

The effects of spatial food distribution and group size on foraging behaviour in a benthic fish

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Abstract

Animals foraging in heterogeneous environments benefit from information on local resource density because it allows allocation of foraging effort to rich patches. In foraging groups, this information may be obtained by individuals through sampling or by observing the foraging behaviour of group members. We studied the foraging behaviour of goldfish (*Carassius auratus*) groups feeding in pools on resources distributed in patches. First, we determined if goldfish use sampling information to distinguish between patches of different qualities, and if this allowed goldfish to benefit from a heterogeneous resource distribution. Then, we tested if group size affected the time dedicated to food searching and ultimately foraging success. The decision of goldfish to leave a patch was affected by whether or not they found food, indicating that goldfish use an assessment rule. Giving-up density was higher when resources were highly heterogeneous, but overall gain was not affected by resource distribution. We did not observe any foraging benefits of larger groups, which indicate that grouping behaviour was driven by risk dilution. In larger groups the proportion searching for food was lower, which suggests interactions among group members. We conclude that competition between group members affects individual investments in food searching by introducing the possibility for alternative strategies, such as scrounging or resource monopolisation.

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1. Introduction

Resources are generally distributed heterogeneously in time or space. If animals can track changes in resource availability, they may take advantage of this heterogeneity by spending more time in more

profitable patches (Morgan et al., 1997; Thompson et al., 2001). When individuals have complete information on resource quality among patches, the optimal strategy is to leave a patch when the harvest rate drops below the average value of the environment according to the marginal value theorem (MVT) (Charnov, 1976). This means that the forager should stay longer (i.e., have a longer patch residence time (PRT)) and harvest more food in rich patches compared to poor patches. In contrast, incomplete information of environmental

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quality may force foragers to use simple rules, such as spending a fixed time or catching a fixed number of prey per patch (Iwasa et al., 1981; Green, 1984). Green (1984) used modelling to show that a simple fixed-time strategy prevents individuals from fully benefiting from encounters with rich patches. Therefore, it is likely that individuals, by previous experience, are aware of the properties of the environment in terms of patch quality distribution and use that experience when foraging in a new patch (Green, 1980; Valone and Brown, 1989; Olsson and Holmgren, 1998). Green (1984) suggested that the optimal strategy is to use an assessment rule, in which the patch-leaving decision is based both on expected harvest rate from previous experience and information gained in the present patch. If patch-leaving decisions are based on information gained in a patch, then the forager needs to sample the patch before it can decide whether or not to stay in the patch (Lima, 1984). Hence, a forager's patch use strategy should, according to theory, reflect its ability to assess environmental quality (Iwasa et al., 1981; Valone and Brown, 1989; Schmidt and Brown, 1996), and should affect its ability to take advantage of heterogeneity in resource distribution.

Another principle solution among foragers for coping with unpredictable environments is joining groups and sharing information. Information sharing within a group may result in shortened search time for food (Pitcher et al., 1982) and lower variation in food intake (Caraco, 1981; Clark and Mangel, 1984; Ranta et al., 1993; Ruxton et al., 1995). Behavioural studies of goldfish (*Carassius auratus*) and minnows (*Phoxinus phoxinus*) have shown that members of larger groups stay longer in food patches and cover larger areas than members of small groups (Magurran and Pitcher, 1983). Pitcher et al. (1982) also showed that the time required to find a food patch decreased with group size. Although these studies suggest a foraging advantage for fish in groups, there are other mechanisms, such as risk dilution and corporate vigilance that may create qualitatively similar results as sharing of foraging information. Moreover, sharing of information introduces the possibility of alternative strategies, such as the scrounger tactic (Barnard and Sibly, 1981), through which receivers of public information do not necessarily contribute to the collecting of that information. Our ultimate goal is to separate group-size effects on individual foraging return generated by information

Table 1
Predictions from patch use models

Patch-leaving rule	Patch residence time (PRT)	Giving-up density (GUD)
MVT	Longer in rich patches	"Equalised"
Assessment	Sampling to assess patch value, then longer in rich patches	Higher in rich patches, but driven towards equalisation
Fixed time	Same in all visited patches	Higher in rich patches

MVT = marginal value theorem.

sharing, predation risk, and alternative foraging strategies. One step towards this goal is to find patterns of group-size-dependent time allocation to different activities and its consequences for foraging return in different environments.

