



## Temperature and food availability affect risk assessment in an ectotherm



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Risk assessment in ectotherms is strongly affected by an organism's energy expenditure and acquisition because these will alter the motivation to feed, which is balanced against antipredator behaviours. Temperature and food availability are known to affect the physiological condition of ectotherms, but how interactions between these variables may influence predator–prey dynamics is still poorly understood. This study examined the interactive effects of food availability and temperature on the trade-offs between predator avoidance behaviour and foraging in juveniles of a marine damselfish, *Pomacentrus chrysurus*. Predator avoidance behaviour was tested by exposing fish to chemical alarm cues obtained from skin extract of conspecifics. When detected, these cues elicit an antipredator response in fish, typically characterized by decreased foraging. Fish maintained under high food ration displayed distinct antipredator responses to chemical alarm cues, regardless of temperature. However, fish maintained in conditions of low food ration and 3 °C above ambient temperature did not display an antipredator response when exposed to chemical alarm cues, whereas those in ambient temperature did. These results suggest that individuals in low physiological condition because of limited food availability are more susceptible to increased temperature and may therefore take greater risks under predation threats to satisfy their energetic requirements.

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Predation is known to drive behavioural patterns associated with foraging, reproduction and other fitness-related activities (Candolin, 1997; Houston, McNamara, & Hutchinson, 1993; Lima & Dill, 1990). Decisions made by an organism under the risk of predation are often described as a trade-off between avoiding predation and obtaining resources (Abrams, 1993; Lima, 1998). Predator avoidance decreases mortality rates but often at the cost of future growth and reproductive investment because of reduced foraging activity (Abrahams & Pratt, 2000; Cressler, King, & Werner, 2010). The extent to which individuals allocate their time to such activities depends on how an individual assesses the potential gains to overall fitness, given their current physiological state (Houston et al., 1993; Lima & Dill, 1990; Mathot & Dall, 2013; McNamara & Houston, 1986). Consequently, these state-dependent decisions can be heavily influenced by environmental parameters that impose an energetic cost, such as temperature (Abrahams, Mangel, & Hedges, 2007; Caraco et al., 1990). Although the importance of environmental parameters in determining antipredator strategies has been acknowledged, few studies have directly tested how interactions between different parameters affect risk assessment.

Theoretical and empirical studies have stressed the importance of an individual's physiological state as a driving component that should influence the trade-off between foraging and avoiding predation. According to these studies, animals exposed to conditions of higher physiological demands should be willing to take greater risks in the presence of a predator (Caraco et al., 1990; Houston et al., 1993; Lima & Dill, 1990; Mangel & Clark, 1986). Killen, Marras, and McKenzie (2011) found that the combined effects of high metabolic rate and food deprivation on risk taking during foraging led to an increased tendency for fish to ignore a visual threat. In keeping with this finding, feeding history has been shown to affect risk-taking behaviour, with hungry animals reducing their antipredator response when presented with conspecific alarm cues (Chivers, Puttlitz, & Blaustein, 2000; Giaquinto & Volpato, 2001; McCormick & Larson, 2008; Smith, 1981). Although food availability and its effect on physiological condition have been shown to influence behavioural decisions in fishes, there has been a lack of studies investigating how other environmental factors may further affect threat-sensitive trade-offs between the benefits of antipredator behaviour and foraging behaviour.

For most organisms temperature is one of the major environmental influences on life history processes. This is especially true for ectothermic species, such as amphibians (Touchon & Warkentin, 2011), reptiles (Rhen, Schroeder, Sakata, Huang, & Crews, 2011) and

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fishes (Green & Fisher, 2004), for which changes in their thermal environment directly affect physiology. Temperature influences fundamental properties of their energy budgets, metabolic demands, digestion rates, assimilation efficiencies (Clarke & Fraser, 2004; Englund, Ohlund, Hein, & Diehl, 2011; Roessig, Woodley, Cech, & Hansen, 2004) and associated behaviours (Biro, Beckmann, & Stamps, 2010; Nowicki, Miller, & Munday, 2012). Indeed, the influence of temperature on physiological processes is so universally important that it has been described as an 'abiotic master factor' (Brett, 1971).

