Monopolization of food by zebrafish (*Danio rerio*) increases in risky habitats

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Abstract: Dominant zebrafish (*Danio rerio*) previously have been shown to reduce their monopolization of food when foraging in structurally complex habitats compared with open habitats. Complex habitats may be more difficult to defend but may also be safer. To decouple these effects, we compared aggression and monopolization of food in groups of zebrafish foraging in an open habitat and one with overhead cover, as well as in an open habitat and a complex (vegetated) habitat. Covered and open habitats should have been equally defendable. In our experiments, fish used covered habitats more than open ones, suggesting that the perceived risk of predation was lower in covered habitats. There was no difference in use of vegetated and open habitats, suggesting that these habitats, which should differ in defendability, did not differ in safety. We found that the degree of food monopolization (expressed in the coefficient of variation within groups) at risky feeders was significantly greater in open habitats than in covered, but not vegetated, habitats. We did not find a difference in aggression between habitats. These results indicate that resource monopolization in groups of zebrafish is greater in risky habitats and support the hypothesis that the lower monopolization of food in complex habitats could result from greater safety in those habitats rather than, or in addition to, the reduction in defendability.

Résumé : Des recherches antérieures ont démontré que les poissons-zèbres (*Danio rerio*) dominants réduisent leur monopole sur la nourriture lorsqu'ils recherchent leur nourriture dans des habitats de structure complexe plutôt que dans des habitats ouverts. Les habitats complexes sont sans doute plus difficiles à défendre, mais ils sont aussi plus sécuritaires. Pour séparer ces effets, nous avons comparé l'agressivité et la monopolisation de la nourriture chez des groupes de zèbres en milieu ouvert et dans un habitat couvert, ainsi qu'en milieu ouvert et dans un habitat complexe (garni de végétation). Les milieux couverts et les milieux ouverts devraient être également défendables. Dans nos expériences, les poissons se tenaient de préférence dans les habitats couverts plus que dans les habitats ouverts, ce qui indique que les poissons perçoivent les habitats couverts comme moins exposés à la prédation. Il n'y a pas de différence dans l'utilisation des habitats garnis de végétation et des habitats ouverts, ce qui semble indiquer que ces milieux, qui devraient ne pas être également défendables, sont tout aussi sécuritaires l'un que l'autre. Nous avons constaté que le degré de monopolisation de la nourriture (exprimé comme le coefficient de variation au sein des groupes) aux mangeoires à risque est significativement plus élevé en milieu ouvert qu'en milieu couvert, mais pas plus élevé que dans les habitats garnis de végétation. Nous n'avons pas trouvé de différences dans le degré d'agressivité d'un habitat à l'autre. Nos résultats indiquent que la monopolisation des ressources chez les groupes de poissons-zèbres est plus fréquente dans les habitats à risque et corroborent l'hypothèse selon laquelle la monopolisation moins importante de la nourriture dans les habitats complexes résulte probablement de la sécurité supérieure de ces habitats plutôt que de la difficulté qu'il y a à les défendre; il se peut aussi que les deux facteurs soient impliqués.

[Traduit par la Rédaction]

Introduction

The ability of animals to monopolize resources can influence the behavioural decisions of themselves and others (Grant 1997), the dynamics of populations (Sutherland 1996), and the composition and stability of communities (Fryxell and Lundberg 1998). Current understanding of resource monopolization is based on the principle of economic defendability (Brown 1964), which states that resources should only be defended when the benefits of doing so exceed the costs. This is more likely to be so when resource density is relatively high, resources are clumped in space, but not in time, and are predictable in both space and time, and competitor density is low (Grant 1997). Structural complexity of the habitat can also influence resource defendability, as resources and competitors are more difficult to detect visually in a complex habitat (Eason and Stamps 1992; Basquill and Grant 1998; Hamilton and Dill 2003).

