AN EXPERIMENTAL STUDY OF FORAGING AGGRESSION IN TWO SOUTHEASTERN MINNOWS:

IMPLICATIONS FOR AN ONGOING INVASION

by

C. MICHAEL WAGNER

(Under the Direction of Gary D. Grossman)

ABSTRACT

Competitive aggression is a trait often assumed important in the establishment of invasive species. I examined the effects of competitive aggression on the group foraging dynamics of two southeastern minnows, the native rosyside dace (*Clinostomus funduloides*), and the introduced yellowfin shiner (*Notropis lutipinnis*). Specifically, my research addressed three primary objectives: (1) to examine the functional value of aggression to non-territorial, socially foraging stream fishes; (2) to identify mechanisms related to competitive aggression that may have promoted the establishment yellowfin shiner in Coweeta Creek, N.C.; and, (3) to determine if interspecific competition between rosyside dace and yellowfin shiner is mediated by flow. Both yellowfin shiner and rosyside dace readily developed social hierarchies in the presence of food where behaviorally dominant (i.e., aggressive) individuals gained a significant feeding advantage by defending positions upstream of conspecifics. Increasing food abundance within the range of natural variation did not affect this relationship. Increasing food abundance did result in an increase in per capita aggression rates for yellowfin shiner, but not rosyside dace, partially supporting the predictions of resource defense theory. Overall, the yellowfin shiner was both more aggressive and more likely to exhibit aggression than the rosyside dace. A patch-choice experiment also revealed yellowfin shiner were more capable than rosyside dace of meeting a key prediction of the Ideal Free Distribution (input-matching) when food was abundant. In concert, these findings suggest the invasive yellowfin shiner may be better at detecting high quality patches, and more able to acquire the best positions in those patches, when competing with the native rosyside dace. However, the rosyside dace is a more efficient forager in high velocity patches. In a test of foraging success in mixed-species groups, the heightened aggression of the invasive species did allow it to monopolize the forward positions at two velocities (10 and 20 cm s^{-1}) and two group sizes (four and eight fish). However, the greater foraging efficiency of the rosyside dace allowed it to feed at a higher rate than the invasive at high velocities despite occupying subordinate positions in the hierarchy. This ability was reduced at the larger group size.

INDEX WORDS: Aggression, *Clinostomus*, Condition-specific competition, Dominance, Food abundance, Foraging, Ideal free distribution, Interspecific competition, Intraspecific competition, Invasive species, *Notropis*, Resource defense, Social hierarchy, Stream fish.

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INTRODUCTION AND LITERATURE REVIEW

In his seminal book, C. S. Elton (1958) warned "... we must make no mistake; we are seeing one of the greatest convolutions of the world's flora and fauna." He was speaking of the human-mediated biological invasions which accompany the expansion of human civilization (Crosby 1986) and greatly alter patterns of global biodiversity (Vitousek et al. 1997). In fact, the impact of biological invasions on native biota is so great, it is considered second in importance only to habitat destruction (Wilson 1992). Freshwater ecosystems have proven especially vulnerable to this 'rising tide' of invasive species (Claudi and Leach 1999, Fuller et al. 1999, Kolar and Lodge 2000). In the United States alone, the rate of fish introductions has tripled in the last half of the twentieth century (Fuller et al. 1999). The introduction of new species dramatically reduces the faunal distinctiveness of biogeographic regions (Brown 1989, Lodge 1993, Rahel 2002), imperils unique indigenous faunas (Reinthal and Kling 1997, Scott and Helfman 2001), and may even compromise human health (Bright 1998).

Although we currently lack a general theory of biological invasions (Parker et al. 1999), ecologists have long wondered why some animals readily establish in new environments, while others, often closely related, do not (Elton 1958, Ehrlich 1989). Early efforts to identify the general traits of an invasive organism based on cataloging the ecological, genetic, and life-history characteristics of successful invaders have met with limited success (Lawton and Brown 1986, Ehrlich 1989, Lodge 1993), prompting some to call for a change in focus to more reductionist approaches based on well-developed theoretical mechanisms of community assembly (Shea and Chesson 2002). For example, recent studies have successfully employed manipulative field and laboratory experiments to test hypotheses concerning the factors controlling invasion success (Bergelson et al. 1993, D'Antonio 1993, Dick et al. 1995) and identify the competitive mechanisms responsible for invader superiority (Petren et al. 1993, Petren and Case 1996, Thebaud et al. 1996, Juliano 1998, Holway 1999). It is becoming increasingly clear that testing the specific mechanisms that promote the success of invasive species will lead to a broader understanding of both invasion biology and the natural process of community assembly (Karieva 1996, Kolar and Lodge 2001, Sakai et al. 2001, Shea and Chesson 2002).

One trait commonly invoked to explain the success of invasive animals is competitive aggression (Holway and Suarez 1999). This observation arises from studies across a range of taxa and habitats, with examples from studies of amphipods (Dick et al. 1995), ants (Human and Gordon 1999), bees (Winston 1992), crayfish (Gamradt et al. 1997), geckos (Bolgar and Case 1992), and fishes (Rincón et al. 2002). A central theme of this dissertation is the behavioral ecology of foraging aggression. The main objective is to develop a mechanistic understanding of the consequences of aggressive behavior for socially foraging stream fishes, using ecologically similar native and invasive species as test subjects. By doing so, I hope to reveal behavioral mechanisms which promote the establishment of invasive species in a context which adds to our theoretical understanding of aggression.

Aggressive behavior is very common among vertebrates, and it usually arises when the interests of individuals come into conflict (Huntingford and Turner 1987, Archer 1988). If it is advantageous for an individual to fight for food, then instead of fighting over each item, it can be energetically more efficient to defend a space which grants priority access to food (Wilson 1975). The decision to defend space is affected by extrinsic and intrinsic factors. The distribution of resources in the environment must be defensible, and the decision to fight for access must yield a greater fitness than alternative tactics such as scrambling (Brown 1964). The defense of space can lead to the emergence of several forms of social organization, with territoriality and the formation of dominance hierarchies being the most common (Maher and Lott 2000). Territoriality appears relatively rare among freshwater fishes (Barlow 1993), although general mechanisms which suppress the development of territorial behavior in aquatic ecosystems remain elusive. Alternatively, dominance hierarchies are frequently observed in laboratory and field studies of socially foraging stream fishes (e.g., Metcalfe et al. 1989, 1990, Hughes 1992).

Studies of aggression with stream-dwelling organisms demonstrate that variation in the rate of aggression is often directly related to the renewal rates of food within the habitat (salmonid fishes, Grant and Noakes 1988, Grant 1993, Hutchinson and Iwata 1997; water striders, Blanckenhorn et al. 1988). These organisms are typically drift-feeders who maintain stationary feeding positions and intercept prey carried downstream by the current. The benefits of intraspecific dominance in territorial stream dwelling salmonid fishes are particularly well studied and a general model has emerged. Individuals of high rank defend discrete territories at the forward end of favorable habitat patches which afford them priority access to drifting prey (Hughes 1992). Dominance hierarchies form such that an individual's social rank will match the rank desirability of an individual's spatial position (Hughes 1992). High social rank often is associated with high aggression rate (Fausch 1984, Grant 1990), and has been correlated with increases in body size and growth rate (Mason and Chapman 1965, Li and Brocksen 1977, Sloman et al. 2000). Ultimately, intraspecific aggression can contribute to density-dependent population regulation in these species as subordinate individuals that are excluded from profitable foraging sites often show reduced growth, emigrate, or die (Li and Brocksen 1977, Elliot 1990, Grant and Kramer 1990, but see Höjesjö et al. 2002). Given the potential strong linkages between aggression, resource use, and population regulation, it is crucial to know the extent to which the salmonid model applies to stream-dwelling fishes overall, especially given that most stream fishes are non-salmonids. This dissertation builds upon the foraging aggression models developed largely for salmonid fishes, and adds to the literature by exploring their validity with native and invasive cyprinid fishes.

In this study, I quantified the relative effects of foraging aggression on the feeding behavior of two stream cyprinids, the native rosyside dace (*Clinostomus funduloides*) and the introduced yellowfin shiner (*Notropis lutipinnis*). My goals were to quantify the dynamics of foraging aggression in a laboratory setting, and to determine what role heightened behavioral aggression may play in the establishment of yellowfin shiner in Coweeta Creek, N.C. I pursued an experimental approach to these problems. I mapped the functional relationships between foraging aggression, position within a fish shoal, and foraging success in intraspecific groups of rosyside dace and yellowfin shiner (Chapter 1). I also examined the effect of increasing food abundance on the patterns of foraging aggression within groups, comparing the findings to a well-described general model of resource defense (Chapter 2). Chapters three and four focus on two mechanisms of invasion success which may derive from aggressive foraging behavior. In Chapter 3, I investigated the relative ability of native and invasive minnows to track and match the distribution of resources in a two-patch habitat, applying the Ideal Free Distribution (Fretwell and Lucas 1970, Fretwell 1972) as a null expectation. Finally, I investigated how a feature of hydrology (velocity variation) influences the outcome of interspecific competition between rosyside dace and yellowfin shiner (condition-specific competition, Chapter 4).

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CHAPTER 1

COMPETITIVE AGGRESSION AND FORAGING SUCCESS IN SMALL GROUPS OF NATIVE AND INVASIVE DRIFT-FEEDING MINNOWS

Wagner, C. M. and G. D. Grossman. Submitted to *Animal Behaviour*.

Abstract

The aggressive monopolization of foraging positions is an important mechanism of competition in group-living species. This is particularly true in streams where the predominantly unidirectional flow of drifting prey imposes a natural ranking template onto foraging positions. We used eight replicate intraspecific groups of native (rosyside dace, *Clinostomus funduloides*) and invasive (yellowfin shiner, *Notropis lutipinnis*) minnows to: 1) determine whether groups of foraging minnows assemble into detectable social hierarchies; 2) test the general prediction that aggressive individuals will acquire forward positions in foraging groups and capture a larger proportion of drifting prey items; and, 3) evaluate the effect of a natural range of food abundance on the functional value of foraging aggression. Each group of six adult fish competed for drifting prey released from the upstream end of a laboratory artificial stream at two rates. Aggression was common only when drifting prey were available. At the onset of feeding positional arrangements within groups changed significantly and stabilized after 10-15 minutes of aggressive interactions. As predicted, the most aggressive foragers of both species acquired forward positions in groups and captured a greater proportion of drifting prey. Fifteen of 16 groups assembled into significant social hierarchies when observations from both prey treatments were combined, although rank switching between hierarchy neighbors was common between treatments. Increasing food abundance had no effect on the functional value of aggression for either species, and there were no marked differences in the utility of aggression between native and invasive species. Aggression in these non-territorial cyprinids appears to be a flexible tactic which potentially increases the fitness of dominant individuals. These patterns are in conceptual agreement with current models of territorial aggression in resource queues.

Introduction

Competition for food frequently is determined by relative foraging success. When socially foraging animals compete intraspecifically, competitive dominance often is maintained through the use of behavioral aggression (Huntingford and Turner 1987, Archer 1988). It is generally assumed, but rarely demonstrated, that individuals with high feeding ranks will display high growth rates and ultimately enjoy high reproductive success (Giraldeau and Caraco 2000). Such feeding hierarchies have been observed in a variety of vertebrate taxa including fishes (e.g., Metcalfe et al. 1989, 1990, Petursdottir 2002). Socially foraging animals should use aggression when competing for access to a limiting resource only if the benefits of defense exceed the costs (i.e., resources are 'economically defensible' sensu Brown, 1964). Thus, the social behavior of animals reveals a dynamic social structure that connects a population to its habitat (Krause and Ruxton 2002).

Several studies have demonstrated that resources become defensible when they: 1) are spatially clumped (Isbell 1991, Grant and Guha 1993); 2) are temporally dispersed (Blanckenhorn 1991a, Grant and Kramer 1992, Bryant and Grant 1995); 3) occur in large patches (van Schaik 1989); 4) are not easily partitioned (Elgar 1986); or, 5) are temporally persistent (Janson 1990, Isbell et al. 1998). Under these conditions access to food is easily monopolized and dominant individuals may usurp resources from subordinates through behavioral acts such as supplantation or competitive aggression (Francis 1988, Drews 1993, Grant 1993). Thus, the distribution of food in the environment is a key economic factor which mediates the ability of an aggressive forager to effectively monopolize access to food. Ultimately, such conditions are thought to contribute to the evolution of foraging aggression, social dominance hierarchies, and territoriality in group-living species (Isbell 1991, Lott 1991, Krause and Ruxton 2002).

Natural streams are variable at multiple spatial and temporal scales (reviewed in Resh et al. 1988). Barlow (1993) contended such variation may explain the general rarity of feeding territoriality among freshwater fishes. Although certain environmental conditions in streams (e.g., discharge, temperature) routinely undergo significant temporal variation on scales from hours to seasons, it appears the larger scale habitat features around which the distributions of fishes are largely organized (e.g., pool-riffle sequences) are fairly stable (Allan 1995, Weins 2002). Within these mesohabitats, fishes routinely form foraging aggregations in patches of high food availability (Power 1984, Freeman and Grossman 1992). In temperate streams, high quality foraging patches are not continuous and occur as discrete patches contained within a less favorable matrix. There is substantial evidence that resident fishes know and respond to the distribution of favorable and unfavorable patches within their local habitat (Power 1984, Hughes 1998, Matthews 1998). An additional feature of streams is the predominantly unidirectional nature of prey delivery (i.e., drifting insect larvae) for many drift-feeding organisms. It is this feature, overlaying the distribution of high quality patches within mesohabitat units, that establishes an economically favorable template for the evolution of aggression among drift-feeding fishes. Unfortunately, we know little about the aggressive behavior of the majority of stream fishes, with the exception of salmonids.

Several studies of aggression in stream organisms do show that variation in the rate of intraspecific aggression can be directly related to the renewal rates of food within a habitat (salmonid fishes, Grant and Noakes 1988, Grant 1993, Hutchinson and Iwata 1997; water striders, Blanckenhorn et al. 1988). These organisms generally hold feeding positions in streams and intercept prey items carried downstream by the current. The benefits of intraspecific dominance in territorial stream dwelling salmonid fishes are particularly well studied and a general model has emerged. Individuals of high rank defend discrete territories at the forward end of favorable habitat patches which afford them priority access to drifting prey (Hughes 1992). Dominance hierarchies form such that an individual's social rank will match the rank desirability of an individual's position (Hughes 1992). High social rank often is associated with high aggression rate (Fausch 1984, Grant 1990) and has been correlated with increased body size and growth rate (Mason and Chapman 1965, Li and Brocksen 1977, Sloman et al. 2000). Nonetheless, it is unclear whether large body size is the cause or an effect of aggression (Huntingford et al. 1990, Adams et al. 1998). Ultimately, intraspecific aggression may contribute to density-dependent population regulation in these species as subordinate individuals that are excluded from profitable foraging sites often show reduced growth, may emigrate, or die (Li and Brocksen 1977, Elliot 1990, Grant and Kramer 1990, but see Höjesjö et al. 2002). Given the potential strong linkages among aggression, resource use, and population regulation, it is crucial to know the extent to which the salmonid model applies to stream-dwelling fishes in general, especially given that most stream fishes are not salmonids.

A recent area of interest in behavioral ecology is the relationship between aggression and successful establishment of invasive fishes (e.g., Savino and Kolar 1996, Rincón et al. 2002, Warburton and Madden 2003). When a new species is introduced into a community, we are presented with an opportunity to identify the mechanisms by which invaders potentially gain their competitive advantage (Brown 1989, Petren and Case 1996, Juliano 1998, Melville 2002). Because an invasive species (yellowfin shiner, *Notropis lutipinnis*) had recently been introduced into a system that we have been studying for 20 years (see Grossman et al. 1998, 2002), we chose to compare the aggressive behavior of this species to that of an ecologically similar native species (rosyside dace, *Clinostomus funduloides*) (Grossman and Ratajczak 1998, Grossman et al 2002). Our aim was to evaluate the role of aggression in the foraging success of non-territorial stream fishes across a natural range of prey availability, and to explicitly compare the functional value of aggression between native and introduced species. Specifically, we experimentally evaluated whether: 1) minnows exhibited large variation in their aggressive tendencies; 2) this variation in aggression supported the generation of linear social hierarchies; 3) differences in body size were associated with social rank within the hierarchies; 4) dominant individuals acquired forward positions in foraging groups; and, 5) individuals occupying forward positions acquired a significantly greater share of the drifting food items. We also investigated whether the nature of these relationships change as a function of food abundance.

Methods

Study System

The rosyside dace, (aka smoky dace, Warren et al. 2000), *Clinostomus funduloides*, is native to streams of the Little Tennessee River drainage in western North Carolina where it is currently listed as a Species of Special Concern (North Carolina Wildlife Resources Commission). In Coweeta Creek NC, rosyside dace forage continuously during daylight hours in pools and select microhabitats (focal point velocities) that maximize prey capture success (Grossman and Freeman 1987, Facey and Grossman 1992, Hill and Grossman 1993, Grossman and Ratajczak 1998, Grossman et al. 2002).

Rosyside dace forage alone or in groups on drifting invertebrates (Stouder 1990), and occasionally direct aggression to neighboring foragers (Grossman and Freeman 1987, Freeman and Grossman 1992). Their aggression rates are generally low and consistent with a tactic of maintaining position relative to other foragers vs. an exclusive-use territory (Rincón and Grossman 2001). Conversely, the yellowfin shiner (*Notropis lutipinnis*) was introduced into the headwaters of the Little Tennessee River system around 1990 and has been progressively expanding its distribution in this drainage (Johnston et al. 1995, W. McClarney pers. comm.). Yellowfin shiners were well established in Coweeta Creek by the mid-1990's and are now sympatric with rosyside dace. Both yellowfin shiner and rosyside dace occupy similar focal point velocities and choose these focal points using an energy-maximization strategy (Grossman et al. 2002). Although little is known of the general foraging ecology of yellowfin shiners, preliminary observations suggest that it is more aggressive than rosyside dace.

Laboratory Apparatus

We conducted the experiment in an artificial stream (Fig. 1.1) equipped with an automatic feeder (Fig. 1.2). The plexiglass tank measured 305 cm × 152 cm × 76 cm (l × w × d) and was vertically divided into upper (fish observation) and lower (water return) reaches separated from each other by a 6 mm-thick opaque plexiglass false-bottom. Upper and lower reaches were further divided into two separate channels by an opaque plexiglass partition running the entire length of the tank. Within each of the upper channels, we confined the fish to a 70 × 75 cm (length × width) feeding area with a 30 cm water depth and a substrate of pebbles (5-15 mm in diameter and 2-4 cm deep) interspersed with cobbles (30-100 mm) to simulate natural pool habitats in Coweeta Creek (Grossman and

Freeman 1987). For each trial, we adjusted the flow such that water velocities throughout each feeding area (50 uniformly dispersed measurements) lay within ± 1 cm s^{-1} of the test velocity (see Experimental Procedures). The tank was completely clad with an opaque cover to ensure the fish could not see the observer during any stage of the experiment. We made behavioral observations from within a completely enclosed and darkened booth adjacent to the artificial stream. We observed the fishes through small, complementary slits in the booth and the cladding of the tank. The experimental fish never responded to movements or sounds generated by the observer.

We constructed an automatic feeder (Fig. 1.2) to supply prey at rates which were set individually for each feeding area. Prey items were kept in suspension in a 17-l brine shrimp hatching tank via aeration. A stand-alone controller (programmable dual-mode repeat-cycle timer) operated 9 mm pinch valves encased in a sound-proofed box which opened and closed according to operator settings. Aliquots of prey were released when a valve was opened, allowing water to flow from the feeder tank into the experimental reach of the fish tank via a silicone tube. We ran the feeding tubes under the gravel and dispensed prey at the level of the substrate at the head of each feeding area to simulate the natural entry of food items into the drift. We sub-divided each tube to yield two entry points 25 cm apart in each channel. In addition, we fitted the ends of the tubes with Y-connectors to effectively disperse the prey over a 50 cm-wide area simulating a single diffuse patch (Fig 1.1). To calibrate the feeder we developed a regression relationship between prey release rate and the amount of prey loaded into the feeder for a single commercial supplier of chironomid larvae (number of prey released per one second opening = -0.34 + 0.69 * total prey load in the feeder in grams; $r^2 = 0.89$, $P < 0.0001$).

Capture, Holding, and Preparation of Experimental Subjects

We captured wild, adult yellowfin shiner (means ± SD: standard length, 62.1 ± 2.0 mm; weight, 3.41 ± 0.38 g) and rosyside dace (standard length, 70.4 ± 4.2 mm; weight, 5.01 ± 0.92 g) approximately weekly between 15 July and 30 October 2001 from Coweeta Creek, a fifth-order tributary stream of the Little Tennessee River located in the highlands of western North Carolina. To minimize stress we encircled the fish with deep seine nets, removed them from the stream by hand in small containers of water, and transported them in an insulated live-well equipped with a recirculating pump, chiller, and aeration. Upon return to the laboratory, we transferred the fish into one of two 550-l recirculating holding tanks and maintained them at conditions typical for Coweeta Creek during late summer (18° C with a constant flow ranging from 3-10 cm s^{-1}). A 14:10 h light:dark schedule was maintained in the laboratory with 60 minute crepuscular periods to simulate normal sunrise/sunset cycles.

Within three days of capture, each fish was anaesthetized in a dilute solution of tricaine methane sulfonate (70 mg l^{-1} MS-222, Ross and Ross 1999), weighed (nearest 0.01 g), measured (SL and TL, nearest 1 mm), and tagged with a small colored disc (1.5 mm dia.) on fine monofilament thread inserted through the musculature posterior to the dorsal fin (technique modified from Chapman and Bevan 1990). We then placed the newly tagged fish into buckets of chilled, aerated water for a period of 15-20 minutes to recover from the stress of handling. After the recovery period we returned the fish to the holding tanks to await the beginning of the foraging experiment. Tagged fish were held for an additional four days to facilitate full recovery from the tagging procedure and to ensure they fed normally. Preliminary trials indicated a few fish (< 3 %, rosyside dace only) were vulnerable to infection by the ubiquitous bacterium *Columnaris flexibacter* in the immediate post-tagging period. To prevent any post-tagging infection while the incision healed we added a very low dose of kanamycin sulfate (3 mg L^{-1}) to the holding tank for the first two days of the post-tagging recovery period. All the tagged fish quickly recovered from the anaesthesia (< 3 min), fed actively within two hours, and exhibited no obvious signs of distress in terms of behavior or body coloration.

During the recovery period and prior to selection for treatment groups, we fed the experimental fish frozen chironomid larvae two times a day during the recovery period for a total ration of 2-3% body weight. After the four day holding period we haphazardly formed two groups of six fish and transferred each to one of the feeding areas in the artificial stream. Once placed in a feeding area, a group was left to acclimatize for an additional two days. In preparation for trials, we fed the fish with the automatic feeders for a one-hour period on the second day of acclimation and observed to ensure normal feeding behavior.

Experimental Procedures

To examine relationships between competitive aggression, spatial position, and foraging success, we used two single-species (intraspecific) experimental treatments of either six yellowfin shiner or six rosyside dace. This group size is representative of rosyside dace groups in Coweeta Creek (1-9 individuals, Freeman and Grossman 1992, 1993) and we assumed the same pattern held for yellowfin shiner. Eight replicate groups were tested for each species. In addition, we tested each group at high (44.9 larvae min^{-1} m^{-2} of stream cross-sectional area) and low (21.6 larvae min^{-1} m^{-2} of stream cross-sectional area) food levels on subsequent days to determine whether prey availability affected the aggressive behavior/foraging success of either species (see below). High and low prey delivery rates represent one standard deviation above and below the mean availability of prey in the size range consumed by drift-feeding minnows in Coweeta Creek (Hill 1989, Freeman 1990, Stouder 1990). More generally, these treatment levels represent the range in quality of commonly encountered foraging patches in Coweeta Creek. The order of prey treatment was assigned by coin flip for each replicate. All trials were conducted at water temperatures of 18° C and velocities of 12 cm s^{-1} to simulate normal summer conditions and the observed habitat preferences of these species in the Coweeta Creek collection sites (Grossman and Freeman 1987, Grossman and Ratajczak 1998, M. D. Farr and G. D. Grossman unpub. data).

We conducted trials once per day between 0900 and 1300 hours, on two consecutive days. A single trial consisted of three observation periods: 10-min pre-trial, 60-min feeding trial, 10-min post-trial. During the pre- and post-trial periods, no food was delivered to the feeding areas. Two groups were tested simultaneously, one in each channel. Trials in the two channels were run sequentially with the order being determined by a coin flip. In order to alleviate any effect of olfactory cues across species only conspecific groups were tested together. In addition, we performed large water changes (~ 50 %) and filtration with unadulterated activated carbon after each trial to remove any residual scent. We assigned the order of replicate groups randomly to reduce the effects of any seasonal changes in behavior. Finally, we approximately size-matched fish (< 20 % difference in total length) within a group to reduce any confounding effects of large size differences (i.e., to ensure that we were dealing with inter-individual behavioral differences alone).

Three behavioral properties were of greatest interest in this experiment: individual rates of aggression and feeding, and the spatial positions adopted by each fish relative to other foraging group members. We continuously recorded the number of prey captures, and the number of direct attacks performed and received for each individual on audio tape. For each aggressive act we recorded the identity of both the initiator and the recipient. Every two minutes we took a scan sample of the position of each fish (ranked from 1 [front] to 6 [back]) relative to the upstream end of the feeding area and every other group member. Unless otherwise noted, all measures of aggression, positional rank, and foraging success were estimated from the last 40 minutes of the feeding trials to ensure that relationships within a group had stabilized.

We conducted several preliminary trials during the spring and early summer of 2001 to develop an ethogram of aggressive behaviors exhibited by either species in intraspecific groups. Behaviors included color changes, displays (fin posturing, exaggerated swimming, parallel swims), and overt aggressive acts similar to those described for other stream fishes (i.e., displacements, charges, chases, nips). During the main experiment displays were rare, only performed by the most aggressive individuals, and always preceded an overt aggressive act. Consequently, we only included overt aggressive acts in the analyses described below.

We used repeated-measures ANOVA and ANCOVA to control for inter-individual and inter-group variation in behavioral metrics. All percentage data were arcsine-squareroot transformed and tested for normality before inclusion in parametric tests (Kolmogorov-Smirnov test, all $P > 0.25$). Our null hypothesis for all tests was one of equality (i.e., no difference between groups) and all tests were two-tailed with $P = 0.05$.

Experimental Questions and Data Analysis

Do minnows vary in their aggressive tendencies? – We examined inter-individual variation in aggressive behavior within both species using two approaches. First, we plotted aggression rates of individual fish (Y) in a descending rank-series (X) to look for the presence of disjunctions or gaps which may indicate the existence of discrete aggression classes (after Rincón and Grossman 2001). Second, we performed a χ^2 goodness-of-fit test to test the null hypothesis that all individuals within a feeding group perform an equal number of one-sided aggressive acts (i.e., all individuals displayed similar patterns of aggressive behavior). The presence of a generally continuous rank series and a rejection of the chi-square tests would suggest that inter-individual differences in aggressive behavior were substantial enough to warrant further examination (see below).

Do minnows form stable linear social hierarchies? – We constructed matrices of one-sided aggressive acts (aggressor vs. recipient) for each group and tested for the presence of linear social hierarchies by calculating the linearity index h' (de Vries 1995). This index is based on Landau's index h (Landau 1951) and varies from 0 (no linearity in the hierarchy) to 1 (completely linear hierarchy). The use of h' is an improvement over many previous measures because it takes into account unknown relationships within the interaction matrix (de Vries 1995, 1998). We tested for significant h' values using a two-step Monte Carlo randomization technique (10 000 replicates, see de Vries 1995 for statistical details). Groups with significant h' values ($P < 0.05$) were then reordered to yield a ranked social hierarchy. We tested for the effects of food abundance on the mean h' values with repeated-measures ANOVA and post-hoc Tukey-Kramer tests.

Social rank typically is estimated from large data sets collected over a range of conditions (Côté 2000, de Vries 1998). Because our study was based on short-term laboratory experiments, we combined the low and high food abundance interaction matrices into a single “consensus” matrix and calculated a new linearity score for each group (hereafter referred to as the consensus hierarchy). We then tested the null hypothesis of no difference in mean consensus hierarchy scores between species using students t-test. We also assigned a social rank to each individual based on the consensus hierarchy for use in subsequent tests. We performed all hierarchy calculations and randomization tests with the MatMan 1.0 add-in for Microsoft Excel.

Are individual aggression rates correlated with measures of body size? – Because we approximately size-matched individuals within each replicate group we had limited ability to detect relationships between body size and social rank. Nevertheless we investigated associations between measures of relative body size (mass and TL) and patterns of aggression and social rank using plots and Pearson product-moment correlations. We compared mean relative individual size (size of target individual/size of largest individual in the group) to consensus hierarchy social rank (1-6).

Do the most aggressive individuals maintain positions at the front of foraging groups? – We tested whether the most aggressive individuals occupied foraging positions at the front of a group by regressing average positional rank (arithmetic mean) against the average aggression rate (arc-sine square-root transformed %) for all individuals within each species (n=48 for each species). Because we could not ascertain the aggressive ranking of individuals prior to the experiment, we calculated individual aggression rates (and subsequent ranks) as the percentage of the group total. To assess the effect of food level on aggression-positional relationships, we calculated separate regressions for each food level. We also investigated the effect of aggression received (arc-sine square-root transformed %) on these relationships by including this variable in a forward-selection step-wise multiple regression ($P < 0.10$ for inclusion). We tested for the effects of food level (within species) and species (within food level) on model slopes (aggression vs. positional rank) with repeated measures analysis of covariance (ANCOVAR) and post-hoc Tukey tests. Finally, to determine if individual fish maintained stable positional ranks during trials (feeding vs. non-feeding periods), we: (1) directly compared the average pre-trial rank to the average rank during the final 40 minutes of the feeding trial (Pearson correlation test); and, (2) calculated the coefficient of variation in average positional rank in 10-minute intervals for each species during all three periods (pre-trial, trial and post-trial).

Do fish at the front of groups get most of the food? – As above, we tested whether fish at the front of groups receive a larger share of the drifting prey with separate linear regression models for each level of food abundance. We regressed an individual's relative foraging success (arc-sin squareroot transformed % of total captures in the group) against the arithmetic mean of its positional rank for all individuals within a species ($N = 48$ for each species). We tested for differences in the model slopes as a function of food abundance (within species) and as a function of species (within food level) with ANCOVAR and post-hoc Tukey tests.

