Predators favour mimicry in a tropical reef fish

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Batesian mimicry evolves when the 'umbrella' of protection provided by resemblance to a conspicuous unpalatable model species is sufficient to overcome increased predation risk associated with greater conspicuousness. However, the shape and extent of this umbrella, that is, how the level of protection provided by mimicry changes with degree of resemblance between model and mimic, is poorly known. We investigated the response of wild predatory fishes to plastic replicas of a model-mimic species pair of tropical reef fishes, *Canthigaster valentini* (a toxic pufferfish, the model) and *Paraluteres prionurus* (the putative mimic), and additional replicas with progressively lower degrees of resemblance to the mimic species. Our results reveal a relatively broad region of protection, indicated by a reduced approach rate by piscivorous fishes, surrounding the colour pattern of the model species. Protection increased with increasing resemblance. By contrast, the response of non-piscivorous fishes was unrelated to degree of resemblance of replicas to the model. Our results suggest that piscivorous fishes on the reef are educated regarding the toxicity of *C. valentini*, and that avoidance of fish having the pufferfish colour pattern has generated selection favouring mimetic resemblance by the palatable *P. prionurus*. The relatively broad protective umbrella has probably facilitated the initial evolution of resemblance in the palatable prey species despite the potential hazards of greater conspicuousness.

Keywords: Batesian mimicry; predation; natural selection; coral reef fish

1. INTRODUCTION

Batesian mimicry appears to be widespread, but we still know little about the process of selection driving mimetic convergence in the wild (Waldbauer 1988; Brodie 1993; Brodie & Janzen 1995; Pfennig *et al.* 2001). One contribution of field studies to the study of mimicry is to provide a measure of the 'umbrella' of protection thought to surround the phenotype of conspicuous, unpalatable prey species (models), and to favour resemblance in palatable prey (the mimics). Knowledge of the shape and extent of this protective umbrella is crucial to addressing numerous issues in the evolution of mimicry, including the following: whether selection by predators is the mechanism driving evolution of resemblance to an unpalatable model; whether precise resemblance is weakly or strongly favoured by selection; whether even crude resemblance to a model has a detectable effect on survival; and whether the required initial stage in the evolution of mimicry (i.e. increased conspicuousness but only slight resemblance) represents a significant hurdle to the evolution of Batesian mimicry. Field studies provide further information on the behaviour of wild predators in response to varying degrees of mimetic resemblance by edible prey.

Here, we present the results of a field study designed to measure the protection from predators generated by a conspicuous, unpalatable pufferfish species, the black-saddled toby, *Canthigaster valentini* (Tetraodontidae) (figure 1), to colour patterns that resemble it. This species

co-occurs with a presumed Batesian mimic, the mimic leatherjacket *Paraluteres prionurus* (Monacanthidae) (Tyler 1966; figure 1), on coral reefs throughout the Indo-Pacific (Myers 1999). Puffer fish in general are highly unpalatable. Their skin and other tissues contain tetrodotoxin, a potent neurotoxin that is lethal to a wide variety of fish species (Halstead 1967). Tetrodotoxin has not been isolated specifically from *C. valentini* but is known from at least one of its congeners, *Canthigaster bennetti*, and from numerous species in related genera (Halstead 1967). After ingesting a *C. valentini*, captive naive piscivorous fishes have been observed to eject and subsequently avoid them (Gladstone 1987).

P. prionurus is the only known putative mimic of *C. valentini*. Its flesh is palatable to some wild piscivorous fishes (M. J. Caley and D. Schluter, unpublished data), suggesting that it is a harmless (i.e. Batesian) mimic. We cannot yet be certain that it lacks noxious properties entirely, and we do not address this here. Two other species of *Paraluteres*, *P. arqat* in the Red Sea and *P.* sp. in the Indian Ocean, are supposed Batesian mimics of two other conspicuous canthigasterine pufferfish, *Canthigaster margaritatus* and *Canthigaster solandri*, respectively (Tyler 1966; Lieske & Myers 1994). The taxonomic distribution of the association suggests parallel evolution of mimicry in closely related species or, more likely, cospeciation of model and mimic lineages. By contrast, species of *Brachaluteres*, the probable sister genus to *Paraluteres* (B. Hutchins, personal communication), are cryptic (Hutchins & Swainston 1986).

