Testing the effects of resource distribution and inherent habitat riskiness on simultaneous habitat selection by predators and prey

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Theoretical models have extended the Ideal Free Distribution model to examine predator–prey systems having three trophic levels, when both predator and prey are allowed to move freely. One consistent prediction made by such models is that the spatial distribution of prey should be mainly determined by the inherent habitat riskiness (e.g. cover level), with prey avoiding the inherently riskier habitats regardless (or nearly so) of resource distribution. To test this prediction, we conducted laboratory experiments in which both predators (creek chub, Semotilus atromaculatus) and prey (northern redbelly dace, Phoxinus eos) were free to move between feeding patches differing in resource quantity and habitat riskiness. When alone, creek chub and northern redbelly dace both preferred the more food-rich patch. The spatial distribution of dace was also inversely related to that of creek chub in the presence of chub fenced into feeding patches. When the patches differed in both riskiness and resource quantity, the spatial distribution of dace was mainly influenced by resource distribution and, to a lesser extent, by the inherent habitat riskiness in the absence of predators. In the presence of creek chub, the dace significantly decreased their use of the inherently riskier patch compared to when predators were absent. However, contrary to the models' prediction, food distribution still significantly influenced dace distribution when predators were present. Finally, dace aggregated increasingly in a third, totally safe area (but one offering no food) as the number of chub present in both patches increased. Thus, the influence of resource distribution and inherent habitat riskiness on prey distribution seems to vary with the level of predation risk.

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Understanding the responses of predators and prey to each other is a central topic in behavioural ecology, with a key issue being their use of habitats (Sih 2005). Many studies have explored habitat use by prey and predators, and there is ample evidence that prey prefer the low-predator habitats and that predators prefer the prey-rich habitats (Lima & Dill 1990; Lima 1998; Sih 2005). However, these studies mostly focused on the behaviour of prey or predators when the distribution of the other species was fixed in space (e.g. using caged predators, chemical cues, or immobile prey). Lima (2002) highlighted the scarcity of both theoretical and empirical knowledge of predator and prey space use when both are allowed to move freely. Intuitively, it could be expected that

predators favour prey-rich habitats, which should cause a shift in prey habitat use, after which predators follow the prey, and so on. However, the consequences of this behavioural race on predator–prey spatial distribution are not obvious; that is, whether an equilibrium distribution would result, and what it would be.

Game theory (Maynard Smith 1982) has provided a conceptual framework for theoretical studies investigating this issue (e.g. Iwasa 1982; Van Baalen & Sabelis 1993; Hugie & Dill 1994; Alonzo 2002; Abrams 2007). Typically, these theoretical studies have extended the Ideal Free Distribution (IFD; Fretwell & Lucas 1970; Kacelnik et al. 1992) model to examine three-level trophic systems, in which a predator species feeds on a prey species, which feeds on a resource fixed in space. Predator and prey can move freely among habitats that differ in their resource quantity and/or in their inherent habitat riskiness (a habitat feature that is independent of predator density, such as cover, structural complexity or light level; Hugie & Dill 1994). On one hand, predators use habitats in a manner that maximizes their foraging success, which is a function of prey density, competition level and inherent habitat riskiness. On the other hand, prey use habitats to balance their risk of predation and the benefits of foraging (which is a function of resource quantity

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and competition level). These theoretical studies showed that spatial distributions of predators and prey can reach an evolutionary stable strategy (ESS), where no individual can improve its fitness by shifting habitat (e.g. Iwasa 1982; Van Baalen & Sabelis 1993; Hugie & Dill 1994; Alonzo 2002; but see Abrams 2007). Although the models differ in their details, one consistent prediction is that habitat use by prey should not be affected by resource distribution, or be only slightly affected, depending on the level of competition among prey and among predators (e.g. Hugie & Dill 1994; Sih 1998; Bouskila 2001; Alonzo 2002; Krivan & Schmitz 2003; Luttbeg & Sih 2004). If habitats differ in both their resource quantity and inherent habitat riskiness, the spatial distribution of prey should be mainly determined by riskiness, with prey avoiding the inherently risky habitat, regardless (or nearly so) of resource distribution (Hugie & Dill 1994; Sih 1998; Luttbeg & Sih 2004). This prediction is quite different from results of theoretical and empirical studies that consider a fixed difference in predation risk between habitats. Indeed, these studies have shown that prey respond to both resource distribution and predation risk when choosing a feeding habitat (Gilliam & Fraser 1987; Abrahams & Dill 1989; Lima & Dill 1990; Grand & Dill 1997).

A few studies have focused on habitat selection by predators and prey when both can move freely (Sih 1984, 2005; Formanowicz & Bobka 1989; Bouskila 2001; Hammond et al. 2007; Luttbeg et al. 2009). These studies determined the effect of either resource distribution (Bouskila 2001; Sih 2005; Hammond et al. 2007; Luttbeg et al. 2009) or inherent habitat riskiness (Sih 1984; Formanowicz & Bobka 1989; Bouskila 2001) on habitat selection by both prey and predators, but not of both factors simultaneously. The objective of our study was thus to test the prediction that the spatial distribution of prey should be mainly determined by riskiness, with prey avoiding the inherently riskier habitat, regardless (or nearly so) of resource distribution. To test this prediction, we conducted laboratory experiments in which both predators and prey were free to move between habitats differing in both inherent riskiness and resource quantity.

METHODS

The experiments were performed in a tank separated into two parts, each of which was 55 cm wide, 25 cm deep and 465 cm long (Fig. 1a), that we used as independent experimental units to perform two trials simultaneously. Water temperature was maintained at $14 \pm 0.2\,^{\circ}C$ and light intensity was kept low during trials (2.8 lx). Magnan & FitzGerald (1984) showed that adult creek chub are mainly active at night and feed as efficiently under low (0.17 lx) as under high light intensity (22 lx). A black curtain was placed around the tank to reduce the effects of external factors on fish behaviour. An automatic feeder was placed at each end of the experimental tanks to deliver different quantities of trout pellets (Fig. 1a). We considered the area around each feeder (55 × 45 cm) as an alternative feeding patch. Trout pellets not eaten by fish were collected in a plastic container on the bottom of the tank (Fig. 1b). A grid covered the container so that the fish did not have access to this uneaten food. Fish were filmed in each feeding patch from the top of the tank with four video cameras (Sony CCD-TR400; Fig. 1b) connected to a recording system.

