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ARTICLE

Neotropical dancing frog: the rich repertoire of visual displays in a hylodine species

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Abstract

During reproductive season, males usually must defend their territory against competitor males and attract females for reproduction. Acoustic signals evolved as an alternative to physical attacks, thus reducing injuries to both opponents during a territorial dispute, but they are also the primarily trait used by female frogs to select males. However, there is some recent evidence that visual signalling also can be important during social interactions in frogs. Here, for the first time, we describe the sophisticated visual behaviour of *Hylodes meridionalis*, a diurnal species that is endemic to the southern Atlantic Forest, where it inhabits fast streams. We submitted resident males to mirror self-image presentations to simulate the presence of an intruder male in their territories. Furthermore, we collected observations from close-range interactions between individuals of this very shy species. We observed seven types of visual displays: toe flagging (slow up-and-down movements of one or more toes), arm lifting (rapid up-and-down movements of one arm), leg lifting (rapid up-and-down movements of one leg), arm waving (lifting an arm and waving it in an arc), both legs kicking (rapidly stretching both hind limbs towards the back), foot flagging (slowly raising one hind limb in a semi-arch movement) and throat display (pulsation of one or both paired lateral vocal sacs without sound production). Only the kicking of both legs was displayed exclusively by females; toe flagging and foot flagging were displayed by males only during agonistic interactions. The frequency of visual displays (7 types, 117 events) was much greater than that of acoustic signals (3 types, 66 events). Our data demonstrate that the visual repertoire of the genus *Hylodes* is richer than previously noted and that visual display behaviour in anurans could be more common than previously believed. Therefore, this characterisation study aids our understanding of the function of the rich repertoire of visual displays in frog species and highlights that ethologists should be directing more of their attention towards this poorly explored anuran behaviour.

Keywords Visual displays · Territoriality · Courtship · Limb lifting · Foot flagging · Arm waving · *Hylodes* · Anuran

Introduction

Communication involves information transfer between individuals via signals, which act by modifying the behaviour of the receiver and can occur at both intra- and interspecific levels (Rendall et al. 2009). In anuran amphibians, intraspecific communication occurs mainly during the reproductive season, when males typically attract females for mating and defend their territory against any competing males (Wells 2010). In most species, males produce advertisement calls to attract females and to facilitate territorial spacing among males, territorial calls during territorial disputes, and courtship calls for close-range communication between a male and a female aimed at stimulating and orientating the female (Wells 2010; Toledo et al. 2015). Although anurans communicate mostly by acoustic signals (Ryan 2001), there is some

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evidence that visual signalling also can be important during social interactions (e.g. *Micrixalus saxicola*, Preininger et al. 2013; *Staurois parvus*, Grafe and Tony 2017).

According to Hödl and Amézquita (2001), for a visual signal to be effective, it must be redundant, visible, and stereotyped, and it must elicit an immediate response in the receptor. Sexual selection and intraspecific competition, such as territorial disputes among males, can constitute evolutionary pressure and character divergence pressure (Nosil 2012). Recently, various visual displays have been described for anurans in different social contexts (Hödl and Amézquita 2001; Biju et al. 2014; Furtado et al. 2017). As an example, in the anuran family Hylodidae, among the dynamic behaviours displayed during intraspecific communication, limb movements and posture raising are the most common visual displays reported during aggressive and/or reproductive interactions (Caldart et al. 2014; Forti and Castanho 2012; de Sá et al. 2016).

The Hylodidae family is a monophyletic group with three genera (*Crossodactylus*, *Hylodes* and *Megaelosia*) and 47 known species (Frost 2019). To date, visual displays have been reported for all hylodines (10 species) in which this behaviour has been investigated: *Crossodactylus schmidti* (Caldart et al. 2014), *C. gaudichaudii* (Weygoldt and Silva 1992), *Hylodes japi* (de Sá et al. 2016), *H. perere* (Silva and Benmaman 2008), *H. dactylocinus* (Narvaes and Rodrigues 2005), *H. asper* (Haddad and Giaretta 1999; Hartmann et al. 2005), *H. nasus* (Wogel et al. 2004), *H. cardosoi* (Forti and Castanho 2012), *H. heyeri* (Lingnau 2003) and *H. phyllodes* (Hartmann et al. 2005). Hödl and Amézquita (2001) suggested that the genus *Hylodes* is the most promising group for studying the evolution of visual communication in anurans due to their diurnality and their reproduction in noisy streams. Daylight facilitates signal visualisation and information transfer, and noisy environments such as waterfalls can reduce the efficiency of acoustic signals, favouring the use of visual signals (Hödl and Amézquita 2001; Caldart et al. 2014). For example, males of *Staurois parvus* present a diurnal habit and increase foot flagging displays and decrease advertisement call emission during intraspecific interactions when submitted to high levels of stream noise (Grafe and Tony 2017).

