

Carotenoid-based coloration is associated with predation risk, competition, and breeding status in female convict cichlids (*Amatitlania siquia*) under field conditions

C. Anderson · S. C. Wong · A. Fuller · K. Zigelsky ·
R.L. Earley

Received: 5 February 2014 / Accepted: 30 July 2014
© Springer Science+Business Media Dordrecht 2014

Abstract The signaling function of carotenoid-based orange ventral coloration expressed by female convict cichlids (*A. siquia*) is still largely unknown. This field study examined the relationship between breeding female *A. siquia* orange coloration and predation stress, territorial competition, and offspring developmental stage. Female orange coloration decreased significantly with increased behavioral interactions with predators and heterospecific competitors, and the presence of wrigglers, fry, or juveniles was significantly associated with a lack of orange coloration. Multiple alternative explanations for these observations are discussed, including body carotenoid re-allocation and variation in environmental characteristics.

Keywords Convict cichlid · Carotenoids · Brood defense · Reversed sexual dichromatism

Introduction

Carotenoid pigments, which are used by numerous taxa to express colorful visual ornaments, have garnered great interest in signaling theory because animals cannot synthesize them *de novo* and must obtain them from their diet (Olson and Owens 1998). Expression of

carotenoid-based color signals might therefore be interpreted by conspecifics as an indication that an individual's diet is of high quality. However, carotenoids have many physiological uses beyond being allocated to sexual signals. Aquaculture research has repeatedly demonstrated that carotenoid supplementation is an effective method of increasing growth rates in adult fish (Güroy et al. 2012; Sheikhzadeh 2013; Teimouri et al. 2013). Carotenoids also contribute to aspects of reproduction such as egg production and hatching rates (Güroy et al. 2012) and embryonic development (Levi et al. 2011). The relationship of carotenoids with immune function is a particularly appealing topic because of its potential application to aquaculture and conservation issues. For example, Amar et al. (2012) found that synthetic astaxanthin supplementation significantly reduced mortality from a viral pathogen challenge in rainbow trout. Increased dietary β -carotene enhances lymphocyte proliferation (Tachibana et al. 1997), indicating a pathway by which carotenoids may directly bolster the immune response. Dietary carotenoids also may improve immune function by serving as antioxidants. Carotenoid supplementation experiments have demonstrated that multiple indices of oxidative stress are inversely correlated with dietary carotenoid levels (Wang et al. 2006; Pan et al. 2011). Studies of fish immune response to environmental pollutants also have indicated that carotenoids may reduce oxidative stress (Elseady and Zahran 2013) or protect against oxidative damage (Pereira et al. 2011).

Because animals derive carotenoids solely from the diet, a low-quality diet might result in an animal lacking

C. Anderson · S. C. Wong · A. Fuller · K. Zigelsky ·
R. Earley (✉)
Department of Biological Sciences, University of Alabama,
300 Hackberry Lane, Box 870344, 35487 Tuscaloosa, AL,
USA
e-mail: rlearley@as.ua.edu

the body carotenoid levels necessary to satisfy all of the competing uses of carotenoids simultaneously. In a carotenoid-limited situation, it is hypothesized that a trade-off would occur in which allocation of carotenoids to one physiological mechanism would reduce allocation to other mechanisms, e.g. reducing skin carotenoid pigmentation in order to support the immune response. The potential trade-off between exhibiting color and coping with various stressors suggests that only high-quality individuals have sufficient body carotenoids to express intense coloration and thus honestly signal their quality (Lozano 1994). The carotenoid trade-off hypothesis has been tested in birds such as American goldfinches (Rosenthal et al. 2012) and Eurasian kestrels (Casagrande et al. 2011) and fishes such as Midas cichlids (Lin et al. 2010), fighting fish (Clotfelter et al. 2007), and guppies (Grether et al. 2004). These laboratory studies have demonstrated trade-offs in some species but not in others. Lin et al. (2010) conducted a laboratory experiment that demonstrated a lack of trade-offs in Midas cichlids even with a carotenoid-limited diet. Studies of carotenoid limitation under controlled conditions have provided a framework for understanding the consequences of trade-offs, but few studies have examined those consequences in naturally occurring animal populations.