Recently, Basquill and Grant (1998) found that aggression and monopolization of food within groups of zebrafish (*Danio rerio*) were greater when those groups were foraging in an open habitat than when they were foraging in a structurally complex habitat. They suggested that items in the vegetated habitat were more difficult to detect, and thus, to defend. However, structural complexity may also increase the safety of a habitat for fish (Gotceitas 1990; Pettersson and Bronmark

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1993; Lonzarich and Quinn 1995; Eklov and Persson 1996). High predation risk is often considered to reduce monopolization of resources because resource-defence behaviours may be conspicuous to predators (e.g., Martel and Dill 1995) and because predator avoidance by dominant foragers may allow subordinates access to resources from which they are otherwise excluded (Martel and Dill 1993; Koivula et al. 1994; Reinhardt 1999). However, high predation risk could result in increased monopolozation of food for at least three reasons. First, subordinate fish may be less willing to challenge dominants for resources when risk of predation is high. Martel and Dill (1995) found that juvenile coho salmon (*Oncorhynchus kisutch*) were more likely to be detected by predators when acting aggressively. However, dominant juvenile coho salmon also are less likely to defend resources when risk is high, allowing subordinates greater opportunities to feed (Martel and Dill 1993; Reinhardt 1999). Second, dominant fish may be more willing than subordinates to accept high predation risk and feed at riskier but more productive sites (Grand 2002). Finally, if there is some benefit to grouping, such as dilution of predation risk, subordinate fish may be reluctant to leave groups when foraging in risky habitats, even when resources are monopolized. This would result in dominants being able to take a larger share of resources without the threat of subordinate departure (Hamilton 2000).

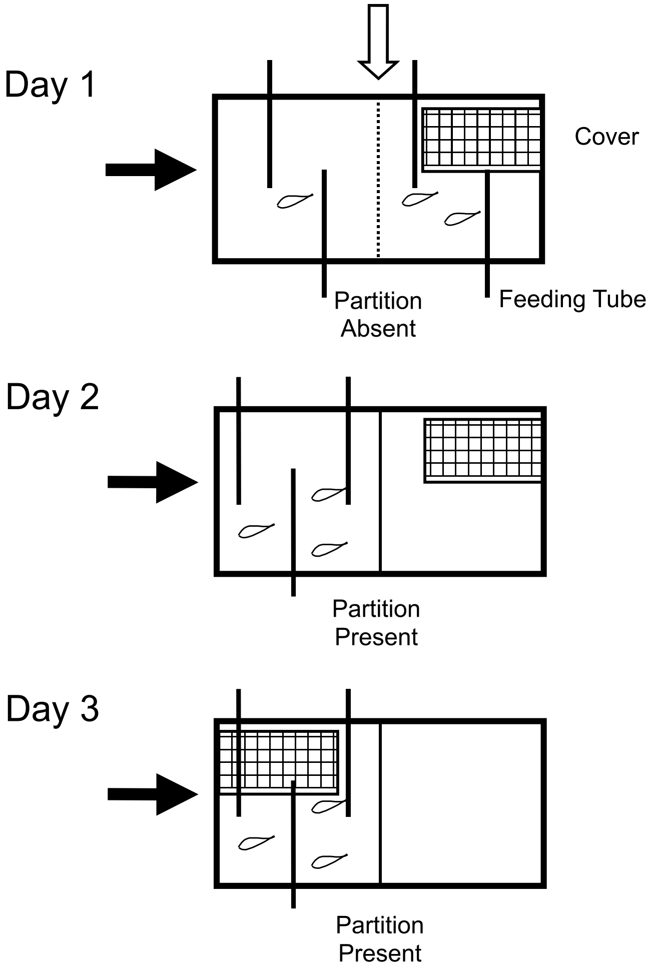
We tested whether increased predation risk alone could explain the observed high monopolization of resources in zebrafish groups foraging in open habitats. To do this, we used the same treatments as Basquill and Grant (1998) but added a habitat with overhead cover of plastic mesh. Zebrafish often respond to an alarm substance by staying close to the bottom of tanks (Rehnberg and Smith 1988), suggesting that these fish perceive the risk of mortality from aerial predators to be high. Providing overhead cover, therefore, should reduce the perceived risk of predation from surface feeding. The cover allowed sufficient light through that fish should have been equally able to detect food and competitors in the open and covered habitats, which therefore should have been equally defendable. Food was delivered in each patch (half of a 20-L aquarium) so that a subordinate fish could choose between feeding at sites frequently used by dominants and those less frequently used. If monopolization is influenced by habitat defendability alone, we predicted lower monopolization in vegetated habitats than in open habitats but no difference in these measures between covered and open habitats. If monopolization is also influenced by predation risk, we predicted lower monopolization in both protected habitats (i.e., vegetated or covered) relative to the open ones.

