



# Non-sex-biased Dominance in a Sexually Monomorphic Electric Fish: Fight Structure and Submissive Electric Signalling

Gervasio Batista\*, Lucía Zubizarreta\*†, Rossana Perrone\*† & Ana Silva\*‡

\* Unidad Bases Neurales de la Conducta, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay

† Departamento de Neurofisiología, Instituto de Investigaciones Biológicas Clemente Estable, Montevideo, Uruguay

‡ Laboratorio de Neurociencias, Facultad de Ciencias, Universidad de la República, Montevideo, Uruguay

## Correspondence

Ana Silva, Unidad Bases Neurales de la Conducta, Instituto de Investigaciones Biológicas Clemente Estable, Avda. Italia 3318, 11600 Montevideo, Uruguay.  
E-mail: asilva@iibce.edu.uy

Received: October 6, 2011

Initial acceptance: November 17, 2011

Final acceptance: January 2, 2012

(W. Koenig)

doi: 10.1111/j.1439-0310.2012.02022.x

## Abstract

Males and females commonly compete for limited resources. When interaction costs are similar for both sexes and there are no sexual differences in resource value estimation, a non-sex-biased dominance is expected. Moreover, only non-sex-biased assessment of contenders fighting ability (Resource Holding Potential, RHP) should influence contest decisions. To test these predictions, we evaluated non-breeding agonistic intra- and intersexual dyadic interactions in the weakly electric fish, *Gymnotus omarorum*. During the non-breeding season, resource value is not expected to depend on individuals' reproductive status and should thus be equal for males and females. In addition, as *G. omarorum* presents no sexual differences in body size, interaction costs can be considered symmetric between sexes. We confirmed that body size differences, but not individuals' gender, is the best predictor of dominance. We correlated RHP asymmetries with contest duration and evidenced that body size but not sex influences assessment in intrasexual and intersexual encounters. All dyads tested engaged in agonistic interactions ( $N = 33$ ) in which a clear dominant emerged. The analysis of conflict phases evidenced the submissive role of electric displays. Electric organ discharge (EOD) interruptions appear early in the contest as an electric hiding attempt, whereas chirps are post-resolution signals of subordinate status. Interestingly, the decision of interrupting the EOD was also influenced by RHP asymmetries, whereas chirping activity was influenced by the intensity of the attacks received. Our results confirm that body size is the best RHP proxy in non-breeding intra- and intersexual contests of this monomorphic species and demonstrated a sequential pattern of submissive signalling by means of two different electric displays.

## Introduction

Animal contests mediate the acquisition and defence of valuable resources such as mates, territory, shelter and food (King 1973). However, agonistic encounters are also costly in terms of time investment, energetic requirements, predation risk and physical damage. Costs and benefits are evaluated by both contenders to proceed or to give up a fight and thus, maximize

absolute fitness pay-offs. Foundational theoretical studies on animal conflict predict that contest outcome should be determined by the asymmetries between the contenders in this cost-benefit relationship (Maynard Smith & Parker 1976; Parker & Rubenstein 1981). Cost asymmetries arise from differences in fighting ability Resource Holding Potential (RHP) (Maynard Smith 1974) that depends on various traits such as size, weaponry and/or

energetic status. Similarly, resource value might be variable among individuals depending on their reproductive state, residency and/or resource availability.

The fitness consequences of intrasexual competition for common resources are obvious, whereas the evolutionary stability of intersexual aggression is not. However, agonistic behaviour is observed both in intrasexual and in intersexual encounters. In accordance with asymmetric contest models (Maynard Smith & Parker 1976; Parker & Rubenstein 1981), when neither sex asymmetries in RHP nor in resource value are expected between contenders, the contest outcome should be sex-independent. The problem is that factors influencing RHP and the estimation of resource value are usually the subject of intersexual variation. Even in species in which fighting costs are similar for males and females (e.g., monomorphism in size or weaponry), contest outcome has been shown to be determined by an asymmetric resource value for one sex. For example, sex asymmetry in resource value has been proposed to explain the singular female dominance in size-monomorphic Madagascar lemurs (Dunham 2008). Therefore, it has been difficult to test the prediction of sex-independent outcome in intersexual contests so far. One possible way to test this prediction in a natural scenario is to evaluate intersexual territorial interactions during the non-breeding season of a monomorphic species.

Resource Holding Potential assessment is expected to influence fighting decisions and modify contest duration. This assessment may be based only on the information of each contender's own fighting ability (self-assessment) or depend on the evaluation of the opponent's RHP (mutual assessment; Enquist & Leimar 1983; Briffa & Sneddon 2010). Theoretical models of RHP assessment can be tested empirically after identifying specific RHP indicators (size, sex, weaponry) and several factors must be considered to precisely discriminate among different assessment strategies (Taylor & Elwood 2003; Arnott & Elwood 2009a). Aggressive behaviours are commonly present during the breeding season when androgen levels increase to facilitate reproduction (Wingfield et al. 2001; Hau et al. 2004). However, some vertebrate species display territorial behaviours during the non-breeding season (Soma et al. 1999; Jasnow et al. 2002; Hau et al. 2004; Boonstra et al. 2008). Previous studies in several species reported sex-dependent variation in agonistic behaviour that can be the basis of sexual differences in RHP assessment strategies (Draud et al. 2004; Briffa & Dallaway 2007; Arnott & Elwood 2009b). In monomorphic species, in which

sex is not expected to be a RHP proxy, we can predict that information about individuals' sex will not be used for the assessment. Thus, contest duration should not be influenced by the sex of the contenders.

The unusual electric channel of communication makes weakly electric fish valuable model systems for the study of social behaviour. The diverse though simple structure of electric signals contributed to the understanding of different evolutionary processes of signal design from ecological and behavioural levels to their molecular bases (Stoddard 2002; Zakon et al. 2006). In particular, after the foundational work of Black-Cleworth (1970) on the agonistic behaviour of *Gymnotus carapo*, different studies have reported distinctive agonistic electric displays in several species of South American freshwater electric fish (Westby 1975a,b; Hagedorn & Zelick 1989; Hupé et al. 2008; Triefenbach & Zakon 2008; Perrone et al. 2009; Fugère et al. 2011). Among these species, agonistic electric displays can be identified as part of the behavioural repertoire of both dominants and subordinates. Some electric signals, such as sharp rate increases decreases (SIDs in *Gymnotus carapo*, Black-Cleworth 1970), chirps (brief and acute high rate signals) in *Apteronotus leptorhynchus* (Triefenbach & Zakon 2008) and in *Brachyhypopomus pinnicaudatus* (Perrone et al. 2009) have been interpreted as threat signals. On the other hand, the cessation in the emission of electric signals (offs) has been recognized as a submissive behaviour in *G. carapo* (Black-Cleworth 1970; Westby 1975b). The rigorous evaluation of the role of electric signals and their temporal pattern during contest is imperative to fully understand agonistic behaviour in electric fish.

