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Adaptation for crypsis versus conspicuous social signalling following transitions across an extreme ecotone

Shizhi Yao and Terry J. Ord*

Evolution and Ecology Research Centre, and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia

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*Corresponding author: Terry J. Ord, Evolution and Ecology Research Centre, and the School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, Australia. Email: t.ord@unsw.edu.au

Abstract

A key selection pressure in most habitats is predation, and a common strategy adopted by prey is crypsis through background matching. Many marine blenny fishes are in the process of a dramatic transition across one of the world's most extreme ecotones: the invasion of land across the intertidal zone. We investigated the impact of this transition on body crypsis versus the conspicuousness of visual signals across 56 blenny taxa relative to 59 biologically relevant backgrounds, as viewed by conspecifics and four representative fish and avian predators. We computed 33 colour and 23 pattern indices from standardised digital photographs of six individuals for each taxa (median sample). Six of these indices were selected for detailed analysis following phylogenetic Principal Component Analysis. While phylogenetic regressions revealed some aspects of body crypsis appeared to have changed adaptively with the progressive transition to land (specifically a reduction in body colour saturation), colonisation was primarily facilitated by a generalist form of crypsis. That is, the colours and patterns of aquatic blennies were already well matched to the range of terrestrial backgrounds where amphibious and terrestrial species were observed out of water. Predation appears to have been an important selection pressure constraining the colour and pattern of the dorsal fins used in social communication, which also matched visual backgrounds. Our data implies anti-predator strategies that translate well across habitats and different predator regimes will facilitate colonisation by either reducing predation risk or allowing species to persist long enough to respond adaptively to environmental change.

Keywords: amphibious fish, biological invasions, camouflage, ecological determinism, historical contingency, land blenny, natural selection

Introduction

The colonisation of new environments is of special interest to evolutionary ecologists. This is because invading species often face new selective challenges that result in adaptation that herald the emergence of new species through adaptive radiation (Beltman et al., 2004; Parent and Crespi, 2006). A notable example includes the colonisation of land by aquatic species during the Devonian, the descendants of which ultimately diversified into all living land vertebrates in existence today (Ashley-Ross et al., 2013; Graham and Lee, 2004). The success of a colonisation event will depend on the invading species capacity to cope with the novel conditions experienced in the new environment. Some species might already possess attributes that happen to be at least partly suited to the conditions experienced in the new environment. Here, invading species are essentially filtered by their ecological suitability to a particular type of environment (e.g., Gearty et al., 2021). Alternatively, phenotypic plasticity or behavioural shifts can allow species to remain in a novel habitat long enough to progressively adapt to the new conditions (e.g., Ord et al., 2016). This can be further facilitated by transitional habitats or ecotones, such as grasslands (transitional between desert and forest), estuaries (between saltwater and freshwater) or the intertidal zone (between marine and terrestrial; Lacasella et al., 2015; Shumilovskikh et al., 2018; Warda et al., 1999). These ecotones offer an opportunity to adapt to the novel conditions of the new environment while still allowing intermittent returns to an ancestral habitat or by providing a stepping-stone environment where some conditions are shared between habitats.

A key factor impacting a species capacity to establish in a new area is the threat of predation. Invading species that lack appropriate anti-predator strategies can be more susceptible to predation compared to native prey species that are better defended (Augustyniak et al., 2023; Sih et al., 2010). For example, the invasion of California bays by the European green crab *Carcinus maenas*, which has been a successful invader in many areas, has had its distribution limited because of encountering unfamiliar predators such as sea otters (Jensen et al., 2007). One strategy for minimising predation risk is camouflage and in particular the evolution of cryptic morphologies in which animals match the overall colour (hue and saturation), brightness (luminance) and pattern of habitat backgrounds (Smithers et al., 2018; Stevens and Merilaita, 2008). However, crypsis is typically background specific (e.g., Morgans and Ord, 2013; Salisbury and Peters, 2019; Vignieri et al., 2010), and transitions into a new environment can effectively 'break' background matching if visual backgrounds differ from that encountered in the ancestral environment. Possessing a generalist form of camouflage that is reasonably suitable for a variety of environments could facilitate colonisation by helping to reduce predation risk

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(Briolat et al., 2021; Endler, 1984). Otherwise, species must rapidly adapt their appearance or behaviour to successfully establish in a new area (e.g., Marshall et al., 2015; Stuart-Fox et al., 2004).

In addition, animal colouration is often critical for sexual and territorial signalling (Endler, 1992; How et al., 2007; Ptacek, 2000), and signal colours are expected to standout from—rather than match—visual backgrounds to successfully attract mates and intimidate rivals (Caves et al., 2024). This results in a trade-off, where animals attempt to remain cryptic to reduce predation risk, but still need to be conspicuous to communicate effectively with conspecifics. In some species, the adaptive solution to this selection trade-off has resulted in the evolution of conspicuous colouration on regions of the body that only become visible once extended or displayed. For example, many lizards possess cryptic dorsal colouration that is in the direct line-of-sight of aerial predators but exhibit conspicuous ventral colouration that is only visible through posturing to ground-based conspecifics (Stuart-Fox and Ord, 2004). In an additional innovation, some lizards have evolved an extendible throat fan or dewlap that is brightly coloured and only extended during signal bouts but is otherwise invisible when not on display (Ord et al., 2015, 2021). Following the colonisation of a new environment, changes in the background could in turn impact the conspicuousness (and subsequent efficiency) of visual signals, while also potentially altering its balance with predator avoidance (e.g., Klomp et al., 2016; Michel et al., 1990).

In this study, we investigated the interplay between cryptic colouration and conspicuous visual signalling in a family of fishes undergoing a dramatic transition across one of the world's most extreme ecotones, the intertidal zone. Blenny fishes are a diverse family found globally in various benthic marine environments. While most are aquatic, there are a number of intertidal species exhibiting a range of amphibious behaviour, which has evolved independently across the family as many as seven times (Ord and Cooke, 2016). These amphibious species move freely between water and land to spend varying amounts of time above the waterline at mid- to high-tide, but usually return to the water remaining in tidepools at low tide (Ord and Cooke, 2016). In addition, other blenny species are exclusively terrestrial and never voluntarily return to water (Ord and Hsieh, 2011; Ord et al., 2017). These terrestrial blennies are active above the waterline on the exposed rocks at mid-tide in the splash zone and retreat to non-submerged rock holes and crevices at high and low tide (Ord and Cooke, 2016; Ord and Hsieh, 2011). Each lifestyle—aquatic, amphibious, and terrestrial—effectively represent separate stages in the colonisation process, from the starting ancestral aquatic environment through to the final colonisation of land, with amphibious species representing the transitional stage in the process.

Aquatic and amphibious blennies are primarily targeted by larger predatory fish. For example, the return of predatory fish with the incoming tide prompts amphibious blennies to leave tidepools and emerge onto the exposed rocks in the splash zone to escape aquatic predation (Ord et al., 2017). Out of the water, both amphibious and terrestrial blennies are still subject to predation from land crabs, lizards, but especially birds (Morgans and Ord, 2013). Yet the risk of predation is considerably lower on land for amphibious and terrestrial blennies than for aquatic blennies (Ord et al., 2017). This ecological release from predation (Ord et al., 2017), and to a lesser extent the ecological opportunity provided by resource availability on land (Ord and Hundt, 2020), appears to have instigated the repeated evolution of amphibious behaviour in blennies (that in turn culminated in the evolution of fully terrestrial species; see Ord and Cooke, 2016).

