



Colour, size and movement as visual subcomponents in multimodal communication by the frog *Allobates femoralis*

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Multimodal signals convey information that can be detected by receivers using two or more sensory modalities. The information transmitted through secondary channels may be mostly useless, redundant, complementary, or essential. Although each option implies different evolutionary scenarios, the relative role of signal subcomponents in a secondary channel has rarely been tested. Anuran amphibians are known for their extensive use of auditory signals, but growing evidence suggests their common use of multimodal signals where the visual component represents the secondary channel. Territorial males of the nontoxic frog *Allobates femoralis* use bimodal (acoustic + visual) signals to recognize conspecific intruders. We used playback experiments to test the relative importance of three visual subcomponents (body coloration, body size and body movement) in a multimodal signal to elicit agonistic reactions in males. The probability of attack was highly related to the movement and size of a dummy frog but very poorly related to dummy's coloration. The results suggest that any body movement, and not only vocal sac movement, is a nonredundant component of a bimodal signal that probably modulates male aggression. Against our expectations, males readily attacked dummy frogs painted to mimic the co-occurring frog *Ameerega trivittata* as well as models lacking some of their own pattern's subcomponents (white lines and yellow patches). Colourful frogs did not use body coloration as a visual cue for conspecific recognition. Both patterns recall the importance of carefully manipulating the availability of visual information in interpreting the origin and evolution of multimodal signals.

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Signals in animal communication are usually classified after the sensory modality in which they are perceived. The classification scheme, however, may be rather simplistic, since signal production often involves energetic modalities other than the essential nature of the signal (Smith 1977). For instance, visual dynamic displays often imply some production of sound or vibration (Lewis et al. 2001; Uetz & Roberts 2002), and the production of auditory signals often implies the movement of body structures that can be visually perceived (Smith & Evans 2008). Because receivers often react to unimodal signals (i.e. perceived by a single sensory modality) under experimental conditions, 'secondary' perturbations can be erroneously assumed to be by-products of signal production that do not carry useful information for receivers (epiphenomena). Indeed, many animal groups are well known for their predominant use of a single communication modality (Gerhardt & Huber 2002; Nicholson et al. 2007; Zakon et al. 2008).

Growing evidence suggests, however, that both eavesdroppers and receivers often perceive and make use of the 'secondary' information produced with a signal, which could then be considered to be multimodal (Partan & Marler 1999, 2005). Female wolf spiders, for example, react more to male courtship signals that combine visual and vibrational components (Uetz & Roberts 2002), or visual and chemical components (Rypstra et al. 2009) than they do to signals containing information in a single sensory modality. The information transmitted through secondary channels may, at one extreme, be completely essential for the appropriate detection and recognition of the signal by the receiver (Acquistapace et al. 2002; Narins et al. 2003). At the other extreme, most of this information may be essentially useless, perhaps redundant, or eventually act as an enhancer of the central message transmitted through the main communication channel (Partan & Marler 2005). Dissecting the relative importance of different information elements (i.e. subcomponents) transmitted through the secondary channel should improve our understanding of the way in which animals integrate multimodal signal components (Lovelace & Partan 2001) and the costs and benefits of using several channels for communication (Roberts et al. 2006). By keeping constant the information transmitted through the main communication

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channel, while experimentally manipulating the availability of information transmitted through a secondary channel, we address here the question of the relative importance of different visual subcomponents within a bimodal (acoustic + visual) signal.

Anuran amphibians are primarily known as acoustically communicating animals (Ryan 1988; Gerhardt & Huber 2002). However, a review of anecdotal and experimental evidence on the possible use of visual information during communication in frogs (Hödl & Amézquita 2001) concluded that dynamic episodes such as postural changes and appendage movements would have evolved as ritualized visual signals that subserve communication during courtship and agonistic encounters (Lindquist & Hetherington 1996). Anurans may also profit from available visual cues during essentially acoustic interactions. Strictly speaking (Bradbury & Vehrencamp 1998), visual cues provide information to perceivers but they did not evolve as ritualized signals. Examples include medium- to long-term states such as body coloration or body size, and dynamic episodes such as movements associated with sound production (Hödl & Amézquita 2001). Because several frog species show temporal or permanent sexual dimorphism in dorsal (Ries et al. 2008), throat (Rosenthal et al. 2004; Hirschmann & Hödl 2006), or appendage coloration (Grafe & Wanger 2007), both males and females might use colour or brightness to identify the sex of another individual. This possibility, however, has rarely been tested. The conspicuous coloration of the poison frogs, known as an advertising signal of toxicity and distastefulness for potential predators (Saporito et al. 2007; Noonan & Comeault 2009), may also have a role in intraspecific communication. Females of at least one polymorphic species appear to use information on body coloration to recognize and select males of the same area (homotypic males) against heterotypic males (Summers et al. 1999; Reynolds & Fitzpatrick 2007; Maan & Cummings 2008).