*Gymnotus omarorum* (Richer-de-Forges et al. 2009) is a highly aggressive territorial pulse-type species of weakly electric fish that displays inter- and intrasexual agonistic behaviour across seasons. The absence of sexual dimorphism and the non-seasonality of its aggressive behaviour make this model system especially suitable to test predictions derived from theoretical studies on animal conflicts. With this aim, we focused on dyadic encounters of *G. omarorum* during the non-breeding season. We first tested whether size and sex asymmetries influenced contest outcome and assessment and confirmed that sex did neither affect dominance nor the assessment strategy in this species. We also identified a precise pattern of emission and an unequivocal role of electric signals associated with submission, whose magnitude depended on the levels of overt aggression. Our results confirmed specific predictions of theoretical models on animal conflicts and allowed us to speculate about the evolu-

tionary processes underlying agonistic behaviour in electric fish.

## Materials and Methods

### Animals

We used 66 adults of *Gymnotus omarorum*, formerly *Gymnotus carapo* (Richer-de-Forges et al. 2009), 38 males and 28 females, ranging from 7 to 78.4 g in body weight and 14.5–30 cm in body length. Sex in *G. omarorum* is not externally apparent (neither morphologically nor electrophysiologically) and was identified after the behavioural experiments by gonadal inspection. No sexual dimorphism was found in body weight or in body length (two-sample unpaired *t*-test,  $p = 0.93$ ,  $p = 0.78$ , respectively).

### Fish Collection and Housing

Fish were detected and collected as described elsewhere (Silva et al. 2003) from Laguna del Sauce (34°51'S, 55°07'W, Department of Maldonado, Uruguay). In this austral population of Gymnotiformes from the temperate zone, the breeding season occurs from November to February (Silva et al. 2003). Collections and experiments were performed during the non-breeding season (April–Aug. 2009). Fish were housed in individual compartments in 500-l outdoor tanks for at least 10 days before the behavioural experiments. All environmental variables were kept within the normal range they exhibit in the natural non-breeding habitat (Silva et al. 2003). Water temperature ranged from 8 to 21°C, and temperatures below this range were avoided using plastic covers. Natural photoperiod ranged from around LD10:14–LD11:13. Water conductivity was adjusted and maintained at 150 µS/cm by the addition of deionized water. Aquatic plants covered the surface of the water and provided shelter for the fish. Fish were fed with *Tubifex tubifex ad libitum*.

### Laboratory Settings

Fish were placed in an experimental setup that allowed simultaneous video and electric recordings as described elsewhere (Silva et al. 2007). The experimental tanks (55 × 40 × 25 cm) were divided into two equivalent compartments by a removable glass gate. These compartments allowed electrical sensing but prevented physical aggression during 2 h prior to the experiment. The day–night cycle and the physicochemical parameters (water temperature, conductiv-

ity and pH) of the outdoor housing tanks were reproduced in the indoor aquaria. All the experiments were performed in total darkness illuminated by an array of infrared LEDs (L-53F3BT; Fablet & Bertoni Electronics, Montevideo, Uruguay) located above the tank. An infrared-sensitive video camera (SONY CCD-Iris, Montevideo, Uruguay) was focused upon the bottom of the tank. The electric signals of freely moving fish were detected by two pairs of fixed electrodes, connected to two high-input impedance amplifiers (FLA-01; Cygnus Technologies Inc., Delaware Water Gap, PA, USA). Images and electric signals were captured by a video card (Pinnacle Systems, PCTV-HD pro stick) and stored in the computer for further analysis.

### Behavioural Protocol

We evaluated the agonistic behaviour of *Gymnotus omarorum* in dyadic encounters ( $N = 33$ ). To explore the influence of asymmetries (body weight differences, body length differences and sex) on contest outcome, we used a plain arena and assumed that territory was the only limited resource individuals competed for. We provided equal resources (territory and residency) for both contestants by placing fish in equally sized compartments. To give symmetrical resource value to males and females, we carried out our experiments during the non-breeding season. As experience can modify the self-perceived fighting ability in future encounters (Hsu et al. 2006), we housed fish individually to ensure that the fish had no agonistic experience during 10 days preceding the test. Fighting costs obviously depend on the magnitude of size asymmetries, and extreme asymmetries may even distort the integration of potential costs and benefits of the contest (Hsu et al. 2006). We thus selected adults that showed a range of intra-dyadic size differences below 50% (weight differences: from 0.2% to 50%, length differences: from 0% to 23.3%). The removable glass gate was raised 10 min after sunset, and fish were separated 10 min following conflict resolution. Dominant and subordinate fish were then removed from the tank, euthanized with an overdose of 2-phenoxyethanol (0.1%), and their sex was identified by visual gonadal inspection. Of the 33 dyads, 10 were female–female, 15 were male–male and 8 were male–female.

### Behavioural Data Processing

#### *Locomotor displays*

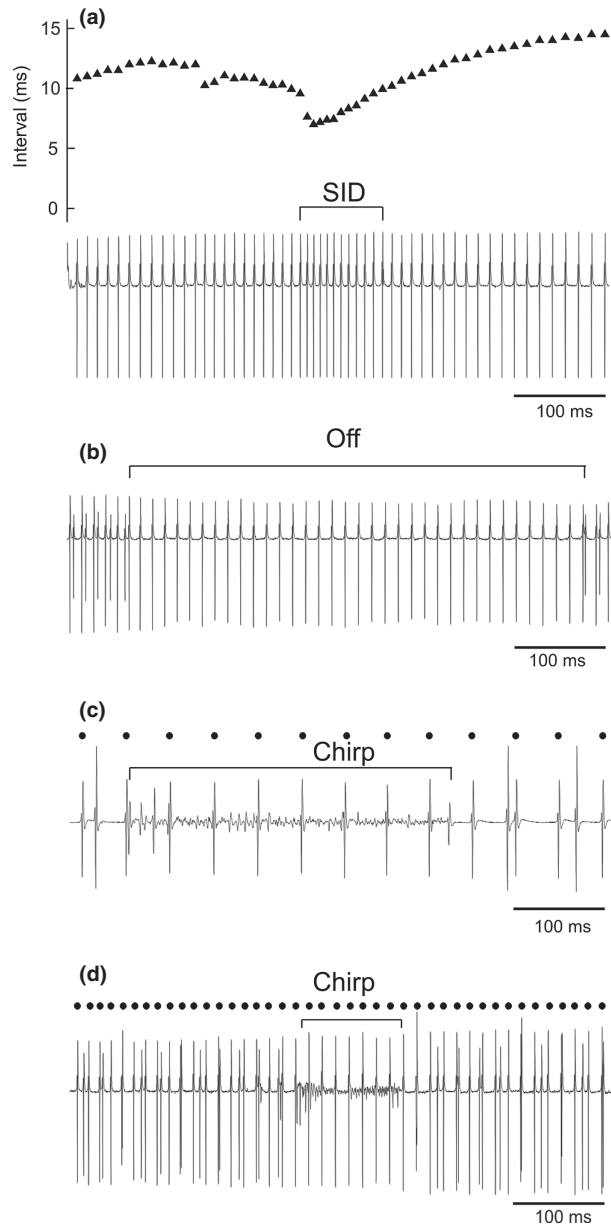
During agonistic encounters, fish exhibited a number of locomotor displays previously described in

*Gymnotus carapo* by Black-Cleworth (1970) and Westby (1975a,b). Although *G. omarorum* displayed all the motor patterns identified in these pioneer studies in the same genus, we focused on attacks including bites, nudges, nips and jaw locks of former descriptions. We analysed video recordings of agonistic encounters to establish the dynamics of the contest: (1) pre-contest: from gate removal (time 0) to the occurrence of the first attack; (2) contest: from the occurrence of the first attack to conflict resolution (resolution time); and (3) post-resolution: 10 min after conflict resolution (Fig. 2).