We tested the hypothesis of mimicry in *P. prionurus* by measuring the advantage of colour pattern resemblance to the black-saddled toby. Advantage was assessed by rec-

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Proc. R. Soc. Lond. B (2003) **270**, 667–672
DOI 10.1098/rspb.2002.2263

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ording the responses of wild fishes on the Great Barrier Reef to a series of plastic replicas presenting a range of colour patterns. Our goals were to test whether similarity to the pufferfish pattern reduced the frequency of approaches by piscivorous predators, and to measure the breadth of patterns yielding at least some protection.

2. MATERIAL AND METHODS

(a) *Replica construction*

A preserved individual of the pufferfish species *C. valentini* was used to construct several casting moulds with alginate flexible moulding compound (Espe Gmbh & Co., Seefeld, Germany). A set of 18 replicas was made by pouring clear casting resin (Huntsman Chemical Company Pty Ltd, Footscray, Australia) into the moulds and allowing the resin to cure. The casts were then removed, air-dried and painted with acrylic craft paints (Vynol Derivan Pty Ltd, Mortlake, Australia). Each replica was about 8 cm in total length (TL), which approaches the maximum TL of both model and mimic species on the Great Barrier Reef (9–10 cm; Randall *et al.* 1990). To limit the role of other sources of variation in predator response, we did not vary replica size or shape in this initial study so that the effect of colour pattern alone could be assessed. These model and mimic species have similar, although not identical, body shapes (figure 1; Randall *et al.* 1990). *P. prionurus* and *C. valentini* differ in the size and number of dorsal and anal fins, but these features are colourless in live specimens. All fins except the caudal were lacking from the plastic replicas (figure 2).

Fifteen out of the 18 replicas were painted to resemble the model and mimic species by degrees, using a sequence of five colour patterns (figure 2). The first pattern resembled that of the model species, *C. valentini*, as closely as possible (figure 2*a*). We focused on duplicating the conspicuous dark dorsal bands, the yellow-brown lateral spots and the yellow wash over the back and caudal fin. We did not attempt to paint the subtle colours and hues around the eyes (figure 1). The second pattern was similar to the first but resembled the mimic species, *P. prionurus*, in having fewer, browner lateral spots (figure 2*b*). Colour patterns of the model and mimic replicas were copied from a live specimen of each. The remaining three patterns were progressively more distant from the mimic (figure 2*c–e*). Choice of these three patterns was somewhat arbitrary, but our goal was to gradually reduce resemblance to the model species by breaking up the distinctive brown dorsal bands and removing the yellow accents from the caudal fin, upper back and lateral spots, while simultaneously maintaining conspicuousness of the overall colour patterns. The resulting range of colour patterns is broad in the sense that it extends far beyond the range of perceptible differences between the putative model and mimic species in these traits (figure 1). Because we reduced both traits progressively, our rank ordering of resemblance of these replicas to the model and mimic replicas should be robust if piscivores use either of these traits separately, or in concert, in evaluating similarity to the model. This strategy solves the problem that predators and human researchers do not rank otherwise unordered prey patterns in the same way (Dittrich *et al.* 1993).

Clearly our replicas were not identical in colour pattern to wild fish. It was not our goal, however, to estimate the predation risk faced by real models and mimics in the wild. Instead, our goal was to test relative degrees of protection afforded by different levels of resemblance to the model phenotype. As shown below, piscivores responded differently to these different colour patterns. This suggests that the replicas presented a sufficiently broad range of resemblance to the wild pufferfish to enable us to estimate characteristics of the umbrella of protection available to mimics of *C. valentini*.

The remaining three replicas were painted with a non-mimetic colour pattern completely distinct from the rest, having a bluish-grey back and white belly (figure 2*f*). This colour combination was intended to gauge responses of piscivores and non-piscivores to a simple pattern crudely approximating that seen in many pelagic fish species (Helfman *et al.* 1997). This pattern provided an additional baseline for testing the protective benefits of mimicking *C. valentini*.

An alternative approach to gradually reducing resemblance to the pufferfish would be to use the historical sequence of colour patterns, from the cryptic supposed ancestor of the mimic (e.g. *Brachyluteres*), to its present form. Unfortunately, this sequence is not known and may be impossible to determine, given the variety of colour patterns that exist even among close relatives in *Canthigaster* and in *Paraluteres*. For now, we restrict attention to the umbrella of protection generated by the current phenotype of *C. valentini*, while acknowledging that the historical colour patterns remain to be evaluated.