Results

Do minnows vary in their aggressive tendencies? – During the trials we observed a total of 13 667 one-sided aggressive acts (yellowfin shiner 9517 acts, rosyside dace 4150 acts). Overt aggression took the form of displacements, charges, chases, and nips in yellowfin shiner groups, and displacements, charges, and chases in rosyside dace groups, and clearly was a response to the presence of food for both species (Fig. 1.3). With the onset of feeding, per capita aggression rates rose quickly to a plateau which was maintained during the trials, and then declined steadily after prey delivery was discontinued. A simple linear fit to the slope of the decline indicates aggression would have ceased within 25 minutes of the end of the feeding trial.

Aggression rank series data for yellowfin shiner showed no distinct breaks in the distribution (Fig. 1.4). However, there was evidence of a non-aggressive class of rosyside dace (approximately rank 30 and lower). Above rank 30, aggressive rosyside dace formed a continuous distribution, demonstrating a lack of further aggression classes. Regardless of food level, there were significant differences in individual aggression rates within groups for both yellowfin shiner (low food: χ^2_5 range117.42 - 649.43, all *P's* < 0.001; high food: χ^2_5 range 47.67 - 384.62, all *P's* < 0.001) and rosyside dace (low food: χ^2_5 range 101.95 - 588.37, all *P's* < 0.001; high food: χ^2_5 range 210.29 - 563.39, all *P's* < 0.001).

Do minnows form stable linear social hierarchies? – Estimated linear hierarchy scores were high for both species (i.e., > 0.70) indicating the presence of social hierarchies (Fig. 1.5). Food abundance significantly affected hierarchy scores, which decreased with increasing food abundance (ANOVAR, food main effect, $F_{1,14} = 6.38$, $P = 0.02$). However, a posteriori tests indicated that this effect only was significant for rosyside dace (Tukey-Kramer test, $P \leq 0.05$). We did not detect significant differences between species ($F_{1,14} = 0.40$, $P = 0.53$) or significant interaction effects ($F_{1,14} = 0.23$, $P = 0.64$). Additionally, Monte Carlo tests revealed that increasing food abundance caused a slight decrease in the number of groups forming significant hierarchies (yellowfin shiner, five of eight at low food and four of eight at high food; rosyside dace, six of eight at low food and five of eight at high food). These findings suggest that increasing food abundance either destabilized or reduced detectability of hierarchies.

Approximately half of all individuals maintained consistent positions within the hierarchies across food treatments (Fig. 1.6). There was a significant correlation between a fish's hierarchy rank in both high and low food treatments (paired Pearson product moment correlation of social rank: yellowfin shiner, $R = 0.76$, $P < 0.001$; rosyside dace, $R = 0.76$, $P < 0.001$), although rank in one treatment only explained 58% of the variance in the other treatment. When individuals did switch ranks, they typically moved a single step (Fig. 1.6). When we combined low and high food aggression matrices into a single consensus matrix, mean hierarchy scores were high (means ± SE: yellowfin shiner, 0.88 ± 0.05; rosyside dace, 0.94 ± 0.03) and 15 of 16 Monte Carlo simulation tests were significant at the $P < 0.05$ level (the single exception was a group of yellowfin shiner, h' = 0.65 $P = 0.21$ which was excluded from further tests of consensus hierarchy scores or individual ranks). A Students-*t* test revealed no differences in consensus hierarchy scores between species ($t_7 = 0.93$, $P = 0.35$). Although both species formed social hierarchies in the lab, our data suggest that these hierarchies did not have a completely rigid structure.

Are individual aggression rates correlated with measures of body size? – Relative body size measures for individuals were weakly, but significantly, correlated with consensus social rank in yellowfin shiner (mass, $R = -0.43$, $R^2 = 0.19$, $P = 0.002$; total length, $R = -0.33$, $R^2 = 0.11$, $P = 0.023$) and rosyside dace (mass, $R = 0.30$, $R^2 = 0.09$, $P = 0.040$; total length, $R = 0.31$, $R^2 = 0.10$, $P = 0.034$, Fig. 1.7). Interestingly, this relationship reversed across species. Large relative size was associated with high social rank in yellowfin shiner groups, whereas small relative size was associated with high social rank in rosyside dace groups.

Do the most aggressive individuals maintain positions at the front of foraging groups? – Mean individual positional ranks during the pre-trial period were not significantly correlated with ranks during the feeding trial for either species or prey levels (yellowfin shiner, low food $R = 0.15$, $P = 0.29$, high food $R = 0.13$, $P = 0.31$; rosyside dace, low food $R = 0.17$, $P = 0.24$, high food $R = 0.16$, $P = 0.23$). Positional ranks also appeared to stabilize after the onset of feeding (i.e., C.V. of positional ranks decreased, Fig. 1.8). These findings suggest that the presence of prey triggered a rearrangement of ranks within groups. Stabilization of positional ranks lagged behind the build-up of aggression by 10-15 minutes which suggests active interactions are necessary cues in the process of social rank assessment and hierarchy formation for these species. Simple linear regression revealed a significant positive relationship between an individual's aggressive tendencies (the fraction of total aggressive acts performed within the group by an individual) and average positional rank within the group for both species (Fig. 1.9, Table 1.1). This relationship was stronger in rosyside dace groups (low food $R^2 = 0.61$, high food $R^2 = 0.63$) than yellowfin shiner groups (low food $R^2 = 0.41$, high food $R^2 = 0.34$). Adding a aggression received term to the model significantly increased the predictive power for yellowfin shiner (multiple regression: low food $F = 26.17$, $R^2 = 0.54$, P for new term=0.0008, overall $P < 0.0001$; high food $F = 19.92$, $R^2 = 0.47$, P for new term = 0.0015, overall $P < 0.0001$). The aggression received term did not contribute significantly to rosyside dace models (low food $P = 0.62$, high food $P = 0.45$). Despite being generally less aggressive (Fig. 1.9), a few of the most aggressive individuals in rosyside dace groups performed a larger fraction of the total aggression within a group than their counterparts in yellowfin shiner groups. Nevertheless, regression model slopes for positional rank-aggression relationships did not differ significantly either for food level within a species or between species (ANCOVAR, all *P's* > 0.10). Overall, the use of aggression allows dominant individuals to acquire high positional rank. Furthermore, regardless of species, a dominant fish must perform approximately the same relative rate of aggression (% of group total) to remain in the front position.

Do fish at the front of groups get most of the food? – Fish with high positional ranks had greater foraging success regardless of food level or species (Fig. 1.10, Table 1.1, all *P's* < 0.001). As before, this relationship was stronger for rosyside dace (low food $R^2 = 0.77$, high food $R^2 = 0.73$) than for yellowfin shiner (low food $R^2 = 0.58$, high food $R^2 = 0.57$). Nonetheless, ANCOVAR revealed no significant effects of food or species on the model slopes (all *P's* > 0.10), indicating that individuals acquire foraging benefits as a function of their positional rank relative to the direction of food delivery regardless of food abundance or species identity.

Discussion

Competitive aggression can play a significant role in the success of socially foraging animals (Huntingford and Turner 1987, Archer 1988). Nonetheless, little is known about the role of aggression in social interactions and resource acquisition in most fishes. Our studies of an invasive (yellowfin shiner) and native (rosyside dace) stream minnow demonstrate that both species formed social hierarchies, and that more aggressive individuals occupied positions at the front of groups. Being at the front of a group ensured that an individual had increased access to food, a critical resource in many habitats. Given the unidirectional delivery of prey experienced by drift-feeding stream fishes, occupying positions at the front of a group probably has a strong effect on individual fitness. In addition, our results indicate that the salmonid model of intraspecific aggression-habitat choice can be applied to some cyprinid fishes.

In numerous species, aggression mediates conflict over access to resources, and the level of aggression typically is positively correlated with dominance status (Huntingford and Turner 1987). In our study, aggression was a weaker predictor of an individual's positional rank than positional rank was of foraging success. Thus, position within a resource queue may ultimately be a better predictor of net energy intake than aggression rate for non-territorial group foragers. Similar results have been reported for drift-feeding salmonid fishes competing for feeding positions (Metcalfe et al. 1989, Hughes 1992, Nakano 1995), and male water striders (Hemiptera: Gerridae) competing for access to both drifting prey and mates (Blanckenhorn et al. 1998). These patterns have also been observed in lotic marine environments where fishes feed on drifting prey (Forrester 1991). The longitudinal delivery of prey by water currents appears to be a compelling environmental factor in establishing the economic utility of foraging aggression. By contrast, positional proximity to defensible resources was less effective (vs. an aggression index) in predicting foraging success for a lake-dwelling species (Arctic charr, *Salvelinus alpinus*, Bailey et al. 2000).

Dominant trout and salmon frequently occupy the most profitable positions in streams (Fausch 1984), and the fitness benefits of foraging dominance generally manifest through higher growth rates and increased metabolic efficiency (Magnuson 1962, Abbott and Dill 1989, Blanckenhorn 1991b, Bryant and Grant 1995, Fraser et al. 1995). Under natural stream conditions, individuals occupying the forward positions in groups should also enjoy priority access to numerically rare but energetically valuable prey items (i.e., 'the right of first refusal', Freeman and Grossman 1992). Krause (1993) observed a reduction in feeding rate and a transition from high quality planktonic prey to low quality benthic prey with decreasing positional rank in mixed shoals of roach (*Rutilius rutilius*) and chub (*Leuciscus cephalus*). It appears that linearly arrayed groups operate as a sieve, with the number and quality of prey items ever reducing with distance from the front.

Although not included in our laboratory study, there also are risks associated with the maintenance of forward positions in groups in nature. For example, individuals at the front of groups may be more visible to predators and ultimately incur a higher risk of mortality. Bumann et al. (1997) allowed groups of creek chub (*Semotilus atromaculatus*) to forage in large aquaria with a partially hidden predator (rock bass, *Ambloplites rupestris*). In 25 of 30 trials the lead forager was attacked, with all remaining attacks limited to fishes in the front half of the shoal. Similar phenomena have been reported in group-foraging birds (Black et al. 1992). Subordinates are therefore less likely to be attacked, and probably are more likely to detect the presence of a predator by observing the responses of dominants. Nonetheless, a previous study of habitat use by Coweeta Creek fishes have shown limited effects of the presence of predators (Grossman et al. 1998).

Direct movements from the back to the front of stationary foraging groups in streams have been associated with poor nutritional condition (i.e., a potentially risk-prone behavior). Experimentally food-deprived individuals show preferences for positions at the front and periphery of foraging groups where prey is ostensibly more accessible and foragers are more vulnerable to attack (roach, Krause et al.1992, Krause 1993; whirligig beetles, Romey 1995). Increased risk of predation has also been associated with a reduction in territorial defense in reproductively active male fathead minnows, *Pimephales promelas* (Jones and Paszkowski 1997). Such costs may ultimately underlie the observation that the establishment of exclusive-use foraging territories are rare in freshwater fishes (Barlow 1993). Barlow’s observation notwithstanding, the all-or-nothing defense of territories is generally rare in nature (Wolf 1978, Wittenberger 1981, Craig and Douglas 1986, Grant et al. 2002). Territoriality divorces an individual from the well documented anti-predator benefits of group membership (Pitcher and Parrish 1993).

Dominant rosyside dace and yellowfin shiner performed approximately the same amount of relative aggression (35 - 40% of the group total) to acquire the best foraging positions. Because group foraging fishes shoal preferentially with conspecifics of similar size (Krause et al. 2000), aggressive tendencies at the species level may be principally tuned by intraspecific interactions. This tendency may prevent individual yellowfin shiner, which are on average smaller than rosyside dace, from frequently invading rosyside dace groups, unless other costs (e.g., the increased cost of predation risk due to the oddity effect) are outweighed by the foraging benefits of high rank. This seems unlikely because only the top 15 - 20% of yellowfin shiner were more aggressive than the dominant rosyside dace. Nonetheless, it is possible that small groups of yellowfin shiner will be able to supplant similar sized groups of rosyside dace from high quality patches. Thus, the effect of the invasion may be most detectable at the scale of patch occupation, and not necessarily microhabitat use by individuals.

When data from both food treatments were combined, both dace and shiner groups could be sorted into highly linear social hierarchies in all but one case. Such results are common in socially foraging vertebrates when group sizes are small and a sufficiently large number of encounters are observed (Andries and Nelissen 1990, Chase et al. 2002). Our findings were in contrast to those of Rincón and Grossman (2001) who failed to detect linear hierarchies when observing small groups of rosyside dace in a laboratory artificial stream. It is likely their ability to construct hierarchies was compromised by a smaller sample size (6 groups, 237 aggressive acts observed vs. 8 groups, 4150 acts observed in the current study). The short observation times (3 min) in the Rincón and Grossman (2001) study also probably contributed to the higher proportion of individuals assigned to the non-aggressive class (60% vs. 38% in the current study). Individuals with low aggression rates could have been mis-classified as non-aggressive. Finally, the artificial stream utilized by Rincón and Grossman (2001) had larger experimental arenas which allowed for solitary foraging, thus reducing the opportunity for individuals to interact during the observation periods.

Linear feeding hierarchies have repeatedly arisen in laboratory and field investigations of fishes when prey are defensible (e.g., cichlids, Oliveira and Almada 1996; salmonids, Nakano and Furukawa-Tanaka 1994, Nakano 1995; sparids, Castro and Caballero 1998). However, both yellowfin shiner and rosyside dace established feeding hierarchies only in response to prey delivery. We base this conclusion on the following observations: 1) aggression was uncommon in the absence of prey; 2) individuals maintained positions within groups only after the onset of aggression; 3) both behavioral patterns diminished after the cessation of feeding; 4) rank switches between hierarchical neighbors were common between trials; and, 5) aggression was commonly directed against higher and lower ranked individuals. Facultative hierarchy formation may be a feature of foraging behavior when species occupy variable environments. Stochastic and seasonal variation in hydrology best predict the patterns of habitat use observed in Coweeta Creek fishes (Grossman and Ratajczak 1998, Grossman et al. 1998). Additionally, exposure to spates and reductions in mean stream depths associated with drought can destabilize feeding hierarchies and remove the growth advantages for dominant fish in groups of drift-feeding stream fishes (Sloman et al. 2000, 2002). Storm flows may also alter the composition of foraging groups when fishes are periodically displaced downstream, requiring individuals to continually reassess the quality of competitors. Even under base-flow conditions the membership of foraging groups in Coweeta Creek are dynamic, with individuals routinely switching group affiliation (Freeman and Grossman 1992, 1993). These factors in concert should require aggressive fishes to continually reassess both the quality and defensibility of resources within a patch.

In addition to defensible resources, the establishment of stable hierarchies generally requires visual attributes of high dominance rank (i.e., an individual can assess its own status by observing or interacting with others). Pre-existing attributes such as physical size, age, sex, coloration, and aggressive behavior all have been associated with social rank in artificially constructed foraging groups (see Chase et al. 2002 and references therein). Interestingly, yellowfin shiner and rosyside dace displayed different relationships between social rank and measures of body size. Each yellowfin shiner was aggressive, albeit at different intensities, and there were positive correlations between body size (biomass) and social rank of individuals. These patterns are commonly observed in aggressive fishes (Grant 1993). Conversely, the rosyside dace exhibited a mixed-strategy (aggressive vs. non-aggressive), and non-aggressive individuals were generally larger than their aggressive counterparts. However, our ability to detect correlations between body size and aggression rates were hampered by the fact that we purposefully did not use a broad size range of individuals in groups (i.e., we were more interested in focusing on innate behavioral differences). A more detailed study would be required to confirm these patterns. It also is possible that the observed differences in aggressive behavior between species may reflect the action of phylogenetic constraints on aggressive behavior (Hutchinson and Iwata 1997). In nature, non-aggressive rosyside dace are both more likely to forage alone, and more likely to leave a foraging group if a highly aggressive individual is present (Freeman and Grossman 1992). In our experiment, group membership was compelled by the apparatus, and may have reduced the ability of larger, non-aggressive rosyside dace to forage alone. Nonetheless, our size-matching of individuals within groups should have minimized this potential bias. Höjesjö et al. (2002) recently demonstrated the value of non-aggressive foraging tactics for stream-dwelling juvenile brown trout. They brought individuals into the lab and assessed their dominance status (dominant, subordinate, or non-aggressor) in dyadic trials before releasing them back into the stream. Dominants grew more than subordinates, but not more than non-aggressors.

In conclusion, our results support the general hypothesis that the unidirectional nature of prey delivery in natural streams establishes a template that promotes the utility of aggression in two group foraging drift feeders. When invoked, aggression clearly mediated the acquisition of food resources through the monopolization of profitable positions in groups of cyprinid fishes. These patterns are in conceptual agreement with existing models of territorial aggression in resource queues. There were no marked functional differences in the use of foraging aggression for intraspecific groups of native and invasive taxa. The instability of linear feeding hierarchies may reflect the invocation of a common and flexible behavioral tactic in response to environmental conditions.

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Table 1.1: Linear regression analysis of the relationships between aggression and positional rank, and positional rank and foraging success in minnow groups. All error terms are ± 95% confidence interval.

		Regression Statistics ($y = y_0 + ax$)				
Species	Treatment	y_0	a	r	r^2	p
Aggression Performed vs. Positional Rank (Fig. 1.9)						
Yellowfin Shiner	Low	4.93 ± 0.63	-4.06 ± 1.41	0.64	0.41	< 0.0001
	High	5.09 ± 0.78	-4.48 ± 1.82	0.58	0.34	< 0.0001
Rosyside Dace	Low	4.68 ± 0.41	-4.01 ± 0.94	0.78	0.61	< 0.0001
	High	4.78 ± 0.41	-4.18 ± 0.92	0.79	0.63	< 0.0001
Positional Rank vs. Foraging Success (Fig. 1.10)						
Yellowfin Shiner	Low	0.60 ± 0.06	-0.06 ± 0.013	0.77	0.58	< 0.0001
	High	0.57 ± 0.04	-0.05 ± 0.012	0.76	0.57	< 0.0001
Rosyside Dace	Low	0.62 ± 0.04	-0.06 ± 0.010	0.88	0.77	< 0.0001
	High	0.58 ± 0.04	-0.05 ± 0.008	0.86	0.73	< 0.0001

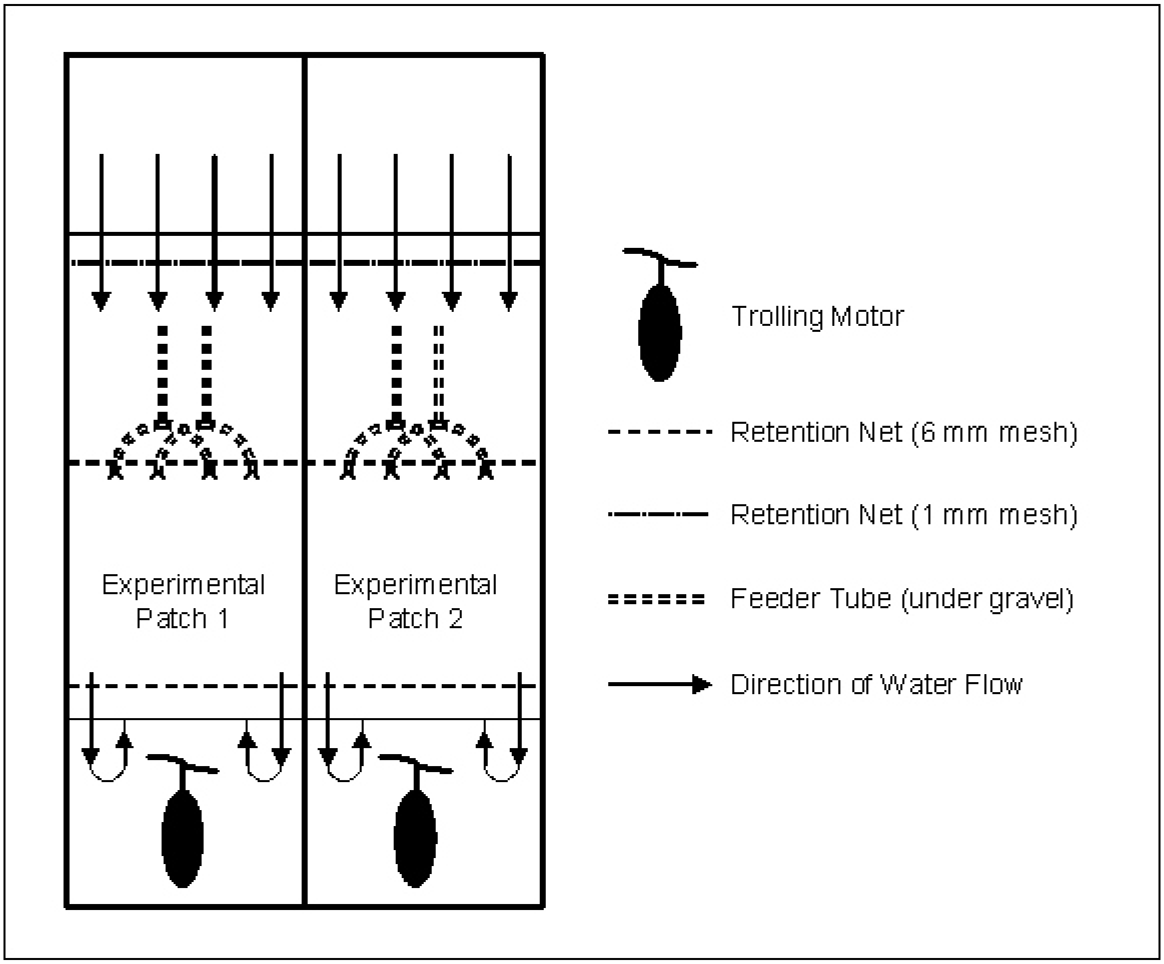

Fig. 1.1. Schematic diagram of the experimental tank (top view). The fish were contained between the 6 mm retention nets. The 1 mm retention net prevented unconsumed food items from re-entering the feeding areas.

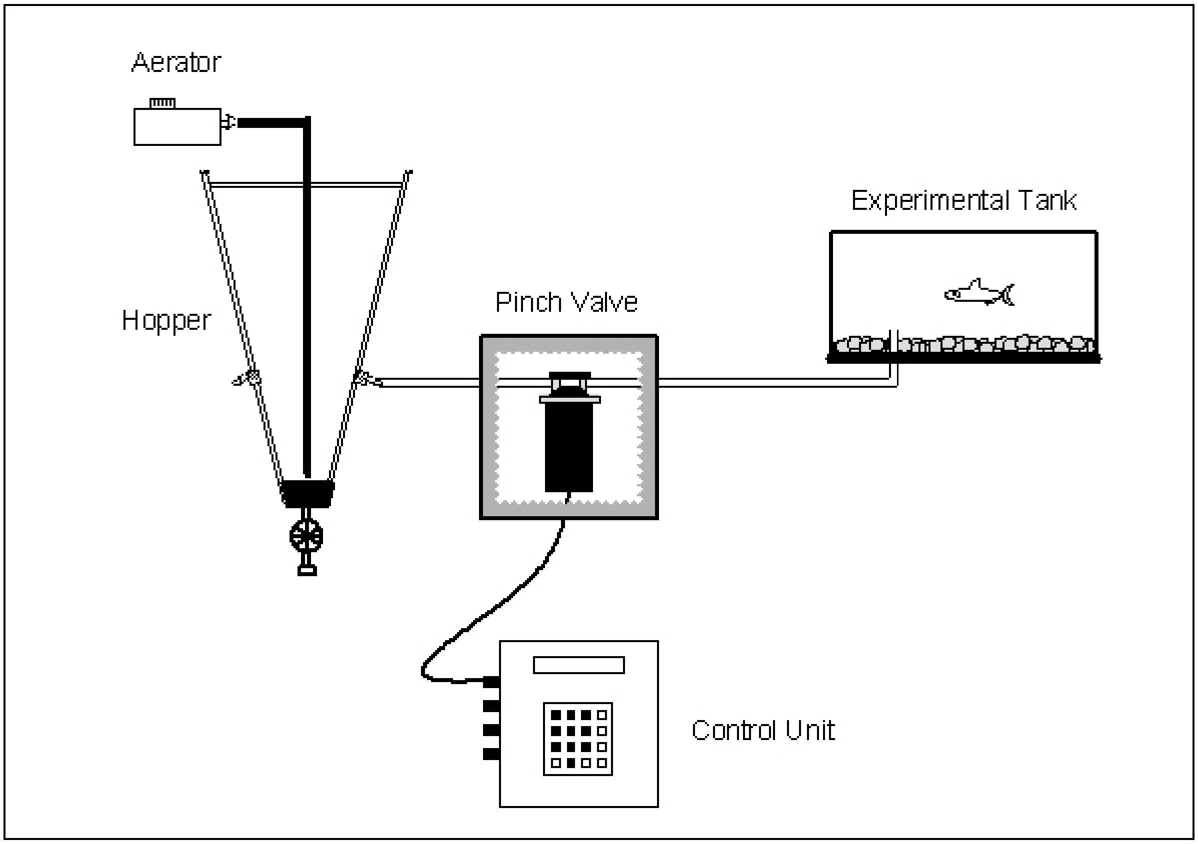

Fig. 1.2. Schematic diagram of the automatic feeder. Prey are suspended via aeration in the hopper. A silicone tube connects the hopper to the experimental tank. Pinch valves were contained in a sound-proofed box and open and close to permit the flow of prey into the experimental tank. Only one valve is shown for simplicity (four were used in the experiment).

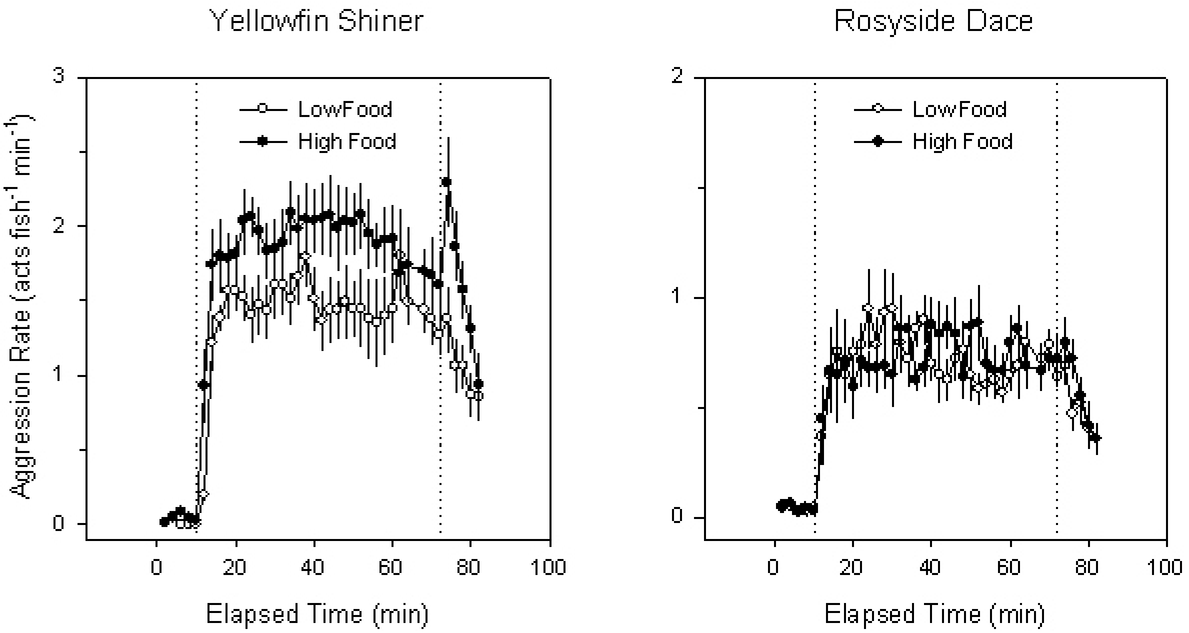

Fig. 1.3. Per capita aggression rate (means ± 1 SE, *N* = 8) for groups in two minute intervals for the entire trial. Dotted lines denote the beginning and end of the feeding trial. Points outside the dotted lines are the pre- and post-trial data (10 min each).

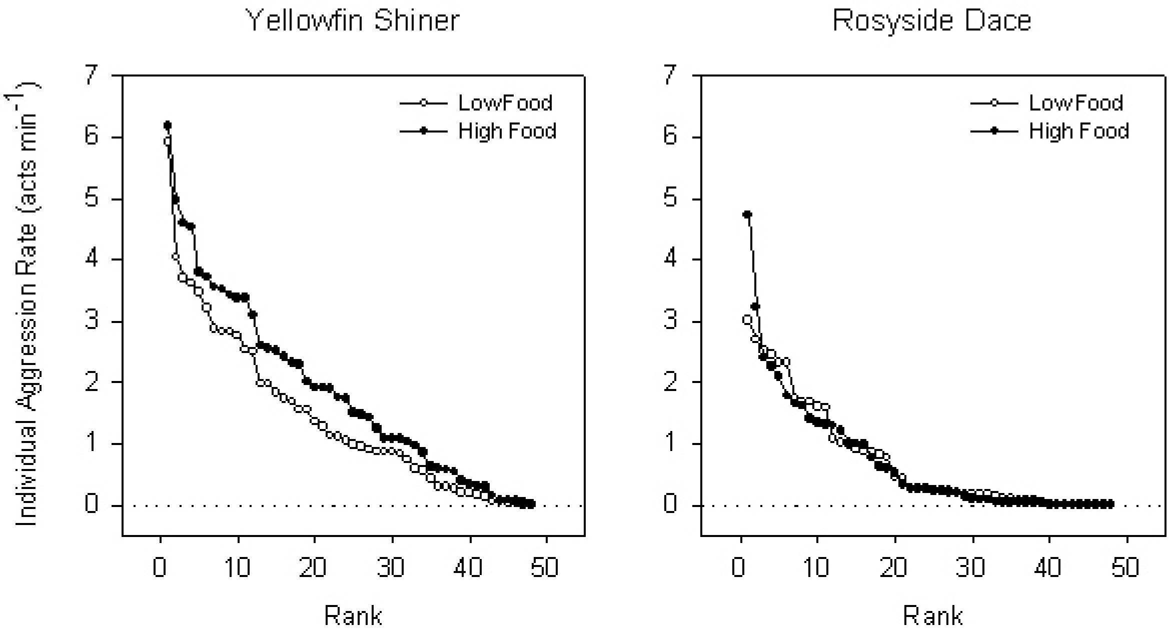

Fig. 1.4. Aggression rank series for each experimental population. Individuals are ranked from most aggressive (rank = 1) to least aggressive (rank = 48) based on their individual aggression rate calculated from the last 40 minutes of the trials. All individuals used in the trials are represented.

