acta ethologica (2023) 26:139–143
https://doi.org/10.1007/s10211-023-00422-8

SHORT COMMUNICATION

Experimental evidence that toe-tapping behavior in the green-and-black poison frog (*Dendrobates auratus*) is related to prey detection

Lisa M. Schulte[1] · **Yannis König**[1]

Received: 9 January 2023 / Revised: 6 April 2023 / Accepted: 26 April 2023 / Published online: 6 May 2023
© The Author(s) 2023

Abstract
Toe-tapping, the quick movement of the middle toes of the hind legs, has been observed in many frogs and toads, and is usually associated with feeding, calling, or courtship behaviors. While plenty of observations of toe-tapping exist for different species, experimental evidence regarding the stimuli triggering this behavior is almost non-existent. Here, we systematically tested the influence of different stimuli on the toe-tapping behavior in the green-and-black poison frog (*Dendrobates auratus*, Dendrobatidae) from a captive colony in the Zoo Frankfurt. We found that, compared to a control, both big and small prey animals (crickets and fruit flies) elicited much more toe-tapping behavior, and that toe-tapping was positively correlated to feeding events. Playback advertisement calls in contrast did not trigger toe-tapping. We further showed that also juvenile frogs already toe-tap, but less frequently than adults. Our results support the observation-based data that toe-tapping is associated with hunting behaviors. While the auditory part of courtship does not seem to trigger toe-tapping, experimental evidence regarding visual and/or tactile courtship stimuli is still lacking.

Keywords Advertisement calls · Amphibia · Dendrobatidae · Predation · Vibrational communication

Introduction

Many animal species use multimodal communication to interact with con- and heterospecifics (Higham and Hebets 2013). In some cases, single behavioral components may serve as multimodal stimuli, such as specific movements, which can be detected in the visual, tactile, and/or auditory domain (Sloggett and Zeilstra 2008). Such specific movements can be found, for example, in many spiders (e.g., Elias et al. 2012), insects (for review, see Virant-Doberlet et al. 2022), and amphibians. The latter move their limbs or digits during hunting and/or courtship, potentially to influence the behavior of prey or mates. These so-called pedal luring, toe-waving, and toe-tapping/twitching behaviors have been observed in a large variety of anuran species and families (for overview see Sloggett and Zeilstra 2008; Erdmann 2017; Claessens et al. 2020). While pedal luring (in horned frogs, *Ceratophrys*; Murphy 1976) and toe-waving (in cane toads, *Rhinella marina*; Hagman and Shine 2008) have been shown to function as visual lure for specific prey items (particularly other anurans), the function of toe-tapping, the fast up- and down-movement of the middle toes of the hind legs (Fig. 1), is still less clear. Sloggett and Zeilstra (2008) suggest that the substrate vibration caused by toe-tapping might not attract, but agitate prey (i.e., trigger movement), making the prey animals easier to detect for the frogs. This was further underlined by a multi-species analysis based on online-video material: toe-tapping behavior was observed more frequently when prey animals were inactive than when they were moving (Claessens et al. 2020). Contrary to this, Erdmann (2017) showed that toe-tapping vibrations in Gulf Coast toads (*Incilius nebulifer*) caused prey to move less, but change movement directions toward the predator. This supports another hypothesis made by Sloggett and Zeilstra (2008), stating that toe-tapping behavior might serve as a prey-mimicking vibrational lure.