Although all six colour patterns of painted replicas were conspicuous, variation in conspicuousness among patterns was difficult to eliminate. Nevertheless, by progressively removing a bright colour (yellow) and the bold dark bars we assumed that colour patterns more distant from the model would be no more conspicuous than replicas painted to resemble the model, and hence that predators should find them no more attractive under the null hypothesis. Additionally, we compared the behaviour of different classes of fish attracted to the replicas to test the importance of variation in conspicuousness. If variation in conspicuousness *per se*, rather than degree of mimetic resemblance, is the cause of differences in piscivore responses to different colour patterns, then we expect fishes that are unlikely to interact with *C. valentini*, such as non-piscivorous and nocturnal species, to respond to replicas in the same way as diurnal piscivores. By contrast, if degree of mimetic resemblance is the cause of variation in piscivore responses, then non-piscivorous and nocturnal species should pay little attention to degree of mimetic resemblance in replicas.

(b) *Field trials*

We placed our replica fish at depths of 5–10 m on, or adjacent to, submerged reefs in the lagoon and on fringing reefs of Lizard Island (14°40′ S; 145°28′ E) in the northern section of Australia's Great Barrier Reef. Both *C. valentini* and *P. prionurus* are encountered at these depths and in these habitats in the study area. A trial involved observing a single replica placed at a fixed location for 5 min by a solitary diver (one of the authors) in a prone position on the substrate 3–6 m away, as far away as visibility allowed. We chose locations close to steep walled reefs, small caves or overhangs, features often used as cover by predatory fishes. Each replica was given buoyancy by attaching one end of a 2 m section of monofilament line to a point on its upper back, above the centre of gravity, and attaching the other end to an inverted clear plastic 5 ml vial filled with air. A second monofilament line was attached to the nose of each replica, passed under a lump of coral lying on the substrate, and extended to the observer. This second line was used by the observer to impart motion to the replica. Pulling on the line cause the replica to tip forward and 'swim' down to the substrate. Releasing the line caused the replica to rise up to 2 m

above the substrate while remaining horizontal. A regular sequence of upward and downward movements was carried out during each trial.

A single dive by an observer yielded 3–12 trials using the same individual replica. Separate trials on a single dive were spaced at least 20 m apart to ensure that the same potential predators were not repeatedly exposed to the same replica. We treated all the results obtained from a dive as a single independent observation, since separate trials on the same dive were not independent. Individual replicas were used during no more than one dive per day, and were repainted before reuse. All trials were conducted between 0830 and 1200 Australian Eastern Standard Time and each of two divers conducted two dives each day. Replica type was randomized among dives, divers and days, and all replica types were tested in both lagoon and fringing reef habitat. Individual sites were visited only once throughout the study.

(c) *Responses to replicas*

The authors recorded the number of individual fish approaching a replica. An approach was considered to be any instance in which an individual fish swam towards the replica and either halted and visually inspected it within a distance of 2 m or actually bit or engulfed the replica. Repeated approaches by the same fish were counted as a single approach.

Fish species attracted to the replicas were identified using the guide by Randall *et al.* (1990) and classified as piscivores or non-piscivores. Piscivores included groupers (Serranidae; mainly *Cephalopholis cyanostigma* and *Cephalopholis microprion*), snappers (Lutjanidae; mainly *Lutjanus carponotatus* and *Lutjanus fulviflammus*) and wrasses (Labridae; mainly *Cheilinus diagrammus*). Soldierfish and squirrelfish (Holocentridae; mainly *Sargocentron spiniferum*) were classified as non-piscivores because they are chiefly nocturnal and feed mainly on invertebrates (Randall *et al.* 1990). Nevertheless, holocentrids were encountered under overhangs, and in caves, along the reef walls where we carried out our trials, and they frequently approached and bit the replicas.

(d) *Analysis*

All analyses of data were carried out using S-PLUS 6.0 (Insightful Corp. 2001). We used single-factor ANOVA to compare mean predator responses to replicas having different colour patterns. We also compared the fit of this 'full' ANOVA model with the fit of a reduced model in which mean predator response to replicas was a monotonic, non-decreasing function of decreasing replica resemblance to the pufferfish (Barlow *et al.* 1972). The monotonic fit was calculated using the isoreg function, written by T. R. Johnson (Department of Psychology, University of Illinois at Urbana, USA) for S-PLUS. This monotonic model had one less parameter than the full ANOVA model because it collapsed means for two of the five replicas to a single value. The fits of the full and reduced models were compared using a standard *F*-test. Subsequently, we used rank correlation to compare responses to replicas by different groups of fishes.

