An investigation of toe-tapping behaviour in anurans by analysis of online video resources

L. S. A. Claessens, N. O. Ganchev, M. M. Kukk, C. J. Schutte & J. J. Sloggett
Maastricht Science Programme, Maastricht University, Maastricht, The Netherlands

Keywords
Anura; Dendrobatidae; toe-tapping; pedal movements; feeding; internet videos; YouTube.

Abstract
Toe-tapping is a widespread anuran behaviour commonly associated with feeding where the anurans move the middle toes of their hind legs up and down. Previous studies have interpreted it as a pedal lure, a prey localization method and a stimulus used to transfix prey. A database of online videos was constructed in order to study this behaviour across species, with a particular focus on arrow poison frogs (Dendrobatidae); tapping occurrence, prey characteristics and environmental factors were recorded. The data collected include 19 species that have, as of yet, not been recorded to tap, 16 of which exhibit feeding-related tapping, while in the three other species, tapping seemed to be related to courtship. Across dendrobatid species, a significant correlation was found between prey activity and the occurrence of tapping, which supports a prey localization hypothesis. The database proved to be a valid method of research as it provided a sample size large enough for detailed data analysis across the Dendrobatidae. The utility of the data was partially limited by the available number of observations per species and the inconsistency in video quality, however.

Introduction
The understanding of anuran, and other amphibian, feeding behaviours is far from complete and misconceptions about stereotyped feeding mechanics resulting from studies on a limited number of model taxa are being replaced by the concept that there is a far greater variety of behaviours than previously thought (Deban, James & Nishikawa, 2001). Anuran diets range from insects to crustaceans to small vertebrate species, with some species exhibiting cannibalistic behaviour (Harvey Pough, 2007). While specialist anurans have been reported (e.g. Toft, 1981), adult anurans are mostly opportunistic generalist sit-and-wait predators (Santos, Almeida & Vasconcelos, 2004). Their diets and the stimuli used to locate food may vary since the particular species present in an anuran’s habitat constitute its prey (Browne, 2009). Terrestrial anuran species require live prey as visual prey detection is dependent on movement (Harvey Pough, 2007). As a result of the relatively sedentary predation mode, anurans generally have less opportunities for catching prey than actively hunting species do. This challenge might be responsible for the evolution of behaviours that could increase the likelihood of feeding taking place when opportunities arise (Hagman & Shine, 2008).

Among these behaviours are various pedal movements. Pedal movements have been reported in 42 amphibian species across 12 families (Erdmann, 2017), the majority of which are anurans. In anurans, pedal movements have been theorized to function as a visual lure that attracts vertebrate prey to the predator (Murphy, 1976; Hagman & Shine, 2008). For example, Murphy (1976) described the pedal luring behaviour of horned frogs (Ceratophrys calcarata) which is suggested to lure the prey to the front of the predator using the elevation and flexing of hind legs. Hagman & Shine (2008) postulated that the waving of specific toes of hind legs by cane toads (Rhinella marina) has the function of a lure for smaller vertebrate prey. However, it is possible that toe waving has another function since toes were additionally waved in presence of invertebrate prey that did not respond to the visual lure (Hagman & Shine, 2008). An alternative hypothesis, accounting for pedal movements in presence of invertebrate prey, was proposed, which suggested that toe-tapping could also serve as a vibrational stimulus that keeps the prey moving in order to allow continued detection by the predator, after initial visual contact has been established (Sloggett & Zeilstra, 2008). Sloggett & Zeilstra (2008) also suggested that toe-tapping might be a prey-mimicking lure by which the anurans mimic invertebrate vibrational communication. Finally, another explanation for pedal movements was proposed by Erdmann (2017), who concluded that pedal movements of Incilius nebulofer may serve as a transfixing stimulus which causes the prey to slowly approach the source of the stimulus, allowing the toad to strike it.

Thus, there is no widely accepted consensus about the function of toe-tapping that would be applicable for all amphibians which exhibit pedal movements. Additionally, tapping-related heterogeneity has been observed within species – they do not tap on every occasion when food is present, suggesting the existence of factors that influence toe-tapping, for example...
increased feeding drive (Erdmann, 2017). Furthermore, toe-tapping does not appear to be limited to feeding-related behaviours – its occurrence during amplexus has been noted in Petlophryne guentheri, suggesting mating-related usage for the behaviour in this species (Landestoy T. & Ortiz 2015).

