Electric fish use electrocommunication signals to fine tune relative dominance and access to resources

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Abstract

Social animals establish dominance hierarchies to regulate access to resources. Although communication signals could reduce costs in negotiating dominance, their detailed role and emergence in non-mammalian vertebrates is not well researched. We tracked electrocommunication signals and agonistic behaviors of the gymnotiform fish *Apteronotus leptorhynchus* in staged competition experiments. Subordinates emitted the majority of so called "rises" in dependence on the competitor's relative size and sex. Rises provoked ritualized biting or chasing behaviors by dominant fish. Already after 25 minutes losers were accurately predictable based on rise numbers, but they continued to emit rises. We suggest the interplay between communication and aggression to fine tune relative dominance without questioning dominance rank. This communication system regulates the skewness of access to resources within a dominance hierarchy and allows *A. leptorhynchus* to populate neotropical rivers with high abundances.

Keywords animal behavior | weakly electric fish | staged competition | dominance hierarchy | communication

Introduction

The abundance and distribution of resources influences the dispersion and density of animals within a habitat. When resources are limited animals compete for territories and their resources (Chapman et al., 1995; Markham et al., 2015). Often dominance hierarchies emerge, where resources are distributed unequally between individuals, favoring those of higher social rank (e.g. Janson, 1985; Wauters and Dhondt, 1992; Sapolsky, 2005; Taves et al., 2009). Dominant animals have various benefits over subordinates, including higher reproductive success, higher net food intake, and a reduced predation risk (Kappeler and Schäffler, 2008; Janson, 1990; Webster and Hixon, 2000; Charpentier et al., 2005). Dependent on species and environmental conditions dominance hierarchies can have various structures. In bottom-up egalitarian hierarchies resources are more equally distributed (Sapolsky, 2005), whereas in top-down despotic hierarchies access to resources is strongly skewed in favor for dominant individuals (Kappeler and Schäffler, 2008). Here dominance is often attained and re-enforced through aggressive encounters or psychological intimidation (Creel et al., 1996; Janson, 1985; Clutton-Brock et al., 1979).

By means of communication signals and behavioral cues animals can assess each other's physical condition, motivational state, and also dominance status (Fernald, 2014). The comparison of these attributes are often sufficient to clarify the social order and the corresponding access to resources between animals. Communication signals and other cues are an important part of social interactions since they prevent costly, repetitive fights. Animals avoid fights with competitors when their chances of success are low and rather rely on dominance cues to regulate access to various different resources than repetitively fight for them (Parker, 1974; Clutton-Brock et al., 1979; Janson, 1990). Nevertheless, how active communication signals are used in negotiating and signaling dominance is primarily researched in mammals (e.g. Bolt et al., 2019), but not so in other vertebrates.

Dominance hierarchies have also been suggested for the gymnotiform electric fish *Apteronotus leptorhynchus* (Dunlap and Oliveri, 2002; Stamper et al., 2010; Raab et al., 2019), which is known for its rich repertoire of various types of electrocommunication signals (Smith, 2013) used in courtship (Hagedorn and Heiligenberg, 1985; Henninger et al., 2018) as well as in agonistic contexts (Batista et al., 2012; Hupé and Lewis, 2008; Triefenbach and Zakon, 2008; Fugère et al., 2011). This makes *A. leptorhynchus* an interesting species for studying the utility and specificity of a range of communication signals and behaviors in establishing and maintaining dominance hierarchies.

Already by means of the sexually dimorphic frequency of their continuous electric organ discharge (EOD) they signal identity and sex, with males having higher EOD frequencies (EODfs) than females (Meyer et al., 1987). Whereas some studies found larger, more dominant fish to have higher EODfs (Hagedorn and Heiligenberg, 1985;

Dunlap and Oliveri, 2002; Cuddy et al., 2012; Henninger et al., 2018; Raab et al., 2019), others were not able to replicate this correlation (Triefenbach and Zakon, 2008). In electric fish in general, dominance has been shown to correlate with body size (Batista et al., 2012; Triefenbach and Zakon, 2008; Dunlap and Oliveri, 2002). The role of the sexes within electric fish dominance hierarchies is still unclear. While some studies suggest female electric fish to either form no dominance hierarchy (Hagedorn and Heiligenberg, 1985) or only a very distinct one whereby females with lower EODf were more likely be found outside of shelters (Dunlap and Oliveri, 2002), others find dominance to be independent of sex (Batista et al., 2012; Zubizarreta et al., 2020).

For generating electrocommunication signals electric fish modulate their EODf on various time scales (Benda, 2020). So called "chirps" are different types of brief (10 – 500 ms), transient increases in EODf (Engler et al., 2000; Zakon et al., 2002; Hupé et al., 2008). "Small" and "long chirps" are used in courtship for synchronizing spawning (Henninger et al., 2018) and at the same time the very same small chirps are used as submissive signals to reduce attacks in agonistic encounters (Hupé and Lewis, 2008; Henninger et al., 2018).

The function of another category of electrocommunication signal, so called "rises", is discussed controversially. Rises are characterized by a moderate increase in EODf by no more than a few tens of Hertz followed by an approximately exponential decay back to baseline EODf over a second to almost a minute (Hopkins, 1974; Engler et al., 2000; Tallarovic and Zakon, 2002; Zakon et al., 2002). Rises have been suggested to be signals of aggression or motivation to attack (Tallarovic and Zakon, 2005; Triefenbach and Zakon, 2008), submission (Hopkins, 1974; Serrano-Fernández, 2003), "victory cries" (Dye, 1987), to evoke or precede attacks (Hopkins, 1974; Triefenbach and Zakon, 2008), or to just a general expression of stress (Smith, 2013).

Using recently developed techniques for tracking electrocommunication signals in freely behaving electric fish (Henninger et al., 2018; Madhav et al., 2018; Henninger et al., 2020) in addition with infrared video recordings, we recorded electric and physical interactions of pairs of *A. leptorhynchus* in staged competitions over a superior shelter. Compared to previous studies we significantly expanded the observation times (from ten minutes to six hours) and the number of interacting pairs of fish. After analyzing the effects of physiological parameters, including size, weight, EODf, and sex, for the establishment of dominance, this allowed us to link dominance to a detailed analysis of the usage of rises, correlate the timing of rises to agonistic interactions, and evaluate the sex-specific function of this communication signal in negotiating dominance.

Methods

Aminals

A total of 21 *A. leptorhynchus* (9 males, 12 females), obtained from a tropical fish supplier, were used in the competition experiments. All fish were mature and not in breeding condition. Fish were selected randomly from multiple populations to reduce familiarity effects and sorted into four mixed-sex groups of five or six fish (males/females in group 1: 2/4, 2: 1/4, 3: 3/2, 4: 3/2). Males were identified by their higher EODf (see below) and elongated snout. The sex of half the fish was verified after the competition experiments via post mortem gonadal inspection in the context of electrophysiological experiments (approved by Regierungspräsidium Tübingen, permit no. ZP 1/16). Fish were housed individually in 54 l tanks at a light-dark cycle of 12 h/12 h prior to the experiments and in between competition trials. Each tank was equipped with a plastic tube for shelter, a water filter, and an electrical heater. Water temperature was constant at $25 \pm 0.5\,^{\circ}\mathrm{C}$ and water conductivity $200\,\mu\mathrm{S/cm}$. Fish were fed frozen *Chironomus plumosus* on a daily basis. The competition experiments complied with national and European law and were approved by the Regierungspräsidium Tübingen (permit no. ZP 04/20 G).

Setup

The competition experiments were run in a larger 100 l tank equipped with a 10 cm long and 4 cm wide PVC half-tube as a superior shelter in the center, surrounded by four additional, less optimal shelters (two 5 cm long, 4 cm diameter PVC half-tubes and two $3 \times 5\,\mathrm{cm}^2$ tables) arranged at a distance of about 25 cm. Water temperature and conductivity as well as light-dark cycle were identical to those in the housing tanks. To maintain water temperature a heating mat was placed below the tank and powered with DC current to minimize electrical noise. Two air-powered water-filters were placed behind PVC boards with netted windows in the corners of the tank to not offer additional shelter. A total of 15 monopolar electrodes at low-noise buffer headstages were used to continuously monitor the electric behavior of the fish. Four electrodes were aligned on both long sides of the tank with a center line of six electrodes between them. One electrode was mounted in the central superior shelter. A reference electrode was placed in one corner of the tank behind a PVC board. Electric signals were amplified ($100\times$ gain, 100 Hz low-pass filter, EXT-16B, npi electronic, Tamm, Germany) digitized at 20 kHz per channel with 16 bit resolution (USB-1608GX-2AO, Measurement Computing) and stored on 64 GB USB sticks using custom written software running on a Raspberry PI 3B. Water temperature was measured every 5 min (Dallas DS18B20 1-wire temperature sensor read out by the Raspberry PI). Infrared-videos were recorded at 25 frames per second for all competition

trials of groups 3 and 4 with a camera (Allied Vision Guppy PRO) mounted on top of the tank. During the trials the tank was continuously illuminated by 2×4 infrared lights (ABUS 840 nm) located on the long sides outside the tank. The tank, camera and illumination was placed inside a faraday cage to further reduce electric noise.