The convict cichlid *Amatitlania siquia* (Schmitter-Soto 2007) presents an unusual opportunity to investigate trade-offs associated with color signals (Brown et al. 2013). Female *A. siquia* exhibit bright orange carotenoid-based ventral coloration that males lack (Fig. 1). The function of this coloration as a sexual signal has not been fully established but there is evidence that females exhibit more intrasexual aggression toward more brightly colored individuals (Beeching et al. 1998). Individuals of this species form breeding pairs and the male and female jointly defend their offspring and nest until the offspring reach the juvenile developmental stage, at which point the breeding pair disbands. During this period of parental defense, breeding pairs must cope with a range of stressors including predation risk and territorial disputes with both conspecifics and heterospecifics (Itzkowitz et al. 2005; Snekser et al. 2011). Increased stress might necessitate re-allocation of integument carotenoids to immune or antioxidant functions according to the carotenoid trade-off hypothesis (Svensson and Wong 2010). Re-allocation of carotenoids also has been linked to breeding status in fish. For example, Garner et al. (2010) found that

rainbow trout re-allocate muscle carotenoids to the skin and eggs as their breeding season progresses. In most species, breeding status is associated with factors such as the expression of parental behaviors and increased predation risk. Thus, numerous, perhaps non-mutually exclusive factors relating to *A. siquia* reproduction and brood defense could result in a reduction or elimination of female orange coloration as those carotenoids are repurposed to help the animal cope with environmental stressors or egg production.

This study aimed to evaluate changes in the coloration status of female *A. siquia* within their natural range in Central America. Lake Xiloá, a volcanic crater lake near the western coast of Nicaragua, contains a large population of *A. siquia* that allows for observation of numerous breeding pairs within a relatively small area. The lake experiences little seasonal temperature variation due to its geographic location and lack of surface inputs other than precipitation. Studies of the temperature characteristics of Lake Xiloá indicate that there is little variation within the top 30 m layer (Barlow et al. 1976) and across the lake surface (Oppenheimer 1997). Like the other cichlid species in Lake Xiloá, *A. siquia* will breed year-round, but the population exhibits breeding peaks coinciding with the middle of the dry season (March–April) and the middle of the rainy season (August–September) (McKaye 1977). Non-breeding individuals cannot be tracked and observed easily at this site because they exhibit no site fidelity and instead move freely among shallow vegetation. In contrast, breeding pairs establish discrete nesting sites, exhibit strong site fidelity, and can be monitored easily. Focusing on breeding pairs enables examination of female color in relation to offspring developmental status instead of the coarser measure of pair-bonded status. Predation and territorial stress both can be measured through observation of breeding pairs' behavioral interactions with conspecifics and heterospecifics. It is hypothesized that female orange coloration would vary concomitantly with offspring developmental stage, predation risk, and the intensity of territorial competition. If female *A. siquia* re-allocate integument carotenoids to egg production and for purposes that mitigate the physiological effects of stress, it is predicted that their orange coloration will decrease around the time of egg deposition. In addition, it is predicted that orange coloration will decrease in response to increasing numbers of interactions with predators and territorial competitors.



Fig. 1 Examples of breeding and non-breeding coloration of female *A. siquia*. The breeding female (*left*) lacks ventral orange coloration and the pair-bonded male can be seen in the background. The non-breeding female (*right*) displays the ventral orange patch. It should be noted that the blue-green coloration of

the dorsal and anal fins displayed by the non-breeding female may be expressed by both sexes of *A. siquia* and thus is not an aspect of the sexual dichromatism in this species. Photograph credit: Mark McKaye

Materials and methods

Behavioral data were collected during March 2010 and from September 2011 through February 2012. Two adjacent sites in Lake Xiloá were used during both observation periods. The 2011 and 2012 data were pooled for the purpose of comparison with the 2010 data. At both sites, two 9 m transects were constructed along each of four depth contours (9, 10.5, 12, and 13.5 m) using forestry flags. The number of breeding pairs of *A. siquia* present at the sites was evaluated weekly by a pair of SCUBA divers swimming along the length of each transect and marking nests with numbered forestry flags. Following these weekly monitoring dives, individual divers conducted behavioral observation dives on randomly chosen breeding pairs; breeding pairs were observed only once. Initial attempts to observe unpaired fish were unsuccessful; after the fish retreated from the approaching observer, it would not return to its initial location, making stationary observation impossible. All observation dives were conducted between 10:00 and 17:00 h and each dive lasted between 60 and 90 min. Because the rate of SCUBA air consumption increases with depth, the number of observations that could be conducted per dive varied based on the depth of the randomly selected breeding pairs. Behavioral observation began with a 2 min settling period where the observer would kneel on the substrate approximately 1 m from the focal pair's nest and note the time,