Therefore, in order to gain more insight into the function of tapping and into the factors which contribute to the manifestation of this behaviour, it is necessary to obtain more observations and data on toe-tapping. However, conducting studies with a large pool of species is impractical. Direct live observations have mostly been made on a small number of species and individuals per study (Murphy, 1976; Radcliffe et al., 1986; Bavetz, 1994; Bertoluci, 2002; Sloggett & Zeilstra, 2008; Erdmann, 2017). Hence, specimen availability is an obstacle for the establishment of a taxonomical overview of tapping species, as well as for the qualification of influencing criteria. In order to extrapolate any conclusions on a scale larger than a few species, an alternative method to making direct observations on live specimens is preferred.

Since the advent of video-sharing platforms such as YouTube, videos from the general public have been utilized as a tool to study animal behaviour. Nelson & Fijn (2013) used YouTube videos to gather evidence of dogs engaging in interspecies play, horses playing with objects and animal responses to iPads. Other examples of such video use include investigations of vocal entrainment in various species (Schachner et al., 2009) and dogs responding to tablet computers (Baskin, Anavi-Goffer & Zamansky, 2015). Nelson & Fijn (2013) have recommended the use of videos to gather a large amount of evidence from which to pick promising research areas, and videos of behavioural curiosities have served as inspiration for experimental studies (Patel et al., 2009). Hence, there is precedent for using videos to amass a large and varied sample size that would not be practically achievable using live specimens exclusively. Based on videos gathered of pet amphibians, feeding is a well-documented behaviour among pet owners (Measey et al., 2019). As such, this method is suitable for qualitative research on toe-tapping phenomena across species in order to expand the currently existing lists compiled by Sloggett & Zeilstra (2008) and Erdmann (2017). The goal of the present study was to investigate the viability of this method for the study of toe-tapping in anurans. For this purpose, a video database was established and used to analyse feeding-related pedal movements, or lack thereof, across anuran species with a focus on dendrobatids since certain species are commonly maintained as pets.

Materials and methods

Compiling the online video database

In order to maximize the number of videos found, through Google searches, the video-sharing platforms YouTube and Vimeo were explored using different phrases: ‘Toad feeding’, ‘toads feeding’, ‘frog feeding’, ‘frogs feeding’, ‘anuran feeding’, ‘toe-tapping’, ‘toe twitching’, ‘pedal luring’, ‘Dendrobatidae feeding’, ‘Amphibian feeding’, ‘feeding frogs’ and ‘feeding toads’. Additionally, all Latin and common English names of bufonid and dendrobatid species listed on Amphibiaweb (www.amphibiaweb.org) were combined with the term ‘feeding’ to create over 900 additional search terms used separately on both Google and YouTube (see Appendix S1). Only videos that featured identifiable anurans with visible toes and the occurrence of tapping and/or feeding were included. It is worth noting the possible selection bias present in looking for videos which comes from using phrases such as ‘toe-tapping’, ‘toe twitching’ or ‘pedal luring’ as search terms; however, such terms yielded only a very small number of the videos recorded in the database, making the effect of the bias very limited.

A number of criteria were observed and recorded in the database in order to quantify the occurrence of toe-tapping in different species as well as factors suspected to have an effect on it (Table 1). In the end, species size, prey activity and substrate hardness as tapping-affecting factors were selected for analysis. Others, such as duration of tapping and prey quantity, are included in our database, but were not analysed here, as in some cases, they were difficult to conclusively assess due to predator and prey individuals moving in and out of frame.

Initially, the research focused on bufonid and dendrobatid species as a lot of work has already been carried out on pedal movements in bufonids (Hagman & Shine, 2008; Sloggett & Zeilstra, 2008; Erdmann, 2017), while dendrobatids are very commonly kept in captivity and were thus thought to be common video subjects. However, video material of bufonids was insufficient for analysis. Thus, the analytical aspect of this research was specifically aimed at tapping behaviour in Dendrobatidae.

