

Ecological Release from Aquatic Predation Is Associated with the Emergence of Marine Blenny Fishes onto Land

Terry J. Ord,^{1,*} Thomas C. Summers,¹ Mae M. Noble,² and Christopher J. Fulton^{3,*}

1. Evolution and Ecology Research Centre and School of Biological, Earth, and Environmental Sciences, University of New South Wales, Kensington, New South Wales 2052, Australia; 2. Fenner School of Environment and Society, Australian National University, Canberra, Australian Capital Territory 2601, Australia; 3. Research School of Biology, Australian National University, Canberra, Australian Capital Territory 2601, Australia

Submitted October 4, 2016; Accepted December 7, 2016; Electronically published March 2, 2017

Online enhancements: appendix. Dryad data: <http://dx.doi.org/10.5061/dryad.0c614>.

ABSTRACT: An ecological release from competition or predation is a frequent adaptive explanation for the colonization of novel environments, but empirical data are limited. On the island of Rarotonga, several blenny fish species appear to be in the process of colonizing land. Anecdotal observations have implied that aquatic predation is an important factor in prompting such amphibious fish behavior. We provide evidence supporting this hypothesis by demonstrating that amphibious blennies shift their abundance up and down the shoreline to remain above predatory fishes that periodically move into intertidal areas during high tide. A predation experiment using blenny mimics confirmed a high risk of aquatic predation for blennies, significantly higher than predation experienced on land. These data suggest that predation has played an active role in promoting terrestrial activity in amphibious blennies and provide a rare example of how ecological release from predation could drive the colonization of a novel environment.

Keywords: Blenniidae, intertidal zone, land invasion, niche expansion, water-land transition.

Introduction

Adaptation is now recognized as a key engine of evolutionary diversification by driving divergences among populations that occupy different environments (Schluter 2009; Losos 2010; Yoder et al. 2010; Schoener 2011; Richardson et al. 2014). Less clear, however, is what motivates taxa to initially move from one environment to another. There are a number of theoretical reasons for why taxa might occupy different habitats, including the abiotic and biotic conditions required

for the establishment of colonizers (niche models; Leibold 1995; Soberon 2007), the extent to which competition determines those species that can coexist in a given habitat (competition models; MacArthur and Levins 1967; Levine and HilleRisLambers 2009), or simply the likelihood of taxa reaching locations and persisting through random adverse events (neutral and demographic models; Lande 1988; Hubbell 2001; Wootton and Pfister 2013). But the situation that most likely promotes adaptive differentiation is one in which individuals colonize an environment where the abiotic or biotic conditions, which determine the selection regime operating on the phenotype, are distinct from the ancestral environment. In this context, individuals might abandon one environment in favor of another to gain an “ecological release,” for example, to escape competition (Bolnick et al. 2010) or predation (Refsnider et al. 2015).

Empirically testing whether an ecological release might have prompted the colonization of a new environment in nature is challenging, and examples are rare (e.g., Stamps 1983; Refsnider et al. 2015). To do so requires reliable identification of the ancestral environment, quantification that the selection pressure experienced by individuals was reduced following colonization of the novel environment, and some measure showing how movement of individuals between environments is associated with changes in that selection pressure. The best opportunity for meeting these requirements is a situation in which the colonization of a novel environment is actively under way.

A remarkable example of this situation is occurring on the South Pacific island of Rarotonga. On this island there are four fish species that emerge from water to spend various amounts of time on the exposed rocks in the littoral zone (see fig. A1; figs. A1, A2 are available online). Each of these fishes belongs to a separate genus within the family Blenniidae, which appear to have independently evolved amphibious lifestyles (Ord and Cooke 2016). Although there

* Corresponding authors; e-mail: t.ord@unsw.edu.au; christopher.fulton@anu.edu.au.

ORCID: Ord, <http://orcid.org/0000-0002-2608-2150>; Summer, <http://orcid.org/0000-0002-8743-1545>; Fulton, <http://orcid.org/0000-0002-1140-1999>.

Am. Nat. 2017. Vol. 189, pp. 570–579. © 2017 by The University of Chicago. 0003-0147/2017/18905-57310\$15.00. All rights reserved. DOI: 10.1086/691155

are amphibious blennies on other islands throughout the North Pacific, South Pacific, and Indian Oceans (Brown et al. 1991; Bhikajee and Green 2002; Shimizu et al. 2006; Ord and Hsieh 2011; Ord and Cooke 2016), Rarotonga is one of the few places where species representing multiple independent origins of an amphibious lifestyle are found together. Of the four terrestrially active species on the island, three divide their time between water and land (and are the main focus of this study), while the fourth species rarely (if ever) returns to water (C. J. Fulton, M. M. Noble, and T. J. Ord, unpublished data) and likely spends its entire adult life above the waterline within the splash zone (e.g., Ord and Hsieh 2011; Platt et al. 2016).