Experimental procedure

In each competition trial two fish were freely swimming and interacting in the experimental tank for 6 h. Participating fish were taken from their housing tanks and simultaneous released into the experimental tank. The first 3 h of each trial took place during the dark-phase and the second 3 h during the light-phase of the circadian rhythm the fish were accustomed to. This limited the experiment to one trial per day. The winner of each trial was identified by its presence within the superior shelter during the light-phase of the trial. Fish were transferred back into their housing tanks after the trial. Pairings for each trial were selected systematically to (i) ensure all possible combinations within each group to be tested (10 combinations for groups of five fish, 15 for the six-fish group), (ii) keep the experience level for all fish equal, and (iii) prevent a single fish to be tested on two consecutive days. Weight and length (body size) of each fish was assessed once a week starting in the week before the competition trials.

With 21 fish in four groups we ended up with a total of 45 pairings and trials. Technical failure lead to loss of the electric recordings for the initial four trials of group four. In another three trials we were unable to extract EODf traces and electrocommunication signals from the electric recordings because the EODf difference between fish were to low (< 0.5 Hz). In a single trial, that we discuss separately, we were unable to determine the winner, because both fish shared the superior shelter at the end of the trail. The remaining 37 trials were analyzed in detail.

Detection and tracking of electric signals

After computing spectrograms for each channel with fast Fourier transformation (FFT, $n_{\text{fft}} = 2^{15}$, corresponds to 1.63 s, 80 % overlap) we first detected peaks in a power spectrum summed of the channels and assigned them to the fundamental EODfs and their harmonics of the two fish. Based on EODfs and the distribution of power in the channels we tracked electric signals over time and obtained EODf traces for each of the two fish (Henninger et al., 2018, 2020; Madhav et al., 2018).

Electric fish produce electrocommunication signals by transiently increasing their EODf (Benda, 2020). To asses baseline EODf we computed the 5th percentile of non-overlapping, 5 minute long EODf trace snippets. EODf is sensitive to temperature changes, which were inevitable throughout the single trials and averaged at 1 °C. We computed the Q_{10}-values resulting from temperature and EODf differences of each 5 minute snippet and used the median of 1.37 over all fish to adjust each fish's EODf to 25 °C (EODf_{25}). The EODf_{25} was used to assess an

individuals sex, with $EODf_{25} > 740\,Hz$ assumed to originate from males. As noted above, the sex of half of the fish was verified via post mortem gonadal inspection.

EODf difference for each pair of fish was estimated from the difference of the median baseline EODfs of the competitors during the light-phase of each trial, where EODfs stayed comparably stable. Rises were identified by detecting their characteristic onset peak in each EODf trace based on a minimum difference of 5 Hz between a peak and the preceding trough (Todd and Andrews, 1999). Then the size of the rise, its maximum increase in EODf, was calculated by subtracting the baseline EODf from this peak frequency.

Detection and characterization of agonistic interactions

We manually extracted two categories of agonistic interactions from the infrared video recordings using the event logging software BORIS (Friard and Gamba, 2016). For agonistic interactions without physical contact that were characterized as high velocity, directed movements towards a competitor (e.g. chasing behavior) we recorded onset and end times. Agonstic physical contacts between competitors like ritualized biting or head bumping were detected as point events. For the synchronization of video and electric recordings we used LED-light pulses of 100 ms duration triggered by the computer-amplifier system in intervals of 5 seconds. The LED was mounted on the edge of the tank not perceivable by the competing fish, but detectable in the video-recordings.

Data analysis

Data were analyzed in Python version 3.6.8 using numpy (van der Walt, 2011), scipy (Oliphant, 2007) and matplotlib (Hunter, 2007) packages . All averages are given with their standard deviation. Mann-Whitney U tests were used to asses significance of differences between two populations and Pearson's test and correlation coefficient r for assessing correlations. The influence of various factors on competition outcome was quantified by paired t-tests and by the area under the curve (AUC) of a receiver-operating characteristics (ROC). Generalized linear mixed models (GLM)

$$y = \frac{1}{1 + \exp\left(c_0 + \sum c_i \cdot x_i\right)} \tag{1}$$

with a logistic link function were used to estimate the combined effects of several factors x_i (continuous: EODf, size, ΔEODf and Δsize, categorical: sex), linearly combined with coefficients c_i and an offset c_0, on the outcome of the competitions y (winner or looser). The performance of the GLMs was again assessed by the AUC of a ROC-analysis. Standard deviations of AUC values were obtained by 1000 times bootstrapping the data.

Temporal coupling between rises and agonistic interactions was quantified by a cross-correlation analysis, i.e.

by estimating the averaged rate of rises centered on agonistic events (onset of chasing behaviors or physical contact). For this the temporal differences, Δtime, between agonistic onsets and rises up to ± 60 sec were convolved with a Gaussian kernel with a standard deviation of 1 s. Statistical significance was assessed by a permutation test. The null hypothesis of rises not being correlated with agonistic interaction events was obtained by computing the cross-correlation as described above from 1000 random variants of shuffled rise intervals. From this distribution we determined the 1st and 99th percentiles. Any measured cross-correlation outside this range was considered as a significant deviation from chance level. In addition, we computed the 98 % confidence interval for the estimated cross-correlation by 1000 times jackknife resampling where we randomly excluded 10 % of the rises. Regions where the mean of the null hypothesis was outside the confidence interval also indicated significant cross-correlations.

We used a time window 5 s prior to agonistic onsets to quantify the average number of rises per agonistic event and to compare them to the corresponding time fractions, the number of agonistic events multiplied with the 5 s window relative to the total dark-period time of 3 h . The time window of 5 s was chosen to approximately cover the time of significantly elevated rise rates that we observed before the agonistic events in the cross-correlation analysis.

Results

In 37 trials we observed and analyzed pairs of *A. leptorhynchus* competing for a superior shelter. The trials were composed of 6 male pairs, 10 female pairs, and 21 mixed-sex pairs. The 9 males differed from the 12 females by their higher EODf as expected from the sexual dimorphism in EODf in *A. leptorhynchus* (see methods for details). The fish's size ranged from 9 to 19 cm and was independent of sex ($U = 51.5$, $p = 0.443$, fig. 1 A). Fish size strongly correlated with body weight (3.3–20.3 g, $r = 0.94$, $p < 0.001$, fig. 1 B) and we therefore excluded weight from the following analysis.

We were able to consecutively track electric behaviors of the competitors based on the individual specific EODf traces, including the detection of rises. Complementary infrared-video recordings obtained during the 20 trials of group 3 and 4 were used to detect agonistic behaviors. In a typical competition trial (fig. 2) the overall activity of the two fish was much higher during the initial, three hour dark phase as demonstrated by the high rates of chasing and contact events as well as of rises (electrocommunication signals). During the subsequent three hour light phase, the activity ceased almost entirely and one fish spent substantially more time within or closer to the superior shelter (99.27 ± 0.006 %). This fish were identified as the winner of the competition trial. EODfs of the two fish usually

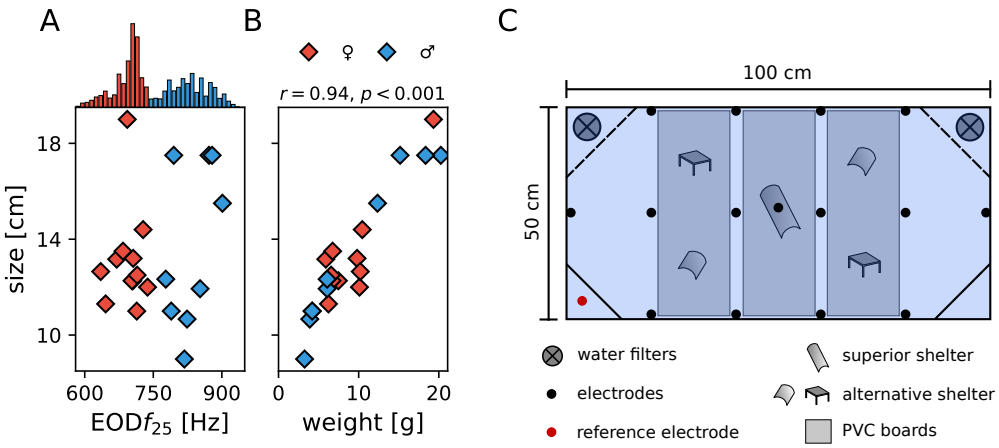


Figure 1: Physical characteristics of the fish and experimental setup. **A** EODf and size (length) of each of the 21 *A. leptorhynchus* participating in the competition experiments. EODf was not correlated with size, neither for all fish nor within the sexes. EODfs were temperature corrected to 25 °C. *A. leptorhynchus* males (blue) were identified by their higher EODfs compared to the EODf of females (red). The histogram on top shows the distribution of EODfs of either sex measured in all trials for every five minutes. **B** Weight and size of the fish were independent of sex and increase proportional to each other, i.e. fish grow mainly in length. **C** Setup for the staged competition experiments. The tank was equipped with one high quality shelter (center tube) and four low quality shelters (two short tubes and two tables) attached to PVC-boards to keep them in place. A total of 15 electrodes (black circles) were distributed in the tank to record electric behaviors of interacting fish. Two air-powered water-filters were placed in the corners behind PVC boards with netted windows (dashed lines). The other two corners were shielded with PVC boards (black lines), one of them contained the reference electrode (red circle).

differed clearly and decreased over the course of the experiment because of slightly decreasing water temperature.