Analysing the video database

Microsoft Excel 2013 was used for data analysis. To explore the relationship between size and tapping, different dendrobatid species were ranked in size, represented as snout–vent length (SVL), from lowest to highest based on the medians calculated from size ranges obtained from Amphibiaweb and additional sources (see Appendix S1). The probability of tapping was estimated for species with observations of ≥10 individuals by calculating the number of individuals observed tapping divided by the total number of individuals per species. A Spearman’s rank correlation coefficient was obtained in order to explore the link between species size and probability of tapping.

A 2 x 2 chi squared test was used to analyse the relationship between prey activity (active/inactive: see Table 1) and individuals tapping or not and substrate hardness (hard/soft: see Table 1) and individuals tapping or not. For these two tests, all dendrobatid species were pooled together in order to acquire a desirable sample size.

Results

Video database and new observations of tapping

The completed database (Appendix S1) featured 222 videos of 389 feeding and/or tapping anurans representing 63 species, 28 of which were members of the Dendrobatidae. Of these
species, feeding-related tapping was observed in 32 species (50.8%). The videos showed evidence of feeding-related tapping by individuals from 16 species which had previously not been reported to tap (Erdmann, 2017 and incl. refs.). Of these, five were bufonid species – Anaxyrus boreas, Anaxyrus terrestris, Nectophrynoideos asperginis, Sclerophrys mauritanica and Sclerophrys regularis, ten were dendrobatids – Adelphobates galactonotus, Ameerega bassleri, Ameerega picta, Ameerega peperi, Ameerega trivittata, Dendrobates truncatus, Phyllobates aurotaenia, Phyllobotes bicolour, Phyllobates lugubris and Phyllobates vitatus and one was a member of Pyxicephalidae – Pyxicephalus adspersus. Despite recording 16 species that have not previously, in literature, been described to perform feeding-related tapping behaviour, our search did not yield any tapping results for a number of species that had been included in the most recent taxonomic overview (Erdmann, 2017), namely Anaxyrus quercicus, Anaxyrus woodhousii and Bufo bufo. Additionally, tapping was observed in a number of situations where individuals were not presented with prey. These ranged from calling and/or courting to amplexus to seemingly random occurrences. Tapping during amplexus was observed in Incilius leucomyos was observed in two individuals, Phyllobates aurotaenia (one individual), Phyllobates bicolour (two individuals), while tapping during courting, calling or mating was observed in P. aurotaenia (one individual), P. bicolour (four individuals), Ranitomeya reticulata (one individual), Ranitomeya summersi (two individuals), Ranitomeya uakarii (one individual), Ranitomeya variabilis (three individuals) and A. bassleri (one individual).

Eight dendrobatid species (Phyllobates terribilis, R. ventrimaculata, P. vitatus, Dendrobates auratus, Dendrobates leucomelas, P. bicolour, Dendrobates tinctorias, A. peperi) had a sufficient number of observed individuals (n ≥ 10) to be included in the size analysis. There was no significant relationship between SVL and the probability of toe-tapping behaviour in the presence of food items (Rs = −0.24; 6 d.f.; P > 0.50; Fig. 1). Across the entirety of the family, tapping probability was higher for inactive prey than for active prey ($X^2 = 10.21; 2$ d.f.; $P = 0.0014$; Fig. 2).

While tapping probability was observed to be higher on hard substrates, the difference between the probability observed on soft substrates was not statistically significant ($X^2 = 1.39; 2$ d.f.; $P = 0.24$; Fig. 3).

### Discussion

No tapping behaviour was observed for A. quercicus, A. woodhousii and B. bufo, species that have previously been reported to tap (Erdmann, 2017 and incl. refs.). These observations reaffirm that tapping varies within species and imply that tapping is not a constant accompaniment to feeding, as its occurrence is situational and depends on the individual.

While the focal point of the research was feeding and related factors, certain species were found to tap during amplexus, courting, calling or mating. Tapping during amplexus was observed in R. ventrimaculata, I. leucomyos and P. guentheri, while tapping during courting, calling or mating was observed in two Phyllobotes species, four other Ranitomeya species and A. bassleri. These instances were recorded in the database as anecdotal examples which may point to the possible adaptation of toe-tapping as a behaviour for tactile stimulation, potentially related to mating, in some anuran species as described by Landestoy T. and Ortí (2015), but were not studied further in this research. It should be acknowledged that in some videos, prey items could have been present but remained out of view. Nevertheless, it is also an intriguing possibility that toe-tapping has a different or additional function.

