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Temperature and its impact on predation risk within aquatic ecosystems

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Abstract

Metabolic rates of fish and their activity levels have thermal optima. When environmental temperatures are below their optimum, increasing temperature will increase their rates of energy consumption resulting in a corresponding increase in the risk of starvation. For that reason we predicted that within this temperature range food is of greater value at higher temperatures so fish should be willing to incur greater costs to obtain it. To test this hypothesis we measured how the activity and foraging rates of the fathead minnow changed with temperature at 4, 15, and 24 C. As expected, fish activity and foraging were greater at higher temperatures. We then measured the impact of predation risk on foraging decisions at 5, 15, and 23 C. At 5 and 15 C the risk of predation had a significant effect on foraging decisions, but no effect at 23 C. These results demonstrate that increasing temperatures below their optimal level diminish the impact of predation risk on foraging behaviour and may mean that the direct consumptive effect of predators on aquatic communities will be greater at warmer temperatures while the risk of predation will become a less important factor, and vice versa.

Keywords: predator-prey interaction, predation risk, temperature effects, climate change, freshwater fishes, freshwater, environmental effects

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Introduction

Predators play an important role structuring aquatic environments (Brodeur and Pearcy 1992; Caley 1995; Jackson et al. 2001; Baum and Worm 2009; Palkovacs and Post 2009) and do so through both direct (consumption) and indirect (habitat use patterns, group vigilance, competition, etc) effects (Sih 1987; Mittelbach and Chesson 1987). Short-term responses to predation risk are common and include hiding and “waiting out” a predator (Johansson and Englund 1995) and a reduction in prey activity (Rahel and Stein 1988; Eklöv and Werner 2000). However, individuals cannot hide indefinitely. They must acquire enough energy to meet their metabolic demands, as well as growth, reproduction, and predator avoidance -- the presence of predators imposes the constraint that food be obtained without becoming food for others (Abrahams 2006). In aquatic ecosystems where fishes are ectothermic (Wootton 1990), energy requirements for both predator and prey should be strongly affected by temperature.

There is an obvious role of physiology in predator-prey interactions as the mechanism that links the physical environment to changes in behaviour (Abrahams 2006). For ectothermic individuals there is a strong relationship between metabolic rate and temperature. In a meta-analytic review of this relationship for 69 species of fish, Clarke & Johnston (1999) found a curvilinear relation between resting oxygen consumption and environmental temperature with a tropical fish at 30 C consuming six times as much oxygen as a polar fish at 0 C. A manifestation of the increased metabolic rate will be a requirement for more energy that will increase foraging rates. At high temperatures, prey should be increasingly affected by these energetic considerations: the hungrier an individual, the more energy it will devote to finding food (Dill and Fraser

1984; Godin and Crossman 1994) and the less it will respond to stimuli associated with predators (Lienhart et al. 2014). A consequence may be that fish will require additional energy since more time will be spent escaping predators. A field study (Smith 2008) conducted over a temperature difference of 8 C (21.1 – 29.4 C) suggested that the feeding rate of a herbivorous fish increases with increasing temperature, though this result was not consistent across sites and the amount of food available was not measured. A mean temperature increase of 2 C was also enough to increase the feeding rate of another subtropical fish (Mendes et al. 2009) and a change of 3 C was sufficient to change personality traits of two species of juvenile coral reef fish (Biro et al. 2010).

While prey requirements for energy likely increase with increasing temperature, the same is probably true of their aquatic predators. They too will incur increasing metabolic costs at warmer temperatures and will therefore require more food to meet their energetic demands. It is within this context that we believe the role of predators within aquatic ecosystems may change. Predators are well known to impact dynamics within aquatic ecosystems (see Clark & Levy 1988) and alter foraging decisions (see Lima & Dill 1990 for a review). At cooler temperatures with reduced metabolic rates, the probability of dying due to starvation should be reduced. Animals that must make decisions to acquire food and avoid predators should place a greater emphasis on safety since the incremental increase in feeding rate would likely not have the same impact on reducing death by starvation. However, as temperature increases so too will metabolic rates, accompanied by an increased likelihood of starvation. Under these conditions we believe that animals are less likely to avoid predators to gain access to additional food

1 and therefore the impact of predation risk on habitat selection decisions should be
2 diminished.