Hylodes meridionalis (Mertens 1927) belongs to the *Hylodes lateristrigatus* group (Frost 2019) and is endemic of the southern mountain slopes of the Atlantic Forest (Kwet et al. 2010). During the reproductive season (October–February), males call during daytime along fast streams of clean water, mostly on rocks or perched on fallen logs (Kwet et al. 2010). *Hylodes meridionalis* males are territorial and defend their calling sites using acoustic signals (Lingnau et al. 2013). Their advertisement and territorial calls were described by Lingnau et al. (2013). Kwet et al. (2010) observed leg movements displayed by individuals under natural conditions. However, the visual repertoire of *H. meridionalis* has not been described in detail.

Several sample designs can be employed to study anuran visual behaviour: (1) observations of natural encounters between individuals (Wogel et al. 2004); (2) mirror self-image presentations (Pombal et al. 1994); (3) picture or video presentations (Reichert and Höbel 2015); (4) introducing adult males/females next to resident individuals (Lindquist and Hetherington 1998); and (5) presentations of artificial models (Preininger et al. 2013). In the present paper, we report a study in which we used mirror self-image presentations to simulate the presence of conspecific intruder males (i.e. the reflection in the mirror simulates the presence of a signal receiver; Furtado et al. 2017) with the purpose of describing the visual repertoire of *H. meridionalis* males during agonistic interactions. In addition, we describe the types and frequency of visual displays during natural close-range encounters between individuals. Comments on other aspects of natural history, such as acoustic communication, are also presented.

Materials and methods

Study site

This study was conducted in January, September and November 2016 and in February 2017 over the course of 20 nonconsecutive days, with an average of five to six work hours in the field per day, in three fast streams in the Atlantic Forest (Fig. 1); specifically, the São Francisco de Paula National Forest (Flona-SFP) in southern Brazil (29°29′13.3″S and 050°13′12″W). Flona-SFP has an area of 1606 ha, of which 56% is native forest (Narvaes et al. 2005). The vegetation consists mainly of a mosaic of moist *Araucaria* forests, steppe formations, and introduced *Pinus* plantations (Backes et al. 2005). The Flona-SFP region has a temperate climate with an average annual rainfall of 2200 mm and a mean temperature of 14.5 °C (Ferreira and Eggers 2008). However, when the data were collected (the summer season), the air temperature varied from 17 to 24.4 °C and the relative humidity varied from 78 to 96% (measured with a TFA digital thermo-hygrometer). The relief in Flona-SFP is wavy, and is permeated by rivers in which groups of *Hylodes meridionalis* individuals can be observed feeding and calling (pers. obs.).

Data collection

We observed 18 males and two females of *Hylodes meridionalis* (87 min of recordings) in natural conditions. We identified the males through the calls they produced, and we identified the females through an absence of call

