REVIEW

Behavioral ecology, endocrinology and signal reliability of electric communication

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Summary

The balance between the costs and benefits of conspicuous animal communication signals ensures that signal expression relates to the quality of the bearer. Signal plasticity enables males to enhance conspicuous signals to impress mates and competitors and to reduce signal expression to lower energetic and predation-related signaling costs when competition is low. While signal plasticity may benefit the signaler, it can compromise the reliability of the information conveyed by the signals. In this paper we review the effect of signal plasticity on the reliability of the electrocommunication signal of the gymnotiform fish *Brachyhypopomus gauderio*. We (1) summarize the endocrine regulation of signal plasticity, (2) explore the regulation of signal plasticity in females, (3) examine the information conveyed by the signal, (4) show how that information changes when the signal changes, and (5) consider the energetic strategies used to sustain expensive signaling. The electric organ discharge (EOD) of *B. gauderio* changes in response to social environment on two time scales. Two hormone classes, melanocortins and androgens, underlie the short-term and long-term modulation of signal amplitude and duration observed during social interaction. Population density drives signal amplitude enhancement, unexpectedly improving the reliability with which the signal predicts the signaler's size. The signal's second phase elongation predicts androgen levels and male reproductive condition. Males sustain signal enhancement with dietary intake, but when food is limited, they 'go for broke' and put extra energy into electric signals. Cortisol diminishes EOD parameters, but energy-limited males offset cortisol effects by boosting androgen levels. While physiological constraints are sufficient to maintain signal amplitude reliability, phenotypic integration and signaling costs maintain reliability of signal duration, consistent with theory of honest signaling.

Background

The sensory drive model for evolution of sexually selected display signals views organisms as balancing the benefits of mate attraction against the physiological and environmental costs of signaling (Endler, 1992; Maynard Smith and Harper, 1995; Otte, 1974). The energetic cost of sexual signaling is thought to create an energy imbalance that results in physiological stress that can affect survival and reproduction. However, species and individuals differ in their vulnerability to stress and in the ways they cope with it (Boonstra and McColl, 2000; Breuner et al., 2008; Creel et al., 1996; McEwen, 2002; Romero et al., 2009; Sapolsky, 2000; Wingfield, 2005; Wingfield and Sapolsky, 2003). Species capable of behavioral plasticity might have an advantage that could enable them to reduce reproductive trade-offs by adjusting their behavior to the energy supply and demand of the current environment (Tomkins et al., 2005; West-Eberhard, 1989).

In the context of sexual communication, animals produce signals that can be used by their competitors to learn about the fighting ability of the sender or by potential mates to infer the quality of the signaler (Andersson, 1994). Plastic signals could allow signalers to transiently escape environmental and physiological constraints of signaling and portray themselves as being of better quality than they actually are. Conversely, signal plasticity could help signalers save

on signaling costs by reducing the intensity of otherwise honest signals when return on signal investment is low.

We are interested in understanding the evolution of signal plasticity. Signal plasticity could offer great advantages to the signaler, allowing it to exaggerate its signal to mates and competitors and decrease it in the absence of conspecific receivers or in the presence of predators. However ideal this system from the signaler's standpoint, dishonest signaling is disadvantageous for receivers, who should be selected to ignore such signals. Thus, signal plasticity is not certain to be evolutionarily stable. For signal plasticity to remain evolutionarily stable it must balance the benefits to the signaler and the cost to the receiver. We hypothesized that first, plastic signals must retain at least some information useful to receivers; and second, plasticity should provide an advantage to signalers, such as reduction in signaling costs. To test these hypotheses, we need a species with an easy to measure plastic communication signal, in which we can estimate the type and quality of the information conveyed. In addition, the signal must have measurable costs that are high enough to provide incentive for energy savings. Signals of electric fish meet these criteria handsomely, as we detail below.

We have studied how an electric fish species with a plastic communication signal uses that plasticity to mitigate reproductive trade-offs and we have explored the consequences of signal plasticity

on the reliability of the information conveyed by the signal. In this paper, we (1) discuss the endocrine mechanisms that regulate signal plasticity in males, (2) explore whether those mechanisms are also present in females, (3) examine the information conveyed by the signal, (4) examine how that information changes when the signal changes, and finally (5) consider the energetic strategies used to sustain expensive signaling.

Introduction to the focal taxon, *Brachyhypopomus gauderio*

Electric fish offer special opportunities for the study of signaling behavior. The constant generation of electric signals offers an exceptional opportunity to continuously monitor their behavior in a non-invasive manner. The ease of recording their behavior, the consistent hormonal and behavioral response to changes in the social environment, along with the tight correspondence of behavior to hormone administration, make electric fish unique models to study the interaction between the environment and endocrine state, and their effect on behavior. In particular, electric fish are exceptional model organisms for studying behavioral flexibility linked to the neuroendocrine response.

Neotropical electric fish of the order Gymnotiformes are distributed from northern Argentina to southern Mexico, largely contributing to the ichthyofauna diversity of South America (Albert and Crampton, 2005; Crampton, 1996). Gymnotiforms produce electric organ discharges (EODs) for electrolocation and communication. Their nocturnal habits and the murky waters they inhabit suggest the importance of the EOD for navigation and communication (Moller, 1995). We have studied *Brachyhypopomus gauderio* (Giora and Malabarba, 2009), a marsh dwelling species that inhabits Uruguay, southern Brazil and northern Argentina. Its sister species, *B. pinnicaudatus*, is found in the Amazon, Orinoco and Guyana Shield drainages to the north (Hopkins, 1991). *Brachyhypopomus gauderio* reproduces throughout the austral summer in its natural habitat (Silva et al., 2003). *Brachyhypopomus gauderio* appears to be annual under field conditions, as only immature fish can be found during the austral winter (Silva et al., 2002). The primary sex ratio is unity (Gavassa et al., 2012a), but reproductive males disappear quickly from the population as the breeding season advances, leaving sex ratios of approximately 1:4 (male:female) after 1 month of breeding effort (Gavassa et al., 2012a; Miranda et al., 2008).

While both sexes generate electric signals, the biphasic EOD of *B. gauderio* is sexually dimorphic (Franchina and Stoddard, 1998; Hopkins, 1981; Hopkins et al., 1990). Males generate EODs with higher amplitude and longer duration. At night, males further enhance EOD amplitude and duration in comparison to females (Fig. 1) (Bass and Hopkins, 1983; Franchina et al., 2001; Franchina and Stoddard, 1998; Hagedorn, 1995; Hopkins et al., 1990). The increase in waveform amplitude and duration is accompanied by an increase in energetic cost (Salazar and Stoddard, 2008). Additionally, the elongation of the EOD's second phase shifts the spectrum of the signal towards the lower frequencies, which are detectable by electric fish predators such as catfish. Consequently, the male EOD is energetically more expensive (Salazar and Stoddard, 2008) and is under greater predation risk than the female EOD (Stoddard, 1999; Stoddard, 2002b).

Some electric fish modulate their discharge rates, increasing the rates during courtship or agonistic interactions, and between daytime rest and nighttime activity (Bass and Hopkins, 1983; Dunlap, 2002; Franchina et al., 2001; Franchina and Stoddard, 1998; Hagedorn, 1995; Silva et al., 2007; Zakon et al., 1991). *Brachyhypopomus gauderio* enhances its EOD following a circadian rhythm: reducing rate, amplitude and duration of the EOD during the day and increasing them during nighttime activity (Silva et al., 2013; Franchina et al., 2001; Franchina and Stoddard, 1998; Silva et al., 2007; Stoddard et al., 2007). Both males and females follow this circadian pattern, but it is accentuated in males (Stoddard et al., 2007). The decline of the EOD parameters during the day could be explained as a strategy to avoid predation and reduce signal production cost (Salazar and Stoddard, 2008; Stoddard, 1999; Stoddard, 2002a; Stoddard, 2002b). Electric signals of males are costly handicaps: they are energetically expensive, consuming an average of 22% of the daily energetic budget (compared with 3% for females) (Salazar and Stoddard, 2008).