Stark differences between the aquatic and aerial environments create numerous challenges for fishes in terms of respiration, physiology, and locomotion (for recent reviews, see Martin 2014; Wright and Turko 2016). Yet transitions across the water-land interface are common in fishes (see the meta-analysis by Ord and Cooke 2016). Within the family Blenniidae, there have been as many as seven independent transitions onto land (Ord and Cooke 2016). Given that these amphibious taxa often have body plans that are very similar to those of their aquatic relatives (e.g., see Morgans and Ord 2013), the obvious question is why fish so clearly adapted to an aquatic lifestyle should make the seemingly dramatic shift to land. Many hypotheses have been proposed (Sayer and Davenport 1991), which range from abiotic motivations (e.g., to escape adverse fluctuations in water conditions; Martin 1996; Gibson et al. 2015) to biotic motivations (e.g., to exploit the availability of food or nest site resources on land; Graham 1973; Shimizu et al. 2006; van Wassenbergh 2013). However, the avoidance of aquatic predation is arguably one of the most common explanations (reviewed in Sayer and Davenport 1991). There are numerous anecdotal reports of fish leaping out of water and stranding themselves on land to avoid attacks from aquatic predators (e.g., Graham 1970; Baylis 1982). Aquatic predation has also been implicated in the terrestrialization of various life stages in amphibians (e.g., Touchon and Warkentin 2008) and experimentally shown to force newts to abandon aquatic habitats almost entirely for land (Winandy et al. 2015). In the specific case of amphibious blennies, there is evidence of predictable changes in life history that are consistent with an ecological release from predation following the move onto land (Platt and Ord 2015; Platt et al. 2016).

To test the hypothesis that fishes on Rarotonga are moving onto land to escape aquatic predation, we combined surveys of predator and amphibious blenny abundance across the water-land interface with an experiment designed to document predatory attacks on blennies in aquatic and terrestrial environments. In the first instance, we quantified fish abundances along transects positioned in the subtidal (permanently aquatic), intertidal (periodically submerged

and emerged by the tide), and littoral (permanently aerial) zones. These surveys were complemented by systematic visual observations of the abundance of potential terrestrial predators (which were found to be birds). We then deployed plasticine blenny mimics along transects in the subtidal and littoral zones and recorded the proportion of mimics showing signs of predator strikes. If aquatic predation was an important instigator of terrestrial activity in blennies, we expected to observe an inverse relationship between the abundance of amphibious blennies and the abundance of aquatic predators, which should track the position of the water-land interface as it shifted elevation with the incoming and outgoing tides. Furthermore, attack rates on blenny mimics should be higher in subtidal than in littoral zones. Taken together, these findings would provide a rare example of an ecological release from predation promoting an active transition between two contrasting environments.

Methods

Data (deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.0c614>; Ord et al. 2017) were collected during what was anticipated to be the peak breeding period for blenny fishes on the island (midsummer; e.g., Bhikajee et al. 2006). Shoreline fish surveys and the predation experiment were conducted consecutively at the same sites near Avana Point and the adjacent island of Motutapu (~150 m from Avana Point) near the locality of Muri (fig. A2). The typical shoreline profile at these sites was composed of a shallow reef flat (0–1.5 m depth) that rose abruptly into a near-vertical wall of ancient coral reef carbonate. A very shallow (<0.1 m deep) reef shelf extended seaward for 4–8 m from the base of this wall before deepening to 0.5–2.0 m as it progressed seaward to the reef crest. At low tide the water level was at the base of the vertical wall, and the incoming tide submerged 0.7–0.9 m of the wall during our study period (December 6–18, 2015).

Quantifying Abundance Shifts

Data Collection. Blenny abundances were assessed along 30 × 1-m belt transects deployed parallel to the waterline at three levels on the shore: subtidal (always submerged; 0.5–1.5 m below low-tide water level and a minimum of 10 m offshore of the intertidal transect), intertidal (periodically emerged and submerged; 0–1.0 m above low-tide level), and littoral (splash zone above high-tide mark; 1.5–2.5 m above low-tide level). A single observer (C.J.F.) worked slowly along the shore and visually recorded the number and species of every blenny present within the littoral and intertidal belt transects, and he then did the same in a return swim along the subtidal transect. Surveys of putative aquatic predators of these small-bodied blennies were assessed by the same observer (C.J.F.) within the same sections of shoreline (as

