A Highly Social, Land-Dwelling Fish Defends Territories in a Constantly Fluctuating Environment

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Abstract

The Pacific leaping blenny (*Alticus arnoldorum*) is a marine fish that has made a highly successful transition to land. We report an extensive field study on the behavior of this remarkable fish and how it has coped with life on land. The fish occurs in great abundance above the waterline along the rocky coastlines of Micronesia. We found them to be terrestrial in all aspects of their adult daily life, but heavily constrained by large fluctuations in both tide and temperature with almost all activity limited to a brief period at mid-tide. Despite this, the fish were highly social and data were consistent with males defending exclusive territories on land. A variety of metrics – the use of visual displays, the allometry of ornaments, and sexual dimorphism – further imply sexual selection on both sexes was strong. Despite being restricted to an extremely narrow habitable zone in which conditions change constantly, the Pacific leaping blenny is remarkably adapted to life on land and rarely returned to water. The genus is unique among the living fishes in its degree of terrestriality and serves as a useful model of the constraints and adaptations that accompany major ecological transitions.

Introduction

The invasion of land by fish in the late Devonian was a critical step in vertebrate evolution. How these early fish adapted physiologically and morphologically to the dramatic change in environment associated with the transition to land can be partly inferred from fossils (e.g., Coates & Clack 1990; Daeschler et al. 2006; Long et al. 2006). Yet, the selective pressures experienced in a terrestrial environment by an animal that, at least initially, retained much of its ancestral aquatic phenotype are difficult to appreciate from fossils alone. Of particular relevance is behavior, because the way in which animals interact with one another and the environment determines the nature of selection experienced by species. Obtaining behavioral information on extinct species is generally limited to extrapolation from the fossil record (e.g., Varricchio et al. 2008; Mazin et al.

2009). A unique opportunity to examine the consequences of a water–land transition on behavior is offered by a number of contemporary examples where fish have made a similar transition onto land (Sayer & Davenport 1991; Martin 1995; Sayer 2005). While these present-day fishes differ in important ways from the first colonizers of land in the Devonian, they are useful living examples of the ways in which land colonization can be achieved from an aquatic origin.

The comb-toothed blennies (family Blenniidae) consist of slender, elongate-bodied fishes that are ancestrally aquatic and benthic in habit (Patzner et al. 2009). However, there are several species of blenny that are noteworthy because of their frequent terrestrial activity on rocks in the intertidal zone (Sayer & Davenport 1991; Martin 1995; Hsieh 2010). Previous observations on some of these species suggest that they seldom, if ever, voluntarily

submerge themselves underwater and can stay indefinitely on land if they remain moist (Brown et al. 1991; Bhikajee & Green 2002; Hsieh 2010). Surprisingly, despite their high abundance at localities throughout the tropical Pacific, very little is known about the behavioral ecology of these remarkable land-dwelling fishes. Here, we report the first behavioral study of the Pacific leaping blenny, *Alticus arnoldorum*. While amphibious behavior seems quite common in fish generally (Sayer & Davenport 1991; Martin 1995; Martin et al. 2004; Sayer 2005), the Pacific leaping blenny is one of the rare living examples of a fish that spends the vast majority of its time on land. Our aim was to determine the consequences of a terrestrial lifestyle on the behavioral ecology of this fish, which has apparently made a highly successful transition cross the water–land interface.

The Pacific leaping blenny is a small marine fish (4–8 cm in length) that occurs in high densities along the rocky coastline of Guam (Fig. S1). The fish are extremely agile on land, moving quickly over complex rocky surfaces using a unique tail-twisting behavior combined with expanded pectoral and tail fin morphology that allows them to adhere to almost any firm surface (Hsieh 2010). Nevertheless, life on land still comes with severe constraints for these fish. Like other marine amphibious fishes, blennies do not possess an air-breathing organ (lung), but rely on the exchange of O_2 and CO_2 through the skin and gills when on land (Martin & Lighton 1989; Brown et al. 1992). Terrestrial blennies must consequently remain moist to avoid asphyxiation. This restricts these fish to the wet intertidal rocks within the splash zone. With this in mind, we began our field study by first determining how the extremes in tide level and air temperature impacted the activity of the Pacific leaping blenny. We then conducted a detailed investigation into the social behavior of adults and found that intrasexual and intersexual interactions were frequent and mediated by conspicuous visual signals in both sexes. Finally, we attempted to identify the cues encoded in a set of these visual signals; in particular, the color and allometry of the brightly colored dorsal fin 'flashed' during aggressive disputes by both sexes, as well as a prominent fleshy head crest possessed by males.