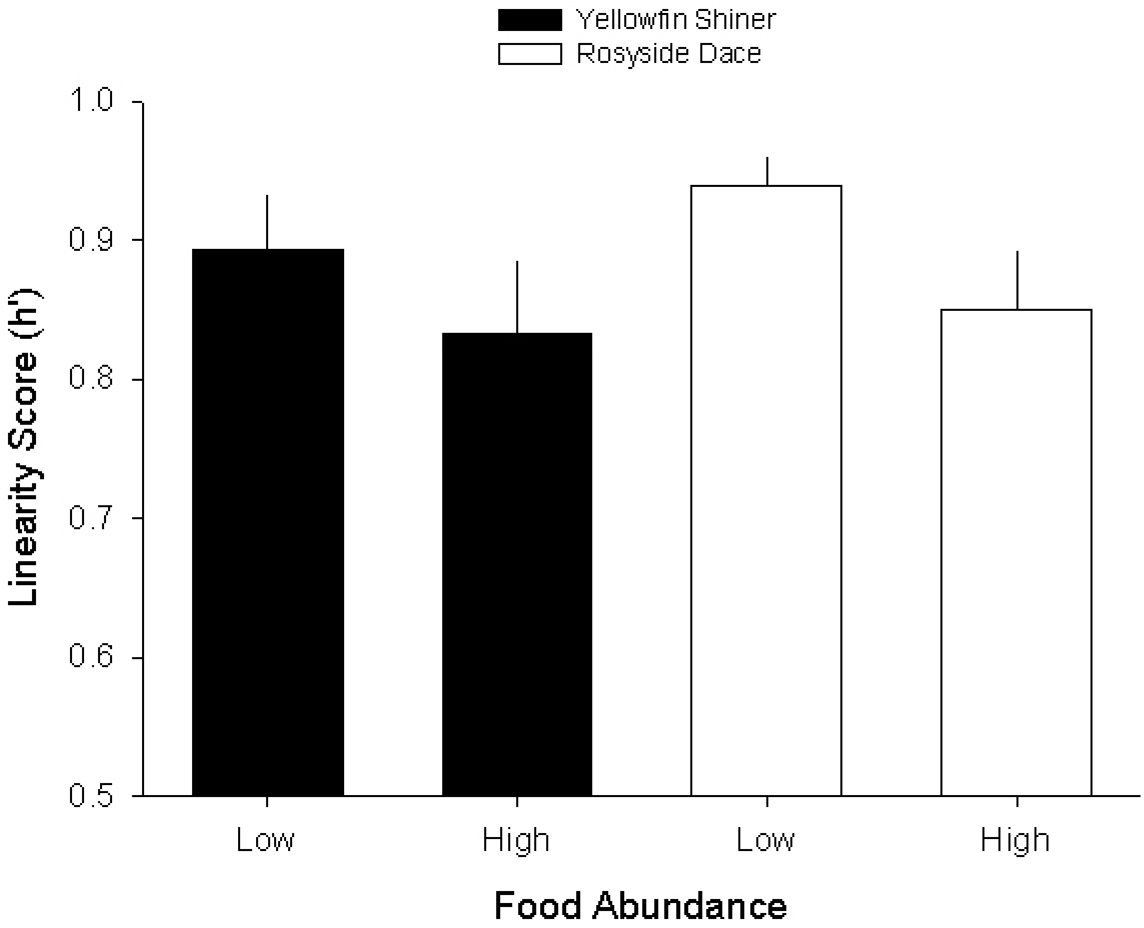

Fig. 1.5. Linearity score (means ±1 SE, $N = 8$) as a function of food abundance.

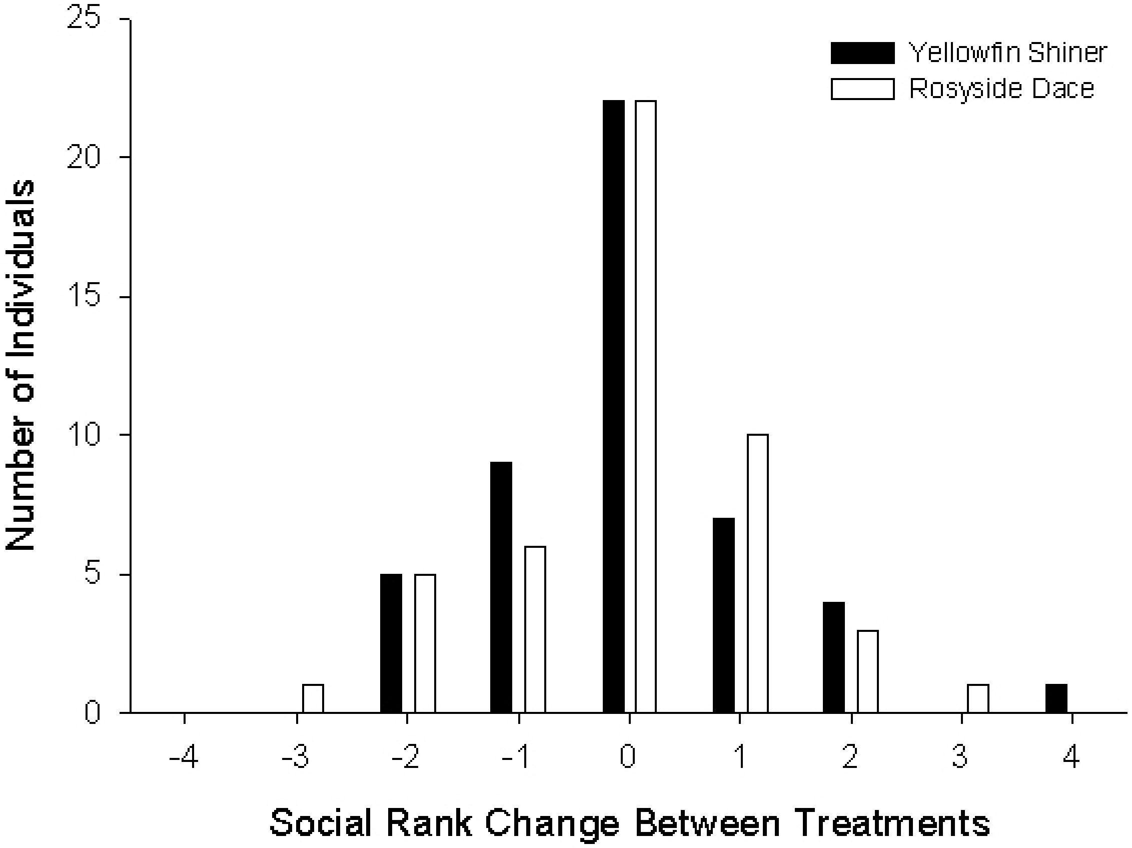

Fig. 1.6. Frequency histogram of the number of social rank switches between food treatments (from low to high food abundance).

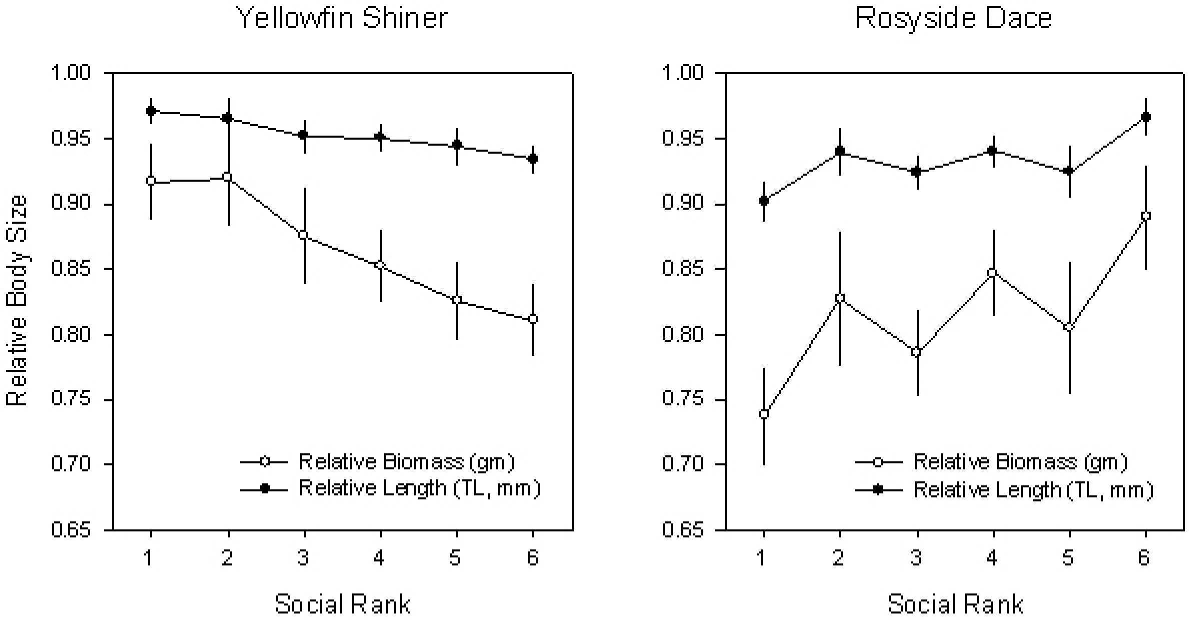

Fig. 1.7. Relative size (size/size of largest individual in the group) of all individuals as a function of their social rank. Values are arithmetic means (± 1 SE, *N* = 7 for yellowfin shiner, *N* = 8 for rosyside dace).

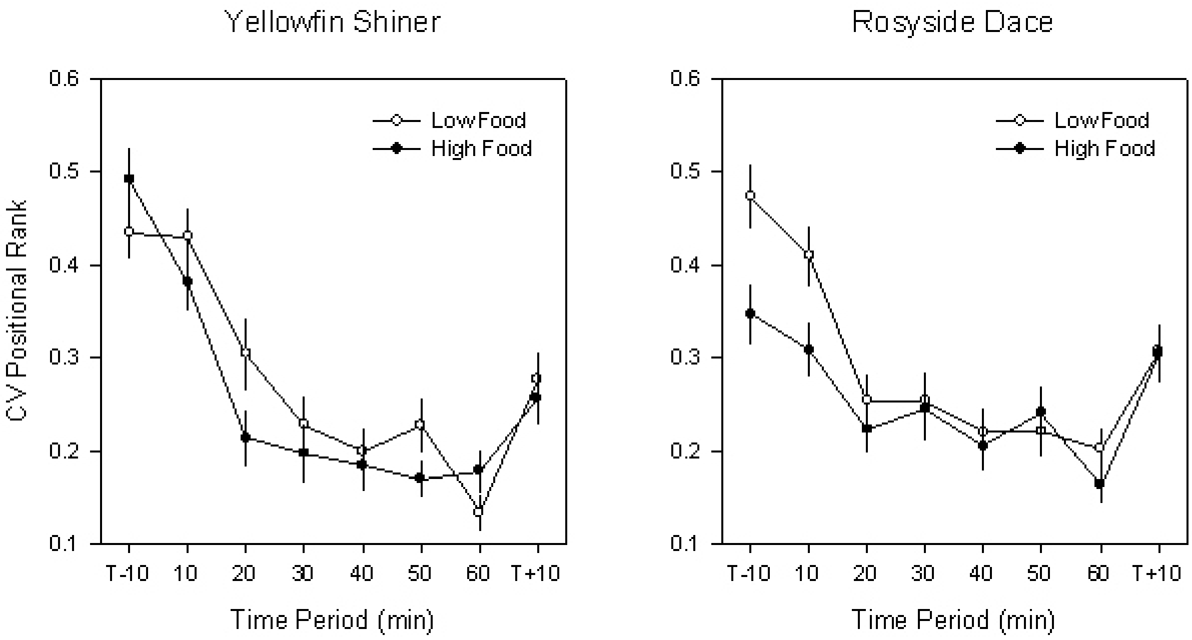

Fig. 1.8. Time-series of the coefficient of variation (CV) in positional rank during the experimental trials. Values represent the mean CV of positional rank (± 1 SE, *N* = 48) measured in 10-minute intervals. T-10 indicates the pre-trial period, T+10 indicates the post-trial period. No feeding took place during the pre- and post-trial periods.

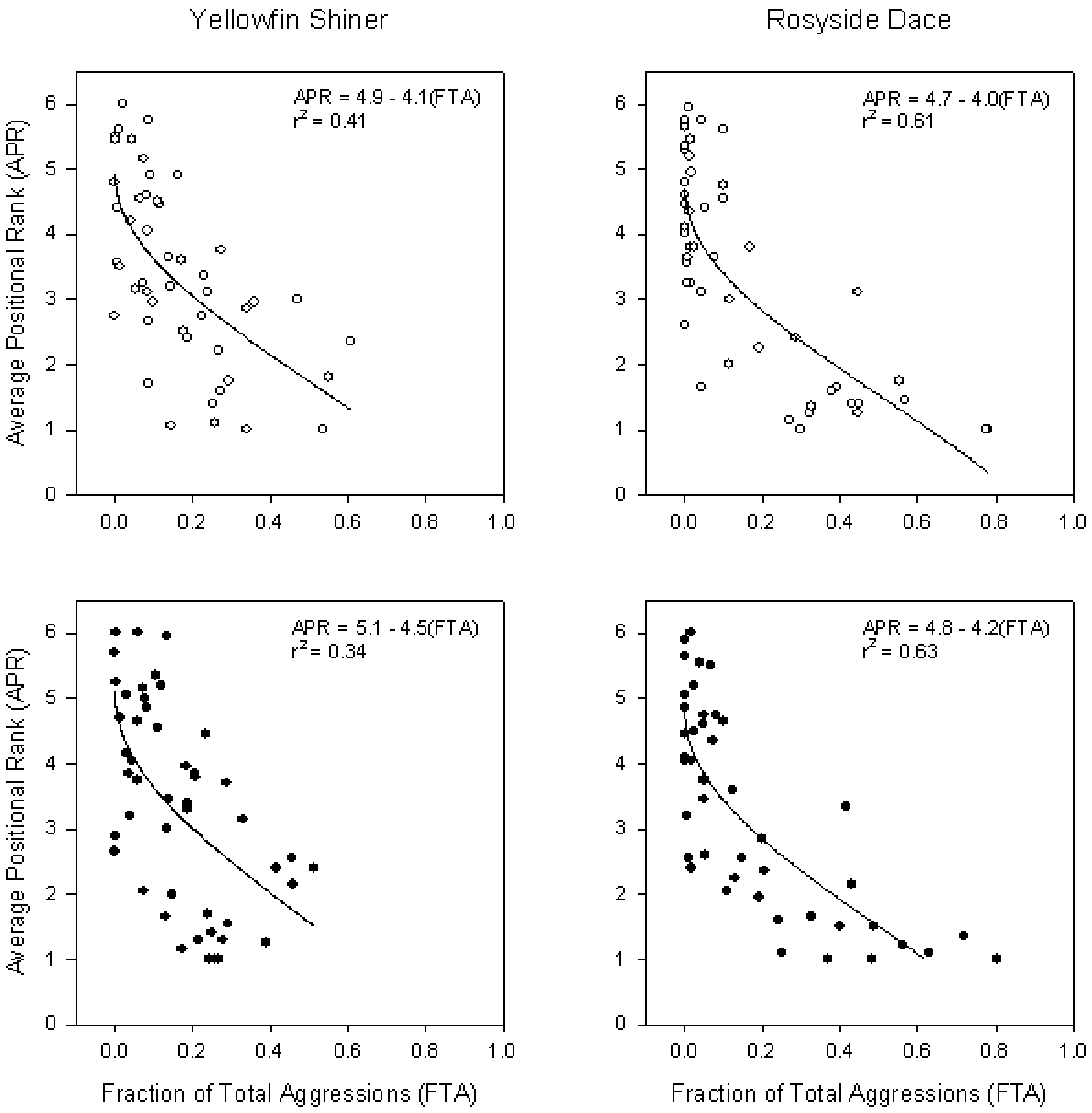

Fig. 1.9. Linear regression of average positional rank as a function of the total fraction of aggression performed (○ = low food treatment, ● = high food treatment). All 48 individuals for each species are represented. Lines are the regression models (Table 1.1). The fractional values (data and regression) have been back-transformed to percentages for ease of interpretation, the regression equation is not back-transformed.

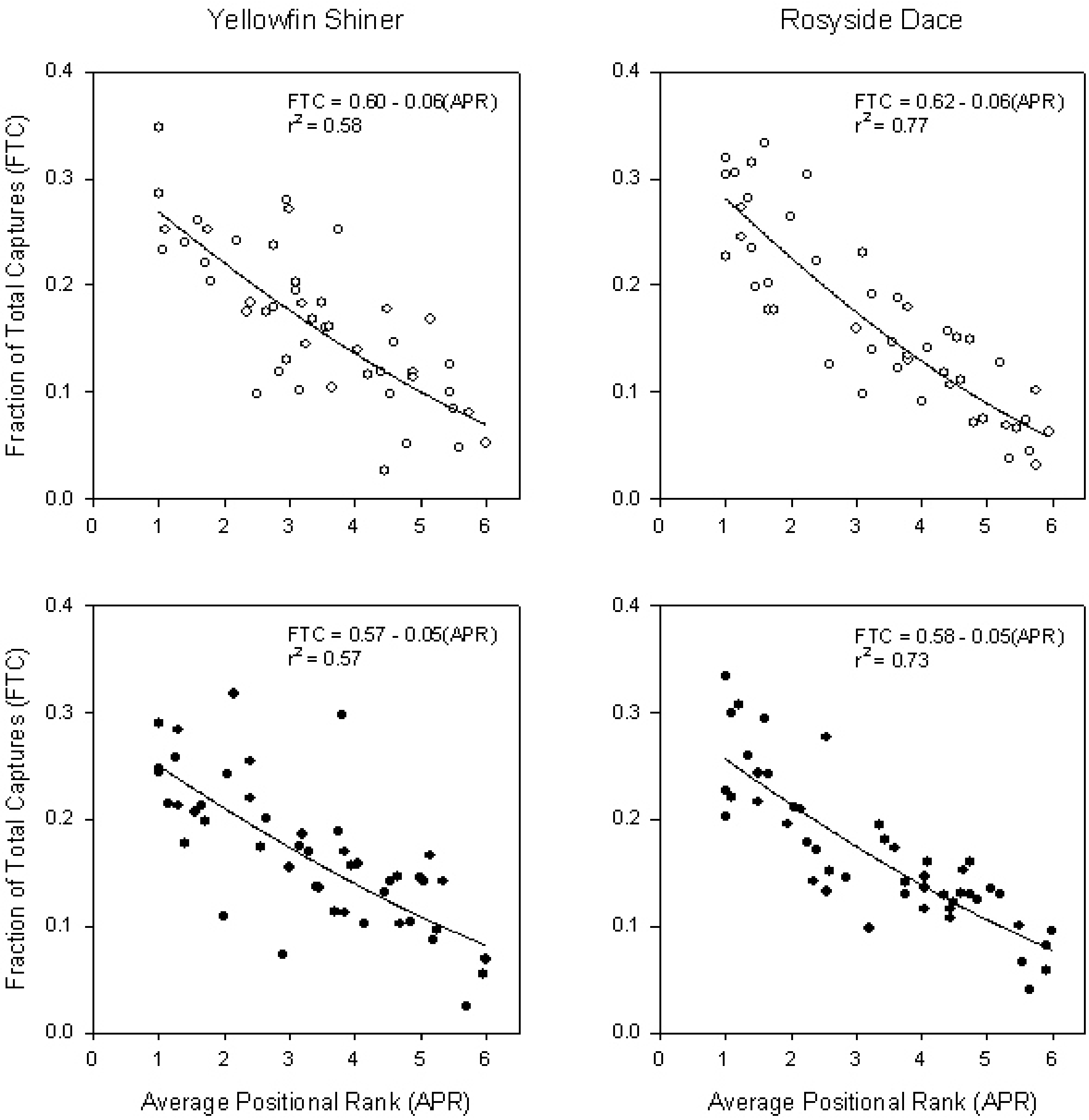

Fig.1.10. Linear regression of fraction of total captures as a function of the average positional rank (○ = low food treatment, ● = high food treatment). All 48 individuals for each species are represented. Lines are the regression models (Table 1.1). The fractional values (data and regression) have been back-transformed to percentages for ease of interpretation, the regression equation is not back-transformed.

CHAPTER 2

EFFECT OF FOOD ABUNDANCE ON COMPETITIVE AGGRESSION IN SMALL GROUPS OF NATIVE AND INVASIVE STREAM FISHES (PISCES: CYPRINIDAE)

Wagner, C. M. and G. D. Grossman. Submitted to *Animal Behaviour*.

Abstract

Animals that forage in groups often use aggression to acquire the best foraging positions. We tested whether group aggression rates in small groups of native (rosyside dace, *Clinostomus funduloides*) and invasive (yellowfin shiner, *Notropis lutipinnis*) drift-feeding minnows responded to increases in food abundance. At low-moderate food abundances resource defense theory predicts: 1) an increase in aggression rate as food abundance increases; and, 2) a decrease in the rate of aggressive investment (number of aggressive acts per prey capture). We found that invasive yellowfin shiner both increased aggression and decreased aggressive investment as predicted by the model. Native rosyside dace showed no significant increase in aggression rate, but decreased aggressive investment. Further, the decrease in aggressive investment was less for rosyside dace than yellowfin shiner, suggesting that each species has a unique aggression-food abundance curve. For both species, dominant individuals were more likely to decrease aggression rates with increasing food abundance, whereas subordinates were more likely to increase their aggression rates. When dominants decreased aggression they also shifted to positions further back in the foraging groups where their intake rates declined. Invasive yellowfin shiner were at least twice as aggressive as the native rosyside dace. We compare these results to the predictions of resource defense theory for groups of ranked individuals and discuss their implications for invasion success.

Introduction

When animals forage in groups they often compete for food. This social interaction can lead to flexibility in competitive strategies, ranging from low interference scrambles to the aggressive defense of exclusive territories. Our understanding of foraging aggression has been greatly aided by the application of cost-benefit and optimization models which employ currencies associated with individual fitness (e.g., food intake rate), and ultimately allow us to evaluate individual strategies from an evolutionary perspective (Stephens and Krebs 1986, Giraldeau and Caraco 2000). Many of these models have their inception in the concept of 'economic defensibility' (Brown 1964). This concept predicts that animals competing for access to a limiting resource will only use aggression when the benefits of resource defense exceed the costs. Economic defensibility provides a powerful conceptual framework for understanding how an individual's behavior is adapted to life in a particular environment, as well as how social behavior responds to variation in habitat quality.

Changing food abundance is a key factor affecting the intensity of competitive aggression in animals (Grant 1993). Conceptual cost-benefit models predict the onset of resource defense when food reaches a threshold abundance where the energetic cost of aggression yields a greater net fitness vs. a non-aggressive strategy (Warner 1980, Meyers et al. 1981, Carpenter 1987, Grant 1993). As the net benefits of foraging aggression increase, the frequency and intensity of aggression also may increase, reaching its apex in the exclusion of all competitors from a stable feeding territory (Carpenter and MacMillen 1976, Craig and Douglas 1986, Grant et al. 2002). Finally, as food abundance increases to high levels, the benefits of aggression decline substantially. Defense should cease altogether when scrambling subordinates acquire the same amount of food as the dominants without paying the energetic cost of aggressive behaviors. Thus, the relationship between foraging aggression and food abundance is a hump-shaped curve, peaking at intermediate levels of food abundance (summarized by Carpenter 1987 and Grant 1993, 1997). Although originally designed to explain the existence of feeding territories (reviewed in Maher and Lott 2000), this general model has been useful in understanding non-territorial resource defense in a number of organisms (Isbell 1991, Grant 1993).

A simple graphical depiction of the resource defense theory outlined above reveals an interesting pair of related and testable hypotheses relating food abundance to competitive aggression (Fig. 2.1). First, when food abundance is low but within the range of economic defendability, an increase in food abundance should elicit an increase in individual, and consequently per capita, rates of aggression. Second, over the range of food abundance that elicits aggression, the rate of aggressive investment (defined here as a per capita rate equal to the number of acts performed per prey item received) should linearly decline with increasing food abundance. Aggressive investment is an instantaneous measure of the slope of the original curve and decreases due to the ever-decreasing slope of a hump-shaped curve. The shape of the aggressive investment function also allows the existence of a curvilinear relationship between food abundance and aggression to be detected without circumscribing the entire curve. A decrease in aggressive investment with increasing food abundance only occurs with a decreasing slope in the original function, thereby implying a peaked or asymptotic relationship between food abundance and aggression. If there is a simple linear relationship between aggression rate and food abundance then the rate of aggressive investment would be the slope of that line, remaining fixed as food abundance increases. Finally, on the right-hand side of the hump, where prey are abundant, the model predicts a decrease in both aggression rate and aggressive investment.

Drift-feeding organisms provide an excellent opportunity to explore the applicability of this model to the behavior of animals in natural foraging situations. Drift feeders consume aquatic and terrestrial invertebrates that are carried by water currents, and the predominantly unidirectional (i.e., downstream) delivery of prey ensures that certain foraging positions will be more profitable than others (Blanckenhorn et al. 1998, Grant 1993, Grant and Noakes 1988, Hughes 1992, Hutchinson and Iwata 1997, Chapter 1). In such 'continuous input' systems, behaviorally dominant individuals typically defend profitable positions at the upstream end of high quality patches (e.g., Hughes 1992, Rincón and Grossman 2001, Chapter 1). Thus, drift-feeding fishes are likely to have evolved social behaviors which maximize their access to spatially predictable resources, and are good candidates for testing the resource defense model described above.

In this study we used two species of drift-feeding minnow to test the general hypothesis that increasing food abundance, within the range observed in a natural stream (Coweeta Creek, North Carolina), would alter aggressive tendencies in intraspecific groups of foraging minnows in accordance with the hump-shaped resource defense theory. We chose rosyside dace (aka smoky dace, Warren et al. 2000), *Clinostomus funduloides*, as our primary test species because they readily defend foraging positions in artificial laboratory streams and the field at comparable rates (Freeman and Grossman 1992a, Rincón and Grossman 2001, Chapter 1). We also chose the rosyside dace to evaluate the effects of a recent invasion by our second study species, the yellowfin shiner, *Notropis lutipinnis*. Although regionally abundant in the southeastern United States, the yellowfin shiner was introduced into the Little Tennessee River drainage ca. 1990 and is rapidly spreading (Johnston et al. 1995, W. McClarney pers. comm.). This species was well established in Coweeta Creek by the mid-1990's and has been observed sympatrically with the rosyside dace. Microhabitat use of yellowfin shiner shows substantial overlap with that of rosyside dace in Coweeta Creek and both species use foraging aggression to establish positional dominance in feeding groups (M.D. Farr and G.D. Grossman unpub. data, Freeman and Grossman 1992a, Rincón and Grossman 2001, Chapter 1).

In a previous study (Chapter 1) we demonstrated that competitive aggression led to the acquisition of profitable foraging positions and increased foraging success for both rosyside dace and yellowfin shiner. In this paper we address four additional questions: 1) does the dome-shaped graphical model predict the behavioral response of foraging groups to increased food abundance; 2) are there significant differences in aggression rates between native and introduced species; 3) do dominant and subordinate individuals display different behavioral responses to increases in food abundance; and, 4) what implications do these results have for the ultimate outcome of the invasion? Our overall goals are to assess the effects of increasing food abundance on aggression in light of current resource defense theory, and to determine whether dominants or subordinates are more likely to alter their behavioral tactics when habitat quality is improved.

Methods

This study is based on the same experimental methods and specimens used in a companion paper (Chapter 1). Descriptions of laboratory apparatus and procedures below are reduced and interested readers should refer to the previous material.

Capture and Preparation of Experimental Subjects

We obtained wild, adult rosyside dace (means ± SD: standard length, 70.4 ± 4.2 mm; weight, 5.01 ± 0.92 g) and yellowfin shiner (standard length, 62.1 ± 2.0 mm; weight, 3.41 ± 0.38 g) approximately weekly between 15 July and 30 October 2001 from Coweeta Creek, a fifth-order tributary of the Little Tennessee River located in the highlands of western North Carolina. Experimental subjects were held in one of two holding tanks at conditions typical for pools in Coweeta Creek during late summer (18° C, a constant flow ranging from 3-10 cm s^{-1}, a 14:10 h light:dark schedule with 60 minute crepuscular periods to simulate normal sunrise/sunset cycles). Within three days of capture, each fish was anesthetized (70 mg l^{-1} MS-222, Ross and Ross 1999), weighed (nearest 0.01 g), measured (standard length, total length, nearest 1 mm), and uniquely tagged (procedure modified from Chapman and Bevan 1990). Newly tagged fish quickly recovered from the anaesthesia (< 3 min), fed within two hours, and exhibited no obvious signs of distress in terms of behavior or body coloration.

Laboratory Apparatus

We conducted all experimental trials in a plexiglass laboratory flow tank measuring 305 cm × 152 cm × 76 cm (length × width × depth) equipped with an automatic feeder that has previously been described in detail (see Chapter 1). Fish were confined to one of two 70 × 75 cm (l × w) feeding areas within the separate experimental channels. Water depth (30 cm), substrate (pebbles, 5-15 mm diameter and 2-4 cm deep interspersed with cobbles, 30-100 mm diameter), and water velocity (12 cm s^{-1}) were designed to mimic typical conditions in the pool habitats preferred by these species during summer months (Grossman and Freeman 1987, Grossman and Ratajczak 1998, M.D. Farr and G.D.

Grossman unpub. data). The automatic feeder supplied prey at rates which were set individually for each patch. We ran the feeding tubes under the gravel and dispensed prey at the level of the substrate at the head of each feeding area to simulate the natural entry of food items into the drift. Tubes were sub-divided to yield four entry points per patch to effectively disperse the prey over a 50 cm-wide area. The tank was completely clad with an opaque barrier and all behavioral observations were performed from within a completely enclosed and darkened booth to ensure the fish never saw the observer during trials or when the feeders were being loaded.

Experimental Procedures

To examine the effects of food abundance on group aggression rates, and to determine whether there were any differences between the two species, we used two single-species (intraspecific) experimental treatments in which either six rosyside dace or six yellowfin shiner were placed in the experimental patches. Group size was based on the approximate mid-point of frequently occurring groups in Coweeta Creek (1-9 individuals, Freeman and Grossman 1992a, 1993). A total of eight replicate groups of six individuals were tested for each species. We chose a repeated-measures design in order to control for inter-individual, and consequently, inter-group variation in aggressive tendencies. We tested two groups simultaneously, one each in the separate channels. In order to alleviate any effect of olfactory cues across species only conspecific groups were tested together, and we performed large water changes (~ 50 %) and filtration with unadulterated activated carbon after each trial to remove any residual scent. The order of groups was randomly assigned to reduce the effects of any seasonal changes in behavior. Finally, we approximately size-matched fish within a group (< 20 % difference in length) to reduce any confounding effects of large size differences.

