

## INFERRING COMPETITIVE BEHAVIOR FROM POPULATION CENSUS AND HABITAT DATA

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### ABSTRACT

Theories of density-dependent habitat selection predict that competitive interference should produce curvilinear relationships when the population densities in adjacent habitats are graphed against each other. We tested the theory by manipulating population densities of brook trout (*Salvelinus fontinalis*) in four separate natural-stream enclosures containing flat and riffle habitats. Brook trout distributions in streams typically reflect a size-based dominance hierarchy. As predicted by theory, interference among individuals was revealed by curved regressions of density in the paired habitats (isodars). Brook trout exhibited no strong preference for either habitat at low population densities. Habitat preferences emerged clearly at higher densities, apparently reflecting the distribution of suitable sites in the habitat pairs. Predicted body-size distributions between flat and riffle were mirrored consistently by those observed in the population. The isodar analysis, based only on density data, revealed the competitive behaviors that underlie brook trout distributions in real streams.

*Keywords:* density-dependent habitat selection, isodar, brook trout, *Salvelinus fontinalis*, interference competition, preemptive interference, competitive behavior

### INTRODUCTION

Density-dependent habitat selection provides a mechanistic link between the optimal behavior of individuals and their distribution across heterogeneous environments (Morris and Brown, 1992; Morris, 1994, 2003). It should be possible, therefore, to infer underlying optimal behaviors from the various density patterns they create (Rosenzweig and Abramsky, 1985; Morris, 1994; Rodríguez, 1995). Interference by dominant or established individuals that prevents later-arriving individuals from occupying preferred sites, for example, should lead to a preemptive distribution across habitats (Pulliam, 1988, 1996; Pulliam and Danielson, 1991; Rodenhouse et al., 1997). We examine

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whether we can use the shape of isodars (Morris, 1987a, 1987b, 1992, 1995, 1997), lines of equal fitness, to document mechanisms of density-dependent habitat selection in brook trout. Whereas exploitation competition for resources produces straight-line isodars, interference and preemptive competition should frequently produce curved isodars (Morris, 1994; Morris et al., 2000a).

We begin by briefly reviewing some density-dependent habitat selection theory that underpins isodars. We then describe a series of procedural and statistical protocols to determine whether the distribution of individuals across habitats lets us infer the competitive interactions responsible for the pattern. Our results demonstrate that we can use ecological patterns at one scale in space and time to reveal the processes that create them at lower scales and that we can link individual behavior with its population consequences.

#### *DENSITY-DEPENDENT HABITAT SELECTION AND ISODAR THEORY*

Habitat-selection models generally characterize a habitat in terms of its basic suitability (fitness) for an individual in the absence of competition, and assume that fitness declines with increasing densities of conspecifics or heterospecifics competing for resources (Morris, 1988, 1989, 1997; Rodríguez, 1995). The negative effects of density on a given habitat-selecting individual, however, will depend on its competitive behavior.

With exploitation competition, individuals often scramble for non-defensible resources that are spread throughout their environment (Nicholson, 1954). Exploitation leads to an ideal free distribution in which the mean fitness of each phenotype is equalized among habitats, and fitness of all individuals declines with each new entrant into the habitat (Fretwell and Lucas, 1970; Fretwell, 1972; Parker and Sutherland, 1986; Łomnicki, 1988; Rodenhouse et al., 1997).

With interference competition, however, dominant or established individuals reduce the fitness of new arrivals (ideal-despotic or ideal preemptive distribution, Fretwell and Lucas, 1970; Fretwell, 1972; Pulliam, 1988, 1996; Pulliam and Danielson, 1991; Rodenhouse et al., 1997), such that "perceived" habitat suitability (i.e., fitness discounted by the interference experienced by an individual) is equalized. An ideal-despotic distribution is produced when subordinate individuals choose habitats on the basis of each habitat's mean perceived quality. A preemptive distribution emerges when dominant or early-colonizing individuals occupy the best available sites (e.g., territory, feeding station, refuge, etc.; Pulliam, 1988; Danielson, 1991, 1992; Pulliam and Danielson, 1991), and preempt their use by subordinates or late colonizers (also called site-dependent population regulation, Rodenhouse et al., 1997; McPeck et al., 2001). Mean fitness will typically be higher in some habitats than in others, but the fitness of individuals occupying the poorest sites will be the same in each habitat (Milinski and Parker, 1991; Morris, 1991, 1994, 1995; Pulliam and Danielson, 1991; Rodríguez, 1995; Rodenhouse et al., 1997).

