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Interpopulation Variation in a Condition-Dependent Signal: Predation Regime Affects Signal Intensity and Reliability

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ABSTRACT: In many models of sexual selection, conspicuous ornaments are preferred by mates because they indicate heritable signaler viability. To function as indicators, ornaments must exhibit a proportional relationship between expression and viability. In cases where the evolutionary interests of signaler and receiver diverge, selection favors exploitative exaggeration by low-viability individuals producing unreliable signals. Theory suggests that the evolutionary stability of such communication systems requires costs that prevent low-viability males from expressing disproportionately intense signals. Therefore, given ecological variation in signaling cost, the reliability of signaling systems will vary concomitantly. In this study, we assess the effect of a variable signal cost, predation, on signal intensity and reliability among 16 populations of Bahamas mosquitofish (*Gambusia hubbsi*) that use colorful dorsal fins in courtship displays. We found that fin coloration was more intense in low-predation sites and could be used to predict body condition. However, this predictive relationship was apparent only in populations subject to predation risk. We demonstrate an important role for ecological signaling cost in communication and show that ecological heterogeneity drives interpopulation variation in both the intensity and the reliability of a sexual signal.

Keywords: honest signaling, animal communication, signal cost, sexual selection, the Bahamas, mosquitofish.

Introduction

Many good-genes models of sexual selection posit that receivers (typically females) evolve preferences for elaborate signals because they function as indicators of genetically based signaler viability (Fisher 1930; Williams 1966; Zahavi 1975; Andersson 1986; Pomiankowski 1987; Iwasa et al. 1991; Maynard-Smith 1991; Andersson 1994). In order to function as indicators of viability, these signals must exhibit

a proportional relationship between expression and an individual's ecological performance (e.g., health, growth rate). Such indicator traits can be amplified and reinforced by the evolution of mating biases, often resulting in elaborate, conspicuous structures that play important roles in sexual selection (Kokko et al. 2003). Crucially, the evolutionary stability of good-genes sexual selection systems in which the interests of signaler and receiver diverge relies on signaling costs (Grafen 1990) and the reliable, condition-dependent signaling systems they produce.

Energetic demands and various risks involved with signal display, production, and/or development impose a range of viability costs, such as decreased immune function (Hamilton and Zuk 1982; Folstad and Karter 1992), compromised locomotion efficiency (Møller and de Lope 1994; Langerhans et al. 2005), reduced growth rate (Basolo 1998), agonistic interactions with conspecifics (Enquist 1985), and increased likelihood of predation (Zuk and Kolluru 1998). The diversity and magnitude of these signaling costs vary over time (Robinson et al. 2008) and space (Endler 1983) and are associated with marked variation in signal form. A prevailing framework for adaptive signal variation focuses on the suppressive effect of costs on signal elaboration or intensity (Endler 1980, 1983). However, theory predicts that signaling costs can shape the evolutionary stability of signaling systems as well. Hypothetically, in environments without signaling costs, condition-dependent relationships that produce honest indicator systems should deteriorate as signals become increasingly unreliable because of low-viability signalers adaptively exploiting prevailing mating preferences through signal exaggeration (Krakauer and Johnstone 1995; Chapman et al. 2003). An adaptive propensity for low-viability individuals to exaggerate their signals in low-cost environments should lead to destabilization of the communication system as a result of elimination or reduction in the information content of the signal (i.e., signal reliability; Maynard Smith and Harper 2003; Searcy and Nowicki 2005). Evidence of cost-mediated reliability has been

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shown for a number of organisms, including sticklebacks (Milinski and Bakker 1990; Candolin 1999), fiddler crabs (Blackwell et al. 2000), stromatopods (Hughes 2000), crayfish (Wilson et al. 2007), beetles (Sadd et al. 2006; Nielsen and Holman 2012), and crickets (Copeland and Fedorka 2012). Together, these studies show that reliable signaling can be driven by ecological costs. But despite extensive theoretical research and supporting experimental work, little empirical evidence from natural contexts is available to evaluate this relatively simple hypothesis (Kotiaho 2001; Busière et al. 2008; but see Martin and Johnsen 2007; Robinson et al. 2008, 2012).

A remarkable variety of communication systems exist in nature and include a broad taxonomic range (e.g., Anderson 1994). Reconciling this diversity and prevalence with the hypothetical pervasiveness of exploitative signaling has been a theoretical challenge for decades (Maynard Smith 1991; Searcy and Nowicki 2005). Yet the assumptions of condition-dependent signaling are infrequently assessed—almost never so in natural populations—leaving a significant gap in our understanding of how signaling systems persist despite exploitative pressures from signalers. In this study, we investigated the effect of natural variation in signaling cost on a condition-dependent signaling system and tested the hypothesis that interpopulation variation in signaling cost would drive concomitant variation in a condition-dependent sexual signal. First, in accordance with existing empirical evidence, we expected signaling costs to be inversely related with signal intensity. Second, our primary hypothesis was that signaling cost would be positively associated with the reliability of the signal. To test these hypotheses, we examined individual variation in fin coloration and body condition among 16 populations of the Bahamas mosquitofish, *Gambusia hubbsi*, that differed in an important signaling cost, predation pressure. Bahamas mosquitofish reveal brightly colored dorsal fins during courtship displays. Previous research has shown that fin coloration in Bahamas mosquitofish is condition dependent and subject to predator biases (Martin et al. 2013; Heinen-Kay et al. 2015). Here, we evaluate the prediction that populations coexisting with piscivorous fishes (predator populations) would exhibit more reliable, condition-dependent relationships than those with low levels of predation (fig. 1).