3. RESULTS

A total of 283 fishes approached the plastic replicas during 267 trials. A wide variety of piscivorous and non-piscivorous fish species approached and occasionally attacked the replicas. No fish of any primarily planktivorous, herbivorous or detritivorous species approached the replicas. We assumed, therefore, that the frequency of approaches

and attacks was a reasonable estimator of predation risk. Groupers predominated, accounting for 49% of observations, followed by snappers (17%). Wrasses (14%) and holocentrids (14%) accounted for most of the remaining observations.

Piscivore behaviour changed significantly in response to colour pattern (figure 3). Replicas most resembling the unpalatable pufferfish received few visits by piscivores, whereas replicas weakly resembling the pufferfish received more visits (ANOVA; $F_{4,20} = 7.56$, $p = 0.0007$). Replicas painted in the baseline grey/white pattern were approached by piscivores at roughly the same rate as the most divergent colour patterns in the pufferfish resemblance series (figure 3). This similarity of responses of piscivores to these two replica types suggests that the most divergent colour pattern provided a reasonable baseline predation risk in the absence of any mimetic resemblance. In contrast to the adjustable responses of piscivores to varying degrees of mimetic resemblance, no significant change was detected in the behaviour of non-piscivores to different colour patterns in the resemblance series (figure 4; ANOVA; $F_{4,20} = 1.34$, $p = 0.29$).

The approach rate by piscivores increased approximately monotonically with decreasing resemblance between replicas and pufferfish (figure 3), and full ANOVA fitted the data hardly any better than a constrained monotonic fit having one less parameter ($F_{1,20} = 0.043$, $p = 0.84$). For this reason, subsequent tests involved use of a simple one-tailed rank correlation between approach rate and replica resemblance with the grey/white baseline colour pattern excluded. The approach rate by piscivores was correlated with the resemblance of replicas to pufferfish (Kendall's $\tau = 0.53$, $n = 25$, $p = 0.0001$), whereas the approach rate by holocentrids (non-piscivore control) was uncorrelated with replica resemblance ($\tau = 0.13$, $n = 25$, $p = 0.16$). The difference between piscivores and non-piscivores in their approach rates was also correlated with resemblance ($\tau = 0.45$, $n = 25$, $p = 0.0006$), indicating that the behaviour of the two categories of fish diverged significantly with decreasing resemblance of replicas to pufferfish.

Piscivores from the two main families responded similarly to the replicas (figure 5). A trend towards increasing predator approach rate with decreasing resemblance was significant in the groupers (Serranidae), the most frequent visitors to the replicas ($\tau = 0.37$, $n = 25$, $p = 0.004$), and in the snappers (Lutjanidae) ($\tau = 0.40$, $n = 25$, $p = 0.0011$). Piscivorous wrasses (Labridae) were uncommon and the trend in approach rate with resemblance of replicas was noisy ($\tau = 0.11$, $n = 25$, $p = 0.16$). Nevertheless, the approach rate was highest with the most different replica even in this group (figure 5).

4. DISCUSSION

Our results confirm the presence of an 'umbrella' of protection surrounding the colour pattern of an unpalatable species of pufferfish. Prey resembling the pufferfish are protected from piscivorous predators, whereas protection declines with decreasing resemblance of mimic to model. The results indicate that piscivorous fishes on the reef are educated regarding the toxicity of *C. valentini* or that they have an innate aversion to the colour pattern
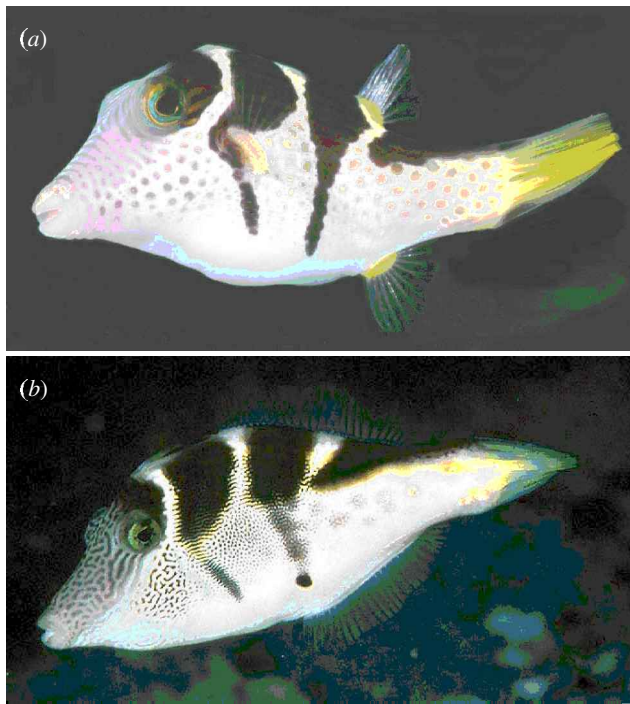
Figure 1. (*a*) The pufferfish, *Canthigaster valentini* (Tetraodontidae). (*b*) The putative Batesian mimic, *Paraluteres prionurus* (Monacanthidae). Photographs: David Wachenfeld and John Randall, respectively; reproduced with permission.

