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„Exploring the speed-accuracy trade-off (SAT) regarding the territory-defence-behaviour in the dendrobatid frog *Allobates femoralis*"

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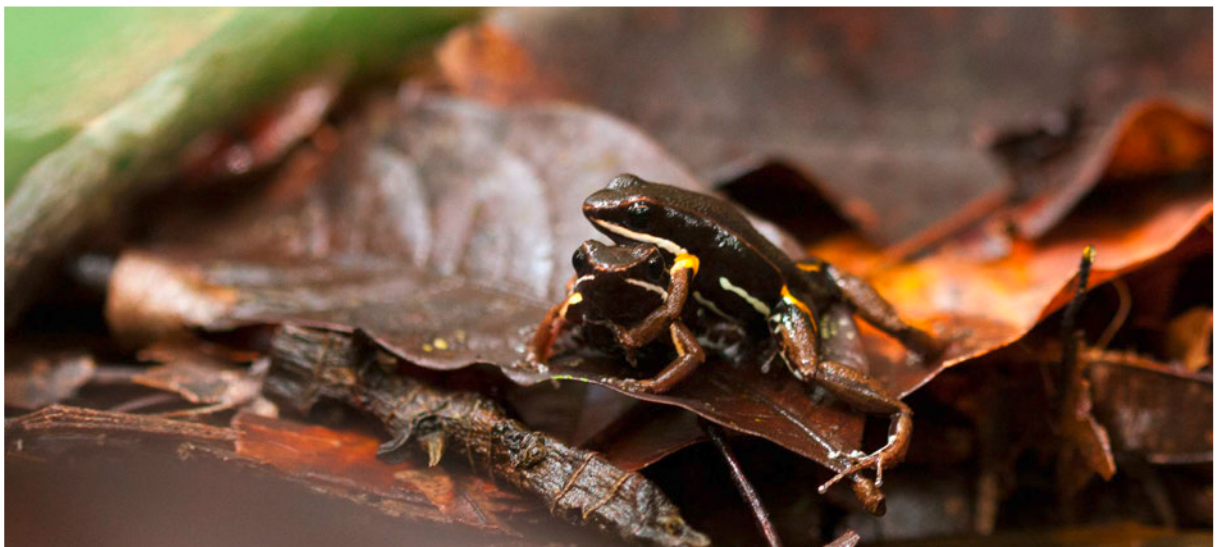
Allobates femoralis males fighting in the Nouragues Natural Reserve, French Guiana
Photo: Andrius Pašukonis

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Abstract

A trade-off between speed and accuracy is known to affect many behavioural processes such as predator avoidance, foraging and nest site selection, and has been found in mammals, insects and fish. Meanwhile, we have limited knowledge about the influence of this trade-off on territory-defence-behaviour. In amphibians, many poison frogs (Dendrobatidae) are known to engage in territorial defence, for instance males of the model species *Allobates femoralis*, widespread across Amazonia and the Guiana Shield, chase and pounce on calling intruders in their territory during the reproductive period. However, attacks need to be well considered, as they are usually energetically costly and bear the risk of getting injured.

We hypothesise the existence of a speed-accuracy trade-off regarding the territory-defence-behaviour in *A. femoralis*. Thus, we expect males that react faster to the call of an intruder to be less accurate and therefore more likely attack 'wrong' i.e. non-threatening individuals that do not show the pulsating vocal sac. We conducted an experiment in which we simultaneously presented a playback mimicking a non-visible threatening intruder and a robotic frog representing a visible non-threatening intruder. Contrary to our hypothesis, we ascertained that neither the decision time nor the approach speed of tested individuals predicted attack likelihood. However, we found that younger individuals were more likely to attack the robotic frog than older individuals, which we interpret as a lack of experience. *A. femoralis* individuals probably have to learn about the role of the vocal sac and how to distinguish between calling and non-calling frogs as well as between males and females. In summary, our study suggests that experience plays an essential role in identifying and distinguishing potential threat in territorial defence behaviour.

Introduction

It is well known that animals spending more time accumulating information before performing a behavioural response are facing lower error rates than faster acting individuals [1]. This so-called speed-accuracy trade-off (SAT) implies that speed and accuracy in decision-making processes cannot be maximised simultaneously; for further information about the neural basis of the SAT see [2,3]. Many behavioural patterns are affected by this trade-off; for example the avoidance of hidden predators which has been shown in mammals [4] and bumblebees [5], the foraging strategies examined in pollinating insects [6,7] and the nest site selection observed in house-hunting ant colonies [8]. However, very little is known about the SAT affecting territory-defence-behaviour.