Material and Methods

Study System

This study was conducted in a series of shallow aquatic habitats on Abaco Island, the Bahamas. Our study animal was the Bahamas mosquitofish, *Gambusia hubbsi*. *Gambusia hubbsi* are small, live-bearing, fish found in a variety of aquatic habitats of the Bahamas, including mangrove wet-

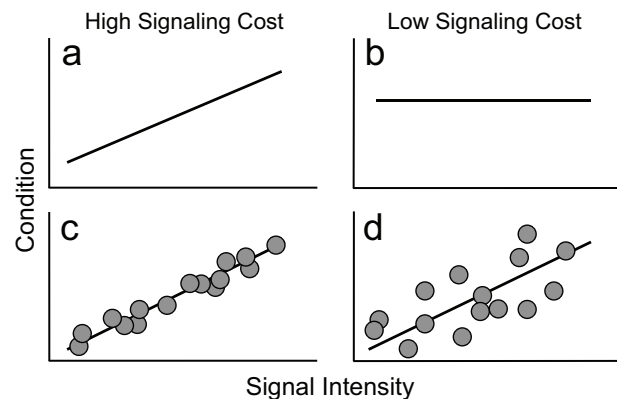


Figure 1: Illustration of the predicted effects of variable signaling cost (high and low) on signal reliability in a hypothetical condition-dependent signaling system. Reliability can be assessed with two statistical measures: (1) a relationship between signal intensity and condition (2) and the amount of residual variation about that relationship. The top panels depict reliability as indicated by a significant relationship between signal and condition. Panel *a* characterizes a proportional relationship between signal and condition that allows receivers to “predict” the viability of the signaler. In *b*, this relationship is lost, possibly because of low-viability signalers exhibiting disproportionately intense signals (e.g., Candolin 1999). The bottom panels depict the effect of variable signaling cost on existing relationships of similar slopes (e.g., Hughes 2000; Carazo and Font 2014). Panel *c* reflects a condition-dependent relationship in which low residual variation (“noisiness”) permits accurate prediction of viability. If signaling costs decrease, as in *d*, increased scatter about the proportional relationship is likely to preclude accurate assessment of viability.

lands, freshwater marshes, hypersaline ponds, and inland blue holes (Langerhans et al. 2007). Because of the diversity of habitats used by *G. hubbsi*, predation risk varies among sites (Martin et al. 2013; Araújo et al. 2014; Chacin et al. 2015; Giery et al. 2015). On the island of Abaco, coastal mangrove wetlands and tidal creeks inhabited by *G. hubbsi* include several species of marine predators, typically snappers (*Lutjanus* spp.), great barracuda (*Sphyrna barracuda*), and redfin needlefish (*Strongylura notata*). In contrast, other systems lack surficial hydrologic connectivity with the ocean, and piscivorous fishes are absent (table A1; tables A1, A2 available online).

Sexual Signaling in *Gambusia* Fishes

Poeciliid fishes, *Poecilia* and *Xiphophorus* species in particular, are well known for a diversity of elaborate sexual signals that are subject to selection by female preferences (Endler 1980, 1983; Rosenthal and Evans 1998). Fishes in the genus *Gambusia* are less understood in this regard. However, many male sexual characters are subject to female preference during courtship, including size, aggres-

sion, pigmentation, and gonopodium length (Gould et al. 1999; Bisazza and Pilastro 2000; Horth 2003; Langerhans et al. 2005; Kahn et al. 2009; Horth et al. 2010). Similar to other poeciliids (Rosenthal and Evans 1998), *G. hubbsi* are sexually dimorphic in coloration, with males exhibiting enlarged, brightly colored dorsal fins subject to female mate choice (Heinen-Kay et al. 2015). Males also possess numerous small, black spots on their fins and body. The function of this trait is not as clear. All ages, and both sexes, possess spotted fins and flanks, suggesting that they may not function as sexual signals. However, previous research in *Gambusia holbrooki* shows a strong link between melanistic patterning and female preference (Gould et al. 1999; Bisazza and Pilastro 2000). In our study, we include both fin coloration and spot number in our analysis to evaluate whether these traits are affected by different viability cost regimes.

Gambusia and Predator Sampling

Gambusia hubbsi populations were sampled in November and December 2012. From each population, 10–30 adult male *G. hubbsi* were collected with dip nets, then photographed live and frozen for later analysis. Photos were taken in a portable “studio” with a Canon 30D and illuminated with a Sigma ringflash. Each photograph included an X-rite Colorchecker standard for exposure correction and white balance. All photos were shot in RAW format and analyzed in Adobe Photoshop CS5 with the CIE (International Commission on Illumination) $L^*a^*b^*$ color space. The CIE $L^*a^*b^*$ color space defines color in a three-dimensional coordinate system where L^* indicates lightness, a^* indicates redness-greenness, and b^* indicates yellowness-blueness. Although the CIE space is based on the human visual system, its biological basis makes it a useful color model for estimating biologically relevant color variation in tri- or tetrachromats (Stevens et al. 2007). The $L^*a^*b^*$ measures were taken from 3×3 -pixel samples from eight points on the dorsal fins. Four readings were located on the distal portion of the fin and four from the region near the fin insertion. The location of each measure was in areas of membrane between fin rays 2,3; 3,4; 4,5; and 5,6. In addition to color, standard length and the number of black spots on the caudal fin, dorsal fin, and right flank were recorded.

