HABITAT SELECTION IN JUVENILE COHO SALMON (*ONCORHYNCHUS KISUTCH*): THE EFFECTS OF INTRASPECIFIC COMPETITION AND PREDATION RISK

by

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ABSTRACT

Habitat selection frequently reflects a compromise between the conflicting demands of growth and survival. Often, an individual's best resolution to this tradeoff will be influenced by the presence of conspecifics, who may decrease a habitat's growth potential via increased competition for resources, and alter its predation risk. I investigated the effects of intraspecific competition and predation risk on habitat selection in juvenile coho salmon, *Oncorhynchus kisutch*.

Given a choice between two habitats differing only in food availability, groups of coho distribute themselves such that the proportion of competitive abilities in each habitat 'matches' the proportion of food available there. The results of this experiment suggest that when deciding where to forage, individual fish are sensitive not only to the number of competitors within a habitat, but also to their ability to compete with those individuals. When I experimentally increased predation risk and added a refuge to the lower growth potential habitat, the proportion of competitive abilities in the higher growth habitat decreased, as expected if fish trade-off growth and survival during habitat selection.

In addition to decreasing growth potential, competitors may also decrease an individual's risk of predation via dilution. I used a game theoretic model to investigate the effects of such risk dilution on habitat selection decisions of individuals differing in competitive ability. When competitor types differ in their susceptibility to predation, and risk is fully diluted by competitor number, the model predicts that all individuals will tend to aggregate in a single habitat. This prediction, together with the results of an experiment investigating the effects of group size and predation risk on risk-taking behaviour, suggests that coho do not benefit greatly from risk dilution.

In general, the resolution of foraging-predation risk tradeoffs will depend upon the relative fitness contributions of growth and survival. For animals who must reach a certain size before progressing to their next life history stage (here, smolting), those contributions will depend on current body size and the future opportunity for growth. Using a state-dependent modeling approach, I investigate how body size and time of year might influence habitat selection in juvenile coho salmon.

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GENERAL INTRODUCTION

The process of habitat selection frequently requires individuals to choose among habitats that differ in growth potential and mortality risk due to predation. When the habitat that provides the highest rate of energetic gain is also the most dangerous, habitat selection will reflect a compromise between the conflicting demands of growth and survival. In many cases, an individual's best resolution to this conflict will be influenced by the presence of conspecifics, who may reduce the growth potential of a habitat via competition for resources and decrease the associated risk of predation via numerical dilution of risk.

In this thesis, I investigate the effects of intraspecific competition and predation risk on habitat selection by juvenile coho salmon, *Oncorhynchus kisutch*. Coho spend their first year of life in freshwater streams, typically maintaining foraging positions from which they dart forward to attack benthic invertebrates and intercept instream drift (Chapman 1962; Hartman 1965; Puckett & Dill 1985). Because food is delivered by water currents, the best feeding sites (i.e., those with the greatest amount of drift per unit time) are likely shallow areas of swift current (Ruggles 1966; Fausch 1984). However, these sites are often without instream structure or cover in which to seek refuge from predators. Thus, habitats with high growth potential are also likely to be associated with relatively high mortality risk. Furthermore, because competition for prey may be intense, an individual's best resolution to this tradeoff will often depend on the habitat choice of conspecifics.

In Chapter 1, I experimentally investigate the effect of resource competition on the habitat choice of juvenile coho salmon. This experiment provides the first clear test of the primary prediction of the unequal competitors ideal free distribution model (IFD; Sutherland & Parker 1985; Parker & Sutherland 1986) and suggests that individual fish are sensitive to both the number of competitors in a habitat and their relative competitive abilities when deciding whether to forage there. In Chapter 2, I experimentally generate between-habitat differences in predation risk by adding a refuge ('cover') to one habitat, and ask how such differences affect the pattern of habitat selection observed in the first experiment. I then use the unequal competitors IFD model as a tool to quantify the energetic equivalence of cover to the fish, and ask whether additional food can offset the fitness benefits of cover.

In addition to influencing a habitat's growth potential, the presence of competitors may also influence an individual's risk of mortality. For example, if predators satiate or are limited in their ability to handle more than a single prey item at a time, an individual's probability of being preyed upon will be inversely related to the total number of individuals present. In Chapter 3, I describe the results of a game theoretic model investigating the effects of such dilution of mortality risk on the equilibrium distribution of competitors across habitats. In developing the model, I consider individual differences in both competitive ability and susceptibility to predation - differences which are likely to be common in nature. I then compare the model's assumptions and predictions to observed patterns of habitat selection in a well-studied assemblage of desert rodents, illustrating how the insights provided by ideal free distribution theory may prove useful for predicting the circumstances under which stable coexistence of competitor types (even of different species) is likely to occur.

Risk dilution is frequently invoked to explain the observation that animals increase their apparent willingness to expose themselves to predators while foraging with conspecifics (see Elgar 1989; Lima 1990; Roberts 1996, for reviews). However, as group size increases, competition for resources may also increase (Lima 1990), and when resources are limited, individuals might be expected to increase their foraging effort in an attempt to obtain a larger share (Clark & Mangel 1986). Such increases in effort will often appear to increase an individual's risk of predation. Thus, increased competition may contribute to the frequently observed relationship between risk-taking behaviour and group size. In Chapter 4, I develop and experimentally test a technique to assess the relative importance of these two mechanisms to the foraging decisions of juvenile coho salmon. In doing so, I argue that to differentiate between the 'risk reduction' and 'increased competition' hypotheses, it is necessary to quantify the effect of predation risk on the form of the relationship between group size and risk-taking behaviour, and thus, to manipulate both group size and predation risk simultaneously.

In general, the resolution of foraging-predation risk tradeoffs will depend upon the relative fitness contributions of growth and survival. For animals who must reach a certain size before progressing to their next life history stage, those contributions will depend on both current body size and the future opportunity for growth (Houston et al. 1993; Clark 1994). In Chapter 5, I present the results of a dynamic optimization model exploring the effects of body size and time of year on patterns of risk-taking behaviour in animals who exhibit considerable flexibility in the timing of life history events. Because juvenile coho salmon are capable of delaying migration to sea ('smolting'), and hence, progression to their next life history stage for a year or more, I use the relevant features of their biology to illustrate the problem of interest. In addition to linking the behavioural decisions of individuals to population level patterns of life history timing, the model also illustrates the importance of considering the life history alternatives available to individuals when investigating foraging-predation risk tradeoffs.

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CHAPTER ONE

Foraging site selection by juvenile coho salmon: ideal free distributions of unequal competitors[*]

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ABSTRACT

When individuals differ in competitive ability, ideal free distribution (IFD) theory predicts that animals should be distributed between habitats such that the distribution of their relative competitive abilities (or 'weights') matches the distribution of resources. At equilibrium, the unequal competitors model predicts that the payoff per unit of competitive weight will be the same in all habitats, such that no individual can increase its payoff by moving. These predictions were tested in juvenile coho salmon, *Oncorhynchus kisutch*, by allowing 15 groups of eight individuals to compete for drifting prey in a two-patch stream channel environment. Competitive weights were quantified a priori as the proportion of prey obtained by each individual when competing with all other members of the group in a single patch. At equilibrium, the distributions of competitive weights did not differ significantly from the distributions of resources, although in most groups, slightly too many competitive weights were in the poor patch relative to that predicted by the model. The mean payoff per unit of competitive weight did not differ between patches. In the good patch, however, 'poor' competitors tended to receive higher payoffs per unit of competitive weight than 'good' competitors, which suggests that competitive abilities did not remain constant across patches as assumed by the model. Although many researchers have found support for the original, equal competitors ideal free distribution model (i.e. total competitor numbers match the distribution of resources) despite the presence of competitive inequalities, the present results suggest that this will not always be true. Distributions of coho salmon numbers were significantly different from both the distributions of resources and the distributions of competitive weights. These results suggest that the incorporation of competitive inequalities into habitat selection models will enhance our abilities to predict animal distributions.

INTRODUCTION

The ideal free distribution theory (IFD; Fretwell & Lucas 1970; Fretwell 1972) was developed to predict how animals, attempting to maximize their fitness, should be distributed in an environment containing habitats of varying quality. If individual fitness declines as the number of competitors in a habitat increases, animals 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). The model assumes that all individuals are of equal competitive ability, that each has perfect or 'ideal' information about the distributions of both competitors and resources, and that animals are 'free' to move to the habitat where their fitness gains will be greatest. At equilibrium, all individuals will receive the same payoff, and no individual can increase its payoff by moving to another habitat. Although IFD theory has successfully predicted the distribution of animals in a number of field and laboratory studies (reviewed in Milinski & Parker 1991; Kacelnik et al. 1992; Tregenza 1995; but see Kennedy & Gray 1993), most researchers report that individuals were not actually of equal competitive ability (e.g., Milinski 1979, 1984; Whitham 1980; Harper 1982; Godin & Keenleyside 1984), and that these competitive inequalities may have influenced the resultant distribution.

Individual differences in competitive ability have been incorporated into IFD theory by Sutherland & Parker (1985) and Parker & Sutherland (1986), who assumed 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 are unaffected by local resource or competitor densities, and thus, remain the same across habitats, their 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). In contrast to the single equilibrium predicted by the equal competitors model, the IFD for unequal competitors predicts a number of potential equilibria, each characterized by having equal payoffs per unit of competitive weight in all habitats.

To date, there have been only two tests of Parker & Sutherland's (1986) model. Sutherland et al. (1988) compared the distribution of goldfish, *Carassius auratus*, of known competitive rank to the distribution of food in a two-patch, laboratory study. They observed that the mean competitive rank of individuals in each patch varied inversely with the number of fish there. Although the input-matching prediction was not tested directly, Sutherland et al.'s (1988) results suggested that individual fish were sensitive both to the number of competitors in a patch and to their relative competitive abilities when deciding where to forage. All fish received higher payoffs in the 'good' patch than in the 'poor' patch, however, suggesting that the distribution was not at equilibrium, or that relative competitive weights differed between patches. In a direct test of the input-matching prediction, Inman (1990) compared the distribution of starlings, *Sturnus vulgaris*, of known competitive weight to the distribution of rewards offered at two experimental patches. The observed distributions differed significantly from that predicted by the unequal competitors model, in part because competitive weights appeared to vary with group size and composition, but perhaps also due to the flocking tendencies of the birds under study. Thus, quantitative support for Parker & Sutherland's (1986) input-matching prediction has yet to be documented.

I tested the input-matching prediction of the unequal competitors IFD model with juvenile coho salmon. Coho spend their first year of life in freshwater streams, typically maintaining foraging positions from which they dart forward to attack benthic invertebrates and intercept instream drift (Chapman 1962; Hartman 1965; Puckett & Dill 1985). Although aggressive defence of territories is often observed in shallow, fast flowing 'riffles', territoriality tends to break down in slow flowing 'glides' and deeper 'pools' where dominance hierarchies predominate (Kalleberg 1958; Mundie 1969). Thus, coho (and other juvenile salmonids) may be appropriate animals with which to test IFD models of continuous input. In addition, small differences in body size influence an individual's position in the dominance hierarchy (Chapman 1962), and are thus likely to result in individual differences in competitive ability within foraging groups.

I quantified the relative competitive abilities of coho salmon competing for food in a single patch and used these measures to compare the observed distributions of fish across two patches to that predicted by the unequal competitors IFD model. Fish distributions were also compared to the predictions of the equal competitors model, to determine whether the inclusion of competitive inequalities resulted in a better 'fit' between the distributions of fish and the distributions of food. I also compared the average payoff per unit of competitive weight in the two patches to test the equilibrium payoff prediction.

METHODS

Experimental Subjects

I captured 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 lab 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, I anaesthetized fish in a dilute solution of 2-phenoxyethanol, determined their mass (nearest 0.01 g) and fork length (nearest 1 mm) and tagged them for individual recognition by attaching pre-made, coloured tags through the musculature posterior to the dorsal fin (e.g., Chapman & Bevan 1990). Each week, two groups of eight fish were formed by selecting individuals ranging in mass from 1.16 to 1.68 g ($\bar{x} \pm SD = 1.42 \pm 0.12$ g, $n = 120$) and in length from 49 to 56 mm ($\bar{x} \pm SD = 52 \pm 2$ mm, $n = 120$), for a total of 15 groups. I 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. Group size was chosen to approximate the density of fish under natural conditions (e.g., 2 - 3 fish $\cdot$ m^{-2}; Dolloff & Reeves 1990; Shirvell 1990; Nickelson et al. 1992; Nielsen 1992).

Four days after tagging, I 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 two days. Fish were fed live, adult brine shrimp (*Artemia* spp.) *ad libitum* while in the flow-through aquaria. No food was provided to the fish once they had been transferred to the stream channel, ensuring that all individuals were motivated to forage when the experiment began.

Apparatus

Stream channel facilities

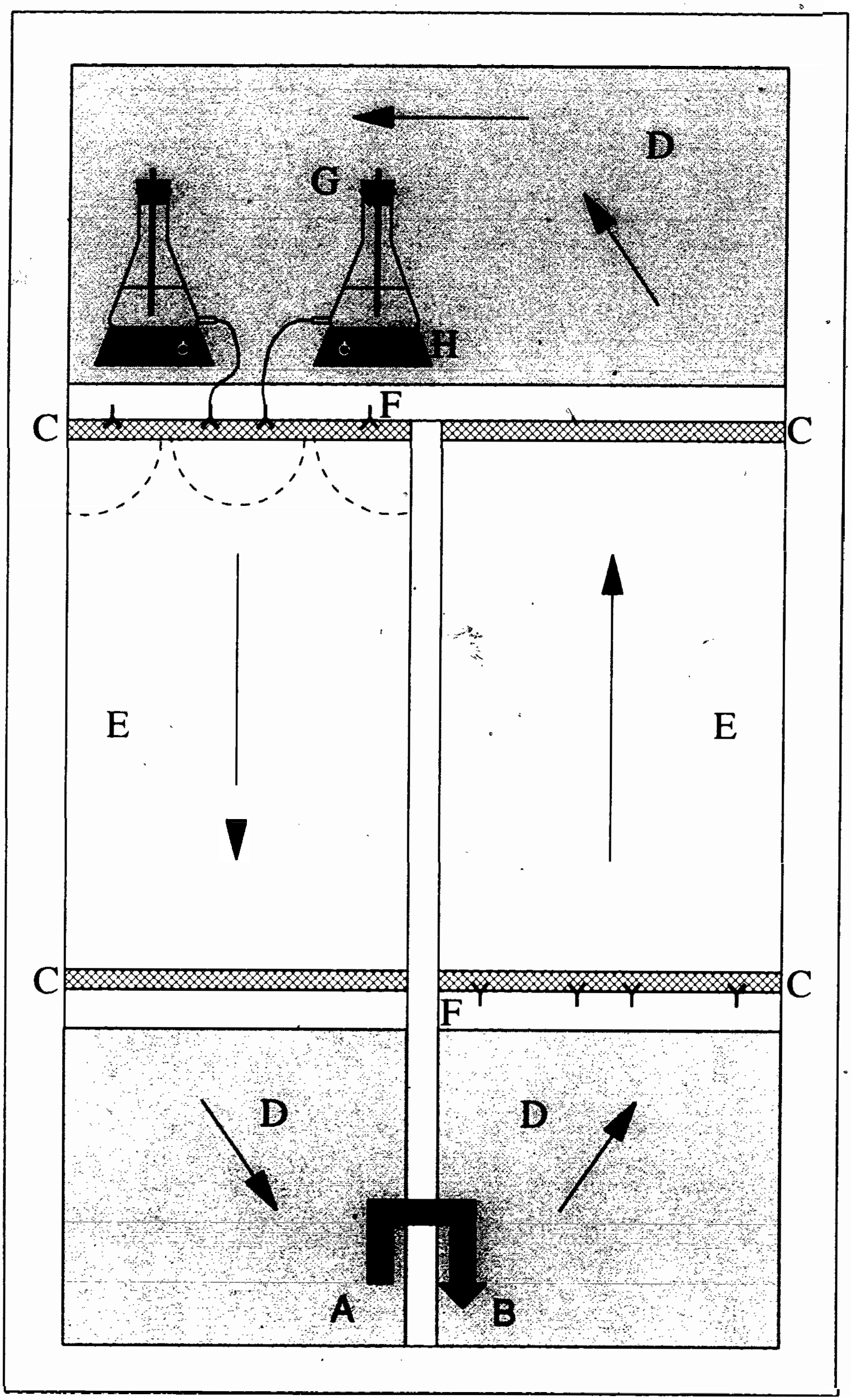
I conducted experiments in an artificial stream channel in the woods of the Burnaby Mountain campus of Simon Fraser University. The concrete channel (562 × 285 × 186 cm; L × W × H; Figure 1.1) consisted of two parallel glides (230 × 115 cm; water depth = 16 cm) separated from each other by a 15 cm-width of concrete and two deep pools (245 × 146 cm; water depth = 77 cm). A 15-cm-wide concrete wall divided one of the pools in two, providing a barrier over which water was pumped to create continuous, circular flow. Although the total volume of water moving through the channels was identical, flow patterns differed between glides. Surface water velocity ranged from 4.31 to 5.28 cm · s^{-1} ($\bar{x} \pm SD = 4.8 \pm 0.36$ cm · s^{-1}, $n = 8$) in the upstream glide and from 7.53 to 11.51 cm · s^{-1} ($\bar{x} \pm SD = 9.7 \pm 1.29$ cm · s^{-1}, $n = 8$) in the downstream glide. These water velocities are similar to those experienced by fish in the field (personal observation). Although differences in current velocity will influence the energetics of foraging site selection (e.g., Puckett & Dill 1985), I expected this effect to be slight relative to the effect of food availability (e.g., Tyler & Clapp 1995), because patches within a glide had relatively similar current velocities. Furthermore, there was no consistent difference in the ability of groups experiencing the two glides to distribute themselves according to the distribution of food. Thus, data from the two glides were pooled for all subsequent analyses. 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) set in wooden frames separated the glides from the pools and prevented movement of the fish between stream channel sections (Figure 1.1). Pools were covered with plywood boards to reduce algal growth and prevent extraneous food (e.g., winged insects) from entering the system. Boards were also used to secure the legs of a plastic tent that was erected over the entire channel. The walls of the tent were made of fine, 'no-see-um' mesh, which prevented both extraneous food and leaf litter from entering the channel. Opaque plastic blinds were attached to the mesh to prevent disturbance of the fish during foraging trials. I made observations of fish behaviour and distributions through small slits cut in the blinds.

Feeding apparatus

Throughout the experiment, fish were fed live, adult brine shrimp obtained weekly from a local aquarium store. Prey were sieved and only those unable to pass through a 1350-µm mesh screen were used. Prey were counted and placed in two 4000-mL Erlenmeyer flasks filled with fresh water collected from one of the pools in the stream channel. Flasks were modified such that a 5-cm glass spout projected from their lower sides (Abrahams 1989). Prey and water drained from the feeders through 70-cm lengths of tygon tubing (diameter = 5 mm), which were fastened to the glass spouts. Each feeding tube emptied into one of four plastic Y-shaped tubes attached to the back side of the mesh barrier at the upstream end of each glide (Figure 1.1). The positions of the Y-tubes on the

Figure 1.1. Overview of the experimental stream channel. Water was pumped over a concrete barrier from (A) to (B) and travelled downstream through a series of four mesh barriers (C) which separated the pools (D) from the glides (E). Four Y-shaped feeding tubes (F) were attached to each of the mesh barriers at the upstream ends of the glides. Prey were dispensed from Erlenmeyer flasks (G) mounted upon magnetic stir plates (H). Arrows indicate the direction of water flow and broken lines the single and paired patches of the one- and two-patch trials, respectively.


D
G
H
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mesh barriers determined the distance between the feeding patches. 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 1.1) or from two spatially distinct lateral patches (Y-tubes placed 30 cm from the edges of the barrier, 55 cm apart). A line was drawn down the center of each glide in indelible ink to delineate the patches for the observer.

Prey in the feeders were kept in suspension by means of a stir bar constantly rotated by a magnetic stir plate. Stirring ensured that prey left the flask at a uniform rate throughout the trial (as determined in preliminary experiments). Flasks were sealed with a rubber stopper penetrated by a glass tube which extended to the bottom of the flask, thus maintaining a constant drain rate of water and prey. A length of tygon tubing was attached to the top of the tube and sealed at the other end with a 23 1/2 gauge syringe. Thus, the feeders could be operated simultaneously and remotely by simply removing the plungers from the syringes, and allowing air to enter the apparatus. Water and prey were dispensed slowly and randomly over the course of the 24-min trial. Trials were halted by re-inserting the plungers in the syringes when 1000 mL of water remained in the flasks. The number of prey remaining in each flask was counted and subtracted 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.

Experimental Procedure

I conducted trials once per day, between 1130 and 1400 hours, on three consecutive days. Experiments in the two glides were run sequentially. After the feeders had been filled and set in place, fish were left undisturbed for 15 min.

On the first two experimental days, 50 brine shrimp were dispensed from each of the two central feeding positions. The wide area over which the prey were broadcast (~ 18 cm) effectively created a single, non-defensible patch. The number of prey captured by each individual fish was recorded on a portable audiocassette recorder and used to determine relative competitive ability. Although the two days' measures of competitive ability were highly correlated ($r = 0.826$, $n = 120$, $p < 0.001$), I assumed that allowing individuals to increase their familiarity with the foraging situation would lead to a better estimate of true competitive ability. Thus, I quantified each individual's competitive weight as the proportion of all available prey it captured during the second one-patch trial.

On the third experimental day, prey were dispensed from the two lateral feeding positions. Patches differed in the number of prey they provided to the fish. Seventy-five brine shrimp were placed 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 such that the actual patch profitability ratio experienced by the fish was approximately 2:1 (as determined from preliminary experiments). I 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. The number and identity of fish in each patch was determined by scan sampling (Martin & Bateson 1986) at 1-min intervals throughout the trial, as well as during the 5 minutes preceding each trial.

To investigate whether an individual's position in the dominance hierarchy was related to its competitive ability, I also collected data on aggression prior to each of the three trials (i.e., independent of the foraging experiment). Fish were observed for 5 min, and all aggressive acts between pairs of individuals were recorded. Aggressive acts were primarily chases, but also included nips and bites (Hartman 1965). For each aggressive interaction, I recorded the identity of both the initiator and the recipient. For each pair of fish in a group, I noted which fish initiated more aggressive acts towards the other. The more 'dominant' of the two received a score of '+1' and the 'subordinate' a score of '-1'. A score of '0' was assigned if the two were equally aggressive towards each other, or if no encounters between the two were observed. Dominance rank within a group was determined by summing these scores over all three pre-trial periods for each fish and assigning rank 1 to the individual with the highest score and rank 8 to the individual with the lowest score (Rubenstein 1981).

Data Analyses

To compare the observed distributions of competitive weights and fish numbers to those predicted by the two IFD models, I determined the average sum of competitive weights and the average proportion of fish in each patch from the scan sample data. To avoid biasing the outcome of the comparisons with pre-equilibrium values, only data from the second half of each trial (i.e., minutes 13 - 24) 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. Thus, although the good patch was expected to provide twice as much food as the poor patch (i.e., a patch profitability ratio of 2:1), the actual patch profitability ratios ranged from 1.97 to 2.62 ($\bar{x} \pm SD = 2.17 \pm 0.17$, $n = 15$). I used paired t-tests to compare the mean sum of competitive weights and the mean proportion of fish in the poor patch to the actual proportion of food available there.

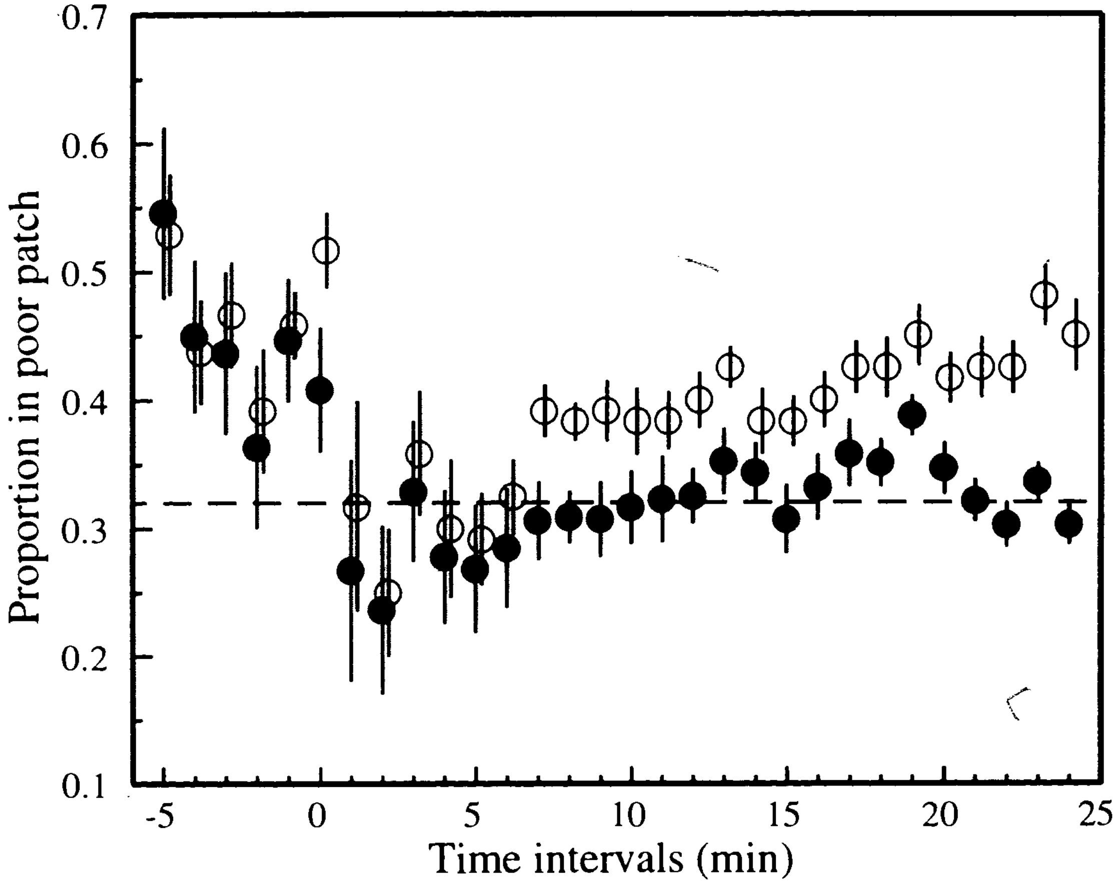
I defined absolute payoffs as the total number of all available prey items consumed by an individual and individual payoffs within patches as the number of prey items obtained per minute spent in the patch per unit of competitive weight. The average payoffs obtained in each patch were calculated by weighting each individual's payoff in the patch by the relative amount of time it spent there and summing these values over all members of the foraging group. To compare the payoffs obtained in the two patches by (1) all individuals and (2) good and poor competitors (i.e., those having competitive weights of ≥ 0.125 and < 0.125, respectively), I used repeated measures analysis of variance (ANOVAR; Wilkinson 1990). Average patch payoffs were compared using paired t-tests. Because all data were normally distributed, transformations were not required. Unless stated otherwise, reported p-values are two-tailed; those associated with multiple comparisons represent Bonferroni-adjusted probabilities (Wilkinson 1990).

RESULTS

Behaviour of the Fish

Prior to 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. This apparent territoriality may have been responsible for the observed deviation from a 50:50 distribution of competitor numbers and competitive weights in the absence of food (Figure 1.2). Upon the beginning of the foraging trial, each 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. In all trials, the majority of the prey were consumed within 20 cm of the mesh barrier. Occasionally, prey items were missed or ignored by the fish, however, these prey were quickly carried downstream and outside of the foraging arena by the current.

Figure 1.2. Mean (± SE) proportion of fish (○) and competitive weights (●) in the poor patch during each minute of the foraging trial. Dashed line indicates the distributions predicted by the equal and unequal competitors IFD models. Distributions of fish were best predicted by the unequal competitors model. *n* = 15 groups of fish.


Proportion in poor patch
0.7
0.6
0.5
0.4
0.3
0.2
0.1
-5
0
5
10
15
20
25
Time intervals (min)

Distributions of Competitive Weights

The distributions of competitive weights varied somewhat over the course of the 24-min trials (Figure 1.2). In most groups, fish were initially attracted to the patch that provided the most food, resulting in an over-representation of competitive weights in the good patch relative to the predictions of the model. Distributions of competitive weights rapidly approached the distributions of resources, however, such that during the second half of the trial, the observed proportion of competitive weights in the poor patch was not significantly different from the proportion of food available there (Table 1.1; $t = 1.632$, $df = 14$, $p = 0.125$). In most cases, deviations from the predicted distributions were characterized by too many competitive weights in the poor patch and too few in the good patch (i.e., 'under-matching' of competitive weights).

Due to the within-group variation in competitive weights, it may not have been possible for a group of individuals to be distributed between the two patches such that the sum of their competitive weights precisely matched the distribution of food. For example, a group of four fish with competitive weights of 0.50, 0.25, 0.20 and 0.05, could not be partitioned precisely between two patches having a 2:1 profitability ratio. The distribution of competitive weights that most closely corresponds to this distribution of food is 0.70:0.30 or 2.333:1. Thus, to determine whether the observed deviations from input-matching resulted from the 'integer effect' described above, I calculated the distribution of competitive weights that most closely approximated the distribution of food for each group of fish (Inman 1990). The observed distributions were then compared with these 'best approximations'. Observed distributions of competitive weights were statistically similar to the 'best approximation' distributions (Table 1.1; $t = 1.734$, $df = 14$, $p = 0.105$), although again there was a tendency towards under-matching of competitive weights (i.e., more competitive weights than expected in the poor patch).

Distributions of Competitor Numbers

Many researchers have found that the proportion of animals in a patch tends to correspond to the proportion of resources available there, despite known differences in competitive ability. Parker & Sutherland (1986) demonstrated theoretically that distributions of unequal competitors can superficially resemble distributions of equal

Table 1.1. A comparison between the observed proportion of competitive weights in the poor patch and the proportion of (1) food provided by the patch, (2) competitive weights that most closely approximates the proportion of food provided by the patch, and (3) fish observed in the patch. $n = 15$ groups.

Competitive weights	Food	Best approximation of competitive weights	Fish
0.3825	0.3367	0.3373	0.4583
0.3012	0.3302	0.3253	0.4063
0.3342	0.3333	0.3299	0.4479
0.3012	0.3113	0.3125	0.4375
0.3731	0.3431	0.2727	0.5341
0.2632	0.3211	0.3158	0.5104
0.2816	0.3048	0.3038	0.3750
0.3155	0.3113	0.3146	0.4167
0.4178	0.2979	0.3000	0.3375
0.3160	0.3211	0.3247	0.4479
0.3947	0.3061	0.3059	0.3977
0.3486	0.3204	0.3239	0.4167
0.3452	0.3333	0.3297	0.3333
0.3660	0.3271	0.3298	0.3500
0.3531	0.3084	0.3043	0.4545
0.340 ± 0.011[a]	0.320 ± 0.003	0.320 ± 0.003	0.422 ± 0.015
Power[b]:	0.71	0.65	---

[a] $\bar{x} \pm$ SE; [b] power of paired *t*-tests comparing (1) and (2) to the observed distribution of competitive weights

competitors, although input-matching of total competitor numbers seems most likely to occur when competitor types are few and when all individuals of the same competitor type have the same competitive ability. In juvenile coho salmon, competitive abilities vary so much between individuals that only rarely do members of a group share the same competitive weight. Thus, I compared the distributions of fish numbers to the distributions of food to determine whether input-matching of total competitive numbers would occur when groups consist of many individuals of different competitive ability. The number of fish observed in the poor patch was significantly different from the proportion of food available there (Figure 1.2, Table 1.1; $t = 7.188$, $df = 14$, $p < 0.001$). In addition, the distributions of competitor numbers were significantly different from the distributions of competitive weights (Table 1.1; $t = 3.905$, $df = 14$, $p = 0.002$), which suggests that, under these experimental conditions, the unequal competitors model is a better predictor of coho salmon foraging distributions than the original, equal competitors IFD.

Individual Payoffs

As predicted by the unequal competitors model, absolute individual payoffs were strongly related to competitive weights (Figure 1.3; $r = 0.727$, $n = 120$, $p < 0.001$). The total number of prey captured by some individuals, however, exceeded that predicted by their competitive weights alone. These differences in payoff could not be explained by differences in patch choice, as might be expected if relative competitive weights changed across patches. Although the proportion of time spent in the good patch decreased with competitive weight rank (Figure 1.4; $F_{1,107} = 3.048$, $p = 0.042$; ANOVA, one-tailed linear contrast), these differences do not explain the observed deviations from the individual payoff-competitive weight regression (ANOVA on residuals; $F_{1,118} = 0.627$, $p = 0.430$). Thus, individuals who received higher payoffs than predicted by their competitive weight alone did not spend significantly more time in the good patch than individuals receiving lower than expected payoffs.

Overall, the payoffs obtained by individuals did not differ between patches (Figure 1.5; $F_{1,114} = 1.223$, $p = 0.271$; ANOVAR). 'Poor' competitors, however, (i.e., individuals with competitive weights < 0.125), tended to receive higher payoffs per unit of competitive weight than did 'good' competitors (i.e., those individuals with competitive weights ≥ 0.125; Figure 1.5; $F_{1,114} = 4.602$, $p = 0.034$; ANOVAR), although this difference was only significant in the good patch ($F_{1,114} = 3.647$, $p = 0.030$; ANOVAR,

Figure 1.3. The number of prey captured by individual fish throughout the trial was positively related to their competitive weight. $n = 120$.