The prey, northern redbelly dace, *Phoxinus eos*, and the predators, adult creek chub, *Semotilus atromaculatus*, used in the experiments were collected with baited minnow traps and fyke nets in Lac de la Grosse of the Mastigouche Reserve (Québec, Canada; 46°40′ N, 73°20′ W; collection permit number 2006-05-24-026-04-S-P) in June 2006. This lake also contained brook trout, *Salvelinus fontinalis*, and white suckers, *Catostomus commersonii*, and dace were subject to both trout and creek chub predation (A. Dupuch, unpublished data). Approximately 1000 northern redbelly dace (mean total length $\pm$ SD = 6.4 $\pm$ 0.5 cm) and 132 creek chub (17 $\pm$ 0.8 cm) were used in the experiments. Dace and chub were
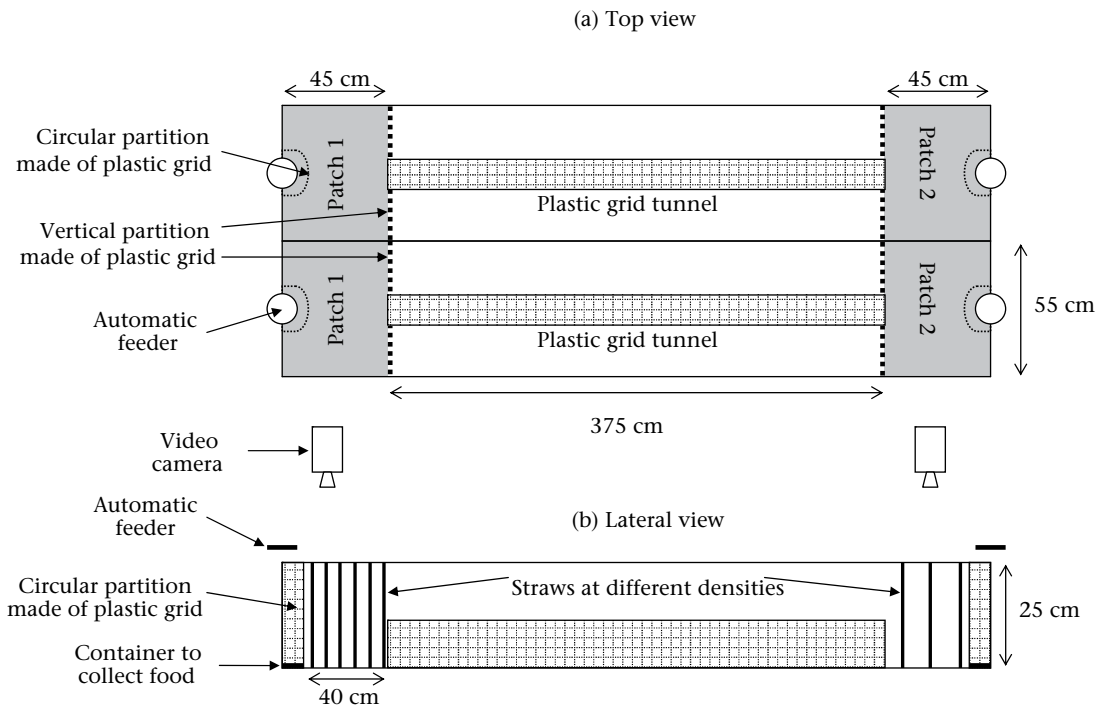

Figure 1. (a) Diagram of the two experimental tanks. The tunnel between the two feeding patches, the vertical partitions and the circular partitions around the feeders (all made of plastic grid) allowed northern redbelly dace, but not creek chub, to pass. The vertical partitions were present only in experiment 3. The tunnel was present in all the experiments. The circular partitions around the feeders were present only in experiments 3, 5 and 6. (b) Lateral view of one experimental tank with different straw densities, which created variable habitat riskiness in the two feeding patches. Containers used to collect trout pellets that were not eaten by fish were present in all the experiments.

held in two and four holding tanks, respectively, at $14 \pm 0.2\,°C$ under a 12 h:12 h light:dark regime. Fish were fed ad libitum once a day with commercial trout pellets (Corey Aquafeeds, Fredericton, New Brunswick, Canada, 0.5 GR and 1.0 GR mixed for dace; Corey Aquafeeds, 1.5 GR for creek chub). Fish were euthanized with an overdose of tricaine methanesulfonate (MS 222) at the end of the experiments.

We conducted six laboratory experiments. In experiments 1 and 2, we tested whether dace and creek chub, respectively, would distribute themselves between two patches according to the resource quantity of each patch (i.e. input matching, as predicted by the IFD model). We also tested whether dace would adapt their spatial distribution to that of the creek chub predators' (experiment 3), or to the inherent riskiness of the habitat in the absence of predators (experiment 4), and whether inherent habitat riskiness affects the match between dace distribution and resource distribution in the absence (experiment 5) or presence (experiment 6) of predators. Experiment 5 was used as a control for experiment 6. We compared the results of experiments 5 and 6 to test the prediction that, in the presence of predators, prey should avoid the inherently riskier patch regardless (or nearly so) of resource distribution.

For all trials, we randomly assigned groups of 50 dace (experiments 1, 3, 4, 5 and 6) or 20 creek chub (experiment 2) to each of the two experimental tanks and introduced them into their centre sections between 0730 and 0930 hours. Immediately after fish were introduced to the experimental tank, automatic feeders began delivering trout pellets in each patch for 7 h. In each experiment, five replicates (six for experiment 1) were performed for each treatment level (i.e. for each food ratio, creek chub ratio, inherent habitat riskiness ratio, or combination of food × inherent habitat riskiness ratio). Fish were returned to their holding tanks at the end of each experiment, but because we alternated the holding tank from which we sampled experimental fish, dace could not be subjected to more than one trial/2 days and creek chub could not be subjected to more than one trial/4 days. The treatment level as well as the food-poor patch and the safer patch in each channel were randomly designated before each trial.