Condition, as in “condition dependence,” reflects fitness components exclusive of competition for mates, such as survivorship and fecundity. Proxy measures such as growth rate (Schluter 2003; Bolnick and Lau 2008), lipid stores (Candolin 1999; Boughman 2007), and condition indices (Bolger and Connolly 2006) are widely employed, highly correlated measures of ecological performance (e.g., foraging success and immune status) that indicate viability. Here, we estimate condition by using the relationship between dry body

mass (individuals dried to constant mass at 60°C) and standard body length. In our analyses, body mass and standard-length values were log transformed and are referred to hereafter as “Mass” and “SL,” respectively. Some reservations have been raised concerning the use of mass-length relationships to estimate condition. For example, Green (2001) and Peig and Green (2009) discuss how nonlinear relationships between mass and body size indices (such as body length) can lead to spurious condition indices. Such nonlinear relationships are typically due to differences between sexes, age classes, or species that lead to different relationships between mass and length for each group; for example, mass/length variation within and among *Gambusia* populations can potentially arise because of sex, ontogeny, and predation regime (Langerhans et al. 2004, 2007). We address these caveats in several ways. First, we restricted our analyses to sexually mature males. Second, we found no significant heterogeneity in the Mass-SL relationship among predation regimes (linear mixed model ANCOVA with population as random: $SL \times \text{predator}$, $F_{1,280} = 1.0$, $P = .323$). And third, the relationship between Mass and SL is strongly linear in our data set ($\text{Mass} = 0.92 + 3.6(\text{SL})$; $r^2 = 0.84$, $F_{1,292} = 1,486$, $P < .001$), as is highly typical of fish of similar age and size (Bolger and Connolly 2006), which accounts for a potential nonlinearity caveat.

To document presence of predatory fish in study sites, we conducted visual surveys (snorkeling or on foot, depending on depth) from June 2012 through May 2013 and recorded the number and species of fish observed during each survey. Our survey method was unbounded; that is, there was no outer radius or belt width in which fishes were counted. As a consequence, these data are qualitative in nature, simply reflecting the presence or absence of predatory fishes in each study wetland (tables 1, A1). For each site, predator status was consistent between surveys; that is, predators were always observed in sites in which they were previously recorded, suggesting that predator status (present/absent) of each population is consistent over periods of months to years (tables 1, A1).

We also sampled the optical environment at each collection site in order to estimate the degree to which predation was confounded by signal transmission properties. Turbidity was sampled with an Oakton T100 turbidimeter, and light transmission was estimated with an Ocean Optics Jaz spectrometer. Transmission was estimated as proportional light attenuation at 570 nm through a 10-cm column of water in a laboratory environment. A beam of light was passed between two fiber optic cables fitted with colimiting lenses arranged 10 cm apart and submerged in a basin of water. Transmission was calculated as the amount of projected light reaching the spectrometer (irradiance) after passing through a water sample collected at a site, proportional to that for a distilled-water control ($T_{570} = \text{water sample/control}$). The

Table 1: Effect of predation regime on morphological variables examined

Dependent variable	Predators ^a		df	F	P
	Present	Absent			
Fin color intensity (PC1)	-1.01 (.25)	.57 (.19)	1,12.9	26.12	<.001
Spots (PC2)	.16 (.39)	-.12 (.30)	1,14	.32	.579
SL	.83 (.03)	.80 (.02)	1,14.1	.63	.441
Mass	3.95 (.11)	3.81 (.08)	1,14	1.05	.322

Note: Population was included as a random term in all models. SL and Mass are log-transformed measures of standard length and body mass, respectively. PC = principal component.

^a Least squares means (1 SE).

wavelength at which we calculated transmission, 570 nm, corresponds to the dominant reflectance wavelength of male dorsal fins (Heinen-Kay et al. 2015) and peak sensitivity for long-wavelength cones in closely related species (guppies: Archer et al. 1987; mollies: Körner et al. 2006) as well as in nearshore marine piscivores (Loew and Lythgoe 1978; Lythgoe et al. 1994).

Analytical Framework

The framework we use to evaluate variable cost effects on signal reliability is illustrated in figure 1. Briefly, the presence of condition dependence can be evaluated with models testing for a relationship between signal and condition, and, if significant, the residual variation around the relationship (r^2) indicates the “noisiness” of the relationship (Hughes 2000; Boughman 2007; Carazo and Font 2014).

Color variation was summarized with principal-component analysis (PCA) conducted in JMP, version 10 (SAS Institute, Cary, NC). Each color component (L^* , a^* , and b^*) was averaged for each individual, log transformed, and entered into a PCA, along with the three spot variables. The first two principal components explained the majority (70%) of the variance in color and spot variables. PC1 loaded heavily with all $L^*a^*b^*$ color components ($L^* = -0.87$, $a^* = 0.94$, $b^* = 0.90$) and weakly with spot variables (all loadings < 0.22). The negative L^* value suggests that fin lightness decreases with increasing a^* and b^* values. Because the background fish were photographed against was white, the observed inverse relationship between L^* , and a^* and b^* is consistent with the interpretation that higher L^* values represent increasing fin transparency due to a lack of fin pigmentation. Positive a^* and b^* loadings indicate that PC1 is correlated with increasing color intensity (more red and yellow). PC2 explained an increasing number of spots (dorsal fin = 0.78, caudal fin = 0.75, lateral = 0.73) but explained little variation in $L^*a^*b^*$ values (all loadings < 0.13). Both principal components were used as predictor variables in subsequent analyses. These results are similar to those reported in Martin et al. (2013) and

Giery et al. (2015), in that the majority of fin color variation in Bahamian mosquitofish corresponds to increasing or decreasing color saturation and hue.

To detect different condition-dependent relationships among predation regimes, we tested for heterogeneity of slopes between predation regimes by using a linear mixed-effects model (LMM) conducted in R (R Development Core Team 2012) with *lme4* (Bates et al. 2011). The model was designed to evaluate the correlation between Mass and morphological variables (i.e., SL, fin coloration, and spots) while allowing random slopes and intercepts for continuous covariates for each population. Fixed main effects in our model were fin coloration (PC1), number of spots (PC2), SL, and predation regime (“predator”). Standard length was included to correct for the effect of length on mass estimates. In effect, this produced a response variable that is a size-corrected estimate of Mass and is interpreted as a proxy for condition (see “*Gambusia* and Predator Sampling”). We also included a predator \times SL term to control for a possible effect of predation on mass-length relationships (Green 2001). The focal terms in our model, that is, the terms that tested our primary hypotheses, were interactions: predator \times PC1 and predator \times PC2. If significant, these terms show that predation has an effect on the relationship between trait value and Mass.