Each form of competition should result in predictable distributions of individuals among habitats. First, consider pure exploitation (scramble) competition. There is a linear decline in fitness for all individuals as population density increases. This trans-

lates into a straight-line isodar (Morris 1987a, 1988). For interference competition other than preemption, the isodar is similar to the case for exploitation competition except the habitat-selecting individuals equalize their perceived fitness between habitats. The isodar could take on either a straight-line form when competition is additive, or follow a logarithmic function when competition is multiplicative (e.g., as when each individual consumes an equal proportion of available resources, e.g., Hassell and Varley, 1969; Sutherland, 1983; Fagen, 1987, 1988; Milinski and Parker, 1991; Morris, 1992, 1994).

With preemptive interference, individual habitat selectors attempt to maximize the quality of the site they occupy within a habitat, as opposed to mean habitat quality. The distribution of individuals between habitats depends on the distribution of site qualities among the habitats. Imagine two habitats with partially overlapping normal distributions of site qualities. The curved site-dependent isodar plotting population densities in these habitats reflects the cumulative distribution of occupied sites (declining site quality as population size increases; Morris, 1994). Even when site qualities follow some other distribution, such as a negative exponential, the resulting isodar is curved. One can, of course, imagine situations where site-dependent isodars are not curved, such as for some rectangular distributions of site quality or when there is no overlap in site qualities among habitats. The point is that when isodars are curved they imply site dependence (Morris, 1994).

#### *DENSITY-DEPENDENT HABITAT SELECTION IN THE FIELD*

Empirical isodars have been constructed for small placental mammals (Morris, 1994; Ovadia and Abramsky, 1995; Knight and Morris, 1996; Abramsky et al., 1997; Morris et al., 2000a,b; Lin and Batzli, 2002), kangaroos (Ramp and Coulson, 2002), mammalian carnivores (Edwards et al., 2002), urban and migratory birds (Fernández-Juricic, 2001; Shochat et al., 2002), salmonid fishes (Rodríguez, 1995), fleas (Krasnov et al., 2003), and many other organisms. Many of these species appear to follow an ideal-free distribution (e.g., Morris, 1994; Abramsky et al., 1997), in which each individual engages in exploitation competition for resources that are widely dispersed. Such resources are not easily defensible so an individual is likely to base its habitat choice on mean habitat quality. As expected, the isodars are mostly straight-line.

Riverine salmonid fishes occupy habitat in a fundamentally different way (Knight, 2000). Lotic salmonids feed on drift. They maximize fitness by maintaining a position in slow-moving water that minimizes their energy expenditure (Bachman, 1984), while being close to fast currents that transport more food per unit time (Fausch and White, 1981; Fausch, 1984; Hughes and Dill, 1990; Hughes, 1992a,b). Competition for resources within and among salmonid species is resolved by interference. Individuals compete for preferred microhabitats by using behaviors ranging from the defense of strict territorial mosaics (e.g., Kalleberg, 1958) to loose dominance hierarchies (e.g., Newman, 1956). In all cases, large size generally confers dominance within species (Newman, 1956; Kalleberg, 1958; Chapman, 1962; Jenkins, 1969; Bohlin, 1977; Noakes, 1980). As a general rule, most salmonid species develop some form of size-structured distribution in streams such that favored sites are occupied by larger, presumably dominant, fish (Fausch, 1984; Heggenes, 1988; Nakano, 1995a,b).