3 We tested this hypothesis by first determining how foraging and activity rates of
4 small minnows were affected by a range of temperatures. We then determined the
5 relative impact of predation risk on habitat selection decisions involving access to
6 measure whether the relative importance of predation risk diminishes with increasing
7 temperature.

8

9 **Methods**

10 Study animals

11 Fathead minnows (*Pimephales promelas*) were used as the prey species for these
12 experiments. Approximately 60 fathead minnows (mean $\pm$ SE length: 48 ± 0.8 mm) for
13 experiment 1 were obtained from small ponds in southern Manitoba, Canada, in the
14 spring of 2007 when the water was less than 5 °C using minnow traps and were held in
15 200-l aquaria at one of three temperatures (4, 15 and 24 °C) under a 12 h light:12 h dark
16 regime at the Animal Holding Facility at the University of Manitoba. They were fed *ad*
17 *libitum* Nutrafin flakes and frozen bloodworms. Fathead minnows for experiment 2 were
18 collected in the fall of 2009 when the water was less than 5 °C at the same locations using
19 the same techniques and held under the same conditions, except that the warmest
20 temperature was 23 °C rather than 24 °C (the difference was due to a limitation of the water
21 supply system within our Animal Holding Facility). Yellow perch (*Perca flavescens*)
22 were used as the predator for these experiments and they were collected from Delta
23 Marsh at the University of Manitoba Field Station at the southern tip of Lake Manitoba

(50°11'N, 98°23'W) in 2006 using minnow traps when the water temperature was less than 5 °C. They were housed in 200-l aquarium at 15 °C under a 12 h light:12 h dark regime at the Animal Holding Facility at the University of Manitoba and fed squid and fish.

Experiment 1: The impact of temperature on behaviour

Approximately 24 h before the start of the experiment, a randomly (haphazardly) selected group of three fish was removed from each of the three tanks and placed in a 76-l aquarium containing water of the same temperature (4, 15 or 24°C). They were not fed during this time. Aquaria were covered on three sides preventing visual contact between individuals occupying separate aquaria. A ruler was placed along the bottom edge of each aquarium to allow for measurements of distances travelled (see below for methods). All trials were conducted in an environmental chamber, which minimized disturbance to the fish. Experiments were conducted between 1400 and 1500 h and lasted for 30 minutes.

The effect of temperature on the activity rate (distance covered/frame) and foraging attempts (number of bites made at the surface/frame) of fathead minnows was observed during thirty-minute trials. The first 15 minutes recorded baseline information in the absence of food. The second 15 minutes provided foraging information in the presence of 0.5 g of Nutrafin flakes. This food was dispersed remotely; a burst of air was delivered from outside the environmental chamber through tubing that entered the chamber. This tubing was connected to a small piece of polyvinyl chloride with two holes – a large hole was used as a means of placing food into the device, which was covered during the trial, and a small hole through which the food exited upon administration of

1 the burst of air. Six trials, each consisting of three fish, were conducted at each
2 temperature. A single Panasonic CCTV WV-CP484 SDIII camera with Pentax 3.5-8mm
3 F/1.4 CS auto iris lenses was used to record each trial. Video data were recorded to
4 Digital Video Disc (DVD) via a Toshiba 1080P UP Conversion D-R7. All tanks were
5 emptied and rinsed between trials to eliminate any remaining food. All video data were
6 converted to stacked frames using VirtualDubMod (Version 1.4.10) and saved as bitmap
7 files. These files were then imported as a sequence to ImageJ (version 1.38, 2007) for
8 further analysis.

9 We recorded the number of foraging attempts conducted by the most active
10 fathead minnow (hereafter, focal individual) during the 15 minutes post food addition.
11 Foraging attempts were classified as movement by the minnow to the surface of the water
12 followed by mouth opening and closing after food was administered (no observation of
13 this behaviour occurred before addition of the food). Nutrafin flakes remained floating at
14 the surface of the aquaria for the remainder of the trial. A single factor ANOVA using
15 $\log_{10}(\text{number of attempts} + 1)$ as the dependent variable and temperature as the
16 independent variable was used to statistically analyze data.