Methods

Adult Abundance

We began our study by conducting a general survey of adult numbers at two locations on the eastern side of Guam during what we anticipated would be the start of the breeding season (April; see Shimizu et al. 2006). The first site was approx. 500 m north of Talofofo Bay at a small cove immediately adjacent to route 4. Here, Pacific leaping blennies were found in high abundance along a 600-m stretch of open rocky shoreline that could be accessed by bush trails or from the water by wading along the reef. The second site was 300 m north of Tagachang Beach and was only accessible by wading through the surf. At this site, blennies were found in high abundance along a 500-m stretch of rocky outcrops under the cliffs. The two sites were roughly 10 km apart and separated by multiple beaches and other terrestrial barriers. We refer to blennies at each location as belonging to the Talofofo and Tagachang populations, respectively.

We established six transects at each location and counted the number of adults, irrespective of sex, at hourly intervals over a single day between 0930 and 1830 hrs (Talofofo: 3 April, 2009; Tagachang: 4 April, 2009). We chose intervals of an hour to minimize the effect of any disturbance to fish in consecutive consensus periods. It is important to note that, while transects varied in length (20–90 m), our objective was to document changes in abundance within transects over time and not to compare densities among transects and populations.

Behavioral Observations

Following abundance surveys, we conducted detail behavioral observations on individual adult males and females. For each population, observations were conducted on consecutive days between 0730 and 1730 h with a median interval between observations of 30 min (Talofofo: 6–11 April, 2009; Tagachang: 13–19 April, 2009). Observations consisted of 15-min focal sampling in which we verbally recorded all behavior performed by the subject on a water-proofed microcassette recorder. During this period, we also performed scan samples at 1-min intervals to note the number of males, females, and subadults (sex unknown) within 20 cm of the subject. At the end of observations, we attempted to catch the subject for morphological measurements and color photography (see 'Morphological Measurements' below). Our catch rate was modest (approx. 63%), reflecting the agility of these fish on land and ability to evade capture by even the most determined researcher.

Audiotape recordings were scored by a single listener (TJO) using JWATCHER ver 1.0 event recorder

software (Blumstein & Daniel 2007). A total of 61 males and 71 females were sampled at Talofofo (33 h of observation), while 66 males and 61 females were sampled at Tagachang (32 h of observation).

Morphological Measurements

Those individuals caught at the end of our observations were weighed using an Ohaus digital balance (Model CS200, Ohaus Corporation, Pine Brook, NJ, USA) to the nearest 0.1 g. Fish were then photographed in natural light using a Canon Rebel XSi digital SLR and 55-mm macrolens against a white standard (X-Rite ColorChecker White Balance Card). Fish were positioned alongside a metric ruler and a mini-Munsell color chart (an X-Rite Mini Color-Checker). A total of 34 males and 42 females were weighed and photographed at Talofofo and 43 males and 44 females at Tagachang.

Photographs were imported into IMAGEJ ver 1.42q (Rasband 1997–2009; NIH) and a single research assistant measured the length of the body, area of the erected dorsal fin, area of the dorsal fin that was colored (typically red), and area of the head crest in males. Measurements were converted from pixels to mm using the ruler positioned alongside fish in photographs. We quantified the color of the dorsal fin following Bergman & Beehner (2008). Briefly, the inCamera plug-in for Photoshop CS4 was used to standardize the color profile of each photograph based on the known color levels of the Munsell color chart positioned in the corner of each photograph. We then quantified the color of the dorsal fin by selecting the colored region of the dorsal fin using the lasso tool. The averaged pixel values over this region were noted for the red, green, and blue channels. Each value is only informative relative to values of the other channels. As we were interested in quantifying the 'redness' of the dorsal fin (because red was the primary color of the fin in both sexes), we computed the ratio of values in the red and green channels (see Bergman & Beehner 2008 for details).