Temperature may also have an impact on risk assessment as many organisms are exposed to substantial changes in temperature on a range of temporal and spatial scales. At the spatial scale of an animal's home range, key drivers of small-scale fluctuations in temperature are season, time of day and microhabitat. Seasonal variability is largely driven by predictable variation in solar radiation (Leichter, Helmuth, & Fischer, 2006). On Heron Island, Great Barrier Reef, Australia, water surface temperature throughout the year has been reported to reach a minimum value of 20 °C in the winter and peak to a maximum value of 29 °C in the summer (Rummer et al., 2013). Additionally, for aquatic organisms, the flow of water through habitats along with tides or floods can lead to dramatic short-term changes in temperature over hours to days (Jimenez, Kuhl, Larkum, & Ralph, 2011; Jimenez, Larkum, Ralph, & Kuhl, 2012). For instance, diurnal changes in temperature in the lagoon of Lady Elliot Island on the Great Barrier Reef can range over 4–8 °C, with peak changes over 12 °C during summertime (McCabe et al., 2010). Consequently, variation in temperature over the short, medium and long term may significantly alter energy demand and risk assessment.

Temperature changes are also expected to have a more marked influence on ectotherms that live close to the equator, where organisms have evolved under relatively stable temperature conditions and live closer to their thermal maxima (Rummer et al., 2013; Tewksbury, Huey, & Deutsch, 2008). The effect of temperature on threat-sensitive behaviour may also be magnified in the transition between life stages, such as the transition from larval to postlarval life stage in organisms with complex life cycles, because the risk is often high owing to unfamiliar predators (e.g. Lönnstedt, McCormick, & Chivers, 2012). During the settlement period, tropical larval fishes are exposed to exceedingly high levels of predation (Almany & Webster, 2006; Houde, 1989) and avoiding predators at this point is central to their chances of survival (Lönnstedt et al., 2012). Thus, tropical fishes at the settlement stage are ideal organisms with which to examine the influence of temperature on risk assessment. Ambient water temperatures over the summer months in the study region (Lizard Island, Australia) can vary by 4–5 °C and food availability can be highly variable and patchy (Rummer et al., 2013). Consequently, the local environment into which juvenile fishes settle may influence how they perceive and respond to predation risk. The aim of our study was to investigate the short-term (5 days) interactive effects of water temperature (27 °C versus 30 °C) and food availability (low versus high) on risk assessment in a model tropical ectotherm, the marine damselfish *Pomacentrus chrysurus*. We experimentally tested the hypothesis that fish subjected to higher energetic demands owing to higher water temperature coupled with limited food availability would decrease their antipredator response when exposed to a threat, as indicated by a conspecific chemical alarm cue.

## METHODS

### *Study Site and Species*

This study was conducted at Lizard Island (145°27'E, 14°41'S), northern Great Barrier Reef, Australia between October and

November 2012. The laboratories and flow-through sea water aquarium system at Lizard Island Research Station were used to conduct all experiments, and fish were collected from the shallow fringing reef.

We used juvenile *P. chrysurus* for all experimental trials. This small damselfish inhabits rocky outcrops in sandy areas and is commonly found in areas high in coral rubble, especially on shallow reef flats (Randall, Allen, & Steene, 1997).

### *Fish Collection, Housing and Release*

*Pomacentrus chrysurus* were collected as newly metamorphosed juveniles using light traps (Meekan, Wilson, Halford, & Retzel, 2001) deployed overnight, or as newly settled fish from the fringing reef using hand nets and a solution of anaesthetic clove oil mixed with alcohol and sea water. Fish were transported back to the research station (approximately 10 min boat trip) in plastic-covered bins (65 × 41 cm and 40 cm deep). Each bin was filled with approximately 60 litres of sea water and contained a maximum of 200 juvenile fishes. The bins were aerated using portable oxygen air pumps to avoid asphyxiation of fishes during transport. Once at the Lizard Island research station, all fish were maintained in 25-litre flow-through aquaria systems for about 24 h, and fed newly hatched *Artemia* twice per day ad libitum to allow for recovery from the stress of capture. Aquaria were maintained under a 12:12 h light:dark regime. Flow-through aquaria systems were fed directly from surrounding lagoon waters so that water temperatures in aquaria mirrored that found in the natural environment (about 27–30 °C). Fish were collected in batches and used in experiments within about 48 h of capture to avoid biases associated with ontogenetic development.

