The effects of the spatial predictability of food on the defence behaviour and distribution of juvenile convict cichlids (*Cichlasoma nigrofasciatum*)

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Abstract

The effects of the spatial predictability of food on the defence behaviour and distribution of juvenile convict cichlids (*Cichlasoma nigrofasciatum*)

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The hypothesis that spatially predictable resources are more easily monopolized and defended than spatially unpredictable resources was tested by allowing groups of six juvenile convict cichlids to compete for *Daphnia magna* prey. One *Daphnia* appeared every 15 s in one of four patches defined by their probability of receiving the prey. Spatial predictability was manipulated by varying how often these probabilities were randomly assigned to the patches over a 3-day experiment: once (Predictable), 6 times (Intermediate), or 36 times (Unpredictable). The distribution of fish and patterns of resource use were compared to those predicted by the ideal free, ideal despotic, and perceptual constraints models of habitat selection.

With increasing resource predictability, dominant fish became significantly more aggressive, more sedentary, and ate a greater share of the food. In the Predictable treatment, the observed distribution was consistent with the

predictions of the ideal despotic model. Dominant fish spent more of their time and obtained more of their food in the best patch than subordinates. In the Unpredictable treatment, aggression was not related to foraging success. Both dominant and subordinate fish under-used the best patch, suggesting they were unable to track its location. The distribution of fish in the Intermediate treatment was not significantly different from an ideal free distribution, despite violating the assumption that individuals are of equal competitive ability.

These results suggest that interference competition, via resource defence, will promote despotic distributions in spatially predictable environments with defendable resources. In unpredictable environments, limitations in the ability of competitors to anticipate local resource availability will favour scramble competition.

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General Introduction

In nature, distributions of resources are often discontinuous in time and space, and these distributions in turn, may influence the distribution, interactions, and adaptations of organisms using the resource (Wiens 1976). Colwell (1974) identified two important components of resource distribution which he referred to as 'constancy' and 'contingency'. Constancy refers to the degree to which resources are clumped in time or space, ranging from uniformly distributed to highly aggregated. Contingency describes the degree to which there are dependable areas or times of resource abundance. In the terminology of Warner (1980), constancy and contingency are comparable to variability and predictability, respectively.

Resource variability in space can be measured as the variance in resource density per unit area (Warner 1980). When the variance in resource density is large, resources are patchy or clumped in their distribution. Temporal variability can be measured as the variance in resource density at a particular place over time, and describes the degree to which resources are synchronous, or clumped in time (Warner 1980).

Spatial predictability describes the degree to which there are dependable concentrations of resource in specific areas (Warner 1980). It can be quantified by ranking

different areas in terms of their relative resource density, and measuring the correlation of these rankings over successive time intervals. When the correlation coefficient is large, resources are predictable in space. Similarly, temporal predictability describes whether there are dependable periods of resource density. It can be quantified by ranking periods of time (i.e. months within a year) in terms of their relative resource density, and measuring the correlation of these rankings over longer periods of time (i.e. years). A high degree of correlation between years indicates a high degree of temporal predictability or seasonality (Warner 1980).

While much attention has focused on individual and population responses to resource variability (for a review see Wiens 1976), relatively few studies have measured or manipulated resource predictability (but see Pimm 1978). This is surprising, given the importance of predictability in most verbal models of spacing, mating and social systems (Brown 1964; Campanella 1975; Wiens 1976; Emlen 1980; Warner 1980; Davies & Houston 1984; Pulliam & Caraco 1984; Lott 1991). Many of the hypotheses stemming from these models are based on the concept of economic defendability (Brown 1964). According to Brown's model, animals should only defend resources when the benefits of defence exceed the costs, and when the net benefits of defence exceed the net benefits of adopting an alternate tactic. Spatial

predictability is thought to increase both the net benefits of defence and a resource's potential for monopolization. Thus, when food or mates are predictable and can be monopolized, territoriality (Wittenberger 1981) and resource defence polygyny (Emlen & Oring 1977) are expected to occur. Spatial predictability is also thought to play an important role in the evolution of life history traits (Stearns 1977; Horn 1978; Warner 1980). When resources are predictable and abundant, reproductive effort is predicted to decrease causing an increase in the mean and a decrease in the variance of adult survival (Ricklefs 1977). In addition, a high degree of spatial predictability is thought to select for philopatry (Horn 1978) and a large energy investment per offspring (Warner 1980).

The purpose of this thesis is to examine changes in the competitive behaviour and distribution of individuals in response to varying levels of spatial predictability of food. In Chapter 1, I investigate the effects of spatial predictability on the ability of juvenile convict cichlids (*Cichlasoma nigrofasciatum*) to defend food. This chapter provides the first test of the hypothesis that spatially predictable resources are more easily monopolized and defended than those which are spatially unpredictable. In Chapter 2, I use the ideal free distribution (Fretwell & Lucas 1970) as a framework for comparing distributions of fish to distributions of resources. Ideal free theory has

been moderately successful in predicting the distributions of animals in environments that are spatially predictable, but has not been applied to less predictable situations. Thus, Chapter 2 tests the general applicability of the model in environments of varying spatial predictability.

Chapter One

Spatial predictability of food influences its monopolization and defence by juvenile convict cichlids

The distribution of a resource in space and time influences its potential for monopolization and defence (Brown 1964; Emlen & Oring 1977; Warner 1980). Most research has focused on two aspects of resource distribution, clumping in space and clumping in time (for a review, see Grant, in press). For example, resources which are clumped in space (Magnuson 1962; Monaghan & Metcalfe 1985; Theimer 1987) or dispersed in time (Blanckenhorn 1991; Grant & Kramer 1992) are more easily monopolized and/or defended than those which are dispersed in space or clumped in time. The spatial predictability of a resource, the degree to which there are dependable concentrations of resources over time (Warner 1980), may also influence defence behaviour. Spatial predictability, also called the contingency of resource distribution in space (Colwell 1974), can be quantified by ranking areas in terms of resource abundance and measuring the correlation of these rankings over successive time units (Warner 1980). A high correlation indicates that good sites are dependably good and poor sites are dependably poor.

Once an individual has located a good site in a spatially predictable environment, it can restrict its

activities to a small, permanent home range. If that individual is of high competitive ability, it may be able to defend and monopolize a large share of the resource. In contrast, an individual must be mobile to locate good sites and to obtain sufficient resources in a spatially unpredictable environment. Hence, sedentariness and the defence and monopolization of resources are predicted to increase with increasing spatial predictability of resources (Wiens 1976; Warner 1980).

Despite the importance of spatial predictability in most verbal models of spacing, mating and social systems (Brown 1964; Campanella 1975; Wiens 1976; Emlen 1980; Warner 1980; Davies & Houston 1984; Pulliam & Caraco 1984; Lott 1991), no study has clearly linked the influence of the spatial predictability of resources to mobility, or to the monopolization and defence of resources. Both Pimm (1978) and Rubenstein (1981) manipulated the spatial predictability and spatial clumping of food simultaneously, making interpretation of their results difficult. The best field evidence for the importance of spatial predictability comes from a comparative study of the mating system of dragonflies. Males defend territories when ovipositing females are spatially predictable but are mobile when females are spatially unpredictable (Campanella 1975).

I tested the hypothesis that sedentariness and the monopolization and defence of resources increase with

increasing spatial predictability of resources, using groups of juvenile convict cichlids (*Cichlasoma nigrofasciatum*) competing for *Daphnia magna* prey. Convict cichlids are a highly aggressive species of freshwater, tropical fish. Males and females jointly defend nest sites and young in both the field and the laboratory (Keenleyside et al. 1990), and will readily defend access to food in the lab. I used juvenile fish to minimize potential sex differences in behaviour related to reproduction.

Methods

Experimental Subjects

The convict cichlids were second generation descendants of crosses between lab stock and wild fish from Costa Rica. Individual fish were captured from stock tanks, weighed to the nearest 0.001 g and measured from snout to caudal peduncle (nearest 0.05 mm). Groups of six fish were formed by selecting individuals ranging in mass from 0.3 to 1.7 g (mean=0.759, SD=0.335, N=198), and in length from 15 to 35 mm (mean=27.08, SD=3.92, N=198). In convict cichlids, dominance rank is related to body size (Keeley & Grant, in press). Thus, to ensure that there was one clear dominant individual in each group, the largest individual weighed a minimum of 0.2 g more than the second largest individual. 1 tagged fish for individual recognition by attaching pre-made, coloured tags through the musculature posterior to the dorsal fin (Chapman & Bevan 1990), and placed them in a small aquarium to recover from the stress of handling and tagging. Tagging rarely took longer than 45 s. Newly tagged fish turned pale in colour and rested on the bottom of the recovery aquarium, but were always swimming and feeding at the surface within 12 hours.

After 4 days, I transferred groups to the experimental tanks, randomly assigned each to one of the three test

treatments, and left the fish to acclimatize for an additional 3 days. Throughout this week, fish were fed by scattering a mixture of frozen brine shrimp (*Artemia* sp.) and "Fry Feed Kyowa" over the surface of the water. Experiments were conducted in a series of 11 blocks, each block consisting of one replicate in each of the three treatments.

Apparatus

I conducted experiments in large aquaria (90 X 46 X 38 cm) maintained at 25°C on a 12:12 light:dark schedule. The bottom of each tank was covered with 5 cm of light-coloured gravel, which acted to anchor two rows of vertically oriented plastic drinking straws. Straws were 20 cm in length, 0.05 cm in diameter and rose to within 2 cm of the surface of the water. They were placed 5 mm apart, creating a partial visual barrier between patches, while still allowing fish to move between them. Aquaria were covered with opaque Plexiglas, into which four holes (1.0 cm in diameter) had been drilled, forming a square of 40 X 40 cm (Fig. 1.1). Food was introduced to the patches via funnels inserted in these holes.

Experimental Procedure

I conducted two trials per day, one in the morning (between 0800 and 1030 hours), and one in the afternoon (between 1500 and 1800 hours) on three consecutive days, for a total of six trials per group of fish. Each trial involved introducing 72 food items to the aquarium. One item arrived every 15 s in one of the four patches. The probability that a food item appeared in each patch was predetermined as either 0.667, 0.167, 0.083, or 0.083. I randomly assigned patch probabilities to the four patches (see below). Trials were 24 min in duration, and were subdivided into six 3-min periods, each consisting of 12 consecutive food items followed by 1 min during which no food was introduced. To signal the beginning of a trial, several ml of water were pipetted into the patch designated to receive the first food item. Fish usually responded immediately by swimming into the patch. Fresh, heat-killed *Daphnia magna* (mean length=3.17 mm, SD=0.46, N=30) were used as prey. An assistant standing behind the aquarium used an eye dropper to deliver one *Daphnia* plus 1 ml of water into the funnel above the appropriate patch.

The identity of the individual eating each food item was recorded on a portable audiocassette recorder. The number and identity of fish in each patch was determined by scan sampling (Martin & Bateson 1986) at 30 s intervals

throughout each of the six trials. During the sixth trial, an additional observer collected data on aggression. Each fish was followed for one 3-min focal period, during which all encounters with other individuals were recorded. Encounters were defined as the number of times the focal fish came to within three body lengths of another fish. Outcomes of encounters were scored as positive (the focal fish initiated an aggressive act), negative (aggression was directed at the focal fish), or neutral (no aggression was observed). Aggressive acts were primarily chases, but also included frontal and lateral displays and bites (Cole et al. 1980).

Data on aggression were also collected both prior to, and following each of the six trials. During the 6 pre-trial and the 6 post-trial baseline periods, each fish was followed for two 1-min focal periods. Again, all encounters and their outcomes were recorded. These baseline data allowed me to determine dominance hierarchies independent of the feeding experiment. For each pair of fish in a group, I determined which 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 one another, or if no encounters between the two were observed. Dominance rank within a group was determined by summing these scores over all six trials for each fish, and

assigning rank 6 to the individual with the highest score and rank 1 to the fish with the lowest score (after Rubenstein 1981).