depth, substrate characteristics, presence or absence of female orange ventral coloration, and developmental stage of any offspring present. Coloration was treated as a binary variable due to the limitations of observing free-swimming fish and because capturing the fish for spectrophotometric quantification of color or measurement of the area of the color patch would require excavating the nest, which would disturb neighboring pairs and increase turbidity to the point where it would prevent effective observation. Offspring were described using three categories: "none/eggs," "wrigglers/fry," and "juveniles." The possible presence of eggs could only be assessed by the observation of guarding behavior generally associated with eggs; direct confirmation of egg presence would have disrupted breeding pair behavior and prevented repeated observations that were conducted for related studies. The "wiggler" stage was defined as recently hatched larval offspring that were not yet free-swimming and moved closely to the substrate, whereas the "fry" stage was defined as free-swimming larval offspring. "Juvenile" offspring were free-swimming and morphologically similar to adult *A. siquia*. The settling period also minimized the effects of observer disturbance on focal pair behavior. After the settling period, the observer would count the focal pair's behavioral interactions for 10 min. Behavioral interactions included any rapid aggressive action directed toward another individual, including chasing, biting, lateral displaying (the fish presenting its side to the intruder

while extending its branchiostegals and unpaired fins) and frontal displaying (the fish facing the intruder while extending its branchiostegals and unpaired fins and flaring its opercular flaps) (adapted from Itzkowitz et al. 2001). Behavioral interactions were categorized by the identity of the target of the interaction: the individual's pair mate, conspecifics other than the pair mate, predators, and any non-predator heterospecifics. Pair mate interactions were defined as any interactions between the two members of a breeding pair. The sole predator species observed in this study was the bigmouth sleeper *Gobiomorus dormitor* (Lacépède, 1800), the primary predator of *A. siquia* in Lake Xiloá. Heterospecifics were other cichlids belonging to the genera *Amphilophus*, *Archocentrus*, *Hypsophrys*, *Parachromis*, and *Thorichthys*.

Results

First, the behavioral data were used to evaluate whether the number of behavioral interactions in each category

varied between years and among stages of offspring development. To achieve normality for parametric analysis, the number of behavioral interactions with predators and with conspecifics was transformed (ANCOVA; Table 1). The number of behavioral interactions with heterospecifics and with pair mates did not meet the assumptions of parametric models, so Kruskal-Wallis tests were used instead (see parametric and nonparametric analyses in Table 1). Pair-bonded *A. siquia* engaged in significantly more behavioral interactions with predators, conspecifics, and heterospecifics but not with their pair mate when they had hatched offspring (wrigglers/fry and juveniles) than when they had no visible eggs or when they displayed behavior indicative of egg presence (Fig. 2, Table 1). The number of behavioral interactions with predators was significantly greater in 2011–2012 than in 2010 while the number of behavioral interactions with conspecifics was significantly greater in 2010 than in 2011–2012 (Table 1); behavioral interactions with heterospecifics and pair mates did not differ significantly between years. There was a significant offspring-stage-by-year effect for predators,

Table 1 Summary of statistical models investigating how interactions between pair-bonded *A. siquia* and other members of the community change between years and across stages of offspring development. Significant effects are shown in bold

Model Effect, transform	F-value, df	P-value	Model Type	Kruskal-Wallis Chi-Square Approx (df)	P-value
Predator, $\ln(x+1)$					
Offspring Stage	60.33 (2, 224)	< 0.0001			
Year	4.819 (1, 224)	0.029			
Offspring Stage x Year	4.426 (2, 224)	0.013			
Depth	5.906 (1, 224)	0.016			
Heterospecific, \sqrt{x}					
Offspring Stage	11.19 (2, 224)	< 0.0001	Offspring Stage, both	26.49 (2)	< 0.0001
Year	0.007 (1, 224)	0.932	Offspring Stage 2010	14.70 (2)	0.0006
Offspring Stage x Year	0.060 (1, 224)	0.942	Offspring Stage 2011	8.238 (2)	0.0163
Depth	0.014 (1, 124)	0.907	Year	3.861 (1)	0.0494
Conspecific, \sqrt{x}					
Offspring Stage	5.578 (2, 224)	0.0043			
Year	34.54 (1, 224)	< 0.0001			
Offspring Stage x Year	13.33 (2, 224)	< 0.0001			
Depth	18.30 (1, 224)	< 0.0001			
Pair mate, $\ln(x+1)$					
Offspring Stage	2.534 (2, 224)	0.082	Offspring Stage, both	4.213 (2)	0.122
Year	0.199 (1, 224)	0.656	Offspring Stage 2010	3.738 (2)	0.154
Offspring Stage x Year	3.890 (2, 224)	0.022	Offspring Stage 2011	8.780 (2)	0.012
Depth	0.415 (1, 224)	0.520	Year	0.105 (1)	0.746