An open question is whether the vocal sac movements associated with sound production act in anuran communication as a useless epiphenomenon, a redundant or a nonredundant component of a multimodal signal. Video playbacks (Rosenthal et al. 2004) and playbacks conducted with an electromechanical model (Taylor et al. 2008) indicate that the availability of visual information on movement (a pulsating vocal sac) increases the attractiveness of an advertisement call during two-choice playback experiments on females of the frog *Physalaemus pustulosus*. Females, however, can still be attracted by the playback of the call without any associated visual information. On the other hand, results of a playback experiment conducted with a robotic frog suggested that vocal sac pulsation, together with the playback of advertisement calls, constituted bimodal requisites for eliciting attacks by males of the territorial frog *Allobates femoralis* to simulated intruders (Narins et al. 2003).

To test the importance for effective communication of different visual subcomponents of a bimodal (acoustic + visual) signal, we investigated the role of body coloration, body size and body movement in agonistic interactions among territorial males. The information transmitted through the acoustic channel was kept constant. Among frogs, the largest repertoires of presumably visual signals occur within the superfamily Dendrobatoidea (Hödl & Amézquita 2001), which includes Neotropical poison frogs and their nontoxic allies (Grant et al. 2006). As in many species of dendrobatoid frogs, *A. femoralis* males are strongly territorial and react to the presence of conspecific calling males by approaching them and then engaging in fights that may last up to several minutes. The successful and prolonged holding of a territory appears to play a pivotal role for the reproductive success of males (Roithmair 1992). The species is basal within Dendrobatoidea compared to the widely known poison frogs (genera *Phyllobates*, *Dendrobates*, *Oophaga*) and, as far as it is known to date, does not

bear skin alkaloids that might deter potential predators from attacking them (Daly et al. 1987; Darst 2006). These frogs, however, have conspicuous body coloration (yellow, red or orange femoral and inguinal patches, as well as white to yellowish dorsolateral lines) that might be used in intraspecific communication.

To test (1) whether body coloration and body size are actually used to discriminate conspecific from heterospecific individuals, we conducted bimodal (auditory–visual) playback experiments to compare the agonistic reaction by *A. femoralis* males towards frog models of the appropriate size and coloration, and frog models with the size and coloration of the frog *Ameerega trivittata*. We predicted that males attracted to a conspecific advertisement call would not attack the associated model if it bore the coloration or size of *A. trivittata*. To test for the specific effect of several coloration elements on conspecific recognition, (2) we tested male reaction towards models that lacked yellow hue but retained (white) line and patch patterning, models that lacked patterning but retained dark background coloration, and models that lacked the dark background coloration and were thus painted entirely yellow. Finally, the previously cited study (Narins et al. 2003) indicated that the vocal sac movements associated with sound production are nonredundant requisites to elicit physical attacks by territorial male *A. femoralis*. (3) We tested the more inclusive hypothesis that any body movement (and not necessarily vocal sac movement) is the prerequisite for eliciting aggression in males.

METHODS

Study System

All experiments took place during October–November 2002 and December 2003–January 2004 in primary lowland forest at the Cercaviva private reserve (4°7'24"S, 69°56'57"W, 90 m elevation), 10.7 km north of Leticia (Colombia). Average annual precipitation is 2800 mm. The rainy season extends between October and May, with the highest amount of rainfall occurring in January and the lowest amount occurring in July. Mean daily temperature is 26.4 °C. As in other species of dendrobatoid frogs (Aichinger 1987; Gottsberger & Gruber 2004), the breeding activity in *A. femoralis* begins several weeks before the rainy season. Our experiments were thus conducted when calling activity was very high, territories were being established, and the first breeding events were occurring.