The full model we began our analysis with was as follows: Mass = SL + PC1 + PC2 + predator + SL \times predator + PC1 \times PC2 + PC1 \times predator + PC2 \times predator + PC1 \times PC2 \times predator + population + SL \times population + PC1 \times population + PC2 \times population. To highlight important variables in our model, we reduced this model, starting with random effects, followed by fixed-effect evaluation. To select an optimal random-variable structure, we compared Akaike information criterion values (AIC) calculated for all combinations of random terms and chose the model with the lowest AIC. Next, fixed effects were trimmed from this new model by means of log-likelihood ratio tests of the new full model against reduced ones. Terms were trimmed if reduced models did not differ in explanatory power (i.e., $P > .05$). The final reduced model was run

in *lme4* (Bates et al. 2011), and *P* values were calculated with Satterthwaite's approximation of denominator degrees of freedom in *lmerTest* (Kuznetsova et al. 2012). To further investigate the effects of predation on condition dependence, residuals (centered by population) from the final LMM were analyzed with simple linear regression. Slopes and r^2 were examined at two levels, predator regime and population, in order to evaluate our hypotheses about the reliability of condition-dependent signaling. Annotated R code for LMM analysis is included as a zip file, available online.¹

Results

Study sites differed in their predator communities. Of the 16 sites sampled, six contained at least two species of piscivorous fishes, typically snappers, great barracuda, and redfin needlefish (tables 1, A1). Optical conditions in all sites were generally permissive to signaling, as indicated by low turbidity (maximum = 2.1 nephelometric turbidity units) and moderate-to-high transmission values ($T_{570} = .69-.99$; tables 1, A1). Optical conditions were also similar across predation regime (turbidity: $t = .15$, $P = .886$; T_{570} : $t = 1.3$, $P = .222$). Male mosquitofish from populations without piscivorous fish were more intensely colored than their no-predation counterparts, indicating a negative effect of predators on average signal intensity (PC1; table 1). An effect of predation was not detected for the remaining morphological variables included in our analysis (spots [PC2], SL, and Mass; table 1).

Variation in Mass was best described by a model including SL, predator, PC1, and predator \times PC1 as fixed terms and heterogeneous slopes for fin coloration as a random term (tables 2, A2). As expected, body length (SL) was positively correlated with body mass (Mass) and explained much of its variation. There was no main effect of predators on body mass, indicating that condition was similar among the predation regimes. Males of higher body mass for their length were more intensely colored than low-mass individuals ("color" in table 2), suggesting that fin coloration is a condition-dependent trait in which intensely colored dorsal fins indicate males of good condition. However, as predicted, this relationship varied according to predation regime (PC1 term), suggesting that predation regime had a significant effect on the condition dependence of fin color (table 2).

Predator presence was associated with a strong positive relationship between fin color and condition indicative of condition dependence. However, in sites lacking predator fishes, no such relationship was found (fig. 2). This posi-

1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

Table 2: Results of linear mixed model evaluating predation-mediated heterogeneity in condition dependence, that is, the relationship between body mass and fin coloration

Source	Estimate	SE	df	<i>F</i>	<i>P</i>
SL	3.56	.07	1,273	2,484.0	<.001
Predator	.09	.07	1,14	1.6	.224
Fin color					
intensity (PC1)	.01	.01	1,11	15.3	.002
Fin color					
intensity (PC1)					
\times predator	.04	.01	1,10	9.8	.010

Note: Population and population \times fin color intensity (PC1) were included as a random terms in the model. PC = principal component.

tive effect of predation on condition dependence was also revealed when we examined populations individually (table 3). All populations in the no-predator regime lacked evidence of condition dependence, that is, they showed no positive linear relationship. In contrast, four of our six populations exposed to predation showed highly significant linear relationships, and of the two predation populations for which linear relationships were not significant ($P > .05$), one was nearly so (Cistern Cay: $P = .069$; table 3). Overall, the effect of predators in our system-wide analysis was observable at the scale of individual populations and was therefore not driven by a subset of strongly condition-dependent populations, consistent with our main hypothesis (table 3).

One caveat of using r^2 as a measure of condition dependence is that comparisons of fit should be made only among models that indicate significant relationships. Otherwise, the r^2 statistic would estimate noisiness of a nonexistent relationship. Condition-dependent relationships (significant *P* values) were not detected in any low-predation-risk populations. Therefore, we did not evaluate the effect of signaling cost on model fit ("signal noisiness"). For predation populations with significant condition-dependent relationships, r^2 values ranged from 0.21 to 0.59, suggesting considerable variation in signal noisiness among populations coexisting with predators (table 3). However, because of the coarse grain at which the study investigated cost variation (i.e., predator presence/absence), further analysis of r^2 was not possible in our data set.