At the end of the experiment fishes from all treatments were maintained for a minimum of 48 h and were fed ad libitum to allow for recovery prior to being released in their natural habitat. No mortality of fish was observed during capture and release of fish. Food availability but not temperature during maintenance of fish affected survival. All fish maintained at the high food ration survived; however, mortality for fish maintained at the low food ration was approximately 5%. All research was conducted under permits from the Great Barrier Reef Marine Park Authority and James Cook University Animal Ethics Committee (permit no. A1720).

### *Experimental Aquaria*

After collection, fish were allocated at random to eight thermally insulated 18-litre aquaria (40 × 30 cm and 15 cm deep) representing two tanks in each combination of the two feeding levels and two temperature treatments. The two feeding levels were either poorly fed (300 *Artemia*/litre twice daily) or well fed (1000 *Artemia*/litre twice daily). These feeding levels were established based on treatments used in similar feeding experiments on congeneric species (Lönnstedt & McCormick, 2011; Lönnstedt et al., 2012). Fish from each feeding treatment were exposed to either ambient temperature (27 °C) or high temperature (30 °C), to match natural fluctuation in summer sea temperature during the recruitment period (e.g. McCormick & Molony, 1995). Electric batten heaters (300 W) were used to control the temperature of the sea water. Fish were acclimated to the high temperature by slowly raising the water temperature over a 48 h period. Fish were kept in the four treatment combinations for 5 days (under a 12:12 h light:dark photoperiod) prior to being used in behavioural trials. Tanks had a slow flow-through sea water system and an airstone within each tank kept the *Artemia* in suspension and distributed throughout the tank, so all fish had similar access to food. As a result of constraints in time and tank availability during

the observation trials, the total number of fish at one time needed to be staggered across different tanks and days. Each experimental aquarium contained approximately 5–10 fishes. Not all fishes were tested for behavioural response; however, morphometric measures were taken for each individual. Sample sizes for behavioural trials and growth analysis were as follows:  $N = 15$  and 35 (low food – 27 °C);  $N = 32$  and 52 (high food – 27 °C);  $N = 24$  and 46 (low food – 30 °C);  $N = 27$  and 52 (high food – 30 °C).

#### Stimulus Preparation

Antipredator responses were tested by exposing fish to chemical alarm cues obtained from conspecifics. These chemical alarm cues are found in the epidermis and elicit distinct antipredator behaviours upon detection by conspecifics and closely related species (Mitchell, Cowman, & McCormick, 2012). The presence of such damage-released chemical alarm cues have been demonstrated in a wide range of fish taxa and other aquatic organisms such as amphibians and invertebrates (Ferrari, Wisenden, & Chivers, 2010). Skin extracts were prepared using *P. chrysurus* collected either from light traps or from the reef (one fish per trial). The donor fish were killed individually through thermal shock by complete immersion in ice slurry (in accordance with James Cook University Animal Ethics; permit no. A1067). Death in juveniles is usually identified as a lack of opercula movement, which generally occurred within 10 s. However, fish were immersed in ice for the full 2 min to ensure complete brain death. Thermal shock was used rather than other killing methods because of the speed of death and because it prevents the release of potentially confounding body odours (in comparison with a blow to the head or a spike through the brain) or the introduction of foreign odours (in comparison with e.g. anaesthesia overdose). A clean scalpel blade was used to make 10 superficial vertical incisions along each flank. Fish were then rinsed with 20 ml of sea water, and the solution was filtered to remove any solid material. Skin extracts were prepared within 5 min of injection into the observation tank to avoid any time-related decrease in potency. For each behavioural trial, we injected chemical alarm cue obtained from one conspecific donor fish.

