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The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied

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Cover is often thought to be an important habitat characteristic for juvenile stream salmonids. In addition to providing protection from predators, cover may be associated with reduced food availability. Thus, an individual's use of cover is likely to reflect a trade-off between the conflicting demands of growth and survival. We measured the influence of cover on foraging-site selection in groups of eight juvenile coho salmon (*Oncorhynchus kisutch*) by examining their distribution across two stream channel patches, one providing access to cover but little food (the "poor" patch), the other providing more food but no cover (the "good" patch). Because fish distributions in the absence of cover conformed to an ideal free distribution (IFD) for unequal competitors (i.e., the distribution of competitive abilities matched the distribution of food), we used IFD theory to quantify the energetic equivalence of cover to the fish. In the presence of cover and a model avian predator, use of the poor patch increased relative to the predictions of the IFD model. Using this observed deviation from an IFD, we calculated how much extra food must be added to the good patch to return the distribution of fish to the previously observed IFD of unequal competitors. As predicted, adding this amount of food caused the fish to return to their previous distribution, demonstrating that IFD theory can be used to relate energy intake and risk of predation in a common currency. *Key words:* coho salmon, foraging, habitat selection, ideal free distribution theory, *Oncorhynchus kisutch*, predation risk, trade-offs, unequal competitors. *[Behav Ecol 8: 437–447 (1997)]*

Foraging theory predicts that individuals attempting to maximize their net rate of energy intake should forage preferentially in areas of high prey density (Stephens and Krebs, 1986). However, when such sites are also associated with high levels of intraspecific competition and/or predation risk, the net fitness value of those sites may decrease relative to areas of lower prey density. Thus, during foraging-site selection, animals may be faced with a trade-off between energy intake and survival (for a review of foraging–predation risk trade-offs, see Lima and Dill, 1990). There are several ways animals can resolve such trade-offs, including the selection of foraging sites adjacent to a refuge or cover (e.g., Brown, 1988; Hogstad, 1988; Newman and Caraco, 1987).

Cover is often speculated to be an important habitat characteristic for stream-dwelling salmonid fishes. Both in-stream structure (e.g., rocks, vegetation) and overhead cover (e.g., undercut banks, streamside vegetation, fallen logs, deep water) are thought to provide protection from predators (Shirvell, 1990; Wilzbach, 1985), as well as reduce energetic expenditure by sheltering individuals from areas of high current velocity (Fausch, 1993; Huntingford et al., 1988). Hence, the preservation of natural cover and the addition of artificial cover are important goals of salmonid enhancement programs. Despite the widely held belief that juvenile salmonids prefer habitats with cover, the results of experiments investigating the effects of cover on fish distributions and abundance are equivocal (e.g., Dolloff, 1986; Fausch, 1993; McMahon and Hartman, 1989; Ruggles, 1966; Taylor, 1988). In some cases cover is preferred (e.g., Taylor, 1988), while in other cases fish are indifferent to its presence (e.g., Bugert and Bjornn, 1991) or avoid it entirely (e.g., Ruggles, 1966). We do not find this surprising given that, in addition to reducing predation risk, cover may also be associated with areas of reduced food availability. Furthermore, in streams where juvenile salmonids co-occur with piscivorous fishes, predation risk may actually be greatest under cover. Thus, rather than expecting the value of cover to be absolute, we view an individual's use of cover as a compromise between the conflicting demands of growth and survival—a compromise that may be extremely context specific.

Juvenile coho salmon (*Oncorhynchus kisutch*) typically maintain foraging positions from which they dart forward to intercept in-stream drift (Chapman, 1962; Hartman, 1965; Puckett and Dill, 1985). The best feeding sites (i.e., those with the greatest amount of drift per unit time) are likely shallow areas of swift current (Fausch, 1984; Ruggles, 1966), often with little in-stream structure or overhead cover. Thus, to gain access to cover, individuals may have to move into areas of slower current and accept a reduction in foraging gains. However, to predict the circumstances under which cover will be used by fish and, consequently, when the addition of natural or artificial cover is likely to reward conservation efforts, it is necessary to quantify the influence of cover on the trade-off between growth and survival, two components of fitness that are usually measured in different currencies.

Abrahams and Dill (1989) used ideal free distribution (IFD) theory (Fretwell, 1972; Fretwell and Lucas, 1970) as a tool to quantify the energetic equivalence of predation risk to guppies (*Poecilia reticulata*). IFD theory predicts that when animals have perfect information about the distributions of competitors and resources ("ideal"), and can move to the habitat where their fitness gains will be highest ("free"), they should distribute themselves such that the proportion of individuals in each habitat matches the proportion of resources available there (i.e., input matching; Parker, 1974). In addition to being "ideal" and "free," the model also assumes that individuals have equal competitive ability. Thus, at equilibrium, all individuals will receive the same payoff and no individual can in-

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crease its payoff by moving to another habitat. After demonstrating that the distribution of guppies between two feeders conformed to an IFD in the absence of predation risk, Abrahams and Dill (1989) added a fish predator to one of the patches and used the observed deviation from an IFD to quantify the energetic equivalence of predation risk. We use a modified version of this 'titration' technique to determine the energetic equivalence of cover to juvenile coho salmon (for further discussion of "behavioral titrations," see Kotler and Blaustein, 1995).

Because small differences in body size influence the rank of coho salmon in a dominance hierarchy (Chapman, 1962) and thus their ability to compete for food, it is unlikely that spatial distributions of coho will conform to the predictions of the original IFD model. In fact, Grand (1997) has recently shown that in the absence of cover and predation risk, distributions of foraging coho salmon are best described by a second-generation IFD model that incorporates competitive inequalities. This IFD model for unequal competitors (Parker and Sutherland, 1986; Sutherland and Parker, 1985) assumes that each individual's payoff is related to its competitive ability or "competitive weight" (i.e., the proportion of a resource it obtains when competing with all other members of a group in a single habitat). When the relative competitive weights of individuals remain constant across habitats, the model predicts that animals should distribute themselves such that the proportion of competitive weights in each habitat matches the proportion of resources available there (i.e., input matching of competitive weights), and juvenile coho do just that (Grand, 1997).

We conducted two experiments to quantify the energetic equivalence of cover to juvenile coho salmon. In the first experiment, groups of fish were allowed to choose between two patches, one providing access to cover but little food, the other providing more food but no cover. We used the observed deviation from an unequal competitors IFD to predict how much additional food must be added to the uncovered patch to return the distribution to that observed in the absence of cover. In the second experiment, we added the calculated amount of food to the uncovered patch and compared the resulting distribution of competitive weights to the previous distribution of food. If our calculation of the energetic equivalence of cover was correct, we expected the distribution of competitive weights to return to that observed in the absence of both cover and additional food, demonstrating that growth and survival can be measured in a common currency.

METHODS

Experimental subjects

We captured 16 wild, young-of-the-year coho salmon by pole seine from the Salmon River, Langley, British Columbia, Canada weekly between 3 July and 28 August 1995. Fish were returned to the laboratory and placed in a 170-l flow-through aquarium where they were maintained at 12°–15°C on a 14:10 h light:dark schedule.