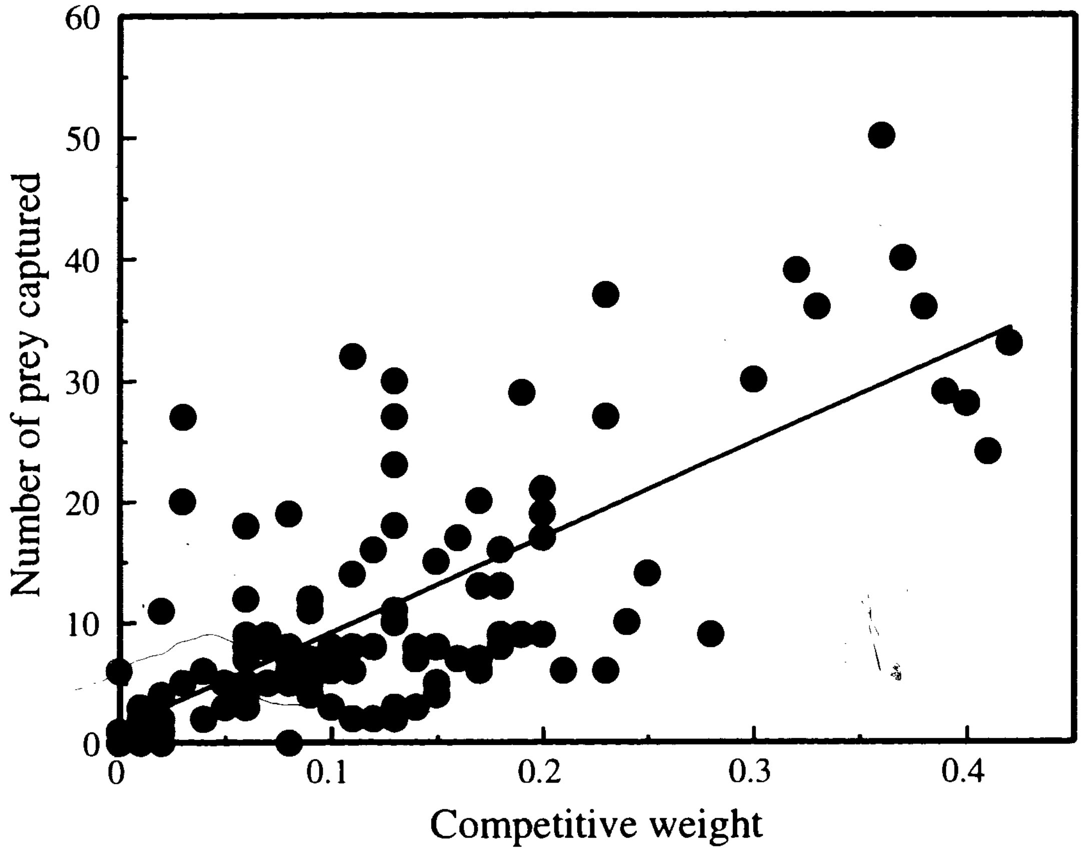

60
50
40
30
20
10
0
0
0.1
0.2
0.3
0.4
Number of prey captured
Competitive weight

Figure 1.4. Mean (± SE) proportion of time spent in the good patch by fish differing in competitive weight rank. The sample sizes used to calculate means (noted in parentheses) varied between ranks as ties for rank occurred in several groups.

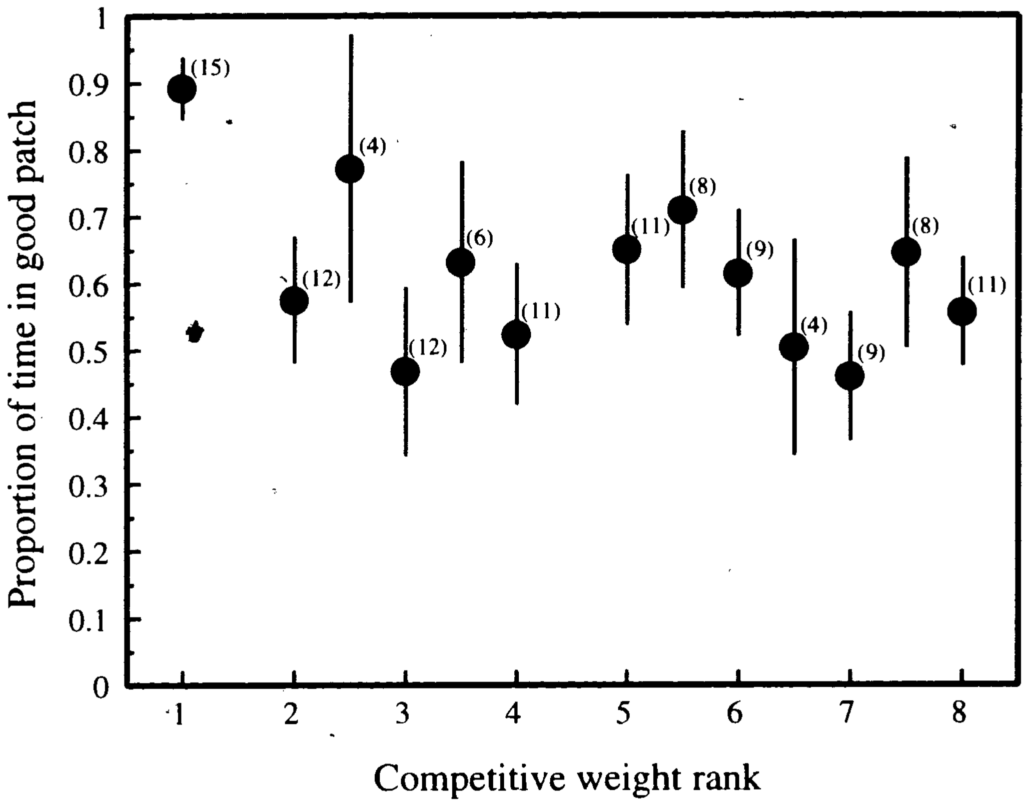
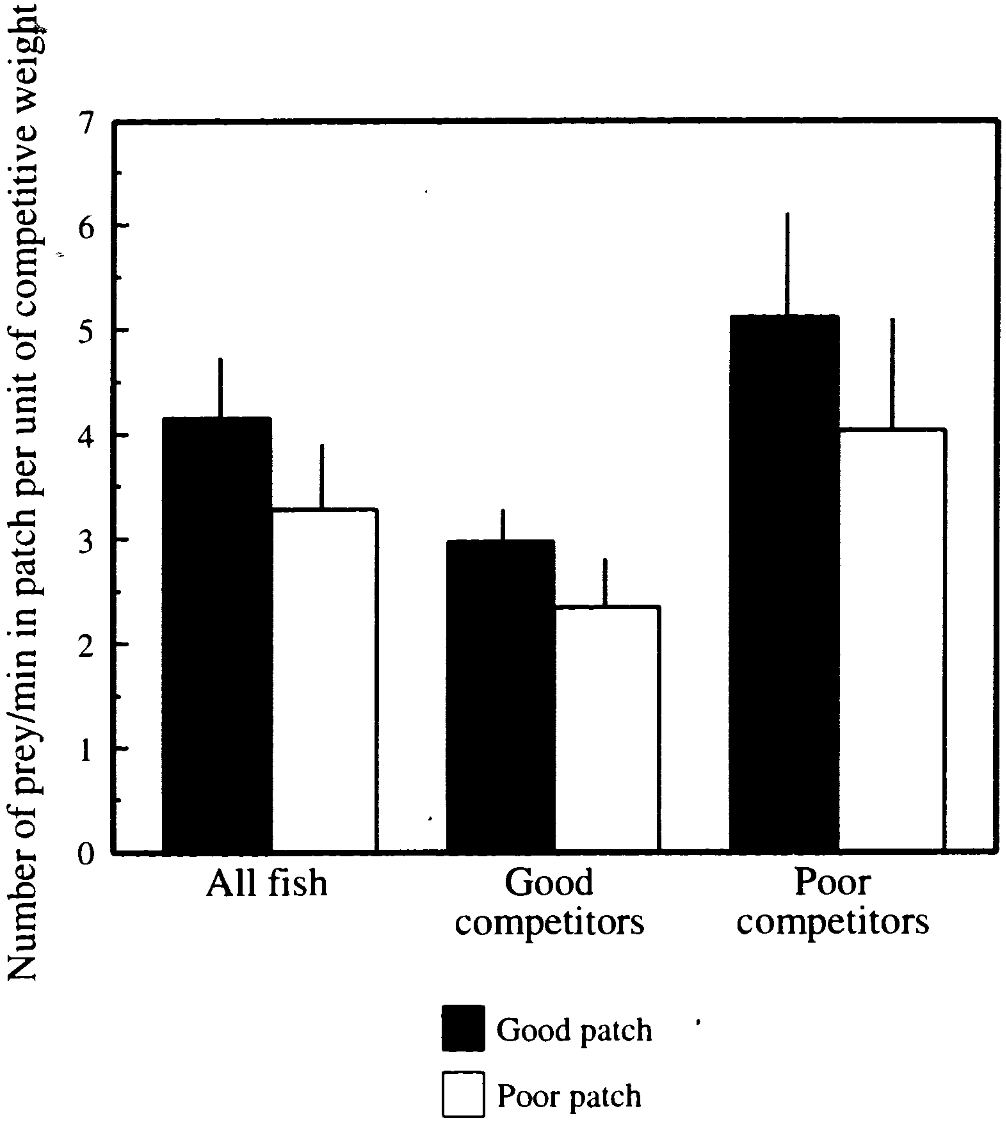

Proportion of time in good patch
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1
1
2
3
4
5
6
7
8
Competitive weight rank
(15)
(12)
(4)
(12)
(6)
(11)
(11)
(8)
(9)
(4)
(9)
(8)
(11)

Figure 1.5. Mean (± SE) number of prey captured per minute per unit of competitive weight by (1) all fish (*n* = 116), (2) good competitors (*n* = 52) and (3) poor competitors (*n* = 64) in the good (solid bars) and poor (open bars) patches, respectively. Four individuals with competitive weights of '0' were omitted from this analysis.



Number of prey/min in patch per unit of competitive weight
0
1
2
3
4
5
6
7
All fish
Good competitors
Poor competitors
Good patch
Poor patch

post-hoc contrast). Failure to find significant differences between the individual payoffs obtained in the two patches by good competitors alone and all competitors combined was not due to lack of statistical power. I estimated the power of the these comparisons to be 0.62 and 0.75, respectively.

Average Patch Payoffs

The unequal competitors IFD model predicts that, at equilibrium, the average payoff per unit of competitive weight will be equal in the two patches. Because individuals spent different amounts of time in the two patches, average patch payoffs cannot be calculated as simply the mean of the individual per unit competitive weight payoffs in each patch (as above). Rather, individual payoffs must be weighted by their contribution to the total number of competitive weight minutes spent in the patch by all members of their foraging group. Thus, for each group of fish, the average payoff in the j th patch, ($\bar{g}_j$), where $j = 1, 2$, will be equal to;

$$\bar{g}_j = \frac{\sum_{i=1}^{n} f_{ij}}{\sum_{i=1}^{n} t_{ij} c_i} \qquad (1.1)$$

where f_{ij} is the number of food items captured by individual i in patch j, t_{ij} is the amount of time spent by individual i in patch j, c_i is the competitive weight of individual i and n is the number of competitors in the group.

Overall, the average payoff per unit of competitive weight did not differ between patches ($t = 1.761$, $df = 14$, $p = 0.201$, power = 0.76; paired t-test), although payoffs tended to be higher in the good patch than in the poor patch ($\bar{x} \pm SD = 8.70 \pm 0.47$ vs. 8.14 ± 0.36 items · min^{-1} · unit of competitive $weight^{-1}$, respectively), presumably as a consequence of slight deviations from input-matching.

Correlates of Competitive Ability

Competitive weights were positively correlated with mass ($r = 0.285$, $n = 120$, $p = 0.016$), negatively correlated with dominance rank ($r = -0.391$, $n = 120$, $p < 0.001$), but not correlated with either fork length (FL) or condition factor (mass · FL^{-3}; $r = 0.232$,

n = 120, p = 0.108, and r = 0.090, n = 120, p > 0.99, respectively), which suggests that heavy, dominant individuals are better competitors than light, subordinate individuals. Because large fish also tend to be high in dominance rank, however (r = –0.477, n = 120, p < 0.001), I used forwards step-wise multiple regression to determine the best predictor of competitive ability. The best fit model included only dominance rank as a significant predictor of competitive ability ($F_{14,105}$ = 2.48, p = 0.004, r^2 = 0.248). Neither mass, FL or condition factor contributed significantly to the total variation in competitive ability once the variance due to dominance rank was explained (partial correlation coefficients; r = 0.088, p = 0.368; r = 0.069, p = 0.485; and r = 0.031, p = 0.754, respectively, all n's = 120). Thus, individuals of high dominance rank in the non-foraging hierarchy also tended to be individuals of high competitive ability.

DISCUSSION

Given a choice between two patches differing in food availability, groups of juvenile coho salmon tend to distribute themselves such that the distribution of their competitive abilities 'matches' the distribution of resources. These results suggest that individual fish are sensitive to both the number of competitors at a site and their relative competitive abilities when deciding where to forage. On average, payoffs per unit of competitive weight were the same in both patches, as predicted by the unequal competitors IFD model (Parker & Sutherland 1986). In the good patch, however, poor competitors tended to receive higher payoffs per unit of competitive weight than good competitors, which suggests that competitive abilities did not remain constant across patches, as assumed by the model.

When competing for food in a two-patch environment, both goldfish (Sutherland et al. 1988) and starlings (Inman 1990) received higher payoffs in the good patch, although for starlings, differences in payoff were also affected by the number of dominant and subordinate birds in the patch (Inman 1990; see also Krause 1994). When the intensity of competition was low (i.e., few subordinates in a patch), dominant starlings were able to defend and monopolize food, and thus received payoffs in excess of those predicted by their competitive weight alone. When competition increased, however (i.e., many subordinates in a patch), resource monopolization declined and the payoffs received by subordinate birds increased to their predicted levels. In coho salmon, only poor competitors benefited from a decrease in the intensity of competition (i.e., between the one- and two-patch trials), and this benefit was observed only in the good patch, where the relative payoffs of poor competitors exceeded those of good competitors. These results suggest that poor competitors increased their foraging rates in response to reduced competition, perhaps by becoming more efficient at searching for or handling prey.

Both Sutherland et al. (1988) and Inman (1990) concluded that the observed differences in payoff between the patches reflect changes in the relative competitive abilities of individuals. In Inman's (1990) experiment, violation of the 'constancy of competitive weights' assumption led to a poor fit between the distribution of birds and the distribution of food (i.e., the distribution of competitive weights did not match the distribution of resources). In the current study, slight changes in the relative competitive abilities of individuals between patches did not appear to affect the ability of fish to reach the predicted equilibrium distribution (Figure 1.2). Although poor competitors tended to receive higher payoffs relative to their competitive weights than did good competitors, the observed proportion of competitive weights in the poor patch did not differ significantly from the proportion of food available there. Furthermore, despite these apparent changes in competitive ability, there was no significant difference between the average payoffs obtained in the two patches, presumably because poor competitors spent very little time in the good patch, thus contributing little to the average payoff obtained there. Thus, this study provides the first quantitative support for Parker & Sutherland's (1986) 'input-matching of competitive weights' prediction.

Given that the unequal competitors model predicts a number of potential equilibria, it is unclear why distributions which are characterized by the best competitor choosing the best patch should occur more frequently than all others. These results cannot be fully explained by Parker & Sutherland's (1986) 'truncated phenotype' distribution, which predicts that when individual competitive abilities differ between patches, competitor types will be truncated across patches such that the best competitors settle in the best patches (i.e., where competitive abilities matter most) and poorer competitors settle in patches of decreasing quality. Although the best competitor in each group of coho foraged almost exclusively in the good patch, fish of lesser competitive ability spent varying amounts of time in both patches (Figure 1.4), suggesting that individuals were not truncated across patches according to competitive ability. The prevalence of this particular type of unequal competitors IFD may be explained in part by the observation that the competitive weights of the best competitors often exceeded the proportion of food provided by the poor patch. For example, an individual of competitive weight 0.37 could never maximize its payoff by choosing to forage in a patch containing one-third of the food, and would always be expected to choose the good patch. Thus, in the present study, the set of all possible equilibria may be limited to those distributions in which the best competitor occurs in the good patch. Alternatively, good competitors may be capable of assessing and matching patch profitabilities more quickly than poor competitors (e.g., Regelmann 1984), who must then make their foraging decisions based upon the reduced resource input ratio.

Despite the similarity between observed and predicted distributions of competitive weights, in no group of fish was the observed distribution identical to the 'best approximation' distribution (Table 1.1). Thus, in all groups, some individuals were receiving slightly lower payoffs than they would have had the group adopted the 'best approximation' distribution. Deviations from input-matching are expected when individuals have less than perfect information about either the distribution of competitors or the distribution of resources (e.g., Abrahams 1986), or when good competitors defend and monopolize access to those resources (Grand & Grant 1994). However, these deviations are always predicted to be characterized by under-matching of total competitor numbers (Abrahams 1986; Grand & Grant 1994) and/or competitive weights (Spencer et al. 1995). In coho salmon, under-matching of competitive weights was observed in only 10 of 15 groups, suggesting that potential violations of the 'ideal' and 'free' assumptions were not wholly responsible for the observed deviations from input-matching. It is possible that imperfect information, in conjunction with changing competitive abilities, might lead to over-matching of competitive weights relative to the distribution of resources, although this possibility has not yet been investigated theoretically.

Unlike other researchers who observed input-matching of competitor numbers despite the presence of competitive inequalities (e.g., Harper 1982; Godin & Keenleyside 1984; Milinski 1984; Grand & Grant 1994), I found the original IFD model to be a relatively poor predictor of coho salmon distributions. Distributions of fish did not match the distributions of resources; in fact, as the trial proceeded, the magnitude of the deviation from input-matching continued to increase, rapidly approaching a random distribution of individuals between the patches by the end of the observation period (Figure 1.2). Furthermore, the distributions of competitor numbers were significantly different from the distributions of competitive weights. Taken together, these results suggest that our ability to predict animal distributions will only be enhanced by incorporating competitive inequalities into models of habitat selection. Before such models can be applied routinely to natural populations, however, researchers must be able to obtain reliable measures of competitive ability.

In many cases, population size and/or time limitations may prohibit direct quantification of competitive ability and thus, require researchers to identify surrogate measures (e.g., body size) which can be easily measured in the field. Although mass is often thought to be a good predictor of the outcome of competitive interactions in fish (see references in Beeching 1992), it is unclear whether it can be used to infer relative competitive ability. In juvenile coho salmon, an individual's position in the dominance hierarchy is the single best predictor of its competitive weight; neither mass nor fork length add significantly to our understanding of what makes an individual a good competitor.

Given the recent interest in applying IFD theory to conservation biology (e.g., Sutherland & Dolman 1994), it may be important to identify situations in which distributions of unequal competitors cannot be expected to resemble distributions of equal competitors. If population density is used to infer habitat quality, habitats containing few, competitively superior individuals may be targeted for 'enhancement' despite being higher in quality than habitats containing greater numbers of inferior competitors. As noted by Holmgren (1995), the relationship between population density and habitat quality will not always be positive. Clearly, information about competitive inequalities in natural populations must be obtained prior to using IFD theories of habitat selection to make management decisions.

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CHAPTER TWO

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

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ABSTRACT

Cover is often thought to be an important habitat characteristic for juvenile stream salmonids. In addition to providing protection from predators, cover may also be associated with reduced food availability. Thus, an individual's use of cover is likely to reflect a tradeoff 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.

INTRODUCTION

Foraging theory predicts that individuals attempting to maximize their net rate of energy intake should forage preferentially in areas of high prey density (Stephens & 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 tradeoff between energy intake and survival (for a review of foraging-predation risk tradeoffs see Lima & Dill 1990). There are several ways in which animals can resolve such tradeoffs, including the selection of foraging sites adjacent to a refuge or cover (e.g., Newman & Caraco 1987; Brown 1988; Hogstad 1988).

Cover is often speculated to be an important habitat characteristic for stream-dwelling salmonid fishes. Both instream 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 (Wilzbach 1985; Shirvell 1990), as well as reducing energetic expenditure by sheltering individuals from areas of high current velocity (Huntingford et al. 1988; Fausch 1993). 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., Ruggles 1966; Dolloff 1986; Taylor 1988; McMahon & Hartman 1989; Fausch 1993). In some cases cover is preferred (e.g., Taylor 1988), while in other cases fish are indifferent to its presence (e.g., Bugert & 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 instream drift (Chapman 1962; Hartman 1965; Puckett & 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 (Ruggles 1966; Fausch 1984), often with little instream 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, in order 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 tradeoff between growth and survival, two components of fitness that are usually measured in different currencies.

Abrahams & Dill (1989) used ideal free distribution (IFD) theory (Fretwell & Lucas 1970; Fretwell 1972) 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 increase 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 & 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 'behavioural titrations' see Kotler & Blaustein 1995).

Because small differences in body size are known to 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 (Sutherland & Parker 1985; Parker & Sutherland 1986) 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 resultant 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 sixteen 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 lab and placed in a 170-L flow-through aquarium where they were maintained at 12 to 15 °C on a 14:10 h light:dark schedule.

Within 36 hours of capture, we anaesthetized fish in a dilute solution of 2-phenoxy-ethanol, determined their mass (nearest 0.01 g) and fork length (nearest mm), and marked them individually by attaching pre-made, colored tags through the musculature posterior to the dorsal fin (Chapman & 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 minutes 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* sp.) *ad libitum* while in the flow-through aquaria.

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 two 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.

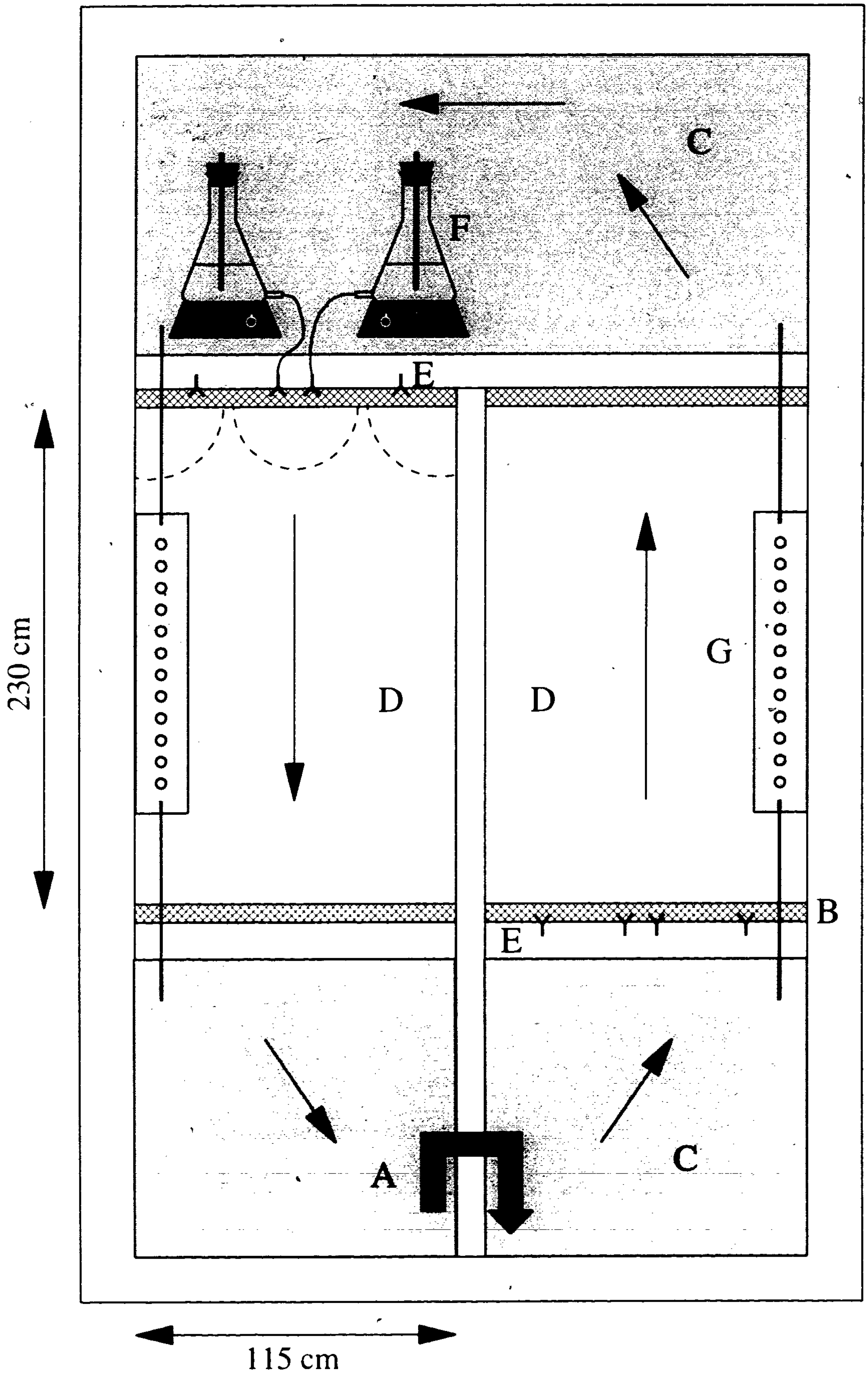
Apparatus and General Methods

We conducted experiments in an artificial stream channel (Figure 2.1) in the woods of the Burnaby Mountain campus of Simon Fraser University. The concrete channel (described more completely in 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 & 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 2.1). 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, 'no-see-um' mesh, was erected over the entire channel to further prevent the entry of both 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 behaviour 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 (diameter = 5 mm) 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 2.1). The positions of the four Y-tubes on the mesh barriers determined the spatial structure of the feeding

Figure 2.1. Schematic top view of the experimental stream channel. Water was pumped over a concrete barrier (A) and travelled 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.


C
F
E
230 cm
D
D
G
B
E
A
C
115 cm

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 2.1) 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-minute trial. Trials were halted by re-inserting the plungers into the syringes when 1000 mL of water remained in the flasks. The number of prey remaining in each flask was counted and subtracted 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 five 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 it's effect on the distribution of competitive weights 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: The effect of cover on foraging site selection

On the first two experimental days, 50 brine shrimp were dispensed from each of the two central feeding positions. The wide area over which prey were broadcast (~ 18 cm) effectively created a single, non-defensible 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 two days were highly correlated ($r = 0.82$, $n = 96$ $p < 0.001$), 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 relatively constant throughout the experiment (see Grand 1997).

On the third experimental day (the 'IFD' trial), prey were dispensed from the two lateral feeding positions. Patches differed in the number of prey they provided to the fish. Seventy-five brine shrimp were placed 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 actual 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 (diameter = 20 cm), suspended 1 cm above the surface of the water (see Figure 2.1). To minimize differences between light levels below the structure and those elsewhere in the channel, we drilled twelve holes (diameter = 1 cm) at regular intervals along the length of the pipe.

On the morning of the fourth day (the 'cover' trial), during the three hours prior to 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. Following 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. The number and identity of fish in each patch and under cover was determined by scan sampling (Martin & 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 prior to 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 towards an increase in the proportion of competitive weights observed in the poor patch in the presence of cover ($\bar{x} \pm$ SE: 0.436 ± 0.044 vs. 0.340 ± 0.021), this difference was not significant ($t = 2.070$, $df = 4$, $p = 0.107$; power = 0.75). In addition, groups of fish responded similarly during the remaining trials regardless of whether or not they had received this additional treatment. Thus, we pooled the data from all twelve groups for the remainder of the analyses.

Experiment #2: The energetic equivalence of cover

We used the ideal free distribution for unequal competitors (Parker & 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:

$$E = \frac{R_g}{C_g} - \frac{R_p}{C_p} \tag{2.1}$$

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 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.

In order 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:

$$\frac{R_g + X_g}{C'_g} = \frac{R_p}{C'_p} + E \tag{2.2}$$

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 (2.2), we can solve for X_g as a function of E. In our experiment,

$$X_g = 0.667E \tag{2.3}$$

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 & 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 prior to the beginning of the foraging trial. 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 are 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 or not. 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 or not 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. Prior to 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 pre-equilibrium values, only data from the second half of each trial (i.e., minutes 13 - 24) 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 analysed similarly. Because all data were homoscedastic and normally distributed, transformations were not required. Unless stated otherwise, reported *p*-values are two-tailed.

RESULTS

General behaviour of the fish

Prior to 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 (~ 1 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.

Experiment #1: The effect of cover on foraging site selection

Distributions of competitive weights varied somewhat over the course of the IFD trial (Figure 2.2a). 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 (minutes 13 - 24), the observed proportion of competitive weights in the poor patch was not significantly different from the proportion of food available there (Figure 2.2a, Table 2.1; $t = 1.211$, $df = 11$, $p = 0.251$, 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.

Figure 2.2. Mean (± SE) proportion of competitive weights in the poor (covered) patch during each minute of the (a) IFD, and (b) cover trials. Dashed lines indicate the mean proportion of food available in the poor patch. *n* = 12 groups of fish.

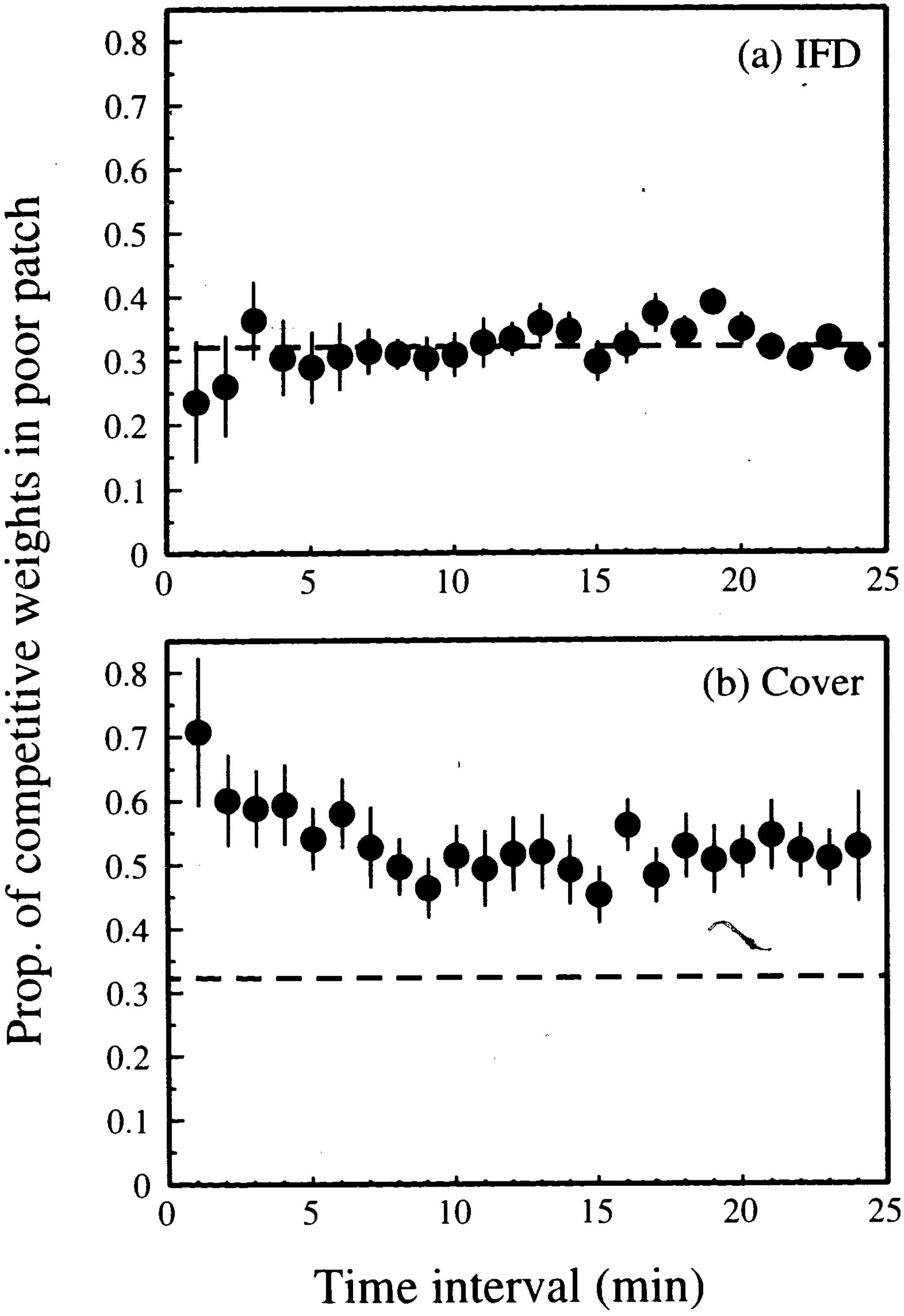

(a) IFD
(b) Cover
Prop. of competitive weights in poor patch
Time interval (min)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0
5
10
15
20
25

Table 2.1. The observed proportion of competitive weights in the poor (covered) patch and the proportion of food available there during minutes 13 to 24 of the IFD, cover and titration trials. The calculated energetic equivalence of cover, *E*, is also indicated for each group of fish. n = 12 groups.

IFD		Cover		Titration		
Comp. wts.	Food	Comp. wts.	Food	Comp. wts.	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
0.338 ± 0.014[a]	0.321 ± 0.004	0.513 ± 0.037	0.322 ± 0.004	0.347 ± 0.037	0.237 ± 0.012	0.839 ± 0.185
$p = 0.251$[b]			$p < 0.001$	$p = 0.519$	$p = 0.012$	

[a] x̄ ± SE; [b] significance of paired *t*-tests comparing distributions of food and distributions of competitive weights

In response to the addition of cover, we observed a shift in the distribution of competitive weights (Figure 2.2b), such that a larger proportion of the competitive weights occurred in the poor patch when cover was present than when it was absent (Table 2.1; $t = 5.033$, $df = 11$, $p = 0.0002$; one-tailed test). The observed distribution of competitive weights was now significantly different from the distribution of food (Figure 2.2b, Table 2.1; $t = 5.001$, $df = 11$, $p < 0.001$), as expected if fish consider the availability of both food and cover during foraging site selection.