During pilot experiments, we observed that antipredator behaviours were elicited in dace only if contact was possible between dace and creek chub (e.g. in contrast to when they were separated by transparent Plexiglas). When we placed both dace ($N = 50$) and creek chub ($N = 7$) together in the experimental tank, we observed that, on average, about seven or eight predation events occurred per trial. As that number of predations was too high, we added a plastic grid tunnel ($12 \times 12 \times 375$ cm long) between the two feeding patches on the bottom of each experimental tank (Fig. 1), allowing dace but not creek chub to pass through. Thus, dace could use this tunnel to swim from one patch to the other without being attacked by creek chub, reducing the number of predation events during trials (to about 2–3 per trial on average). A distance of 40 cm separated the end of the tunnel from each food source (Fig. 1). Thus, creek chub mainly attacked dace when they left the tunnel to reach the food. In these experiments, dace and chub needed only a few seconds (<15 s) to move from one feeding patch to the other, and movements between patches occurred at least once every 2 min (A. Dupuch, personal observation).

Attacks on dace and predation events occurred during experiments 3 and 6. The alarm substance released from dace during these predation events (Dupuch et al. 2004) could thus have biased their behaviour during trials of these experiments, and potentially during trials of experiments 4 and 5, because of the persistence of alarm substance in the experimental system. Ideally, we should have removed the water from the tank (4000 litres) and cleaned it after every trial in which a predation event occurred. However, this

was not possible because of the limited capacity of our water treatment system. To reduce this bias, we changed 75% of the water volume in the tank (about 3000 litres) after performing the trials of experiment 3, and we waited 2 days before performing experiment 4, which did not involve predation. Furthermore, we alternated experiments 5 and 6 in groups of 10–20 trials. When a group of trials without predators followed one with predators, we changed half of the water volume in the tank (2000 litres) and waited 1 day before performing the next pair of trials. Dupuch et al. (2004) found that dace behaviour is not affected by low concentrations of alarm substance in the water. Given the large volume of water in our experimental tank and the water changes that we made, the concentration of alarm substance in these experiments was probably too low to have significantly affected dace behaviour.

Experiments 1 and 2: IFD in Dace and Creek Chub

Differences in habitat profitability were produced by delivering different quantities of trout pellets in the two feeding patches of each experimental tank. A total of 1.4 g of pellets for dace (pellet size 0.5–1.0 mm) and 2.8 g for creek chub (pellet size 1.5 mm) was split between the two patches in the following ratios (patch 1: patch 2): 1:6, 1:3, 1:1, 3:1, 6:1, and continuously input by the automatic feeders over a period of 7 h. On average, 4.8 and 1.6 pellets/min were delivered by both feeders for dace and chub, respectively. The results of pilot experiments (using the two food ratios, 1:3 and 3:1) showed that (1) 3 h after the beginning of the trials, dace distributed themselves as expected from IFD and (2) IFD was usually maintained until the seventh hour of trials. However, in some pilot experiments, IFD was not maintained during the seventh hour, probably because of satiation. Based on this result, we assumed that dace were probably not satiated with these quantities of food and remained sensitive to pellet distribution until the sixth hour of trials. IFD was tested for creek chub (i.e. the predator) because it is an assumption of theoretical models. Dace rather than trout pellets should have been the food source for chub. However, this experiment was not feasible because it would have been necessary to fence dace in cages to create patches of different profitabilities and then chub would not have had access to their prey (see also Sih 2005). The establishment of IFD during the course of trials was not estimated for creek chub because we were not interested in the behaviour of chub vis-à-vis the trout pellets. The behaviour of chub towards dace during trials was addressed in another experiment (see Estimation of Fish Distribution below).

Experiment 3: Effect of Creek Chub Distribution on Dace Distribution

In each feeding patch, the automatic feeders delivered 0.7 g of pellets over a period of 7 h. Creek chub were maintained in each patch by a vertical plastic grid partition that allowed dace but not creek chub to pass through (Fig. 1a). We also placed a circular plastic grid partition around the feeders to allow dace, but not creek chub, to feed on pellets (Fig. 1a). Thus, creek chub were not competing directly with dace. This partition did not greatly reduce the area around the feeders and did not appear to change the behaviour of creek chub or their interactions with dace. A total of seven creek chub were distributed between the two feeding patches in the following ratios (patch 1: patch 2): 1:6, 2:5, 3:4, 4:3, 5:2 and 6:1.

Experiment 4: Effect of Inherent Habitat Riskiness on Dace Distribution in the Absence of Predators

In each feeding patch, the automatic feeders delivered 0.7 g of pellets over a period of 7 h. We simulated variation in inherent

habitat riskiness by varying the densities of straws (to imitate plant stems in lakes) at both ends of the experimental tank (straw densities used were $111/m^2$, $222/m^2$ and $333/m^2$, which are comparable to stem densities in vegetated areas of lakes in the study system). Different combination of straws/m^2 (333:111, 222:111, 222:222, 111:222, 111:333) were used to create the following inherent habitat riskiness ratios (patch 1: patch 2): 1:3, 1:2, 1:1, 2:1 and 3:1. Given that dace show a significant preference for habitats with dense cover over habitats with sparse cover in the littoral zone of lakes containing piscivorous fish (Naud & Magnan 1988), we assumed that (1) patches with more straws would be perceived by dace as being less risky than patches with fewer straws and (2) a patch with more straws would be much safer for dace since the difference in straw density between patches was high. No straws were present just below the feeders to avoid influencing the ability of dace to assess food availability and to access pellets.

