HOW, WHEN, AND WHERE TO PERFORM VISUAL DISPLAYS:
THE CASE OF THE AMAZONIAN FROG HYL A PARVICEPS

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ABSTRACT: We performed intrusion experiments and observed the course of 13 male-male agonistic interactions to gather information on the communicative role of visual signaling in the Amazonian tree frog Hyla parviceps. To obtain information on the ecological context potentially associated with visual signaling, we performed nightly censuses of calling activity and tested whether males differentially used microhabitats in relation to properties that affect both acoustic and visual communication. Among seven behaviors performed by males, two were visual displays. Foot-flagging displays and advertisement calls were used at a similar rate and at similar distances between interactants. Arm-waving displays were less common and used at a closer range than foot-flagging displays. The analysis of a dyadic transition matrix revealed that foot flagging significantly elicited foot-flagging displays by the opponent frog. Furthermore, resident males produced more arm wavings and calls than intruders, although the latter difference was not significant. We conclude that male H. parviceps respond to intruders by combining advertisement calls and visual displays, and that visual signals may serve functionally as a spacing mechanism. Comparing the properties of perches used by calling males with a random sample of available perches indicates that males prefer perches surrounded by denser and higher vegetation. Furthermore, calling activity occurred during or shortly after heavy rains and coincided with calling activity of several co-occurring species of hylid frogs, which probably decreases the locatability of calling males. We suggest that, under these conditions, the simultaneous production of auditory and visual signals may momentarily increase a sender’s locatability when a conspecific receiver is detected.

Key words: Agonistic interactions; Anura; Communication; Habitat selection; Visual signaling

ALTHOUGH anurans are well known to use auditory signals as the primary mode of intraspecific communication (Gerhardt, 1994; Rand, 1988; Wells, 1977), individuals of some species perform remarkable visual displays in variable social contexts (Davison, 1984; Haddad and Giaretta, 1999; Harding, 1982; Lindquist and Hetherington, 1996; Richards and James, 1992). Reviews on the use of visual displays by anuran amphibians (Hödl and Amézquita, 2001), reveal that all species performing visual displays perform acoustic displays as well, which makes it difficult to separate the functional role of each mode of communication. Moreover, most reports on visual displays in anurans remain anecdotal, and controlled experiments have been performed only recently in an attempt to elucidate their communicative role (Lindquist and Hetherington, 1996). Visual signaling can be hypothesized as either an alternative or complementary communication mode in anurans, the prevalence of which depends on the social context and the environmental conditions under which it occurs.

Several environmental conditions may have favored the evolution of visual displays in anurans (Hödl and Amézquita, 2001). Breeding in noisy environments, such as near fast streams or waterfalls, may require that acoustic signals be emphasized by visual displays (Haddad and Giaretta, 1999; Hödl et al., 1997; Lindquist and Hetherington, 1996). In arboREAL hylids, calling from elevated perches in dense vegetation may reduce an emitter’s locatability (Passmore et al., 1984) or attractiveness (Penna and Solís, 1998) and, thus, favor the use of complementary visual displays. The consequences of habitat use for acoustic communication in a single anuran species have been discussed to some extent (Etges, 1987; Wells and Schwartz, 1982). Visual signals, however, differ from auditory signals in both propagation distance and sender’s locatability (Bradbury and Vehrencamp, 1998). Thus, species that perform both acoustic and visual displays may differ in the ecological correlates of communication. An understanding of the evolution of visual displays in anurans requires accurate descriptions of the behaviors and
the social context in which these acts are performed.

The Amazonian tree frog *Hyla parviceps* is considered an opportunistic breeder because its calling activity, mainly nocturnal, seems to be associated with occasional heavy rains (Crump, 1974; Weygoldt, 1986). We incidentally observed males of this species extending both arms and legs during one breeding night, when the density of conspecific and heterospecific calling males was very high. The probability of auditory interference suggested that *H. parviceps* might have aggressive or courtship visual signals redundant with acoustic signals. The observation that males call mainly at night and from dense vegetation suggested that visual signals might be correlated with environmental conditions that favor signal propagation. Therefore, our aims in this study are (1) to describe the visual displays of *H. parviceps* as well as some ecological conditions under which they are performed, (2) to perform intrusion experiments to obtain information about the social context associated with visual signaling, and (3) to test whether males differentially use microhabitats for signaling activity.