However, tapping behaviors have not only been observed in relation to hunting and feeding. Starnberger et al. (2018) observed male spotted reed frogs (*Hyperolius puncticulatus*)

✉ Lisa M. Schulte
Schulte@bio.uni-frankfurt.de

[1] Wildlife-/Zoo-Animal-Biology and Systematics, Faculty of Biological Sciences, Goethe University, Frankfurt, Frankfurt/Main, Germany

Fig. 1 Adult *D. auratus* from the Zoo Frankfurt. The middle toes on the hind legs, which are used for toe-tapping behavior, are marked with white arrows

tapping their feet in response to male playback calls. Toe-tapping during courtship and/or in association with calling behaviors was also reported for several dendrobatid species (Claessens et al. 2020) as well as in female whipping frogs (*Polypedates*; Narins 1995). In the green-and-black poison frog (*Dendrobates auratus*, Fig. 1), where toe-tapping behavior has first been observed in association with feeding (Murphy 1976), a recent field observation reports toe-tapping additionally in association with courtship behavior (Barquero and Arguedas 2022). They suggest that toe-tapping might function as an intraspecific vibratory signal.

Unlike for the more specific pedal luring and toe waving behaviors (Murphy 1976; Grafe 2008; Hagman and Shine 2008), most reports on toe-tapping are based on (single) observations from the wild or from pet frogs (e.g., Gagliardo et al. 2010; Turner 2011; Barquero and Arguedas 2022). Apart from a systematic analysis of online video-recordings of the latter (Claessens et al. 2020), the only experimental data on toe-tapping were, to the best of our knowledge, conducted by Erdmann (2017). He tested toe-tapping behavior in Gulf Coast toads (*Incilius nebulifer*) in relationship to prey animals (and vice versa). Due to the lack of experimental evidence and the observation that toe-tapping may also be related to intraspecific communication, with our study we had three goals: (1) we aimed to proof experimentally that poison frogs react to prey with toe-tapping behavior, (2) we tried to find out if different size prey animals trigger toe-tapping behavior in the same manner, or if this behavior is only directed at small or large prey animals, and (3) we aimed to get first experimental data on toe-tapping in relation to intraspecific communication, focusing here merely on vocal communication (i.e., conspecific calls, triggering territorial and reproductive behavior in males and females, respectively). For this, we systematically tested which of the three stimuli—small prey animals, big prey animals, and conspecific calls—triggered the toe-tapping behavior in green-and-black poison frogs kept in a colony in the Zoo Frankfurt, Germany. Based on previous observations in this species (see above), we hypothesized that all three stimuli would result in increased toe-tapping behavior.

Methods

Study animals

We tested a group of 21 adults and 7 juvenile *D. auratus* between February and March 2022. The animals were kept together in a 4.2 m^3 (2 m × 1.5 m × 1.4 m) large enclosure in the Zoo Frankfurt. Depending on the age of the frogs, they shared the enclosure with their conspecifics already since many years (i.e., the frogs knew each other). The enclosure contained a ca. 0.14 m^2 large water body in the front, several large branches reaching diagonally throughout the tank, plants like blushing bromeliad (*Neoregelia carolinae*), cornstalk dracaena (*Dracaena fragrans*), ferns (*Microlepia hookeriana*) and spider lily (*Crinum asiaticum*), and leaf litter on the ground. The animals were kept together with serrated basilisks (*Laemanctus serratus*), large-headed anoles (*Anolis cybotes*), Smith's tropical night lizards (*Lepidophyma smithii*), and Cuvier's foam froglets (*Physalaemus cuvieri*). Unlike *D. auratus*, *P. cuvieri* are night active and were not visible during the experiments. The reptiles only stayed in the upper part of the enclosure and did not get in contact with the frogs during the experiments. The day/night cycle was dependent on the natural light, with additional artificial light from 10:00 to 17:00. The enclosure was sprayed with an automated sprinkler-system twice per day (9:00 and 15:00). Under non-experimental conditions the animals were fed every other day. The main food source for the animals were crickets (*Acheata domesticus*), regularly complemented with flight-deprived fruit flies (*Drosophila melanogaster*). We could reliably recognize each animal based on its individual abdominal pattern, using picture cards made prior to the experiment when photographing each frog through the glass (i.e., without handling the animals). However, we could not distinguish between males and females. Due to the very regular mating outcome in the communal enclosure, we assumed a relatively even sex ratio.