Larger fish win competition

Larger fish were more likely to win the superior shelter ($t = 5.3$, $p < 0.001$, fig. 3 A). Over all pairings, winners are correctly assigned with a probability of 90 % based on size difference (in the sense of the AUC of a ROC analysis). In particular in trials won by males, most of the winners were larger than the losers (male-male: 5 out of 6, $t = 2.9$, $p = 0.04$; male-female: 11 out of 14, $t = 3.9$, $p = 0.002$). In trials won by females, this influence of size difference was similarly pronounced but not significant (female-female: 8 out of 10 winners were larger, $t = 2.1$, $p = 0.07$; female-male: 6 out of 7 winners were larger, $t = 2.0$, $p = 0.09$). In 12 of the 21 mixed-sex pairings were the males larger than the competing females, of which only a single male lost. Of the nine larger females three lost. Absolute size, on the other hand, did not predict competition outcome (AUC = 67 %, fig. 3 F). Note that neither in males nor in females EODf correlated with size (males: $r = 0.47$, $p = 0.20$; females: $r = 0.04$, $p = 0.90$) and that size was independent of sex (fig. 1 A).

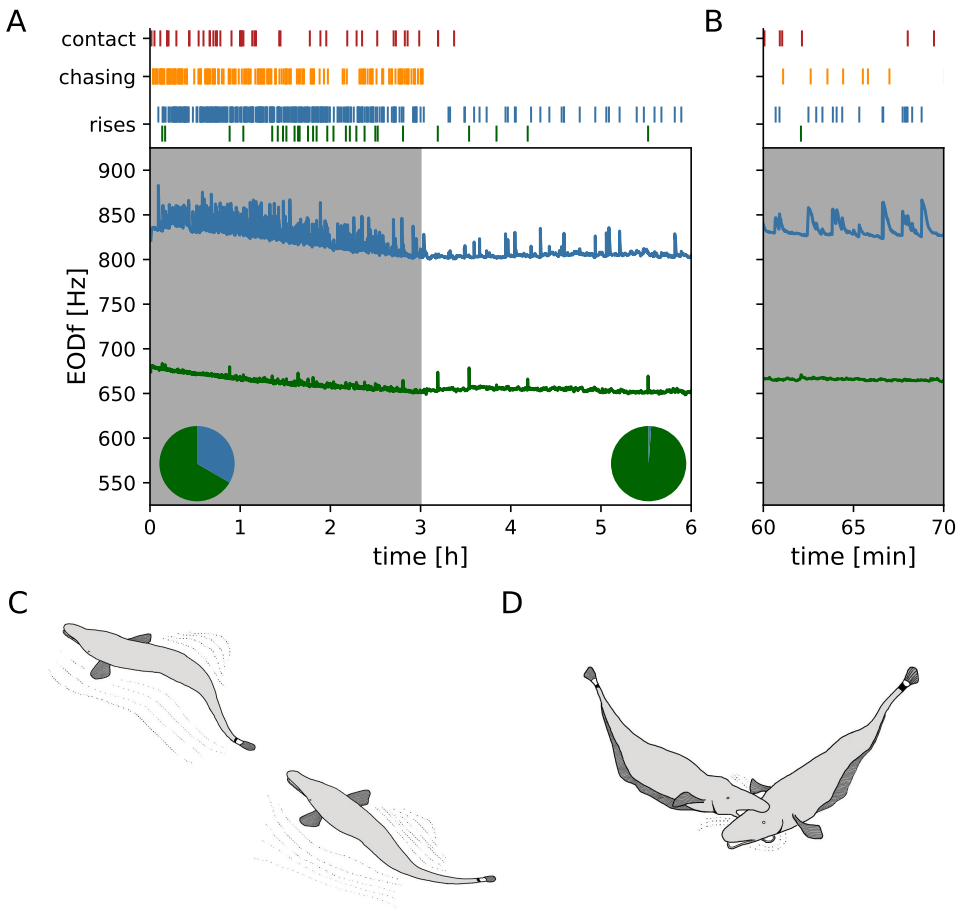


Figure 2: Behaviors and interactions of competitors during a typical competition trial. **A** EODf traces of the two fish (blue male and green female, bottom panel), time points of detected rises of both fish, physical contacts, and onsets of chasing behavior (top panels) recorded during the full 6 h trial with the first 3 h in darkness (gray background) and the last 3 h during light. Pie-charts show the probability for both competitors of being closer to or within the central superior shelter during the dark- (left) and light-phase (right). **B** A 10 min long snippet of the trial shown in A. **C** Chasing behavior as a non-contact agonistic interaction is defined as high velocity movements towards an opponent. **D** Agonistic physical contacts are short, ritualized behaviors like biting or head bumping. Both agonistic behaviors were initiated by fish later winning a trial.

Fish with higher EODf seem to win competition

Winning fish had on average higher EODfs in comparison to their opponents ($t = 2.1$, $p = 0.04$, fig. 4 A). However, in same sex pairings analyzed separately, EODf did not predict competition outcome neither in males ($t = 0.79$, $p = 0.47$, fig. 4 B) nor in females ($t = 1.4$, $p = 0.19$, fig. 4 C), but the positive slope of the logistic regressions suggests a mild influence of higher EODf in predicting the winner. Further, in mixed sex pairings, winning males always had higher EODfs and winning females always lower EODfs than their opponent, because of the sexual dimorphic EODfs in *A. leptorhynchus* (fig. 4 D & E). These mixed-sex competitions were more often won by males

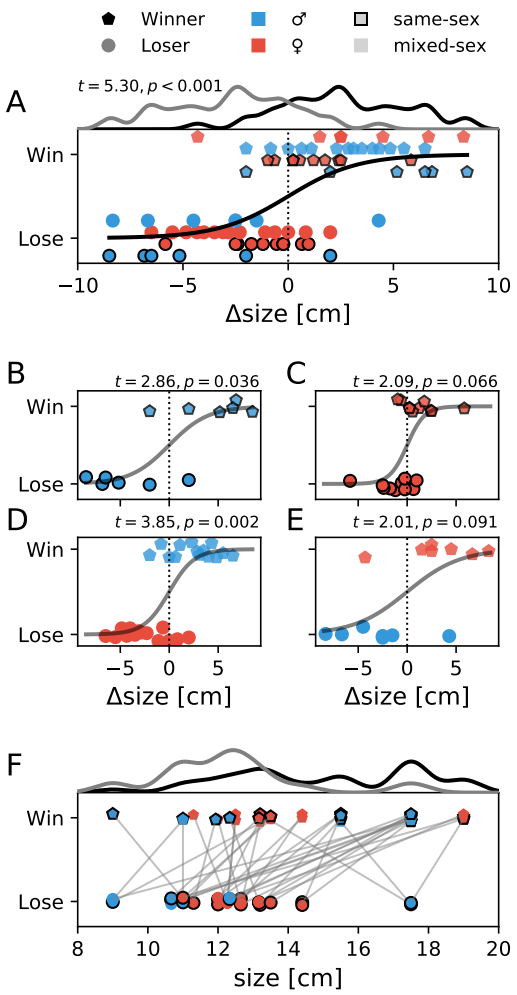


Figure 3: Body size of winners and losers. Colors and marker style indicate different pairings and the outcome of the competition. Each competition trial contributes two data points, one for the winner and one for the loser. Blue represents males, red females. Pentagons indicate winners, circles losers. Black marker edges indicate same-sex pairings. Winners and losers of each sex pairing were offset in panels A and B and jittered in panels C–F. **A** Winners were larger than their opponents as indicated by a logistic fit (black line, $t = 5.3$, $p < 0.001$) and kernel histograms of winners and losers (AUC = 90 %). Size differences are measured relative to the opponent. **B, C, D, E** Winners were larger in all sex pairings. In particular, winning males were larger than their male (B) or female (D) opponent. **F** Distributions of absolute body size of winners and losers largely overlap. The crucial factor determining winners and losers is the difference in size between opponents as shown in A. Grey lines connect pairs competing in a trial.

than by females (14 out of 21, Binomial test 14 or more males winning assuming equal chances for both sexes: $p = 0.10$). This asymmetry results in an AUC = 82 % for discriminating winners from losers based solely on sex as a rough proxy for EODf (males have high, females low EODf). Although the difference in EODfs potentially contains more detailed information than sex alone, it does not discriminate winners from loser better than sex (AUC = 75 %). Absolute EODf is even less informative about competition outcome (AUC = 65 %, fig. 4 F).