Here, we first studied the foraging strategy of goldfish, a group foraging benthic fish by establishing their patch-leaving rule in artificial patches of different qualities. We compared the observed patch use behaviour with predictions derived from MVT, assessment models, and fixed-time (Table 1). With complete knowledge of the environment (an assumption that has to be met for the MVT), goldfish should have larger patch residence time (PRT) in patches with higher than with lower food abundance, and leave patches at the same quitting harvest rate. The giving-up density (GUD) is frequently used as an equivalent to quitting harvest rate in experimental set-ups because it is easier to quantify (Brown, 1988). According to a fixed time strategy, a goldfish should spend equal time in all visited patches, indicating that they are incapable of accurately estimating the resource value in the food patches. A fixed-time strategy would result in GUD being positively correlated with initial resource density. If goldfish use an assessment strategy, we expect that PRT would depend on resource density. We also expect that GUD would be driven towards equalisation, so that equal amounts of food should be left in all patches, regardless of initial resource density.

We then studied the consequences of the strategy by testing how foraging behaviour is affected by the heterogeneity in resource distribution. Foragers that are able to correctly assess their environment should benefit from increased heterogeneity by allocating more time to profitable patches. Lack of knowledge should, on the contrary, lead to a larger cost in more

heterogeneous environments in terms of lower harvest rate, since time will be wasted in unprofitable patches.

Finally, we tested the effects of group size on GUD, individual time allocation for searching, and its consequences for foraging return by investigating whether the proportion of individuals actively searching for resources is dependent on group size. Group-size independence of the proportion foraging would indicate no interactions among group members (providing that accessibility was not limited by patch size) suggesting that groups are formed simply to increase the rate of information gathering or for risk dilution. In the case of information gathering, individuals should spend less time to obtain a certain collective amount of information on patch quality in larger rather than smaller groups, thus reducing individual sampling costs and increasing harvest rate in large groups. In the case of dilution of predation risk, increasing group size should come at a cost of increased competition (between equal competitors), and thus, result in decreased harvest rate. If the proportion of individuals foraging decreases with group size, then interactions among group members may balance costs and benefits.

In the case of group-size-dependent foraging, several mechanisms may generate qualitatively similar results. For example in producer–scrounger models, the proportion producers (individuals searching for food) decreases with group size but increases with patch quality (Giraldeau and Caraco, 2000), which is qualitatively similar to the predictions of models including dominance hierarchy in which some individuals may attempt to monopolise the resource in a competitive environment. It is beyond the scope of this study to experimentally test different social patch models. Instead, our goal is to derive patterns of the group-size dependence of different behavioural variables, and in particular time invested into sampling, that could be used to design future more explicit tests.

2. Materials and methods

2.1. Experimental fish

Experiments were performed with common goldfish 9–11 cm in length. Goldfish are benthivorous, “dig” in the gravel to find food and are group living (Magurran, 1984). Therefore, the experiments were performed with

four fishes (except in group-size experiments) in each trial to avoid biases due to non-natural foraging situations. The fishes were obtained from Simontorp Säteri AB (Blentarp, Sweden).

2.2. Experiments

Three experiments were conducted, two between 22 August and 1 September 2000 (resource distribution and group size) and one in April 2001 (patch quality) to test the effects of patch quality, resource distribution and group size on foraging behaviour. Experiments in 2000 were performed on the roof of the Ecology Building in Lund Sweden, whereas the 2001 experiment was performed in a greenhouse adjacent to the Ecology Building. All trials took place in five circular pools (20001, $h=0.45$ m, $d=2.4$ m). Each pool contained nine clay plates ($d=22$ cm), commonly used as plates for plant pots, which represented food patches. Pellets (mean weight 37 mg) of salmon food, which do not fall apart in the water, were used as food items. The pellets that were left after trials were easily removed and counted. The plates were filled with approximately 15 mm sand and the food items were hidden in the sand to prevent the fishes from seeing them. The resource distribution and group-size experiments were replicated five times, whereas the patch quality experiment was replicated four times. Water temperature was between 14 and 20 °C, but MANCOVAs, with temperature as the covariate, showed no effects ($p>0.05$) of temperature on any of the behavioural variables measured. The fishes were kept in the experimental pools during the duration of the experiments. After each trial, all fish were caught and randomly mixed into new groups for new trials the following day. On days when experiments were conducted, the fish were not fed except during trials to control for hunger level.