#### Experimental Set-up

Our design followed a  $2 \times 2 \times 3$  repeated-measures design, whereby fish maintained under two temperatures (27 °C versus 30 °C) and under two food rations (low versus high) were subsequently observed during three successive periods: during the prestimulus period (baseline), after an exposure to water (control stimulus for disturbance) and finally after an exposure to a chemical alarm cue (experimental stimulus).

Observations of fish behaviour were conducted in 13-litre flow-through aquaria (36 × 21 cm and 20 cm deep). Each tank had a 3 cm layer of sand and a small terracotta pot (5 cm diameter) for shelter at one end and an airstone at the opposite end. A feeding tube and stimulus injection tube were attached to the airstone tube with their ends placed just above the stone to aid rapid dispersal of the chemical stimuli. The injection tubes allowed the food and stimuli to be introduced with minimal disturbance to the fish. Each tank was surrounded on three sides with black plastic and insulation foam to isolate the fish visually and thermally. Fish were observed through small holes cut in a black plastic curtain that was hung in front of the tanks to minimize disturbance to the fish.

The behaviour of the fish was quantified by counting feeding strikes over a specific length of time (3 min in the present study). Many studies have shown that a decrease in foraging is a common behavioural response observed in animals facing a risky situation (Bishop & Brown, 1992; Killen, Gamperl, & Brown, 2007; Lima,

1998; Williams & Brown, 1991), including larval damselfish (e.g. Mitchell, McCormick, Ferrari, & Chivers, 2011). The foraging rate included all feeding strikes on *Artemia* irrespective of whether the fish were successful at capturing prey. *Artemia* has commonly been used in experiments on foraging and antipredator behaviour of fish, partly because feeding rate on these low-calorie prey items is stable over a relatively extended period of time before the fish attain satiation threshold (Holmes & McCormick, 2010; McCormick & Larson, 2008).

Prior to the start of the trial, the fish were given 2.5 ml of food to remove the 'feeding frenzy' effect associated with the sudden presentation of food in the tank. This prefeeding phase consisted of injecting 2.5 ml of food (an *Artemia* solution containing 250 individuals per ml) in the tank, followed by 20 ml of sea water to flush all the food into the tank, hence allowing the fish to reach a stable feeding rate before the trial. The trial started 3 min later.

Each trial consisted of a 3 min prestimulus observation (first observation), another 3 min observation after the injection of water (second observation) and finally a 3 min poststimulus observation after the injection of alarm cues (third observation). The flow-through system was turned off during the trials. At the start of the first observation, 2.5 ml of food was introduced and flushed with 20 ml of saltwater. Subsequently, a second observation was initiated by injecting 2.5 ml of food followed by 20 ml of saltwater and flushed with 20 ml of saltwater. At the start of the third observation, 2.5 ml of food was injected, followed by 20 ml of chemical alarm cue and flushed with 20 ml of saltwater. After observational trials, larvae were photographed in a lateral position on a 0.5 mm plastic grid. Standard length (SL) to the nearest 0.01 mm was estimated from each fish from the digital photograph using image analysis software (ImageJ version 1.45s, National Institute of Health, U.S.A., <http://rsbweb.nih.gov/ij/>).

#### Statistical Analyses

The manipulation of both temperature and food could have resulted in a difference in the size of the fish, which could potentially affect their antipredator response. Thus, we included fish size as a covariate in all analyses. We initially ran a two-way repeated measures ANCOVA, using temperature and food as fixed factors, our three observations as a repeated factor and size as a covariate. Given the difficulty in interpreting potential four-way interactions, we split the analysis to address three simple questions: (1) do food and/or temperature affect the baseline activity of the fish; (2) do they affect the response of fish to disturbance (water); and (3) do they affect the response of the fish to risk (alarm cues)? For the first question, we used the feeding strikes from the first time period as raw data in the analysis. For the second and third questions, we computed the percentage change in feeding strikes (water–baseline)/baseline for question 2 and (alarm cues–water)/water for question 3 to take into account the change in prestimulus baseline. Assumptions of homoscedasticity were met, and we verified that no interaction existed between the covariate and any of the factors. We did not predict any differences in behaviour between the first and second observations (control versus water; question 2). However, we predicted that fish able to display an antipredator response to risk would decrease the number of strikes during the third observations (i.e. after an injection of alarm cues; question 3).