described above) along 30×5 -m belt transects deployed during each of the low-tide (subtidal) and high-tide (subtidal and intertidal) states (NB: at low tide there was no aquatic environment for aquatic predators in the intertidal zone, and there was no aquatic environment in the littoral zone during any tidal phase). The target species were predatory coral reef fishes known to consume other fishes, which at our sites included flounders (e.g., *Bothus*), trevallies (*Carangoides*), groupers (*Epinephelus*), lionfishes (*Pterois*), moray eels (*Siderea*), and the wrasses *Thalassoma purpuraceum* and *Thalassoma lunare* (Connell 1998; Bellwood et al. 2006; Ashworth et al. 2014). This entire procedure was repeated within a 1-h window of a low- and a high-tide state, with a minimum of 72 h separating repeat surveys of the same shoreline section under different tidal states. Apart from setting transects according to the level of the low-tide mark (as described above), transects were not fixed but deployed haphazardly in each section of shoreline. A total of 11 sections of shoreline were surveyed in this way (i.e., $N = 33$ transects per tide state across the three shore zones), with a minimum of 5 m separating adjacent sections (fig. A2).

Finally, the abundance of potential terrestrial predators foraging within the bounds of the littoral to subtidal areas encompassed in the fish surveys was assessed by a single observer (M.M.N.), who sat with binoculars and scanned 200 m of shoreline for about 20 min (median: 21 min; range: 20–30 min). Terrestrial predators at our site potentially included lizards or rats (which were anecdotally observed during the field trip), but the only animals observed during the terrestrial surveys were birds. For these, point surveys recorded those bird species capable of taking an amphibious blenny (which effectively included any predatory bird). At our site, these were the gray-tailed tattler (*Tringa brevipes*; directly observed striking at a blenny mimic in the littoral zone), the brown noddy (*Anous stolidus*), the fairy tern (*Gyrus alba*), and the Pacific reef heron (*Egretta sacra*; directly observed taking a live blenny from the intertidal zone). Each point survey was repeated within each of two 200-m shoreline sections during both a high- and a low-tide state.

Statistical Analyses. We focused our analyses on the total abundance of three amphibious blennies (*Praealticus caesus*, *Entomacrodus striatus*, and *Istiblennius edentulus*) because these were the only fishes found in both aquatic and aerial environments. These species are, therefore, likely to respond to changing risks of both aquatic and terrestrial predation. A number of aquatic blennies were also observed at low densities in the subtidal (*Blenniella bilitonensis*, *Blenniella gibbifrons*, *Blenniella paula*, *Exallias brevis*, *Rhabdoblennius rhabdotrachelus*, and *Salarias fasciatus*) but were never seen out of the water during the study (consistent with observations of the same species and genera on other islands; Ord and Cooke 2016). The single exclusively “terrestrial” blenny

found at the study site (*Alticus* sp. cf. *simplicirrus*) was excluded from our analyses because it was never observed underwater, nor was it expected to ever occur in water as a juvenile or adult (Bhikajee et al. 2006; Ord and Hsieh 2011; Platt et al. 2016); therefore, it is rarely exposed to aquatic predation.

The association between predator and amphibious blenny abundance was tested in a restricted maximum likelihood linear mixed-effects model implemented using the lme4 package (ver. 1.1-8; Bates et al. 2015) in R (ver. 3.2.4; R Development Core Team, R Foundation for Statistical Computing, Vienna). Abundance data were first naturally log transformed ($\ln X + 1$) to improve normality and reduce heteroscedasticity. The model included the fixed effect of predator abundance and a random intercept and slope for tide (coded as 0 for low tide and 1 for high tide). We also applied a second set of analyses to only those transects that were submerged during a given tidal phase using a standard linear regression. The first mixed-effects model provided an overall view of how predator and amphibious blenny abundance varied relative to each other across shore zones and tidal phases. The second regression applied separately to each tidal phase quantified the relative abundances of predator and amphibious blennies exclusively in the aquatic environment. These latter analyses were used to evaluate the extent to which submerged amphibious blennies actively avoided fish predators and also provided a means of predicting the abundance of amphibious blennies in the absence of fish predators (see fig. 1). If amphibious fish moved out of the water to avoid fish predation, then the observed abundance of amphibious fish on land should be comparable to the abundance predicted from aquatic regressions when fish predators were absent. If amphibious fish moved out of water for other reasons, such as to exploit terrestrial resources (e.g., food or nest holes), then abundances on land should be higher than expected in the absence of fish predators.