Calling *A. femoralis* males readily react to the playback of conspecific advertisement calls within their territories. We have previously studied this relatively stereotypic reaction in several populations throughout the Amazon basin (Amézquita et al. 2005, 2006) including the population of Leticia, where we conducted this study. In a typical acoustic playback experiment, we set a loudspeaker within 1–3 m of a calling male, according to the average distance between individuals in the study population. The observer then walked about 2 m away perpendicularly to the line between the frog and the loudspeaker. A second person, situated more than 2 m away, played the stimulus signal after a short (less than 3 min) acclimation period, in which males usually resumed their calling activity. When an appropriate signal was broadcast at a sound pressure level (SPL) surpassing a threshold of about 70 dB (re. 20 µPa), males stopped calling, often reoriented their bodies, and approached the loudspeaker (Ursprung et al. 2009). We terminated the experiment when the male approached within 30 cm of the loudspeaker, which usually occurred within 1 min when average signals (see below) were played back. When males came close to the loudspeaker, they often stopped their fast approach, waited, and sometimes changed their otherwise linear trajectory, always staying within 50 cm of the loudspeaker. We do not know whether this behaviour reflects the lack of spatial auditory resolution at

short distances from the sound source, or the search for a visual representation of the calling frog. In any case, we used 30 cm of male-to-loudspeaker distance as a conservative threshold to define a positive phonotactic reaction. The results of about 600 acoustic playback experiments (i.e. 600 individual tests, 65 of them conducted in Leticia) provide a framework to interpret the results of the bimodal (acoustic and visual) playbacks that we conducted in this study.

Bimodal Playback Experiments

An average auditory signal was synthesized using the average spectral and temporal parameters of the advertisement calls measured in 15 individuals of the same population at Leticia (Amézquita et al. 2005). Each advertisement call consists of four notes uttered in temporally structured series (calling bouts). We first prepared and assembled the four basic types of frequency-modulated notes using the software SoundEdit (Weary & Weisman 1993), and based on the note duration, the internote interval, and the low frequency of the natural notes. The modulation frequency was manipulated to mimic the natural frequency range, and the fade-in and fade-out effects were used to simulate the characteristic note envelope. Other details of the synthesis procedure are described elsewhere (Amézquita et al. 2005). We assembled series of 10 calls followed by silent intervals of similar duration, to mimic the calling bouts of *A. femoralis* under natural conditions (Gasser et al. 2009). Call series were broadcast at SPL values above 72 dB (as measured at the end of the experiment from the frog's initial position) and, since our main questions dealt with the role of visual cues on male reaction, we used the same auditory stimulus with all males.

To investigate the role of body coloration, body size and body movement on the agonistic reaction of males, we conducted bimodal playback experiments. In short, we broadcast average advertisement calls to attract acoustically active males from their calling perches (1.0–1.5 m away) towards a wooden 30 × 30 cm platform containing both the loudspeaker and, at about 5 cm in front of it, a dummy frog. Once the male arrived within 40 cm of the platform and we could safely assume that the dummy was within his visual field, we moved the dummy (except in the experiments with stationary models) 0.5–1 m from the platform and observed the frog's reaction. We moved the dummy by gently pulling two twisted nylon lines that were attached to the model (Fig. 1); repeated pulling at a rate of about 1 Hz makes the dummy look like a hopping and turning frog. Based on preliminary trials, we expected males to call, move around and attack the dummy. Accordingly, our main output variable was binary, whether or not

the male attacked the dummy frog, but we also measured the number of uttered calls and the time elapsed from the beginning of the visual phase of the experiment (when we started to move the dummy) until the male attacked the model. If the male did not attack the model within 4.5 min, we stopped playing the sound and terminated the experiment.

Dummy frogs used as visual stimuli were prepared with cold-hardening clay (Porcelanicom) made from polyvinyl-acetate (PVA). Each model was individually carved to mimic the body shape and average size of the frogs, and then hand-painted with acrylic paints according to the experimental treatments. To reduce the probability of playback pseudoreplication (Kroodsma 1989; Kroodsma et al. 2001), we prepared 10 replicates of each type of dummy (i.e. each experimental treatment), and used the dummy as the biological and statistical unit of analysis. Since models were completely worked by hand, no two of them were identical. The results reported here are based on 80 dummies tested on 57 territorial males. Because reusing some males may influence the generality of the conclusions we expected to draw, a maximum of three experiments were conducted on a single male. Also, a male was never tested twice with the same experimental treatment, and two consecutive tests on the same frog were separated by a period of no calling activity (1 night in *A. femoralis*).

