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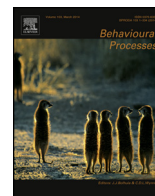
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Does fin coloration signal social status in a dominance hierarchy of the livebearing fish *Xiphophorus variatus*?



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ABSTRACT

In each population of the livebearing fish *Xiphophorus variatus*, only a small portion of the adult males develop bright yellow-red (YR) coloration on the dorsal and caudal fins. Here we characterized the dominance hierarchy in *X. variatus* and tested whether YR coloration is related to a male's position in the hierarchy and can therefore serve as a reliable cue to rival males. Populations varied considerably in the frequency of YR males. Across all populations, males with YR coloration were significantly larger than the rest of the males in the population. Observations of aggressive interactions among males in small groups in the laboratory revealed a sized-based dominance hierarchy with YR males at the top. Aggression was more common among males of a similar size and fighting increased as male body size differences decreased. However, despite the reliability of YR coloration as a signal of dominance status, males at lower social ranks did not avoid aggression with YR males and YR males did not experience fewer aggressive attacks compared to non-YR males. Our findings demonstrate that fin coloration is a reliable cue of a male's social status but rival males appear to not use this information to avoid potentially costly interactions with dominant males, suggesting that YR fin coloration has not evolved as a cue in agonistic interactions.

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1. Introduction

Across the animal kingdom conspicuous visual cues are hallmarks of sexual communication often either advertising an individual's condition to potential mates (Andersson, 1994) or status to potential rivals (Senar, 2006; Fisher and Rosenthal, 2007). Some traits function in both contexts, simultaneously providing information for potential mates and rivals (Rowland, 1984; Fisher and Rosenthal, 2007; Marty et al., 2009). The evolution of conspicuous traits has most often been studied in the context of mate choice and competing hypotheses have arisen. One model suggests that traits do not provide information but rather may serve to exploit female sensory biases (Ryan, 1990). Indicator models on the other hand suggest that a trait indicates a male's condition and that mate choice can provide females with either direct (Hoelzer, 1989) or indirect benefits (Head et al., 2005). However, male traits can also provide information to potential rivals, signaling

an individual's social rank (Setchell and Wickings, 2005), aggressive intent (Moretz and Morris, 2003) or indicate fighting ability (Moretz, 2005). Aggressive interactions can result in injury or negatively affect an individual's reproductive opportunities (Wong and Candolin, 2005).

A priori information about an individual's rank (Setchell and Wickings, 2005), size (Fisher and Rosenthal, 2007), or fighting ability (Moretz, 2005) could help prevent potentially costly interactions with males that are dominant or are better fighters.

Species of the genus *Xiphophorus*, as well as many other poeciliids, have been the subject of a wide variety of behavioral studies on sexual selection especially in the context of male morphology in inter- (Rosenthal and Evans, 1998; MacLaren et al., 2011) and intra-sexual contexts (Benson and Basolo, 2006; Fisher and Rosenthal, 2007) including pigmentation (for review see Culumber, 2014). Yet, surprisingly few studies have characterized dominance hierarchies, and fewer yet have investigated the potential role of coloration in intra-sexual signaling. Here we focus on the platyfish *Xiphophorus variatus* in which only a small portion of the adult male population exhibits bright yellow and red (YR) coloration of the dorsal and caudal fins (Fig. S1). In sibling pairs raised in the laboratory, the development of YR coloration was found to be related with a male's relative size at maturation (Borowsky, 1973). Males

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that matured early did so at a smaller size and without YR coloration, while siblings that matured later went on to attain larger size and developed YR coloration. In that study, the intensity of YR coloration also increased until a male was surpassed in size by another male (Borowsky, 1973). Thus, males that are never the largest within a group never develop YR coloration and instead have fin color similar to that of females. *X. variatus* has proved to be a useful system for studying the maintenance of genetic variation, due to polymorphism in pigmented tailspot patterns within populations (Culumber et al., 2014; Culumber and Rosenthal, 2013). No study has yet examined the potential role of tailspot patterns in male–male interactions.

Supplementary Fig. S1 related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.beproc.2014.08.010>.