Patch probabilities were randomly assigned to the patches prior to the first trial. I manipulated spatial predictability by varying the number of times that these probabilities were randomly reassigned to the patches. In the Predictable treatment, patch probabilities remained the same throughout all trials. In the Intermediate treatment, patch probabilities were randomly assigned prior to each trial, subject to the constraint that no two consecutive trials had the same 'best' patch. In the Unpredictable treatment, patch probabilities were randomly assigned prior to each period within a trial, subject to the constraint that no two consecutive periods had the same 'best' patch. These treatments resulted in fish experiencing 1, 6, or 36 spatial arrangements of the patch probabilities in the Predictable, Intermediate, and Unpredictable treatments, respectively. Each treatment was experienced by 11 groups of fish, each group being used only once in the experiment.

Data Analyses

I quantified mobility from the scan sample data, by counting the number of times each fish switched between patches within a trial. Aggression was quantified as the

total frequency of aggressive acts by each individual. Because the frequency with which individuals encounter one another will influence the frequency of aggression observed, I quantified aggressiveness as the proportion of each individual's encounters which resulted in that individual initiating an aggressive act.

Resource monopolization, the uneven distribution of food among individuals, was expressed in two ways: (1) the proportion of food eaten by the dominant fish (number of food items eaten by dominant fish/total number eaten by all fish) and (2) the coefficient of variation (SD/mean) of food distribution among individuals within a group.

To meet the assumptions required for parametric analyses, mobility and frequency of aggression were $\log_{10}$-transformed, whereas measures of aggressiveness and feeding success were arcsine-square-root transformed. A two-factor repeated measures ANOVA was used to determine the effects of treatment and trial number on resource monopolization and the mobility of fish. I used single degree-of-freedom polynomial contrasts (Wilkinson 1990) to investigate trends in behaviour over time. Because the assumption of compound symmetry of the covariance matrix was never violated, *P*-values did not require adjustment (Potvin et al. 1990). Treatment effects on frequency of aggression and aggressiveness were analyzed by one-way ANOVA, because these data were only recorded during trial six.

Results

Dominance Rank

In 27 of 33 groups, the same fish was dominant in all six trials. In the remaining six groups, one individual was dominant during the first one or two trials and then relinquished its dominant status to another individual for the remainder of the experiment. Because dominance hierarchies remained relatively stable over time, I assigned dominance ranks to individuals based on all 12 baseline periods (see Methods).

In 28 of 33 groups, the dominant fish was also the largest. Correlations between dominance rank and mass were positive and significant for all three treatments (Predictable: Spearman's r_s=0.67, N=66, P<0.001; Intermediate: r_s=0.83, N=66, P<0.001; Unpredictable: r_s=0.80, N=66, P<0.001), even when the dominant fish were excluded (Predictable: r_s=0.46, N=55, P<0.001; Intermediate: r_s=0.73, N=55, P<0.001; Unpredictable: r_s=0.74, N=55, P<0.001).

Resource Monopolization

The total number of food items consumed by groups of fish over the six trials was not affected by resource

predictability ($F_{2,30}$=0.488, P=0.619). Fish ate 94.8% (410/432 items), 95.8% (414/432), and 95.5% (413/432) of the available food in the Predictable, Intermediate and Unpredictable treatments, respectively. An average convict cichlid can eat approximately 60 *Daphnia* in 30 min, so satiation did not occur in the experiments.

Differences in the feeding success of dominant fish were, however, influenced by the spatial predictability of food. Dominant fish were the most successful foragers in 8 of 11 Predictable replicates, 5 of 11 Intermediate replicates, and 2 of 11 Unpredictable replicates (G=6.99, df=2, P<0.05). In addition, the proportion of food obtained by the dominant fish increased with spatial predictability (Fig. 1.2a; $F_{2,30}$=7.83, P=0.002). Moreover, the success of the dominant fish increased over the six trials at all levels of spatial predictability (Fig. 1.2a; $F_{1,30}$=19.73, P<0.001). Dominant fish ate more food than the average subordinate fish (all fish other than dominants) in the Predictable and Intermediate treatments ($F_{1,10}$=30.79, P=0.002 and $F_{1,10}$=7.87, P=0.019, respectively) but not in the Unpredictable treatment ($F_{1,10}$=0.93, P=0.356).

Treatments did not differ significantly in the degree to which resources were monopolized, as measured by the coefficient of variation in food intake within a group (Fig. 1.2b; $F_{2,30}$=2.88, P=0.072). There was, however, a tendency for resource monopolization to be higher in the Predictable

treatment than in the Intermediate and Unpredictable treatments. Although there were differences between trials ($F_{5,150}$=2.15, P=0.062), monopolization did not change consistently over time (Fig. 1.2b; $F_{1,30}$=2.11, P=0.157).

Mobility

Because of a significant interaction between the main effects of treatment and trial number ($F_{10,150}$=2.46, P=0.009), I could not draw conclusions about the effect of spatial predictability on the mobility of dominant fish (Fig. 1.3a). However, this interaction only occurred during trials one to three. When I re-analyzed the data for the final three trials, the frequency of patch switching by dominant fish decreased with increasing spatial predictability of food ($F_{2,30}$=4.52, P=0.019). Furthermore, the proportion of time spent in the best patch by dominant fish increased from (mean ± SE) 0.45 ± 0.019 to 0.59 ± 0.054 to 0.68 ± 0.075 with increasing spatial predictability of food ($F_{2,30}$=4.22, P=0.024). Time trends were investigated by re-analyzing treatments separately. Dominant fish decreased their frequency of patch switching over time in the Predictable treatment(Fig. 1.3a; $F_{1,10}$=11.98, P=0.006), but there were no significant changes in their mobility in either the Intermediate or the Unpredictable treatments ($F_{1,10}$=0.84, P=0.382 and $F_{1,10}$=2.97, P=0.116, respectively).

There was also a significant interaction between treatment and trial number in the frequency of patch switching by subordinate fish ($F_{10,150}$=2.26, P=0.017), but this effect was overwhelmed by the treatment effect (Fig. 1.3b; $F_{2,30}$=13.74, P<0.001). Subordinate fish were more mobile in the Unpredictable treatment than in either the Intermediate or Predictable treatments. In both the Predictable and Intermediate treatments, patch switching declined significantly from trial one to trial six (Fig. 1.3b; $F_{1,10}$=31.96, P<0.001 and $F_{1,10}$=5.86, P=0.036, respectively). No change in the frequency of patch switching occurred in the Unpredictable treatment ($F_{1,10}$=0.25, P=0.627). The frequency of patch switching did not differ between dominant and subordinate fish in any of the three treatments ($F_{1,10}\leq$1.95, $P\geq$0.193).

Resource Defence

The spatial predictability of food did not influence the total frequency of aggression by dominant ($F_{2,30}$=2.65, P=0.088) or subordinate ($F_{2,30}$=0.54, P=0.589) fish, although aggression tended to be most frequent in the Predictable treatment (Fig. 1.4). Dominant fish did, however, perform more aggressive acts than subordinate fish in the Predictable and Intermediate treatments (Wilcoxon matched pairs; z=-2.58, N=11, P=0.010 and z=-2.85, N=11, P=0.004,

respectively), but not in the Unpredictable treatment (z=-1.60, N=11, P=0.109) (Fig. 1.4).

The aggressiveness of dominant fish, measured as the proportion of encounters resulting in aggression, increased from 0.15 to 0.17 to 0.29 with increasing spatial predictability (Fig. 1.5; $F_{2,30}$=3.51, P=0.043). The aggressiveness of subordinate fish did not differ significantly among treatments ($F_{2,30}$=0.85, P=0.439). However, subordinate fish were less aggressive than dominant fish in the Predictable and Intermediate treatments ($F_{1,10}$=30.06, P<0.001 and $F_{1,10}$=14.38, P=0.004, respectively) but not in the Unpredictable treatment ($F_{1,10}$=0.92, P=0.361) (Fig. 1.5).

Resource Acquisition Tactics

I used a partial correlation analysis to identify three variables (body mass, aggressiveness and patch switching) that were related to foraging success, defined as the proportion of food eaten by each fish over the six trials. At all levels of spatial predictability, body mass was positively correlated with foraging success (Fig. 1.6a,d,g). Individual aggressiveness and foraging success were positively correlated in the Predictable treatment (P<0.001), but were not significantly correlated in the Intermediate (P=0.28) or Unpredictable (P=0.092) treatments

(Fig. 1.6b,e,h). Mobility was positively correlated with foraging success in the Unpredictable treatment (P=0.002), but was not significantly correlated in the Predictable (P=0.408) or Intermediate (P=0.14) treatments (Fig. 1.6c,f,i). In summary, large, aggressive fish were successful at acquiring food in the Predictable treatment, large fish were successful in the Intermediate treatment, and large, mobile fish were successful in the Unpredictable treatment.

Although I found significant differences among treatments in both mobility and aggressiveness, much of the variation in behaviour occurred among individuals within groups. Only 17.6% of the variation in frequency of patch switching was due to treatment effects, while differences between individuals within a group accounted for 82.4% (nested ANOVA). Similarly, 1.1% of the variation in aggressiveness was due to the treatments, while 97.1% was explained by differences among fish.

Discussion

With increasing spatial predictability of resources, dominant fish were able to acquire a larger proportion of the food. These results provide quantitative support for the prediction that competitive individuals are able to monopolize a greater share of resources with increasing spatial predictability. This prediction stems primarily from the mating systems literature (Warner 1980), but has not been tested because of the difficulty of manipulating the dispersion of mates (Davies 1991). This study and others (e.g. Grant & Kramer 1992) suggest that foraging systems may be useful for testing hypotheses derived from the theory of mating systems. This result also has implications for studies of social foraging. In spatially unpredictable environments, both dominant and subordinate animals may prefer to forage in groups. However, subordinate individuals pay a higher foraging cost to be in a group when food is predictable than when food is unpredictable. Hence, in predictable environments, subordinate individuals may prefer to forage solitarily (see Rohwer & Ewald 1981; Hodapp & Frey 1982).

All fish became less mobile as the spatial predictability of food increased. For dominant fish, the trend was even stronger than it appeared from the data analysis alone. Most of their time was spent in the most

profitable patch, and much of their apparent mobility was the result of chasing competitors away from the food. These results are consistent with the foraging mode literature which suggests that animals should be relatively sedentary in predictable environments and relatively mobile in unpredictable environments (Wiens 1976; Huey & Pianka 1981; Grant & Noakes 1988).

Dominant fish were twice as likely to chase an encountered conspecific in the Predictable treatment as in the Unpredictable treatment. These results are consistent with the theory (Warner 1980). However, the cost of defence (frequency of aggression) did not increase with resource predictability because fish encountered each other less frequently as predictability increased. Taken together, these results suggest that dominant convict cichlids monopolize more food and become more sedentary and aggressive as the spatial predictability of food increases. Spatial predictability appears to increase the economic defendability (Brown 1964) of a resource because monopolization increased with predictability, but the frequency of aggression did not.

Two previous studies have examined the effects of spatial predictability of resources on defence behaviour. Pimm (1978) allowed three species of hummingbirds (*Archilochus alexandri*, *Lampornis clemenciae*, and *Eugenes fulgens*) to compete for access to artificial feeders

arranged in groups. Because the experimental design manipulated both spatial predictability and spatial clumping simultaneously, his results are difficult to interpret. Nevertheless, when feeders were spatially predictable and dispersed, individuals of the dominant species defended the feeders and excluded individuals of the subordinate species. When feeders were spatially unpredictable and clumped, resource defence ceased, and all three species fed together from the feeders. Rubenstein (1981) allowed pygmy sunfish (*Elassoma evergladei*) to compete for benthic prey that were either randomly dispersed or 'predictably' clumped. Although the effects of spatial predictability were confounded by the effects of spatial clumping, his results suggest that predictably clumped food is more likely to be defended than food that is unpredictably dispersed.