Males further enhance their EODs at night when attracting mates or deterring competing males. Given a choice, females prefer large males, which produce the most enhanced EODs (Curtis and Stoddard, 2003). Social isolation reduces the male's EOD (Salazar and Stoddard, 2009). The EOD partially recovers minutes after the introduction of a conspecific to the tank, and fully recovers after 3 days (Franchina et al., 2001). The EOD recovers faster with the introduction of a male than a female (Franchina et al., 2001).

Neuroendocrine regulation of the EOD waveform

EOD waveform amplitude and duration are regulated peripherally in the electrocytes, electrically excitable cells of the electric organ (Szabo, 1974). In *B. gauderio* the electric organ extends bilaterally from the back of the pectoral fin to the end of the caudal filament. The near simultaneous electric discharge of the anterior and posterior membranes of electrocytes in *B. gauderio* produces a biphasic waveform that varies in amplitude and duration (Markham and Stoddard, 2005). The biphasic waveform is composed of a head-positive phase, followed by a head-negative phase (Fig. 1). The head-positive phase is generated when the spinal motoneurons, which innervate the posterior face of the electrocytes, trigger an action potential stimulating a current flow towards the head. The head-positive action potential triggers a second wave of action potentials by the anterior face of the electrocytes, creating a tailward current. This alternate flow of current generates the characteristic biphasic *B. gauderio* waveform (Bennett, 1971). Variation in signal amplitude and duration is determined by the kinetics of the Na^+ and K^+ currents and the differential distribution of ion channels across the electrocyte membranes (Ferrari et al., 1995; Few and Zakon, 2001; Few and Zakon, 2007; Schaefer and Zakon, 1996).

Changes in EOD waveform are driven by the slow (days to weeks) action of steroid hormones (Allee et al., 2009; Dunlap and Zakon, 1998; Silva et al., 2002; Stoddard et al., 2006) and by the rapid (minutes to hours) action of peptide hormones (Table 1)
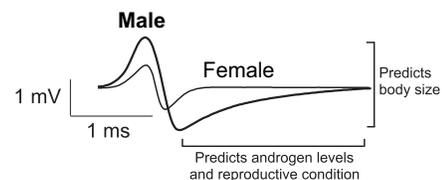

Fig. 1. Male and female electric organ discharge (EOD) in *Brachyhypopomus gauderio*. The male EOD (bold line) is greater in amplitude and longer in duration than the female EOD (thin line). The amplitude of the EOD predicts the body length of the signaler, while the duration of the EOD's second phase predicts androgen levels and reproductive condition.

Table 1. Summary of hormone effects on the electric organ discharge (EOD) of *Brachyhypopomus gauderio*

Hormone	EOD amplitude	EOD duration	Reference
α-MSH/ACTH	↑	↑	Markham and Stoddard, 2005; Goldina et al., 2011
Testosterone	–	↑↑	Goldina et al., 2011
11-KT	↑	↑↑↑	Goldina et al., 2011
Cortisol	↓	↓	Gavassa and Stoddard, 2012

Androgen administration enhances signal parameters over the course of a couple days. Melanocortin (α-MSH/ACTH) injection enhances EOD a few minutes after administration. Cortisol administration decreases both EOD parameters. Arrows indicate direction and intensity of the effect while horizontal bar indicates no effect.

(Markham and Stoddard, 2005; Stoddard et al., 2003). In many electric fish, including African mormyrids and South American gymnotiforms, androgens masculinize the EOD waveform by increasing signal duration and amplitude (Allee et al., 2009; Bass and Hopkins, 1984; Goldina et al., 2011). In *B. gauderio*, the timeline of androgen effects on the EOD is consistent with genomic effects of androgens such as those seen in other electric fish species where androgens initiate transcription of ion channels subunits with altered kinetics of ion channels (Bass and Hopkins, 1983; Bass and Zakon, 2005; Carlson et al., 2000; Liu et al., 2008).

In *B. gauderio* and *B. occidentalis* females, androgen implants increase EOD duration, making it more male-like (Hagedorn and Carr, 1985; Silva et al., 1999). In the field, testosterone and 11-ketotestosterone (11-KT) levels predict EOD duration in males and females (Gavassa et al., 2011). Interestingly, only administration of 11-KT, the dominant androgen produced by teleosts, enhances EOD amplitude, while both testosterone and 11-KT elevate signal duration (Fig. 2, Table 1) (Goldina et al., 2011). This differential regulation of waveform duration and amplitude can serve as a potential mechanism for independent regulation of these signal parameters, enhancing signal plasticity.

Social interaction causes variable effects on *B. gauderio* waveform. In the presence of a social challenger, amplitude and duration of the second phase increase. This increase is accompanied by an increase in androgen and cortisol levels (Gavassa and

Stoddard, 2012; Salazar and Stoddard, 2009). EOD amplitude, cortisol and the variances of circulating 11-KT levels track competition intensity, increasing as the male density in a pool is increased. In contrast, EOD duration and testosterone levels seem to track the presence or absence of competition (Salazar and Stoddard, 2009). In all of the studies on *B. gauderio*, EOD duration is always more responsive to any social stimulus than EOD amplitude (Allee et al., 2009; Franchina et al., 2001; Goldina et al., 2011; Markham and Stoddard, 2005; Salazar and Stoddard, 2009). In *B. gauderio*, 11-KT is significantly more potent than testosterone at enhancing duration, and only 11-KT can elevate signal amplitude (Fig. 2, Table 1) (Goldina et al., 2011). However, 11-KT implants fail to increase EOD amplitude to the level observed during social interaction, suggesting that another hormone might be involved in amplitude modulation during social interactions (Table 1) (Goldina et al., 2011).

Circulating cortisol levels, along with testosterone and 11-KT, increase during social interactions (Gavassa and Stoddard, 2012; Goldina et al., 2011; Salazar and Stoddard, 2009). Interestingly, cortisol is tightly correlated with EOD amplitude when social competition is high [$R^2=0.90$, $P=0.004$ (Salazar and Stoddard, 2009)]. However, cortisol administration reduces EOD amplitude and duration (Fig. 2, Table 1), negating the possibility of cortisol fostering EOD enhancement (Gavassa and Stoddard, 2012). We hypothesize that cortisol release is necessary to sustain the
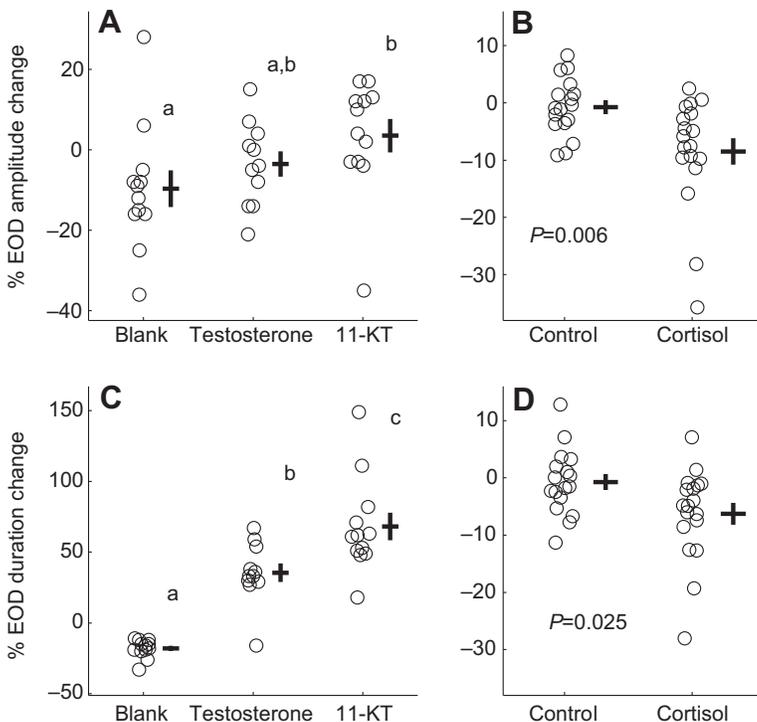