Statistical Analysis

There are multiple ways in which we might expect tide levels and temperature to influence Pacific leaping blenny abundance and activity. Adopting a model selection approach includes this as part of the analytical philosophy (Johnson & Omland 2004). Rather than applying one model, we considered all realistic combinations of predictor variables and weighed the evidence for each model simultaneously. Abundance was assessed as the number of adults of either sex recorded at hourly intervals during transect surveys (see 'Adult Abundance'). Activity data consisted of three behaviors that were among the most common during the 15-min focal samples. Those behaviors were as follows: total time spent moving about on rocks, total time spent feeding off algae on rocks, and total number of aggressive interactions defined as either displacing or being displaced by another conspecific. Tide and air temperature data were obtained from the Center for Operational Oceanographic Products and Services website (http://co-ops.nos.noaa.gov/index.shtml), which was collected at the University of Guam Marine Laboratory located 5 km north of Tagachang Beach. These data were taken at 6-min intervals and were matched to within 2 min of collection times of abundance and activity data.

We used a series of mixed models implemented in the lme4 package in R ver 2.8.1 (Bates 2008; R Development Core Team) to fit realistic combinations of linear and quadratic functions of tide level and temperature. Both authors performed abundance surveys and focal sampling observations, and this was accounted for in models by entering 'observer' as a covariate. Models applied to adult abundance data also included random effects (repeated measures) for transect and population. Models applied to activity behaviors included an additional covariate for subject sex and random effects for observation date and population. For both abundance and activity, we tested a null model in which only covariates and random effects were included; i.e., neither tide nor temperature were assumed to have an effect on the abundance and activity of blennies. Model fit was assessed using the second-order Akaike's information criterion that included a correction for small sample size, AIC_c. The model with the lowest computed AIC_c value is deemed the model of 'best' fit, although any model within two AIC_c units of this lowest model is considered equally supported by the data (i.e., $\Delta AIC < 2.0$; Burnham & Anderson 2002). To further evaluate the relative likelihood of each model, we computed model weights, AIC_w, to determine the level of evidence in favor of a given model relative to all other models analyzed in the same set (see Johnson & Omland 2004 for AIC_c, ΔAIC and AIC_w calculations). We present effect sizes in the form of t values to illustrate the direction and magnitude of relationships in the best-supported models.

We used a MANOVA to examine sex and population differences in behavior. Effect sizes for individual behaviors included in the analysis were computed by taking the square root of the mean sum of squares divided by the total sum of squares to obtain an estimate of r (Field 2005). Sex differences in spacing patterns were assessed using factorial ANOVAs in three steps. First, the length of time it took to find a subject of a given sex to start focal sample observations was used as a proxy for the overall density of males and females in a given population. (Our sampling protocol consisted of observing males and females alternately, and intervals between observations should be comparable if both sexes were equally abundant in the population.) Second, we compared the average number of adults, irrespective of sex, within 20 cm of the subject to determine whether each sex was more or less likely to associate with adult conspecifics. Finally, of the adults within 20 cm of the subject, we compared the number that were of the same sex as the subject to determine whether each sex was more or less likely to associate with same-sex adults.

Our observations suggested that males were defending rock holes, from which they attempted to court females using conspicuous headnodding behavior (see Video S1). We tested this idea using a model selection approach in which we applied a range of logistic regression models with a combination of social and environmental predictors of hole use. Observer was included in all models as a covariate. The relative fit of these models was then assessed against a null model that included no predictors of hole use (see tide and temperate effects on abundance and activity for other analysis details).

Finally, reduced major axis regressions were used to compute allometric exponents for the area of the dorsal fin, the area of the dorsal fin colored red, and the area of the head crest in males. Exponents were extracted from slope estimates of $\log_{10}$ body length on $\log_{10} \sqrt{\text{area}}$ (see Bonduriansky 2007). Allometric exponents within the range of 1.5–2.5 are thought to be consistent with traits under sexual selection (Kodric-Brown et al. 2006; Tomkins et al. 2010; see Bonduriansky 2007 for a cautionary note on interpreting allometric relationships). Ordinal least-squares regression analyses were then used to examine differences in dorsal fin 'redness' as a function of sex, body size, and population (specifically, red/green ratio; see 'Morphological Measurements').

MANOVAs, ANOVAs, and regressions were performed in R ver 2.11.1. In cases where multiple comparisons were performed, we calculated false discovery rates (FDR; Benjamini & Hochberg 1995) based on an initial α of 0.05.