Experimental Design and Treatments

The most conspicuous components of the *A. femoralis* coloration pattern from Leticia are the brilliant yellow patches on the femoral and inguinal areas, and the white to yellowish dorsolateral lines. They all contrast against a black to brown dorsal background. At our study site, other at least partially diurnal frog species bear dorsolateral white lines but either have no patches (*Allobates* sp.), or have no conspicuous patterning at all (e.g. *Leptodactylus* aff. *andreae*, *Rhinella* spp.). In contrast, dorsal coloration of the significantly larger frog *Ameerega trivittata* (Silverstone 1976) consists basically of an alternation of bright green and black longitudinal stripes. To determine whether *A. femoralis* males distinguish conspecific from heterospecific (*A. trivittata*) individuals based on visual cues, we used a factorial (2 × 2) design, manipulating the coloration and size of the dummies to mimic individual of each species. We chose *A. trivittata*'s coloration traits as experimental treatment because both species extensively co-occur throughout the Amazon basin (Fig. 2), are regularly syntopic, and share behavioural and ecological similarities that increase the probability of interspecific encounters (Amézquita et al. 2005).

Other diurnal frogs interspersed within the territories of *A. femoralis* share body coloration components of *A. femoralis* to different degrees. Some species bear a similar brown to black dorsal background, others bear white dorsolateral lines, and others bear essentially the same pattern of yellow/orange/red patches and white-yellowish lines against a dark background. To identify which subcomponents of *A. femoralis* coloration pattern might be involved in conspecific recognition, we prepared dummies of the appropriate (i.e. *A. femoralis*) size but (1) without the yellow coloration (patches and lines were white instead of yellow), (2) without conspicuous patterning (no lines or patches were present and the dummy was uniformly brown), or (3) completely yellow. To our knowledge, no diurnal frog species shows completely yellow coloration in the study area. Males failing to react to one of the dummy types would indicate that the lacking element (yellow patterning, conspicuous patterning or dark background coloration, respectively) is necessary for visual recognition of conspecific individuals.

Finally, to determine whether body movement is a prerequisite for eliciting male agonistic reactions, we conducted 10 additional experiments with stationary models (i.e. dummies not pulled with

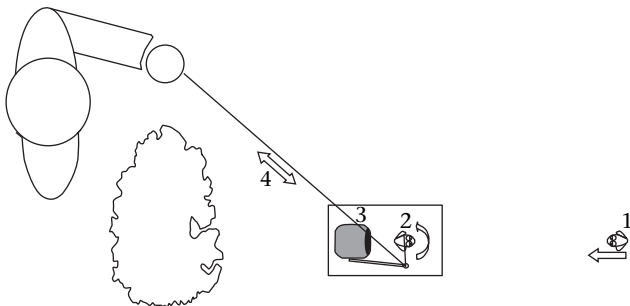


Figure 1. Schematic representation of the bimodal (acoustic and visual) playback experiment conducted on male *Allobates femoralis*. The focal male (1) sees the dummy frog (2) while approaching the acoustic stimulus broadcasted by the loudspeaker (3). The observer controls the movements of the dummy frog by gently pulling and releasing two twisted nylon chords (4).

