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LETTER

Ecology shapes the evolutionary trade-off between predator avoidance and defence in coral reef butterflyfishes

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Abstract

Antipredator defensive traits are thought to trade-off evolutionarily with traits that facilitate predator avoidance. However, complexity and scale have precluded tests of this prediction in many groups, including fishes. Using a macroevolutionary approach, we test this prediction in butterflyfishes, an iconic group of coral reef inhabitants with diverse social behaviours, foraging strategies and antipredator adaptations. We find that several antipredator traits have evolved adaptively, dependent primarily on foraging strategy. We identify a previously unrecognised axis of diversity in butterflyfishes where species with robust morphological defences have riskier foraging strategies and lack sociality, while species with reduced morphological defences feed in familiar territories, have adaptations for quick escapes and benefit from the vigilance provided by sociality. Furthermore, we find evidence for the constrained evolution of fin spines among species that graze solely on corals, highlighting the importance of corals, as both prey and structural refuge, in shaping fish morphology.

Keywords

Chaetodontidae, constraint, coral reef ecology, evolutionary trade-off, foraging strategy, functional morphology, phylogenetic comparative method, predation risk, social behaviour, spines.

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INTRODUCTION

Predation risk is determined by an individual's chance of encountering a predator and their chance of death given an encounter (Lima & Dill 1990). Both of these components can be affected by traits specific to an individual such as behaviour and morphology. Changes in traits that influence predation risk should be adaptive and under strong selection, given their substantial effects on fitness (Abrams 2000). A number of studies have examined the microevolutionary effects of predation risk on adaptive trait changes in behaviour (reviewed in Lima 1998; Bednekoff 2007) and morphology (Brönmark & Miner 1992; Andersson *et al.* 2006; Langerhans 2009; Frommen *et al.* 2011). Few studies have examined the effects of predation risk on a macroevolutionary scale and considered the complexity of integrating gross morphological antipredator adaptations with behavioural decision-making (but see Blanchard & Moreau 2017).

Across teleosts fishes, fin spines and body shape may have evolved synergistically to overcome the limited gape of predators (Price *et al.* 2015). This suggests that the microevolutionary effects of predation risk scale up to macroevolutionary differences in adaptive traits. Given the magnitude of fish shape variation, it is important to explore how predation risk has shaped morphology more specifically and determine whether morphological defences are correlated among closely related species, and whether antipredator adaptations exhibit evolutionary trade-offs with the potential to promote or constrain trait evolution. Butterflyfishes (Family Chaetodontidae) exemplify an extreme body shape and possess potent structural defences, featuring an unusually deep body and numerous, long and strong fin spines. Our initial aim is to determine whether body depth and spine length have evolved synergistically within butterflyfishes.

The evolution of antipredator adaptations can be promoted or constrained through complex interactions between organisms and their environments. Social interactions can increase vigilance for predators (Pitcher 1986; Brandl & Bellwood 2015) and reduce the probability of being predated upon (Domenici & Batty 1997). However, the influence of sociality on the evolution of antipredator adaptations remains unclear (but see Ab Ghani *et al.* 2016). The role of sociality may be particularly important to butterflyfishes because most species feed by biting prey from the benthos, increasing their risk of predation relative to fishes that feed with a horizontal posture (Krause & Godin 1996; Domenici 2010). Furthermore, foraging strategy, comprising prey type, its proximity to refuges, mode of prey detection, foraging frequency, diet specialisation and resource dynamics, may affect predation risk (Webb 1986; Brown & Kotler 2004; Bednekoff 2007; Chivers *et al.* 2008; Preisser *et al.* 2009; Domenici 2010), and the ability of organisms to adapt morphologically. It is not known how foraging strategy influences the evolution of antipredator adaptations in fishes, or how it interacts with social behaviour.

Butterflyfishes comprise both social and solitary species, and while most are benthic biters, foraging strategies vary from actively hunting benthic invertebrates to obligate grazing on corals. Obligate grazers frequently consume readily available prey, often within defended territories (Righton & Mills 2006; Cole & Pratchett 2013), while benthic hunters dynamically search over larger distances for prey items (Roberts & Ormond 1992; Cole & Pratchett 2013). Assuming that benthic hunters and solitary species experience greater predation risk as a consequence of their foraging strategy and social behaviour, we predict they will have evolved more robust morphological defences. Additionally, we predict that morphological

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defences will trade-off with antipredator adaptations that facilitate predator avoidance. Here, we explore how antipredator adaptations have evolved through time, and the breadth of trait space occupied by species with shared ecologies and behaviours, to gain insight into the selective pressures and evolutionary constraints that shape trait diversity. Specifically, we examine how social behaviour and foraging strategy have influenced the evolution of butterflyfish antipredator adaptations on a macroevolutionary scale.