17 The distance travelled (a proxy measure of activity) by the focal individual in
18 each aquarium was measured using the position of the minnow in the aquaria at 5 sec
19 intervals (every 150th frame) using ImageJ. We compared activity levels before and after
20 feeding at each temperature with a paired t-test and analyzed the pooled data if there was
21 no significant difference, or separately if they were statistically different. The analysis
22 used a single factor ANOVA with distance travelled as the dependent variable and

1 temperature as the independent variable for differences in distance travelled/frame among
2 the three temperatures.

3 Each trial represented a single, independent observation as fish were only used
4 once in the experiment. All data were tested for normality and homogeneity of variance
5 employing the Shapiro Wilk W test and Levene's test, respectively. Any non-normal data
6 were transformed to meet normality standards. Alpha values were set at 0.05 for all
7 analysis and all analyses were conducted using STATISTICA software (StatsSoft
8 Software, STATISTICA version 8, 2007).

9

10 Experiment 2: Temperature and Risk of Predation

11 To determine the potential effects of temperature on predator-prey interactions,
12 we designed an experiment to test the relative risk-taking (feeding in a risky location) by
13 minnows held at three temperatures (5, 15 and 23 C), while the temperature of the
14 predator remained constant to keep risk levels independent of temperature.

15 The experimental apparatus consisted of a 40-l aquarium containing the fathead
16 minnows and a 10-l aquarium housing the yellow perch adjacent to the end of the large
17 aquarium. Before the experiment commenced, a solid divider was placed between the two
18 aquaria to prevent visual contact of predator and prey (fathead minnows) and potential
19 habituation. Control treatments were trials with no predators; the solid divider was also
20 placed between those two aquaria in the trials. The small aquarium was randomly placed
21 on either the right or left side of the aquarium to control for any potential side effect in
22 both control and treatment trials. In the minnow's aquarium, two automated feeders were
23 set up to provide equal amounts of food. One feeder was placed 5 cm from the 10-l

1 aquarium (when predator present in the small aquarium, this was designated as the high
2 risk location), the other 5 cm from the end of the opposite end of the aquarium (low risk).
3 Each feeder provided 0.25 g of frozen bloodworm over an approximate 15 minute time
4 period (see Abrahams and Dill 1989 for a description of the feeders) (Figure 1).

5 Both the predator and groups of six similar sized prey were randomly selected and
6 placed in the apparatus 24-h before the experiment started. Once the trial was ready to
7 begin, cameras were activated, the solid divider removed and the automated feeders
8 activated. The feeder was the only source of food for the minnows for the duration of the
9 experiment. Upon completion of the trial, the water was changed and the aquarium
10 cleaned. At each temperature, six replicates of each treatment (predator present or absent)
11 were completed for a total of 36 trials. Groups of fish were used in one trial only (either
12 predator present or predator absent). All trials were completed over 24 days with trials
13 being performed once per day, every second day, in three aquaria.

14 All trials took place between 1100 and 1130 and ran for approximately 15
15 minutes. The total number of minnows using the feeders and their location with respect to
16 the feeders (whether the minnows were feeding at the high risk feeder close to the
17 predator – the 10-l aquarium location – or the safe feeder at the opposite end of the 10-l
18 aquarium) were observed every 30 seconds for the 15 minute duration of the trial. The
19 mean proportion of minnows occupying the high-risk location was calculated in both the
20 predator and no predator treatments. A feeding minnow was considered to be any
21 individual that had consumed or was consuming bloodworms within approximately 5 cm
22 of either side of the feeder. To determine if the predators were affected by the behaviour
23 of the prey among temperature treatments, the proportion of the time spent oriented

1 towards the minnows in the 40-l aquaria during approximately the last 10 minutes of the
2 15 minute trial was assessed. Omitting the first 5 minutes of the trial allowed for any
3 disturbances associated with the removal of the solid divider to be accounted for in the
4 analysis.

5 Statistical Analysis

6 For descriptive statistics, each group of minnows represented a single
7 experimental unit. For statistical analysis, each unique combination of minnows and
8 predator at each temperature was considered an independent observation, since
9 observations depended both upon group identity and the response of the predator to the
10 temperature manipulation (prey behaviour at the various temperatures). A single
11 observation for each experiment was determined by taking the mean of all sequential
12 observations within a trial. The effect of temperature and predator on the mean number of
13 minnows feeding and the proportion using the high-risk feeder (dependent variables) was
14 determined using a two-way factorial ANOVA.