Before each trial, the fish were caught and placed in a covered cage in the pool. The patches were then placed in the pool and the fish were released. All trials lasted for 12 min and were recorded with a video camera. After each trial, all food patches were collected and remaining food items were counted.

Separate experiments were performed on effect of patch quality, resource distribution and group size. The patch quality experiment was performed with initial resource densities (IRD) of 0, 6 or 12 food items in each of three patches within each pool. In the

resource distribution experiment, food was distributed according to one of three resource heterogeneity levels: homogeneous with food in all of the nine patches (CV of patch quality = 0, six food items/patch; 54 items in total), intermediate, with food in five of the nine patches (CV of patch quality = 95; 11 food items/patch; 55 items in total), or heterogeneously, with food in three of the nine patches (CV of patch quality = 150; 18 food items/patch; 54 items in total). The group-size experiment was performed with three group sizes, 2, 4 and 8 individuals and with food distributed heterogeneously (CV of patch quality = 150; 18 food items in three out of the nine patches).

2.3. Analyses of foraging behaviour

We used three response variables to characterise foraging behaviour: total gain, GUD and PRT. Total gain and GUD were obtained directly from the remaining food in the patches after termination. Total gain was defined as the average individual reward in each experiment, and GUD the average remaining number of food items in a specific patch type at the end of each experiment. The harvest rate in each patch is a negative function of amount of food remaining in the patch and GUD is thus an indirect measure of quitting harvest rate (Brown, 1988). Patch residence time was derived from analysis of foraging behaviour from video recordings.

We quantified a separate patch residence time for the case when no food was found or none available (PRT_{sampling}), because a difference in PRT and PRT_{sampling} would indicate that the patch-departure decision followed the MVT or an assessment of patch quality. We quantified PRT as the amount of time any member/members in a group occupied a patch of a given initial quality. PRT is here defined as time actively searching for food (characteristic nose down posture (Pitcher et al., 1982)). PRT_{sampling} is included in PRT in those patches where food was consumed. In the group-size experiments, we also calculated the proportion of the group that was active in either sampling for (i.e., when no food was found) and/or eating (when food was found) the food found by the group. The proportion of individuals actively participating in searching in a patch was obtained by first calculating the average number of individuals engaged in searching, which is the ratio between the sum of time a patch was occupied by each individual and PRT. The average number

of individuals engaged in searching was then divided by group size to obtain the proportion of the group engaged in searching (and/or eating).

2.4. Statistics

All statistical analyses were performed on pool means with SPSS 8.0. (SPSS Inc., Chicago, IL, USA 1989–1997). To test the effects of patch quality, we used a randomised block design with replicate as the block. The differences within resource distribution and group-size experiments were tested with MANOVA. Comparisons between patches with and without food (PRT and the proportion of the group actively searching for food) were done with paired *t*-test.

3. Results

3.1. Effects of patch quality

Patch residence time increased with increasing initial patch quality (Fig. 1a; Table 2). Patch residence time was dependent on whether food was found or not, given that PRT_{sampling} was significantly lower than

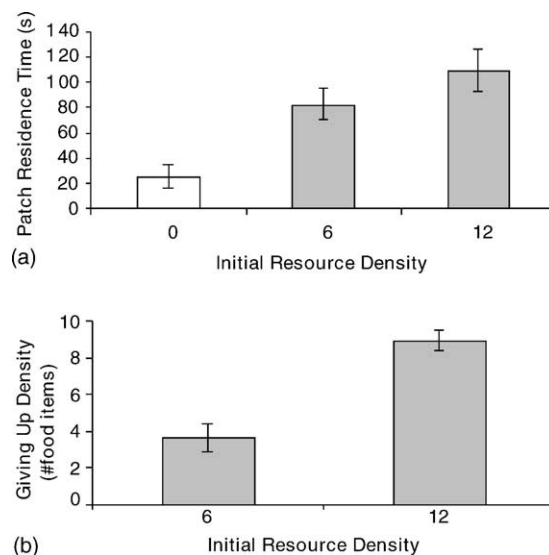


Fig. 1. Patch residence time (a) and giving-up density (b) of goldfish foraging in patches of different initial qualities. Filled and open bars refer to cases when food was found and when food was not found, respectively.