MATERIALS AND METHODS

Sampling and morphometric measurements

We generated a morphological dataset of eight traits that function to defend against attacks or enhance detection and predator avoidance (Fig. 1). Traits that defend against attacks from gape-limited predators include the lengths of the longest dorsal and anal fin spines and their offset, length of the pelvic fin spine, body depth and maximum body size (Hoogland *et al.* 1956; Werner 1974; Hoyle & Keast 1987; Reimchen 1991; Bosher *et al.* 2006). Eye diameter determines a fishes' ability to detect predators (Sadler 1973; Fernald 1990), and caudal fin shape affects how well a fish can avoid predation using unsteady swimming (Blake 2004). Traits were quantified by linear morphometric measurements (mm; see Appendix S1 in Supporting Information for measurement descriptions) from a total of 351 whole, ethanol-preserved or cleared and stained specimens, representing 87 chaetodontid species (Eschmeyer *et al.* 2017; average number of specimens per species = 4; range = [1,7]; see Table S1 in Appendix S2). Specimens were loaned from the Smithsonian National Museum of Natural History, the Field Museum of Natural History, the California Academy of Sciences and P. Wainwright's personal collection (see Table S1 in Appendix S2 for specimen catalogue numbers).

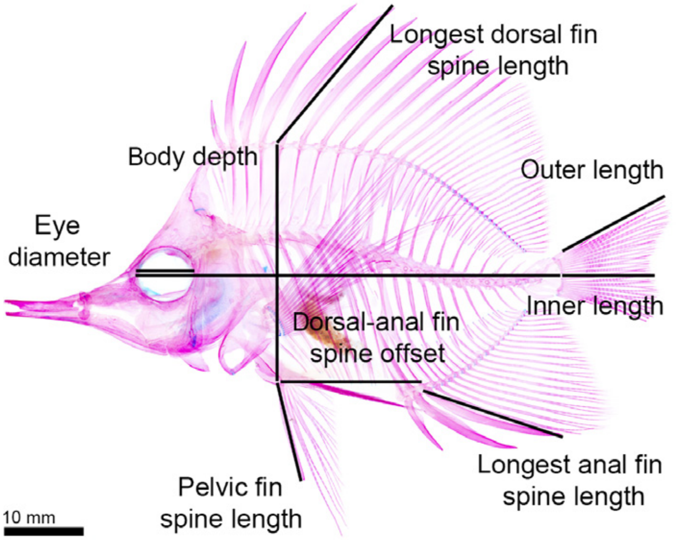

Figure 1 Lateral view of a cleared and stained butterflyfish illustrating the linear morphometric measurements.

Behavioural and ecological data

We collected data on social behaviour and foraging strategy from online databases, identification guides and comprehensive book chapters (Table S1 in Appendix S2). We categorised each species' behaviour as solitary or social based on whether they are most commonly observed alone, or in pairs or groups. When multiple behaviours were cited as the most common, species were categorised by the behaviour affording the least amount of protection from predators (i.e. solitary). We did not consider social behaviour associated with mating. We used available data on dietary habits (Cole & Pratchett 2013) as an indicator of the amount of time spent actively hunting or grazing. Based on this information, we categorised species as either benthic invertebrate hunters, facultative coral grazers that perform both hunting and grazing, obligate coral grazers or pelagic hunters that feed primarily on plankton (Table S1 in Appendix S2). Morphological adaptations of pelagic hunters will be presented in a future paper. Here, we focus on the hunting-grazing spectrum of benthic foragers.

Data handling and analysis

Analyses were conducted in the R statistical computing environment (R Core Development Team 2016). Species means were calculated for each morphometric trait and $\log_{10}$-transformed to better meet the assumptions of parametric statistics. Two exceptions were caudal fin shape, where species' means were quantified as untransformed unit-less ratios, and maximum body size, where the value analysed was the maximum size reported in the literature, not a mean of multiple samples. To correct for evolutionary relatedness, we used the most recent phylogeny of the Chaetodontidae (Hodge *et al.* 2014). The phylogeny was constructed from mitochondrial (16S rRNA, 12S rRNA, *COI*, cytochrome *b*) and nuclear (*TMO-4C4*, *S7* intron 1) DNA, using Bayesian inference with fossil data to simultaneously infer the phylogeny and estimate divergence times. We randomly sampled 100 trees from the posterior distribution of 48 003 trees and appended the maximum-clade credibility (MCC) tree. All 101 trees were pruned to include only those species in our dataset ($n = 87$).

Phylogenetic generalised least-squares regression

We tested the relationship between fin spine length (the sum of the longest dorsal and anal fin spines) and body depth using phylogenetic generalised least-squares regression (PGLS) implemented in the R package CAPER (Orme 2013). We also used PGLS to test the relationship between the longest dorsal and anal fin spines. Each regression was performed using the MCC phylogeny. We accounted for differences in body size by adding $\log_{10}$ standard length as a covariate to each analysis. We controlled the structure of the phylogenetic signal by optimising the branch length transformations of Pagel's lambda using maximum likelihood. For visualisation purposes, we performed both linear models on phylogenetically independent contrasts using the R package APE (Paradis *et al.* 2004).

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Stochastic character mapping

We inferred the evolutionary history of social behaviour and foraging strategy using stochastic character mapping implemented in SIMMAP Version 1.5 (Bollback 2006). Character histories were simulated across 101 tree topologies by specifying an empirical prior on the bias parameter and a branch length prior on the rate parameter, with the branches rescaled. Five character maps were simulated for each tree topology by single draws from the prior distributions, resulting in 505 stochastic character maps each, for social behaviour and foraging strategy. We summarised ancestral state reconstructions on the maximum-clade credibility topology to explore transitions in social behaviour and foraging strategy, and the relative amount of time spent in each character state. We defined transitions in character states as nodes with posterior probability values greater than or equal to 0.80 in support of a transition, and included changes along terminal branches.