15 Finally, to determine if the temperature of the prey affected the proportion of
16 time the predators spend oriented towards the prey a single factor ANOVA was used with
17 temperature as the independent variable and the proportion of time the predator spent
18 oriented towards the prey as the dependent variable. To further examine the potential
19 relationship between the orientation of the predators toward the prey and the prey
20 behaviour, two regression analyses were run. The first regression analysis included the
21 average number of minnows foraging as the independent variable and the proportion of
22 time the predator spent oriented towards the prey as the dependent variable. The second
23 regression analysis used the mean proportion of minnows using the risky feeder as the

independent variable and the proportion of time the predator spent oriented towards the prey as the dependent variable. All data were tested for normality and homogeneity of variance, and any non-normal data were transformed to meet normality standards. All data in the form of proportions were arc-sine square root transformed prior to analysis. Results were considered significant at $\alpha = 0.05$. Alpha values were set at 0.05 for all analyses that were conducted with the STATISTICA software.

Results

Experiment 1

Foraging attempts. There was a significant effect of temperature on foraging attempts made by fathead minnows ($F_{2, 15} = 21.69$, $P = 0.00001$, Figure 2a). Tukey HSD (Honestly Significant Difference) determined that significant differences were observed between mean foraging attempts at both 4 C and 15 C temperatures when compared to mean foraging attempts at 24 C. No difference was observed between mean foraging attempts of minnows held at 4 C and those held at 15 C. The magnitude of change in foraging attempts was greatest between 4 C and 24 C water treatments (a five-fold increase) and an approximate two-fold increase between the 15 and 24 C treatments (Figure 2a).

Distance travelled. There were no significant differences in activity of fish before and after feeding at any of the temperatures (paired t-test: 4 C: $t = 0.28$, $P = 0.79$; 15 C: $t = -1.03$, $P = 0.32$; 24 C: $t = -0.72$, $P = 0.48$; $df = 10$ for all analysis). We therefore used the entire 30 min duration of the trial for each temperature in a single factor ANOVA to determine the effect of temperature on activity rates of fathead minnows. There was a

1 significant effect of temperature on activity rates ($F_{2,15} = 81.37$, $P < 0.0001$; Figure 2b)
2 and a Tukey's HSD test determined that there were significant differences between each
3 temperature treatment. There was a six-fold increase in activity rates between 4 C and 15
4 C, and a 1.5 times increase between 15 C and 24 C (Figure 2b).

6 Experiment 2

7 *Risk of predation and patch preference*

8 At 23 C there were almost three times as many minnows foraging as compared to both 5
9 and 15 C (Figure 3a). This result was not dependent upon whether the predator was
10 present or absent, the total number of animals feeding was significantly greater at 23 C
11 than at 5 and 15 C (Table 1). Statistical analysis of these data demonstrated that the
12 presence or absence of the predator, and its interaction with temperature had no effect on
13 the mean number of minnows foraging in these experiments (Table 1).

14 In the absence of predators fishes distributed themselves equally between the two
15 feeders regardless of the temperature at which they were held (Figure 3b). However, the
16 impact of a predator on this spatial distribution was strongly affected by temperature. At
17 5 C the presence of a predator created the greatest shift away from the high-risk location,
18 while at 23 C the predator had almost no effect. The result at 15 C was intermediate
19 (Figure 3b). Statistical analysis demonstrated that temperature, predator, and their
20 interaction had a significant impact upon the proportion of minnows feeding in the risky
21 location (Table 2).

22 The predator spent significantly more time oriented towards the prey when the
23 prey were at warmer temperatures (one-way ANOVA: $F_{2,17} = 60.96$, $P < 0.000001$).

Both the mean number of fathead minnows feeding ($R^2 = 0.31$, $F_{1,16} = 7.06$, $P = 0.02$; Figure 4a) and the proportion of fathead minnows using the risky feeder ($R^2 = 0.42$, $F_{1,16} = 11.79$, $P = 0.003$; Figure 4b) were significant predictors of the proportion of time the yellow perch spent oriented towards their prey.

