

Generalization of learned predator recognition in coral reef ecosystems: how cautious are damselfish?

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Summary

1. Learned predator recognition provides animals with an adaptive mechanism to rapidly adapt to current levels of predation risk. Prey may be able to reduce the cost associated with learning if they can use information learned about known predators to respond to cues from closely related predators with which they are unfamiliar.
2. The capacity of prey to generalize recognition and distinguish between novel predators and non-predators is poorly understood, particularly in species-diverse communities with many closely related predators and non-predators.
3. Lemon damselfish, *Pomacentrus moluccensis*, conditioned to recognize the odour of a predatory moon wrasse, *Thalassoma lunare*, as a risky stimulus, were subsequently tested for their response to *T. lunare* and a range of closely related predators and non-predators from within the Labridae family, a distantly related non-predator and a saltwater control.
4. *Pomacentrus moluccensis* displayed antipredator responses not only to *T. lunare* odour, but also generalized their recognition to congeneric *T. amblycephalum* and *T. hardwicke* odours. Recognition was not extended to other species within (Labridae; *Coris batuensis* and *Halichoeres melanurus*) or beyond (Pseudochromidae; *Pseudochromis fuscus*) the family. Individuals could not distinguish between the predator *T. hardwicke* and non-predator *T. amblycephalum* when generalizing their recognition to congeneric species based on chemosensory assessment alone.
5. Our results demonstrate that reef fishes may limit their generalization to congeneric species only, and may be unable to distinguish between predators and non-predators using chemosensory cues. Recognition patterns may result from uncertainties in predicting the identities of predators in species-diverse communities.

Key-words: antipredator behaviour, coral reef fish, generalization, learning, predator recognition

Introduction

The ability to recognize and respond to predators is essential for prey to survive and reproduce. Individuals that are best able to identify predators and respond appropriately will maximize their fitness and have the greatest chance of surviving to reproduce (Lima & Dill 1990; Kats & Dill 1998). However, predation often is highly variable in time and space, and prey must acquire sufficient information about each predator to respond in a threat-sensitive way (Helfman 1989; Lima & Bednekoff 1999). Learning allows

prey to maximize overall fitness through the accurate identification and assessment of the risk posed by predators through time (Griffin 2004; Ferrari, Wisenden & Chivers 2010a). Despite the existence of mechanisms allowing prey to learn to recognise predators from a relatively safe location (via chemical cues or social learning), collecting predator information may frequently come at the cost of prey having to survive a potentially deadly first encounter with a predator (Kelley & Magurran 2003a).

Recent work suggests that prey living in multi-predator systems can mitigate some of the cost associated with learning by generalizing recognition of one predator to other closely related novel predators (Griffin, Evans &

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Blumstein 2001; Ferrari *et al.* 2007; Stankowich & Coss 2007). For instance, tammar wallabies (*Macropus eugenii*) trained to recognize the sight of a model red fox (*Vulpes vulpes*) as a threat generalized their antipredator response to an unknown predatory feral cat (*Felis catus*), but they did not respond to a non-predatory juvenile goat (*Capra hircus*) (Griffin, Evans & Blumstein 2001). In a similar study, fathead minnows (*Pimephales promelas*) conditioned to recognize the smell of lake trout (*Salvelinus namaycush*) as a predator subsequently recognized the odour of two other salmonid species (Ferrari *et al.* 2007). Interestingly, the generalized response to each species diminished as they became more distantly related from the lake trout. This suggests that generalized predator recognition is a specific case of stimulus generalization, seen in studies from the psychological literature, with odours that are similar to the conditioned odour eliciting a stronger response than odours that are more dissimilar (Ghirlanda & Enquist 2003; Shettleworth 2010). However, such recognition patterns seem highly adaptive, given that for the majority of species, taxonomic relatedness generally correlates with similarity of foraging patterns; close relatives of a known predator are likely to pose a predation threat as well (Bellwood *et al.* 2006; Cowman, Bellwood & van Herwerden 2010). Being able to generalize predator recognition to novel species provides prey with a way to identify potential predators without the cost associated with learning (Griffin, Evans & Blumstein 2001; Ferrari *et al.* 2007; Burns, Foucaud & Mery 2010).