Fig. 2. Effect of androgens and cortisol on nighttime electric organ discharge (EOD) of *Brachyhypopomus gauderio*. 11-Ketotestosterone (11-KT) increases nighttime EOD amplitude (A), while both testosterone and 11-KT increase EOD duration (C) in comparison to blank implants (adapted from Goldina et al., 2011). In contrast, cortisol decreases both EOD amplitude (B) and EOD duration (D) in comparison to a control group treated with vehicle (adapted from Gavassa and Stoddard, 2012). Horizontal lines indicate group means while vertical lines indicate standard error of the mean. Significant differences between groups are indicated by lowercase letters.

energetic demands of costly signaling; however, its detrimental effect on the EOD may be offset by the simultaneous increase in androgens, which enhance EOD waveform.

While androgens affect EOD waveform on a long-term time scale of days to months, the melanocortin peptide hormones adrenocorticotropic hormone (ACTH) and α-melanocyte stimulating hormone (α-MSH), induce rapid changes in the EOD waveform observable within 6 min of injection (Table 1) (Stoddard et al., 2006). In *B. gauderio* melanocortin receptors activate the cAMP/PKA pathway, which increases EOD amplitude and duration in part by differentially modulating the timing of action potentials of the two excitable membranes of the electrocytes (Markham and Stoddard, 2005). Additionally, melanocortins may increase EOD amplitude by promoting ion channel trafficking to the excitable membranes of the electrocyte, as has been shown for *Sternopygus macrurus* (Markham et al., 2009b). Melanocortin-induced waveform changes appear comparable in timing and magnitude to those observed during social interactions, suggesting a mechanism for social regulation of EOD (Franchina et al., 2001; Markham et al., 2009a; Markham and Stoddard, 2005; Stoddard et al., 2006). As predicted, pharmacological block of the melanocortin receptors prevents the rise in EOD amplitude and duration normally induced by social interactions (Markham et al., 2009a).

Androgens enhance the responsiveness of the EOD to melanocortins (Allee et al., 2009; Goldina et al., 2011). The increase in EOD amplitude and duration in response to melanocortin injections is enhanced multiplicatively by 11-KT, while testosterone enhances duration response to melanocortins additively (Goldina et al., 2011). These differences suggest that 11-KT is much more effective modulating EOD waveform, and that amplitude modulation is 11-KT specific.

The complex regulation of EOD plasticity, with androgens regulating long-term changes and melanocortins regulating short-term changes, allows *B. gauderio* to adjust its behavior to multiple time scale changes in the environment. Melanocortins allow the EOD to respond opportunistically to social encounters and aggressive interactions, while androgens allow the response to long-term conditions such as changes in social status, population composition or reproductive season.

Is female EOD plasticity functionally similar to that of males?

Females increase EOD amplitude and duration at night, albeit to a lesser extent than males (Franchina and Stoddard, 1998; Stoddard et al., 2007). Signal plasticity among females was shown to save energy during the day (Salazar and Stoddard, 2008; Stoddard et al., 2007) but social consequences of female signal plasticity were not understood. Recently, we have found that female signals also respond to changes in the social environment in ways similar to males (Gavassa et al., 2012a). Both in field observations and laboratory manipulations, females increase the amplitude of the EOD in response to increases in population density, while the duration of the EOD's second phase increases in response to a greater ratio of females to males. However in the laboratory, second phase duration also increased with population density (Table 2).

Although females produce EODs of lower amplitude and shorter duration than males, the signal parameters greatly overlap between both sexes (Gavassa et al., 2011; Stoddard et al., 2007). Accordingly, circulating androgen levels, which regulate signal parameters, are also higher in males than in females. Males and females overlap widely in their circulating levels of testosterone, but circulating levels of 11-KT are an order of magnitude greater in males than in females (Fig. 3C,D) (Gavassa et al., 2011).

Females and males respond to intrasexual competition in similar ways. Males increase the duration of their EOD second phase and show elevated levels of androgens in response to male–male competition (Table 2) (Franchina et al., 2001; Salazar and Stoddard, 2009). Females in the field increase EOD second phase duration and androgen levels in proportion to intrasexual competition (Table 2) (Gavassa et al., 2012a). However, in the laboratory, female intrasexual competition increases EOD second phase duration without detectable changes in androgen levels (Gavassa et al., 2012a), although experimental increase of androgen levels reliably and consistently increases EOD duration in both sexes (Allee et al., 2009; Gavassa et al., 2011; Goldina et al., 2011; Pouso et al., 2010; Silva et al., 2002).

We found that female *B. gauderio* respond to increased population density by increasing EOD amplitude and respond to same-sex competition by increasing EOD duration. Males and females show similar changes in EOD parameters in relation to social context (Table 2). The increase in EOD amplitude may signal resource holding potential (Gavassa et al., 2012b) or may aid electrolocation by improving the signal-to-noise ratio. Conversely, EOD duration elongation appears to serve as a signal for intrasexual competition in both sexes. The persistence of female signal plasticity despite the cost predation and energetic cost of signal enhancement indicates that some degree of sexual selection acts on female signals (Gavassa et al., 2012a).

Elaborated and conspicuous advertisement traits in females are common in species with reversed sex roles (Colwell and Oring, 1988; Geberzahn et al., 2009; Geberzahn et al., 2010), and in species where females compete for direct benefits offered by a male (Yasukawa and Searcy, 1982; Sandell and Smith, 1997; Langmore, 1998; Sandell, 1998; Langmore et al., 2002). The presence of sexual selection in *B. gauderio* females is not obvious from their mating system. Neither sex provides parental care and males provide no direct benefits to females. A mark-recapture study

Table 2. Summary of social effects on the EOD and on androgen levels in comparison to isolation

Stimulus	EOD amplitude		EOD duration		Androgens	
	Males	Females	Males	Females	Males	Females
Intrasexual competition	−[a]	− laboratory[c]	↑[a]	↑[c]	↑*,[d]	↑ field − laboratory[c]
Population density	↑[b]	↑[c]	↑[a]	↑ laboratory − field[c]	↑*,[d]	− field[3]

Both males and females increase EOD amplitude in response to population density. Both sexes increase EOD duration in response to intrasexual competition and population density. Arrows indicate direction of the effect while horizontal bar indicates no effect.

*Population density and intrasexual competition were manipulated simultaneously.

[a]S.G., unpublished.