Results

Constraints of Living on Land

Adult abundance, movement, feeding, and aggressive interactions were all heavily dependent on both tide and, in most cases, temperature. The best-supported models were those that included a
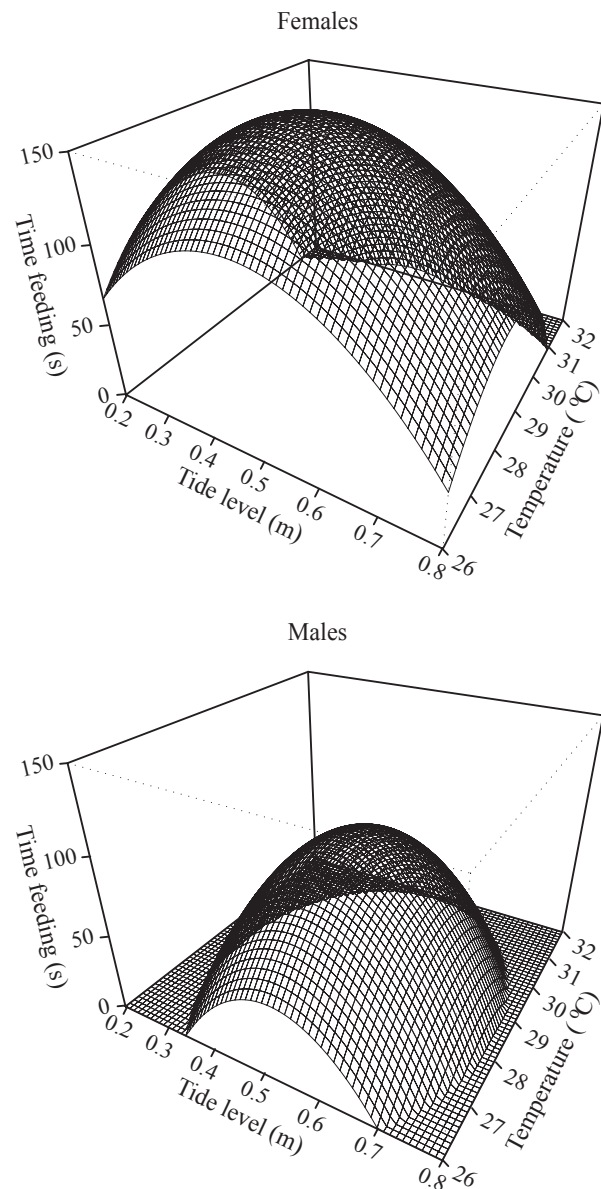
Fig. 1: The dependency of foraging behavior on tide and temperature fluctuations for female and male Pacific leaping blenny.

quadratic function for tide level and temperature (Table S1). That is, terrestrial blennies concentrated most of their activity during mid-tide (0.3–0.7 m) and at moderate temperatures (27–30°C; Fig. 1). The result was a daily activity window of roughly 2–4 h depending on whether tide changes extended into the night (see Fig. S2). At high tide, the waves were often so violent that blennies spent most of their time clinging to rocks or sheltering in crevices and holes above the waterline. At low tide or at high temperatures, blennies were observed to retreat into moist crevices and rock holes to avoid desiccation [A brief visit to one site at night during mid-tide revealed blennies out on the rocks in low density. However, their nocturnal activity appeared very low (T. J. Ord, pers. obs.), and the ambient air temperature was also below the optimum 27–30°C (see Fig. S2).]

There was a strong sex effect for feeding and aggressive interactions (Table S1). Sex-specific analyses showed that females spent approximately twice as long feeding than males and engaged in twice as many aggressive interactions as males (Table S2; Fig. 1).

Sex Differences in Social Behavior

MANOVAs reiterated the extended bouts of feeding and greater number of aggressive interactions for females, but also showed that males performed significantly more visual displays than females (Table 1). Two display types were observed. The first was a close-range aggressive display performed by both sexes (although more frequently by males; Table 1) in which the red dorsal fin was flashed at a nearby conspecific (usually an individual of the same sex within 20 cm of the subject). This display was often accompanied by a dramatic and rapid change in body color in both sexes, from dull green-gray to black. The second display type was an exaggerated headnodding that was performed by males (see Video S1), apparently to entice females to enter a male's rock hole to spawn. Indeed, the best predictor of hole use by males was the frequency of headnodding (Table S3). In contrast, females were much less likely to use rock holes (Talofofo: df = 1, χ^2 = 6.09, p = 0.01; Tagachang: df = 1, χ^2 = 12.30, p < 0.001) and spent most of their time foraging out on rocks (e.g., Fig. 1). The female target of male nodding displays was often quite distant (e.g., up to 2 m away), making this display a long-range signal (e.g., compared to dorsal fin flashes).