We conducted trials once per day between 0900 and 1300 hours on two consecutive days. Each replicate group was tested at two prey delivery rates (22 and 45 larvae min^{-1} m^{-2} of stream cross-sectional area), one per day, which represent one standard deviation above and below the mean availability of prey in the size range consumed by drift-feeding minnows in Coweeta Creek (Hill 1989, Freeman 1990, Stouder 1990). Because Coweeta Creek has low productivity and some fishes feed constantly during daylight hours to obtain a maintenance ration (Freeman 1990), we believe these food levels represent positions on the left limb of the hump-shaped foraging aggression-food abundance model. We assigned the order of prey treatment by coin flip for each replicate. A single trial consisted of three periods: 10-min pre-trial, 60-min feeding trial, 10-min post-trial. During the pre- and post-trial periods no prey were delivered to the feeding areas.

We continuously recorded the number of prey captures and the number of overt aggressive acts performed and received for each individual on audio tape. For each aggressive act we recorded the identity of both the initiator and the recipient. Additionally, every two minutes a scan sample was taken and each fish was assigned a positional rank based on its relative position in the group (from one to six, front to back). We quantified aggression, position, and foraging success from the last 40 minutes of the feeding trials to ensure that relationships within a group had stabilized (see Figs. 1.2 and 1.8 in Chapter 1). All percentage data were arcsine-squareroot transformed and tested for normality (Kolmogorov-Smirnov test, all $P > 0.60$) before inclusion in parametric tests. All quoted probabilities are for two-tailed tests of significance.

Experimental Questions (Model Predictions) and Data Analyses

Do rates of aggression increase when food abundance increases (model prediction 1)? Do rates of aggressive investment decrease when food abundance increases (model prediction 2)? Are there significant differences in the per capita rate of aggression or aggressive investment between species? – We tested for the predicted effects of increasing food abundance on aggressive tendencies, and for differences between the species, with separate repeated-measures analysis of variance (ANOVAR) for each response variable (per capita rates of aggression and aggressive investment). Group (replicate) was the within subject factor and food abundance (low or high food) and species (yellowfin shiner or rosyside dace) were between-subject factors. We applied post-hoc Tukey-Kramer tests to investigate the nature of any significant main effects and only those with adjusted *P*-values $\leq$ 0.05 were interpreted.

Do dominant fish alter their aggression rates when food abundance increases? – Behaviorally dominant minnows defend forward positions in foraging groups and have higher rates of foraging success (Chapter 1). To determine how changes in food abundance affected an individual's aggressive tactics, we evaluated whether changes in positional rank were related to both changes in the number of aggressive acts performed and changes in food capture rate with linear regression analysis. Differences between species were evaluated by directly comparing the 95% confidence intervals of the regression model parameters. To determine if there were any consistent patterns as to which fish were altering their aggressive tactics (dominants vs. subordinates), we assigned a simple aggression rank (1-6, most to least aggressive) to each member of a group at the low food treatment and calculated the mean change in relative aggression (i.e., fraction of total group aggression performed by individual X in high food treatment - fraction of total group aggression performed by individual X at low food treatment) as a function of initial aggression rank.

Results

All fish fed actively throughout the trials and no evidence of satiation was observed. Per capita prey capture rates increased for both species as a function of food abundance (ANOVAR, $F_{1,14}$ = 465.84, $P < 0.0001$) and were not significantly different from each other (Fig. 2.2). However, at the high food abundance level, observed per capita capture rates were slightly lower than anticipated. The capture rate at high food was the same for both species and could indicate a reduction in observer efficiency with increasing strike rate. Overall the evidence suggests there were no perceived differences in habitat quality between species and the treatment effect was sufficiently large to evaluate the effects of food abundance on aggressive behavior.

Do rates of aggression increase when food abundance increases (model prediction 1)? – Repeated-measures ANOVA revealed an overall significant effect of species ($F_{1,14} = 29.25$, $P <$ 0.001) and food abundance ($F_{1,14} = 11.70$, $P = 0.004$) on group aggression rates (Fig. 2.3a). The interaction between these effects was also significant ($F_{1,14} = 6.41$, $P = 0.024$) due to the differential effect of food abundance on each species. As predicted by the model, the per capita rate of aggression increased with increasing food abundance for groups of yellowfin shiner (post-hoc Tukey-Kramer test for the effect of food, $t = 4.21$, adj. P=0.004). Nonetheless, in contrast to model predictions, rosyside dace aggression rates did not increase with increasing food (post-hoc Tukey-Kramer test for the effect of food, $t = 0.63$, adj. $P = 0.921$).

Do rates of aggressive investment decrease when food abundance increases (model prediction 2)? – As predicted by the model, increasing food abundance significantly reduced the aggressive investment in prey capture for both species (Fig. 2.3b, ANOVAR: $F_{1,14} = 35.43$, overall $P < 0.0001$, interaction term $P = 0.65$). Post-hoc Tukey-Kramer tests revealed the effect was significant for both species at the $P < 0.05$ level (yellowfin shiner, $t = 4.53$, adj. $P = 0.001$; rosyside dace, $t = 3.89$, adj. $P = 0.002$).

Are there significant differences in the per capita rate of aggression or aggressive investment between species? – Per capita aggression rates in groups of yellowfin shiner were at least twice those of rosyside dace (Fig. 2.3a). Mean aggression rates observed for the rosyside dace were higher on average (0.70 - 0.76 acts fish^{-1} min^{-1}), but within the range of those observed in the field (mean ± 2 SD: 0.20 ± 0.77 acts fish^{-1} min^{-1}, Freeman and Grossman 1992a). No field estimates of aggression rates for yellowfin shiner are currently available. The higher mean aggression rates were likely due to an increased defendability of resources in the lab. Nevertheless, experimental conditions were identical for each species and the differences between them should reflect genuine interspecific variation in aggressive tendencies. Rosyside dace demonstrated a smaller change in aggressive investment with increasing food than yellowfin shiner (change in acts capture^{-1}, means ± 95% C.I.: rosyside dace, -0.67 ± 0.29; yellowfin shiner, -0.78 ± 0.39), but this difference was not statistically significant.

Do dominant fish alter their aggressive tactics when food abundance increases? – There was a clear effect of altering behavioral tactics on the competitive advantage of dominant fish. Behaviorally dominant individuals who altered their aggressive tactics by reducing their aggression rates as food increased ended up farther back in foraging groups (Fig. 2.4, Table 2.1). These regression relationships were highly significant but had low predictive power (yellowfin shiner, $R^2 = 0.20$, $P = 0.001$; rosyside dace, $R^2 = 0.37$, $P < 0.001$). In addition, when dominant individuals of either species fell back in groups they incurred lower capture rates (Fig. 2.5, Table 2.1). Thus, those individuals who reduced their aggression rates sacrificed positional rank in the group (relative to the direction of food delivery) and suffered reduced feeding rates. We also examined the relative distribution of aggression within the groups as a function of food abundance. As food abundance increased, the most aggressive individuals performed a smaller fraction of the total aggression in a group and vice versa (Fig. 2.6). This pattern obtained for both species, and therefore applied regardless of whether or not group aggression rate increased with food abundance (yellowfin shiner - increase, rosyside dace - no increase). Overall, these patterns suggest there was a transfer of aggressive imperative from dominants to subordinates accompanying a change in positional rank.

We also observed significant differences in the relationship between individual aggression rate (cost) and foraging performance (benefit) between species. According to regression slope parameters (Fig. 2.4, Table 2.1), improving positional rank by one step for yellowfin shiners required a two-fold increase in aggression rate compared to that needed for a one step increase by rosyside dace (means ± SE: 2.33 ± 0.55 acts min^{-1} vs. 1.07 ± 0.17 acts min^{-1}). Thus, yellowfin shiner were both more aggressive on average, and more resistant to displacement from aggressive subordinates. Despite these differences in aggressiveness there was no difference in the foraging value of a step increase in positional rank between species (direct comparison of 95% confidence limits on slope parameter from regression models, Fig. 2.5, Table 2.1).

Discussion

When socially foraging animals compete for food, resource defense theory proposes a dome-shaped relationship between the frequency of aggression and food abundance. A graphical depiction of this theory yields two simple predictions: 1) an increase in per capita aggression rate with increasing food abundance when prey are at low-moderate abundance; and, 2) a decreasing investment in aggressive behavior with increased food abundance under all conditions of economic defendability. Our results for yellowfin shiner agreed with model predictions, whereas those for the rosyside dace only supported prediction two. For rosyside dace, this result could also be explained as a simple dilution effect. If individuals employed a fixed strategy (e.g., be aggressive at a certain rate when food and competitors are present), then aggressive investment would continually decline as food abundance increased while per capita rates of aggression would not change. However, this alternate explanation is inconsistent with the observed changes in individual aggression strategies (i.e., no individual should have changed its aggression rate). In addition, because natural food abundance is low in Coweeta Creek (Freeman 1990, Hill and Grossman 1993) we assume that even our high food treatment was on the left shoulder of the theoretical aggression-food abundance curve (Grant et al. 2002), and thus our experimental design constitutes a reasonable test of model predictions under natural conditions. Although few studies have documented an increase in aggression with increasing food abundance at low food availability, examples do cover a range of taxa and foraging situations (fish, Grant et al. 2002; birds, Ewald and Carpenter 1978; salamanders, Wildy et al. 2001; juvenile hyenas, Wachter et al. 2002).

It is possible that interspecific differences in individual behavior can explain the differential aggressive responses of yellowfin shiner and rosyside dace to increased food. The observed per capita aggression rate in groups of yellowfin shiner and rosyside dace is a consequence of aggregation, but is not intrinsically an attribute of the group as an entity. It is the sum result of a number of individuals acting in proximity, but not in concert. It may therefore be more appropriate to model groups as arrays of individuals, and to evaluate their individual decisions (aggression rate) against the relative value of their position within the group (net energy gain, Fig. 2.7). This approach is particularly apt when either the environment (e.g. stationary fish foraging against a flow) or behavior (e.g., a foraging group moving in a single direction) imposes a known, linear structure onto the relative quality of any position within a group (Brown 1964, Grant 1993). By converting prey delivery rate (a measure of absolute habitat quality) to net energy gain (a measure of realized habitat quality), the dome-shaped model could accommodate the failure of rosyside dace to increase group aggression if either of two situations are true.

First, if rosyside dace are nearer the peak of the curve than yellowfin shiner, we would expect increased food to produce a smaller change in their aggression rate. Because per capita capture rates were nearly identical in the experiments (Fig. 2.2), this would mean the energetic costs of maintaining any position within the rosyside dace group would have to be lower than those for yellowfin shiner. The main costs in our experimental situation were twofold: 1) the energetic cost of holding position against a flow; and, 2) the costs of preforming and receiving aggression. The former were small at the treatment velocity, and likely equal for similar sized rosyside dace and yellowfin shiner (Facey and Grossman 1992, Videler 1993). By contrast, costs to individuals of aggression are hard to quantify and incorporate the energy necessary to engage opponents as well as lost opportunities for acquiring prey (Huntingford and Turner 1987). Nevertheless, yellowfin shiner groups were at least twice as aggressive as rosyside dace groups. It is likely their total energetic costs were higher, and consequently, they suffered reduced net energy gain at the same level of food abundance. The aggression rates we observed in the lab appear to be realistic because mean aggression rates of rosyside dace were similar to those observed in the field, although field estimates are not available for yellowfin shiner.

The second possibility also arises from the differential aggression rates displayed by the species. It is reasonable to assume that maximum aggression rate (the height of the peak) is a trait of the species (or the population), and as a consequence, rosyside dace and yellowfin shiner probably possess distinct aggression curves with disparate geometries. The less aggressive rosyside dace should have a shallower curve than the more aggressive yellowfin shiner (Fig. 2.8). The consequences of the flatter curve are a less pronounced increase in aggression with food abundance, and a smaller decrease in the rate of aggressive investment (slope of the line). In fact, rosyside dace did demonstrate a slower reduction in the rate of change in aggressive investment than did yellowfin shiner. An additional factor that could have produced a shallower dome-shaped curve for rosyside dace is that not all dace were aggressive in the laboratory foraging groups (Chapter 1). Populations of rosyside dace from Coweeta Creek include non-aggressive individuals which may represent a separate behavioral phenotype (Freeman and Grossman 1992a, Rincón and Grossman 2001). Non-aggressive rosyside dace in Coweeta Creek are more likely to both forage alone and to leave a group if a highly aggressive individual is present (Freeman and Grossman 1992a). Nevertheless, foraging groups routinely contain non-aggressive foragers and we believe their inclusion in the experimental groups represents the natural situation. It is therefore unlikely that the observed difference represents a pure experimental artifact of the constructed foraging groups. In addition, if rosyside dace were to the right of yellowfin shiner on the same curve, they should have exhibited a higher average aggression rate. The opposite was observed. Overall, it appears most likely that the observed interspecific differences were due to differences in curve geometry. It is important to note, however, that although our experiment revealed these possibilities, it was not designed to explicitly discern between them.

Extension of the dome-shaped model to arrays of individuals (i.e., a social hierarchy) also provides an intuitively appealing explanation of how aggression within a group should be expressed by each individual forager. Specifically, spatially subordinate individuals should be farther to left on the curve than dominants, and therefore exhibit less aggression in low food situations. Additionally, the imperative to perform aggression should progress backward in the group as the overall habitat quality increases. In other words, the uneven distribution of feeding opportunities amongst the foraging positions establishes a lag in perceived changes in habitat quality. Dominant (and hungry) individuals will occupy forward positions and benefit first from increases in food abundance, and this benefit is proportional to the degree of resource monopolization they can exert. As habitat quality improves, dominant individuals should also reduce aggression first and then drift back in the group into less profitable positions. Our data support this hypothesis because: 1) the most aggressive individuals accounted for a smaller fraction of total group aggression as food abundance increased; and, 2) those aggressive individuals who reduced aggression also lost positional rank within the group and suffered reduced feeding rates. Krause and Ruxton (2002) anticipated this result, suggesting that individual fish within a shoal will exhibit dynamic positioning as the imperative switches from foraging to predator avoidance with increasing stomach fullness (i.e., a trade-off in fitness currencies). As a dominant individual's nutritional condition improves, it should shift to safer, more central positions within the group (Hamilton 1971, Bumann et al. 1997). Our study made no attempt to include or manipulate any perceived predation threat because the presence of predators does not appear to strongly influence microhabitat use by fishes in Coweeta Creek at the reach scale (Grossman et al. 1998). However, our findings are in agreement with the general view that dominance is a trait that allows individuals to maximize the benefits of group association by monopolizing spatial positions within a group.

General differences in aggressiveness between our two experimental species were evident. The invasive yellowfin shiner was both more aggressive and more likely to exhibit aggression (absence of a non-aggressive class, see Chapter 1). Heightened aggression is commonly invoked to explain the success of some invasive animals (Dick et al. 1995, Savino and Kolar 1996, Gamradt et al. 1997, Rincón et al. 2002, Warburton and Madden 2003), although its general importance remains unclear (Holway and Suarez 1999). Interestingly, the reward for aggressively maintaining a profitable position within groups of either species was approximately equal (Fig. 2.5, see also Chapter 1). This suggests an incentive for a dominant yellowfin shiner to join a group of less aggressive rosyside dace. Such a decision may be unusual, as fishes routinely prefer to school with individuals of the same species and size, ostensibly to reduce the effects of oddity on predation risk (reviewed in Krause et al. 2000). Nevertheless, minnows in Coweeta Creek are known to form mixed-species foraging aggregations in favorable habitats (Grossman and Freeman 1987, Freeman and Grossman 1992b, 1993). Ultimately, heightened foraging aggression could be important in the establishment phase of the invasion, when competition for the best feeding positions may balance the heightened predation risk for rare invaders.

Interspecific interference behaviors may also play a role in the relative reproductive success of rosyside dace and yellowfin shiner. Within their native range, both species spawn in aggregations over the nests of large chubs (*Nocomis* spp., Wallin 1989, 1992, Jenkins and Burkhead 1994). Johnston et al. (1995) identified a rosyside dace × yellowfin shiner hybrid cross from southern Appalachian streams suggesting overlap in the use of spawning sites. If the availability of nests is a limiting factor in the spawning of these species, then competition for favorable spawning positions over the nest may be an important mechanism of population regulation and warrants further exploration.

To summarize, our data suggest that the theoretical dome-shaped aggression-food abundance relationship is applicable to both native and introduced drift-feeding minnows. By reducing the scale from groups (averaged behavior) to sorted arrays of individuals, the model also accommodated the observed changes in the behavioral strategies of individual foragers. Dominant fish were more likely to reduce their aggression when food abundance increased. This behavior may be a hallmark of the hypothesized transition of priority from feeding to other benefits of group association, although, we could not test this hypothesis directly. We conclude that the high rate of foraging aggression displayed by the yellowfin shiner ultimately may promote their success in the Little Tennessee River.

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Table 2.1. Linear regression analysis of the relationships between changing individual aggression rates and positional rank improvement (Fig. 2.4), and positional rank improvement and capture rate improvement (Fig. 2.5) for yellowfin shiner and rosyside dace. Estimated regression parameters are ± the 95% confidence interval.

	Regression Statistics ($y = y_0 + ax$)				
Species	y_0	a	r	r^2	P
Aggression Change vs. Positional Rank Improvement (Fig. 2.4)					
Yellowfin Shiner	-0.20 ± 0.30	0.01 ± 0.01	0.45	0.20	0.0014
Rosyside Dace	-0.07 ± 0.32	0.03 ± 0.01	0.61	0.37	< 0.0001
Positional Rank Improvement vs. Capture Rate Improvement (Fig. 2.5)					
Yellowfin Shiner	0.40 ± 0.03	0.10 ± 0.03	0.43	0.18	0.0023
Rosyside Dace	0.36 ± 0.03	0.08 ± 0.02	0.46	0.21	0.0011

Figure 2.1. Hypothetical depiction of resource defense theory for continuous input situations (all units are arbitrary). Aggression rate is modeled as a parabolic function of prey delivery and initiates at some food abundance greater than zero (solid line). The rate of aggressive investment is defined as per capita aggression rate (Y_i) divided by per capita prey capture rate (X_i) at any point on the curve (dashed line). The model assumes handling time is much less than the interval between prey arrival, and all prey items are captured by the group.

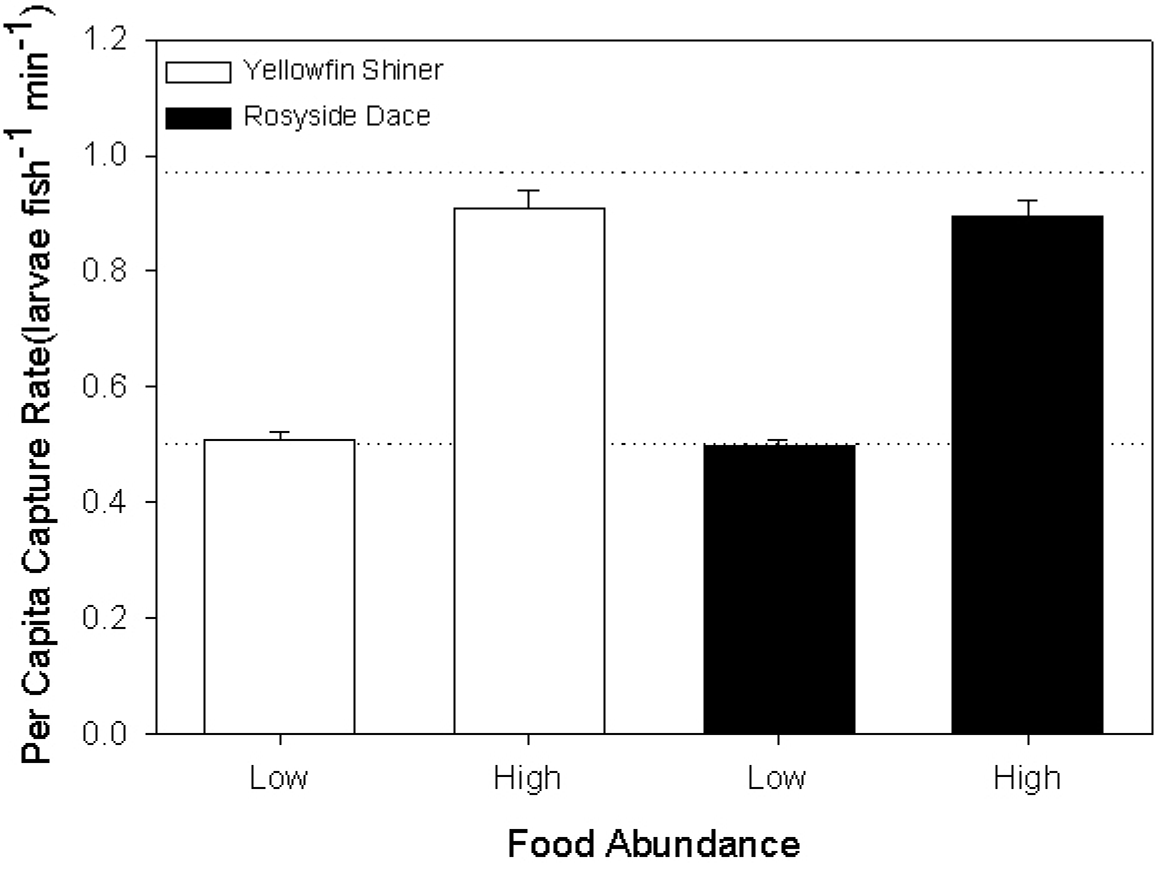

Fig. 2.2. Mean per capita capture rate (± 1 SE, *N* = 8) as a function of food abundance treatment. Dotted lines indicate the target treatment levels for food delivery. Different letters indicate significant differences at the P < 0.0001 level (ANOVAR with post-hoc Tukey-Kramer tests).

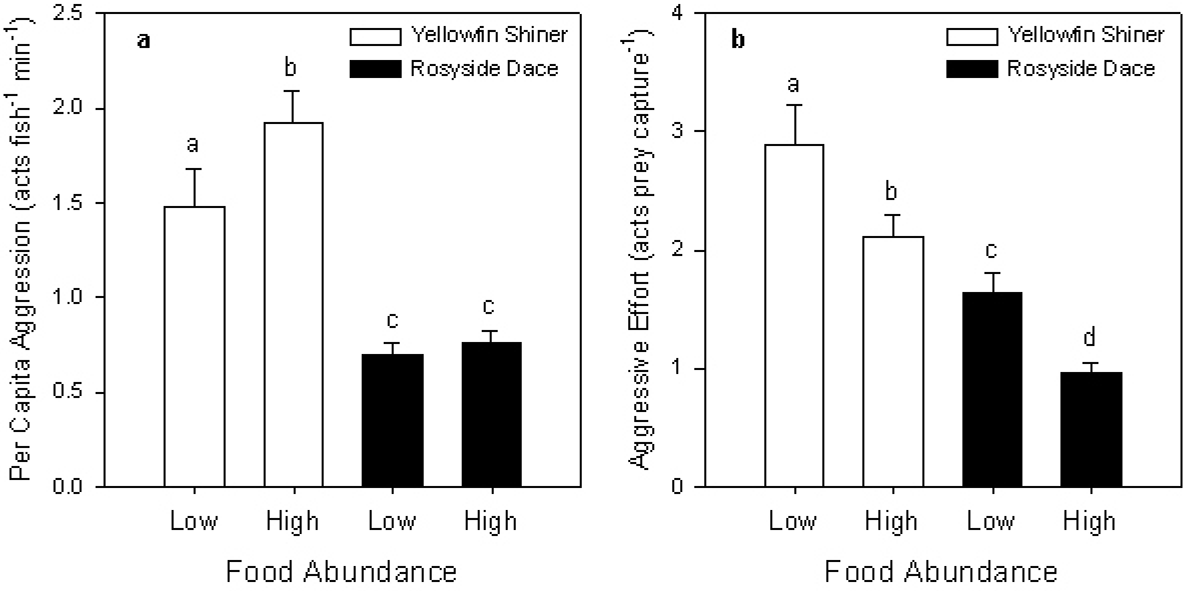

Fig. 2.3. Effect of food abundance on (a) mean group per capita aggression rate (± 1 SE, *N* = 8), and (b) mean per capita rate of aggressive investment (± 1 SE, *N* = 8). Different letters indicate significant differences at the P < 0.05 level (ANOVAR with post-hoc Tukey-Kramer tests).

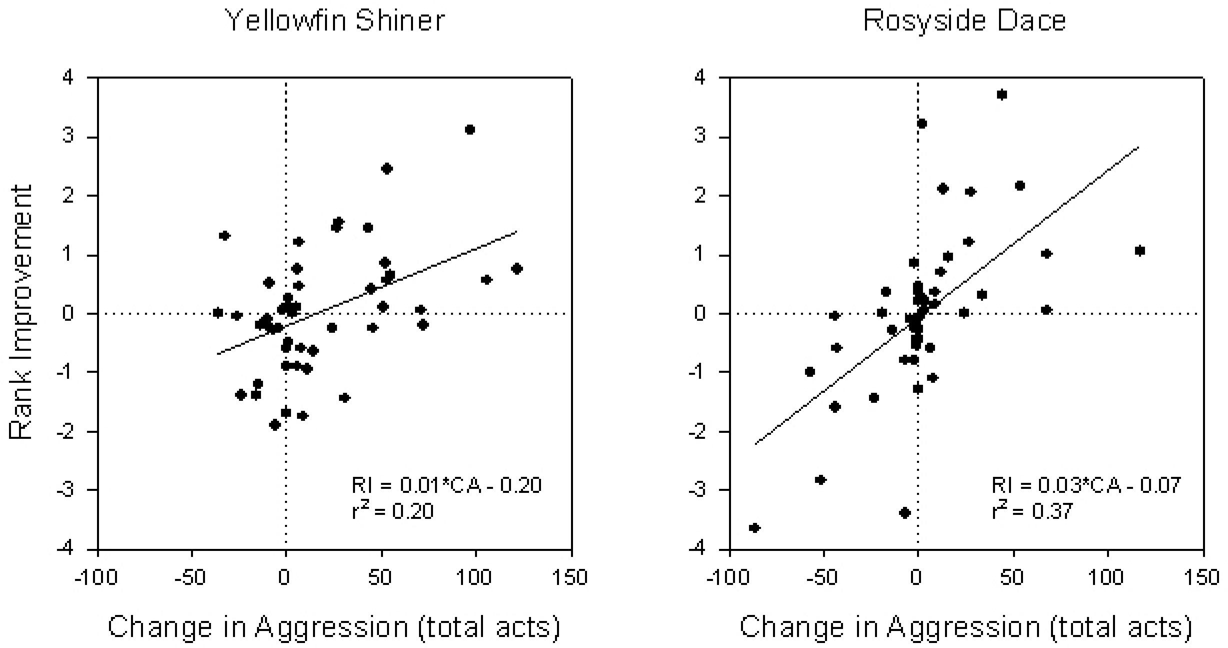

Fig. 2.4. Effect of altering aggression behavior on individual positional rank within foraging groups. Rank improvement is defined as the change in an individual's mean positional rank between low and high food treatments. Both regressions are significant at the *P* < 0.01 level.

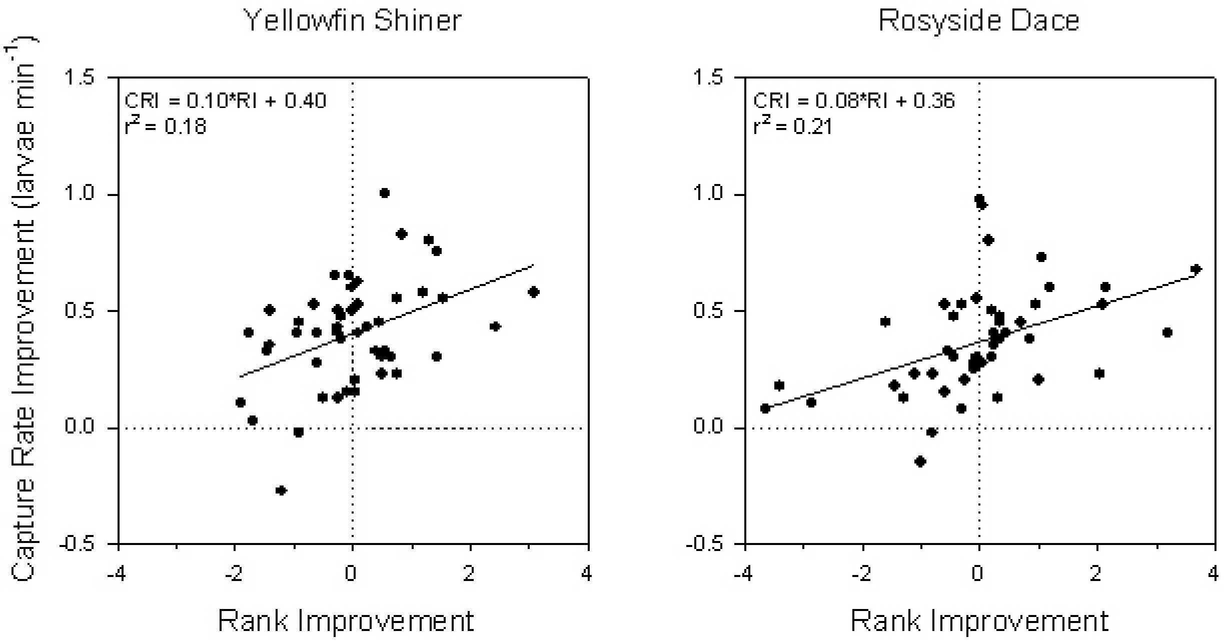

Fig. 2.5. Effect of changing positional rank on individual capture rate. Improvement values are defined as the difference between low and high food treatments (i.e., a positive value indicates an increase in the value when food abundance increased). Both regressions are significant at the *P* < 0.01 level.

