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Lighting environment predicts the relative abundance of male colour morphs in bluefin killifish (*Lucania goodei*) populations

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Animal communication occurs when an animal emits a signal, the signal is transmitted through the environment, and then detected by the receiver. The environment in which signalling occurs should govern the efficacy of this process. In this study, I examine the relationship of lighting environment (light transmission and tree cover), location and the relative abundances of male colour morphs across seven drainages and 30 populations in the bluefin killifish, *Lucania goodei*. I found that males with blue anal fins were more common in populations with low transmission of ultraviolet (UV) and blue wavelengths. By contrast, males with red anal fins (and to a lesser extent, males with yellow anal fins) were more common in populations with high transmission of UV and blue wavelengths. High UV–blue light transmission should create a blue visual background and may make blue males less conspicuous and red males more conspicuous to conspecifics. Colour contrast with the visual background may be more important than total brightness of the colour pattern. These results indicate that natural selection for effective intraspecific communication drives the relative abundance of male colour morphs in different lighting habitats.

Keywords: brightness; contrast; Fundulidae; polymorphism; sensory drive; sexual selection

1. INTRODUCTION

Animal communication occurs when a signaller emits a signal, the signal is transmitted through the environment, and then detected by a receiver (Endler 1992, 1993*a*). The environment in which signalling occurs should have large effects on the efficacy of this process. Signals should be most easily detected when they can be fully transmitted through the environment and when they differ from the background noise against which they are emitted. In terms of visual communication, the wavelengths of a given colour pattern must be transmitted through the environment and the colour pattern must differ from the colour pattern of the visual background. Based on these general principles, we can predict that animals living in habitats with drastically different lighting environments and signal transmission properties should use different colour patterns.

Two different approaches have been adopted for studying the relationship between a colour pattern and the lighting environment. The first approach is to describe the lighting environment in which males of a given species display and ask whether those lighting conditions are a specialized subset of available lighting conditions. These studies require thorough descriptions of colour, background, pattern, ambient light spectra, light transmission and visual capabilities of signallers and receivers (Endler 1990, 1993*b*; Bennett *et al.* 1994; Grill & Rush 2000). Endler & Théry (1996) showed that lekking birds in French Guyana only display in a subset of available lighting conditions. Similarly, Endler (1991) showed that male guppies engage in courtship in lighting environments that maximize their conspicuousness to females but reduce their conspicuousness to predators.

The second method is the comparative approach where comparisons among species (or populations) are made with reference to the lighting environment. Interspecific comparisons seek to demonstrate differences in colour pattern between species inhabiting habitats with different lighting characteristics. For example, Price (1996) showed that finch species occurring in dark, tropical forests tend to be sexually monomorphic in colour pattern whereas species in lighter, temperate forests are more likely to be sexually dimorphic in colour pattern. By contrast, Marchetti (1993) showed that warbler species occurring in darker habitats tended to have more brightly coloured males. The comparative method can also be applied to populations. Seehausen *et al.* (1997) took this approach in a study of two cichlids (*Haplochromis neyererei* and *Neochromis* 'velvet-black'/'blue scraper'). Across populations of *H. neyerei*, the redness of breeding males increases with light transmission. Similarly with *Neochromis*, the blueness of breeding males increases with light transmission. Hence, males of both species are more colourful in populations where such coloration is visible.

In this study, I take a comparative approach and examine the relationship between lighting environment and male colour patterns across several populations within a species. Specifically, I examine the correlation between light transmission, tree cover, location and relative abundance of various male colour morphs for the bluefin killifish, *Lucania goodei*. *L. goodei* is an excellent system for examining the effect of lighting habitat on signals because both the lighting habitats and the signals are highly variable. *L. goodei* occurs in a variety of habitats ranging from crystal clear springs to more tea-stained swamps and from populations with total canopy cover to populations with absolutely no tree cover. The colour pattern among *L. goodei* males is highly polymorphic and the abundance of colour patterns varies widely among populations.

(a) *Breeding biology of the bluefin killifish, Lucania goodei*

The bluefin killifish, *L. goodei*, is a freshwater fundulid found throughout peninsular Florida with a few populations occurring in southeastern Georgia and South Carolina (Page & Burr 1991). The breeding system is promiscuous. Males guard patches of vegetation that serve as substrates for females to attach eggs (Fuller 2001). Gravid females spawn 10–20 eggs each day for 7–10 days. Females visit and inspect males both singly and in groups. Females release one egg per spawn and are assumed to spread their eggs among several males. There is no evidence for male parental care (Fuller & Travis 2001).

Males use their dorsal and anal fins when fighting other males and also when courting females. In fights, males flare their dorsal and anal fins and engage in circular fights (Fuller 2001). One male usually wins and chases the other away. Males also use their fins in the initial stages of courting females. Females approach males. Males then swim circular loops in front of the female and also around her. If the female remains, then the male assumes a position beneath the female where he rapidly twitches his head which makes clicking sounds (Foster 1967). If the female remains, then she and the male swim into the vegetation and simultaneously press their bodies against the vegetation at which time an egg is released, fertilized and deposited onto the vegetation.

The colour pattern is dimorphic between the sexes. Males have a red dot at the base of the caudal fin. The dorsal, anal and pelvic fins are coloured in males but not in females. The anterior three-quarters of the dorsal fin is blue on all males. The posterior quarter of the dorsal fin, the pelvic fins and the anal fin are polymorphic among males. The polymorphism on the pelvic fins and posterior dorsal fin is relatively simple. The posterior quarter of the dorsal fin can be blue, red or yellow. The pelvic fins are either red or yellow.