Resource predictability is often hypothesized to influence the social organization of animals (Brown 1964; Wiens 1976; Emlen 1980; Warner 1980; Davies & Houston 1984; Pulliam & Caraco 1984; Lott 1991). When females, or the resources they require, are found in dependably good sites, males typically defend these sites. Examples include oviposition sites for dragonflies (Campanella 1975) and frogs (Howard 1978) and grazing sites for ungulates (Gosling 1986). When these resources are unpredictable in space, males become mobile to increase their encounter rate with females. The same principles apply to foraging systems.

For instance, juvenile salmonids are often territorial in streams, where food is predictable in space, but are mobile and live in undefended home ranges in pools or lakes, where food is unpredictable in space (Grant & Noakes 1988). Studies such as these imply that the spatial predictability of resources is important to animals in the wild. However, most studies have quantified the behaviour of the animals, but not the dispersion of resources. Field studies are needed that monitor the behaviour of animals while either measuring (Whitten 1983) or manipulating (Ims 1988) resource dispersion.

Resource Acquisition Tactics

Aggression was an effective means of monopolizing food only in the Predictable treatment, whereas mobility was effective only in the Unpredictable treatment. More generally, these data suggest that interference competition, via resource defence, will be favoured when resources are spatially predictable whereas scramble competition will be favoured when resources are unpredictable.

Large fish ate more food than small fish in all treatments, suggesting that body size is important for both interference and scramble competition. The advantage of body size is relatively straightforward in interference competition because dominance rank and body size were

positively correlated. However, body size was also an important predictor of foraging success in the Unpredictable treatment, perhaps because large fish locate, capture and handle food faster than small fish.

Despite the obvious differences in behaviour between treatments, most of the variation in mobility and aggressiveness occurred between individuals within a group. Much of this variation is likely due to the frequency dependant nature of behaviour that occurs in small groups. For instance, in the Predictable treatment, small fish may be prevented from using aggression by the aggressive behaviour of the large, dominant fish. In addition, subordinate fish may become less mobile to avoid being chased by the dominant fish.

If the pattern of variation in this data is applicable to field situations, we should expect to see at least as much variation in behaviour within environments as between environments differing in spatial distribution of resources. To detect differences in behaviour between environments, it will be important to compare individuals of a similar social status (e.g. dominant males). Alternative tactics within populations have been extensively studied in mating systems (Dunbar 1982; Dominey 1984; Gross 1984), but should also be expected in foraging systems (e.g. Barnard & Sibly 1981; Giraldeau 1984; Grant & Kramer 1992).

This experiment also shows that fish can respond

rapidly to changes in resource distribution. By the end of the three-day experiment, dominant fish in the three treatments differed significantly in their aggressiveness and mobility. The proportion of food eaten by dominant fish also increased over time, suggesting that highly competitive individuals can use their skills more effectively when they have more experience with their environment. Differences between individuals will apparently be magnified in stable, predictable environments.

Figure 1.1. Experimental tanks were divided into four patches (A, B, C, and D). Patch boundaries are indicated by rows of straws, while closed circles represent the holes through which food was dispensed.

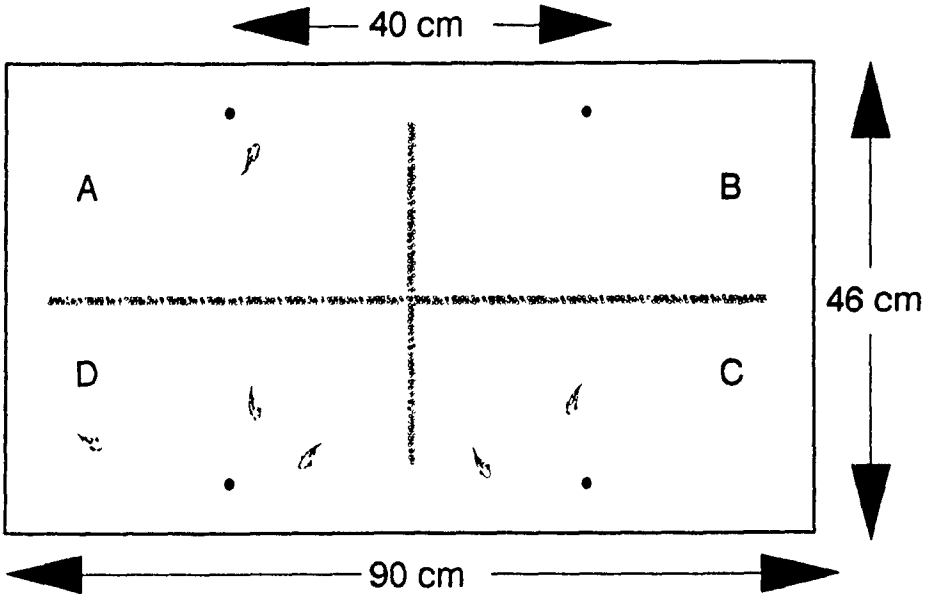
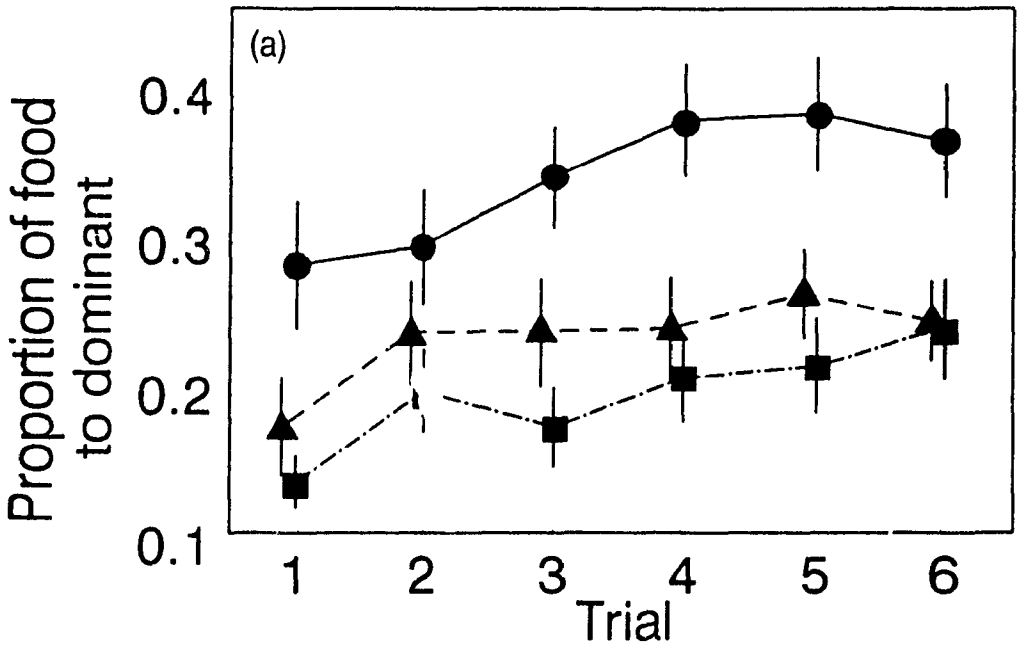

40 cm
A
B
C
D
46 cm
90 cm

Figure 1.2. Change in resource monopolization over time. (a) The mean proportion ± 1 SE (N=11) of total food eaten by the dominant fish and (b) the mean coefficient of variation (CV) ± 1 SE (N=11) in feeding success within a group in the Predictable (solid circles), Intermediate (solid triangles), and Unpredictable (solid squares) treatments.


(a)
Proportion of food to dominant
0.4
0.3
0.2
0.1
1
2
3
4
5
6
Trial

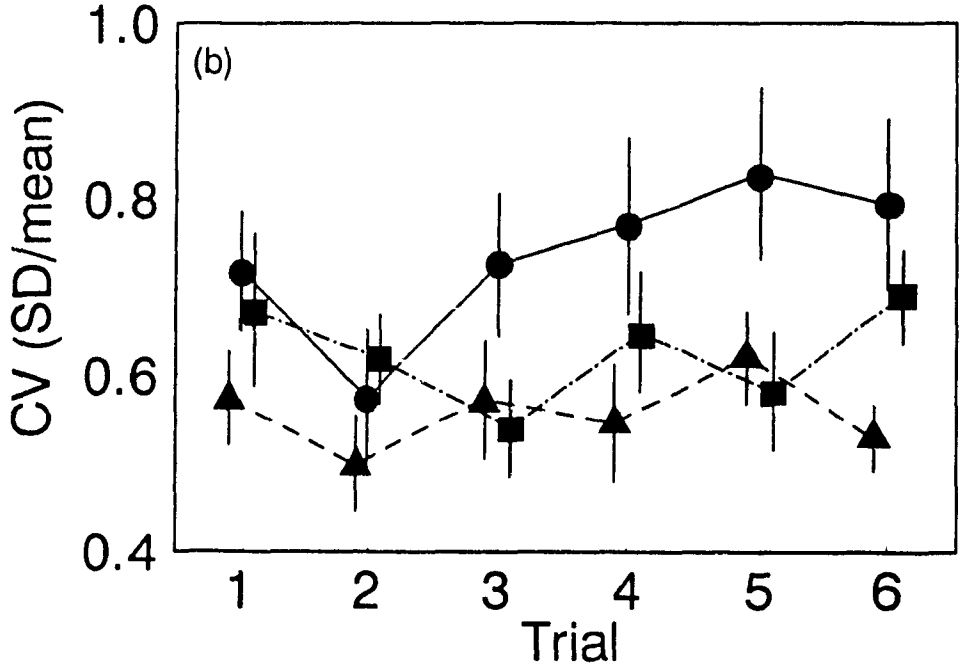
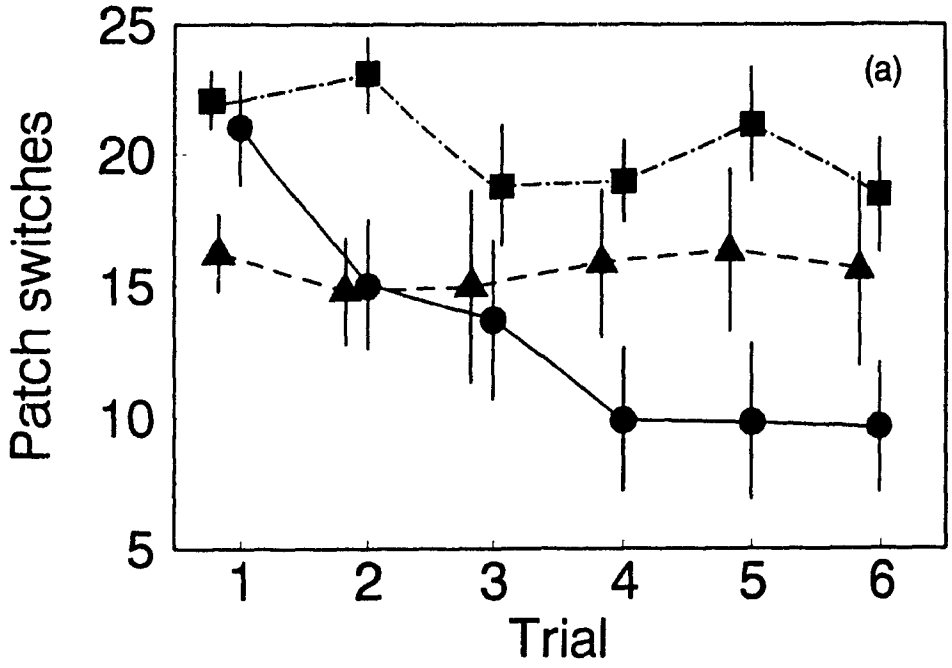

(b)
CV (SD/mean)
1.0
0.8
0.6
0.4
1
2
3
4
5
6
Trial

Figure 1.3. Mean number of patch switches ± 1 SE (N=11) performed by (a) dominant and (b) subordinate fish during trials one to six, in response to Predictable (solid circles), Intermediate (solid triangles), and Unpredictable (solid squares) spatial distributions of food.