The data implied that there is no significant correlation between the probability of toe-tapping in dendrobatid species and species’ size. Such a difference has been observed intraspecifically in R. marina, in which smaller/younger individuals tap less/not at all (Hagman & Shine, 2008); however, this may not apply across species highlighting the multifaceted nature of the phenomenon. Alternatively, while such a relationship could exist, the limits posed by the reliance on video material exclusively could have confounded the results.

A significant conclusion drawn from the database was that, in Dendrobatidae, inactive prey increases toe-tapping probability. This relationship could be explained through the ‘vibrational stimulus’ hypothesis of Sloggett & Zeilstra (2008), which states that toe-tapping disturbs prey, increasing...

### Table 1 Parameters of videos and observations recorded in the database with their measurement criteria

| Video parameters and observations | Criteria |
|----------------------------------|----------|
| Video link                        | -        |
| Species observed                  | Retrieved from video title/description. |
| Species size                      | The median of the species size range obtained from Amphibiweb. |
| Number of specimens in video      | -        |
| Occurrence of tapping (Yes/No)    | Whether at least one individual toe tapped. In cases of multiple specimens present in the same video – how many individuals tapped. |
| Duration of tapping               | Total amount of time individual(s) spent tapping. |
| Substrate characteristics (Soft/Hard) | Qualitative observation-based classification of substrate material. |
| Prey type (Active/Inactive)       | Based on relative mobility of prey item: Arthropods, vertebrates and crustaceans were considered as active, worms and larvae as inactive. |
| Number of prey items              | How many prey individuals the anuran was presented with. |
| Additional factors                | Recorded non-feeding-related tapping behaviour. |
Since active prey is typically on the move and therefore easier to spot, the relative effect of toe-tapping would be small. In inactive, non-moving prey, however, toe-tapping would have a larger effect, as the relative increase in movement and therefore detectability caused by the stimulus would be much bigger. Consequently, toe-tapping would occur more frequently in the presence of inactive prey.

No correlation between substrate hardness and tapping occurrence was found. This may indicate that substrate hardness does not modulate tapping occurrence since the benefits of toe-tapping may outweigh the relatively low energy costs in most cases. It is further possible that such a variety of substrates does not exist in the anuran’s natural habitat, making it unnecessary to assess the substrate type and adjust tapping behaviour accordingly. Additionally, it should be considered that the vibrational component of tapping has been overestimated and does not serve a specific purpose. The acquired results may alternatively be distorted due the binary descriptive approach of the method, as all substrate types had to be divided into two (hard/soft) groups based purely on visual assessment.

While utilizing videos in order to establish the database proved largely adequate, as it provided a large sample size of anuran feeding behaviours, there were some shortcomings consequent on this method. Since most of the videos were not made for scientific research, there were many confounding variables present which could influence feeding behaviours or the researchers’ ability to observe them. The videos were mostly made by different pet owners, resulting in a lack of uniform living and feeding conditions. For instance, it could not be made sure how often the different anurans were fed, and as such, it was impossible to assess the influence of factors such as hunger. Similarly, tapping duration and prey number could not be recorded consistently. Another shortcoming was the sample size per species. For more popular pet species, there was adequate video material; however, for rarer species, there were no or very few usable videos. Dendrobatidae were the main focus of analysis due to their popularity, while bufonid species for instance were excluded from statistical analysis as the number of useable videos proved too little to result in a sufficient sample size. This had an influence over data analyses as it limited the number of taxa analysed.