Experiments 5 and 6: Effects of Habitat Riskiness and Resource Distribution on Dace Distribution in the Absence and Presence of Predators, Respectively

In these experiments, we used the same habitat riskiness ratios as in experiment 4 and food ratios of 1:3 and 3:1. These food ratios were used because the results of experiment 1 showed that the spatial distribution of dace at these two food ratios (1) did not differ from the predictions of the IFD model (the 95% confidence interval, CI, included the expected value from IFD; 1:3: CI = 0.17–0.32; 3:1: CI = 0.47–0.76) and (2) were significantly different from each other (Mann–Whitney U test: $U = 0.0$, $N_1 = N_2 = 6$ trials, $P = 0.004$). Again, we placed a circular plastic grid partition around the feeders to allow dace, but not creek chub, to feed on the pellets (Fig. 1a). The combination of different food and inherent habitat riskiness ratios resulted in 10 different treatments. For the experiment with predators (i.e. experiment 6), seven creek chub were introduced in the central section of the experimental tank at the beginning of the fourth hour of a trial and were free to move from one feeding patch to the other. We introduced creek chub at the beginning of the fourth hour because the results of pilot experiments showed that (1) 3 h after the beginning of the trials, dace distributed themselves as expected from IFD and (2) IFD was maintained until the seventh hour of trials. We therefore assumed that dace needed only 3 h to learn how to use the feeders and to navigate in the experimental tank, and that they had enough time to acquire knowledge about pellet and straw distributions before the introduction of chub. We mimicked creek chub introduction by dumping only water into the central section of the experimental tank at the beginning of the fourth hour of trials in the experiment without predators (i.e. experiment 5). This ensured that results from the experiment with predators were due to the presence of creek chub and not to the disturbance created during creek chub introduction. We counted the number of dace at the end of each trial with predators to determine the number of predation events that occurred.

Estimation of Fish Distribution

Given that chub were not totally naïve to the experimental set-up (we always used the same 132 individuals for the experiments), we assumed that a 1-hour acclimation to the experimental set-up would be sufficient. The fact that attacks on dace and predation events began as early as the first hour after the introduction of creek chub to the experimental tank (experiment 6) supports this point. In several trials, creek chub activity and attacks on dace strongly decreased during the third hour after their introduction (counting the 3 h of dace acclimation before the introduction of

chub, the attacks on dace strongly decreased during the sixth hour after the beginning of an experiment). Based on these observations, the fifth hour of a trial was considered as the most appropriate period to determine the effects of resource distribution and inherent habitat riskiness on the spatial distribution of dace in the presence of predators. To compare results among experiments (1, 3, 4, 5 and 6), we measured the spatial distribution of dace during the fifth hour of trials in all experiments. Furthermore, fish were deprived of food for 24 h before each trial. Given that pellets were delivered as soon as dace were introduced into the experimental tank, we consider that 5 h was sufficient for individuals to meet their short-term energetic demands resulting from food deprivation, ensuring that they would pay attention to food distribution without ignoring predation risk.

To describe the spatial distribution of dace in these experiments, we used the mean proportion of individuals observed in patch 1 (Fig. 1). For each trial, we first counted the number of individuals in each feeding patch every 2 min for dace and every minute for creek chub during the fifth hour of trials. We then used the average number of individuals observed in each patch i (i.e. N_i) during these 60 min to estimate the mean proportion of individuals observed in patch 1 (i.e. $N_1/(N_1 + N_2)$).

For each trial of experiment 6, we also counted the number of dace in each patch every 2 min for 30 min from 2.5 to 3 h after the beginning of the trial (i.e. just before the introduction of creek chub) to estimate the mean proportion of individuals observed in patch 1. It was essential that dace responded to resource distribution before the introduction of creek chub in experiment 6. To meet this condition, we compared the mean proportion of dace in patch 1 before the introduction of creek chub (experiment 6) to the mean proportion observed during experiment 5 for the same combination of food proportion × inherent habitat riskiness. Trials for which the proportion of dace in patch 1 before the introduction of creek chub (experiment 6) was significantly different (i.e. not within the 95% CI) from that seen in experiment 5 were not considered; that is, 1 of 50 trials (experiment 6), which was replaced by a successful trial. This ensured that the spatial distribution of dace in experiment 6 was not different from that in experiment 5 before the introduction of creek chub, so any difference in the spatial distribution of dace between experiments 5 and 6 was due to the presence of predators.

A safe area was present under each automatic feeder because of the partition placed around the feeder to prevent chub from feeding on pellets (Fig. 1). We included dace observed in this safe zone with the number of dace observed in each feeding patch because, to reach this safe area, dace had to go through the dangerous part of the patch having different densities of chub and straws. The decision by dace to reach the safe area probably depended on habitat riskiness and the risk of being preyed upon by chub in each patch, so dace abundance in the safe area probably reflected the effect of both factors on their habitat choice.

We did not consider trials in any experiment in which dace showed abnormal behaviour (i.e. where the entire group of dace stayed motionless in one of the patches). We also did not consider trials in which the group of creek chub were either motionless and/or did not attack dace (1 of 50 trials; experiment 6). All the trials that were thus eliminated were redone to maintain the same sample size.

Statistical Analyses

For each experiment, we used a general linear model (GLM) to determine whether the different treatment levels (independent variables) were significantly related to the proportion of dace or creek chub in patch 1 during the fifth hour of the trial (dependent

variable). The independent variables were the proportion of food delivered in patch 1 (experiments 1, 2, 5 and 6), the proportion of predators in patch 1 (experiment 3), the inherent habitat risk ratio (experiment 4, 5 and 6), and the inherent habitat risk ratio in interaction with the proportion of food delivered in patch 1 without predators (experiment 5) and with predators (experiment 6). The interactions (food proportion × predator) and (habitat riskiness × predator) were also tested (experiments 5 versus 6; predators absent versus present, respectively) to examine model predictions. If, in the presence of predators, prey avoid the inherently riskier habitat regardless (or nearly so) of resource distribution, we expected that the effect of inherent habitat riskiness on dace distribution would increase and that of food proportion would decrease in the presence of creek chub (i.e. both the interactions (habitat riskiness × predator) and (food proportion × predator) would be significant).

We also tested whether the slope of the relationship between resource distribution and fish distribution was significantly different from 1.0 in experiments 1 and 2 to test whether the proportion of dace and creek chub in patch 1 conformed to IFD. Similarly, we tested whether the mean proportion of dace in patch 1 for each combination of food × inherent habitat riskiness ratio differed from the IFD expectation in experiment 5. Here, we considered that the proportion of dace in patch 1 was significantly different from IFD when the expected proportions (25% or 75%) were not included in the 95% CI of the observed distribution.