On land, at least one blenny species that is exclusively terrestrial seems cryptic in general body colouration (saturation and luminance) against terrestrial backgrounds on which they are typically active (Morgans and Ord, 2013). Yet aquatic blennies also exhibit body colours and patterns that would seem generally cryptic as well (see Figure 1), suggesting terrestrial (and amphibious) species simply retained the cryptic body morphology of their aquatic ancestors, rather than adapted to match terrestrial backgrounds after colonisation (discussed by Morgans and Ord, 2013). This could be because the visual backgrounds of terrestrial blennies are the same rocky backgrounds against which many aquatic blennies are seen as well (given an appropriate tide level). Nevertheless, the conspicuousness of prey is dependent on the visual system of predators, such that the same prey against the same background would be more or less cryptic depending on the predator viewing it (e.g., Xiao and Cuthill, 2016). This means that while terrestrial blennies might retain colours and patterns from what were cryptic aquatic ancestors, this does not necessarily result in terrestrial blennies being equally cryptic when viewed by terrestrial predators.

Furthermore, both male and female terrestrial blennies use their dorsal fin during social communication, raising the fin during aggressive interactions with same-sex rivals or to attract prospective mates. When not raised, the dorsal fin remains flat against the body and is effectively invisible. In some terrestrial species, the size of the dorsal fin has become considerably exaggerated (Summers and Ord, 2022b). On one hand, this has apparently occurred because the biomechanical constraints usually imposed by the use of the dorsal fin in swimming have been removed in terrestrial species, while on the other hand sexual selection (e.g., through female mate choice; Summers and Ord, 2022a) has resulted in increasingly larger ornamentation in males (Summers and Ord, 2022b). In other terrestrial species, the dorsal fin is coloured a rich red (e.g., Ord and Hsieh, 2011) that contrasts well against most terrestrial backgrounds (Morgans and Ord, 2013). Taken together, the transition out of the water onto land seems to have allowed terrestrial blennies to solve the selection trade-off between predation risk and conspicuous social signalling by allowing the dorsal fin to only be viewed during social signalling.

If the colonisation of land has been facilitated by a generalist body colour and pattern that is cryptic in a variety of environments, then aquatic, amphibious and terrestrial blennies should all largely match terrestrial backgrounds, and when viewed by both aquatic and terrestrial predators (e.g., fish and birds). Alternatively, if the cryptic appearance of aquatic blennies are specialised to aquatic backgrounds, then the transition to land should have been accompanied by adaptive shifts in colour and pattern to match terrestrial backgrounds and specifically as viewed by terrestrial predators. This predicts terrestrial species will match terrestrial backgrounds the most, whereas aquatic species will match terrestrial backgrounds the least, with amphibious species falling somewhere between the two extremes. Furthermore, the conspicuousness of dorsal fins should be highest in terrestrial species because these species only expose the fin during

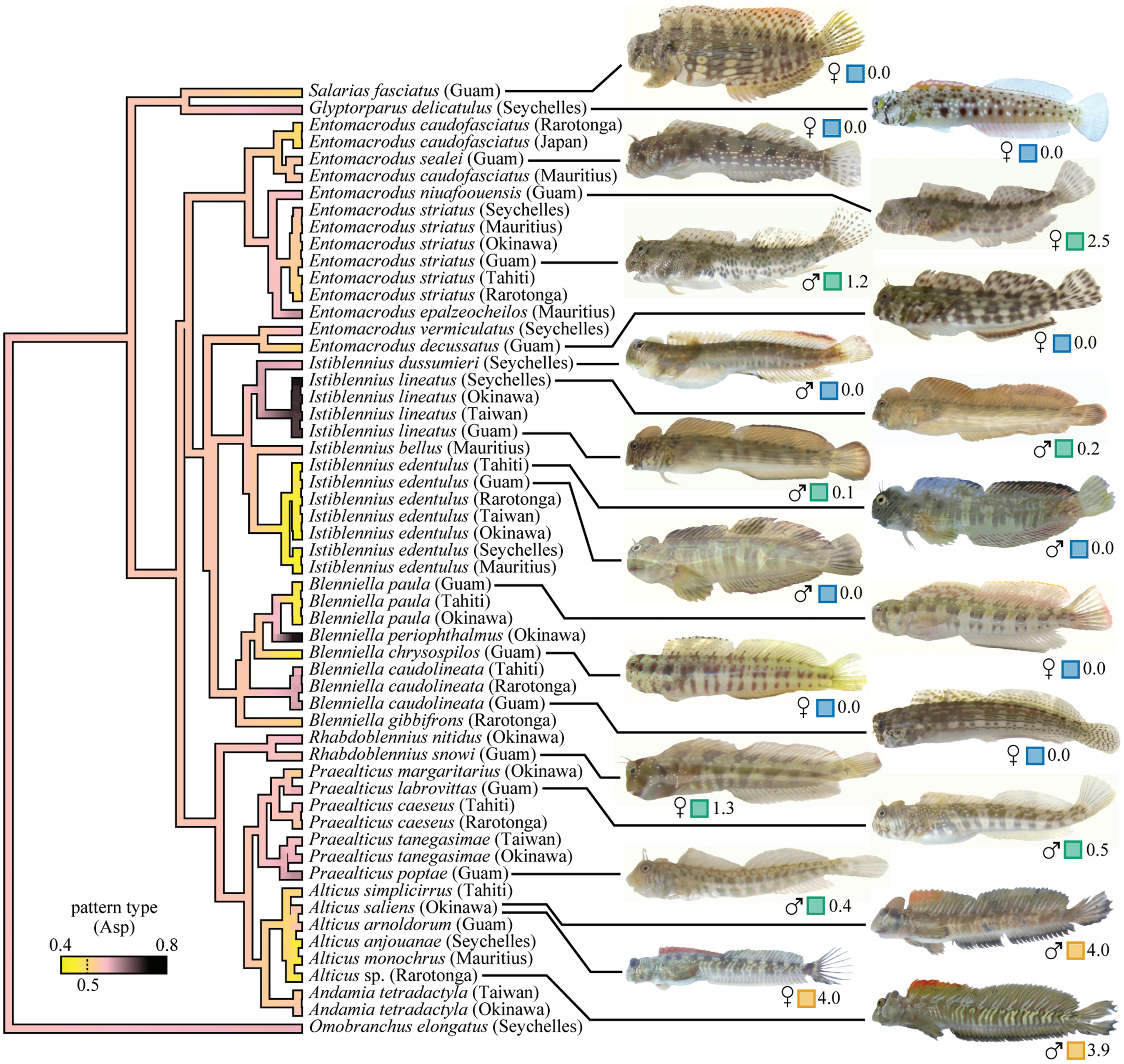


Figure 1. Phylogeny of the colour morphology of blennies illustrated by an ancestor state reconstruction of pattern type (Asp; values of 0.5 correspond to random or globular patterns such as *Entomacrodus decussatus*, while those converging on 1.0 are horizontal patterns such as *Istiblennius lineatus* or 0.0 are vertical patterns such as *Istiblennius edentulus* or *Alticus* sp.). Images of representative species illustrate the diversity of colour morphologies across species, with coloured squares and numerals to the lower right indicating lifestyle (aquatic: blue or 0.0; amphibious: green or 0.1–3.4; terrestrial: orange or 3.5–4.0). Locations for each taxon are given in parentheses.

social communication. More specifically, signal efficiency is improved with high saturation and brightness (Fleishman and Persons, 2001; White et al., 2020) and low pattern complexity relative to backgrounds (Ord and Garcia-Porta, 2012; see also Xiao and Cuthill, 2016). In contrast, the dorsal fin of aquatic species will be frequently exposed to aquatic predators and should converge on similar cryptic colouration and patterns as exhibited in the body to reduce predation risk (i.e., low saturation, dull colours, and high pattern complexity). Amphibious species should again sit somewhere between these two extremes.