Territory-defence-behaviour is widespread across amphibians and is particularly prominent in all dendrobatid frogs that have been studied [9], as for instance *Allobates femoralis*, a small dendrobatid species that is widespread across Amazonia and the Guiana Shield [10]. The reproductive success of male *A. femoralis* appears to be influenced by their ability to hold multi-purpose long-term territories in which pair-formation, courtship, mating and oviposition take place [11,12]. During the reproductive season males establish and proclaim such territories by calling from elevated perches on the forest floor [11,12,13]. Other calling males are not tolerated within a territory and are dislodged by various aggressive behaviour patterns, such as antiphonal calling, direct phonotactic approach or chasing and attacking the intruder [11,13,14,15,16]. The level of male aggressive territorial response depends on the sound pressure level (SPL) of an intruders' calling, measured from the position of the territorial male. SPLs above 56 dB evoke orientation towards the sound source followed either by subsequent antiphonal calling (56-68 dB) or by an approach towards the sound source (above 68 dB) [17]. It is known that it needs vocalisation and either vocal sac pulsations [14] or any body movement [18] to provoke physical combats. Previous preliminary observations in the field have shown that occasionally males might also attack approaching, mute females [E. Ringler pers. obs.]. This led to the question if speed comes at cost of limited precision in the context of territorial defence behaviour in *A. femoralis*. We thus conducted an experiment in which we simulated a non-visible, threatening intruder, using a playback call and a visible, non-threatening intruder, using a robotic frog model (FM). We expected males with faster decision time and/or approach speed to make more "false" decisions (i.e. attacking the model).

Materials and Methods

Field Site

The study was conducted in an experimental *A. femoralis* population that had been installed on a river island in 2012. The small-sized (~ 5 ha) island in the river Arataye is situated in a lowland tropical rainforest in the Nouragues Natural Reserve in French Guiana, close to the "Saut-Pararé" field camp (4°02' N – 52°41' W) of the Nouragues Ecological Research Station. The tropical, wet and humid climate in this area is characterised by an average annual precipitation of 4000 mm and a mean temperature of 26.3 °C [19]. The study was carried out between February and March 2017 and 2019, during the small rainy season when the reproductive period takes place, to ensure abundant calling activities. All trials were conducted from 0700 h to 1200 h and from 1400 h to 1900 h, during the two peaks of calling activity in *A. femoralis* [20].

Experimental Design

To investigate whether decision time and/or approach speed come at cost of lower accuracy, we arranged a bimodal experimental setup (see fig. 1a) by using the FM as the visual cue and a standardised advertisement playback call as the acoustic cue.

We used the same FM-apparatus as described by Narins et al. [14,15], which was made from silicone rubber, painted like an adult *A. femoralis* and fitted to a turntable rotated by a servo motor (Graupner Modellbau, Kirchheim unter Teck, Germany) at an angular velocity: 1,3 rad*s^{-1} that was integrated into an artificial log (size: 0.35 x 0.12 x 0.12 m) made from epoxy resin. In our study, the FM's vocal sac was replaced with modelling clay to mimic a female or a non-threatening, non-calling male. After locating a calling male, the FM was placed in an estimated distance of 2 m to the male.

The acoustic stimulus was broadcast using a portable speaker with an integrated audio player (Creative MUVO 2c, Creative, Singapore). The speaker was elevated to the same height as the FM, oriented towards the calling focal male, and placed semi-randomly to the right or the left side of the FM. We decided on the lateral positioning of the speaker to prevent unintentional direct encounters of the male with the FM when approaching the acoustic signal. FM and the centre of the loudspeaker were 0.10 m apart, which corresponds to an angular distance of 2.9° at a distance of 2 m between focal male and FM, where the

integration of bimodal signals operates well [15]. For the acoustic stimulus we used the artificial 'standard call' *sensu* Ursprung et al. [16], which is based on recordings by Gasser [21]; for a detailed description see [22].