Evolutionary model fitting

To account for variation in body size, we applied a phylogenetic size correction using the phyl.resid function of the PHYTOOLS R-package (Revell 2012). We regressed each morphometric trait (except maximum body size) on standard length measured from the anterior of the orbit (see Table S2 in Appendix S2 for regression statistics). All further analyses were based on the phylogenetic residuals of the seven morphometric traits, and $\log_{10}$-transformed maximum body size.

We used an evolutionary model selection approach to determine how social behaviour and foraging strategy have influenced the evolution of antipredator adaptations. This allowed us to evaluate whether the evolution of antipredator traits is better predicted by sociality or foraging strategy, and to determine whether independent transitions in character states of the best predictor variable have resulted in convergence of antipredator traits to separate adaptive optima. For each trait, we fit evolutionary models using the R package OUWIE (Beaulieu *et al.* 2012). The models included, with increasing complexity, single-rate Brownian motion (BM1), single-optimum Ornstein-Uhlenbeck (OU1), multi-rate Brownian motion (BMS), multi-peak Ornstein-Uhlenbeck (OUM) and multi-peak Ornstein-Uhlenbeck with separate estimates of the stationary variance around the optima (OUMV).

The models differ in whether they incorporate effects of sociality or foraging strategy on the evolution of traits – both BM1 and OU1 allow traits to evolve independently of the predictor variable. The two multi-peak models allow traits to assume separate, regime-dependent optimal values, but they differ in whether stochastic factors (unmeasured selective forces and phylogeny, relative to the primary adaptive force) vary between regimes. Stochastic factors are determined by the stationary variance of the joint OU-BM process and depend on both the rate of trait evolution and the strength of pull towards the primary optima (Hansen 1997). Models that vary either of these parameters between regimes include BMS, and OUMV.

Models with regime-specific parameters are denoted with ‘sb’ for social behaviour (e.g. BMSsb, OUMsb, OUMVsb) or ‘fs’ for foraging strategy (BMSfs, OUMfs, OUMVfs). We selected the best overall model using the Akaike information criterion corrected for small sample size (AICc and AICc weights; Burnham & Anderson 2002; Burnham *et al.* 2011). If either sociality or foraging strategy has influenced the evolution of antipredator traits, we would expect the best-fit model to have multiple optima (OUM or OUMV), or rates (BMS or OUMV). If neither sociality nor foraging strategy has influenced the evolution of antipredator traits, we would expect the best-fit model to be either BM1 or OU1.

Estimates of trait optima are relative to their allometric expectation, with positive values greater than expected given body size, and negative values less than expected given body size. OUwie analyses were run with the assumption that the value of the trait at the root was distributed according to the stationary distribution of the OU process (root.station = TRUE). We examined the eigen-decomposition of the Hessian to ensure the analyses returned the maximum likelihood estimates, and discarded iterations (model results and trees) with negative eigenvalues or unrealistic parameter estimates (values well outside the realm of possibility). ΔAICc values were calculated for each retained iteration and averaged across iterations for each model. Mean ΔAICc values were used to calculate AICc weights, and the model with the highest AICc weight was selected as the best model.

We generated 95% confidence intervals for best-fit model parameters using the parametric bootstrapping function OUwie.boot in the R package OUWIE (Beaulieu *et al.* 2012). For each morphometric trait, we performed 100 bootstrap replicates per stochastic character map under the best-fit model.

Phylogenetic principal component analysis

To visualise how transitions to solitary behaviour have influenced antipredator adaptations for species in each foraging regime, we performed a phylogenetic principal component analysis (PCA) of all seven size-corrected morphological traits and maximum body size in PHYTOOLS (Revell 2012). The analysis applied the correlation matrix and optimisation of Pagel’s lambda. We evaluated the contribution of size to the first principal component via PGLS regression on standard length, implemented in the R package CAPER (Orme 2013). We plotted 95% confidence ellipses around the barycentre of species for each combination of social behaviour and foraging strategy using the function coord.ellipse in the R package FACTOMINER (Lê *et al.* 2008). This allowed us to track the directionality and consistency of change in antipredator adaptations associated with transitions to solitary behaviour across foraging strategies.

RESULTS

Phylogenetic generalised least-squares regression

We found no support for a positive correlation between fin spine length and body depth within butterflyfishes ($t_{2,84} = 0.027$, $P = 0.98$; Fig. 2a). Further examination of the data revealed low variation in body depth among species. The lack of a correlation suggests that either variation in predation risk has had little to no influence on the evolution of body depth in butterflyfishes, or that predation risk does not