**Materials and Methods**

**Study Site, Study Species, and Breeding Activity**

From 8 April–5 May of 1997, we studied a population of *H. parviceps* occurring at about 150 m elevation at the Surumoni River (Venezuela) within the Orinoco drainage (3° 10′ N, 65° 40′ W). The rainy season there extends from April–November, with a rainfall peak during the months of May–July (about 400 mm/mo). Annual precipitation is near 3000 mm but year-to-year fluctuations of about 500 mm are common. Mean annual temperature is 25.5–26.5 C, and average diurnal temperature range (5–10 C) exceeds among-years variation (<4 C). The vegetation at the study site consists primarily of a relatively old, secondary growth forest with a canopy at about 30 m.

At the study site, *H. parviceps* was found at streamside ponds that were formed during water-level rise of Surumoni river at the beginning of the rainy season. Ponds formed in this way existed for only a few weeks before becoming fully connected to the river. Calling males, as well as amplexant pairs, of *H. parviceps* were found in the vegetation above or beside the ponds. Eggs are laid on the water surface, and larvae probably complete their development in a short time interval under temporal restrictions that are imposed by pond flooding. We conducted our study with frogs displaying from two ponds that measured 18 × 6 × 0.3 m (length × width × depth) and 12 × 5 × 0.2 m. Both ponds were completely surrounded by forest. Other anuran species calling at the site during this study included *Allophryne ruthveni, Osteocephalus taurus, Sci- nax sp., Hyla granosa*, and *Leptodactylus knudseni*.

On 37 consecutive days at the onset of the rainy season, we performed daily censuses of the number of calling males at the study ponds. During this time period, water levels in the ponds rose from <2 cm to the level at which they became completely flooded by the Surumoni river. We visited ponds between 2000 h and 0100 h, walking slowly to spot all calling males. When no calls were heard, we waited at least 1 h at each pond before declaring no calling activity. To test for association between rainfall and calling activity, we used data on daily rainfall above the forest canopy from a weather station from less than 200 m from the furthest pond (Szarzynski, J; Surumoni-Project: Climate Monitoring, 1997; Forest-Atmosphere Interaction Research; Department of Geography, University of Mannheim).

**Behavioral Observations and Intrusion Experiments**

We observed 17 male-male interactions to describe visual signaling behavior and the associated social context. Because most of the spontaneous visual signals occurred during the few hours when the density of calling individuals was highest, only 4 observations were made of spontaneous interactions and 13 observations were of intrusion experiments. The procedure consisted of displacing a calling male from its perch to a new perch located at least 50 cm from a calling male. The displaced male was never one of the closest neighbors of the resident (i.e., calling) male. We then waited until one of the males either started to call or made visual contact. Afterwards, one of us dictated sequentially all observed behav-
ioral patterns into a tape recorder (Fagen and Young, 1978; Lehner, 1979). We also noted inter-individual distances (initially expressed in body-length units) at which behaviors were performed. An interaction was considered terminated when one of the individuals jumped away from the other so that visual contact was interrupted.

In the course of inter-individual interactions, we observed two kinds of behaviors that can be classified as visual displays. We name them foot flagging and arm waving, following Hödl and Amézquita (2001). During a foot-flagging display, a male raised one or both hind legs by extending it/them into an arc above the substrate level. The leg was then returned to the body side. At maximum extension, toes were outstretched, spread, and sometimes vibrated (Fig. 1). At maximum extension, hind legs revealed contrasting orange spots, visible only from behind the frog. Hind legs were either simultaneously or alternatively extended. Foot flagging was by far the most frequently observed display during both intrusion experiments and occasional observations. In *H. parviceps*, arm waving consisted of lifting an arm and waving it up and down in an arc above the head. A maximum of five waving movements were performed consecutively without contacting the substrate. The movements were not performed in any recognizable temporal pattern.