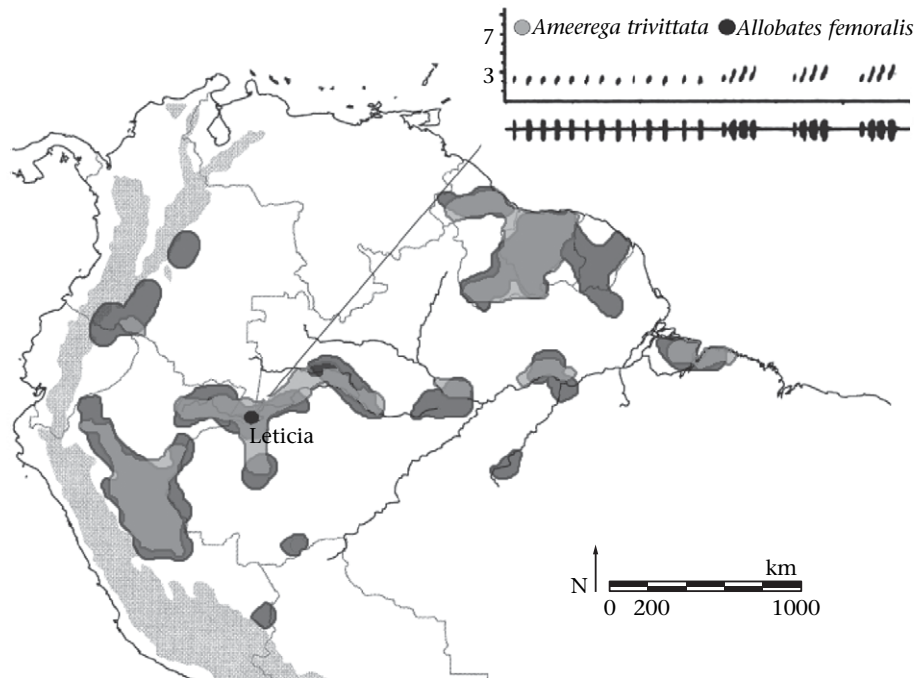


Figure 2. Overlapping geographical distribution of the frogs *Allobates femoralis* (dark grey area) and *Ameerega trivittata* (light grey area) in the Amazon basin, modified after (Silverstone 1976). The map emphasizes elevations above 1000 m. The inset shows a representative advertisement call of each species at the study site (Leticia, Colombia): X axis represents time at 1 s intervals; Y axis represents call frequency (above; spectrogram, in kHz) and arbitrary sound intensity units (below; oscillogram).

the twisted nylon lines but otherwise equal) of the appropriate size and coloration. In these cases, we considered the beginning of the visual phase of the experiment when the phonotactically approaching male arrived within 40 cm of the dummy frog.

To analyse the effect of coloration, body size and body movement on the reaction of males, we ran three ordinal logistic regression analyses (OLR), one per experiment. OLR works as an extension of chi-square contingency table analysis for the special case of several input variables (O'Connell 2006). When there is a single predictor variable, ordinal logistic regression is equivalent to likelihood-ratio estimates of chi-square. Only half of the males attacked the dummy frog, so we ran a single ANOVA to test for differences between treatments in the time to attack the dummy. Because fewer than half of the males called during the experiment, we did not perform inferential tests, and thus, we present only descriptive statistics regarding calling activity. All statistical tests were two tailed.

RESULTS

Tested frogs attacked the models in 41 of 80 experiments. Typically, the male first pushed the model with his forefeet, then jumped onto the model, grabbed its neck and pressed it downwards while supported by the hindlegs (Fig. 3). The male often jumped back and repeated this behavioural attack sequence several times. The time since we started moving the dummy until the first attack varied between 6 s and 178 s, with no apparent relationship with the experimental treatment (ANOVA: $F_{5,35} = 1.61$, $N = 41$ dummies, $P = 0.18$).

When we manipulated model size and coloration to simulate *A. femoralis* and *A. trivittata* intruders (Fig. 4a), males attacked small models more often than large models (ordinal logistic regression: likelihood ratio: $\chi^2_1 = 6.66$, $N = 40$ dummies, $P = 0.014$), regardless of their coloration pattern ($\chi^2_1 = 0.00$, $P = 1.000$). Only three of 40 males called during these experiments, precluding further analyses of calling activity.

When we manipulated subcomponents in models' coloration pattern, males responded similarly towards control, white-patterned and brown models (Fig. 4b). However, significantly fewer males attacked yellow models (likelihood ratio: $\chi^2_3 = 9.50$, $N = 40$ dummies, $P = 0.023$; Fig. 4b). Whereas no male called when exposed to the control models, five (white-patch model, 1–54 calls/male), four (brown model, 1–5 calls/male) and three (yellow model, 5–52 calls/male) of 10 males called in response to the experimental models.

Finally, males showed no observable reaction towards stationary models (likelihood ratio: $\chi^2_1 = 16.91$, $N = 20$ dummies, $P < 0.001$; Fig. 4c). Males typically jumped on and off the platform, often passing by the model without touching it. Nevertheless, males that were exposed to stationary models called more often (5 of 10 males, 23–70 calls/male) than males that were exposed to moving models (no males called) of the same (i.e. control) coloration and size.