Methods

A total of 60 fish were purchased from an aquarium wholesaler and used in these experiments (6 fish per week for 10 weeks). Fish were kept in a 100-L tank with a water temperature of approximately 28°C, 12 h of light, and ad libidum food. All fish had been maintained in the tank for at least 6 weeks prior to the start of the experiment.

We used two 20-L glass tanks (60 × 30 cm) as experimental tanks. Each tank was filled with dechlorinated water to a depth of 30 cm 2 days before the beginning of each set of experimental trials. Water temperature was maintained at 28°C.

Fig. 1. Experimental tanks during the experiment. The order of presentation on days 2 and 3 was randomly determined. Tanks with a vegetated habitat were identical, except that a patch of simulated vegetation replaced the cover. The solid arrow represents the position of the observer during feeding trials. The open arrow in day 1 represents the position of the observer when determining the location of fish after feeding trials. On day 1, fish could forage on both sides of the tank. On days 2 and 3, fish were confined to the side of the tank nearest the observer.



The sides of the tanks were lined with black plastic to prevent fish in one tank from seeing those in the other. However, observers could view the fish through the fronts of the tanks (to the left in Fig. 1).

Tanks could be divided into two equal volumes (30 × 30 × 30 cm) using an opaque Plexiglas divider held in place by a clamp. For each tank, one of the resulting sides was “open”, without cover or vegetation, and the other was “protected” (Fig. 1). The protected side consisted of either a 25 × 15 cm cover of plastic square mesh (mesh size 1 cm) attached so that it hung 1 cm above the water surface (“covered” tank) or 12 strips (1 × 10 cm) of black plastic attached in three rows of four to a piece of translucent green Plexiglas, which was placed on the bottom of the tanks with the plastic strips floating up into the water column (“vegetated” tank). The entire array of black plastic in the complex treatment covered an area of 18 × 10 cm. Overhead cover and simulated vegetation were randomly assigned to experimental tanks each week.

Each week, six fish were haphazardly selected from the holding tank and divided into two groups of three. Group members were selected to differ in size and pattern, both to facilitate identification of individuals and to create competitive inequalities within the group. Cover or vegetation was randomly assigned to one side of each tank. One group was added to each experimental tank, with the partition removed, and allowed to acclimate for 30 min. Fish were then fed commercially available frozen brine shrimp (*Artemia* spp.) that had been thawed and individually placed in 5-mL syringes filled with distilled water. Shrimp were individually delivered into the tank through 29-cm, 5-mL pipette tubes attached to the sides of each tank and extending to just below the water surface in the middle of the tank. On the first day, four tubes were used (two on each of the open and protected sides of the tank; Fig. 1). Eighteen shrimp were delivered randomly among tubes approximately every 30 s, varied by a few seconds in either direction, so that fish were unlikely to be able to predict when a shrimp would appear. By the end of the first day, all fish had eaten at least one shrimp delivered via this method. After all shrimp had been delivered, the observer (I.M. Hamilton) watched from a location midway down the plastic-lined sides of the tank and recorded the location of each fish (open or protected side) at 15-s intervals for a total of 5 min.