The polymorphism on the anal fin is much more complex. There are five main categories of anal fin colour patterns: solid red, solid yellow, solid blue, a combination of red and blue, and a combination of yellow and blue. There is a large heritable component to the male colour pattern (R. Fuller and J. Travis, unpublished data). In the laboratory, most adult males retain the same pattern throughout their life.

2. MATERIAL AND METHODS

I sampled fish across seven drainages and 30 populations in Florida (figure 1). I initially relied on accounts of *L. goodei* populations from the University of Florida Natural History Museum, but also sampled from other sites. I focused on drainages from which there appeared to be a high probability of obtaining three or more populations.

At each population, I collected *L. goodei* using seines and dipnets. I collected until I had obtained a reasonably large number of males (30–60) or until I could no longer catch any fish. For each male, I recorded its colour pattern. I also recorded male body length (standard length in millimetres). For the first two populations sampled (Guaranto Springs and Bradford Springs), I only recorded body length for a fraction of the males (11 out of 33 and 39 out of 58 males measured, respectively). For the remaining populations, I recorded body length for nearly
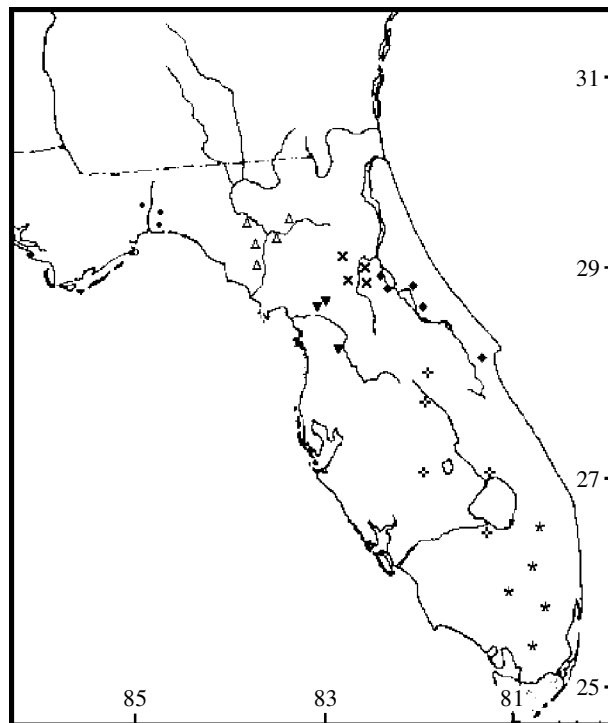

Figure 1. The location of the sampled populations. Only the sampled drainages are shown. Dots, Wakulla; white triangles, Suwanee; crosses, Oklawaha; black diamonds, St Johns; black inverted triangles, Withlacootchee; plus signs, Okeechobee; asterisks, Everglades.

all the males. All fish were released after being processed. Fish were collected between 21 May and 17 July 1999.

At each population, I took measurements of the lighting conditions beginning with the tree cover. There were three categories of tree cover as follows: none (0%), low (10–50%) and high (more than 50%). I measured the transmission of light through the water using an Ocean Optics S2000 spectrophotometer, a tungsten light source (LS1 lamp) and a reflectance probe. I built a sampling chamber that consisted of a flat, white, plastic test cap and a white PVC circular end cap. I drilled a hole into the end cap that matched the diameter of the reflectance probe and helped keep it at an angle of 90° for measurements (figure 2*a*). The reflectance probe emits a beam of light that strikes an object and then bounces back and is measured by the probe.

To measure light transmission, I set the circular PVC end cap on the white flat test cap in a bucket of water from the habitat. I then inserted the reflectance probe through the hole in the circular end cap until the probe touched the flat test cap (figure 2*a*). Here, I took a reference measurement so that I knew the maximum amount of light coming from the light source and being detected by the probe. I then moved the reflection probe so that it was 20 mm away from the end cap and measured the proportion of light detected by the probe (figure 2*b*). I took all measurements under shade to reduce the influence of any light leaking into the sampling chamber. Although this is not a standard measure of light transmission, it provides a relative measure of light transmission and allows for population comparisons in environmental lighting conditions. I measured the light transmission at each population from 12 to 17 July 1999.

For each light transmission reading, the spectrophotometer records the proportion of light detected between 360 and 800 nm in 0.32 nm increments. Hence, each curve comprised

(a)

patchcord to
spectrophotometer
and light source

PVC end cap
(white)

reflectance probe
in contact with
test cap

test cap
(white)