## RESULTS

#### Baseline Activity

The two-way ANCOVA revealed a significant interaction between food and temperature ( $F_{1,93} = 14.84$ ,  $P < 0.01$ ), but no effect

of size ( $F_{1,93} = 0.09$ ,  $P = 0.76$ ) on the response of the fish. Tukey's post hoc tests revealed that basal feeding rate in poorly fed fish maintained at high temperature was significantly higher than that from poorly fed fish maintained at ambient temperature ( $P < 0.01$ ), and from that of well-fed fish maintained at ambient ( $P < 0.01$ ) and high temperature ( $P < 0.01$ ; Fig. 1).

#### Response to Disturbance

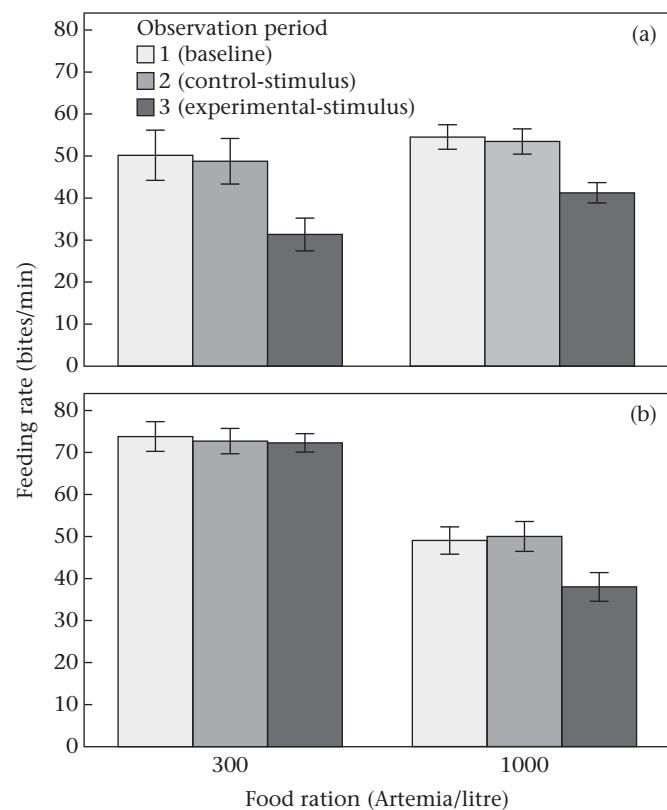
The two-way ANCOVA revealed no effect of food ( $F_{1,92} = 2.47$ ,  $P = 0.12$ ), no effect of temperature ( $F_{1,92} = 2.20$ ,  $P = 0.14$ ) and no interaction ( $F_{1,92} = 0.00$ ,  $P = 0.96$ ) on the behavioural response of the fish (Fig. 1). In addition, the effect of size was not significant ( $F_{1,92} = 3.76$ ,  $P = 0.06$ ).

#### Response to Risk

The two-way ANCOVA revealed a significant interaction between food and temperature ( $F_{1,93} = 16.60$ ,  $P < 0.05$ ), but no effect of size ( $F_{1,93} = 0.09$ ,  $P = 0.77$ ) on the response of the fish. Tukey's post hoc tests revealed that the change in feeding rates for fish in the poorly fed, high-temperature treatment was significantly different from that of poorly fed fish maintained at ambient temperature ( $P < 0.01$ ) and well-fed fish maintained at both ambient ( $P < 0.01$ ) and high temperature ( $P < 0.01$ ; Fig. 1).