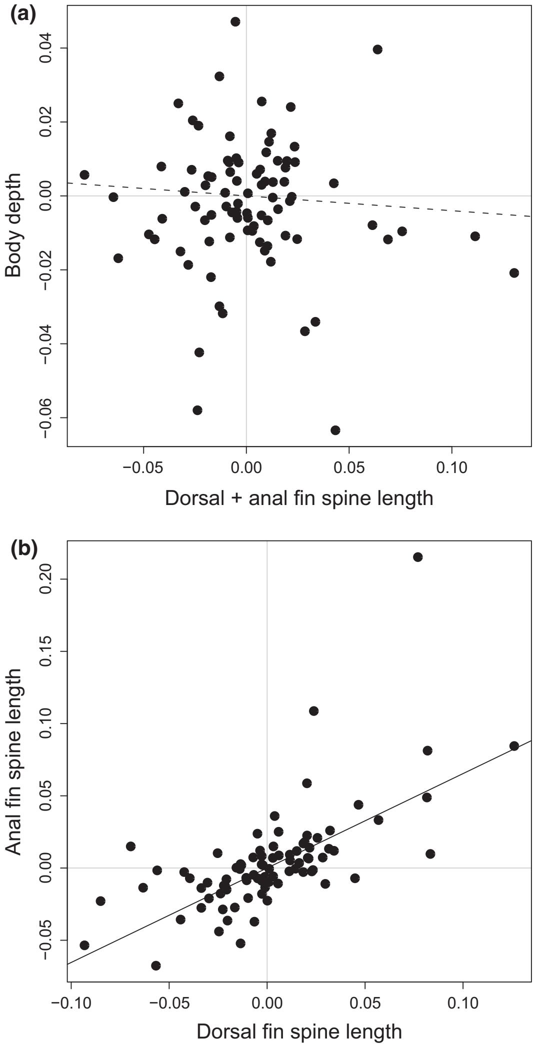

Figure 2 Phylogenetic regressions of (a) body depth vs. the sum of the longest dorsal and anal fin spine lengths, and (b) the longest anal fin spine length vs. the longest dorsal fin spine length. Lines represent linear models fit to phylogenetically independent contrasts. The dashed line (a) indicates a non-significant relationship between body depth and spine length ($t_{1,85} = -0.679$, $P = 0.50$). The solid line (b) indicates a significant relationship between dorsal fin and anal fin spine lengths ($t_{1,85} = 7.816$, $P < 0.001$), demonstrating that these two traits have evolved synergistically. Similar non-significants ($t_{2,84} = 0.027$, $P = 0.98$) and significant results ($t_{2,84} = 5.66$, $P < 0.001$) were obtained from phylogenetic generalised least-squares regression respectively.

vary enough across species to affect differences in defensive morphology. To evaluate these two hypotheses further, we tested the relationship between the longest dorsal and anal fin spine lengths using PGLS. Relative to body depth, the range of dorsal and anal fin spine lengths varied four- and twofold, respectively (based on size-corrected phylogenetic residuals), and we found strong support for their synergistic evolution ($t_{2,84} = 5.66$, $P < 0.001$; Fig. 2b).

Stochastic character mapping

Ancestral state reconstructions revealed 24 independent transitions to solitary behaviour and four reversals to social behaviour (Fig. 3a). Facultative grazing evolved seven times and obligate coral grazing evolved five times (Fig. 3b). Species reverted to benthic hunting seven times (see Appendix S1 for further details). Summaries of the ancestral state reconstructions showed differences between the two trait regimes in the total amount of time spent in each state. Lineages evolved in a social state four times longer than they have in a solitary state (percentage of total time, solitary: 18.8%; social: 81.2%). The total time lineages spent evolving with different foraging strategies was more evenly dispersed among regimes (percentage of total time, benthic hunter: 48.7%; facultative grazer: 25.3%; obligate grazer: 22.1%). The greater frequency of transitions in social behaviour, combined with the relatively low amount of evolutionary time spent in a solitary state, signals lower potential for social behaviour to have influenced long-term morphological trends.

Evolutionary model fitting

Foraging strategy was recovered as the better predictor of all traits except maximum body size (Table 1, Fig. S1 in Appendix S3). All best-fit models had separate adaptive optima, and models best-fit to dorsal and anal fin spine lengths and body depth had differences in variance between foraging strategies (Fig. S2 in Appendix S3, Table S3 in Appendix S2). We recovered strong support for most best-fit models (Table 1). However, multiple models received substantial empirical support (ΔAICc less than two; Burnham & Anderson 2002; see Appendix S1) for several traits, including body depth, maximum body size and pelvic fin spine length. Henceforth, we focus on traits for which all comparable models included multiple adaptive optima explained by the same predictor.

Optimal dorsal, anal and pelvic fin spine lengths were longer than expected given body size among benthic hunters and shorter than expected among facultative and obligate grazers (Fig. 4a and b). Comparatively, dorsal fin spine lengths of benthic hunters can be up to seven times longer than those of obligate coral grazers (based on size-corrected phylogenetic residuals). Benthic hunters had the highest variance in both dorsal and anal fin spine lengths, suggesting that there are additional factors influencing the evolution of median fin spines in species with this foraging mode (Fig. S2a and c in Appendix S3). In contrast, obligate grazers had the lowest variance in both fin spine lengths, suggesting that either the evolution of long fin spines is constrained among coral grazing species, or that long fin spines are energetically costly to develop and maintain, and spine lengths are reduced whenever possible.