On the second day, fish were coaxed to one side of the tank and the Plexiglas divider was inserted. Therefore, fish were confined to one side that was either open or protected (Fig. 1). This protocol was used for all subsequent observations, and the order that fish were confined to the open and protected sides was randomly determined. Three feeding tubes were installed so that two tubes delivered food at the surface, while the third delivered food approximately 5 cm below the surface. On the protected sides of tanks, the lower feeder was also in a safer position. In vegetated tank halves, the lower feeder on the protected side was closer to the vegetation than the surface feeders. In covered tank halves, the lower feeder on the protected side was directly under the cover, while the surface feeders were in the open. Preliminary observation suggested that dominant fish were likely to use the surface feeders (I.M. Hamilton, personal observation). This created a situation where lower ranked fish could feed with the dominant at the surface or use the lower, safer feeder.

Fish were allowed to adjust to their new situation for 10 min prior to testing, which appeared to be sufficient for them to resume their normal activities (i.e., levels of aggression appeared normal and fish were at the surface searching for food). Shrimp were then delivered through the feeding tubes, as described above. The identity of the fish that captured each shrimp and the tube from which it was delivered were recorded. Afterwards, fish were videotaped searching for food (although no food was being delivered) for 2 min. After testing, the cover or vegetation was switched to the opposite side of the tank and the partition removed.

The following day, fish were again confined to the front of the tank. Because the protected and open sides of each tank had been switched, fish were now confined in a habitat different from that of the day before (i.e., if they were tested first on the open side, they were tested on the protected side the next day; Fig. 1). The experimental procedure described in the previous paragraph was repeated. On the last day of the experiment, fish were removed from the tanks and the mass of each fish was measured using a Sartorius balance to determine size ranks. Fish had not fed for at least 3 h prior to weighing.

Statistical analyses

This experimental design assumes that dominant fish are likely to attempt to monopolize resources at the surface feeders and that fish perceive the protected sides of tanks as intrinsically less risky than the open sides. We tested the first of these assumptions by comparing the use of the surface feeders by the large, medium-sized, and small fish in each group. Large fish usually, but not always, initiated chases of other fish. We compared the probability that fish of each size rank captured food from the surface feeders against the null hypothesis that use of these feeders matched the proportion of food delivered through these feeders using repeated-measures ANOVAs for each size rank. The critical *P* values for these tests were adjusted to 0.0167 (0.05/3) because we performed three comparisons: one each for large, medium-sized, and small fish. We included the type of protected side (covered or vegetated) as a between-groups effect in the ANOVA. To test whether large fish were able to obtain more of the prey delivered through the surface feeders than other size classes, we also compared the proportion of prey captured by each size class and the mean of a fish's rank in terms of number of prey captured in each trial over the entire experiment using repeated-measures ANOVAs. The type of protected side was included as a between-groups effect and size rank as a within-groups effect.

All further comparisons were performed separately for covered and vegetated tanks. To test the assumption that fish perceived the protected sides of tanks as safer, we used paired *t* tests to compare the mean number of fish observed in the protected side on day 1, when fish had the opportunity to use both sides of the tank, with the expectation of equal use. The mean rates of delivery of food to the protected and open sides of the tanks were equal on the first day. Therefore, if fish were able to gauge the rate of food delivery, and were not concerned with safety, we expected that they would use both sides of the tank equally. Because we had an a priori expectation that fish would use the protected side more, we used one-tailed tests.