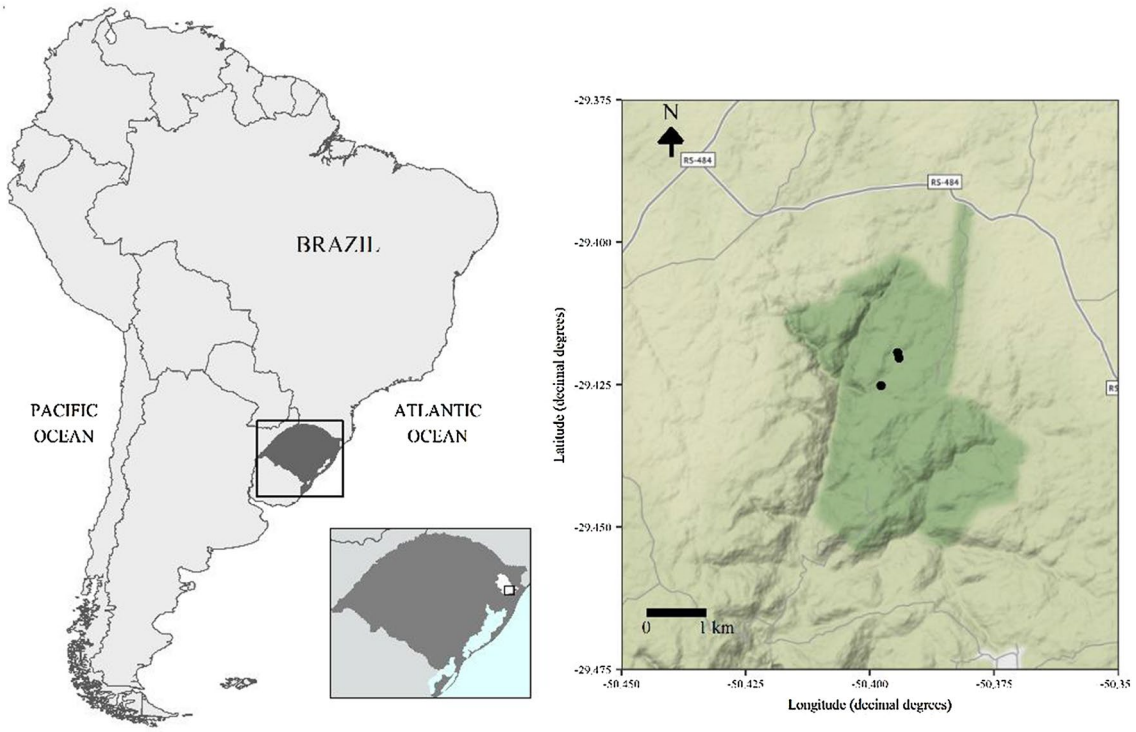

Fig. 1 Map of the study site. *Left*: a map of South America with the Brazilian state of Rio Grande do Sul highlighted. *Lower centre*: a map of the state of Rio Grande do Sul in which the area of the Municipality of São Francisco de Paula is highlighted. *Right*: a map highlighting (in *dark green*) the location of the São Francisco de Paula National Forest. *Black circles* indicate locations at which individuals of *Hylodes meridionalis* were observed during the present study

producing and an absence of an aggressive response from males to these individuals. Observations occurred during the afternoon between 13 and 18 h. Focal males were selected arbitrarily, the approximation was very gentle, and images were captured using a video camera (Panasonic HC-W850) positioned at least 1.5 m from the individual.

We submitted males to mirror self-image presentations to simulate the presence of an intruder male in the resident's territory (Fig. 2). For that, we gently positioned a mirror (15 × 15 cm) supported by a retractable handle 1 m long in the visual field of the resident male. The mirror was 15–25 cm from the actively calling resident male and at an angle of approximately 45° in relation to the male's body position to avoid a possible blind spot at 0° (directly in front of the animal; Fite 1973, Furtado et al. 2017). The behavioural responses of each focal male were recorded for at least 3 min, and both visual and acoustic responses were measured through these recordings. Additionally, during the field work, we also observed close-range interactions between individuals (one male–female and three male–male interactions) and we recorded and scored these natural encounters. The visual responses were classified according to the motor patterns described by Hödl and Amézquita (2001), Hartmann et al. (2005), Caldart et al. (2014) and de Sá et al. (2016), and the acoustic responses following Lingnau et al. (2013).