In accordance with the threat-sensitive predator avoidance hypothesis (Helfman 1989), individuals should be flexible when displaying generalization patterns. They should match the extent of generalization to the probability they will respond correctly to more and more distantly related species (Ferrari, Messier & Chivers 2008). The 'Predator Recognition Continuum Hypothesis' (PRCH) suggests that the extent to which individuals generalize recognition depends on the ratio of predators to non-predators within a community (Ferrari *et al.* 2007; Ferrari, Messier & Chivers 2008). Where the predator to non-predator ratio is low (i.e. relatively few predators compared with non-predators within a given taxonomic group), individuals should learn each predator as they encounter them, or alternatively have a narrow generalization window, as the costs associated with responding to non-predatory species may be too high. Where the ratio is high (i.e. many predators but few non-predators), individuals should have a wider generalization window, as the benefits from avoiding a potentially deadly encounter with novel predators will override the initial cost of responding to a few non-predatory species.

Interestingly, Griffin, Evans & Blumstein (2001) suggested that wallabies might have used characteristics specific to predators (e.g. frontally placed eyes) when generalizing recognition to the cat but not the goat. Such cues relate directly to the predators functional morphology and are therefore absent in non-predators. If prey

are able to use such functional cues, they might be able to distinguish between predators and non-predators when generalizing recognition. Such abilities would allow prey to reduce the risk of misidentifying non-predators and generalize to a greater range of predators than predicted by the PRCH. However, their results were confounded by the fact that the goat was more distantly related to the fox than the cat was. Thus, a lack of significant overlap between the cues in general rather than the specific cues could have resulted in wallabies not responding to the goat. Furthermore, studies investigating how velvet geckos generalize recognition of predator using olfactory cues showed they could not distinguish between snakes that ate them and those that did not (Webb *et al.* 2009, 2010).

In aquatic systems, prey often acquire recognition of predators through associative learning, where the predator cue (generally visual or chemical) is encountered simultaneously with a chemical alarm cue (Kelley & Magurran 2003a,b). Chemical alarm cues (released by mechanical damage to the skin during a predation event) are innately recognized by many prey organisms and elicit dramatic short-term increases in antipredator behaviours upon detection (Ferrari *et al.* 2010a).

The extent to which fishes from species-diverse systems, such as coral reef, are able to generalize predator recognition is unknown. The predictions of the PRCH suggest that prey species on coral reefs will display a limited use of predator generalization because of the unreliability of the information. However, if prey are able to utilize cues that are functionally specific to predators, they should distinguish between predators and non-predators and generalize broadly. Therefore, this study experimentally investigated the ability of a common coral reef fish, the lemon damsel (*Pomacentrus moluccensis*; Bleeker, 1853), to learn to recognize predators, generalize this recognition to other related fishes and distinguish between predators and non-predators. After conditioning *P. moluccensis* to recognize the predatory moon wrasse (*Thalassoma lunare*; Linnaeus, 1758) as a threat, individuals were tested for their response to odours from *T. lunare*, a congeneric predator, the six-bar wrasse (*Thalassoma hardwicke*; Bennett, 1830), a congeneric non-predator, the blunt-headed wrasse (*Thalassoma amblycephalum*; Bleeker, 1856), a confamilial predator, the variegated wrasse (*Coris batuensis*; Bleeker, 1856), a confamilial non-predator, the tail-spot wrasse (*Halichoeres melanurus*; Bleeker, 1851), a distantly related predator, the brown dottyback, *Pseudochromis fuscus* (Müller & Trotschel, 1849), or a saltwater control. We predicted that if *P. moluccensis* were able to generalize their recognition of *T. lunare*, they should display the strongest response to *T. lunare* odour and show a weaker response to novel wrasse odours as they become more distantly related. Additionally, if *P. moluccensis* were able to distinguish between predatory modes, then they should not respond to the odours of the non-predatory *T. amblycephalum* and *H. melanurus*.

Materials and methods

STUDY SPECIES

Pomacentrus moluccensis are a common and abundant coral reef fish, found throughout the Indo-Pacific Ocean and Great Barrier Reef. They settle at the end of the larval phase to shallow reefs and are preyed upon by a diversity of predators that include *T. lunare* and *Ps. fuscus*. The wrasse *T. hardwicke* has an ecology similar to *T. lunare*, whilst the congeneric *T. amblycephalum* is a planktivore. The wrasse *C. batuensis* is generalist predators with a diet generally composed of invertebrates and is known to target early developmental stages of fish (Sano, Shimizu & Nose 1984; Steele 1999). *H. melanurus* is a non-piscivorous invertivore. All species co-occur at the shallow reef front at the study location.