Estimating Predation

Data Collection. Highly realistic blenny mimics were made using latex casts of fresh-caught fish of a terrestrial *Alticus* species from Guam created as part of a previous study (Morgans and Ord 2013). The gross morphology and standard length of this species was typical for amphibious blennies more generally (e.g., amphibious blennies on Rarotonga range in mean standard length from 42 to 70 mm, and our blenny mimics were 60 to 70 mm). A combination of black, white, green, and yellow malleable plasticine (Colorific; Clayton, Australia) was carefully blended by hand and referenced to photographs of live amphibious blennies to mimic their cryptic coloration and patterning (see figs. A1, 2C). The method of quantifying predation using plasticine or clay models has been successful in a variety of taxa (e.g., McLean et al. 2010;

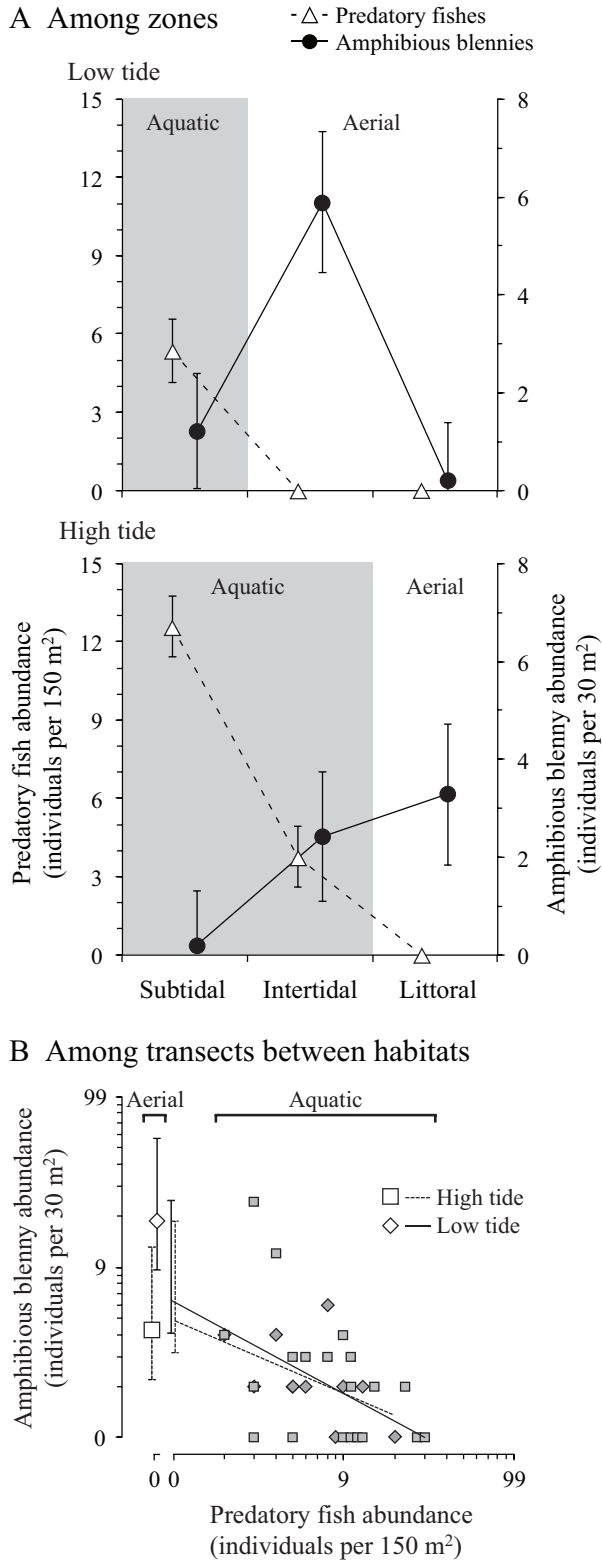


Figure 1: Changes in the abundance of amphibious blennies and their aquatic predators on the island of Rarotonga at low and high tide. Shown in A are back-transformed means and standard errors

Chouteau and Angers 2011; Linnen et al. 2013) and has proven especially useful in estimating predation on amphibious blennies on other islands (Morgans and Ord 2013; Morgans et al. 2014).

We deployed a total of 125 blenny mimics in the subtidal zone and 124 blenny mimics in the littoral zone. Mimics were not deployed in the intertidal, as we could not be sure whether attacks were from aquatic or terrestrial predators in this intermittently submerged zone. Mimics were positioned in the same areas as the belt transects described above and so were known areas of activity for amphibious blennies and their predators (both aquatic and terrestrial). Particular care was also taken to place mimics in locations and against substrate backgrounds typical of amphibious blennies observed during transect surveys (NB: amphibious blennies are demersal and are often found directly on rock substrate; e.g., see fig. A2). Deployments were made in consecutive, spatially nonoverlapping cohorts of 50–68 mimics. To anchor blenny mimics, a small amount of epoxy adhesive putty (Knead-IT Aqua; Selleys, Padstow, Australia) was used to secure mimics to large rocks in subtidal pools or directly to rock outcrops in the littoral zone. Blenny mimics were initially deployed at low tide and left for a minimum of 3 days and (for a subset) a maximum of 8 days. After the completion of the experiment, all foreign material was removed from the study area.