Factors influencing competition outcome

We constructed a generalized linear mixed model (GLM, Eq. (1)) predicting the competition outcome based on all the measured physical factors size, size difference, EODf, EODf difference, and sex (fig. 5 A–C) for estimating an upper bound of discrimination performance. As expected from the single-factor analysis, size difference is the only factor significantly contributing to the prediction of winners ($t = 2.4$, $p = 0.02$). The model correctly predicts the outcome of 34 of the 37 competition trials with an AUC of 94 % (fig. 5 D). Two-factor GLMs based on size differences and either sex or EODf differences perform similarly well (AUC = 93 %) and slightly better than size

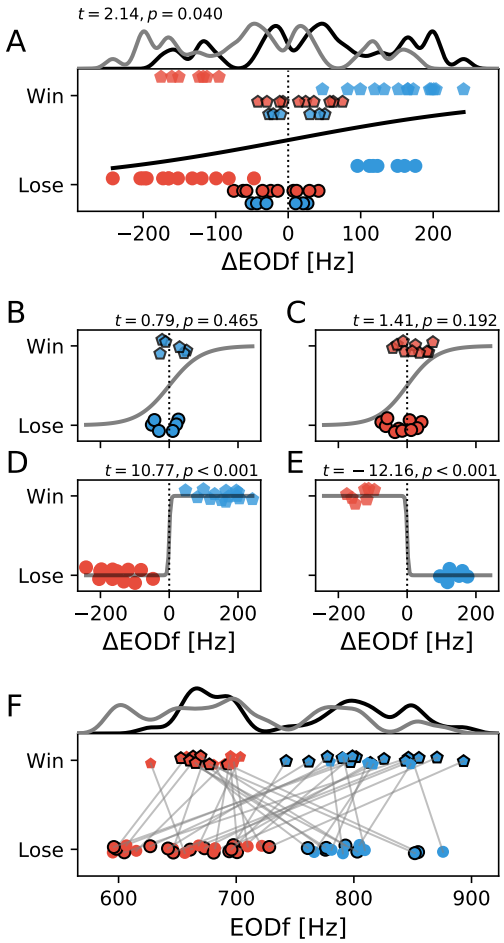


Figure 4: EOD frequencies of winners and losers. Same annotation scheme as in fig. 3. **A** Winners tend to have higher EODfs than their opponents. **B, C** Winners of same-sex encounters do not have significantly higher EODfs than losers (AUC=73 %). **D, E** In mixed sex competitions the sexual dimorphic EODf does not predict competition outcome. Males with their higher EODf can lose against females. More males ($n = 14$) were winning mixed-sex trials than females ($n = 7$), explaining the overall trend of winners having higher EODfs than losers (panel A) **F** Absolute EODf of winners and losers convey even less information about the outcome of the competitions (AUC=65 %).

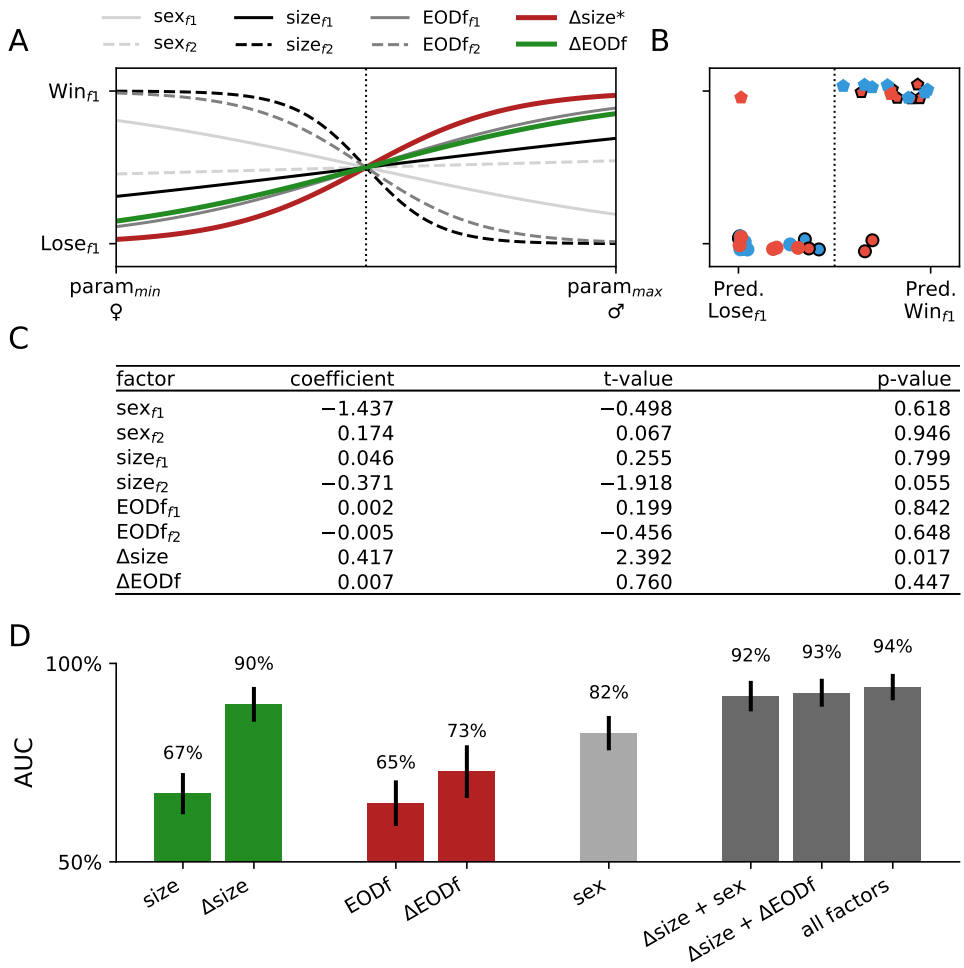
difference alone (AUC = 90 %), further questioning the role of EODfs in predicting competition outcome (fig. 5 D).

Rises

We detected in total 8 530 rises using their characteristic onset peak in EODf (fig. 6 A & B). The size of the rises, the peak EODf relative to baseline EODf before, ranged from the detection threshold of 5 Hz up to 68 Hz with a mean of 17 Hz. The distribution of rise sizes was similar in all four sex-pairing categories (fig. 6 C). We were not able to detect any dependency of our results on the size of rises. Rises categorized in distinct size categories did not behave differentially. In the following we therefore focus on an analysis of rise numbers and timing.

Losing fish emit more rises during the active phase

Rises were primarily emitted during the dark-phases, i.e. when fish were actively interacting with each other ($t = 6.7$, $p < 0.001$). The fish that later in the light phase did *not* occupy the superior shelter, produced ten-fold more rises in the dark phase (184 ± 105) than their winning competitors (18 ± 17, $t = 9.5$, $p < 0.001$, fig. 7 A). Loser rise counts were highly variable, they ranged from 0 to 419 rises per trial with a coefficient of variation of



factor	coefficient	t-value	p-value
sex$_{f1}$	−1.437	−0.498	0.618
sex$_{f2}$	0.174	0.067	0.946
size$_{f1}$	0.046	0.255	0.799
size$_{f2}$	−0.371	−1.918	0.055
EODf$_{f1}$	0.002	0.199	0.842
EODf$_{f2}$	−0.005	−0.456	0.648
Δsize	0.417	2.392	0.017
ΔEODf	0.007	0.760	0.447

Figure 5: Logistic regression models predicting the outcome of the competition experiments. **A** Visual representation of the impact of all factors (sex, absolute size, and EODf of fish $f1$ and $f2$ competing with each other, as well as their differences in size and EODf, see legend) on the generalized linear mixed model with a logistic link function. The steeper the logistic functions the more discriminative the respective factor. Size difference, Δsize, is the only significant factor (*, see C). **B** Predictions of the GLM on fish$_1$ of each of the 37 competition trials being the winner or loser based on all factors shown in A. Same marker code as in fig. 3. **C** Factors i of the GLM shown in A and B and their coefficients c_i, Eq. (1), t-statistics, and significance. The size difference between competitors is the only significant factor of the model, indicating its major influence on predicting the winner. The coefficients set the slope of respective curves shown in A. **D** Area under the curve (AUC, with standard deviation estimated by bootstrapping) extracted from a receiver-operating-characteristic (ROC) analysis to quantify the performance of single factors and combinations of factors to discriminate winners of competitions from losers. Chance level is at AUC $= 50\,\%$.

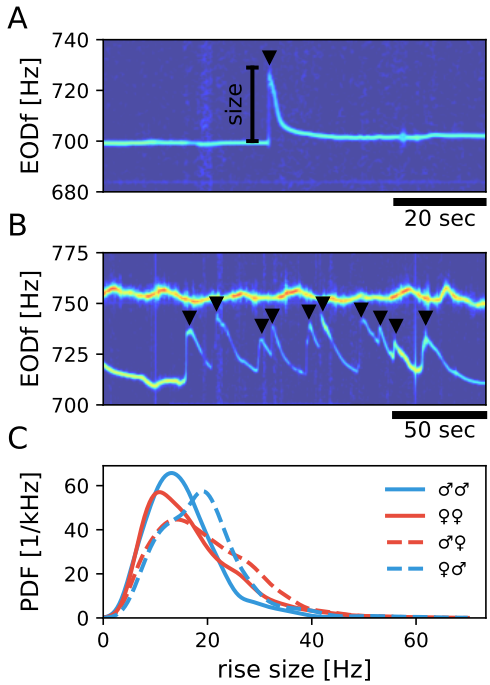


Figure 6: Characteristics of rises. **A** Spectrogram of an electric recording including the EODf trace of a single fish while emitting a rise. Rises are abrupt increases of an electric fish's EODf followed by an exponential decay back to baseline EODf. Rises were detected using their characteristic onset peak (black triangle). The size of each rise is the deviation of the peak EODf from the baseline EODf. **B** Spectrogram of a 200 second snipped of a electric recording showing EODf traces of two fish. In the lower EODf trace a series of 10 rises can be seen. **C** Rise sizes of subordinate individuals. Distributions of all sex-pairing categories (line-styles) are similar.