Discussion

We investigated the role of variable predation risk on the intensity and reliability of sexual signaling in wild populations of the Bahamas mosquitofish. Our results show that populations exposed to predation generally exhibited less intense, but more reliable, condition-dependent signals. The inverse was true for populations without predators. We

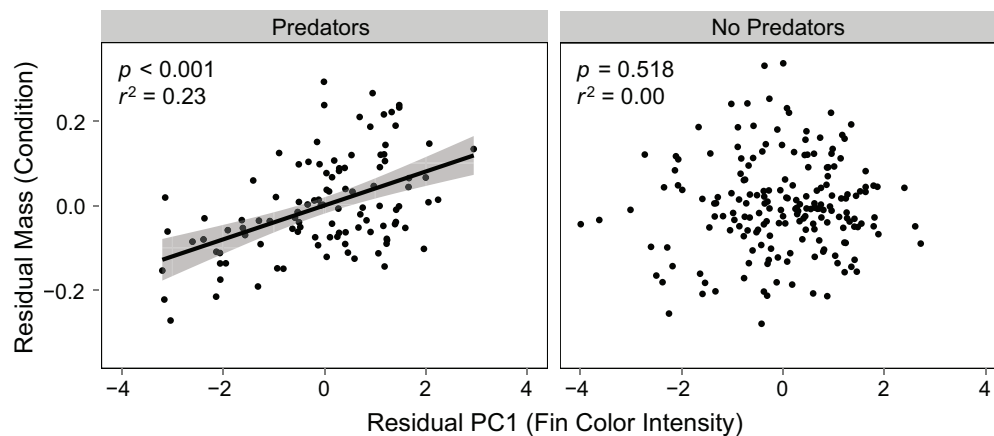


Figure 2: Partial-regression plots showing individual male condition dependence for six *Gambusia hubbsi* populations that co-occur with piscivores (left: $F_{1,105} = 31.7$, $b = .48$), and nine populations that do not (right: $F_{1,185} = .42$, $b = .05$). Data underlying this figure are available in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.977p1> (Gery and Layman 2015).

found that the second trait examined, spotting (PC2), did not exhibit evidence of variation due to predator regime, nor did it exhibit signs of condition dependence. Therefore, the remainder of this discussion examines results of our fin color analysis. Because of the large effect of predators on condi-

tion dependence, we were unable to apply the second part of our analytical approach, that is, comparison of r^2 values among predator regimes (fig. 1c, 1d), to examine variation in reliability more closely. Nevertheless, our data suggest that ecological signaling costs, such as predation, have strong effects on signal reliability, thereby supporting the most widely accepted resolution (costly dishonesty) to the problem of stable communication systems when signaler and receiver interests diverge (Maynard-Smith 1991). Below, we briefly discuss several scenarios, none of which are mutually exclusive, that might explain these findings, and we elaborate on more general implications of natural variation in condition-dependent signaling systems.

Predation has a strong direct effect on signal evolution in poeciliid fishes, especially conspicuous coloration (Ender 1980, 1983; Martin et al. 2013). Generally, empirical data show that predators routinely show a bias toward consuming brightly colored or otherwise conspicuous individuals (Götmark and Olsson 1997; Rosenthal et al. 2001; Godin and McDonough 2003; Lindström et al. 2006; Heinen-Kay et al. 2015), placing a significant, ecologically mediated viability cost on the production of signals. Physical condition also affects predation risk (Guderley 2004; Martínez et al. 2004; Walker et al. 2005). Therefore, because physical condition affects predator avoidance potential via escape performance, low-condition males with conspicuous coloration are at relatively high risk of predation. Consequently, the disproportionately high mortality experienced by individuals that bear both costs (signaling and escape) could maintain a condition-dependent communication system if males exhibiting disproportionately intense coloration are subjected to biased consumption by predators. This would be an example of a “pure epistatic” handicap (Maynard

Table 3: Results of linear regressions of residual variation in condition (mass) and fin color intensity (PC1)

Populations	<i>n</i>	Fin color intensity (PC1)			
		<i>F</i>	β	$P_{\beta} \leq 0$	r^2
Low predation risk:					
Blue Spring	18	.66	-.20	.787	.04
Red Bay Pond	12	.01	.03	.461	.00
Cherokee Sound	18	.00	.02	.524	.00
High Banks Pond	10	.09	-.12	.615	.01
No Man's Land	22	.19	.10	.334	.01
The Old Place	16	.03	-.04	.571	.00
Calcutta Creek	19	.39	.15	.270	.02
Ridge Swamp	18	1.55	.30	.116	.09
Sandy Point	26	.07	.05	.398	.00
Stinky Pond	28	.06	-.05	.593	.00
High predation risk:					
Loggerhead Creek	22	8.65	.55	.004	.30
Baker's Creek	18	8.47	.59	.005	.35
Cistern Cay	12	8.30	.46	.069	.43
Deal's Creek	14	17.55	.77	.001	.59
Double Blocked	13	2.65	.66	.008	.21
Stinky Creek	28	.36	.12	.277	.01

Note: Residuals were derived from mixed models where standard length and population were independent predictors of mass and fin coloration. *P* values are one-tailed, in line with our a priori prediction of a positive relationship between body condition (residual mass) and fin color intensity (PC1). PC = principal component.

Smith 1991). Alternatively, and more in line with theoretical analysis, if individuals modulate signal intensity according to predation risk, they may simply invest in signaling in proportion to their escape ability (“revealing” or “conditional” handicaps; Maynard Smith 1991). In both scenarios, predation risk could result in reliable signaling. We lack data that might enable us to differentiate between these mechanisms; however, support for a direct effect of predators on the prevalence of exaggerators is provided by a positive relationship between condition and predator escape performance in mosquitofish (Langerhans 2009) and other fishes (Guderley 2004; Martínez et al. 2004; Walker et al. 2005).

Signal reliability could also vary according to indirect predator effects, but whether effects mediate reliable signaling probably depends on predation sufficiently affecting the strength of competition within prey/signaler populations. For example, if predators weaken resource competition by reducing prey population size, they could conceivably reduce signal reliability by relaxing viability selection on resource acquisition. Cotton et al. (2004) illustrated this phenomenon in stalk-eyed flies by experimentally relaxing selection on food acquisition. As predicted, their reduced-selection treatment eliminated condition dependence, because individuals were all phenotypically similar despite underlying genotypic variation for signal size. If, however, predators intensify viability selection on resource competition by limiting prey foraging opportunities rather than population size per se (Dill 1983; Diehl and Eklöv 1995; Peckarsky et al. 2008; Heinen-Kay et al. 2013), they could indirectly favor reliable signaling systems by increasing in-trapopulation variance in condition (e.g., Lobón-Cerviá 2010). Notwithstanding the plausibility, if not probability, of indirect predator effects on signal reliability, predation had no detectable effect on mean condition (“predator” term in table 2) or condition variance in our data set (Levene’s test: $F_{1,292} = 0.78$; $P = .38$). Therefore, evidence for indirect predator effects on resource competition-mediated viability costs and condition dependence is lacking here.