Body size of salmonids, including brook trout, is an easily obtained measure of relative dominance (Newman, 1956; Jenkins, 1969; Bachman, 1984; Hughes, 1992b; Keeley and Grant, 1995; Nakano, 1995a,b). If brook trout obey an ideal-despotic distribution, large and dominant individuals would select the best quality habitat and exclude others from it. The largest mean body size would be found in the best habitat and there would be minimal overlap in the body-size distributions between habitats. If brook trout use site-dependent habitat selection (obey an ideal preemptive distribution), then mean body size would be greater in the habitat with the highest mean site quality. Overlap in body size between habitats would be extensive at all population sizes. The pattern of overlapping body sizes would reflect the availability of sites in each habitat, as well as the curved shape of the isodar.

Here, we use brook trout to put isodars to the test. We construct isodars from experiments in which we manipulated brook trout densities in paired flat-riffle enclosures. We demonstrate that the isodars are curved. We then test whether the distribution of brook-trout body-sizes predicted from isodars corresponds with that actually observed in the field.

## MATERIALS AND METHODS

### *OVERVIEW OF EXPERIMENTAL DESIGN*

To construct isodars we required simultaneous estimates of brook trout population density in adjacent sections of flat and riffle habitat over a range of different densities. We generated these data by constructing four natural-stream enclosures. Each enclosure contained a single reach of flat and riffle habitat. We then manipulated population densities of brook trout in a series of experiments. Each enclosure was treated as a separate experimental unit. One isodar was generated from each enclosure.

### *STUDY RIVERS AND FIELD METHODS*

We conducted experiments in Drook and Bristy Cove rivers at Cape Race, southeastern Newfoundland, Canada. We constructed two enclosed reaches in each river, referred to as Upper and Lower enclosures, by installing wire-mesh fences across side-channels. Enclosures ranged in size from 41 m<sup>2</sup> to 83 m<sup>2</sup> (Knight, 2000). We built rock weirs at the upstream openings of the side-channels, allowing us to maintain relatively constant water flows throughout the experimental period. One enclosure per river contained an upstream section of flat habitat contiguous with a downstream section of riffle habitat. The second enclosure had the reverse arrangement. We removed all fish larger than 70 mm from the enclosures with a backpack electrofisher (Model 12, Smith-Root Inc., Vancouver, Washington, USA), before starting the experiments.

We designed our experimental protocol to measure daytime habitat selection by juvenile and adult brook trout during the summer feeding and growth season. We repeated experiments from 6 June to 27 August (Knight, 2000). We captured brook trout ranging in size from 70 to 210 mm fork length from the main river channel using the

electrofisher. We marked all fish with an adipose-fin clip and held them in a flow-through container for at least one hour. We excluded trout that did not appear to be swimming normally within a few minutes after capture and marking (injured or unhealthy individuals). Electrofishing and fin clipping cause minimal disturbance to trout behavior (Bohlin, 1977). Wild trout recover from the physiological effects of electroshocking within 3–6 h and from behavioral modifications within 24 h (there may be some depression in their aggression rates beyond 24 h, Mesa and Schreck, 1989). We introduced all individuals simultaneously into the enclosure at the boundary of the flat and riffle habitats. We left trout undisturbed for three days to recover from handling and to allow for exploration and selection of a preferred location.

On the fourth day we dropped a weighted barrier net between the flat and riffle habitats, effectively dividing the enclosure in two. We then removed all trout from each habitat with the electrofisher. Mean recapture rates were approximately 90%. We measured fork length and weight of each fish and calculated the population density in each habitat. We then returned all fish to the main stem of the river. Individual trout were used in only one four-day experimental run. We repeated the experimental protocol 10 to 14 times in each enclosure over a wide range of randomly assigned trout densities.

#### *HABITAT MEASURES AND ANALYSIS*

We estimated habitat characteristics in a series of stream-width transects (1-m intervals) along the length of each habitat to verify our assumption that riffle and flat habitats were indeed different. We measured water velocity at 2/3 depth (Flo Mate Velocity Meter, Marsh-McBirney, Frederick, Maryland, USA), water depth, and substrate size at five stations spaced at equal distances along each transect. We contrasted mean values of each measure between flat and riffle in each enclosure individually, and for all enclosures combined using empirical distributions from Monte Carlo randomizations.