In the present study we examined the frequency of YR males in natural populations and tested the prediction that, in natural populations, YR males are larger on average than males without YR coloration. We then characterized aggressive interactions to determine whether a dominance hierarchy exists and to explore the factors that affect its structure. We hypothesized that if a size-based hierarchy exists, then YR males should be the dominant males. Since males cease growth at maturity, and a male's YR color formation stops only when he is surpassed in size by a maturing male, then males without YR coloration should avoid potentially costly interactions (e.g., fin damage or reduced reproductive opportunities; for the latter see: Wong and Candolin, 2005) with larger, YR males given that they have no chance of outgrowing them and little chance of taking their place in the hierarchy. We therefore predicted that fin coloration should serve as an informative cue of a male's status, reducing aggression from lower ranking males toward YR males. Though there was no a priori expectation that tailspot types would differ in aggression, work on other melanistic pigmentation traits in *Xiphophorus* has demonstrated variation among phenotypes in aggression (REFS). We therefore tested for an effect of tailspot phenotype on aggression, but predicted no directionality of aggression among tailspot types.

2. Methods

2.1. Study system, phenotyping and fish maintenance

Adult *X. variatus* were collected from multiple streams in two drainages using minnow traps (Table 1). A few populations were phenotyped for YR coloration on-site (YR = present and NYR = not present) and fish were returned to their point of capture as a part of other projects. Those collections were used only for YR frequencies. All other fish were transported alive to the Centro de Investigaciones de las Huastecas Aguazarca, where males were digitally photographed and phenotyped for YR coloration. Fin coloration is

easily distinguished by eye on live fish and in digital photographs (Fig. S1). Digital photographs were then used to measure body size of all adult males using ImageJ software. For all analyses herein, body size was measured as the standard length (tip of the snout to the caudal peduncle) and was averaged between the left and right side of each fish to obtain more exact measures. Fish for behavioral assays were maintained in 200-L mixed sex aquaria separated by population, fed three times daily with TetraMin flake food, and maintained at 25 °C on an ambient light cycle (approximately 14L:10D).

2.2. Coloration and body size

While Borowsky (1973) robustly demonstrated that YR males were larger on average when reared in sibling pairs in the laboratory, the social environment (e.g., sex ratios, population densities, etc.) is different in the wild and can vary among populations. We therefore tested body size using a linear mixed model with standard length as the dependent variable to confirm that YR males are larger than NYR males in natural populations as would be predicted from Borowsky (1973). Fin coloration (YR or NYR) and tailspot phenotype, which has known relationships with body size (Borowsky, 1978), and their interaction were included as fixed effects and population was included as a random effect.

2.3. Aggression

Patterns of aggression among males we assayed by observing social interactions in mixed groups. After 1 month of acclimation to laboratory conditions, adult males and females from two populations, Garces and San Pedro, were assigned to 40-L aquaria. Fish from the same population were assigned to tanks at random except for a consistent density (12 fish/tank), sex ratio (1:1), and male color ratio (1 YR: 2 NYR). This color ratio was chosen as it was similar to frequencies observed in the wild. Females were included due to the fact that contests between males often occur over access to females (Morris et al., 1992). Each tank had a small sponge filter providing aeration, two size-matched rocks and two artificial plants in order to provide structure and limit stress. Fish were allowed to acclimate to the new tank environment for 1 h and were then observed for 300 s during which time all aggressive encounters were recorded including the identity of the aggressor and the target of each aggressive behavior. Aggressive encounters included bites, chases, and lateral displays with a raised dorsal fin. We did not distinguish among the type of behavior in our data set. Variation in male morphology including YR coloration, tailspot type, and body size made it easy to distinguish among the six males in the experimental tanks. For our experiments and the figures herein we use the following nomenclature: YR = Y and NYR = N. Aggressive

Table 1
Collecting localities from the present study. Collections with photos that were used to analyze body size are indicated with an asterisk (*).