Other behaviors observed during agonistic interactions include approaching, jumping away, turning, and uttering advertisement calls. Approaching and jumping away are defined according to the position of the interacting individual, i.e., approaching means walking so that the inter-individual distance is reduced and jumping away means jumping (rarely walking) so that the interacting individual is left behind. Turning describes a group of behaviors in which the observed individual reorients the body without displacing. Turning is characterized by sequential lifting of every foot.

**Perch Use and Perch Availability**

To sample the characteristics of perches used by displaying frogs, the exact place was marked where each calling male was located during the census. In most cases, males that had been momentarily displaced resumed calling within a few minutes at a nearby perch. The perch properties measured were chosen from the literature (Arak and Eiriksson, 1992; Etges, 1987) according to the potential value for increasing the propagation of the signals and for reducing locatability of senders to potential predators. Measured properties included perch height, height of calling site above water level; perch size, leaf area (estimated as an ellipse based on the length of the leaf’s orthogonal axes) or branch thickness (horizontal diameter of trunk at the place where the frog was located); vegetation density, measured as the number of leaves that intersect a vertical cylinder (5 cm width × 70 cm height) centered at the frog’s location; upper cover, as the approximate distance from the frog to the top of the bush or tree where it was perched; and distance to the pond edge, expressed as positive if perches were directly above water and as negative if they were outside the pond. All perch variables were measured the following day to avoid disturbing the animals excessively. When water level rose throughout the night, perch height and distance to pond edge were estimated, based on marks left during the previous night.

To estimate perch availability, we measured the same properties on all potential perches (leaves as well as branches) intersecting vertical planes of two transect lines per pond. The azimuth direction of the first transect plane at each pond was randomly chosen; the second plane was orthogonal to it (in order to reduce the potential effect of environmental gradients). Transect planes extended up to 2 m
outside the pond edge, which represents the maximum distance at which a calling frog was detected.

**Statistical analyses**

To compare the prevalence of behaviors, the inter-individual distance at which they were performed, and their frequency in relation to the status of the individual at the beginning (resident versus intruder) and at the end (winner versus loser) of the interaction, we used the experimentally induced behavioral interactions as the statistical units of analysis (i.e., we calculated one value of each variable for each behavioral interaction). Nonparametric analyses were used because of nonnormal distribution of data.

To analyze behavioral transitions within the same subset of data, behavioral sequences were displayed in the form of a first-order contingency table. Rows represent preceding behaviors and columns represent succeeding behaviors that were performed by another individual (Fagen and Young, 1978). Given the prevalence of low frequency values within the cells, a randomization test was used to evaluate the independence between rows and columns.

To test whether visual displays were significantly preceded by any other behavior, we performed binomial tests between observed and expected behavioral transitions (Baker and Gillingham, 1983; Bels and Crama, 1994).

To test whether perches are selected according to the properties we measured, we compared each property between used and available perches with a Kolmogorov-Smirnov test. Since the null hypothesis is that no selection of perches occurs, we used a Bonferroni procedure to adjust significance levels for the number of variables tested (Scheiner, 1993).

**RESULTS**

Calling and breeding activities are opportunistic in *H. parviceps*. Most breeding activity occurred between 0–2 d of a heavy rainfall. We used daily rainfall and daily temperature (minimum, average, maximum) as predictor variables of presence (1) or absence (0) of nightly calling activity in a logistic regression model. Only daily rainfall was a significant predictor of calling activity (Log likelihood if term removed = −19.13, $P = 0.001$, $n = 31$ d; $P > 0.354$ for other variables), and calling activity most probably occurred when rainfall exceeded 30 mm/d (Fig. 2).