DISCUSSION

Allobates femoralis males readily attacked dummy frogs in our bimodal playback experiments. Probability of attack was highly positively related to model movement and model size but poorly related to model coloration. Models painted to mimic the co-occurring *Ameerega trivittata* and models painted dark brown or brown with white patterning were attacked as frequently as control models. Our results show that not all the information available from the visual (secondary) channel in a multimodal signal is actually used for conspecific recognition among males. Instead, our results suggest a complex scenario involving some visual elements that are required to elicit agonistic reaction, others that may emphasize the main auditory signal, and others that may be essentially irrelevant for information transfer. This scenario adds to the current classification scheme of multimodal signals (Partan & Marler 1999, 2005) by showing that a single signal component

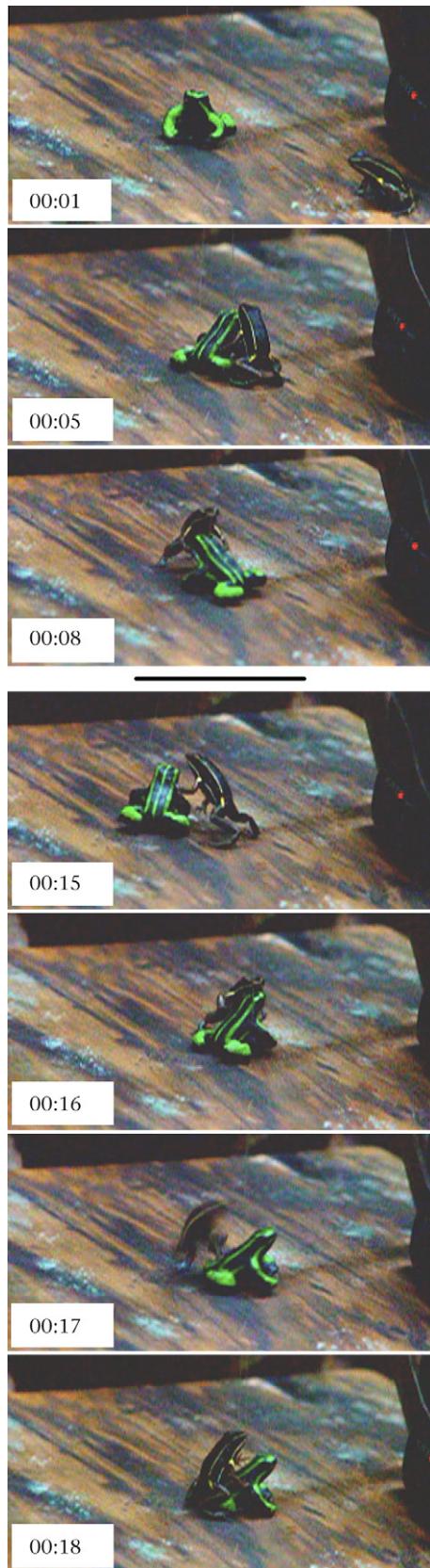


Figure 3. A male *Allobates femoralis* attacking a dummy frog painted with the coloration pattern of *Ameerega trivittata* during a bimodal playback experiment. The images were extracted at approximately 3.5 s (first three images) and 1 s (last four images) intervals from a representative video. The wood platform and the loudspeaker (right, with a red light) are also visible. See *Methods* for further details of the experiment.

(i.e. the visual) contains subcomponents that can be classified in different categories according to their tested functional role.

Body Coloration

Body coloration appears to be a nonessential component of the bimodal signal in *Allobates femoralis* (Partan & Marler 1999), because variation in this trait did not lead to differences in the agonistic reaction by males. That males attacked dummies bearing heterospecific coloration may indicate that coloration does not play a role in species recognition or that males of this species are regularly involved in agonistic interactions with individuals of other species, namely *Ameerega trivittata* (green stripes model) and *Allobates* sp. (brown model). We disfavor the latter explanation for both empirical and theoretical reasons. In the course of other studies at eight Amazonian sites (Amézquita et al. 2006), we have often observed males of other species calling within 1 m (and probably within the visual field) of acoustically active *A. femoralis* males without any indication of agonistic behaviour. Also, if *A. femoralis* males defend their territories against heterospecific intruders, they should, as an acoustically communicating species, react to heterospecific calls. They do not, according to previously conducted experiments in which calls of one (Göd et al. 2007), or four (Panguana, Peru: A. Amézquita, A. Lima, S. Flechas & W. Hödl, unpublished data) co-occurring species were presented to *A. femoralis* males. Our results combined with those of previous studies on male–male communication in this species support the idea that body coloration does not contribute to discrimination between conspecific and heterospecific individuals.