We followed the same procedures outlined in Morgans and Ord (2013) for recording signs of predator strikes on mimics. Specifically, we recorded evidence of puncture wounds and bite marks left in the plasticine that could be attributed to a fish, a bird, or some other terrestrial predator (rat or lizard). These impressions were deep and clearly delivered with some force. They were often accompanied by teeth marks, the outline of what seemed to be a jaw or beak, or large portions of plasticine being removed entirely from the mimic. Examples are presented in figure 2C. However, the key objective was to categorize evidence of predatory attack generally, not the type of predator responsible for any given attack. In the case of subtidal deployments, we confirmed that fish predators were attracted to (and attacked) the mimics by positioning a GoPro3 White video camera in underwater housing adjacent to one subtidal mimic at a distance of 1.5 m in 0.3-m water depth and recorded fish visitations for 60 min

of fish abundance recorded along 11 transects within each of the subtidal, intertidal, and littoral zones. The shaded regions illustrate zones that were submerged at each tidal phase. Data in B are total fish abundances for individual transects submerged at a given tidal phase (and therefore aquatic) relative to back-transformed means and 95% confidence intervals of fish abundances found out of the water on land (aerial). The trend lines are those computed by models in table 1, part B, and illustrate the confidence intervals for intercepts (the inferred abundances of amphibious blennies when there are no recorded predatory fish).

