks in the proportion of time spent moving (Fig. 1) or in aggressive behavior (Fig. 4). The discrepancy may represent sampling error, as the data regarding each attribute come from different subsamples of the fish we observed. Alternatively, this may reflect the impact that unmeasured components of fitness (see above) have on behavior, or reflect constraints on the ability of these very young fish to assess the level of activity where growth rate potential is high. The relationship between behavior and growth rate potential is also more complex than we expected, depending on the rate of foraging attempts as well as the proportion of time spent moving. Superficially, the dependency on foraging rate appears inconsistent with our laboratory experiment, where RNA concentration was unaffected by food ration. In our laboratory experiment, however, none of the fish were deprived of food. In the field, conversely, some fish are not receiving adequate amounts of food, as evidenced by empty digestive tracts (McLaughlin et al. 1994; McLaughlin and Grant 1994).

Concentrations of RNA will decline when charr are deprived of food for periods of 5 days or more (McLaughlin et al. 1995).

Our research on recently emerged brook charr provides a useful complement to the literature on resource polymorphisms in four ways. First, we have focused uniquely on foraging tactics exhibited by behaviorally flexible individuals from a population without distinct morphological variants, whereas the existing literature on resource polymorphisms has focused almost exclusively on fixed differences in behavior exhibited by distinctly different morphotypes (see Smith and Skúlason 1996). For example, the work of Schluter (1993, 1995, 1996) demonstrating foraging and growth rate tradeoffs in three-spine sticklebacks (*Gasterosteus aculeatus*) involved comparisons of species pairs. More recently, Robinson et al. (1996) demonstrated that individual pumpkinseed sunfish (*Lepomis gibbosus*) with extreme benthic and limnetic morphologies had higher condition factors and exhibited faster growth rates than did individuals of intermediate morphology. Their examination was particularly stringent because they focused on intraspecific variation, and the morphological differences among individuals were subtle in the study population. Our brook charr system appears to represent an even more subtle, but similar form of diversification in foraging behavior. Moreover, our findings come from a species where more discrete resource polymorphisms have been reported in other, lake populations (Robinson and Wilson 1994; Bourke et al. 1997). Therefore, our findings are relevant to speculation regarding the role of behavioral diversification during initial steps in the evolution of distinct feeding morphs (Skúlason and Smith 1995; Smith and Skúlason 1996).

Second, despite possessing the pitfalls of a descriptive field study, our study has provided evidence suggesting short-term, divergent selection in a system where individuals exhibit diverse foraging tactics. Testing the hypothesis that behavioral or morphological diversification is brought about by divergent selection for efficient resource use is a significant challenge and examples are uncommon (but see Hori 1993; Smith 1993; Schluter 1993, 1994, 1995; Robinson et al. 1996). Although some uncertainties remain, our findings are even more remarkable because the behavioral tactics we observed are not reinforced by differences in body size or shape (McLaughlin et al. 1994) and individuals can switch between tactics.

Third, because of our ability to observe the behavior directly in the field, our findings complement the large literature for lacustrine fishes where the significance of behavior has been largely inferred from conspicuous differences in foraging morphology and diet, rather than demonstrated through direct observation (see Robinson and Wilson 1994; Robinson et al. 1996). The complementarity is important for improving our understanding of the role of behavior in producing and maintaining resource polymorphisms, particularly because the behavior of fishes is often difficult to observe under natural conditions.

Finally, our system provides a unique example where generalizations regarding the adjustments in prey-searching behavior and the tradeoffs reported in earlier laboratory experiments examining fishes switching between benthic and limnetic niches (e.g., Murdoch et al. 1975; Ehlinger 1989, 1990; Savino and Stein 1989) can be observed and measured, albeit more crudely, in the field. Findings from small-scale, controlled laboratory studies may not extrapolate well to larger-scale, more complex field (lake) environments (e.g., Skúlason et al. 1993), particularly when activity is the significant behavior of interest (Lindsey 1978). Results from this system, however, are pertinent to larger-scale, lake systems, despite the simplicity and smaller scale of the system (see Robinson and Wilson 1994; Biro and Ridgway 1995; Biro et al. 1996; Bourke et al. 1997; McLaughlin and Noakes, in press).

Why the conspicuous morphological variation observed relatively frequently in lacustrine fishes is not observed in our study system, in particular, and rarely in stream fishes in general (Wimberger 1994), is an interesting question. It could be that subtle variation does exist, but has gone undetected. A more likely explanation, however, is that the temporal and spatial variability of benthic and limnetic resources is higher in streams than in lakes. Consequently, generations of stream fishes are less likely to spend significant portions of their lives in a specific niche (e.g., Fausch et al. 1997) in the way some lake fishes are thought to, hence the evolution of alternative morphs would not be expected. With our system in particular, developmental changes in habitat use as well as learning and swimming ability are probably important. The young charr only inhabit the still-water pools during spring and early summer, and later move into deeper, flowing water.

The temporal stability of the behavioral variation observed among the charr in still-water pools remains a related, interesting, but unanswered question because of the logistical difficulties of marking and reobserving these small fish. Short-term repeated measurements of behavior (see Methods), the correlations between activity and both diet and growth rate potential, and longer, qualitative observations in the field, lead us to believe that some individuals exhibit longer-term repeatability in their behavior, while some probably do not. Further, a variety of studies have demonstrated longer-term, repeatable, individual differences in social and foraging behavior for wild salmonids (Bryan and Larkin 1972; Nielsen 1992; Nakano 1995; Bourke et al. 1997). In particular, one recent, field enclosure study with marked, recently emerged brook charr from a lake population has revealed repeatable differences, over several weeks, in the proportion of time spent moving during search for prey (P. Biro, personal communication). In fact, we are unaware of a study on salmonids which has attempted and failed to find individual differences in behavior, although it is also clear that stream-dwelling salmonids will alter their behavior in response to changes in the abundances of benthic and surface prey (Fausch et al. 1997). The fact that the behavioral differences we observe for brook charr may not represent fixed, long-term specializations may seem disadvantageous given the current emphasis on resource polymorphisms exhibiting well-defined morphs. However, from the perspective of understanding the early stages of resource polymorphisms, when individuals are still expected to possess a high degree of behavioral flexibility, it is not. Part of identifying the ecological conditions favoring resource polymorphisms requires that we examine populations with more flexible behavior and less pronounced variation in morphology.

For many years behavioral ecologists have promised that understanding the behavior of individuals could provide valuable insights into population-level processes (Krebs and Davies 1991), with some success (e.g. Metcalfe et al. 1989; Sutherland 1996; Fryxell and Lundberg 1997). Our brook charr system provides an example where ideas developed by behavioral ecologists could be very useful for examining the role adaptive, individual behavior plays in one important population-level phenomenon – the evolution of resource polymorphisms.

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