Experimental design and data collection

Our experiments included four different treatments in the following order: (i) non-fed control ("control-treatment"), (ii) fed with fruit-flies ("fly-treatment"), (iii) fed with crickets ("cricket-treatment"), and (iv) confronted with conspecific calls ("calls-treatment"). For the control-treatment, frogs received their last regular meal the day before and they were not fed during the recordings. The fly treatment as well as the cricket-treatment both took place after 2 days of last feeding, so frogs were most likely hungry. The flies (or crickets) were presented to the frogs by directly dropping them ad libitum at the openable front of the enclosure. The calls-treatment took place at a day when frogs were not fed (i.e., 1 day after feeding). A small bluetooth-operated loud speaker (JPB® Harman, CLIP2 Portable Bluetooth Speaker) was hung on a branch at 30 cm above the ground. Advertisement calls of *D. auratus* (recorded at 26 °C in captivity by T. Ostrowski) were played to the frogs at roughly natural volume in a loop. Even though we cannot exclude other potential intraspecific interactions, the intraspecific stimuli tested here (i.e., the calls) did not occur during any of the other treatments, because none of the frogs called at any time of the experiments. During the control- and the calls-treatment, frogs were purposely not fed to be minimally distracted by prey. Although it is possible that subjects have found small insects crawling through the leaf litter of the tank, these food items were very scarce compared to the fly- and cricket-treatments.

During the treatments, frogs were filmed between 9:00 and 15:00 with a hand-held camera (Panasonic HC-V380) in a randomized order. Our goal was to record each frog for 5 min during each trial in order to measure the duration of toe-tapping behavior during this time. However, frogs often did not stay in sight for long enough, or their toes were not always visible in the recordings. So, recording time ranged from 1 min (only in two cases) to 10 min, with an average recording time of 4:52 min per frog per trial. Each frog was only filmed once per trial. The continuous recordings were analyzed via behavior sampling, with a focus on toe-tapping behavior. The accumulated time (in seconds) was counted for toe-tapping in each frog. To account for the variation in recording time, the average duration per minute was calculated. In addition to the toe-tapping behavior we also recorded all events (or attempts) of feeding for each frog per trial.

The juveniles were recorded and analyzed in the same manner as the adults in order to compare the average duration of their toe-tapping behavior with that of the adults. However, because their toe-tapping behavior varied from that of the adults, they were excluded from the statistical analyses.

Statistical analysis

We performed a generalized linear mixed-effect model of the relationship between the duration of toe-tapping behavior as response variable and the treatments (i–iv) as explanatory variable, with a poisson error distribution, using the Template Model Builder package glmmTMB (Magnusson et al. 2017) in R 4.2.0 (R-Core-Team 2022). We entered the ID of each frog as well as the daytime of measurement (morning: 9:00–11:00, midday: 11:00–13:00, afternoon: 13:00–15:00) as random effects into the model. Because our data were overdispersed, observation-level random effects (OLRE) were fitted to the model (Browne et al. 2005). *p*-values were obtained by likelihood ratio tests of the full models with the effect in question (i.e., the different treatments) against the model without the effect in question (i.e., without the different treatments; Winter 2013). In order to find which of the treatments had an influence on the toe-tapping behavior, a Tukey-corrected post-hoc test (multicomp-package; Hothorn et al. 2008) was conducted.

To see if feeding events (or attempts) were correlated to toe-tapping behavior, we calculated a Spearman's rank correlation in R (after showing with a Shapiro–Wilk normality test that our data were not normally distributed). We did not observe any calling behaviors during any of the trials, so no analysis was conducted regarding this behavior.

Results

Toe-tapping behavior during the different trials

Adult frogs tapped their toes during our recordings for up to 56 s per minute, with an average of 16.30 s per minute. Juveniles also showed toe-tapping behavior, but with an average of 5.98 s per minute less than the adults (leading to an exclusion from the statistical analyses).