$CV = 0.63$.

The difference of the number of rises between the winner and the loser emitted during the dark phase almost perfectly predicts the winner (AUC = 99.9 %, figs. 7 B). Initially, discrimination performance exponentially increases from chance level to maximum discrimination starting at 5 min after the beginning of a trial with a time constant of about 5 min (figs. 7 C). The prediction level of 94 % based on the physical factors (fig. 5) is clearly surpassed after about 20 min. In that time the losing fish emitted on average 7.0 ± 5.7 rises and the winner just 1.2 ± 1.2.

The losing fish kept emitting higher numbers of rises than the winning fish throughout the dark phase of trials (figs. 7 D). In none of the trials did the competitors switch this behavior (figs. 7 E). The few instances were the fractions of rise counts of losing fish fall below 50 % are time windows with very few numbers of rises. Despite the ongoing emission of rises by the losing fish they failed to win the superior shelter.

Because of the low numbers of rises produced during the day and by winning fish, we focus in the following on rises produced by losing fish during the night. As detailed in the following, the number of rises produced by losing fish were dependent on the competitor's sex, their physical differences, and the number of trials the fish already participated in. In contrast, we found no such dependencies for the number of rises emitted by winning fish.

Loser against females emit more rises

In trials won by males, the losing competitor of either sex produced less rises than in trials won by females ($U = 98.0$, $p = 0.02$; fig. 8 A). The sex of the losing fish did not have a strong effect in both cases (male winning:

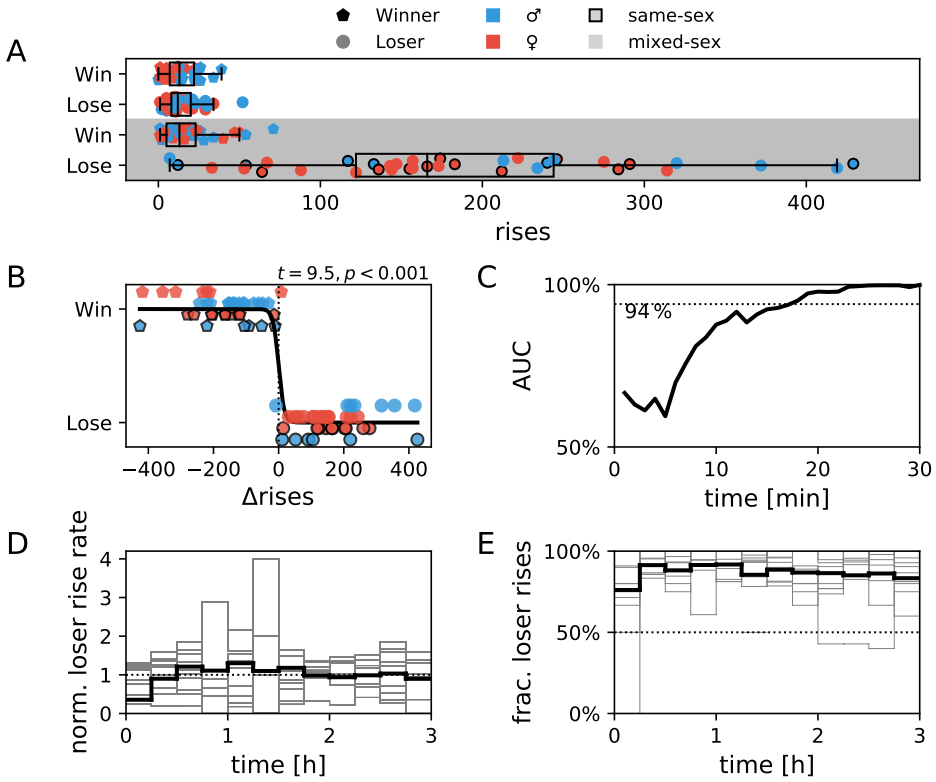


Figure 7: Rise rates of winners and losers. **A** EODf Rises were predominantly produced by losers of the competitions during the dark-phase (shaded). Winners during the dark-phase produced equally little rises as both winners and losers during the light-phase (white background). **B** Losers of competitions reliably produced more rises than winners in the dark, although absolute and relative numbers of rises varied considerably between trials. **C** Time resolved discrimination performance between winners and losers based on differences in cumulative rise counts for the first 30 min of the trials. The AUC of ROC analysis asymptotes to almost 100 % after about 25 min, indicating the outcome of the trials to be already determined the latest from this time on. For comparison, the dashed line at 94 % indicates the performance of the GLM including all physical characteristics of the fish from fig. 5 D. **D** Time course of loser rise rates during the dark phase. Rise rates of each trial (gray) were normalized to their mean rate. On average (black) rise rates reached a constant level after about 30 min. **E** Fraction of rises of losing fish quantified in 15 min time windows is consistently larger than 50 % (dashed line) throughout the whole dark period. Individual trials in gray, average over trials in black.

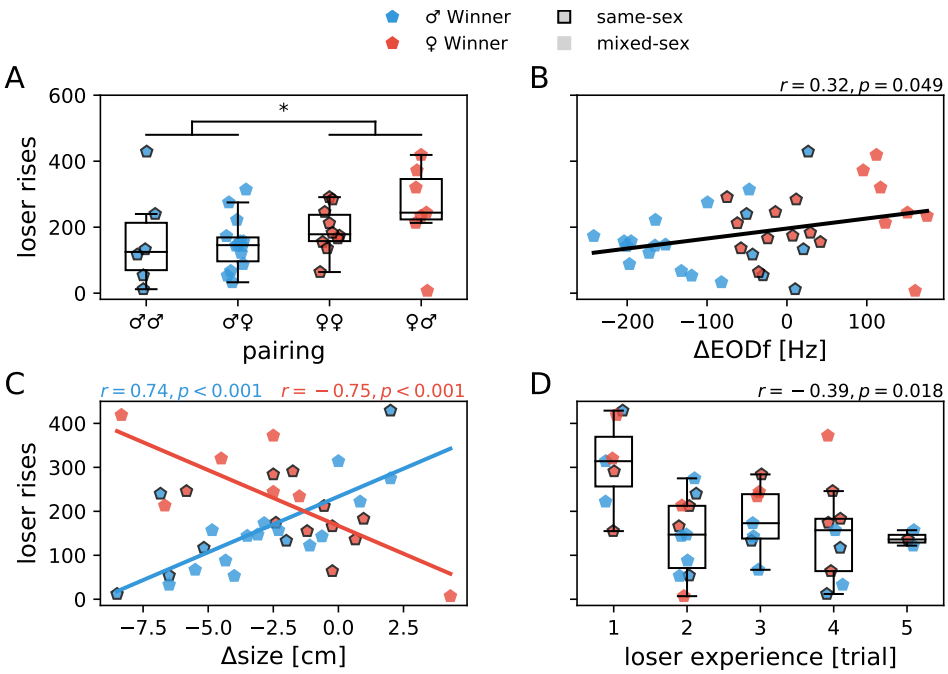


Figure 8: Dependence of rise counts of *losing* fish on physical differences between competitors and experience in the experiment. **A** Number of rises emitted by losers in different sex pairings. Markers indicate sex of winning opponent, first symbol in pairing category indicates sex of winner. In trials won by females (red) slightly more rises of the losing fish were observed than in trials won by males (blue). **B** With increasing difference in EODf to the winning fish ($\Delta\text{EODf} = \text{EODf}_{\text{loser}} - \text{EODf}_{\text{winner}}$), losing fish produced more rises. This effect rests on losing males emitting on average more rises than losing females in mixed-sex competitions (panel A) and males having higher EODfs than females. **C** In trials won by males (blue), the smaller the size difference to the winner ($\Delta\text{size} = \text{size}_{\text{loser}} - \text{size}_{\text{winner}}$) the more rises were produced by the losing opponent of either sex. In trials won by females (red), the opposite effect was observed. The larger the size difference the more rises were emitted by the losing fish. Correlation coefficients and their significance are displayed in corresponding colors. **D** With increasing experience in the experiments, losing fish produced less rises per trial.

$U = 37.0$, $p = 0.36$; female winning: $U = 19.0$, $p = 0.07$). Consequently, the number of rises produced by losing fish correlated positively with the difference in EODfs, because of the sexually dimorphic EODfs in *A. leptorhynchus* ($r = 0.32$, $p = 0.05$; fig. 8 B).