(b)

patchcord to
spectrophotometer
and light source

PVC end cap
(white)

reflectance probe
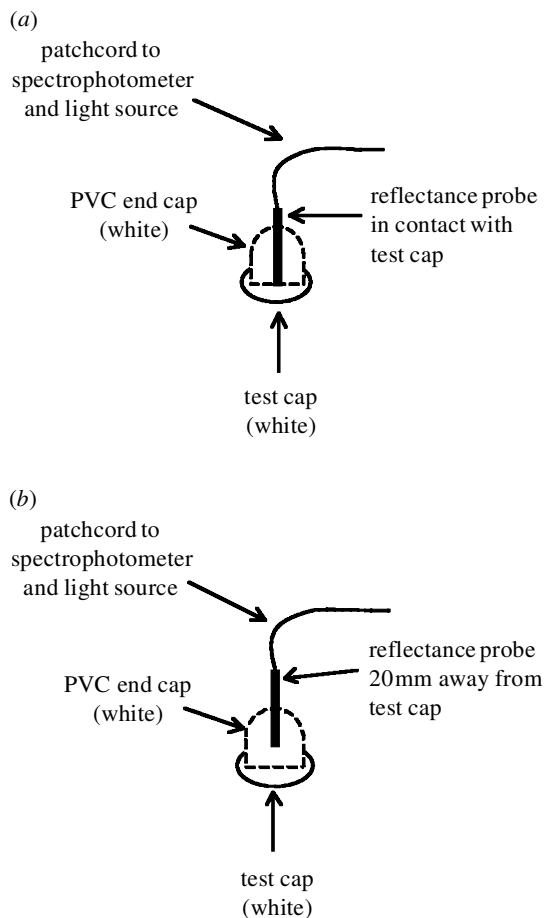20mm away from
test cap

test cap
(white)

Figure 2. Schematic diagram of apparatus used to measure light transmission through the water. A white PVC end cap sits on a white test cap. The end cap is opaque and does not allow any sunlight to enter the chamber. The dashed line denotes that the schematic diagram is showing what happens inside the chamber. The reflectance probe fits snugly through a small hole in the top of the end cap. *(a)* Reflectance probe in contact with test cap. Light emerges out of the probe, is reflected off the test cap, and is then detected by the sensors in the probe. This determines the maximum amount of light detectable. *(b)* Reflectance probe 20 mm away from the test cap. Light emerges out of the probe, is transmitted through the water, bounces off the test cap and the inside of the end cap, and then is detected by the sensors in the probe. The proportion of light transmitted through the water can be calculated by comparing the amount of light detected here with the maximum amount of light possible and the minimum amount of light possible (complete darkness).

1363 points. I reduced the number of points in each curve and only considered the transmission at every 2 nm (i.e. 360, 362, ... 800 nm). This resulted in light transmission curves with 221 points each, where each location is an observation of data for these 221 variables (transmission at each of the 221 wavelengths). I examined these data using principal components analysis on correlations in order to derive a smaller number of variables that could account for most of the variance among the locations in light transmission. Finally, I calculated the overall light transmission across all wavelengths for each population; this is the average of transmission across all of these wavelengths.

Usually when performing principal components analysis, one

wants to have many more observations than variables going into the analysis. If the associations among the variables are somewhat loose, then the analysis can produce a spurious structure due to low sample size (Stevens 1986). However in this case, the 221 variables are tightly correlated. In fact, we are not really measuring 221 separate variables but are instead describing a continuous function with 221 data points. To confirm that the high number of variables was not a problem, I smoothed out the light transmission curves in two separate ways. I created one set of light transmission curves described by 14 data points where each point on the curve was 32 nm apart. I then created a second set of light transmission curves described by seven data points where each point on the curve was 64 nm apart. I conducted two separate principal components analyses to ascertain whether the results of the original analysis was affected by the number of variables.

I returned to 29 of the 30 populations in December 2001–January 2002 and measured light transmission through the water using an alternative method. The reason for measuring the light transmission again was to ensure that the method described earlier produced similar results to the beam transmission method (Endler 1990). In the beam transmission method, a light source is placed at various distances from a sensor that records the total amount of light detected. Regressing the log of the amount of light detected by the sensor on distance provides an attenuation coefficient that is another measure of light transmission. The beam transmission method produced data similar to the light transmission measured by the reflectance probe method used in this study. Hence, the method I used in this study adequately captured the major components of variation in light transmission across the populations. Further details and data are provided in electronic Appendix A available on The Royal Society's Publications Web site.

To simplify the analysis, I considered only the anal fin colour pattern. I described each male as having either a solid red, solid blue, solid yellow, red–blue combination or yellow–blue combination anal fin. For Newport Springs, three males could not be placed in any of these categories (see table 1 legend). For each colour (red, blue and yellow), I calculated the proportion of males with a solid coloured anal fin (e.g. number of males with a solid blue anal fin divided by the total number of males). In addition, I calculated the proportion of males with red–blue combination anal fins and the proportion with yellow–blue combination anal fins.

For each of the five colour morphs, I performed a backwards stepwise analysis of a general linear model to determine which variables accounted best for the variation in the relative abundance of that colour morph among populations. The original model included six variables: drainage, tree score, latitude, longitude and two principal components. Latitude and longitude plus the two principal components were continuous variables. Drainage and tree score were categorical variables and were treated as dummy variables in the model (Draper & Smith 1981, p. 241). Independent variables were removed from the model if the F-ratio for their effect was less than unity. I continued removing terms until all terms had an F-ratio greater than unity. This occasionally resulted in a situation where some effects were left in the model even though the p-value did not reach statistical significance ($p < 0.05$). My rationale for this approach is that effects should be dropped from the model if there is more variation within than among groups ($F < 1$). When the F-ratio is greater than unity, this indicates that the effect is accounting for some variation even if the effect is not statistically

Table 1. Data for male colour morphs across the 30 sampled populations.
(Newport Springs also contained two males that were classified as having orange anal fins and one male that was classified as having a yellow–red–blue combination anal fin.)