Material and methods

Digital calibrated photography

Data was extracted from an archive of 486 high-resolution photographs of 264 individual blennies representing 56 taxa (across 39 species) collected as part of fieldwork on seven islands in the North and South Pacific and Indian Oceans (Guam, Japan, Taiwan, Rarotonga, Tahiti, Mauritius, and Seychelles; e.g., see Ord and Cooke, 2016). Where possible, at least three females and three males were measured for each taxa, although some species had fewer fish because of low abundance (several species were quite rare; median individuals sampled, range: 6, 1–41). In many cases, different island populations of the same species were examined because there was variation in appearance and lifestyle among populations within species (e.g., see Ord and Cooke, 2016). Fish were photographed out of water against a white standard (X-Rite ColorChecker White Balance Card) with a metal ruler and Munsell colour chart visible in a frame (X-Rite mini ColorChecker; see Morgans and Ord, 2013 for details). In blennies, colour change can occur from a base (cryptic) colour pattern to uniform charcoal or jet black during aggressive interactions (Heflin et al., 2009; Ord and Hsieh, 2011) or because of capture stress (TJO personal observation), or to dull grey or almost white as a receptive signal during courtship (females only; Bhikajee and Green, 2002; TJO personal observation). In the context of the current study, photographs were only taken of fish that exhibited their base colour pattern (e.g., see Figure 1) and no colour change was observed while photographs were being taken (see also Morgans and Ord, 2013). To obtain a standardised area of the body for subsequent analysis (with an equivalent area of visual backgrounds also analysed; see next paragraph), photographs of each fish were cropped to a common rectangular region of the body, starting behind (but not including) the pectoral fin to a length representing approximately half the standard length of the body, with a height that included as much of the body as possible without the dorsal, ventral or pectoral fins being included. A second rectangular crop was made of the first dorsal fin that included as much of its full length and height as possible without encroachment on the white background. The first dorsal fin was selected because this fin is used for social communication (see Ord and Hsieh, 2011). The overall size and region of the rectangle cropped were carefully chosen to include a representative sample of the dominant colours and patterns exhibited on the body and fin or in visual backgrounds.

This approach of cropping to a standardised rectangle of the body, fin, and background ensures the visual area analysed is proportionally comparable across all samples. While it is possible to isolate the entire body and full area of the dorsal fin, these areas would individually differ in size (e.g., the first dorsal fin is less than a quarter of the area of the body on most species), which would in turn complicate the selection of areas of the background. Identical regions of interest for every fish and feature would have to be replicated across all visual backgrounds, which was not tractable. Regardless, we considered it important to apply a standardised area for comparison across species and visual backgrounds to ensure the subsequent calculation of image indices were not confounded by variation in the size of regions analysed. This is because the size of sampled regions has a direct impact on the value of computed colour, luminance, and pattern indices: the smaller the area analysed, the more the image is homogenised to single dominant colours and their mean luminance, and reduced pattern complexity.

Data was also extracted from 59 photographs of terrestrial backgrounds taken where amphibious and terrestrial blennies were observed to be active on three islands in the North Pacific and Indian Oceans (Guam, Japan, and Mauritius). The backgrounds photographed at these locations were typical of the environments on all other islands where we have studied amphibious and terrestrial blennies (Ord and Cooke, 2016), as well as those described in the literature (e.g., Depczynski and Gagliano, 2007). Photographs were taken with the Munsell colour chart held in the frame and against the substrate of the background, which also provided a scale to standardise the spatial area covered by the image. Visual backgrounds ranged from largely homogenous to those exhibiting greater heterogeneity in colour and pattern. To accommodate this variation, we selected six areas of the background to provide a broad, representative sample of the visual appearance of backgrounds. These six rectangular regions were cropped from each photograph to an area equivalent to the size cropped for the body of individual blennies, again based on the Munsell colour standard used as a scale.

Fish (out of the water) and terrestrial background images were photographed with the same Canon EOS 7D digital SLR using an EFS 15-85mm, f/3.5-5.6 IS USM zoom lens. Multiple photographs were taken to ensure adequate lighting and positioning of fish/backgrounds within the visual field. The camera used provided a reasonable resolution of colour and luminance over the 400 to 700 nm range (see Morgans and Ord, 2013). Although images did not capture Ultra-Violet (UV) reflectance (< 400 nm), photographs provided a broad representation of the appearance of fish across species and relative to terrestrial backgrounds. The impact of any UV reflectance that might be seen by aquatic or terrestrial predators needs a highly specialised approach that is difficult to implement in the field. It requires either a spectrophotometer, which subsequently limits estimates to point samples rather than a holistic analysis, or specialised camera lens, filters, and often some method of standardised lighting, which circumvent the point sample constraint but are difficult to implement for field photography of live fish and in situ images of habitat backgrounds.

Behavioural data on lifestyle was available for each individual blenny photographed and was taken from the archive associated with Ord and Cooke (2016). These data provided a quantitative, continuous index of behaviour over a range of 0 to 4, with 0 being fully aquatic and 4 being fully terrestrial. This scoring was determined for each fish as part of the collection protocol of capturing fish in the field prior to photography and is described in detail in Ord and Cooke (2016). For some illustrative purposes, this continuous index was categorised into three lifestyles, with a score of 0 indicative of exclusively 'aquatic', scores greater than 0 but less than 3.5 considered 'amphibious', while scores greater than 3.5 considered 'terrestrial'.

The work followed protocols approved by the UNSW Sydney's Animal Care and Ethics Committee in projects 11/36B and 13/21B.

Colour analysis

Images were processed through the Multispectral Image Analysis and Calibration (MICA) Toolbox plugin version 2.2.2 (Troscianko and Stevens, 2015) for ImageJ version 1.54b (imagej.nih.gov/ij). Prior to regions of interest being cropped (see previous section), all jpg photographs (i.e., those of both fish and backgrounds) were first standardised by creating a specified linearisation model based on the grey reflectance values of the Munsell colour chart positioned in the frame of the photograph. This generated an image calibrated to the known RGB colour channel. This calibrated image was then transformed into a separate image based on one of five visual models to provide an image as it would be potentially seen by either predators or conspecifics.

Visual models used as representative predators or conspecifics were selected from the library available within the MICA Toolbox. This library allows researchers to select from a range of ready-made visual models for easy implementation. Readers interested in the specific details of how the visual models were parameterised are referred to the MICA website and user manual. Our choice of species and general information on species visual sensitivities are given below.