[b]Gavassa et al., 2012b.
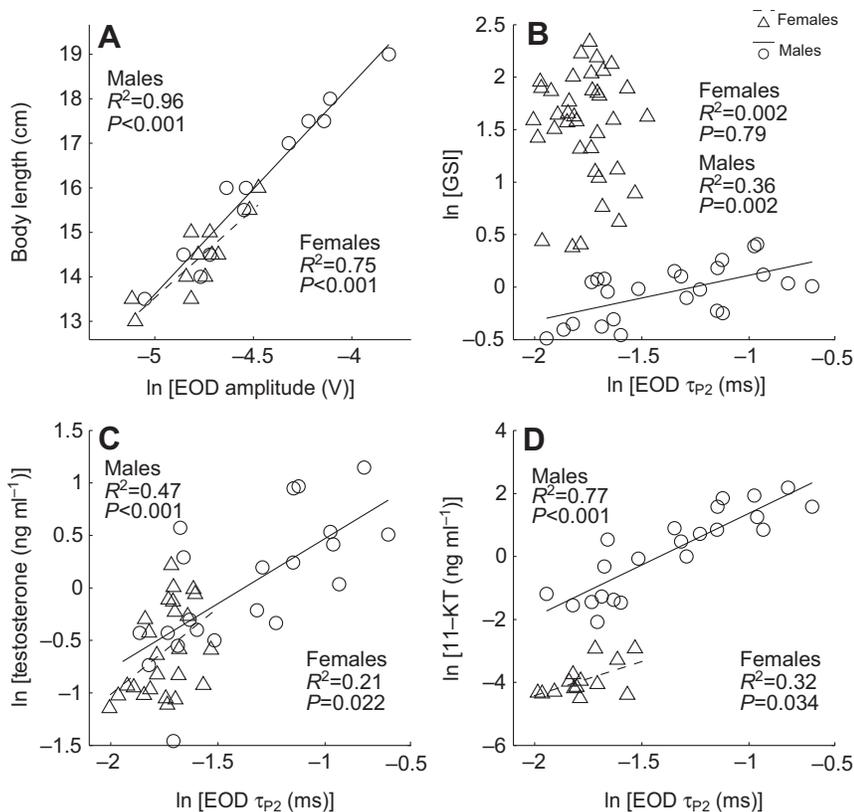
[c]Gavassa et al., 2012a.

[d]Salazar and Stoddard, 2009.

Fig. 3. Information conveyed by the electric organ discharge (EOD) in *Brachyhypopomus gauderio*. (A) The amplitude of the EOD predicts body length in both sexes. Data are shown from the sampling date with the highest population density (adapted from Gavassa et al., 2012b). (B) The duration of the EOD (τ_{P2}) predicts reproductive condition [gonadosomatic index (GSI)] in males. Moreover, EOD duration also predicts circulating levels of testosterone (C) and 11-ketotestosterone (D) in both sexes (adapted from Gavassa et al., 2011).

showed that female *B. gauderio*, in contrast to males, do not hold territories (Miranda et al., 2008). Nonetheless, female *B. gauderio* may compete for access to high quality males, particularly at the beginning of the breeding season, when sexually mature males are scarce (Gavassa et al., 2012a).

Can a hormone-responsive signal convey reliable information about the endocrine state of the signaler?

Sex steroids coordinate reproduction by orchestrating changes in a broad suite of physiological and behavioral traits (Wingfield et al., 1990). Androgens in particular regulate the expression of traits relevant for sexual communication (Moore et al., 2005; Ball et al., 2008; Bass, 2008; Godwin, 2010). Nonetheless, communication signals that are regulated by sex steroids rarely reflect sex steroid levels at the time the signals are produced (Adkins-Regan, 2008), which should make it even less likely that signals could accurately reflect other behaviorally relevant phenotypic traits regulated by sex steroids. Various factors can mask or impair phenotypic integration and ultimately compromise signal reliability, for instance differences in tissue sensitivity, receptor density or binding affinity, the time scale of the response to hormone levels, the plasticity of the signal, or the intervention of other hormonal regulators (Adkins-Regan, 2008; Ball et al., 2008; Kempenaers et al., 2008; Karubian et al., 2011). Despite these theoretical limitations, endogenous androgen levels (testosterone and 11-KT) are tightly linked to the duration of the EOD's second phase (Fig. 3) (Gavassa et al., 2011). Moreover, androgens also link the duration of the EOD's second phase to other androgen-mediated traits such as gonad size in males (Fig. 3B) and estrogen (which is produced by the aromatization of testosterone) in females (Gavassa et al., 2011). These correlations are readily observed in field samples with near simultaneous EOD recording and hormone sampling, but have

proven more difficult to obtain under laboratory conditions where variation in hormone levels and EOD parameters is less extreme.

Information about circulating androgen levels should be relevant to same-sex receivers to assess the motivation state of the signaler to fight. Females implanted with androgens are more likely to attack and bite other females (Allee et al., 2009; P. Perez, S.G. and P.K.S., unpublished), and we infer that intrasexual aggression in both sexes is regulated by androgens. Consequently, conspecifics can gather valuable information about the behavioral and physiological state of the signaler from the duration of its EOD: females benefit by inferring the reproductive state of males, while both sexes benefit from inferring the motivational state of same-sex signalers.

Does EOD modulation degrade its reliability as an honest indicator of body size?

As mentioned earlier, signal plasticity could allow signalers to exaggerate their signals and portray themselves as being of better quality than they are, thereby decreasing the reliability of the signal. To explore hypotheses related to signal reliability, it helps greatly to know what information the signals can convey to receivers. The EOD of *B. gauderio* could serve as an indicator of body length because the amplitude of the signal physically depends on the length of the electric organ, which runs the length of the fish's body (Curtis and Stoddard, 2003; Hopkins, 1999; Hopkins et al., 1990). Moreover, body length is key for mate choice and male–male interactions, as longer males are more attractive to females (Curtis and Stoddard, 2003) and are more likely to win agonistic encounters (Salazar, 2009; Zubizarreta et al., 2012). Therefore, receivers should pay particular attention to any information about body length coded in the signal. Additionally, the energetic and predation costs of generating electric signals make them costly handicaps.
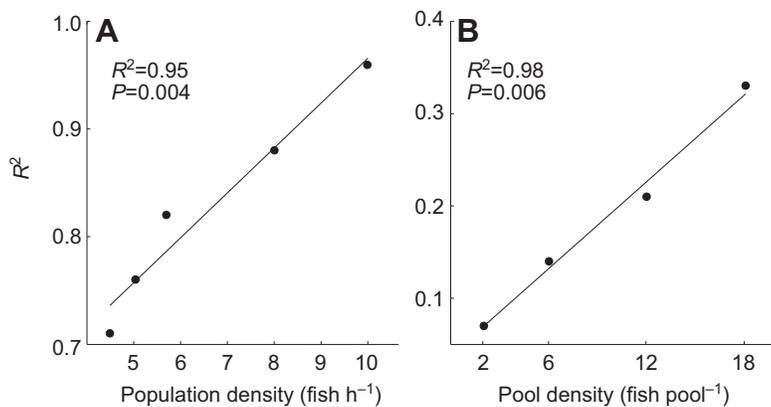
Fig. 4. Signal reliability increases with population density in *Brachyhypopomus gauderio* observed in the field (A) and experimentally manipulated in the laboratory (B). R^2 values were obtained from the linear regression between body length and the natural logarithm of EOD amplitude [reprinted from Animal Behaviour, 83, Gavassa, S., Silva, A. C., Gonzalez, E. and Stoddard, P. K., Signal modulation as a mechanism for handicap disposal, 935-944, Copyright (2012), with permission from Elsevier].