Conflict resolution was established as the moment we observed the third consecutive retreat of one fish without attacking back. This criterion unambiguously defined subordination status; fish fulfilling this requirement were never observed to change their status in the following 10 min of interaction. We calculated dominant attack rate dividing the number of attacks by contest duration time in seconds. To emphasize the relationship between locomotor and electric displays, we split the aggressive acts observed during the contest into three levels based on dominant attack rate: low ( $<0.2$ ), medium ( $\geq 0.2, <0.4$ ) and high ( $\geq 0.4, <0.6$ ). Because only 2 dyads exhibited high levels of dominant attack rate, we only tested statistical comparisons between low and medium levels of aggression (Fig. 4).

*Electric signals*

Simultaneous electric and video recordings allowed us to continuously record the electric organ discharge (EOD) of both fish regardless of their position, and to distinguish which fish was the sender of each EOD. Electric signals were digitized, and the EOD intervals and amplitude determined using Clampfit (Molecular Devices Corporation, Sunnyvale, CA, USA). Distinctive electromotor displays were observed during agonistic encounters: SIDs, offs and chirps (Fig. 1). Following Perrone et al. (2009), we characterized offs and chirps by measuring the following parameters: (1) off duration: from the last basal EOD before the interruption to the first normal basal EOD after the interruption; (2) chirp duration: from the first intra-chirp EOD to the next basal EOD; (3) intra-chirp EOD amplitude: as the percentage of EOD basal amplitude measured in the intra-chirp EOD localized at 50% of chirp duration; and (4) intra-chirp EOD interval: as percentage of the EOD basal interval measured between two intra-chirp EODs localized at 50% of chirp duration (Table 1).



**Fig. 1:** Social electric signals recorded during agonistic interactions. (a) Sharp increase decrease (SID) produced by the dominant fish during an interruption of the subordinate fish. Only one individual's electric organ discharge (EOD) is observed in the lower trace because the other fish had turned off its discharge. Filled triangles show the interval time plot of the trace below. (b) Interruption of the EOD produced by the subordinate fish (Off). The EOD of smaller amplitude was turned off for approximately 500 ms. (c, d) Two examples of chirps: brief increases in rate of EODs of reduced amplitude emitted by the subordinate fish while the dominant fish remained discharging regularly (dots).

To explore the role of the electric displays in the agonistic behaviour of *G. omarorum*, we calculated first off and first chirp latency as the time to first off/chirp minus the time of occurrence of the first



**Table 1:** Characterization of offs and chirps

	Median	IQR
Offs		
Duration (ms)	1370	6450
Chirps		
Duration (ms)	403.3	589.0
Intra-chirp amplitude (%)	6.7	6.5
Intra-chirp interval (%)	6.7	4.1

Median and interquartile range (IQR) of the selected parameters are shown (See Materials and methods for definition of parameters). N offs = 209, N chirps = 193.

attack. We calculated off and chirp rate (separately for contest and post-resolution phases) dividing the number of offs and chirps produced in each phase, respectively, by the corresponding phase duration in seconds, and we measured the duration of the interrupted time as the time of EOD cessation in percentages of contest and post-resolution durations, respectively.

**Statistics**

*Contest outcome*

To determine the factors (dyad asymmetries) that influence the outcome of an agonistic encounter, we ran a binomial regression using a logit model in which the dependent variable (contest outcome) was 1 for the dominant and 0 for the subordinate. We tested as independent variables: weight difference = (body weight focal fish – body weight contender fish)/body weight focal fish; length difference = (body length focal fish – body length contender fish)/body length focal fish; sex of the individuals; and dyad sex (intra-sexual or intersexual) in all the dyadic agonistic encounters (N = 33 dyads and N = 66 individuals). Therefore, the model can be expressed by the following equation in which  $\Omega$  adopts a logit function, and  $\varepsilon$  an error  $N(0, \sigma^2)$ :

Contest outcome =  $\Omega (\beta_1 \times \text{weight difference}, \beta_2 \times \text{length difference}, \beta_3 \times \text{sex}, \beta_4 \times \text{dyad sex} + \varepsilon)$ . Based on this equation, the independent variables that influence contest outcome are those whose  $\beta$  are significantly different from 0 when tested using a *t*-test. As this model requires the observations to be independent between individuals, we randomly selected one individual of each dyad as focal fish and ran the model for this sample (Wooldridge 2002). To avoid sampling bias and guarantee robustness of the results, we replicated the model in 10 different samples of N = 33 focal individuals and present average values of coefficients and parameters in Table 2.

**Table 2:** Binomial regression using logit model to test the influence of weight difference, length difference, individual sex and dyad sex upon contest outcome

Factors	Contest outcome (N = 33, R <sup>2</sup> = 0.2988, Predictive power: 0.806)			
	$\beta$	p	Min	Max
Weight difference	9.2911	0.019*	1.60	16.982
Length difference	-1.5227	0.6926	-10.692	7.6464
Sex	-0.1064	0.49	-1.9664	1.7535
Dyad sex	-0.3863	0.5177	-2.5755	1.8029
Constant term	0.5882	0.3535	-1.5531	2.7296

The values for the regression coefficients ( $\beta$ ) are averages of 10 random samples (see Materials and methods).

\* $\beta$  significantly different from 0. Note that the range between minimum and maximal values of  $\beta$  includes 0 for all the independent variables except weight difference

*Assessment strategies*

To test the factors that influence assessment, we employed multiple linear regressions between the asymmetries in weight [weight difference = (body weight dominant fish – body weight subordinate fish)/body weight dominant fish], dyad sex and the subordinate’s sex, as independent variables, and contest duration as the dependent variable (N = 32, Table 3). Using the combination of the variables sex and subordinate sex allowed us to evaluate the three possible combinations of dyad sex (male–male, male–female and female–female). To distinguish between self- and mutual assessment strategies (which both show an inverse correlation between size difference and contest duration), it is necessary to test the influence of the absolute RHP of dominants and subordinates on contest duration (Taylor & Elwood 2003; Arnott & Elwood 2009a). We employed two multiple linear regressions with absolute weight (dominant and subordinate, respectively), dyad sex and subordinate’s sex as independent variables; and contest duration as dependent variable (N = 32).

**Table 3:** Results of multiple linear regression analysis: effect of weight difference, sex asymmetry and subordinate sex on contest duration

Variable	Contest duration (F <sub>3,28</sub> = 3.11, *p = 0.04)		
	b	t	p
Weight difference	-7.1	-2.2	0.03*
Sex difference	-38	-0.61	0.54
Subordinate’s sex	15	0.22	0.83
Constant term	316	5.98	0.0001*

*Electric displays*

Electrical behavioural data were analysed using non-parametric statistical tests: Wilcoxon matched-pairs test for paired variables in the same fish and Mann-Whitney *U*-test for independent variables using sets of data from different fish. For the same reason, data are expressed as median and interquartile range (IQR) throughout. To test the submissive role of electric displays, we compared the number of offs and chirps emitted by dominants and subordinates 3–5 min after resolution. To test the timing profile of the emission of electric displays with respect to conflict resolution, we used chi-square tests ( $\chi^2$ ). Chirp parameters (chirp duration, intra-chirp EOD amplitude and intra-chirp EOD interval) did not show obvious differences, and it was not possible to visually discriminate them into groups; thus, they were further analysed by PCA and k-means cluster analysis, as described in Perrone et al. (2009). These parameters were also tested between males' chirps (N = 108) and females' chirps (N = 85) by two independent samples *t*-tests.