Fig. 2 Mirror self-image presentation to a male of *Hylodes meridionalis* in the São Francisco de Paula National Forest, southern Brazil. The reflection of the animal in the mirror (15 × 15 cm), positioned at an angle of approximately 45° in relation to the male body position, simulated the presence of an intruder male in the resident territory

After the recording, the individuals were captured to measure their snout to vent length (SVL) using Mitutoyo calipers with a precision of 0.02 mm. To ensure that each individual was observed only once, we placed the focal animals in terrariums until the end of each sampling period (not

exceeding 3 days). All the animals were released at their capture site in apparent good health. Each sampling period was conducted in a different stream or in a different section of the same stream. The possibility of observing the same male at different sampling sites was low because species of this genus are very territorial (Haddad and Giaretta 1999; Lingnau 2003; Wogel et al. 2004; Forti and Castanho 2012; de Sá et al. 2016).

Results

We localised and observed *Hylodes meridionalis* individuals only in the native forest, where males called in full daylight along fast streams of clean water, mostly on rocks or perched on fallen logs. The present study represents the first observations of *H. meridionalis* males performing calling activities during September. The females were observed during the months of November 2016 and February 2017. Although we did not observe males vocalising alone during the field work (the groups observed comprised 3–7 males performing calling activities), the distances between males were more than 2 m. The males and one female were found very close to the water (only a few centimetres away) or with the posterior part of the body underwater (Figs. 2, 3). The other female was recorded while she was sitting inside a small cave formed by a big rock above the ground, 2 m from the water. Although we could not capture the females to measure their SVLs, our observations indicate that the females ($N=2$) may have been larger than the males (SVL: 39.38 ± 1.96 mm; $N=8$ males measured; Fig. 3). We also observed lighter body colouration in the females when compared to the males (Fig. 3).

Fig. 3 A male (smaller and darker colour; SVL = 39.2 mm) and a female (larger and a lighter colour) *Hylodes meridionalis* in the São Francisco de Paula National Forest, southern Brazil

This species is very shy. The males stopped calling and jumped into the water even before we arrived at the margin of the fast stream. However, if the observers remained motionless and silent, they often returned to their initial position after a few minutes. Unlike the males, the females did not return to their initial position after escaping from our approach. Additionally, females were observed only twice during the field work, and no amplexus, eggs or tadpoles were seen by us.

Visual repertoire

Despite the difficulty involved in observing *H. meridionalis* in natural conditions, we witnessed a large visual repertoire, with seven visual displays performed by the males and females:

- *Toe flagging*. Slow up-and-down movements of one or more toes. Toes may be moved independently without a fixed sequence or in sequence in a wave-like pattern. Toe flagging was performed with right, left or both feet, and it was mainly performed immediately before or after a foot flagging display (see descriptions below and Video S1 in the Electronic supplementary material (ESM) for a resident male). On two occasions, a male displayed toe flagging and emitted advertisement calls simultaneously. During our observations, only one focal male performed toe flagging (male 3), but he did so in a highly repetitive way (10 events) during a close-range agonistic interaction with another male (Table 1).
- *Arm lifting*. Rapid up-and-down movement of one arm without extending it (Video S1 (intruder male) and Video S2 in the ESM). This was a high-speed display that was performed with the right or left arm. Additionally, the behaviour was observed immediately before or after a leg lifting display (see descriptions below). This behaviour was performed by seven males in an agonistic context and by one female in a reproductive context (Table 1).
- *Leg lifting*. Rapid up-and-down movement of one leg without extending it (Video S2 in the ESM). This was a high-speed display that was performed with a right or left limb. This behaviour was performed immediately before or after an arm lifting display. Leg lifting was performed by ten males in both agonistic and reproductive contexts and by one female in a reproductive context (Table 1). During our study, we observed the same male performing both arm and leg lifting displays (Table 1, Video S2 in the ESM).
- *Arm waving*. Lifting an arm and waving it up and down in a gentle arc beside the head (Video S3 in the ESM). Both the right and left arms were used to perform high-speed arm waving. Arm waving was performed by seven males in both agonistic and reproductive contexts and by one

Table 1 Emission of visual and acoustic behaviours and physical attacks by 18 males and one female *Hylodes meridionalis* during agonistic and reproductive interactions