Discussion

Both foraging and activity rates of fathead minnows increased with increasing temperature. When compared to fishes occupying 4 C water, fishes held at 24 C increased their distance travelled per frame by a magnitude of nearly nine-fold. A ten-fold increase in foraging attempts was observed between fishes held at 4 C and those held at 24 C. In measures of both foraging and activity, fish held at 15 C displayed intermediate foraging and activity levels. These increases in foraging as temperatures increase is similar to that observed in an herbivorous marine fish foraging under different thermal regimes (Smith 2008). Increased foraging with temperature has also been observed in juvenile brown trout, *Salmo trutta* (Ojanguren et al. 2001) and brook trout, *Salvelinus fontinalis* (Taniguchi et al. 1998). Increases in activity with temperature agrees with the results of Krause and Godin (1995) who also observed fishes held at warmer temperatures moved more rapidly and made quick turns.

These results suggest that temperature is a driving force influencing the activity and energy budgets of fathead minnows, and that the effect of temperature may be exacerbated by positive feedback. This will be true only within a certain temperature range since physiological responses are governed by biochemical reactions that have thermal optima and generate temperature preferences for ectotherms (Huey and

1 Kingsolver 1989). Below these optima warmer temperatures cause fish to increase their
2 foraging to meet their higher energetic demands by increasing their level of activity.

3 Above these optima further increases in temperature may have the opposite effect.

4 At temperatures below the optima, the relation between increasing temperature
5 and increasing requirements for food mean that fish will be less likely to integrate
6 predation risk into their decision-making processes (Dill and Fraser 1984; Godin and
7 Crossman 1994) as incorporating risk of predation into the decision to forage or not is a
8 state-dependent decision (Magnhagen 1988; Gregory 1993). A satiated individual is less
9 likely to take a risk to obtain food as compared to a hungry individual; the satiated
10 individual can rely on its energetic reserves, which negates the need to forage under risk
11 of predation. Hungry individuals are therefore more likely to take the risk and forage
12 while predators are present which in turn may result in increased detection and capture
13 rates by predators.

14 Anderson et al. (2001) found that increasing temperatures increased growth of
15 larval anurans (*Hyla regilla*), which was expected to reduce the mortality rates of these
16 larger individuals, as their predators were gape limited. This increased growth decreases
17 the number of gape-limited predators that can consume prey (Magnahagen and Heibo
18 2001) and offers a potential refuge for prey (Urban 2007). However the increase in
19 growth of larval anurans resulted in increased mortality at higher temperatures. While
20 activity and foraging rates were not measured in that study, it is probable that they
21 increased at high temperatures and may partially account for this result. This would
22 increase encounters between prey and predators as foraging/activity of prey increased
23 with increased temperature. Increased activity has also been linked to increased mortality

1 rates in the damselfly, *Coenagrion hastulatum* (Brodin and Johansson 2004) and
2 flounder, *Pseudopleuronectes americanus* (Taylor and Collie 2003) when predators are
3 also ectothermic.

4 The study by Anderson et al. (2001) suggests that high temperatures results in
5 higher predation risk. However there is a possibility that low temperatures and the
6 resulting low activity rates observed in this study may not necessarily result in a
7 reduction in predation risk. Muscle function and swim speed are reduced when
8 temperatures are low (Claireaux et al. 2006; Jones et al. 2008) and may result in a
9 reduction in the ability to escape faster swimming predators. Johnston et al. (2004)
10 observed the activity of young-of-year Atlantic salmon (*Salmo salar*) and determined that
11 at low temperatures ($< 7^{\circ}\text{C}$) salmon become less active (as observed in this study) and
12 spend more time hiding – they also become nocturnal at low temperatures. If only the
13 prey are ectothermic, a reduction in muscle function and swim speed may actually
14 increase the vulnerability of fish to predation – a possible explanation for the observation
15 of a switch to nocturnal behaviour of the salmon to avoid their endothermic predators at
16 low temperatures (Johnston et al. 2004).

17 If increased temperature results in increased encounters between predators and their
18 prey, the potential detrimental effects to prey as a result of increased temperatures may be
19 beneficial to a predator assuming it is able to meet its increased energy demands. Prey
20 are more active at higher temperatures and therefore less cryptic (Gotceitas and Godin
21 1991) and predators have demonstrated a preference for active prey (Krause and Godin
22 1995). With an increase in activity and foraging rates with temperature, it is expected that
23 fathead minnows would experience an increase in predation risk with increasing

temperature. Mitigating effects of increased predation risk might include increased mobility and escape capabilities at increased temperatures (Persson 1986) as muscle function and swim performance are temperature dependent (Logue et al. 1995).

