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Mass movement and potential vibratory toe signalling in the Green and Black Poison-Dart Frog, *Dendrobates auratus* (Amphibia: Dendrobatidae)

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Mass movements of amphibians are commonly related to migration for reproductive purposes or with dispersal, when conditions in the natal habitat limit the chances of survival or reproduction (Russell et al., 2005; Semlitsch, 2008). In the first case, adult individuals typically move unidirectionally from terrestrial habitats to aquatic breeding sites during the night at specific times of the year (Semlitsch, 2008). This has been extensively documented in species of Salamandridae (true salamanders), Ranidae (true frogs), and Bufonidae (toads) from temperate areas (Arnfield et al., 2012; Heemeyer and Lannoo, 2012; Mettouris et al., 2018). For example, California Red-Legged Frogs (*Rana draytonii*) move overland in approximately straight lines to aquatic sites that are up to 2800 m apart, with up to 22% of the adult population performing this migration every year (Bulger et al., 2003). In the case of dispersal, both juvenile and adult individuals move either small or large distances to explore new areas, particularly to avoid inconvenient conditions such as microhabitat desiccation. For example, a literature review on the African Clawed Frogs (*Xenopus laevis*) revealed that most observational studies report the simultaneous overland movement of very large numbers of individuals, despite the fact that this species is considered purely aquatic (Measey, 2016).

There have been no reports of breeding migrations of Dendrobatidae (poison frogs) and species of this family are usually considered poor dispersers (Caldwell and Summers, 2003; Wells, 2007). However, they can move short distances, either horizontally or vertically, to transport tadpoles on their backs to waterbodies (Pašukonis et al., 2019). Many dendrobatid species can reproduce during several months of the year or even year-round, although the transportation of tadpoles is not performed in a coordinated fashion and breeding is asynchronous (Savage, 2002; Caldwell and Summers, 2003; Wells, 2007). The Green and Black Poison-Dart Frog, *Dendrobates auratus* (Girard, 1855), is a common forest floor denizen where it occurs. This species ranges from southern Nicaragua through both the Pacific and Caribbean lowlands of Costa Rica and Panama into eastern Colombia (Savage, 2002; Leenders, 2016). Adult individuals are relatively small (25–42 mm snout–vent length) and active diurnal foragers, feeding upon small arthropods (e.g., ants, mites, flies; Savage, 2002; Caldwell and Summers, 2003). Territoriality seems to be density-dependent (Caldwell and Summers, 2003), with both males and females engaging in aggressive interactions (Wells, 1978). Mass movements have not been reported in this species, although individuals can move up to 6000 body lengths in a day and climb up to 45 m in the canopy (Savage, 2002; Wells, 2007).

On 15 April 2019, at approximately 13:30 h, we observed a mass movement of adult *Dendrobates auratus* crossing a cemented trail in Carara National Park, Puntarenas Province, Costa Rica (9.7790°N, 84.6058°W, elevation 38 m). Our observations occurred on a 50-m section of the trail, which is ~100 m apart from and parallel to a busy highway. The frogs seemed oblivious to our presence and some individuals voluntarily approached us up to a distance of < 20 cm (Video S1, available at the Kérwá repository of the University of Costa Rica, https://hdl.handle.net/10669/84342). Some individuals moved along the trail for a few minutes, but eventually all of them followed the same direction from west to east, moving away from the highway and into the forest. We estimated that at least 60 individuals were actively hopping across the trail, and even a few groups of 2–3 individuals were observed moving very close together (Video S1). We

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started detecting these frogs after a moderate rain shower, and we observed their movements for about 30 min, by which time most individuals had disappeared from sight into the forest.

During the observation period, we identified several behaviours typical of the species, such as locomotion (making short, quick hops), foraging (leaning forward and striking the substrate with the tongue), and courtship (individuals touch and move around each other; Fig. 1). In addition, we observed a particular toe-tapping behaviour previously reported for *Dendrobates auratus* during feeding (Murphy, 1976), but that we associate with mating behaviour. We detected a male calling in the leaf litter and a possible female that was < 20 cm apart. The female approached the male and both individuals made several short hops, touching each other in the process. At the same time, the male started to quickly twitch the fourth toe (the longest in this species) of both feet, pounding the leaf litter slightly (Video S2, available at the Kérwá repository of the University of Costa Rica, https://hdl.handle.net/10669/84349). The male moved away from the female a few centimetres, repeating the vibrations of the fourth toes, and the female followed him. It seemed that the male was guiding the female through the leaf litter by calling and toe-tapping, since the female approached to the location of the male. However, the female eventually jumped to the cemented trail and moved away from the male. Raindrops were falling onto the leaf litter during the entire observation.