We used the leopard coral trout (Plectropomus leopardus; spectral sensitivities, l_{max}: 455 nm and 522 nm; visual acuity: 12.7 cycles per degree; Caves et al., 2017; Cortesi et al., 2016) and the white-banded triggerfish (Rhinecanthus aculeatus; spectral sensitivities, l_{max}: 413 nm, 480 nm, and 528 nm; visual acuity: 2.75 cycles per degree; Champ et al., 2014; Cheney et al., 2013) as representative aquatic fish predators. These fish species were selected because (i) they were located within the same geographic region as several of our aquatic blenny species, (ii) are known to predate blennies or similar-sized fishes (based on information provided in www.fishbase.se), and (iii) have visual acuities that likely encompass a range of other intertidal predatory fish. Ideally, birds known to similarly predate blennies would have also been preferable as terrestrial predators, but basic information on common shorebirds present on each of the seven islands was generally unavailable to confidently identify these species. Instead, we selected the Indian peafowl (*Pavo cristatus*; spectral sensitivities, l_{max}: 432 nm, 477 nm, 537 nm, and 605 nm; visual acuity: 20 cycles per degree; Hart, 2002) and the blue tit (*Cyanistes caeruleus*; spectral sensitivities, l_{max}: 371 nm, 448 nm, 503 nm, and 563 nm; visual acuity: six cycles per degree; Moore et al., 2013; Silvasti et al., 2021) as proxies, despite these birds not feeding on fish or occupying the intertidal zone. We focussed on these two birds because our objective was to provide a reasonable approximation of how blennies might be viewed by a predatory bird, and the visual acuities and spectral sensitivities of peafowl and tits can be expected to cover at least some range of the visual perception abilities of intertidal seabirds that do feed on blennies. Last, we selected the two-spotted goby (*Gobiusculus flavescens*; spectral sensitivities, l_{max}: 456 nm, 531 nm, and 553 nm; visual acuity: 8.7 cycles per degree; Caves et al., 2017; Utne-Palm and Bowmaker, 2006) as a proxy visual model for blenny conspecifics in analyses of the dorsal fin and its conspicuousness in social communication. The two-spotted goby is similar in size and occupies similar marine environments to many aquatic blennies. Both the goby visual model and Salariini blennies (specifically those examined in the current study) do not appear to have spectral sensitivities in the UV range (< 400 nm; Cortesi et al., 2018). That is, the goby is likely to provide a reasonable proxy of the colours and patterns observed by conspecific blennies.

These visual models were used to generate a cone-catch model to apply the Quantitative Colour and Pattern Analysis framework (van den Berg et al., 2020). The pre-set Weber fractions within MICA were used for the bird and goby species. In the case of the triggerfish, the cone abundance ratio of 1:2:2:2 (short wavelength, sw: medium wavelength, mw: long wavelength, lw: luminance, dbl) with the base Weber fraction of 0.05 was used following a previous study (van den Berg et al., 2024). The cone abundance of coral trout is unknown, but its spectral sensitivities are likely processed by double cones like most fish (Cortesi et al., 2016; da Silva et al., 2020), so the same Weber faction inputs were used as the triggerfish. The viewing distance of the predator visual models were set to 30 cm as a standardised distance that would be biologically relevant for both fish and bird predators. In the case of the conspecific visual model, viewing distance was set to 20 cm to reflect that terrestrial blennies have been observed displaying to each other within this general range (e.g., Ord and Hsieh, 2011). Images were then processed using the Receptor Noise Limited ranked filter using default inputs.

In addition to the multitude of indices computed by MICA following image calibration, cropping and visual model conversion, we also used the R package ‘pavo2’ version 2.7.1 (Maia et al., 2019) to measure the R/G ratio of image regions as an alternative estimate of ‘redness’ (a common dominant colour of the dorsal fin when used in social communication) and the proportional sum of the R, G, and B channels as an alternative estimate of luminance (following Morgans and Ord, 2013).

Statistical analysis

All statistical analyses were implemented using R version 4.0.5 (R Core Team, 2021) and the phylogeny developed by Ord and Cooke (2016) for the same taxa examined in the current study. Data obtained represented a weighted mean of the colour, luminance, and pattern of the body of individual fish (see ‘Colour analysis’ below), which was then summarised by taking a mean estimate across individuals of the same species from the same island. In the case of data taken for the dorsal fin, data were further separated by sex because males and females potentially experience a different balance of selection pressures on fin conspicuousness. For example, males display the dorsal fin as part of a courtship signal to prospective mates and during aggressive interactions with rival males, whereas females only display the dorsal fin during aggressive interactions with other females (and on occasion with males as well; e.g., Ord and Hsieh, 2011). Furthermore, the colouration and size of the dorsal fin can be different between the sexes in some species (Ord and Hsieh, 2011; Summers and Ord, 2022b). Data for the six background regions were averaged within each photo under the assumption that a blenny will generally need to match the colour, luminance, and pattern of the background within its immediate vicinity to remain cryptic (with the immediate vicinity represented by the background visible within a given photograph). Subsequent statistical analyses were conducted in four stages.

First, MICA and pavo together compute an extensive range of potential colour morphology indices for consideration. We narrowed this range down manually to the subset we considered to have the most potential to explain biologically relevant differences in crypsis or conspicuous social signalling in blenny fishes. This resulted in 19 chromatic (colour), 14 achromatic (luminance) and 23 pattern indices (see Supplementary Tables S1 and S2). These were then entered into a phylogenetic Principal Component Analysis (pPCA) using the λ evolutionary model in ‘phytools’ version 0.7-80 (Revell, 2012). These pPCAs identified indices representing orthogonal axes that could reflect evolutionary independent attributes of colour, luminance, and pattern. pPCAs were repeated for all five visual models, with loadings found to be broadly consistent regardless of the visual model used. We then selected two chromatic (colour complexity, Hc; colour saturation, MSsat), two achromatic (luminance, ML; internal luminance contrast between adjacent colours, MSL), and two pattern indices (pattern complexity, C; pattern type, Asp) for subsequent examination of crypsis. The selection of indices for the dorsal fin were more straightforward because we had a priori hypotheses of how visual signals should maximise contrast against complex visual backgrounds to increase the probability of conspecific detection: high contrasting colour, high contrasting luminance, and simple pattern. Nevertheless, we entered the same 56 indices outlined above for the dorsal fin into pPCAs to confirm the selection of these indices were broadly representative of dorsal fin appearance. Specifically, we focussed on the degree of 'redness' of the dorsal fin (measured using the MICA index 'RNLx'; see justification in the previous section for why red is of biological relevance for social communication), its luminance (ML) and pattern complexity (C). The output of pPCAs for select visual models are presented in Supplementary Tables S1 and S2 and are not discussed further.

Second, evolutionary shifts in each of the six body indices (and computed from the four predator visual models) and the three dorsal fin indices (computed from the predator visual models and one representing conspecifics) were evaluated as a function of lifestyle using phylogenetic regressions. These phylogenetic regressions were implemented as Ornstein-Uhlenbeck (OU) evolutionary regressions using 'phylolm' version 2.6.2 (Ho and Ane, 2014). Two model sets were applied. The first was a null or intercept-only model that effectively assumed evolutionary shifts in the index variable were either the product of stochastic evolutionary differentiation among taxa or otherwise the result of some unknown selection pressure not measured. The second model included the predictor variable of lifestyle based on the quantitative behavioural score from 0 (aquatic) to 4 (terrestrial). The Akaike information criterion with a modification for sample size (AIC_c) computed by 'MuMIn' version 1.46.0 (Bartoń, 2022) was used to identify the better-supported model (indicated by the lower AIC_c value). Nevertheless, any model within two units of the lower model was still considered to be equally plausible. If the lifestyle model was determined to be the better-supported model or within two units of the null model, the magnitude and direction of its effect was evaluated using the computed t value. A $t \geq 2$ was used as a general benchmark of an effect likely to be statistically distinguishable from zero, which was then confirmed based on a 95% confidence interval of the slope estimate that did not overlap zero (confidence intervals were computed using 1,000 bootstrap replicates). Identified shifts in appearance as taxa became increasingly more terrestrial in behaviour were visualised using 'ggplot2' version 3.3.5 (Wickham, 2016).