Population	Date	Stream (drainage)	Coord.	N	YR Freq.
Achiquihuixtla*	2013	Huazalingo (Panuco)	20.987, –98.374	20	0.250
Atlapexco*	2013	Atlapexco (Panuco)	21.014, –98.339	51	0.176
Cacahuatengo*	2013	Grande (Tuxpan)	20.781, –98.032	46	0.283
Garces*	2013	Garces (Panuco)	20.939, –98.281	71	0.155
Guaguaco	2013 (January)	Grande (Tuxpan)	20.784, –98.070	28	0.250
Guaguaco*	2013 (August)			99	0.141
Huextetitla	2013	Xiliatl (Panuco)	21.161, –98.559	16	0.188
Limantitla	2012	Candelaria (Panuco)	21.077, –98.420	31	0.290
Puente Agua Fria	2012	Sasaltitla (Panuco)	20.926, –98.224	10	0.100
San Pedro	2012	Huazalingo (Panuco)	20.950, –98.925	34	0.382
San Pedro*	2013			68	0.176
Vinazco*	2013 (June)	Santa Cruz (Panuco)	21.158, –98.520	30	0.167
Vinazco	2013 (August)			16	0.125

encounters were designated based on the identification (Y or N) of the male initiating the attack as the first letter, and the male it attacked as the second letter. In this way, an encounter initiated by an NYR male toward another NYR male was designated as NN, aggression initiated by an NYR male toward a YR male was NY, and so on.

We first tested the role of body size in dominance and aggressive encounters. A generalized linear model (GzLM) with a binomial distribution and log link was used to model predictors that explained whether or not males exhibited aggressive behavior. Males were coded as a 0 if they never exhibited aggression. Any male that initiated aggression at least once was coded as a 1. The GzLM was constructed with the predictor variables population, replicate tank, coloration, tailspot phenotype and body size as a covariate. Non-significant factors ($P > 0.05$) were removed in a stepwise manner beginning with the largest P -value until the final model contained only significant predictors. Next, an analysis of variance (ANOVA) was used to test the difference in body size of each male pair that engaged in aggressive behavior with the male's identity (as the 'aggressor' or 'target' of the behavior) and encounter type (NN, NY, YN, or YY) as fixed effects and population as a random effect. Based on the results of the ANOVA, post hoc t -tests were then used to evaluate differences between opponent sizes within encounter types. In order to determine whether aggression was more likely between males of a similar size, the absolute difference in body size between each male pair that engaged in aggressive behavior was compared to the mean pairwise difference in body size among all males within the same tank using a paired t -test. Estimates of effect size, Cohen's d , were calculated for t -tests (Cohen, 1988), and all tests were two-tailed. Finally, because the count data contained did not meet the assumption of normality (Shapiro–Wilk $P < 0.05$) and the mean and variance were not equal, a GzLM with a negative binomial distribution was used to evaluate the relationship between the difference in body size of each male pair that engaged in aggressive behavior and the total number of encounters between that pair. A stepwise removal of the same predictors as described above was conducted until only significant predictors remained.

In order to then characterize overall patterns of aggression and determine whether YR males receive less aggression than other males, Pearson's chi-squared tests were first used to test for deviations in the observed and expected frequencies of encounters among males based on the male color frequencies in the tanks. All aggressive encounters were classified according to which male type (NYR = N or YR = Y) initiated the encounter (NN, NY, YN, or YY) and data were combined between populations due to low counts of encounter types within populations (5 of 8 counts were less than 10 observations). Some males engaged in aggressive encounters with the same opponents multiple times within the 300 s observation period. Counts of encounter types were partitioned in two ways. First we summed the total number of encounters of each type for which multiple fights between the same males were included. Second, we summed only the unique encounters for which aggression between any two males was counted only once and subsequent fights between the same males were excluded. Each χ^2 was conducted on both the total fights and unique fights. Lastly, we used GzLMs to evaluate predictor variables for the number of aggressive encounters males initiated toward YR males and the number of aggressive encounters received by males. As above, since the count data did not meet normality and differed in the mean and variance, a negative binomial distribution was specified. Both GzLMs began with the predictor variables population, replicate tank, and coloration with body size as a covariate. A stepwise backwards selection procedure was used as described above until only significant predictors remained in the model. All tests were conducted in SPSS v17.0.