The overall findings of this study and observations made throughout point to several different conclusions, indicating the potential value of this method in describing animal behaviour across species. Firstly, toe-tapping is a multifaceted, mainly hunting-related behaviour with potential species-specific usages, notably in courtship and amplexus. Although the video quality
limited statistical analysis for some factors, a significant correlation between exposure to inactive prey and an increase in tapping probability in Dendrobatidae was found. We postulate that for these species, toe-tapping is related to providing a vibrational stimulus that induces movement in prey, allowing for improved detection, which falls in line with the hypothesis proposed by Sloggett & Zeilstra (2008). Room for future research is also present for determining the exact role of toe-tapping in hunting and feeding, its triggers and its connection to prey type and other factors as well as its other possible roles such as in courting and amplexus. Lastly, another matter which warrants investigating is the presence of toe-tapping in other anuran families as well as its occurrence as a preserved trait in non-anuran taxa.

References
Baskin, S., Anavi-Goffer, S., & Zamansky, A. (2015) Serious games: is your user playing or hunting? In Entertainment computing - ICEC 2015. ICEC 2015. Lecture notes in computer science, vol 9353, pp. 475–481. Chorianopoulos, K., Divitini, M., Baalsrud, H.J. Jaccheri, L. & Malaka, R. (eds.). Cham: Springer.
Bavetz, M.J. (1994). Pedal movements in two ambystomatid salamanders. J. Herpetol. 28, 504–506.
Bertoluci, J. (2002). Pedal luring in the leaf-frog Phyllomedusa burmeisteri (Anura, Hylidae, Phyllomedusinae). Phyllomedusa 1, 93–95.
Browne, R.K. (2009). Amphibian diet and nutrition. http://www.amphibiark.org/research/Amphibian-diet-and-nutrition.pdf Retrieved 18 December 2019.
Deban, S.M., James, C.O.R. & Nishikawa, K.C. (2001). The evolution of the motor control of feeding in amphibians. Am. Zool. 41, 1280–1298.
Erdmann, J. (2017). The Function of Toe Movement in Feeding by the Gulf Coast Toad (Incilius nebulifer). Master’s thesis. Southeastern Louisiana University, Hammond, Louisiana.
Hagman, M. & Shine, R. (2008). Deceptive digits: the functional significance of toe waving by cannibalistic cane toads, Chaunus marinus. Anim. Behav. 75, 123–131.
Harvey Pough, F. (2007). Amphibian biology and husbandry. ILAR J. 48, 203–213.
Landestoy T., M. & Ortíz, R. (2015). Rediscovery of the eastern crested toad (Peltophyne fracta), with comments on conservation, vocalization, and mating behavior. Reptile Amphib. 22, 50–55.
Measey, J., Basson, A., Rebelo, A.D., Vimercati, G., Louw, M. & Mohanty, N. (2019). Why have a pet amphibian? Insights from YouTube. Front. Ecol. Evol. 7, 52.
Murphy, J. (1976). Pedal luring in the leptodactyld frog, Ceratophrys calcarata Boulenger. Herpetologica 32, 339–341.
Nelson, X.J. & Fijn, N. (2013). The use of visual media as a tool for investigating animal behaviour. Anim. Behav. 85, 525–536.
Patel, A.D., Iversen, J.R., Bregman, M.R. & Schulz, I. (2009). Experimental evidence for synchronization to a musical beat in a nonhuman animal. Curr. Biol. 19, 827–830.
Radcliffe, C.W., Chiszar, D., Estep, K., Murphy, J.B. & Smith, H.M. (1986). Observations on pedal luring and pedal movements in Leptodactyld Frogs. J. Herpetol. 20, 300–306.
Santos, E.M., Almeida, A.V. & Vasconcelos, S.D. (2004). Feeding habits of six anuran (Amphibia: Anura) species in a rainforest fragment in Northeastern Brazil. Iheringia. Sér. Zool. 94, 433–438.
Schachner, A., Brady, T.F., Pepperberg, I.M. & Hauser, M.D. (2009). Spontaneous motor entrainment to music in multiple vocal mimicking species. Curr. Biol. 19, 831–836.
Sloggett, J.J. & Zeilstra, I. (2008). Waving or tapping? Vibrational stimuli and the general function of toe twitching in frogs and toads (Amphibia: Anura). Anim. Behav. 5, e1–e4.
Toft, C. (1981). Feeding ecology of panamanian litter anurans: patterns in diet and foraging mode. J. Herpetol. 15, 139–144.

Supporting Information
Additional Supporting Information may be found in the online version of this article:
Appendix S1. Search terms, database and data analysis.