Table 1: Activity during the intertidal window for two populations of the Pacific leaping blenny. Differences in behavior occurred as a function of sex and population (a). A significant observer effect was found and the analysis was repeated for the main observer (b)

	df	Pillai	$F_{5,249}$	p
(a) Both observers				
MANOVA				
Sex	1	0.20	12.18	<0.001[a]
Site	1	0.08	4.55	<0.001[a]
Observer	1	0.15	8.98	<0.001[a]
Residuals	253			
		Sex	Population	Observer
Effect size (r)				
Time spent moving		0.04	−0.19[a]	−0.05
Time spent grazing		−0.37[a]	−0.14	0.32[a]
Aggressive interactions		−0.20[a]	−0.01	−0.21[a]
Displays: dorsal fin		0.30[a]	0.29[a]	0.13
Displays: headnod		0.30[a]	−0.23	0.19[a]
	df	Pillai	$F_{5,148}$	p
(b) Main observer				
MANOVA				
Sex	1	0.23	9.04	<0.001[a]
Site	1	0.06	2.01	0.081
Residuals	152			
		Sex	Population	
Effect size (r)				
Time spent moving		0.01	−0.003	
Time spent grazing		−0.31[a]	−0.05	
Aggressive interactions		−0.24[a]	−0.02	
Displays: dorsal fin		0.28[a]	0.23[a]	
Displays: headnod		0.30[a]	0.18	

Coding for sex: females, 0, males, 1; Population: Talofofo Bay, 0, Tagachang Beach, 1. The main observer recorded the majority of the observations (155∕257), with an even proportion distributed among each sex (77 males: 78 females).
[a]Statistically significant effects following false discovery rates adjustment for 12 tests: two MANOVAs and 10 multiple regression analyses used to calculate r-values.

Although both sexes were equally abundant (Fig. S3a) and equally likely to associate with other adult conspecifics (Fig. S3b), males were rarely found in the vicinity of other males (i.e., same-sex neighbors within 20 cm were significantly lower for males compared to females; Table 2; Fig. S3c). Taken together, our data were consistent with our initial anecdotal observations that males defended small territories centered on rock holes that were used for mating, while the heightened aggression of females reflected site defense over foraging resources rather than territoriality.

Table 2: The spacing patterns of adult Pacific leaping blenny. A general index on density is reflected by the length of time it took to find subjects for focal sampling. Neighbors were defined as mean number of adult conspecifics within 20 cm of the focal fish

	df	F	Effect size, r	p
(a) Interval between observations				
Sex	1	0.17	−0.03	0.676
Population	1	3.16	−0.11	0.076
Observer	1	6.07	−0.15	0.014[a]
Sex*population	ns			
Residuals	256			
(b) Adult neighbors				
Sex	1	0.56	−0.05	0.456
Population	1	3.30	0.11	0.071
Observer	1	0.69	0.05	0.408
Sex*population	ns			
Residuals	256			
(c) Same-sex neighbors				
Sex	1	159.59	−0.62	<0.001[a]
Population	1	3.31	0.11	0.070
Observer	1	1.75	0.08	0.187
Sex*population	1	6.09	−0.15	0.014[a]
Residuals	255			

Sex*site was only included as a term if statistically significant.
[a]Statistically significant effects following false discovery rates adjustment for three factorial ANOVAs.
ANOVA coding for sex: females, 0, males, 1; Site: Talofofo Bay, 0, Tagachang Beach, 1.

Morphology of Visual Signals

The allometric scaling exponents of the dorsal fin, the area colored red on the dorsal fin, and the head crest of males were statistically greater than isometry in almost all cases (i.e., 95% confidence intervals, CI, did not overlap 1; Table 3; Fig. 2). Furthermore, the exponents were within the range suggested for morphological traits under sexual selection (1.5–2.5; Kodric-Brown et al. 2006; Tomkins et al. 2010; our data: 1.31–2.61).

