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Natural selection in novel environments: predation selects for background matching in the body colour of a land fish

Courtney L. Morgans*, Terry J. Ord

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

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The invasion of a novel habitat often results in a variety of new selective pressures on an individual. One pressure that can severely impact population establishment is predation. The strategies that animals use to minimize predation, especially the extent to which those strategies are habitat or predator specific, will subsequently affect individuals' dispersal abilities. The invasion of land by a fish, the Pacific leaping blenny, *Alticus arnoldorum*, offers a unique opportunity to study natural selection following the colonization of a novel habitat. Various studies have examined adaptations in respiration and locomotion, but how these fish have responded to the predation regime on land was unknown. We studied five replicate populations of this fish around the island of Guam and found their body coloration converged on the terrestrial rocky backgrounds on which the fish were most often found. Subsequent experiments confirmed that this background matching significantly reduced predation. Natural selection has therefore selected for background matching in the body coloration of the Pacific leaping blenny to minimize predation, but it is a strategy that is habitat specific. A subsequent comparative study of closely related blenny species suggested that the evolutionary ancestor of the Pacific leaping blenny might have resembled the rocky backgrounds on land prior to invasion. The ancestors of the Pacific leaping blenny may therefore have already been ideally suited for the predator regime on land. More generally our results imply that animals must either already possess antipredator strategies that will be effective in new environments, or must adapt very quickly to new predation pressures if successful establishment is to occur.

Adaptive divergence among taxa often arises when populations invade new environments (reviewed by Schluter 2001). This is because changes in the selection regime experienced by invaders can lead to changes in phenotype (adaptation). The colonization of novel environments has therefore been of special interest to evolutionary biologists because of the opportunity it brings to study natural selection in the wild (e.g. Losos et al. 1993, 1997; Rundle et al. 2003; Wagner et al. 2012). However, if new habitats are different enough from home environments, invading individuals may not survive long enough to establish a viable population. A key factor that can determine colonization success in this regard is predation, as high predation rates or the presence of different types of predators can prevent population establishment (Lodge 1993; Schoener & Spiller 1995). There are a number of strategies that animals might employ to reduce predation, but the best strategy is often to minimize encounters with predators altogether. This can include behavioural changes in habitat use or activity; for example being arboreal in the presence of terrestrial predators (Losos et al. 2004) or avoiding diurnal predators by becoming nocturnal (Berger & Gotthard 2008). Often, however, the option of shifting habitat use or activity is not viable and animals must resort to other measures.

If an individual is indistinguishable from other aspects of the environment, it is less likely to be attacked than one that is not. Tactics used to reduce detection and recognition by predators in this way include masquerading as an unpalatable food item (Skelhorn et al. 2011) or other adverse stimuli (Clucas et al. 2008), disruptive patterning in heterogeneous environments (Zylinski et al. 2011), or some form of background matching when backgrounds are static or otherwise predictable (Stuart-Fox et al. 2008; Wang & Schaefer 2012). These methods of camouflage are specific to the environment that an individual inhabits or to the predator that prey are trying to avoid (Stuart-Fox et al. 2008). This has obvious ramifications for the ability of animals to disperse into new environments. If an organism can no longer effectively camouflage itself (because the habitat or predators differ too much), predation could prevent population establishment entirely. However, if

* Correspondence: C. L. Morgans, School of Biological, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia.
E-mail address: courtney.morgans@unsw.edu.au (C. L. Morgans).

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establishment does occur, animals may be restricted to certain areas within that habitat where individuals are less conspicuous. Predation may still be a problem, but selection has the opportunity to drive the evolution of greater crypsis or some other strategy to minimize predation. Species in this latter scenario offer a means to study how predation can affect the colonization process and provide a wonderful opportunity to study the process of natural selection more generally (e.g. Losos et al. 2004; Vervust et al. 2007).

The Pacific leaping blenny, *Alticus arnoldorum*, is a small tropical fish (4–8 cm in length) found on the island of Guam and has made one of the most extreme ecological transitions possible; it is a fish that has successfully colonized land. To achieve this, it has evolved various adaptations including cutaneous respiration capabilities (while still relying on its gills, respiration also occurs through the skin: Martin & Lighton 1989; Brown et al. 1991; Martin 1995) and the ability to move effectively about on land using a unique axial tail twisting behaviour (Hsieh 2010). To avoid desiccation (and subsequent asphyxiation), the fish is limited to the splash zone of intertidal areas around Guam. For all appearances, however, the fish is exclusively terrestrial and almost never returns to water (Ord & Hsieh 2011). The fish spends much of its time feeding on exposed rocks and other areas out of the water (Ord & Hsieh 2011). Furthermore, both sexes display conspicuously using flashes of a conspicuous, red dorsal fin during courtship and aggression (Ord & Hsieh 2011). How the Pacific leaping blenny has coped with the potential change in predation regime that has followed the transition to land has not been studied. It follows from the observation that the Pacific leaping blenny resembles the rocks on which they spend most of their time (see Supplementary material, Figs S1, S2) that camouflage has potentially been a key strategy for this species in predator avoidance. On land, predation of the Pacific leaping blenny is most likely from diurnal predators such as birds, land crabs or lizards (C. L. Morgans, personal observation). In contrast, predation in the ancestral marine environment was probably from other fish (reviewed by Norton & Cook 1999) and to a lesser extent birds (see Cheney 2009). Furthermore, the visual environment is different on land than in the marine environment: on land, fish have an immediate backdrop of rocks, while in water fish have a general background of water and to some extent rocks if marine species occupy the intertidal zone (e.g. Marshall & Jennings 2003).