Individual	Context	Time	Behaviour										
			Toe flagging	Arm lifting	Leg lifting	Arm waving	Both legs kicking	Foot flagging	Throat display	Advertisement call	Unknown call	Territorial call	Physical attack
Male 1	Mirror self-image	03:00	0	0	0	0	0	0	0	1	0	0	0
Male 2		03:00	0	0	0	5	0	1	0	7	0	0	1[a]
Male 3		03:00	1	2	1	0	0	0	0	7	0	0	1[a]
Male 4		03:00	0	0	0	0	0	0	0	0	0	0	0
Male 5		03:00	0	3	0	0	0	0	0	1	0	0	1[a]
Male 6		05:36	0	0	3	3	0	3	0	4	0	0	0
Male 7		03:00	0	1	0	0	0	0	0	2	0	0	0
Male 8		03:00	0	0	1	0	0	0	0	0	0	0	0
Male 9		03:01	0	0	0	0	0	0	0	2	0	0	0
Male 10		03:01	0	0	0	0	0	0	0	0	0	0	0
Male 11		07:45	0	0	0	7	0	0	0	4	0	0	0
Male 12		03:02	0	0	1	0	0	0	0	0	0	0	2[a]
Male 13		03:07	0	1	0	5	0	0	0	0	0	0	0
Male 3	Male–male interaction	10:25	10	0	1	10	0	8	0	19	0	0	1
Male 14[b]			0	3	1	4	0	2	0	3	0	0	0
Male 15	Male–male interaction	5:56	0	1	2	2	0	0	10	0	0	0	0
Male 16			0	1	2	0	0	0	0	0	0	0	0
Male 17	Male–male interaction	3:21	0	0	2	4	0	0	2	0	0	13	0
Male 18			0	0	0	0	0	0	0	0	0	0	0
Male 11	Male–female interaction	12:03	0	0	1	8	0	0	1	0	3	0	0
Female 1			0	1	1	5	1	0	0	0	0	0	0
Total		78:17	11	13	16	49	1	14	13	50	3	13	6

Agonistic interactions consisted of the presentation of the mirror self-image to simulate the presence of an intruder male in their territories and in observations of close-range male–male interactions. Reproductive interactions consisted of observations of close-range male–female interactions. *Time* represents the duration of the observation (min:s)

[a]The male attacked the mirror

[b]Intruder male

female in a reproductive context (Table 1). Arm waving was the most frequent visual display observed during our study (49 events, 41.88% of visual displays).

- *Both legs kicking*. Rapid stretching of both hind limbs at the same time towards the back above the ground, after which they are returned to the normal position, as if the individual was kicking the air (Video S4 in the ESM). This display was performed only once by a female during a very close-range male–female interaction (Table 1). It was performed 5 s after the male displayed arm waving (Video S4 in the ESM). The male did not visually or acoustically respond to the kicking display; after some time (approximately 80 s), he moved away from the female, who did not follow him. Some minutes later the male returned to the proximity of the female and both the male and the female started to display visually to each other again.
- *Foot flagging*. Raising slowly one hind limb, in a semi-arc movement, above the substrate level and returning it to the body side (Video S1 in the ESM). Foot flagging was performed with the right or left leg, and sometimes there was alternation of sides (Video S5 in the ESM). The lifted foot could simultaneously perform toe flagging. Foot flagging was performed by four males exclusively during agonistic encounters (Table 1).
- *Throat display*. Pulsation of the throat (inflation and deflation of the vocal sac) without audible sound production. This was performed once or repeated several times (Video S6 in the ESM). In contrast to the production of advertisement calls, where both paired lateral vocal sacs are inflated (Video S7 in the ESM), a throat display can be performed by inflating only one lateral vocal sac (Video S6 in the ESM). Throat displays can be performed by males in both agonistic and reproductive contexts (Table 1), but in different ways. During an agonistic interaction, one male performed ten throat displays consecutively, inflating only the left vocal sac (Video S8 in the ESM), and other male performed two throat displays alternating with territorial calls (it was not possible to determine if the male inflated one or both vocal sacs; Video S8 in the ESM; Table 1). However, when in the presence of a female, the male performed only one throat display, inflating only the left vocal sac, immediately after leg lifting and before the emission of unknown vocalisations (see details below; Video S9 in the ESM).