The optimal dorsal-anal fin spine offset was positive for facultative grazers and benthic hunters (indicating anterior placement of the longest dorsal fin spine) and negative for obligate grazers (indicating posterior placement of the longest dorsal fin spine; Fig. 4b). Optimal eye size was largest among benthic hunters and smallest among obligate coral grazers (Fig. 4c). Measurements of caudal fin shape ranged from rounded (inner:outer length ratio = 1.07) to emarginate (inner:outer length ratio = 0.76; Fig. S3 in Appendix S3). Obligate coral grazers had the roundest optimal caudal fin shape, whereas

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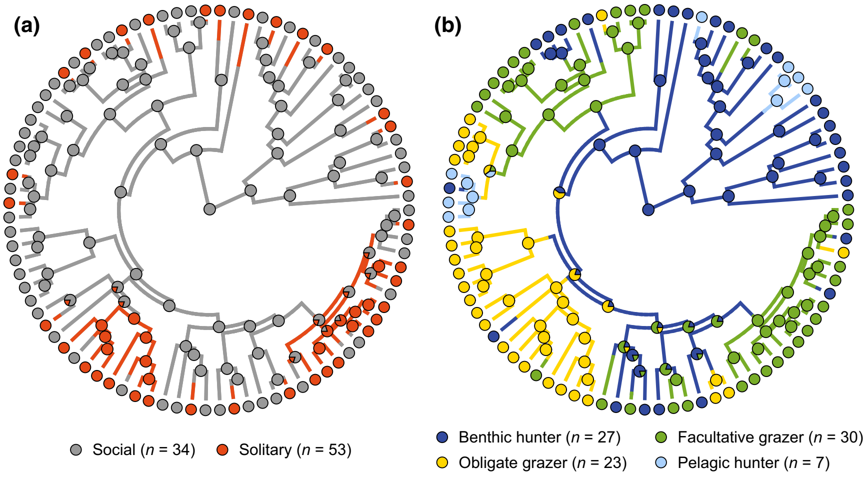

Figure 3 Evolutionary history of (a) social behaviour and (b) foraging strategy in butterflyfishes shown on the maximum-clade credibility topology (adapted from Hodge *et al*. 2014). Sample stochastic character maps are shown on branches and posterior probability estimates summarised from five SIMMAPs are indicated by pie charts at the nodes.

Table 1 Evolutionary models best-fit to morphological traits important in predator defence, detection and avoidance, as predicted by social behaviour and foraging strategy, their mean ΔAICc values, and AICc weights. Models with ΔAICc values less than two were considered to have comparable support (Comp. models; Burnham & Anderson 2002).

Trait	No. retained iterations	Best model	ΔAICc	AICc weight	Comp. models	ΔAICc	AICc weight
Anal fin spine length	382	OUMVfs	0.000	1.000	–	–	–
Body depth	483	OUMVfs	1.168	0.430	OU1	1.608	0.345
Caudal fin shape	458	OUMfs	0.036	0.857	–	–	–
Dorsal-anal fin spine offset	497	OUMfs	1.065	0.646	–	–	–
Dorsal fin spine length	500	OUMVfs	0.298	0.981	–	–	–
Eye diameter	493	OUMfs	0.018	0.837	–	–	–
Maximum body size	500	OUMsb	1.467	0.312	OUMVfs	1.577	0.296
Pelvic fin spine length	411	OUMfs	0.602	0.564	OUMVfs	1.118	0.436

the optimal shape for benthic hunters was the most emarginate (Fig. 4c).

Phylogenetic principal component analysis

The phylogenetic principal component analysis (PCA) showed a gradual transition from species that perform benthic hunting to obligate coral grazing, with the first principal component (PC1) explaining 27.6% of the variation (Fig. 5a and b). All eight morphological traits loaded in the same direction on PC1 (Fig. 5a), which often indicates that the primary driver of variation is body size. However, by including maximum body size in our analysis, we can show that size does not load heavily on PC1. Furthermore, a phylogenetic regression of PC1 on standard length showed no significant relationship ($F_{1,85}$ = 2.29, P = 0.1339). The second principal component (PC2) explained 16.7% of the variation. The proportion of solitary species in each foraging regime is provided in Table S4 (see Appendix S2).

PC1 was most strongly correlated with all three fin spine lengths and eye diameter, where species with long fin spines and large eyes are on the negative end (Fig. 5a). PC2 was predominantly driven by body depth and caudal fin shape, where species with deep bodies and rounded caudal fins are on the positive end (Fig. 5a). For all three foraging strategies, transitions to solitary behaviour resulted in a negative shift of the barycentre along PC1, and to a lesser extent along PC2 (Fig. 5c), demonstrating concomitant shifts to more robust defensive morphologies. Transitions to solitary behaviour result, on average, in the evolution of longer fin spines and larger eyes. The mean shift in morphology between social and solitary species was most pronounced in benthic hunters, where species that hunt alone have the longest fin spines and the largest eyes (Fig. 5b and c). The mean shift in morphology between social and solitary obligate grazers was the least pronounced, but with a notable change in the size of the area of confidence along PC2 (Fig. 5b and c). Species that graze alone have greater variation in defensive morphology, especially in their body depth and caudal fin shape. Interestingly, there is virtually no change in the area of confidence along PC2 for facultative grazers and a negative shift in the mean along PC1 (Fig. 5b and c).