Third, the degree of overlap for a given body or dorsal fin index relative to terrestrial backgrounds was assessed based on a direct comparison of the distribution of values across taxa grouped by lifestyle (categorised as aquatic, amphibious, or terrestrial) with the distribution of values measured across all visual backgrounds. This degree of overlap was used to determine the extent to which blennies likely exhibited colours, luminance values, or patterns that offer a generalised form of background matching across multiple terrestrial backgrounds. It also provided a conservative means of benchmarking the extent to which aquatic blennies possess colour morphologies that were likely to be broadly suitable for terrestrial environments. These distribution comparisons were examined using colour-coded histograms created using 'ggplot2'.

Finally, Blomberg's K (Blomberg et al., 2003) and Pagel's λ (Pagel, 1999) estimates of phylogenetic signal were estimated to assess the extent descendent taxa have retained attributes from evolutionary ancestors. These two statistics were estimated separately for each of the six body and three dorsal fin indices using 'phytools'. An instance where K and λ converge on zero is consistent with a phenotypic characteristic that has retained little from evolutionary ancestors (has a low phylogenetic signal) and has been potentially free to adapt. Conversely, an instance where K and λ approach 1 (or exceed 1 in the case of K) is consistent with a characteristic that retains much of its properties from evolutionary ancestors (has a high phylogenetic signal). The extent to which K was statistically distinguishable from 0 was determined through 100,000 simulations in a randomisation test, while a log-likelihood ratio test was used to determine whether the estimated λ was significantly distinguishable from a value of 0. For purely illustrative purposes, a maximum likelihood ancestor state reconstruction was made for the single index (pattern type; Asp) consistently found to be statistically distinguishable from zero using 'phytools'. These reconstructions are presented in Figure 1.

Results

Transitions in habitat that led to adaptive change in colour morphology

Irrespective of the predator visual model considered (aquatic or terrestrial), colour saturation (MSsat) of the body was the only colour morphology index consistently identified as differing among taxa as a function of lifestyle (Table 1; Supplementary Table S3). Specifically, the weighted average of the 'richness' of body colours has progressively declined in taxa that have become increasingly amphibious, reaching its lowest saturation among terrestrial taxa (Figure 2). That is, amphibious and terrestrial blennies have body colours closer to grey (MSsat = 0) than aquatic blennies, although the differences were subtle. For example, the body of aquatic blennies have a phylogenetic mean MSsat value somewhere between 4.2 and 8.5 depending on the predator viewer (corresponding to the OU regression intercepts reported in Supplementary Table S4), while the body of terrestrial taxa have a phylogenetic mean MSsat value somewhere between 2.9 and 6.5 (corresponding to the OU regression slope estimate for a lifestyle score of 4 in Supplementary Table S4). These body colour saturation values generally lie within the distribution of background colour saturation values for terrestrial environments for both aquatic and terrestrial blennies viewed by both aquatic and terrestrial blennies (Figure 2). Nevertheless, the colour saturation of the body in amphibious and terrestrial blennies viewed by a terrestrial bird predator appears marginally more closely matched to terrestrial backgrounds than the body of aquatic blennies viewed by an aquatic fish predator (compare blenny body saturation values to the colours typically seen in backgrounds represented by the distributions in the left and right panels of Figure 2). This implies the change in colour saturation of the body as blennies have progressively colonised land has potentially been an outcome of selection for improved crypsis in the context of the visual system of terrestrial predators.

There were no credible changes in dorsal fin redness (RNLx), luminance (ML) or pattern complexity (C) for either sex as blennies have progressively invaded land, as viewed by conspecifics (Table 2) and most predators (Supplementary Table S5). There was a single instance in which the colour of female

Table 1. Ornstein-Uhlenbeck evolutionary regression models comparing the extent to which lifestyle is a credible predictor of potential evolutionary change in body colour morphology relative to null (intercept only) models of stochastic evolutionary change, based on blennies being viewed by a representative (a) predatory fish (coral trout) and (b) predatory bird (peafowl; Supplementary Table S3 provides full results for all predator visual models considered). Lifestyle models with ΔAIC_c values ≤ 2.0 are presented with *t* values to highlight the magnitude and direction of statistical effects. Those models with statistically distinguished effects greater than zero are highlighted by an asterisk.

Model	AIC_c	ΔAIC_c	*t*
(a) Blenny body, as seen by predatory fish			
Colour complexity (Hc)			
Null	38.94	0.66	
Lifestyle	38.27	0.00	−1.02
$N_{taxa} = 56$			
Colour saturation (MSsat)			
Null	208.38	4.04	
Lifestyle	204.33	0.00	−2.32*
$N_{taxa} = 56$			
Luminance, internal contrast (MSL)			
Null	307.14	0.00	
Lifestyle	308.74	1.61	0.83
$N_{taxa} = 56$			
Luminance, average (ML)			
Null	−127.00	0.00	
Lifestyle	−126.02	0.98	−1.16
$N_{taxa} = 56$			
Pattern complexity (C)			
null	−320.41	0.00	
lifestyle	−318.09	2.32	
$N_{taxa} = 56$			
Pattern type (Asp)			
Null	−158.56	0.00	
Lifestyle	−156.89	1.67	−0.83
$N_{taxa} = 56$			
(b) Blenny body, as seen by predatory birds			
Colour complexity (Hc)			
Null	46.29	0.00	
Lifestyle	47.48	1.19	−0.69
$N_{taxa} = 56$			
Colour saturation (MSsat)			
Null	233.95	5.22	
Lifestyle	228.73	0.00	−2.61*
$N_{taxa} = 56$			
Luminance, internal contrast (MSL)			
Null	329.95	0.35	
Lifestyle	329.60	0.00	1.63
$N_{taxa} = 56$			
Luminance, average (ML)			
Null	−123.81	0.00	
Lifestyle	−123.39	0.43	−1.40
$N_{taxa} = 56$			
Pattern complexity (C)			
Null	−317.31	0.00	
Lifestyle	−315.50	1.81	0.71
$N_{taxa} = 56$			
Pattern type (Asp)			
Null	−160.15	0.00	
Lifestyle	−159.55	0.60	−1.37
$N_{taxa} = 56$			