How individual prey make tradeoffs between increased energy acquisition and predation risk can dictate the flow of energy within an ecosystem (Trussell et al. 2006). The energy flow within an ecosystem is itself determined by prey being consumed by predators and the rate of food consumed by these prey (Schmitz et al. 1997). Both of these factors are affected by temperature and interact with one another. As temperature increases at ranges below a species' thermal optima, food consumption and activity rates of prey increase making it increasingly difficult to meet their energetic demands. It is likely that these individuals will be less concerned with predation risk when it comes to decision making as their efforts are focused on food consumption. Not only are these individuals likely not incorporating predation risk as fully into decision making as individuals inhabiting cooler temperatures, but the increased activity observed at high temperatures probably renders these individuals more easily detected by predators.

Determining the overall response of an aquatic ecosystem to increasing temperature requires an understanding of how all organisms respond to this change. This paper focused only on the response of the prey. Abrahams et al. (2007) have developed an individual-based computer simulation that modeled the physiological and behavioural response of predators (brown trout, *Salmo trutta*) and their prey (charr, *Salvelinus alpinus*) to 3 and 7 °C increases in their environment over 100 years. This simulation demonstrated increased interactions between predators and their prey at warmer temperatures as described above but also produced the surprising result that predator

- 1 growth rates declined with warmer temperature due to their increased metabolic costs.
- 2 Understanding how an entire ecosystem will respond to a changing climate requires
- 3 considerably more information but it is reasonable to assume that the thermal
- 4 environment will affect the role of predation risk within temperate aquatic ecosystems.
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Table 1: Results of the two-way factorial ANOVA examining the relationship between temperature and predator presence or absence (independent factors) on the mean number of minnows foraging. Significant differences are indicated with bold values.

Source of variation	<i>df</i>	F	P
Temperature	2	35.31	0.00001
Predator	1	0.25	0.63
Temperature*Predator	2	0.18	0.84

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Table 2: Results of the two-way factorial ANOVA examining the relationship between temperature and predator presence or absence (independent factors) on the mean proportion of minnows using the risky feeder. Significant differences are indicated with bold values.

Source of variation	<i>df</i>	F	P
Temperature	2	8.45	0.0012
Predator	1	40.20	0.000001
Temperature*Predator	2	8.63	0.0011

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1 Figure Captions

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3 Figure 1: Diagram of the experimental apparatus used to determine the effects of
4 temperature on response of minnows to a predator. F_1 represents the high-risk feeder, F_2
5 the low-risk feeder; they are located approximately 5 cm from the side of the 40-l
6 aquarium. The solid divider prevented the minnows from becoming habituated to the
7 presence of the predator.

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9 Figure 2: The change in the behaviour of minnows associated with the three temperature
10 regimes as measured by (a) the mean number of foraging attempts per frame and (b) the
11 distance travelled. Bars represent standard error around the mean and letters above the
12 bars represent significant differences at $\alpha = 0.05$ using Tukey post hoc tests.

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14 Figure 3: The mean response of the fathead minnows to the presence of a predator as
15 measured by (a) the average total number of fish feeding per trial and (b) the mean
16 proportion of fish feeding on the treatment (aquarium) side, at each temperature in the
17 presence and absence of a predator. Bars represent standard error around the mean and
18 illustrate how increasing temperature increases the number of fish feeding and the
19 diminished impact of predation risk. These results are statistically significant and the
20 details are provided in Tables 1 and 2.

21

22 Figure 4: The relationship between prey activity and predator orientation towards the
23 prey as measured by (a) the number of fish active per trial and the proportion of time the
24 predator spent oriented towards the prey and (b) the proportion of fish using the risky

1 feeder and the proportion of time the predator spent oriented towards the prey. The
2 regression line was fitted through all data, with temperature specific data identified within
3 the key.

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Pink & Abrahams Figure 1

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Pink & Abrahams, Figure 2

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Pink & Abrahams, Figure 3

Pink & Abrahams, Figure 4