#### *INNATE HABITAT PREFERENCE*

Habitat-selection theory assumes that habitat preferences at low density are modified by increasing population size. We attempted, therefore, to reveal the innate habitat preference of brook trout by documenting habitat use in all replicates for which density in the enclosure was less than 0.5 individuals  $m^{-2}$ . We used a *t*-test comparing mean trout density in the two habitats for each enclosure to determine whether flat or riffle habitat was used most frequently.

#### *MODEL SELECTION: FINDING THE BEST ISODAR*

We fitted a series of linear and polynomial regressions of population density in flat habitat against density in riffle for each of the enclosures. We excluded any density pair in which one habitat had a zero value, unless one or more individuals had occupied that habitat in a replicate with fewer trout in the enclosure. Dropping zero values is a standard procedure when calculating isodars because it ensures that intercepts are not drawn to the origin by low-density replicates (Hansson, 1996; Knight and Morris, 1996). We used the results of least-squares regression (Data Fit Version 8.2, Oakdale Engineering)

to select the best isodar. We used five hierarchical screening criteria to select the best model.

- i) We assessed graphs of residuals plotted against predicted values, and rejected all models where the visual pattern illustrated an inappropriate fit (Sokal and Rohlf, 1995).
- ii) We graphed the isodars and rejected those polynomial models where predicted densities implied erratic or otherwise implausible shifts in population distribution back and forth between habitats. Note that this criterion was a conservative test of preemptive habitat selection because it could reject only curved models.
- iii) We calculated and ranked the adjusted  $R^2$  values of the remaining models to ensure that each one explained a reasonable proportion of the common variance in density.
- iv) We compared model likelihoods with the Akaike information criterion corrected for small sample sizes ( $AIC_c$ ) (Akaike, 1973; Sakamoto et al., 1986; de Leeuw, 1992; Hilborn and Mangel, 1997) and Akaike weights ( $w_i$ ) calculated for the best curved, log-log, and straight-line isodar solutions. We selected the model with the smallest  $AIC_c$  (e.g., Johnson and Omland, 2004).
- v) When all criteria were similar, we selected the simplest model possible.

#### *TESTING ISODARS WITH TROUT BODY-SIZE DISTRIBUTIONS*

Model selection yielded curved isodars, reinforcing our a priori expectation that habitat selection by brook trout is based on a form of interference competition. To distinguish between despotic interference and preemptive habitat selection, we examined whether the assortment of individuals was consistent with predictions of selection at the scale of mean habitat quality (despotic distribution) or at the scale of individual sites (preemptive distribution).

We first tested for preemptive interference. Using each isodar equation, we predicted the sequential order in which habitats would be filled and thereby generated cumulative site-quality frequency distributions for flat and riffle habitats. Then, we used data from the replicate with highest trout density, for which the most sites would be occupied, to predict the size distribution for brook trout in flat and riffle habitats for each enclosure (Fig. 1). We did this by sorting the data such that the largest fish was assigned to the habitat with the best site, the second-largest fish to the habitat with the second-best site, and so on. We then predicted the expected difference in the mean and the difference in the coefficient of variation (CV) of trout length between flat and riffle habitat and tested whether those differences were likely to be significant with Monte Carlo randomizations. Finally, we calculated the same test statistics using our observed data, compared the observed differences with predicted ones, and evaluated the statistical significance of those combined results with a sign test. This procedure allowed us to test the differences in actual trout-length distributions that would be caused by preemptive habitat selection in each experimental enclosure.