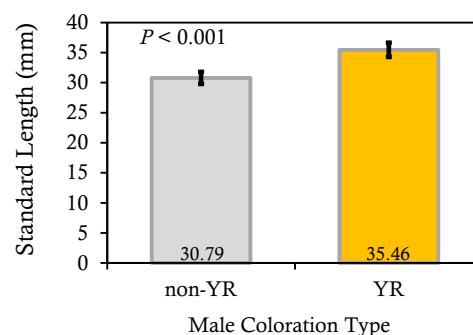


Fig. 1. Results from a linear mixed model showed that YR males were significantly larger than NYR males within populations.

3. Results

3.1. YR frequencies and body size

Populations varied in the frequency of YR males (Table 1). Though only a few populations were collected more than once, it appeared that the frequency of YR males within populations varies temporally. Males with YR coloration were larger than non-YR males from the same collections ($F_{1,368} = 37.817$, $P < 0.001$; Fig. 1). There was no effect of tailspot genotype ($F_{6,30} = 1.320$, $P = 0.279$), the interaction coloration*tailspot genotype ($F_{6,368} = 0.516$, $P = 0.796$), nor the random effect population (Wald $Z = 1.66$, $P = 0.097$).

3.2. Aggression

The GzLM on the tendency to exhibit aggressive behavior revealed that body size was the only significant predictor (Wald $\chi^2 = 7.32$, $df = 1$, $P = 0.007$). Small males were less likely to have exhibited aggression, while aggression was considerably more common with increasing body size. In the ANOVA on difference in opponent body sizes, there was an interaction between whether a male was the aggressor or target and the encounter type ($F_{3,3} = 9.62$, $P = 0.048$; Fig. 2A). Aggressor and opponent body sizes differed in NN ($t = 2.65$, $df = 55$, $P = 0.01$; Cohen's $d = 0.67$) and YN encounters ($t = 4.55$, $df = 37$, $P < 0.001$; Cohen's $d = 1.19$; Fig. 2B), but not in NY ($t = 0.85$, $df = 19$, $P = 0.40$; Cohen's $d = 0.38$) nor YY encounters ($t = 0.27$, $df = 15$, $P = 0.79$; Cohen's $d = 0.14$; Fig. 2B). There was no effect of population on the difference in opponent sizes ($F_{1,1} = 0.039$, $P = 0.883$). The difference in body size between opponents was also significantly smaller than the pairwise difference in size among all males within tanks (Garces: $t = 3.86$, $df = 30$, $P < 0.001$, Cohen's $d = 0.90$; San Pedro: $t = 7.06$, $df = 31$, $P < 0.001$, Cohen's $d = 1.04$). The absolute difference in opponent body size predicted the frequency of aggressive encounters between opponents (Wald $Z = 11.770$, $df = 1$, $P = 0.001$). Aggression was more frequent between male pairs of a similar size.

The frequency of encounters initiated by YR and NYR males did not deviate from expected based on their frequencies in the tanks ($\chi^2 = 1.94$, $P = 0.16$), demonstrating no overall difference in aggression between male types. However, aggressive encounters between YR and NYR males were initiated by NYR males less often than expected, and this was true for unique ($\chi^2 = 7.87$, $P = 0.005$) and total encounters ($\chi^2 = 18.67$, $P < 0.001$). Aggression initiated by YR males exhibited random directionality within unique encounters ($\chi^2 = 1.56$, $P = 0.21$), and a trend of increased aggression toward other YR males in total number of encounters ($\chi^2 = 3.75$, $P = 0.053$). Aggression initiated by NYR males exhibited a trend of reduced aggression toward YR males in unique encounters ($\chi^2 = 2.96$, $P = 0.085$) and random directionality in total encounters ($\chi^2 = 1.17$,