In sum, strong support for a specific mechanism generating the patterns we observed is lacking at this time. Yet we provide compelling evidence that predators affect signal reliability and believe that resource competition may play an important role. Clearly, much remains to be understood about signaling costs and the evolutionary ecology of communication systems in the wild. For example, exploring the role of social environment (e.g., Gavassa et al. 2012) or life-history variation on dishonest signaling (Bonduriansky 2014) deserves further effort. To address these topics and others, we advocate additional studies like ours, in which natural ecosystems are employed to evaluate the ecological underpinnings of sexual-signal reliability (Cornwallis and Uller 2010).

Our results strengthen empirical support for a long-hypothesized role for ecological costs in the evolution of signaling-system reliability. We also believe that our results cast new light on a generation of research examining inter-population variation in sexual signals (e.g., Houde 1997; Magurran 2005). For example, the evolution of sexually selected ornaments is often portrayed as the net effect of opposing selection: ecological signaling costs (often predation) and signaling benefits via female mating preferences (Endler 1980, 1983). In agreement with this “balance-of-selection” framework, our results indicate a negative effect of predation on signal intensity among populations (table 1). However, we found that signal costs have alternate, less direct, effects on sexual signal evolution as well. That is, predation affects not only the average conspicuity of signals but also the reliability of qualities theoretically transmitted by them (fig. 2). Understanding the importance of these correlated responses for sexual selection systems and the mechanisms that produce them will require further study.

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Literature Cited

- Andersson, M. 1986. Evolution of condition-dependent sex ornaments and mating preferences: selection based on viability differences. *Evolution* 4:804–816.
- . 1994. *Sexual selection*. Princeton University Press, Princeton, NJ.
- Araújo, M. S., R. B. Langerhans, S. T. Giery, and C. A. Layman. 2014. Ecosystem fragmentation drives increased diet variation in an endemic live-bearing fish of the Bahamas. *Ecology and Evolution* 4: 3298–3308.
- Archer, S. N., J. A. Endler, J. N. Lythgoe, and J. C. Partridge. 1987. Visual pigment polymorphism in the guppy *Poecilia reticulata*. *Vision Research* 27:1243–1252.
- Basolo, A. L. 1998. Evolutionary change in a receiver bias: a comparison of female preference functions. *Proceedings of the Royal Society B: Biological Sciences* 265:2223–2228.
- Bates, D., M. Maechler, and B. Bolker. 2011. lme4: linear mixed-effects models using S4 classes. R package version 0.999375-42. <http://CRAN.R-project.org/package=lme4>.
- Bisazza, A., and A. Pilastro. 2000. Variation of female preference for male coloration in the eastern mosquitofish, *Gambusia holbrooki*. *Behavioral Genetics* 30:207–212.