Ethical Note

In experimental studies of predation, special consideration should be given to reducing the pain and suffering that must inevitably be experienced by study animals (Huntingford 1984).

Testing model predictions in the present study required that predator and prey physically encounter one another. To reduce the number of predation events during experiments, we added a plastic grid tunnel between the two feeding patches on the bottom of each experimental tank (Fig. 1), allowing dace, but not creek chub, to pass through. Thus, dace could use this tunnel to swim from one patch to the other without being attacked by creek chub. Furthermore, the numbers of dace and chub used were kept to the minimum, given the sample size needed for a rigorous statistical test of the hypothesis.

This research received prior approval from the Animal Care Committee of Université du Québec à Trois-Rivières and, thus, adheres to the guidelines for the care and use of experimental animals of the Canadian Council on Animal Care and to legal requirements in Canada (protocol approval number no. 2006-05-24-026-04-S-P).

RESULTS

The spatial distributions of both northern redbelly dace and creek chub responded to the resource quantities in the alternate patches (experiments 1 and 2; Fig. 2). However, these relationships did not conform to the predicted IFD because their slopes were significantly lower than 1.0 (dace: $F_{1,28} = 23.31$, $P < 0.001$; creek chub: $F_{1,23} = 27.77$, $P < 0.001$). This deviation from IFD results from an underuse of patch 1 by dace when it was the richer patch and an overuse of patch 1 by creek chub when it was the poorer patch. The proportion of dace was also inversely related to that of creek chub in patch 1 (experiment 3; Fig. 3) and to the inherent habitat riskiness in patch 1 in the absence of predators (experiment 4; Fig. 4).

In the absence of predators, when patches differed in both riskiness and resource quantity (experiment 5), the spatial distribution of dace was mainly influenced by resource distribution
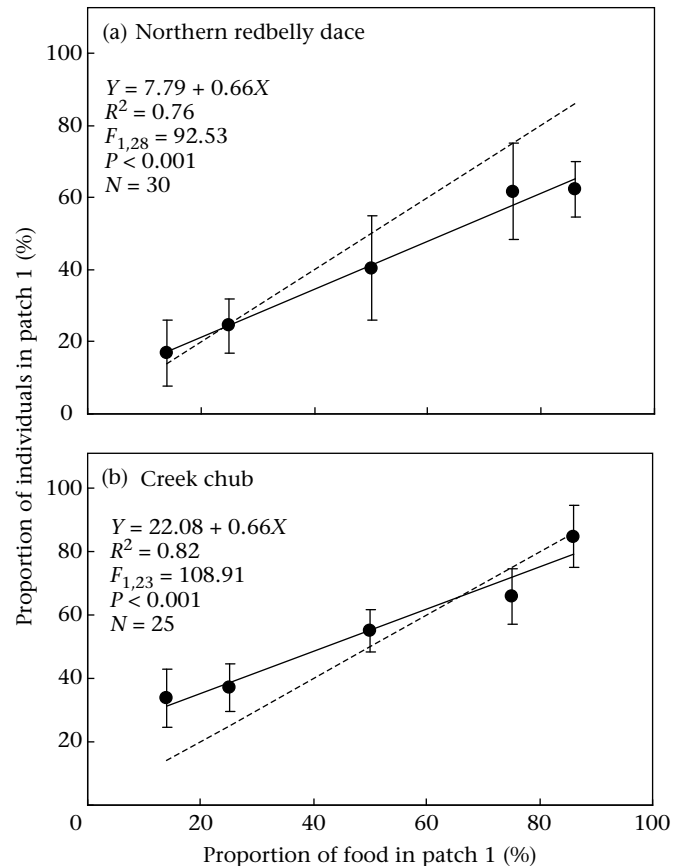
Figure 2. Variations in the proportion of (a) dace and (b) creek chub in patch 1 according to the proportion of food delivered in patch 1 (experiments 1 and 2, respectively). On the X axis, 14%, 25%, 50%, 75% and 86% correspond to the following food ratios (patch 1: patch 2): 1:6, 1:3, 1:1, 3:1 and 6:1, respectively. Dashed lines represent the expected perfect match between resource distribution and the spatial distribution of fish under an Ideal Free Distribution model. Values are means ± SE.

($R^2_{\text{partial}} = 0.59$; Table 1, Fig. 5) and, to a lesser extent, by the inherent habitat riskiness ($R^2_{\text{partial}} = 0.08$; Table 1, Fig. 5). Furthermore, the fact that feeding patches differed in their inherent riskiness decreased the expected match between resource quantity and the spatial distribution of dace. Indeed, dace distribution approached IFD only when the richer patch was substantially safer
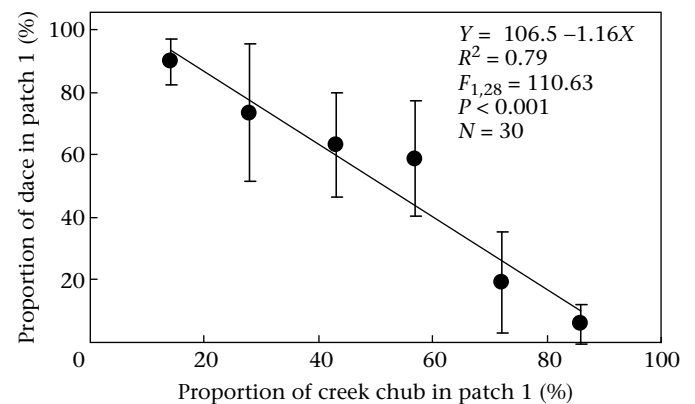
Figure 3. Variations in the proportion of dace in patch 1 according to the proportion of creek chub in patch 1 (experiment 3). On the X axis, 14%, 28%, 43%, 57%, 71% and 85% correspond to the following creek chub ratios (patch 1: patch 2): 1:6, 2:5, 3:4, 4:3, 5:2 and 6:1, respectively. Values are means ± SE.
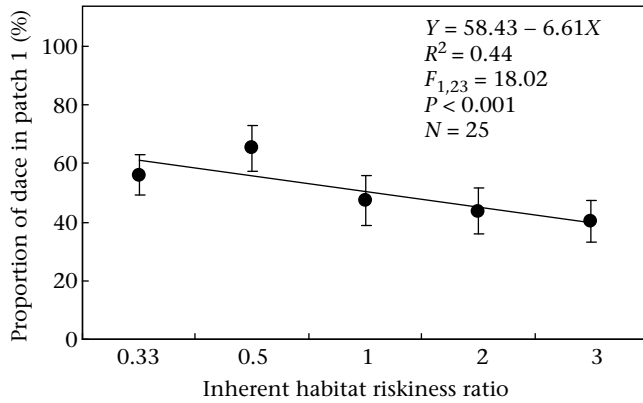
Figure 4. Variations in the proportion of dace in patch 1 according to the inherent habitat riskiness ratio (experiment 4). On the *X* axis, 0.33, 0.5, 1, 2 and 3 correspond to the following inherent habitat riskiness ratios (patch 1: patch 2): 1:3, 1:2, 1:1, 2:1 and 3:1, respectively. Values are means ± SE.
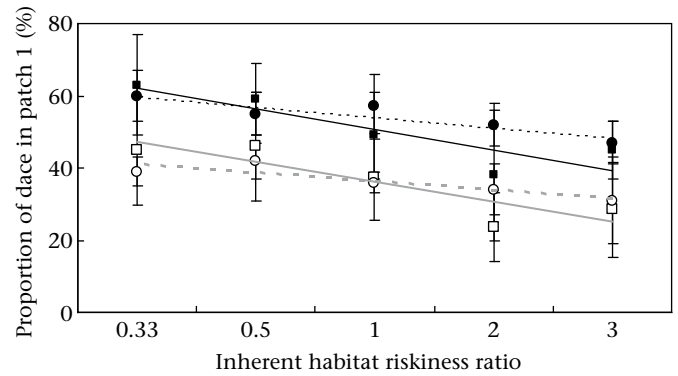