DISCUSSION

Butterflyfishes have evolved exceptionally deep bodies that undoubtedly afford them protection from gape-limited predators. Given their size, their body depth lies above the 97th

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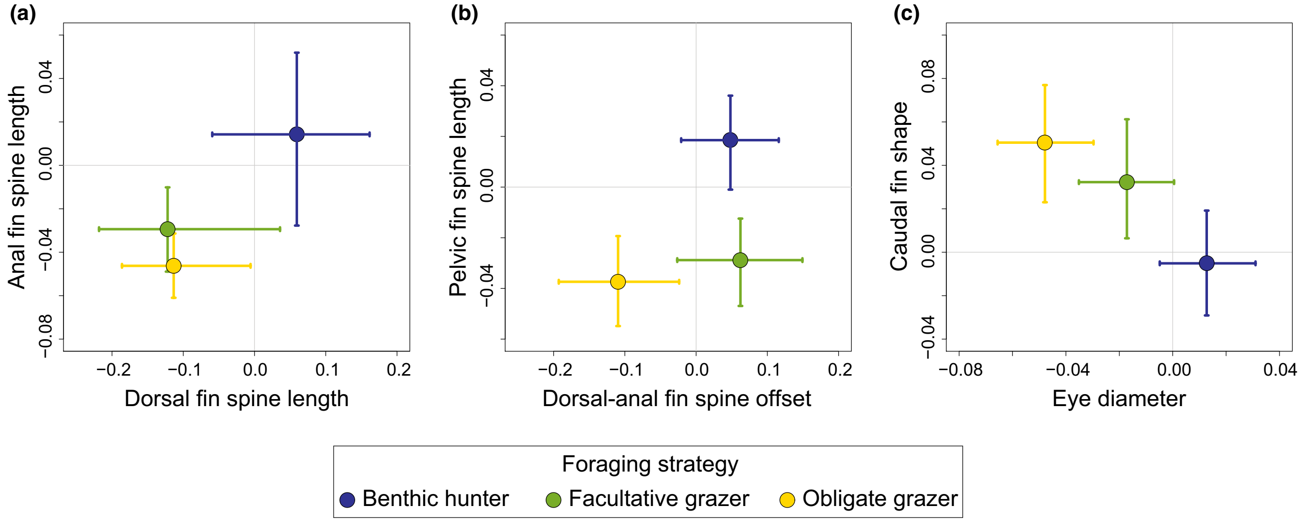

Figure 4 Estimated median optima and 95% confidence intervals of traits important in predator defence, detection and avoidance that were best-fit by a multi-peak evolutionary model. Axes represent size-corrected phylogenetic residuals, where zero is the allometric expectation. Benthic hunters have positive optima for traits important in predator defence and detection, including all three fin spine lengths, the offset of the longest dorsal fin spine from the longest anal fin spine, and eye diameter (a–c). In contrast, obligate grazers show a reduction from the allometric expectation in the aforementioned traits, but a positive optimum for caudal fin shape [i.e. a more rounded caudal fin (c)], a trait important in predator avoidance.

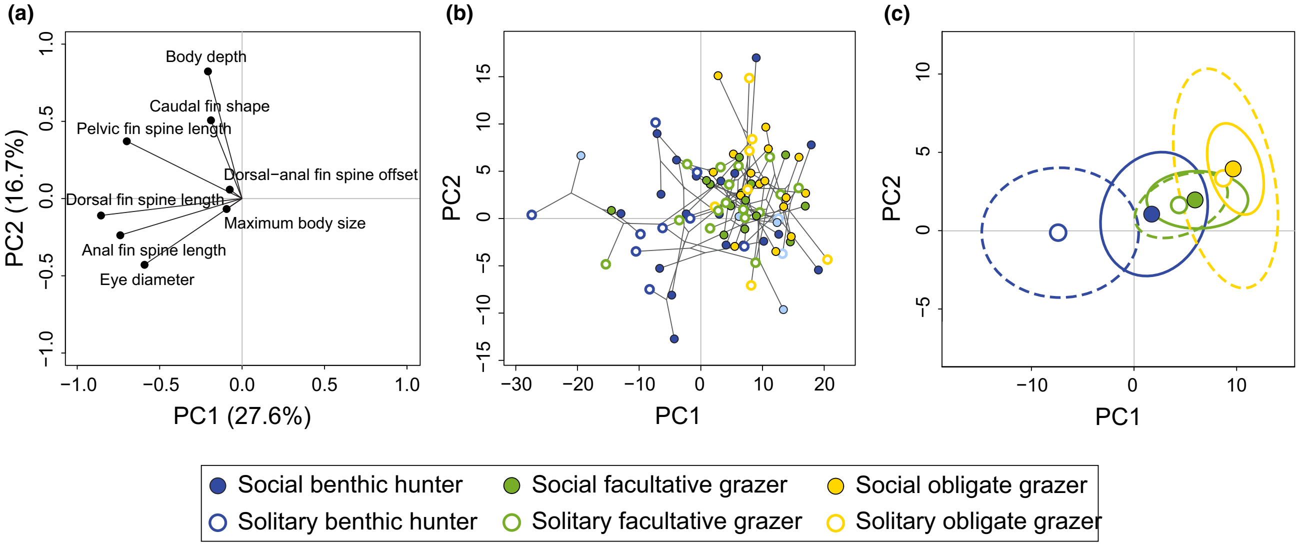

Figure 5 Social behaviour interacts with foraging strategy to influence defensive morphology. (a–c) Phylogenetic principal component analysis of eight morphological traits important in predator defence, detection and avoidance. (a) All three spine lengths and eye diameter are the main traits driving differentiation along PC1, where species with long spines and large eyes are located on the negative end of the axis. Differentiation along PC2 is predominantly driven by body depth and caudal fin shape, where species with deep bodies and rounded caudal fins are located on the positive end of the axis. (b) The phylomorphospace projection of species on the first two principle components, coloured by their foraging strategy and social behaviour. Light blue denotes pelagic hunters. (c) The 95% confidence ellipses around the barycentre for each combination of foraging strategy and social behaviour where transitions to solitary behaviour produce consistent shifts to more robust morphological defences.