Within 36 h of capture, we anesthetized fish in a dilute solution of 2-phenoxy-ethanol, determined their mass (nearest 0.01 g) and fork length (nearest millimeter), and marked them individually by attaching pre-made, colored tags through the musculature posterior to the dorsal fin (Chapman and Bevan, 1990). Each week, two groups of eight fish were formed by selecting individuals ranging in mass from 1.16 to 1.68 g ($\bar{x}$ = 1.42 g, SD = 0.125, n = 96) and in length from 49 to 56 mm ($\bar{x}$ = 51.8 mm, SD = 1.54, n = 96), for a total of 12 groups. We placed groups of fish in buckets of cold, aerated water for 30 min to recover from the stress of handling and tagging and then returned each group to a separate flow-through aquarium to await the beginning of the foraging experiment. Fish were fed live, adult brine shrimp (*Artemia* spp.) ad libitum while in the flow-through aquaria.

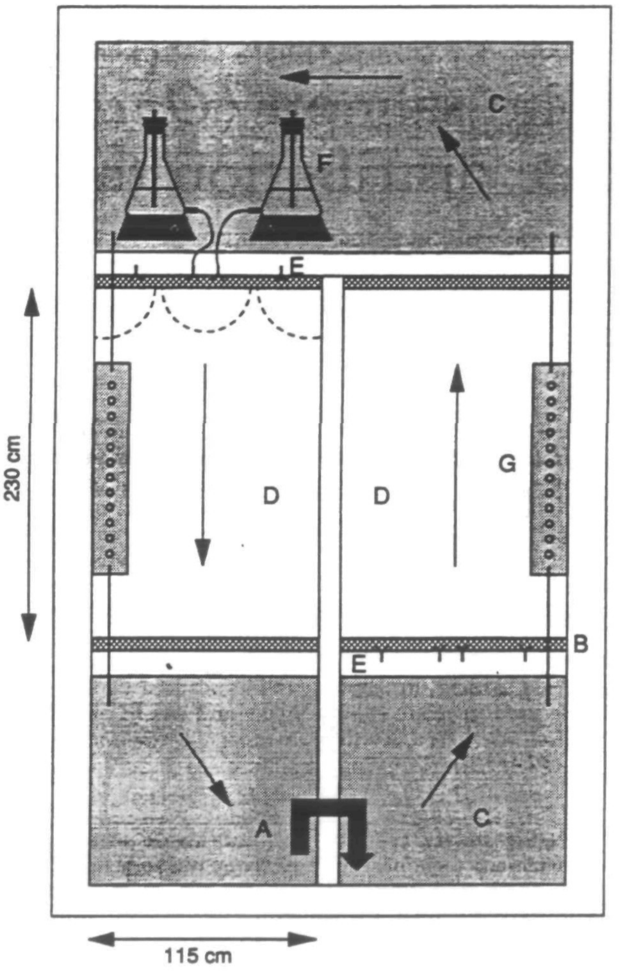

Figure 1
Schematic top view of the experimental stream channel. Water was pumped over a concrete barrier (A) and traveled downstream through a series of four mesh barriers (B) which separated the pools (C) from the glides (D). Four Y-shaped feeding tubes (E) were attached to the mesh barriers at the upstream end of each glide. Prey were dispensed from Erlenmeyer flasks (F) mounted on magnetic stir plates. A single cover structure (G) could be placed along either wall of each glide. Arrows indicate the direction of water flow and broken lines the single and paired patches of the one- and two-patch trials, respectively.

Four days after tagging, we transferred each group to one of two glide sections of the artificial stream channel in which experiments were conducted (see below), and left the fish to acclimatize for an additional 2 days. No food was provided to the fish during this acclimation period, ensuring that all individuals were hungry and foraged actively when the experiment began.

Apparatus and general methods

We conducted experiments in an artificial stream channel (Figure 1) in the woods of the Burnaby Mountain campus of Simon Fraser University. The concrete channel (described more completely elsewhere; Grand, 1997) consists of two shallow, rectangular glides separated from one another by a width of concrete and two deep pools. An additional concrete wall divides one of the pools in two, providing a barrier over which water is pumped to create continuous, circular flow (for a description of similar methodology and apparatus, see Tyler and Gilliam, 1995). Water temperature increased gradually throughout the summer from 15°C in early July to 17°C in late August.

Four plastic mesh screens (mesh opening = 5 mm) separated the glides from the pools and from one another, thus restricting the movement of each group of fish to a single glide (see Figure 1). Pools were covered with plywood boards to reduce algal growth and prevent extraneous food (i.e., winged insects) from entering the system. A plastic tent, with walls of fine mesh, was erected over the entire channel to further prevent the entry of extraneous food and leaf litter. Opaque plastic blinds were attached to the mesh to prevent disturbance of the fish during foraging trials. We made observations of fish behavior through small slits cut in these blinds.

Throughout the experiment, fish were maintained exclusively on the live, adult brine shrimp provided during the foraging trials. Prey were sieved, and only those unable to pass through a 1350-μm mesh screen were used. Prey were counted and placed in two 4-l Erlenmeyer flasks filled with fresh water collected from the stream channel. Prey and water drained from the flasks through 70 cm lengths of tygon tubing (5 mm diam) fastened to glass spouts attached to the bottom of the flasks (after Abrahams, 1989). Each feeding tube emptied into one of two plastic Y-shaped tubes attached to the back side of the mesh barrier at the upstream end of each glide (see Figure 1). The positions of the four Y-tubes on the mesh barriers determined the spatial structure of the feeding patch(es): food could be dispensed from either a single central patch (Y-tubes placed in the center of the barrier, 8 cm apart, as illustrated in Figure 1) or from two spatially distinct lateral patches (Y-tubes placed 30 cm from the edges of the barrier, 55 cm apart). A line down the center of each glide delineated the patches for the observer.

Prey in the flasks were kept in suspension by means of a stir bar constantly rotated by a magnetic stir plate, ensuring that prey left the flask at a uniform rate throughout the trial (as determined from preliminary experiments). Flasks were sealed with a rubber stopper penetrated by a glass tube extending to the bottom of the flask, thereby maintaining a constant drain rate of water and prey. A length of tygon tubing was attached to the top of the glass tube and sealed at the other end with a hypodermic needle fastened to a syringe. Thus, the flasks could be operated simultaneously and remotely by simply removing the plungers from the syringes and allowing air to enter them. Water and prey were dispensed slowly over the course of the 24-min trial. Trials were halted by reinserting the plungers into the syringes when 1000 ml of water remained in the flasks. We counted the number of prey remaining in each flask and subtracted this number from the number of prey originally placed there. Thus, for all trials, the actual number of prey available to the fish in each patch was known.