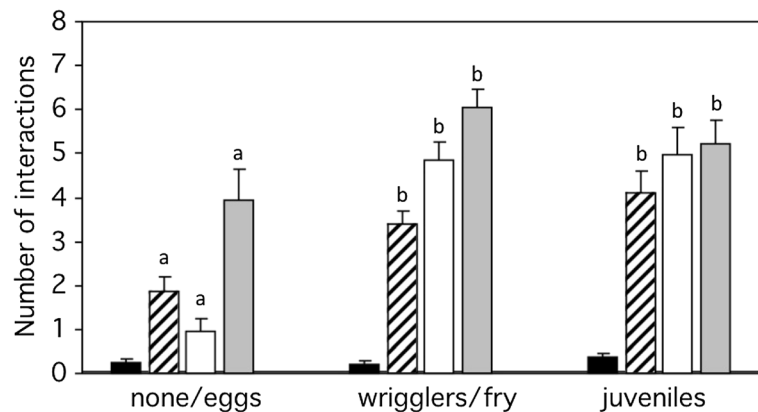


Fig. 2 Changes in the frequency of interaction between pair-bonded *A. siquia* and their pair mate (black bars), heterospecific competitors (hatched bars), predators (white bars), and conspecific intruders (grey bars) across the stages of offspring development. Data are shown as untransformed means \pm SEM. Within each class of interactant (e.g., predator), bars with different letters are

significantly different as determined by Tukey's HSD (for ANCOVA on predators and conspecifics) or Dunn's Multiple Comparisons Test (for Kruskal-Wallis tests on heterospecifics and pair mate). There were no significant changes in the frequency of pair mate interactions across the stages of offspring development, so no letters are shown

conspecifics, and pair mates, but Tukey's HSD revealed trends notably different than those reported in Fig. 2 only for behavioral interactions with conspecifics. In 2010, *A. siquia* interacted with conspecifics to a greater extent than in 2011–2012 but the number of behavioral interactions did not vary across offspring stages, whereas in 2011–2012, *A. siquia* interacted with conspecifics significantly more when defending hatched offspring (Fig. 3). Dunn's multiple comparisons test revealed that, in 2011–2012, interactions with pair mate were more frequent when juveniles were present than with no/possible eggs ($Z = -2.93$, $P = 0.01$; conducted on Kruskal-Wallis test for 'Offspring Stage 2011' effect on interactions with pair mate; Table 1). Regression analyses on the relationship between depth and interactions between predators and conspecifics confirm the results reported in Table 1 indicating that interactions with predators increase as a function of increasing depth ($F_{1, 229} = 4.16$, $P = 0.042$; equation: Interactions with predators (Y) = $0.625 + 0.016 \times \text{Depth}$) and that interactions with conspecifics decrease as a function of increasing depth ($F_{1, 229} = 34.71$, $P < 0.0001$; equation: Interactions with conspecifics (Y) = $3.79 + 0.057 \times \text{Depth}$).

Second, the behavioral data were used to determine whether environmental variables (e.g. depth), predation risk, intensity of competition with heterospecifics or conspecifics, and the frequency of interaction with the pair mate could predict the probability that females possessed orange ventral coloration. The data from

2011–2012 were omitted from these analyses because only one female was observed with orange coloration during that time (Fig. 4). Females were significantly less likely to possess orange coloration when defending hatched offspring (Table 2, Fig. 4). The probability that female *A. siquia* possessed orange coloration also decreased significantly as a continuous function of increased predation risk and increased competition with