percentile of teleost families (based on data from Price *et al.* 2015). Our results show that in contrast to the macroevolutionary pattern found across teleosts (Price *et al.* 2015), body depth is constrained within butterflyfishes and has not evolved synergistically with spine length (Fig. 2a). The lack of correlation between body depth and spine length could reflect lack of variation in predation risk among species. Under this scenario, we would expect similar non-correlative evolution between other defensive traits. Instead, we found a significant correlation between dorsal and anal fin spine lengths (Fig. 2b), suggesting that predation risk is likely variable enough among species to affect the morphology of some defensive traits.

Over all traits, estimated values of the adaptive optima agree with our predictions that benthic hunters have evolved more robust morphological defences, which likely permit them to actively search for prey items over large distances (Fig. 4).

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Interestingly, the adaptive optima of obligate coral grazers were farthest away from the allometric expectation for several key defensive traits, revealing a reduction in all three fin spine lengths and eye diameter, but a rounder caudal fin (Fig. 4). Obligate coral grazers are less structurally defended than benthic hunters, with reduced capabilities for detecting predators, but potentially better at avoiding predation through increased unsteady swimming performance. Fishes commonly seek shelter within the reef structure when threatened and, apart from morphological defences, refuges provided by structural habitat complexity constitute their primary defensive mechanism (Beukers & Jones 1997; Almany 2004; Hixon 2015). We argue that because coral grazers have such an intimate association with corals (Righton & Mills 2006) they are able to rely more on the corals themselves for protection from predation (predator avoidance), and less on morphological defences in the form of long fin spines.

Predator avoidance mechanisms, such as fleeing and occupying refuges, are thought to trade-off evolutionarily with antipredator defences, like fin spines that reduce the probability of predation going to completion (Brodie *et al.* 1991; Sansom *et al.* 2009). The evolution of either antipredator defences or predator avoidance mechanisms should reduce the selective pressures on the other, or the probability of evolution of the other. Evolutionary trade-offs in antipredator adaptations have been reported in other organismal groups (Losos *et al.* 2002; Blanchard & Moreau 2017). Among fishes, such trade-offs have been proposed (McLean & Godin 1989; Brainerd & Patek 1998) and supported by evidence at the population-level for a select number of fish species (Andraso & Barron 1995; Bergstrom 2002; Leinonen *et al.* 2011). We believe this is the first study to demonstrate a trade-off in antipredator adaptations on a macroevolutionary scale, among closely related fish species. Both predator avoidance and defence likely influence survival in natural systems (Brodie *et al.* 1991) – obligate grazers still have spines and benthic hunters still seek refuge – and the dominance of one strategy over the other may be evolutionarily constrained by factors specific to the ecology of the organism.

Benthic hunters forage widely and do not typically defend territories – for these species long fin spines are likely beneficial, given their lower chance of finding suitable refuge within the reef when under threat. This is consistent with previous work showing that fishes with adequate structural defences rely less on their ability to flee, and they do so in a manner that is decoupled with refuge proximity (McLean & Godin 1989). Morphological defences can release ecological constraints imposed by predator avoidance requirements, thereby freeing organisms to exploit their habitats more effectively and increase their niche space (Arbuckle *et al.* 2013). Thus, longer fin spines have likely allowed benthic hunters to retain a broader diet niche than obligate coral grazers (some of which consume just a handful of coral species) through the facilitation of active hunting over large areas.

Contrary to benthic hunters, our results imply that obligate coral grazers rely predominately on predator avoidance and that the defensive benefits of long fin spines are compensated for by shelter of the coral habitat. Obligate coral grazers have been shown to use highly predictable routes when travelling around spatially complex home ranges (Reese 1989), demonstrating their ability to learn areas with reduced predation risk, as well as areas with easy access and effective refuge (Markel 1994; Stamps 1995). Experimental work has shown that close proximity to refuge decreases reaction distances in fishes (Grant & Noakes 1987; Dill 1990; Gotanda *et al.* 2009), and this is thought to produce greater fitness benefits for species that graze on small prey items (Webb 1986). Thus, the evolution of specialist grazing may impart ecological constraints on antipredator adaptations that favour predator avoidance over defence. Moreover, long fin spines may actually be a hindrance to species closely associated with corals. Butterflyfishes typically flare their spines when threatened. In close proximity to corals, longer fin spines have a higher chance of catching on the coral, which may result in injury or compromise the fishes' ability to escape the threat.