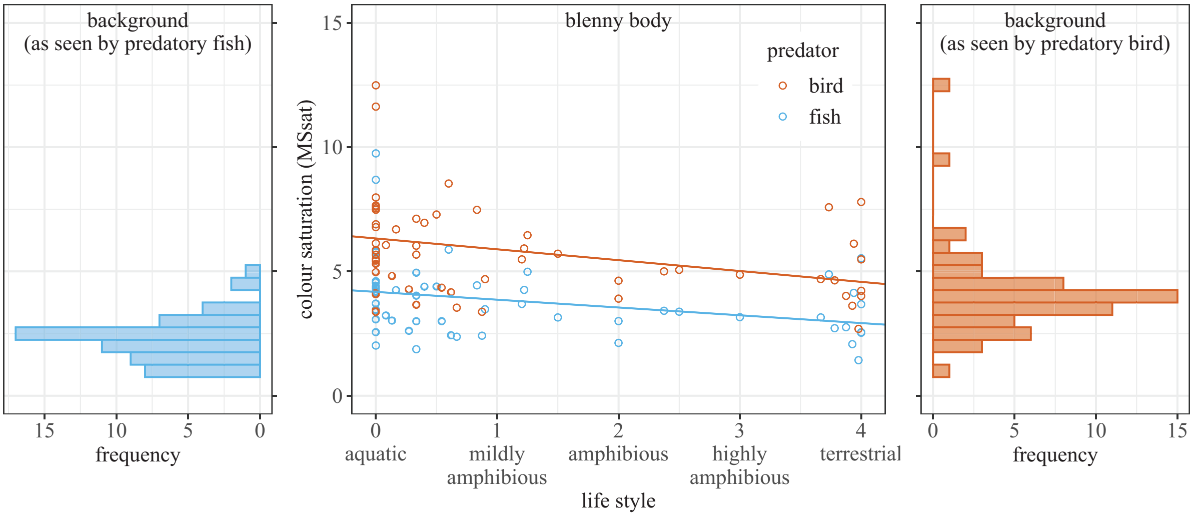


Figure 2. The colour saturation (MSsat) of the body has progressively declined as blennies have progressively colonised terrestrial environments, as viewed by representative aquatic (light blue; coral trout) and terrestrial predators (orange; peafowl) and benchmarked against the colour saturation of diverse terrestrial backgrounds.

Table 2. Ornstein-Uhlenbeck evolutionary regression models comparing the extent to which lifestyle is a credible predictor of potential evolutionary change in the colour morphology of the first dorsal fin, relative to null (intercept only) models of stochastic evolutionary change. See Table 1 legend for other details.

Model	AIC_c	ΔAIC_c	*t*
(a) Female fins, as seen by conspecifics			
Redness (max RNLx)			
Null	1.03	0.00	
Lifestyle	2.51	1.48	1.02
$N_{taxa} = 42$			
Luminance, average (ML)			
Null	−24.02	0.00	
Lifestyle	−22.03	2.00	−0.69
$N_{taxa} = 42$			
Pattern complexity (C)			
Null	−207.15	0.00	
Lifestyle	−205.86	1.29	−1.06
$N_{taxa} = 42$			
(b) Male fins, as seen by conspecifics			
Redness (max RNLx)			
Null	25.02	0.00	
Lifestyle	27.61	2.59	
$N_{taxa} = 28$			
Luminance, average (ML)			
Null	−16.60	1.05	
Lifestyle	−17.66	0.00	−1.94
$N_{taxa} = 28$			
Pattern complexity (C)			
Null	−164.97	0.00	
Lifestyle	−163.18	1.78	−0.97
$N_{taxa} = 28$			

dorsal fins might have become more red as taxa have become increasingly amphibious or terrestrial, but this was limited to a single predator viewer (blue tit; Supplementary Table S5) and was not subsequently considered to be broadly applicable finding. There was some evidence that the luminance of male dorsal fins has decreased (not increased as predicted) as blennies have transitioned onto land (Supplementary Table S6). Evaluation of model outputs (Supplementary Table S7) indicated the 95% confidence intervals for the decline in male dorsal fin luminance was statistically distinguishable from zero as viewed by conspecifics, one of the fish predators, and both bird predators (Supplementary Table S7). The dorsal fins of male aquatic blennies varied widely in luminance, while those of male terrestrial blennies have converged on darker overall colours that appear to match the luminance of terrestrial backgrounds well (Supplementary Figures S1 and S2).

Terrestrial background matching across lifestyles

Of the remaining colour morphology indices, the body of most blennies—irrespective of whether aquatic, amphibious, or terrestrial—was generally well suited for crypsis in terrestrial environments. Body colour complexity (Hc), luminance (ML), internal luminance contrast (MSL) and pattern complexity (C) for the vast majority of blennies generally overlapped the characteristics of most terrestrial backgrounds, and irrespective of whether viewed by aquatic or terrestrial predators (Figure 3). This was despite colour, luminance, and pattern complexity tending to vary widely amongst taxa (Figure 3). The range of colour morphologies exhibited was largely comparable across aquatic, amphibious, and terrestrial taxa (Figure 3). The type of body pattern exhibited by blennies was the only index that appeared not to converge on terrestrial backgrounds. Across taxa, the body pattern of blennies ranged from horizontal through to vertical patterns (e.g., *Istiblennius lineatus* and *Istiblennius edentulus*, respectively; Figure 1), whereas terrestrial backgrounds had random or globular patterns centred on Asp values of 0.5 (Figure 3).

The amount of red (RNLx) and pattern complexity (C) of female and male dorsal fins were generally comparable to most terrestrial backgrounds as viewed by conspecifics, which implies these attributes of the social signal would probably be difficult to see (not conspicuous as predicted) against these backgrounds. There appeared to be a tendency for female fins to exhibit more red as taxa have become more terrestrial (and potentially being more conspicuous; Figure 4a), but this effect was not statistically distinguishable from zero (see Supplementary Table S5a). In some taxa, both sexes tended to have simpler fin patterns than terrestrial backgrounds (particularly male dorsal fins of terrestrial and some amphibious taxa; Figure 4b), but again this was not predicted by lifestyle (Supplementary Tables S5a and S6a; terrestrial taxa were expected to have simpler fin patterns compared to aquatics). The luminance of both female and male dorsal fins for many aquatic and amphibious taxa was often brighter than terrestrial backgrounds, while terrestrial taxa converged on darker colours that overlapped those of terrestrial backgrounds (see