Despite our good understanding of the neuroendocrine mechanisms underlying signal modulation in *B. gauderio*, the effects of this signal plasticity on the reliability of the signal were unknown until recently. Salazar and Stoddard proposed that signal enhancement could provide information about the body condition of the signaler (Salazar and Stoddard, 2008). An alternative hypothesis was that EOD modulation would be used for dishonest communication purposes, to exaggerate the signaler's size. The former hypothesis was supported by a correlation between the residuals of EOD amplitude (obtained from a linear regression between body length and EOD amplitude) and the residuals of body mass (obtained from a linear regression between body length and body mass) (Salazar and Stoddard, 2008). All prior studies had assumed a linear relationship between EOD amplitude and body length (Curtis and Stoddard, 2003; Hopkins et al., 1990; Salazar and Stoddard, 2008). However, residual analyses are very sensitive to the shape of the relationships between the variables (Green, 2001; Jakob et al., 1996) and large sample sizes are needed to distinguish between fits of different regression models. Our extensive field data set allowed us to test the fit of a linear regression between both (1) EOD amplitude and body length, and (2) body length and body mass. We found that neither of these relationships is linear: EOD amplitude and body mass both increase exponentially with body length (Fig. 3A) (Gavassa et al., 2012b). Therefore, the apparent connection between body condition and EOD amplitude reported by Salazar and Stoddard (Salazar and Stoddard, 2008) appears to have been an artifact of a linear model fit to underlying exponential functions. Moreover, we found that in the field, body length determines up to 96% of the variation in EOD amplitude (Fig. 4), leaving no room for another factor to explain significant variation in EOD amplitude. In fact, the 4% of the variation left unexplained corresponds to our measuring error of 0.2 cm for body length measurements (Gavassa et al., 2012b).

We propose that the exponential relationship between body length and EOD amplitude comes from the combination of two linear effects of body size on EOD amplitude. The first is that longer fish have longer electric organs with more electrocytes connected in series (Hopkins, 1999), from which we expected a linear relationship between length and EOD amplitude. Second, a fish generating an electric discharge resembles an electric dipole, and dipole separation is a proportion of the signaler's body length (Stoddard et al., 1999). The strength of the electric field is determined by magnitude of the charges times the distance between the poles. Thus, the two effects of body length on EOD amplitude combine multiplicatively, accounting for the exponential relationship between body length and EOD amplitude.

Despite the improvement in the model of signal production, our field data revealed a great degree of natural variation in the tightness of the correlation between body length and EOD amplitude. Based on the dishonest communication hypothesis, we expected the reliability of the relationship between EOD amplitude and body length to decrease as males enhanced EOD amplitude. However, we found the opposite. The tightest relationship between EOD amplitude and body length occurred at the highest population densities when EOD amplitude is the highest, precisely when males should gain the greatest benefits from exaggerating or bluffing (Fig. 4A). We replicated the field observations in a controlled laboratory experiment and again showed that the relationship between EOD amplitude and body length tightens with social density (Fig. 4B) (Gavassa et al., 2012b). Population density explained 95% of the variation in the strength of the relationship between body length and EOD amplitude in the field and 98% in the laboratory (Fig. 4).

The exponential relationship between body length and EOD amplitude reinforces the honesty of the EOD, because for a male fish to effectively exaggerate his size, he has to increase his EOD amplitude exponentially. The expected EOD amplitude doubles with every 3.3 cm difference in length (Gavassa et al., 2012b). For example, for a 15 cm male to increase his EOD amplitude to equal that of a typical 18 cm male, he would have to double the amplitude of his EOD, an energetically expensive and perhaps physiologically unattainable undertaking.

Our data show that signal enhancement increases the reliability of the information conveyed by the signal, thus refuting our initial hypothesis that signal enhancement degrades the reliability of communication. Conversely, when males reduce their signal parameters, they decrease the reliability of their signals at encoding information about body size, which has the individual benefit of energy savings during periods of low social competition.

Life history and signal plasticity
The life history of *B. gauderio* indicates a high probability of death in adults following the reproductive season, and males seem to perish at high frequency midseason (Silva et al., 2002; Gavassa et al., 2012a; Miranda et al., 2008). This pattern closely resembles a semelparous life history. Based on this life history, we expect *B. gauderio* to resist stress and continue to reproduce even when glucocorticoids levels soar. A previous study in the laboratory found that cortisol levels increased with social competition, and, interestingly, cortisol associated tightly with EOD amplitude [R^2=0.90, P=0.004 (Salazar and Stoddard, 2009)]. The concurrent increase in cortisol levels with signal enhancement plus the
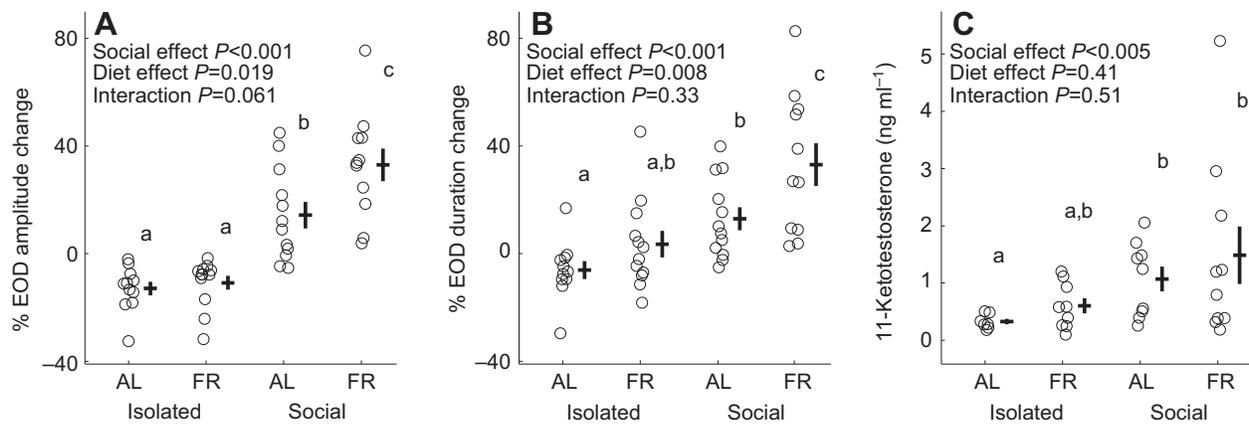
Fig. 5. Effect of food restriction and social treatment on the electric organ discharge (EOD) and circulating levels of 11-ketotestosterone in *Brachyhypopomus gauderio*. Social stimulation increases EOD amplitude (A) and duration (B); however, fish under food restriction (FR) increase both parameters more than fish on an *ad libitum* (AL) diet. Likewise, 11-ketotestosterone levels increase with social stimulation (C) (adapted from Gavassa and Stoddard, 2012).

relationship between cortisol and signal amplitude suggests that the electric signal of *B. gauderio* is resistant to cortisol inhibition. This pattern suggested that cortisol might even enhance EOD amplitude, but we found that experimental cortisol administration diminished EOD waveform parameters (Fig. 2B,C) (Gavassa and Stoddard, 2012). Thus, we do not think the relationship between circulating cortisol levels and EOD amplitude is direct. Instead, it may result from pleiotropic action of the melanocortin ACTH, which releases cortisol from the teleost interrenal tissues and enhances EOD amplitude through direct action on the electrocytes (Markham et al., 2009a). In addition, androgens synergize with melanocortins to enhance their effects on EOD amplitude (Allee et al., 2009; Goldina et al., 2011). Thus, as androgens levels increase during social interaction, the effect of endogenous melanocortins on the amplitude of the EOD increases as well, resulting in the observed correlation between circulating cortisol levels and EOD amplitude. It appears that *B. gauderio* does not resist cortisol inhibition of reproduction-associated behavior (e.g. signal amplitude) as prior correlations in our laboratory had suggested, and as is commonly found in other semelparous species. Rather, the inhibitory effects of cortisol seem to be compensated by melanocortins and androgens; however, this hypothesis still needs to be tested explicitly. Moreover, other stress-resistance mechanisms may exist for more intense stressors.