The consistency of our results across spine lengths in all three fins, showing reduced adaptive optima for obligate grazers supports the notion that long spines are a hindrance. Pelvic fin spines have shorter adaptive optima despite their role in locomotor function, allowing fishes to stop and maintain position (Harris 1938; Yamanoue *et al.* 2010; Konow & Ferry-Graham 2013). This function is especially important for butterflyfishes because most species feed on benthic prey. Therefore, they require precise control of their speed upon approach, and then the ability to stop to bite prey items. This contrasts with many other fishes that use body ram in prey capture, effectively swimming beyond the original position of the prey item (Norton & Brainerd 1993; Wainwright *et al.* 2001). Although most butterflyfishes require the ability to stop and maintain position, obligate and facultative grazers have shorter pelvic fin spine optima (Fig. 4b). Furthermore, if long fin spines are a hindrance for species closely associated with corals, we would expect the placement of their longest spine to be posterior to the allometric expectation (across chaetodontid species), and farther away from their mouth, and the coral during feeding. Indeed, we found that obligate coral grazers have shifted their longest dorsal spine posteriorly, thereby also reducing the area of the body over which the longest spines provide protection. Collectively, this suggests that the evolution of fin spines may be constrained in species that rely on corals for shelter and food.

Visual acuity is important in the detection of predators, as well as prey. In fishes, eye size is one of the primary determinants of visual acuity because of its direct relationship with the collection of light, the lens diameter and focal length (Sadler 1973; Fernald 1990). Relative to other reef fishes, butterflyfishes have large eyes that are thought to have played an important role in the evolution of their high-precision benthic feeding (Goatley & Bellwood 2009; Goatley *et al.* 2010). However, until now variation in eye size among butterflyfish species was unknown outside the context of jaw length variation. Here, we show that benthic hunters have the largest optimal eye size (Fig. 4c), indicating they are better at detecting predators and prey. In contrast, obligate grazers have the smallest optimal eye size. This could reflect a reduction in their predation risk – early detection of predators may not be as critical for butterflyfishes that maintain close contact with corals. It could also indicate that coral prey are easier to detect and

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require less light collection and visual acuity to capture. Benthic hunters are presumed to feed opportunistically (Birkeland & Neudecker 1981). They actively search for appropriate prey items, often inspecting crevices, reef interstices and the undersides of overhangs where light penetration is reduced. Many factors, including light penetration in foraging microhabitats (Herler 2007) and prey type (Pankhurst 1989), likely influence the evolution of eye size in diurnal coral reef fishes. Our results suggest that predator detection abilities vary between foraging regimes as a result of differences in eye size.

Butterflyfishes swim using body-caudal undulation augmented by pectoral fin strokes to produce thrust (Fulton 2007) that is capable of high acceleration and slow sustained swimming speeds (Walker & Westneat 2000). They primarily use pectoral fin strokes, along with movements of the soft dorsal and anal fins, to manoeuvre while feeding, and body-caudal undulation almost exclusively when swimming above the reef or when threatened. Rounded caudal fins have a larger surface area – an adaptation associated with good unsteady swimming (Blake 2004), specifically c-starts (Borazjani 2015) and faster sprint speeds (Oufiero *et al.* 2011). We found that as morphological defences are reduced from benthic hunters to obligate grazers, caudal fins become more rounded (Fig. 4c). This suggests that obligate grazers rely on their ability to avoid predation by fleeing into the reef structure via short bursts of speed with efficient manoeuvrability. Experimental work has shown that predators attacking prey with higher acceleration performance were more likely to abort attacks and less likely to chase prey (Webb 1986), suggesting that the method of predator avoidance employed by obligate grazers may also function effectively by deterring predator pursuit.

Social behaviour should increase vigilance, thereby increasing the ability of fishes to detect and avoid predators. The phylomorphospace shows that the loss of this trait that aids in predator avoidance results in the amplification of a suite of traits that aid in predator defence (Fig. 5). In terms of investment in morphological defences, benthic hunters gain the most from being social as the shift in their average defences is most pronounced following transitions to solitary behaviour. Facultative grazers have a similar, less pronounced response to the loss of sociality, whereby their defences also become more robust. When obligate grazers lose the protection afforded by sociality, their morphological response is more variable, and they become deeper bodied with rounder caudal fins, or more slender-bodied with emarginate caudal fins. The decrease in the magnitude of defensive trait response to the loss of sociality from benthic hunters through facultative to obligate grazers demonstrates a concomitant increase in the evolutionary constraint of spine lengths associated with coral grazing. Facultative coral grazers, as intermediates, are less constrained than obligate coral grazers, presumably due to the increased flexibility of their foraging strategy. As a whole, defensive morphology of grazing species is reduced regardless of their sociality.

Our results show that antipredator adaptations trade-off in a complex manner that varies with both ecology and behaviour. Species that actively hunt benthic prey items, especially those that forage alone, are the most well-defended morphologically. These enhanced morphological defences have likely evolved in response to greater predation risk associated with benthic hunting. Species that graze on corals have reduced morphological defences, due in part to the hindrance posed by long fin spines in close association with corals during escape and feeding, and the added protection they receive from corals within their foraging territory. Obligate coral grazers rely predominately on predator avoidance rather than defence, and the consequences of habitat loss for these species are obviously dire, in that they would be left almost defenceless against predators.

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COMPETING INTERESTS

The authors declare no competing financial interests.

AUTHORSHIP

JRH and NGB conceived the study. JRH, CA, NGB and PCW developed the study design. JRH, CA, NGB, WL, BT and PCW collected the data. JRH designed and led the analyses with considerable input from SAP. JRH wrote the manuscript with contributions from all authors.

DATA ACCESSIBILITY STATEMENT

Data used in this study are available in Table S1 in Appendix S2. The data and phylogenetic trees are also available for download from Figshare (DOI: 10.6084/m9.figshare.6030656).

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