Experiment #2: The energetic equivalence of cover

The calculated energetic equivalence of cover varied markedly among groups of fish (see Table 2.1). 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 2.1; $t = 2.698$, $df = 11$, $p = 0.010$; one-tailed test). Furthermore, the distribution of competitive weights was significantly different from the current distribution of food (Table 2.1, Figure 2.3; $t = 2.99$, $df = 11$, $p = 0.012$), 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, prior to the addition of extra food (Table 2.1, Figure 2.3; $t = 0.667$, $df = 11$, $p = 0.519$, power = 0.94) as expected if we had correctly calculated the energetic equivalence of cover.

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 eight minutes of the trial, and thereafter, did not appear to differ from the proportion of food available there. Furthermore, the equilibrium proportions of competitive weights observed in the poor patch were similar for each of the three trials (Table 2.2). Thus, given that we have used only data from the second half of each trial (i.e., minutes 13 to 24) to test our main hypotheses, we are confident that the

Figure 2.3. Mean (± SE) proportion of competitive weights in the poor (covered) patch during each minute 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 minutes 23 and 24 reflect the reduced number of groups represented by those means (*n* = 8 and *n* = 4, respectively). All other *n* 's = 12 groups of fish.

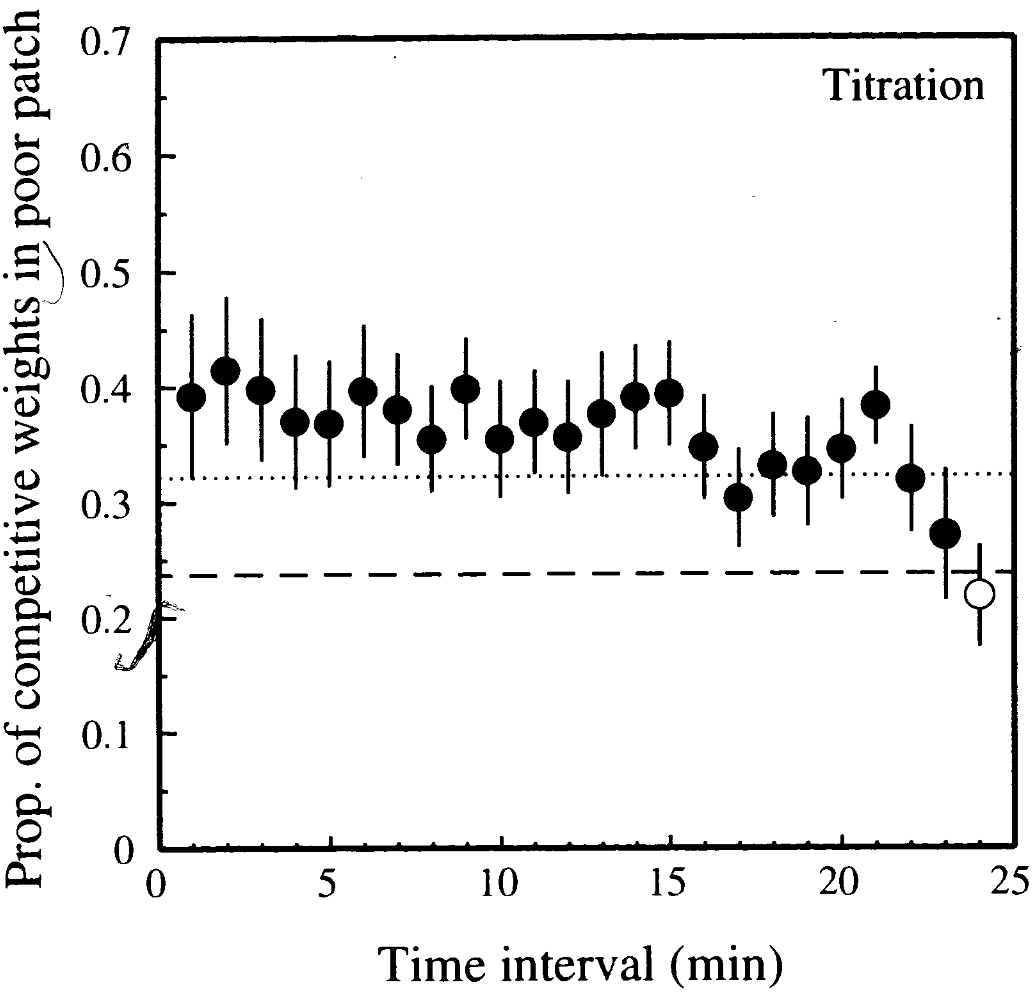

Titration
Prop. of competitive weights in poor patch
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20
25
Time interval (min)

Table 2.2. The mean proportion of competitive weights observed in the poor patch during the 'carry-over' and 'predator habituation' control experiments. Two separate groups of fish were used for each experiment.

	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	.018	0.413	.010	--	--
Group 2	0.499	.020	0.456	.006	--	--

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

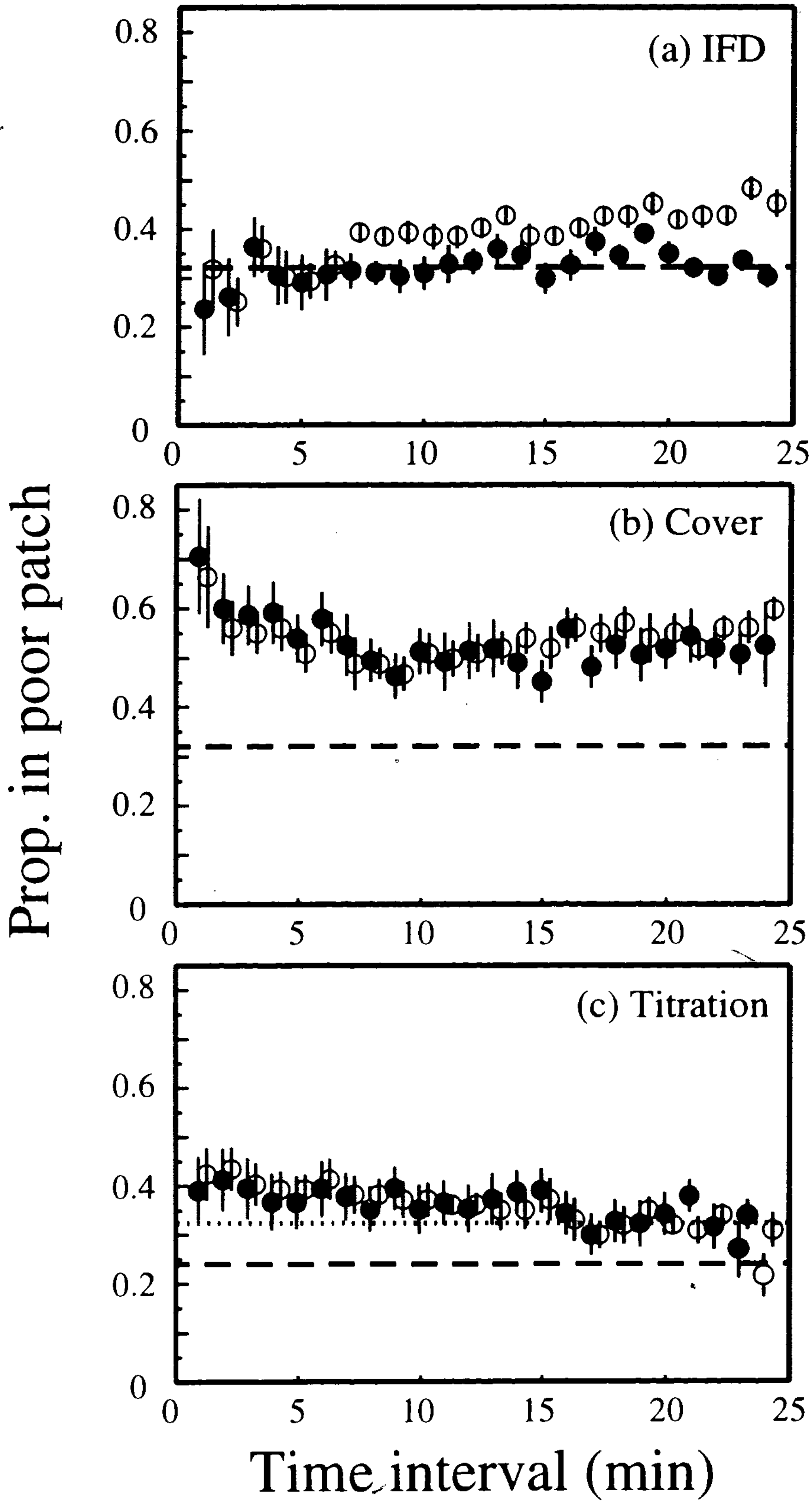
The equilibrium proportion of competitive weights observed in the covered patch did not differ between trials (Table 2.2; $t = -1.00$, $df = 1$, $p = 0.500$, power ~ 0.97). This result suggests that the observed change in the distribution of competitive weights between the cover and titration trials 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.

Individual differences in risk-taking

In contrast to the single equilibrium predicted by the original IFD model for equal competitors (Fretwell & 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 & 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 Figure 5.4 in Milinski & Parker 1991). 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 2.1; $t = 0.213$, $df = 11$, $p = 0.835$; 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 2.4a vs. 3.4c; $t = 1.898$, $df = 11$, $p = 0.084$). 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 2.4b,c; $t = 1.078$, $df = 11$, $p = 0.304$, power = 0.86 and $t = 0.238$, $df = 11$, $p = 0.816$, power = 0.98, respectively), there was a significant difference between their distributions during the IFD trial (Figure 2.4a; $t = 2.838$, $df = 11$, $p = 0.016$). 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

Figure 2.4. Mean (± SE) proportion of fish (○) and competitive weights (●) in the poor (covered) patch during each minute of the (a) IFD, (b) cover, and (c) titration trials. Dashed lines indicate the mean proportion of food available in the poor patch. Competitive weight data are the same as those shown in Figures 2.2 and 2.3. For clarification, open circles have been offset slightly to the right. Shaded symbols for minutes 23 and 24 in (c) reflect the reduced number of groups represented by those means (*n* = 8 and *n* = 4, respectively). All other *n* 's = 12 groups of fish.


(a) IFD
(b) Cover
(c) Titration
Prop. in poor patch
Time interval (min)
0
0.2
0.4
0.6
0.8
0
5
10
15
20
25

competitors of relatively 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 2.5a), this effect was not significant ($F_{12,83} = 1.540, p = 0.127$; ANOVA) and there was no overall effect of competitive weight rank on the proportion of time spent in the poor patch (Figure 2.5a,b,c; $F_{12,83} = 1.179, p = 0.312$; 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 good competitors (Figure 2.6a,b; $F_{12,83} = 3.361, p = 0.001$; ANOVAR). The significance of this relationship, however, appears to be generated primarily by the behaviour 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 ($F_{11,76} = 1.265, p = 0.261$; ANOVAR). Thus, although good competitors may increase their use of the poor patch with the addition of cover, they are less likely than the poorest competitors to be found directly under the cover structure.

Figure 2.5. Mean (± SE) proportion of time spent in the poor (covered) patch by fish differing in competitive weight rank during the (a) IFD, (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.

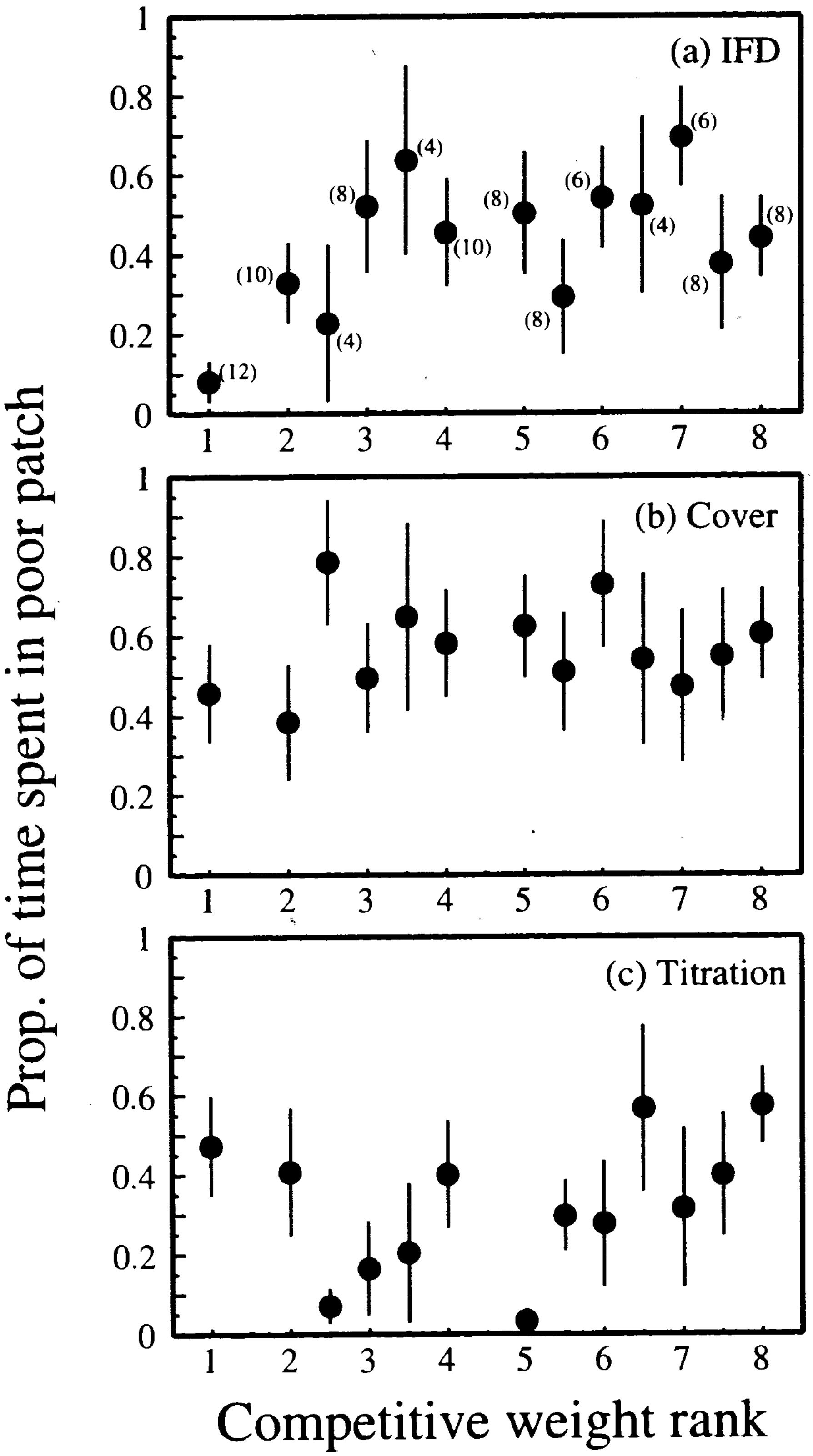
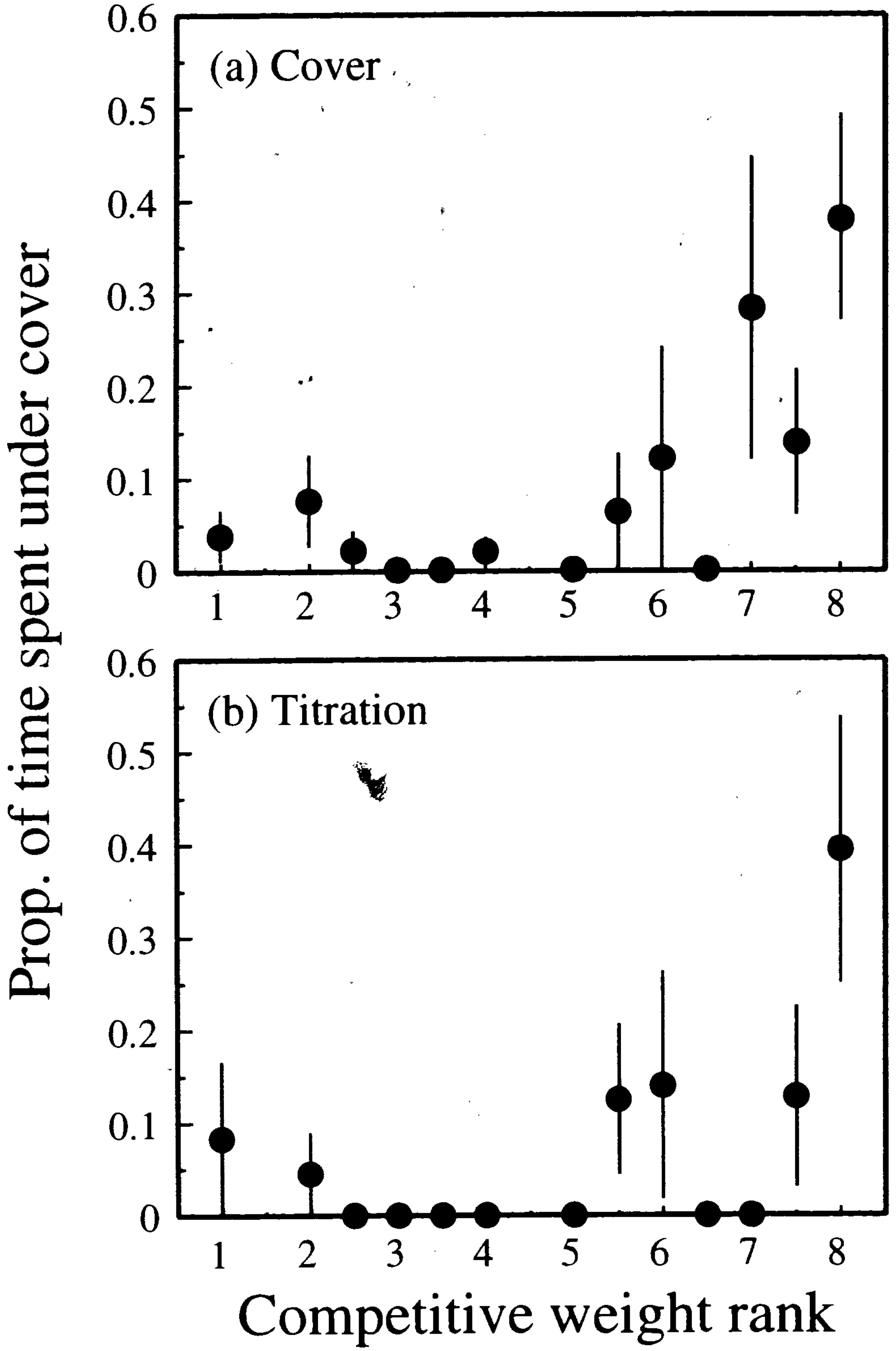

(a) IFD
(b) Cover
(c) Titration
Prop. of time spent in poor patch
Competitive weight rank
0
0.2
0.4
0.6
0.8
1
1
2
3
4
5
6
7
8
(12)
(10)
(4)
(8)
(4)
(10)
(8)
(8)
(6)
(4)
(6)
(8)
(8)

Figure 2.6. Mean (± SE) proportion of time 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 2.5.


(a) Cover
(b) Titration
Prop. of time spent under cover
Competitive weight rank
0
0.1
0.2
0.3
0.4
0.5
0.6
1
2
3
4
5
6
7
8

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 tradeoff 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 behaviour of salmonid fishes (e.g., Ruggles 1966; Dolloff 1986; Huntingford et al. 1988 McMahon & Hartman 1989; Shirvell 1990; Bugert & Bjornn 1991; Bugert et al. 1991; Fausch 1993), 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 tradeoff 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 2.2b). Furthermore, data from the five groups of fish who 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 tradeoff is a continuous one.

Using ideal free distribution theory for unequal competitors (Sutherland & Parker 1985; Parker & Sutherland 1986), it is possible to describe foraging-predation risk tradeoffs 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 & 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 coloured 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 2.3), 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 & Clark 1988) provides another method by which foraging-predation risk tradeoffs 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 behaviour (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 & Fraser (1987) developed an analytic model which 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 to it, 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 & 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 2.4). Thus, these two ideal free distributions 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 the 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 2.5). 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 2.6). 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, having 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 & Godin 1991; see also Damsgård & Dill in prep). 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, who 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 2.6). 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 & 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 & 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 & 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. Thus, the preservation of natural cover and the addition of artificial structures will not increase population densities in all types of habitats. In order 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 tradeoff 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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CHAPTER THREE

Predation risk, unequal competitors, and the ideal free distribution*

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ABSTRACT

Ideal free distribution theory (IFD) has frequently been used to investigate habitat selection when fitness payoffs are frequency-dependent. To date, however, researchers have not considered the possibility that individuals may differ in both their ability to compete for resources and in their susceptibility to predation. Such differences might be expected to occur as a consequence of differences in body size, morphology or behaviour. Here, we develop a model to investigate the effects of differences in competitive ability and mortality risk on the equilibrium distribution of competitors across habitats. For simplicity, we consider the case of two competitor types competing for resources in an environment containing two habitats: a productive, but risky habitat and a less productive, but safer habitat. In general, the model predicts that when individual mortality risk is independent of the density of competitors within a habitat, competitor types will tend to be assorted by competitive ability, with the competitor type experiencing the higher ratio of mortality risk across the habitats ('risk ratio') occurring predominantly in the safer, but less productive habitat. In contrast, when individual mortality risk within a habitat is diluted by competitor number, the model predicts that both competitor types will tend to aggregate in the same habitat, the choice of which depends on which competitor type experiences the higher ratio of mortality risk across the habitats. When good competitors experience a higher risk ratio than poor competitors, both competitor types will tend to aggregate in the risky, but more productive habitat. However, when poor competitors experience the higher risk ratio, both competitor types will tend to aggregate in the safer, but less productive habitat. Because our model can be applied to both intra- and interspecific resource competition, its results may help to predict circumstances under which stable coexistence of competitor types within a habitat is likely to occur.

INTRODUCTION

The process of habitat selection often requires individuals to choose among habitats that differ in growth potential and mortality risk due to predation. When the habitat providing the highest rate of energetic gain is also the most dangerous, habitat selection should reflect a compromise between the conflicting demands of growth and survival. Indeed, many studies have demonstrated that animals are sensitive to both energetic gains and mortality risk during habitat selection, and are capable of responding to such tradeoffs in an adaptive manner (for recent reviews see Lima & Dill 1990; Lima in press). In some cases, however, the fitness consequences of choosing a particular habitat depend not only on the characteristics of the habitat itself, but also on the number of other individuals present (i.e., fitness consequences are density-dependent).

Ideal free distribution theory (IFD; Fretwell & Lucas 1970; Fretwell 1972) has often been used to study the effects of density-dependent resource competition on habitat selection (see Tregenza 1995 for a recent review). Assuming that all individuals are of equal competitive ability, that each has perfect or 'ideal' information about the distributions of both competitors and resources, and is 'free' to move to the habitat where its resource payoff will be greatest, the model predicts that, at equilibrium, the distribution of competitors across habitats will 'match' the distribution of resources (i.e., 'input-matching'; Parker 1974). Implicit in this approach is the assumption that individual resource payoffs decline as the number of competitors in a habitat increases. In some situations, however, individual survival may increase with increasing local population density (Pulliam & Caraco 1984). Group members may experience reduced risk of mortality as a consequence of shared vigilance (Elgar 1989), predator confusion (Milinski & Heller 1978), or simple numerical dilution (Foster & Treherne 1981; Morgan & Godin 1985), particularly when predators are limited in their ability to capture more than a single prey item per attack.

Although a number of researchers have considered the effects of density-dependent growth and mortality on habitat selection within the framework of IFD theory (e.g., McNamara & Houston 1990; Hugie & Dill 1994; Moody et al. 1996), none have allowed for the possibility that competitors might differ both in their ability to compete for resources and in their susceptibility to predation. There are many reasons why such differences might exist. For example, body size may influence an individual's ability to detect and acquire resources (Grand 1997) and its probability of being captured by a predator (Werner & Gilliam 1984). Similarly, individuals may possess morphological features that enhance competitive ability (Price 1978) and/or reduce vulnerability to predators (Abrahams 1995). Thus, differences in body size and morphology among competitors may affect each individual's best resolution to the conflicting demands of growth and survival and, consequently, the equilibrium distribution of competitors across habitats.

Individual differences in competitive ability have already been incorporated into IFD theory by Sutherland & Parker (1985) and Parker & Sutherland (1986), who assumed that an individual's resource 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 are unaffected by local resource or competitor densities, and thus remain the same across habitats, their 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; see Grand 1997).

Here, we model the effect of mortality risk on the unequal competitors IFD model and ask how differences in both competitive ability and susceptibility to predation might influence an individual's choice of habitat and, hence, the equilibrium distribution of competitors across habitats. As with other models of this sort, we assume that competitors have 'ideal' information about all habitat parameters and are 'free' to move to the habitat where their fitness payoff is greatest. We begin by considering situations where individual mortality risk is unaffected by competitor density, and then consider the effect of dilution of mortality risk on habitat selection. Finally, we compare the predictions of our model to the patterns of habitat selection exhibited by a well-studied assemblage of desert rodents, illustrating how the insights provided by IFD theory may prove useful for understanding patterns of species coexistence and community structure.

THE MODEL

We model the distribution of a large number of competitors of two types: 'poor' competitors (type 1) and 'good' competitors (type 2). The total number of type 1 and 2 competitors is given by N_1 and N_2, respectively. We define K as the competitive ability of good competitors relative to poor competitors (i.e., $K > 1$), and assume that K remains constant across habitats. We consider an environment containing two habitats: a 'good' habitat (A) and a 'poor' habitat (B), with resource availability in each given by R_A and R_B (energy $\cdot$ time^{-1}), respectively. We assume that resources are continually renewing, and therefore non-depleting, and that the rate of energy gain per unit of competitive ability is inversely proportional to the number of competitive units in a habitat ('continuous input' scenario of Tregenza 1995). For a summary of all constants and variables used in the model, see Table 3.1.

In addition to differing in resource availability, habitats also differ in their associated mortality risk, such that the risk of death due to predation for type i competitors in habitat j is given by μ_{ij} (probability $\cdot$ time^{-1}). We assume that competitor types are encountered at random by the predator who exhibits no diet selectivity. Predation risk might be expected to differ between habitats as a consequence of differences in structural complexity, light levels, or the availability of refuge sites. The risk of mortality experienced by the two competitor types might be expected to differ as a consequence of differences in their morphology, body size and predator avoidance behaviour, including flight initiation distance and flight speed (Lima & Dill 1990). Some competitor types may also be more easily detected by predators than others, particularly when competitive ability is correlated with body size. Initially, we assume μ_{ij} to be independent of the number of competing individuals in a habitat. In keeping with our interest in foraging-predation risk tradeoffs, we consider only scenarios where $\mu_{iA} \geq \mu_{iB}$ (i.e., the more productive habitat is at least as dangerous as the less productive habitat), for both competitor types.

We seek the equilibrium distribution of competitor types across the habitats, assuming that all individuals seek to maximize their fitness. We describe the distribution of the i th competitor type (where $i = 1, 2$) by the proportion of those competitors in habitat A, p_i ; their proportion in habitat B is given by $1 - p_i$. To incorporate both energetic gains and mortality risk in a single currency, we calculate fitness in terms of expected lifetime production of offspring. We assume that population size is held constant

Table 3.1. Summary and definitions of all constants and variables used in the model.

Symbol	Definition	Units
$i = 1, 2$	competitor type	--
N_i	total number of type i competitors	--
K	competitive ability of type 2 competitors relative to type 1 competitors	--
$j = A, B$	habitat	--
R_j	prey availability in habitat j	energy · time^{-1}
μ_{ij}	mortality risk for type i competitors in habitat j	probability of death · time^{-1}
p_i	proportion of competitor type i in habitat A	--
$1 - p_i$	proportion of competitor type i in habitat B	--
$l(i, j)$	lifespan of competitor type i in habitat j	time
$e(i, j)$	net energy intake of competitor type i in habitat j	energy · time^{-1}
F	proportion of energy available for growth	--
M_i	metabolic requirement of competitor type i	energy · time^{-1}
O	energetic cost per offspring	energy · offspring^{-1}
$w(i, j)$	fitness of competitor type i in habitat j	offspring
$\hat{p}_i$	equilibrium proportion of type i competitors in habitat A	--
c_j	sum of competitive abilities in habitat j	--
n_j	total number of competitors in habitat j	--
$\mu_{ij}(n_j)$	mortality risk for type i competitors in habitat j as a function of the number of competitors there	probability of death · time^{-1}
d	dilution exponent	--

due to density-dependent factors (i.e., parasitism or disease) and impose no maximum lifespan (as in Hugie & Dill 1994).

Since we begin by assuming that mortality risk is independent of competitor density, the expected lifespan of competitor type i in habitat j ($l(i, j)$) is simply:

$$l(i\,,j) = \frac{1}{\mu_{ij}} \tag{3.1}$$

The expected net energy intake rate of competitor type i in habitat j ($e(i, j)$), however, depends on the distribution of both type 1 (p_1) and type 2 (p_2) competitors. As a consequence of differences in competitive ability, energy intake rates differ for good and poor competitors. For good competitors, expected net energy intake rates in habitats A and B are equal to:

$$e(2\,,A) = K\left(\frac{R_A}{p_1\,N_1 + p_2\,N_2\,K}\right)F - M_2 \tag{3.2}$$

and

$$e(2\,,B) = K\left(\frac{R_B}{(1-p_1)\,N_1 + (1-p_2)\,N_2\,K}\right)F - M_2\,, \tag{3.3}$$

respectively, where F is the proportion of acquired energy that is available for reproduction and M_i is the metabolic requirement (energy · time^{-1}) of competitor type i. The corresponding expected net energy intake rates of poor competitors are equal to:

$$e(1, A) = \left(\frac{R_A}{p_1\,N_1 + p_2\,N_2\,K}\right)F - M_1 \tag{3.4}$$

and

$$e(1, B) = \left(\frac{R_B}{(1-p_1)\,N_1 + (1-p_2)\,N_2\,K}\right)F - M_1 \tag{3.5}$$

For simplicity, we assume that F is the same for both competitor types, and that F and M_i are independent of habitat. Thus, fitness of the i th competitor type in the j th habitat ($w(i\,,j\,)$) equals:

$$w(i\,,j\,) = \frac{l(i\,,j\,)\,e(i\,,j\,)}{O} \tag{3.6}$$

where O is the energy required to produce a single offspring. We assume that all individuals in the population are capable of reproduction, and therefore can translate energy directly into offspring.

The distribution of competitor type i will be at equilibrium when its fitness payoffs in the two habitats are equal:

$$w(i, A) = w(i, B) \tag{3.7}$$

Substituting in the appropriate expressions for $l(i, j)$ and $e(i, j)$, and solving equation (3.7) for the equilibrium distribution of each competitor type as a function of the other produces two straight lines, each having a negative slope and a positive intercept:

$$\hat{p}_2 = -\left(\frac{N_1}{N_2 K}\right)p_1 + \left(\frac{R_A \mu_{2B}}{R_A \mu_{2B} + R_B \mu_{2A}}\right)\left(\frac{N_1 + N_2 K}{N_2 K}\right) \tag{3.8}$$

and

$$\hat{p}_1 = -\left(\frac{N_2 K}{N_1}\right)p_2 + \left(\frac{R_A \mu_{1B}}{R_A \mu_{1B} + R_B \mu_{1A}}\right)\left(\frac{N_1 + N_2 K}{N_1}\right) \tag{3.9}$$

where $\hat{p}_1$ and $\hat{p}_2$ are the equilibrium proportions of type 1 and type 2 competitors in the good habitat (A). Equations (3.8) and (3.9) represent the fitness isoclines for good and poor competitors, respectively, such that all points on competitor type i's fitness isocline denote distributions of the two competitor types for which the fitness payoff obtained by the i th competitor type is the same in each habitat. In order to compare their slopes and intercepts directly, we plot these two isoclines on a common set of axes (i.e., p_2 vs. p_1) by rearranging equation (3.9) and solving for p_2. Thus, the fitness isocline for type 1 competitors becomes:

$$p_2 = -\left(\frac{N_1}{N_2 K}\right)\hat{p}_1 + \left(\frac{R_A \mu_{1B}}{R_A \mu_{1B} + R_B \mu_{1A}}\right)\left(\frac{N_1 + N_2 K}{N_2 K}\right) . \tag{3.10}$$

Note that the fitness isoclines for type 1 and 2 competitors have the same, negative slope and differ only with respect to intercept. As a consequence, these isoclines will never intersect and the usual method of solving for the simultaneous equilibrium of the two competitor types (or more generally, two alternative strategies) cannot be used (see Hugie

& Grand in press). Instead, we use the graphical methods of Rosenzweig & MacArthur (1963) to determine what the combined equilibrium distribution of type 1 and 2 competitors will look like under a variety of conditions. We confirm these equilibria and their stability by computer simulation, using the evolutionary difference equations described in Appendix 3.1.