Brachyhypopomus gauderio has a relatively long breeding season (~3 months) compared with most semelparous species (ranging from 1 to 20 days). If *B. gauderio* gains fitness by surviving the duration of the breeding season, it should conserve energy or acquire extra energy when possible. In support of this hypothesis, when we experimentally limited food availability and increased social competition, *B. gauderio* males paid for their signal enhancements by increasing foraging intensity before compromising their energetic reserves (Gavassa and Stoddard, 2012). However, when we limited available food while intensifying competition, male *B. gauderio* burned through energetic reserves to increase reproductive signaling effort in a manner typical of semelparous species (Fig. 5) (Gavassa and Stoddard, 2012).

From these data we conclude that male *B. gauderio* employ a flexible stress resistance strategy that changes with food availability and the urgency to breed. Social stimulation and food limitation both trigger an investment in reproductive signaling. When possible, male *B. gauderio* increase food intake to fuel signaling, but when food is limited, instead of compromising signaling, they go for broke by consuming body reserves to increase signal output. This flexible strategy puts reproductive output ahead of survival, but extends survival through the breeding season where possible.

Energetics–hormone vocalization model

According to the energetics–hormone vocalization (EHV) model (Emerson, 2001), signaling output should decrease as energy reserves decline. The EHV model proposes that energetically expensive signaling would elevate circulating androgens, as predicted by the challenge hypothesis (Wingfield et al., 1990), but it would also elevate glucocorticoids to fuel signaling. Prolonged signaling should decrease energetic stores until glucocorticoids rise to a level at which they inhibit androgen release. The resultant drop in circulating androgen then causes signaling output to decline (Emerson, 2001; Moore and Jessop, 2003).

Intermediate levels of intra-sexual competition (one male intruder) had no effect rising cortisol levels (Gavassa and Stoddard, 2012). However, higher competition intensity (five additional males) resulted in cortisol increase (Salazar and Stoddard, 2009). This pattern seems to follow the predictions of Emerson's EHV model. However, we believe *B. gauderio* has circumvented the inhibitory regulation of cortisol predicted under the EHV model, allowing concomitant elevation of cortisol and EOD enhancement (Salazar and Stoddard, 2009). We hypothesize that *B. gauderio* prevents cortisol from inhibiting signaling through a compensatory increase in androgen levels and the synergistic effects of androgens on melanocortin-mediated signal enhancement. Although social stimulation increases androgen levels in all socially stimulated fish, we found that the group with social competition and food limitation showed the greatest increase in androgen levels (Fig. 5C) (Gavassa and Stoddard, 2012). Compensatory androgen release has been proposed as a mechanism for stress resistance in other species, such as male olive baboons and male Arctic ground squirrels (Boonstra et al., 2001; Sapolsky, 1982; Wingfield and Sapolsky, 2003).

What we have learned and where to go from there

We found that information about body size, reproductive state and aggressive motivation is encoded in the signal waveform. We also show that the quality of the information improves instead of degrading when males boost their EOD parameters. We have not shown whether potential mates and potential competitors use the

information encoded in the signal to make behavioral decisions. Future studies are needed to show whether receivers can assess the information conveyed by the signal and what degree of discrimination receivers show for multiple signals.

Male and female *B. gauderio* regulate EOD parameters in response to social cues. If we can generalize, EOD amplitude is most sensitive to social density, whereas EOD duration responds to same-sex competition. The latter is particularly relevant because EOD duration tracks androgen levels in both sexes, and androgens increase the likelihood of intrasexual aggression, including in females (Allee et al., 2009).

In conclusion, signal plasticity allows *B. gauderio* to adjust signaling effort according to the demands of the current physical and social environment. Energy saving strategies are favored during periods of low social competition but are abandoned when competition increases. Signal plasticity remains evolutionarily stable as signalers benefit from saving in costly signaling when return is low and receivers benefit from the improvement in the information quality when the signals are enhanced.

List of abbreviations

11-KT	11-ketotestosterone
ACTH	adrenocorticotropic hormone
EHV	energetics–hormone vocalization model
EOD	electric organ discharge
α-MSH	α-melanocyte stimulating hormone

Author contributions

S.G., A.G. and P.K.S. carried out analysis and interpretation of laboratory findings; S.G., A.C.S. and P.K.S. carried out analysis and interpretation of field data. S.G. and A.G. drafted the manuscript; P.K.S., A.C.S., S.G. and A.G. carried out article revisions.

Competing interests

No competing interests declared.

References

Adkins-Regan, E. (2008). Review. Do hormonal control systems produce evolutionary inertia? *Phil. Trans. R. Soc. B* **363**, 1599-1609.

Albert, J. S. and Crampton, W. G. R. (2005). *Diversity and Phylogeny of Neotropical Electric Fishes (Gymnotiformes).* New York, NY: Springer.

Allee, S. J., Markham, M. R. and Stoddard, P. K. (2009). Androgens enhance plasticity of an electric communication signal in female knifefish, Brachyhypopomus pinnicaudatus. *Horm. Behav.* **56**, 264-273.

Andersson, M. (1994). *Sexual Selection.* Princeton, NJ: Princeton University Press.

Ball, G. F., Tlemçani, O. and Balthazart, J. (2008). Individual variation and the endocrine regulation of behaviour and physiology in birds: a cellular/molecular perspective. *Phil. Trans. R. Soc. B* **363**, 1699-1710.

Bass, A. H. (2008). Steroid-dependent plasticity of vocal motor systems: novel insights from teleost fish. *Brain Res. Rev.* **57**, 299-308.

Bass, A. H. and Hopkins, C. D. (1983). Hormonal control of sexual differentiation: changes in electric organ discharge waveform. *Science* **220**, 971-974.

Bass, A. H. and Hopkins, C. D. (1984). Shifts in frequency tuning of electroreceptors in androgen-treated mormyrid fish. *J. Comp. Physiol. A* **155**, 713-724.

Bass, A. H. and Zakon, H. H. (2005). Sonic and electric fish: at the crossroads of neuroethology and behavioral neuroendocrinology. *Horm. Behav.* **48**, 360-372.

Bennett, M. V. L. (1971). Electric organs. In *Fish Physiology* (ed. W. S. Hoar and D. J. Randall), pp. 347-491. London: Academic Press.

Boonstra, R. and McColl, C. J. (2000). Contrasting stress response of male arctic ground squirrels and red squirrels. *J. Exp. Zool.* **286**, 390-404.

Boonstra, R., Hubbs, A. H., Lacey, E. A. and McColl, C. J. (2001). Seasonal changes in glucocorticoid and testosterone concentrations in free-living arctic ground squirrels from the boreal forest of the Yukon. *Can. J. Zool.* **79**, 49-58.

Breuner, C. W., Patterson, S. H. and Hahn, T. P. (2008). In search of relationships between the acute adrenocortical response and fitness. *Gen. Comp. Endocrinol.* **157**, 288-295.

Carlson, B. A., Hopkins, C. D. and Thomas, P. (2000). Androgen correlates of socially induced changes in the electric organ discharge waveform of a mormyrid fish. *Horm. Behav.* **38**, 177-186.