In the course of 13 male–male behavioral interactions, we observed 309 behaviors performed by 27 different males. Sixty-seven of these acts (21.7%) were foot-flagging displays, and 18 (5.8%) were arm-waving displays. Foot flagging was performed in 9 and arm waving in 8 of 13 male-male interactions. Within a single interaction, foot-flagging displays were as common as acoustic signals (Fig. 3), whereas arm-waving displays were less common than acoustic signals.

**When Are Visual Displays Performed?**

To know whether visual displays are preferentially performed when males approach each other beyond a threshold distance, we compared the inter-individual distance at which behaviors were performed. For each single interaction, we calculated the minimum, median, and maximum distance at which each category of behavior was performed. Foot flagging distance (average minimum – average maximum; 8–21 cm) was slightly shorter than...
calling distance (15–26 cm). Arm waving was performed at shorter distances (11–13 cm) than calling (Fig. 4).

Resident males performed more arm-waving displays (Fig. 5a; Wilcoxon signed ranks test; $Z = -2.23$, $P = 0.026$; $n = 13$ interactions) and tended to produce more calls ($Z = -1.75$, $P = 0.081$; $n = 13$ interactions) than intruders. There was no difference in the number of arm-waving displays between males that remained at the calling perches at the end of the interactions (winning males) and fleeing (losing) males (Fig. 5a; Wilcoxon signed ranks test; $Z = -0.21$, $P = 0.832$; $n = 13$ interactions). Likewise, the number of foot flagging displays did not differ between resident and intruder (Fig. 5a; Wilcoxon signed ranks test; $Z = -0.85$, $P = 0.397$; $n = 13$ interactions), and between winner and loser (Fig. 5a; Wilcoxon signed ranks test; $Z = -1.19$, $P = 0.236$; $n = 13$ interactions) males.

The first-order sequential analysis on a dyadic matrix (Table 1) revealed that the probability of one individual performing a behavior was associated with the preceding act performed by another individual (Monte Carlo Test on a $7 \times 7$ contingency table: number of trials $= 100,000$, $P = 0.0013 \pm 0.0001$, $n = 161$ transitions). To know the potential role of any behavior in eliciting a visual display, we performed binomial tests between those behavioral transitions that presented the largest differences between observed and expected frequencies according to the dyadic matrix (Baker and Gillingham, 1983; Bels and Crama, 1994). We corrected the significance levels for the tests performed using a sequential Bonferroni adjustment (Scheiner, 1993). Footflagging displays were significantly preceded by foot flagging of the interacting individual (Binomial randomization test; one-tailed test $P = 0.0001$, critical $P$-value $= 0.0500$) and turning movements were significantly preceded by turning movements of the interacting individual (Binomial randomization test; one-tailed $P = 0.0046$, critical $P$-value $= 0.0250$). Otherwise, calling tended to follow approaching (Binomial randomization test; one-tailed test $P = 0.0302$, critical $P$-value $= 0.0125$); and approaching tended to follow moving away (Binomial randomization test; one-tailed test $P = 0.0201$, critical $P$-value $= 0.0063$). Arm waving was not significantly preceded by any behavior (one-tailed test $P > 0.1769$ in all cases).
Where Are Visual Displays Performed?

Male *H. parviceps* differentially used perches in relation to vegetation density and cover height (Fig. 6). More males were found at perches that were surrounded by dense vegetation (Kolmogorov-Smirnov test; \( Z = 3.30, P < 0.001 \)) and that were part of high trees (\( Z = 2.75, P < 0.001 \)). Males, however, did not differentially use perches in relation to their height (\( Z = 1.15, P = 0.141 \)), their distance to pond edge (\( Z = 0.73, P = 0.670 \)), their area (for leaf perches; \( Z = 1.31, P = 0.066 \)), or their thickness (for branch perches; \( Z = 1.00, P = 0.273 \)).