COLLECTION AND MAINTENANCE

This research was conducted with fishes collected from the fringing reef around Lizard Island, northern Great Barrier Reef, Australia (14°40'S, 145°28'E). *P. moluccensis* recruits were collected prior to settling, using light traps (see small light trap design, Meehan *et al.* 2001) moored overnight 50–100 m off the reef crest at Lizard Island during November 2010. Collecting recruits prior to settlement ensured they would be naïve to the odours of reef-associated predators. The fish were maintained in 60-l flow-through aquaria, at ambient seawater temperature (29 °C) under a 14:10 light:dark photoperiod. They were fed freshly hatched *Artemia* sp. twice daily.

Five wrasse species, *T. lunare* (17.1 and 23.5 g, individual weights), *T. hardwicke* (26 and 41.4 g), *T. amblycephalum* (5.3, 6.4–3.7, 4.2 and 6.5 g), *C. batuensis* (21.9 and 14.3 g) and *H. melanurus* (9.3, 8.8, 9.6 and 2.4 g) and a distantly related predator, *Ps. fuscus* (6.4, 5.0, 6.9, 4.8 and 5.0 g), were collected from reefs at Lizard Island using barrier nets and clove oil. All fish were maintained in aerated 60-l aquaria.

STIMULUS PREPARATION

Alarm cues were prepared daily, 10 min before the conditioning phase. One *P. moluccensis* per trial was killed by a quick blow to the head. Using a scalpel blade, fifteen superficial cuts were made along each flank of the fish. Fish were rinsed with 15 mL of sea water, and the solution was filtered through filter paper to remove any solid material.

For odour collection, fish were fed squid for 2 days before the start of the experiment, to remove any potential fish cues from their digestive tract. The aquaria flow-through system was turned off during the experiment, except during the daily water exchange, to allow the odour to concentrate. Eighty per cent of the tank water was exchanged at 1600 h daily to ensure odour concentration was constant throughout the experiment. Each aquarium contained at least two individuals of one species. To standardize the concentration of odour between species, the water volume in each aquarium was adjusted so that there was 1 L of sea water per 1.1 g of fish. Sea water containing fish odours was collected directly from these maintenance aquaria.

OBSERVATION TANKS

Experiments were conducted in 13-l flow-through aquaria (36 × 21 × 20 cm, flow at 0.6 L min⁻¹). Tanks were set up as described in Mitchell *et al.* (2011) with a layer of sand, shelter (5 cm diameter) at one end, an airstone at the opposite end and 4 × 6 grid (grid size = 5 × 6 cm) drawn onto the tank. One feeding and one stimulus injection tube were attached to the airstone tube.

CONDITIONING PHASE

Pomacentrus moluccensis were acclimated individually in tanks for at least 2 h before conditioning. The flow-through system was turned off during conditioning to prevent the stimuli from flushing out. We then injected either 15 mL of alarm cue or 15 mL of sea water, both paired with 30 mL of *T. lunare* odour into the tanks. The fish were left for 1 h, after which the flow-through system was turned on again. We conditioned a total of 255 fish, 24 fish per day (1.18 cm ± 0.06; mean size ± 1 SD), between 1400 and 1500 h.

RECOGNITION TRIALS

Trials were conducted between 0730 and 1430 h the day after conditioning. Each trial consisted of an initial 5-min feeding period, a 5-min pre-stimulus observation and 5-min post-stimulus observation. The flow-through system was turned off before the trials started. Fifteen milli litres of sea water was removed from both injection tubes and discarded to remove stagnant water. A further 65 mL was removed and retained for flushing. At the start of the feeding period, we injected 2.5 mL of food (*Artemia* solution, 250 individuals per mL), flushed with 15 mL of sea water, allowing the fish to reach a stable feeding rate before the behavioural observations. At the start of the pre-stimulus observation, an additional 2.5 mL of food was introduced and flushed with 15 mL of sea water. Following the pre-stimulus observation period, we injected 2.5 mL of food, followed by 30 mL of stimulus odour; both were flushed with 15 mL of sea water. The stimulus odours were randomly assigned to each tank and consisted of one of seven odours: *T. lunare*, *T. hardwicke*, *T. amblycephalum*, *C. batuensis*, *H. melanurus*, *Ps. fuscus* and a saltwater control. This ensured that all treatments were run simultaneously.