Figure 5. Proportion of dace in patch 1 as a function of the inherent habitat riskiness ratio and proportion of food in patch 1 (open symbols, grey lines = 25%, solid symbols, black lines = 75%) before (circles, dashed lines) and after (squares, solid lines) introduction of the creek chub (groups of seven individuals per trial). On the *X* axis, 0.33, 0.5, 1, 2 and 3 correspond to the following inherent habitat riskiness ratios (patch 1: patch 2): 1:3, 1:2, 1:1, 2:1 and 3:1, respectively. Values are means ± SE (based on five trials; *N* = 50). See text and Tables 1 and 3 for statistics.

than the poorer patch (Table 2). The large confidence intervals around the mean proportion of dace in patch 1 (Table 2) also indicate that there was great variability in the spatial distribution of dace for a given combination of food proportion and inherent habitat riskiness, which could have reduced the statistical power of our test for detecting significant deviation from matching.

In the presence of predators (experiment 6), the proportion of dace significantly decreased in the inherently riskier patch compared to trials when predators were absent (habitat riskiness × predator was significant; Table 3, Fig. 5). However, contrary to expectations, the presence of predators did not change the effect of food distribution on dace distribution. The proportion of dace was always higher in the richer patch relative to the poorer one, even in the presence of predators (food proportion × predator was not significant; Table 3, Fig. 5). Resource distribution and the inherent habitat riskiness ratio explained 20% and 24%, respectively, of the variation in the proportion of dace in patch 1 in the presence of predators (Table 1).

In the experiments where dace and chub were alone in the experimental tank (i.e. experiments 1, 2, 4 and 5), a high proportion of individuals were in the feeding patches (dace: 72%; chub: 65%). The mean number of dace observed per minute in the two patches combined was about 36 individuals in the experiments without creek chub, but was significantly lower in experiments with creek chub ($F_{6,278} = 25.08$, $P < 0.001$; Fig. 6). In the presence of creek chub (experiments 3 and 6), the mean number of dace observed per minute in the two patches combined was reduced to about 28 individuals (i.e. 56% of dace in the experimental tank). Furthermore, when creek chub were free to move between patches (experiment 6), the proportion of

dace leaving the feeding patches after the introduction of chub increased significantly with the mean number of chub observed per minute in the two patches combined, to a maximum of 75% (Fig. 7). Individuals that were not in the feeding patches were in the tunnel, not in the open habitat between feeding patches (A. Dupuch, personal observation).

The number of predation events occurring during a trial varied from 0 to 6 (mean ± SD = 2.2 ± 1.6) and significantly increased with the mean number of chub observed per minute in the two patches combined (Spearman rank correlation: $r_S = 0.41$, $N_{trials} = 48$, $P = 0.004$), but significantly decreased with the mean number of dace observed there ($r_S = -0.39$, $N_{trials} = 48$, $P = 0.006$).

Creek chub distribution was not significantly affected by either resource distribution or inherent habitat riskiness (GLM: $N = 50$, $P > 0.05$).

DISCUSSION

As predicted, both dace and creek chub preferred the richer patch when alone (experiments 1 and 2), but resource matching was imperfect. Many studies have shown that consumers generally undermatch the resource distribution for various reasons (Kennedy & Gray 1993), such as travel cost between habitats, imperfect knowledge of resource distribution (Abrahams 1986), and competitive interference among consumers (Sutherland 1983). Also, it is likely that all the individuals present in feeding patches were not actively feeding and thus competing for food (leading to imperfect resource matching). Dace especially can benefit from dilution and confusion effects by grouping with other individuals in the feeding patches, leading to a higher number of dace in a patch than expected from IFD. Aggressiveness among creek chub

Table 1
Results of the general linear model to test for the effects of inherent habitat riskiness and food proportion on the proportion of dace in patch 1, with and without creek chub in the experimental tank (i.e. experiments 5 and 6, respectively)

Model variables	Estimate	df	F	P	Partial R^2	R^2 model
Without predators		2	48.62	<0.001		0.67
Intercept	49.63					
Food proportion	− 17.84	1	85.02	<0.001	0.59	
Habitat riskiness	− 3.37	1	12.21	0.001	0.08	
Food prop. × habitat risk.				NS		
With predators		2	18.51	<0.001		0.44
Intercept	39.72					
Food proportion	− 14.72	1	16.68	<0.001	0.20	
Habitat riskiness	− 8.10	1	20.35	<0.001	0.24	
Food prop. × habitat risk.				NS		

Table 2
Mean proportion of dace in patch 1 (with 95% CI) for each combination of food proportion × inherent habitat riskiness ratio during the experiment without predators (experiment 5)

Food proportion in patch 1	Inherent habitat riskiness ratio (patch 1/patch 2)				
	1/3	1/2	1/1	2/1	3/1
75%	**60 (41–79)**	55 (41–69)	**57 (33–81)**	52 (40–64)	47 (34–57)
25%	39 (29–48)	42 (29–54)	36 (29–44)	**34 (17–51)**	**31 (2–61)**

Bold values indicate that the mean proportion of dace in patch 1 did not differ from IFD (CI includes the expected value from the IFD; i.e. 75% and 25%, respectively).