Patch switches
25
20
15
10
5
(a)
1
2
3
4
5
6
Trial

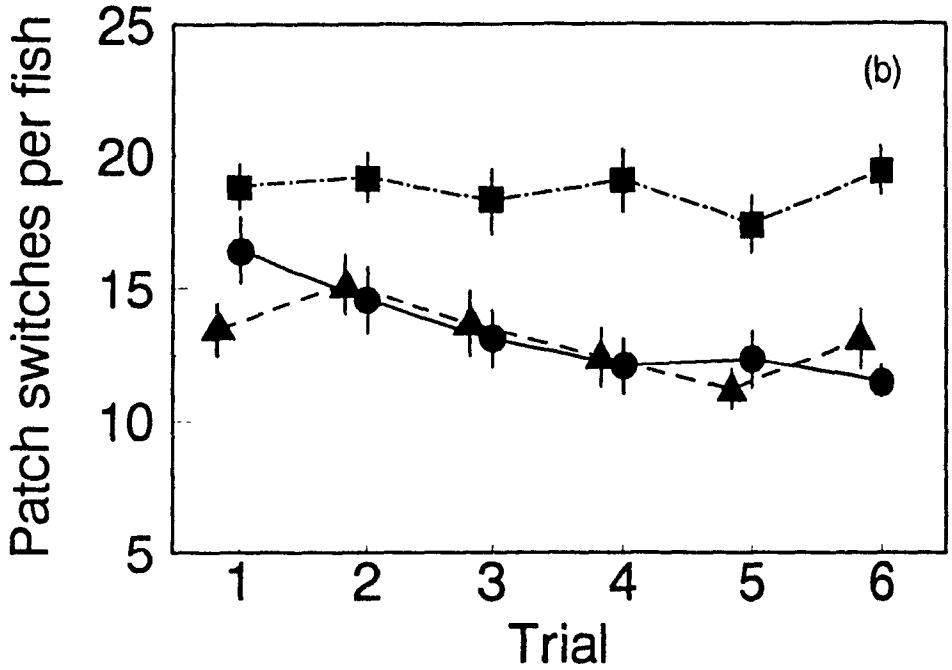

Patch switches per fish
25
20
15
10
5
(b)
1
2
3
4
5
6
Trial

Figure 1.4. Mean number of aggressive acts ± 1 SE (N=11) performed by dominant (solid bars) and subordinate fish (open bars) during trial six, in response to increasing spatial predictability of resources.

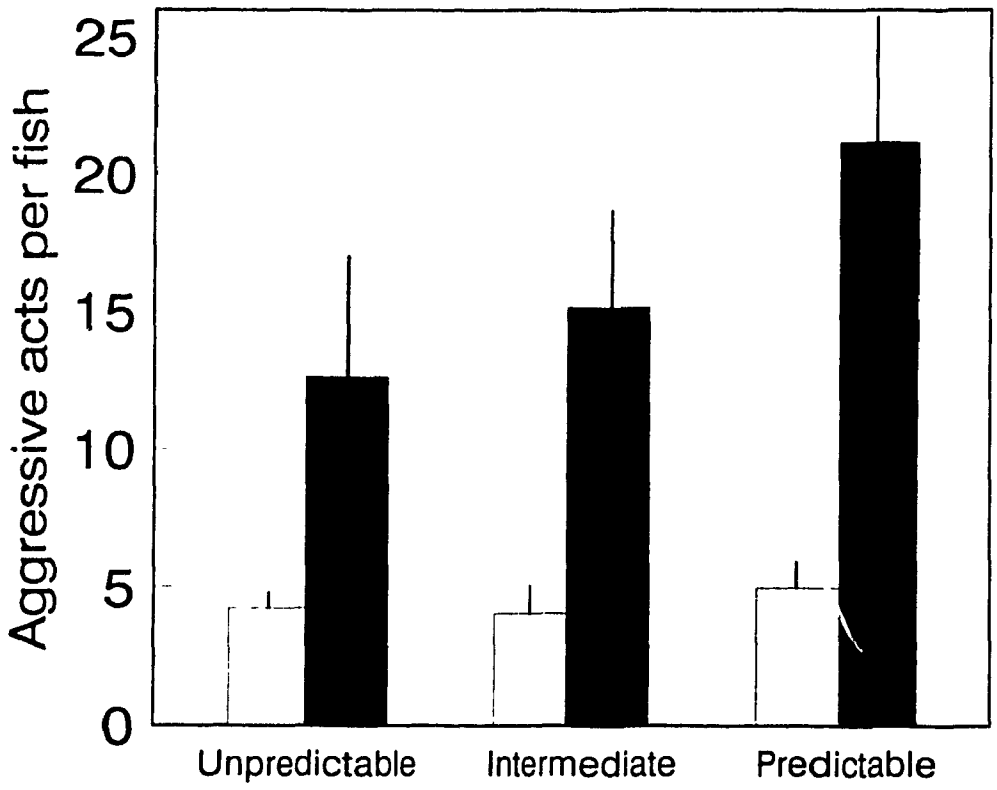

Aggressive acts per fish
25
20
15
10
5
0
Unpredictable
Intermediate
Predictable

Figure 1.5. Mean proportion of conspecifics chased ± 1 SE (*N*=11) by dominant (solid bars) and subordinate fish (open bars) during trial six, in response to increasing spatial predictability of resources.

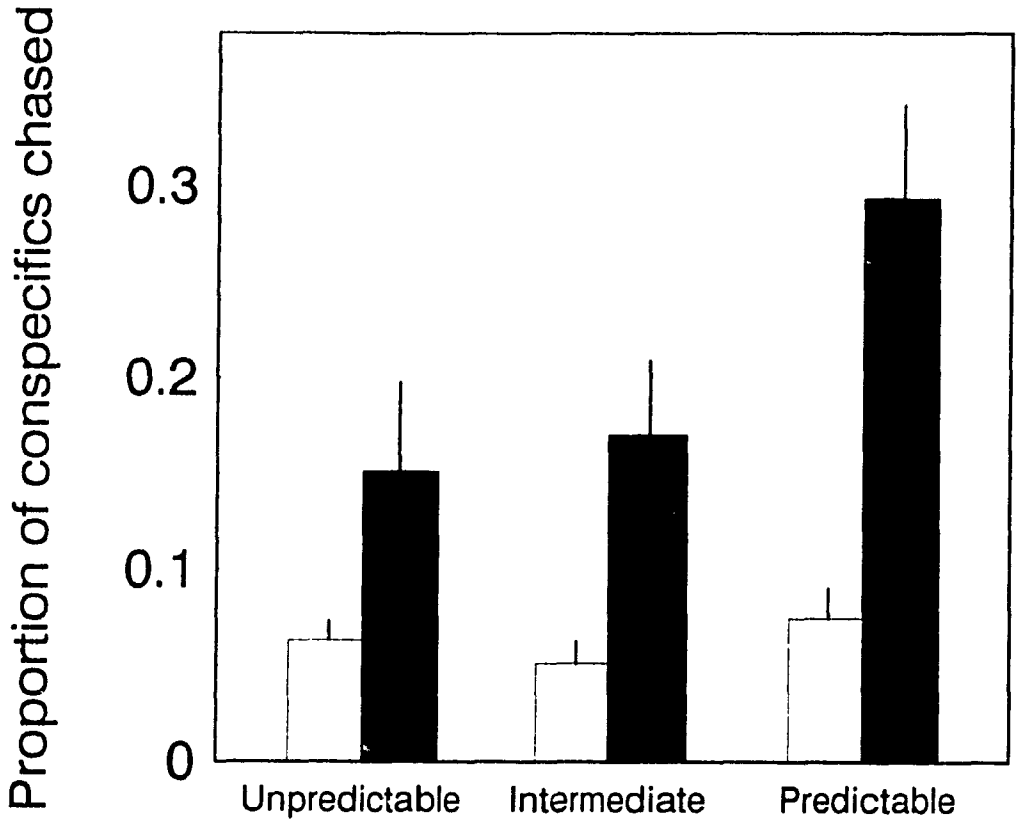
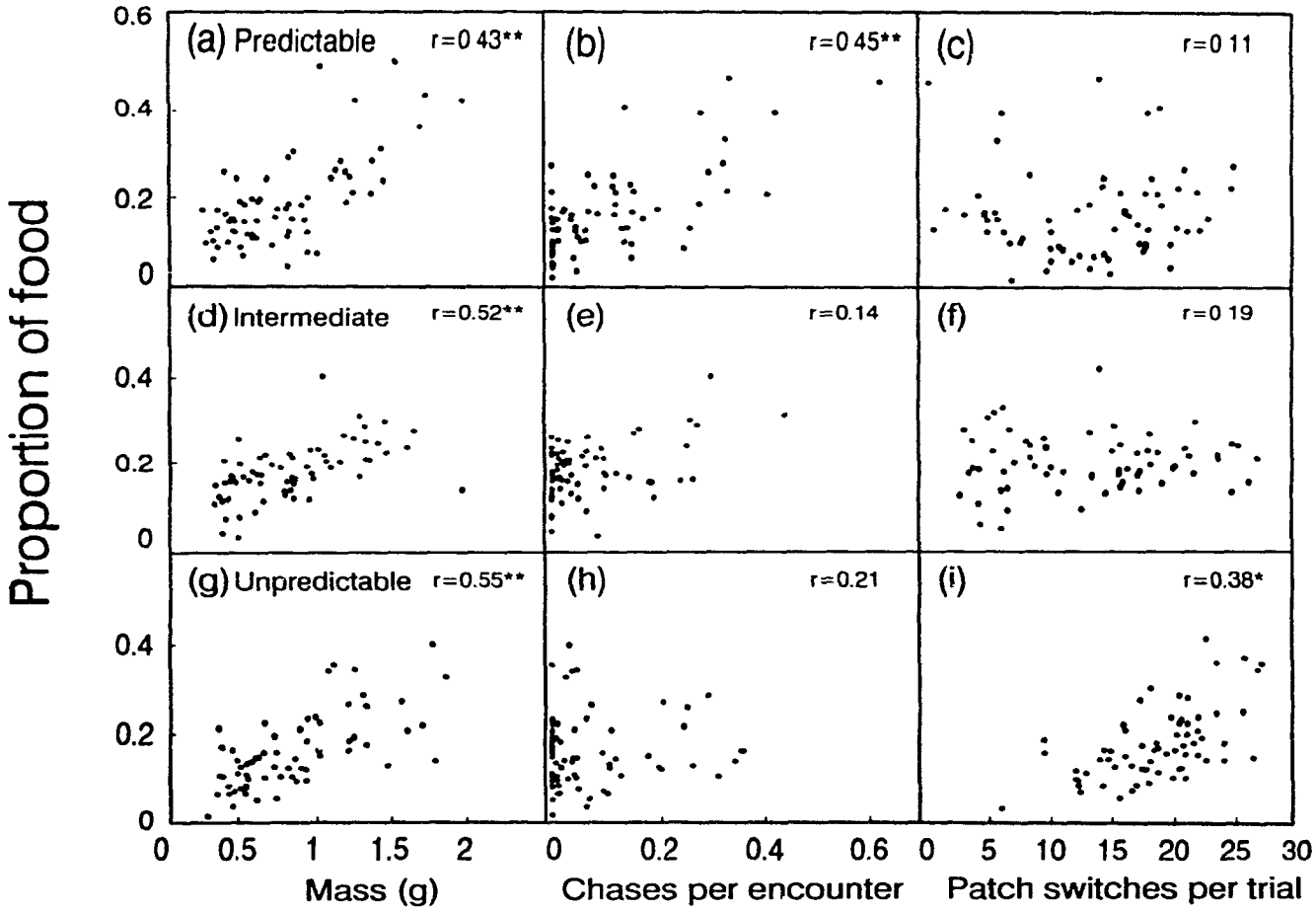

Proportion of conspecifics chased
0.3
0.2
0.1
0
Unpredictable
Intermediate
Predictable

Figure 1.6. Scatter plots relating foraging success of individual fish to their body mass (a,d,g), aggressiveness (b,e,h), and mobility (c,f,i) in the Predictable, Intermediate, and Unpredictable treatments. Partial correlation coefficients are shown for each (*P<0.01, **P<0.001). When all three variables are combined in a multiple regression, the multiple r^2 are 0.53, 0.38, and 0.55 (N=66, P<0.001), for the Predictable, Intermediate, and Unpredictable treatments, respectively.