Colwell, M. A. and Oring, L. W. (1988). Sex ratios and intrasexual competition for mates in a sex-role reversed shorebird, Wilson's phalarope (*Phalaropus tricolor*). *Behav. Ecol. Sociobiol.* **22**, 165-173.

Crampton, W. G. R. (1996). Gymnotiform fish: an important component of Amazonian floodplain fish communities. *J. Fish Biol.* **48**, 298-301.

Creel, S., Creel, N. M. and Monfort, S. L. (1996). Social stress and dominance. *Nature* **379**, 212.

Curtis, C. C. and Stoddard, P. K. (2003). Mate preference in female electric fish, *Brachyhypopomus pinnicaudatus. Anim. Behav.* **66**, 329-336.

Dunlap, K. D. (2002). Hormonal and body size correlates of electrocommunication behavior during dyadic interactions in a weakly electric fish, *Apteronotus leptorhynchus. Horm. Behav.* **41**, 187-194.

Dunlap, K. D. and Zakon, H. H. (1998). Behavioral actions of androgens and androgen receptor expression in the electrocommunication system of an electric fish, *Eigenmannia virescens. Horm. Behav.* **34**, 30-38.

Emerson, S. B. (2001). Male advertisement calls: behavioral variation and physiological processes. In *Anuran Communication* (ed. M. J. Ryan), pp. 36-44. Washington, DC: Smithsonian Institution Press.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.* **139**, S125-S153.

Ferrari, M. B., McAnelly, M. L. and Zakon, H. H. (1995). Individual variation in and androgen-modulation of the sodium current in electric organ. *J. Neurosci.* **15**, 4023-4032.

Few, W. P. and Zakon, H. H. (2001). Androgens alter electric organ discharge pulse duration despite stability in electric organ discharge frequency. *Horm. Behav.* **40**, 434-442.

Few, W. P. and Zakon, H. H. (2007). Sex differences in and hormonal regulation of Kv1 potassium channel gene expression in the electric organ: molecular control of a social signal. *Dev. Neurobiol.* **67**, 535-549.

Franchina, C. R. and Stoddard, P. K. (1998). Plasticity of the electric organ discharge waveform of the electric fish *Brachyhypopomus pinnicaudatus.* I. Quantification of day-night changes. *J. Comp. Physiol. A* **183**, 759-768.

Franchina, C. R., Salazar, V. L., Volmar, C. H. and Stoddard, P. K. (2001). Plasticity of the electric organ discharge waveform of male *Brachyhypopomus pinnicaudatus.* II. Social effects. *J. Comp. Physiol. A* **187**, 45-52.

Gavassa, S. and Stoddard, P. K. (2012). Food restriction promotes signaling effort in response to social challenge in a short-lived electric fish. *Horm. Behav.* **62**, 381-388.

Gavassa, S., Silva, A. C. and Stoddard, P. K. (2011). Tight hormonal phenotypic integration ensures honesty of the electric signal of male and female *Brachyhypopomus gauderio. Horm. Behav.* **60**, 420-426.

Gavassa, S., Gonzalez, E., Silva, A. C., Molina, J. and Stoddard, P. (2012a). Social competition masculinizes the electric communication signal of female *Brachyhypopomus gauderio. Behav. Ecol. Sociobiol.* **66**, 1057-1066.

Gavassa, S., Silva, A. C., Gonzalez, E. and Stoddard, P. K. (2012b). Signal modulation as a mechanism for handicap disposal. *Anim. Behav.* **83**, 935-944.

Geberzahn, N., Goymann, W., Muck, C. and Ten Cate, C. (2009). Females alter their song when challenged in a sex-role reversed bird species. *Behav. Ecol. Sociobiol.* **64**, 193-204.

Geberzahn, N., Goymann, W. and ten Cate, C. (2010). Threat signaling in female song-evidence from playbacks in a sex-role reversed bird species. *Behav. Ecol.* **21**, 1147-1155.

Giora, J. and Malabarba, L. R. (2009). *Brachyhypopomus gauderio*, new species, a new example of underestimated species diversity of electric fish in the southern South America (Gymnotiformes: Hypopomidae). *Zootaxa* **2093**, 60-68.

Godwin, J. (2010). Neuroendocrinology of sexual plasticity in teleost fishes. *Front. Neuroendocrinol.* **31**, 203-16.

Goldina, A., Gavassa, S. and Stoddard, P. K. (2011). Testosterone and 11-ketotestosterone have different regulatory effects on electric communication signals of male *Brachyhypopomus gauderio. Horm. Behav.* **60**, 139-147.

Green, A. J. (2001). Mass/length residuals: measures of body condition or generators of spurious results? *Ecology* **82**, 1473-1483.

Hagedorn, M. (1995). The electric fish *Hypopomus occidentalis* can rapidly modulate the amplitude and duration of its electric organ discharges. *Anim. Behav.* **49**, 1409-1413.

Hagedorn, M. and Carr, C. (1985). Single electrocytes produce a sexually dimorphic signal in South American electric fish, *Hypopomus occidentalis* (Gymnotiformes, Hypopomidae). *J. Comp. Physiol.* **156**, 511-523.

Hopkins, C. D. (1981). The neuroethology of electric communication. *Trends Neurosci.* **4**, 4-6.

Hopkins, C. D. (1991). *Hypopomus pinnicaudatus* (Hypopomidae), a new species of gymnotiform fish from French Guiana. *Copeia* **1991**, 151-161.

Hopkins, C. D. (1999). Design features for electric communication. *J. Exp. Biol.* **202**, 1217-1228.

Hopkins, C. D., Comfort, N. C., Bastian, J. and Bass, A. H. (1990). Functional analysis of sexual dimorphism in an electric fish, *Hypopomus pinnicaudatus*, order Gymnotiformes. *Brain Behav. Evol.* **35**, 350-367.

Jakob, E. M., Marshall, S. D. and Uetz, G. W. (1996). Estimating fitness: a comparison of body condition indices. *Oikos* **77**, 61-67.

Karubian, J., Lindsay, W. R., Schwabl, H. and Webster, M. S. (2011). Bill coloration, a flexible signal in a tropical passerine bird, is regulated by social environment and androgens. *Anim. Behav.* **81**, 795-800.

Kempenaers, B., Peters, A. and Foerster, K. (2008). Sources of individual variation in plasma testosterone levels. *Phil. Trans. R. Soc. B* **363**, 1711-1723.

Langmore, N. E. (1998). Functions of duet and solo songs of female birds. *Trends Ecol. Evol.* **13**, 136-140.

Langmore, N. E., Cockrem, J. F. and Candy, E. J. (2002). Competition for male reproductive investment elevates testosterone levels in female dunnocks, Prunella modularis. *Proc. Biol. Sci.* **269**, 2473-2478.

Liu, H., Wu, M. M. and Zakon, H. H. (2008). A novel Na$^+$ channel splice form contributes to the regulation of an androgen-dependent social signal. *J. Neurosci.* **28**, 9173-9182.

Markham, M. R. and Stoddard, P. K. (2005). Adrenocorticotropic hormone enhances the masculinity of an electric communication signal by modulating the waveform and timing of action potentials within individual cells. *J. Neurosci.* **25**, 8746-8754.

Markham, M. R., Allee, S. J., Goldina, A. and Stoddard, P. K. (2009a). Melanocortins regulate the electric waveforms of gymnotiform electric fish. *Horm. Behav.* **55**, 306-313.

Markham, M. R., McAnelly, M. L., Stoddard, P. K. and Zakon, H. H. (2009b). Circadian and social cues regulate ion channel trafficking. *PLoS Biol.* **7**, e1000203.