To evaluate the effects of size asymmetry on electric displays (first off and chirp latency, post-resolution off and chirp rates, and post-resolution interrupted time), we ran linear regressions using weight difference as independent variable (Table 4, conflict duration N = 25, first off latency N = 25, and first chirp latency N = 21).

**Ethical Note**

To achieve reliable and repeatable behaviours, our collection, transportation, housing and recording conditions were adjusted to minimize stress on the animals. To reduce stress and injuries during agonistic encounters that are inevitably harmful, we terminated behavioural experiments 10 min after conflict resolution. Also, we refined our statistical strategies to allow us conclusive interpretations using a minimum number of fish. All research procedures complied with ASAP/ABS *Guidelines for the Use of Animals in Research* and were approved by the Universidad de la República Institutional Ethical Committee (Comisión Bioética, Instituto Clemente Estable, MEC, 07-28-2008).

**Results**

**Fight Structure and the Emission of Electric Signals**

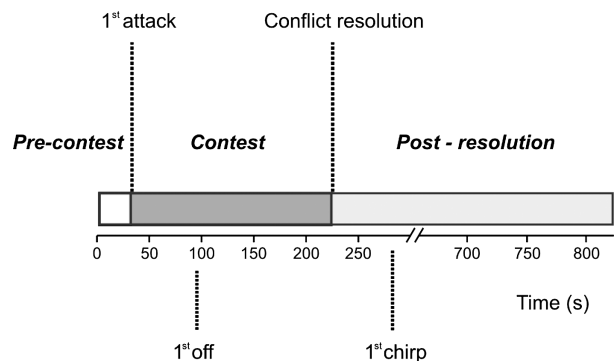
After gate removal, all 33 dyads engaged in agonistic interactions that ended in the establishment of stable

**Table 4:** Results of simple linear regression analysis: effect of weight difference on contest duration, first off latency and first chirp latency

Variable	Contest duration		
	$(F_{1,30} = 5.72, R^2 = 0.21, *p = 0.02)$		
	<i>b</i>	<i>t</i>	<i>p</i>
Weight difference	-7.24	-2.39	0.02*
Constant term	296	4.73	0.0001*
	First Off latency		
	$(F_{1,23} = 6.82, R^2 = 0.22, *p = 0.02)$		
	<i>b</i>	<i>t</i>	<i>p</i>
Weight difference	-10	-2.61	0.02*
Constant term	309	3.44	0.002*
	First Chirp latency		
	$(F_{1,19} = 3.73, R^2 = 0.25, *p = 0.07)$		
	<i>b</i>	<i>t</i>	<i>p</i>
Weight difference	-13.7	-1.93	0.07
Constant term	506	3.78	0.01*

dominance relationships. All interactions followed the same 3 phases (Fig. 2): (1) a short pre-contest phase (first attack latency = 30.5 (36)s, median (IQR), N = 33); (2) a contest phase (contest duration, 147 (184)s, N = 33) characterized by overt aggressive behaviours; and (3) a post-resolution phase in which the reversion of dominance relationship was never observed.

Agonistic behaviour in *Gymnotus omarorum* included locomotor and electric displays. Fish produced a number of electric displays easily identified from basal EOD: SIDs (sharp increases decreases in EOD rate,



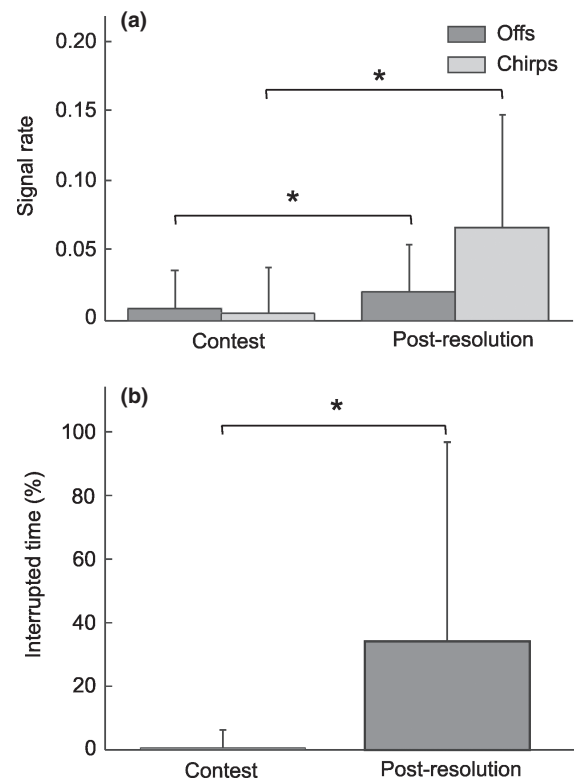
**Fig. 2:** Temporal structure of agonistic encounters in *Gymnotus omarorum*. Representation of the duration contest phases (median values) related to electric signals occurrence.

Fig. 1a); offs (complete cessation of EOD activity, Fig. 1a, b); and chirps (transient and brief increases in EOD rate accompanied by a decrease in EOD amplitude and distortion of EOD waveform, Fig. 1c, d). Chirps and offs showed a wide and continuous range of durations (Table 1). Chirps were often emitted during an EOD interruption, that is, when a fish showed an EOD interruption, it sometimes chirped and then continued with the interruption. We did not identify distinctive chirp types in terms of internal structure in *G. omarorum* (no clusters were identified by PCA followed by k-means cluster analysis of the parameters presented in Table 1). It should be noted that these parameters did not show sexual differences (two-sample independent *t*-test, duration:  $p = 0.54$ , intra-chirp EOD amplitude:  $p = 0.28$ , intra-chirp EOD interval:  $p = 0.63$ ).

Offs and chirps were interpreted as submissive electric signals. During the contest phase, both contenders interrupted their EODs even simultaneously (double offs observed in 7 of 33 dyads). After resolution, only subordinates produced offs and chirps (subordinate offs vs. dominant offs: Wilcoxon matched-pairs test,  $T = 3.5$ ,  $N = 27$ ,  $p < 0.001$ ; subordinate chirps vs. dominant chirps: Wilcoxon test,  $T = 0$ ,  $N = 27$ ,  $p < 0.001$ ).

Offs were produced during both contest and post-resolution phases, whereas chirps were mostly produced in the post-resolution phase. As shown in Fig. 2, the first off occurred during the contest (first off latency = 92 (213)s,  $N = 25$ , median [IQR]), whereas the first chirp occurred during the post-resolution phase (first chirp latency = 273 (326)s,  $N = 21$ ). The emission of submissive electric signals showed a consistent temporal pattern: the first off preceded conflict resolution in 76% of the interactions ( $\chi^2 = 6.76$ ,  $p < 0.01$ ) and conflict resolution preceded the first chirp emission in 71.4% of the interactions ( $\chi^2 = 3.86$ ,  $p < 0.05$ ). In addition, the first off preceded the first chirp in 76% of the interactions ( $\chi^2 = 5.76$ ,  $p < 0.05$ ).