Proportion of food
(a) Predictable r=0 43**
(b) r=0 45**
(c) r=0 11
(d) Intermediate r=0.52**
(e) r=0.14
(f) r=0 19
(g) Unpredictable r=0.55**
(h) r=0.21
(i) r=0.38*
0.6
0.4
0.2
0
0 0.5 1 1.5 2
Mass (g)
0 0.2 0.4 0.6
Chases per encounter
0 5 10 15 20 25 30
Patch switches per trial

Chapter Two

Spatial resource predictability and the ideal free distribution

In nature, the spatial distribution of organisms is often patchy in response to patchily distributed resources. The theory of ideal free distribution (IFD) (Fretwell & Lucas 1970; Fretwell 1972) was developed to describe how animals, attempting to maximize their fitness, should distribute themselves in an environment containing patches of varying suitability. If patch suitability declines as the density of animals in the patch increases, animals should distribute themselves such that the proportion of individuals in each patch matches the proportion of resources available (i.e. input matching; Parker 1974). The model assumes that all animals have perfect information about the relative suitabilities of the patches ('ideal') and are able to move between patches at will ('free'). The model predicts that at equilibrium the average rate of resource gain in each patch will be the same and individuals can expect equal rates of gain regardless of which patch they choose. No individual can increase its success by moving to another patch (for assumptions and predictions see Table 2.1).

IFD theory has successfully predicted the distribution of individuals in a number of studies (for reviews see

Milinski & Parker 1991; Kacelnik et al. 1992), despite violating a key assumption that all individuals are of equal competitive ability (e.g. Whitham 1980; Harper 1982; Godin & Keenleyside 1984; Milinski 1984). However, most of these studies were either two-patch laboratory studies with fixed patch profitabilities (Godin & Keenleyside 1984; Milinski 1984; Abrahams 1989; Korona 1990) or field studies with only two habitats of predictable suitability (Parker 1974; Davies & Halliday 1979; Whitham 1980; Harper 1982; Courtney & Parker 1985). Hence, it is unclear whether the IFD is applicable in more realistic laboratory environments or more complex field situations.

The purpose of this study is to test the applicability of the IFD in laboratory environments of varying spatial predictability. The results of Chapter 1 suggest that deviations from an IFD are to be expected when resources vary in the degree to which they are spatially predictable. Table 2.1 summarizes the predictions that result from changing the assumptions of the IFD model. In the Predictable treatment, dominant fish were sedentary and apparently used aggression to defend and monopolize food. Because the 'free' assumption of the model may have been violated, I expected an ideal despotic distribution (IDD) (Fretwell & Lucas 1970; Fretwell 1972). In contrast, when food was Unpredictable in space, fish moved continually between patches, apparently unable to track the location of

the best patch and perhaps violated the 'ideal' assumption. If individuals are limited in their ability to perceive differences between patches of differing suitability, good sites will always be under-used relative to IFD. Abrahams (1986) calls this an ideal free distribution under perceptual constraints. Although the IDD and the perceptual constraints models make similar qualitative predictions, they can be distinguished by comparing the phenotypes of competitors in the best patch. The despotic model predicts that dominants will spend more time than subordinates in the best patch, whereas the perceptual constraints model predicts no relationship between dominance rank and patch occupancy (Table 2.1). Hence, a despotic distribution will be characterized by a positive relationship between dominance rank and foraging success, while a distribution mediated by perceptual constraints will not. In the Intermediate treatment, foraging success was not related to aggression or mobility, hence I had no *a priori* expectation about the resulting distribution.

I allowed groups of juvenile convict cichlids (*Cichlasoma nigrofasciatum*) to compete for food in four-patch environments of varying spatial predictability. The observed distributions and patterns of resource gain were compared to those predicted by the IFD, IDD and the perceptual constraints model (summarized in Table 2.1). I expected deviations from an IFD in the direction of an IDD

in the Predictable treatment and in the direction of the perceptual constraints model in the Unpredictable treatment.

Methods

The data used for the following analyses were gathered from the experiment described in Chapter 1.

Data Analyses

To compare the observed distributions of fish to those predicted by each of the models, I determined the average number of fish in each patch, from the scan sample data. Because food was delivered randomly to the four patches, the actual amount of food arriving in a patch within a period differed slightly from the expected patch probability. However, the magnitude of this error was always less than one-third the magnitude of the error associated with each of the dependent variables, permitting the use of least squares regression methods (McArdle 1988). The mean dominance rank of fish in each patch was quantified by multiplying each individual's dominance rank by the proportion of time it spent in the patch, summing these values over all group members, then dividing by the summed proportions of time spent in the patch by all six members of the group. Individual rates of resource gain were defined as the proportion of the total food consumed by an individual, and individual rates of gain within each patch were quantified as the number of food items eaten by each fish per minute

spent in the patch.

As demonstrated in Chapter 1, the behaviour of individuals changed significantly over the six trials. Similarly, fish distributions changed over time, and appeared to be most stable during the sixth trial (Fig. 2.1). Consequently, I calculated each variable using data from the six periods of the final trial (periods 31-36), when fish had the most experience about the experimental environment. Values for the two poorest patches (0.083) were averaged, thus contributing one data point to each of the analyses. Because all data were not significantly different from a normal distribution, transformations were not required.

Results

Spatial Distributions of Fish

Even though fish distributions changed over time (Fig. 2.1), the proportion of fish in the best patch did not vary significantly between trials (Predictable: $F_{5,60}=1.95$, $P=0.099$; Intermediate: $F_{5,60}=0.19$, $P=0.964$; Unpredictable: $F_{5,60}=0.16$, $P=0.977$; repeated measures ANOVA), but did vary between periods within trials. In the Predictable and Unpredictable treatments the proportion of fish in the best patch decreased from period 1 to 6 within each trial (Fig. 2.1a,c; $F_{1,60}=8.20$, $P=0.006$ and $F_{1,60}=26.54$, $P<0.001$, respectively). This decrease was presumably due to an increase in the effectiveness of defence by the dominant fish in the Predictable treatment. In the Unpredictable treatment, the observed decrease may be an artefact of the experimental design; fish were attracted to the best patch by the cue used to signal the beginning of each trial, but thereafter were unable to track its location effectively. In contrast, use of the best patch increased from the beginning to the end of each trial in the Intermediate treatment (Fig. 2.1b; $F_{1,60}=6.47$, $P=0.014$), apparently due to the tendency of fish during the first period to visit the patch which provided the most food during the previous trial.

In each of the three treatments, the distribution of individuals deviated significantly from an IFD. The slopes of regression lines comparing the mean proportion of fish in each patch to the proportion of food available were significantly lower than the slope of 1.0 predicted by IFD theory (Table 2.2), i.e. there were too few fish in the best patch and an excess of fish in the poor patches (Fig. 2.2). The magnitude of this deviation was greatest in the Unpredictable treatment (Fig. 2.2c) where the slope was significantly lower than those of Predictable and Intermediate treatments (t-tests, df=62; t=5.06, P<0.001 and t=6.28, P<0.001, respectively). Furthermore, the slopes for the Predictable and Intermediate treatments did not differ significantly from one another (t=1.47, df=62, 0.10<P<0.20). When data from the first period was excluded from the analysis (for the reasons mentioned above), fish distributions in the Predictable and Unpredictable treatments deviated even further from an IFD. However, in the Intermediate treatment, the distribution of fish during periods 32 to 36 was not significantly different from that predicted by IFD theory (b=0.96, r^2=0.95, P<0.001; t=-1.08, df=31, P>0.20).

Both dominant and subordinate fish switched between patches throughout the experiment (Chapter 1), suggesting that they partitioned their foraging effort between the four patches by allocating a proportion of their time to each

patch. I compared the proportion of time spent by dominant and subordinate fish to the proportion of food available in each of the patches. In both the Predictable and Intermediate treatments, dominant fish allocated their time to each patch according to its probability of receiving food (Fig. 2.3a,b; Table 2.3), whereas subordinate fish were only able to 'input match' in the Intermediate treatment (Fig. 2.3b). In all other cases, fish under-exploited the best patch and over-exploited the two poorest patches (Fig. 2.3; Table 2.3). Differences in the slopes for dominant and subordinate fish were only significant in the Predictable treatment (Table 2.3), with dominant fish spending more time in the best patch than subordinate fish (Fig. 2.3a).

To determine where individuals were acquiring their food, I compared the proportion of food obtained from each patch to the total proportion of food available, for both dominant and subordinate fish. At all levels of spatial predictability, dominant fish obtained food from the various patches in direct proportion to its availability (Fig 2.4a,b,c; Table 2.4). Subordinate fish were able to 'input match' only in the Unpredictable treatment (Fig. 2.4c), and under-used the best patch in both the Predictable and Intermediate treatments (Fig. 2.4a,b; Table 2.4). Slopes differed significantly for dominant and subordinate fish in the Predictable treatment (Fig. 2.4a; Table 2.4), but not in the Intermediate or Unpredictable treatments (Fig. 2.4b,c;

Table 2.4).

Individual Payoffs

Contrary to an assumption of the IFD, individuals within a group did not have equal rates of resource gain in the Predictable, Intermediate or Unpredictable treatments (Fig. 2.5; $F_{5,50}$=15.38, P<0.001; $F_{5,50}$=3.43, P=0.010; $F_{5,50}$=3.93, P=0.004, respectively; 1-way ANOVA). Both mass (Chapter 1, Fig. 1.6a,d,g) and dominance rank were positively correlated with the proportion of the total food that was eaten by an individual in each of the three treatments (Predictable: r_s=0.651, N=66, P<0.001; Intermediate: r_s=0.377, N=66, P<0.005; Unpredictable: r_s=0.498, N=66, P=0.001; Spearman's rank correlation). At all levels of predictability, larger, dominant fish ate more food than smaller, subordinate fish.

IFD theory also predicts that, at equilibrium, individual fish should experience equal rates of resource gain in each of the four patches. To test this prediction, I compared the mean number of food items eaten per minute spent in each patch by dominant and subordinate fish. In the Predictable treatment, feeding rates increased with patch quality (Fig. 2.6a; $F_{1,20}$=8.89, P=0.007) but dominant fish had higher feeding rates than subordinate fish in all patches ($F_{1,20}$=6.82, P=0.017). The interaction between patch

quality and dominance status was not significant ($F_{2,40}$=0.89, P=0.421). In the Intermediate treatment, feeding rates of dominant and subordinate fish did not differ significantly across patches ($F_{2,40}$=0.13, P=0.877), and only differed from one another in the best patch (Fig. 2.6b; t=2.28, df=10, P=0.046; paired t-test), although dominant fish obtained more food than subordinates overall (Chapter 1, Fig. 1.3). Again, the interaction between patch quality and dominance status was not significant ($F_{2,40}$=2.74, P=0.177). There was, however, a significant interaction between patch quality and dominance status in the Unpredictable treatment (Fig. 2.6c; $F_{2,40}$=3.81, P=0.031), but this effect was overwhelmed by the patch quality effect ($F_{2,40}$=27.00, P<0.001). The feeding rates of both dominant and subordinate fish increased with increasing patch quality. However, dominant fish had a higher feeding rate than subordinate fish only in the best patch (t=2.90, df=10, P=0.016; paired t-test).