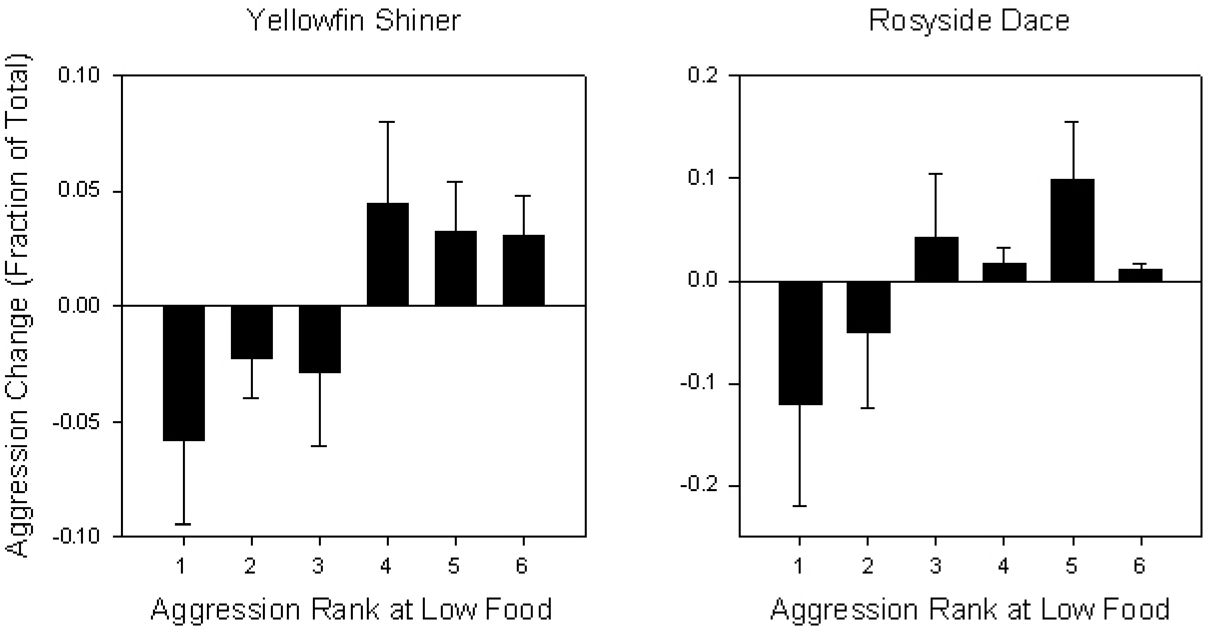

Fig. 2.6. Change in mean relative aggression rate (± 1 SE, $N = 8$) as a function of aggression rank at low food. Aggression difference is the change in individual contribution to the total group aggression rate expressed as a percentage of the group total (e.g., a value of + 0.05 indicates that individuals of that rank performed 5% more of the total group aggression at high food than at low food).

Fig. 2.7. The dome-shaped relationship between aggression and habitat quality measured as food abundance (absolute habitat quality) or net energy gain (realized habitat quality). Circles represent individuals joined into groups with a linear dominance structure.

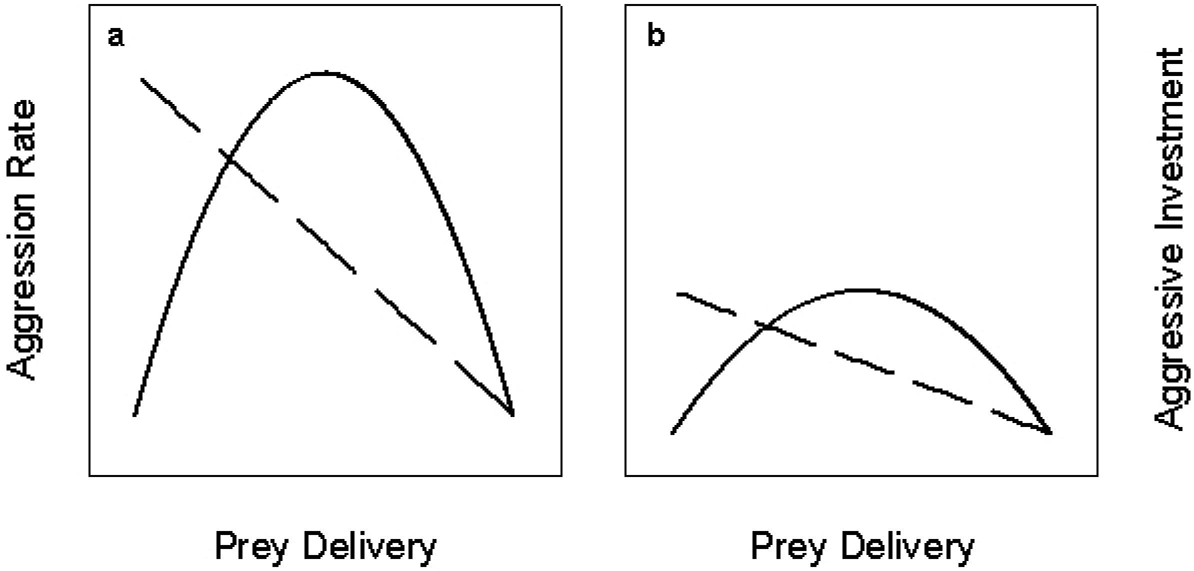

Fig. 2.8. The dome-shaped relationship between food abundance and per capita aggression rate (solid line) or per capita aggressive investment rate (dashed line) for two hypothetical species which differ in maximum aggression rate. Panel (a) represents a highly aggressive species, panel (b) represents a weakly aggressive species.

CHAPTER 3

IDEAL INVADERS?

THE EFFECT OF INCREASING FOOD ABUNDANCE ON INPUT-MATCHING BY NATIVE AND INVASIVE STREAM FISHES

Wagner, C. M. and G. D. Grossman. To be submitted to *Oikos*.

Introduction

Invasions by non-indigenous species pose a serious threat to the integrity of the Earth's freshwater ecosystems (Vitousek et al. 1997, Claudi and Leach 1999, Kolar and Lodge 2000). In the United States alone the rate of fish introductions has tripled in the last half of the twentieth century (Fuller et al. 1999). However, for reasons not well understood, many introductions either fail or do not result in serious impacts to native communities. Why do some species establish and spread where others fail? What attributes of invaders are critical to their establishment? The inability to answer these questions underlies the general failure to accurately predict the impact of introductions into aquatic ecosystems (Lodge 1993, Moyle and Light 1996), and is placing a significant strain on already limited management resources (Parker et al. 1999). Studies of the mechanisms that allow introduced species to establish are needed to improve both theoretical understanding of the invasion process and the accuracy of predictions (Karieva 1996, Byers et al. 2002).

Habitat selection by many drift-feeding stream fishes is a dynamic process. To forage efficiently, each fish must continually assess swimming costs, the supply rate and capture efficiency of food items, and the risk of predation, all of which vary greatly along spatial and temporal gradients (Hughes and Dill 1990, Kramer et al. 1997). When individuals make accurate assessments they feed more efficiently, and ultimately enjoy a higher fitness relative to less efficient competitors (Dill 1983). Therefore, it is not surprising that several studies show drift-feeding stream fishes select foraging microhabitats that maximize their net rate of energy intake (e.g., Fausch 1984, Hughes and Dill 1990, Hill and Grossman 1993, Tyler and Gilliam 1995, Guensch et al. 2001, Grossman et al. 2002). These studies support the general contention that stream fishes have both the ability to assess variation in critical environmental parameters that mediate foraging success, and sufficient behavioral flexibility to respond appropriately (Dill 1983).

Because profitable foraging habitat is patchily distributed in streams, non-territorial stream fishes often will form aggregations in the best patches as a result of similar, but independent, habitat choices (Freeman and Grossman 1993, Matthews 1998). Social foraging may lower patch quality through increased exploitation of its resources. Thus, socially foraging fishes must have sufficient ability to assess and respond to the distribution of both food and competitors. If individuals are free to move among patches within the stream, this ability may lead to a dynamic ideal-free distribution (IFD; Fretwell and Lucas 1970, Fretwell 1972). The central prediction of the IFD is termed input- or habitat-matching (Sutherland 1983, Pulliam and Caraco 1984). It states, when there is a continuous input of resources, the distribution of organisms across the environment should match the distribution of resources. This prediction obtains from the general assumptions that animals: (1) are well informed as to the distribution of resources in each habitat patch (i.e., are 'ideal'); (2) can freely move about the environment (i.e., are 'free'); and (3) are of equal competitive ability. Given these constraints, IFD theory predicts that the equilibrium distribution of competitors will be one where the benefits to each individual are equal across habitat patches, and no competitor can increase its foraging rate by switching patches.

Numerous studies have confirmed the ability of fishes to achieve an IFD in the laboratory (reviewed in Tregenza 1995), though field tests of model predictions remain rare (Fraser and Size 1980, Power 1984). It has been argued that the input-matching 'rule' is sufficiently established to be employed as a bioassay technique to compare the habitat-selection behaviors of competing species (Rosenzweig and Abramsky 1997). In laboratory experiments with stream fishes, the input-matching rule has been applied as a null hypothesis to evaluate the effects of velocity on patch selection (Tyler and Gilliam 1995), the energetic value of predation risk (Grand and Dill 1997), and the mitigating effect of visual isolation on aggressive interactions (Giannico and Healey 1999). Our study also employs the input-matching prediction as a null expectation, and tests the relative abilities of two North American minnows (one native, one invasive) to track changes in food abundance in a laboratory artificial stream. This investigation was prompted by the appearance of an invasive species (the yellowfin shiner, *Notropis lutipinnis*) in Coweeta Creek, North Carolina, a system we have been studying for over 20 years (see Grossman and Ratajczak 1998, Grossman et al. 2002). We chose to examine its input-matching behavior in tandem with an abundant, ecologically similar species whose foraging ecology is known (the rosyside dace, *Clinostomus funduloides*). We suspected the ability to accurately match the spatial distribution of food in a frequently changing environment is important to the process of invader establishment in streams, and may have aided yellowfin shiner in their establishment in the Coweeta Creek drainage.

To test for input-matching, we examined the distribution of intraspecific groups of minnows between two patches that differed in relative food distribution (2:1 ratio) under two conditions of habitat quality (high food and low food). The following questions were addressed: (1) Do yellowfin shiner and rosyside dace input-match as predicted by the IFD? (2) Does increasing food abundance (i.e., within the natural range observed in Coweeta Creek) affect the accuracy of input-matching by either species? and (3) Is the invasive species better at matching resource distributions than the native?

Methods

Input-Matching Models

Because both yellowfin shiner and rosyside dace display intraspecific aggression that affects foraging success (Freeman and Grossman 1992; Rincón and Grossman 2001; Chapters 1 and 2), our design potentially violates two of the basic premises of IFD theory (i.e., minnows are not equal competitors and they may not be entirely 'free'). Nevertheless, these species are non-territorial group foragers (Freeman and Grossman 1992, M.D. Farr and G.D. Grossman, unpub. data), and the distribution of individuals in single-species IFD tests may superficially match one or more of the predicted input-matching scenarios even though specific predictions about relative intake rates between patches presumably would not hold (Kacelnik et al. 1992, Sutherland 1996). IFD theory has successfully been applied to the analysis of patch-use in a variety of vertebrates which employ foraging aggression including fishes (e.g., Grand 1997, Koops and Abrahams 1999), birds (e.g., Kennedy and Gray 1994), and mammals (e.g., Halama and Dueser 1994; Beckmann and Berger 2003). Violation of the IFD assumptions does result in a characteristic deviation from input-matching termed undermatching (i.e., when fewer competitors than predicted occupy the resource-rich patch). Undermatching is predicted to occur when: (1) individuals cannot make complete assessments of relative patch quality ('perceptual constraints hypothesis', Abrahams 1986); (2) the best competitors defend the best foraging positions ('unequal competitors hypothesis', Grand and Grant 1994); or (3) organisms must physically sample each patch to make an assessment (Gotceitas and Colgan 1991, Houston et al. 1995).

If undermatching occurs due to competitive inequalities, we expect the distribution of foragers will either match the ideal despotic distribution (IDD: Fretwell and Lucas 1970; Fretwell 1972) or the unequal competitors IFD (Sutherland and Parker 1985; Parker and Sutherland 1986). The IDD model assumes some individuals use territorial aggression to limit the entry of subordinates into high quality patches and should result in extreme undermatching. Further, patch switching should be infrequent at equilibrium and the dominant fish should always occupy the ‘rich’ patch. If competitive aggression does not exclude individuals from a patch, but does reduce their foraging success, then the unequal competitors IFD may apply. Under these conditions the distribution of ‘competitive weights’ (defined as the proportion of resource an individual receives when competing with all other members of a group in a single patch) should match the distribution of resources, whereas competitor numbers would not (e.g., Grand 1997). If perceptual constraints or sampling behavior underlies the undermatching phenomena, Abrahams (1986) predicted that increasing overall food abundance would increase the information content of the system and allow more foragers to accurately match the distribution of resources. By contrast, the unequal competitor models predict no change in the distribution with increasing food (assumes the best competitor is always the best competitor when group membership does not change). We also tested this assumption by comparing the competitive weights of individuals across food treatments.

Field and Laboratory Procedures

We collected wild, adult rosyside dace and yellowfin shiner between 15 July and 30 October 2001 with seine nets from Coweeta Creek, North Carolina. Experimental subjects were maintained in holding tanks at conditions typical for pools in Coweeta Creek during late summer (18° C, 3-10 cm s^{-1} flow,) with a 14:10 h light:dark schedule and 60 minute crepuscular periods to simulate normal sunrise/sunset cycles. We acclimated the fish for a total of six days in the laboratory. Prior to the experimental trials each fish was weighed (electronic balance, nearest 0.1 g), measured (SL, TL, nearest mm), and uniquely tagged with a small colored disc (1.5 mm dia.). The tag was attached with fine monofilament thread inserted through the musculature posterior to the dorsal fin (technique modified from Chapman and Bevan 1990).

We conducted all experimental trials in a 1000-l laboratory artificial stream equipped with an automatic feeder (Fig. 3.1, described in greater detail in Chapter 1). Water depth (30 cm), substrate (5-15 mm diameter pebbles 2-4 cm deep interspersed with 30-100 mm diameter cobbles), and water velocity (12 cm s^{-1}) were designed to mimic typical conditions in the pool habitats preferred by these species during summer months (Grossman and Freeman 1987; Grossman and Ratajczak 1998; M.D. Farr and G.D. Grossman, unpub. data). After the holding period we transferred groups of six fish to a 70 × 75 cm (length × width) feeding area in the artificial stream and allowed them to acclimatize to the experimental conditions for an additional two days. We selected the experimental group size based on the range of group sizes commonly observed in Coweeta Creek (1-9 individuals, Freeman and Grossman 1992, 1993). Before a group was used in a test, we fed the fish via the automatic feeders for a period of one hour on the second day of acclimation to ensure a normal feeding response.

We chose chironomid larvae as the experimental prey due to its prevalence in the diet of drift-feeding minnows from Coweeta Creek (Stouder 1990). To simulate the natural entry of larvae into the drift, we ran the feeder tubes under the gravel and dispensed prey at the level of the substrate at the head of each feeding area. We used two configurations in each feeding area: single-patch and split-patch (Fig. 3.1). For single-patch trials, we sub-divided the two primary tubes to yield four entry points each 10 cm apart in the central region of each channel. In addition, we fitted the ends of the tubes with Y-connectors to effectively disperse the prey over a 50 cm-wide area simulating a single diffuse patch (a total of eight release points). For split-patch trials, we reconfigured the tubes to yield two lateral patches 25 cm apart, each approximately 20 cm wide and with four prey release points.

Experimental Procedures

We used single-species treatments (eight replicates each) in which monospecific groups of either six rosyside dace or six yellowfin shiner were placed in an experimental patch. In order to measure individual competitive abilities (single-patch trial), and then the distribution of individuals across patches (input-matching), it was necessary to use the same group of fish in consecutive trials (i.e., a repeated-measures design). We tested two groups simultaneously in the separate channels. In order to alleviate any effect of olfactory cues across species we only placed conspecific groups together. We also assigned the order of groups randomly to reduce the effects of any seasonal changes in behavior. Finally, fish within a group were approximately size-matched fish to reduce confounding effects of large size differences (> 20 %). We conducted trials once per day between 0900 and 1300 hours on four consecutive days. A single trial consisted of three periods: 10-min pre-trial, 60-min feeding trial, 10-min post-trial. During pre- and post-trial periods no prey were delivered to the feeding areas. We ran trials in the two channels sequentially each day, the order was determined by coin flip.

On the first two days of the experiment we ran single-patch trials to determine relative competitive weights. On consecutive days we dispensed chironomid larvae at one of two prey delivery rates (22 or 45 larvae min^{-1} m^{-2} of stream cross-sectional area) which represent one standard deviation above and below the mean availability of prey in the size range consumed by drift-feeding minnows in Coweeta Creek (Hill 1989; Freeman 1990; Stouder 1990). We chose these treatment levels to represent the range in quality of commonly encountered foraging patches in Coweeta Creek (hereafter referred to as low and high). The order of prey treatment (low vs. high) on consecutive days was assigned randomly for each replicate. We recorded the number of larvae captured by each individual fish. To determine relative competitive ability, we generated rank orders of the capture rates for individuals within each group. The individual fraction of total prey captures was used to determine the relative abilities of the fish, a measure equivalent to Sutherland and Parker's (1985) competitive weights. On the third and fourth experimental days we ran split-patch trials where the total prey delivery within a channel was divided into a 2:1 ratio between the two patches. We randomly assigned the position of the 'rich' patch (left or right) for each trial. We recorded the number and identity of the fish in each patch by scan sampling (Martin and Bateson 1986) at 1-min intervals throughout the trial. Again, we tested each group at the two prey delivery rates on subsequent days. We transcribed all data from audio tape recordings made during the trials.

Experimental Questions and Data Analyses

Do rosyside dace or yellowfin shiner input-match? – We compared the observed distributions of fish numbers and competitive weights with those predicted by the IFD models by directly comparing the mean fish distributions (± 95% C.I.) with the proportion of food delivered to the poor patch. If the confidence interval of the fish distribution overlapped the random expectation of a 1:1 distribution of fish between patches, then no matching behavior occurred. We also used paired t-tests to compare the mean sum of competitive weights and the mean proportion of fish numbers in the poor patch. If conversion of fish numbers to competitive weights improves the fit to the input-matching prediction, we expect a significant difference between the measures, with the mean competitive weight more closely approximating the input-matching distribution. We calculated all means from the final 40 minutes of the feeding trial to avoid biasing the outcome with non-equilibrium values (see Chapter 1).

Does food abundance affect input-matching?– Increasing overall food abundance increases the information content of the system, and may improve the accuracy of input-matching (Abrahams 1986). To determine whether this occurred, we again compared the observed mean (± 95% C.I.) distributions of fish numbers and competitive weights with the input-matching prediction at high food. If the 95% confidence interval of the observed distribution overlapped the input-matching prediction at high food, but undermatched at low food, an improvement in input-matching accuracy may have occurred. To determine if this improvement was significant, we performed one-tailed paired t-tests on the mean distribution of fish numbers and competitive weights (low vs. high food). Because we expected both species to undermatch at low food, we were only interested in testing a reduction in the quantity of fish occupying the poor patch (i.e., an improvement in the accuracy of input-matching), hence, one-tailed tests. We also repeated the paired t-test analysis to determine whether there was a significant difference in the distributions of fish numbers and competitive weights at high food.

Does food abundance affect the relative competitive ability of individuals? – Most of the unequal competitor IFD models rely on the assumption that individual competitive weights do not change as a function of habitat quality, if the group membership remains the same. We tested this assumption by regressing competitive weights of individuals at high food against their competitive weights at low food. If the slope (± 95% CI) deviates significantly from a value of one, we can conclude that the relative competitive weights were significantly affected by food abundance. To determine whether a change in competitive weight was associated with a change in rank within a group, we also calculated the frequency of rank switches between low and high food treatments.

Do individuals prefer one foraging patch over the other? – To evaluate the tendency of individuals to prefer one patch over the other, we classified individual yellowfin shiner and rosyside dace into one of two categories modified from previous studies by Milinski (1984), Godin and Keenleyside (1984), Talbot and Kramer (1986), and Brännäs and Eriksson (1999): 1) stayers, defined as active foragers which show a clear preference for one patch, and 2) switchers, defined as active foragers which show a tendency to use both patches. We classified fish relative to the proportion of time spent in the rich patch as follows. Individuals which spent $\geq$80% of the observation time in a single patch were classified as stayers, and those that spent < 80% of the observation time in one patch were classified as switchers. We pooled all individuals from the groups and plotted frequency histograms in 10% increments to investigate differences in the ratio of stayers to switchers between species.

Do the best competitors select the best foraging patches? – The IDD and unequal competitor IFD models predict the best competitors will monopolize (IDD) or simply prefer (UC IFD) the rich patch. We used Pearson correlation statistics to test whether competitive weight was significantly correlated with the fraction of time (% of scan samples) spent in the rich patch.

Results

General Behavior of the Fish – We previously have reported the general aggression patterns arising during the single-patch trials (Chapters 1 and 2). Where necessary to augment the interpretation of the split-patch trials, we will refer specifically to those findings rather than repeat them.

During the pre-trial periods individual fish maintained relatively stationary positions in the pools and rarely engaged in aggressive interactions with their neighbors. At the beginning of the feeding trial the fish quickly moved towards the front half of the patch and began to feed as well as contest for forward positions. Aggression levels were stable during feeding and quickly diminished when prey delivery ceased (Chapter 1, Fig. 1.3). Fish fed actively and no more than five prey escaped the feeding areas uneaten in any given trial (mean ± 1 SE: 3.3 ± 1.2 larvae). The distribution of fish clearly responded to both the onset of feeding and the disparate proportions in the split-patch trials (Fig. 3.2). Distributions during the feeding trials were generally more stable than the pre-trial period (i.e., smaller standard error terms) suggesting the fish were actively choosing foraging patches when prey was delivered.

Do rosyside dace or yellowfin shiner input-match? – At low food abundance individual yellowfin shiner were approximately randomly distributed between the patches (Fig. 3.2a). After 20 minutes of feeding the fish approached a numeric distribution which undermatched the general IFD prediction (i.e., too many fish in the poor patch), but this distribution was not stable. The average number of fish in the poor patch (mean ± 95% C.I., 0.40 ± 0.06) was significantly less than the random expectation (0.50), but also was significantly greater than the IFD prediction (0.33). The relatively high variance in this value was clearly due to shifting distributions between the patches (i.e., the wave-like trend in Fig. 3.2a). The distribution of competitive weights for yellowfin shiner also quickly responded to the delivery of prey at low food (Fig. 3.2a). However, the mean distribution of competitive weights did not differ significantly from that of fish numbers (paired t-test: low food, $t_7 = 0.94$, $P = 0.38$). The distribution of yellowfin shiner clearly responded to the distribution of food, but generally undermatched the input-matching prediction.

Similarly, individual rosyside dace were distributed randomly during the pre-trial period at low food (3.2b). Rosyside dace approached a numerical distribution which slightly under-matched the IFD prediction more quickly than the yellowfin shiner groups (~ 5 min). The average number of fish in the poor patch was significantly less than the random expectation, and significantly higher than the IFD prediction (mean ± 95% C.I.: 0.38 ± 0.03). The distribution of fish numbers also appeared to achieve a more stable equilibrium throughout the trial versus that of yellowfin shiner under identical food conditions. As with yellowfin shiner, conversion of fish distributions to competitive weights did not improve the fit to the IFD prediction. The distribution of mean competitive weights was not significantly different from the distribution of mean numbers (paired t-test: low food, $t_7 = 0.15$, $P = 0.88$). Thus, the final distribution of rosyside dace also responded to the distribution of food, but undermatched the input-matching prediction.

Does food abundance affect input-matching? – Increasing food abundance clearly affected the accuracy of input-matching for yellowfin shiner (Fig. 3.2c). At high food the yellowfin shiner groups responded more quickly to the distribution of resources (~ 5 min), stabilized at a single distribution of fish numbers, and matched the general IFD input-matching prediction for the poor patch (mean ± 95% C.I.: 0.31 ± 0.03). However, as with low food treatments, the distribution of competitive weights did not differ from that of fish numbers (paired t-test: high food, $t_7 = 0.08$, $P = 0.99$; Fig. 3.3a). The average decrease in proportion of fish in the poor patch at high food (vs. low food) was significant whether measured by competitive weight (one-tailed paired *t*-test, $t_7 = 2.77$, $P = 0.01$) or by fish numbers ($t_7 = 2.00$, $P = 0.04$).

By contrast, there was no detectable response to increased food abundance for rosyside dace. At high food the number of rosyside dace also responded quickly to the distribution of resources (Fig. 3.2d). However, there was no indication of increased input-matching (one-tailed paired t-test: fish number, $t_7 = 0.13$, $P = 0.45$; competitive weights, $t_7 = 0.06$, $P = 0.47$, Fig. 3.3b). As with yellowfin shiner, conversion of numerical fish distributions to competitive weights did not improve the fit to the IFD prediction. Mean competitive weights were not different from the distribution of mean numbers (paired t-test: low food, $t_7 = 0.15$, $P = 0.88$; high food, $t_7 = 0.04$, $P = 0.94$). Interestingly, the groups of yellowfin shiner tended to shift towards the high quality patch during the post-trial periods, although not initially during the low food treatment. Rosyside dace tended to return towards a random distribution during the post-trial periods.

Does food abundance affect the relative competitive ability of individuals? – Competitive weights of individuals ranged broadly within groups during the single-patch trials (yellowfin shiner, 0.03 - 0.35; rosyside dace, 0.03 - 0.33), and were highly correlated between the low and high food single patch trials (Fig. 3.4, linear regression: yellowfin shiner, $R^2 = 0.70$, $P < 0.0001$; rosyside dace, $R^2 =$

0.56, $P < 0.0001$). However, the slope of the line was significantly less than one for both species (slope ± 95% CI: yellowfin shiner, 0.78 ± 0.16; rosyside dace 0.60 ± 0.16). This indicates that relative competitive abilities changed with increased food abundance, and that the best competitors at low food were more likely to lose advantage with increasing food abundance. The observed change in relative competitive ability in our experiment arose from a reduction in aggression by the dominant individuals resulting in a reduced ability to monopolize the best foraging positions within the group (as reported in Chapter 2).

Within groups, competitive rank switches were less common for yellowfin shiner (54%) than rosyside dace (67%, Fig. 3.5). The majority of changes involved a single step in rank for yellowfin shiner (± 1 step, 84%; ± 2 steps, 16%), whereas rosyside dace exhibited larger rank changes (± 1 step, 72%; ± 2 steps, 16%; ± 3 steps, 12%). For both species the most stable positions were the highest and lowest ranked individuals. These findings indicate that relative competitive abilities of intermediately ranked foragers routinely change with time or with the exact nature of the foraging situation. Increasing food abundance clearly altered the behavior of moderately ranked individuals.

Do individuals prefer one foraging patch over the other? – The majority of yellowfin shiner were classified as stayers regardless of treatment level (low food, 69%, high food, 79%), and their distribution was skewed towards the rich patch as predicted by the general IFD (Fig. 3.6). When food abundance increased, the overall distribution of stayers shifted towards the rich patch (ratio of fish numbers, rich patch:poor patch: low food, 1.54:1, high food 2.45:1). These findings indicate that yellowfin shiners actively track relative patch quality, and can respond by shifting to higher quality patches when prey becomes more abundant. Rosyside dace also made strong site selections, and the number of stayers increased from 75% at low food to 85% at high food. However, the distribution of stayers did not change when food abundance was increased (ratio of fish numbers, rich patch:poor patch: low food, 1.76:1, high food 1.73:1). In fact, it is apparent from Fig. 3.6 that rosyside dace became increasingly polarized in their patch selections as food increased (i.e., the number of individuals in the highest 'stayer' bins increased). This is a striking difference from the behavior of yellowfin shiner. The greater tendency for yellowfin shiner to track and respond to changes in patch quality likely represents a mechanism underlying the differential response of group distributions to resource distributions reported above (Figs. 3.2, 3.3).

Do the best competitors select the best foraging patches? – We found no significant correlation between an individual's competitive weight and proportion of time spent in the rich patch for either yellowfin shiner (low food, $R = -0.10$, $P = 0.50$; high food, $R = 0.03$, $P = 0.81$) or rosyside dace (low food, $R = 0.02$, $P = 0.89$; high food, $R = 0.01$, $P = 0.99$). Similarly, there was no difference in competitive weights between fishes classified as switchers, stayers (poor patch), and stayers (rich patch) for any combination of species and food abundance (ANOVAR, all *P's* > 0.10).

Discussion

In structurally simple laboratory habitats with a 2:1 difference in food abundance between patches, the spatial distribution of both rosyside dace and yellowfin shiner responded numerically to input rate of food as predicted by the general IFD. However, in keeping with many previously published studies, the numerical distribution of both yellowfin shiner and rosyside dace consistently undermatched the food input rate (three of four cases). Although numerical undermatching was common, final fish distributions between patches were significantly different from random. Random selection of patches would have spread competitors evenly between patches, and cannot cause the frequency distributions observed during the feeding trials (Abrahams 1986, Kacelnik et al. 1992). These results confirm our general hypothesis that drift-feeding minnows are able to track resource distributions, and can chose between patches which differ in competitor density and food abundance in a manner consistent with the ideal free distribution.

Aggressive interactions were common, although there was no evidence that dominants prevented subordinates from entering either patch (i.e., when under-matching occurred it was not severe). The ideal despotic distribution was therefore not supported by our results. Although aggression clearly affects an individual's foraging performance within a patch, it does not appear to inhibit input-matching by non-territorial fishes (Grand 1997, Tregenza and Thompson 1998, Koops and Abrahams 1999). Within foraging patches, dominant minnows acquire and defend the most profitable positions, usually at the front of groups (Chapter 1). Despite the broad range of competitive abilities exhibited by rosyside dace and yellowfin shiner, there were no significant differences in the distribution of foragers when measured by number or competitive weight. Further, there were no significant correlations between competitive weight and time spent in the rich patch for either species. The unequal competitors IFD model of Parker and Sutherland (1986), which predicts input-matching of competitive weights and the truncated distribution of phenotypes (i.e., the best competitors preferring the best patch), was therefore also no better at predicting the distribution of these species than the equal competitors IFD. Our findings contrast with those of Grand (1997) who found: (1) that the distribution of drift-feeding juvenile coho salmon (*Oncorhyncus kistuch*) competitive weights accurately matched prey delivery rates in a laboratory stream; and (2) that numerical distributions of coho diverged significantly from the competitive weight distribution (tending towards random) by the end of the trial. Small group sizes can blur the distinction between numerical and competitive weight input-matching (Milinski 1988), although, both group size (6 fish vs. 8 fish) and the range of competitive weights (0.03 - 0.35 vs. 0 - 0.42) were similar between our study and Grand's (range of competitive weights estimated from Fig. 3 in Grand, 1997). Several previous researchers have observed input-matching of competitor numbers to resources despite the presence of competitive inequalities (e.g., Harper 1982, Godin and Keenleyside 1984, Milinski 1984, Grand and Grant 1994).