Sex-specific dependence of rise emission on body size differences

The dependence on sex of the winner was even stronger when considering differences in body size. In pairings won by males, the number of rises emitted by the loser of either sex increased when the size of the losing fish approached and exceeded the size of the winning male ($r = 0.74$, $p < 0.001$, fig. 8 C). On the contrary, in pairings won by females the number of rises of the losers decreased the more similar the competitors were in size ($r = -0.75$,

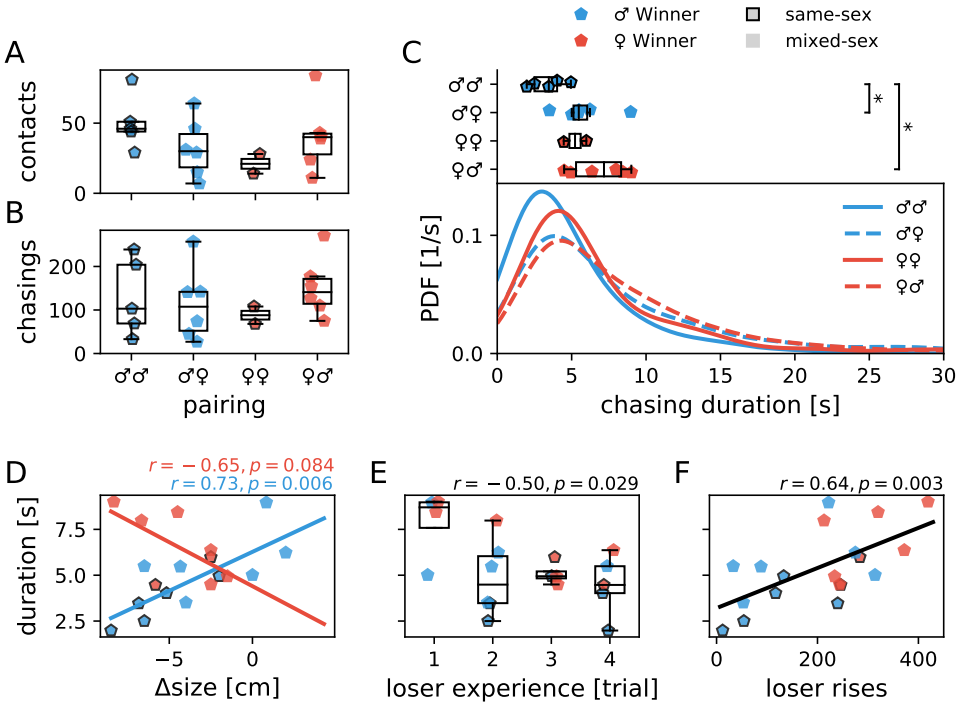


Figure 9: Agonistic interactions. While the number of agonistic interactions was independent of the physical characteristics of the opponents, the duration of chasings showed similar dependencies as the number of rises. **A** Number of agonistic contacts and **B** chasing behaviors during the active phase were independent of the different sex pairings. **C** Chasings were the shortest in male-male interactions. Probability densities (bottom) show distributions of durations of all chasing events in each sex-pairing category, box-whiskers and markers (top) their median duration per trial. In the annotations of the sex pairings the first symbol indicates the winner. **D** In trials won by males the median chasing duration increased with losers approaching and exceeding the size of the winner ($\Delta\text{size} = \text{size}_{\text{loser}} - \text{size}_{\text{winner}}$). In trials won by females the opposite effect was observed. Correlation coefficients and their significance are shown in corresponding colors. **E** With increasing experience in the experiments the median chasing duration decreased. **F** The median chasing duration increased with the number of rises emitted by losers.

$p < 0.001$, fig. 8 C).

Habituation of rise rates

The fish's experience in the experiment also influenced the number of emitted rises. With increasing experience, that is the higher the number of trials a fish participated in, the number of rises produced by the losing fish decreased ($r = -0.39$, $p = 0.02$; fig. 8 D). This habituation was independent of the paired sexes.

Agonistic interactions

We detected in total 2 480 chasing behaviors and 804 agonistic interactions involving physical contact in the 19 trials were we recorded and evaluated these behaviors with infrared video. Agonistic interactions were exclusively detected during the dark-phase of each trial and stopped with or shortly after the onset of the light-phase (fig. 2). In random visual inspections of video recordings we found agonistic attacks to always be initiated by those fish later identified as winners. Per trial we observed on average 128 ± 72 chasing behaviors lasting each 7.4 ± 6.5 seconds and in addition 36 ± 21 physical contacts. The number of physical contacts between the competitors tended to increase with the number of chasings ($r = 0.37$, $p = 0.12$). Interestingly, none of the so far discussed factors had an impact on the number of both categories of agonistic interactions, including the competitor's sexes (fig. 9 A & B), their size and EODf differences, and their experience in the experiment. In particular and similar to the rises, the number of interactions per trial were highly variable (contacts: $CV = 0.55$, chasings: $CV = 0.58$) and neither the number of contacts ($r = -0.27$, $p = 0.24$) nor the number of chasings ($r = 0.30$, $p = 0.20$) correlated with the number of rises.

Sex-specific dependence of the duration of chasing behaviors on body size differences

However, the duration of the chasing behaviors were sensitive to these factors. The median chasing durations were shorter in male-male competitions compared to other pairings ($U = 5$, $p = 0.003$). In other pairings the median chasing durations were indistinguishable (fig. 9 C).

In trials won by males the duration of chasings increased with the size of the losing fish relative to the size of the winner ($r = 0.73$, $p = 0.006$, fig. 9 D). Contrary, in trials won by females we observed a trend towards shorter chasings with decreasing size difference ($r = -0.65$, $p = 0.08$, , fig. 9 D). Chasing durations were not correlated with differences in EODf between the competitors ($r = 0.18$, $p = 0.45$).

Habituation of the duration of chasing behaviors

Beyond physical differences, the experience of the competitors in the experiment influenced the duration of chasing behaviors. The duration of chasings decreased with the number of trials the losing fish had experience with ($r = -0.50$, $p = 0.03$, fig. 9 E). The number of chasing behaviors was unaffected by experience ($r = 0.05$, $p = 0.83$). Finally, the observed communication behavior had an impact on the duration of chasings. In trials where losers produced more rises chasings lasted longer ($r = 0.64$, $p = 0.003$, fig. 9 F).

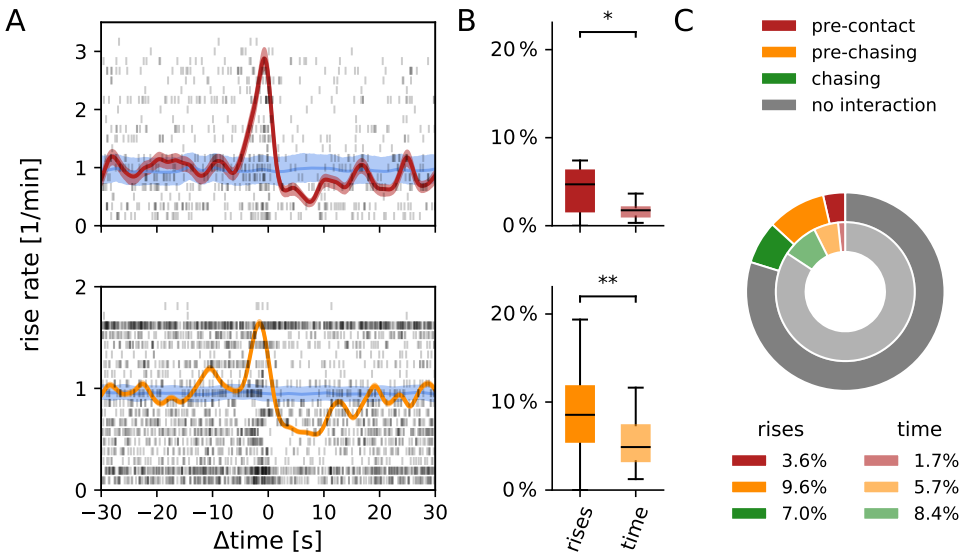


Figure 10: Rises trigger dominants into initiating agonistic attacks. **A** Rise times and rates relative to physical contacts (top) and the onset of chasing behaviors (bottom). Each line of the rasters (black) shows rise times aligned to all agonistic events of a single competition trial. Corresponding rise rates (red/orange) were obtained by convolving rise times with Gaussian kernels with standard deviation of 1 s and normalizing by the number of agonistic events and trials. 98 % confidence intervals (reddish/orangish areas) were estimated by jackknifing. The Null-hypothesis (mean in blue, 1st and 99th percentile in bluish) was obtained by randomly permuting rise intervals. **B** Fraction of all rises within the dark phase of a trial that occurred within five seconds prior to agonistic contacts (top) or the onset of chasing behaviors (bottom) and the corresponding times these five-second windows make up relative to the total dark-phase lasting three hours. **C** Mean fractions of rises (outer circle) occurring within five seconds prior to physical contacts (red), prior to the onset of chasing behaviors (orange), and during chasings (green) and the corresponding times (inner circle) over all trials, indicating that in most cases rises did not evoke agonistic interactions.

Some rises triggered agonistic interactions

Within about five seconds prior to agonistic interactions, rise rates accumulated over all agonistic interactions were increased (fig. 10 A & B). Because the baseline rate of rises is just one rise per minute this does *not* imply that a burst of rises triggered agonistic interactions. Rather, the probability of a single rise to evoke an agonistic interaction is increased. In particular, chances for agonistic contacts were higher 0.7 s after a rise and chances for chasing behaviors were higher 1.6 s after a rise. Consequently, the fraction of rises occurring within five seconds prior to agonistic onsets exceeded the fraction expected from the corresponding times, the number of agonistic interactions times five seconds (agonistic contacts: 3.6 % versus 1.7 %, $t = 2.9$, $p = 0.01$; chasing behaviors: 9.6 % versus 5.7 %, $t = -3.1$, $p = 0.007$; fig. 10 B).