To measure inequality in resource use, we used two measures: (1) the coefficient of variation (CV = $s/\bar{x}$) in the number of prey captured by each fish at the surface feeders, where s is the standard deviation in prey captured by each fish within the group and $\bar{x}$ is the mean number of prey captured by each fish in the group, and (2) the proportion of food delivered at the surface feeders that was captured by the top-ranked fish. The top-ranked fish was defined as the fish that had the highest mean rank in terms of number of prey caught per day averaged over both days of the experiment. If two fish in a group were tied for the top rank, we selected the one that captured the greatest number of shrimp over the entire experiment. If a fish did not attempt to feed at all during the trials, it was not included in the calculation of the CV. CVs were compared between open and protected

Table 1. Comparisons of CVs in prey capture at surface feeders on open and protected sides of experimental tanks when fish were confined to one side (days 2 and 3).

	Open	Protected	T	N	P
Covered tanks	0.67 (0.79–0.56)	0.41 (0.66–0.13)	19.5	10	0.02
Vegetated tanks	0.38 (0.66–0.30)	0.42 (0.58–0.22)	8.5	10	0.22

Note: Median CVs and quartile ranges of these coefficients (in parentheses) for the 10 trials are presented along with results of one-tailed Wilcoxon's signed-ranks tests. All tests use a critical P value of 0.025 to adjust for the two comparisons within tanks (open versus covered and open versus vegetated).

Table 2. Comparisons of the proportions of food at the surface feeders and the lower feeder that were captured by the top-ranked fish (in terms of the number of prey captured) in open and protected sides of experimental tanks when fish were confined to one side (days 2 and 3).

	Open	Protected	Open – protected	t_9	P
Surface feeders					
Covered tanks	0.54 (0.69–0.39)	0.36 (0.48–0.23)	0.18 (0.34–0.03)	2.67	<0.025
Vegetated tanks	0.35 (0.46–0.23)	0.40 (0.49–0.31)	–0.05 (0.19 to –0.08)	–0.89	>0.5
Lower feeder					
Covered tanks	0.32 (0.58–0.06)	0.33 (0.51–0.16)	–0.01 (0.28 to –0.31)	–0.13	>0.5
Vegetated tanks	0.36 (0.59–0.13)	0.32 (0.50–0.14)	0.04 (0.35 to –0.27)	0.29	>0.5

Note: Means and 95% CIs (in parentheses) of the 10 trials are presented along with results of one-tailed paired t tests for surface feeders and two-tailed paired t tests for lower feeders. All tests use a critical P value of 0.025 to adjust for the two comparisons within tanks (open versus covered and open versus vegetated).

sides with separate Wilcoxon's signed-ranks tests. In this and all of the following comparisons between open and protected sides, each group contributed one data point, resulting in $N = 10$ for comparisons in each of the covered and vegetated tanks. In these comparisons, we used a critical P value for α adjusted to 0.025 (0.05/2) because we performed two tests (open versus covered and open versus vegetated). We used paired t tests to compare the proportion of food taken by the top-ranked fish in terms of prey capture. Paired t tests were used in this and all following comparisons because the differences in each measure were normally distributed. Because we tested the a priori prediction that resource monopolization at surface feeders would be greater in open habitats, we used one-tailed tests. We also compared the proportions of food captured by the top-ranked fish at the lower, safer feeder using two-tailed paired t tests.

We used the videotaped searching episodes to measure aggression. Every 15 s, we recorded whether any of the fish were acting aggressively towards the others. Aggression was defined as chases, displays with fins erect, or sudden movements directed towards another fish that fled. We combined all aggressive acts within the group for each trial and compared these between open and protected sides using paired t tests with the critical P value adjusted to 0.025.