Taken together, these results suggest that competitive ability varied markedly within groups. In fish, an individual's ability to compete for food may be related to aggression, swimming speed, prey recognition abilities, or a combination of the three. To examine the effect of unequal competitive abilities on habitat selection, I compared the mean rank of individuals in each patch with the density of competitors there. For this comparison, I assumed that dominance rank was a reliable indicator of an individual's

competitive ability. If individuals consider the abilities of competitors when deciding where to forage, patches with high ranked individuals should have fewer competitors than patches with low ranked individuals (Sutherland et al. 1988). Although mean rank and competitor density were negatively correlated in 8 of 9 conditions (Table 2.5), the correlation was only significant in the best patch of the Predictable treatment.

Discussion

In the Predictable and Unpredictable treatments, the observed distributions of fish deviated significantly from an ideal free distribution. On average, too many fish exploited the poor patches and too few fish exploited the best patch. These results were not unexpected, as one or more of the assumptions of the model were thought to have been violated in these treatments.

In the Predictable treatment, the observed distribution was qualitatively consistent with an ideal despotic distribution. Dominant fish were more aggressive than subordinates and foraging success was positively correlated with aggressiveness (Chapter 1). Furthermore, dominant fish spent more time and obtained a greater proportion of their food in the best patch than subordinates. However, the foraging rates of subordinate fish were also highest in the best patch, suggesting that they too prefer to forage where resources are most abundant. Taken together, these results are consistent with the hypothesis that dominant fish use aggression to exclude subordinates from the best patch, thus violating the 'free' assumption of IFD theory.

In the Unpredictable treatment, distributions of fish deviated from an IFD in a manner qualitatively consistent with the perceptual constraints model. On average, too few

fish used the best patch and both dominant and subordinate fish spent an equal proportion of their time there. Despite their apparent inability to anticipate the location of the best patch, all individuals obtained food from the various patches in direct proportion to its availability. Although the spatial patterns of resource use were similar for dominant and subordinate fish, individuals differed in the total number of prey captured. These differences were not, however, related to differences in aggressive behaviour (Chapter 1). Fish that switched frequently between patches obtained more food than sedentary individuals (Chapter 1), presumably because they encountered prey more often or were faster to respond to its arrival. Foraging success was also positively correlated with body mass and dominance rank. In fish, both swimming speed (Webb 1978) and visual capabilities (Li et al. 1985) increase with body size, so large individuals may be better scramble competitors than small individuals. These differences appear to be most important in the best patch, where dominant fish had higher foraging rates than subordinates.

The closest approximation to an IFD occurred in the Intermediate treatment. Although it appeared that too few fish used the best patch, when data from the first period are excluded, the proportion of fish in the best patch did not differ significantly from that predicted by IFD theory. Furthermore, dominant and subordinate fish spent a similar

amount of time in the best patch, and obtained a similar proportion of their diet from it. Individual differences in foraging success were not related to aggressiveness (Chapter 1). Hence, the distribution of fish did not appear to be mediated by despotism. As suggested by Fretwell & Lucas (1970), aggressive behaviour does not necessarily influence habitat selection directly, but may function as a means by which individuals assess the density of competitors within a patch. Foraging success was, however, positively correlated with body size and dominance rank, thus violating the IFD assumption of equal competitive ability.

The distribution of unequal competitors relative to resources has been formally modelled by Parker & Sutherland (1986). The competitive IFD model assumes that each individual's rate of resource gain is related to its competitive ability, or 'competitive weight' (i.e. the proportion of the resource it obtains were competing with all members of the group at a single patch), and predicts that the sum of the competitive weights in each patch is equal to the proportion of resources available there. However, my study and others (Harper 1982; Godin & Keenleyside 1984; Milinski 1984; McNamara & Houston 1988) demonstrate that IFD's can occur despite differences in competitive ability.

The results of my study suggest that the spatial predictability of resources influences both the ability of

individuals to perceive differences in patch profitabilities and their freedom to choose between those patches. At one extreme, spatial predictability encourages resource monopolization and despotism, with dominant individuals actively expelling subordinates from preferred sites. However, spatial predictability alone is not sufficient to lead to a despotic distribution; resources must also be economically defendable (Brown 1964). In environments where resources are both spatially predictable and defendable, territoriality or resource defence behaviour may limit the density of individuals in the preferred habitat, forcing some individuals to settle in inferior habitats. For example, great tits (Kluyver & Tinbergen 1953) and convict cichlids (Patterson 1984) settled in non-preferred habitats in response to the aggression exhibited by territorial owners, even though empty nest sites remained available in the preferred habitat. When resources are spatially predictable but defence is uneconomical, distributions are more likely to be 'ideal free' (e.g. Godin & Keenleyside 1984; Milinski 1984; Abrahams & Dill 1989). In spatially unpredictable environments, the IFD will be a poor predictor of competitor distributions, presumably because individuals cannot track or perceive differences in patch profitabilities (Abrahams 1986). Therefore, my results suggest that the likelihood of observing ideal free distributions will depend upon both the spatial

predictability of patch quality and the economic defendability of resources within those patches.

More generally, my study and others suggest that the quantitative predictions of IFD theory may not be applicable in complex environments. When the number of habitats (Talbot & Kramer 1986) or competitors (Gillis & Kramer 1987) is large, or resource abundance fluctuates rapidly in time (Recer et al. 1987), individuals may have difficulty assessing habitat suitability, and hence, tracking resource availability. Hence, too few animals are found in the best patches in complex environments. The predictive power of the IFD in natural populations will depend on the magnitude of these deviations.

Table 2.1. Assumptions and predictions of the ideal free, ideal despotic, and perceptual constraints models of habitat selection (from Fretwell & Lucas 1970 and Abrahams 1986).

Model	Assumption(s)	Predictions			
		Distribution of fish		Payoffs	
		Numbers	Phenotype	Individual	Patch
Ideal free	'ideal', 'free'	-prop. of fish in each patch equals the prop. of food in the patch	-n.a. equal competitors	-all fish have equal intake rates	-individuals obtain equal payoffs in each patch
Ideal despotic	'ideal'	-too few fish in the best patch, too many in the poor patch, relative to ideal free	-dominants settle in the best patch	-intake rate is correlated with dominance rank	-individuals obtain higher payoffs in good patches
Perceptual constraints	'free'	-too few fish in the best patch, too many in the poor patch, relative to ideal free	-dominance rank not related to distribution	-intake rates of fish are unequal and unrelated to dominance rank	-individuals obtain higher payoffs in good patches

Table 2.2. Least squares regressions of the proportion of fish versus the proportion of food in each patch for the Predictable, Intermediate and Unpredictable treatments.

Treatment	Slope	r^2[a]	t-value[b]
Predictable	0.831	0.95*	-4.694*
Intermediate	0.874	0.97*	-5.500*
Unpredictable	0.596	0.74*	-6.413*

[a] r^2-tests of the significance of the regression lines (df=1,31).

[b] t-tests comparing the observed slope to 1.0 (df=31).

* P<0.001

Table 2.3. Least squares regressions of the proportion of time spent in each patch versus the proportion of resources available for dominant (D) and subordinate (S) fish.

Treatment	Status	Slope	r^2 [a]	t-value[b]	Dominant[c] vs. Subordinate
Predictable	D	1.175	0.69*	1.250	t=4.31*
	S	0.706	0.65*	-3.128*	
Intermediate	D	0.950	0.66*	0.410	t=0.32
	S	0.923	0.91*	-1.510	
Unpredictable	D	0.304	0.13*	-5.438*	t=1.67
	S	0.451	0.74*	-11.438*	

[a] F-tests of the significance of the regression lines (df=1,31).

[b] t-tests comparing the observed slope to 1.0 (df=31).

[c] t-tests comparing the slopes of dominant and subordinate fish (df=62).

* P<0.01, ** P<0.001

Table 2.4. Linear regressions of the proportion of food eaten by dominant (D) and subordinate (S) fish in each patch and the proportion of resources available there.

Treatment	Status	Slope	r^2 [a]	t-value[b]	Dominant[c] vs. Subordinate
Predictable	D	1.106	0.65**	0.726	t=2.65*
	S	0.817	0.75**	2.153*	
Intermediate	D	0.869	0.50**	0.840	t=0.23
	S	0.893	0.92**	2.277*	
Unpredictable	D	1.064	0.66**	0.467	t=0.29
	S	1.037	0.94**	0.771	

[a] *F*-tests of the significance of the regression lines (*df*=1,31).

[b] *t*-tests comparing the observed slope to 1.0 (*df*=31).

[c] *t*-tests comparing the slopes of dominant and subordinate fish (*df*=62).

* $P<0.05$, ** $P<0.001$

Table 2.5. Spearman correlation coefficients relating mean dominance rank to competitor density for each of the three patch probabilities in the Predictable, Intermediate and Unpredictable treatments (N=11).

Treatment	Patch probability	r
Predictable	0.667	-0.765*
	0.167	-0.300
	0.083	-0.182
Intermediate	0.667	-0.159
	0.167	0.173
	0.083	-0.473
Unpredictable	0.667	-0.333
	0.167	-0.269
	0.083	-0.501

* $P<0.05$

Figure 2.1. The mean proportion of fish ± 1 SE (N=11) in the best patch during periods 1 to 36 for the (a) Predictable, (b) Intermediate and (c) Unpredictable treatments. The proportion predicted by IFD theory is indicated by the dashed line.

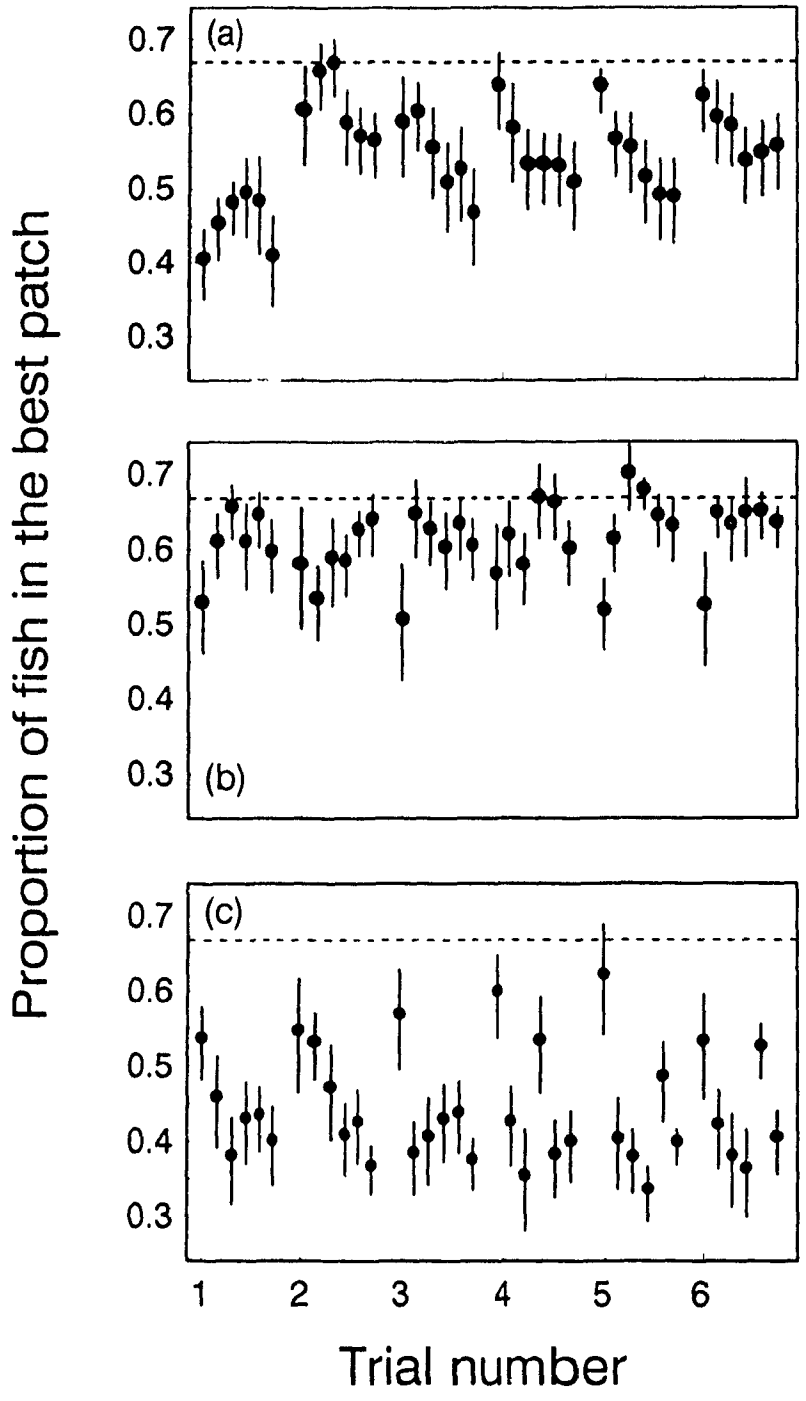

Proportion of fish in the best patch
0.7
0.6
0.5
0.4
0.3
(a)
(b)
(c)
1
2
3
4
5
6
Trial number

Figure 2.2. Least squares regressions of the proportion of fish in relation to the proportion of food in each patch for the (a) Predictable, (b) Intermediate and (c) Unpredictable treatments. The observed relationships (dotted lines) are compared with the predicted ideal free distribution (solid lines). Mean proportions of fish ± 1 SE (N=11) are indicated for each patch.