population	drainage	total	solid blue	solid red	solid yellow	red–blue combination	yellow–blue combination
East Canal	Everglades	23	16	3	1	1	2
26-Mile Bend	Everglades	73	30	9	6	16	12
I-75 Reststop	Everglades	33	16	3	1	7	6
Payhayokee	Everglades	67	12	8	12	22	13
Tamiami Canal	Everglades	50	22	9	8	8	3
Arbuckle Creek	Okeechobee	34	23	1	0	10	0
Lake Marion	Okeechobee	31	13	0	0	14	4
Lake Okeechobee	Okeechobee	46	15	8	0	17	6
Lake Tohopekalagia	Okeechobee	48	16	15	4	12	1
West Canal	Okeechobee	16	5	0	2	5	4
Delk's Bluff, Oklawaha River	Oklawaha	34	4	10	4	8	8
Lake Eaton	Oklawaha	14	10	0	0	2	2
Orange Lake	Oklawaha	35	14	3	0	9	9
Mill Dam Lake	Oklawaha	9	2	4	2	1	0
Alexander Creek	St Johns	24	1	10	10	0	3
Crow's Bluff, St Johns River	St Johns	20	5	9	1	5	0
Melbourne	St Johns	28	12	5	1	6	4
Ponce de Leon Springs	St Johns	32	6	16	5	5	0
Salt Springs	St Johns	26	1	21	3	1	0
Blue Springs	Suwanee	43	1	25	15	2	0
Bradford Springs	Suwanee	58	0	42	16	0	0
Duncans Landing, Santa Fe River	Suwanee	7	1	2	4	0	0
Guaranto Springs	Suwanee	33	1	22	10	0	0
Hart Springs	Suwanee	26	3	11	9	2	1
Newport Springs	Wakulla	7	0	1	3	0	0
St Marks Refuge	Wakulla	33	0	11	5	15	2
Wakulla River	Wakulla	38	1	9	26	1	1
Dunnellon, Rainbow River	Withlacootchee	23	5	7	6	2	3
Hernando, Tsala Apopka Lake	Withlacootchee	25	6	6	4	6	3
K-P Park, Rainbow River	Withlacootchee	49	1	10	28	3	7

significant. In this case, it is possible that effect really does contribute to the pattern (but there is a lack of power) or that the F-ratio is greater than unity simply due to random chance. In either case, leaving the effect in the model makes subsequent tests for other effects more conservative. Type three sums of squares were used in all analyses.

I visually examined the residuals from the models for departures from normality. In all cases, the residuals appeared to be normally distributed. Hence, no transformations of the raw colour morph frequencies were necessary.

Finally, I compared the male body length between drainages, populations and colour morphs using a nested ANOVA. All factors were treated as fixed effects. I nested individuals within populations within drainages. Furthermore, I examined the interaction between colour morph and drainage, and the interaction between colour morph and population nested within drainage. Provided that they were not statistically significant, I removed the interactions from the model. For body length data, I report means ± standard errors (in millimetres).

All analyses were performed with the SAS statistical package v. 8. All tests were considered significant at $p < 0.05$.

3. RESULTS

Two principal components summarized over 90% of the total variation in light transmission. The first component accounted for 77.87% of variation and correlated positively with all wavelengths (figure 3a). Principal component (PC) 1 was highly correlated with the overall light transmission for each population ($r = 0.9952$, $p < 0.0001$, $n = 30$) as well as with the light transmission at each measured wavelength ($p < 0.01$ for all correlations). For the remainder of this paper, I refer to PC1 as overall transmission. The second component accounted for 13.3% of the variation and loaded positively onto UV and blue wavelengths (figure 3a). PC2 was significantly correlated with light transmission from 360 to 478 nm, but not with light transmission from 480 to 800 nm. For the remainder of this paper, I refer to PC2 as UV–blue transmission. The third and fourth principal components together accounted for most of the remaining variation (9%) but failed to predict the relative abundance of male colour morphs.