Moreover, the temporal pattern of the emission of offs and chirps differed among phases: both off and chirp occurrence increased in the post-resolution phase compared to the contest phase (Fig. 3a, off rate: Wilcoxon test,  $T = 91$ ,  $N = 25$ ,  $p = 0.05$ ; chirp rate: Wilcoxon test,  $T = 52$ ,  $N = 21$ ,  $p = 0.02$ ); and the time the submissive fish remained interrupted increased from contest phase to post-resolution phase (Fig. 3b per cent of interrupted time: Wilcoxon test,  $T = 17$ ,  $N = 25$ ,  $p < 0.01$ ).



**Fig. 3:** Distribution of electric submissive signals with respect to conflict phases. (a) Off rate and chirp rate increased from contest phase to post-resolution phase. \* $p < 0.05$ , Wilcoxon test,  $N = 25$  and  $N = 21$  respectively. (b) The per cent of interrupted time increased from contest phase to post-resolution phase. \* $p < 0.05$ , Wilcoxon test,  $N = 25$ . Values are expressed as medians, error bars represent interquartile range (IQR).

### Contest Outcome

We evaluated the effects of differences in body weight and body length, and the effects of individual sex and dyad sex on contest outcome by binomial regression. Only weight difference was statistically significant in explaining contest outcome; there was no significant effect of individual sex, dyad sex and length differences as shown in Table 2 with the averaged values of coefficients and parameters. The model was consistently significant for weight difference in each one of the 10 samples with  $R^2$  always above 0.25 (minimum  $R^2 = 0.27$ , maximum  $R^2 = 0.35$ ). The model was also validated by its predictive power, which succeeded in the prediction of the actual outcome in above 70% of the cases (minimum of correctly classified percentage = 73.3%, maximum of correctly classified percentage = 85.3%).

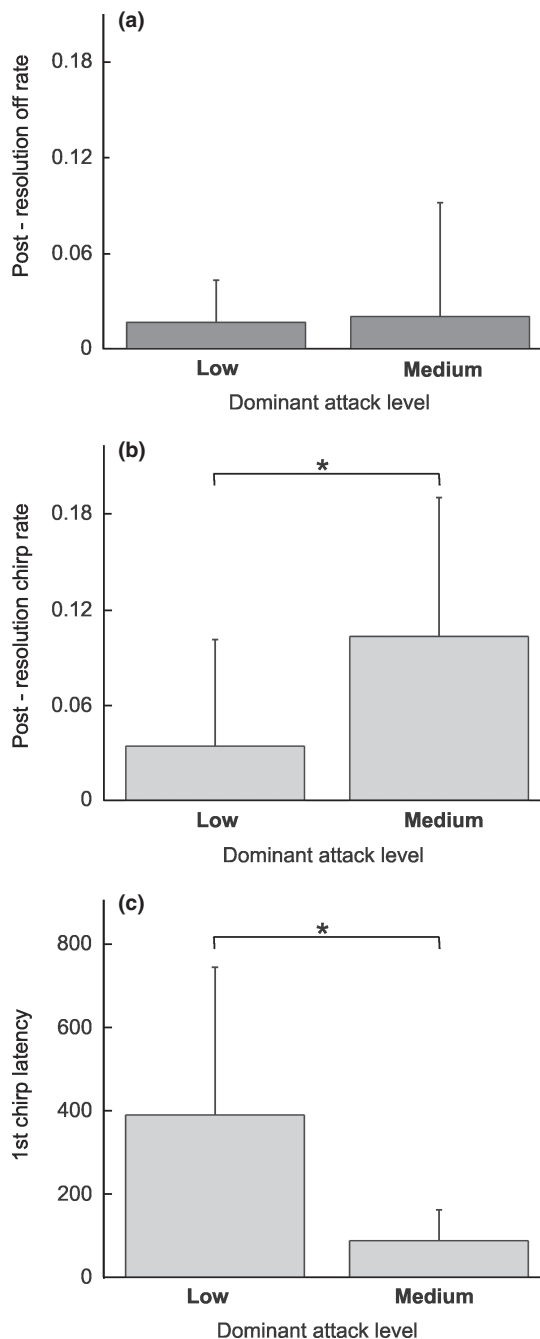
### Influence of Size Differences on Contest Dynamics

Only weight differences among contestants, but neither subordinate sex nor dyad sex, influenced contest duration (Table 3). These results suggest that body size is a good predictor of fighting ability in this species independent of the sex of the individuals in both intra- and intersexual encounters. We were unable to discriminate between both assessment strategies, as dominant and subordinate weight exhibited non-significant correlations with contest duration ( $F_{3,28} = 0.36$ ,  $p = 0.77$ , dominant;  $F_{3,28} = 0.36$ ,  $p = 0.78$ , subordinate; multiple linear regression with absolute weight, dyad sex and subordinate's sex as independent variables vs. contest duration as dependent variable).

As shown in Table 4, we confirmed that weight differences among contenders had significant predictive power not only for contest duration but also for first off latency. Although not significant, a negative relation between weight asymmetry and first chirp latency was also observed (Table 4). Nonetheless, weight had no predictive power for post-resolution off rate ( $F_{1,23} = 0.16$ ,  $p = 0.69$ ), post-resolution interrupted time ( $F_{1,23} = 0.08$ ,  $p = 0.78$ ) and post-resolution chirp rate ( $F_{4,19} = 1.15$ ,  $p = 0.3$ ). No sexual differences were found in these parameters (Mann–Whitney  $U$ -test for the following: post-resolution off rate,  $N_1 = 14$ ,  $N_2 = 11$ ,  $p = 0.98$ ; post-resolution interrupted time,  $N_1 = 14$ ,  $N_2 = 11$ ,  $p = 0.30$ ; post-resolution chirp rate,  $N_1 = 12$ ,  $N_2 = 9$ ,  $p = 0.19$ ; first off latency,  $N_1 = 14$ ,  $N_2 = 11$ ,  $p = 0.07$ ; first chirp latency,  $N_1 = 12$ ,  $N_2 = 9$ ,  $p = 0.55$ ). These results suggest that the decision for EOD cessation (and probably for chirping as well) is made based on evaluation of relative body size of the contestants.

### Aggression Levels and Submissive Electric Signals

We tested the relationship between dominant aggressive behaviour and subordinate submissive electric displays. In this sense, post-resolution off rate in subordinates was similar regardless of the level of aggression they received during the contest (low or medium, Fig. 4a). Nevertheless, post-resolution chirp rate was significantly higher in subordinates that received higher levels of aggression than in those that received lower levels (Mann–Whitney  $U$ -test,  $N_{Low} = 14$ ,  $N_{Medium} = 5$ ,  $p = 0.03$ ); and first chirp latency was significantly shorter among subordinates that received higher levels of aggression than in those that received lower levels



**Fig. 4:** Subordinate electric performance in relation to dominant aggression levels. (a) Post-resolution off rate, (b) post-resolution chirp rate, (c) first chirp latency of subordinates receiving low and medium levels of aggression. \* $p < 0.05$ , Mann–Whitney  $U$ -test,  $N_{Low} = 14$ ,  $N_{Medium} = 5$ . Values are expressed as medians, error bars represent interquartile range (IQR).