We conducted trials once per day, between 1130 and 1400 h, on 5 consecutive days. Experiments in the two glides were run sequentially. The first three trials were used to quantify relative competitive abilities and to test the input matching prediction of the unequal competitors IFD model (see Grand, 1997, for further discussion of these data). During the fourth ("cover") trial, cover was added to the poor food patch, and its effect on the distribution of competitive weights was quantified. From these data we calculated the energetic equivalence of cover (i.e., the amount of food that we predicted should be added to the good food patch to cause the fish to return to the distribution observed in the absence of cover). This quantity of food was then added during the fifth ("titration") trial and the resultant distribution of competitive weights observed.

Experiment 1: effect of cover on foraging-site selection

On the first 2 experimental days, 50 brine shrimp were dispensed from each of the two central feeding positions. The wide area over which prey were broadcast effectively created a single, nondefensible patch. The number of prey captured by each fish was recorded on a portable audiocassette recorder and used to determine relative competitive ability. Although the measures of competitive ability on the 2 days were highly correlated ($r = .82$, $p < .001$, $n = 96$), we assumed that allowing individuals to increase their familiarity with the foraging situation would lead to a better estimate of true competitive ability. Thus, we quantified each individual's competitive weight as the proportion of all available prey it captured during the second of these one-patch trials. These a priori measures of competitive weight were assumed to remain constant throughout the experiment (see Grand, 1997).

On the third experimental day (the IFD trial), we dispensed prey from the two lateral feeding positions. Patches differed in the number of prey they provided to the fish. We placed 75 brine shrimp in one flask (the good patch) and 35 in the other (the poor patch). The location of the good patch (i.e., left or right half of the glide) was determined randomly for each group. Because trials were always terminated before the flasks had drained completely, a small proportion of the total prey was usually unavailable to the fish. Initial numbers of prey were chosen (based on preliminary experiments) such that the patch profitability ratio experienced by the fish was approximately 2:1.

After the completion of the foraging trial, a single cover structure was placed along the length of the patch that had recently provided the most food. This patch would be the poor food patch during the following day's trial. Cover consisted of a 132-cm long half-round of PVC pipe (20 cm diam), suspended 1 cm above the surface of the water (see Figure 1). To minimize differences between light levels below the structure and those elsewhere in the channel, we drilled 12 holes (1 cm diam) at regular intervals along the length of the pipe.

On the morning of the fourth day (the cover trial), during the 3 h before the foraging trial, a cardboard replica of a kingfisher (*Alcedo atthis*; wing span = 23 cm) was plunged repeatedly into the center of each glide at random intervals for a total of 12 predator presentations per group. The predator was suspended on monofilament thread guided through a series of pulleys attached to the roof and walls of the enclosure, allowing it to be operated remotely, beyond the view of the fish. After the final presentation of the predator, fish were left undisturbed for 30 min, after which a two-patch foraging trial was conducted. As before, the good patch provided roughly twice as many prey items as the poor patch, which now possessed the additional benefit of cover. (Note that the terms "good" and "poor" reflect the relative amounts of food available in the patches and are used interchangeably with the terms "uncovered" and "covered," respectively). Immediately following the trial, the cover structure was moved to the opposite wall of the glide, thus reversing the locations of the good and poor patches prior to the fifth trial (part of experiment 2).

During each of the IFD and cover trials, we recorded the identity of the individual eating each prey item and the location of the patch from which the item originated on a portable audiocassette recorder. We determined the number and identity of fish in each patch and under cover was determined by scan sampling (Martin and Bateson, 1986) at 1-min intervals throughout the trial. Differences in the distributions of competitive weights during the IFD and cover trials were used to indicate the presence of a foraging–predation risk tradeoff.

To determine whether the fish responded as if cover were beneficial even in the absence of the model predator, we exposed a subset of the fish ($n = 5$ groups) to an additional treatment. On the day immediately preceding the cover (plus predator) trial, we conducted an additional two-patch foraging trial. The cover structure was placed in the poor patch, but fish were not exposed to the predator before the trial. We recorded the number and identify of fish in each patch and under cover at 1-min intervals throughout the trial and compared the distribution of competitive weights to the distribution of food to determine whether cover provided some perceived benefit to the fish, even in the absence of the artificial predator. Although there was a tendency toward an increase in the proportion of competitive weights observed in the poor patch in the presence of cover (±SE; 0.436±0.044 versus 0.340±0.021), this difference was not significant ($t = 2.070$, df $= 4$, $p = .107$; power $= 0.75$). In addition, groups of fish responded similarly during the remaining trials regardless of whether they had received this additional treatment. Thus, we pooled the data from all 12 groups for the remainder of the analyses.

Experiment 2: energetic equivalence of cover

We used the IFD for unequal competitors (Parker and Sutherland, 1986) to determine the energetic equivalence of cover to the fish. IFD theory predicts that when food is the only variable contributing to fitness, individuals should be distributed such that the sum of their competitive weights in each patch matches the proportion of food available there. At equilibrium, the mean payoff per unit of competitive weight will be equal in the two patches. However, if one patch has the additional benefit of cover and the other does not, a smaller proportion of competitive weights is expected to use the uncovered patch than predicted by the distribution of food alone. Consequently, those individuals continuing to use the uncovered patch will receive higher foraging payoffs per unit of competitive weight than those switching to the covered patch. If we assume that this new equilibrium distribution of competitive weights is also an IFD for unequal competitors, individuals using the covered and uncovered patches will receive identical fitness payoffs, although foraging payoffs obtained in the two patches will differ. Those individuals in the poor patch are compensated by having a lower risk of predation. Thus, we can calculate the energetic equivalence of cover per unit of competitive weight (E) as the difference in the per competitive weight foraging payoffs between the patches:

$$E = \frac{R_g}{C_g} - \frac{R_p}{C_p}, \tag{1}$$

where R_g and R_p represent the quantity of prey (items·trial^{-1}) provided by the good (uncovered) and poor (covered) patches, respectively, and C_g and C_p represent the observed sums of the competitive weights in those patches. Thus, E indicates how much food individuals are willing to give up (per unit of competitive weight) to gain access to cover.

To return the distribution of competitive weights to that observed previously (i.e., C_g and C_p, as predicted by the distribution of food alone), we must add sufficient food to the uncovered patch to offset the fitness benefit of cover provided by the alternate patch. When this quantity of extra food (X_g) is added to the good patch, the mean fitness payoff per unit of competitive weight should be the same in the two patches. Thus, the fitness benefits of food obtained in the good patch should be equal to the combined fitness benefits of food and cover obtained in the poor patch:

$$\frac{R_g + X_g}{C'_g} = \frac{R_p}{C'_p} + E. \tag{2}$$

Given knowledge of E and the initial distribution of resources between the patches (R_g and R_p), we can calculate how much extra food (X_g) must be added to the good patch to return the distribution of competitive weights to that observed in the absence of cover and elevated risk. In our experiment, this calculation is based on the IFD prediction that if one patch is twice as valuable to the fish as the other, there should be twice as many units of competitive weight there at equilibrium (i.e., $C'_g = 0.667$, $C'_p = 0.333$). Thus, by substituting the appropriate values for R_g, R_p, C'_g and C'_p into Equation 2, we can solve for X_g as a function of E. In our experiment,

$$X_g = 0.667E. \tag{3}$$

This calculation necessarily assumes that the presence of cover increases the fitness of all individuals by a fixed amount per unit of competitive weight and implies that individuals of high competitive ability will require absolutely greater foraging payoffs than individuals of low competitive ability to offset the benefit of cover. We return to this point later. We also assume that there is no dilution of predation risk (see Moody et al., 1996) or competition for access to cover and that the relationship between energy intake and fitness is linear (see Abrahams and Dill, 1989 for further discussion of the implications of this last assumption).