Table 3
Results of the general linear model to test for the effects of inherent habitat riskiness, food proportion and their interactions with predation risk (creek chub absent or present) on the proportion of dace in patch 1 (i.e. experiments 5 versus 6)

Model variables	Estimate	df	F	P	R^2
Full model		5	20.36	<0.001	0.52
Intercept	39.72				
Food proportion	−14.72	1	63.34	<0.001	
Habitat riskiness	−8.10	1	31.66	<0.001	
Predator	9.90	1	5.83	0.018	
Habitat riskiness × predator	4.73	1	5.39	0.022	
Food proportion × predator				NS	

(A. Dupuch, personal observation) could partly explain their imperfect resource matching. Furthermore, we found that dace preferred patch 2 and creek chub preferred patch 1, an inherent tank effect that we cannot explain (this side preference was observed in both the experimental tanks). This resulted in an underuse of patch 1 by dace when it was the richer patch and an overuse by creek chub when it was the poorer patch.

Like many prey, dace avoided predator-rich (experiment 3) and refuge-poor patches (experiments 4 and 5) (Lima & Dill 1990; Kramer et al. 1997; Lima 1998). Our results are consistent with the hypothesis that patches with more straws were perceived as being less risky than patches with fewer straws. However, given the weak effect of riskiness on dace distribution in all the experiments testing this (4, 5 and 6), our results also suggest that dace did not view the patch with three times more straws as actually being three times safer. One explanation for this finding is that the straws affected feeding efficiency or competitive interactions among individuals and potentially added noise to our results. However, despite this potential noise, the observed effect of straw density on dace
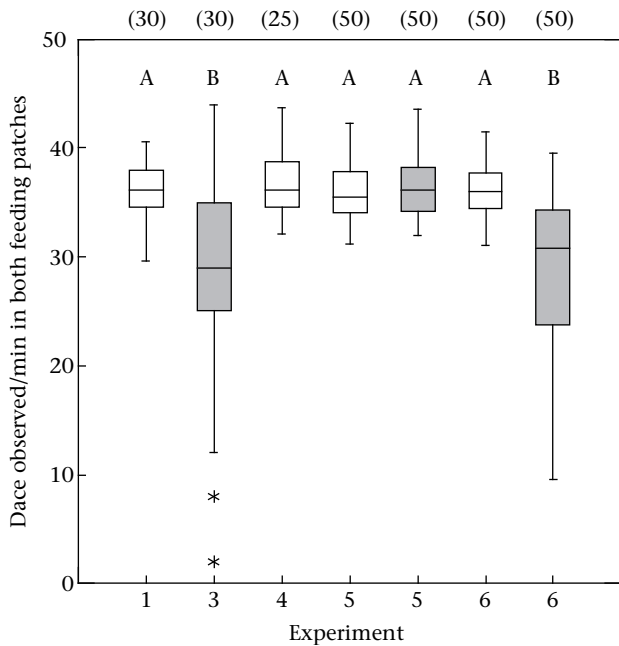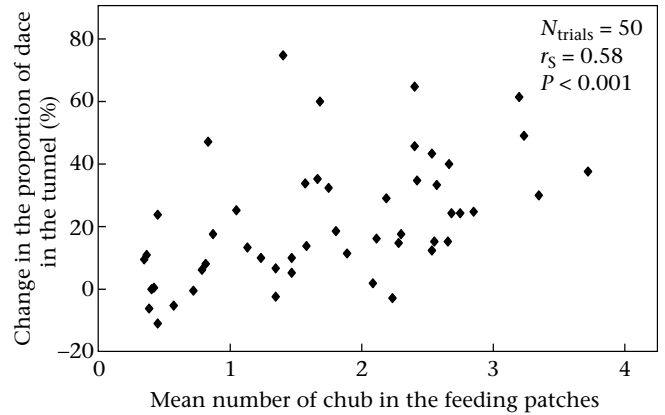

Figure 7. Change in the proportion of dace in the tunnel after introduction of creek chub in the experimental tank (experiment 6) according to the mean number of chub observed per minute in the two feeding patches. Negative values indicate that fewer dace were present in the tunnel after the introduction of chub.

distribution is in accordance with the hypothesis that dace perceive the patch with the highest density of straws to be safer.

Generally, prey balance energetic gains and predation risk when choosing a feeding habitat (Lima & Dill 1990). When patches differed in both resource quantity and inherent habitat riskiness, and predators were absent, dace underused the richer patch (relative to IFD predictions), especially when it was also the inherently riskier patch. This suggests that either (1) dace use the habitat's structural complexity as a proxy of predation risk, and trade-off energetic gains and predation risk even in the absence of a real predation threat, or (2) dace do not perceive zero risk in the absence of predators, explaining their slight preference for the patch with a higher straw density (see also experiment 4; Fig. 4).

Contrary to model predictions, dace distribution was determined by both resource distribution and inherent habitat riskiness in the presence of predators free to move (experiment 6). Given that prey and predator distributions should affect each other, one explanation could be that creek chub distribution was not as predicted by the models. Usually, models predicting that prey distribution should not be affected (or only slightly) by resource distribution also predict that predators should prefer habitats containing the highest resource quantity, even when they do not consume those resources (Hugie & Dill 1994; Sih 1998; Luttbeg & Sih 2004). However, in our experiment, creek chub distribution was relatively uniform. The presence of the grid around the automatic feeders prevented creek chub from feeding on trout pellets (i.e. the resource), and may have prevented them from assessing the resource quantity in each patch and responding accordingly. Our finding that creek chub did not prefer the richer patch could thus explain why resource distribution significantly influenced dace distribution.