Territorial dispute between males

In total, we observed six types of visual displays performed by males during territorial disputes: toe flagging, arm lifting, leg lifting, arm waving, foot flagging, and throat display (99 events; Table 1). Arm waving behaviour was the most frequent visual display during both mirror self-image presentations and male–male interactions (Table 1). Although the emission of acoustic signals (63 events) was much less frequent than the presentation of visual displays (117 events), we video-recorded two known acoustic signals for males of *H. meridionalis*: an advertisement call (Video S7 in the ESM) and a territorial call (Video S8 in the ESM; Lingnau et al. 2013). An advertisement call was the most frequent acoustic signal emitted by males during aggressive interactions (50 events, 79.4% of calls produced; Table 1). Additionally, the simultaneous emission of advertisement calls and toe flagging (2 events, 2 males) by resident males only occurred after the approach of intruding males.

The males' aggressiveness during male–male competition could be identified not only through the production of visual displays and acoustic signals but also by observing physical attacks against intruders. Four males of *H. meridionalis* jumped towards the mirror during recordings, probably physically attacking their reflection, which resembled a conspecific intruder male (Table 1; Video S7 in the ESM). Aggressive physical contact was also observed during close-range male–male interactions, but in a different way. We observed a male pushing away an intruder from his territory by putting its head under the intruder's head and pushing it out. After that, the resident male followed the intruder while emitting advertisement calls and performing toe flagging and foot flagging displays until the complete exit of the intruder from the rock (Video S10 in the ESM).

Male–female interaction

We observed only a single interaction between a male and a female (Fig. 3). The female approached the male and both started to display visually to each other. During a period of approximately 15 min, the male emitted arm waving (8 events), leg lifting (1 event) and throat displays (1 event), and the female emitted arm waving (5 events), arm lifting (1 event), leg lifting (1 event) and both legs kicking (1 event; Table 1). The female emitted the both legs kicking display immediately after the male emitted an arm lifting display. During the exchange of visual displays, the distance between the male and female animal varied from adjacent (Fig. 3) to 25 cm.

After the performance of visual displays by both individuals, which did not follow any apparent order, the male emitted four consecutive unknown vocalisations (Video S9 in the ESM) immediately after the emission of leg lifting and a throat display. In contrast to the production of advertisement calls, where both paired lateral vocal sacs are inflated, the male alternated the use of the vocal sacs to produce undescribed vocalisations. After vocalising, the male began to move towards the riverside. However, the female moved towards the opposite site and jumped into the

water. In summary, no advertisement call by *H. meridionalis* males during close-range interactions with a female was ever observed.

Discussion

Almost all visual displays described for *Hylodes meridionalis* have previously been described for other hylodine frogs (Table 2). The both legs kicking display, however, was first reported for the genus *Hylodes* in the present study, and it was performed only by females of *H. meridionalis* (Table 2). These observations further emphasise the trend in this genus for visual communication, which is largely attributable to its characterised behavioural aspects of diurnality and reproduction in noisy streams (Haddad and Giaretta 1999; de Sá et al. 2016). Environmental factors are believed to be related to the evolution of visual signalling in anurans (Hödl and Amézquita 2001), but this has not been checked so far.

Arm waving was the most frequent visual display performed by *H. meridionalis*, especially during agonistic interactions between two males. For example, one focal male did not perform arm waving displays during mirror self-image presentations, but it performed several arm waving displays after the approach of another male into its territory. Therefore, it seems that the reflection in the mirror alone did not trigger an increase in the display of this particular behaviour. In addition, arm waving behaviour could be a visual display originating in a combination of rapid movement with a colour contrast against the background. In contrast to other anuran species (e.g. *Atelopus zeteki*, Lindquist and Hetherington 1996, 1998; *Brachycephalus ephippium*, Pombal et al. 1994), the arms of *H. meridionalis* individuals moved fast during arm waving displays. Conspicuous colouration in the supra-labial area in hylodines is commonly observed (Haddad et al. 2008). De Sá et al. (2016) suggested that the rapid arm movement associated with the colour contrast between the dark arm and the bright whitish-yellow colouration in the supra-labial area in *H. japi* can produce a flashing signal for the conspecific receiver. However, the present study is merely a starting point to elucidate the function of arm waving in *H. meridionalis*, and future experimental studies are required.