Body coloration may still mediate the recognition of conspecific females. Typically, males shift from advertisement to buzz-like courtship calls once an approaching female enters their visual field (Roithmair 1992). If the male perceives advertisement calls that can be temporally and spatially integrated with a visual representation of another frog (Narins 2005), body coloration would be basically unimportant and other visual subcomponents (namely body movement and body size) would play the role of confirming the intruder's presence and location. In the absence of advertisement calls, body coloration may still work as an independent visual signal or cue mediating the recognition of conspecific females. Very often, however, we have seen *A. femoralis* males uttering courtship calls while a heterospecific individual was passing by. Thus, the possibility that males require more strict visual information to recognize conspecific females than they do to recognize conspecific males demands further experimental testing.

Why be colourful if coloration does not convey any advantage in intraspecific communication? Conspicuous coloration in dendrobatid frogs is thought to serve interspecific communication, particularly the announcement of toxicity to potential predators (Summers & Clough 2001; Noonan & Comeault 2009). The coloration pattern of *A. femoralis* is widespread among toxic dendrobatid frogs. Since no studied population of *A. femoralis* has been reported to be toxic (Daly et al. 1987; Darst 2006), conspicuous coloration in this species may subserve Batesian mimicry on toxic syntopic species that bear similar coloration patterns, such as *Ameerega* (*Epipedobates*) *hahneli* in Ecuador (Darst 2006). This hypothesis is supported by our own extensive sampling of geographical variation in coloration pattern of *A. femoralis* and its candidate models for Batesian mimicry. Although we found no toxic species bearing a similar coloration pattern in our study site at Leticia, a population of *A. hahneli* co-occurs with *A. femoralis* a few kilometres away (J. D. Lynch, personal communication). If body coloration communicates information to predators rather than to conspecifics, then the visual element of the bimodal signal that is most conspicuous to humans, the coloration pattern, would be essentially irrelevant for

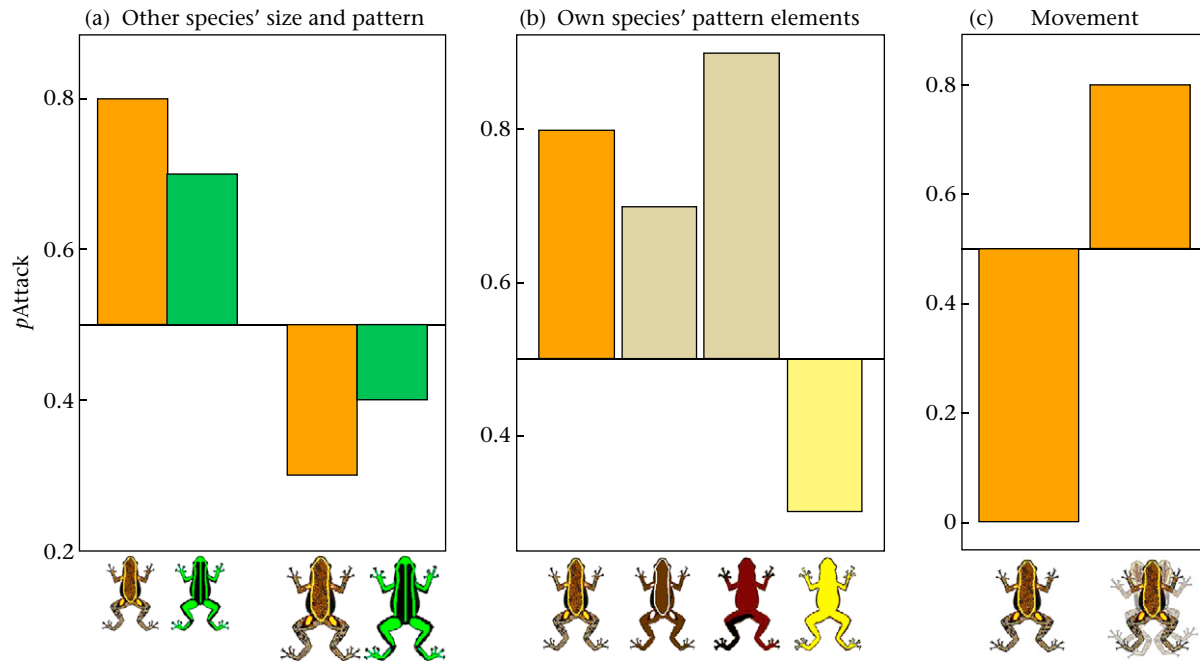


Figure 4. Probability that phonotactically attracted male *Allobates femoralis* would attack dummy frogs that (a) simulated the size and coloration of a co-occurring species, *Ameerega trivittata*, (b) lacked subcomponents (yellow patches and lines, patterning, or brown background) of *A. femoralis* coloration pattern, or (c) lacked movement. To improve data visualization, bars are oriented representing probabilities of attack above or below 0.5.

conspecific frogs. This scenario calls for more careful interpretations on the nature of multimodal signals when the relative importance of different subcomponents has not been explicitly tested.