For the purpose of measuring the approach-speed, a finish line depicted with small branches was indicated 0.25 m in front of the artificial log (see fig. 1). After log, loudspeaker and finish line had been positioned, the observer moved about two metres away from the experimental setup not to disturb the movement of the frog. The behaviour of individual frogs during the trials was noted down by using a voice recorder (ICD-PX333, Sony Corporation, Tokio, Japan). To avoid decisive time lags between the actual movement and the recorded one, abbreviations for every single action were used (e.g. jumping "JUMP", reaching the finish line "LINE" and attacking the FM "ATTACK"). Each trial started as soon as the loudspeaker and the rotating turntable were activated and lasted for 25 bouts (1 bout = 10 calls; 402.4 seconds).

The exact initial distance between the male and the FM (distance: $\bar{X} \pm SD = 2.23 \pm 0.30$ m) was measured with a laser rangefinder (DLE 50, Bosch GmbH, Stuttgart, Germany) at the end of each trial. Additionally, we measured the temperature (T: $\bar{X} \pm SD = 25.9 \pm 0.8$ °C) and humidity using a digital hygro-/thermometer (GFTH 95, Greisinger, Regenstauf, Germany). As humidity was always shown at 100%, it was not considered for further analysis. The SPL of the playback signal at the initial position of the focal male was measured after each trial using a sound level meter (VOLTCRAFT SL-100, Conrad Electronic, Hirschau, Germany). Due to the structural complexity of the forest floor, the received SPL of the playback signal differed among trials between 64.5 dB and 76.9 dB (SPL: $\bar{X} = 72,0$ dB; The mean value was calculated using linear values, for which a conversion from SPL in dB to sound pressure in Pa was performed). For individual identification and determining age, we took pictures of the individually distinct ventral belly patterns of all tested frogs to subsequently compare them with our long-term monitoring data set [23] using the pattern matching software Wild-ID [24]. Regarding the age we differentiated between young individuals (i.e. new encounters in this year) and old ones (i.e. recaptured males already known from previous years). Furthermore, we took pictures of each frogs' back in front of a reference grid for measuring snout-urostyle length (SUL: $\bar{X} \pm SD = 0.0286 \pm 0.0012$ m) using the freeware Fiji [25].

We used the software Solomon Coder [26] to transcribe observational recordings into timetables of behaviour. The decision time was defined as the time measured from the beginning of the trial (i.e. start of the playback along with the activation of the turntable-

rotation) until the male performed its first jump. The approach speed was calculated by dividing the distance between the tested male and the finish line (which was determined from the exact initial distance between the male and the FM) and the time it took the individual from its first jump to reach the finish line.
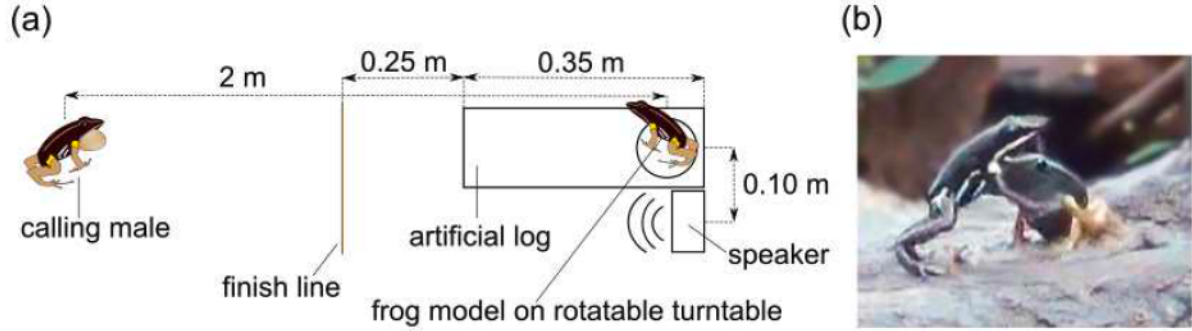

Figure 1. (a) Schematic diagram of the experimental setup. The frog model (FM) was positioned on a rotatable turntable that was integrated into an artificial log (0.35 x 0.12 x 0.12 m) and placed in a distance of about 2 m to a calling male. A standard advertisement call was presented by using a loudspeaker that was placed semi-randomly to the right or the left side of the frog model. Schematic figure is not to scale. (b) Extracted picture from video footage showing an *A. femoralis* male attacking the frog model.

Data Analysis

Fifty-one males were tested. We had to exclude four individuals that did not move at all and eight individuals that did not reach the finish line. Hence, our data included 39 males, thereof 22 old individuals and 17 young ones. 19 trials were conducted in 2017, 20 in 2019.