Together, arm and leg lifting displays were the second most frequently performed visual display by males of *H. meridionalis*, and limb lifting displays have been reported in six other hylodine frogs. Hödl and Amézquita (2001) suggested that limb lifting behaviour (including both arm and leg movements) was one of the most widespread visual displays in anurans. This visual display has been reported in species from eight anuran families (Micrixalidae, Biju et al. 2014; Ranidae, Stangel et al. 2015; Hylidae and Centrolenidae, Hartmann et al. 2005; Aromobatidae, Narins et al. 2003; Dendrobatidae, Hödl and Amézquita 2001; Bufonidae, Lindquist and Hetherington 1996; and Hylodidae, present study). Although ethologists do not usually separate arm lifting from leg lifting during anuran visual repertoire description (e.g. Hödl and Amézquita 2001; Hartmann et al. 2005), and individuals of *H. meridionalis* are able to perform both displays, de Sá et al. (2016) highlighted that individuals of *H. japi* were observed performing arm lifting displays only. In addition, while leg stretching (i.e. the stretching of only one leg) display has been reported for all the other *Hylodes* species in which visual communication has been studied, it is performed by males in particular. Here, we observed a both legs kicking display performed by a female *H. meridionalis*. However, the present study is not the first to report a both legs kicking display by a member of the Hylodidae family. Caldart et al. (2014) described *Crossodactylus schmidti* individuals performing both legs kicking, but only during agonistic encounters between two males. Therefore, we suggest that future studies should not only investigate the adaptive function of visual displays emitted by each sex of hylodines, but also how the diversity of visual displays is distributed across the phylogeny of the group.

Among the visual displays performed by males of *H. meridionalis* in agonistic contexts (toe flagging, arm lifting, leg lifting, arm waving, foot flagging and throat display), throat display was the only one exclusively performed during a close-range interaction between individuals. This result agrees with other studies (Pombal et al. 1994; Lindquist and Hetherington 1998; Haddad and Giaretta 1999; Furtado and Nomura 2014) which indicate that mirror self-image presentations can be a good method of investigating the visual repertoires of visually oriented animals. However, it is not perfect; in future studies, we strongly suggest the use of a proper control to confirm or reject any effect caused by the close proximity of an object on the behaviour of focal animals. A control treatment would also make it possible to verify whether the individuals produce visual displays even in the absence of a signal receiver. In this case, visual displays would probably not represent visual signals, but displacement activities (Furtado and Nomura 2014).

Displacement activities are unintentional behaviours with apparent irrelevance during ongoing activity (Tinbergen 1952; Maestripieri et al. 1992). This kind of display does not have a communicative function but can be very stereotyped and easily misinterpreted as a signal display (Furtado and Nomura 2014). However, signals evolve from pre-existing cues (e.g. unintentional behaviours) or other signals (Tinbergen 1952). Therefore, it is possible that some visual displays in *H. meridionalis* represent bona fide visual signals, while others do not. In the latter case, these displacement activities may have not evolved into signals yet.

During our observations, a male *H. meridionalis* inflated only one of his paired sacs during throat display after a

Table 2 Visual displays emitted by male (♂) and/or female (♀) of anurans from the genus *Hylodes* (family Hylodidae) during various social contexts

Species	Toe/finger trembling	Toe posture	Toe flagging	Limb lifting*	Arm waving	Leg stretching	Both legs kicking	Foot flagging	Mouth opening	Head bobbing	Head snaking	Throat display	Body lowering	Body raising	Upright posture	Back raising	Two-legged pushing	Body jerking	References
Hylodes asper	–	–	♂[a]	♂♀[b]	–	♂♀[b]	–	♂[b]	–	–	–	–	–	♂[b]	–	–	–	–	1, 2, 3, 4
H. japi	–	♂[b]	♂[b]	♂♀[b]	♂♀[b]	♂[a]	–	♂[b]	–	♂[b]	♂[r]	♂[b]	♂[a]	♂[b]	♂[b]	–	♂[a]	♂♀[b]	5
H. perere	–	–	–	–	–	♂	–	–	–	–	–	–	–	–	–	–	–	–	6
H. dactylocinus	♂	♂	♂	♂	–	♂	–	♂[b]	–	–	–	–	–	–	–	♂[a]	–	–	3,7
H. nasus	–	–	–	–	♂[a]	♂[a]	–	♂	–	–	–	–	–	–	♂[a]	–	–	–	8
H. cardosoi	–	–	–	♂[a]	–	♂[b]	–	♂♀[b]	–	–	–	–	–	♂[b]	–	–	–	–	9,10
H. heyeri	–	♂	♂	♂[a]	–	♂[a]	–	–	♂	–	–	–	♂	–	♂	–	–	–	11
H. phyllodes	–	–	♂[a]	♂	–	♂[b]	–	♂	♂[a]	–	♂	♂	♂[a]	♂[b]	♂[a]	–	–	–	4,12
H. meridionalis	–	–	♂[a]	♂♀[b]	♂♀[b]	–	♀[r]	♂[a]	–	–	–	♂[b]	–	–	♂[a]	–	–	–	Present study