The behaviour of the fish was observed during the pre- and post-observation periods. We quantified two response variables: number of feeding strikes and number of line crosses. Decreased foraging rate and activity are well-known antipredator responses in a number of prey species (Ferrari *et al.* 2010b). Foraging rate included all feeding strikes irrespective of whether they were successful at capturing prey. Line crosses were counted every time the entire body of the fish crossed a grid line.

STATISTICAL ANALYSIS

Residual analyses revealed that data for feeding strikes met the assumptions of homogeneity of variance and normality, but the data for line crosses were arcsine-transformed to meet parametric assumptions. The proportional change in behaviour from the pre-stimulus baseline ((post-pre)/pre) was calculated and used in the following analysis. The effects of conditioning (alarm cue vs. salt water) and test odour (six fish odours and salt water) were analysed using a two-factor MANOVAS on the number of foraging strikes and line crosses. The MANOVA approach was used due to the correlative nature of the two behaviours (fish feeding more are also likely to be the ones that moved the most).

Due to a significant interaction between the two factors, we divided the analysis into three parts: (i) we performed a one-factor MANOVA to test the effect of test cues on the responses of *P. moluccensis* conditioned with *T. lunare* paired with salt water. This determined whether *P. moluccensis* have an innate response to any of the fish species in the absence of true conditioning. (ii) We performed a series of *t*-tests (or *t'*-tests) comparing the response of *P. moluccensis* conditioned with water to those conditioned with alarm cues to each of the seven odours. This told us which odours were generalized by *P. moluccensis*. (iii) A one-factor ANOVA was performed to test whether there was a difference in the intensity of antipredator responses displayed to all generalized odours.

Results

The two-factor MANOVA revealed a significant interaction between conditioning and test odour on the response of *P. moluccensis* ($F_{12,444} = 2.02$, $P < 0.05$). The univariate tests showed there was a significant interaction between conditioning and test odour for foraging rate, but there was no effect of either conditioning or foraging rate on line crosses (Table 1). There was no effect of test odour on foraging rate for fish conditioned with the *T. lunare* odour and salt water (one-factor ANOVA, $F_{6,123} = 0.581$, $P = 0.745$; Fig. 1). Juvenile *P. moluccensis* did not respond differently to the odour of six fishes or the saltwater control, indicating no innate response to any of the fish used in our experiment.

Independent *t*'-tests revealed that there was a significant effect of conditioning on foraging rate for *P. moluccensis* responding to *T. lunare* ($t_{(23.78)} = -3.011$, $P = 0.004$), *T. hardwicke* ($t_{(34)} = -3.38$, $P = 0.002$) and *T. amblycephalum* ($t_{(35)} = -2.97$, $P = 0.005$) odours. Conditioning had no effect on the response of *P. moluccensis* to *C. batuensis* ($t_{(35)} = -0.27$, $P = 0.79$), *H. melanurus* ($t_{(31)} = -0.94$, $P = 0.36$), *Ps. fuscus* ($t_{(34)} = -0.49$, $P = 0.62$) or salt water ($t_{(33)} = -0.68$, $P = 0.5$). When comparing the intensity of response to the three species eliciting antipredator responses, our results indicated that *P. moluccensis* did not respond differently to the three congeneric species ($F_{2,51} = 0.38$, $P = 0.69$).

Discussion

Naïve juvenile *P. moluccensis* conditioned with *T. lunare* odour and alarm cues learned to recognize *T. lunare* odour as a threat, displaying a distinct antipredator response when subsequently exposed to *T. lunare* odour alone. Juveniles also displayed antipredator responses to the odours of *T. hardwicke* and *T. amblycephalum* but not to odours of species beyond the *Thalassoma* genus. This result demonstrates that reef fish can generalize antipreda-

Table 1. Comparison of the behaviour of juvenile *Pomacentrus moluccensis* in response to the odours of one of six fish species or salt water ('Test odour') after being conditioned with *Thalassoma lunare* odour paired with either a chemical alarm cue or salt water ('Conditioning'). Two-factor ANOVAs were conducted on (a) foraging rate and (b) line crosses (adjusted $\alpha = 0.025$)