Fitness isoclines of the two competitor types will overlap completely when their intercepts are identical:

$$\left(\frac{R_A\,\mu_{2B}}{R_A\,\mu_{2B}+R_B\,\mu_{2A}}\right)\left(\frac{N_1+N_2\,K}{N_2\,K}\right)=\left(\frac{R_A\,\mu_{1B}}{R_A\,\mu_{1B}+R_B\,\mu_{1A}}\right)\left(\frac{N_1+N_2\,K}{N_2\,K}\right) \tag{3.11}$$

or more simply, when the ratio of mortality risk across the habitats (hereafter referred to as the 'risk ratio') is the same for both competitor types:

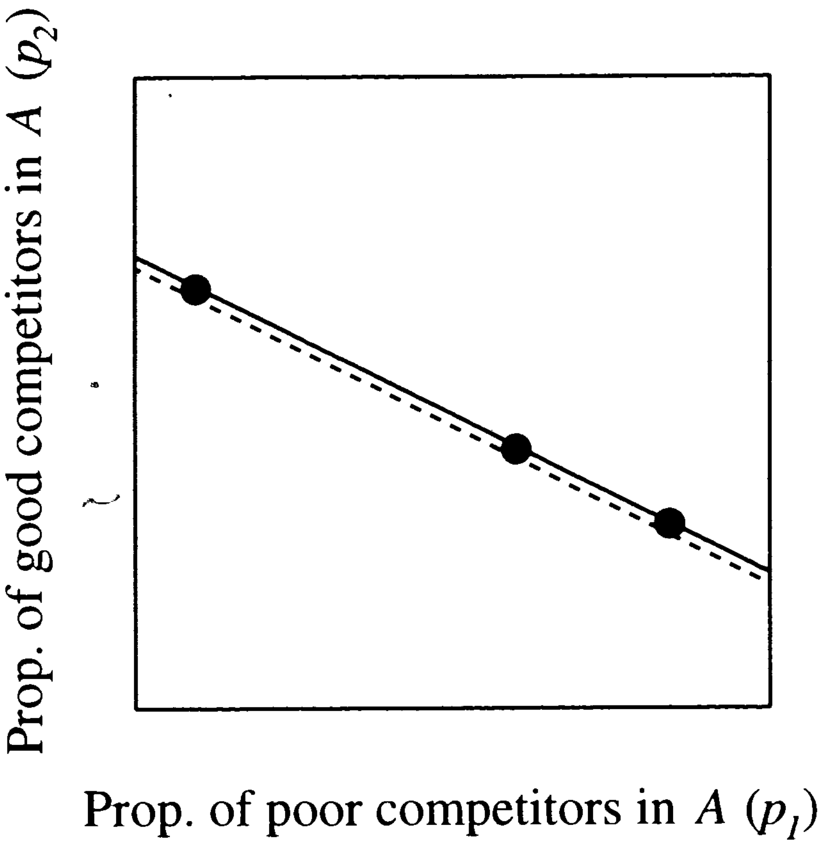
$$\frac{\mu_{1A}}{\mu_{1B}}=\frac{\mu_{2A}}{\mu_{2B}} \tag{3.12}$$

In this case, the simultaneous equilibrium of type 1 and 2 competitors can occur anywhere along the shared fitness isocline, its exact location depending only upon the initial distribution of competitor types, $(p_1, p_2)_{t=0}$ (Figure 3.1). When $(p_1, p_2)_{t=0}$ lies below the shared isocline, both competitor types experience higher fitness payoffs in habitat *A*. As a consequence, both will increase their proportion in *A* until payoffs in the two habitats are equal. Similarly, when $(p_1, p_2)_{t=0}$ lies above the isocline, both competitor types experience higher fitness payoffs in habitat *B* and will decrease their proportion in *A* until fitness payoffs in the two habitats are equal. All points along the shared isocline represent stable distributions of competitor types 1 and 2 (see Appendix 3.1). For all such $(\hat{p}_1, \hat{p}_2)$:

$$\frac{c_A}{c_B}=\frac{\hat{p}_1\,N_1+\hat{p}_2\,N_2\,K}{(1-\hat{p}_1)\,N_1+(1-\hat{p}_2)\,N_2\,K}=\left(\frac{R_A}{R_B}\right)\left(\frac{\mu_{1B}\,\mu_{2B}}{\mu_{1A}\,\mu_{2A}}\right)\left(\frac{\mu_{2A}-\mu_{1A}}{\mu_{2B}-\mu_{1B}}\right) \tag{3.13}$$

where c_A and c_B are the sums of competitive weights in habitats *A* and *B*, respectively. Hence, when competitor types experience the same ratio of mortality risk across the habitats (i.e., when expression (3.12) is true), regardless of the absolute mortality risk in each, the ratio of the sum of competitive weights across the two habitats will be

Figure 3.1. Fitness isoclines for type 1 (- - -) and type 2 (—) competitors when both experience the same ratio of mortality risk across the two habitats. The combined equilibrium (●) can occur anywhere along the shared isocline, depending on the initial distribution of competitor types.

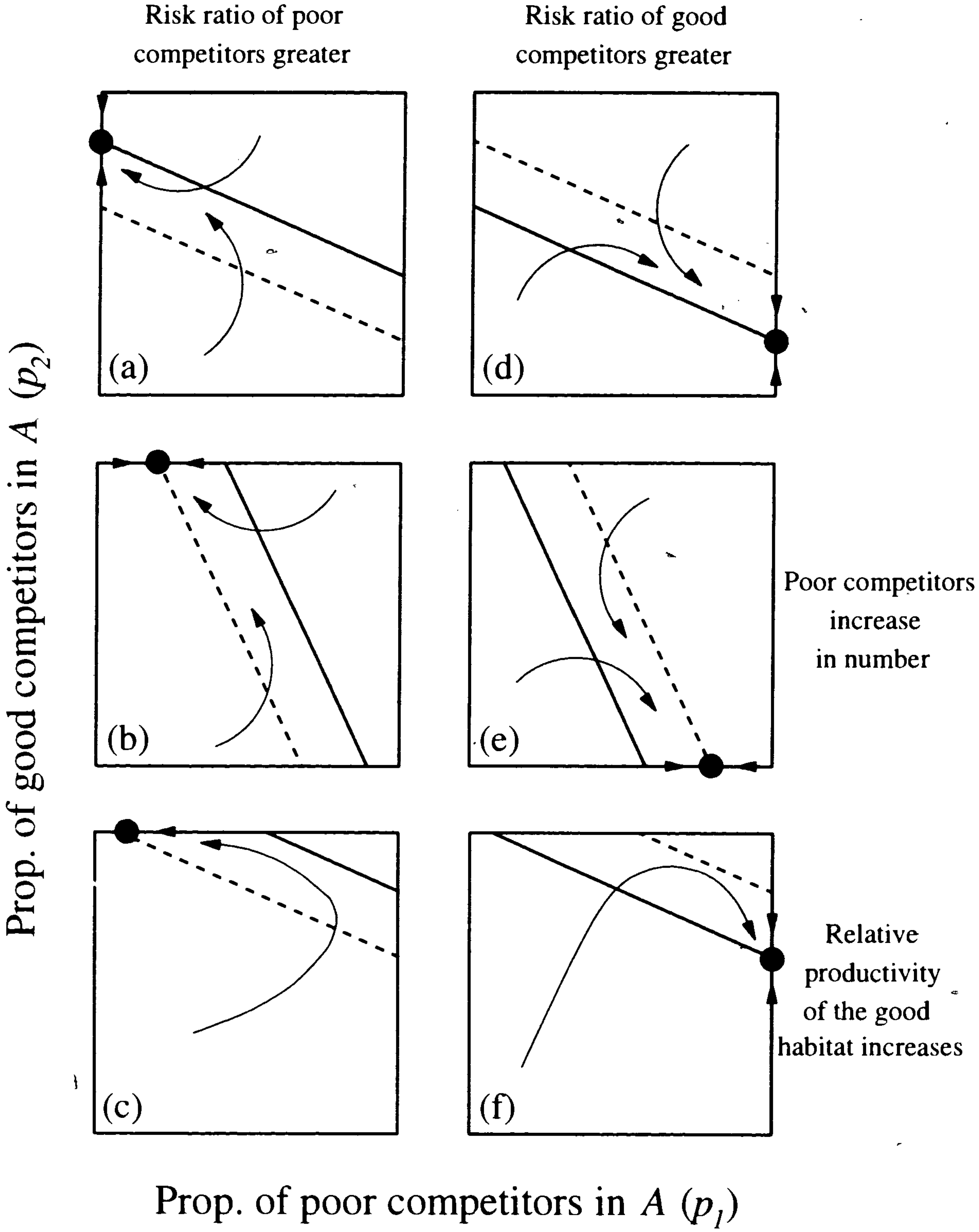

Prop. of good competitors in A (p_2)
Prop. of poor competitors in A (p_1)

proportional to (1) the ratio of resource availabilities, (2) the inverse of each competitor type's risk ratio, and (3) the ratio of the within-habitat differences in mortality risk between competitor types. All equilibria that satisfy equation (3.13) are characterized by under-matching of competitive weights (i.e., there are fewer competitive weights in the good patch than predicted by the distribution of resources alone), given that both competitor types experience a higher risk of mortality in habitat *A* than in habitat *B*. Note that when habitats have the same mortality risk (i.e., $\mu_{1A} = \mu_{1B}$ and $\mu_{2A} = \mu_{2B}$), the distribution of competitive weights matches the distribution of resources, as originally predicted by Parker and Sutherland (1986).

When competitor types experience different ratios of mortality risk across the habitats (i.e., when expression (3.12) is false), their fitness isoclines no longer share a common intercept. The fitness isocline of the competitor type with the higher risk ratio is lower in elevation, corresponding to a decrease in the proportion of that competitor type in habitat *A* for any given distribution of the other competitor type. Intuitively, this makes sense, since the competitor type whose risk of mortality is most greatly reduced by using the poor habitat should be more likely to be found there.

The location of the combined equilibrium ($\hat{p}_1$, $\hat{p}_2$) now depends primarily on which competitor type experiences the higher ratio of mortality risk across the habitats. When poor (type 1) competitors have a higher risk ratio than good (type 2) competitors, their fitness isocline is lower in elevation than that of good competitors. The combined equilibrium usually occurs at the intersection of the type 2 competitors' isocline and the y-axis, regardless of the initial distribution of competitor types (Figure 3.2a). However, depending on the steepness and elevation of this isocline (see below), its intersection with the y-axis may occur at $p_2 > 1$, in which case, the equilibrium occurs at the intersection of the type 1 competitors' isocline and the line $p_2 = 1$ (Figure 3.2b). In both cases, the combined equilibrium is characterized by at least one competitor type occurring exclusively in a single habitat. Either good competitors occur exclusively in habitat *A*, accompanied by only a small proportion of poor competitors (Figure 3.2b), or poor competitors occur exclusively in habitat *B*, accompanied by only a small proportion of good competitors (Figure 3.2a). Note that at this equilibrium, only the competitor type that occurs in both habitats experiences the same fitness payoff in each habitat (i.e., only for this competitor type will equation (3.7) be satisfied).

Figure 3.2. The effects of changing relative competitor density (N_1:N_2) and relative habitat productivity (R_A:R_B) on the fitness isoclines of type 1 (- - -) and type 2 (—) competitors, when (a, b, c) poor competitors experience a higher ratio of mortality risk across the habitats, or (d, e, f) good competitors experience a higher ratio of mortality risk across the habitats. The location of the combined equilibrium and sample trajectories of the change in the proportion of each competitor type in habitat *A* for all $(p_1, p_2) \neq (\hat{p}_1, \hat{p}_2)$ are indicated by ● and →, respectively. In all cases, $\mu_{1A} = \mu_{2A} = 0.5$, $K = 2$ and $N_2 = 1000$. Remaining parameter values for (a) $R_A = 1.2$, $R_B = 0.8$, $\mu_{2B} = 0.5$, $\mu_{1B} = 0.3$, $N_1 = 1000$; (b) $R_A = 1.2$, $R_B = 0.8$, $\mu_{2B} = 0.5$, $\mu_{1B} = 0.3$, $N_1 = 3000$; (c) $R_A = 1.6$, $R_B = 0.4$, $\mu_{2B} = 0.5$, $\mu_{1B} = 0.3$, $N_1 = 1000$; (d) $R_A = 1.2$, $R_B = 0.8$, $\mu_{2B} = 0.3$, $\mu_{1B} = 0.5$, $N_1 = 1000$; (e) $R_A = 1.2$, $R_B = 0.8$, $\mu_{2B} = 0.3$, $\mu_{1B} = 0.5$, $N_1 = 3000$; (f) $R_A = 1.6$, $R_B = 0.4$, $\mu_{2B} = 0.3$, $\mu_{1B} = 0.5$, $N_1 = 1000$.


Risk ratio of poor competitors greater
Risk ratio of good competitors greater
(a)
(d)
(b)
(e)
Poor competitors increase in number
(c)
(f)
Relative productivity of the good habitat increases
Prop. of good competitors in A (p_2)
Prop. of poor competitors in A (p_1)

When good competitors have a higher ratio of mortality risk across the habitats than poor competitors, the fitness isocline of type 2 competitors is lower in elevation than that of type 1 competitors, and the combined equilibrium usually occurs where the type 2 competitors' isocline intersects the line $p_1 = 1$, regardless of the initial distribution of competitor types (Figure 3.2d). However, depending on the steepness and elevation of the isocline (see below), this intersection may occur below the x-axis (i.e., at $p_2 < 0$), in which case the equilibrium occurs at the intersection of the type 1 competitors' isocline and the x-axis (Figure 3.2e). Again, the combined equilibrium is characterized by at least one competitor type occurring exclusively in a single habitat. Either poor competitors occur exclusively in habitat *A*, accompanied by only a small proportion of good competitors (Figure 3.2d), or good competitors occur exclusively in habitat *B*, accompanied by only a small proportion of poor competitors (Figure 3.2e).

Thus, when competitor types experience different ratios of mortality risk across the habitats, equilibria tend to be characterized by segregation of competitor types (i.e., animals tend to be assorted by competitive ability). The competitor type with the higher risk ratio tends to avoid the risky habitat, regardless of which competitor type is at absolutely greater risk there. Again, distributions of competitive weights are always under-matched relative to the distribution of resources, assuming that both competitor types experience a higher risk of mortality in habitat *A* than in habitat *B*.

The slopes and elevations of the two fitness isoclines, and therefore the location of the combined equilibrium, are influenced by the values of N_1, N_2 and K, and R_A, R_B, and μ_{ij}, respectively. As the abilities of the competitor types become more similar (i.e., $K \rightarrow 1$), or the number of poor competitors increases relative to the number of good competitors, the slopes of both isoclines increase (Figure 3.2a,b and Figure 3.2d,e) and become bounded by the line $p_2 = 1$. This bounding also occurs as the productivity of the good patch increases relative to that of the poor patch and the isoclines increase in elevation (Figure 3.2a,c and Figure 3.2d,f). As a consequence of increases in isocline slope, both competitor types increase their proportion in habitat *A*, as long as poor competitors experience a higher ratio of mortality risk across the habitats than do good competitors (e.g., Figure 3.2a,b). This occurs because the 'resource space' required by good competitors decreases with their competitive advantage, leaving vacancies to be filled in habitat *A* (in the case of decreasing *K*) and because increasing numbers of poor competitors in both habitats reduce the benefits associated with the safer habitat, particularly for good competitors (in the case of increasing N_1:N_2). In contrast, when good competitors have a higher risk ratio than poor competitors, increases in isocline slope result in both competitor types decreasing their proportion in A (e.g., Figure 3.2d,e). This is because the energetic benefits received by good competitors no longer outweigh the mortality cost associated with the riskier habitat.

Increase in the elevation of fitness isoclines result in both competitor types increasing their proportion in habitat A, regardless of which competitor types experiences the higher ratio of mortality risk across the habitats (compare Figures 3.2d and 3.2f or Figures 3.2d and 3.2f), solely as a consequence of increased resource availability. Finally, the magnitude of the difference in elevation between the isoclines depends on the difference in the risk ratios of the two competitor types: as the difference between risk ratios increases, the difference in elevation between the fitness isoclines increases as well.

Regardless of the parameter values chosen, when competitor types experience different ratios of mortality risk across the habitats and risk is undiluted by competitor number, individuals will tend to be assorted by competitive ability, with the competitor type experiencing the higher risk ratio occurring predominantly in the less productive (but safer) habitat.

Incorporating dilution of mortality risk

Thus far, we have assumed that the mortality risk experienced by each individual is independent of the number of individuals in the habitat. However, as with foraging payoffs, mortality risk may also be density-dependent, if for example, predators are constrained in their ability to pursue, capture and handle more than one prey item at a time. We now consider the effect of dilution of mortality risk on the equilibrium distribution of competitor types. Per capita mortality risk experienced by the i th competitor type in the j th habitat, μ_{ij} (i.e., where μ_{ij} is defined as the risk experienced by a single competitor of the i th type in the j th habitat), is now a function of the total number of competitors in that habitat, $\mu_{ij}(n_j)$, independent of their respective competitive abilities. For example, in habitat A, the mortality risk experienced by type 2 competitors is equal to:

$$\mu_{2A}(n_A) = \frac{\mu_{2A}}{(p_1 N_1 + p_2 N_2)^d} \qquad (3.14)$$

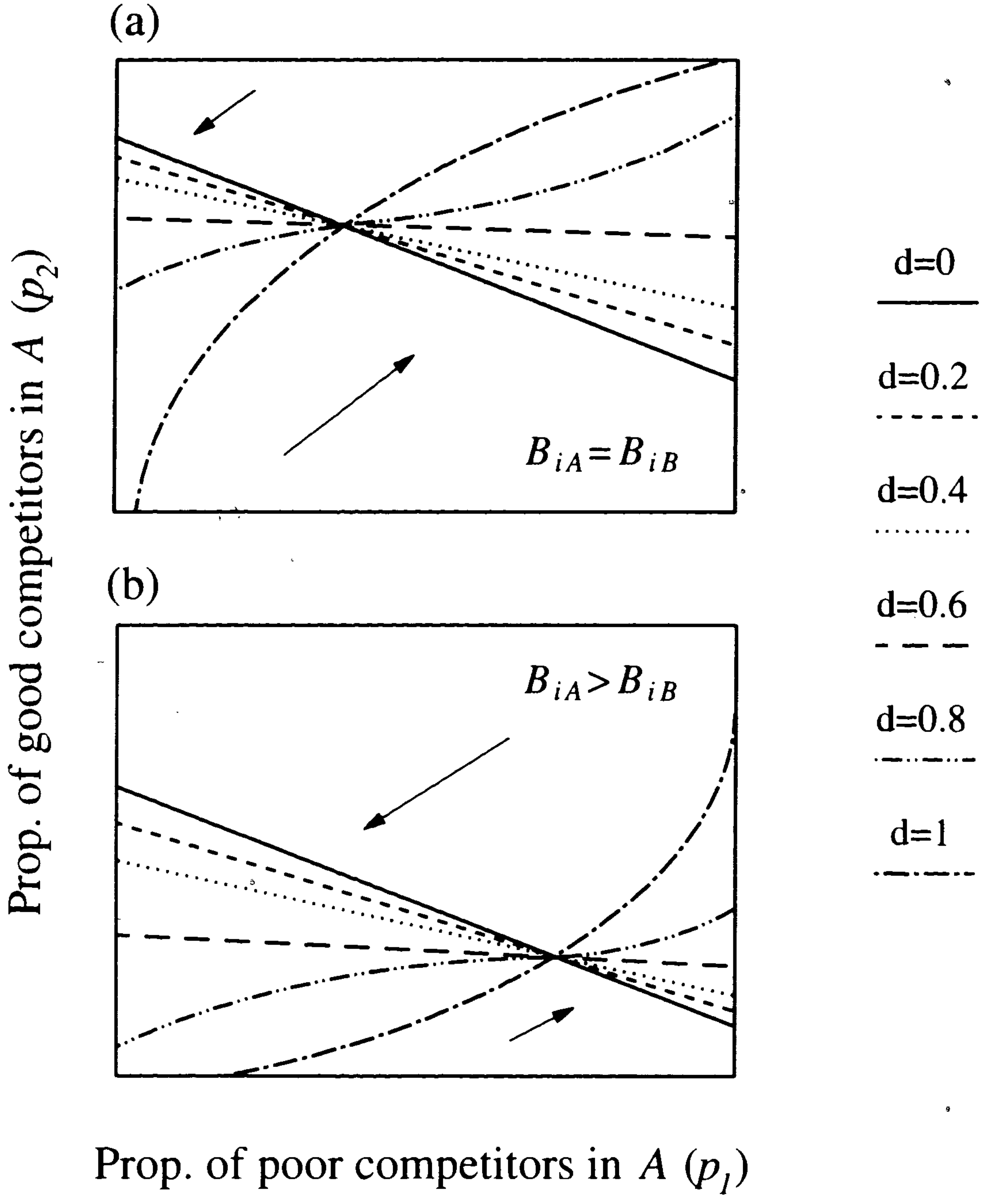
where d scales the relationship between competitor number and risk of mortality ($0 \leq d \leq 1$). When $d = 0$, there is no dilution of mortality risk and the risk experienced by each individual in the habitat is as described earlier. When $d = 1$, mortality risk is fully diluted, and all individuals in the habitat experience a reduction in risk that is directly proportional to the number of individuals there. Again, we assume that competitor types are encountered at random and that there is no diet selectivity on the part of the predator.

With the addition of the dilution exponent, the equilibrium distribution of competitor type i can no longer be expressed as a simple function of the distribution of the other competitor type (i.e., in the terms of equations (3.8) and (3.9)). We can, however, approximate the fitness isoclines of the two competitor types numerically. In doing so, we ask what distribution of type i competitors is required to satisfy expression (3.7), given a variety of distributions of the other competitor type. As before, we use these isoclines to determine what the combined equilibrium distribution of type 1 and 2 competitors will look like under a variety of conditions and confirm the equilibria and their stability via computer simulation (see Appendix 3.1).

As shown previously, when $d = 0$, the fitness isocline of each competitor type is a straight line with negative slope and positive intercept. As d increases, both isoclines rotate counter-clockwise, their slopes first decreasing to 0 then increasing positively, in some cases, decelerating or accelerating as $d \to 1$ (Figure 3.3a,b, respectively).

Once again, when the mortality risk ratios of the two competitor types are identical, their fitness isoclines overlap completely. The combined equilibrium can occur anywhere along the shared fitness isocline, its exact location depending on both the initial distribution of competitor types, $(p_1, p_2)_{t=0}$, and the degree of dilution. When $(p_1, p_2)_{t=0}$ lies below the shared isocline, both competitor types experience higher fitness payoffs in habitat A than in habitat B. As a consequence, both competitor types will alter their proportion in A until payoffs in the two habitats are equal (see arrows in Figure 3.3). Similarly, when $(p_1, p_2)_{t=0}$ lies above the isocline, both competitor types experience higher fitness payoffs in B than in A, and will alter their distribution until fitness payoffs in the two habitats are equal. All points along the shared isocline represent stable distributions of competitor types 1 and 2. Regardless of the initial distribution of good and poor competitors, for all such $(\hat{p}_1, \hat{p}_2)$ it can be shown that:

Figure 3.3. The effect of increasing the strength of dilution on the shared fitness isocline of type 1 and 2 competitors when (a) inherent mortality risk in the two habitats is equal and (b) habitat *A* is inherently riskier than habitat *B*. Arrows indicate sample trajectories of the change in the proportion of each competitor type in habitat *A* for all $(p_1, p_2) \neq (\hat{p}_1, \hat{p}_2)$. In both (a) and (b), $R_A = 1.2$, $R_B = 0.8$, $N_1 = N_2 = 1000$, $K = 2$ and $\mu_{1A} = \mu_{2A} = 0.5$. In (a), $\mu_{1B} = \mu_{2B} = 0.5$. In (b), $\mu_{1B} = \mu_{2B} = 0.3$.


(a)
$B_{iA}=B_{iB}$
(b)
$B_{iA}>B_{iB}$
Prop. of good competitors in A (p_2)
Prop. of poor competitors in A (p_1)
d=0
d=0.2
d=0.4
d=0.6
d=0.8
d=1

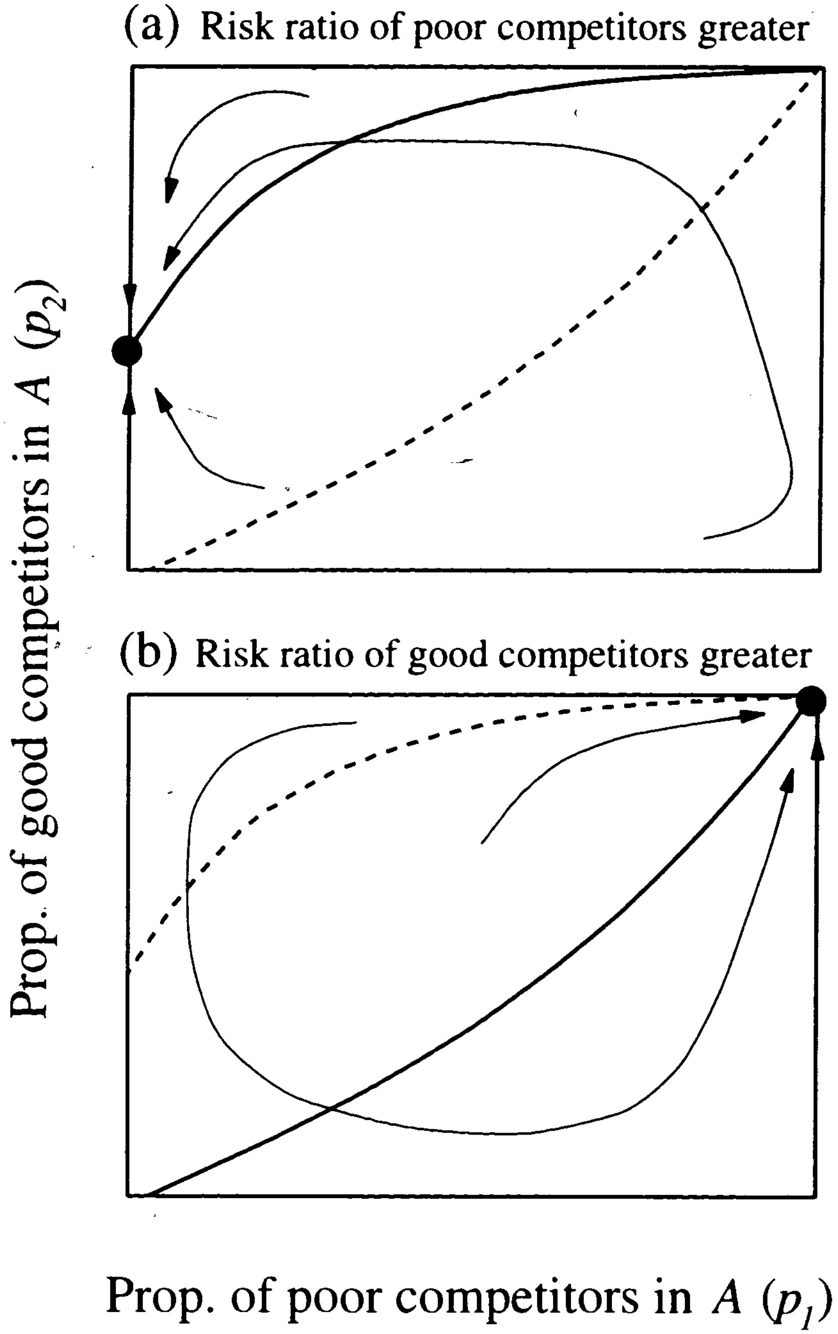
$$\frac{c_A}{c_B} = \left(\frac{R_A}{R_B}\right)\left(\frac{\mu_{1B}\,\mu_{2B}}{\mu_{1A}\,\mu_{2A}}\right)\left(\frac{\mu_{2A} - \mu_{1A}}{\mu_{2B} - \mu_{1B}}\right)\left(\frac{\hat{p}_1 N_1 + \hat{p}_2 N_2}{(1 - \hat{p}_1) N_1 + (1 - \hat{p}_2) N_2}\right)^d \tag{3.15}$$

Hence, when competitor types experience the same ratio of mortality risk across the habitats, the ratio of the sum of competitive weights across the habitats will be proportional to (1) the ratio of resource availabilities, (2) the inverse of each competitor type's risk ratio, (3) the ratio of the within-habitat differences in mortality risk between competitor types, (4) the ratio of competitor numbers across the habitats, and (5) the strength of dilution. Equilibria that satisfy equation (3.15) may be characterized by input-, under- or over-matching of competitive weights, depending on the relative risk of mortality in the two habitats and the degree of dilution. In general, when habitats differ greatly in mortality risk and the strength of dilution is weak, under-matching of competitive weights is usually observed.

When the risk ratios of competitor types differ, their fitness isoclines are no longer identical. As was the case without risk dilution, the fitness isocline of the competitor type with the higher risk ratio is lower in elevation, corresponding to a decrease in the proportion of that competitor type in habitat *A* for any given distribution of the other competitor type. Again, this makes intuitive sense, since the competitor type whose probability of survival is most greatly increased by using the poor habitat should be more likely to be found there.

As before, the location of the combined equilibrium $(\hat{p}_1, \hat{p}_2)$ depends primarily on which competitor type experiences the higher ratio of mortality risk across the habitats. When poor competitors have a higher risk ratio than good competitors, their fitness isocline is lower in elevation than that of good competitors, and the combined equilibrium usually occurs at the intersection of the type 2 competitors' isocline and the y-axis, regardless of the initial distribution of competitor types (Figure 3.4a). Depending on the steepness and elevation of this isocline, particularly when dilution is weak, the intersection may occur beyond (0, 1), in which case, the equilibrium occurs where the type 1 competitors' isocline crosses the line $p_2 = 1$ (see Figure 3.2b). In either case, poor competitors tend to occur almost exclusively in habitat *B*, with the proportion of good competitors occurring there increasing as the dilution exponent increases. Competitive weights are always under-matched relative to the distribution of resources, given that habitat *A* is riskier than habitat *B* for both competitor types.

Figure 3.4. Fitness isoclines for type 1 (- - -) and type 2 (—) competitors under full dilution of mortality risk ($d = 1$), when (a) poor competitors experience a higher ratio of mortality risk across the habitats, and (b) good competitors experience a higher ratio of mortality risk across the habitats. The location of the combined equilibrium and sample trajectories of the change in the proportion of each competitor type in habitat A for all $(p_1, p_2) \neq (\hat{p}_1, \hat{p}_2)$ are indicated by ● and →, respectively. In both (a) and (b), $R_A = 1.2$, $R_B = 0.8$, $\mu_{1A} = \mu_{2A} = 0.5$, $K = 2$ and $N_1 = N_2 = 1000$. In (a), $\mu_{2B} = 0.5$ and $\mu_{1B} = 0.3$. In (b), $\mu_{2B} = 0.3$ and $\mu_{1B} = 0.5$.



(a) Risk ratio of poor competitors greater

(b) Risk ratio of good competitors greater

Conversely, when good competitors have a higher risk ratio than poor competitors, their fitness isocline is lower in elevation than that of poor competitors, and the combined equilibrium occurs at the intersection of the type 2 competitors' isocline and the line $p_1 = 1$ (Figure 3.4b). Again, depending on the steepness and elevation of this isocline, and the magnitude of d, the intersection may occur at $p_2 < 0$, in which case, the equilibrium occurs at the intersection of the type 1 competitors' isocline and the x-axis (e.g., Figure 3.2e). Poor competitors tend to occur almost exclusively in habitat A, with the proportion of good competitors occurring there increasing as the dilution exponent increases. Depending on the difference in competitor type risk ratios and the degree of dilution, $(\hat{p}_1, \hat{p}_2)$ may be characterized by input-, under- or over-matching of competitive weights. In general, the greater the difference in the risk ratios of competitor types and the weaker the effect of dilution, the more frequently under-matching is expected to occur.

Note that as the strength of dilution increases, the tendency of competitor types to aggregate in the same habitat also increases, such that $(\hat{p}_1, \hat{p}_2)$ approaches (1, 1) when the risk ratio of good competitors is higher than that of poor competitors, and (0, 0) when the risk ratio of poor competitors is higher than that of good competitors (compare Figure 3.2a to 3.4a and Figure 3.2d to 3.4b).

The slopes and elevations of the two fitness isoclines, and consequently, the location of the combined equilibrium, are influenced by the values of N_1, N_2 and K, and R_A, R_B, and μ_{ij}, respectively, in the same manner as previously described. Regardless of the parameter values chosen, however, when competitor types experience different ratios of mortality risk across the habitats and mortality risk is diluted by competitor number, competitors tend to aggregate in a single habitat. Furthermore, as the strength of dilution increases, the tendency to aggregate also increases. The habitat chosen depends on which competitor type experiences the higher ratio of mortality risk across the habitats. When good competitors experience the higher risk ratio, both competitor types tend to aggregate in the good habitat (i.e., $(\hat{p}_1, \hat{p}_2) \rightarrow (1, 1)$; compare Figure 3.2d to 3.4b). When the risk ratio of poor competitors is higher than that of good competitors, both competitor types tend to aggregate in the poor habitat (i.e., $(\hat{p}_1, \hat{p}_2) \rightarrow (0, 0)$; compare Figure 3.2a to 3.4a).

Equal competitors – unequal risk: a comparison with Moody et al. (1996)

Recently, Moody et al. (1996) investigated the effects of mortality risk and risk dilution on Fretwell & Lucas' (1970) original equal competitors IFD model. Assuming that individuals are equally susceptible to predation and that current conditions do not alter future fitness expectations, their model predicts that individuals will tend to aggregate in the more productive of two habitats when risk is fully diluted by competitor number and the fitness value of food is relatively high. In contrast, our model predicts that competitor types will sometimes aggregate in the less productive and safer of those habitats under full dilution of mortality risk. In an attempt to understand why such similar models make different predictions, we evaluate our model under the conditions assumed by Moody et al. (1996). Again, we generate fitness isoclines by computer simulation and use them to determine what the equilibrium distribution will look like under a variety of conditions.

Although we generally expect animals to differ in their ability to compete for resources, in some cases, individuals differing in phenotype may be more or less equal in competitive ability (i.e., $K \approx 1$). As was the case for $K > 1$, when $d = 0$, the fitness isocline of each *equal* competitor type is a straight line with negative slope and positive intercept. Now, however, as d increases, isoclines no longer change in slope. Instead, the fitness isoclines increase in elevation, corresponding to an increase in the proportion of both competitor types in habitat A with an increase in the strength of dilution (Figure 3.5).

When competitor types experience the same risk of mortality within a habitat (i.e., $\mu_{1A} = \mu_{2A}$, $\mu_{1B} = \mu_{2B}$), as assumed by Moody et al. (1996), their fitness isoclines overlap completely. The combined equilibrium can occur anywhere along the shared fitness isocline, its exact location depending on the initial distribution of competitor types, $(p_1, p_2)_{t=0}$, and the magnitude of the dilution exponent (Figure 3.5). When $(p_1, p_2)_{t=0}$ lies below the shared isocline, both competitor types experience higher fitness payoffs in habitat A and consequently, increase their proportion in A until payoffs in the two habitats are equal. Similarly, when $(p_1, p_2)_{t=0}$ lies above the isocline, both competitor types experience higher fitness payoffs in habitat B and decrease their proportion in A until fitness payoffs in the two habitats are equal. The stronger the effect of risk dilution, the greater the equilibrium proportion of both competitor types in the riskier habitat.