Reduced rise rates during chasings

Rise rates were approximately halved during chasings (fig. 10 A, bottom). After the onset of chasings rise rate was reduced for about ten seconds, clearly outlasting the average duration of chasing behaviors (7.4 s). Again this just implies that the chances to observe a single rise during chasing is reduced. About 7.0 % of rises occurred during chasings, less than expected from the corresponding time covered by the chasings (8.4 %, $t = 3.4$, $p = 0.003$).

Most rises did not trigger agonistic interactions

All the rises emitted within five seconds prior to agonistic contacts and chasings as well as during the chasings make up 20 % of all rises (fig. 10 C). Although this is disproportional more than expected from the corresponding times, the majority of the rises (80 %) did not trigger any obvious interaction. Also note that the fish engaged in actual agonistic interactions in form of chasing behaviors in just 8.4 % of the time. Vice versa, agonistic interactions were *not* exclusively triggered by rises emitted by losers. Rises preceded 15.6 % of all chasings and 19.4 % of physical contacts, respectively.

Discussion

In staged competition experiments between pairs of the electric fish *A. leptorhynchus* of either sex we found size difference between competitors to be the best predictor for the fish winning the superior shelter. In addition, difference in EODf slightly improved the prediction. During the initial three hour dark (active) phase of the competition experiment, fish engaged in physical interactions like head bumping, biting and chasing behaviors, and emitted electrocommunication signals of which we analyzed rises. These signals were primarily emitted by those fish later identified as losers. Based on the numbers of rises we have demonstrated that the outcome of the competition was set the latest after the initial 25 minutes of a trial. Nevertheless losing fish consistently continued to emit rises with a higher rate than winners. In none of the trials did we observe a switch in rise emission changing the competition outcome. Rises were costly for the loser in that they raised chances to be attacked and chased for a longer time by the winner. Further, the number of emitted rises of the loser increased the closer it was in size to a winning male, but decreased the closer in size to a winning female. Our results suggests that losers emit rises to raise their social status and to claim resources beyond winning the shelter.

Dominance in A. leptorhynchus

Animals often compete over limited resources with conspecifics in their proximity. To avoid costly, repetitive fights they often establish a dominance hierarchy that regulates the access to resources (e.g. Janson, 1985; Webster and Hixon, 2000; Sapolsky, 2005). *A. leptorhynchus* can be found in small groups in the field (Stamper et al., 2010) and loosely aggregated in microhabitats offering suitable shelter in large laboratory tanks (Raab et al., 2019). Only in breeding season they compete for mates (Hagedorn and Heiligenberg, 1985; Henninger et al., 2018). During the day these nocturnal fish mainly compete for optimal shelter (Dunlap and Oliveri, 2002; Batista et al., 2012). This rivalry leads to the establishment of a dominance hierarchy in *A. leptorhynchus* where more dominant fish have priority access to these resources (Dunlap and Oliveri, 2002; Hagedorn and Heiligenberg, 1985; Henninger et al., 2018). Our experiments tested initial encounters, where fish were unfamiliar to each other and still needed to establish a dominance hierarchy between each other. In such situations animals would need to rely on dominance cues and communication signals to assess each other's social status and claim on resources in order to avoid costly fights (Fernald, 2014).

Body size as proxy for dominance

Across species the social status of an individual is determined by its ability and motivation to compete with conspecifics (Parker, 1974; Dunham, 2008). In our experiments body size difference between competitors was the best predictor for the outcome of the competitions (figs. 3 & 5). This is not unusual. Larger animals are often found to be more dominant, since their physical advantages reflect their fighting abilities (Parker, 1974). Larger animals also have increased metabolic costs, increasing their valuation of food (Wauters and Dhondt, 1992). Since a higher social status is associated with increased food intake, this further reinforces the link between body size and dominance (Parker, 1974; Dunham, 2008).

In our experiments mixed-sex competitions were slightly more often won by males than females, but mainly because of a bias of males being larger than females in these trials (fig. 3). Overall, body size was independent of sex (fig. 1 A), and associated metabolic requirements and fighting abilities can therefore be assumed to be similar for both sexes (Parker, 1974; Dunham, 2008). Further, fish were not in breeding condition, eliminating the possibility of additional, asymmetric metabolic requirements for either sex (Wauters and Dhondt, 1992). The similar physical conditions and metabolic requirements of fish of either sex when not in breeding season suggest dominance in *A. leptorhynchus* to be independent of sex (Parker, 1974). Our results together with recent studies on other gymnotiform electric fish support this expectation (Batista et al., 2012; Zubizarreta et al., 2020) and reject

previous conclusions of less distinct dominance hierarchies in females (Hagedorn and Heiligenberg, 1985; Dunlap and Oliveri, 2002).

Male *A. leptorhynchus* have been described as more territorial and to be more aggressive (Bastian et al., 2001; Zupanc and Maler, 1993; Cuddy et al., 2012), making males slightly more motivated to acquire and/or hold a higher social status and associated benefits. In addition, the sexual dimorphic EODf in *A. leptorhynchus* might incur higher metabolic cost for males to generate EODs of higher frequency (Lewis et al., 2014). This could be another reason why males in *A. leptorhynchus* might be more eager to insist on a higher social status. Indeed, when evaluated separately, the correlation between body size and dominance was more distinct in trials won by males (fig. 3 B & D).

EODf is not a primary predictor of competition outcome

Anecdotal observations in the lab and in the field show that *A. leptorhynchus* males with higher EODf fertilize more eggs (Hagedorn and Heiligenberg, 1985; Henninger et al., 2018), suggesting EODf to signal dominance at least in males in breeding season. Indeed, mature males increase both EODf and the androgen 11-ketotestosterone following environmental cues simulating the onset of breeding season (Cuddy et al., 2012). Outside the breeding season males with higher EODf have been found to solitarily occupy their preferred shelter (Dunlap and Oliveri, 2002) and to be more territorial during the day (Raab et al., 2019). Also in *Sternarchorhynchus* sp. did higher frequency fish win the shelter over lower frequency ones (Fugère et al., 2011). In contrast, in our sample with approximately similar numbers of fish we found only an insignificant influence of EODf on dominance (figs. 4 & 5). At the same time, EODf was not correlated with body size in our fish (fig. 1 A), whereas in Dunlap and Oliveri (2002) EODf was weakly but significantly correlated with body size. This further supports our observation of body size being the primary cue for dominance at least in non-breeding contexts. A possible influence of EODf on dominance appears as a secondary effect only in cases where EODf happens to be correlated with body size.

Electrocommunication with rises

A. leptorhynchus has been shown to use a rich repertoire of electrocommunication signals in social interactions (Smith, 2013). Some of the various types of chirps, transient elevations of EODf within less than about 500 ms, are used in agonistic, same sex encounters, to deter agonistic attacks (Hupé and Lewis, 2008; Henninger et al., 2018) and in courtship where synchronization of spawning is probably only one of their many functions (Hagedorn and Heiligenberg, 1985; Triefenbach and Zakon, 2003; Cuddy et al., 2012; Henninger et al., 2018). In contrast, evidence for the function of rises is scarce and inconsistent. Rises are characterized by smaller but much longer increases

in EODf in comparison to chirps (Hopkins, 1974; Hagedorn and Heiligenberg, 1985). They vary considerably in their size (a few up to several tens of Hertz, fig. 6) and over three orders of magnitude in their duration (less than a second to up to a few minutes, Tallarovic and Zakon, 2002). Some authors attempted to categorize them into small, medium, and long rises (Hagedorn and Heiligenberg, 1985; Tallarovic and Zakon, 2002), or to single out specific types of rises, like "yodels" (Dye, 1987). On the other hand, others acknowledged rises to rather form a continuum of signals ("gradual frequency rises", Triefenbach and Zakon, 2008). The large number of rises we detected in our experiments clearly formed a continuous distribution of sizes (fig. 6 C) and we found no obvious indication of distinct functional roles of rises of different sizes.

At time scales longer than a few seconds electric fish produce another category of signals where EODf stays at an elevated or reduced EODf. These have been discussed as jamming avoidance responses in *Eigenmannia* (Bullock et al., 1972). In contrast, *A. leptorhynchus* has been shown to use similar signals (non-selective responses, Dye, 1987) to battle with their EOD frequencies, both in the lab between females (Triefenbach and Zakon, 2008) and in the field (Benda, 2020). A recent field study also observed similar active jamming behaviors in *Eigenmannia* in the field (Fortune et al., 2020). If at all we observed only a few of such signals, but they appeared more like merged rises. On smaller, sub-second timescales rises overlap with chirps, but these were not detected by our analysis because of the 1.6 s long FFT windows we used. However, these long analysis windows allowed us to automatically track EODf traces and long rises, that stood out as prominent and frequently emitted signals between the freely interacting fish.