Source of variation	df	F	P
(a) Foraging rate			
Test odour	6	3.273	<0.005
Conditioning	1	14.458	<0.0001
Test odour*Conditioning	6	2.950	<0.01
Error	239		
(b) Line crosses			
Test odour	6	1.128	0.347
Conditioning	1	0.215	0.644
Test odour *Conditioning	6	0.545	0.773
Error	239		

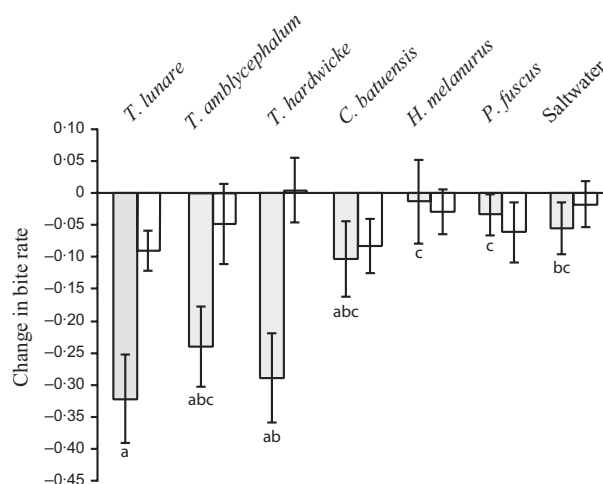


Fig. 1. Proportional change in bite rate (per 5 min observation; mean \pm 1 S.E.) for *Pomacentrus moluccensis* conditioned with *Thalassoma lunare* odour paired with a chemical alarm cue (grey bars) or salt water (white bars) and tested for their response to the odour of *T. lunare*, *T. hardwicke*, *T. amblycephalum*, *Coris batuensis*, *Halichoeres melanurus*, *Ps. fuscus* or a saltwater control. Wrasse species are presented in order of the degree to which they are related to *T. lunare*, with *T. amblycephalum* being the closest and *H. melanurus* being the most distantly related. Letters below bars indicate Tukey's HSD groupings for the individuals conditioned with chemical alarm cue and *T. lunare* odour only.

tor responses associated with a predator odour to the odours of congeneric species that had not previously been associated with risk, similar to findings from fathead minnows (Ferrari *et al.* 2007), wood frogs (*Rana sylvatica*, Ferrari *et al.* 2008; Ferrari & Chivers 2009), tamar wallabies (Griffin, Evans & Blumstein 2001) and geckos (Webb *et al.* 2009, 2010). Interestingly, our results show that whilst individuals could generalize predator recognition to other related species, they were only able to extend recognition to very closely related species and could not distinguish between predators and non-predators. Differences in the patterns of generalization may arise from differences in the taxonomy of coral reef fishes compared with other fish groups such as salmonids, with predator odours diverging at a greater rate in confamilial fish from coral reefs. Alternatively, recognition patterns might reflect the difference in predation risk and the reliability of information available to fish on coral reefs.

As predicted by the PRCH, *P. moluccensis* only generalized recognition to closely related species, within the same genus as the reference predator. By restricting how far they generalized recognition of *T. lunare*, they were able to enhance their chances of correctly generalizing antipredator responses to closely related predators (Ferrari *et al.* 2007; Ferrari, Messier & Chivers 2008). Previous studies have demonstrated that fathead minnows are capable of generalizing recognition to species beyond the genus level (Ferrari *et al.* 2007), and both wallabies (Griffin, Evans & Blumstein 2001) and larval wood frogs (Ferrari & Chivers 2009) generalized recognition to species from different orders. Whilst these differences between the various studies

may arise from methodological idiosyncrasies (such as alarm cue concentration during conditioning) or the rate at which odours differentiate between species within the various taxonomic groups, it is likely that they reflect differences in the composition of the predator community to which prey species were exposed (Ferrari *et al.* 2007). The high species and trophic diversity of genera within coral reef systems complicates the prediction of whether a closely related species is a predator or not. This coupled with the inability to distinguish between predatory status of a novel species would explain why *P. moluccensis* generalized recognition of known predators to only the most closely related species. In contrast, minnows and wood frogs come from systems where predators are generally closely related phylogenetically to one another, thereby increasing the chances of correctly predicting their identity (Ferrari & Chivers 2009). By matching the extent to which they generalize with the probability of correctly responding to a novel predator, they gain the benefits of generalization whilst minimizing the potential costs of unnecessarily losing time and energy on antipredator behaviours.