It is tempting to suggest these findings would allow us to monitor the relative distributions of group forming non-territorial species in the wild without assessing individual competitive abilities. However, significant difficulties may affect the application of small-scale laboratory studies of the IFD in field situations. For example, in a four-week laboratory study with an aggressive salmonid fish (amago, *Oncorhynchus masou ishikawae*), Hakoyama and Iguchi (2001) observed a clear transition from random to ideal free to ideal despotic distribution over the experimental time period. They concluded that growth depensation (on the scale of weeks) was the mechanism underlying the changes in the spatial distribution of resource use by competitors. The distribution of amago approached but under-matched the IFD after 4-6 days, approximately equal to time spent together in the experimental tank by our groups prior to the split-patch trials. However, although large-scale movements are probably rare in Coweeta Creek (Hill and Grossman 1987), the membership of stream fish foraging groups in Coweeta Creek changes frequently in response to fluctuations in prey availability and the behavior of competitors (minutes to hours; Freeman and Grossman 1992, 1993). The ability to respond to short-term changes in patch profitability caused by the actions of competitors or stochastic fluctuations in prey delivery are thought to be generally important for organisms which inhabit heterogeneous environments (Dill 1983, Milinski 1994). Long-term experiments which constrain membership over several weeks may not adequately represent the natural situation in North American streams.

Strong and consistent habitat associations with mesohabitat units (10-50 m, e.g., pools vs. riffles) have been noted in many fishes which occupy geomorphologically diverse stream ecosystems. These patterns are thought to arise from the evolutionarily-driven morphological constraints imposed by an organisms lifestyle (Matthews 1998). At the microhabitat scale (< 1 m), many drift-feeding fishes choose positions which represent an energetic compromise between the cost of reduced capture efficiency and the benefit of increased prey encounter rate at higher velocities (Fausch 1984, Hughes and Dill 1990, Hill and Grossman 1993, Tyler 1993, Guensch et al. 2001, Grossman et al. 2002). Between the meso- and microhabitat scales are patches. Having established that fish often choose habitat patches consistent with a strategy of maximizing intake rate, it is puzzling that so many fish spend a significant portion of their time in the low quality patch (undermatch). At least three mechanisms have been proposed to account for this behavior: (1) when individuals cannot make complete assessments of relative patch quality (‘perceptual constraints hypothesis’, Abrahams 1986); (2) when the best competitors defend the best foraging positions (‘unequal competitors hypothesis’, Grand and Grant 1994); or (3) when organisms must physically sample each patch to make an assessment (Gotceitas and Colgan 1991, Houston et al. 1995). Abrahams (1986) proposed a means to distinguish between the first two competing explanations. By increasing food abundance throughout the environment while keeping the relative distribution between patches unchanged, he predicted two responses by the foragers. If perceptually constrained, individual foragers should make better assessments of patch quality when food abundance increases, and shift to full input-matching. If competitive inequalities are more important, then there should be no change in distribution. This latter pattern requires relative competitive abilities to remain unaffected by habitat quality. We were ultimately unable to fully test the Abrahams (1986) contention as relative competitive abilities clearly changed for some individuals in our groups when food abundance was increased (Chapters 1 and 2). However, certain features of the fishes behavior did provide insight into the probable causes of undermatching.

Perhaps our most striking finding was that as food abundance increased, groups of nonindigenous yellowfin shiner shifted to conform with the input-matching prediction, whereas native rosyside dace continued to undermatch. Three features of the yellowfin shiner distributions suggest this difference arose from differences in sampling behavior. First, yellowfin shiner failed to achieve a clear equilibrium distribution at low food (Fig. 3.2a). The wave-like form of the distribution suggests individuals were regularly shifting between patches, ostensibly to monitor their relative quality. Second, yellowfin shiner were less likely to settle in one patch then rosyside dace (ratio of switchers to stayers, Fig. 3.6). When food abundance increased, the yellowfin shiner groups maintained a significant number of switching foragers, whereas the rosyside dace groups became increasingly polarized towards stayers. Third, yellowfin shiner tended to remain in the rich patch after the cessation of feeding, whereas rosyside dace returned toward a random distribution. These findings suggest the yellowfin shiner were actively monitoring the position of the high quality patch, and may settle there during non-feeding periods in anticipation of high prey delivery in the future. Overall, our results are consistent with the two previous studies of movement patterns for yellowfin shiner and rosyside dace (Hill and Grossman 1987, Goforth and Foltz 1998). Both home range size (42.9 ± 79.0 m^2 vs. 19.3 ± 8.0 m^2) and maximum distance moved (521 m vs. 98.4 m) were greater for yellowfin shiner. In our experiment, sampling behavior may have been promoted by small differences in quality between the patches, where an individual experiences a small decrease in intake rate when it leaves its optimal patch.

Another potential explanation for the improved input-matching at high food is that foraging yellowfin shiner observed the aggressive behavior of conspecifics as an additional measure of patch quality. In the single patch experiments, the per capita rate of aggression significantly increased with increasing food abundance in groups of yellowfin shiner, but not rosyside dace (Chapter 2). Additionally, yellowfin shiner are 2-3 times more aggressive than rosyside dace in laboratory situations (Chapter 2). By observing the behavior of other foragers, an animal may increase its ability to perceive differences in patch quality and conform more closely to the distribution of resources (Templeton and Giraldeau 1996, Koops 1998). However, in a recent test Koops and Abrahams (1999) found the distribution of foraging fish matched that of the food, but was unaffected by the distribution of aggression. In Coweeta Creek, non-aggressive rosyside dace (i.e., weak competitors in groups) will actually avoid groups when highly aggressive fish are present (Freeman and Grossman 1992). If aggression was strongly influencing the inter-patch distribution of rosyside dace in this experiment, we would also expect the worst competitors to be restricted to the low quality patch (i.e., a truncated phenotype distribution). Neither rosyside dace nor yellowfin shiner exhibited this pattern during our experiments, though longer trials (days to weeks) may be necessary for such fine-tuning of distributions (Sutherland 1996). Overall, our data do not support the role of aggression as information which promotes input-matching.

Our third aim was to ascertain whether differences in input-matching behavior may have contributed to the rapid establishment of yellowfin shiner in the Little Tennessee River system. Although the application of ideal free distribution theory to conservation biology has received increasing interest in the last decade (Sutherland and Dolman 1994, Gosling and Sutherland 2000), we are not aware of other studies that have used it to compare behavioral traits of native and invasive taxa. In fact, the study of behavioral flexibility, though long thought to be a general trait that provides significant advantages to animals in novel environments (e.g., Mayr 1965), is rarely tested as a mechanism of invader establishment (Holway and Suarez 1999). Behavioral flexibility allows individuals to respond more rapidly to novel environments by tracking changes in the distribution of resources, and can affect the establishment of introduced species. For example, in New Zealand, invading birds are more likely to establish new populations when they have relatively large brains and a high frequency of foraging innovations in their native range (Sol and Lefebvre 2000, Sol et al. 2002). Our studies suggest drift-feeding minnows must be able to track two features of habitat quality which affect foraging success. First, fish must be able to detect spatial variation in velocity in order to chose microhabitats (i.e., focal point velocities, FPV) which maximize prey capture success. Studies of the rosyside dace demonstrate this ability (Hill and Grossman 1993, Grossman et al. 2002), however, yellowfin shiner are less 'optimal' in their selection of FPVs (Grossman et al. 2002). This finding may be partially explained by the higher rate of patch sampling observed for yellowfin shiner, which should naturally lead to an overuse of suboptimal habitats. It is less clear why yellowfin shiner, on average, occupy velocities higher than predicted by their capture efficiency in Coweeta Creek (Grossman et al. 2002). Second, individuals must be able to accurately assess differences in patch quality to adjust their distributions appropriately (present study). In contrast to microhabitats, yellowfin shiner are better at making this discrimination at fine differences in patch quality (a 1:2 ratio may be viewed as a relatively small difference vs. 1:5 or 1:10 ratios typical of IFD studies). Although this ability obtained only at the high food level, this concentration of prey is well within the natural range encountered in Coweeta Creek.

Interest in the relevance of behavioral mechanisms to conservation biology has grown considerably in recent years (Clemmons and Buchholz 1997, Caro 1998, Gosling and Sutherland 2000). Our study has demonstrated the utility of the IFD input-matching rule as an assay to test the relative competitive abilities of native and invasive species in stream ecosystems. Because highland streams exhibit a high degree of spatial and temporal variability, the ability to track changing resource distributions is advantageous. Our findings suggest the recently introduced yellowfin shiner can track and match resource distributions in high quality habitats better than an ecologically similar native. Such native invasions, where species are displaced into new habitats over relatively short distances, represent one of the greatest challenges to the conservation of the incredibly high species diversity in southern Appalachian freshwater fish assemblages (Scott and Helfman 2001).

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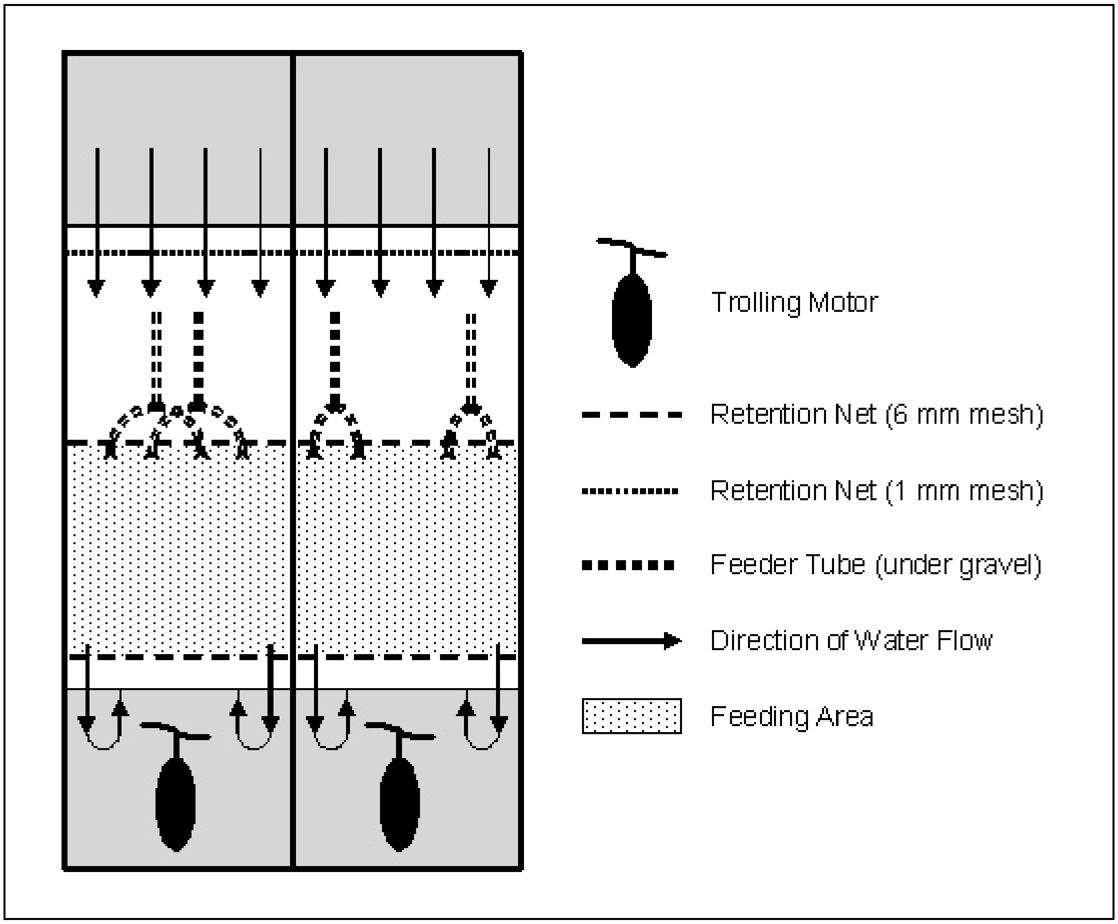

Fig. 3.1. Schematic diagram of the experimental tank (top view). The left channel is configured for a single-patch trial, the right channel for a split-patch trial.

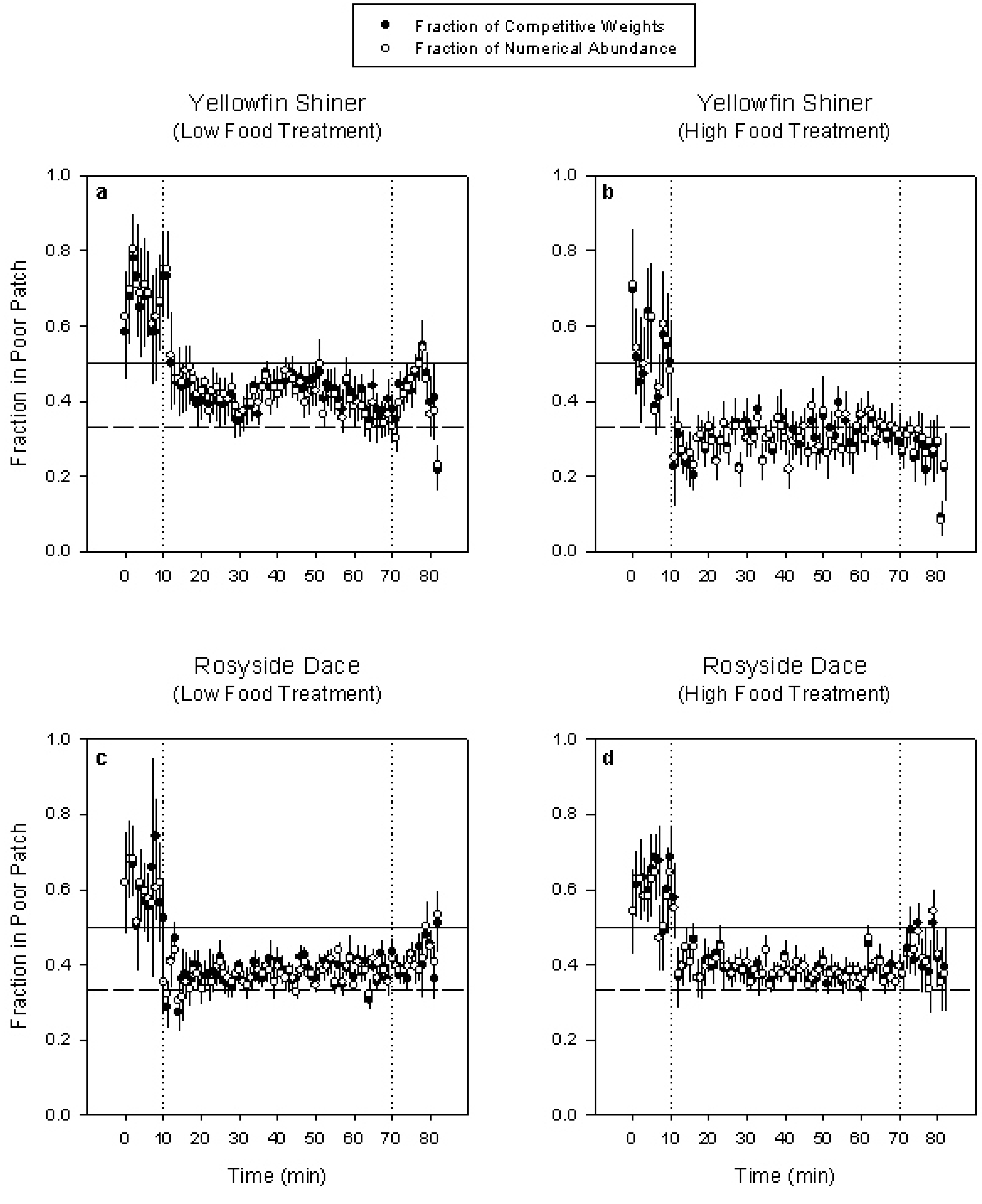

Fig. 3.2. Mean (± 1 SE) proportion of fish and competitive weights in the poor patch during each two-minute interval of the foraging trial ($N = 8$ groups of fish). Solid and dashed lines indicate the predictions of random and IFD distributions, respectively.

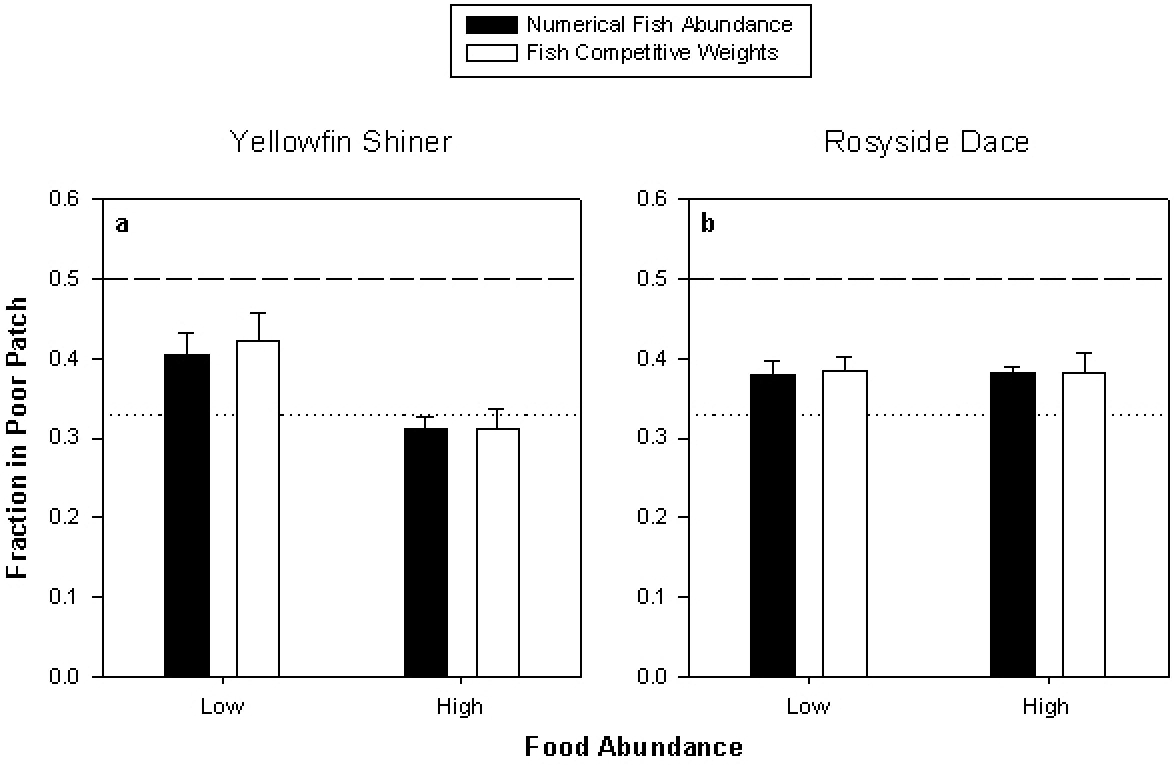

Fig. 3.3. Mean (± 1 SE) fraction of fish in the poor patch during the last 40 minutes of the feeding trials. The dashed line represents the random expectation of a 1:1 distribution between rich and poor patches. The dotted line represents the input-matching prediction (2:1 distribution between rich and poor patches).

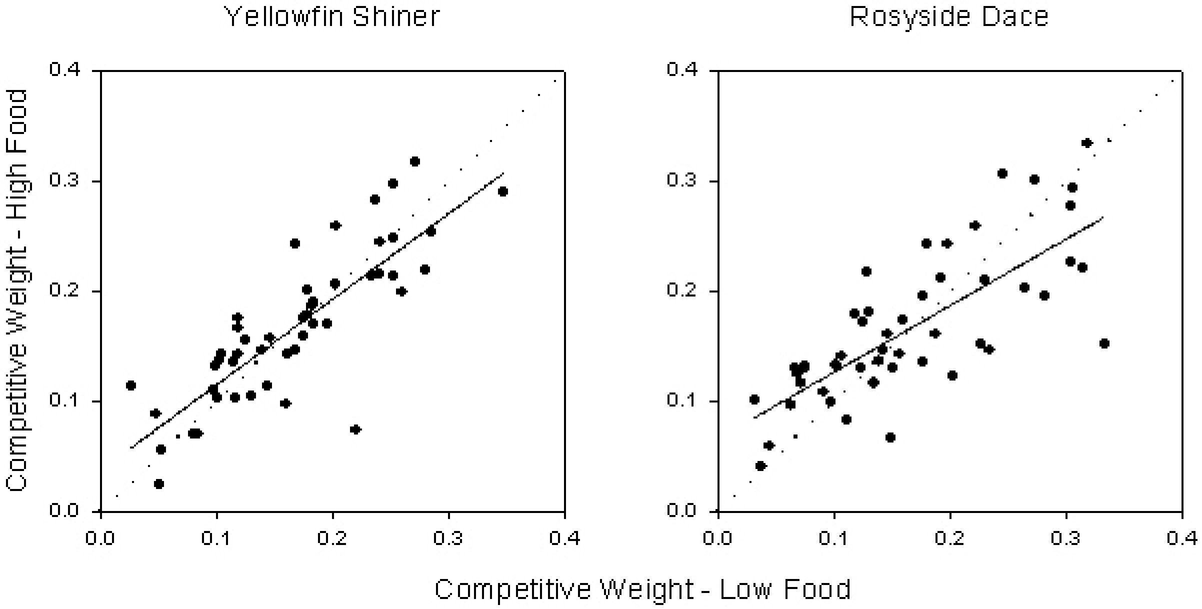

Fig. 3.4. Competitive weights of individual fish at high and low food abundance (*N* = 48). The dotted line represents a one-to-one relationship, the solid line is the relationship determined by linear regression.

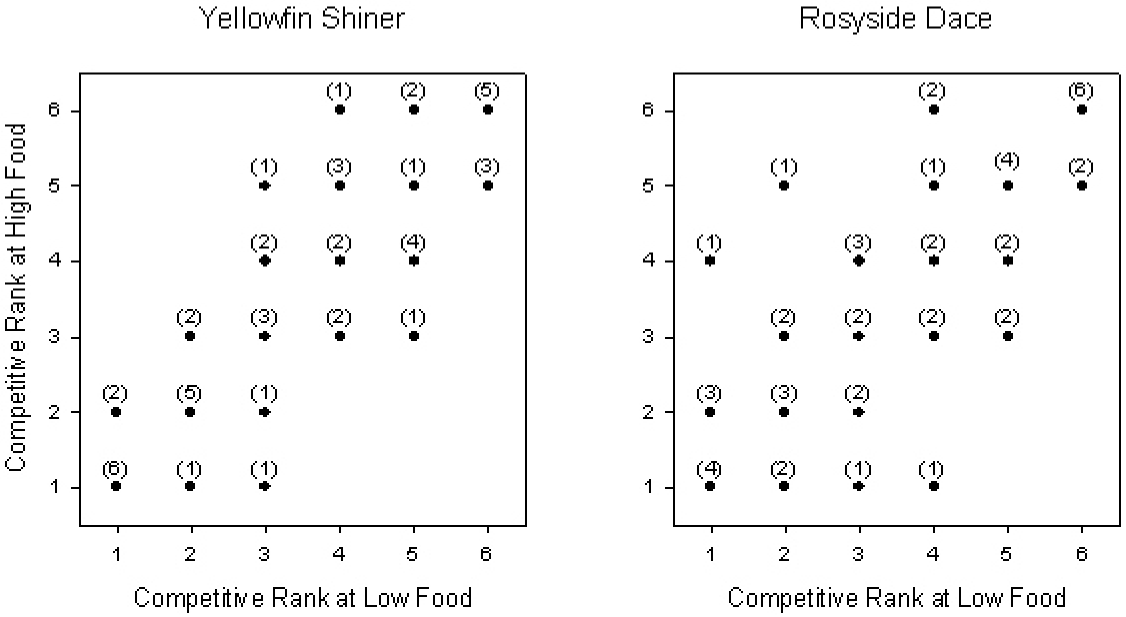

Fig. 3.5. Frequency of rank switches between low and high food treatments. A point indicates that a rank switch occurred, unless it falls on the one-to-one diagonal. The number in parentheses above the point indicates the number of times that rank switch occurred (maximum possible value is 8).

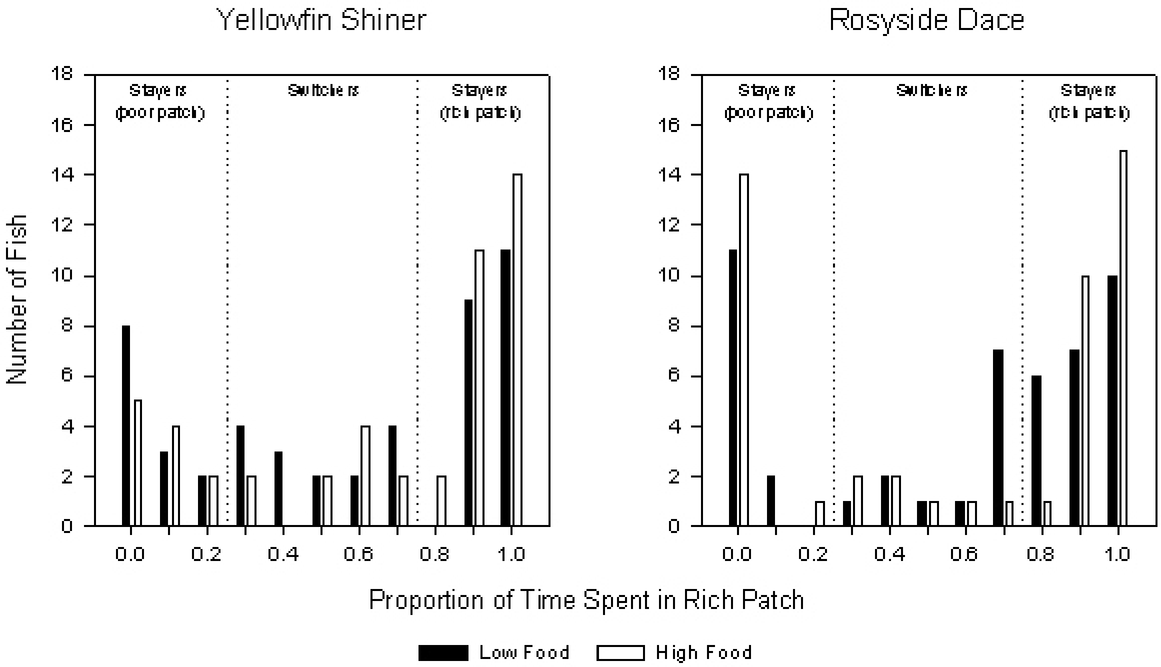

Fig. 3.6. Frequency histogram of stayers (≥ 80% of time in one patch) and switchers (< 80% of time in one patch) during feeding trials for shiner and dace (*N* = 48 for each species).

CHAPTER 4

FLOW MEDIATES INTERSPECIFIC COMPETITION BETWEEN NATIVE AND INVASIVE STREAM FISHES

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Introduction

The integrity of the Earth’s freshwater ecosystems is rapidly degrading under a rising tide of invasive species (Vitousek et al. 1997, Claudi and Leach 1999, Fuller et al. 1999, Kolar and Lodge 2000). The introduction of new species dramatically reduces the faunal distinctiveness of biogeographic regions (Brown 1989, Lodge 1993a, Rahel 2002), imperils unique indigenous faunas (Reinthal and Kling 1997, Scott & Helfman 2001), and may even compromise human health (Bright 1998). Although we currently lack a general theory of biological invasions (Parker et al. 1999), understanding why some communities are vulnerable to invasion while others are not is a major challenge for invasion biology (Ehrlich 1989). Elton (1958) proposed that a community’s resistance to invasion is proportional to its diversity, often referred to as biotic resistance. Theoretically, diverse communities with strongly interacting members establish an “activation barrier” that repels invasions by ecologically similar species (Case 1990). Although biotic resistance can pose a significant barrier to invasion in some systems (Tilman 1997, Stachowitz et al. 1999, Naeem et al. 2000), abiotic factors unrelated to species diversity often dominate native-invader interactions in aquatic systems (Moyle and Light 1996a, Levine and D’Antonio 1999, Fausch et al. 2001), and may interact with biotic factors to influence the outcome of a particular invasion.

Understanding the interplay between biotic and abiotic factors in determining the outcome of species interactions is also important to the general study of community ecology. For example, condition-specific competition has been proposed as a major structuring force in many natural communities (Hutchinson 1961, Jaeger 1970, Wilbur 1987). It occurs when the ability of one species to dominate another in sympatry is contingent upon the physical environment (Dunson and Travis

1991), and has principally been employed to explain the adjacent, but non-overlapping distributions of ecologically similar species along continuous environmental gradients (Diamond 1970, Schluter 1982). The influence of abiotic conditions on competitive interactions may be greatest in habitats where environmental gradients strongly influence individual fitness. Under these conditions, the tendency for the physical environment to mitigate species-level differences in competitive ability could promote species coexistence, thereby influencing patterns of species diversity (Chesson 1986, Tilman and Pacala 1993). Although ecologists have long been interested in these phenomena, there remain relatively few experimental studies of the actual mechanisms underlying condition-specific competition (Kingsolver 1989, Dunson & Travis 1991, Warner et al. 1993, Taniguchi and Nakano 2000, Holway et al. 2002). It is becoming increasingly clear that testing the specific mechanisms that promote the success of invasive species will lead to a broader understanding of both invasion biology and the natural process of community assembly (Karieva 1996, Kolar and Lodge 2001, Sakai et al. 2001, Shea and Chesson 2002).