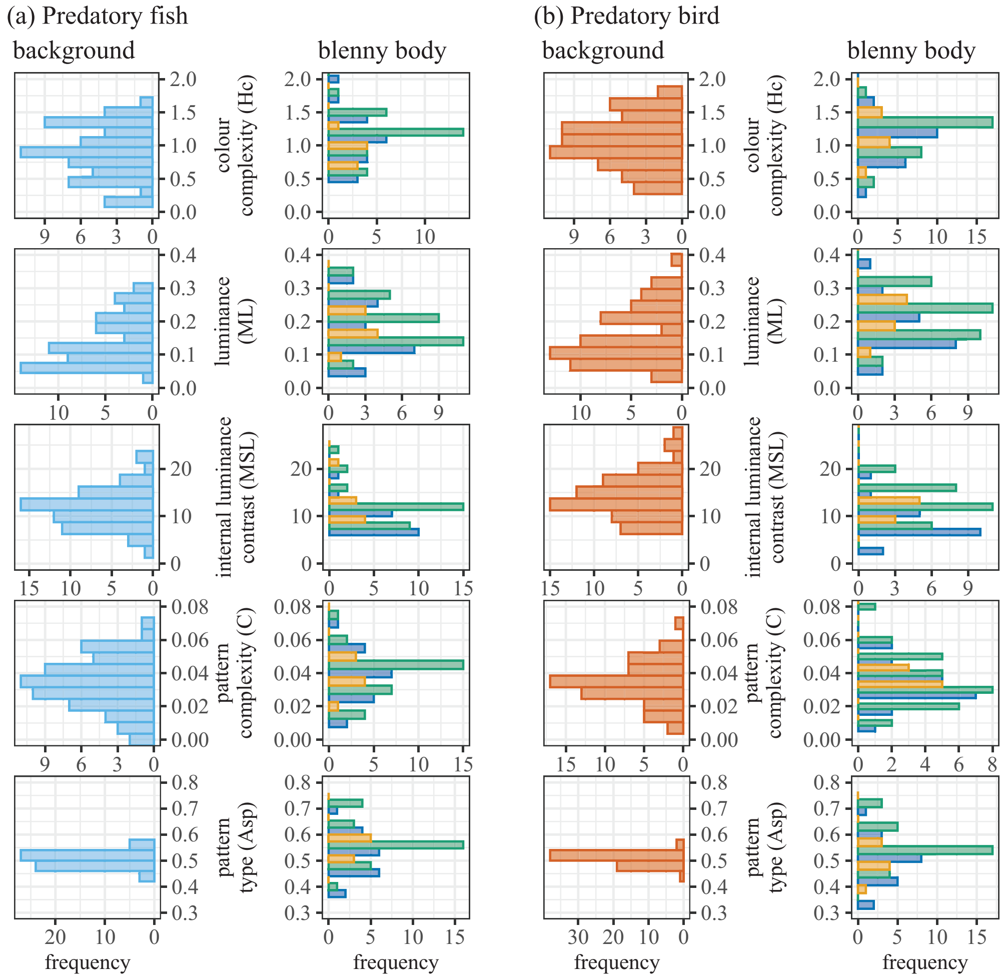


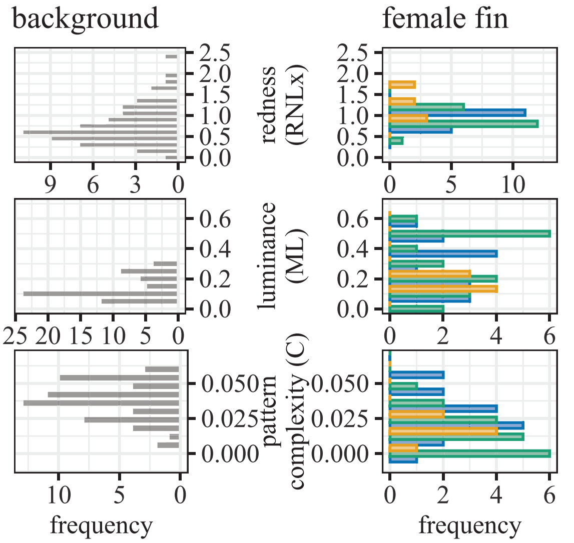
Figure 3. The distributions of body colour morphologies exhibited by aquatic (dark blue), amphibious (green) and terrestrial (tan) species of blenny, and as viewed by representative aquatic (light blue; coral trout) and terrestrial (orange; peafowl) predators and benchmarked against multiple terrestrial backgrounds.

also Supplementary Table S7; dorsal fins were predicted to be brighter than terrestrial backgrounds as taxa have become more terrestrial).

Historic predispositions in colour morphology

Estimates of phylogenetic signal for most colour morphology indices, for both the body and dorsal fin (Table 3), and irrespective of predator or conspecific viewer (Supplementary Table S8), were low implying very little of the colour morphology of blennies has been retained from evolutionary ancestors. The exceptions were body colour complexity and saturation, and the luminance and pattern complexity of the dorsal fin, which were estimated to have moderate to high phylogenetic signal and were statistically distinguished from zero (i.e., no phylogenetic signal), but these estimates were largely contingent on the type of evolutionary model applied (K or λ) and the predator or conspecific viewer considered (Table 3; Supplementary Supplementary Table S8). The phylogenetic signal of body pattern type (Asp) and the pattern complexity (C) of the male dorsal fin (specifically) were the only indices found to consistently differ from zero (Table 3; Supplementary Table S8). Body pattern type varied widely among taxa and was estimated to have low or high phylogenetic signal depending on the evolutionary model applied (K = 0.05 to 0.12 vs. λ = 0.86 to 0.97; Supplementary Table S8). In general, taxa from the same species from different islands or those belonging to the same genus tended to exhibit similar body patterns (see Figure 1). Similar conflicting estimates of the magnitude of phylogenetic signal were found for male dorsal fin pattern complexity (K = 0.08 vs. λ = 0.75; Supplementary Table S8), but again closely related taxa—particularly terrestrial species and some amphibious species (Figure 4b)—tend to exhibit moderate complexity male dorsal fin patterns (which were nevertheless simpler in complexity than most terrestrial backgrounds; Figure 4b).

(a) Female dorsal fin (as seen by conspecific)



(b) Male dorsal fin (as seen by conspecific)

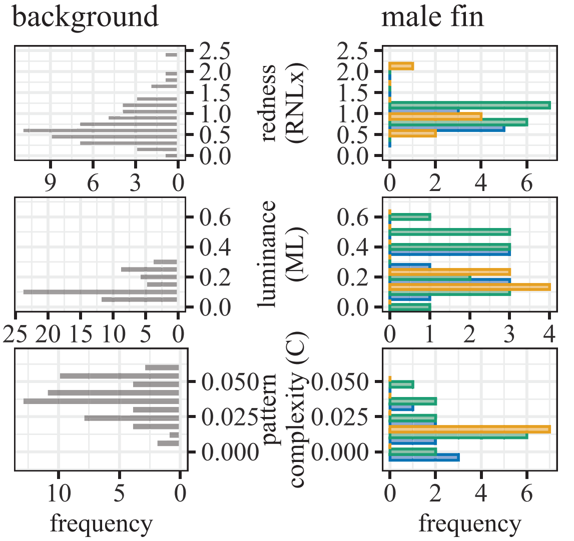


Figure 4. The distributions of dorsal fin colour morphologies exhibited by aquatic (dark blue), amphibious (green) and terrestrial (tan) species of blenny, and as viewed by a potential conspecific and benchmarked against multiple terrestrial backgrounds (grey).

Discussion

Our findings suggest blennies possess a range of colour morphologies that are largely cryptic in various terrestrial environments, regardless of whether taxa were currently aquatic, amphibious, or terrestrial, or viewed by fish or bird predators. While there was considerable diversity in appearance among individual species (Figure 1), differences among species were largely independent of phylogeny (i.e., most characteristics did not seem to have been retained from evolutionary ancestors) and remained within the broad bounds of what would be reasonably considered a cryptic phenotype. There were exceptions, with colour saturation of the body appearing to progressively converge on neutral (grey) colours as blennies have progressively transitioned from water to land, especially as viewed by terrestrial bird predators (Figure 2). There is evidence that bird predators are more likely to target prey with greater contrast in body colour saturation against visual backgrounds (Miller and Hollander, 2010). This suggests the change in colour saturation in blennies could reflect an adaptive response to selection imposed by terrestrial bird predation. In general, though, the morphology of blennies seems to conform to a generalist palette of colours and patterns that are likely cryptic in a variety of terrestrial (and presumably aquatic) environments. By extension, this has likely allowed blennies to more easily transition across one of the world's most extreme ecotones, at least in the context of reducing likely predation risk.