Our test for despotic interference was less precise as it was not possible to make

**DROOK LOWER      DROOK UPPER      BRISTY COVE LOWER      BRISTY COVE UPPER**

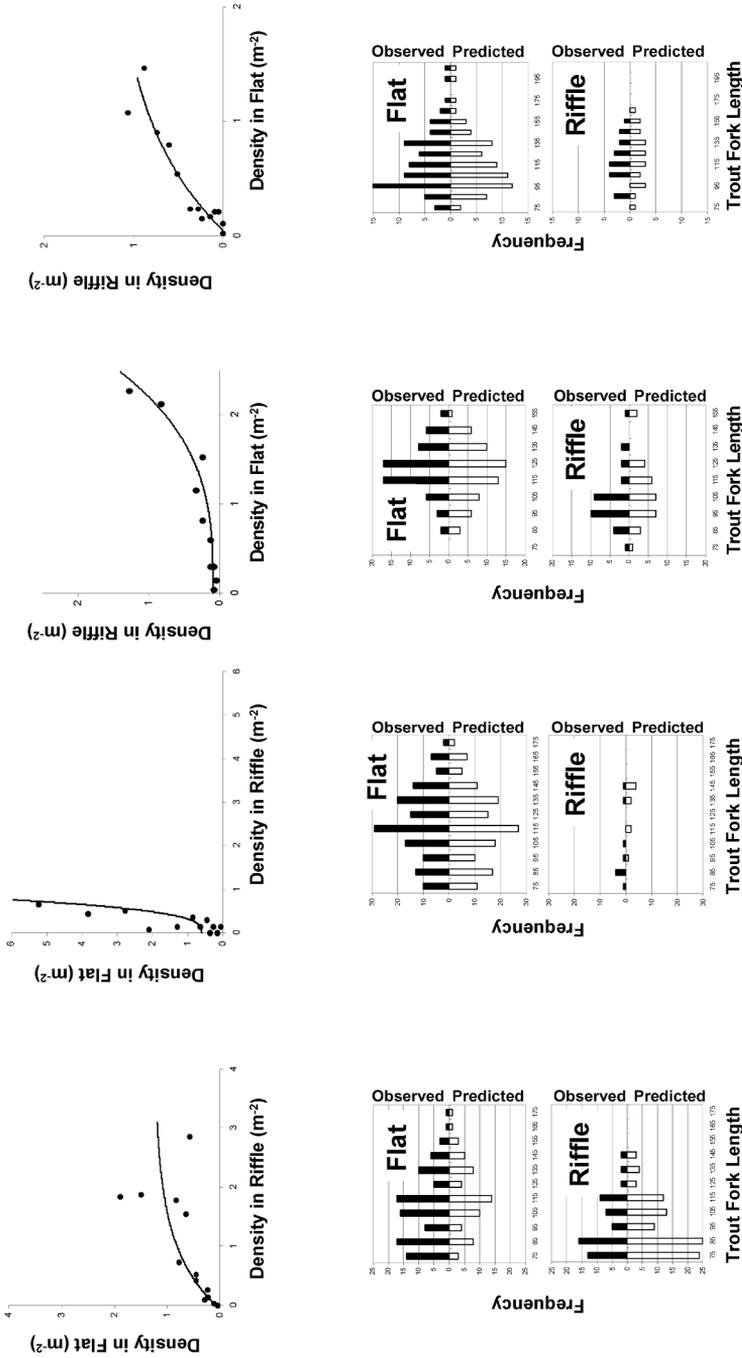


Fig. 1. Best-fit brook trout isodars (top) and comparison of the predicted versus actual body-size distributions (bottom) for the four enclosures at Cape Race, Newfoundland. The isodars are curved, suggesting site-dependent habitat selection (Table 2). To test whether body-size distributions were consistent with site-dependent habitat selection, we used the isodar equations to predict the size distribution of individuals in flat and riffle habitats for each enclosure and compared these predicted distributions with observed data from the experimental run with most trout (bottom).

definitive predictions about the variation in body size between habitats. For each enclosure, we used a *t*-test of the Y-intercept for the log–log isodar to identify whether a significant habitat preference existed (Morris, 1987a). We predicted that the largest mean body size should be found in the preferred habitat. We then compared predicted mean body sizes with observed data.