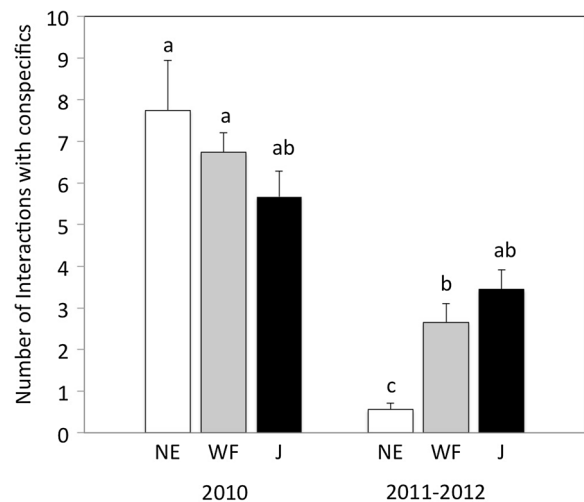
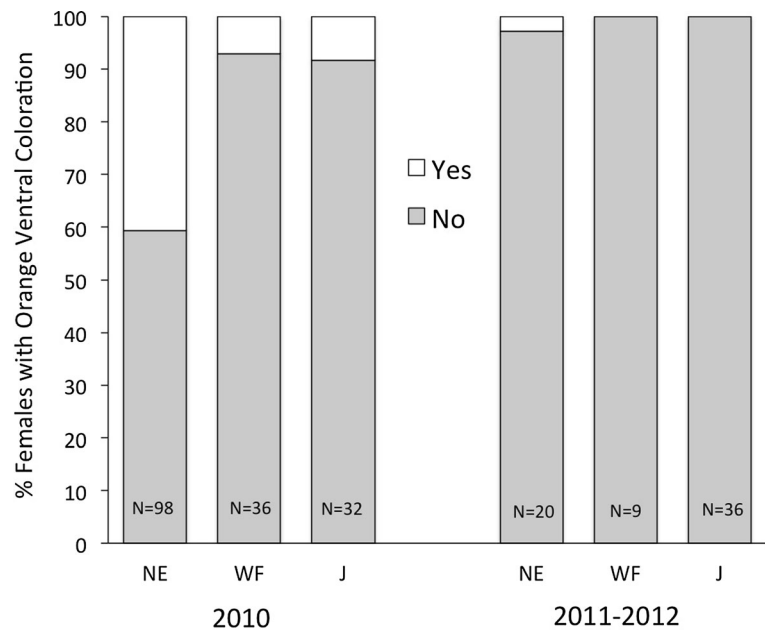


Fig. 3 Annual variation in the relative frequency of interactions between pair-bonded *A. siquia* and conspecific intruders. NE=no eggs/possible eggs; WF=wrigglers/fry; J=juveniles. Bars sharing a letter are not significantly different from one another (Tukey's HSD $P > 0.05$)

Fig. 4 Percentage of female *A. siquia* possessing orange ventral coloration categorized according to breeding status (offspring developmental stage). *NE*=no eggs/possible eggs; *WF*= wrigglers/fry; *J*=juveniles. There was a highly significant difference in 2010 in the percentage of females possessing orange across offspring developmental stages ($\chi^2=19.26$, $df=2$, $P<0.0001$ with $NE < WF = J$); no such difference existed in 2011. See also Table 2



heterospecifics (Table 2). Behavioral interactions with conspecifics or pair mates and depth of the nest site had no significant effects on the probability of females possessing orange coloration (Table 2).

Discussion

These results support the predictions that the probability of female *A. siquia* possessing orange coloration would decrease between egg deposition and hatching and also with increasing numbers of behavioral interactions with

predators and heterospecific competitors. The frequencies of interaction with conspecifics and pair mates were not significant predictors of coloration status. Although conspecific and heterospecific predation on *A. siquia* offspring does occur (e.g., Wisenden and Keenleyside 1992), most aggressive interactions in these two categories are related to territorial competition in Lake Xiloá. The increased aggression toward predators displayed by breeding pairs with hatched offspring (Fig. 2) may result from increased predation risk associated with free-swimming fry and juveniles. By contrast, the increased aggression toward heterospecifics and conspecifics

Table 2 Summary of logistic analyses examining whether the probability that female *A. siquia* possessed orange ventral color varied as a function of interactions with predators, heterospecifics or conspecifics, depth, and offspring developmental stage. Estimates reflect the relationship between increased number of interactions with, for example, predators and the probability that the

females possess orange color. Likelihood ratio (L-R) chi-square is presented as the test statistic. Odds ratios reflect the odds per unit change in the regressor (e.g., number of interactions with a predator). Odds and p-values for offspring status are presented for comparisons of both wrigglers/fry (WF) and juveniles (J) with no eggs/eggs (NE), which was the baseline (see also Fig. 4)

Model Effect	Estimate	L-R χ^2	P-Value	Odds Ratio
Predator	-1.429	21.87	< 0.0001	0.239
Heterospecific	-0.578	5.34	0.021	0.562
Conspecific	-0.002	0.0001	0.992	0.998
Pair mate	+0.997	2.73	0.098	2.711
Depth	-0.011	0.153	0.696	0.989
Offspring Status		19.25	< 0.0001	
WF vs. NE (baseline)	-0.784		< 0.0001	8.895
J vs. NE (baseline)	-0.617		0.0013	7.526

displayed by breeding pairs with hatched offspring (Fig. 2) may result from the breeding pair defending a larger area around hatched offspring (personal observation) or from an increased heterospecific or conspecific intrusion rate on the nest. Future studies of the factors underlying changes in *A. siquia* breeding pair aggression could elucidate the observations in this study.