McEwen, B. S. (2002). Sex, stress and the hippocampus: allostasis, allostatic load and the aging process. *Neurobiol. Aging* **23**, 921-939.

Miranda, M., Silva, A. and Stoddard, P. K. (2008). Use of space is consistent with exploded lek polygyny in the gymnotiform electric fish *Brachyhypopomus pinnicaudatus*. *Environ. Biol. Fishes* **83**, 379-389.

Moller, P. (1995). *Electric Fish: History and Behavior.* New York, NY: Chapman and Hall.

Moore, I. T. and Jessop, T. S. (2003). Stress, reproduction, and adrenocortical modulation in amphibians and reptiles. *Horm. Behav.* **43**, 39-47.

Moore, F. L., Boyd, S. K. and Kelley, D. B. (2005). Historical perspective: hormonal regulation of behaviors in amphibians. *Horm. Behav.* **48**, 373-383.

Otte, D. (1974). Effects and functions in the evolution of signaling systems. *Annu. Rev. Ecol. Syst.* **5**, 385-417.

Pouso, P., Quintana, L., Bolatto, C. and Silva, A. C. (2010). Brain androgen receptor expression correlates with seasonal changes in the behavior of a weakly electric fish, *Brachyhypopomus gauderio*. *Horm. Behav.* **58**, 729-736.

Romero, L. M., Dickens, M. J. and Cyr, N. E. (2009). The reactive scope model – a new model integrating homeostasis, allostasis, and stress. *Horm. Behav.* **55**, 375-389.

Salazar, V. K. (2009). The effect of male-male competition and its underlying regulatory mechanisms on the electric signal of the gymnotiform fish *Brachyhypopomus gauderio*. PhD dissertation, Florida International University, Miami, FL, USA.

Salazar, V. L. and Stoddard, P. K. (2008). Sex differences in energetic costs explain sexual dimorphism in the circadian rhythm modulation of the electrocommunication signal of the gymnotiform fish *Brachyhypopomus pinnicaudatus*. *J. Exp. Biol.* **211**, 1012-1020.

Salazar, V. L. and Stoddard, P. K. (2009). Social competition affects electric signal plasticity and steroid levels in the gymnotiform fish *Brachyhypopomus gauderio*. *Horm. Behav.* **56**, 399-409.

Sandell, M. I. (1998). Female aggression and the maintenance of monogamy: female behaviour predicts male mating status in European starlings. *Proc. R. Soc. B* **265**, 1307-1311.

Sandell, M. I. and Smith, H. G. (1997). Female aggression in the European starling during the breeding season. *Anim. Behav.* **53**, 13-23.

Sapolsky, R. M. (1982). The endocrine stress-response and social status in the wild baboon. *Horm. Behav.* **16**, 279-292.

Sapolsky, R. M. (2000). Stress hormones: good and bad. *Neurobiol. Dis.* **7**, 540-542.

Schaefer, J. and Zakon, H. H. (1996). Opposing actions of androgen and estrogen on in vitro firing frequency of neuronal oscillators in the electromotor system. *J. Neurosci.* **16**, 2860-2868.

Silva, A. C., Quintana, L., Galeano, M., Errandonea, P. and Macadar, O. (1999). Water temperature sensitivity of EOD waveform in *Brachyhypopomus pinnicaudatus*. *J. Comp. Physiol. A* **185**, 187-197.

Silva, A. C., Quintana, L., Ardanaz, J. L. and Macadar, O. (2002). Environmental and hormonal influences upon EOD waveform in gymnotiform pulse fish. *J. Physiol. Paris* **96**, 473-484.

Silva, A. C., Quintana, L., Galeano, M. and Errandonea, P. (2003). Biogeography and breeding in Gymnotiformes from Uruguay. *Environ. Biol. Fishes* **66**, 329-338.

Silva, A. C., Perrone, R. and Macadar, O. (2007). Environmental, seasonal, and social modulations of basal activity in a weakly electric fish. *Physiol. Behav.* **90**, 525-536.

Silva, A. C., Perrone, R., Zubizarreta, L., Batista, G. and Stoddard, P. K. (2013). Neuromodulation of the agonistic behavior in two species of weakly electric fish that display different types of aggression. *J. Exp. Biol.* **216**, 2412-2420.

Smith, M. J. and Harper, D. G. C. (1995). Animal signals: models and terminology. *J. Theor. Biol.* **177**, 305-311.

Stoddard, P. K. (1999). Predation enhances complexity in the evolution of electric fish signals. *Nature* **400**, 254-256.

Stoddard, P. K. (2002a). Electric signals: predation, sex, and environmental constraints. *Adv. Study Behav.* **31**, 201-242.

Stoddard, P. K. (2002b). The evolutionary origins of electric signal complexity. *J. Physiol. Paris* **96**, 485-491.

Stoddard, P. K., Rasnow, B. and Assad, C. (1999). Electric organ discharges of the gymnotiform fishes: III. *Brachyhypopomus*. *J. Comp. Physiol. A* **184**, 609-630.

Stoddard, P. K., Markham, M. R. and Salazar, V. L. (2003). Serotonin modulates the electric waveform of the gymnotiform electric fish *Brachyhypopomus pinnicaudatus*. *J. Exp. Biol.* **206**, 1353-1362.

Stoddard, P. K., Zakon, H. H., Markham, M. R. and McAnelly, L. (2006). Regulation and modulation of electric waveforms in gymnotiform electric fish. *J. Comp. Physiol. A* **192**, 613-624.

Stoddard, P. K., Markham, M. R., Salazar, V. L. and Allee, S. (2007). Circadian rhythms in electric waveform structure and rate in the electric fish *Brachyhypopomus pinnicaudatus*. *Physiol. Behav.* **90**, 11-20.

Szabo, T. (1974). Anatomy of the specialized lateral line organs of electroreception. In *Handbook of Sensory Physiology* (ed. A. Fessard), pp. 13-58. Berlin: Springer-Verlag.

Tomkins, J. L., Kotiaho, J. S. and Lebas, N. R. (2005). Phenotypic plasticity in the developmental integration of morphological trade-offs and secondary sexual trait compensation. *Proc. Biol. Sci.* **272**, 543-551.

West-Eberhard, M. J. (1989). Phenotypic plasticity and the origins of diversity. *Annu. Rev. Ecol. Syst.* **20**, 249-278.

Wingfield, J. C. (2005). The concept of allostasis: Coping with a capricious environment. *J. Mammal.* **86**, 248-254.

Wingfield, J. C. and Sapolsky, R. M. (2003). Reproduction and resistance to stress: when and how. *J. Neuroendocrinol.* **15**, 711-724.

Wingfield, J., Hegner, R. E., Dufty, A. M., Jr and Ball, G. (1990). The 'challenge hypothesis': theoretical implications for patterns of testosterone secretion, mating systems, and breeding strategies. *Am. Nat.* **136**, 829-846.

Yasukawa, K. and Searcy, W. A. (1982). Aggression in female red-winged blackbirds – a strategy to ensure male parental investment. *Behav. Ecol. Sociobiol.* **11**, 13-17.

Zakon, H. H., Mills, A. C. and Ferrari, M. B. (1991). Androgen-dependent modulation of the electrosensory and electromotor systems of a weakly electric fish. *Semin. Neurosci.* **3**, 449-457.

Zubizarreta, L., Perrone, R., Stoddard, P. K., Costa, G. and Silva, A. C. (2012). Differential serotonergic modulation of two types of aggression in weakly electric fish. *Front. Behav. Neurosci.* **6**, 77.