- Blackwell, P. R. Y., J. H. Christy, S. R. Telford, M. D. Jennions, and N. I. Passmore. 2000. Dishonest signalling in a fiddler crab. *Proceedings of the Royal Society B: Biological Sciences* 267:719–724.
- Bolger, T., and P. L. Connolly. 2006. The selection of suitable indices for the measurement and analysis of fish condition. *Journal of Fish Biology* 34:171–182.
- Bolnick, D. I., and O. L. Lau. 2008. Predictable patterns of disruptive selection in stickleback in postglacial lakes. *American Naturalist* 172:1–11.
- Bonduriansky, R. 2014. Background mortality can modulate the effects of male manipulation on female fitness. *Evolution* 68:595–604.
- Boughman, J. W. 2007. Condition-dependent expression of red color differs between stickleback species. *Journal of Evolutionary Biology* 20:1577–1590.
- Bussière, L. F., J. Hunt, K. N. Stölting, M. D. Jennions, and R. Brooks. 2008. Mate choice for genetic quality when environments vary: suggestions for empirical progress. *Genetica* 134:69–78.
- Candolin, U. 1999. The relationship between signal quality and physical condition: is sexual signalling honest in the threespine stickleback? *Animal Behaviour* 58:1261–1267.
- Carazo, P., and E. Font. 2014. “Communication breakdown”: the evolution of signal unreliability and deception. *Animal Behavior* 87:17–22.
- Chacin, D. H., S. T. Giery, L. Yeager, C. A. Layman, and R. B. Langerhans. 2015. Does hydrological fragmentation affect coastal bird communities? a study from Abaco Island, the Bahamas. *Wetland Ecology and Management*. doi:10.1007/s11273-014-9389-8.
- Chapman, T., G. Arnqvist, J. Bangham, and L. Rowe. 2003. Sexual conflict. *Trends in Ecology and Evolution* 18:41–47.
- Copeland, E. K., and K. M. Fedorka. 2012. The influence of male age and parasitic infection on producing a dishonest sexual signal. *Proceedings of the Royal Society B: Biological Sciences* 279:4740–4746.
- Cornwallis, C. K., and T. Uller. 2010. Towards an evolutionary ecology of sexual traits. *Trends in Ecology and Evolution* 25:145–152.
- Cotton, S., K. Fowler, and A. Pomiankowski. 2004. Condition dependence of sexual ornament size and variation in the stalk-eyed fly *Cyrtodiopsis dalmanni* (Diptera: Diopsidae). *Evolution* 58:1038–1046.
- Diehl, S., and P. Eklöv. 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. *Ecology* 76:1712–1726.
- Dill, L. M. 1983. Adaptive flexibility in the foraging behavior of fishes. *Canadian Journal of Fisheries and Aquatic Sciences* 40:398–408.
- Endler, J. A. 1980. Natural selection on color patterns in *Poecilia reticulata*. *Evolution* 34:76–91.
- . 1983. Natural and sexual selection on color patterns in poeciliid fishes. *Environmental Biology of Fishes* 9:173–190.
- Enquist, M. 1985. Communication during aggressive interactions with particular reference to variation in choice of behaviour. *Animal Behavior* 33:1152–1161.
- Fisher, R. A. 1930. *The genetical theory of natural selection*. Clarendon, Oxford.
- Folstad, I., and A. J. Karter. 1992. Parasites, bright males, and the immunocompetence handicap. *American Naturalist* 139:603–622.
- Gavassa, S., A. C. Silva, E. Gonzalez, and P. K. Stoddard. 2012. Signal modulation as a mechanism for handicap disposal. *Animal Behaviour* 83:935–944.
- Giery, S. T., and C. A. Layman. 2015. Data from: Interpopulation variation in a condition-dependent signal: predation regime affects signal intensity and reliability. *American Naturalist*, Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.977p1>.
- Giery, S. T., C. A. Layman, and R. B. Langerhans. 2015. Anthropogenic ecosystem fragmentation drives shared and unique patterns of sexual signal divergence among three species of Bahamian mosquitofish. *Evolutionary Applications*. doi:10.1111/eva.12275.
- Godin, J.-G., and H. E. McDonough. 2003. Predator preference for brightly colored males in the guppy: a viability cost for a sexually selected trait. *Behavioral Ecology* 14:194–200.
- Götmark, F., and J. Olsson. 1997. Artificial colour mutation: do red-painted great tits experience increased or decreased predation? *Animal Behavior* 53:83–91.
- Gould, J. L., S. L. Elliott, C. M. Masters, and J. Mukerji. 1999. Female preference in a fish genus without female mate choice. *Current Biology* 9:497–500.
- Grafen, A. 1990. Biological signals as handicaps. *Journal of Theoretical Biology* 144:517–546.
- Green, A. 2001. Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* 82:1473–1483.
- Guderley, H. 2004. Locomotor performance and muscle metabolic capacities: impact of temperature and energetic status. *Comparative Biochemistry and Physiology B: Biochemistry and Molecular Biology* 139:371–382.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds—a role for parasites. *Science* 218:384–387.
- Heinen, J. L., M. W. Coco, M. S. Marcuard, D. N. White, M. N. Peterson, R. A. Martin, and R. B. Langerhans. 2013. Environmental drivers of demographics, habitat use, and behavior during a post-Pleistocene radiation of Bahamas mosquitofish (*Gambusia hubbsi*). *Evolutionary Ecology* 27:971–991.
- Heinen-Kay, J. L., K. E. Morris, N. A. Ryan, S. L. Byerley, R. E. Venezia, M. N. Peterson, and R. B. Langerhans. 2015. A trade-off between natural and sexual selection underlies diversification of a sexual signal. *Behavioral Ecology* 26:533–542.
- Horth, L. 2003. Melanic body colour and aggressive mating behaviour are correlated traits in male mosquitofish (*Gambusia holbrooki*). *Proceedings of the Royal Society B: Biological Sciences* 270:1033–1040.
- Horth, L., C. Binckley, R. Wilk, P. Reddy, and A. Reddy. 2010. Color, body size, and genitalia size are correlated traits in eastern mosquitofish (*Gambusia holbrooki*). *Copeia* 2010:196–202.
- Houde, A. E. 1997. *Sex, color, and mate choice in guppies*. Princeton University Press, Princeton, NJ.
- Hughes, M. 2000. Deception with honest signals: signal residuals and signal function in snapping shrimp. *Behavioral Ecology* 11:614–623.
- Iwasa, Y., A. Pomiankowski, and S. Nee. 1991. The evolution of costly mate preferences. II. The “handicap” principle. *Evolution* 45:1431–1442.
- Kahn, A. T., B. Mautz, and M. D. Jennions. 2009. Females prefer to associate with males with longer intromittent organs in mosquitofish. *Biology Letters* 6:55–58.
- Kokko, H., R. Brooks, M. D. Jennions, and J. Morley. 2003. The evolution of mate choices and mating biases. *Proceedings of the Royal Society B: Biological Sciences* 270:653–664.
- Körner, K. E., I. Schlupp, M. Plath, and E. R. Loew. 2006. Spectral sensitivity of mollies: comparing surface- and cave-dwelling Atlantic mollies, *Poecilia mexicana*. *Journal of Fish Biology* 69:54–65.
- Kotiaho, J. S. 2001. Costs of sexual traits: a mismatch between theoretical considerations and empirical evidence. *Biological Reviews* 76:365–376.