We calculated E and X_g for each group of fish based on their observed distribution of competitive weights and the actual distribution of prey during the cover trial. We then added the appropriate quantity of additional prey to the uncovered patch and conducted the fifth and final (titration) trial. As previously, predation risk was increased by repeatedly introducing the model predator to the channel before the foraging trial began. Once again, we recorded the identify of the individual capturing each prey item, the patch from which the item originated, and the locations of all individuals at 1-min intervals throughout the trial.

Control experiments

Carry-over effects

Because the locations of the good and poor patches were alternated between trials, we were concerned that any observed increase in the proportion of competitive weights using the poor patch during the cover trial might be due to carry-over effects rather than to an increase in the perceived value of the poor patch with the addition of cover. If, in the absence of information about the current availability of resources, fish were initially attracted to the patch that provided the most food during the previous trial, the proportion of the competitive weights observed in the poor patch should increase between trials regardless of whether cover has been added. To test this hypothesis, we performed an additional experiment on two new groups of fish, in the absence of cover and elevated predation risk. After quantifying relative competitive weights (as described above), we conducted a series of three two-patch foraging trials, reversing the locations of the good and poor patches each day. We compared the proportion of competitive weights using the poor patch across trials for each group of fish.

Predator habituation effects

Because fish were repeatedly exposed to the artificial predator, we were concerned that any observed increase in the proportion of competitive weights using the uncovered patch between the cover and titration trials might be a result of habituation. If, during their second exposure to the predator, individual fish perceived it to be less of a threat, we might expect them to increase their use of the uncovered patch, regardless of whether food availability had increased. To test this hypothesis, we performed a second control experiment on two additional groups of fish. After quantifying relative competitive weights (as described above), we conducted two two-patch foraging trials. Before each trial, fish were repeatedly exposed to the artificial predator (as described above). The locations of the good and poor patches (and hence, the location of cover) remained fixed between trials, as did the rates of prey delivery to the patches. We compared the proportion of competitive weights using the covered patch in the two trials for each group of fish.

Data analyses

To compare the observed distributions of competitive weights to one another and to the distributions of food, we determined the average sum of competitive weights in each patch from the scan sample data. To avoid biasing the outcome of the comparisons with preequilibrium values, only data from the second half of each trial (i.e., 13–24 min) were included. Because food was allocated stochastically to the patches, the actual number of prey arriving in a patch often differed slightly from the expected patch profitability (see Grand, 1997). Therefore, we used paired t tests to compare the mean sum of competitive weights in the poor patch to the actual proportion of food available there. To investigate the effect of competitive ability on foraging-site selection, we used repeated-measures analysis of variance (ANOVAR) to compare the proportion of time spent in the poor patch by individuals of different competitive weight rank across the three two-patch trials. Differences between trials in the proportion of time spent under cover by individuals differing in competitive-weight rank were analyzed similarly. Because all data were homoscedastic and normally distributed, transformations were not required. Unless stated otherwise, reported p values are two tailed.

RESULTS

General behavior of the fish

Before the introduction of food, individual fish maintained relatively stationary positions along the length of the glide and engaged in occasional aggressive interactions with their neighbors. Upon the beginning of a foraging trial, most fish moved to the upstream end of the glide and engaged in scramble competition for individual prey items at one of the two point sources. Initially, movement between patches occurred frequently (approximately one switch per fish per minute), but gradually decreased as the trial progressed. During the cover and titration trials, one or two fish would often remain under the cover structure for several minutes at a time, occasionally venturing upstream to compete for prey. In all trials, the majority of the prey were consumed within 20 cm of the mesh barrier and thus could not be captured by individuals positioned directly under the cover structure or by fish in the other patch. Occasionally, prey items were missed or ignored by the fish, but these items were quickly carried downstream and outside the foraging arena by the current.

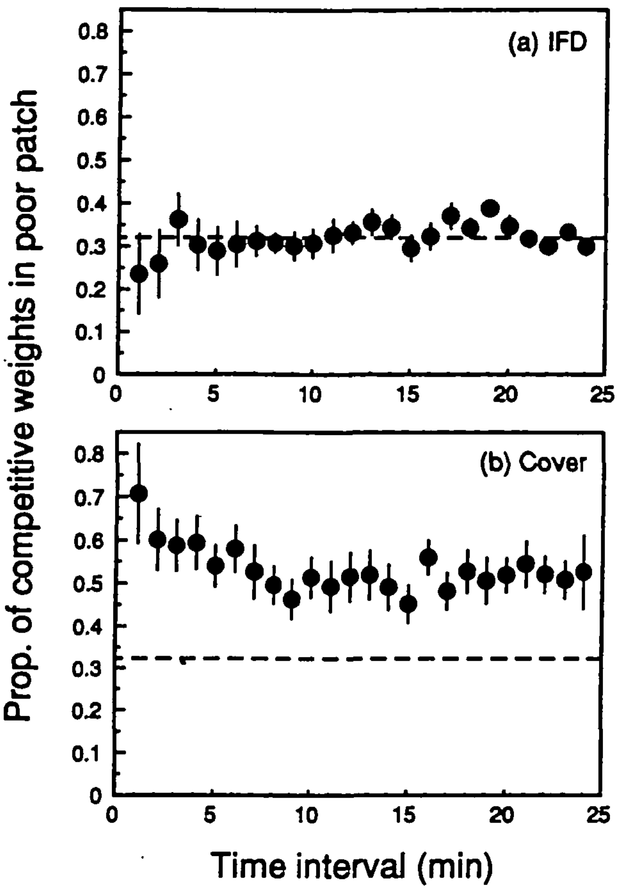

Figure 2
Mean (± SE) proportion of competitive weights in the poor (covered) patch during each min of the (a) ideal free distribution, and (b) cover trials. Dashed lines indicate the mean proportion of food available in the poor patch; n = 12 groups of fish.

Experiment 1: effect of cover on foraging-site selection

Distributions of competitive weights varied somewhat over the course of the IFD trial (Figure 2a). In most cases, fish were initially attracted to the patch that provided the most food, resulting in an under-representation of competitive weights in the poor patch relative to the predictions of the unequal competitors model. However, distributions of competitive weights rapidly approached the distribution of resources, such that during the second half of the trial (13–24 min), the observed proportion of competitive weights in the poor patch was not significantly different from the proportion of food available there (Figure 2a, Table 1; $t = 1.211$, df = 11, $p = .251$, power = 0.84; see also Grand, 1997). Thus, with this apparatus, the unequal competitors IFD model appears to be a good predictor of the distribution of juvenile coho salmon.