Previous studies found that the intensity of response to novel predators waned as differences between novel predator and reference predator increased (Griffin, Evans & Blumstein 2001; Ferrari *et al.* 2007; Stankowich & Coss 2007). In contrast, we found *P. moluccensis* appeared to display a hypersensitive antipredator response: responding equally to the reference predator, *T. lunare*, and the odours of species recognized through generalization, matching the findings for juvenile rainbow trout (Brown *et al.* 2011). Whilst the consistent responses to odours may reflect the inability of *P. moluccensis* to differentiate between closely related predators (Brown *et al.* 2011), the lack of differentiation between species might relate to how individuals perceive risk within their environment. Response patterns are dependent not only on current perception of risk (Kelley & Magurran 2003a,b) but also on the predation history to which populations have been exposed (Magurran *et al.* 1992; Brown *et al.* 2009). Given the high levels of predation experienced following settlement (Almany & Webster 2006), it may be beneficial to extend recognition to only a few species and display strong antipredator behaviour when these species are encountered (Helfman & Winkelman 1997; Brown *et al.* 2009). However, as predation risk fluctuates through time, prey may shift between threat-sensitive and hypersensitive responses to maintain maximal fitness (Brown *et al.* 2006).

Pomacentrus moluccensis were unable to distinguish between predators and non-predators when generalizing recognition, matching the findings for velvet geckos using olfactory cues (Webb *et al.* 2009, 2010) but contrasting findings for tamar wallabies (Griffin, Evans & Blumstein 2001) using visual cues. The disparity between the findings for olfactory and visual cues suggests that prey gain different information from each sensory mode. Visual cues appear to provide predator-specific cues (Griffin, Evans & Blumstein 2001). Prey may discriminate between aspects of morphol-

ogy or behaviour that are functionally specific to predators, allowing them to differentiate between predators and non-predators. Predators that are closely related share specific aspects of their morphology that allow efficient detection, capture and handling of prey, such as eye shape and location, mouth shape and size, or body silhouette (Karplus & Algom 1981; Karplus, Goren & Algom 1982; Blumstein *et al.* 2000; Griffin, Evans & Blumstein 2001; Stankowich & Coss 2007). Our results suggest that such functionally distinct cues are missing from non-diet-related predator odours. Future studies should manipulate the availability of predator cues from multiple sensory modes to assess how prey use particular sources of information differentially to assess predation risk within their environment.

Whilst controlled for in this study, diet cues have the potential to act as olfactory markers of the trophic level of the cue source. As previously mentioned, closely related predators often have a significant overlap in diet composition (Cowman, Bellwood & van Herwerden 2010). Prey may therefore be able to recognize differences in diet cues to distinguish between predators and non-predators. A number of studies have demonstrated the importance of diet cues in predator recognition (Mirza & Chivers 2003; Ferrari *et al.* 2010b), and a recent study has even demonstrated that there are predator-specific components to urine for carnivorous mammals (Ferrero *et al.* 2011). 2-Phenylethylamine purified from bobcat urine elicited antipredator responses in rats and mice and was found to be present in high concentration across a range of mammalian carnivores but in low concentrations in herbivores (Ferrero *et al.* 2011). Such chemical compounds may act to supplement information gained from the predator odour alone, allowing prey to further generalize predator recognition across a wide range of predators.

This study demonstrates that even in species-rich communities, it is still advantageous to generalize predator recognition to closely related species. The extent to which individuals generalize may be a result of their species experience with predators over multiple generations. Interestingly, fish generalized recognition to both predators and non-predators despite the fitness costs (i.e. energy expenditure, lost opportunities to forage or mate etc.) associated with misidentifying non-predators. By being cautious and restricting, the extent to which they generalize individuals are able to balance the costs of mislabelling non-predators with the benefits of generalization. Juvenile fish are subjected to a predation-induced bottleneck in the first few days following settlement onto a coral reef (60–90% mortality; Almany & Webster 2006). At such critical times, during development, there is a need to prioritize survival in order to enhance overall fitness. Overestimating risk is therefore likely to be beneficial. Predator recognition can then be refined to enhance fitness with experience (e.g. learned irrelevance; Hazlett 2003) and latent inhibition (Ferrari & Chivers 2006; Mitchell *et al.* 2011) or using additional information from other sensory systems (Ferrari *et al.* 2008).