The intensity of red in dorsal fins differed between the sexes in unexpected ways. First, the dorsal fin was significantly 'redder' in females than males (Table 4; in many other fish, males are typically the more colorful sex; e.g., Houde & Endler 1990; Milinski & Bakker 1990; Seehausen et al. 2008). Second, the intensity of red was positively correlated with body size in females, but negatively correlated with body size in males (Table 4; Fig. S4).

Population Variation

Male-biased sexual size dimorphism was significantly greater at Tagachang (95% CI in body length:

Table 3: The allometry of visual signals in the Pacific leaping blenny. Reduced major axis (RMA) regression was used to compute allometric exponents, β

|	Males		Females	
	df	β (lower 95% CI, upper 95% CI)	df	β (lower 95% CI, upper 95% CI)
(a) Talofofo Bay				
Dorsal fin area	32	1.65 (1.30, 2.00)	40	1.50 (1.36, 1.64)
Dorsal fin, area red	32	1.56 (0.61, 2.50)	40	2.22 (1.79, 2.66)
Head crest area	32	2.61 (1.69, 3.53)		
(b) Tagachang Bay				
Dorsal fin area	41	1.31 (1.02, 1.61)	42	1.52 (1.33, 1.70)
Dorsal fin, area red	41	1.71 (0.85, 2.57)	42	2.28 (1.84, 2.72)
Head crest area	40	2.16 (1.61, 2.72)		

Females lack head crests entirely.

1.093–1.117, n = 75) than Talofofo (1.065–1.091, n = 85). Adult males from the Tagachang population were generally much larger (Fig. 2), spent more time flashing their dorsal fins in aggressive displays (Table 1), and were less likely to be near other males than those from the Talofofo population (reflected by the significant interaction term in Table 2c; Fig. S3). Although the allometry of signal traits was similar between populations (Table 3), the intensity of red in the dorsal fin was significantly lower in both sexes in the Tagachang population (Table 4; Fig. S4). All other measured characteristics were comparable between populations.

Discussion

The Pacific leaping blenny offers a unique opportunity to discover how a water–land transition has taken place in an extant genus. It is well established that tetrapods evolved from sarcopterygian (i.e., lobe-finned) fishes and likely made only short initial forays on land owing to structural and respiratory constraints (Coates & Clack 1990; Clack 2002; Long & Gordon 2004). Because all known extant sarcopterygian fishes are aquatic, it is not possible to study these fishes for clues on how living intermittently in two environments may have affected the behavioral patterns of transitional forms. The Pacific leaping blenny is behaviorally terrestrial while continuing to be constrained by its dependence on water for respiration. These fish can therefore provide valuable insight into how life in a highly dynamic environment impacts the behavioral ecology of a species.