#### Size

Despite the absence of any significant effect of size as a covariate, we ensured that the fish did not differ in size between



**Figure 1.** Feeding rate (bites/min  $\pm$  1 SE) for juvenile *Pomacentrus chrysurus* maintained at either (a) 27 °C or (b) 30 °C and either 300 or 1000 *Artemia*/litre twice a day, for 5 days. Time periods 1, 2 and 3 represent, respectively, the behavioural response (feeding rate) of fish to nothing (first observation: baseline), water (second observation: control) and chemical alarm cue (third observation).

treatments. Two-way ANOVA indicated that the standard length of fish was not significantly influenced by food availability and temperature (food availability:  $F_{1,181} = 3.70$ ,  $P = 0.06$ ; temperature:  $F_{1,181} = 0.70$ ,  $P = 0.40$ ; interaction:  $F_{1,181} = 0.54$ ,  $P = 0.46$ ). Standard length (mean  $\pm$  SD) of fish across all treatments was  $13.75 \pm 1.20$  mm.

#### DISCUSSION

Environmental variability in food availability and temperature are known to play major roles in the bioenergetics of ectotherms and has been shown to affect a wide range of traits including physiological condition, growth rate, reproduction and behaviour (Donelson, Munday, McCormick, Pankhurst, & Pankhurst, 2010; McLeod et al., 2013; Nicieza & Metcalfe, 1997; Wildhaber & Crowder, 1990). However, whether the interaction of these environmental variables influences antipredator behaviour in prey organisms and in particular the trade-offs between foraging and predator avoidance remains poorly understood. The results of the present study clearly show that temperature and food level interact to have substantial effects on the energetic requirements of *P. chrysurus* and that this in turn influences the trade-off between predator avoidance and foraging. Fish maintained in the high-temperature–low-food treatment had a significantly higher baseline foraging rate than fish maintained in other temperature and food level combinations, suggesting these fish were subjected to significantly higher energetic demands. Consequently, these differences influenced decisions about how individuals responded to risky situations. Well-fed fish maintained at either ambient or 3 °C above ambient temperature, and fish maintained under low food rations and ambient temperature, all showed a typical antipredator response when exposed to chemical alarm cues. In contrast, fish maintained on low food rations and 3 °C above ambient temperature did not display a measurable antipredator response when exposed to chemical alarm cues. These results highlight how natural variation in environmental parameters may interact to have detrimental effects on the trade-off between satisfying energetic demands and avoiding predation.

Theoretical models, supported by some experimental work, suggest that animals increase their foraging behaviour as their energetic state declines, often at the cost of increased exposure to predators (Caraco et al., 1990; Houston et al., 1993; Lima & Dill, 1990; Lönnstedt & McCormick, 2011; Mangel & Clark, 1986). For example, fish deprived of food exhibited significantly reduced alarm responses when presented with conspecific alarm substances (Chivers et al., 2000; Giaquinto & Volpato, 2001; Lönnstedt & McCormick, 2011; McCormick & Larson, 2008; Smith, 1981). Our study indicates that environmental factors, such as temperature and food availability, may change the basal energetic cost of daily activities and alter the level of sustenance required for the individual to stay below the threshold where they are willing to increase risk. According to the foraging models developed by McNamara and Houston (1986) and Mangel and Clark (1986), the choice of actions made by an animal should be dependent upon its 'metabolic state'. Although many factors induce changes in metabolic rate, it has been suggested that body size, food availability and temperature are key drivers of metabolic rates through their effects on growth rates (Parry, 1983). Increased energetic requirements in individuals with a higher metabolic demand require them to forage more often or take more risks to achieve a higher rate of food intake (Killen et al., 2011).