In response to the addition of cover, we observed a shift in the distribution of competitive weights (Figure 2b), such that a larger proportion of the competitive weights occurred in the poor patch when cover was present than when it was absent (Table 1; $t = 5.033$, df = 11, $p = .0002$; one-tailed test). The observed distribution of competitive weights was now significantly different from the distribution of food (Figure 2b, Table 1; $t = 5.001$, df = 11, p .001), as expected if fish consider the availability of both food and cover during foraging-site selection.

Table 1

Observed proportion of competitive weights in the poor (covered) patch and the proportion of food available there during min 13–24 of the ideal free distribution (IFD), cover, and titration trials, as well as calculated energetic equivalence of cover, *E*, for each group of fish (*n* = 12 groups).

	IFD		Cover		Titration		
	Competitive wt.	Food	Competitive wt.	Food	Competitive wt.	Food	*E*
	0.3825	0.3367	0.6813	0.2929	0.3831	0.1897	1.7888
	0.3012	0.3302	0.3213	0.3069	0.6090	0.2778	0.0660
	0.3342	0.3333	0.7277	0.3271	0.3419	0.1576	2.0217
	0.3012	0.3113	0.4214	0.3431	0.4396	0.2555	0.3211
	0.3731	0.3431	0.4881	0.3300	0.2952	0.2672	0.6328
	0.2632	0.3211	0.5383	0.3241	0.1206	0.2482	0.8619
	0.2816	0.3048	0.5559	0.3241	0.4241	0.2138	0.9389
	0.3155	0.3113	0.3596	0.3333	0.3324	0.2846	0.1142
	0.4178	0.2979	0.6596	0.3100	0.2593	0.1951	1.5570
	0.3947	0.3061	0.4400	0.3241	0.2460	0.2619	0.4704
	0.3486	0.3204	0.5352	0.3300	0.2484	0.2263	0.8249
	0.3452	0.3333	0.4322	0.3158	0.4670	0.2703	0.4743
Mean ± SE	0.338 ± 0.014	0.321 ± 0.004	0.513 ± 0.037	0.322 ± 0.004	0.347 ± 0.037	0.237 ± 0.012	0.839 ± 0.185
p	.251[a]		<.001		.519	.012	

[a] Significance of paired *t* tests comparing distributions of food and distributions of competitive weights.

Experiment 2: energetic equivalence of cover

The calculated energetic equivalence of cover varied markedly among groups of fish (see Table 1). On average, we added 40.6 (± 8.84, SE) prey items to the uncovered patch, resulting in a new mean resource input ratio of 3.34:1 (± 0.29, SE). The addition of extra food offset the distribution of competitive weights, such that a significantly smaller proportion of the competitive weights was observed in the poor patch during the titration trial than during the cover trial (Table 1; $t = 2.698$, df = 11, $p = .010$; one-tailed test). Furthermore, the distribution of competitive weights was significantly different from the current distribution of food (Table 1, Figure 3; $t = 2.99$, df = 11, $p = .012$), as expected if fish integrate the fitness benefits of food and cover during foraging-site selection. However, there was no significant difference between the proportion of competitive weights observed in the poor patch during the titration trial and the proportion of food provided by that patch during the preceding cover trial, before the addition of extra food (Table 1, Figure 3; $t = 0.667$, df = 11, $p = .519$, power = 0.94), as expected if we had correctly calculated the energetic equivalence of cover.

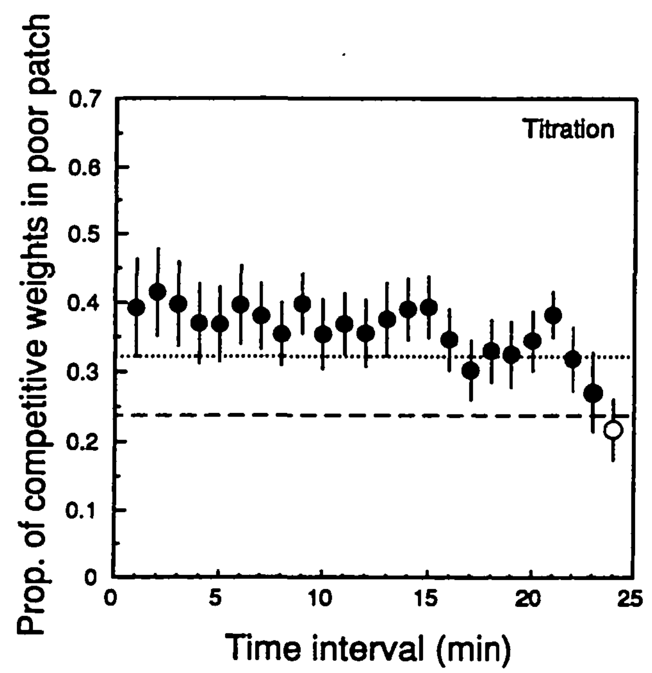

Figure 3
Mean (± SE) proportion of competitive weights in the poor (covered) patch during each min of the titration trial. Dashed and dotted lines indicate the mean proportion of food available in the covered patch during the current and previous day's trials, respectively. Shaded symbols for min 23 and 24 reflect the reduced number of groups represented by those means ($n = 8$ and $n = 4$, respectively); All others, $n = 12$ groups of fish.

Control experiments

Carry-over effects

Although fish had an initial tendency to forage in the patch that had previously provided more food, the proportion of competitive weights observed in the poor patch decreased rapidly over the first 8 min of the trial and thereafter did not appear to differ from the proportion of food available. Furthermore, the equilibrium proportions of competitive weights observed in the poor patch were similar for each of the three trials (Table 2). Thus, given that we have used only data from the second half of each trial (i.e., 13–24 min) to test our main hypotheses, we are confident that the observed increase in the proportion of competitive weights using the poor patch was a result of the addition of cover to that patch rather than to carry-over effects.

Predator habituation effects

The equilibrium proportion of competitive weights observed in the covered patch did not differ between trials (Table 2; $t = -1.00$, df = 1, $p = .500$, power ~ 0.97). This result suggests that the observed change in the distribution of competitive weights between the cover and titration trials occurred in response to the addition of prey to the uncovered patch rather than to a decrease in the value of cover with repeated exposure to the artificial predator.

Table 2

Mean proportion of competitive weights observed in the poor patch during the carry-over and predator habituation control experiments

	Trial 1		Trial 2		Trial 3	
Experiment	Mean	SE	Mean	SE	Mean	SE
Carry-over						
Group 1	0.366	0.016	0.387	0.016	0.311	0.016
Group 2	0.353	0.019	0.389	0.013	0.359	0.023
Habituation						
Group 1	0.414	0.018	0.413	0.010	—	—
Group 2	0.499	0.020	0.456	0.006	—	—

Two separate groups of fish were used for each experiment.