The mechanisms that explain the observed differences in female *A. siquia* coloration based on breeding status are not well resolved. One potential explanation for these observations is that female *A. siquia* experience increased energy expenditure during territorial brood defense and alter their carotenoid allocation to cope with the associated challenges they face (e.g., stress, immune function, lower body condition). If brood defense requires the maintenance of elevated testosterone and/or 11-ketotestosterone levels, steroid hormones often associated with aggression (e.g. Rodgers et al. 2013), the immunosuppressive effects of this androgenic steroid could be mitigated via carotenoid re-allocation (Folstad and Karter 1992). The putative link between androgen-induced immunosuppression and carotenoid re-allocation has yet to be fully elucidated, but there is accumulating evidence that supports the hypothesis. For example, Dijkstra et al. (2007) found a negative correlation between the size of red nuptial coloration and immune response in a haplochromine cichlid fish, and they also noted a positive correlation between nuptial coloration and 11-ketotestosterone levels. Such a response would not alter an individual's overall body carotenoid levels, but rather change the concentration of carotenoids in different tissues. An alternative hypothesis is that breeding female *A. siquia* display reduced orange coloration because they re-allocate integument carotenoids to developing eggs, which would result in decreased orange coloration following egg deposition as observed in this study. This hypothesis has not been tested extensively, but studies of female Arctic charr (Nordeide et al. 2008) and Chinook salmon (Gardner et al. 2010) found no relationship between skin coloration and egg carotenoid content. Brown et al. (2013) found that carotenoid supplementation increased ovary carotenoid content in female *A. siquia* but did not change carotenoid allocation to the skin. In contrast to the carotenoid allocation predictions associated with immunocompetence, allocation of carotenoids to eggs would result in decreased whole-body carotenoid levels in female *A. siquia* following egg deposition.

Another alternative hypothesis is that environmental factors contribute to the observed decrease in female orange coloration when defending hatched offspring. Behavioral observations conducted during this study indicated that breeding female *A. siquia* do not travel far from the nest until their offspring reach the juvenile stage. If female convict cichlids deplete carotenoid-rich plant matter near the nest during territory establishment, nest building, and egg deposition, then changes in female coloration may reflect decreased carotenoid availability. Although carotenoid limitation-induced trade-offs have been demonstrated in laboratory studies, it is largely unknown whether the carotenoid content of laboratory diets is ecologically relevant. For example, although Lin et al. (2010) used a low-carotenoid diet treatment based on diets used in previous trade-off studies, the average dietary carotenoid intake of wild Midas cichlids has not been evaluated. Likewise, the dietary carotenoid content of *A. siquia* in Lake Xiloá is currently unknown. Reduction of color ornaments in breeding female *A. siquia* might also serve to decrease the conspicuousness of the nest, thereby reducing offspring predation risk from *G. dormitor* or heterospecifics. Conversely, presence of orange coloration might serve as a conspicuous indicator of sexual receptivity, a phenomenon that has been observed in numerous fish species including three-spined stickleback (Sparkes et al. 2013) and two-spotted gobies (Svensson et al. 2006). Future work on these topics should examine how predation pressures change throughout *A. siquia* ontogeny and whether or not male *A. siquia* exhibit mate choice preferences related to female coloration (e.g., Beeching et al. 1998; Santangelo and Itzkowitz 2004).

Morphological characteristics may also contribute to the observed variation in color. Erythrophores (carotenoid-containing chromatophores) in fish integument can rapidly aggregate or disperse pigments to alter color expression, a process that is under neuroendocrine control and that may be induced by certain wavelengths of light (Fujii 2000). However, erythrophores can alter color expression on a much shorter time scale than re-allocation of carotenoids between tissues, so daily observations would not effectively capture this potential source of variation. The findings of this study indicate that breeding status and the intensity of brood defense both are associated with the expression of carotenoid-based coloration in female *A. siquia*, but causality cannot be assigned based on these data. Future field and laboratory studies of carotenoid-based traits should

manipulate these parameters independently to determine which factors best predict flexibility in the expression of carotenoid-based coloration and to elucidate the mechanisms by which trade-offs take place. Few studies have addressed the potential behavioral outcomes of carotenoid trade-offs in a field setting and further work is needed to interpret trade-off theory in a more ecologically relevant context.