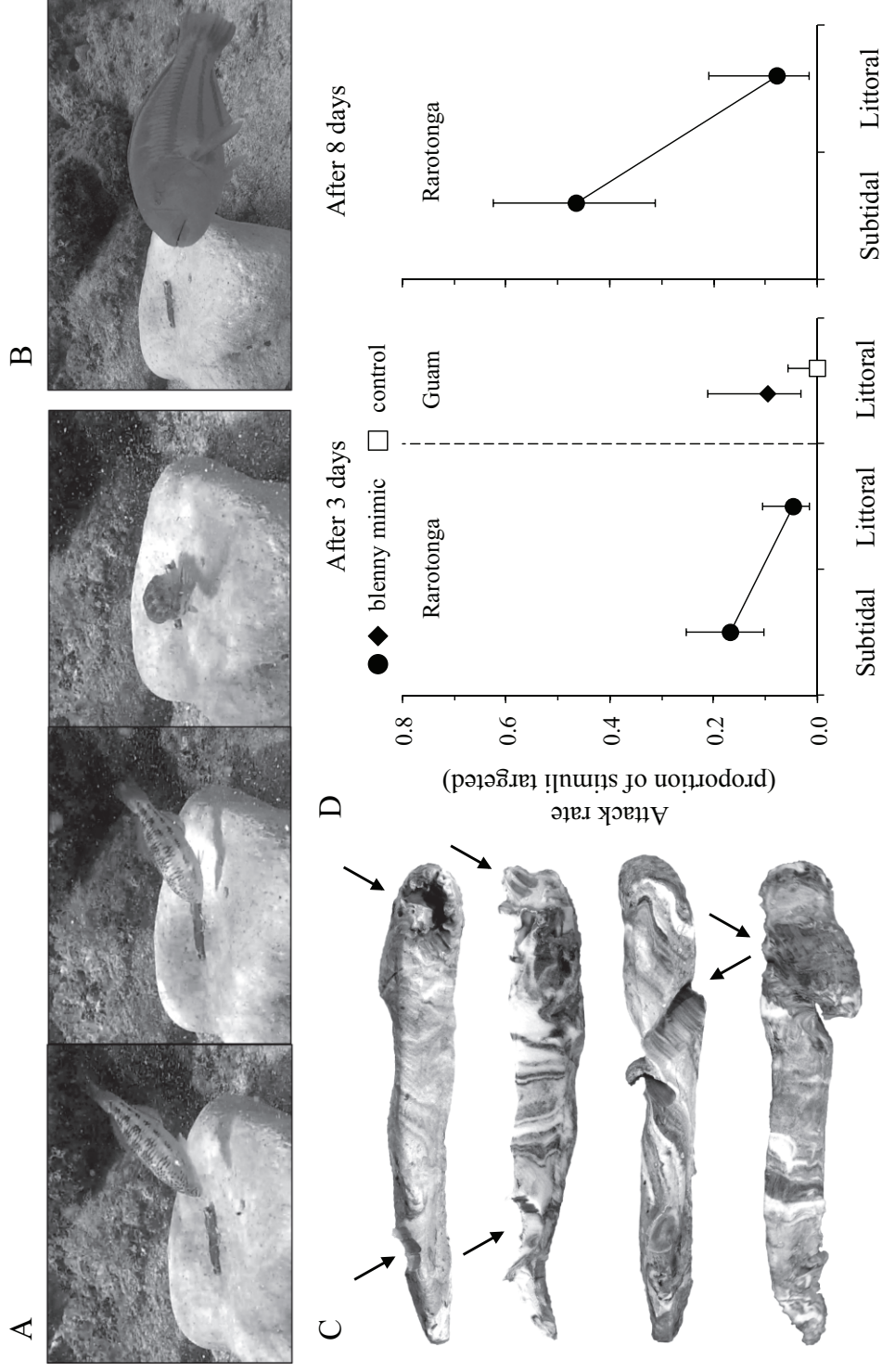


Figure 2: Predation on blenny mimics. Video stills in *A* illustrate a wrasse (*Thalassoma purpuraceum*) attacking a blenny mimic, and the still in *B* illustrates inspection of a mimic by a terminal-phase male of the same species. Examples of predator attacks on blenny mimics are given in *C*, with the first three showing attacks made on mimics deployed in subtidal pools and the last showing an attack made on a mimic deployed out of the water in the littoral zone. *D*, Proportions and associated 95% confidence intervals of blenny mimics attacked in subtidal pools and on land in the littoral zone, after 3 days (compared with equivalent data from an earlier study conducted on Guam; Morgans and Ord 2013) and 8 days of deployment. A color version of this figure is available online.

during the incoming morning tide. Representative examples of predators seen attacking the mimic during this time period are shown in figure 2A and 2B.

To provide a benchmark, we compared our data with those obtained from blenny mimics and a conspicuous control stimulus deployed in the littoral zone on Guam as part of a previous study (Morgans and Ord 2013; the control was a ring of highly visible pink plasticine of the same thickness and length as blenny mimics). The objective of this earlier experiment was to document differences in terrestrial predation on a terrestrial blenny (*Alticus arnoldorum*) in two adjacent terrestrial habitats (rocky outcrops vs. open sandy beach; Morgans and Ord 2013). The experimental procedure was otherwise comparable to that used in the current study.

Statistical Analyses. The proportion of blenny mimics showing evidence of predator attack was compared between the subtidal and littoral deployments (and to benchmarks from the previous study on Guam) through a comparison of 95% confidence intervals (CIs) and effect size estimates. CIs of proportions were computed using the formula presented in Zar (1999). Effect sizes and corresponding 95% CIs were computed as an odds ratio that was then converted to an r value using the formula presented in Ord et al. (2011). Proportions and effect sizes with 95% CIs that did not overlap were considered statistically distinguishable from one another (equivalent to $P < 0.05$).

Results

Predator and Amphibious Blenny Abundance

The abundances of aquatic predators and amphibious blennies were inversely correlated across tide phases (table 1, pt. A). At low tide the peak abundance of amphibious blen-

nies was in the intertidal zone and, to some extent, subtidal pools, where aquatic predators were in low abundance (fig. 1A). At high tide, however, amphibious blennies moved upward on the shore so that their greatest abundance was in the littoral zone, ahead of an increase in aquatic predators who followed the water rising in the intertidal (fig. 1A).

Comparisons among submerged transects showed that amphibious blennies were found in higher abundance within transects with fewer aquatic predators (table 1, pt. B), which is consistent with the notion that blennies were actively avoiding areas of high predation risk, even within the aquatic environment. The intercept values of these regressions—that is, the expected abundances of amphibious blennies in the absence of aquatic predators—were statistically indistinguishable from the observed abundances of amphibious blennies on land (where aquatic predators are absent; fig. 1B). This is consistent with the notion that amphibious blennies have moved onto land primarily to avoid aquatic predation.

Direct statistical analysis was not possible for estimates of bird predator abundances, partly because methods of assessment could not be standardized to those used for fish and partly because sightings of bird predators were generally infrequent (NB: birds were the only potential terrestrial predator of blennies observed during surveys). Nevertheless, sightings of bird predators were consistently made across tide phases, with mean sightings (weighed by observation time) of 3.81 birds per 20 min (95% CI: 2.61 to 5.01) during low tide and 4.30 birds per 20 min (95% CI: -0.30 to 8.91) during high tide.