Individual differences in risk-taking

In contrast to the single equilibrium predicted by the original IFD model for equal competitors (Fretwell and Lucas, 1970), the IFD for unequal competitors predicts a number of potential equilibria, each of which is characterized by the distribution of competitive weights matching the distribution of resources (Parker and Sutherland, 1986). However, each of these equilibria will be composed of a unique combination of individuals and thus a different distribution of total competitor numbers between the patches (see Milinski and Parker, 1991:Figure 5.4). Therefore, by comparing the change in the distributions of competitor numbers relative to the distributions of competitive weights in the presence and absence of cover, it may be possible to determine whether individuals of different competitive ability also differ in their willingness to expose themselves to predation risk.

Although the distributions of competitive weights in the IFD and titration trials did not differ significantly from one another (Table 1; $t = 0.213$, df = 11, $p = .835$, power = 0.98), there was a tendency for a larger proportion of the fish to use the poor patch during the IFD trial than during the titration trial (Figure 4a versus 4c; $t = 1.898$, df = 11, $p = .084$). Although this difference is not significant, it suggests that the composition of the groups using the poor patch may have differed between trials. Furthermore, although distributions of competitive weights and competitor numbers did not differ from one another during the cover or titration trials (Figure 4b,c; $t = 1.078$, df = 11, $p = .304$, power = 0.86 and $t = 0.238$, df = 11, $p = .816$, power = .98, respectively), there was a significant difference between their distributions during the IFD trial (Figure 4a; $t = 2.838$, df = 11, $p = .016$). These results suggest that in the absence of cover and elevated risk, the group of individuals choosing to forage in the poor patch consisted of many competitors of low average competitive ability. However, when cover was available and the quantity of food provided by the good patch increased, fewer individuals, of presumably higher competitive ability, were observed to forage in the poor patch.

To directly determine whether individuals of different competitive ability differed in their use of the patches, we used the scan sample data to calculate the equilibrium proportion of time spent by each individual in the poor patch during each of the three two-patch trials. Although there was a tendency for individuals of high competitive ability to forage almost exclusively in the good patch during the IFD trial (Figure 5a), this effect was not significant ($F_{12,83} = 1.540$, $p = .127$, ANOVÅ), and there was no overall effect of competitive-weight rank on the proportion of time spent in the poor patch (Figure 5a–c; $F_{12,83} = 1.179$, $p = .312$, ANOVAR).

The amount of time spent directly under cover was, however, influenced by competitive ability. During both the cover and titration trials, poor competitors tended to spend a larger proportion of their total time in the poor patch directly under cover than did good competitors (Figure 6a,b; $F_{12,83} = 3.361$, $p = .001$; ANOVAR). The significance of this relationship, however, appears to be generated primarily by the behavior of the poorest competitors. When individuals of competitive-weight rank 8 are removed from the analysis, the relationship between competitive ability and time spent under cover is no longer significant ($F_{11,76} = 1.265$, $p = .261$; ANOVAR). Thus, although good competitors may increase their use of the poor patch with the addition of cover, they are less likely than the

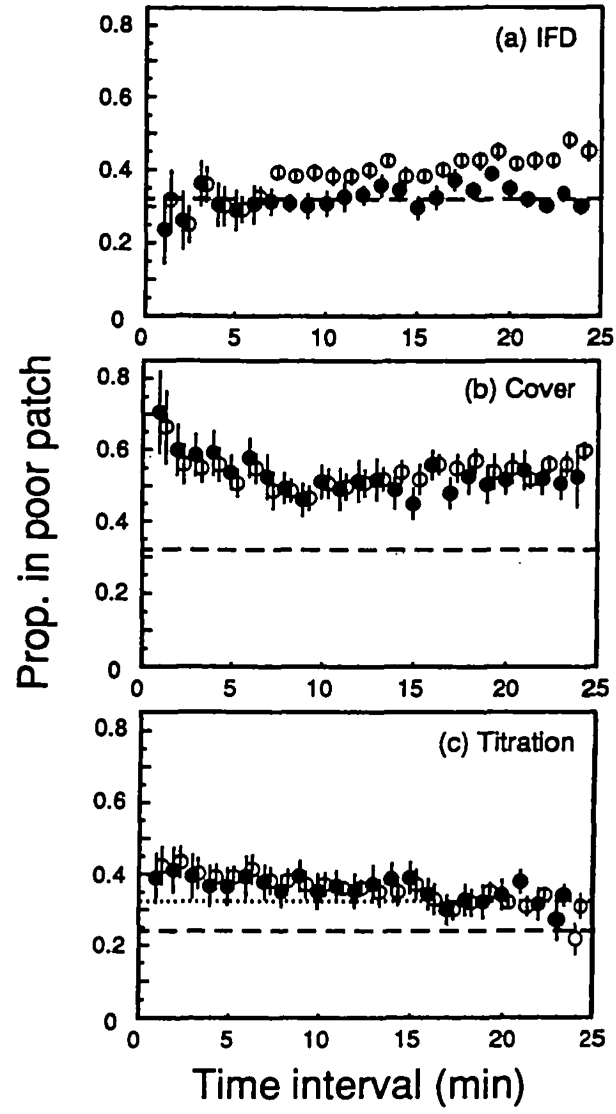

Figure 4
Mean (± SE) proportion of fish (open circles) and competitive weights (closed circles) in the poor (covered) patch during each min of the (a) ideal free distribution, (b) cover, and (c) titration trials. Dashed and dotted lines as in Figure 3. Competitive weight data are the same as those shown in Figures 2 and 3. For clarification, open circles have been offset slightly to the right. Shaded symbols for min 24 and 23 in (c) reflect the reduced number of groups represented by those means ($n = 8$ and $n = 4$, respectively); all others, $n = 12$ groups of fish.