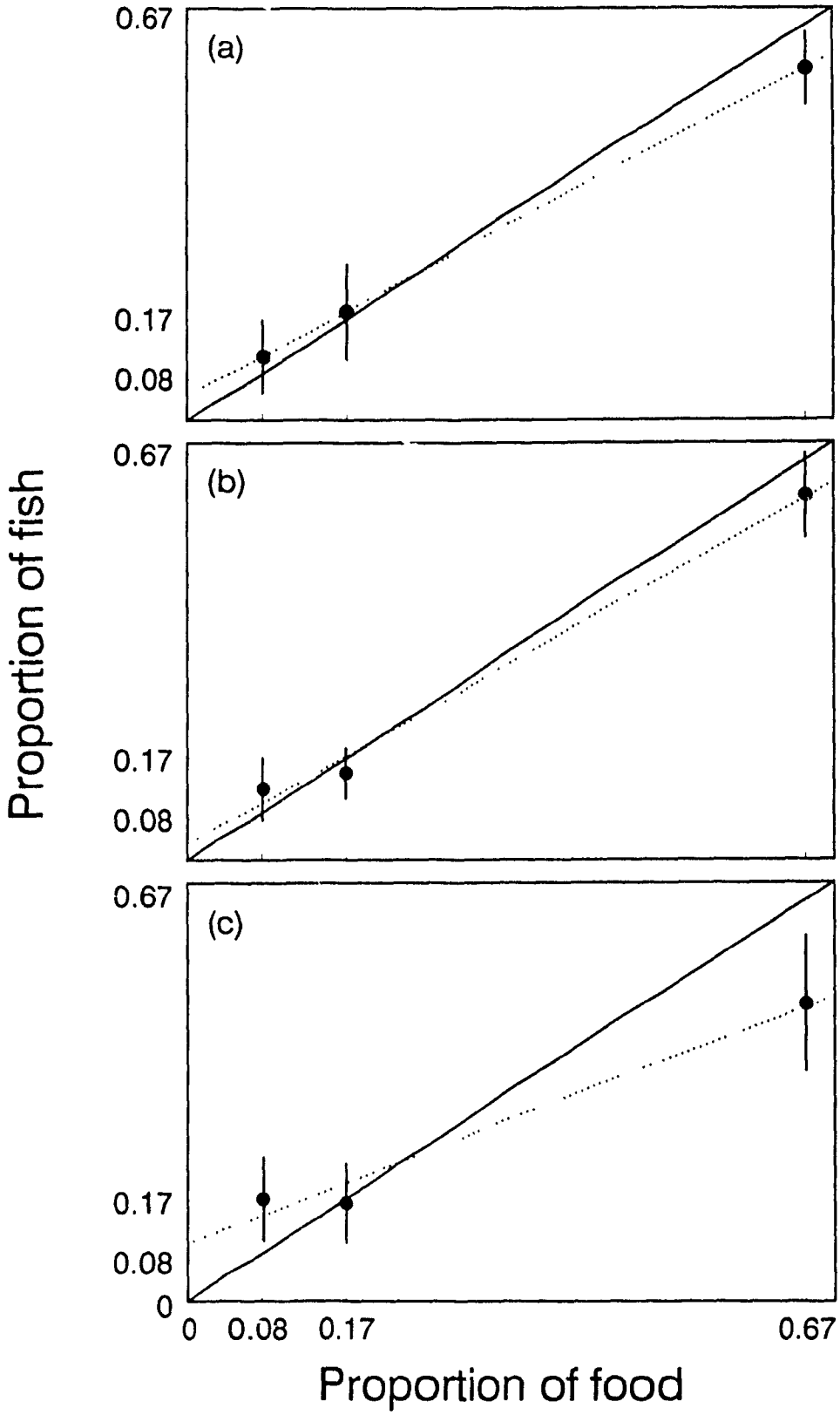

0.67
(a)
0.17
0.08
0.67
(b)
0.17
0.08
0.67
(c)
0.17
0.08
0
0
0.08
0.17
0.67
Proportion of fish
Proportion of food

Figure 2.3. Least squares regressions of the proportion of time spent in each patch in relation to the proportion of food in each patch for dominant (circles) and subordinate fish (triangles) for the (a) Predictable, (b) Intermediate and (c) Unpredictable treatments. The observed relationships are compared with the input matching slope of 1 (solid line). Mean proportions ± 1 SE (N=11) are indicated for each patch.

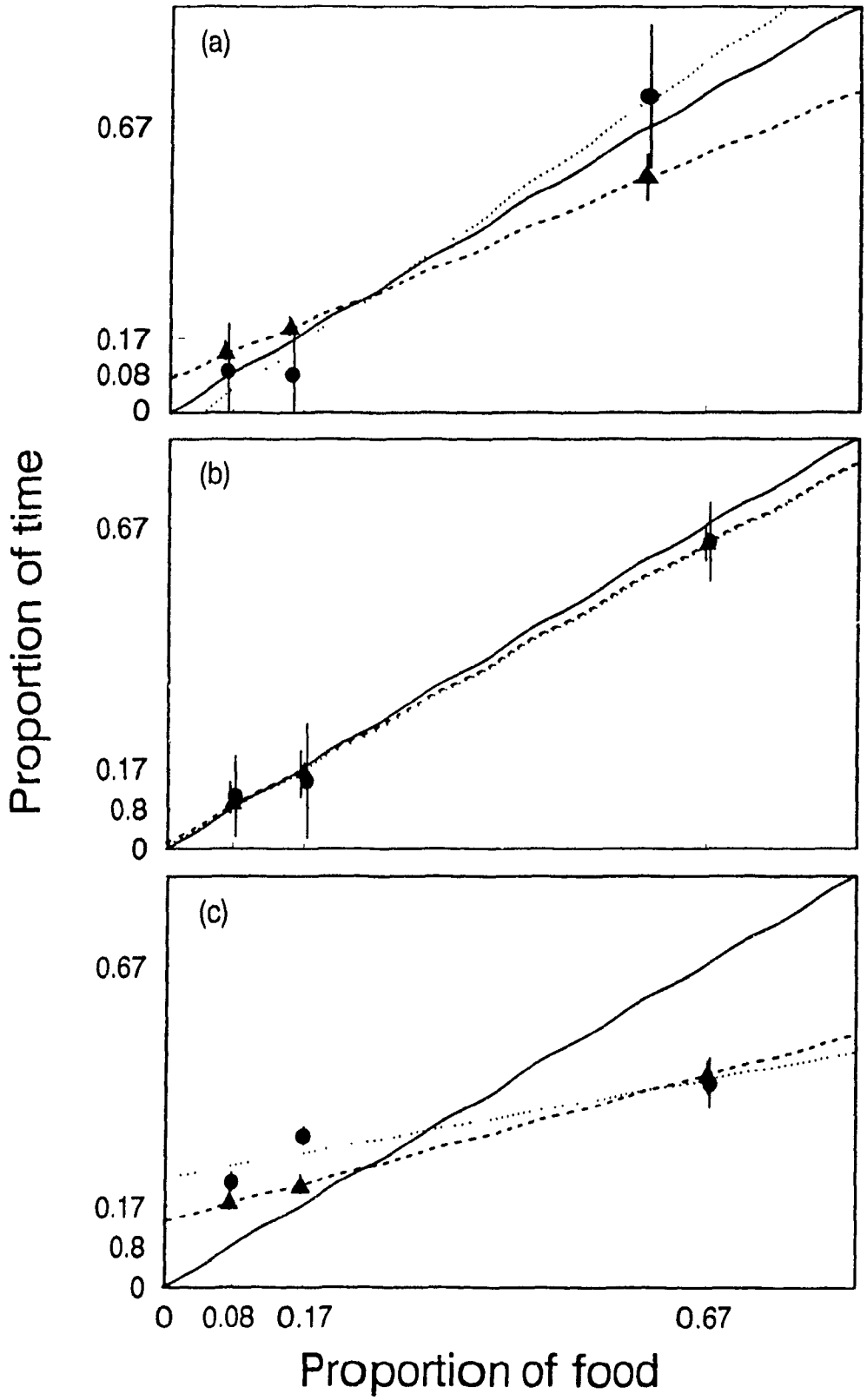

(a)
0.67
0.17
0.08
0
(b)
0.67
0.17
0.8
0
(c)
0.67
0.17
0.8
0
0
0.08
0.17
0.67
Proportion of time
Proportion of food

Figure 2.4. Least squares regressions of the proportion of an individual's diet originating from each patch in relation to the proportion of the food available in each patch for dominant (circles) and subordinate fish (triangles) in the (a) Predictable, (b) Intermediate and (c) Unpredictable treatments. The observed relationships are compared with the input matching slope of 1 (solid line). Mean proportions ± 1 SE (N=11) are indicated for each patch.