of this specific pufferfish species. The results support the hypothesis that protection from predators is a mechanism of selection favouring increased resemblance to the pufferfish. This finding in turn supports the hypothesis of mimicry in the palatable leatherjacket, *P. prionurus*.

Our findings also indicate a relatively broad region of protection surrounding the colour pattern of the unpalatable model species. Protection extends well beyond the colour pattern of the putative mimic species. All but the fifth-most divergent colour pattern in the resemblance series appeared to give some protection from predators relative to the baseline (figure 3). The fact that we detected varying degrees of protection in a series of painted replicas, even the most similar of which was not an exact match to the pufferfish (figures 1 and 2), further suggests a relatively broad 'umbrella'. This result counters one potential hypothesis for the rarity of pufferfish mimicry in reef fish communities: that protection is provided only when resemblance is strong, and that the evolution of mimicry required a fortuitous close resemblance to the model in the initial stage. Instead, it is reasonable to conclude that mimicry in this system could have begun with only moderate resemblance, and that closer resemblance between model and mimic evolved gradually thereafter. Conversely, the rise in piscivore approach rate at the outer extreme of the colour pattern series, that least resembling the puffer fish (figure 3), further underscores the price of high conspicuousness unaccompanied by resemblance to an unpalatable model species.

Our result is based on a series of replicas in which even those patterns departing moderately from the model-mimic colour patterns are novel and not found in the local reef community. In real life, the protection provided by a
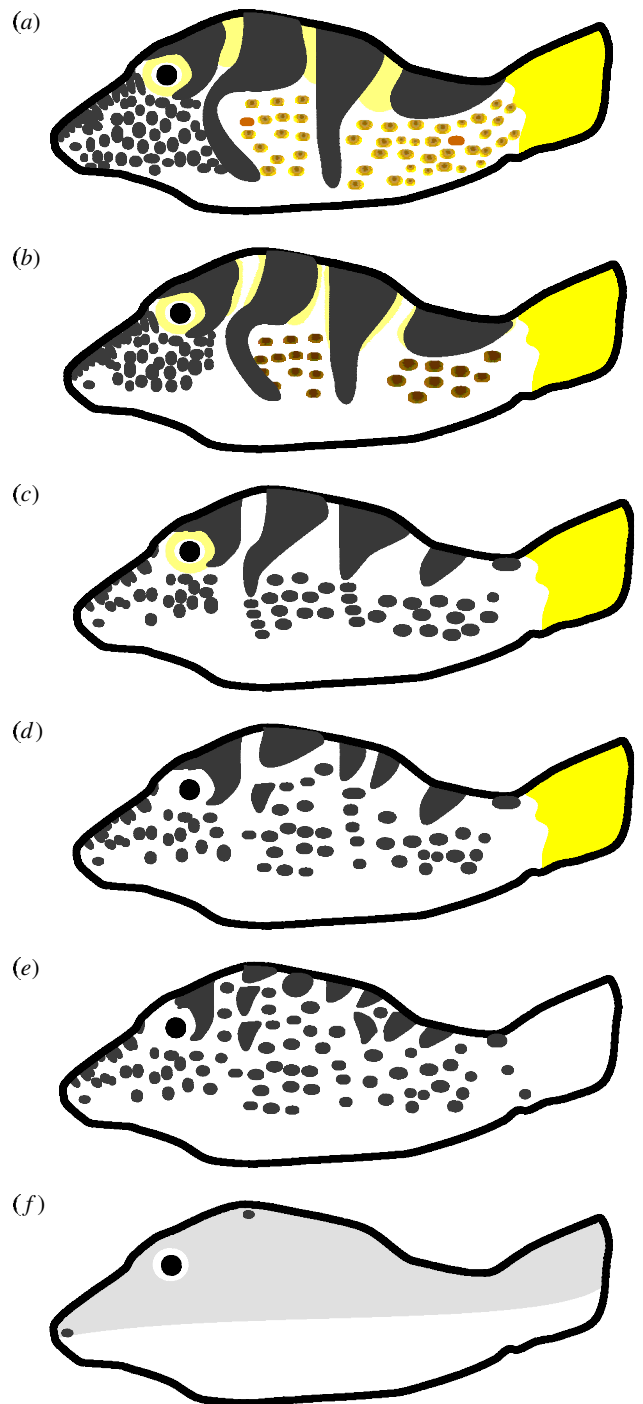