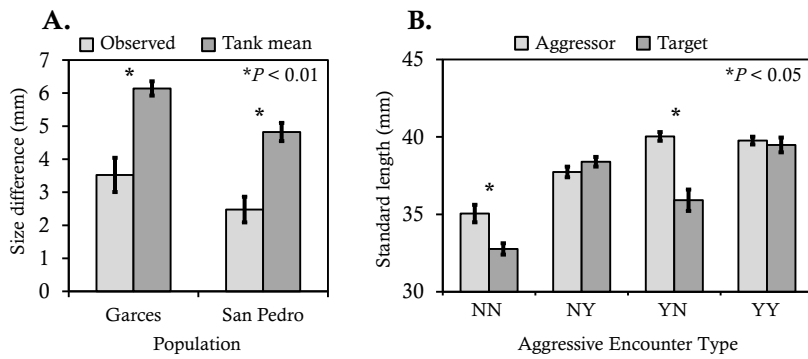


Fig. 2. Males that engaged in aggressive behavior were significantly closer in body size than the tank pairwise mean differences in body size for both populations (A). Males that initiated aggressive encounters were significantly larger in NN and YN encounters, but there was no difference in body size of male pairs in NY and YY encounters (B). Asterisks in panel B indicate significant differences between opponent sizes within encounter types (for both $P < 0.05$, Cohen's $d > 0.6$).

$P = 0.28$). Body size was the only significant predictor retained in both GzLMs for aggressive behavior initiated toward YR males (Wald $\chi^2 = 19.323$, $df = 1$, $P < 0.001$; Fig. 3A) and total aggression received by males (Wald $\chi^2 = 5.612$, $df = 1$, $P = 0.018$; Fig. 3B). Fin coloration was not a significant predictor of whether or not males exhibited aggression toward YR males or in the number of aggressive attacks received from other males.

4. Discussion

Observations across multiple populations demonstrated that YR fin coloration varies in frequency among localities and rarely surpasses thirty percent of the males in any population. Males with YR fin coloration were larger than their counterparts that lacked bright YR fins, suggesting that YR coloration is a reliable cue of a male's relative body size within a population. The dominance hierarchy in male *X. variatus* was sized-based with large males at the top. Since YR males are the largest within populations, YR coloration appears to be a reliable cue of a male's social status. However, data on aggressive encounters suggested that a male's coloration does not affect the amount of aggression they receive and NYR males do not exhibit reduced aggression toward YR males. Males therefore do not appear to assess a potential rival's coloration in the context of the dominance hierarchy.

The frequency of YR males varied across populations and between collections within populations. The social environment has strong control over YR color formation (Borowsky, 1973) such that adult male size distributions, frequencies, and population densities could all play a role in determining the frequency of YR males

within a population. We did not observe any noticeable fading of YR coloration of any males in the laboratory, and this together with the sometimes high frequency of YR males in the wild (e.g., up to 38%) suggests that YR males may retain their coloration even once they are surpassed in size by another male. The laboratory observations that YR coloration is determined by a male's relative size within a group appear to hold true in natural populations. Within populations, males with YR fin coloration were larger than males without YR coloration and only a fraction of the adult male population had YR coloration. Female *Xiphophorus* prefer larger males (MacLaren et al., 2011) and small differences in body size of male *X. variatus* lead to disproportionate benefits to reproductive success (Borowsky, 1981). Together with the importance of body size in agonistic interactions (discussed below), the larger body size of YR males could confer an advantage in terms of sexual selection.

Dominant behavior could have an important effect on male fitness. While *Xiphophorus* are not considered territorial in the classical sense, males often do exhibit some degree of site fidelity, "patrolling" small home ranges and chasing off potential competitors (Morris et al., 1992; Franck and Ribowski 1993; Morris et al., 1995). Aggression toward smaller rivals provides greater access to females and a mating advantage for large males (Morris et al., 1992). Additionally, in the related *X. birchmanni*, dominant males are more likely to gain access to a food resource than subordinates, suggesting a potential advantage to resource acquisition in the wild (Wilson et al., 2013).