In this study, we examine how a feature of hydrology (velocity) influences the potential competitive impact of invasive yellowfin shiner (*Notropis lutipinnis*) on an ecologically similar native species, the rosyside dace (*Clinostomus funduloides*). North American stream fish assemblages are excellent systems to evaluate the importance of condition-specific competition during biotic invasions. The physical isolation of drainages promotes the formation of distinct, moderately diverse assemblages with high degrees of endemism (Hocutt and Wiley 1986, Allan and Flecker 1993), and low saturation of species (Gido and Brown 1999). Thus, they have proven especially likely to incorporate invasive species (Lodge 1993b). Streams also consist of a network of heterogeneous habitats on local and regional scales (Frissell et al. 1986, Pringle et al. 1988). In particular, many of the physical features of streams that impinge on the ability of predators to locate and acquire prey, including substrate, flow, and light availability, are quite variable in space and time. For instance, drifting insect larvae are generally more abundant as flow increases (Allan and Rusek 1985), but this abundance is countered by reduced strike efficiency for drift-feeding fishes at high velocities (Hill and Grossman 1993, Tyler 1993). As a consequence, many fishes occupy microhabitats that maximize their net intake rate, a parameter considered to be strongly correlated with individual fitness (Chapman 1966, Werner and Hall 1979, Hill and Grossman 1993, Wootton 1999, Grossman et al. 2002). These suitable foraging sites are not continuous and generally occur as discrete patches imbedded in a largely unfavorable matrix (Matthews 1998). Additionally, the predominantly unidirectional nature of prey delivery in streams ensures certain positions within patches will be more profitable than others. Dominant individuals typically defend these positions in social groups (Blanckenhorn et al. 1998, Grant 1993, Grant & Noakes 1988, Hughes 1992, Hutchinson & Iwata 1997, Chapter 1, Chapter 2). Thus, competition with native species for high quality foraging positions may be generally important to the establishment of invasive species in variable environments.

The yellowfin shiner was introduced into the Little Tennessee River, North Carolina around 1990 and is believed to be rapidly expanding its distribution throughout the drainage (Johnston et al. 1995, Fuller et al. 1999). Yellowfin shiner occupy microhabitats (focal point velocities) that overlap significantly with an abundant native minnow, the rosyside dace (Fig. 4.1a), and both employ aggression to defend profitable positions in social foraging groups (Freeman and Grossman 1992, Rincón and Grossman 2001, Chapter 1). In laboratory tests of intraspecific aggression rates, yellowfin shiner are two to three times more aggressive than native minnows (Chapter 2), and may therefore be behaviorally dominant over native minnows in mixed-species groups. However, the yellowfin shiner's ability to displace native minnows may be contingent on abiotic factors. For instance, in Coweeta Creek, yellowfin shiner are less efficient foragers than several native minnows, particularly at high velocities (Fig. 4.1b; Grossman et al. 2002). Because minnows in Coweeta Creek predominantly occur in small groups (1-9 individuals; Freeman & Grossman 1992, 1993), this reduced efficiency may reduce their impact on native fishes when foraging in mixed groups.

Here we employ a mechanistic experimental approach to test the extent to which water velocity (via reduced strike efficiency) limits the ability of an aggressive invader to displace native stream fishes from profitable foraging positions. Our results demonstrate how biotic and abiotic effects may interact to mitigate the impact of a recent invasion.

Methods

Fish Collection and Laboratory Procedures

During July-October 2002 we collected adult rosyside dace and yellowfin shiner approximately weekly from Coweeta Creek, a fifth-order highland tributary to the Little Tennessee River in North Carolina. Experiments were conducted in a laboratory artificial stream equipped with an automatic feeder at the Whitehall Forest fisheries laboratory of the University of Georgia (described in detail in Chapter 1). Upon return to the lab each fish was measured to standard length (SL, nearest mm), weighed (nearest 0.01 gm), and individually tagged with a small, colored disc. Individuals of each species were maintained in separate 550 L holding tanks with flowing water at 18°C and a natural photoperiod (adjusted weekly) with 45 minute crepuscular periods to simulate average summer conditions in Coweeta Creek. We fed the fish once per day with insect larvae (Chironomidae) at a ration of 3% body weight per day. All experimental fish were acclimated to the laboratory conditions for a total of eight days to ensure full recovery from capture and tagging. After the holding period, we transferred each group into the experimental tank for an additional three-day acclimation period. On the last two days, we fed the fish via the automatic feeders to ensure normal feeding behavior and to allow natural dominance relationships to form within the group (Chapter 1). To prevent any disturbances during acclimation or experimental trials, we clad the tanks with an opaque barrier to a height of 2.25 m. During the experiment we observed the fish from within a completely darkened booth adjacent to the stream.

The artificial stream is equipped with two isolated experimental channels which allowed us to test two groups simultaneously. Within each channel, we confined the fish to a 75 × 70 × 30 cm (length × width × depth) test area with 6 mm mesh nets. The microhabitats experienced by the fish in the feeding areas are similar to those reported for group foraging minnows in small Coweeta Creek pools (Grossman & Freeman 1987; Grossman & Ratajczak 1998). The substrate was a mixture of pebbles (5-15 mm diameter) interspersed with cobbles (30-100 mm diameter). We configured the automatic feeders to release prey from multiple points at the level of the substrate to simulate the natural entry of insect larvae into the drift. Environmental conditions within the feeding areas were generally homogenous. Flow varied no more than ± 1 cm s^{-1} from the target velocities, except at the benthic boundary layer, and temperature varied no more than ± 0.1 °C from the target condition (18°C).

Experimental Design and Behavioral Observations

We based our experimental design on the response surface approach described by Inouye (2001). We crossed two densities (four or eight fish, hereafter low density and high density) and three species combinations (100% dace, 100% shiner, 50% dace and 50% shiner) for a total of six treatments. We chose group sizes comparable to those of natural mixed-species foraging groups in Coweeta Creek (typically 1-9 individuals, Freeman & Grossman 1992, 1993). We also subjected each treatment group to feeding trials at two velocities on consecutive days (10 and 20 cm s^{-1}). We chose these velocities for two reasons. First, both rosyside dace and yellowfin shiner typically occupy focal point velocities between 10 and 25 cm s^{-1} in Coweeta Creek (Fig. 4.1a, Grossman & Freeman 1987, Grossman & Ratajczak 1998, Grossman et al. 2002, M.D. Farr and G.D. Grossman unpub. data). Second, foraging efficiency for rosyside dace and yellowfin shiner is approximately equal at 10 cm s^{-1}, but is most different at 20 cm s^{-1} (Fig. 4.1b, Grossman et al. 2002). Therefore, these treatments represent a natural range of effects velocity may impose on foraging competition in Coweeta Creek. We performed six replicates for each treatment for a grand total of 36 experimental groups and 216 fish. The order of treatments was randomly assigned.

Because food intake rate is considered a limiting factor for drift-feeding stream fishes (Chapman 1966, Hill & Grossman 1993, Grossman et al. 2002), we assigned competitive superiority based on which species captured the most prey items (per capita rates). We chose insect larvae from the Family Chironomidae as experimental prey because they are frequently eaten by drift-feeding minnows in Coweeta Creek (Stouder 1990). Because our objective was to observe competitive interactions under simulated natural conditions, we set the prey delivery rate at 33 larvae min^{-1} m^{-2} of stream cross-sectional area, which represents the mean drift rate of larval insect prey consumed by these minnows in Coweeta Creek (Hill 1989, Freeman 1990, Stouder 1990). This yielded a release rate of 6.9 larvae per minute in each of the experimental feeding areas. Larvae that passed through the feeding areas without being captured were retained on a 1-mm mesh net. However, virtually all of the prey were consumed upon release, and we never observed an unconsumed prey item re-entering the feeding areas. During the trials we continuously recorded all prey captures on audio tape.

To minimize behavioral differences between species due to size, we used specimens of similar size within and between species (< 10% difference in standard length within a group). The size range across all replicates was 57-77 mm SL (mean ± SE, 64.3 ± 0.4 mm for rosyside dace, 63.1 ± 0.3 mm for yellowfin shiner), and 2.46-6.21 g wet weight (mean ± SE, 3.72 ± 0.08 g for rosyside dace, 3.51 ± 0.06 g for yellowfin shiner). Size differences within this range have little to no effect on dominance relations within these species (Chapter 1). We also initiated the experiment after the reproductive season (April-June, DeHaven et al. 1992) to minimize any effects of reproductively associated aggression.

In natural streams, locations near pool inlets at the front of foraging groups provide the best access to drifting prey items (Huntingford 1993, Nakano 1995). To acquire these profitable positions, rosyside dace and yellowfin shiner employ a range of foraging aggression behaviors including displays, displacements, nips, charges, and chases (Freeman & Grossman 1992, Rincón and Grossman 2001, Chapters 1 and 2). During the trials we continuously recorded all overt aggressive interactions on audio tape, noting the identity of the instigator and recipient, and the direction of the action (forward, lateral, rearward). We also measured the position of each fish relative to each other and the direction of prey delivery at two minute intervals. We ranked the position of each individual from 1-6 (upstream to downstream) and calculated the mean positional rank from the last 40-minutes of each trial, when positional ranks should have stabilized (Chapter 1).

Predictions and Data Analyses

Determining Competitive Advantage – A previous study determined that yellowfin shiner are two to three times more aggressive than rosyside dace in monospecific experimental tests (Chapter 2). Thus, we first sought to establish that heightened aggression can translate into competitive superiority under conditions most favorable to the yellowfin shiner (i.e., low velocity), but within the natural range of microhabitat overlap with rosyside dace. We tested this hypothesis by comparing the per capita foraging rates of rosyside dace and yellowfin shiner at low intraspecific density (4 fish) to both high intraspecific (8 fish) and high interspecific (4 dace + 4 shiner) densities. The difference in foraging rate between the low and high intraspecific treatments represents the effect due to intraspecific competition. If intraspecific competitor density has an effect on individual foraging rates under simulated natural conditions (velocity and prey delivery rate), then (1) increasing fish density from four to eight fish will decrease the per capita foraging rate of rosyside dace and yellowfin shiner in single-species groups. Similarly, the difference in foraging rate between the low intraspecific and high interspecific treatments represents the effect due to interspecific competition. If yellowfin shiner are superior competitors, we predict: (2) rosyside dace foraging rates will be reduced more by adding four shiner than four dace (interspecific effect > intraspecific effect); and, in contrast, (3) yellowfin shiner foraging rates will be reduced more by adding four shiner than four dace (intraspecific effect > interspecific effect). We tested these predictions with separate one-way ANOVAs for each species. We followed up significant ANOVAs with post-hoc Tukey PSD tests ($P < 0.05$) to identify significant differences in mean per capita foraging rates.

Influence of Water Velocity and Group Size on Rates of Aggression – Because foraging success in small groups is influenced by relative aggression rates for both species (Chapter 1), we also investigated whether the treatment conditions (velocity, density) would significantly alter per capita aggression rates. In particular, if increasing water velocity suppresses the aggressive tendencies of one species but not the other, then interpreting the mechanism(s) underlying condition-specific competition becomes more complicated. This obtains because minnows fight for position, not individual prey items, and a change in position has a significant effect on foraging rate (Chapter 1). However, because these fishes routinely occupy the test velocities in nature (Grossman et al. 2002), and increasing velocity from 10 to 20 cm s^{-1} does not appear to impose significant physiological costs to small stream fishes (Facey & Grossman 1992), we predicted there would be no significant effects of the increasing velocity on per capita aggression rates for either species.

In contrast, resource defense theory does predict a decrease in the rate of aggression as group size increases (Brown 1964, Giraldeau and Caraco 2000). When groups compete for the same resources, increasing group size reduces the ability of aggressive individuals to defend those resources. Dominants who spend too much time fighting may miss foraging opportunities while expending energy on costly aggressive behaviors, and will ultimately suffer a reduced net energy intake rate. We predict increasing group size in the intraspecific treatments will decrease per capita aggression rates, and the magnitude of the change (as a proportion) will be similar for yellowfin shiner and rosyside dace. We have previously determined that yellowfin shiner are more aggressive than rosyside dace (Chapter 2). Because both species fight for position, and in proportion to the quality of that position, we expect aggression in the interspecific groups will be additive. Thus, per capita aggression rates should also decrease in interspecific groups, and the magnitude of the change will be intermediate to that of yellowfin shiner and rosyside dace intraspecific treatments. We tested these predictions separately with repeated-measures ANOVAs (ANOVAR) for each species. Group (replicate) was the within subject factor and velocity and group size were between-subject factors. We applied post-hoc Tukey-Kramer tests to investigate the nature of any significant main effects and only those with adjusted *P*-values ≤ 0.05 were interpreted.

Condition-Specific Competition (Mixed-species treatments) – We made the following predictions regarding the effects of velocity on interspecific competition between yellowfin shiner and rosyside dace. Because foraging efficiency is approximately equal at 10 cm s^{-1}, we predict yellowfin shiner will be competitively superior to rosyside dace by showing higher per capita rates of aggression, acquiring the forward positions in mixed-species groups, and hence, achieving a higher per capita prey capture rate. These predictions should apply at both low and high densities. At 20 $cm \cdot s^{-1}$, yellowfin shiner should continue to show higher per capita rates of aggression and acquire the forward positions in mixed species groups; however, rosyside dace will achieve a greater per capita capture rate due to its superior foraging efficiency at high velocity. We expect the foraging advantage for rosyside dace will be greater at low density than high density. This final prediction arises from the expectation that more yellowfin shiner in the front of the rosyside dace at high density (4 fish vs. 2 fish) will result in more captures by yellowfin shiners. We tested these predictions with separate ANOVARs for each density.

Group (replicate) was the within subject factor and species and velocity were between-subject factors. We applied post-hoc Tukey-Kramer tests to investigate the nature of any significant main effects and only those with adjusted *P*-values ≤ 0.05 were interpreted.

Unless otherwise noted, all tests were two-tailed with α set at 0.05 and all reported *P* values are adjusted for multiple comparisons as described above. We $\log_{10}(x+1)$ transformed the data to meet the assumptions of normality and homogeneity of variance for ANOVAs and ANOVARs. However, we present untransformed data in the figures to ease interpretation of the results. SAS version 8.2 was used for all statistical analyses.

Results

Competitive Advantage

One-way ANOVA revealed a strong main effect of competition treatment on per capita foraging rate for both species at low velocity (rosyside dace, F = 449.95, df = 2, $P < 0.0001$; yellowfin shiner, F = 77.26, df = 2, $P < 0.0001$). Per capita foraging rates in rosyside dace groups were reduced by 54% when intraspecific density was increased from four to eight individuals (Tukey HSD, $P < 0.01$, Fig. 4.2a). Increasing intraspecific density had a similar effect on yellowfin shiner foraging, reducing the per capita foraging rate by 47% (Tukey HSD, $P < 0.01$, Fig. 4.2b). In contrast to the intraspecific treatments, the magnitude of the foraging rate reduction that occurred by adding heterospecifics was different across species. Rosyside dace foraging rates were reduced by 69% in the presence of yellowfin shiner (Tukey HSD, $P < 0.01$), a further average decrease of 15% (vs. the high density intraspecific treatment). Conversely, yellowfin shiner foraging benefitted from the presence of rosyside dace, reducing foraging rates by an average of 31%, a net increase of 16% from the high density intraspecific treatment (Tukey HSD, $P < 0.01$). Hence, the results support our first three predictions.

Influence of Water Velocity and Group Size on Aggression

The results of our ANOVAR analyses revealed no effect of velocity on per capita aggression rates for any of the competition treatments (Table 4.1, Fig. 4.3). As predicted, yellowfin shiner groups were more aggressive than rosyside dace (mean factor of 2.9X, range 1.9-4.0), and mixed-species groups displayed intermediate per capita aggression rates. Increasing group size decreased aggression rates in intraspecific groups as predicted by resource defense theory; however, there was a large difference in the magnitude of the reduction between species. Aggression in yellowfin shiner groups decreased an average of 19% while rosyside dace groups reduced an average of 58%. There were no significant interactions between velocity and group size ($P = 0.21$-0.57). The data support our predictions regarding the effects of water velocity (no effect) and group size (reduction) on per capita aggression rates.

Condition-Specific Competition

Aggression Rate – Interspecific competition had a range of interesting effects on per capita aggression rates (Table 4.2, Fig. 4.4). As predicted, yellowfin shiner initiated significantly more aggressive acts than rosyside dace at both densities (species main effect: low density, $F_{1,10} = 68.83$, adj. $P < 0.0001$; high density, $F_{1,10} = 728.40$, adj. $P < 0.0001$) and there was no effect of velocity on whole group per capita aggression rates (velocity main effect: low density, $F_{1,10} = 1.41$, adj. $P = 0.26$;

high density, $F_{1,10} = 0.01$, adj. $P = 0.97$). There were also no significant interactions between species and velocity (low density, $F_{1,10} = 0.92$, adj. $P = 0.41$; high density, $F_{1,10} = 0.56$, adj. $P = 0.44$). However, even though whole group per capita aggression rates were intermediate to the intraspecific treatments of equal density as predicted (Fig. 4.3), species-specific rates were not. Compared to the intraspecific treatments, yellowfin shiner aggression rates in mixed groups were 7-30% higher, whereas rosyside dace per capita aggression rates were 51-74% lower (vs. the same intraspecific factorial combination). Also in contrast to the intraspecific treatments, separate ANOVAR analyses for each species revealed no significant reduction in species-specific per capita aggression rates as density increased (density main effect: yellowfin shiner, $F_{1,10} = 3.48$, $P = 0.09$; rosyside dace, $F_{1,10} = 2.61$, $P = 0.14$).

Interestingly, both yellowfin shiner and rosyside dace targeted conspecifics more often than heterospecifics (Table 4.3). Yellowfin shiner were 1.4-1.7 times more likely to attack another shiner, and rosyside dace were 3.7-22 times more likely to target another dace. The higher and more variable ratios for rosyside dace likely are an artifact of the lower number of total attacks. If we adopt a null hypothesis that attacks are random and therefore each member of the group is equally likely to be attacked, the expectation is actually a heterospecific bias of 2:1 for small groups and 1.33:1 for large groups.

Positional Rank – Interspecific competition led to a clear spatial hierarchy within mixed species foraging groups (Table 4.2, Fig. 4.5). At low density, yellowfin shiner consistently occupied the two forward positions (ANOVAR: $F_{1,22} = 28.32$, $P < 0.0001$). Yellowfin shiner positional ranks (means ± 1 SE) averaged 1.68 ± 0.17 at low velocity and 1.92 ± 0.26 at high velocity. In contrast, rosyside dace ranks averaged 3.33 ± 0.14 at low velocity and 3.08 ± 0.20 at high velocity. Velocity treatment had no significant effect on positional rank (ANOVAR: $F_{1,22} = 0.01$, $P = 0.96$), and there were no significant interactions ($F_{1,22} = 0.63$, $P = 0.52$). At high density, yellowfin shiner again occupied the forward half of mixed foraging groups (ANOVAR: $F_{1,46} = 65.57$, $P < 0.0001$). Yellowfin shiner positional ranks averaged 2.86 ± 0.29 at low velocity and 2.99 ± 0.30 at high velocity. In contrast, rosyside dace ranks averaged 6.14 ± 0.27 at low velocity and 6.01 ± 0.32 at high velocity. Velocity treatment had no significant effect on positional rank (ANOVAR: $F_{1,46} = 0.01$, $P = 0.91$), and there were no significant interactions ($F_{1,46} = 0.58$, $P = 0.46$).

Although we did not measure inter-individual distances, we did not observe any evidence that two distinct groups were forming. Individuals from both species frequently moved forward and back in the group and generally interacted with all other members during the course of a trial. The differing range of values for positional rank (1-4 vs. 1-8) prevented a direct comparison of the effects of density on species-specific mean positional ranks. However, inspection of the plots suggests there were no major differences, with yellowfin shiners consistently ahead of rosyside dace regardless of density (Fig. 4.5).

Foraging Rate – ANOVAR revealed significant effects of species and species × velocity interaction on foraging rates in mixed groups (Table 4.2, Fig. 4.6). At low density, yellowfin shiner foraged at a rate significantly higher than rosyside dace in low velocity treatments, acquiring 66% of total prey captures and achieving a per capita foraging rate (means ± 1 SE) of 1.08 ± 0.01 larvae fish^{-1} min^{-1} (vs. 0.58 ± 0.03 larvae fish^{-1} min^{-1} for rosyside dace; adj. $P < 0.0001$). However, when velocity was increased, a complete competitive reversal occurred. Rosyside dace foraged at a rate of 0.94 ±

0.03 larvae fish^{-1} min^{-1}, that was significantly higher than for yellowfin shiner (adj. $P < 0.0001$), and comprised 61% of total group captures. In contrast, yellowfin shiner foraged at a rate of 0.61 ± 0.02 larvae fish^{-1} min^{-1}, a 56% reduction vs. the low velocity treatment. As predicted, this condition-specific effect produced a significant interaction between species and velocity main effects (ANOVAR: $F_{1,10}$ = 245.90, adj. $P < 0.0001$).

Similar patterns were observed at high density, where yellowfin shiner again foraged at a higher rate than rosyside dace at low velocity (adj. $P < 0.0001$). Individual yellowfin shiner foraged at an average rate of 0.59 ± 0.03 larvae fish^{-1} min^{-1} whereas rosyside dace only achieved a rate of 0.28 ± 0.01 larvae fish^{-1} min^{-1}. When velocity was increased, rosyside dace again increased their foraging rate at the expense of yellowfin shiner (Fig. 4.6). However, unlike the low density treatment, there was no significant difference in foraging rates between species (yellowfin shiner, 0.45 ± 0.01 larvae fish^{-1} min^{-1}; rosyside dace, 0.44 ± 0.03 larvae fish^{-1} min^{-1}; adj. $P = 0.98$). This also led to a significant interaction effect in the ANOVAR model ($F_{1,10}$ = 65.21, adj. $P < 0.0001$).

Discussion

Although heightened behavioral aggression is commonly cited as a characteristic of successful invaders, few studies have documented the underlying mechanisms (Holway and Suarez 1999). Our results suggest aggressive invaders usurp preferred foraging positions in mixed groups, but the ability to translate greater aggression into competitive dominance is partly a function of the physical environment. Regardless of group size or velocity, yellowfin shiner initiated more aggressive interactions and occupied the lead positions in mixed foraging groups. At low velocity (10 cm s^{-1}), this behavioral dominance allowed yellowfin shiner to consume more drifting prey than rosyside dace. However, when velocity was increased to 20 cm s^{-1}, the superior strike efficiency of the native outweighed (small groups) or balanced (large groups) the behavioral dominance of yellowfin shiner. Thus, our original hypothesis that a competitive reversal will occur as a function of velocity was supported. Previous studies that document the effects of abiotic factors on competitive interactions among stream fishes have largely focused on temperature (Baltz et al. 1982, De Staso and Rahel 1994, Taniguchi et al. 1998, Taniguchi and Nakano 2000). To the best of our knowledge this is the first study to demonstrate experimentally the interplay among velocity, group size, and interspecific competition for native and invasive stream fishes.

The importance of interspecific competition can only be effectively evaluated relative to intraspecific competition (Connell 1983, Underwood 1986). Our results clearly demonstrate the presence of asymmetric interspecific competition under simulated natural conditions. For rosyside dace, interspecific competition at high density reduced foraging rates 15% more than intraspecific competition (at low velocity). Conversely, yellowfin shiner enjoyed a 16% increase in per capita foraging rate in the presence of rosyside dace vs. the same density of conspecifics. In general, there has been little agreement on the importance of competition in structuring stream communities (see reviews by Kohler 1992, Fausch 1988, 1998). Largely due to their variable flow regimes, streams are viewed as physiologically taxing environments, and many stream ecologists have come to emphasize the importance of abiotic factors to the population and community dynamics of lotic faunas (Hynes 1970, Townsend 1989, Grossman et al. 1990, Grossman et al. 1998). However, flow regimes vary greatly across the landscape, and can oscillate significantly within a given stream across seasons or years (e.g., flood vs. drought; Poff and Ward 1989). Even in flood prone streams, resource limitation and biotic interactions can become important during periods of relatively stable flow (e.g., Fisher et al. 1982, Power et al. 1985, Dudley et al. 1990).

Aggression rates were generally unaffected by velocity, and decreased with increasing group size as predicted by resource defense theory (Brown 1964, Grant 1993, 1997). Although the total per capita aggression rates in mixed groups were intermediate to the intraspecific rates of equal density (Fig. 4.3), there were striking differences in the species-specific rates which clearly indicated different responses to interspecific competition. Rosyside dace aggression rates in mixed groups were 51-74% lower than complementary intraspecific treatments. In contrast, yellowfin shiner aggression rates in mixed groups were 7-30% greater than the intraspecific treatments. Both yellowfin shiner and rosyside dace defend positions in groups relative to the profitability of that position, and individual aggression rates decrease with increasing distance from the front of the group (Chapter 1). This spatial hierarchy could offer some explanation for the unanticipated aggression responses to interspecific competition. Because yellowfin shiner were generally in the front half of mixed groups, it may be more appropriate to compare their per capita rate to that of the two or four highest ranked individuals in the intraspecific treatments. Doing so reveals that dominant yellowfin shiner in mixed groups were actually 16-30% less aggressive than their equally ranked counterparts in shiner-only groups. This makes more sense as interacting with the less aggressive rosyside dace should reduce the amount of aggression yellowfin shiner need to perform to maintain high positional ranks in mixed groups. A similar reversal occurs for rosyside dace, who interact with more aggressive yellowfin shiner in mixed groups. Rosyside dace in mixed groups were actually 47-77% more aggressive than low ranking dace in dace-only groups.

However, if rosyside dace applied aggression solely in response to their foraging rate (i.e, the perceived quality of a foraging position), we would have expected the rosyside dace to increase aggression when the quality of their positions improved (i.e., with increasing velocity in mixed groups). This did not occur. It appears the identity of group members also contributes to an individual's aggression rate.

Yellowfin shiner were 6-20 times more aggressive than rosyside dace in interspecific groups, but targeted conspecifics 1.4-1.7 times more often than rosyside dace. Rosyside dace also showed a conspecific bias in agonistic activity, targeting other dace 4-22 times more often than yellowfin shiner. The conspecific bias can also be explained by the spatial hierarchy. Both yellowfin shiner and rosyside dace use aggression to defend against displacement by lower ranked individuals (i.e, those farther back in the group; Chapter 1). As a general consequence, most aggressive acts are directed towards hierarchical neighbors. Thus, the species segregation in groups (yellowfin shiner in the front, rosyside dace at the back) probably increased the likelihood of encounters between conspecifics. Overall, the aggression data support the view that flexible foraging behavior plays an important role in the success of stream fishes (Dill 1987, Chapter 3).

We found that manipulating the size of foraging groups can alter the effect of velocity on the outcome of interspecific competition. At low density and high velocity, rosyside dace made 61% of the total captures despite being relegated to rear positions in the foraging group. However, increasing density mitigated the superior capture efficiency of the rosyside dace, and both species acquired approximately 50% of the available prey. Because the high velocity treatment (20 cm s^{-1}) represents the greatest difference in foraging efficiency between rosyside dace and yellowfin shiner (Fig. 4.1b), this finding implies rosyside dace will only find a competitive refuge in small groups when yellowfin shiner enter high velocity patches, and that yellowfin shiner may be limited in their ability to invade headwaters. The effect of increasing density on condition-specific competition was clearly a statistical phenomenon that arose from the longitudinal segregation of the species. The capture efficiency (total captures/total prey encountered) of a single yellowfin shiner foraging alone at 20 cm s^{-1} is 34% (Grossman et al. 2002). However, when four yellowfin shiner are arrayed approximately linearly, their individual efficiencies are additive, and the four shiners together should have a combined efficiency of 81%. Thus, a position within a patch becomes less profitable as prey are ‘sieved’ from the water column by individuals situated upstream. Interestingly, the difference between the theoretical maximum capture efficiency (81%) and the realized capture efficiency from the interspecific treatments (51%) may approximate the strength of the intraspecific interference effect of aggression for yellowfin shiner.

The effect of velocity on interspecific competition was quite unlike that reported for temperature in previous studies of condition-specific competition. The mechanism by which temperature mediates competition appears to be dominated by species-specific physiological responses to changing environmental conditions. For example, Argentine ants have widely displaced native ants in mesic habitats of California through a mix of interference and exploitative behaviors (Human and Gordon 1996, 1999, Holway 1999). However, in xeric habitats, high temperature and low soil moisture depress worker activity rates and increase mortality in Argentine ant colonies (Holway et al. 2002). As a consequence, their ability to outcompete native ants depends largely on the physiological suitability of the habitat (Holway et al. 2002). In streams, temperature has been shown to mediate interspecific competition by differentially affecting aggressive tendencies (DeStaso and Rahel 1994), metabolic rates (Baltz et al. 1982), appetite suppression (Taniguchi et al. 1998), or some combination thereof

(Taniguchi and Nakano 2000). In our study, the species-specific effect of velocity on foraging efficiency was clearly modified by the social context (group size and composition). Whether or not there are additional differences in the effects of velocity on the species (e.g., the cost of holding position in high velocity patches) is unknown. However, the range of velocity we tested does not impose a significant metabolic cost to rosyside dace, and presumably this applies to other small, streamlined minnows (Facey and Grossman 1992).

The key role of velocity in mediating the impact of an aggressive new species likely stems from its broader importance to stream fish ecology in general (Dill 1983, Matthews 1998). As pointed out by Ricklefs (1990), differential competitive abilities often arise from asymmetries in autecology and natural history. In the southeastern United States the rosyside dace is commonly found in pool areas of clear, cool rocky streams (Etnier and Starnes 1993). The Little Tennessee River form is thought to be an undescribed new species (B. Burr, pers. comm.), and has been classified as a highland endemic (Mayden 1987, Scott and Helfman 2001). Highland streams exhibit a high degree of mesohabitat diversity (e.g., riffles, runs, chutes, torrents, woody debris, pools, etc.) with predominantly coarse substrates, heavy shading by riparian vegetation, and low to moderate primary and secondary productivity. In contrast, the yellowfin shiner is most abundant in lower elevation creeks and rivers where waters are often warmer, more turbid, and nutrient rich. It is therefore not surprising that a recent optimal foraging model found that yellowfin shiner in Coweeta Creek were generally less capable of choosing microhabitats which maximize their intake rates vs. native minnows (Grossman et al. 2002).

Although it is thought the introduction of yellowfin shiner was a bait bucket transfer from the Savannah River drainage (W. McClarney, pers. comm.), an additional mechanism has been identified which may support the establishment of more ‘downstream’ generalist species in Coweeta Creek. The availability of water column habitat is inversely correlated with species diversity in Coweeta Creek, largely due to the upstream migration of species during periods of drought (Grossman et al. 1998). Drought reduces average water column velocities, potentially reducing the availability of habitats that provide a refuge for high velocity ‘specialists’ from the impact of aggressive migrants. Coweeta Creek experienced several years of drought during the 1990's, the period when yellowfin shiner were establishing throughout the Little Tennessee River (Grossman et al. 1998). Habitat diversity may generally mediate the effect of introduced species in terrestrial environments as well. For example, Petren and Case (1998) demonstrated that reducing the structural complexity of foraging habitats increased the strength of interspecific competition between native and invasive geckos on Pacific islands.