Table 2

ANOVA table of the effects of patch quality (randomised block; pool as block) on patch residence time (PRT)

Source	d.f.	F-test	p-value
Patch residence time (PRT)			
Initial resource density (IRD)	2	8.509	0.018
Block	3	0.383	0.770
Error	6		

Giving-up density (GUD)

Paired <i>t</i> -test, IRD = 6 vs. IRD = 12	d.f.	<i>t</i>	<i>p</i>
	3	−5.657	0.011

The table also presents results from paired sample *t*-tests of the differences in giving-up density (GUD) between patches containing 6 vs. 12 food items. Bold *p*-values refer to significant effects.

PRT (Fig. 1a; Table 2). However, initial resource density did not affect the time spent in patches where food was found, which resulted in giving-up density (GUD) increasing with increasing initial resource density (Fig. 1b; Table 2).

3.2. Effects of resource distribution

There was a significant effect of resource distribution on the behaviour of goldfish (MANOVA, Wilks' $\lambda = 0.016$, $p < 0.001$). As in the patch quality experiment, PRT was significantly longer than PRT_{sampling} (Fig. 2a; Table 3). GUD was higher in patches with higher initial resource density (Fig. 2b; Table 3). However, gain over the whole trial was not affected by resource distribution (Fig. 2c; Table 3).

Table 3

ANOVA table of the effects of resource distribution on patch residence time (PRT), PRT_{sampling}, giving-up density (GUD) and gain

	d.f.	F-test	p-value
Patch residence time (PRT)	2	0.1130	0.894
PRT _{sampling}	2	1.413	0.284
Giving-up density (GUD)	2	156.2	<0.001
Gain	2	0.190	0.830

Paired <i>t</i> -test, PRT vs. PRT _{sampling}	d.f.	<i>t</i>	<i>p</i>
CV of patch quality = 0%	4	7.341	0.002
CV of patch quality = 95%	4	2.569	0.062
CV of patch quality = 150%	4	3.515	0.025

The table also presents results from paired sample *t*-tests of the differences between PRT and PRT_{sampling} in each resource distribution experiment. Bold *p*-values refer to significant effects.

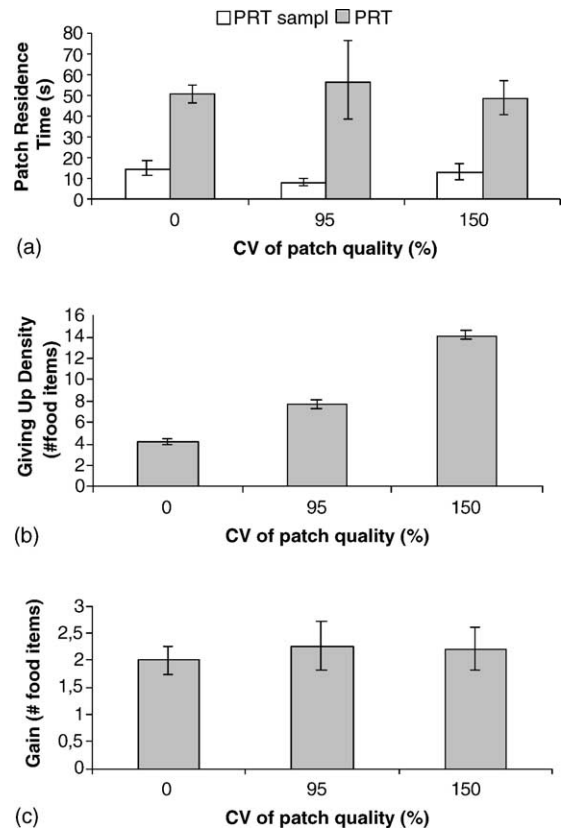


Fig. 2. Patch residence time (a), giving-up density (b) and average individual gain over the whole experimental trial (c) of goldfish foraging in patch environments with different resource distributions. Filled and open bars refer to cases when food was found and when food was not found, respectively.

3.3. Effects of group size

There was a significant effect of group size on goldfish behaviour (MANOVA, Wilks' $\lambda = 0.004$, $p < 0.001$). Group size did not affect PRT (Fig. 3a; Table 4), but PRT_{sampling} was significantly shorter for two individuals than for larger groups (Fig. 3a; Table 4). All group sizes devoted significantly longer time in a patch when they found food compared to sampling time (Fig. 3a; Table 4). GUD decreased with group size (Fig. 3b; Table 4), whereas the pattern for gain tended to be the opposite, i.e., small groups had higher average individual gains (Fig. 3c; Table 4).