Our study showed that life on land for a marine fish is heavily dependent on tide and temperature fluctuations, so much so that almost all activity is
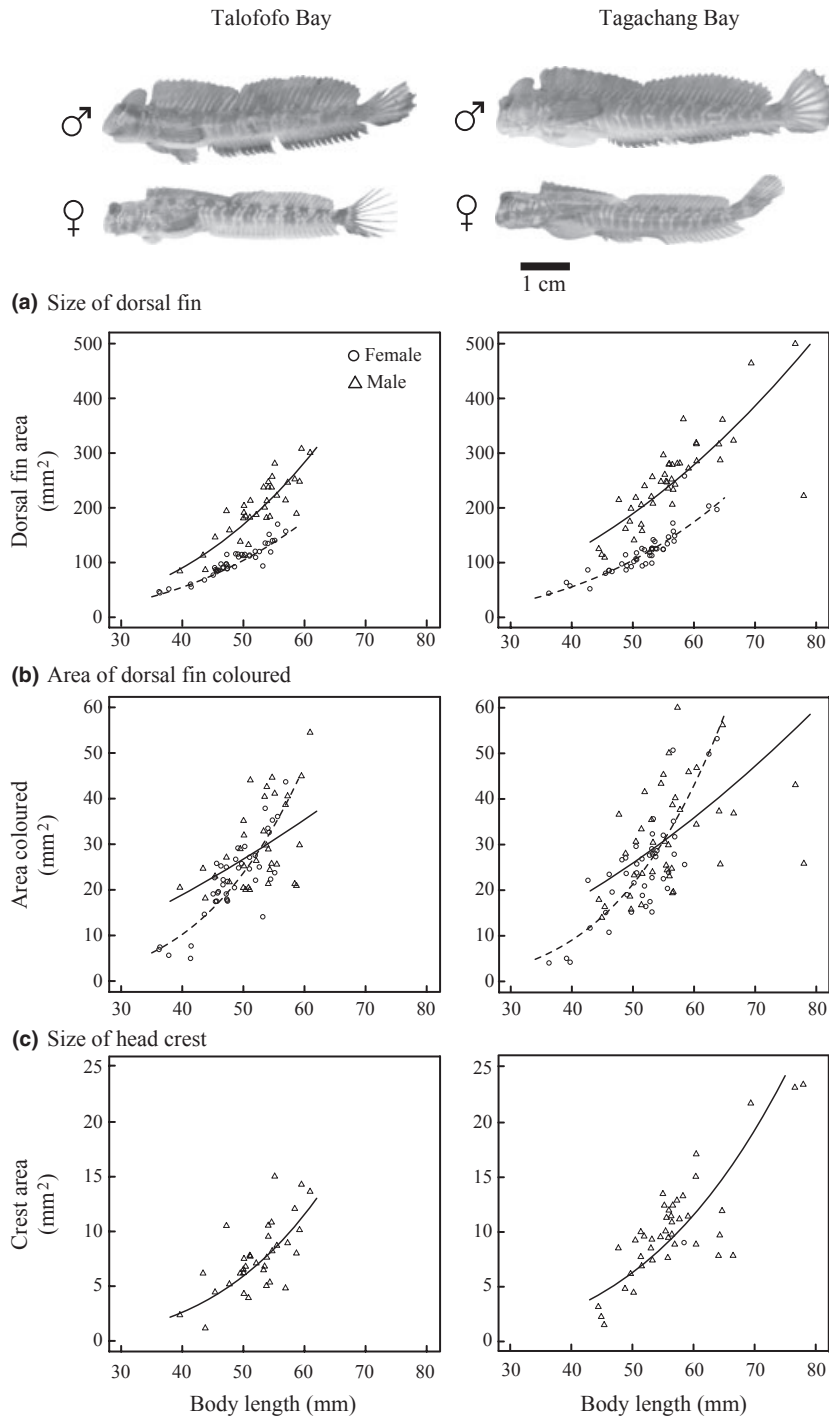
Fig. 2: The allometry of visual signals in the Pacific leaping blenny: the area of the dorsal fin (a), area colored red on the dorsal fin (b), and the area of the fleshy head crest in males (c).

restricted to a brief period at mid-tide, the timing of which changes daily (see Fig. S2). Yet, the Pacific leaping blenny was never observed to voluntary return to water and spent much of its time actively

avoiding submersion by incoming waves. Indeed, rather than jump into water, the typical escape response of the Pacific leaping blenny to a simulated predator attack (attempted capture by a researcher)

Table 4: Degree of dorsal fin 'redness' in adult Pacific leaping blennies

	β	t	Effect size, r	p
Both sexes ($F_{4,148}$ = 11.35, p < 0.001[a])				
Intercept	1.00	5.71	0.42	<0.001[a]
Sex	0.59	2.52	0.20	0.013[a]
Body length	0.08	2.30	0.19	0.022
Population	−0.09	−3.18	−0.25	0.002[a]
Sex*body length	−0.01	−3.10	−0.25	0.002[a]
Males ($F_{2,70}$ = 10.64, p < 0.001[a])				
Intercept	0.59	13.71	0.85	<0.001[a]
Body length	−0.01	−2.75	−0.31	0.008[a]
Population	−0.08	−2.80	−0.32	0.007[a]
Females ($F_{2,77}$ = 3.14, p = 0.049[a])				
Intercept	0.99	4.71	0.47	<0.001[a]
Body length	0.01	1.92	0.21	0.059
Population	−0.09	−2.05	−0.23	0.044[a]

Coding for sex: females, 0, males, 1; Site: Talofofo Bay, 0, Tagachang Beach, 1.

The interaction term population*body length was considered but was not statistically significant and dropped from the final model.

[a]Statistically significant effects following false discovery rates adjustment for three regression analyses.

was to hop rapidly along the rocks and hide in crevices above the waterline (T. J. Ord, pers. obs.).