To investigate whether a speed-accuracy trade-off exists or if and which other environmental (T, SPL, year of data sampling) or individual (age, SUL) effects influence the probability of an attack, we created Generalized Linear Models (glm) with binomial error structure. We used 'attack' as the response variable and 'approach speed', 'decision time', 'T', 'SPL', 'age', 'year' and 'SUL' as the predictors.

There was no multicollinearity between the predictors (variance inflation factor VIF ≤ 2.1 for all predictor variables). We standardised all variables to make their effect sizes comparable independent from the scale. For model selection we followed an information-theoretic approach [27] and created a set of candidate models with all possible combinations of the predictor variables from the respective full model. We ranked the models based on

Akaike's second order information criterion (AICc) [28] and selected the subset of best models within ΔAICc ≤ 6 [cf. 29] and calculated model-averaged coefficients. All statistical analyses were done in R [30] using the packages lme4 [31], car [32] for calculating the VIF and MuMIn [33] for model averaging.

Results

Overall, seven individuals (n = 39) attacked the frog model, six of these were first-year adults i.e. young individuals. The estimates of the model-averaged coefficient of age had the highest relative importance and a very strong, negative effect on the probability to attack (estimate = -2.44, SE = 1.5, RI = 0.91; table 1). Also SPL had a quite high relative importance, with a strong positive effect on the probability to attack. This means that young individuals were more likely to attack the FM, and the probability of an attack increased with the SPL of the playback signal at the initial location of the tested male.

Five males approached the artificial log although the intensities of the playback sounds were below the proposed threshold of 68 dB SPL (with 64,5 dB SPL as the lowest) to elicit phonotactic response, as suggested by Hödl [17].

Decision time had a strong negative effect on the probability to attack, but a much smaller relative importance and a comparably large standard error and is therefore hard to interpret. Approach speed, SUL, year and T had a very low relative importance and small effect sizes and are therefore least likely to have affected attack behaviour in our experiment.

Table 1. Model-averaged coefficients including standard errors (SE) and relative importance (RI) to explain how the variables influence the probability of an attack.

	Estimate	SE	RI
Intercept	-2.64	1.03	-
Age	-2.44	1.50	0.91
Sound pressure level (SPL)	2.10	1.89	0.76
Decision time	-2.28	3.03	0.55
Approach speed	0.29	0.79	0.27
Snout-urostyle length (SUL)	-0.30	0.80	0.28
Year of data sampling	0.35	0.96	0.26
Temperature (T)	0.28	0.88	0.25

Discussion

Contrary to our hypothesis, neither decision time nor approach speed affected the accuracy of attack behaviour in *A. femoralis* in this study. Our results rather suggest a fundamental role of experience on the accuracy of territorial decision-making, as age was of utmost importance in influencing the probability of an attack.

Although it has been shown that any body movement (and not specifically the vocal sac pulsation) in addition to the acoustic cue might elicit attack behaviour in *A. femoralis* [18], the comparatively low attack rate in our study (7 out of 39) confirms the findings of Narins [14] that demonstrated high attack rates only occur when acoustic and visual (i.e. vocal sac pulsation) cues are presented in synchrony. Furthermore, it is in line with the general assumption that fighting is energetically costly and involves the risks of getting injured. Furthermore, attacking a female by mistake leads to the loss of a mating opportunity. Therefore, any attack needs to be well considered.

Our finding of young individuals being less accurate in decision-making during territorial defence might be a consequence of a lack of experience. It is known that experience plays a major role in various behaviour patterns such as hunting [34,35,36], foraging [37,38] as well as mating [39,40] and might also influence territory defence [41]. We assume that older *A. femoralis* individuals, in comparison to younger ones, are more experienced and therefore might have already learned how to distinguish between a calling male and a non-calling one as well as between a male and a female in general. Therefore, older frogs might be

better in discriminating between a threatening intruder and a non-threatening individual. The idea that frogs might need to learn to discriminate between sexes and potential threatening intruders is supported by observations in the field where males sometimes attack females sojourning in their territory while another male is calling close by [E. Ringler & R. Sonnleitner pers. obs.], and males performing courtship calls towards non-calling males [E. Ringler pers. obs.].

Although attacking a non-threatening intruder possibly causes a lack of a mating opportunity, young individuals still might benefit from doing so. We assume that such a rash acting might help to establish a territory for the first time, which could be even more important than single mating, as it may increase the reproductive success over a longer period of time.