Observations of aggressive interactions overwhelmingly indicated that body size is the principal factor underlying patterns of aggression and dominance in *X. variatus*. Body size was the only

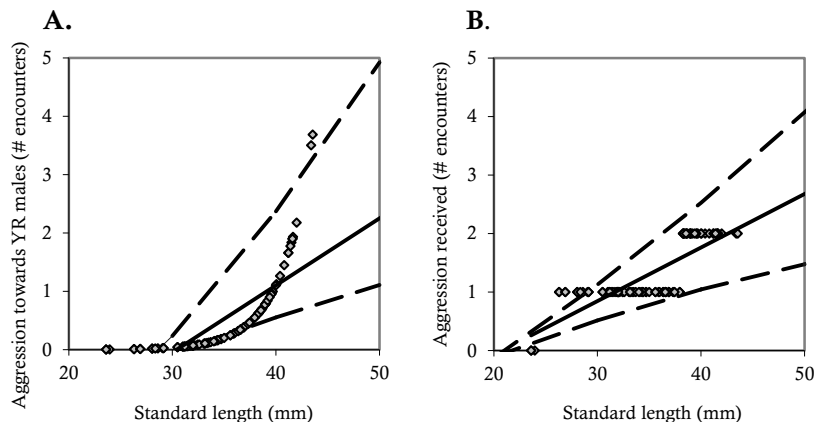


Fig. 3. Standard length was the only significant predictor of aggressive encounters initiated toward YR males (A) and aggression received from other males (B). Each panel shows the predicted means and 95% confidence intervals produced from the two generalized linear models (for both $P < 0.05$).

significant predictor of whether or not males exhibited aggression toward other males, and small males were least likely to exhibit aggression. Our results were consistent with those for *X. hellerii*, demonstrating the importance of body size in establishing stable dominance hierarchies (Franck and Ribowski, 1993). In our study, males that engaged in aggressive encounters did so with males that were significantly closer to their own body size than if aggression was random among males, and the intensity of fighting (the number of repeated fights between two particular males) increased as males became closer in size regardless of the fin color of the males involved. The increased frequency of aggressive encounters between individuals as opponent size decreased is consistent with observations in *X. nigrensis*. In the laboratory *X. nigrensis* males use body position and chasing to block an opponent's access to females. The frequency of this behavior is greater when the size difference between the males is smaller (Morris et al., 1992). In our experiment, males that initiated aggression were also significantly larger than the males which they targeted, indicating a sized-based pecking order in which larger males exert their dominance by chasing, biting, and displaying to males in the same and immediately adjacent social ranks (just above or below). While initiating males were not larger in NY and YY encounters, this makes intuitive sense. The fact that body size did not differ in NY encounters indicates that only the largest NYR males (closest in rank to YR males) exhibited aggression up the dominance hierarchy. Similarly, since YR males are clumped at the upper end of the size distribution within populations, there is reduced size variability among YR males and body size therefore did not differ in YY encounters.

Given the sized-based hierarchy we predicted that YR males, which are the largest within populations, would receive less aggression from other males since rivals can assess their coloration as a signal of dominance. Rival males could prevent potentially costly interactions by avoiding the larger and dominant YR males. The tests of frequencies of encounters appeared to support this as aggression between YR and NYR males was initiated significantly less often by NYR males than expected due to chance alone. There was no evidence to support an overall difference in aggression between YR and NYR males, and only a marginal trend suggesting that YR males tended to exhibit more aggression to other YR males. However, those tests did not account for differences in body size. The generalized linear models revealed that only body size and not fin coloration predicted the number of aggressive behaviors exhibited toward YR males and the number of aggressive attacks received by males. There was no evidence that YR males received less aggression from rivals after controlling for body size.

Due to the importance of body size in aggressive interactions and that YR males are the largest males in natural population, YR coloration appears to be a reliable signal of a male's position at the top of the dominance hierarchy. Despite the reliability of this cue of social status, YR coloration did not alter the aggressive behavior of other males and therefore is likely not assessed by rival males. A variety of other livebearing fishes including other members of the genus *Xiphophorus* exhibit variation in fin coloration, and larger males often tend to have the most conspicuous color (ZWC personal observation). Our study provides the first evidence to demonstrate that this coloration likely has a limited role in intra-sexual signaling, at least in the context of aggressive encounters. However, the benefits of increased access to females (Morris et al., 1992), resources (Wilson et al., 2013) or mate choice for body size (MacLaren et al., 2011) may generate a reproductive or survival advantage for YR

males. Future studies should address these other hypotheses for the evolution of conspicuous fin coloration in *X. variatus* and related species such as the potential reproductive or survival advantages that colorful males may experience.

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