Acknowledgments This work was supported by a National Science Foundation award to R. L. Earley (IOS-1051682), a University of Alabama Graduate Council Fellowship to S.C. Wong and a Sigma Xi Grants-in-Aid to S.C. Wong. The authors thank E. Clotfelter and A. Brown for insightful discussions about the data presented herein. In addition, two anonymous reviewers provided constructive comments on the manuscript. M. McKaye provided the *A. siquia* images used in Fig. 1. The authors also are grateful to K. McKaye for the opportunity to use his facilities at Lake Xilao and to M. McKaye, E. Van den Berghe, and L. Canda for logistical support. This research was supported by a permit issued by MARENA to R. L. Earley and was approved by the University of Alabama IACUC (Protocol #10-345).

References

- Amar EC, Viswanath K, Akutsu T, Satoh S, Watanabe T (2012) Resistance of rainbow trout *Oncorhynchus mykiss* to infectious hematopoietic necrosis virus (IHNV) experimental infection following ingestion of natural and synthetic carotenoids. *Aquacult* 330–333:148–155
- Barlow GW, Baylis JR, Roberts D (1976) Chemical Analyses of some Crater Lakes in Relation to Adjacent Lake Nicaragua. Investig of the Ichthyofauna of Nicaraguan Lakes Paper 4. <http://digitalcommons.unl.edu/ichthyonicar/4>
- Beeching SC, Gross SH, Bretz HS, Hariatis E (1998) Sexual dichromatism in convict cichlids: the ethological significance of female ventral coloration. *Anim Behav* 56:1021–1026
- Brown AC, McGraw KJ, Clotfelter ED (2013) Dietary carotenoids increase yellow nonpigment coloration of female convict cichlids (*Amantitlania nigrofasciata*). *Physiol Biochem Zool* 86:312–322
- Casagrande S, Dell’Omo G, Costantini D, Tagliavini J, Groothuis T (2011) Variation of a carotenoid-based trait in relation to oxidative stress and endocrine status during the breeding season in the Eurasian kestrel: a multi-factorial study. *Comp Biochem Physiol A* 160:16–26
- Clotfelter ED, Ardia DR, McGraw KJ (2007) Red fish, blue fish: trade-offs between pigmentation and immunity in *Betta splendens*. *Behav Ecol* 18:1139–1145
- Dijkstra PD, Hekman R, Schulz RW, Groothuis TGG (2007) Social stimulation, nuptial coloration, androgens and immunocompetence in a sexual dimorphic cichlid fish. *Behav Ecol Sociobiol* 61:599–609
- Elseady Y, Zahran E (2013) Ameliorating effect of β -carotene on antioxidant response and hematological parameters of mercuric chloride toxicity in Nile tilapia (*Oreochromis niloticus*). *Fish Physiol Biochem* 39:1031–1041
- Folstad I, Karter AJ (1992) Parasites, bright males, and the immunocompetence handicap. *Am Nat* 139:603–622
- Fujii R (2000) The regulation of motile activity in fish Chromatophores. *Pigment Cell Res* 13:300–319
- Gardner SR, Neff BD, Bernards MA (2010) Dietary carotenoid levels affect carotenoid and retinoid allocation in female Chinook salmon *Oncorhynchus tshawytscha*. *J Fish Biol* 76:1474–1490
- Grether GF, Kasahara S, Kolluru GR, Cooper EL (2004) Sex-specific effects of carotenoid intake on the immunological response to allografts in guppies (*Poecilia reticulata*). *Proc R Soc Lond B* 271:45–49
- Güroy B, Şahin İ, Mantoğlu S, Kayalı S (2012) *Spirulina* as a natural carotenoid source on growth, pigmentation and reproductive performance of yellow tail cichlid *Pseudotropheus acei*. *Aquacult Int* 20:869–878
- Itzkowitz M, Santangelo N, Richter M (2001) Parental division of labour and the shift from minimal to maximal role specializations: an examination using a biparental fish. *Anim Behav* 61:1237–1245
- Itzkowitz M, Santangelo N, Cleveland A, Bockelman A, Richter M (2005) Is the selection of sex-typical parental roles based on an assessment process? A test in the monogamous convict cichlid fish. *Anim Behav* 69:95–105
- Levi L, Ziv V, Admon A, Levavi-Sivan B, Lubzens E (2011) Insight into molecular pathways of retinal metabolism, associated with vitellogenesis in zebrafish. *Am J Physiol Endocrinol Metab* 302:E626–E644
- Lin SM, Nieves-Puigdollér K, Brown AC, McGraw KJ, Clotfelter ED (2010) Testing the carotenoid trade-off hypothesis in the polychromatic Midas cichlid, *Amphilophus citrinellus*. *Physiol Biochem Zool* 83:333–342
- Lozano G (1994) Carotenoids, parasites, and sexual selection. *Oikos* 70:309–311
- McKaye KR (1977) Competition for breeding sites between the cichlid fishes of Lake Jilóá, Nicaragua. *Ecology* 58:291–302
- Nordeide JT, Mohus Å, Nicolaisen O, Volden R, Egeland ES (2008) Offspring or ornaments? Is carotenoid-based ornamentation in female Arctic charr, *Salvelinus alpinus* (L.), condition-dependent and traded off against offspring? *Ecol Freshw Fish* 17:328–339
- Olson VA, Owens IPF (1998) Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol Evol* 13:510–514
- Oppenheimer C (1997) Remote sensing of the colour and temperature of volcanic lakes. *Int J Remote Sens* 18:5–37
- Pan CH, Chien YH, Wang YJ (2011) Antioxidant defense to ammonia stress of characins (*Hyphessobrycon eques* Steindachner) fed diets supplemented with carotenoids. *Aquacult Int* 17:258–266
- Pereira AA, van Hattum B, Brouwer A (2011) Hepatic retinoid levels in seven fish species (teleosts) from a tropical coastal lagoon receiving effluents from iron-ore mining and processing. *Environ Toxicol Chem* 31:408–416
- Rodgers CMC, Neff BD, Knapp R (2013) Androgen-mediated nurturing and aggressive behaviors during paternal care in bluegill sunfish (*Lepomis macrochirus*). *Horm Behav* 63:454–461