Predator Attack Rates

The proportion of blenny mimics showing compelling signs of predator attacks (e.g., fig. 2C) was higher for those de-

Table 1: Amphibious blenny abundance as a function of predator abundance along belt transects positioned in the subtidal, intertidal, and littoral zones (pt. A; see also fig. 1A; tide level was included as a random intercept and slope) or submerged at low or high tide (pt. B; see fig. 1B)

Variable	Estimate (95% CI)	Effect size (t)	One-tailed P
A. Among all transects ($N_{\text{transects}} = 66$, $N_{\text{tides}} = 2$):			
Intercept	1.27 (.84 to 1.69) ^a	5.79	... ^b
Predator abundance	-.29 (-.54 to -.03) ^a	-2.18	... ^b
B. Among aquatic transects only:			
Low tide ($N_{\text{transects}} = 11$):			
Intercept	1.59 (.55 to 2.62) ^a	3.46	.007
Predator abundance	-.43 (-.96 to .10)	-1.83	.051
High tide ($N_{\text{transects}} = 32$):			
Intercept	1.84 (.77 to 2.90) ^a	3.61	.001
Predator abundance	-.54 (-1.02 to -.06) ^a	-2.35	.015

^a Confidence intervals (CIs) that do not overlap zero.

^b P values could not be formally computed for this model.

ployed in the subtidal pools than for those deployed in the littoral zone; this effect increased dramatically with deployment time (95% CIs of effect size r : for after 3 days, 0.103 to 0.558, $N_{\text{subtidal}} = 107$, $N_{\text{littoral}} = 106$; for after 8 days, 0.272 to 0.711, $N_{\text{subtidal}} = 43$, $N_{\text{littoral}} = 39$; fig. 2D). Notably, the littoral mimic attack rates were comparable to those deployed on Guam over the same number of days and were statistically indistinguishable from control stimuli (i.e., 95% CIs overlapped; fig. 2D). This suggests that terrestrial predation on Rarotonga was probably negligible and not unusually so compared with that on other oceanic islands. Furthermore, the proportion of mimics attacked in the littoral zone on Rarotonga changed little over time, while evidence of aquatic predation increased substantially the longer mimics were left in subtidal pools (fig. 2D).

Discussion

The aquatic ancestral environment of blenny fishes is clear (see historic reconstructions in Ord and Cooke 2016 and Hundt et al. 2014a). The intertidal zone represents a dynamic ecotone between this ancestral (subtidal) environment and the adjacent (littoral) terrestrial environment. Daily tidal fluctuations produced spatial shifts in the aquatic-aerial boundary through the intertidal zone, which in turn caused significant shifts in the abundance of aquatic predators at different levels on the shore. This provided an unusual opportunity to observe how the movements of amphibious blennies between the aquatic and aerial environments were related to predator movements. Within the intertidal, aquatic predators were generally more abundant when deeper water was present at high tide, while many amphibious blennies moved into aquatic areas away from these predators (fig. 1B) or left the aquatic environment altogether in favor of terrestrial refuges in the littoral zone (fig. 1A). At low tide, aquatic predator abundance was noticeably reduced, and those remaining were restricted to deep subtidal pools. At the same time, amphibious blennies returned to the intertidal zone in high numbers (fig. 1A) and occasionally to shallow subtidal pools away from predatory fish (fig. 1B). Bird predators were observed foraging in all zones (and were the only terrestrial predators observed during point surveys), but their abundance was generally low and unrelated to tide. Our predation experiment (fig. 2D) subsequently confirmed higher attack rates on blenny mimics in subtidal pools than on the exposed rocks of the littoral zone typically frequented by amphibious blennies (fig. 1B). These data imply a significant release from predation for any fish that crosses the aquatic-aerial boundary, which appears to have been an active force prompting terrestrial activity in amphibious blennies on Rarotonga.

Factors associated with an ecological release have often been speculated in the evolution of amphibious behavior

in fishes (Sayer and Davenport 1991), including the putative role of aquatic predation causing fish to temporarily strand themselves on land (e.g., Graham 1970). Yet basic ecological data on why fish leave their aquatic environments for a life on land are lacking (for rare examples, see Martin 1996; Gibson et al. 2015), despite numerous cases of amphibious activity in living fishes (documented in at least 33 families and 73 genera; Ord and Cooke 2016) and its central role in the evolutionary origin of terrestrial vertebrates (Coates et al. 2008; Laurin 2010). Our data provide the best evidence to date that predation may have been an important ecological instigator of terrestrial activity in marine fishes (Sayer and Davenport 1991; Ord and Cooke 2016; Wright and Turko 2016).