Figure 3.5. The effect of increasing the strength of dilution on the shared fitness isocline of *equal* type 1 and 2 competitors. $R_A = 1.2$, $R_B = 0.8$, $N_1 = N_2 = 1000$, $K = 1$, $\mu_{1A} = \mu_{2A} = \mu_{1B} = \mu_{2B} = 0.5$.

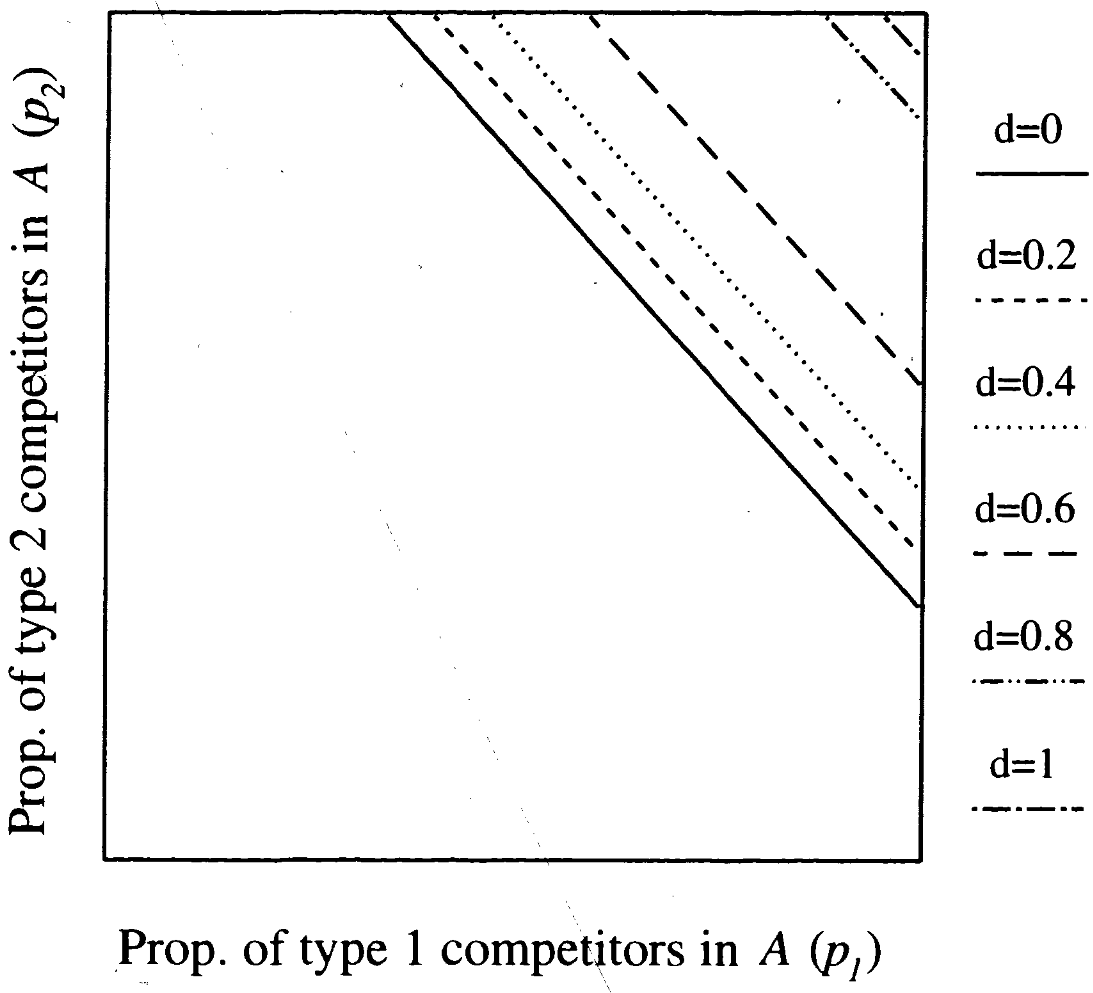
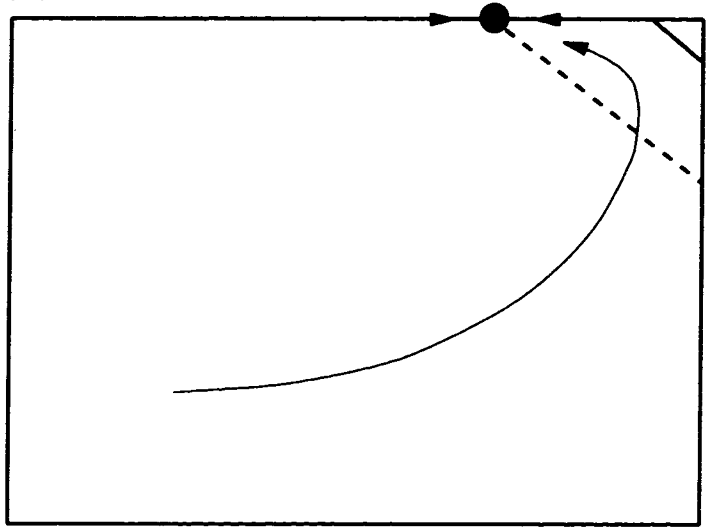
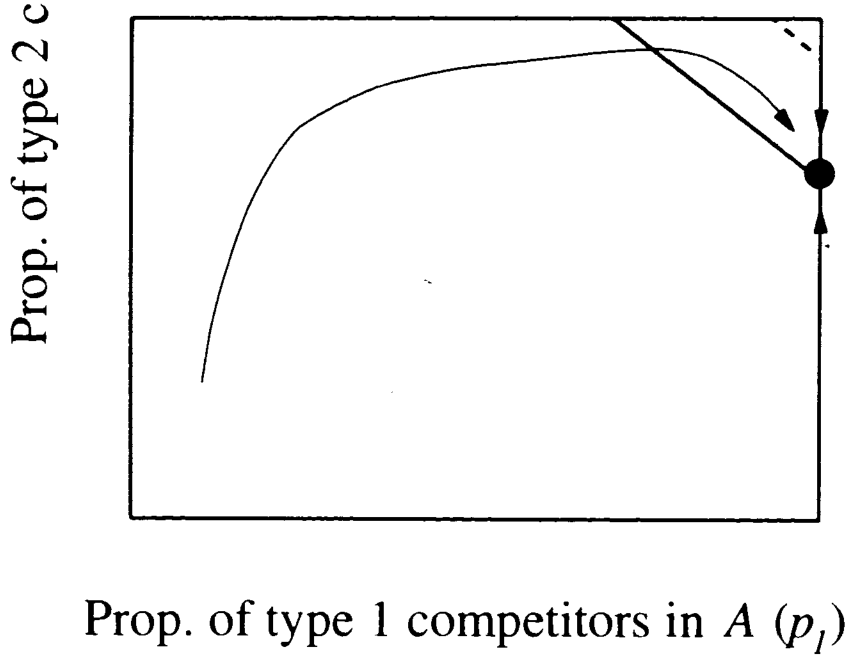

Prop. of type 2 competitors in A (p_2)
d=0
d=0.2
d=0.4
d=0.6
d=0.8
d=1
Prop. of type 1 competitors in A (p_1)

Figure 3.6. Fitness isoclines for *equal* type 1 (- - -) and type 2 (—) competitors under strong dilution of mortality risk ($d = 0.9$), when (a) type 1 competitors experience a higher ratio of mortality risk across the habitats, and (b) type 2 competitors experience a higher ratio of mortality risk across the habitats. The location of the combined equilibrium and sample trajectories of the change in the proportion of each competitor type in habitat A for all $(p_1, p_2) \neq (\hat{p}_1, \hat{p}_2)$ are indicated by ● and →, respectively. In both (a) and (b), $R_A = 1.2$, $R_B = 0.8$, $\mu_{1A} = \mu_{2A} = 0.5$, $K = 1$ and $N_1 = N_2 = 1000$. In (a), $\mu_{2B} = 0.5$ and $\mu_{1B} = 0.4$. In (b), $\mu_{2B} = 0.4$ and $\mu_{1B} = 0.5$.

(a) Risk ratio of type 1 competitors greater



(b) Risk ratio of type 2 competitors greater



In many cases, however, 'equal' competitors may experience different mortality risk in the same habitat, perhaps as a consequence of differences in morphology or anti-predator behaviour. When such differences in habitat-specific mortality risk lead to competitor types having identical ratios of mortality risk across the habitats (i.e., when expression (3.12) is true), the above conclusions are unchanged. However, if competitor types experience different risk ratios, the fitness isocline of the competitor type with the higher risk ratio is lower in elevation (e.g., Figure 3.6), and the location of the combined equilibrium will depend on the relative risk ratios of the two competitor types.

When the risk ratio of type 1 competitors is higher than that of type 2 competitors, $(\hat{p}_1, \hat{p}_2)$ tends to occur at the intersection of the type 1 competitors' isocline and the line $p_2 = 1$ (Figure 3.6a). Similarly, when type 2 competitors experience the higher risk ratio, $(\hat{p}_1, \hat{p}_2)$ tends to occur at the intersection of the type 2 competitors' isocline and the line $p_1 = 1$ (Figure 3.6b). In both cases, the combined equilibrium is characterized by relatively large proportions of both competitor types in habitat *A*, proportions that increase as the strength of dilution increases. Thus, when competitors are equal in their ability to compete for resources, both competitor types tend to aggregate in the riskier, but more productive habitat, regardless of which competitor type experiences the higher risk ratio.

Although our analysis of the equal competitors case confirms the results obtained by Moody et al. (1996), our earlier consideration of competitive inequalities demonstrates the lack of generality of this conclusion. Our model predicts that both unequal competitor types tend to reside in the same habitat when the effects of dilution are strong. However, the chosen habitat need not always be the one with the higher input rate, as predicted by Moody et al. (1996). When poor competitors experience a higher ratio of mortality risk across the habitats than do good competitors, the combined equilibrium is characterized by both competitor types occurring almost exclusively in the poor habitat (see Figure 3.4a). Hence, aggregation in either the good or poor habitat can occur, depending on the relative risk ratios experienced by the competitor types, the strength of risk dilution, and the relative abilities of competitor types to compete for resources.

DISCUSSION

We have considered the effect of differences in habitat-specific mortality risk on the equilibrium distribution of unequal competitors. We have shown that such distributions are characterized by either segregation of competitor types across habitats or aggregation of both competitor types within a single habitat, depending on the strength of risk dilution and the ratio of each competitor type's mortality risk across the habitats. Distributions of competitive weights no longer match the distribution of resources, as predicted by the original unequal competitors IFD model (Sutherland & Parker 1985; Parker & Sutherland 1986), but rather, are usually under-matched (i.e., there will be too few competitive weights in the good habitat), as expected if individuals are willing to accept a reduction in foraging gains to decrease their risk of predation (Grand & Dill 1997).

In the absence of ~~risk~~-dilution, our model predicts that competitor types tend to be assorted by competitive ability. The competitor type who experiences the higher ratio of mortality risk across the habitats occurs predominantly in the safer, less productive habitat, regardless of the absolute risk of mortality experienced by either competitor type. As the strength of dilution increases, the reduction in foraging gains associated with choosing a habitat where competitor density is high is increasingly compensated by a reduction in mortality risk, resulting in both competitor types aggregating in the same habitat. Which habitat is preferred depends primarily on which competitor type experiences the higher ratio of mortality risk across the habitats. When the risk ratio of good competitors is greater than that of poor competitors, both competitor types tend to aggregate in the risky, more productive habitat. The safer, less productive habitat is preferred, however, when poor competitors experience the higher risk ratio. This is because good competitors, by virtue of their great competitive ability, experience a smaller absolute reduction in foraging payoffs as competitor density increases than do poor competitors; a reduction that is balanced by a decrease in mortality risk for them, but not for poor competitors.

When competitor types experience the same ratio of mortality risk across the habitats, regardless of the strength of dilution or the absolute risk of mortality experienced by either competitor type, a number of stable equilibrium distributions are possible. Almost all such equilibria are characterized by both competitor types occurring in both habitats, and thus, receiving equal fitness payoffs in each. However, as with Parker & Sutherland's (1986) original IFD for unequal competitors, which of these equilibria is actually observed depends on the initial distribution of competitor types.

In nature, individuals frequently exhibit differences in morphology, body size and behaviour that may influence their susceptibility to predation (see Lima & Dill 1990).

Furthermore, morphological and behavioural differences may interact with the physical features of the habitat to modify an individual's risk of predation, such that the relative risks of mortality experienced by competitor types differ across habitats. For example, the relative vulnerability of competitor types may depend on the degree of structural complexity within a habitat (Savino & Stein 1982, 1989; Schramm & Zale 1985; Christensen & Persson 1993), such that one competitor type gains a greater reduction in mortality risk by choosing a particular habitat than do other competitor types, perhaps as a consequence of small body size (e.g., Werner & Gilliam 1984; Power 1987) or the absence of protective armour (e.g., McLean & Godin 1989; Abrahams 1995). In general, we expect that competitor types will experience different ratios of mortality risk across habitats, and thus, that a single, stable distribution of competitor types will usually exist. This equilibrium will tend to be characterized by either segregation of individuals by competitive ability (in the absence of risk dilution) or aggregation of competitors in a single habitat (when risk is diluted by competitor number).

There is much evidence to suggest that given a choice, individuals prefer to forage with competitors of similar body size (Theodorakis 1989; Krause 1994; Peuhkuri et al. 1997) and phenotype (Wolf 1985; Allan & Pitcher 1986). Often, researchers attribute such assortment to the 'oddity effect' (Landeau & Terborgh 1986), assuming that individuals who least resemble the group are more conspicuous to predators, and thus, more likely to be targeted during a predatory attack. However, if differences in phenotype or body size are correlated with differences in competitive ability (e.g., Godin & Keenleyside 1984; Grand & Grant 1994; Grand 1997), it is not necessary to invoke an oddity effect to explain assortment by competitor phenotype. Segregation of competitor types is also frequently predicted to occur as a consequence of differences between competitor types in their habitat-specific resource utilization efficiency. Many habitat selection models, particularly those developed for multi-species systems, assume that each competitor type is most efficient at exploiting resources in a different habitat (e.g., MacArthur and Levins 1967; Lawlor and Maynard Smith 1976; Vincent et al. 1996). In our model, good competitors are better at obtaining resources than poor competitors in both habitats, and relative resource utilization efficiencies are assumed to remain constant across habitats. Thus, segregation of competitor types can occur in the absence of such 'distinct preferences' (Rosenzweig, 1991) and 'oddity effects', as long as competitor types experience different ratios of mortality risk across the habitats and risk dilution is weak.

Traditionally, IFD theory has been used to investigate the effects of intraspecific competition on habitat selection (see Tregenza 1995). However, the theory (and modifications of it) may also enhance our understanding of interspecific patterns of habitat use, particularly in communities where multiple species compete for access to a common resource pool. For example, habitat partitioning has been frequently observed within North American assemblages of granivorous desert rodents. In general, large, bipedal species (e.g., kangaroo rats, *Dipodomys*) tend to forage in open areas, where the risk of encountering predators is high (Kotler et al. 1988; 1991), while small, quadrupedal species (e.g., deer mice, *Peromyscus*) restrict their foraging to bushes and other relatively safe habitats (Kotler 1984, 1985). Two general mechanisms have been proposed to explain this pattern: (1) species differ in the habitat in which they are competitively superior, and (2) species differ in the habitat in which they are most vulnerable to predation. According to the predictions of our model, this pattern of habitat selection could also result if (1) both species are at greater risk in the open habitat, but quadrupedal species experience a higher ratio of mortality risk across the habitats than bipedal species, (2) the relative competitive abilities of bipedal and quadrupedal species are similar across habitats, (3) open habitats are at least as productive as bush habitats (i.e., $R_A \geq R_B$), and (4) dilution of mortality risk is weak.

Both bipedal and quadrupedal species are more likely to be captured by predators in open habitats than in bush habitats (Kotler 1984, 1985; Kotler et al. 1988, 1991). However, bipedal species are less likely to be captured than quadrupedal ones in open habitats (Kotler et al. 1991), presumably as a consequence of the former's enlarged auditory bullae and bipedal locomotory habits, which enhance predator detection and avoidance abilities, respectively (Rosenzweig 1973). Assuming that bipedal species are at least as vulnerable to predators in bush habitats as are quadrupedal species, quadrupeds will experience a higher ratio of mortality risk across the habitats than bipeds (see Table 1 of Kotler et al. 1988), as required by our model.

Although differences in morphology, body size and locomotory ability may influence the relative abilities of species to harvest resources in open and bush habitats (see Kotler 1984), it is unclear how different the competitive abilities of bipedal and quadrupedal species actually are and whether they remain constant across habitats. However, large (bipedal) species are generally able to harvest (Price & Heinz 1984) and husk (Rosenzweig & Sterner 1970) seeds more rapidly than small (quadrupedal) species. Such skills are likely to reflect competitive ability and are unlikely to vary greatly with habitat type, although large species may have more difficulty searching for food in the bush habitats than smaller species (Brown et al. 1988). Although relative habitat productivities have not been rigorously quantified, open areas are perceived to contain richer seed resources than bush habitats (Kotler 1984), as required by our model.

To date, the effect of competitor density on per capita predation rates has not been studied in this system, although Rosenzweig et al. (1997) have found evidence for a dilution effect in small populations of old-world desert gerbils. If, however, North American desert rodents do not gain a significant reduction in mortality risk by associating with conspecific or heterospecific competitors, our model predicts that quadrupedal and bipedal species should occur in different habitats, given the relationships between body form, competitive ability and habitat-specific mortality risk discussed above.

Unlike previous explanations for habitat segregation in desert rodent communities, our explanation does not require competitor species to rank habitat profitabilities differently (e.g., Rosenzweig 1973; Brown et al. 1988) or to differ in the habitat in which they experience the highest mortality risk (e.g., Longland & Price 1991). Furthermore, species that occur predominantly in open habitats need not experience an absolutely lower risk of mortality there than species which occur predominantly in bush habitats. Thus, in comparing the assumptions and predictions of our model to the patterns of habitat use exhibited by desert rodents, we have provided an alternate explanation for the coexistence of species who exploit the same resources.

As is true of all models, ours makes a number of assumptions which may have influenced the predictions generated. For simplicity, we have assumed that relative competitive abilities remain constant across habitats, such that both competitor types rank habitat profitabilities identically. However, if competitor types disagree on which habitat is the most profitable, or relative competitive abilities change across habitats, segregation of competitor types is likely to be absolute, even in the absence of mortality risk (e.g., Lawlor & Maynard Smith 1976; Parker & Sutherland 1986). We have also assumed that the fitness value of food remains constant over time and is the same for all type *i* competitors. However, as demonstrated by Moody et al. (1996) and McNamara & Houston (1990), relaxation of these assumptions can lead to competitor distributions which reflect neither the distribution of resources nor the spatial distribution of mortality risk. Finally, we have assumed that mortality risk is spatially fixed, such that predators are unable to alter their distribution in response to the distribution of their prey. However, if predators are also free to move to the habitat where their fitness gains are highest, competitors may no longer benefit from the dilution effect (Hugie & Dill 1994). Under such circumstances, it is unlikely that competitor types will aggregate in a single habitat.

Because our model can be applied to both intra- and interspecific resource competition, its results may help to predict circumstances under which stable coexistence of competitor types is likely to occur, and when we should expect divergent habitat 'preferences' and the beginnings of niche specialization. Ideal free distribution theory has long been heralded as a potential method of linking individual decision-making to population and community-level phenomenon (see Kacelnik et al. 1992; Rosenzweig 1995; Sutherland 1996). By considering more than a single competitor type, and differences between competitor types in habitat-specific patterns of mortality risk, we believe that we have strengthened this link.

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APPENDIX 3.1

Stable distributions of competitor types

We simulated solutions to the model and examined the stability of all equilibria produced using the finite evolutionary game dynamics described by equation (A3.1), based on the evolutionary difference equation described by Maynard Smith (1982) and Hofbauer & Sigmund (1988). In doing so, we assume that fitness represents the multiplication 'rate' (R_0) defined over the generation time. The finite change in the proportion of the i th competitor type in habitat A, Δp_i, over one time unit will be equal to:

$$\Delta p_i = p_i \frac{w_{iA} - \bar{w}_i}{\bar{w}_i} \qquad \text{(A3.1)}$$

where $\bar{w}_i$ is the mean fitness of all type i competitors, given by:

$$\bar{w}_i = p_i \, w_{iA} + (1 - p_i) \, w_{iB} \qquad \text{(A3.2)}$$

When $\Delta p_i = 0$, the distribution of type i competitors will be at equilibrium, such that no individual can increase its fitness payoff by switching habitats. When competitor type i occurs in both habitats, for any equilibrium, $w(i, A) = w(i, B)$. When competitor type i occurs exclusively in a single habitat (for example, habitat A), for any equilibrium, $w(i, A) > w(i, B)$ for all p_i.

To test for local stability of equilibria, we add a perturbation factor (ε) to our simulations:

$$\Delta p_i = p_i \frac{w_{iA} - \bar{w}_i}{\bar{w}_i} \pm \varepsilon \qquad \text{(A3.3)}$$

such that at each time step, a small, random number of type *i* competitors are either added to or subtracted from the habitat. We might think of ε as representing individuals who occasionally move between habitats as a consequence of imperfect information (e.g., Abrahams 1986), or to escape from predators, search for mates or avoid agonistic encounters (e.g., Hugie & Grand 1997). If, despite these random perturbations, an equilibrium is repeatedly returned to once reached, it can be said to be locally stable. In all cases, simulations rapidly converged on a single, stable equilibrium distribution of type 1 and 2 competitors ($\hat{p}_1$, $\hat{p}_2$).

CHAPTER FOUR

The effect of group size on the foraging behaviour of juvenile coho salmon: reduction of predation risk or increased competition?

ABSTRACT

Animals often increase their apparent willingness to incur risk when foraging with conspecifics, presumably because group membership reduces an individual's risk of predation. As group size increases, however, competition for resources may also increase, resulting in a decrease in the quantity of resources available to each member of the group. When resources are scarce, individuals might be expected to increase their foraging effort in an attempt to increase their share of the resource. Such increases in effort will often appear to increase an individual's risk of predation. Thus, increased competition may contribute to the frequently observed relationship between risk-taking behaviour and group size. To date, no experimental assessment of the relative importance of these two mechanisms exists, in part because it is unclear how to separate their effects. We argue that to differentiate between the 'risk reduction' and 'increased competition' hypotheses, it is necessary to quantify the effect of predation risk on the form of the relationship between group size and risk-taking behaviour, and thus, to manipulate both group size and predation risk simultaneously. We conducted an experiment to determine the relative importance of risk reduction and increased competition to the foraging decisions of juvenile coho salmon (*Oncorhynchus kisutch*). Predation risk and group size were varied together, the foraging behaviour of 18 focal individuals being recorded in the presence and absence of a predator and in the company of zero, one and three conspecifics. As group size increased from one to four, focal fish captured more prey items, ventured closer to the feeder (and predator) to intercept them, and decreased their use of cover. Furthermore, although focal individuals captured fewer prey items and intercepted them farther from the feeder in the presence of the predator than in its absence, the form of the relationship between risk-taking behaviour and group size was not affected by the overall level of predation risk. We argue that the results of this experiment are consistent with the hypothesis that increases in risk-taking behaviour with group size occur primarily as a consequence of increased competition for scarce resources.

INTRODUCTION

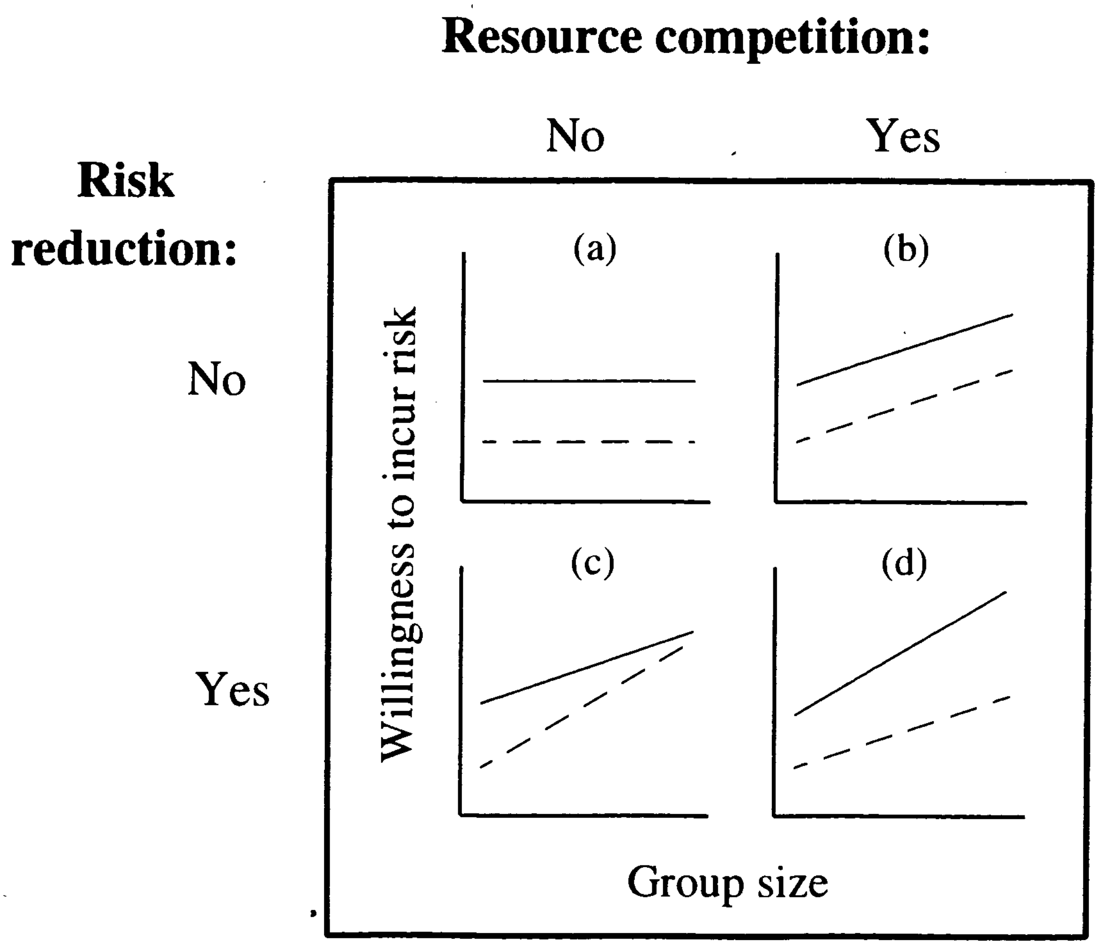
It is generally accepted that animals can reduce their risk of predation by associating with conspecifics (see Pulliam & Caraco 1984; Lima & Dill 1990, for reviews). A number of mechanisms may render group membership safer than solitary existence, including earlier detection of approaching predators (i.e., 'many eyes'; Pulliam 1973; Powell 1974; Lazarus 1979), 'confusion' of attacking predators (Neill & Cullen 1974; Milinski & Heller 1978) and, when predators are limited in their ability to capture more than a single prey item per attack, simple numerical 'dilution' of risk (Foster & Treherne 1981; Morgan & Godin 1985). As a consequence of such risk reduction, individuals are expected to behave in a less 'cautious' manner when in the presence of conspecifics, engaging in what might appear to be increasingly 'risky' behaviour as group size increases. Such apparent changes in 'risk-taking' behaviour with group size (i.e., the 'group size' effect) have been frequently demonstrated. For example, animals are often observed to decrease their level of vigilance as group size increases (see Elgar 1989; Lima 1990; Roberts 1996, for reviews), despite evidence that non-vigilant individuals are more likely to be captured by a predator (Fitzgibbon 1989). Similarly, animals have also been observed to make fewer visits to protective cover (Magurran & Pitcher 1983), inspect predators more closely (Magurran 1986), remain longer in the presence of a predator before fleeing (Dill & Ydenberg 1987), and resume feeding more quickly after exposure to a predator (Morgan 1988) when in the presence of conspecifics.

As group size increases, however, competition for resources may also increase, particularly when those resources are scarce and essential for survival (Lima 1990). As a consequence of increased competition, individuals may be forced to exert greater effort in order to obtain their share of the available resource (Clark & Mangel 1986), and hence, may appear more willing to engage in high risk behaviours than when alone (e.g., Barnard et al. 1983; Dill & Fraser 1984). Thus, increased competition may represent an alternative explanation for the frequently observed relationship between risk-taking behaviour and group size (see Elgar 1989; Lima 1990; Roberts 1996). These two mechanisms need not be mutually exclusive: both risk reduction and increased competition may contribute to the group size effect. However, no experimental assessment of the relative importance of the two mechanisms exists (Lima 1990), in part because most authors have been content to accept the risk reduction hypothesis (see Lima 1990; Roberts 1996), but also, because it is unclear how to separate their effects.

To date, most studies which claim to provide support for the risk reduction hypothesis have consisted of a comparison of the vigilance behaviour of individuals in small and large groups (see Roberts 1996). Rarely is predation risk manipulated and its effect on the relationship between risk-taking behaviour and group size reported (but see Morgan 1988). However, a comparison of the form of the relationship between group size and risk-taking at different overall levels of predation risk may provide information about the relative importance of risk reduction and increased competition. For example, consider the behaviour of a small bird, foraging within a flock which varies in size over time. For any given level of predation risk, we might expect the bird to increase the distance from protective cover at which it forages with increasing flock size. Now imagine that a predatory hawk has recently been sighted in the area. As a consequence of an increase in the perceived overall level of predation risk, we might expect the bird to decrease its distance from cover. However, as we shall show, the magnitude of this decrease for any given flock size will depend on whether increasing group size reduces predation risk, increases resource competition, or both.

If we assume that the bird experiences only a reduction in predation risk as a consequence of increasing group size, the relative reduction in perceived risk with the addition of another flock mate will be greater when the overall level of predation risk is high (i.e., $\left(\frac{2p}{n} - \frac{2p}{n+1}\right) > \left(\frac{p}{n} - \frac{p}{n+1}\right)$; where n is the number of birds in the flock and p is the probability of being captured by a predator). Thus, we might expect the bird to increase its distance from cover more rapidly with increasing group size when the overall risk of predation is relatively high (Figure 4.1c). However, if increased competition is the only consequence of an increase in flock size, the relative increase in distance from cover with group size should be independent of the overall level of predation risk (Figure 4.1b). When increasing group size both reduces predation risk and increases resource competition, the strength of competition experienced within a flock of a given size will be independent of the overall level of risk. However, the reduced cost of high risk behaviour, and thus, the net benefit of increasing foraging effort with increasing flock size will be greater when the overall level of predation risk is relatively low. Thus, we might expect the bird to increase its distance from cover more rapidly with increasing group size when risk is low (Figure 4.1d). Note that in generating these predictions we have assumed that (1) all individuals, regardless of group size, experience a higher risk of predation in the presence of a predator than in its absence (see Figure 4.1a), (2) groups of different sizes are attacked by the predator with equal probability, (3) the strength of competition is

Figure 4.1. Hypothesized form of the relationship between group size and risk-taking behaviour under high (- - -) and low (—) levels of predation risk when (a) risk of predation and the strength of competition are independent of group size, (b) competition increases with increasing group size, (c) predation risk decreases with increasing group size and, (d) predation risk decreases and the strength of competition increases with increasing group size.


Resource competition:
No
Yes
Risk reduction:
No
Yes
(a)
(b)
(c)
(d)
Willingness to incur risk
Group size

inversely proportional to group size and, (4) resources are in short supply and valued equally by all individuals.

We conducted an experiment to assess the relative importance of risk reduction and increased competition to the foraging decisions of juvenile coho salmon (*Oncorhynchus kisutch*). Although previous work has indicated that the foraging behaviour of these fish is sensitive to both predation risk and the presence of conspecifics (e.g., Dill & Fraser 1984; Grand & Dill 1997), it is unclear whether individuals experience either a reduction in risk or an increase in the strength of competition with increasing group size. In the experiment described here, predation risk and group size were manipulated simultaneously, permitting examination of the effect of predation risk on the form of the relationship between group size and risk-taking behaviour, and thus, differentiation between the risk reduction and increased competition hypotheses. Because previous experiments suggest that coho can reduce their perceived risk of predation by decreasing their foraging activity (e.g., Dill & Fraser 1984) and increasing their use of cover (Grand & Dill 1997; Reinhardt & Healey in press), we assumed that an individual's willingness to incur risk was inversely correlated with the amount of time it spent under cover, its reticence to attack prey, and the distance from the predator at which it captured prey. In order to hold overall resource availability constant across group size treatments, focal individuals were separated from group members by a clear, plexiglass barrier, thus preventing actual, but not perceived competition for resources (see below).

METHODS

Experimental Subjects

We captured a total of 90 wild, young-of-the-year coho salmon by pole seine from the Salmon River, Langley, British Columbia, Canada, on July 22 and August 13, 1996. Individuals were chosen such that they ranged in mass from 1.4 to 2.0 g ($\bar{x} \pm SD = 1.68 \pm 0.16$ g, $n = 90$) and in fork length from 50 to 60 mm ($\bar{x} \pm SD = 54.8 \pm 1.7$ mm, $n = 90$). 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 until they were to be used in the experiment. Fish were fed live, adult brine shrimp (*Artemia* sp.) *ad libitum* while in the flow-through aquarium.