Principal components analyses on both the 14 data point transmission curves and the seven data point transmission curves produced results nearly identical to the original analysis. For both analyses, the first two components accounted for more than 90% of the variation; the first component loaded positively onto all wavelengths, and the second component loaded positively onto the UV–blue wavelengths and negatively (although weakly) onto the longer wavelengths. Hence, the results of the principal components analyses are robust to changes in the number of variables used to describe the light transmission curves.
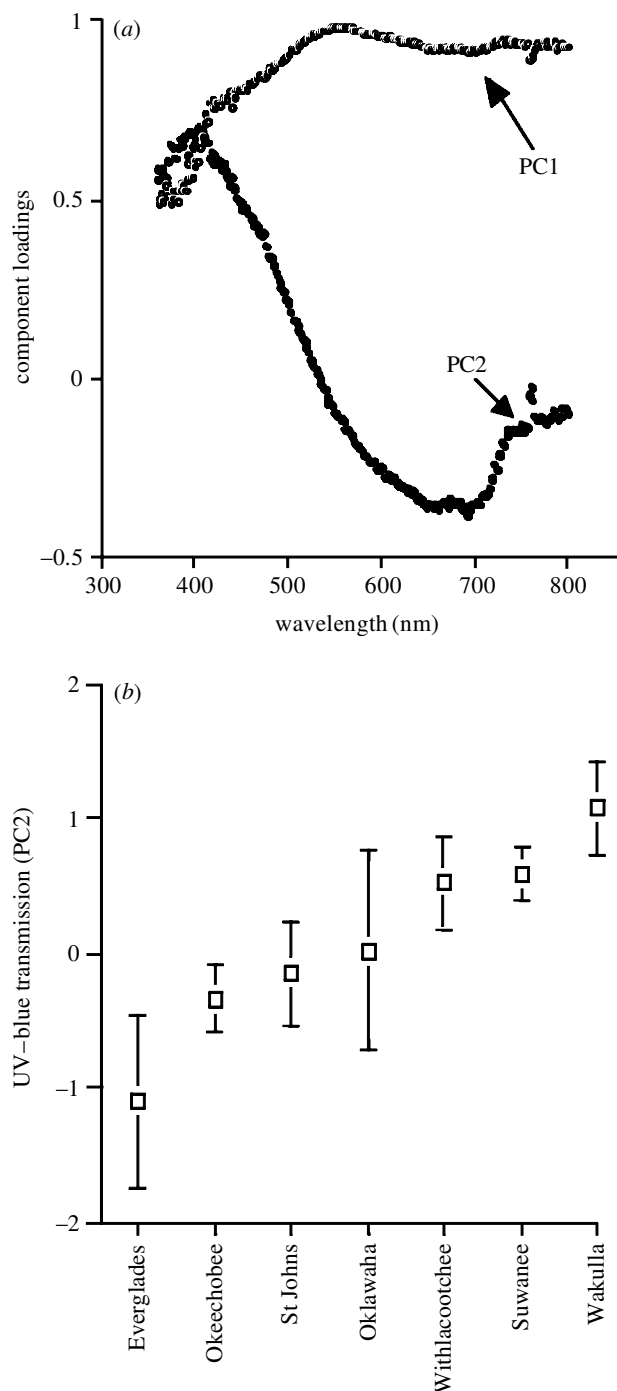
higher tree cover than the Suwanee and Wakulla sites (Mann–Whitney *U*-test for multiple comparisons, $p < 0.05$) (Siegel & Castellan 1988, p. 213).

The male anal fin colour patterns were highly polymorphic (table 1). At least two different male anal fin colour patterns were present in all the populations, and most populations had three or more colour patterns. Bradford Springs contained the fewest colour patterns with males with solid red anal fins and males with solid yellow anal fins. All populations contained both males with some type of yellow anal fin (solid yellow or yellow–blue combination) and males with some type of red anal fin (solid red or red–blue combination) with the exception of Arbuckle Creek. In Arbuckle Creek, only males with solid blue, solid red or red–blue combination anal fins were found.

Males with solid blue anal fins were more common in populations where the UV–blue light transmission was low (table 2, figure 4*a*). Throughout the stepwise process, the UV–blue light transmission was statistically significant in all models ($p < 0.0064$ in all models, final model: $F_{1,21} = 18.023$, $p = 0.0004$, $r = -0.742$). Hence, the UV–blue transmission had a large effect even when all other independent variables were included in the model. UV–blue transmission, overall transmission and drainage were the only terms in the final model—although the latter two terms were not statistically significant (drainage: $F_{6,21} = 1.806$, $p = 0.1465$; overall transmission: $F_{1,21} = 3.407$, $p = 0.0791$). Removal of the leftmost outlying point did not alter the results nor the effect of the UV–blue transmission ($F_{1,20} = 9.123$, $p = 0.0068$). Longitude, latitude and tree score were dropped from the model.

The abundance of males with solid red anal fins was affected by UV–blue transmission and drainage (table 2, figure 4*b,c*). Both terms were statistically significant in both stepwise models. Therefore, both terms had strong effects in the presence of all other independent variables. Figure 3*b* shows that males with solid red anal fins were more common in populations with a high transmission of the UV–blue wavelength ($F_{1,18} = 9.94$, $p = 0.0055$, $r = 0.406$). Figure 3*c* shows the mean and standard error for each drainage ($F_{6,18} = 6.55$, $p = 0.0008$). There were significantly higher proportions of males with solid red anal fins in the Suwanee and St Johns drainages than there were in the Everglades and Okeechobee drainages. In addition, the proportion of males with solid red anal fins was significantly higher in the Suwanee than in the Oklawaha drainage. Overall transmission, tree score and longitude remained in the model although none was statistically significant (overall transmission, $F_{1,18} = 2.88$, $p = 0.1071$; tree score, $F_{2,18} = 2.41$, $p = 0.1185$; longitude, $F_{1,18} = 3.48$, $p = 0.0783$). Again, removal of the outlier did not alter the results for UV–blue transmission ($F_{1,18} = 8.15$, $p = 0.0105$) or drainage ($F_{6,18} = 7.90$, $p = 0.0003$), although overall transmission and longitude did drop from the model.

Both UV–blue transmission and overall transmission had positive, significant effects on the abundance of males with solid yellow anal fins. There was a positive relationship between UV–blue transmission and the abundance of males with solid yellow anal fins (table 2, figure 5*a*, $F_{1,25} = 6.965$, $p = 0.0141$, $r = 0.539$). Similarly, figure 5*b* shows that males with solid yellow anal fins were more common in populations with high overall light trans-

Figure 3. (*a*) Component loading of PC1 and PC2 onto the light transmission of each wavelength between 360 and 800 nm. (*b*) Means and standard errors of UV–blue transmission (PC2) across the drainages.

In addition, running the principal components analysis on covariates produced nearly identical results.