Results

Large fish were more likely to use the two surface feeders during the experiments than expected based on the relative rates of prey delivery through the three tubes. This difference was significant using a Bonferroni-adjusted critical P value of 0.0167 (repeated-measures ANOVA, $F_{[1,18]} = 10.8$, $P < 0.005$). The degree to which large fish made more use of the surface feeders did not differ between covered and vegetated tanks (repeated-measures ANOVA, $F_{[1,18]} = 0.11$, $P > 0.7$). Medium-sized and small fish did not use the surface feeders significantly more often than expected (repeated-measures ANOVA, medium: $F_{[1,18]} = 2.6$, $P > 0.1$; small: $F_{[1,18]} = 0.5$, $P > 0.45$). These differences did not differ between covered and vegetated tanks (repeated-measures ANOVA, medium: $F_{[1,18]} = 1.5$, $P > 0.2$; small: $F_{[1,18]} = 1.3$, $P > 0.25$). At the two surface feeders, the largest fish captured significantly more prey than did smaller fish (repeated-measures ANOVA: $F_{[2,17]} = 10.1$, $P < 0.01$; contrasting only large and medium: $F_{[1,18]} = 6.8$, $P < 0.025$; contrasting only large and small: $F_{[1,18]} = 12.7$, $P < 0.005$). This effect did not differ significantly between covered and vegetated tanks ($F_{[2,17]} = 0.5$, $P > 0.6$). The mean rank of fish was significantly influenced by size class, with large fish ranked significantly higher (and therefore capturing more food) than small fish ($F_{[2,17]} = 5.24$, $P < 0.025$; contrasting only large and medium-sized: $F_{[1,18]} = 2.83$, $P > 0.1$; contrasting only large and small: $F_{[1,18]} = 10.85$, $P < 0.005$).

Covered versus open sides

On the first day of the experiment, when fish were able to choose to forage in either the open or covered side of tanks, fish used the covered side significantly more often than expected by chance (observed $\bar{x}$ ± 95% confidence interval (CI) for the 10 trials: 12.0 ± 2.3 observations; expected: 10 observations; one-tailed paired t test: $t_9 = 2.0$, $P < 0.05$). On subsequent days, the extent to which the three fish differed in success at capturing food delivered from the surface feeders (CV) and the proportion of food captured there by the top-ranked fish were significantly higher for fish confined to the open side than for fish confined to the covered side (Tables 1 and 2). There was no difference between open and covered sides in the proportion of food taken by the top-ranked fish at the lower feeder (Table 2). The number of aggressive interactions did not differ significantly between open and covered sides (Table 3).

Table 3. Comparisons of the combined number of aggressive acts performed by all three individuals in the group during the observation period in open and protected sides of experimental tanks when fish were confined to one side (days 2 and 3).

	Open	Protected	Open – protected	t_9	P
Covered tanks	6.8 (8.6–5.0)	6.5 (8.3–4.7)	0.3 (3.3 to –2.7)	0.23	0.41
Vegetated tanks	6.2 (8.1–4.3)	6.3 (8.0–4.6)	–0.1 (2.2 to –2.4)	–0.10	>0.5

Note: Means and 95% CIs (in parentheses) for the 10 trials are presented along with results of paired *t* tests. All tests use a critical *P* value of 0.025 to adjust for the two comparisons within tanks (open versus covered and open versus vegetated).

Vegetated versus open sides

Fish did not use the vegetated side of tanks significantly more often than the open side (observed $\bar{x}$ ± 95% CI for the 10 trials: 10.7 ± 1.6 observations; expected: 10 observations; one-tailed paired *t* test: $t_9 = 0.9$, $P > 0.15$) on the first day of the experiment. On subsequent days, we did not find a significant difference between sides in CV of prey captured from surface feeders or the proportion of food captured there by the top-ranked fish (Tables 1 and 2). There was also no difference between sides in the proportion of food taken by the top-ranked fish at the lower feeder (Table 2). Aggressive acts were also not significantly more frequent in the open side of these tanks (Table 3).

Discussion

Our results supported the prediction that monopolization of food within groups of zebrafish would increase in habitats where perceived predation risk was higher, but only when the safer habitat was covered. We found that resource monopolization decreased in a protected habitat, even when there were no visual barriers to prevent the detection of resources and competitors. Furthermore, foraging fish used the covered side of tanks more often than expected by rates of prey input to the covered side. This suggests that the covered side was perceived as intrinsically safer (cf. Abrahams and Dill 1989; Grand and Dill 1997).