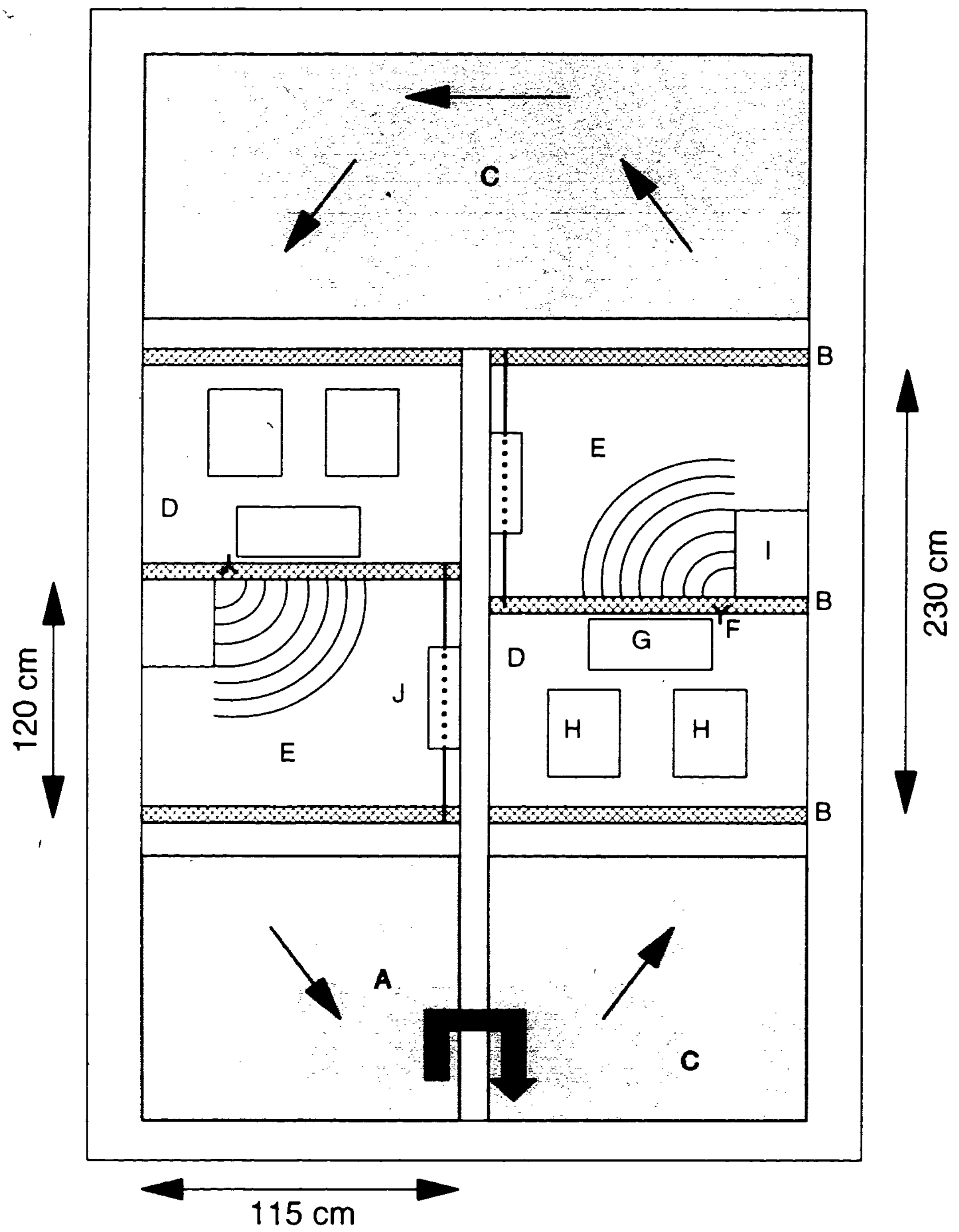
Three days before each experiment began, five fish, of similar mass (coefficient of variation; x̄ ± SD = 2.14 ± 1.11, n = 18 groups of five fish) and fork length (CV; x̄ ± SD = 1.27 ± 0.517, n = 18), were chosen from the stock tank. Individuals were randomly designated as either the focal individual, a solitary 'companion' or one of a group of three companion fish. Fish were then transferred to one of two 'glide' sections of the stream channel in which experiments were to be conducted (see below). The focal individual was released into the 'foraging arena', while solitary and grouped companions were placed upstream of the foraging arena, in two flow-through enclosures (see below). Experiments were conducted over a period of 1 month; beginning August 3 and ending September 5, 1996.

Apparatus and General Methods

We conducted experiments in an artificial stream channel (Figure 4.2) in the woods of the Burnaby Mountain campus of Simon Fraser University. The concrete channel (described more completely in Grand 1997) consists of two shallow, rectangular 'glides' (water depth = 18 cm) 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. 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, 'no-see-um' mesh, was erected over the entire channel to further prevent the entry of both extraneous food and leaf litter. Opaque plastic blinds attached to the mesh prevented disturbance of the fish during foraging trials; we made observations of fish behavior through small slits cut in these blinds.

Each glide was further divided into two sections; a downstream 'foraging arena' (120 × 115 cm; L × W) and an upstream 'holding' area (110 × 115 cm; L × W) which contained both the predator and the two, flow-through, companion group enclosures (Figure 4.2). Sections of the glides were separated from one another, and the pools at each end, by mesh dividers (mesh opening = 5 mm), thus restricting the movement of each focal fish to the foraging arena within a single glide (see Figure 4.2). The predator, a single, 1+ coho salmon (FL = 15 cm), was housed in a small, glass aquarium (41 × 21 × 24 cm; L × W × D; water depth = 18 cm), placed lengthwise against the mesh barrier which separated the upstream holding area from the foraging arena. Because coho of this size are capable of preying on smaller members of other salmonid species (Parker 1971), and

Figure 4.2. Schematic top view of the experimental stream channel. Water was pumped over a concrete barrier (A) and traveled downstream through a series of six mesh barriers (B) which separated the pools (C) from the holding areas (D) and the foraging arenas (E). A Y-shaped feeding tube (F) was attached to the mesh barrier at the upstream end of each foraging arena, directly adjacent to the predator aquarium (G). Companion groups were transferred between clear plexiglass enclosures in the upstream holding area (H) and the foraging arena (I). A single cover structure was placed along the opposite wall of the foraging arena (J). Arrows indicate the direction of water flow and solid arcs the lines used to delineate 10-cm intervals to the observer.


C
B
E
D
I
B
F
G
D
J
H
H
E
B
A
C
120 cm
230 cm
115 cm

small coho are often preyed upon by both coho smolts (McMahon & Holtby 1992) and other salmonids (Sandercock 1991), we believe that focal individuals perceived the larger fish as a predator rather than merely a very large competitor. The predator aquarium was surrounded on three sides by opaque plexiglass, thus preventing the companion fish from directly observing the predator between trials. The front face of the predator aquarium was fitted with two removable opaque plexiglass blinds, which prevented the focal fish, and any companion fish present, from seeing the predator both between trials and during 'no predator' trials.

Companion groups were housed in two clear plexiglass enclosures (42 × 31 × 31 cm; L × W × D), the narrow ends of which were covered with mesh screen (mesh opening = 5 mm), permitting continuous circulation of water through them. An identical, empty, companion group enclosure was placed in the foraging arena, immediately adjacent to the point from which prey were delivered (see Figure 4.2). A single, cover structure (34 cm long half-round of PVC pipe; diameter = 11 cm) was suspended above the surface of the water along the opposite wall of the foraging arena. To minimize differences between light levels below the structure and those elsewhere in the channel, we drilled eight holes (diameter = 1 cm) at regular intervals along the length of the pipe.

Throughout the experiment, fish were fed live, adult brine shrimp obtained weekly from a local aquarium store. Prey were sieved and only those unable to pass through a 1350 µm mesh screen were used. Brine shrimp were placed in a single 4 ℓ Erlenmeyer flask filled with fresh water collected from the channel. Prey and water drained from the flask through a 70 cm length of tygon tubing (diameter = 5 mm) fastened to a glass spout attached to the bottom of the flask (after Abrahams 1989). The feeding tube emptied into a Y-shaped plastic tube attached to the back side of the mesh barrier at the upstream end of each glide (see Figure 4.2). Prey in the feeder were kept in suspension by means of a stir bar constantly rotated by a magnetic stir plate. The flask was sealed with a rubber stopper penetrated by a glass tube which extended to the bottom of the flask. A length of tygon tubing was attached to the top of the tube and sealed at the other end with a 23 1/2 gauge syringe. The feeder could be operated remotely by simply removing the plunger from the syringe, and allowing air to enter the apparatus.

A series of 7 arcs, drawn at 10 cm intervals along the bottom of each glide, radiated outward from the point at which prey were delivered (see Figure 4.2), thus, delineating prey capture 'zones' for the observer. Hereafter, we refer to the interval nearest the feeder as zone 1 and the interval farthest from the feeder as zone 7. All trials were video-taped from above, using a High-8 Sony Camcorder suspended 120 cm above the surface of the water.

Experimental Procedures

Each focal fish (*n* = 18) experienced all six combinations of 'predator'/'no predator' and companion group size ('0', '1' and '3') treatments. To reduce the possibility of 'carry-over' effects between trials, the order of treatment combinations was varied between individuals. Companion group size treatments were blocked within 'predator'/'no predator' treatments, such that each focal fish experienced a block of three 'predator' trials and a block of three 'no predator' trials. We randomized the order of treatment blocks between focal individuals, such that half of the fish experienced the three 'predator' treatments first, while the other half experienced the three 'no predator' treatments first. Within 'predator'/'no predator' treatment blocks, companion group size treatments were randomized, such that focal individuals experienced the three companion group sizes in different orders.

Each focal fish experienced all treatment combinations within a single day, at 0930, 1100, 1230, 1400, 1530 and 1700 h. Experiments in the two glides were conducted on alternate days. At 0800h on the morning of each experiment, the feeder was filled and set on the stir plate and the companion group for the first trial was dip-netted and gently transferred to the plexiglass enclosure in the foraging arena. Fish were then left undisturbed for the next 90 min.

Immediately preceding each trial, we removed either one or both opaque plexiglass blinds from the front of the predator aquarium, allowing the focal fish and any companion fish present, to view either the second piece of plexiglass (during 'no predator' trials) or the predator (during 'predator' trials). After waiting an additional 10 min, we activated the video camera remotely and began the foraging trial. During each 15 min trial, a single brine shrimp was introduced to the focal fish approximately every 3-min, for a total of five prey items per trial. For each item introduced, we recorded whether the prey was captured and if so, the foraging zone (1 to 7; i.e., within 10, 20, 30, 40, 50, 60 or 70 cm of the feeder) in which it was intercepted. Because distances beyond foraging zone 7 could not be accurately quantified (either visually or on video), prey interceptions occurring beyond this point were arbitrarily (and conservatively) given a value of '8'. During the 3 min following the introduction of each prey item, the location of the focal fish (i.e., foraging zone 1 - 7, under cover or elsewhere) was determined by scan sampling (Martin & Bateson 1986) at 30 s intervals. At the end of each trial, the camera was turned off and the plexiglass blind(s) returned to the front of the predator aquarium. The companion group was returned to the upstream enclosure and replaced with the group to be used in the next trial. After the final trial of the day, all fish were captured, removed from the stream channel, and replaced with the next focal individual to be tested and its companions. Companion fish were never used with more than a single focal individual.

Data Analyses

For each focal individual, we recorded (1) the total number of prey captured (max = 5), (2) the distance at which prey were intercepted (foraging zone 1 to 7 or beyond), (3) the proportion of time spent under cover and, (4) the proportion of time spent in foraging zones 1 to 7. Data were collected from the videotape and used to confirm and clarify observations made visually at the time of the trials. We used a two-factor repeated measures analysis of variance (ANOVAR), with predator presence/absence and companion group size as factors, to examine the effects of predation risk and competition for resources on foraging behaviour. Initially, data were coded according to whether the focal individual experienced the predator block of treatments first or second, and within each block, the order in which the focal individual experienced companion group sizes. However, because all such 'order' effects and their interactions with main effects were non-significant (all *p*'s > 0.25), they were subsequently dropped from the model. Thus, all *p*-values reported represent those from the simple two-way ANOVAR's and are two-tailed, unless stated otherwise. To investigate linear trends in behaviour over trials, we used single degree-of-freedom polynomial contrasts (Wilkinson 1990).

RESULTS

General behaviour of the fish

Foraging behaviour and patterns of space use varied widely among focal fish. Some individuals treated the cover structure as a 'central place', venturing out from it only to intercept prey. Others ignored the structure entirely, instead remaining upstream, displaying to their competitors and scanning the surface for prey. Companion fish usually remained at the upstream end of their enclosure, darting towards prey items as they entered the foraging arena. In some cases, it appeared that focal individuals were alerted to the arrival of prey by the behaviour of companion fish.

Prey capture

The total number of prey items captured by focal individuals was influenced by both the presence of the predator and the number of companion fish present (Figure 4.3). Focal fish captured fewer prey items in the presence of the predator than in its absence ($F_{1,17} = 14.106$, $p = 0.002$), and the number of prey captured increased with increasing companion group size ($F_{1,17} = 10.552$, $p = 0.005$; single degree-of-freedom linear contrast).

Prey capture distance was also influenced by the presence of the predator and the number of companion fish present (Figure 4.4). Focal fish captured prey closer to the feeder (i.e., closer to the predator) in the predator's absence than in its presence ($F_{1,17} = 18.104$, $p = 0.001$) and prey capture distance decreased with increasing companion group size ($F_{1,17} = 22.695$, $p < 0.001$; single degree-of-freedom linear contrast). In both cases, interactions between predator presence and the number of companion fish were not significant ($F_{2,34} = 1.150$, $p = 0.329$, and $F_{2,34} = 1.230$, $p = 0.305$, respectively), suggesting that the observed change in foraging behaviour with increasing group size was primarily a consequence of increased resource competition (see Figure 4.1).

Use of space

The proportion of time spent by focal individuals under cover and within 70 cm of the feeder (i.e., within foraging zones 1 to 7) was also influenced by companion group size, but not by the presence of the predator (Figure 4.5). Focal individuals spent less time under cover (Figure 4.5a; $F_{1,17} = 16.861$, $p < 0.001$; single degree-of-freedom linear contrast) and more time within 70 cm of the feeder (Figure 4.5b; $F_{1,17} = 7.978$, $p = 0.012$; single degree-of-freedom linear contrast) as companion group size increased from zero to three, although the greatest change in space use appeared to occur between the solitary and single companion fish treatments. However, focal individuals did not alter the relative amounts of time spent under cover (Figure 4.5a; $F_{1,17} = 0.849$, $p = 0.370$) or in close proximity to the feeder (Figure 4.5b; $F_{1,17} = 0.041$, $p = 0.842$) in response to the presence of the predator.

Figure 4.3. Mean (+ SE) number of prey items captured by focal individuals in the presence of 0, 1 and 3 companion fish, in the predator (□) and no predator (■) trials. $n = 18$.

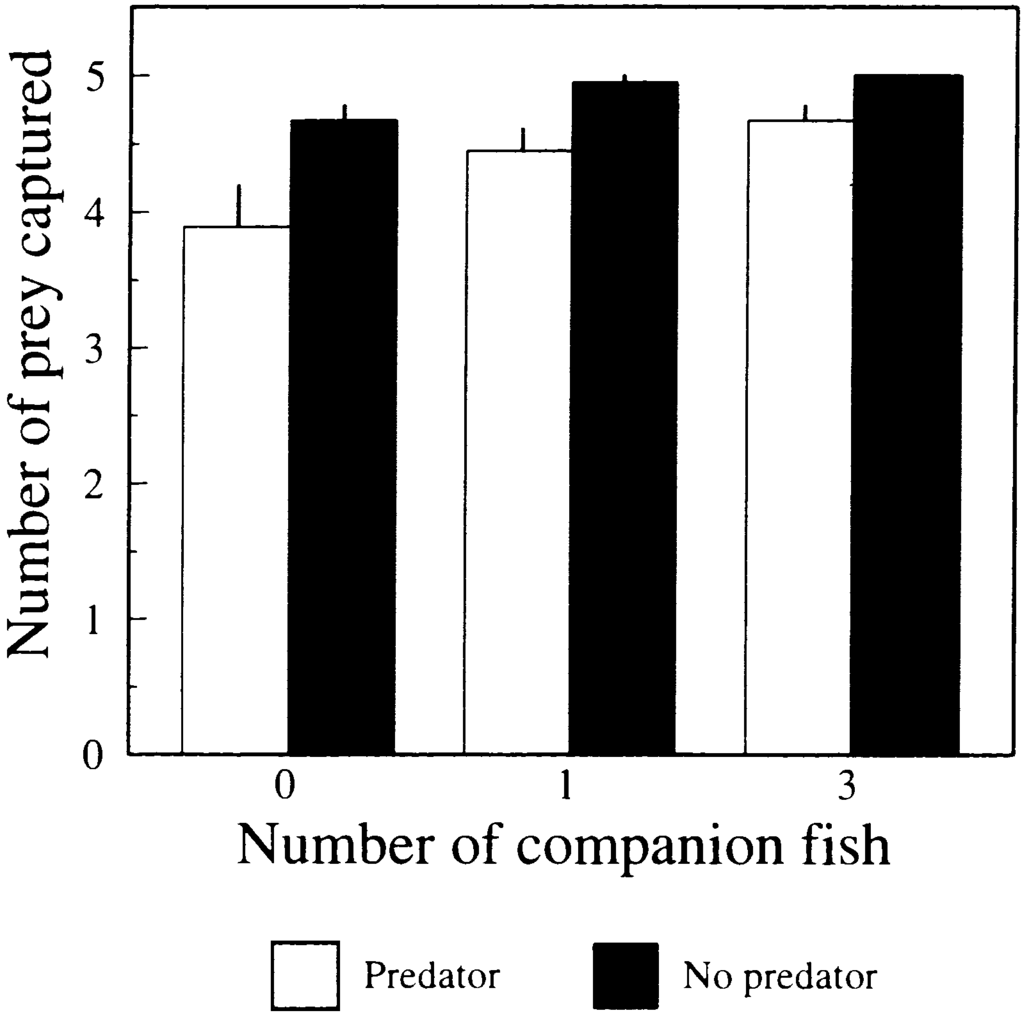

Number of prey captured
0
1
2
3
4
5
0
1
3
Number of companion fish
Predator
No predator

Figure 4.4. Mean (+ SE) zone of prey capture by focal individuals in the presence of 0, 1 and 3 companion fish, in the predator (□) and no predator (■) trials. $n = 18$.

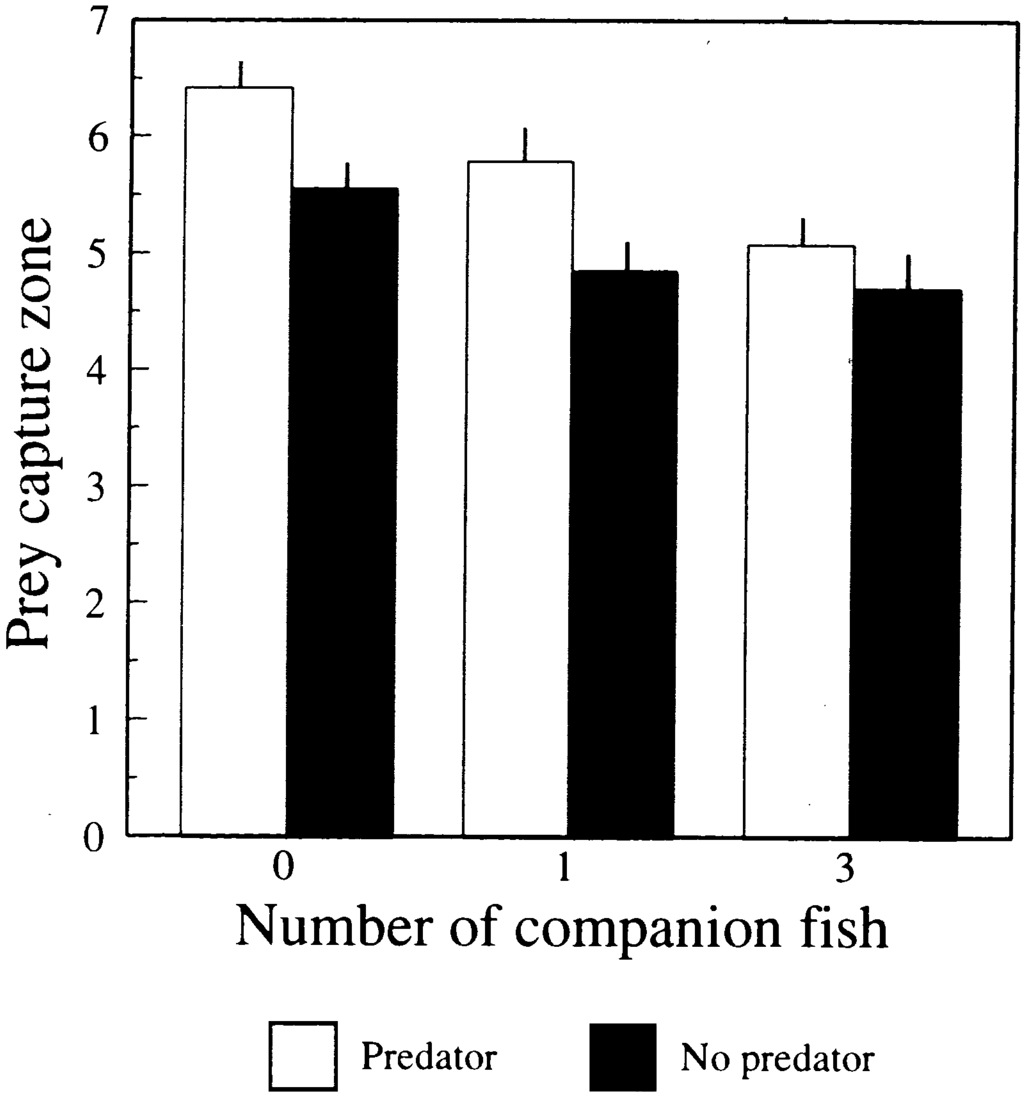
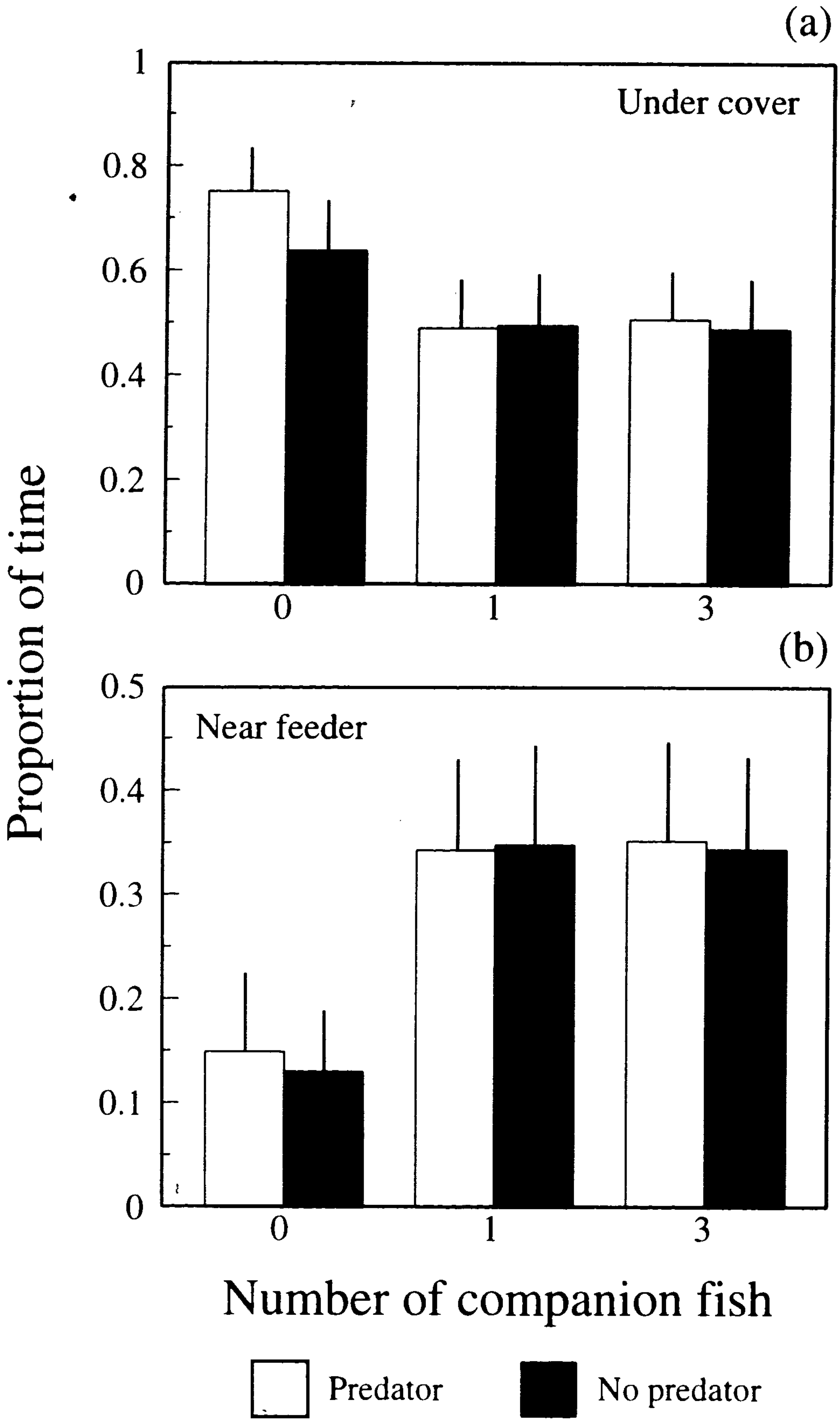

7
6
5
4
3
2
1
0
Prey capture zone
0
1
3
Number of companion fish
☐ Predator
■ No predator

Figure 4.5. Mean (+ SE) proportion of time spent by focal individuals (a) under cover, and (b) within 70 cm of the feeder, in the presence of 0, 1 and 3 companion fish, in the predator (□) and no predator (■) trials. *n* = 18.


(a)
Under cover
1
0.8
0.6
0.4
0.2
0
0
1
3
(b)
Near feeder
0.5
0.4
0.3
0.2
0.1
0
0
1
3
Proportion of time
Number of companion fish
Predator
No predator

As before, interactions between predator presence and the number of companion fish did not significantly affect the proportion of time spent either under cover or within 70 cm of the feeder ($F_{2,34} = 1.649, p = 0.207$, and $F_{2,34} = 0.043, p = 0.958$, respectively). Again, these results suggest that the observed effect of group size on space use occurred primarily as a consequence of increased resource competition, rather than being due to a reduction in perceived risk of predation with increasing group size.

DISCUSSION

Juvenile coho salmon varied their foraging behaviour in response to both group size and predation risk. Focal individuals captured fewer prey items and intercepted them farther from the feeder in the presence of the predator than in its absence, regardless of the number of conspecifics present, as expected if increased activity and proximity to the feeder (and predator) increase an individual's perceived risk of predation (Dill & Fraser 1984). As group size increased from one to four fish, focal individuals captured a greater number of the available prey, ventured closer to the feeder to intercept prey and decreased their use of cover, as expected if associating with conspecifics either decreases predation risk or increases the strength of competition. However, the form of the relationship between risk-taking behaviour and group size was not affected by the presence of the predator, as indicated by the lack of any statistical interaction between group size and predation risk effects. Thus, the results of this experiment are consistent with the hypothesis that changes in risk-taking behaviour with group size occur primarily as a consequence of increased resource competition (see Figure 4.1b).

Many other studies have demonstrated a similar effect of group size on risk-taking behaviour (see Lima 1990; Roberts 1996 for reviews). Despite acknowledging that their results might be explained in part, by increased competition for resources, most authors have been content to attribute the effect to risk reduction. Indeed, much of the literature on the group size effect has focused on elucidating the specific mechanism by which increasing group size might reduce predation risk (e.g., 'confusion', 'vigilance', or 'dilution'; Roberts 1996), to the exclusion of non-risk related alternatives (i.e., the 'confounding variables' of Elgar 1989). However, many of these experiments did not manipulate predation risk (e.g., Bertram 1980; Magurran & Pitcher 1983; Magurran et al. 1985), and hence, cannot rule out increased competition as a contributing factor. Similarly, experiments which attribute group size effects in the absence of a predator entirely to increased competition (e.g., Barnard et al. 1983) cannot rule out the possibility that risk reduction contributed to the observed effect. While animals presumably perceive a non-zero risk of predation in the presence of a predator, they may not perceive zero risk in its absence (Lima & Dill 1990). Thus, to evaluate the relative importance of risk reduction and increased competition to any observed group size effect, it is necessary to compare the form of the relationship between group size and risk-taking behaviour at various levels of predation risk: risk of predation and group size must be manipulated simultaneously.

We are aware of only one other study in which both group size and predation risk were varied. Morgan (1988) examined the roles of hunger, group size and predator presence on the foraging behaviour of bluntnose minnows (*Pimephales notatus*). She observed that latency to forage was greater in the presence of the predator than in its absence, and decreased as group size increased from three to twenty. Similarly, foraging rates were lower in the presence of the predator and increased with increasing group size. From these results, Morgan (1988) concluded that the observed decrease in foraging activity with decreasing group size was primarily a response to an increased need to be vigilant for predators (i.e., the risk reduction hypothesis). However, all interactions between group size and predation risk effects were non-significant, suggesting that the form of the relationship between group size and risk-taking behaviour was the same, both in the presence and absence of the predator. Thus, Morgan's (1988) results are consistent with the hypothesis that increases in risk-taking behaviour with group size, at least in fishes, are primarily a consequence of increased competition for resources.

The idea that increases in group size might lead to increased competition for resources and thus to greater risk-taking, is not new. Barnard et al. (1983) and Dill & Fraser (1984) sought experimental evidence for such an effect over a decade ago. Dill & Fraser (1984) observed that juvenile coho salmon increased their foraging activity in the presence of an apparent companion (i.e., the focal individual's mirror image). Their conclusion that increases in risk-taking behaviour with increasing group size were primarily due to competition seems appropriate, given that the mirror was placed such that focal individuals saw themselves leaving the safety of their companion when attempting to capture prey. However, because the relationship between risk-taking behaviour and group size was only quantified at a single level of predation risk (i.e., in the presence of a model predator), the possibility that focal individuals perceived their risk of predation to be lower in the presence of the companion than in its absence cannot be ruled out. Similarly, Barnard et al. (1983) observed that common shrews (*Sorex araneus* L.) increase their allotment of time to foraging activity when in the presence of a conspecific. They attributed these results solely to increased resource competition, presumably because no predator was present during the experiment. However, if shrews perceive a non-zero risk of predation, even in the absence of any immediate threat, they may have perceived their risk of predation to be even lower in the presence of the conspecific and adjusted their behaviour accordingly.

In generating predictions about the effect of predation risk on the form of the relationship between group size and risk-taking behaviour, a number of simplifying assumptions were made. Relaxation of these assumptions may lead to predictions other than those illustrated in Figure 4.1. For example, we assumed (as was certainly the case in this experiment) that predator attack rate was independent of group size, which may not be true if large groups are more visible and more easily detected by predators than small groups. In this case, risk-taking behaviour might be expected to increase less quickly with increases in group size, thus making it difficult to distinguish between the scenarios depicted in Figures 1b and 1c. However, the simple verbal models developed here can easily be altered to include the relevant biological features of any animal's foraging ecology. The specific predictions generated here are less important than the approach advocated.

Despite the considerable research effort into understanding the relationship between group size and risk-taking behaviour (see reviews in Elgar 1989; Lima 1990; Roberts 1996), it is still unclear whether animals adjust their behaviour in response to a reduction in predation risk or an increase in the strength of resource competition with increasing group size. Most research has focused on the risk reduction hypothesis and the various mechanisms by which it might arise (Roberts 1996). Relatively little attention has been paid to non-risk related hypotheses, although much of the evidence used in support of risk reduction can also be attributed to increased resource competition. Future research should be directed towards explicit consideration of the two effects and empirical tests to distinguish their relative importance.

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CHAPTER FIVE

Risk-taking behaviour and the timing of life history events: consequences of body size and season

ABSTRACT

When faced with behavioural options differing in energetic gain and mortality risk due to predation, an individual's best compromise to the conflicting demands of growth and survival will depend upon both its current energetic state and the future opportunity for growth. Such state and time-dependent tradeoffs are often investigated using dynamic programming. By specifying the relationship between fitness and the state variable of interest at the time of some relevant life history event, fitness-maximizing solutions for all state and time combinations can be found. To date, however, no dynamic programming model has considered the possibility that animals may be capable of delaying life history events beyond the time period modeled. In such cases, in addition to being influenced by future life history events, short term behavioural responses to foraging-predation risk tradeoffs may also indirectly affect the timing of those events. I use dynamic programming (1) to investigate the effects of body size and time of year on patterns of risk-taking behaviour in animals capable of postponing life history events, and (2) to explore the outcome of such individual decisions on the subsequent timing of life history events and the states of individuals undergoing those events. In doing so, I relax the basic dynamic programming assumption of a finite time horizon and allow individuals to postpone initiating the life history event until some future favourable period of time. Such delays are frequently observed in anadromous fishes, including coho salmon, *Oncorhynchus kisutch*, hence, I use the relevant features of their biology to develop the model and illustrate the general problem of interest.

INTRODUCTION

Animals may often have to choose among behavioural options (i.e., foraging sites, foraging modes, prey types etc.) which differ in energetic gain and mortality risk due to predation. When the option that provides the highest rate of energetic gain is also the most dangerous, observed behaviours will reflect a compromise between the conflicting demands of growth and survival (see Lima & Dill (1990) for a review of foraging-predation risk tradeoffs). An individual's best resolution to this tradeoff will depend on the fitness benefits of energy acquisition, which in turn, will depend on both its current energetic state and future opportunity for growth (Houston et al. 1993; Clark 1994). Therefore, the time remaining from the moment that a decision is made to some future life history event (e.g., migration, maturation, or reproduction) may influence the optimal balance between growth and survival, and thus, the optimal behavioural option.

Dynamic programming (Houston et al. 1988; Mangel & Clark 1988) provides a powerful method by which the effects of state and time on the tradeoff between growth and survival can be investigated (Houston et al. 1993; Clark 1994). Beginning with some specified relationship between the state variable and fitness at the end of the time period to be modeled, fitness-maximizing solutions for all state and time combinations are found by backwards iteration. The resulting size distribution and growth trajectories of a population of individuals following this 'optimal policy' can then be found by forward simulation (Mangel & Clark 1988). Hence, the technique provides a direct link between the short term, behavioural decisions of individuals and the life history patterns characteristic of entire populations (Houston et al. 1988; Clark 1993).