(Mann–Whitney  $U$ -test,  $N_{Low} = 14$ ,  $N_{Medium} = 5$ ,  $p < 0.01$ ), as shown in Fig. 4b, c.



## Discussion

*Gymnotus omarorum* is a sexually monomorphic solitary species that displays territorial aggression independent of sex and season. We confronted non-breeding dyads of different sex to evaluate contest outcome and assessment strategies when resource value remained equal for both sexes. We confirmed that body size, but not sex, is a good RHP proxy thus influencing contest resolution. We also focused on the role of electric signals in agonistic encounters of this species and confirmed a sequential pattern of electric submission.

### The Integration of Locomotor and Electric Displays in the Agonistic Behaviour of *Gymnotus omarorum*

Social behaviours in Gymnotiformes include electric displays in addition to locomotor ones (Moller 1995). Dominance is established by a hierarchal order of EOD rates in *Gymnotus carapo* and in several wave-type species (Westby 1975b; Hagedorn & Heiligenberg 1985; Hagedorn & Zelick 1989; Fugère et al. 2011). In addition, transient social electric signals have been reported to play a role in agonistic encounters of *G. carapo* and other gymnotiforms (Black-Cleworth 1970; Maler & Ellis 1987; Dunlap & Larkins-Ford 2003; Hupé & Lewis 2008; Triefenbach & Zakon 2008; Perrone et al. 2009).

In this study, we observed two main types of social electric signals in dyadic encounters of *G. omarorum*: (1) offs (Fig. 1a, b), already described in (Black-Cleworth 1970; Westby 1975b); (2) and chirps (Fig. 1c, d), a conspicuous electric display not previously identified in this genus. Both social electric signals, offs and chirps were produced by subordinates regardless of whether they were males or females or whether they participated in inter- or intrasexual dyads. Furthermore, neither the duration of offs and chirps nor the chirp structure differed significantly among sexes. Although offs and chirps can be interpreted as submissive signals, not all individuals signalled submission electrically: six of 33 dyads exhibited neither offs nor chirps and still the conflict was resolved. SIDs were more rarely observed (Fig. 1a) but indistinguishable from those reported in *G. carapo* (Black-Cleworth 1970) in both the amplitude of the rate increase and in its temporal pattern. We also interpreted SIDs in *G. omarorum* as threat signals emitted by dominants as shown in Fig. 1a, in which one SID occurred while the subordinate fish had turned off its EOD.

Distinctive types of chirps have been associated with different behaviours in Gymnotiformes: for example, specific agonistic chirps have been described in *Apteronotus* and *Brachyhyppopomus* (Zupanc et al. 2006; Perrone et al. 2009). Although chirps emitted by *Gymnotus omarorum* were extremely variable in duration and shape (Table 1, Fig. 1c, d), no chirp types were identified. We therefore conclude that all chirps, long or short, emitted by males or females, carry information about submission. This contrasts with previous findings in *A. leptorhynchus* (Triefenbach & Zakon 2008) and in male–male encounters of *B. gauderio* (Perrone et al. 2009), in which chirps are not exclusively emitted by one of the contenders, but appear to be produced mostly by dominant fish.

The behavioural protocol used in this study, in which territory was the only resource contenders could fight for, allowed us to observe complete agonistic encounters in all the 33 tested dyads. Moreover, the agonistic behaviour of *Gymnotus omarorum* always followed a robust sequence of three phases: (1) an extremely short pre-contest phase, taken from the moment of barrier removal to the first observed attack; (2) a contest phase of overt aggression in which both individuals perform aggressive displays (bites, nudges, nips and jaw locks) until the subordinate fish stops attacking and retreats; and (3) a post-resolution phase, recorded arbitrarily for 10 min after the resolution time, in which the dominant fish persists attacking the already defeated contender. Interestingly, if we add to this framework the analysis of the social electric signals (offs and chirps), we can obtain a more comprehensive understanding of the temporal profile of the agonistic behaviour of *G. omarorum*. As shown in Fig. 2, the first off occurs during the contest phase, whereas the first chirp appears after conflict resolution. Therefore, the first submissive electric signal is emitted long before the subordinate fish makes the decision to retreat. After resolution, the pattern of electric signalling is completely different; the subordinate keeps emitting more profuse and longer offs and adds a novel probably more unambiguous submissive signal, the chirp (Fig. 3). We argue, as discussed later, that the subordinate fish communicates its decision of giving up the fight by electric signalling and that it uses both signals in sequence to reduce the level of ambiguity at different stages of surrender.

### Non-Sex-Biased Dominance in *Gymnotus omarorum*

The theoretical analysis of the evolution of behavioural strategies in contest situations predicts that

when there are no sex asymmetries (neither in the resource value nor in the fighting ability) among contenders, the contest outcome should be independent of sex (Maynard Smith & Parker 1976; Parker & Rubenstein 1981). During the non-breeding season, territory is a valuable resource for males and females of *Gymnotus omarorum*. As predicted by Game-theory models, we found that dominance is not influenced by individuals' sex during the non-breeding season of this monomorphic species. The binomial model used in this study supported that only weight asymmetry, but not length asymmetry, individual sex or dyad sex influenced the contest outcome (Table 2). Weight is the most direct and widespread indicator of physical strength. Therefore, it was likely that weight asymmetry would be an important predictor of dominance in the escalated contests of *G. omarorum*. However, although body weight and body length are strongly correlated, body length was not a relevant predictor of dominance in *G. omarorum*, in contrast to the results previously reported in other Gymnotiformes (Triefenbach & Zakon 2008; Fugère et al. 2011).

As a complementary prediction of the cost-asymmetry hypothesis, in species with sexual size monomorphism, in which the fighting abilities of the two contestants are comparable, the outcome will depend on the value of the resources to be won for each contestant, that is, size symmetry may be counterbalanced by asymmetric resource values. This issue has been elegantly supported in lemurs in which female dominance over males is the norm (Dunham 2008). Despite the similarity in size of the sexes, female lemurs, with their added reproductive costs (i.e., pregnancy, lactation, maternal care, etc.), are expected to have substantially higher nutritional demands overall than males. As such, a female has more to lose in terms of fitness by not attaining the resource, is more motivated to fight and therefore is more likely to win a contest with a male of equal size. In Columbian ground squirrels, *Spermophilus columbianus*, males and females show no consistent patterns of dominance until after the mating season, when females have high resource needs and become dominant over males (Murie & Harris 1988). In the case of *Gymnotus omarorum*, we expect that non-breeding sex symmetric intersexual contests will reverse to asymmetric during breeding. We predict and will test in the future that the sex with the higher costs of reproduction (probably the female) will have higher payoff for winning a fight during breeding, resulting in an asymmetric intersexual contest.