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References

- Almany, G. & Webster, M. (2006) The predation gauntlet: early post-settlement mortality in reef fishes. *Coral Reefs*, **25**, 19–22.
- Bellwood, D.R., Wainwright, P.C., Fulton, C.J. & Hoey, A.S. (2006) Functional versatility supports coral reef biodiversity. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **273**, 101–107.
- Blumstein, D.T., Daniel, J.C., Griffin, A.S. & Evans, C.S. (2000) Insular tammar wallabies (*Macropus eugenii*) respond to visual but not acoustic cues from predators. *Behavioral Ecology*, **11**, 528–535.
- Brown, G.E., Bongiorno, T., DiCapua, D.M., Ivan, L.I. & Roh, E. (2006) Effects of group size on the threat-sensitive response to varying concentrations of chemical alarm cues by juvenile convict cichlids. *Canadian Journal of Zoology*, **84**, 1–8.
- Brown, G.E., Macnaughton, C.J., Elvidge, C.K., Ramnarine, I. & Godin, J.-G.J. (2009) Provenance and threat-sensitive predator avoidance patterns in wild-caught Trinidadian guppies. *Behavioral Ecology and Sociobiology*, **63**, 699–706.
- Brown, G.E., Ferrari, M.C.O., Malka, P.H., Russo, S., Tressider, M. & Chivers, D.P. (2011) Generalization of predators and nonpredators by juvenile rainbow trout: learning what is and is not a threat. *Animal Behaviour*, **81**, 1249–1256.
- Burns, J.G., Foucaud, J. & Mery, F. (2010) Cost of memory: lessons from 'mini' brains. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **278**, 923–929.
- Cowman, P.F., Bellwood, D.R. & van Herwerden, L. (2010) Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. *Molecular Phylogenetics and Evolution*, **52**, 621–631.
- Ferrari, M.C.O. & Chivers, D.P. (2006) The role of latent inhibition in acquired predator recognition by fathead minnows. *Canadian Journal of Zoology*, **84**, 505–509.
- Ferrari, M.C.O. & Chivers, D.P. (2009) Sophisticated early life lessons: threat-sensitive generalization of predator recognition by embryonic amphibians. *Behavioral Ecology*, **20**, 1295–1298.
- Ferrari, M.C.O., Messier, F. & Chivers, D.P. (2008) Can prey exhibit threat-sensitive generalisation of predator recognition? Extending the Predator Recognition Continuum Hypothesis. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **275**, 1811–1816.
- Ferrari, M.C.O., Wisenden, B.D. & Chivers, D.P. (2010a) Chemical ecology of predator-prey interactions in aquatic ecosystems: a review and prospectus. *Canadian Journal of Zoology*, **88**, 698–724.
- Ferrari, M.C.O., Gonzalo, A., Messier, F. & Chivers, D.P. (2007) Generalisation of learnt predator recognition: an experimental test and framework for future studies. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 1853–1859.
- Ferrari, M.C.O., Vavrek, M.A., Elvidge, C.K., Fridman, B., Chivers, D.P. & Brown, G.E. (2008) Sensory complementation and the acquisition of predator recognition by salmonid fishes. *Behavioral Ecology and Sociobiology*, **63**, 113–121.
- Ferrari, M.C.O., Brown, G.E., Bortolotti, G.R. & Chivers, D.P. (2010b) Linking predator risk and uncertainty to adaptive forgetting: a theoretical framework and empirical test using tadpoles. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **277**, 2205–2210.
- Ferrero, D.M., Lemon, J.K., Fluegge, D., Pashkovski, S.L., Korzan, W.J., Datta, S.R., Spehr, M., Fendt, M. & Liberles, S.D. (2011) Detection and avoidance of a carnivore odor by prey. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 11235–11240.
- Ghirlanda, S. & Enquist, M. (2003) A century of generalization. *Animal Behavior*, **66**, 15–36.
- Griffin, A.S. (2004) Social learning about predators: a review and prospectus. *Learning & Behavior*, **32**, 131–140.