- Krakauer, D. C., and R. A. Johnstone. 1995. The evolution of exploitation and honesty in animal communication: a model using artificial neural networks. *Philosophical Transactions of the Royal Society B: Biological Sciences* 348:355–361.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2012. lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). R package version 2.0. <http://CRAN.R-project.org/package=lmerTest>.
- Langerhans, R. B. 2009. Morphology, performance, fitness: functional insight into a post-Pleistocene radiation of mosquitofish. *Biology Letters* 5:488–491.
- Langerhans, R. B., M. E. Gifford, and E. O. Joseph. 2007. Ecological speciation in *Gambusia* fishes. *Evolution* 61:2056–2074.
- Langerhans, R. B., C. A. Layman, and T. J. DeWitt. 2005. Male genital size reflects a tradeoff between attracting mates and avoiding predators in two live-bearing fish species. *Proceedings of the National Academy of Sciences of the USA* 102:7618–7623.
- Langerhans, R. B., C. A. Layman, A. M. Shokrollahi, and T. J. DeWitt. 2004. Predator-driven phenotypic diversification in *Gambusia affinis*. *Evolution* 58:2305–2318.
- Lindström, L., J. J. Ahtiainen, J. Mappes, J. S. Kotiaho, A. Lyytinen, and R. V. Alatalo. 2006. Negatively condition-dependent predation cost of a positively condition-dependent sexual signaling. *Journal of Evolutionary Biology* 19:649–656.
- Lobón-Cerviá, J. 2010. Density dependence constrains mean growth rate while enhancing individual size variation in stream salmonids. *Oecologia* (Berlin) 164:109–115.
- Loew, E. R., and J. N. Lythgoe. 1978. The ecology of cone pigments in teleost fishes. *Vision Research* 18:715–722.
- Lythgoe, J. N., W. R. A. Muntz, J. C. Partridge, J. Shand, and D. M. Williams. 1994. The ecology of the visual pigments of snappers (Lutjanidae) on the Great Barrier Reef. *Journal of Comparative Physiology A: Sensory, Neural, and Behavioral Physiology* 174:461–467.
- Magurran, A. E. 2005. *Evolutionary ecology: the Trinidadian guppy*. Oxford University Press, New York.
- Martin, C. H., and S. Johnsen. 2007. A field test of the Hamilton-Zuk hypothesis in the Trinidadian guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology* 61:1897–1909.
- Martin, R. A., R. Riesch, J. L. Heinen-Kay, and R. B. Langerhans. 2013. Evolution of male coloration during a post-Pleistocene radiation of Bahamas mosquitofish (*Gambusia hubbsi*). *Evolution* 68:397–411.
- Martínez, M., M. Bédard, J. D. Dutil, and H. Guderley. 2004. Does condition of Atlantic cod (*Gadus morhua*) have a greater impact upon swimming performance at U_{crit} or sprint speeds? *Journal of Experimental Biology* 207:2979–2990.
- Maynard Smith, J. 1991. Theories of sexual selection. *Trends in Ecology and Evolution* 6:146–151.
- Maynard Smith, J., and D. Harper. 2003. *Animal signals*. Oxford University Press, Oxford.
- Milinski, M., and T. C. M. Bakker. 1990. Female sticklebacks use male coloration in mate choice and hence avoid parasitized males. *Nature* 344:330–333.
- Møller, A. P., and F. de Lope. 1994. Differential costs of a secondary sexual character: an experimental test of the handicap principle. *Evolution* 48:1676–1683.
- Nielsen, M. L., and L. Holman. 2012. Terminal investment in multiple sexual signals: immune-challenged males produce more attractive pheromones. *Functional Ecology* 26:20–28.
- Peckarsky, B. L., P. A. Abrams, D. I. Bolnick, L. M. Dill, J. H. Grabowski, B. Luttbeg, J. L. Orrock, et al. 2008. Revisiting the classics: considering nonconsumptive effects in textbook examples of predator-prey interactions. *Ecology* 89:2416–2425.
- Peig, J., and A. J. Green. 2009. New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. *Oikos* 118:1883–1891.
- Pomiankowski, A. 1987. The costs of choice in sexual selection. *Journal of Theoretical Biology* 128:195–218.
- R Development Core Team. 2012. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Robinson, M. R., J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2008. Environmental heterogeneity generates fluctuating selection on a secondary sexual trait. *Current Biology* 18:1–7.
- Robinson, M. R., G. S. van Doorn, L. Gustafsson, and A. Qvarnström. 2012. Environment-dependent selection on mate choice in a natural population of birds. *Ecology Letters* 15:611–618.
- Rosenthal, G. G., and C. S. Evans. 1998. Female preference for swords in *Xiphophorus helleri* reflects a bias for large apparent size. *Proceedings of the National Academy of Sciences of the USA* 95:4431–4436.
- Rosenthal, G. G., T. Y. F. Martinez, F. J. García de León, and M. Ryan. 2001. Shared preferences by predators and females for male ornaments in swordtails. *American Naturalist* 158:146–154.
- Sadd, B. M., L. Holman, H. Harmitage, F. Lock, R. Marland, and M. T. Siva-Jothy. 2006. Modulation of sexual signaling by immune-challenged male mealworm beetles (*Tenebrio molitor*, L.): evidence for terminal investment and dishonesty. *Journal of Evolutionary Biology* 19:321–325.
- Schluter, D. 2003. Frequency dependent natural selection during character displacement in sticklebacks. *Evolution* 57:1142–1150.
- Searcy, W. A., and S. Nowicki. 2005. *The evolution of animal communication: reliability and deception in signaling systems*. Princeton University Press, Princeton, NJ.
- Stevens, M., C. A. Párraga, I. C. Cuthill, J. C. Partridge, and T. S. Troscianko. 2007. Using digital photography to study animal coloration. *Biological Journal of the Linnean Society* 90:211–237.
- Walker, J. A., C. K. Chalambor, O. K. Griset, D. McKenney, and D. N. Reznick. 2005. Do fast starts increase the probability of evading predators? *Functional Ecology* 19:808–815.
- Williams, G. C. 1966. *Adaptation and natural selection*. Princeton University Press, Princeton, NJ.
- Wilson, R. S., M. J. Angilletta Jr., R. S. James, C. Navas, and F. Seebacher. 2007. Dishonest signals of strength in male slender crayfish (*Cherax dispar*) during agonistic encounters. *American Naturalist* 170:284–291.
- Zahavi, A. 1975. Mate selection: a selection for a handicap. *Journal of Theoretical Biology* 53:205–214.
- Zuk, M., and G. R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology* 73:415–438.

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