* Including both arm and leg lifting behaviours. Contexts: [a] agonistic, [r] reproductive, or [b] both

References: [1]Heyer et al. (1990); [2]Haddad and Giaretta (1999); [3]Hödl and Amézquita (2001); [4]Hartmann et al. (2005); [5]de Sá et al. (2016); [6]Silva and Benmaman (2008); [7]Narvaes and Rodrigues (2005); [8]Wogel et al. (2004); [9]Lingnau et al. (2008); [10]Forti and Castanho (2012); [11]Lingnau (2003); [12]Forti (pers. obs.)

female approached. This is the second anuran species that is known to independently use each lateral vocal sac (this ability was first noted for *H. japi* in de Sá et al. 2016, but is also discussed in Elias-Costa et al. 2017). We also observed males of *H. meridionalis* alternatively inflating their lateral vocal sacs during the production of undescribed calls. Therefore, these results indicate that these animals can voluntarily control each vocal sac, and that the use of a specific paired lateral vocal sac or both of them may be selected.

Species that employ visual signalling can also use acoustic signalling during social interactions (Narins et al. 2003). This makes it difficult to separate the function of each signal modality during communication (Amézquita and Hödl 2004). In contrast to other anuran species that also exhibit mirror presentations (e.g. *Boana albomarginatus*, Furtado and Nomura 2014; *B. raniceps*, *Dendropsophus nanus* and *Lysapsus limellum*, Furtado et al. 2017), the visual displays were more frequent than acoustic signals in *H. meridionalis*. Since the visual displays actually represent displacement activities in *B. albomarginatus*, *B. raniceps*, *D. nanus* and *L. limellum* (Furtado and Nomura 2014; Furtado et al. 2017), this result may indicate a high possibility that the visual displays performed by *H. meridionalis* individuals actually represent visual signals. Despite the low emission of calls by males of *H. meridionalis*, we recorded advertisement and territorial calls (described by Lingnau et al. 2013) and one unknown type of call that was emitted only by a male during a close-range male–female interaction. Therefore, future studies are needed to confirm the production of courtship calls by males of *H. meridionalis*. In addition, bimodal stimulation (e.g. acoustic and visual signals) can result, for example, in the strongest behavioural response of focal animals (Narins et al. 2003). Therefore, the possibility that males of *H. meridionalis* could increase their aggressive response when confronted by a calling intruder male performing visual displays should be investigated to complement the findings reported in this study.

Visual displays during intraspecific communication have been reported for only a small number of anuran species, despite the evidence of its importance in social interactions. Here, we have reported a diverse visual repertoire in *H. meridionalis* in both aggressive and reproductive contexts, including a throat display in which only one lateral vocal sac is displayed. Studies of natural history provide the primary information needed to elucidate the adaptive functions and eco-evolutionary aspects of anuran behaviour, especially in this field, which is poorly explored by ethologists.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no potential conflict of interest.

Ethical approval This study was carried out in accordance with the guidelines of the Ethics Committee on the Use of Animals of the Instituto Chico Mendes de Conservação da Biodiversidade—ICMBio, Brazil. ICMBio permitted the fieldwork with anuran species in the National Forest of São Franscisco de Paula (no. 51201-2). No animals were sacrificed during the study, and all of the animals used for the study were released back into nature.

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