**DISCUSSION**

In the course of male-male agonistic interactions in *H. parviceps*, visual signals are at least as frequently used as acoustic signals. Both types of signals were observed in most interactions and were produced at similar rates during a single interaction. The extensive use of visual signals suggests that they are functional components of the communication system and poses interesting questions about their communicative role and the evolutionary scenario under which they evolved. Below we discuss our results from two perspectives: (1) the probable communicative role of the visual signals and (2) the possible ecological correlates of the visual signaling in *H. parviceps*.

**The Communicative Role of Visual Signals**

Social interactions have favored the evolution of 2–3 across-species categories of signals in anurans (Bogert, 1960; Duellman and Trueb, 1986; Kluge, 1981; Rand, 1988): advertisement calls, aggressive/territorial calls, and, in some species, courtship calls. Spontaneous (i.e., in the absence of other individuals) performance of visual signals has been reported for some anuran species that evolved visual communication (Hödl et al., 1997; Pavan et al., 2001), suggesting a communicative role comparable to the role of advertisement calls: to indicate a male’s reproductive disposition to potential receivers of either sex (Grafe, 1995; Harrison and Littlejohn, 1985; Ryan and Rand, 1998; Schwartz and Wells, 1985). We believe, however, that visual signaling in *H. parviceps* does not serve advertisement purposes, because we
never observed visual displays performed by individuals that were not approached by a second male. There is still a good possibility that visual displays play a role as courtship signals that allow, for example, sex recognition between males and females (Rand, 1988; Wells, 1977; Zimmermann and Zimmermann, 1988).

In addition to the male-male interactions described in this paper, we observed two male-female encounters that involved 21 behaviors, six of them consisting of arm-waving displays that were performed by a single male in one of the interactions. This interaction did not lead to amplexus and oviposition.

From our data, the functional role of visual signals in *H. parviceps* can be compared to the role of aggressive calls. Because males in almost all intrusion experiments performed some kind of visual displays, we interpret arm waving and foot flagging as behaviors that signal aggressive motivational states. Furthermore, foot flagging significantly elicited foot flagging by interacting males. Advertisement calls were also produced after the intrusion of a second male, but we did not find any evidence of a distinctive aggressive call in *H. parviceps*. Instead, most males responded to intruders by combining advertisement calls and visual displays, suggesting that visual signals may function as aggressive calls (mediating spacing) in other species.

Most visual displays occurred at inter-individual distances below 30 cm, which may be partly attributed to an experimental artifact, i.e., experimental observations were initiated by placing a male within 50 cm of a focal male. However, during both registered and non-registered spontaneous interactions that involved visual displays, we always estimated inter-individual distances shorter than 50 cm. In other anuran species (Grafe, 1995; Schwartz and Wells, 1985; Wells and Schwartz, 1984), focal males produced more, more complex, or longer aggressive calls when experimental stimuli simulated one individual excessively approaching the calling male. In this study, resident males tended to perform more arm waving (significant differences) and to call more (nonsignificant differences) than intruders (Fig. 5). In our opinion, the sum of our results strongly suggests that visual signals play a role in the evolution of agonistic interactions.

### Ecological Correlates of Visual Signaling

In another study, we have explored several hypotheses about ecological correlates for the evolution of visual communication: diurnality, aposematism, signaling from acoustically complex environments, and signaling from noisy environments (Hödl and Amézquita, 2001).
The repertoire of visual signals is relatively low in *H. parviceps*, which agrees with previous predictions on the relative importance of diurnality in the evolution of anuran visual communication. Whereas the frog species exhibiting the largest repertoires of visual displays are diurnal, *H. parviceps* is primarily nocturnal and only occasionally extends its breeding activity to the first hours of the daytime. Furthermore, the coloration pattern of *H. parviceps* in the resting position does not seem to contrast against natural backgrounds. We, therefore, discuss below the possible importance of visual signaling for communication in environments where the locatability of sender is reduced.