Members in the small group were much less active than fish in larger groups and spent a larger fraction of the 12-min trials motionless. When actively searching,

they went quickly to a patch and then back to the side again, especially when no food was found, as indicated by shorter PRT_{sampling} (Fig. 3a). The groups of four and eight were more active and group members visited patches for most of the trial. However, there was a significant negative group-size effect on the proportion of the group actively searching for food, both when food was and was not found (Fig. 4; Table 4). Moreover, this proportion was significantly lower when food was not found compared to when food was found (Fig. 4; Table 4). Still, all members of the group stayed next to the patch and had access to information from the group members that were searching. Aggressive behaviour took place more frequently with larger group sizes than with two fish (visual observations).

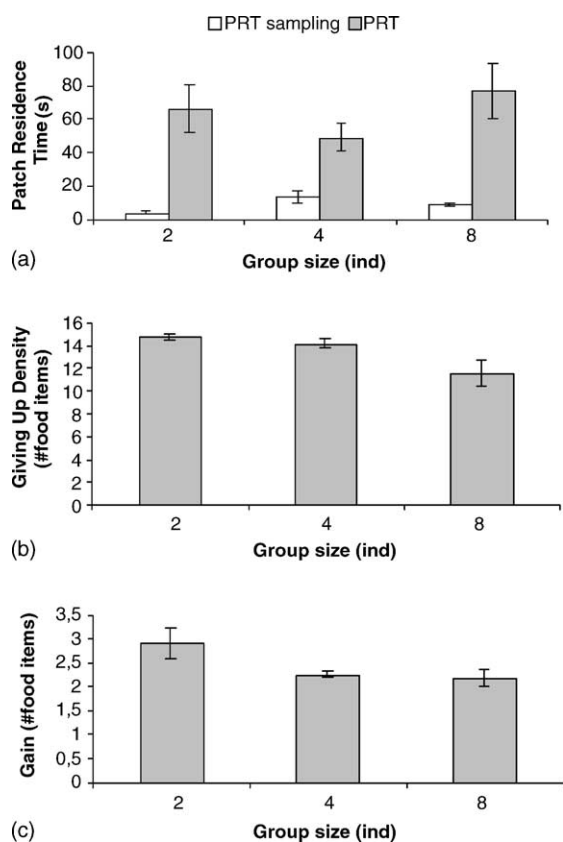


Fig. 3. Patch residence time (a), giving-up density (b) and average individual gain (c) of goldfish foraging in differently sized groups. Filled and open bars refer to cases when food was found and when food was not found, respectively.

Table 4

ANOVA table of the effects of group size on patch residence time (PRT), PRT_{sampling} , giving-up density (GUD), gain, proportion of group actively eating and proportion of group actively searching

	d.f.	<i>F</i> -test	<i>p</i> -value
Patch residence time (PRT)	2	1.093	0.366
PRT_{sampling}	2	4.235	0.041
Giving-up density (GUD)	2	5.742	0.018
Gain	2	3.317	0.071
Proportion active _{eating}	2	25.272	<0.001
Proportion active _{sampling}	2	121.390	<0.001

Paired <i>t</i> -test	d.f.	<i>t</i> -test	<i>p</i> -value
PRT vs. PRT_{sampling} (individuals)			
2	4	−4.388	0.012
4	4	−3.515	0.025
8	4	−4.306	0.013
Prop.eating vs. Prop.sampling (individuals)			
2	4	−2.467	0.069
4	4	−7.282	0.002
8	4	−4.217	0.014

The table also presents results from paired sample *t*-tests of the differences between PRT and PRT_{sampling} and between prop.eating vs. prop.sampling for each group-size treatment. Bold *p*-values refer to significant effects.

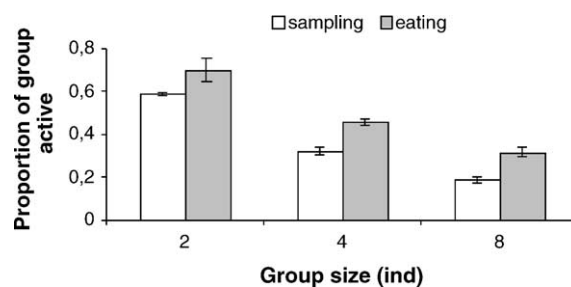


Fig. 4. Proportion of the foraging goldfish groups actively searching in resource patches. Filled and open bars refer to cases when food was found and when food was not found, respectively.

