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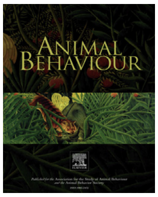

Temperature and food availability affect risk assessment in an ectotherm

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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.

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