Calling males were disproportionally found at perches with high vegetation density. From the acoustic point of view, this result is unexpected since sound propagation may be diminished under these conditions (Ellinger and Hödl, 2003; Penna and Solís, 1998; Richards and Wiley, 1980). One can speculate that perches within dense vegetation reduce locatability of senders to aerial predators such as bats. Calling male *Physalaemus pustulosus* (Ryan, 1985; Tuttle and Ryan, 1981) and *Smilisca sila* (Da Silva Nunes, 1988) change their behavior in the presence of bats. Indeed, during the course of this study, we observed bats preying upon frogs such as *Osteocephalus taurinus* that were calling from elevated perches. In spite of the potential benefits as antipredator strategy, calling from relatively hidden perches reduces the locatability of males to potential conspecific receivers, which could in turn reduce mating opportunities or increase the costs (time, energy, predation risk) of repelling other males. Under this scenario, the simultaneous production of auditory and visual signals may momentarily increase a sender’s locatability when a conspecific receiver is detected. Moreover, calling activity of males of *H. parviceps* is strongly associated with heavy rains (this study; Crump, 1974; Weygoldt, 1986), when the cacophony produced by other breeding species may negatively affect acoustic communication (Narins and Zelick, 1988; Schwartz and Wells, 1983). Visual signaling may thus favor species recognition in species breeding within large assemblages, when acoustic and visual environments become too complex. These hypotheses deserve further testing by comparing, for example, phylogenetically close species that vary in signal stereotypicity, signal repertoire, and microhabitat used for displaying.

**Acknowledgments.**—This research was funded by the Austrian Science Foundation (FWF) grant to W. Hödl (P 11565-Bio). We thank I. Strausz for invaluable field assistance and personal support; B. Rojas, V. Flechas, and L. Castellanos for help in data organization; and J. Szarzynski and N. Ellinger for providing data on the local weather.

**LITERATURE CITED**


**A REPATRIATION STUDY OF THE EASTERN MASSASAUGA (SISTRURUS CATENATUS CATENATUS) IN WISCONSIN**

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The use of relocations, repatriations, and translocations as amphibian and reptile conservation strategies has received much debate. In the case of endangered species, their use may outweigh the potential negative consequences. We performed an experimental repatriation of the eastern massasauga (*Sistrurus catenatus catenatus*), which has experienced range-wide population declines and extirpations. The experiment included measures to minimize negative conspecific effects to the donor populations as well as inter-species effects on the release and donor sites. Snakes released during late July had lower mortality rates, larger home ranges, and gained more mass than snakes released in early September. The July release cohort also successfully reproduced, while no breeding activity was observed with September release snakes. Results of this study suggest that repatriation *may* be a viable method of restoring eastern massasauga populations. We hope the methods and conservation measures used in this experiment will serve as a template for future repatriations.

**Key words:** ecology; recovery; repatriation; *Sistrurus*; snakes

Although herpetologists undoubtedly have been conducting transplants for decades, only recently has the efficacy of transplanting or repatriating individuals received rigorous debate (Burke, 1991; Dodd and Seigel, 1991; Griffith et al., 1989; Plummer and Mills, 2000; Reinert, 1991; Sealy, 1997). Ultimately, the need for repatriation (Dodd and Seigel, 1991) involves balancing two opposing issues: (1) the need to recover a species, which often includes expanding populations into formerly occupied habitats and (2) the obligation to do no harm to the individuals being released as well as resident animals.

The purpose of this study was development of an ethical repatriation method for a species that clearly warrants it, the eastern massasauga (*Sistrurus catenatus catenatus*), in the hope that it will serve as a template for future repatriations. We chose a study design that minimizes impacts on the founder and resident snake populations. To achieve this, the study sites had to meet the following criteria: (1) sites had to be void of eastern massasaugas, which by definition eliminated any impacts on resident massasaugas; (2) the sites had to have harbored eastern massasaugas in the past, which demonstrates the sites’ ability to harbor massasaugas if habitat conditions are right; and (3) the cause of extirpation, in this case habitat degradation, must have been reversed prior to the study (Dodd and Seigel, 1991).

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