Blennies seem to be a group prone to terrestrial activity (Ord and Cooke 2016). For example, there are other genera (*Alticus* and *Andamia*) on Rarotonga and other islands that have effectively made a permanent transition to land within the splash zone (Bhikajee and Green 2002; Bhikajee et al. 2006; Shimizu et al. 2006; Depczynski and Gagliano 2007; Cooke et al. 2016; Ord and Cooke 2016). Out of water, blennies continue to use the same respiratory surfaces as their aquatic relatives (gills and, to some extent, the skin; Martin and Lighton 1989; Brown et al. 1992) and have both a feeding ecology (a diet of epilithic algae and detritus; Hundt et al. 2014b) and a cryptic body coloration that easily translates to a lifestyle in the littoral splash zone (Morgans and Ord 2013). Amphibious blennies have also co-opted the tail-to-head movement of the aquatic C-start escape response in a terrestrial hop that allows them to be highly mobile on terrestrial substrates (Hsieh 2010). These predispositions, combined with the apparent significant selection pressure imposed by aquatic predation reported in this study, offers a plausible explanation for why these intertidal fishes might have so frequently invaded land.

While the notion of “a fish out of water” might imply that amphibious fish are an extraordinary example of an ecological transition, the puzzle of why fish emerge onto land is effectively the same question of what motivates any organism to move into an environment starkly different from its ancestral condition. The ecological causes of terrestrial activity in amphibious blennies are therefore broadly relevant for our general understanding of how environmental transitions might occur in nature. Given that most animals are subject to some form of predation and that in many cases it imposes a critical selection pressure on prey, the benefits of moving into a predator-free environment seem obvious. While other factors might also promote amphibious behavior in fishes, including competitor-free ecological opportunities for resource exploitation on land, the results of this study and others (Graham 1970; Sayer and Davenport 1991; Shimizu et al. 2006; Platt and Ord 2015; Platt et al. 2016) implicate an important role for predation.

Captive experiments that manipulate the likelihood of aquatic predation while maintaining similar levels of competitive pressure and resource availability are the next obvious step for confirming a link between terrestrial activity in amphibious fishes and predator avoidance (e.g., Graham 1970; Winandy et al. 2015).

More generally, the concepts of ecological release and opportunity following the colonization of a new environment are key explanations for why transitions into novel environments might promote adaptive diversification (reviewed in Losos 2010; Yoder et al. 2010). Most discussions around these topics have focused on a release from competition and implicitly consider ecological release or opportunity as phenomena operating over evolutionary timescales (Bolnick et al. 2010). For example, the vast majority of investigations have relied on phylogenetic comparative analyses to determine whether the colonization of new environments has preceded accelerated adaptive evolution or speciation (e.g., Losos and de Queiroz 1997; Harmon et al. 2008; Parent and Crespi 2009; Mahler et al. 2010; Setiadi et al. 2011; Wagner et al. 2012; Garcia-Porta and Ord 2013; Price et al. 2014; Schluter 2016). While an ecological release might promote adaptive diversification through niche expansion (e.g., Lister 1976; Knudsen et al. 2006; McCormack and Smith 2008), as a hypothesis for why taxa colonize novel environments this often operates at local spatial scales (i.e., transitions between immediately adjacent environments; Stamps 1983; Refsnider et al. 2015) and on the behavior of individuals rather than whole populations or species (e.g., Stamps 1983; Bolnick et al. 2010). Predation is known to impact colonization in a number of ways (e.g., restricting the abundance of taxa colonizing new areas; Schoener and Schoener 1978; Schoener and Spiller 1995; deRivera et al. 2005; Buckley and Jetz 2007) and to be a powerful force in the evolution of predator-avoidance strategies more generally (e.g., the evolution of nocturnality; Rydell and Speakman 1995). Our study offers one of the few empirical investigations of an ecological release from predation, and it is a rare example of an experiment conducted at a scale likely to be relevant for understanding the colonization of novel environments by animals in nature.

Acknowledgments

This study was funded by a Discovery Project grant from the Australian Research Council to T.J.O. (DP120100356) and by funding from the Research School of Biology, Australian National University, to C.J.F. The work described in this study followed protocols outlined in the University of New South Wales Animal Care and Ethics Committee applications 13/21B and 16/2B and was approved by the Cook Island Research Committee through the Office of the Prime Minister under research permit 19/15. Jack and Jasmine

Ord provided considerable distraction during the making of blenny mimics, while Claire Fulton provided the motivation for prolonged in-water surveys. All data from this publication have been archived in the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.0c614>).

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Natural History Editor: Mark A. McPeck



Entomacrodus striatus is one of several blennies found on Rarotonga that frequently emerges from water and is active on land. Photo credit: Christopher J. Fulton.