## RESULTS

### TWO HABITATS

Riffles in each enclosure (and in all enclosures combined) were significantly shallower ( $p < 0.001$ ), and had significantly faster currents ( $p < 0.001$ ) than flat habitats. Substrate size was not different between habitats (with the exception of one enclosure [Drook Upper], in which substrate was larger in riffle than in flat [ $p < 0.001$ ]).

### HABITAT PREFERENCE

Brook trout at low densities tended to be somewhat more abundant in the flat habitat, but the mean preference between flat and riffle was not statistically significant (Table 1). Similar habitat preferences at low density suggest, in the case of ideal-free or despotic habitat selectors, that there is no clear fitness difference between habitats at small population sizes. The lack of habitat preference for preemptive habitat selectors, on the other hand, suggests simply that individuals are able to locate high-quality sites in both habitats at small population sizes.

### ISODARS

Significant isodar regressions described habitat use in each experimental enclosure. In all cases, the best-fit isodar model was curved, the second-best was log–log, and the poorest was a straight line (Table 2). In all enclosures, Delta AIC<sub>c</sub> ( $\Delta_i$ ) between the curved model and straight-line model was greater than two, indicating considerably less support for the straight-line solution (Burnham and Anderson, 2002). The relatively poor fits of the straight-line isodars indicate that a form of interference competition, not

Table 1

Mean brook trout population density in flat ( $N_f$ ) and riffle ( $N_r$ ) habitats for 46 experimental runs at low density (less than 0.5 trout/m<sup>2</sup>) in four stream enclosures near Cape Race, Newfoundland. *t*-tests indicate that brook trout had no significant mean preference for flat or riffle in any of the enclosures

Location	<i>df</i>	$N_f$ (± SE)	$N_r$ (± SE)	<i>t</i>	<i>p</i>
Drook Lower	14	0.25 (± 0.05)	0.21 (±0.07)	0.57	0.579
Drook Upper	10	0.31 (± 0.09)	0.12 (±0.04)	1.96	0.078
Bristy Cove Lower	8	0.27 (± 0.09)	0.09 (±0.02)	1.949	0.087
Bristy Cove Upper	14	0.17 (± 0.03)	0.14 (±0.05)	0.46	0.650

Table 2

A comparison of the straight-line, log-log, and curved isodar solutions for the four brook trout enclosures at Cape Race, Newfoundland. The best model for each enclosure, based on five screening criteria, is highlighted in bold text and includes the actual values for its regression coefficients. The Akaike Information Criterion corrected for small sample size ( $AIC_c$ ) values provide a measure of the model's likelihood, with lower  $AIC_c$  values indicating better fit. Akaike weights ( $w_i$ ) provide the relative probability that  $i$  is the best model, given the data set and set of candidate models evaluated. In all four enclosures, the best-fit isodar was curved, followed by the log-log and linear solutions

Model	F	df <sub>n</sub>	df <sub>d</sub>	P	R <sup>2</sup>	AIC <sub>c</sub>	w <sub>i</sub>
Drook Lower							
<b><math>N_f = 1.24 - 1.16 e^{(-N_f)} + \epsilon</math></b>	<b>14.22</b>	<b>1</b>	<b>11</b>	<b>0.003</b>	<b>0.52</b>	<b>-19.9</b>	<b>0.30</b>
Log-log	11.53	1	11	0.006	0.47	-18.4	0.15
Straight line	8.37	1	11	0.015	0.38	-16.4	0.05
Drook Upper							
<b><math>N_f = 0.60 + 12.4 (N_f)^3 + \epsilon</math></b>	<b>32.07</b>	<b>1</b>	<b>10</b>	<b>&lt;0.001</b>	<b>0.74</b>	<b>2.89</b>	<b>0.20</b>
Log-log	25.89	1	10	<0.001	0.69	4.79	0.08
Straight line	18.00	1	10	0.002	0.61	7.78	0.02
Bristy Cove Lower							
<b><math>N_f = 9.45 + 8.98 (N_f)^3 + \epsilon</math></b>	<b>127.12</b>	<b>1</b>	<b>8</b>	<b>&lt;0.001</b>	<b>0.93</b>	<b>-37.7</b>	<b>0.31</b>
Log-log	73.19	1	8	<0.001	0.89	-32.6	0.03
Straight line	31.67	1	8	<0.001	0.77	-25.4	<0.01
Bristy Cove Upper							
<b><math>N_f = 1.30 - 1.36 e^{(-N_f)} + \epsilon</math></b>	<b>64.02</b>	<b>1</b>	<b>9</b>	<b>&lt;0.001</b>	<b>0.86</b>	<b>-38.5</b>	<b>0.28</b>
Log-log	53.05	1	9	<0.001	0.84	-36.8	0.11
Straight line	47.38	1	9	<0.001	0.82	-35.7	0.07