We consider that toe-twitching might function as a potential intraspecific vibratory signal in this species (Claessens et al., 2020). Toe-tapping has been identified to occur in a wide range of amphibian species (Sloggett and Zeilstra, 2008; Claessens et al., 2020), although it has been commonly regarded as a visual stimulus to attract prey (Hagman and Shine, 2008). However, intraspecific vibratory signals are commonly used by amphibians in several contexts (Narins et al., 2018). Anurans are recognized for having a highly sensitive saccule that detects frequencies below 100 Hz, such as substrate-borne vibrations (Wells, 2007). Most anurans use this seismic sense to detect approaching predators, although in some species it also serves as an extra-tympanic pathway to detect vibratory signals from conspecifics (Narins et al., 2018). Whether individuals of *D. auratus* are using such a mechanism for intraspecific communication is yet to be tested. However, we speculate that toe-tapping could serve as a reinforcement of the call, whose frequency averages 3.5 kHz and lasts up to 4 s (Savage, 2002), especially because of the background noise produced during rainy conditions. The noise of raindrops dropping onto the leaf litter could reduce the effective transmission of the call, and a vibratory signal might mitigate message transmission.

Figure 1. Two *Dendrobates auratus* observed performing courtship behaviour during a mass movement at Carara National Park, Costa Rica. Photo by Marco D. Barquero.

The effects of rain on frogs are uneven throughout the year at the Carara National Park, which presents a clear regime of wet (May–November) and dry (December–April) seasons, with an average annual rainfall of 2000–3000 mm and an average annual temperature of 27°C (Vargas Ulate, 1992). Thus, we were interested in examining the weather conditions during the day the observations occurred and the previous six weeks. We obtained meteorological data from the Instituto Meteorológico Nacional that included daily total rainfall and daily temperature (average, minimum and maximum) from 1 March–15 April 2019, as well as hourly rainfall and temperature for the day when observations occurred. These data came from the two closest stations located 13.5 km and 15.8 km distant from the national park. We used these data to determine the daily variation in the climatic conditions during the previous six weeks to the events reported and the hourly variation during the day of our observations. We found that air temperatures during the 6-week period ranged between 23°C (minimum) and 36°C (maximum), and was around 32°C when the mass movement of frogs took place (Fig. 2). In addition, our observations took place at the onset of the rainy season, since only two soft showers (0.2 mm on 10 April and 0.6 mm on 14 April) had been recorded prior to the day of our observations. This suggests very dry and hot conditions at the Carara National Park previous to and during the mass movement of the frogs observed.

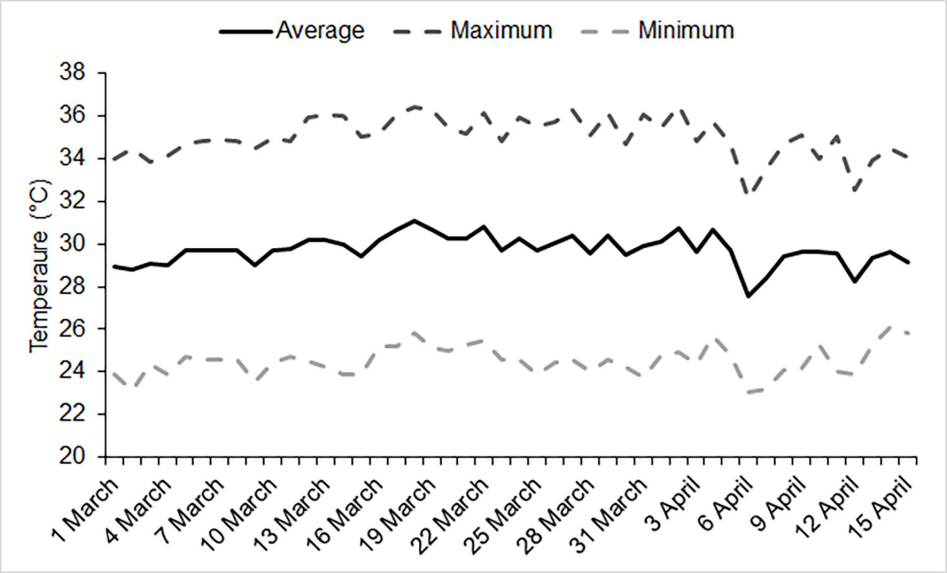

Figure 2. Air temperature variation from 1 March–15 April 2019. Data obtained from two meteorological stations close to Carara National Park, Costa Rica.

Gray and Green (2000) reported refuge use by *D. auratus* under leaf litter at Taboga Island, Panama, where frogs found a relatively moist place to hide and survive very dry conditions produced by the 1997–1998 El Niño event. They observed at least 40 frogs emerging from the refuge (a depression 85 cm wide covered by 55 cm of leaf litter) when one of the researchers stepped close to it. This would potentially explain our observations on the mass movement of this species. We argue that the frogs we observed could have been surviving the high temperatures and low rainfall experienced during the dry season by using refuges similar to that described for Panama (Gray and Green, 2000). Therefore, with the first rains, frogs began to emerge from one of these refugia to disperse across the forest. Our observations pose the challenge to test refugium use in this frog species, as well as whether vibratory signals could be a component of the repertoire of many amphibians that should receive more attention.

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