Furthermore, the attack rate was increased by a higher SPL at the initial location of the tested male. We assume that the SPL of the intruder's call provides information about its threat potential, for which increased SPL might indicate a closer [22] intruder, representing a more immediate threat to the territory owner than a distant invader and therefore lowers the territory owner's accuracy in decision-making.

Our results show no effect of SUL on accuracy regarding attack behaviour. The reason for this might be that we only tested calling males, i.e. territorial adult individuals, whose body sizes do not differ a lot (SUL: $\bar{X} \pm SD = 0.0286 \pm 0.0012$ m).

Our findings suggest that T does not influence the attack behaviour. This might be due to the fact that our experiments were conducted at times when overall calling activity was high, and calling activity is strongly dependent on precipitation [42], which negatively correlates with T [20]. Since we only tested calling males, we probably tested them in their preferred temperature range for acting.

No difference in attack behaviour was observed between the two sampling years, which allowed for the merging of our two datasets.

We conclude that experience plays an important part in optimising individual decision-making. In species without sexual dimorphism, individuals might need to learn to discriminate between males and females, which is likely to be achieved via the integration of multimodal stimuli.

Ethics

This study was approved by the scientific committee of the "Nouragues Ecological Research Station" and the ethics board of the University of Veterinary Medicine Vienna (ETK09012017). All sampling was conducted in strict accordance with current French and EU law and followed the ASAB guidelines.

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Deutsche Zusammenfassung

Der Kompromiss zwischen Geschwindigkeit und Genauigkeit beeinflusst das Verhalten von Tieren in vielfältiger Weise, wie beispielsweise die Vermeidung von Prädatoren, die Nahrungssuche, sowie auch die Auswahl von Nistplätzen. Dieser sogenannte Geschwindigkeits-Genauigkeits-Ausgleich (GGA) wurde vor allem bei Säugetieren, Fischen und Insekten erforscht. Bisweilen ist nur wenig über die Existenz des GGAs bei Amphibien bekannt, insbesondere über dessen Einfluss auf territoriales Verteidigungsverhalten.

Bei Pfeilgiftfröschen (Dendrobatidae) ist territoriales Verhalten weit verbreitet, so auch bei *Allobates femoralis*. Die Männchen dieser in den tropischen Regenwäldern Südamerikas beheimateten Art sind bekannt dafür, sich während der Fortpflanzungsperiode hoch territorial zu verhalten. Mittels Anzeigerufen grenzen sie ihr Revier gegenüber männlichen Artgenossen ab, wobei nur rufende Eindringlinge verjagt und attackiert werden. Attacken müssen aber gut überlegt sein, da sie energetische Kosten sowie Verletzungsrisiken mit sich bringen.

Wir wollten testen, ob Männchen, die sehr schnell auf potenzielle Eindringlinge mit aggressivem Abwehrverhalten reagieren, gleichzeitig auch eine höhere Wahrscheinlichkeit für Fehlentscheidungen aufweisen. In unserer Versuchsanordnung wurde territorialen Männchen mit Hilfe eines Roboterfrosches ein sichtbarer, aber „ungefährlicher" Eindringling ohne pulsierende Schallblase präsentiert und zeitgleich durch Abspielen eines Anzeigerufes mittels Lautsprecher ein nicht sichtbarer, aber „gefährlicher" Eindringling simuliert. Entgegen unserer Hypothese konnten weder die Reaktionszeit noch die Annäherungsgeschwindigkeit die Wahrscheinlichkeit einer Attacke vorhersagen. Stattdessen stellten wir fest, dass junge Individuen den Roboterfrosch mit größerer Wahrscheinlichkeit attackieren als ältere, was möglicherweise auf fehlende Erfahrung zurückzuführen ist. Es erscheint uns naheliegend, dass *A. femoralis* Individuen erst im Laufe ihres Lebens über die Rolle der Schallblase als wichtigen Teil des Lautäußerungssystems bei Männchen lernen und damit in weiterer Folge auch über die Unterscheidung zwischen rufenden und nicht rufenden Individuen sowie zwischen Männchen und Weibchen. Zusammenfassend zeigt unsere Studie, dass Erfahrung eine essentielle Rolle bei der Erkennung und Unterscheidung von potentieller Gefahr im territorialen Verteidigungsverhalten spielt.

"It is just like man's vanity and impertinence to call an animal dumb because it is dumb to his dull perceptions."

Samuel Langhorne Clemens (1835-1910), "What Is Man?"

Allobates femoralis individual, Photo: Ria Sonnleitner