### Assessment Strategies and the Process of Electric Submission

Decision-making during agonistic contest is influenced by RHP assessment. Our results (Table 3) strongly suggest that body mass is the best predictor of RHP and sex is not affecting the decision-making process in the non-breeding territorial agonistic behaviour of *Gymnotus omarorum*. We therefore confirmed in this monomorphic species the predicted non-sex-biased assessment strategy in intra- and intersexual encounters. In coherence with the non-sex-biased dominance, evolution has also favored a sex-independent RHP assessment in *G. omarorum* during the non-breeding season. Following the same rationale, in the hermit crab (*Pagurus bernhardus*), dominance that is biased towards the male sex in size-matched intersexual contests has been correspondingly related with different contest dynamics among sexes (Briffa & Dallaway 2007).

In contrast to self-assessment, mutual assessment models predict that contest resolution should emerge from the detection of RHP asymmetries but not from the individuals' RHP (Enquist & Leimar 1983). In both models, individuals are expected to employ longer interaction times when RHP differences are small. In this study, we were unable to discriminate between self-assessment, in which the RHPs of both contestants are expected to be positively correlated with contest duration, and mutual assessment, in which this relation is expected to be negative in winners and positive in losers (Taylor & Elwood 2003; Arnott & Elwood 2009a).

In electric fish, RHP assessment is likely to take into account electric cues. Early studies demonstrated that dominance is established by a hierarchal order of EOD rates in pulse and wave-type species (Westby 1975b; Hagedorn & Heiligenberg 1985). More recently, EOD rate and its modulations were proven to correlate with RHP in two wave-type species (Triefenbach & Zakon 2008; Fugère et al. 2011). Other lines of evidence suggest that, besides rate, EOD amplitude can also predict RHP in pulse-type species (Stoddard & Salazar 2011). In our study, we were unable to obtain reliable measurements of EOD amplitude and basal rate because these measurements require either a precise and stable spatial relationship between the fish and the recording electrodes or stability impossible to obtain with freely interacting animals (Franchina & Stoddard 1998). EOD traits (amplitude and rate) could act as remote indicators of RHP in *Gymnotus omarorum*, allowing fish to detect fighting ability asymmetries through

the electric communication channel avoiding the costs of escalated aggression. It is probable that the confinement we imposed on the fish in a small arena prevented the occurrence of remote assessment, and shortcut the sequence of agonistic behaviour to the overt aggression phase that could have been avoided by early retreats. The fact that SIDs were only rarely observed in our study may be also a result of the size of the arena that induced individuals to enter directly into escalated phases of the fight.

*Gymnotus omarorum* submission includes three successive decisions: to turn off the EOD, to retreat and to chirp. Interestingly, RHP assessment in this species not only influences the decision to retreat but also the decision to interrupt the EOD (Table 4). Moreover, RHP asymmetry seems to influence (although not significantly, Table 4) the decision to chirp.

#### Qualitative Changes of Signalling during Submission

Formal theoretical models propose that submissive signalling is likely to occur when animals cannot flee away, injuries are frequent and/or RHP relative estimations are accurate (Matsumura & Hayden 2006). In *Gymnotus omarorum*, EOD cessation makes subordinates less conspicuous and thus, harder to be detected by electrolocation. However, in proximity, dominants may still perceive an electric shadow of their rival's body. Offs could be interpreted both as a hiding strategy ('electric hiding'; Black-Cleworth 1970) or as an attempt to communicate the aim of not entering into an escalated conflict. Supporting the communicative function of offs, their timing (mostly before contest resolution and gradually increasing in intensity and rate during the post-resolution phase) is expected for a graded signal of intention (Figs 2 and 3). This temporal pattern resembles the darkening behaviour during territorial encounters in the Atlantic salmon (*Salmo salar*), which is proposed to act also as a submission signal (O'Connor et al. 1999).

Dominants could interpret the EOD restart as a provocative behaviour if it is not accompanied by retreat behaviour. Our experimental conditions, in which confinement impedes fish to retreat, may still be a plausible scenario for studying agonistic behaviour of this species during high population density stages. In nature, individuals with their EOD interrupted would flee until out of the dominant's attack range. Nevertheless, long interruptions during which

fish cannot electrolocate imply higher risks; therefore, EOD restart would be unavoidable. It is conceivable that this trade-off between the cost of submission signalling and EOD interruption is the evolutionary cause for the emergence of chirps as a second and more unambiguous subordination signal. Chirps are emitted only after conflict resolution (Fig. 3). Post-resolution chirping rate was not correlated with body asymmetries, although individuals receiving higher levels of aggression chirped more intensely and sooner (Fig. 4). As individuals in close proximity of more aggressive dominants have to deal with higher costs, it would be advantageous for them to signal their subordinate status intensively and unambiguously. In summary, submission in *Gymnotus omarorum* employs different electric displays that accompany a loss of ambiguity in subordination signalling.

#### Speculations about Assessment in Electric Fish Contests

Electric displays carry remote and reliable information about individual RHP. Thus, we predict that evolution should have favoured mutual RHP assessment strategy in most electric fish species. Despite the diversity and complexity of RHP assessment strategies, the richness of electric information makes pure mutual assessment strategy the most likely to be adopted by electric fish. Although we were unable to discriminate between assessment strategies in *Gymnotus omarorum*, our results allow us to speculate about the natural sequence in the contests of this species that could also be expected for any other electric fish species. In nature, without confinement artefact, individuals would start with a low-cost remote assessment of relative RHP, employing information conveyed by both EOD amplitude and rate. Subsequently, individuals should evaluate each other's intention to escalate by employing transient increases in EOD rate (such as the chirps reported in *Apteronotus leptorhynchus* or the SIDs observed in *G. carapo* (Black-Cleworth 1970; Triefenbach & Zakon 2008)). Then, only if RHP asymmetry is small and difficult to be detected by remote mutual assessment, contenders should engage in overt aggression phases to determine relative RHP differences reliably but costly, as predicted by mutual assessment models. Finally, in gregarious species or in cases in which retreat is impossible, we also expect the emergence of submissive electric signals and the establishment of permanent electric ranks.

## Acknowledgements

We wish to thank Patricia Black, Philip Stoddard, Betina Tassino and Laura Quintana for their generous revision and suggestions to our manuscript. We are especially grateful to Maira Colacce and Alexis Gerschuni for their help with statistical analysis. This research was supported by ANII, project FCE2007\_569, FCE\_2657, FCE\_2472 and PEDECIBA.