Most applications of dynamic programming to date have assumed that animals must either (1) survive to a fixed time at which some relevant life history event must occur, with fitness depending on state at that time (e.g., Bednekoff & Houston 1994a), or (2) reach a fixed state before the life history event can take place, with fitness depending on when, within the period of time specified by the modeler, that state is attained (e.g., Beauchamp et al. 1991; Bednekoff & Houston 1994b). In some cases, however, both final state and final time may be sufficiently flexible that an individual can decide what its state will be when the life history event takes place, and when that event will occur. Such tradeoffs between state and the timing of life history events have been modeled by Ydenberg (1989), Ludwig and Rowe (1990) and Rowe and Ludwig (1991). However, none of these researchers considered the possibility that individuals could postpone the life history event beyond the time period modeled.

Although the timing of life history events will often be limited to a single favourable period (e.g., fledging seabirds, Ydenberg 1989; metamorphosing tadpoles, Ludwig & Rowe 1990), postponement of the event until some future favourable period (i.e., the next morning, the next lunar or tidal cycle, or the following year) may be possible for some animals. For example, pandalid shrimp, whose reproductive period is seasonally constrained, may delay their first breeding attempt for a year or more (Charnov 1989). Similarly, the transformation to adulthood by dobsonfly larvae, which is triggered by a seasonal decline in the size of their prey, can be delayed for one to three years (Hayashi 1994). Often, individuals who delay the life history event differ in state from those who do not. Thus, in addition to being influenced by future life history events, short term behavioural responses to foraging-predation risk tradeoffs may also indirectly affect the timing of those events, and consequently, the life history characteristics of entire populations, via their effects on the states of individuals.

Here, I develop a dynamic programming model (1) to investigate the effects of body size and season on patterns of risk-taking behaviour in animals capable of postponing life history events, and (2) to explore the outcome of such individual decisions on the subsequent timing of life history events and the states of individuals initiating those events. In doing so, I relax the basic dynamic programming assumption of a finite time horizon and allow individuals to delay initiating the life history event until some future favourable period. I ask what the optimal pattern of risk-taking behaviour is, assuming that the life history event must be initiated before reproduction can take place, and that an individual's state at the time of the event reflects its expected future reproductive success. Because both individual variation in risk-taking behaviour (Dill & Fraser 1984; Grand & Dill 1997; Reinhardt & Healey in press) and flexibility in the timing of life history events (Sandercock 1991 and references therein) have been reported in coho salmon (*Oncorhynchus kisutch*), I use the relevant features of their biology to illustrate the general problem of interest.

SMOLTING IN COHO SALMON: AN EXAMPLE OF A DELAYABLE LIFE HISTORY EVENT

Like other anadromous salmonids, the life cycle of coho salmon is characterized by a juvenile period of freshwater residency followed by migration to sea as 'smolts' and a period of rapid oceanic growth. After several years at sea, maturing adults return to their natal stream to deposit eggs in the gravel, dying once spawning is complete (Sandercock 1991). In order to attain the body size required to reproduce successfully, juvenile fish must first make the transition from freshwater to seawater. This life history event usually occurs at the beginning of the second year in freshwater, although the timing and breadth of the smolting period can vary considerably between populations, as can the size of individuals undergoing the transition (Sandercock 1991). Furthermore, in many populations, some individuals forego smolting for an additional year or two, often initiating the seaward migration at a larger size (e.g., Fraser et al. 1983; Holtby 1988; Holtby et al. 1990).

During the freshwater residency period, juvenile coho typically maintain foraging positions from which they dart forward to attack benthic invertebrates and intercept instream drift (Chapman 1962; Hartman 1965; Puckett & Dill 1985). Within the stream, sites may differ in food availability (Ruggles 1966; Fausch 1984) and predation risk, such that safety from predators may sometimes be acquired only through a reduction in foraging gains (e.g., Grand & Dill 1997). Hence, risk-taking behaviour will be reflected in patterns of foraging-site selection and may represent a compromise to the conflicting demands of growth and survival. For each individual, the best resolution to this conflict will depend on the fitness benefits of growth, which in turn, will depend on the individual's size and the time remaining before the seaward migration. Furthermore, current risk-taking behaviour will influence future size, which will in turn influence both future willingness to incur risk and the timing of smolting. Because I only consider behaviour during the non-reproductive part of the life cycle, I treat the probability of successfully smolting as a surrogate measure of individual fitness.

Formulation of the model

Let the state of each individual at the beginning of each time period, t, in each year, y, be characterized by its mass, $x\,(t\,,\,y)$, in grams. Mass has both upper and lower physiological limits such that:

$$x_{min} \leq x\,(t\,,y) \leq x_{max} \tag{5.1}$$

If $x\,(t\,,\,y)$ falls below x_{min}, the animal dies of starvation.

I define 20 equally spaced time periods, beginning in early April ($t\ = 1,\,y$) and ending in late March of the following year ($t\ = 20,\,y$), in which individuals can choose among behavioural options. At the beginning of each time period, individuals can either elect to remain in freshwater, foraging in one of three habitats and thus, accepting one of three levels of risk, or initiate seaward migration. Freshwater habitats, $i = 1, 2, 3$, are characterized by two parameters: (1) probability of death per time period due to predation, B_i, and (2) expected growth rate per time period, expressed as a function of body size, $g_i(x)$. For further information about the derivation of $g_i(x)$ see the Appendix.

Initially, I assume mortality risk to be independent of body size. However, because increasing body size may benefit individuals by reducing their probability of being captured by a predator (e.g., Patten 1977), I also explore the effects of size-dependent mortality risk, such that:

$$B_i = f(\mu_i, x) \tag{5.2}$$

where μ_i scales the relationship between body size and mortality risk. For simplicity, I assume that B_i (and in the case of size-dependent predation, μ_i) remains the same-year round. However, $g_i(x)$ is reduced during time periods 12 through 17 to simulate the seasonal reduction in food availability and metabolic rate associated with reduced water temperatures in winter (Sandercock 1991). For a complete description of the functions used in the model, see Table 5.1.

For juvenile stream salmonids, whose prey are delivered by water currents, the best feeding sites are likely shallow areas of relatively high current velocity (Ruggles 1966; Fausch 1984), but often with little instream structure or overhead cover to shelter

Table 5.1. Definitions and ranges of parameter values producing qualitatively similar results for all symbols and functions in the model with sources of literature estimates indicated below.

Definition	Symbol	Values Investigated
time period within a year	t	1, 2, ..., 20
year	y	---
body size at (t, y) expressed as mass, in grams	$x(t, y)$	1 to 15[a]
minimum size before starvation	x_{min}	1
maximum size attainable	x_{max}	15
behavioural options	i, s	$i = 1, 2, 3$, s = smolt
per period potential increase in mass associated with option i, as a percent of body size	$e_i(x)$	8.91 to 89.1 (s)[b] 0.891 to 8.91 (w)[b]
per period decrease in mass associated with option i, as a percent of body size	$\alpha_i(x)$	0.285 to 16.3 (s)[c] 0.02855 to 1.63 (w)
per period probability of successfully acquiring food associated with option i	λ_i	0.1 to 0.9 (s) 0 to 0.5 (w)
per period expected growth rate associated with option i, as a function of body size	$g_i(x)$[d]	---
per period probability of mortality associated with option i	B_i	0.0267 to 0.2136[e]
relationship between body size and mortality risk associated with option i	$f(\mu_i, x)$	$\frac{\mu_i}{x(t, y)}$
coefficient scaling size-dependent mortality risk associated with option i	μ_i	0.0801 to 0.2314
coefficient scaling size-dependent survival at smolting	k	1 to 6
minimum mass required to smolt, in grams	x_s	4[f]
coefficient scaling the breadth of the favoured smolting period	A	0.2 to 0.9

[a] Sandercock (1991) and references therein

[b] the range reported reflects the minimum and maximum values explored for the safest and riskiest options, respectively, in summer (s) and winter (w)

[c] per period mass losses were chosen such that they ranged from 3 to 50% of the per period mass increases associated with successful acquisition of prey

[d] $e_i(x)$, λ_i and $\alpha_i(x)$ were chosen such that $g_i(x)$ produced daily growth rates similar to those reported by Parker (1971) and Shelbourn et al. (1973) and seasonal changes in mass as reviewed by Sandercock (1991)

[e] calculated from seasonal mortality estimates reported by Godfrey (1965), Fraser et al. (1983) and Gregory & Levings (1996)

[f] derived from estimates reported by Sandercock (1991) and references therein

individuals from predators. Therefore, habitats with high growth potential are also likely to be associated with high mortality risk, such that:

$$B_1 > B_2 > B_3 \tag{5.3}$$

and

$$g_1(x) > g_2(x) > g_3(x) \tag{5.4}$$

As a consequence of choosing to remain in freshwater and forage in habitat i during time period t, in year y, an individual's expected body size during the subsequent time period, $x\,(t + 1, y)$, will be:

$$x\,(t + 1, y) = x\,(t, y) + g_i(x) \tag{5.5}$$

and its expected future probability of successfully smolting, $F_i(x, t, y)$, will equal:

$$F_i(x\,,\,t\,,\,y) = (1 - B_i)\,\left[F_i\left(x\,(t\,,\,y) + g_i(x),\, t + 1,\, y\right)\right] \qquad \text{for all } x\,(t\,,\,y) \geq x_{min} \tag{5.6}$$

$$F_i(x\,,\,t\,,\,y) = 0 \qquad \text{for all } x\,(t\,,\,y) < x_{min} \tag{5.7}$$

If, however, the individual elects to smolt during period t, in year y, its expected probability of success, $S\,(x\,,\,t\,,\,y)$, will depend on body size and time of year (Foerster 1954; Holtby et al. 1990). In general, I assume that an individual's probability of surviving smolting will be positively related to body size, and will be highest each spring and lowest during the fall. Although many of the biological details required to estimate the true relationship between body size, time of year, and smolting success are unknown, for the purpose of this example I assume that $S\,(x\,,\,t\,,\,y)$ can be characterized by a function of the following sort:

$$S\,(x\,,\,t\,,\,y) = \frac{x\,(t\,,\,y)^3}{k^3 + x\,(t\,,\,y)^3} + A \text{ cosine } \left(\frac{2\pi t}{t_{max}}\right) - 0.6 \qquad \text{for all } x\,(t\,,\,y) \geq x_s \tag{5.8}$$

$$S\,(x\,,\,t\,,\,y) = 0 \qquad \text{for all } x\,(t\,,\,y) < x_s \tag{5.9}$$

where x_s is the minimum mass required for physiological salt water tolerance. Thus, I assume that smolting can take place at any time during the year, however, the probability of success will be greatest for large individuals who initiate migration during the favoured spring period, the breadth of which is influenced by the amplitude (A) of the cosine function in expression (5.8) (Figure 5.1). For all combinations of (x , t , y), the behavioural option (high risk, intermediate risk, low risk, or smolt) providing the highest expected return defines the optimal policy. Thus, we have the dynamic programming equation:

$$F(x, t, y) = \max_i \begin{cases} (1 - B_i)\, F(x + g_i(x), t + 1, y) & \text{for } i = 1 \text{ to } 3 \\ S(x, t, y) & \text{for } i = s \end{cases} \tag{5.10}$$

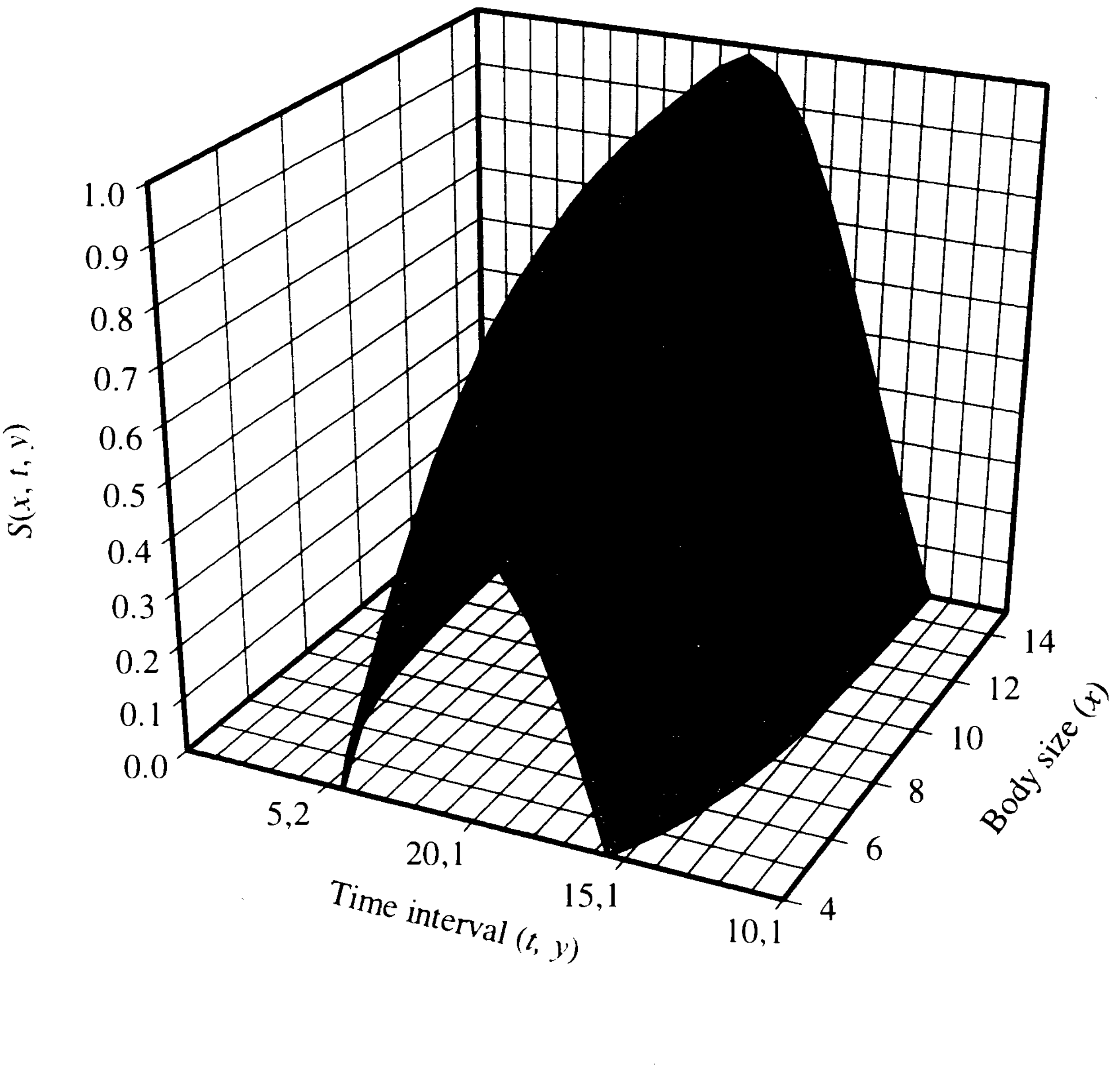
For simplicity, I assume that each individual's decision is independent of the decisions made by other members of the population (but see Discussion).

Unlike most dynamic programming models, this model has no fixed time horizon. Rather, fish can obtain the 'terminal' reward (given by expression (5.8)) at any time and elect to remain in freshwater for a second, third or even fourth year without loss of fitness (but see Discussion). The normal backward induction approach must therefore be modified, since the fitness consequences of choosing behavioural option 1, 2 or 3 at the end of the year ($t = 20$, y) will depend on some unknown value - the fitness associated with the individual's expected state at the beginning of the following year ($t = 1$, $y + 1$). The solution is found by repeated backward iteration. Expected fitness values for all x ($t = 20 + 1$, y) in the current iteration are replaced with those calculated for x ($t = 1$, y) in the previous iteration such that when $t = 20 = T$, the dynamic programming equation becomes:

$$F(x, T, y) = \max_i \begin{cases} (1 - B_i)\, F(x + g_i(x), 1, y + 1) & \text{for } i = 1 \text{ to } 3 \\ S(x, T, y) & \text{for } i = s \end{cases} \tag{5.11}$$

The process is repeated until the solution stabilizes; typically, 4 or 5 iterations are required. The computational process is analogous to the biological scenario being modeled, in which the behavioural option which maximizes fitness at the end of the first year depends on the expected consequence of that behaviour at the beginning of the next

Figure 5.1. General form of the terminal reward function. An individual's probability of successfully smolting will depend on both body size and the time remaining before the annual smolting period. For details, see equations (5.8) and (5.9).


1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
S(x, t, y)
5,2
20,1
15,1
10,1
Time interval (t, y)
4
6
8
10
12
14
Body size (x)

year, in essence, tomorrow or the next time period. As a consequence of this procedure, a 'decision matrix' is created, illustrating the optimal behavioural policy for all combinations of x, t, and y. In reality, because I assume that environmental conditions do not vary between years, the optimal policy for each combination of x and t will be the same regardless of the number of years spent in freshwater, and thus, can be simply illustrated with respect to x and t alone (see Figure 5.2).

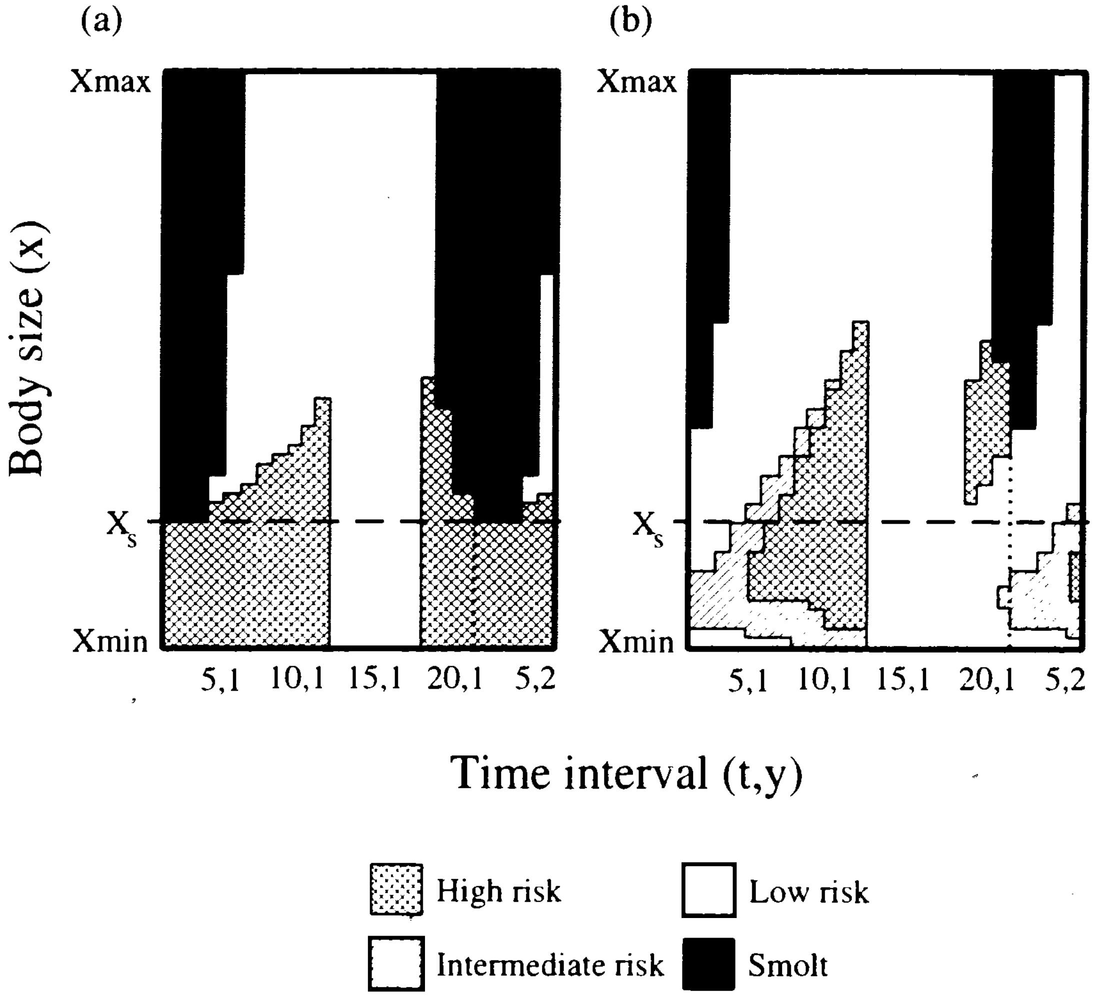
Due to lack of information about the specific values parameters might take (i.e., habitat-specific growth rates, mass losses due to metabolism, and mortality risks), I initially chose values that produced a range of daily and seasonal growth rates, fry to smolt mortality rates, and size distributions at smolting similar to those described in the literature (see Sandercock 1991 and references therein). I then examined how changes in these parameter values might influence the state- and time-dependent optimal policy and, through sequential forward iteration (i.e., individuals remaining in freshwater at $t = 20$ were 'run' through the decision matrix a second, third or fourth time, as necessary), the resultant distribution of smolt sizes and times of seaward migration, both within and between years. To simulate the variation in size at and timing of emergence of juvenile fish from the gravel, I varied the starting conditions for each forward iteration by randomly assigning some proportion of the original population to each of the first two x and t intervals. Sensitivity analyses were conducted on each of the model's parameters, including the function describing the 'terminal' reward. As suggested by Gladstein et al. (1991) and Houston et al. (1992), I report the range of values over which qualitatively similar results were obtained (Table 5.1).

Results

General patterns of risk-taking behaviour

Despite the broad range of parameter values investigated, only two general patterns of risk-taking behaviour are generated by the model (e.g., Figure 5.2a, 5.2b). In both cases, the predicted effects of body size and season on risk-taking behaviour are similar. In general, large individuals (i.e., $x(t, y) >> x_s$) are predicted to favour lower risk behavioural options than small individuals, protecting the large expected fitness associated with their body size until such time as smolting is favoured ('asset protection'; Clark 1994). Small individuals are generally predicted to accept higher levels of mortality risk, in part, to avoid starvation, but also because high-risk behaviour may allow them to attain the minimum size required for smolting (x_s) in the current year. Individuals of all sizes are

Figure 5.2. General patterns of risk-taking behaviour when (a) mortality risk is independent of body size, and (b) when increasing body size reduces mortality risk. Optimal policies for time periods 1 through 5 in year 2 are indicated on the right hand side of each decision matrix to facilitate illustration of the predicted smolting period. Parameter values associated with high, intermediate and low risk behavioural options, respectively, in (a) λ_i (summer) = 0.5625, 0.375, 0.225, λ_i (winter) = 0.15, 0.075, 0.0375, B_i = 0.0712, 0.064, 0.0534, and (b) λ_i (s) = 0.75, 0.5, 0.3, λ_i (w) = 0.2, 0.1, 0.05, μ_i = 0.2136, 0.1424, 0.0801. In both (a) and (b), $e_i(x)$ (s) = 0.1958, $e_i(x)$ (w) = 0.01958, $\alpha_i(x)$ (s) = 0.01958, 0.00979, 0.005874, $\alpha_i(x)$ (w) = 0.001958, 0.000979, 0.000589, k = 4, and A = 0.6.


(a)
(b)
Xmax
Xmax
Body size (x)
X_s
X_s
Xmin
Xmin
5,1 10,1 15,1 20,1 5,2
5,1 10,1 15,1 20,1 5,2
Time interval (t,y)
High risk
Low risk
Intermediate risk
Smolt

predicted to reduce their level of risk-taking during the winter months, when the growth potentials of higher risk habitats are too low to offset the associated mortality costs.

The size range of individuals accepting high levels of mortality risk is predicted to increase as the year progresses, in part, because individuals who had previously 'played it safe' must protect themselves against the lower growth rate and potential mass loss associated with winter, but also, because high-risk behaviour may lead to the attainment of the body size required for smolting in their second spring of life (i.e., shaded regions at t = 19, 20, y = 1 and t = 1, 2, 3, y = 2). Small fish tend to make the transition from low-risk to high-risk behaviour earlier in the year than large fish, as they require a longer period of high growth to reach smolting size.

As a consequence of the general shape of the terminal reward function (see Figure 5.1), smolting tends to occur in the spring (i.e., t = 19, 20, y = 1 and t = 1, 2, 3, y = 2), with the predicted minimum size of smolting individuals first decreasing, then increasing as the smolting period draws to a close (Figure 5.2a, 5.2b). For individuals whose body size places them on the steepest part of the terminal reward function, delaying smolting for an additional time period or two, and increasing body size via high-risk behaviour, can dramatically increase the payoff obtained when smolting eventually occurs.

When mortality risk is independent of body size and behavioural options differ significantly in growth potential, the predicted area of high risk-taking behaviour extends to the bottom of the decision matrix, including even the smallest individuals, who must accept high levels of risk to avoid starvation (Figure 5.2a). However, when mortality risk decreases with increasing body size, the predicted area of high risk-taking behaviour shrinks and is replaced by areas of intermediate risk behaviour, both earlier in the year and by individuals of relatively small body size (Figure 5.2b). Fish who continue to accept high levels of risk are those for whom increased body size has decreased their risk of being captured by a predator, and who can anticipate smolting in the current year if a high rate of growth is maintained. However, even individuals who are unlikely to attain the size required for smolting the following spring may favour high risk behaviours in an attempt to 'outgrow' their predators. Again, small individuals (with the exception of fish close to x_{min}, who experience the highest risk of mortality) are predicted to shift to higher risk behaviours earlier in the season than large individuals, as they require a longer period of high growth to reach the body size required for smolting.

As a consequence of individuals adopting the patterns of risk-taking behaviour described above, fish populations will be characterized by one of two size-frequency distributions over time. When mortality risk is independent of body size, all individuals initially incur the same level of risk (see Figure 5.2a, $t = 1, 2, 3$, $y = 1$), and hence, grow at a similar rate. The size-frequency distribution of fish tends to be unimodal and increases in breadth over time, in response to the probabilistic nature of prey capture, and consequently, fish growth. Depending on both relative and absolute growth rates and mortality risks, the surviving population either smolts in a single year or over several consecutive years, with the largest fish smolting at the end of the first year and the remainder smolting a year or two later (Figure 5.3).

When large body size reduces mortality risk, the smallest individuals initially accept lower levels of risk than those slightly larger in size and thus, grow at a slower rate (see Figure 5.2b, $t = 1, 2, 3$, $y = 1$). As a consequence of these behavioural differences, size-frequency distributions of fish can be either unimodal or bimodal, depending on the initial size distribution of fish in the population and the relative locations of high and low risk-taking behaviours in the decision matrix. When the size-frequency distribution of fish is bimodal, 'upper mode' individuals (*sensu* Thorpe 1977), having experienced relatively high growth rates, tend to smolt after spending only a single year in freshwater, while lower, slower-growing mode individuals delay smolting until the second year (Figure 5.4).

Sensitivity Analysis

Although the general behavioural patterns discussed above are generated consistently over a broad range of parameter values (see Table 5.1 for the range of parameter values over which qualitatively similar results were generated), both the shape of the predicted parameter space of high-risk taking behaviour and the breadth of the predicted smolting period vary with the values chosen.

Effects of increasing growth potential

For both types of decision matrices (e.g., Figures 5.2a, 5.2b), increasing growth potential results in both a horizontal narrowing and a vertical elongation of the range of (x, t) combinations that are predicted to accept high levels of risk, as small individuals (i.e., $x(t, y) \approx x_s$) reduce their level of risk-taking early in the year and larger individuals increase their level of risk-taking later on (Figures 5.5, 5.6). As growth potential increases, the fitness benefits of incurring risk increase for fish of intermediate size,

Figure 5.3. Temporal changes in the size-frequency distribution of a population of fish following the pattern of risk-taking behaviour predicted when mortality risk is independent of body size. For each time period illustrated, the proportion of the original population (i.e., 1 at $t = 0$, $y = 1$) that has survived and remains in freshwater is indicated by the upper limit on the corresponding frequency axis. Note that population size decreases over time as a consequence of the death of some individuals and the decisions of other to initiate seaward migration. Parameter values are the same as those for Figure 5.2a.

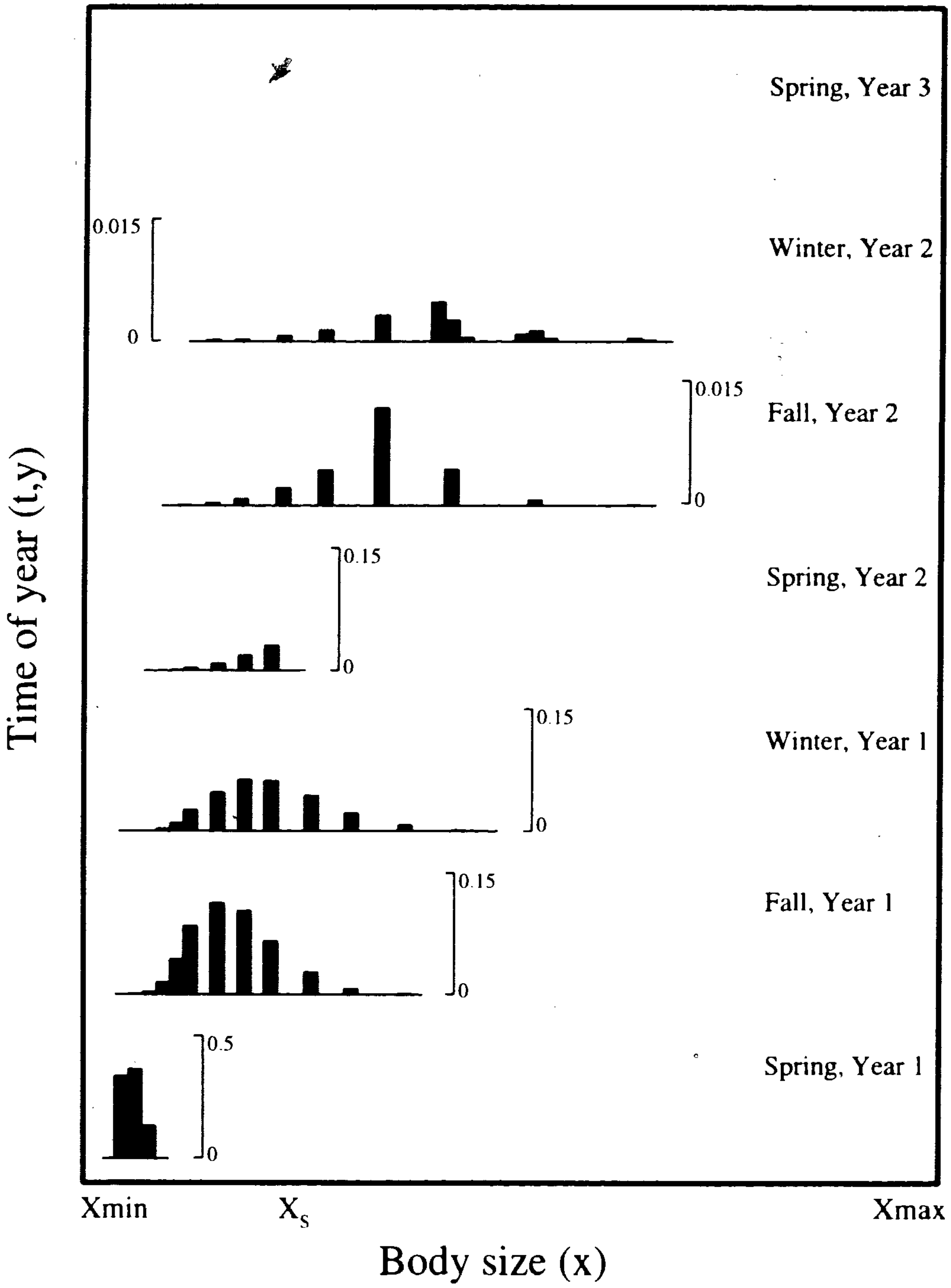

Spring, Year 3
0.015
0
Winter, Year 2
0.015
0
Fall, Year 2
0.15
0
Spring, Year 2
0.15
0
Winter, Year 1
0.15
0
Fall, Year 1
0.5
0
Spring, Year 1
Time of year (t,y)
Xmin
X_S
Xmax
Body size (x)

Figure 5.4. Temporal changes in the size-frequency distribution of a population of fish following the pattern of risk-taking behaviour predicted when increasing body size reduces mortality risk. For each time period illustrated, the proportion of the original population (i.e., 1 at $t = 0, y = 1$) that has survived and remains in freshwater is indicated by the upper limit on the corresponding frequency axis. Note that population size decreases over time as a consequence of the death of some individuals and the decisions of other to initiate seaward migration. Parameter values are the same as those for Figure 5.2b.