For tanks with a vegetated side, fish did not significantly use that side more often than the open (unprotected) side when given the opportunity to use both. This suggests that fish did not perceive the vegetated side as safer. Neither monopolization nor aggression differed significantly between sides of these tanks. These are contrary to the findings of Basquill and Grant (1998). The differences in results between our study and theirs may reflect differences in the structure of the complex habitat. The simulated vegetation used in our experiment was shorter than theirs, so the effects of both safety and resource defendability may have been more important in their experiment.

Increased perceived predation risk may have resulted in increased monopolization because subordinates were less willing to challenge for resources in the open (risky) patch, because dominants were more willing to accept higher predation risk and remain close to productive but risky feeders, or because subordinates were more willing to remain in groups when risk of predation was high. We did not find a difference in aggression between habitats, suggesting that subordinates were equally willing to challenge dominants and dominants were equally willing to defend in protected and risky habitats.

We found that large fish, which were generally high ranked in terms of the proportion of prey captured, used surface feeders more often than expected based on the relative rates of food delivery to these and lower feeders, while medium-sized and small fish did not. This suggests that dominant fish were more willing to forage at these productive sites, despite the higher risk. These fish may have been less vulnerable to predators than smaller fish, which generally captured fewer prey at the surface feeders; large fish are faster swimmers and may therefore be better able to avoid aerial predators (Godin 1997). Although smaller fish may have avoided the risky, productive patch, we did not find that competitive types were segregated, as all fish continued to capture food at the safer, less productive lower feeder (Table 2).

Finally, subordinates may have been more willing to remain in groups in risky habitats, despite monopolization by dominants, if grouping reduced predation risk through dilution. Zebrafish in larger shoals tend to forage in more open habitats than those in smaller shoals, and shoaling zebrafish increase polarization, cohesion, and synchronization of swimming when exposed to an alarm substance (Rehnberg and Smith 1988). These behaviours suggest that shoaling does influence perceived predation risk in zebrafish. If the antipredator benefits of shoaling were more important in risky habitats in this experiment, subordinates may have accepted a smaller share of resources to remain in the group in these habitats. This would have allowed greater monopolization by dominants, as is predicted by transactional skew models (Hamilton 2000). To determine if monopolization by dominant zebrafish is influenced by the amount of resources subordinates require to remain in the group, it is necessary to establish whether the threat of subordinate departure influences resource monopolization. This could be experimentally tested by providing subordinate fish with the opportunity of foraging in a safe site far away from the site preferred by dominant fish and varying the productivity of that secondary patch. Transactional models predict that the degree of monopolization (skew) at the patch used by dominants should increase as the expected success of subordinates that leave the group decreases (Keller and Reeve 1994; Hamilton 2000). Therefore, monopolization should be greater as the value of the secondary patch decreases.

Our results also suggest that experimental observations that resource monopolization changes with habitat complexity (e.g., Eason and Stamps 1992; Basquill and Grant 1998) must be interpreted with caution because complex and open habitats may differ in safety. The effects of this difference in safety may differ among systems. In our experiment, resource monopolization decreased with increasing safety, while in others, increased safety can increase competitive inequalities among foragers. In several other studies, subordinates were found to be more likely to accept high risk to gain access to resources (e.g., coho salmon, Reinhardt 1999; willow tits (*Parus montanus*), Koivula et al. 1994). In those experiments, the amount of food available was equal in risky and safe patches, and dominants chose safer patches in which to forage. In our experiment, the risky positions (the surface feeders) were also more productive because two-thirds of the shrimp were delivered at the surface, and large individuals that tended to be dominant in terms of prey capture tended to use the risky but productive patch. Our results demonstrate that when patches differ in both productivity and riskiness, increased risk of predation may increase competitive inequalities among group-foraging animals. This finding emphasizes the need to decouple risk and defendability in interpreting the results of experiments investigating the effects of habitat complexity on resource defence.

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