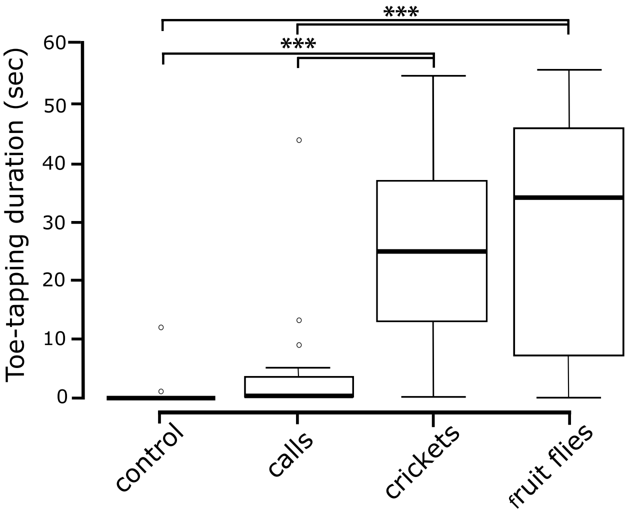

Fig. 2 Duration of toe-tapping behavior per minute during the different treatments (control, calls, crickets, fruit flies). The horizontal lines represent the median, the boxes delimitate the 25th and 75th percentile of the data, and the whiskers the minimum and maximum values (excluding the outliers presented by the circles). $^{***}p < 0.001$

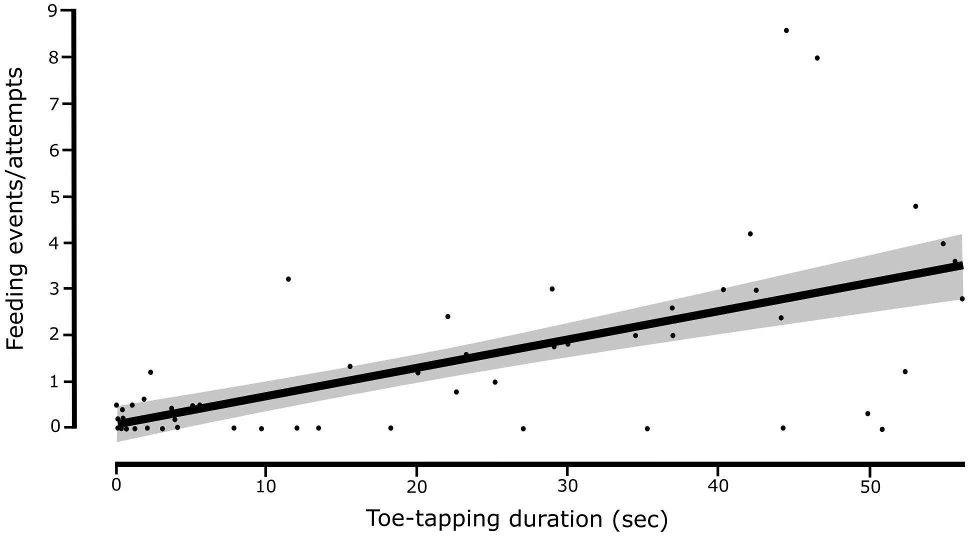

Fig. 3 Relationship between feeding events and toe-tapping behavior (pooled from all four treatments). The plot was made in the R-package ggplot 2 (Wickham et al. 2016). Dots represent the data points. The dark line indicates the regression line, with the grey shade marking the 95% confidence interval

Our comparison of the null versus the full model showed that the duration of toe-tapping behavior in the adults was significantly influenced by the different treatments ($\chi^2(2) = 60.77$, $p < 0.001$). When we compared the effects of the trials individually, we found that the effect of the calls-treatment did not differ from the control-treatment ($z = 2.08$, $p = 0.153$). The two treatments including food (i.e., fly-treatment and cricket-treatment), were, however, significantly different from both, the control-treatment (flies vs. control: $z = 6.20$, $p < 0.001$; crickets vs. control: $z = 6.15$, $p < 0.001$), as well as the calls-treatment (flies vs. calls: $z = 5.78$, $p < 0.001$; crickets vs. calls: $z = 5.71$, $p < 0.001$). Both food-treatments elicited much more toe-tapping behavior (Fig. 2). There was no difference in effect between the different types of food offered ($z = 0.11$, $p = 1.0$).