The primary goal of our study was to test the general hypothesis that visually oriented predators on land have selected for a body coloration in the Pacific leaping blenny that matches the rocky backgrounds against which the fish are typically found. We tested this hypothesis in two ways. First, we examined five populations of blenny around Guam and determined the extent to which the body coloration of each population matched their environments (we measured both the hue (chromatic) and brightness (achromatic) properties of fish and backgrounds). We replicated our study across five populations because initial observations suggested habitat backgrounds varied subtly from location to location. Given this, we predicted that populations would converge on the colour properties specific to their location. To provide a suitable benchmark for this colour comparison, we also quantified the colour of the dorsal fin, which is an important signal in social interactions for both males and females (Ord & Hsieh 2011) and should therefore be conspicuous in the environment (e.g. Stuart-Fox & Moussalli 2009; Zylinski et al. 2011). If predation has selected for crypsis in the Pacific leaping blenny, we expected to find the body of individuals, which is always visible, to match the appearance of habitat backgrounds. Conversely, the dorsal fin, which is only visible when erected during signal bouts, should exhibit high contrast with habitat backgrounds to facilitate its role in communication. Second, we performed an experiment to confirm that cryptic body coloration reduces predation. The experiment compared predation rates on naturalistic model blennies to conspicuously coloured controls in two adjacent, visually different land environments. The Pacific leaping blenny was found in both environments, but differed substantially in density (C. L. Morgans & T. J. Ord, personal observation). If blenny body coloration has been selected for background matching, then predation should be lowest in the environment most often used by blennies and in which blennies appear most cryptic.

To provide some resolution of the evolutionary history of body coloration, and whether it might have facilitated or challenged the invasion of land by the Pacific leaping blenny, we supplemented these two studies with an ad hoc examination of body coloration in representative specimens of several closely related marine species found around the island. This comparative study was not meant to provide a formal phylogenetic reconstruction of ancestor phenotype, which would require detailed and extensive sampling of species across the blenny phylogeny (as well as their environments). Rather, the goal was to reveal the extent to which the Pacific leaping blenny differed or resembled its marine relatives and, by extension, the likelihood that the fish has evolved its present-day body coloration prior to, or following, the colonization of land.

METHODS

Population Colour Analysis

Adult male and female Pacific leaping blennies and specimens of closely related species were captured using hand nets at five locations around Guam between June and August 2011 (overlapping with the probable breeding season of this genus; see Shimizu et al. 2006). The locations were: Pago bay (13°25′39″N, 144°47′56″E), Taga'chang (13°24′16″N, 144°46′53″E), Talofofo (13°20′34″N, 144°46′21″E), Umatac (13°17′40″N, 144°39′29″E) and Adelup Point (13°28′52″N, 144°43′44″E; see Results, Fig. 1). Of the Pacific leaping blenny, a total of 95 males and 95 females were sampled, with a median of 24 males and 25 females per population. All individuals were released at the point of capture after study, except for a small subset from Taga'chang that was euthanized to make prey models (see next section). Of the marine species, a few whole specimens were caught opportunistically as part of tissue collections made for a separate study on the phylogeny of the Blenniidae family. These individuals were ultimately euthanized following procedures outlined in the University of New South Wales Animal Care and Ethics Committee (UNSW ACEC) protocol 11/36B for later molecular analysis. However, before being euthanized, we used this whole specimen collection to examine one representative adult individual for each species. Both the Pacific leaping blennies and its relatives are capable of changing their body coloration from their normal patterning. For example, the colour of the Pacific leaping blenny can change to either a uniform ash grey or charcoal black within minutes (Ord & Hsieh 2011; see also Abel 1993; Heflin et al. 2009). These colour changes seem to be limited to social interactions (e.g. Ord & Hsieh 2011), but to minimize colour variation that might also be induced from the initial stress of capture, individuals were isolated in moist opaque plastic containers and left in a sheltered, shady area for at least 1 h prior to photography. At no time did we observe any noticeable colour change while taking photos of the Pacific leaping blenny or any other species.

Full body photographs were taken of individuals positioned side-on to the camera with the dorsal fin raised against a white standard background (X-Rite ColorChecker White Balance Card) and beside a ruler and a Munsell colour chart (X-Rite mini ColorChecker; Fig. S1). Photographs were taken with a Canon EOS 7D digital SLR using an EFS 15–85 mm, f/3.5–5.6 IS USM zoom lens and stored as high-resolution jpegs. Multiple photographs were