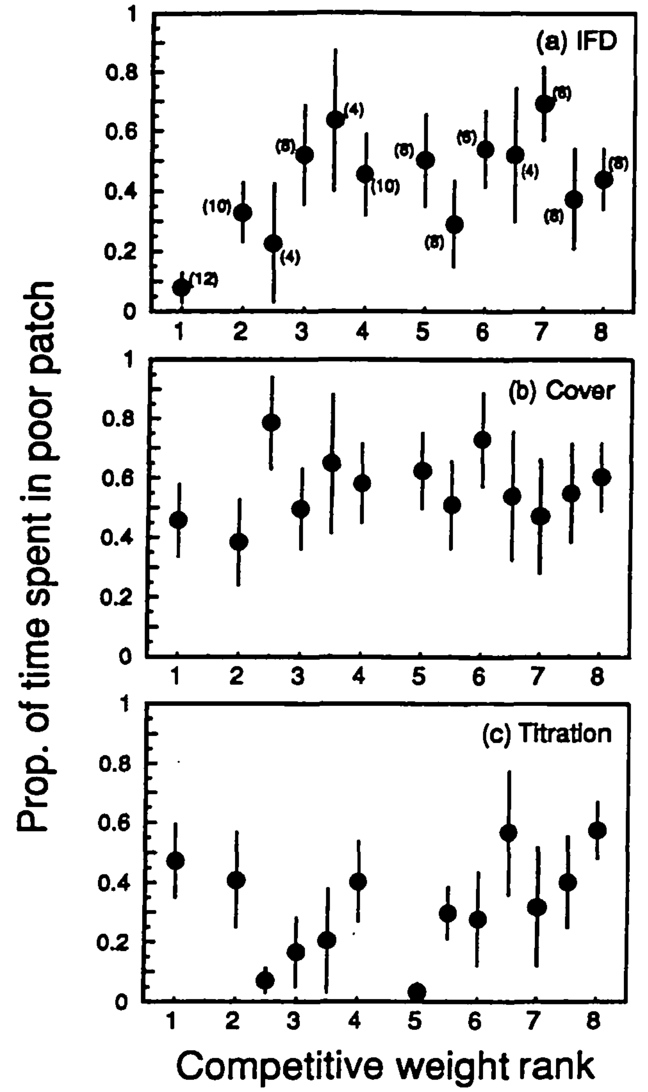

Figure 5
Mean (± SE) proportion of time spent in the poor (covered) patch by fish differing in competitive-weight rank during the (a) ideal free distribution, (b) cover, and (c) titration trials. The sample sizes used to calculate means (noted in parentheses) varied between ranks because ties for rank occurred in several groups. Rank 1 denotes the individual of highest competitive weight within a group.

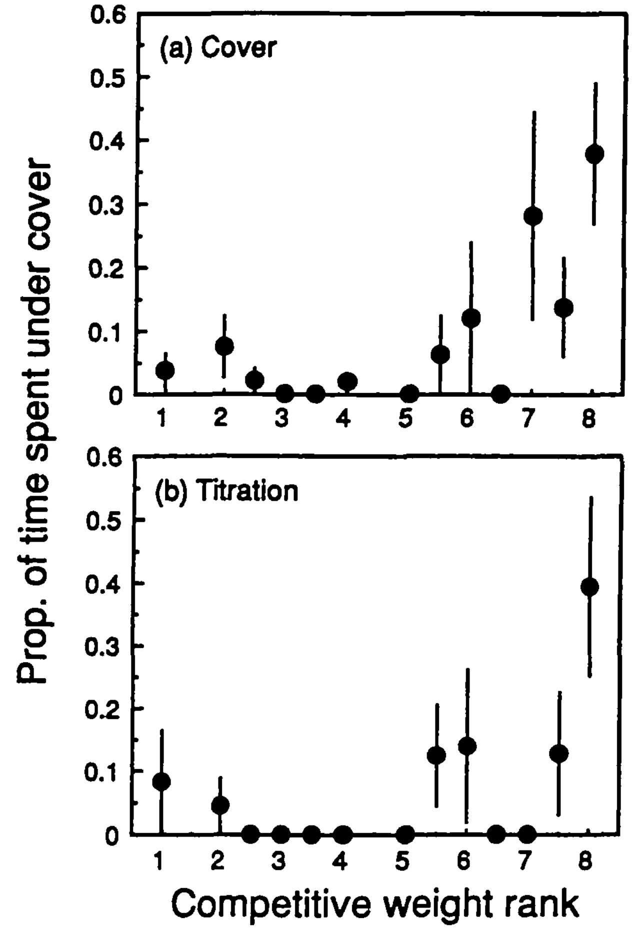

Figure 6
Mean (± SE) proportion of time in the poor patch spent under cover by fish differing in competitive-weight rank during the (a) cover and (b) titration trials. Sample sizes and ranks as in Figure 5.

poorest competitors to be found directly under the cover structure.

DISCUSSION

Given a choice between two patches differing in food availability, groups of juvenile coho salmon tend to distribute themselves such that the sum of their competitive weights in each patch matches the availability of resources (see also Grand, 1997). When cover is added to the poor food patch and predation risk elevated, the proportion of competitive weights in the poor patch increases, as expected if both energetic gains and predation risk influence foraging-site selection. We quantified the trade-off between energy intake and predation risk by measuring the energetic equivalence of cover. When this extra food was subsequently added to the uncovered patch, the distribution of competitive weights returned to that observed in the absence of cover and elevated risk. Thus, our results demonstrate that the fitness benefits of cover can be measured in units of energy and can be offset by sufficient food.

Although many studies have investigated the effects of cover on the distribution and behavior of salmonid fishes (e.g., Bugert and Bjornn, 1991; Bugert et al., 1991; Dolloff, 1986; Fausch, 1993; Huntingford et al., 1988; McMahon and Hartman, 1989; Ruggles, 1966; Shirvell, 1990), few have simultaneously manipulated food availability, cover, and predation risk (but see Wilzbach, 1985), thereby viewing the use of cover by individual fish as a trade-off between the conflicting demands of growth and survival. Indeed, our experiment appears to be the first to demonstrate that juvenile coho salmon will accept a reduction in energetic intake to be near cover when the risk of predation is high (Figure 2b). Furthermore, data from the five groups of fish that received the extra cover treatment indicate that fish may prefer to be near cover even in the absence of elevated risk, which suggests that the trade-off is a continuous one.

Using IFD theory for unequal competitors (Parker and Sutherland, 1986; Sutherland and Parker, 1985), it is possible to describe foraging–predation risk trade-offs in a common currency and thus quantify the energetic equivalence of cover to the fish. When we calculated how much food was required to offset the fitness benefits of cover, we made three necessary assumptions: (1) there is no dilution of predation risk, (2) the relationship between energetic intake and fitness is linear, and (3) cover increases the fitness of all individuals by a fixed amount per unit of competitive weight. If an individual's risk of predation decreases as the number of conspecifics foraging in a patch increases, we would not expect distributions of competitive weights to match the distribution of food (see Moody et al., 1996, for a discussion of the effects of risk dilution on the IFD). Rather, fish would be expected to give up foraging opportunities to join larger groups and, depending on the distribution of competitor numbers, there would be either too few or too many competitive weights in the covered patch relative to the predictions of the unequal competitors IFD model. Furthermore, adding the calculated energetic equivalence of cover to the uncovered patch would not result in the distribution of competitive weights returning to its previous distribution. Similarly, if the relationship between energetic gains and fitness was not linear, at least over the range of resource input rates provided, we would have added either too much or too little food to offset the benefit of cover, and we would not expect the distribution of competitive weights to return to that observed previously (see Abrahams and Dill, 1989).

The third assumption implies that risk of predation is proportional to competitive weight, which may be true if good competitors are larger or more conspicuously colored than poor competitors or if they spend a larger proportion of their time interacting with conspecifics, thereby reducing their level of vigilance. In juvenile coho salmon, competitive ability is positively correlated with both dominance rank and body size (Grand, 1997) and thus may be similarly correlated with risk of predation. Because the addition of the calculated energetic equivalence of cover resulted in distributions of competitive weights that did not differ significantly from those observed in the absence of cover and elevated risk (Figure 3), all three assumptions appear to be justified. Furthermore, we appear to have approximated the true energetic equivalence of cover to the fish.