Toe-tapping behavior in relation to feeding

As expected, we could count more feeding events (and attempts) during the fly- and cricket-treatments (on average 1.78 and 1.96 per minute) than during the control- and calls-treatments (0.15 and 0.08 per minute). The Spearman's rank correlation revealed that there was a significant positive relationship between toe-tapping behavior and feeding events ($r_s = 0.62$, $p < 0.001$; Fig. 3).

Discussion

In this study, we show for the first time experimental evidence for the relationship between toe-tapping behavior and feeding in dendrobatids, supporting part of our hypothesis. However, unlike Starnberger et al. (2018), who showed that different types of playback calls (advertisement and aggression) triggered foot-tapping behavior in *H. puncticulatus* (Hyperoliidae), for *D. auratus*, we could not find a relationship between playback advertisement calls and toe-tapping. This contradicts our hypothesis that advertisement calls would have the same effect as food. We can, however, not exclude the possibility at this point that the frogs, due to their communal enclosure, are generally less interested in conspecific interactions. In addition, we were not able to differentiate between sexes and cannot rule out if only one and not both sexes react with toe-tapping to the calls. However, the generally low amount of toe-tapping observations during this trial rather suggests that neither males nor females reacted to the calls. But our results do not exclude the possibility that toe-tapping behavior is displayed during the physical part of courtship, as reported from field observations (Barquero and Arguedas 2022). However, the question to what extent we are dealing with multimodal communication evolved to communicate visually and vibrationally with conspecifics still awaits further testing.

Regarding the relationship between toe-tapping and feeding, the size (or species) of prey presented to the frogs during the food treatments (flies vs. crickets) did not affect the predators' response, leading to the conclusion that prey in general triggers toe-tapping. However, this behavior seems to be less pronounced in juveniles, possibly because, due to their smaller size, toe-tapping has a weaker effect on the prey animals. What effect this exactly is and if it differs between prey species still needs further investigation, since predictions here diverge (attraction vs. movement stimulation; Erdmann 2017; Sloggett and Zeilstra 2008). All in all, our experimental results support the online-video analysis based on observational reports from different poison frog species (Claessens et al. 2020). Being visual hunters, it is most likely that the frogs' reaction to prey is based on visual cues (i.e., prey movement; Eibl-Eibesfeldt 1951). However, it remains unknown if for example also the smell or 2D-visual stimuli (i.e., video recordings) of prey can trigger toe-tapping in these animals. Corresponding results would be especially interesting with regard to enrichment of captive (zoo) animals without the involvement of food—a subject that is still largely ignored in amphibians (Michaels et al. 2014).

Acknowledgements We are very grateful to the Zoo Frankfurt for their financial support and for providing the facilities for this study. We want to especially thank Johannes Köhler, Gerrit Wehrenberger, Thomas Tikatsch, and the rest of the animal care taker team of the Exotarium for their organizational help. We further thank Thomas Ostrowski for providing us with a recording of the natural call of the study species.

Author contribution Study conception and methodology: LMS; performance of the experiments: YK; data analysis: YK, LMS; writing/manuscript preparation: LMS, YK.

Funding Open Access funding enabled and organized by Projekt DEAL. Financial support of the Lab by the Zoo Frankfurt.

Availability of data and materials The datasets generated during and/or analyzed during the current study are available from the authors on reasonable request.

Code availability Not applicable.

Declarations

Ethics approval Not applicable.

Consent to participate Not applicable.

Consent for publication All authors gave their consent for the publication of the manuscript.

Competing interests The authors declare no competing interests.