Figure 2. Colour pattern series used in the field experiment.

novel pattern only moderately resembling an unpalatable model might be temporary, and become quickly reduced as predators learned to discriminate between the novel pattern in the palatable species and the familiar pattern in the unpalatable model. Perhaps in this way predator learning could narrow the protective umbrella relative to that demonstrated here. On the other hand, a broad umbrella of protection would still be expected if the cost to a predator of making a mistake (attacking a pufferfish instead of a mimic) is high or the chance of making such a mistake is high because of inability of predators to resolve differences in colour patterns (Edmunds 2000). It is thought that a high cost of error is one reason why venomous snakes appear to have so many imperfect mimics
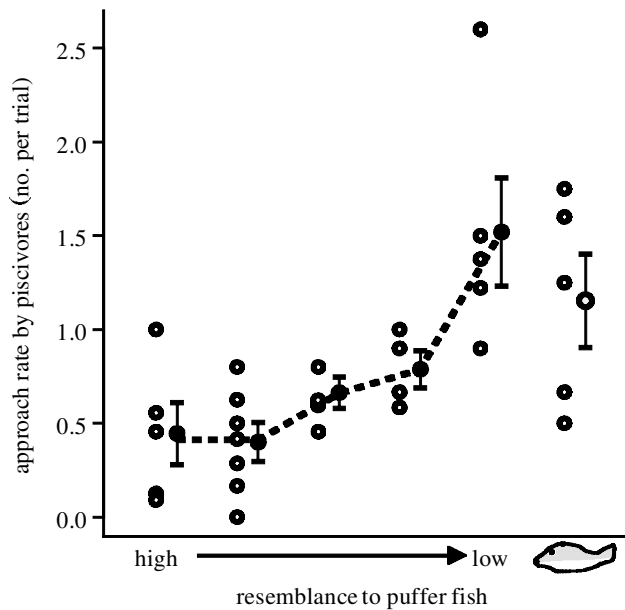
Figure 3. Predator response to colour pattern of replicas. The sequence of replicas, from high to low resemblance, is that illustrated in figure 2. Each open symbol represents the mean of 3–12 individual trials. Filled symbols and error bars are means and standard errors. The dashed line is the best-fit function constrained to be monotonic and non-decreasing.

(Greene & McDairmid 1981; Pough 1988; Brodie 1993). Unfortunately, we do not yet have information on this cost in our pufferfish system.

Protection of mimetic forms has also been demonstrated in the few other field studies of putative Batesian mimicry systems. For example, Brodie (1993), Brodie & Janzen (1995), Hinman *et al.* (1997) and Pfennig *et al.* (2001) have shown that predatory birds avoid plasticine replicas of snakes that resemble highly venomous coral snakes, even when mimicry is only partial (e.g. Hinman *et al.* 1997). Protection provided to a given mimetic colour pattern disappeared in an area outside the geographical range of the venomous models (Pfennig *et al.* 2001). Sternburg *et al.* (1977) and Jeffords *et al.* (1979) showed that predators differentially attack male promethea silk-moths painted with a pattern that reduced their otherwise strong resemblance to unpalatable pipevine swallowtail butterflies. Field studies of Mullerian mimicry, in which both model and mimic are unpalatable, have also shown that greater protection from predators is provided to colour pattern phenotypes that resemble the dominant warning colour phenotype in the site (Mallet & Barton 1989; Kapan 2001). The present study differs from previous field studies in that we used a gradation of colour patterns ranging from resemblance to the model to weak or no resemblance, which allows finer estimation of the shape and extent of the umbrella of protection.