The UV–blue transmission differed among the drainages studied (figure 3*b*, $F_{6,23} = 3.012$, $p = 0.025$). The UV–blue transmission was lower in the Everglades drainage than in the Wakulla drainage. Tree cover was lower in the Everglades, Okeechobee, Oklawaha and St Johns drainages than in the Suwanee, Wakulla and Withlacootchee drainages (Kruskal–Wallis, $\chi^2 = 13.57$, d.f. = 6, $p = 0.0348$; Mann–Whitney *U*-test for multiple comparisons, $p < 0.05$). In addition, the Withlacootchee sites had

Table 2. Summary of results for each colour morph.
(Factors significant in the initial model refers to effects that are statistically significant in the presence of all the other variables. 'Robust to removal of outlier?' refers to whether or not the significant factors in either the initial or final model still have statistically significant effects upon removal of the outlier.)

colour morph	factors significant in initial model	factors significant in final model	additional factors remaining in final model	robust to removal of outlier?
solid blue	UV–blue transmission	UV–blue transmission	overall transmission, drainage	yes
solid red	UV–blue transmission, drainage	UV–blue transmission, drainage	overall transmission, tree score, longitude	yes
solid yellow	nothing	UV–blue transmission, overall transmission	tree score	UV–blue transmission drops from model, overall transmission not significant in final model
yellow–blue combination	longitude, drainage	longitude, drainage	nothing	longitude and drainage marginally significant in all models $p \approx 0.08$–0.05
red–blue combination	nothing	nothing	UV–blue transmission, drainage, tree score, latitude	drainage becomes significant in final model only

mission ($F_{1,25} = 10.337$, $p = 0.0036$, $r = 0.480$). However, neither of these terms accounted for significant amounts of variation in the first three models. Hence, these results should be interpreted with caution. Tree score remained in the model but was not statistically significant ($F_{2,25} = 2.712$, $p = 0.0859$). Drainage, longitude and latitude were dropped from the model. Removal of the far outlier had a large effect on this analysis. Without the far outlier, the UV–blue transmission dropped from the model. Longitude and latitude also dropped from the model. Overall transmission, tree score and drainage remained in the model although none accounted for significant amounts of variation.

Longitude and drainage accounted for significant variation in the abundance of males with yellow–blue combination anal fins. Both factors were significant in all models, and no other factors remained in the model. Males with combination yellow–blue anal fins were less common in populations in the northern part of their range as shown by the effect of longitude ($F_{1,22} = 6.85$, $p = 0.0158$, $r = 0.472$). The abundance of yellow–blue males also differed across the drainages ($F_{6,22} = 2.80$, $p = 0.0356$) being most common in the Oklawaha and least common in the Suwannee. Removal of the outlier resulted in a similar model selection, but the effects of longitude and drainage were marginally significant in all models ($0.08 < p < 0.05$).

The abundance of males with red–blue combination anal fins was not significantly predicted by any of the independent variables. The stepwise analysis resulted in a model containing drainage, tree score, latitude and UV–blue light transmission, but none of these variables accounted for a significant amount of variation, although the overall model was statistically significant. Removal of the outlier did result in a final model where drainage was statistically significant ($F_{6,20} = 2.96$, $p < 0.031$).

Male body length differed between the colour morphs, drainages and populations nested within the drainages (colour morphs, $F_{4,903} = 3.55$, $p = 0.0069$; drainages, $F_{6,903} = 117.29$, $p < 0.0001$; populations (drainages),

$F_{23,903} = 17.79$, $p < 0.0001$). None of the interactions was statistically significant. Hence, both were removed from the model. Males with yellow anal fins were significantly larger than males with red, red–blue combination or blue anal fins (yellow, 29.949 ± 0.284, $n = 177$; red, 29.101 ± 0.232, $n = 247$; red–blue, 28.805 ± 0.284, $n = 182$; blue, 28.585 ± 0.275, $n = 240$; yellow–blue, 29.181 ± 0.455, $n = 91$). However, these differences were quite small. Males with yellow anal fins were only 4.7% larger than males with blue anal fins and 2.9% larger than males with red anal fins. The differences in body length among drainages were much larger. For example, Withlacootchee males were significantly larger than males from all other drainages and were 29% larger than Everglades males.

4. DISCUSSION

The main result to emerge from this study is that environmental lighting conditions are strongly associated with the relative abundance of male colour morphs between populations. This effect occurs despite the effect of drainage, and presumably does not reflect a historical constraint. Furthermore, the fact that all populations had at least two colour morphs and that all drainages had all five colour morphs indicates that a lack of genetic variation in colour pattern does not cause these patterns.