State-dependent modeling ("dynamic programming"; Houston et al., 1988; Mangel and Clark, 1988) provides another method by which foraging–predation risk trade-offs can be expressed in a common currency. Both growth and the probability of mortality are expressed in terms of their contribution to fitness or reproductive value. Although this approach has been quite successful in generating qualitative predictions about risk-taking behavior (see Clark, 1994), it cannot specify the quantitative relationship between growth and survival unless habitat-specific growth and mortality rates are known. Using a precursor to the state-dependent approach (i.e., optimal control theory), Gilliam and Fraser (1987) developed an analytic model that successfully predicted how much additional food was required to induce juvenile creek chub (*Semotilus atromaculatus*) to forage in a riskier habitat. Their model predicts that when an individual has several habitats available, including an absolute refuge, it should forage preferentially in the habitat with the lowest ratio of mortality rate to feeding rate. However, as pointed out by the authors, this prediction is not general and is only expected to occur when several important assumptions about the life history of the animal under study are met (see Gilliam and Fraser, 1987).

Although the distributions of competitive weights were similar both before the addition of risk and cover and after extra food had been added to the uncovered patch, distributions of competitor numbers differed between trials (Figure 4). Thus, these two IFDs of unequal competitors appear to be composed of different combinations of fish using the good and poor patches. In the absence of cover and elevated risk, the proportion of fish using the poor patch exceeded the proportion of competitive weights observed there. After the addition of extra food to the good patch, distributions of competitor numbers and competitive weights did not differ significantly from one another. These results suggest that in the presence of cover and predation risk and the addition of extra food to the good patch, the group of individuals foraging in the poor patch decreased in number but increased in average competitive weight, as might be expected if individuals of different competitive ability trade off growth and survival differently. Specifically, these results suggest that individuals of low competitive ability are more willing to incur risk to gain access to the richer food patch.

To investigate individual differences in patch use more directly, we compared the proportion of time fish of different competitive-weight rank spent in the poor patch and under cover during each of the trials. Although the best competitors appeared to spend the majority of their time foraging in the good patch in the absence of cover and elevated risk, when all trials were considered simultaneously, there was no evidence for a relationship between competitive-weight rank and patch use (Figure 5). All individuals were observed to increase their use of the poor patch with the addition of cover and elevated risk. Cover, however, was not used in the same way by individuals of different competitive ability (Figure 6). Poor competitors were more likely than good competitors to be found directly under cover, during both the cover and titration trials. In contrast to the results obtained by the comparison of competitor number and competitive-weight distributions, these results suggest that good competitors, rather than poor competitors, are more likely to risk exposure to a predator to gain access to the richer food patch.

Given the apparent contradictory nature of our results, it remains unclear how competitive ability and willingness to take risk are related in juvenile coho salmon. Both positive and negative relationships between competitive ability and risk taking are equally plausible. If good competitors are at greater risk of predation than poor competitors, either because they represent more profitable prey items to their predators or because they are more easily detected, they should be less willing to expose themselves to risk than poor competitors. Furthermore, because foraging payoffs are positively related to competitive weight (see Grand, 1997), good competitors are more likely to be satiated than poor competitors, as they received a larger proportion of the food during the previous day's trial. Consequently, good competitors may also be less motivated to forage than poor competitors, who may need to expose themselves to higher levels of risk to compensate for their previous lack of foraging success (e.g., Gotceitas and Godin, 1991; see also Damsgård B and Dill LM, in preparation). This phenomenon has also been reported in a number of bird species (e.g., Hegner, 1985; Hogstad, 1988; Koivula et al., 1995).

Alternatively, we might expect good competitors to be more willing to incur risk while foraging than poor competitors, if competitive ability is positively correlated with body size (as in our experiment; see Grand, 1997) and selection for large body size is strong (see Johnsson, 1993). Additionally, if individuals had already 'decided' at the time of our experiment whether they would smolt (i.e., migrate to sea) the following spring or spend an additional summer in freshwater, large and small fish may have been on different growth trajectories. Because size at the time of migration influences the probability of surviving the early marine phase (Holtby et al., 1990; McGurk, 1996, and references therein), those individuals smolting the following spring may place a higher premium on immediate growth and hence incur greater risks than individuals who defer migration for an additional year. This phenomenon has been observed in juvenile Atlantic salmon (*Salmo salar*), where large, dominant fish, which tend to smolt after a single year in freshwater (Metcalfe et al., 1990), are less likely to move to poorer foraging areas upon exposure to a piscine predator than smaller, later-migrating, subordinate individuals (Huntingford et al., 1988).

Despite the observed effect of cover on the distribution of coho salmon competitive weights, the actual amount of time spent under cover by individuals was relatively small (Figure 6). On average, individual fish spent only 8% of their time in the poor patch directly under the cover structure. In addition, the uncovered patch only needed to provide between three and four times as much food as the covered patch to return the distribution of competitive weights to that observed in the absence of cover and elevated risk. Our results are similar to those obtained by Abrahams and Dill (1989), who observed that guppies required the safe patch to provide 1.25–3 times as much food as the risky patch before they became indifferent to risk (although several groups of males continued to avoid the risky feeder even when it provided more than 17 times the amount of food provided by the safe feeder). In a similar experiment, Kennedy et al. (1994) estimated that food would have to be approximately 28 times more abundant in the patch containing a piscine predator to induce foraging bullies (*Gobiomorphus breviceps*) to become indifferent to risk. Although differences between our results and those described above might be explained by our use of a model rather than a live predator, we believe they are more likely to be a consequence of coho salmon life history. Unlike bullies and male guppies, coho salmon are limited to a narrow seasonal window during which progression to the next life-history stage can occur (Sandercock, 1991). Thus, all individuals, regardless of competitive ability, may place a higher premium on growth than either guppies or bullies and therefore expose themselves to greater levels of risk to obtain food. Furthermore, juvenile coho are more likely than three other species of Pacific salmon to escape capture by a piscine predator (Abrahams and Healey, 1993), which suggests that, even in apparently risky habitats, coho may perceive themselves to be at relatively low risk of predation.

Recently, fisheries biologists have expressed concern over the observed decrease in salmon numbers in British Columbia streams. Much of this loss in productivity has been attributed to a reduction in the quality and quantity of available stream habitat as a result of human activities, including clear cutting and channelization (Bugert and Bjornn, 1991). Habitat enhancement programs have suggested that the addition of instream structure and overhead cover may increase the availability of protected nursery habitats and thus increase the numbers of salmonids (Boussu, 1954; Dolloff, 1986). However, our results suggest that the value of cover to fish will not be universal, but will depend on the costs and benefits associated with its use. The preservation of natural cover and the addition of artificial structures will not increase population densities in all types of habitats. To predict the environmental conditions in which cover will have its greatest effect on salmonid productivity and hence increase the efficacy of stream enhancement programs, it is important to be able to quantify the trade-off between energy intake (as reflected by growth) and predation risk (as reflected by survival). Ideal free distribution theory appears to provide a method by which this can be done.

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