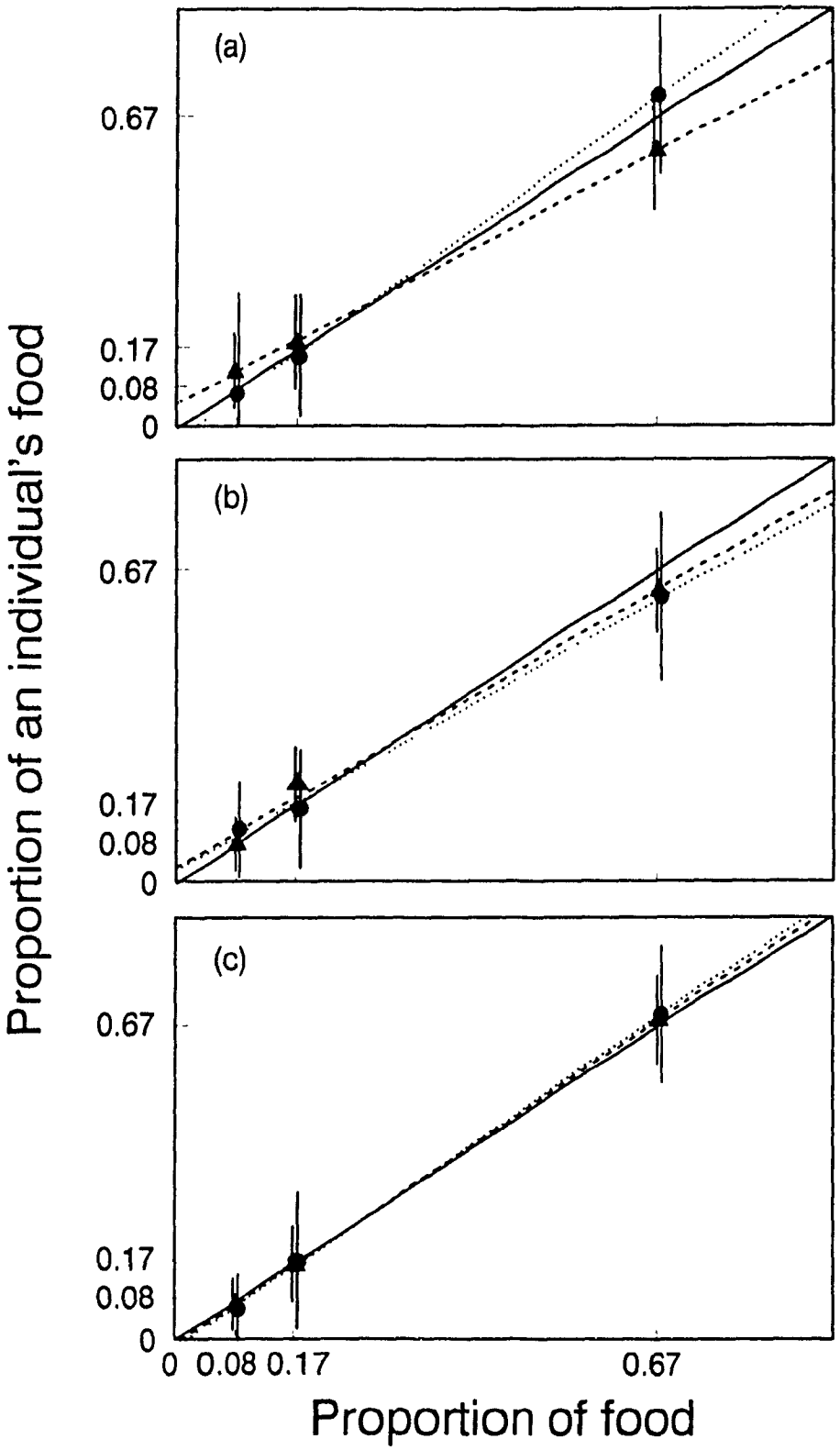

(a)
(b)
(c)
0.67
0.17
0.08
0
0 0.08 0.17
0.67
Proportion of an individual's food
Proportion of food

Figure 2.5. The mean proportion of food ± 1 SE (N=11) obtained by individuals of different dominance rank in the (a) Predictable, (b) Intermediate and (c) Unpredictable treatments. Dominant fish are ranked 6.

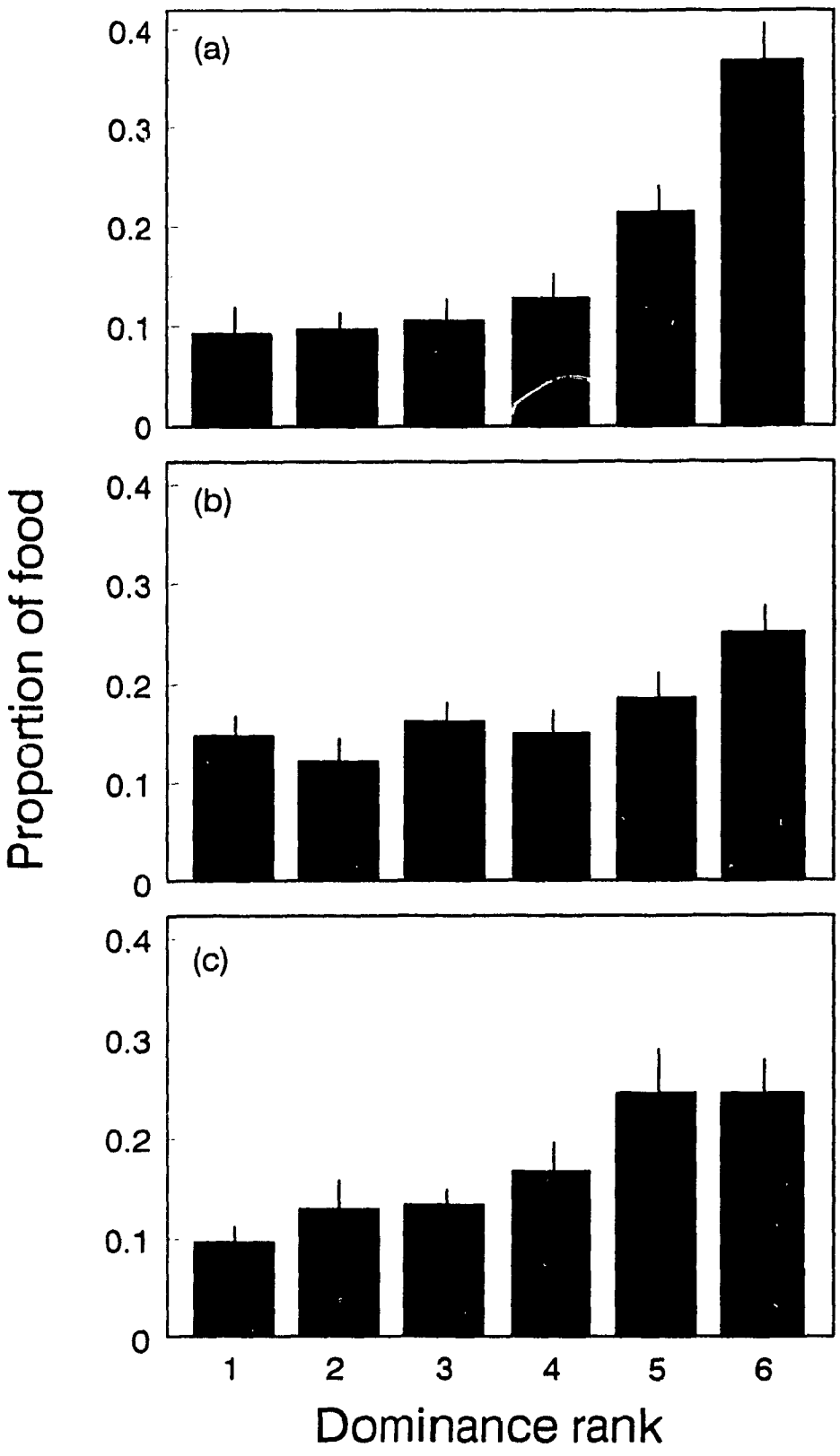
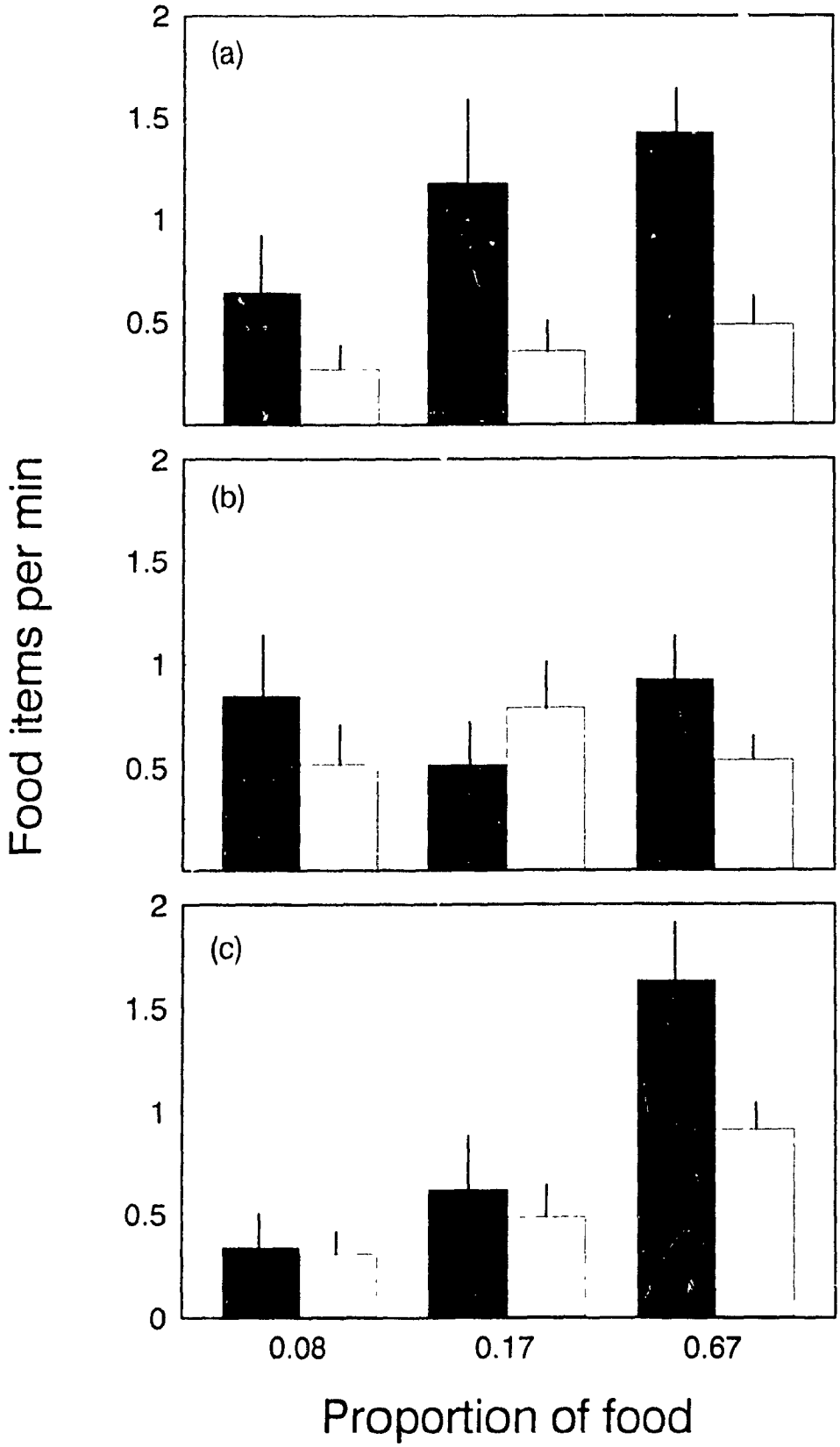

(a)
(b)
(c)
0.4
0.3
0.2
0.1
0
Proportion of food
1
2
3
4
5
6
Dominance rank

Figure 2.6. A comparison of the mean number of food items per minute ± 1 SE (N=11) obtained from each patch by dominant (solid bars) and subordinate fish (open bars), in the (a) Predictable, (b) Intermediate and (c) Unpredictable treatments.


(a)
(b)
(c)
2
1.5
1
0.5
0
0.08
0.17
0.67
Food items per min
Proportion of food

Summary

Although spatial predictability is often invoked to explain the behaviour and distribution of individuals, few studies have measured or manipulated predictability. Chapter 1 provides the first quantitative test of the hypothesis that spatially predictable resources are more easily monopolized and defended than spatially unpredictable resources. This hypothesis is central to resource defence theory (Brown 1964) and is also important in the theories of mating, spacing and social systems (Wiens 1976; Emlen 1980; Warner 1980; Davies & Houston 1984; Pulliam & Caraco 1984; Lott 1991).

In the second chapter, I examined the influence of spatial predictability on the distribution of individuals relative to resources, within the context of an 'ideal free' framework (Fretwell & Lucas 1970). Resource predictability was shown to have two primary effects on habitat selection. When resources were predictable and defendable, fish distributions were mediated by the despotic behaviour of the dominant individual. When resources were unpredictable in space, groups of fish under-used the best patch, and appeared to be unable to differentiate between patches differing in quality. These results suggest that resource predictability may play an important role in habitat selection.

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