How to identify which introduced species will become a problem in the future is an important question for invasion biology (Moyle et al. 1986, Moyle and Light 1996b, Kolar and Lodge 2002). Although human alteration of the landscape (or riverscape, Faush et al. 2002) can promote the establishment of invasive species that are less sensitive to habitat disturbance (Moyle and Light 1996a), biotic interactions with natives also can be important. In a review of post-invasion mechanisms structuring stream fish assemblages, competition and predation were important in 62% of the reviewed studies, although direct mechanisms were only investigated in five cases (Ross 1991). Our findings suggest the active transfer of species into high quality streams may ‘seed’ the system with new species poised to take advantage of future habitat degradation. This is a particularly important problem in the southeastern United States which houses the most diverse assemblage of temperate freshwater fishes in the world (Lydeard and Mayden 1995, Warren et al. 2000). Habitat alteration in southeastern streams is dominated by the removal of riparian forests leading to sedimentation of coarse substrates, increased turbidity, and warmer temperatures. In extreme cases these alterations may functionally convert cool upland streams with high habitat diversity into facsimiles of lowland creeks. This habitat homogenization generally progresses upstream and may lead to widespread faunal homogenization and the eventual loss of rare native taxa (Scott and Helfman 2001).

In conclusion, we have shown how post-establishment effects of a behaviorally dominant invader hinge upon environmental variation. Specifically, differences in foraging efficiency at various velocities (a scramble mechanism) can reverse the effects of competitive aggression (an interference mechanism) for socially foraging stream fishes. Consequently, we suggest that the ability of rosyside dace to withstand the invasion by yellowfin shiner in Coweeta Creek will rely partly upon the maintenance of high habitat diversity, particularly flows. Additional field and laboratory experiments designed to identify the interactions between behavioral mechanisms and attributes of the physical environment will be required to determine if condition-specific competition is generally important to the establishment of invasive species. The need for such studies has been exacerbated by the accelerating rate of habitat loss and degradation in areas with unique faunal assemblages.

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Table 4.1. Results of individual ANOVARs for effects of velocity and group size on per capita aggression rates of yellowfin shiner, rosyside dace, and mixed-species groups.

Source	*F*	df	*P*
A) Yellowfin Shiner			
Velocity	0.80	1, 10	0.39
Group Size	14.40	1, 10	<0.001
Velocity × Group Size	0.77	1, 10	0.40
B) Rosyside Dace			
Velocity	0.74	1, 10	0.41
Group Size	27.33	1, 10	<0.001
Velocity × Group Size	0.34	1, 10	0.57
C) Mixed-species Groups			
Velocity	3.71	1, 10	0.09
Group Size	6.52	1, 10	0.03
Velocity × Group Size	1.79	1, 10	0.21

Table 4.2. Summary of repeated-measures ANOVA results for the effects of species and velocity on aggressive behavior, positional rank, and foraging success.

Response variable	Source	df	*F*	*P*
A) Low Density				
Aggression Rate	Species	1,10	68.63	<0.0001
	Velocity	1,10	1.41	0.262
	Species × Velocity	1,10	0.92	0.413
Positional Rank	Species	1,22	28.32	<0.0001
	Velocity	1,22	0.01	0.955
	Species × Velocity	1,22	0.63	0.520
Foraging Rate	Species	1,10	5.21	0.046
	Velocity	1,10	9.54	0.011
	Species × Velocity	1,10	245.90	<0.0001
B) High Density				
Aggression Rate	Species	1,10	728.40	<0.0001
	Velocity	1,10	0.01	0.970
	Species × Velocity	1,10	0.56	0.439
Positional Rank	Species	1,46	65.57	<0.0001
	Velocity	1,46	0.01	0.914
	Species × Velocity	1,46	0.58	0.457
Foraging Rate	Species	1,10	57.84	<0.0001
	Velocity	1,10	0.91	0.364
	Species × Velocity	1,10	65.21	<0.0001

Table 4.3. Summary aggression counts by direction (conspecific vs. heterospecific), density, and velocity treatment for mixed-species groups. YF = yellowfin shiner, RD = rosyside dace. Counts only include one-sided acts performed during the last 40 minutes of the trials, all replicates are combined.

Density	Velocity	Aggressor	Recipient	Total Acts	% Acts
Low	Low	YF	YF	851	0.63
Low	Low	YF	RD	502	0.37
Low	High	YF	YF	653	0.58
Low	High	YF	RD	467	0.42
Low	Low	RD	RD	115	0.79
Low	Low	RD	YF	31	0.21
Low	High	RD	RD	158	0.80
Low	High	RD	YF	40	0.20
High	Low	YF	YF	1236	0.60
High	Low	YF	RD	814	0.40
High	High	YF	YF	940	0.58
High	High	YF	RD	678	0.42
High	Low	RD	RD	84	0.84
High	Low	RD	YF	16	0.16
High	High	RD	RD	198	0.96
High	High	RD	YF	9	0.04

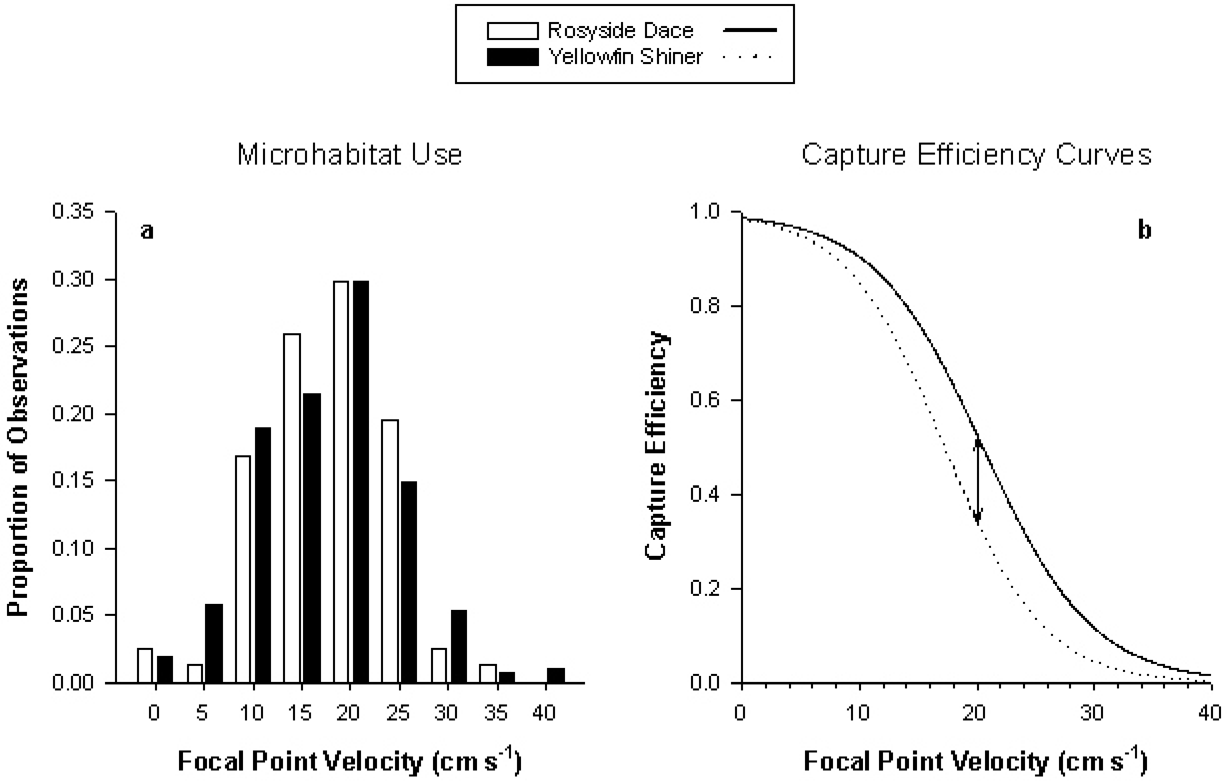

Fig. 4.1. Use of focal point velocities in Coweeta Creek (a) and laboratory capture efficiency curves (b) for yellowfin shiner and rosyside dace. Field data were collected during the summers of 1996-1997 by M. D. Farr (unpub. data). Capture efficiency curves were calculated from equations included in Grossman et al. (2002). The bi-directional arrow represents the point of greatest difference between the yellowfin shiner and rosyside dace curves (20 cm s^{-1}).

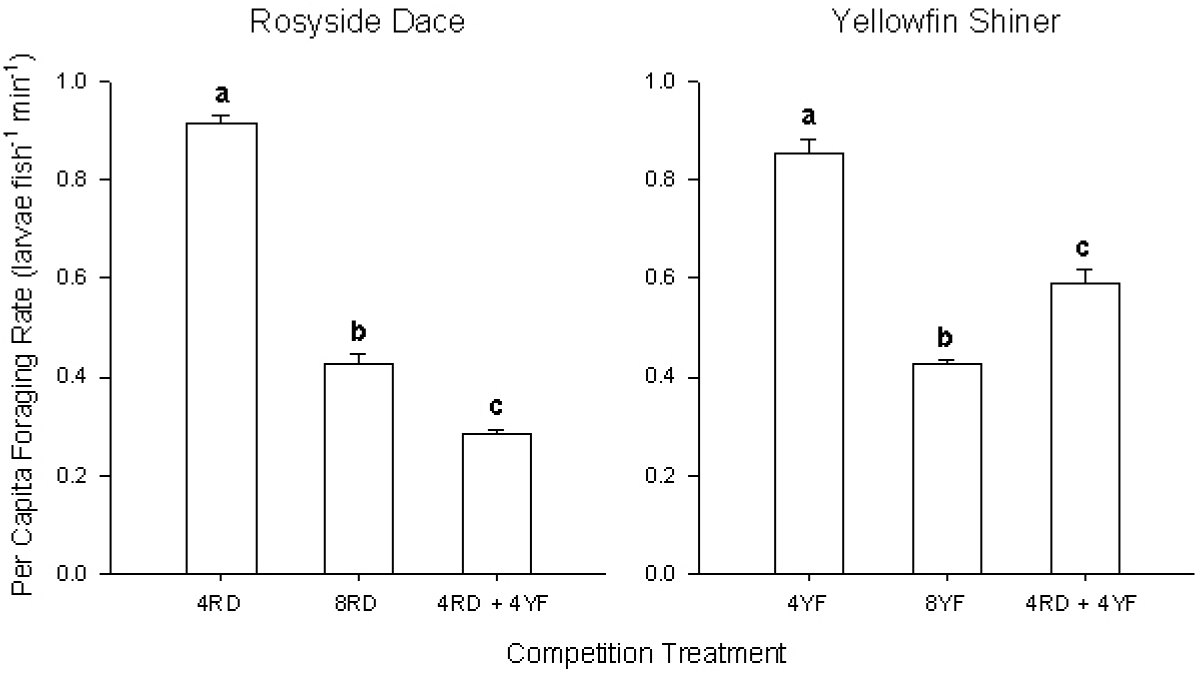

Fig. 4.2. Effects of the competition treatments on (means ± 1 SE) per capita foraging rates for rosyside dace (A) and yellowfin shiner (B). Means labeled with the same letter are not significantly different at the $P < 0.05$ level (ANOVA with Tukey HSD test). $N = 6$ for each factorial combination. RD = rosyside dace, YF = yellowfin shiner.

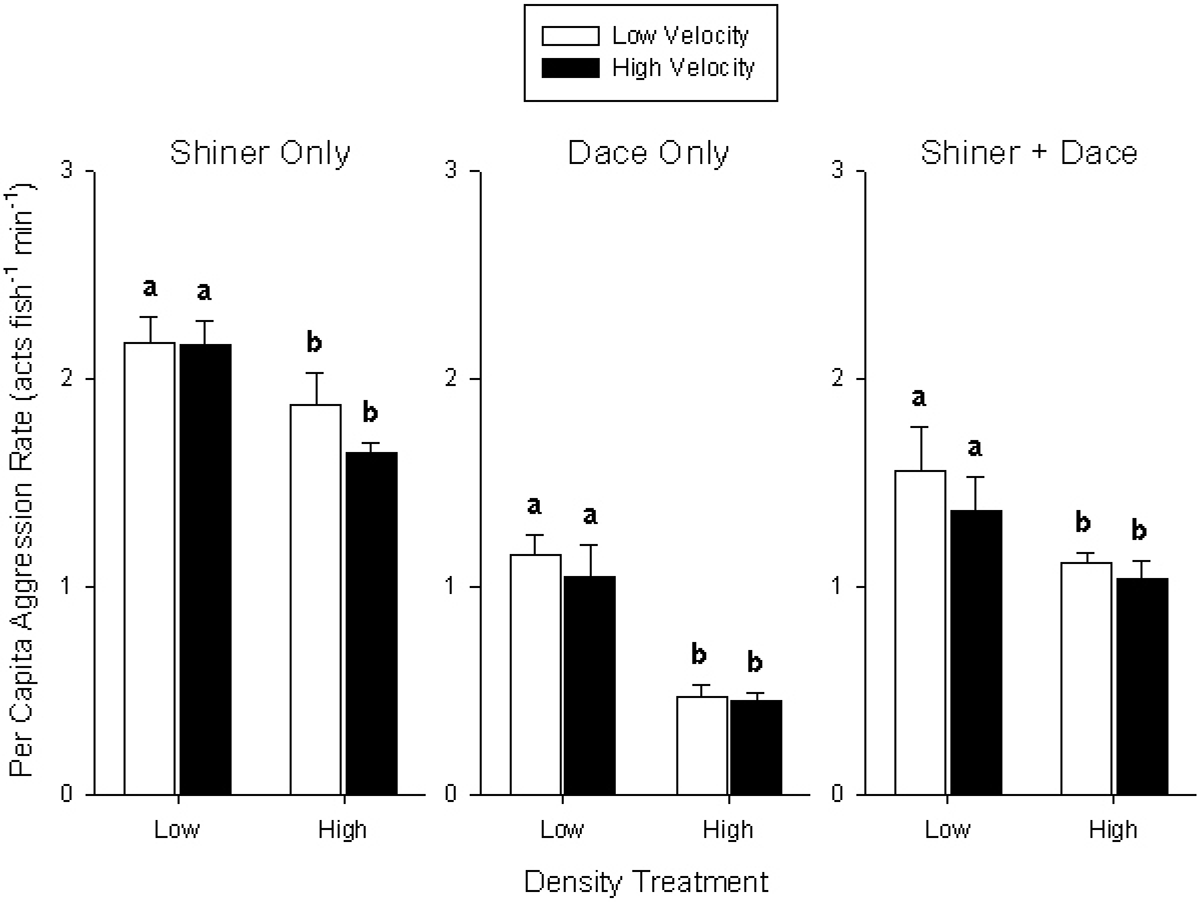

Fig. 4.3. Summary of the effects of velocity and group size on per capita aggression rates (means ± 1 SE) in rosyside dace, yellowfin shiner, and mixed-species groups. Means labeled with the same letter are not significantly different at the $P < 0.05$ level (ANOVAR with post-hoc Tukey-Kramer tests). Significant differences only apply within a frame. $N = 6$ for each factorial combination.

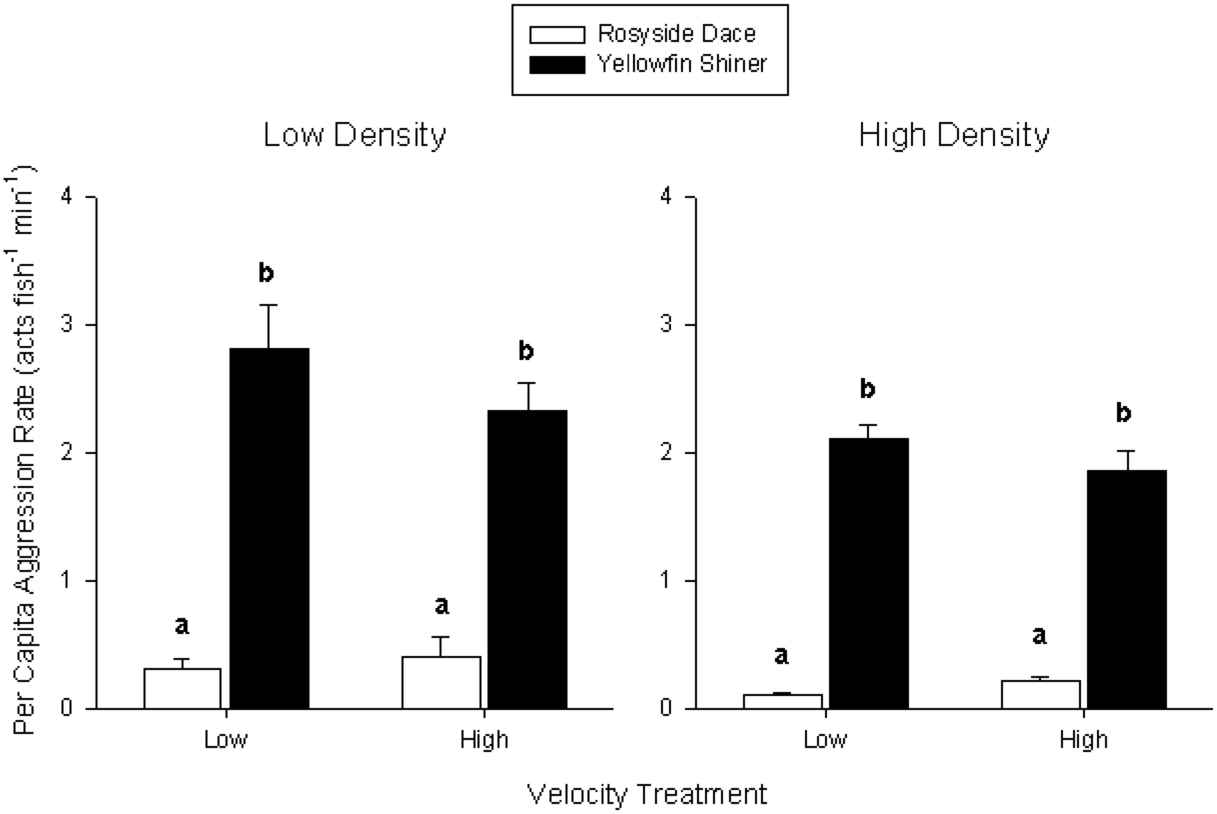

Fig. 4.4. Per capita aggression rates (means ±1 SE) in mixed-species groups as a function of velocity and density. Means labeled with the same letter are not significantly different at the $P < 0.05$ level (ANOVAR with post-hoc Tukey-Kramer tests). Significant differences only apply within a density treatment. $N = 6$ for each factorial combination.

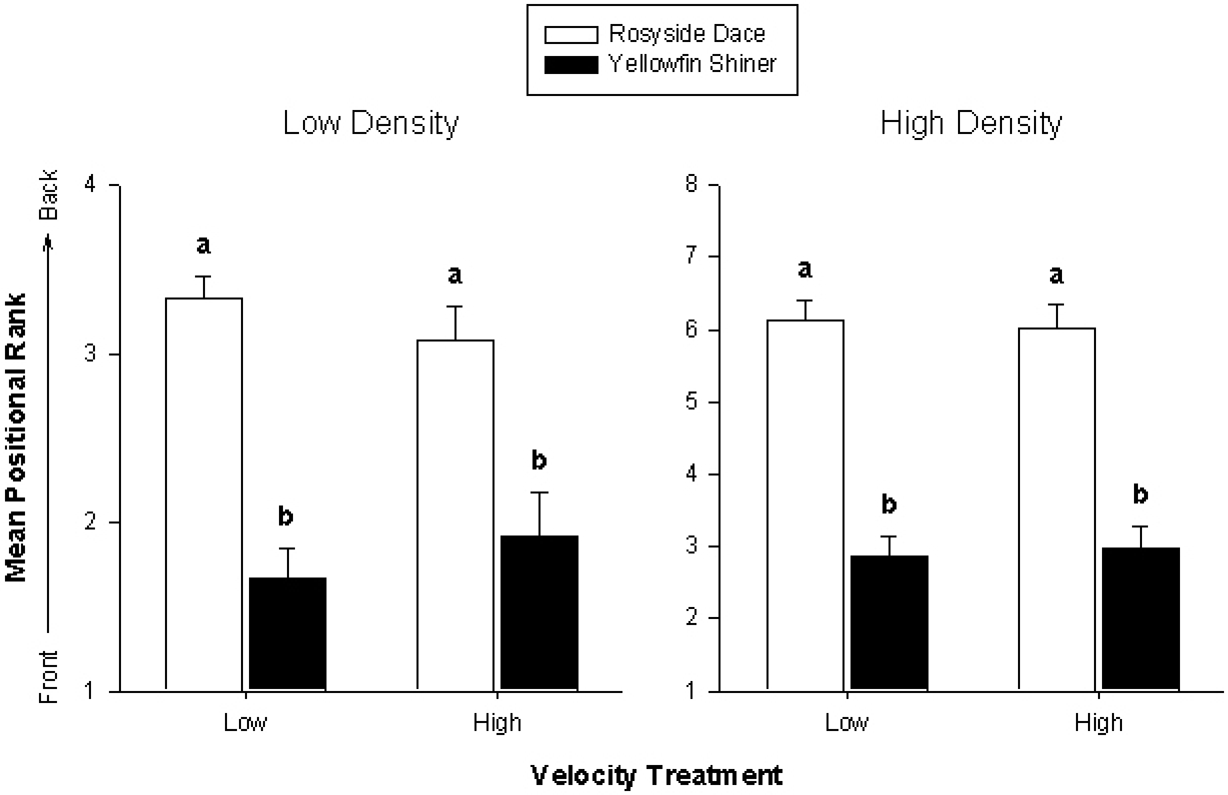

Fig. 4.5. Positional ranks (means ±1 SE) in mixed-species groups as a function of velocity and density. Individuals are ranked from 1-4 (front to back, low density) or 1-8 (front to back, high density). Means labeled with the same letter are not significantly different at the $P < 0.05$ level (ANOVAR with post-hoc Tukey-Kramer tests). Significant differences only apply within a density treatment. $N = 12$ for each low density factorial combination. $N = 24$ for each high density factorial combination.

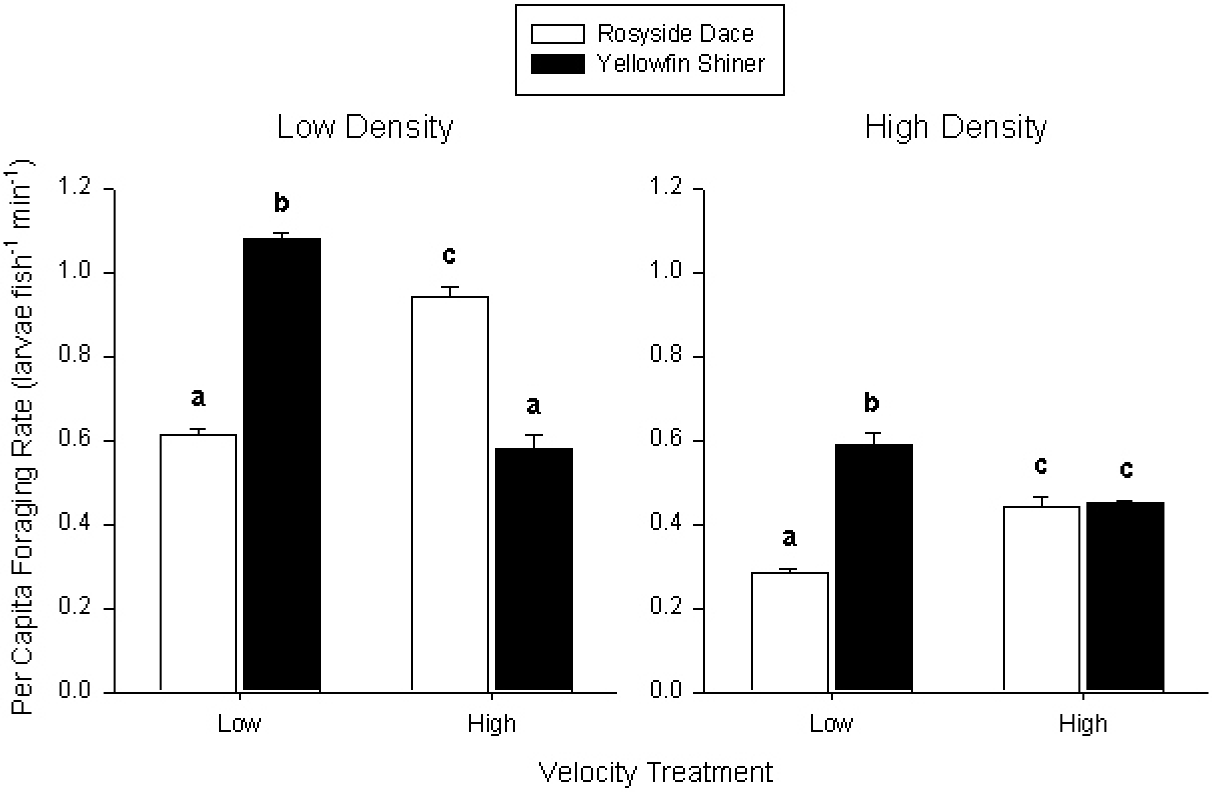

Fig. 4.6. Per capita foraging rates (means ±1 SE) in mixed-species groups as a function of velocity and density. Means labeled with the same letter are not significantly different at the $P < 0.05$ level (ANOVAR with post-hoc Tukey-Kramer tests). Significant differences only apply within a density treatment. $N = 6$ for each factorial combination.

SUMMARY AND CONCLUSIONS

Understanding how behaviors maximize individual fitness is the cornerstone of behavioral ecology. Numerous laboratory and field studies have revealed the importance of fitness-maximizing behaviors to the process of habitat selection by fishes. Using a combination of theoretical models and empirical studies, I examined the importance of competitive aggression to foraging interactions between stream fishes. Because an invasive species (yellowfin shiner, *Notropis lutipinnis*) had recently been introduced into a system that we have been studying for 20 years (Coweeta Creek, N.C.), I chose to examine its behavior in tandem with an ecologically similar native species (rosyside dace, *Clinostomus funduloides*). Previous research with rosyside dace led to the development of a general mechanistic model of microhabitat selection for stream fishes, based on the profitability of occupying varying focal point velocities in a stream (Hill and Grossman 1993, Grossman et al. 2002). I 'scaled-up' from microhabitat to patches and examined the utility of competitive aggression in groups of socially foraging minnows.

Both yellowfin shiner and rosyside dace readily develop dominance hierarchies in the presence of food, and dominant individuals gain a significant feeding advantage in social groups by defending positions upstream of conspecifics (Chapter 1). Variation in total food abundance within the range of natural variation does not appear to affect this functional relationship. Interestingly, the dominant individuals in either species were required to perform the same relative amount of aggression (~ 30% of the group total) to maintain the best foraging position in the group. The dominance hierarchies which formed appeared ephemeral, arising when food delivery began, and dissipating when food delivery ceased. Thus, foraging aggression was a facultative response to the presence, or perhaps defensibility, of food.

Resource defense theory predicts an increase in per capita aggression rates in groups when food abundance increases from initially low levels, then decreasing at high food abundance (i.e., a hump-shaped curve). This theory led me to consider the effects of food abundance on individual aggression rates within a linear dominance structure (Chapter 2). I discovered that dominant individuals were more likely to decrease aggression with increasing food while subordinates were more likely to increase aggression (i.e., dominants travel over the ‘hump’ first). Because dominants reduced aggression, they also fell back into more central positions within the group. Central positions are thought to provide superior refugia from predators, although I did not include predation as a factor in the experiments. However, it appears likely that behavioral dominance generally allows fish to monopolize spatial resources within groups, trading off foraging and anti-predator benefits as a function of habitat quality (Krause and Ruxton 2002).

Yellowfin shiner were both more aggressive (higher per capita rate, Chapter 2) and more likely to exhibit aggression (absence of a non-aggressive class, Chapter 1). Heightened foraging aggression could have been important in the establishment phase of the invasion. Although heightened aggression may make a forager more conspicuous to predators, there is little evidence for strong predator effects on the foraging behavior of fishes in Coweeta Creek (Grossman et al. 1998). Coupled with the observation that yellowfin shiner generally limit their aggressive behavior (i.e., they are aggressive when food is available and defensible), competition for the best feeding positions may more than balance the heightened predation risk for new invaders.

Using a fitness maximization patch-use model (the Ideal Free Distribution), I measured the relative ability of native and invasive minnows to track changes in patch quality under a range of natural prey abundances (Chapter 3). Because yellowfin shiner move between patches more frequently than rosyside dace, they were able to match the IFD when overall food abundance was high, whereas the native dace continued to overuse low quality patches (i.e., undermatching). The general ability of an invasive species to maximize its average fitness more than a native competitor could explain its ability to invade the system, as could its greater tendency to disperse, regardless of interactions. Hence, yellowfin shiner may be more able to detect high quality patches, and more able to acquire the best positions in those patches (vs. rosyside dace). To the best of my knowledge, this is the first study to demonstrate the IFD as a potential mechanism that promotes the establishment of new species.

I also discovered condition-specific competition may mediate the effects of the invasion at the patch-scale (Chapter 4). Although yellowfin shiner are more aggressive than rosyside dace, they are also less efficient foragers, particularly at higher velocities. As a consequence, yellowfin shiner always acquired the best positions in mixed-species groups, but their ability to monopolize prey captures was mitigated by water velocity. At high velocities (but within the natural range of microhabitat overlap) the rosyside dace acquire equal or superior competitive status (feeding rate) due to their superior capture efficiency. Condition-specific competition is thought to be a primary force in the structuring of natural assemblages, and may also be important to the naive interactions between native and invasive species.

How to identify which introduced species will become a problem in the future is an important question for invasion biology. Although human alteration of the landscape can promote the establishment of invasive species that are less sensitive to habitat disturbance, my findings suggest biotic interactions with natives also can be important. It is intriguing to suggest that the maintenance of habitat diversity, especially in terms of flow regimes, may prevent the loss of species in Coweeta Creek by mediating the impact of an aggressive invader, although much work remains before such a conclusion is fully supported.

The relationships between native and invasive organisms have often been examined as retrospective case studies after significant negative effects have occurred. My work provides evidence that well established theoretical mechanisms (e.g., ideal free distributions, condition-specific competition) can provide significant insight into the outcome of interactions between invasive fishes and their receiving communities early in the invasion process. These findings should also be applicable to introduced phenotypes (e.g., when aggressive hatchery fish are introduced into native populations). Understanding the mechanisms of invader-native-environment interactions will provide a deeper understanding of how species are ecologically and evolutionarily linked in biological communities, and should lead to the development of effective conservation practices.

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