exploitation competition, is the habitat-selecting behavior controlling the distribution of brook trout in streams. The isodars do not differentiate as clearly between preemptive interference at the site scale and despotic interference at the habitat scale. Bristy Cove Lower was the only enclosure for which  $\Delta_i$  between the curved model and the log-log model was greater than two. For the remaining three enclosures,  $AIC_c$  was lower for the curved models but  $\Delta_i$  ranged from 1.5 to 1.9. In these three enclosures, Akaike weights ( $w_i$ ) suggest that the curved model was more likely than the log-log model by a factor of 2.1 in Drook Lower, 2.6 in Drook Upper, and 2.4 in Bristy Cove Upper, given the final set of three isodar models tested in each enclosure.

#### TEST OF INTERFERENCE COMPETITION

Differences in size distributions between flat and riffle habitats supported the interpretation from the isodar analysis of preemptive habitat selection. Our predicted relative differences in mean fork length between habitats were correct for three of four enclosures, and the relative differences in the CV of body size were correct in every instance (Table 3, Fig. 1). The combined results were significantly different from chance (1 out of

Table 3

Comparison of mean trout size and variation in trout size between flat and riffle habitats from four stream enclosures at Cape Race, Newfoundland. Each row provides a comparison of results for the highest-density replicate in one enclosure. Predicted differences in mean body size for despotic interference were identified from isodar intercepts. Predicted differences for preemptive interference were generated from distributions of site quality inferred from the isodars, and *p*-values were based on Monte Carlo randomizations. Observed differences are the actual values obtained in the field. A double asterisk in the Agree column indicates whether the predicted difference and the observed difference correspond. Top: Mean fork length as an index of trout size. Bottom: Coefficient of variation for trout fork length as an index of variability in dominance. Note that no predictions about the variance in body size could be made for despotic interference

Mean fork length (mm)		Predicted differences			Predicted differences			Observed differences			
Enclosure	Flat	Despotic interference		<i>p</i>	Flat	Preemptive interference		<i>p</i>	Flat	Observed differences	
		Riffle	Agree			Riffle	Agree			Riffle	<i>p</i>
Drook Lower	Flat =	Riffle		0.109	115.2 >	95.3 <	0.001	**	107.1 >	96.3	0.005
Drook Upper	Flat >	Riffle	**	<0.001	115.6 =	128.6	0.133		117.6 >	97.2	0.017
Bristy Cove Lower	Flat >	Riffle	**	0.003	118.9 >	106.9	0.003	**	121.3 >	102.7	<0.001
Bristy Cove Upper	Flat >	Riffle		0.008	115.8 =	121.5	0.461	**	117.2 =	117.1	0.986

Coefficient of variation in fork length (mm)		Predicted differences			Predicted differences			Observed differences			
Enclosure	Flat	Despotic interference		<i>p</i>	Flat	Preemptive interference		<i>p</i>	Flat	Observed differences	
		Riffle	Agree			Riffle	Agree			Riffle	<i>p</i>
Drook Lower	20.1 =	20.3	**	0.950	22.7 =	19.7	0.185				
Drook Upper	21.5 =	14.0	**	0.086	20.6 =	24.8	0.407				
Bristy Cove Lower	14.3 =	17.5	**	0.151	12.9 =	16.8	0.079				
Bristy Cove Upper	23.5 =	20.1	**	0.460	24.1 =	16.9	0.086				

8 “negative” results,  $p < 0.05$  assuming positive vs. negative results were equally likely; two-tailed sign test).