Within this brief window at mid-tide, our data suggest males defend small territories centered on rock holes. The defense of these rock holes is probably critical for a male's reproductive success. Males were often observed vigorously headnodding at the entrance of their hole (e.g., Table 3; see Video S1) and would occasionally succeed in attracting a female who would subsequently enter. Similar observations on two closely related blennies suggest that females were inspecting a male's hole for the possibility of depositing eggs, which would then be fertilized by the resident male (Bhikajee & Green 2002; Shimizu et al. 2006). It also follows that male parental care in the form of egg guarding is likely in Pacific leaping blenny (both female inspection of male nest sites and male egg guarding are common in blenniid; e.g., Sunobe et al. 1995; Gonçalves & Almada 1998; Oliveira et al. 1999; Shimizu et al. 2006).

Females were not territorial in the same sense as males. We often found females aggregated together in rock crevices at low and high tide. However, once females emerged from these refuges at mid-tide, they spent the vast majority of their time feeding on epilithic algae and were frequently aggressive toward any individual that encroached on a feeding site. Our study was conducted close to the start of the breeding season, and it is probable that the high energetic requirements of egg production, aggravated by the brief tidal window in which feeding can occur, explain the heightened aggression exhibited among females as they foraged (Tables 1 and 2).

Allometric scaling exponents and the intensity of red in the dorsal fin flashed during aggressive disputes were generally greater in females than in males (Tables 3 and 4). Positive allometry in morphological traits within the range documented here (1.5–2.5) is often assumed to reflect the outcome of sexual selection. That is, larger adults are able to incur the costs associated with developing disproportionately larger ornaments compared to smaller adults, leading to an ornament that is an honest indicator of condition (reviewed in Kodric-Brown et al. 2006). Red pigmentation in many fish is also condition dependent (Milinski & Bakker 1990; see also Grether 2000). Whether fin allometry and pigmentation are honest signals of condition in blennies will need to be confirmed in future studies. However, taken together with our behavioral observations, our results are consistent with the notion that the intensity of sexual selection, via aggressive competition, is strong on females and potentially even greater on females than on males.

Our study also hinted at potentially important differences between populations. The frequency of aggressive dorsal fin displays and spacing patterns among males were greater at Tagachang Bay than Talofofo Bay. Male-biased sexual size dimorphism, another common metric used to infer the intensity of aggressive competition within populations (among males), was also significantly greater at Tagachang Bay. While it is difficult to draw anything conclusive from these differences (or reconcile, for that matter, why the dorsal fin in both sexes was *less* red at Tagachang Bay), an expanded survey of other populations around the island is warranted. Although it is currently unknown whether the larvae of the Pacific leaping blenny remain inside rock holes above the waterline or become aquatic, blenniids as a family are notoriously sedentary (Gonçalves & Faria 2009). Populations of land-dwelling fish that are physically isolated from one another are therefore likely to be reproductively isolated as well. Any difference between populations in factors potentially associated with selection would be of special interest because of the obvious implications it has for evolutionary divergence among populations.

Finally, within the family Blenniidae, there are two genera that are highly terrestrial (one of which, *Alticus*, includes the Pacific leaping blenny), two

sister genera that are amphibious – spending part of their time on land and part of their time in water – and a variety of genera that retain the ancestral aquatic phenotype (Sayer & Davenport 1991; Hsieh 2010). Representative species of all these genera are found on or around Guam. Collectively, these species provide a unique opportunity to study the various steps – essentially evolutionary 'snapshots' – in the invasion of land by marine fish as well as the selection pressures faced at different stages during a major ecological transition.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1: The Pacific leaping blenny occurs in high density along the rocky shores of Guam.

Figure S2: Daily tide and temperature changes and periods that were optimal for Pacific leaping blenny activity.

Figure S3: The spacing patterns of adult Pacific leaping blenny.

Figure S4: The intensity of red in female (a) and male (b) dorsal fins in two populations of Pacific leaping blenny.

Table S1: The constraints of a terrestrial lifestyle on the activity of the Pacific leaping blenny.

Table S2: Sex differences in feeding and social behavior of a fish living on land.

Table S3: Predictors of hole use by the Pacific leaping blenny.

Video S1: In this video, a male Pacific leaping blenny at Tagachang Bay performs courtship head-nodding at the entrance of his rock hole while a female approaches.

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