4. Discussion

Individuals foraging in an uncertain environment may use different strategies to optimise foraging return (McNamara, 1982; Green, 1980; Valone and Brown, 1989; Olsson and Holmgren, 1998). With complete knowledge, foragers feeding on depletable patches should follow the predictions from the marginal value theorem and deplete all patches to the same density (Charnov, 1976). Our experiment did not support this prediction, because GUD was dependent on initial

resource density. With no knowledge of the quality of the current patch, foragers may use previous experience to define a fixed-time or a fixed-number patch-departure rule (Iwasa et al., 1981; McNair, 1983; Valone and Brown, 1989). A fixed-time strategy predicts that animals spend the same amount of time in all visited patches, which was not the case in our experiment. Instead, fish first invested a short time to sample patches and only continued foraging in that patch if rewarded. Hence, our results suggest that goldfish use an assessment rule when searching for food. In variable environments, frequent re-evaluations of previous experience and recent sample information that track changes in the environment may yield a higher foraging return in comparison to a fixed strategy (Green, 1984; Iwasa et al., 1981; Olsson and Holmgren, 1999; Hirvonen et al., 1999). As indicated by patch residence time in patches where no food was found, sample time was short and with a low probability of actually yielding a food item. The cost of using this strategy is that the fish not only disregard empty patches, but also sometimes profitable ones.

Patch assessment has previously been observed in avians (Lima, 1984; Olsson and Holmgren, 1999; van Gils et al., 2003) and mammals (Valone and Brown, 1989), but has to our knowledge never been reported for fish. Lima (1984) showed that Downy woodpeckers (*Picoides pubescens*) used gained information about food distribution in the patch visited, and made use of this information when entering the next patch. If the woodpecker did not find food after a certain amount of sampling effort, it continued to the next patch. An assessment rule is thus useful, and generally the optimal solution in a heterogeneous environment if animals have incomplete information on patch value (Green, 1984; Green, 1987; Olsson and Holmgren, 1999; van Gils et al., 2003). However, we did not confirm our prediction that a patch assessment strategy is most profitable in heterogeneous environments, given that gain did not vary among treatments in the resource distribution experiment.

The advantages of detecting patchiness in resource availability should be positively related to the patchiness of the environment (Schmidt and Brown, 1996). Hence, there is more to be gained if the variance in patch quality is high. In our experiments, giving-up density increased with increasing resource density and

the fish seemed to stay a fixed time in a patch once food was found. Hence, goldfish could not fully take advantage of the heterogeneity of the environment, although the assessment rule reduced time spent in empty patches. Consequently, goldfish were successful in assessing if a patch was empty or not, but did not appear to access the information required to differentiate between patches with unequal amounts of food. Inability in assessing patch resource density has previously been found in avian granivores (Valone and Brown, 1989; Garb et al., 2000; Hayslette and Mirarchi, 2002) and fish (DeVries et al., 1989; Marschall et al., 1989). The ability to distinguish between patches with different values is likely to be affected by foraging scale of the consumer, i.e., the grain size of the environment perceived by the consumer (Ritchie, 1998), and the amount of information that is gathered in each patch. If patches are small and/or if little information is gained by exploiting them, a forager may not be able to assess patch value appropriately. In our experiment, patches contained only a few food items and goldfish left patches after partial exploitation. The information gained in each patch may have been insufficient to distinguish between food patches, at least not between patches that differed in resource density by a factor of two, which was the case in the patch quality experiment.

Goldfish always avoided solitary foraging, but since individual gain tended to decrease with group size, grouping behaviour was more likely driven by risk dilution than information sharing. In larger groups, the fraction of the group searching for food was lower, suggesting interactions among group members. Hence, the observed behaviours could not simply be explained by either obtaining more information or risk dilution. Instead, we conclude that competition between group members affects the individual investments into sampling, either by introducing the possibility for alternative strategies such as scrounging, or because some individuals attempt to monopolise the resource.