Further aspects of the evolution of mimicry in the leatherjacket–pufferfish system may be tested using a similar approach. In particular, the question of whether the initial stage in the evolution of mimicry (greater conspicuousness accompanied by only weak resemblance to the pufferfish) represents an adaptive hurdle might be addressed with additional colour pattern series that include ancestral
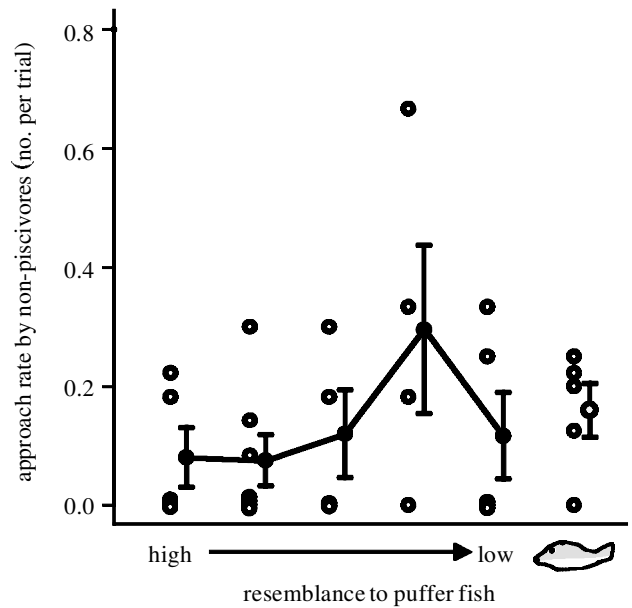

Figure 4. Response of non-piscivores (holocentrids: squirrelfish and soldierfish) to colour pattern of replicas. Each open symbol represents a set of 3–12 individual trials. Filled symbols and error bars are means and standard errors.
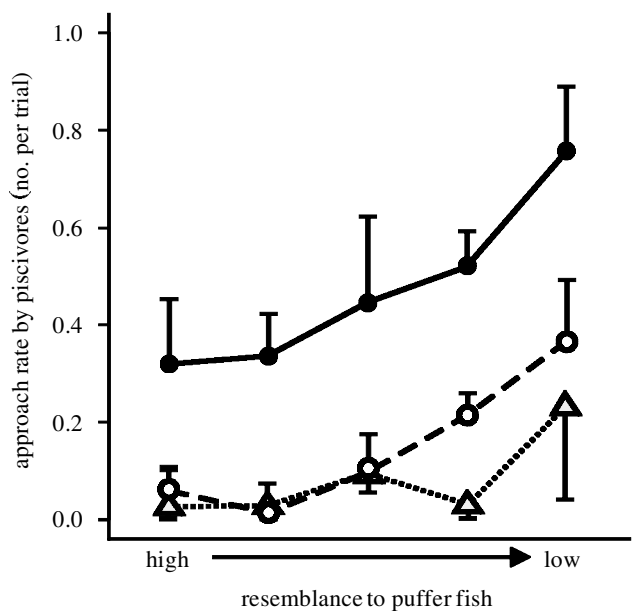

Figure 5. Response of piscivores in different families to colour pattern of replicas. Symbols and error bars are means and standard errors (one-sided only, to minimize overlap). Filled circles, Serranidae; open circles, Lutjanidae; triangles, Labridae.

cryptic forms. Other components of mimicry by *P. prionurus* might also be addressed. To our eyes *P. prionurus* resembles *C. valentini* in body shape (figure 1) to a greater extent than do other leatherjackets. Perhaps resemblance in shape has also been favoured by predators. Or, fortuitous similarity in shape resulting from other selection pressures may have increased the effectiveness of selection for colour pattern resemblance, and favoured the evolution of mimicry in colour pattern. The hypothesis of Batesian mimicry also assumes that the pufferfish gains no advantage (indeed, it may be harmed) by resembling the

leatherjacket. Finally, *P. prionurus* shows remarkable similarity to *C. valentini* in habitat affinity and in some aspects of behaviour. For example, we have observed individuals of *P. prionurus*, when approached by a diver, join parties of *C. valentini*. It seems likely that many aspects of the biology of these mimics continue to be shaped by predator selection against conspicuous phenotypes that resemble the unpalatable model less well.

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