The most striking pattern is the relationship between UV–blue transmission and the relative abundance of male colour morphs. Males with blue anal fins are more common in turbid south Florida sites with low UV–blue transmission, whereas males with red anal fins (and to a lesser extent males with yellow anal fins) are more common in clear spring populations with high UV–blue transmission (table 2). At first consideration, these results seem paradoxical because they indicate that there are more males with blue anal fins in populations where UV–blue wavelengths do not travel very far. Using blue in such an environment should reduce the total brightness of the col-
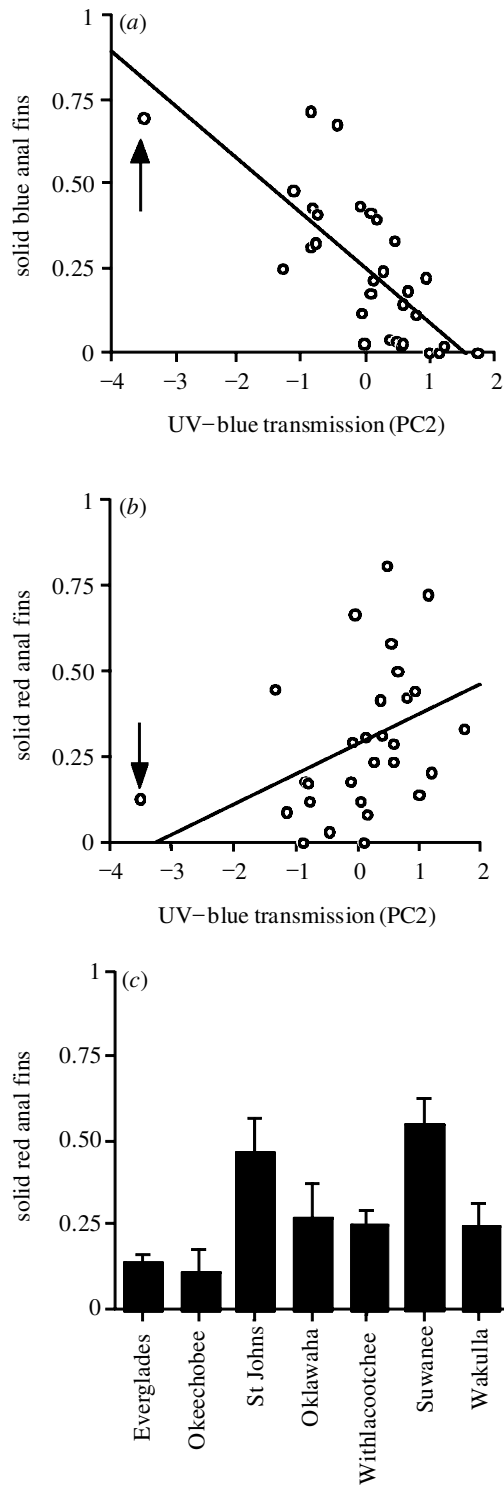
Figure 4. The factors accounting for significant amounts of variation in blue and red morph abundance. Each data point represents a population. The arrows point to the outliers with high leverage. (*a*) The relationship between the abundance of males with solid blue anal fins and UV–blue transmission (PC2). (*b*) and (*c*) Proportion of males with solid red anal fins as a function of (*b*) UV–blue transmission (PC2) and (*c*) drainage. The means and standard errors are shown.

our pattern (Endler 1993*b*). There are two potential explanations for these findings.

The first explanation is that blue males may actually be less conspicuous in populations with high UV–blue trans-
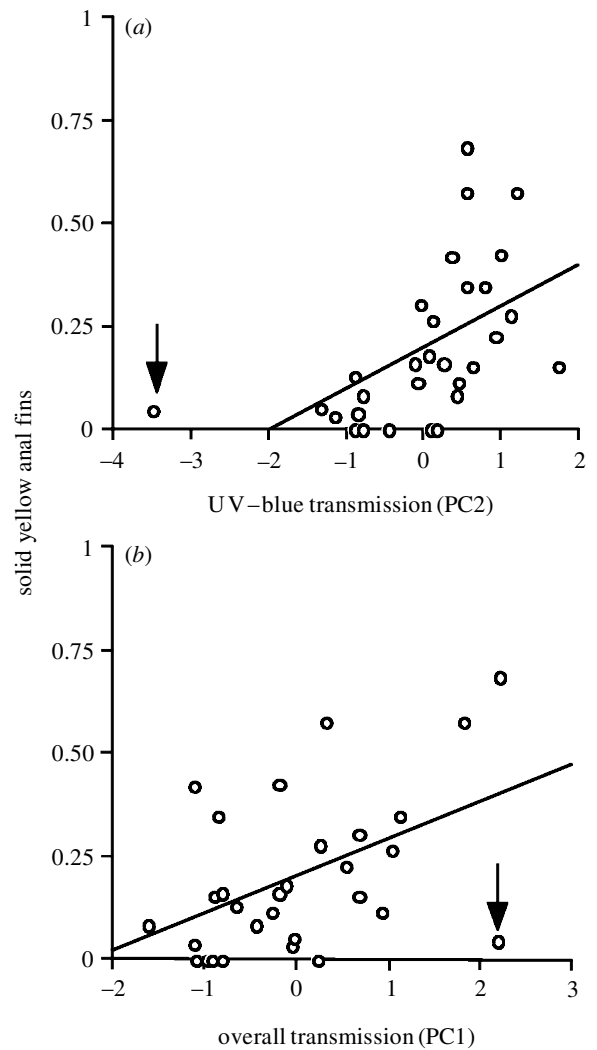
Figure 5. Factors affecting the abundance of yellow morphs. The proportion of males with solid yellow anal fins versus (*a*) UV–blue transmission (PC2) and (*b*) overall transmission (PC1).

mission. Although total brightness may be greater in clear water populations, the contrast between the colour pattern and the background (brightness contrast) may be low (Endler 1993*b*). The water in populations with high UV–blue transmission frequently takes on a blue tint (e.g. Blue Springs). While males are undoubtedly at times viewed against a background of green vegetation, they are likely also to be viewed with the water column serving as a background. Blue males may not be very conspicuous in such populations because they do not differ from their visual background. In comparison, red males should be very conspicuous in such populations. Provided that conspicuousness leads to higher mating success, males with red anal fins would have a selective advantage, while males with blue anal fins would have a disadvantage in populations with high UV–blue transmission.