Foraging in a group has been suggested as a way to reduce risk and to enhance the amount of information regarding where to find food and how long to stay in a patch of a certain quality. In our experiment, all individuals of the group more or less entered and left patches simultaneously. Individual gain decreased with group size. If groups were formed due only to the benefits of either information sharing or risk dilution,

one would expect that individual gain would increase or decrease, respectively, with group size. Hence, risk dilution or increased vigilance seems to be driving the group formation in the first place. Indeed, sampling time (PRT_{sampling}) was shorter and activity was lower for the small group (two individuals) compared to larger groups, which suggests that smaller groups experienced higher perceived predation risk. However, if groups were formed solely based on such benefits, group size would not affect foraging behaviour. In our study, the proportion of the group actively searching for food declined with increasing group size, which suggests that goldfish foraging in groups should be viewed as a balance between these benefits and the cost of sharing resources between group members.

We could not obtain data on individual foraging return, which makes it essentially impossible to test different social patch models. However, based on our data on search times, we can qualitatively evaluate different alternatives. One process that causes this group-size-dependent searching is monopolisation of resources by some individuals in a patch. If competition increases with group size, monopolisation behaviour would be stronger in larger groups and would lead to a lower proportion being allowed to search for food. The proportion searchers in the larger groups was significantly higher in patches where food was found, which shows the individual behaviours were driven at least partly by the information gained on patch quality and introduces the possibility for alternative strategies. If group members can gain information from others on where and when to find food, some individuals may decide to feed opportunistically at resource hot spots and spend the rest of the time on other fitness generating activities than searching, such as looking for predators or observing the food searching of others. If the benefits of these activities are shared within the group, e.g. by a public warning of an approaching predator, it qualifies as information sharing. However, if the benefits are invested in increased mating success or survival, it approaches a producer–scrounger game (Barnard and Sibly, 1981; Vickery et al., 1991; Giraldeau and Beauchamp, 1999). In our experiment, non-searching group members stayed next to the patch, and thus, may have had access to information from the searching part of the group. The lower proportion of active group members in larger groups is indeed in accordance with theoretical prediction from producer–scrounger

models (Giraldeau and Caraco, 2000), if group members next to the patch only are involved in searching for feeding opportunities. It is likely, however, that fish are engaged in other activities, such as scanning for predators, which violates the assumptions of producer–scrounger models (Giraldeau and Caraco, 2000).

The tendency towards a cost in individual gain for members of large groups may be due to the experimental design that forced larger groups to share a similar total amount of food as small groups. This resulted in patches being revisited to a larger extent in experiments with larger groups. However, individual gain was lower for members in larger groups, despite small groups being less active than larger groups in the sense that fewer patches were visited. This supports the results by (Magurran and Pitcher, 1983) that goldfish in groups of two spent a lower fraction of time foraging compared to groups of five. In theory, larger groups, therefore, have to forage over larger areas to reach the same individual gain as smaller groups, which may result in higher travelling costs in larger groups. This cost is important to consider, because it is generally easier to achieve benefits of group foraging when travelling time is short (Sermland et al., 2003). Any foraging benefit of group foraging may, therefore, be counteracted by the need for larger groups to cover larger areas. In fact, recent theoretical studies show that the foraging advantage of information sharing generally does not exceed the cost of sharing food among group members (Livoreil and Giraldeau, 1997; Rita and Ranta, 1998; Sermland et al., 2003). Another explanation for the tendency for lower gain of larger groups could reflect overuse of relatively safe patches to reduce risky or costly travelling between patches.

Hence, both models and our empirical evidence suggest that average per capita gain may decrease with group size. In our study, the costs of competition did not seem to be sufficient to motivate solitary foraging or splitting groups, although aggressive behaviour and kleptoparasitism took place more frequently with eight individuals than with two individuals. This suggests that there are other benefits of being a group member, such as reduced variance in intake rate (Brown, 1988) or better protection against predators (Pulliam and Caraco, 1984; Turner and Pitcher, 1986; Clark and Mangel, 1986; Dehn, 1990; Wrona and Dixon, 1991; Krause et al., 1998; Krause and Ruxton, 2002),

and that these benefits are sufficiently large to maintain the widespread phenomena of group living. However, higher competition in larger groups introduced the possibility for alternative strategies and future studies should identify which strategies are present and how group size affects the frequency distribution of these strategies.

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