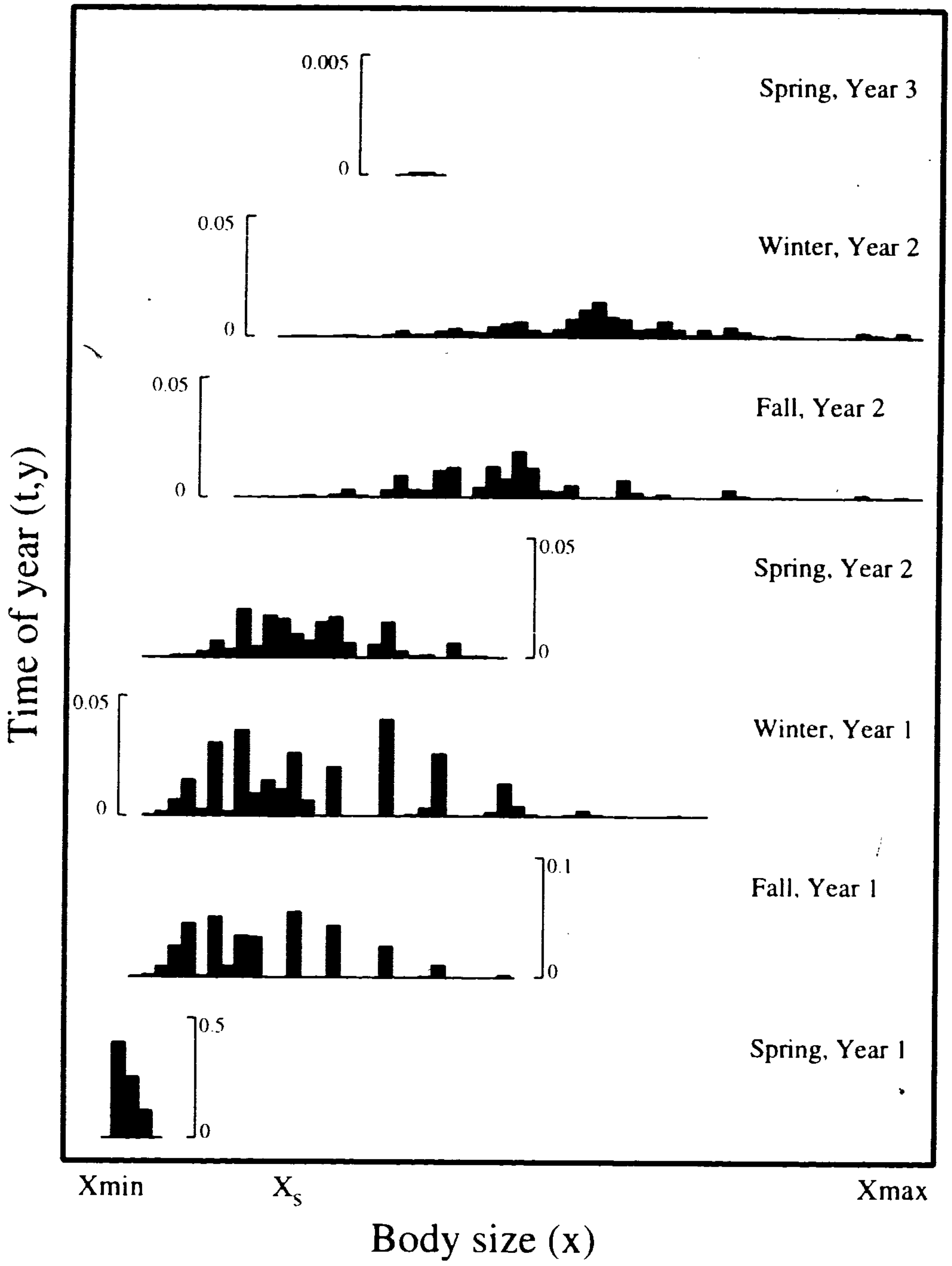

0.005
0
Spring, Year 3
0.05
0
Winter, Year 2
0.05
0
Fall, Year 2
0.05
0
Spring, Year 2
0.05
0
Winter, Year 1
0.1
0
Fall, Year 1
0.5
0
Spring, Year 1
Time of year (t,y)
Xmin
X_s
Xmax
Body size (x)

Figure 5.5. Effects of increased growth potential and mortality risk on the predicted patterns of risk-taking behaviour when mortality risk is independent of body size. Optimal policies for time intervals 1 through 5 in year 2 are indicated on the right hand side of each decision matrix to facilitate illustration of the predicted smolting period. Parameter values associated with high, intermediate and low risk behavioural options, respectively, when growth potential is low (a, d) [$e_i(x)$ (summer) = 0.1424, $e_i(x)$ (winter) = 0.01424], intermediate (b, e) [$e_i(x)$ (s) = 0.1958, $e(x)$ (w) = 0.01958], and high (c, f) [$e_i(x)$ (s) = 0.267; $e_i(x)$ (w) = 0.0267] and when mortality risk is low (a, b, c) [B_i = 0.0356, 0.03204, 0.0267], and high (d, e, f) [B_i = 0.0712, 0.064, 0.0534]. In all cases, $k = 4$ and $A = 0.6$. Per period mass losses and probabilities of successfully acquiring food are the same as those for Figure 5.2a.

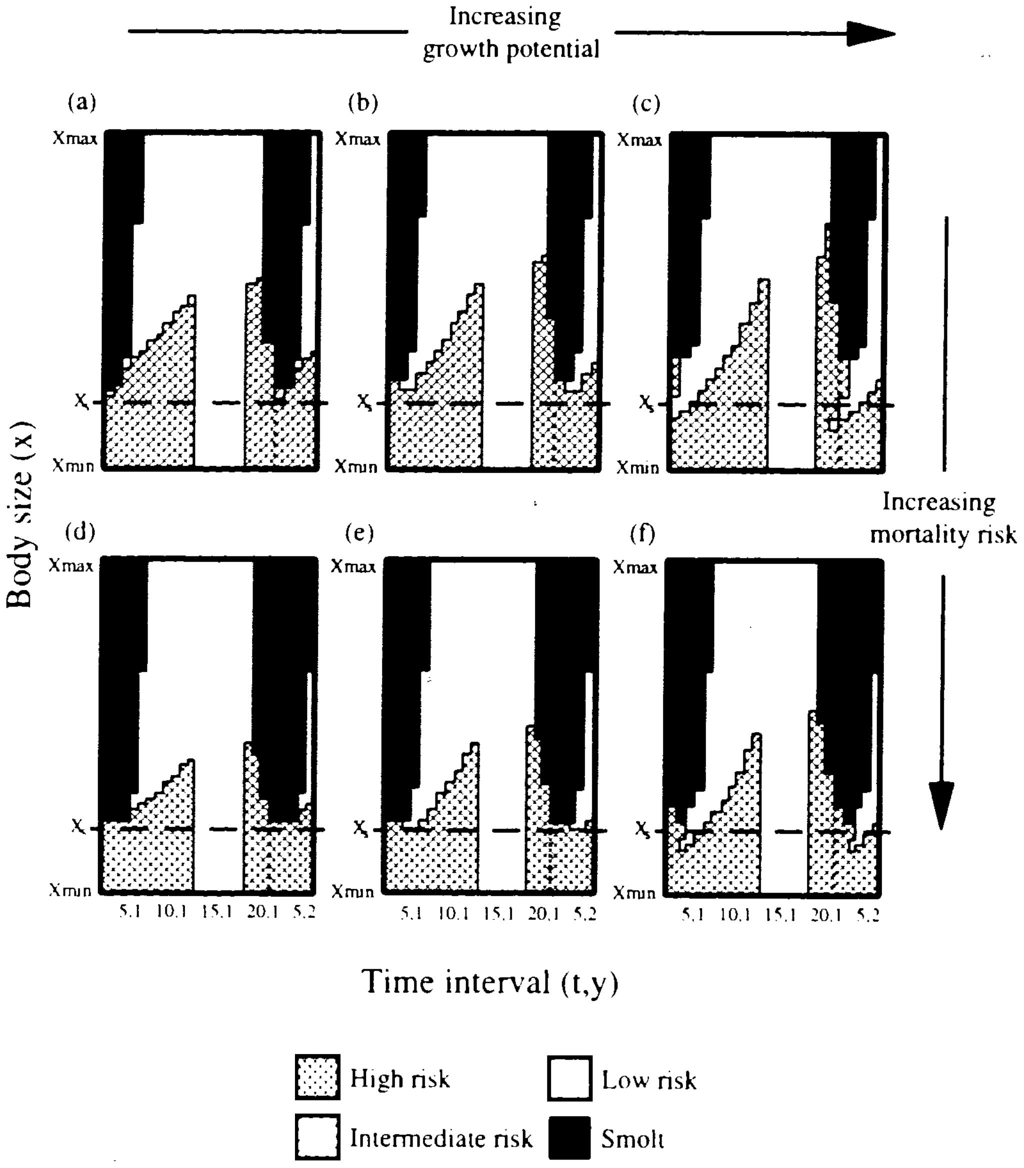
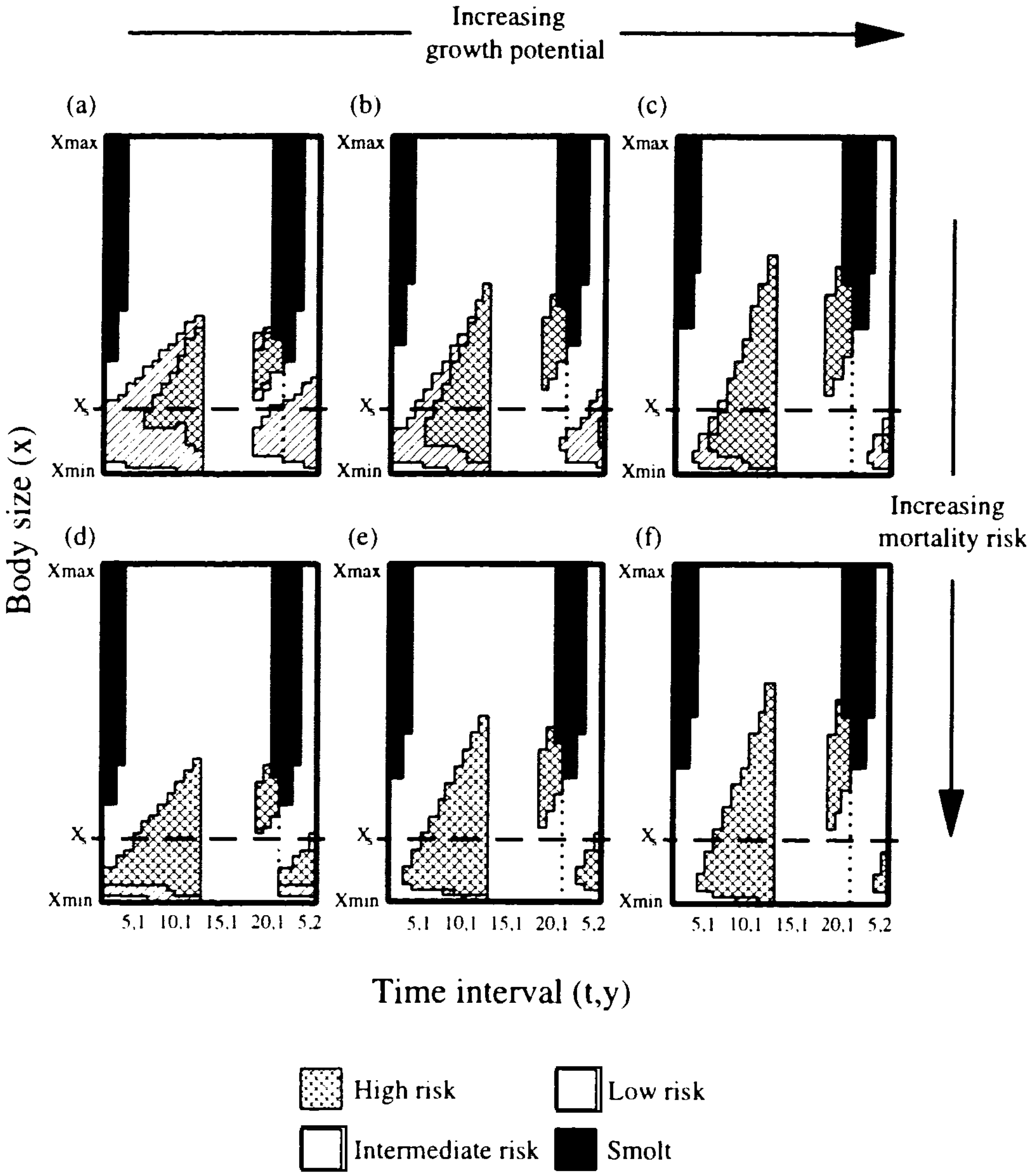
Increasing growth potential
Increasing mortality risk
(a)
(b)
(c)
(d)
(e)
(f)
Xmax
Xs
Xmin
Body size (x)
5.1
10.1
15.1
20.1
5.2
Time interval (t,y)
High risk
Low risk
Intermediate risk
Smolt

Figure 5.6. Effects of increased growth potential and mortality risk on the predicted patterns of risk-taking behaviour when mortality risk is size-dependent. Optimal policies for time intervals 1 through 5 in year 2are indicated on the right hand side of each decision matrix to facilitate illustration of the predicted smolting period. Parameter values associated with high, intermediate and low risk behavioural options, respectively, when growth potential is low (a, d), intermediate (b, e) and high (c, f), and when mortality risk is low (a, b, c) [$\mu_i = 0.2136, 0.1424, 0.0801$] and high (d, e, f) [$\mu_i = 0.2314, 0.1602, 0.089$]. In all cases, $k = 4$ and $A = 0.6$. Potential increases in mass are as described for Figure 5.5 and per period mass losses and probabilities of successfully acquiring food are the same as those for Figure 5.2b.


Increasing growth potential
(a)
(b)
(c)
(d)
(e)
(f)
Xmax
Xs
Xmin
Body size (x)
Increasing mortality risk
5.1 10.1 15.1 20.1 5.2
Time interval (t,y)
High risk
Low risk
Intermediate risk
Smolt

particularly those whose body size places them on the steepest part of the terminal reward function (see Figure 5.1). Because low risk behaviours are less likely to lead to starvation, small fish can delay incurring higher levels of risk until later in the year. Increasing growth potential also results in an increase in the predicted minimum size of smolting individuals (Figures 5.5b, 5.5c and 5.6b, 5.6c).

As a consequence of increasing growth potential, cumulative mortality decreases slightly (Table 5.2), in part because fewer individuals starve to death, but also because a larger number of individuals reach the size where the adoption of safer behaviours is predicted. Having grown at a faster rate, fish tend to smolt both earlier in the year and at a larger size, resulting in an overall decrease in the proportion of the population delaying smolting until year two (Table 5.2).

Effects of increasing mortality risk

Increasing overall mortality risk (B_i) results in an increase in the range of (x , t) combinations favouring the lowest risk option (Figures 5.5, 5.6), although the magnitude of the effect depends upon the relationship between mortality and body size. The size of the largest risk-takers tends to decrease, particularly when mortality risk is independent of body size, because the fitness benefits of increased growth no longer outweigh the risk of being captured by a predator. This decline is less noticeable when mortality risk is size-dependent, presumably because the increase in risk is relatively small for larger fish (e.g., Figure 5.6b, 5.6e). However, fish who are slightly smaller than the minimum size required for smolting (x_s) may actually increase their level of risk-taking (compare Figure 5.5c to 5.5f, Figure 5.6a to 5.6d and Figure 5.6b to 5.6e). Because small fish can 'escape' their predators through growth, incurring risk for a short period of time will both increase body size and decrease future risk of mortality (see equation (5.2)).

As a consequence of increasing mortality risk, the proportion of the population that survives to smolting decreases (Table 5.2). Fish tend to smolt at a smaller size and to extend the smolting period until later in the year (i.e., $t = 1, 2, 3, y = 2$), often incurring high levels of risk in the periods immediately preceding seaward migration (see Figures 5.5, 5.6).

Effects of the terminal reward function

I investigated the effects of changing (1) the breadth of the favoured smolting period, and (2) the steepness of the relationship between body size and fitness, on the

Table 5.2. The effects of increasing growth potential ($e_i(x)$)and mortality risk due to predation (B_i)on the cumulative proportion of the original population dying each year, and the size and proportion of the original population smolting after spending one or two years in freshwater.

B_i[a]	$e_i(x)$[b]	Cumulative Mortality		Year 1 Smolts			Year 2 Smolts		
		Year 1	Year 2	t, y	Prop.	Size	t, y	Prop.	Size
0.0356, 0.03204, 0.0267	0.1424, 0.01424	0.5201	0.5752	20, 1	0.0032	6.695	20, 2	0.0642	9.447
				1, 2	0.3564	5.012			
	0.1958, 0.01958	0.5176	0.5303	20, 1	0.0809	8.577	19, 2	0.0152	11.593
				1, 2	0.3485	6.515	20, 2	0.0001	7.574
				2, 2	0.0249	5.034			
	0.2670, 0.0267	0.5016	0.5026	20, 1	0.4023	11.536	20, 2	0.0012	12.889
				1, 2	0.0908	7.976			
				2, 2	0.0030	5.982			
0.0712, 0.064, 0.0534	0.1424, 0.01424	0.7572	0.7744	1, 20	0.0420	5.350	19, 2	0.0042	7.712
				1, 2	0.1407	4.752	20, 2	0.0016	6.863
				2, 2	0.0234	4.322			
				3, 2	0.0138	4.322			
	0.1958, 0.01958	0.7476	0.7499	19, 1	0.0165	8.271	19, 2	0.0006	8.96
				20, 1	0.1400	6.724	20, 2	4.87E-5	7.416
				1, 2	0.0862	5.282			
				2, 2	0.0047	4.322			
				3, 2	0.0021	4.322			
	0.2670, 0.0267	0.7240	0.7241	19, 1	0.1865	10.007	19, 2	2.42E-5	10.532
				20, 1	0.0712	8.302	20, 2	1.59E-6	8.364
				1, 2	0.0178	6.584			
				2, 2	0.0030	4.797			
				3, 2	0.0001	4.797			

[a] per period probability of mortality due to predation associated with high risk, intermediate risk and low risk behaviours, respectively

[b] per period potential increase in mass associated with successful prey acquisition in summer and winter, respectively; parameter values as described in Figure 5.2a.

predicted pattern of risk-taking behaviour. This was done by altering the amplitude of the cosine function ($A = 0.2$ to 0.9) and the magnitude of the exponent scaling the relationship between body size and fitness ($k = 1$ to 6), respectively (see equation (5.8)). Although varying these components of the terminal reward function resulted in quantitative changes in both the predicted size distributions of smolting individuals and the proportion of the population smolting at the end of the first year, general features of the decision matrices remained the same. Therefore, I conclude that the general patterns of risk-taking behaviour predicted by the model are relatively insensitive to the specific parameter values chosen, and are likely to be applicable as long as the relationship between body size and the probability of successfully smolting is positive and environmental conditions favour an annual smolting period.

DISCUSSION

Risk-taking behaviour in juvenile salmon

Using the methods of dynamic programming (Houston et al. 1988; Mangel & Clark 1988), I have shown that state- and time-dependent responses to options differing in growth potential and mortality risk can affect the timing of life history events and the body size at which they occur. In general, the model predicts that, over the entire possible size range (i.e., x_{min} to x_{max}), an individual's willingness to accept risk while foraging will be negatively correlated with its body size ('asset protection'; Clark 1994) and with the amount of time remaining before the seaward migration. However, because individuals can delay migration for a year or more, the generality of these predictions will depend on both the size range and developmental pathways of the individuals considered.

When mortality risk is independent of body size, all members of a recently emerged cohort are predicted to accept the same level of risk initially (Figure 5.2a). Individuals will grow at a fairly similar rate, although some will grow more quickly than others due to the probabilistic nature of acquiring food, and the population will be characterized by a unimodal size-frequency distribution of fish over time (Figure 5.3). In contrast, when body size is negatively correlated with mortality risk (bigger fish are safer), the largest members of a recently emerged cohort will often favour higher risk behavioural options than their smaller contemporaries (Figure 5.2b). As a consequence of these behavioural differences, large individuals will experience higher rates of growth than small individuals, and population size-frequency distributions may become bimodal over time (Figure 5.4).

In both cases, an individual's probability of smolting successfully after only a single year in freshwater will be positively correlated with its body size, however, in bimodally distributed populations large fish will have achieved their size via higher risk behaviour rather than by chance encounters with prey.

In general, the results of experiments investigating foraging-predation risk tradeoffs in a number of anadromous salmonids support the patterns of risk-taking behaviour predicted by the model. While investigating the effects of cover on the habitat choices of recently emerged coho salmon, Grand and Dill (1997) observed that large, dominant fish were less likely to be found directly under cover than their smaller subordinates, suggesting that willingness to incur risk was positively correlated with body size (but see Figure 2.4 for an alternative interpretation). Similarly, Johnsson (1993) observed that large individuals within a cohort of recently emerged rainbow trout (*Oncorhynchus mykiss*) were more willing to expose themselves to predation while foraging than were smaller individuals. Such patterns of risk-taking behaviour are predicted to occur when increased body size confers some survival advantage prior to smolting (see Figure 5.2b). However, due to the short time period over which these experiments were conducted, it is unclear whether the observed individual differences in risk-taking behaviour correspond to differences in developmental pathway and consequently, to differences in the timing of life history events.

The link between risk-taking behaviour and life history timing has been more clearly demonstrated in Atlantic salmon (*Salmo salar*), whose populations are often characterized by markedly bimodal size-frequency distributions (Thorpe 1977). Large, upper modal group fish, who tend to smolt after a single year in freshwater (Metcalfe et al. 1988), are less likely to move to poorer foraging areas upon exposure to a predator than small, lower modal group individuals (Huntingford et al. 1988a, 1988b), who frequently defer migration for a year or more. These differences in growth rate and life history timing are thought to occur as a direct consequence of the observed reduction in appetite and feeding motivation of lower modal group fish in the summer of their first year of life (Metcalfe & Thorpe 1992). Indeed, when such a 'developmental switch' is incorporated into a dynamic programming model exploring the effects of climate change on salmonid life histories, a bimodal size-frequency distribution of individuals is always produced (Mangel 1994).

It is unclear, however, whether developmental switches are a general characteristic of salmonid biology, and it is difficult to understand how unimodal size distributions of fish might arise given their presence. Thus, rather than impose a reduction in feeding motivation on individuals who happen to be below some size threshold at a particular time (see Mangel 1994), I have allowed fish to repeatedly choose the level of growth, and hence, the level of mortality risk, that maximizes their probability of successfully smolting. As a consequence, both unimodal and bimodal size-frequency distributions of fish can occur, depending on relative growth rate and mortality risk, and the relationship between body size and mortality risk. It is interesting to note, however, that bimodality is only predicted to occur when small differences in body size lead to the adoption of different risk-taking behaviours in the spring and summer of the first year in freshwater, precisely the same time that individual decisions to maintain growth or reduce appetite become evident in bimodally distributed populations of Atlantic salmon (Metcalfe et al. 1986, 1988; Thorpe et al. 1992). Thus, the model suggests the types of environments in which developmental switches are likely to have evolved and provides a potential explanation for their timing.

In an attempt to simplify the model and increase its generality, I have made a number of important assumptions, several of which may affect the predicted patterns of risk-taking behaviour and life history timing. Although water temperature is known to influence salmonid energetics (e.g., Brett & Glass 1973), other than mimicking the effects of low winter temperature on food availability and energetic expenditure, I have ignored its effect on growth. However, catabolism increases with water temperature (Ursin 1979), and the proportion of an individual's daily intake which is available for growth will either increase or asymptote with increasing temperature, depending on its overall level of energy intake (Elliot 1976). Therefore, temperature will affect growth potential and hence, the optimal balance between growth and survival. Although I have not explicitly accounted for temperature-dependent growth in the model, in exploring the effects of increasing growth potential on risk-taking behaviour, I have illustrated how whole-stream increases in water temperature might influence growth rate and life history timing. Seasonal variation in water temperature can be easily incorporated into the dynamic programming framework by specifying the effects of temperature on metabolic rate and utilization efficiency (e.g., Mangel 1994), and generating a function which translates time of year into water temperature (e.g., Bednekoff & Houston 1994a).

When calculating the fitness payoff associated with each behavioural option, I have assumed both growth rate and mortality risk to be independent of local population density (i.e., density independent). However, when food or space is limited, or predators are constrained in their ability to handle more than a single prey at a time, the fitness payoff associated with a particular behavioural option may depend on the number of individuals adopting that behaviour. For juvenile salmonids, energetic gains will often be density-dependent, particularly in environments which favour territoriality (Kalleberg 1958; Mundie 1969). Preferred foraging sites may become saturated, forcing some individuals to settle in sites of lower quality (Fretwell & Lucas 1970), thereby reducing the number of fish adopting high risk behaviour and consequently, the proportion of the population smolting after a single year in freshwater. Furthermore, because out-migrating smolts provide a spatially predictable source of food for their predators, early marine survival may also depend on smolt density (but see Holtby et al. 1990). Thus, incorporating density-dependent fitness payoffs into the dynamic programming model described here will not only influence the predicted patterns of risk-taking behaviour (for an example, see McNamara & Houston 1990), but may also lead to increased synchronicity in the within-year timing of smolting.

Finally, I have assumed that fish who delay migration for a year or more do not incur any fitness cost, other than the cost of surviving until the next favourable smolting period. However, if individuals who smolt early also mature and reproduce early (e.g., 'jacks'; Gross 1991), their lifetime fitness may be greater than those who remain in freshwater for an extra year, particularly when those individuals are members of an expanding population (Roff 1992). Imposing a penalty for delaying smolting will likely have a similar effect on life history timing as that of decreasing growth potential; fish will tend to smolt earlier and at a smaller size.

Risk-taking behaviour and life history timing

In recent years, evolutionary ecologists have become interested in understanding the factors influencing the timing of life history events, particularly those that are accompanied by some abrupt ontogenetic transformation or shift in habitat use (Werner & Gilliam 1984; Ydenberg 1989; Ludwig & Rowe 1990). Such shifts are thought to have arisen primarily in response to differences between habitats in size-specific growth and mortality rates and therefore, can be viewed as strategies for achieving an optimal balance between growth and survival during ontogeny (Werner & Gilliam 1984). When shifts in habitat use are seasonally constrained (e.g., by temperature or resource availability), a tradeoff exists between the timing of the shift and the size at which it occurs (Rowe & Ludwig 1991). Theoretical investigations of this tradeoff are typically characterized by two simplifying assumptions: (1) all individuals within a population follow the same growth trajectory and consequently, incur the same level of risk, prior to the habitat shift, and (2) individuals who don't initiate the transition by the end of the time period modeled receive a fitness payoff of zero (Ydenberg 1989; Rowe & Ludwig 1991). While both assumptions may be appropriate for the decisions modeled by these authors (i.e., timing of fledging in seabirds and metamorphosis in tadpoles, respectively), their biological generality is not universal.

By allowing individuals to choose repeatedly amongst behavioural options differing in both energetic gain and mortality risk and delay their habitat shift until some future favourable period of time, I have demonstrated that individual differences in risk-taking behaviour will influence growth trajectories and consequently, the timing of life history events, including ontogenetic habitat shifts. Like previous models of life history timing, this model predicts that the size of individuals initiating the habitat shift will decrease as the favoured transition period draws to a close (see Table 5.2). However, the pattern arises not because individuals who postpone the shift face certain reproductive death, but rather, because the fitness increase associated with smolting at a larger size does not offset the mortality risk incurred by remaining in freshwater for an extra year. Furthermore, as a consequence of relaxing the assumptions of Ydenberg (1989) and Rowe and Ludwig (1991), my model allows for the emergence of alternative developmental pathways and hence, alternative life history strategies within a single population, a phenomenon which is frequently observed (see examples below).

The results of the model are likely to be quite general, applying not only to anadromous salmonids, but to any animal whose temporally constrained life history events may be postponed beyond some current favourable period of time. Examples include shrimp (Pandalidae) whose reproductive period is seasonally constrained, and who can delay their first breeding attempt for a year or more (Charnov 1989), predatory dobsonfly larvae (*Protohermes* spp.), whose transformation to adulthood is triggered by a seasonal decline in prey size and can be delayed for up to three years (Hayashi 1994), and burnet moths (*Zygaena hippocrepidis*), who can either develop directly and reproduce in a single year, or delay reproduction by a year or more through the addition of late instar diapause and aestivation (Wipking 1990). In each case, individuals are likely to be faced with short term behavioural options differing in both energetic gain and mortality risk. Clearly, in order to fully understand how animals resolve the conflicting demands of growth and survival, future studies of risk-taking behaviour must consider not only the effects of state and time on the tradeoff between growth and survival (e.g., Clark 1994), but also the life history alternatives available to individuals.

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APPENDIX 5.1

Expected growth rates

As a consequence of choosing to foraging in habitat i, during time period t, an individual of mass x will either be successful at acquiring food (with probability λ_i) and increase in mass, or fail to acquire food (with probability $(1 - \lambda_i)$), and decrease in mass. In this example, λ_i reflects the overall availability of food within a habitat, such that:

$$\lambda_1 > \lambda_2 > \lambda_3 \qquad \text{(A5.1)}$$

For simplicity, I assume that λ_i is independent of body size.

If successful at acquiring food, the individual will increase its mass by $e_i(x) - \alpha_i(x)$, where $e_i(x)$ represents the potential increase in mass per time period resulting from prey capture, and $\alpha_i(x)$ represents the expected decrease in mass per time period resulting from metabolic expenditure. However, if the individual fails to acquire food during time period t, its mass will decrease by $\alpha_i(x)$. Both $e_i(x)$ and $\alpha_i(x)$ are expressed as percentages of body size. For simplicity, I assume that then energetic content of captured prey is independent of habitat, and thus, that:

$$e_1(x) = e_2(x) = e_3(x) \qquad \text{(A5.2)}$$

However, because prey are delivered by water currents, high prey encounter rates will often correspond to high rates of metabolic expenditure, such that:

$$\alpha_1(x) > \alpha_2(x) > \alpha_3(x) \qquad \text{(A5.3)}$$

Thus, an individual's expected growth rate $(g_i(x))$ in habitat i, per time period, t will be equal to:

$$g_i(x) = \lambda_i \, (e_i(x) - \alpha_i(x)) + (1 - \lambda_i) \, (-\alpha_i(x)) \qquad \text{(A5.4)}$$

I chose values of λ_i, e_i, and α_i such that:

$$g_1(x) > g_2(x) > g_3(x) \tag{A5.5}$$

GENERAL CONCLUSIONS

In his recent book, W. J. Sutherland (1996) advocates the use of ideal free distribution theory (IFD; Fretwell & Lucas 1970; Fretwell 1972) as a tool for linking the habitat selection decisions of individuals to population-level phenomenon. He argues that, because the fitness consequences of choosing a particular habitat will often depend on the behaviour of conspecifics (i.e., will be frequency-dependent), a game theoretic approach must be employed when studying habitat selection. However, despite an impressive array of illustrative examples and potential applications of the theory, Sutherland (1996) limits himself almost exclusively to cases in which fitness is determined primarily by the rate of resource acquisition. Differences in mortality risk between habitats are rarely considered, and the potential effects of competitors on an individual's risk of predation are virtually ignored.

In nature, habitats will frequently differ in their associated risk of mortality due to predation. Thus, an individual's choice of habitat will reflect its response to the conflicting demands of growth and survival. Indeed, my studies have demonstrated that animals are sensitive to both energetic gains and mortality risk during habitat selection, and are capable of responding to such tradeoffs in an adaptive manner (for recent reviews see Lima & Dill 1990; Lima in press). As noted by Sutherland (1996), an individual's best choice will often depend on the behaviour of conspecifics, both because they can reduce a habitat's growth potential via competition, and because they can decrease each individual's risk of predation within that habitat via earlier detection of predators (i.e., 'many eyes'; Pulliam 1973), 'confusion' of predators (e.g., Neill & Cullen 1974), and/or numerical dilution of risk (e.g., Foster & Treherne 1981). Clearly, in order to predict population-level patterns of habitat use, both components of fitness, and the manner in which each is influenced by competitors, must be considered.

In this thesis, I have considered the effects of intraspecific resource competition and predation risk on habitat selection in juvenile coho salmon (*Oncorhynchus kisutch*). In doing so, I have illustrated how differences between individuals in competitive ability and vulnerability to predation might influence an individual's choice of habitat, and consequently, the population distribution of competitors across habitats.

In Chapter 1, I showed experimentally that coho salmon consider not only the number of competitors in a habitat when deciding whether to forage there, but also the ability of those individuals to compete for limited resources. This chapter provides the first empirical support for Parker & Sutherland's (1986) unequal competitors IFD model, and suggests that in order to accurately predict the spatial distribution of a population, information about the relative competitive abilities of individuals within that population must be considered.

In Chapter 2, I experimentally generated between-habitat differences in predation risk and, by comparing the consequent pattern of habitat selection to that observed in the absence of risk, demonstrated that juvenile coho salmon consider both energy intake and risk of predation during habitat selection. Using the unequal competitors IFD model (Parker & Sutherland 1986) as a tool, I quantified the energetic equivalence of safety to the fish, and thus, the tradeoff between energy intake and predation risk. The results of this experiment demonstrate that the fitness benefits of safety can be measured in units of energy and can be offset by sufficient food.

In Chapter 3, I described a game theoretic model developed to investigate the effects of differences between competitors in both their ability to compete for resources and their vulnerability to predation on their choice of habitat and the subsequent distribution of competitors across habitats. In doing so, I considered how density-dependent predation risk might influence the predicted distribution. In the absence of such risk dilution, individuals are predicted to assort themselves according to competitive ability, with the competitor type experiencing the higher ratio of mortality risk across the habitats occurring primarily in the safer, less productive habitat. In contrast, when risk is fully diluted by competitor number, all members of the population are predicted to aggregate in a single habitat.

In Chapter 4, I reported the results of an experiment designed to determine the relative importance of risk dilution to the foraging decisions of juvenile coho salmon. The results of this experiment suggest that risk dilution is not an important determinant of coho foraging behaviour, rather, conspecifics influence the tradeoff between growth and survival primarily through their effect on the availability of resources. These results are consistent with the data presented in Chapter 2; even under elevated predation risk, fish distributions were never characterized by aggregation in a single habitat, as expected when risk is fully diluted by the presence of competitors.

In general, the manner in which individuals resolve foraging-predation risk tradeoffs, and consequently, the distribution of individuals across habitats, will depend upon the relative fitness contributions of growth and survival. In Chapter 5, I considered the effects of body size and the future opportunity for growth on the habitat choices of juvenile coho salmon and other animals who exhibit considerable flexibility in the timing of important life history events. The results of a dynamic programming model suggested that an individual's willingness to expose itself to predation risk, and hence, its choice of habitat, should depend on its body size and the time remaining before the annual period of seaward migration (i.e., 'smolting'). For simplicity, I assumed that the fitness consequences of choosing a particular habitat were independent of the number of competitors there. However, as demonstrated in Chapters 1, 2, and 4, the presence of competitors will often reduce a habitat's growth potential, and hence, might be expected to influence the state and time-dependent tradeoff between growth and survival, and consequently, the distribution of individuals across habitats.

Clearly, in order to link individual behaviour to population level phenomenon, future studies of habitat selection must consider not only individual differences in competitive ability, vulnerability to predation, body size, and anticipated future opportunity for growth, but also the effects of conspecifics on the tradeoff between growth and survival. Furthermore, because the population-level consequences of individual behaviour may depend strongly on population dynamics, when extending the results of simple models and small scale experiments to natural systems, researchers must also consider the effects of population size.

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