A second explanation could be that game models that predict no effect of resource distribution on prey distribution consider prey fitness to be independent of an individual's state (such as energy reserves or individual experience). Yet, empirical data suggest that models that incorporate individual state in the feeding–mortality trade-off better predict behavioural decision making in prey (Skalski & Gilliam 2002). Alonzo's (2002) model considered that energy reserves affect prey fitness and it predicted that prey should favour the habitat with more resources when their energy reserves are low (i.e. if the risk of starvation is high), but that prey distribution should be unaffected by resource distribution when energy reserves of prey are high. Given that dace were fed ad libitum each day, we had no reason to predict that dace would select the richer patch because their risk of starvation was high.

Figure 6. Box plots representing the mean number of dace observed per minute in both feeding patches during a trial for experiments 1, 3, 4, 5 and 6. In experiment 3, creek chub were present (grey box) for the duration of each trial. For experiments 5–6, in which we introduced creek chub (experiment 6) or mimicked introduction of creek chub (experiment 5) values are means for trials before (open boxes) and after (grey boxes) the introduction (or mimicked ones). Numbers in parentheses indicate the number of trials for each experiment. Experiments accompanied by different letters were significantly different (*P* < 0.001). Asterisks denote outliers.

Because there was no food in the plastic grid tunnel between the two feeding patches, we expected that dace would mainly use the patches to forage and use the plastic grid tunnel only to move from one patch to the other. However, in the presence of creek chub (experiments 3 and 6), dace used the patches less often and their movements between patches were reduced compared to experiments without creek chub (A. Dupuch, personal observation). Accordingly, the mean number of dace observed per minute in the two patches combined was significantly lower in experiments with than without creek chub (Fig. 6). Furthermore, when creek chub were free to move between patches (experiment 6), the proportion of dace leaving the feeding patches to take refuge in the tunnel increased significantly with the mean number of chub observed per minute in the feeding patches (Fig. 7). Sih (1984) also showed that in the presence of a refuge, prey distribution was negatively related to predator distribution, with prey avoiding areas with numerous predators, and that prey movements decreased as predator movements increased. In fact, in addition to the two feeding patches, the tunnel offered a third, totally safe area for dace, but without food. After the introduction of creek chub, our results suggest that dace reduced their use of the least complex patch in favour of the refuge habitat (i.e. the tunnel) or the more structurally complex feeding patch. As the number of creek chub in the patches increased, dace aggregated and stayed motionless in the tunnel to avoid them.

Similarly, Gilliam & Fraser (1987) studied juvenile creek chub (prey) habitat selection among a refuge habitat and two feeding areas in which predation risk (i.e. the number of adult piscivorous creek chub) and resource levels were varied experimentally. As in our experiment, juvenile creek chub (prey) spent significantly more time in the refuge habitat as the number of adult creek chub (predator) increased in the feeding areas. Although we always introduced seven creek chub to the experimental tank (experiment 6), the predation risk intensity probably varied from one experiment to another because of variation in the activity level of creek chub and the attack rate on dace. Indeed, the number of predation events occurring during a trial varied and significantly increased with the mean number of chub observed per minute in the two patches combined, but significantly decreased with the mean number of dace observed there. This result suggests that dace used the refuge habitat more often as the overall level of predation risk in the experimental tank increased. Therefore, given the use of the refuge habitat (relative to both feeding patches), our results suggest that dace considered inherent habitat riskiness as being more important than resource distribution as predation risk intensity increased.

These results support the prediction of Luttbeg & Sih's model (2004). Their model predicts that if prey fitness is body-mass dependent (which is often the case), the relative contribution of resources and riskiness in determining prey distribution depends on the level of predation risk. When the level of predation risk is low, their model predicts that prey should favour the richer habitat even if it is the inherently riskier one. But when the level of predation risk is high, prey distribution should be mainly determined by the habitat riskiness ratio. Both the models of Hugie & Dill (1994) and Sih (1998) predict that the influence of resource distribution on prey distribution should increase with competition among predators. Given that, in these models, an increase in competition among predators decreases the predation risk of prey, both models also indirectly predict that the importance of resource distribution in prey distribution is inversely related to the level of predation risk. As in our study, the intensity of predation risk would also explain the variations of distribution between habitats differing in inherent riskiness in kangaroo rats (*Dipodomys* spp.; the prey) in response to snake (*Crotalus cerastes*; the predator) distribution (Bouskila 2001), and in bottlenose dolphins, *Tursiops*

aduncus, dugong, *Dugong dugon*, and pied cormorants, *Phalacrocorax varius*, in response to tiger shark, *Galeocerdo cuvier*, distribution (Heithaus & Dill 2002, 2006; Heithaus 2005; Wirsing et al. 2007).

In conclusion, the dace's use of the refuge habitat (relative to both feeding patches) suggests that the influence of resource distribution and inherent habitat riskiness on prey distribution varies with the level of predation risk. In fact, dace aggregated in the refuge habitat in direct proportion to the number of creek chub in the two patches combined. Thus, predator avoidance seems to determine habitat choice of dace as predation risk increases. In accordance with these results, a negative correlation between prey and predator distribution has commonly been observed (Sih 1984, 2005; Bouskila 2001; Hammond et al. 2007), regardless of habitat characteristics (i.e. resource quantity and inherent habitat riskiness). This suggests that predator avoidance has a stronger effect on habitat selection by prey than resource distribution, inherent habitat riskiness or conspecific avoidance (see also Hammond et al. 2007). On the other hand, some dace did not shelter in the tunnel even when the level of predation risk was high. For these dace that were outside the refuge habitat, our result showed that they considered resource quantity as being as important as inherent habitat riskiness when choosing a feeding patch (Fig. 5). This suggests that when prey accept the risk imposed by predators, both foraging success and mortality risk drive their habitat choice. The fact that some fish accept the risk imposed by predators could be due to factors like hunger and innate boldness.

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