## Literature cited

- Arnott, G. & Elwood, R. W. 2009a: Assessment of fighting ability in animal contests. *Anim. Behav.* **77**, 991–1004.
- Arnott, G. & Elwood, R. W. 2009b: Gender differences in aggressive behaviour in convict cichlids. *Anim. Behav.* **78**, 1221–1227.
- Black-Cleworth, P. 1970: The role of electrical discharge in the non reproductive social behavior of *Gymnotus carapo* (Gymnotidae, Pisces). *Anim. Behav.* **3**, 1–77.
- Boonstra, R., Lane, J. E., Boutin, S., Bradley, A., Desantis, L. & Newman, A. E. M. 2008: Plasma DHEA levels in wild, territorial red squirrels: seasonal variation and effect of ACTH. *Gen. Comp. Endocrinol.* **158**, 61–67.
- Briffa, M. & Dallaway, D. 2007: Inter-sexual contests in the hermit crab *Pagurus bernhardus*: females fight harder but males win more encounters. *Behav. Ecol. Sociobiol.* **61**, 1781–1787.
- Briffa, M. & Sneddon, L. U. 2010: Contest behavior. In: *Evolutionary Behavioral Ecology* (Westneat, C. W. & Fox, D. F., eds). Oxford Univ. Press, New York, pp. 246–265.
- Draud, M., Macias-Ordóñez, R., Verga, J. & Itzkowitz, M. 2004: Female and male Texas cichlids (*Herichthys cyanoguttatum*) do not fight by the same rules. *Behav. Ecol.* **15**, 102–108.
- Dunham, A. 2008: Battle of the sexes: cost asymmetry explains female dominance in lemurs. *Anim. Behav.* **76**, 1435–1439.
- Dunlap, K. D. & Larkins-Ford, J. 2003: Diversity in the structure of electrocommunication signals within a genus of electric fish, *Apteronotus*. *J. Comp. Physiol. A* **189**, 153–161.
- Enquist, M. & Leimar, O. 1983: Evolution of fighting behaviour: decision rules and assessment of relative strength. *J. Theor. Biol.* **102**, 387–410.
- Franchina, C. R. & 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.
- Fugère, V., Ortega, H. & Krahe, R. 2011: Electrical signaling of dominance in a wild population of electric fish. *Biol. Lett.* **7**, 197–200.
- Hagedorn, M. & Heiligenberg, W. 1985: Court and spark: electric signals in the courtship and mating of gymnotoid fish. *Anim. Behav.* **33**, 254–265.
- Hagedorn, M. & Zelick, R. 1989: Relative dominance among males is expressed in the electric organ discharge characteristics of a weakly electric fish. *Anim. Behav.* **38**, 520–525.
- Hau, M., Stoddard, P. K. & Soma, K. K. 2004: Territorial aggression and hormones during the non-breeding season in a tropical bird. *Horm. Behav.* **45**, 40–49.
- Hsu, Y., Earley, R. L. & Wolf, L. L. 2006: Modulation of aggressive behaviour by fighting experience: mechanisms and contest outcomes. *Biol. Rev.* **81**, 33–74.
- Hupé, G. J. & Lewis, J. E. 2008: Electrocommunication signals in free swimming brown ghost knifefish, *Apteronotus leptorhynchus*. *J. Exp. Biol.* **211**, 1657–1667.
- Hupé, G. J., Lewis, J. E. & Benda, J. 2008: The effect of difference frequency on electrocommunication: chirp production and encoding in a species of weakly electric fish, *Apteronotus leptorhynchus*. *J. Physiol. Paris* **102**, 164–172.
- Jasnow, A. M., Huhman, K. L., Bartness, T. J. & Demas, G. E. 2002: Short days and exogenous melatonin increase aggression of male syrian hamsters (*Mesocricetus auratus*). *Horm. Behav.* **42**, 13–20.
- King, J. A. 1973: The ecology of aggressive behavior. *Annu. Rev. Ecol. Syst.* **4**, 117–138.
- Maler, L. & Ellis, W. G. 1987: Inter-male aggressive signals in weakly electric fish are modulated by monoamines. *Behav. Brain Res.* **25**, 75–81.
- Matsumura, S. & Hayden, T. J. 2006: When should signals of submission be given? A game theory model. *J. Theor. Biol.* **240**, 425–433.
- Maynard Smith, J. 1974: The theory of games and the evolution of animal conflicts. *J. Theor. Biol.* **47**, 209–221.
- Maynard Smith, J. & Parker, G. A. 1976: The logic of asymmetric contests. *Anim. Behav.* **24**, 159–175.
- Moller, P. 1995: *Electric fishes: history and behavior*. Chapman & Hall, London.
- Murie, J. O. & Harris, M. A. 1988: Social interactions and dominance relationships between female and male Columbian ground squirrels. *Can. J. Zool.* **66**, 1414–1420.
- O'Connor, K., Metcalfe, N. & Taylor, A. 1999: Does darkening signal submission in territorial contests between juvenile Atlantic salmon, *Salmo salar*? *Anim. Behav.* **58**, 1269–1276.
- Parker, G. A. & Rubenstein, D. I. 1981: Role assessment, reserve strategy, and acquisition of information in asymmetric animal conflicts. *Anim. Behav.* **29**, 221–240.



- Perrone, R., Macadar, O. & Silva, A. 2009: Social electric signals in freely moving dyads of *Brachyhypopomus pinnicaudatus*. *J. Comp. Physiol. A* **195**, 501—514.
- Richer-de-Forges, M. M., Crampton, W. G. R. & Albert, J. S. 2009: A new species of *Gymnotus* (Gymnotiformes, Gymnotidae) from Uruguay: description of a model species in neurophysiological research. *Copeia* **2009**, 538—544.
- Silva, A., Quintana, L., Galeano, M. & Errandonea, P. 2003: Biogeography and breeding in Gymnotiformes from Uruguay. *Environ. Biol. Fish* **66**, 329—338.
- Silva, A., Perrone, R. & Macadar, O. 2007: Environmental, seasonal, and social modulations of basal activity in a weakly electric fish. *Physiol. Behav.* **90**, 525—536.
- Soma, K. K., Sullivan, K. & Wingfield, J. 1999: Combined aromatase inhibitor and antiandrogen treatment decreases territorial aggression in a wild songbird during the nonbreeding season. *Gen. Comp. Endocrinol.* **115**, 442—453.
- Stoddard, P. K. 2002: The evolutionary origins of electric signal complexity. *J. Physiol. Paris* **96**, 485—491.
- Stoddard, P. K. & Salazar, V. L. 2011: Energetic cost of communication. *J. Exp. Biol.* **214**, 200—205.
- Taylor, P. W. & Elwood, R. W. 2003: The mismeasure of animal contests. *Anim. Behav.* **65**, 1195—1202.
- Triefenbach, F. A. & Zakon, H. H. 2008: Changes in signalling during agonistic interactions between male weakly electric knifefish, *Apteronotus leptorhynchus*. *Anim. Behav.* **75**, 1263—1272.
- Westby, G. W. M. 1975a: Comparative studies of the aggressive behaviour of two gymnotid electric fish (*Gymnotus carapo* and *Hypopomus artedi*). *Anim. Behav.* **23**, 192—213.
- Westby, G. W. M. 1975b: Further analysis of the individual discharge characteristics predicting social dominance in the electric fish, *Gymnotus carapo*. *Anim. Behav.* **23**, 249—260.
- Wingfield, J. C., Lynn, S. & Soma, K. K. 2001: Avoiding the “costs” of testosterone: ecological bases of hormone-behavior interactions. *Brain Behav. Evol.* **57**, 239—251.
- Wooldridge, J. 2002: *Econometric Analysis of Cross Section and Panel Data*. MIT Press, Cambridge.
- Zakon, H. H., Lu, Y., Zwickl, D. J. & Hillis, D. M. 2006: Sodium channel genes and the evolution of diversity in communication signals of electric fishes: convergent molecular evolution. *Proc. Natl Acad. Sci. USA* **103**, 3675—3680.
- Zupanc, G. K. H., Sîrbulescu, R. F., Nichols, A. & Ilies, I. 2006: Electric interactions through chirping behavior in the weakly electric fish, *Apteronotus leptorhynchus*. *J. Comp. Physiol. A* **192**, 159—173.