- Griffin, A.S., Evans, C.S. & Blumstein, D.T. (2001) Learning specificity in acquired predator recognition. *Animal Behavior*, **62**, 577–589.
- Hazlett, B.A. (2003) Predator recognition and learned irrelevance in the crayfish *Orconectes virilis*. *Ethology*, **109**, 765–780.
- Helfman, G.S. (1989) Threat-sensitive predator avoidance in damselfish-trumpetfish interactions. *Behavioral Ecology and Sociobiology*, **24**, 47–58.
- Helfman, G.S. & Winkelman, D.L. (1997) Threat sensitivity in bicolor damselfish: effects of sociality and body size. *Ethology*, **103**, 369–383.
- Karplus, I. & Algom, D. (1981) Visual cues for predator face recognition by reef fishes. *Zeitschrift für Tierpsychologie*, **55**, 343–364.
- Karplus, I., Goren, M. & Algom, D. (1982) A preliminary analysis of predator face recognition by *Chromis caeruleus* (Pisces, Pomacentridae). *Zeitschrift für Tierpsychologie*, **58**, 53–65.
- Kats, L.B. & Dill, L.M. (1998) The scent of death: chemosensory assessment of predation risk by prey animals. *Ecoscience*, **5**, 361–394.
- Kelley, J.L. & Magurran, A.E. (2003a) Learned predator recognition and antipredator responses in fishes. *Fish and Fisheries*, **4**, 216–226.
- Kelley, J.L. & Magurran, A.E. (2003b) Effects of relaxed predation pressure on visual predator recognition in the guppy. *Behavioural Ecology Sociobiology*, **54**, 225–232.
- Lima, S.L. & Bednekoff, P.A. (1999) Temporal variation in danger drives antipredator behaviour: the predation risk allocation hypothesis. *American Naturalist*, **153**, 649–659.
- Lima, S.L. & Dill, L.M. (1990) Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology*, **68**, 619–640.
- Magurran, A.E., Seghers, B.H., Carvalho, G.R. & Shaw, P.W. (1992) Behavioral consequences of an artificial introduction of guppies, *Poecilia reticulata*, in N. Trinidad: evidence for the evolution of antipredator behaviour in the wild. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **248**, 117–122.
- Meekan, M.G., Wilson, S.G., Halford, A. & Retzel, A. (2001) A comparison of catches of fishes and invertebrates by two light trap designs, in tropical NW Australia. *Marine Biology*, **139**, 373–381.
- Mirza, R.S. & Chivers, D.P. (2003) Predator diet cues and the assessment of predation risk by juveniles brook char: do diet cues enhance survival? *Canadian Journal of Zoology*, **81**, 126–132.
- Mitchell, M.D., McCormick, M.I., Ferrari, M.C.O. & Chivers, D.P. (2011) Friend or foe? The role of latent inhibition in predator and non-predator labelling by coral reef fish. *Animal Cognition*, **14**, 707–714.
- Sano, M., Shimizu, M. & Nose, Y. (1984) *Food Habits of Teleostean Reef Fish in Okinawa Island, Southern Japan*. University of Tokyo Press, Tokyo.
- Shettleworth, S.J. (2010) *Cognition, Evolution and Behaviour*, 2nd edn. Oxford University Press, New York.
- Stankowich, T. & Coss, R.G. (2007) The re-emergence of felid camouflage with the decay of predator recognition in deer under relaxed selection. *Proceedings of the Royal Society of London Series B-Biological Sciences*, **274**, 175–182.
- Steele, M.A. (1999) Effects of shelter and predators on reef fishes. *Journal of Experimental Marine Biology and Ecology*, **233**, 65–79.
- Webb, J.K., Du, W.G., Pike, D.A. & Shine, R. (2009) Chemical cues from both dangerous and non-dangerous snakes elicit antipredator behaviours from a nocturnal lizard. *Animal Behavior*, **77**, 1471–1478.
- Webb, J.K., Du, W.G., Pike, D.A. & Shine, R. (2010) Generalization of predator recognition: Velvet geckos display antipredator behaviours in response to chemicals from non-dangerous elapid snakes. *Current Zoology*, **56**, 337–342.

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