Similar patterns have been found among two colour morphs in the three-spined stickleback, *Gasterosteus aculatus*. Reimchen (1989) showed that males with red throat patches were more common in clear waters while males with black throat patches were more common in stained water populations on the Queen Charlotte Archipelago, Canada. That study indicated that a red throat viewed

against a blue water column in clear-water populations maximizes contrast and presumably breeding success. In stained waters, this contrast may be reduced. This pattern has been subsequently documented for other *G. aculatus* populations (Boughman 2001; Scott 2001). Milinski & Bakker (1990) later showed that lighting environment affects male mating success. Females preferred males with red throat patches when viewed under white light, but not when viewed under green light. This presumably occurs due to a lack of red reflectance under green light. Whether or not such visual habitats occur in nature is unclear. In a slightly different aquarium experiment on guppies (*Poecilia reticulata*), Long & Houde (1989) showed that females do not exert preferences for males with orange spots when viewed under orange light. This effect occurs due to a lack of contrasting reflectance between orange spots and other body parts. Hence, the high transmission of orange wavelengths does not make orange males more conspicuous (Houde 1997).

The other potential explanation for the abundance of blue morphs in populations with low UV–blue transmission is that blue colour elements serve as a private channel for communication. Males use their fins in signalling to conspecific males and females over short distances (less than 0.5 m). Blue signals may be effective over such short distances but may attenuate over longer distances such as those from which predators would view them. If this were true, the survival of males with blue anal fins would be higher in populations with low UV–blue transmission. Endler (1987, 1991) has indicated a similar phenomenon in guppies (*P. reticulata*). Guppies modify their behaviour to reduce the conspicuousness to predators and to increase their conspicuousness to females. By displaying at certain times and places, males use wavelengths that travel far enough to be effective in attracting females but should attenuate over longer distances.

While this system is similar to that found in guppies (freshwater fish species, highly polymorphic colour pattern), there are important differences between these two species. In guppies, most of the variation in colour patterns has been explained in terms of differences in the predation regime (Endler 1978, 1980, 1982). In the guppy system, there are entire suites of predators that are present in some populations, but not in others (Reznick *et al.* 1990; Reznick & Travis 1996). In *L. goodei*, differences in predation communities probably cannot independently account for the observed differences in colour morph abundance. Large fishes (bass), insects (dragonflies) and avian predators (kingfishers, herons) are present in all the sampled populations (for fish records see the University of Florida Museum of Natural History database). The most divergent predator communities most probably occur in the Everglades and Okeechobee drainages where exotic species are quite common (Loftus & Kushlan 1987). Admittedly, relative predator abundance could explain some residual variation in colour morph abundance. Predators in different lighting environments probably differ in which male colour morphs they see most easily and can prey upon. However, differences in the predator communities probably do not independently drive the pattern demonstrated in this study.

In comparison to the guppy system, the lighting environment has a much larger effect on the relative abun-

dance of colour morphs in *L. goodei*. Guppies may use certain lighting environments preferentially at certain times of the day (Endler 1991; Reynolds *et al.* 1993). Endler (1980) has demonstrated that there is increased predation on guppies whose spot size differs from the average size of a cobble. In addition, light transmission does affect the absolute measures of conspicuousness (Endler 1991). Still, there is little research demonstrating that colour morph abundances in guppies (e.g. red, blue, yellow, black) differ dramatically across populations in relation to lighting environment independent of predation regime.

The large amount of variation within *L. goodei* populations remains unexplained. If these morphs have a genetic basis, then there must be a mechanism allowing for the maintenance of such high genetic variation. Heterogeneity in the lighting environment is one potential explanation. The transmission properties of light change with the water depth (Endler 1990, 1991). Also, fish occurring close to the bottom may be viewed against a different visual background. Females can ovoposit eggs on floating, vertical or bottom vegetation. If females have consistent preferences for such substrates, then this would indicate that females also differ consistently in the background against which they observe males. Alternatively, temporal variation in lighting environment could have a role, although this hypothesis requires that the environment varies over a smaller time-scale than the lifespan or generation of the organism (Ellner & Hairston 1994). Lighting environment could vary between the wet and dry seasons especially in non-spring populations. Populations occurring in irrigation ditches and canals would be particularly prone to temporal variation in the lighting environment. In addition, other mechanisms such as frequency dependent selection through female mate choice or male–male competition (Andersson 1994), mutation–selection balance or heterozygote advantage could be important in the maintenance of this polymorphism (Lynch & Walsh 1998). These alternatives remain to be tested.

Finally, these results raise the obvious question of whether the vision physiology of *L. goodei* also varies among populations. Sensory exploitation and sensory bias hypotheses would indicate that these differences in colour morphs represent the solutions adopted by males to stimulate the same receiver physiology under different environmental conditions (Basolo 1990, 1991; Ryan 1991). By contrast, coevolutionary models of female mating preferences and male traits rely on evolvable preferences and, therefore, evolvable sensory physiology (Iwasa & Pomiankowski 1994; Widemo & Saether 1999). It is possible that the vision physiology has been adapted to local conditions and male colour patterns evolve to match the vision physiology. In this scenario, the signalling and receiving systems coevolve to maximize communication under a wide variety of lighting conditions. I am currently investigating whether population and genetic variation is present in *L. goodei* sensory systems to resolve these issues.

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