Function of rises

Previous studies suggested various divergent functions of rises. Rises have been observed to be followed by attacks or bouts of aggression, both in *Eigenmannia* (Hopkins, 1974) and *A. leptorhynchus* (Triefenbach and Zakon, 2008), and to primarily be emitted by subordinates in *Apteronotus albifrons* (Serrano-Fernández, 2003). We quantified these behaviors and also found rises in *A. leptorhynchus* to be primarily emitted by subordinates during the dark-phase of each trial (fig. 7 A & B) and to trigger dominants into initiating agonistic attacks within a few seconds (fig. 10). These common findings further support the hypothesis of rises being conserved signals for social interactions in gymnotiform electric fish (Turner et al., 2007).

Rises also have been described as submissive signals (Hopkins, 1974; Serrano-Fernández, 2003). Our data rule out this interpretation. Rises did not prevent but rather triggered the dominant fish into agonistic behaviors (fig. 10), chasings lasted longer the more rises the subordinate produced (fig. 9 F), and the number of agonistic behaviors was not reduced by higher number of rises but was completely independent of rises. Our findings do not support

rises to function as "victory cries" after an EOD mimic was switched off (Dye, 1987). In our setting, however, such situations were not possible, because the fish were not able to evade each other. Further, both rises triggering agonistic attacks and rise rates being decreased during chasing behaviors (fig. 10) does not support them to be a general expression of stress (Smith, 2013), since stress levels are usually increased during agonistic encounters (Creel et al., 1996). Long rises have also been suggested as an advertisement of status or reproductive condition (Tallarovic and Zakon, 2002), or to signal attack motivation (Triefenbach and Zakon, 2008). Our data allow to substantiate and refine these more subtle roles of rises in negotiating dominance as we discuss in the following.

Rises aim to decrease dominance differences

In our experiments winners could reliably be predicted within the initial 25 min of each trial based on the numbers of rises emitted by either fish (fig. 7 C). Nevertheless, subordinates continued to emit more rises than the winner until the end of the dark-phase (fig. 7 D). Never did we observe a switch in communication behavior indicating a switch in dominance (fig. 7 E). Therefore, rises were apparently not used to obtain dominance. What then is the purpose of rises?

Communication signals in general aim to alter the behavior of receivers in a net beneficial fashion for the sender and they are only produced if the potential benefits resulting from it outweigh the costs (Endler, 1993; Seyfarth et al., 2010). Accordingly we expect subordinates to have a benefit from their continuous efforts to emit rises. The more so because the produced rises provoked attacks by the competitor (fig. 10). We suggest rises to be produced not to switch dominance, but to decrease the dominance difference, or relative dominance, to a conspecific and therefore increase an individual's access to resources by signaling a partial claim. Consequently, the production of rises should reflect a subordinate's potential and motivation to compete with conspecifics.

Indeed, the number of rises was dependent on physical differences between competitors (Triefenbach and Zakon, 2003) and their social experience in the experiment, factors which can be associated with an individuals ability and motivation to compete (fig. 8). In trials won by males less rises were recorded in comparison to trials won by females (fig. 8 A), but their number increased with decreasing size difference between competitors (fig. 8 C). Dominant males are more territorial (Dunlap and Oliveri, 2002), can be assumed to be more aggressive (Zupanc and Maler, 1993), show more distinct dominance displays (Raab et al., 2019), and can be assumed to have higher intrinsic motivation to keep their dominance status. Thus, raising a claim against males comes with higher potential costs, resulting in less rises produced by subordinates in general. With decreasing size difference potential costs decrease and chances of success increase (Clutton-Brock et al., 1979). Emitting more rises against a male of similar or even smaller size might have better chances to pay off. Hagedorn and Heiligenberg (1985) reported

female *Eigenmannia* to emit many rises in early morning hours. One possible explanation could be that the females claimed shelters for the upcoming day against males.

Females, in contrast, are less territorial and more tolerant against conspecifics (Zupanc and Maler, 1993; Dunlap and Oliveri, 2002; Cuddy et al., 2012). Chances of subordinates to successfully raise a claim and reduce relative dominance might be higher. Indeed, in female dominated trials rises were slightly more frequent (fig. 8 A) and the number of rises emitted by the subordinate male or female even increased with size difference (fig. 8 C). Stronger inferiority would not make it impossible to raise a claim but would simply require more efforts by subordinates to be acknowledged in their claim to improve access to resources.

Agonistic attacks reinforce dominance

In addition to communication signals, agonistic interactions, often ritualized, are an important element in establishing dominance. Especially when competitors are of similar physical condition and have similar interests in acquiring dominance or to raise in social status, cues and signals become insufficient to enforce the social order and agonistic interactions emerge (Parker, 1974). In our experiments we observed biting and head bumping as well as chasing behaviors to be initiated by dominants (Triefenbach and Zakon, 2008). The number of both types of agonistic interactions was not dependent on any of the measured parameters (e.g. fig. 9 A & B), whereas the duration of chasing events showed similar correlations as those of rises (fig. 9 D – F). This similarity suggests a direct link or a common reason for both.

Dominants initiated agonistic attacks against subordinates. About a third of the contacts and chasings followed within a few seconds of about 13 % of rises emitted by subordinates (fig. 10), quantifying earlier observations in *A. leptorhynchus* (Hopkins, 1974; Triefenbach and Zakon, 2008) and detailing findings in *A. albifrons* (Serrano-Fernández, 2003). This causal relation between rises and attacks clearly qualify rises as communication signals. In dominance hierarchies agonistic interactions are often used to reinforce dominance, especially when the behavior of subordinates interferes with the interests of dominants (Creel et al., 1996; Janson, 1985). While being chased subordinates emitted less rises (fig. 10 C). The increased intimidation caused by the ongoing agonistic attack could decrease their motivation to interfere with the dominant's interest and inhibit their rise production.

As mentioned before, behavioral characteristics and potentially higher resource valuation of males suggests them to be more eager to raise in dominance or to defend their higher social status and associated resources. However, with decreasing size difference to a dominant male, fighting abilities of competitors can be assumed to converge and the motivation of subordinates to compete increase. Then subordinates take their chances and challenge the competitors with more rises (fig. 8 C), while dominants attack subordinates for longer to emphasize

and defend their dominance (fig. 9 D).

On the contrary, in female dominated trials the duration of chasing behavior decreased the smaller the size difference between competitors (fig. 9 D). The smaller a subordinate in comparison to a winning female the more rises it produced (fig. 8 C), making it necessary for the female to more strongly emphasize its dominance by longer chasings.

Negotiating skewness in a dominance hierarchy

In summary, our experiments suggest that by means of rises subordinates try to reduce the relative dominance to their competitors without questioning their rank and thereby to gain better access to resources. This is to some extend tolerated by dominant fish, because they initiated agonistic attacks in response to only about 13 % of rises (fig. 10 C). The agonistic attacks are most likely launched to keep subordinates under control, since they try to interfere with the dominant's interests. The interplay and balance of rises of subordinates on the one hand and agonistic attacks of dominants on the other hand could define the dominance difference between the competitors and thereby the skewness in access to resources. The independence of rise counts and number of agonistic interactions in our experiments support this hypothesis. Both rise counts and number of agonistic behaviors varied a lot between trials and did not correlate with any of the measured characteristics of the fish. This would fit our assumption of these signals and behaviors to reflect status and motivation of the fish.

Only once did we observe the dominant fish to share the superior shelter with the subordinate at the end of a trial. In this mixed-sex trial, the smaller male (11.9 cm) was continuously emitting 180 rises during the dark phase and apparently succeeded in reducing relative dominance difference to the larger female (12.5 cm, no rises during dark-phase) by gaining access to the shelter. Unfortunately we do not know whether the dominant female attacked the male to keep the dominance difference, since this was one of the early trials without video recordings. Nevertheless, this exceptional trial further supports our hypothesis of subordinates emitting rises in order to gain partial access to resources.

Rises have been observed to be produced by fish interacting in a huge laboratory tank where plenty of suitable shelters were available (Raab et al., 2019), as well as in the field where fish could easily evade each other (personal observation TR & JB). Together with our finding that subordinates never managed to gain dominance it seems unlikely that rises are used to only negotiate about currently present resources, like the shelter in the competition experiment. We rather suggest that rises play a major role in improving dominance status in general, in order to gain access to currently absent but relevant resources, like for example food.

Conclusion

Social status in dominance hierarchies regulates access to resources (Janson, 1985; Wauters and Dhondt, 1992; Webster and Hixon, 2000; Taves et al., 2009). Most often dominance is attained and reinforced solely using physical interactions (e.g. mammals: Wauters and Dhondt, 1992; Clutton-Brock et al., 1979; birds: Rat et al., 2015; fish: Webster and Hixon, 2000; Taves et al., 2009). Therefore, an individual's body size reflecting its fighting ability usually is the best proxy for dominance. However, when social hierarchies are exclusively shaped by agonistic interactions, social status can only be improved by subduing a more dominant conspecific. With their large repertoire of electrocommunication behaviors electric fish employ an additional modality to interact with each other and to potentially communicate intents, needs, and motivations (Smith, 2013). Our results demonstrate that *A. leptorhynchus* might use rises to fine tune the social hierarchy within the persisting social order and without further escalating agonistic interactions. This communication system allows them to populate neotropical rivers in high densities (Albert and Crampton, 2005), without costly physical interactions.

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Author contributions

T.R. designed the experiment, measured and analyzed data, and wrote the manuscript. S.B. and S.E. measured and analyzed the data. J.B. discussed the experiment, advised data analysis, and edited the manuscript.

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