- Rosenthal MF, Murphy TG, Darling N, Tarvvin KA (2012) Ornamental bill color rapidly signals changing condition. *J Avian Biol* 43:553–564
- Santangelo N, Itzkowitz M (2004) Sex differences in the mate selection process of the monogamous, Biparental convict cichlid, *Archocentrus nigrofasciatum*. *Behaviour* 141:1041–1059
- Schmitter-Soto JJ (2007). A systematic revision of the genus *Arcocentrus* (Perciformes: Cichlidae), with the description of two new genera and six new species. *Zootaxa* 1603:1–78
- Sheikhzadeh N (2013) Influence of dietary vegetable crops on rainbow trout (*Oncorhynchus mykiss*) immune system and growth performance. *Acta Sci Veterinariae* 41: 1109
- Snekser JL, Santangelo N, Nyby J, Itzkowitz M (2011) Sex differences in biparental care as offspring develop: a field study of convict cichlids (*Amatitlania siquia*). *Environ Biol Fish* 91:15–25
- Sparkes TC, Rush V, Kopp DA, Foster SA (2013) Reproductive success in a natural population of male three-spined stickleback *Gasterosteus aculeatus*: effects of nuptial colour, parasites and body size. *J Fish Biol* 82:1720–1727
- Svensson PA, Wong BBM (2010) Carotenoid-based signals in behavioural ecology: a review. *Behaviour* 148:131–18
- Svensson PA, Pélabon C, Blount JD, Surai PF, Amundsen T (2006) Does female nuptial coloration reflect egg carotenoids and clutch quality in the Two-Spotted Goby (*Gobiussculus flavescens*, Gobiidae)? *Funct Ecol* 20:689–698
- Tachibana K, Yagi M, Hara K, Mishima T, Tsuchimoto M (1997) Effects of feeding of β -carotene-supplemented rotifers on survival and lymphocyte proliferation reaction of fish larvae (Japanese parrotfish (*Oplegnathus fasciatus*) and Spotted parrotfish (*Oplegnathus punctatus*)): preliminary trials. *Hydrobiologia* 358:313–316
- Teimouri M, Amirkolaie AK, Yeganeh S (2013) The effects of *Spirulina platensis* meal as a feed supplement on growth performance and pigmentation of rainbow trout (*Oncorhynchus mykiss*). *Aquacult* 396–399:14–19
- Wang Y, Chien Y, Pan C (2006) Effects of dietary supplementation of carotenoids on survival, growth, pigmentation, and antioxidant capacity of characins, *Hyphessobrycon callistus*. *Aquacult* 261:641–648
- Wisenden BD, Keenleyside MHA (1992) Intraspecific brood adoption in convict cichlids: a mutual benefit. *Behav Ecol Sociobiol* 31:263–269