These results contrast with expectations from a despotic distribution. Predicted differences in mean trout fork length for the log–log isodars were correct for only two of the four enclosures (Table 3).

## DISCUSSION

All of our best-fit isodars were curved regressions, suggesting that brook trout compete via interference as opposed to exploitation of resources. The isodars did not clearly differentiate between curved (preemptive) and log–log (despotic interference) regressions but support was much stronger for the curved preemptive models. Body-size distributions between habitat pairs bolster the preemptive isodar interpretation, as does a detailed behavioral study of brook trout habitat selection (Knight, 2000) in which Newfoundland brook trout selected some sites preferentially over others, sites were occupied in the order of their preference, and large fish occupied higher-preference sites than did smaller fish. The fact that our isodar analysis documents a form of interference competition in brook trout probably is little surprise to those who study salmonid behavior. Prior residence (Jenkins, 1969; Bohlin, 1977; Glova and Field-Dodgson, 1995) and dominance-based competition (Newman, 1956; Jenkins, 1969; Bachman, 1984; Heggenes, 1988) are both recognized as primary determinants of habitat selection in salmonids. But our approach is unique. The isodars allowed us to predict competitive interactions between individuals based only on population census data. Our isodar analysis of habitat selection in brook trout thus reinforces the perspective that density-dependent habitat selection is a key process linking individual and population levels of ecological organization (Rosenzweig and Abramsky, 1985; Rosenzweig, 1991; Morris, 1997).

Was our experimental protocol suitable to detect the behavioral ecology of individuals? Brook trout were captured by electrofishing, introduced into a novel environment, given three days to select preferred locations, and were then recaptured during daylight hours. Physical conditions such as water flow and temperature varied among runs through the season. Five lines of evidence suggest that our protocol was indeed suitable.

1. Bult et al. (1999) varied the acclimation period of electrofished Atlantic salmon parr in an experimental stream from three to 13 days. There was no detectable effect of acclimation period on the distribution of parr among pool, riffle, and run sections of three enclosures (Bult et al., 1999).
2. All individuals were used once only and all were treated the same.
3. Although salmonids feed heavily in the early morning and late evening (e.g., Hoar, 1942; Kalleberg, 1958), they maintain feeding positions throughout daylight hours with little variation in their activity patterns (e.g., Bachman, 1984).
4. Replicate experiments were conducted in random order. All used the same protocol. Any patterns in population distribution that emerged must have been caused primarily by the interactions among brook trout at different population densities.

5. The isodar regressions were all highly significant with minimal residual variation despite the short duration of the experiments and varying physical conditions among runs. The variation among runs should, if anything, have reduced our chances of finding consistent and significant patterns in habitat selection.

We thus interpret the consistent pattern of curved models as preemptive interference, as opposed to multiplicative interference or exploitation competition, in this species. The predicted variation in body size between habitats, and the agreement between observed and predicted differences for mean body size in three of four enclosures, confirm that brook trout were distributed according to a dominance-based occupation of the most profitable sites available. This interpretation also agrees with observations of brook trout habitat selection in an experimental stream tank (Knight, 2000).

Our study documents a correspondence among theory, spatial patterns in abundance, inferred habitat quality, and the size distribution of brook trout. Our experimental manipulations demonstrate that brook trout distributions are mediated by interference competition, a result consistent with numerous behavioral studies on this species. Our study thus supports theories of habitat selection as well as our ability to infer mechanisms of habitat selection from the patterns they create (isodars). There is a reciprocal linkage between the optimal behavior of individuals and their resulting distribution across habitats.

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