Many natural objects (including environmental backgrounds) and the bodies of at least some blennies reflect in the ultraviolet (UV < 400 nm; Cheney and Marshall, 2009). However, our investigation was limited to the non-UV spectral sensitivities of the digital camera used. The peak sensitivities of the image sensors of this camera are not published by the manufacturer, but most likely occur around 475, 550, and 625 nm with the associated sensitivity curves around these peaks overlapping extensively to provide broad colour representation across the 400–700 nm spectrum (see Morgans and Ord, 2013 for discussion). Our analyses were therefore limited to the RGB colour space or short, medium, and long wavelengths of light reflectance. While some fish predators do see into the UV, the observation that many prey species appear to rely on UV reflectance as a private channel for social communication implies most fish predators probably do not rely on UV reflectance to localise prey (Marshall et al., 2019). Nevertheless, there are various predatory shorebirds that do see UV (e.g., Odeen et al., 2010). Given blennies exhibit colours, luminance, and patterns that overlap those of a diverse range of terrestrial habitats, and that there has been minimal adaptive divergence in appearance with the progressive transition onto land (colour saturation), it would seem likely that blennies similarly match any UV reflectance of visual backgrounds as well to remain cryptic. Nonetheless, the degree of UV matching requires explicit investigation in future research. In the context of social signalling, the subfamily of blennies examined in our study (Salariini) are unlikely to see any UV reflectance (Cortesi et al., 2018), obviating its probable relevance for visual signalling.

In the absence of a generalist phenotype, would-be colonisers potentially face considerable selective challenges limiting the odds of establishment in novel habitats. Plasticity or behavioural changes can help buffer against local extinction (Yeh and Price, 2004), while allowing colonisers enough time to ultimately adapt to new conditions (Härer et al., 2017; Le Gros et al., 2016; Yeh et al., 2007). Yet species that possess characteristics that are at least partly suited to the new environment are subsequently more likely to survive and establish after colonisation (Blackburn et al., 2011). Examples include the invasive African sharptooth catfish (*Clarias gariepinus*) that were established in the Malay Peninsula because it was already well adjusted to the higher temperatures and open stream environments, which were also free of ecological competitors (Low et al., 2022). Intertidal blennies and their progressive transition across an extreme habitat boundary are a case that seems to have been instigated by adaptive change for enhanced crypsis in aquatic environments, which in turn translated well to the environment on land.

The impact of predation is particularly salient for the colonisation of new environments because it can result in a critical trade-off. On one hand, there is considerable pressure on prey to remain inconspicuous in the environment to reduce predation risk (e.g., Ioannou and Krause, 2009; Vignieri et al., 2010), while on the other hand, social signals require prey to disclose their location to communicate effectively to conspecifics (e.g., Driessens et al., 2017; Hornsby et al., 2013; Roberts and Uetz, 2008). The balance of this trade-off will necessarily change when prey transition between habitats that differ in the type and abundance of predators, not to mention if visual backgrounds differ as well. For example, the new habitat can have fewer predators, and prey can consequently establish larger populations because of this ecological release from predation (Des Roches et al., 2011). A similar ecological release has been implicated in at least one species of terrestrial blenny, where the dorsal fin used in social communication appears highly conspicuous (bright red) against terrestrial backgrounds, compared to the cryptic fins of aquatic blennies (Morgans and Ord, 2013). While this conclusion might hold true for certain individual terrestrial species (Figure 4), our broader analysis across multiple terrestrial, amphibious and aquatic blennies indicate the dorsal fin exhibits colours, luminance, and patterns more generally matched to the visual backgrounds of terrestrial environments. This seems inconsistent with the use of the dorsal fin in social communication (Ord and Hsieh, 2011), which predicts visual signals should instead standout against visual backgrounds (Fleishman and Persons, 2001; White et al., 2020). It is not unusual for predation to impose limits on how the colour and size of visual signals are expressed in favour of better survival over higher reproductive success (Endler, 1980; Gotmark, 1993). In other systems, species that occupy high predation environments trade-off conspicuous colour for larger, but more drab visual signals (Klomp et al., 2016). A similar scenario is suggested when our data is combined with past studies of the size of the dorsal fin across blenny species. At least in the case of male dorsal fins, terrestrial species have consistently larger fins than amphibious and aquatic taxa, with some terrestrial blennies exhibiting wildly enlarged fins (Summers and Ord, 2022b). The movement or abrupt presentation of a visual signal, such as raising the dorsal fin during social interactions by terrestrial blennies (this study) or the extension of the dewlap by

Table 3. Estimates of phylogenetic signal using two alternative measures (K and λ) for the colour morphology of the body (as viewed by a representative predatory fish (coral trout) and predatory bird (peafowl; Supplementary Table S8 provides full results for all predator visual models considered) and first dorsal fin (as likely seen by conspecifics). A randomisation test (based on 100,000 random samples) and a likelihood ratio test were used to evaluate the extent K or λ were statistically distinguishable from zero (highlighted in bold).

	K	$p_{100,000}$	λ	p_{LR}	K	$p_{100,000}$	λ	p_{LR}
(a) Blenny body	(i) As seen by predatory fish				(ii) As seen by predatory bird			
Colour complexity (Hc)	0.02	.23	**0.59**	**.01**	0.02	.36	0.43	.20
Colour saturation (MSsat)	0.02	.22	**0.57**	**.04**	0.02	.19	**0.64**	**.01**
Internal luminance contrast (MSL)	0.02	.60	0.00	1.00	0.01	.74	0.36	.07
Luminance, average (ML)	0.02	.28	0.00	1.00	0.03	.13	0.69	.62
Pattern complexity (C)	0.03	.09	**0.72**	**.0026**	0.02	.14	0.67	.08
Pattern type (Asp)	**0.08**	**.0002**	**0.97**	**.0000**	**0.12**	**<.0001**	**0.98**	**<.0001**
(b) Female fin	(i) As seen by conspecifics							
Redness (max RNLx)	0.04	.09	0.69	.53				
Luminance, average (ML)	**0.05**	**.01**	0.78	1.00				
Pattern complexity (C)	**0.05**	**.04**	0.48	1.00				
(c) Male fin	(i) As seen by conspecifics							
Redness (max RNLx)	0.07	.10	0.00	1.00				
Luminance, average (ML)	0.04	.32	0.49	1.00				
Pattern complexity (C)	**0.08**	**.04**	**0.75**	**.04**				

visually displaying lizards (Ord et al., 2013), can also enhance signal detection by conspecifics while minimising its detection by predators (Ord et al., 2021; see also Stevens and Cuthill, 2007; Stuart-Fox and Ord, 2004). What is clear from our study and others is the impact of predation on social signals, particularly during colonisation, is complex and dependent on a variety of factors beyond just the colour morphology of the signal.

The capacity to transition between different environments has implications beyond historical colonisation events and adaption. Future environmental change will likely see more species struggling to survive in existing habitats and forced to move into neighbouring habitats to escape adverse abiotic changes in temperature and other factors (Ehrlén and Morris, 2015; Pecl et al., 2017). These neighbouring environments can present their own challenges in the form of predation risk. Our data suggests that any anti-predator strategy that translates effectively across habitats (or more specifically predator regimes) will facilitate the colonisation process. Crypsis through background matching is usually thought to result in a specialised form of camouflage that is highly specific to certain environments (e.g., Vignieri et al., 2010). The dramatic transition occurring in the blenny fishes between two extreme environments (aquatic and terrestrial) presents an example where prey species can evolve diverse colour morphologies that are cryptic against a variety of visual backgrounds and when viewed by a range of predators with very different visual systems.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

All data used in this paper can be found in the Dryad Digital repository: https://doi.org/10.5061/dryad.c59zw3rkh.

Author contributions

Shizhi Yao (Conceptualization [supporting], Data curation [lead], Formal analysis [equal], Writing—original draft [lead]), and Terry Ord (Conceptualization [lead], Data curation [supporting], Formal analysis [equal], Funding acquisition [lead], Supervision [lead], Writing—review & editing [lead])

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Conflicts of interest

None declared.

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