Body Size, Body Movement and the Role of the Vocal Sac

Our results suggest that body size may act as a nonredundant and independent subcomponent of the visual signal (Partan & Marler 1999), although the classification depends upon the interpretation of males' reaction or lack thereof. That male *A. femoralis* attacked large models (i.e. average size of *A. trivittata* males) less frequently suggests two alternative explanations. Males in our study might have recognized large models as conspecific individuals, regardless of their coloration, but attacked them less frequently because larger individuals are more difficult to subdue. The ability to estimate opponent size and the predisposition to avoid attacking larger conspecifics is widespread among animals (Kratochvíl & Frynta 2002), including frogs (Davies & Halliday 1978; Wagner 1989; Bee et al. 1999). Alternatively, males may not have attacked large models because size is a visual cue used to discriminate conspecific against heterospecific individuals. The essential difference between both explanations is whether large models are interpreted as 'hard to beat' males or as 'heterospecific' males. The lack of overlap in body size between males of both species apparently favours the latter interpretation, because large models might look unnaturally large to *A. femoralis* males. However, many animals react to stimuli representing a trait that is exaggerated to a degree not occurring in nature (Enquist & Arak 1993). To discriminate between both explanations, bimodal playback experiments could be conducted in which unnaturally small models (i.e. with a body size comparable to that of a co-occurring small species not overlapping in size with *A. femoralis*) are presented to territorial males. If males attack small models despite their size, it could be concluded that body size is not used to discriminate between conspecific and heterospecific individuals.

Body movement can be unambiguously interpreted as an essential, independent and nonredundant component of the bimodal signal. Our results support the previous claim that a bimodal (visual and auditory) signal is required to elicit attacks by territorial *A. femoralis* males (Narins et al. 2003). They further suggest that any movement, rather than the pulsating movements of the vocal sac specifically, is the visual subcomponent of the bimodal signal. In Narins et al.'s (2003) experiment, an electro-mechanical model (i.e. a robotic frog) was combined with a loudspeaker to present different kinds of bimodal (auditory + visual) stimuli to territorial males. Males never attacked the model when the vocal sac was stationary, regardless of whether it was deflated or inflated. A pulsatile vocal sac, however, invariably led to male attacks. Although the model was sometimes rotated on its vertical axis to simulate body movement, this stimulus was always presented together with the pulsation of the vocal sac. Therefore, the experiment could not discriminate between vocal sac pulsation and body movement as visual cues that elicited male aggressive behaviour. Our technically much simpler experiment did not include a fake vocal sac in the dummy. Our experiment nevertheless showed that neither the presence nor the pulsation of the vocal sac is necessary, whereas body movements are enough to elicit attacks on the tested males.

In summary, although *A. femoralis* males required bimodal signals to engage in aggressive behaviour towards other males, these signals were only basic visual cues, namely movements, and perhaps, body size and some dark dorsal coloration were also used. The components (auditory + visual) of the bimodal signal can be considered nonredundant because neither of the more relevant visual subcomponents (body or sac movement) alone is sufficient to elicit aggressive reactions (Narins et al. 2003; Partan & Marler 2005). In turn, the visual component alone could be better described as a modulator of the auditory signal. If one considers male attacking behaviour as the only relevant reaction, then body movement is better described as part of a 'bimodal signal requisite' to elicit aggression (Narins et al. 2003). If, on the other hand, one

considers male reaction as manifold (Partan & Marler 2005), consisting of approaching, calling, searching and attacking, then the visual subcomponent of the signal would modulate male reaction in the sense of including attacks. In any case, our study shows that frogs include visual information in multimodal signals although in a way that enriches the actual classification schemes. In view of this new evidence, we strongly advocate for a more experimental and detailed analysis of the information transmitted through secondary channels before making inferences on the origin and adaptive value of multimodal signals.

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