In isolation, temperature did not significantly affect risk assessment. Well-fed juvenile fish reared at 27 °C showed reductions in foraging activity that were similar in magnitude to those observed at 30 °C. These findings are consistent with similar work done with juvenile temperate fish reared at 3 or 8 °C (Killen &

Brown, 2006). Although water temperature seemed to have a direct impact on their lipid composition and energy storage abilities, newly hatched ocean pout, *Macrozoarces americanus*, at the higher temperature showed a decrease in foraging activity similar in magnitude to that observed at the lower temperature. This is surprising, as it was expected that fish reared at a higher temperature might have continued foraging even while under the threat of predation. The results from the present study indicate that temperature in conjunction with food availability appeared to interact to influence risk assessment in *P. chrysurus*. A threshold towards a risk-prone foraging behaviour was attained for fish reared at 30 °C and in conditions of low food availability. This leads to the suggestion that individuals with a lower physiological condition because of limited food availability are more susceptible to increased temperature and may therefore take greater risks under predation threats to satisfy their energetic requirements. Killen and Brown (2006) may have failed to detect a 'hunger' response at the higher temperature for ocean pout because they used a food ration that may still have been too high to induce an increase in their willingness to engage in risky behaviour.

Although there is a lack of comparative data on threat-sensitive behaviour across a latitudinal gradient, tropical fishes are expected to be more sensitive to elevated temperature because they generally experience less annual variation in water temperature than temperate species (Addo-Bediako, Chown, & Gaston, 2000; Tewksbury et al., 2008). Many tropical ectotherms live much of the year in environments in which body temperatures are near or above optimal temperatures for performance (Nguyen et al., 2011; Rummer et al., 2013; Sunday, Bates, & Dulvy, 2011). Some ectothermic species are able to thermoregulate behaviourally by selecting habitats with preferred temperatures (Breau, Cunjak, & Peake, 2011; Gibson et al., 1998; Vickers, Manicom, & Schwarzkopf, 2011). However, a broad range of tropical ectothermic species, including *P. chrysurus*, are relatively sedentary (McCormick & Makey, 1997), which makes them particularly vulnerable to local environmental changes such as temperature and food availability. How species will be affected by spatial and temporal variability in temperature regimes will mainly depend on their capacity to acclimate thermally and the shape of the species' thermal reaction norm for that geographical locality (Niehaus, Angilletta, Sears, Franklin, & Wilson, 2012; Pörtner & Farrell, 2008). The extent to which individuals are pushed over the optimum of performance characteristics by temperature changes, and the frequency and duration of these occurrences, will determine how food and temperature regimes interact to affect the balance between vigilance and foraging. Future research should therefore further investigate sensitivity of species and populations to changes in temperature, as small increases of just a few degrees appear to have dramatic effects on behavioural and physiological traits of ectothermic species.

Although natural variation in single environmental parameters might not have significant effects on risk assessment, when fish are simultaneously exposed to multiple environmental stressors anti-predator behaviours can be compromised, as shown in the present study. Short-term changes in environmental parameters may therefore play a significant role in predator–prey dynamics, with ramifications for population dynamics. This may be particularly relevant for communities in which supply-side processes play a major role in structuring communities, for example coral reef fishes and larval amphibians. Both juvenile coral reef fishes and tadpoles must grow rapidly to pass through a predation bottleneck if they are to survive to become adults (Almany & Webster, 2006; Doherty et al., 2004; Ferrari, Brown, Bortolotti, & Chivers, 2011). During this time, short-term changes in the environment may significantly alter survival rates, as risk assessment plays a critical role in determining survival (Lönnstedt et al., 2012).

Our results underscore the importance of understanding how the interactive effects of environmental conditions on physiological demands determine behavioural decisions. The balance of information from visual, olfactory and other senses, on which behavioural decisions are based, may also play a crucial role in predator risk assessment. McCormick and Manassa (2008) reported that fish can react with a similar magnitude of antipredator response to a strong visual cue or olfactory alarm cue. Although organisms usually show a graded response to cue intensity (e.g. Holmes & McCormick, 2011), studies have shown that cues from different sources with threat-relevant information tend to lead to an additive response when cues are well represented (e.g. McCormick & Manassa, 2008; Smith & Belk, 2001). It may therefore be expected that under conditions with high energetic requirements, the threshold towards a risk-prone foraging behaviour could be further postponed if additional sensory information is available. We therefore stress the need for further studies assessing cue-based sensitivity in risk taking while foraging, across a range of environmental conditions.

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