Additional declarations for articles in life science journals that report the results of studies involving humans and/or animals Data collection conducted with the approval of the Zoo Frankfurt.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Barquero MD, Arguedas V (2022) Mass movement and potential vibratory toe signalling in the green and black poison-dart frog, *Dendrobates auratus* (Amphibia: Dendrobatidae). Herpetol Notes 15:79–82

Browne WJ, Subramanian SV, Jones K, Goldstein H (2005) Variance partitioning in multilevel logistic models that exhibit overdispersion. J R Stat Soc 168:599–613

Claessens LSA, Ganchev NO, Kukk MM, Schutte CJ, Sloggett JJ (2020) An investigation of toe-tapping behaviour in anurans by analysis of online video resources. J Zool 312:158–162

Eibl-Eibesfeldt I (1951) Nahrungserwerb und Beuteschema der Erdkröte (*Bufo bufo* L.). Behaviour 4:1–34

Elias DO, Maddison WP, Peckmezian C, Girard MB, Mason AC (2012) Orchestrating the score: complex multimodal courtship in the *Habronattus coecatus* group of *Habronattus* jumping spiders (Araneae: Salticidae). Biol J Linn Soc 105:522–547

Erdmann JA (2017) The function of toe movement in feeding by the gulf coast toad (*Incilius nebulifer*). Master's thesis. Southeastern Louisiana University, Hammond, Louisiana

Gagliardo R, Griffith E, Hill R, Ross H, JR MI, Timpe E, Wilson B, (2010) Observations on the captive reproduction of the horned marsupial frog *Gastrotheca cornuta* (Boulenger 1898). Herpetol Rev 41:52–58

Grafe TU (2008) Toe waving in the brown marsh frog *Rana baramica*: pedal luring to attract prey? Sci Bruneiana 9:3–5

Hagman M, Shine R (2008) Deceptive digits: the functional significance of toe waving by cannibalistic cane toads, *Chaunus marinus*. Anim Behav 75:123–131

Higham JP, Hebets EA (2013) An introduction to multimodal communication. Behav Ecol Sociobiol 67:1381–1388

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. Biometrical J 50:346–363

Magnusson A, Skaug H, Nielsen A, Berg C, Kristensen K, Maechler M, van Bentham K, Bolker B, Brooks M, Brooks MM (2017) Package 'glmmtmb.' R Packag Version 02 0

Michaels CJ, Downie JR, Campbell-Palmer R (2014) The importance of enrichment for advancing amphibian welfare and conservation goals. Amphib Reptil Conserv 8:7–23

Murphy JB (1976) Pedal luring in the leptodactylid frog, *Ceratophrys calcarata* Boulenger. Herpetologica 339–341

Narins PM (1995) Comparative aspects of interactive communication. In: Flock A, Ottoson D, Ulfendahl M (eds) Active hearing. Elvesier Science, London, pp 363–372

R-Core-Team (2022) R: a language and environment for statistical computing. In: Found. Stat. Comput. https://www.r-project.org/

Sloggett JJ, Zeilstra I (2008) Waving or tapping? Vibrational stimuli and the general function of toe twitching in frogs and toads (Amphibia: Anura). Anim Behav 76:e1–e4

Starnberger I, Maier PM, Hödl W, Preininger D (2018) Multimodal signal testing reveals gestural tapping behavior in spotted reed frogs. Herpetologica 74:127–134

Turner GS (2011) Toe-twitching in juvenile Sudell's frog *'Neobatrachus sudelli'*. Vic Nat 128:147–149

Virant-Doberlet M, Stritih-Peljhan N, Žunič-Kosi A, Polajnar J (2022) Functional diversity of vibrational signaling systems in insects. Annu Rev Entomol 68:191–210

Wickham H, Chang W, Wickham MH (2016) Package 'ggplot2'. Create elegant data visualisations using the grammar of graphics. Version 2:1–189

Winter B (2013) Linear models and linear mixed effects models in R with linguistic applications. arXiv 1308:5499

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.