Topic Summary

Cane toads (*Rhinella marina*) and many other amphibians engage in the mating position known as amplexus, in which the male dorsally grasps the female with his forelimbs and externally fertilized her eggs. This behaviour is quite easy to visually observe, and cane toads can engage in mating and courtship behaviours on land, in the shallow waters of their habitats, or further away (Duellman and Trueb 1994). Once eggs have been externally fertilized, females typically release them into streams (Najar and Ferrante 2020). Due to concentrating their reproductive activities during short time windows in the year (explosive breeders), selection has occurred overtime for this behaviour to be highly efficient in cane toads, but often inaccurate (Carvajal-Castro et al. 2020)

In terms of the emergence and persistence of this behaviour through evolution, amplexus is believed to have evolved for the male to ensure the fidelity of the female while mating, thus increasing the chance of egg fertilization (Carvajal-Castro et al. 2020). Within the 'nuptial clasp' itself, differing durations and positions have been observed in species within the order Anura (Duellman and Trueb 1994). Through phylogenetic analyses, it was determined that axillary amplexus, which happens to be the most common position in cane toads in which the male clasps the female under her forelimbs, is basal to most Anurans (Carvajal-Castro et al. 2020). In this position, the anurans orifices for gamete release are close to each other, ensuring high fertilization efficiency. However, in species with pronounced size dimorphism, males have evolved different stances that still ensure that their sperm is released closed to the female's orifice (Duellman and Trueb 1994).

Aside from the production of gametes and physiological allocation of energy during mating, the action of amplexus can confer additional costs on both the male and female. The magnitude of these costs was typically studied by measuring and comparing locomotion speeds of amplectant individuals and free toads (Bowcock et al. 2009; Bowcock et al. 2008). Researchers found that the female's ability to sprint and swim was greatly reduced due to the weight of the male on her back, and that both sexes had decreased feeding rates while mating (; Bowcock et al. 2008).

There are several adaptations for amplexus that confer an advantage to males and enhance their ability to compete for females and hence maximize their reproductive success. Of these, researchers studied forelimb muscle size and body size respectively (Clark and Peters 2006; Bowcock et al. 2013). They found that the larger a male's body size, the more successful he is in outcompeting his rivals and dislodging them for his spot atop the female; a similar large-size advantage was found for males with larger forelimbs (Clark and Peters 2006; Bowcock et al. 2013). Researchers also found that size may play a role in males' selection criteria for female mates in a size-associative manner, with divergence from this pattern when a female was already engaged in amplexus as the rival male would be unable to correctly assess her size (Bowcock et al. 2013).

Cane toads must be able to communicate with members of their own species to evaluate potential partners, terminate amplexus, and assess the suitability of their surrounding habitat for breeding (Bowcock et al. 2008; Bowcock et al. 2013). This complex process involves integrating

signals from the environment across many sensory systems (Bowcock et al. 2008; Bowcock et al. 2013). Researchers that were interested in studying the inter and intrasexual interactions between cane toads during mating first stimulated reproductive readiness in the laboratory by administering a leuprorelin acetate (a GnRH-like hormone) injection to males and observing their consequent behaviours (Bowcock et al. 2008; Bowcock et al. 2013). When it comes to misdirected amplexus clasps, which often occur in cane toads, clasped males will produce a release call and vibrations of their body wall muscles. Females will not produce a call at all but will still vibrate if they wish to terminate mating (Bowcock et al. 2008; Clark et al. 2006). Due to these mechanical cues, Clark and others (2019) predicted that males would not use visual cues when mate searching, or at least to a lesser degree. However, counterevidence to this prediction was provided by observations made by Gray and Mackenzie (2016), in which rival males were attempting to jump onto amplectant pairs in water from a vantage point, suggesting that visual information helped them decipher the female's location from afar. Gray and Mackenzie (2016), as well as another group of researchers (Najar and Ferrante 2020) conducted purely observational field studies of different amplexus pairs and commented on their undisturbed ecological interactions. Gray and Mackenzie (2016) saw two rival males attempt to dislodge an amplectant male from a female using various physical tactics, whereas Najar and Ferrante (2020) observed an unusual case of two males attempting to mate with a dead female. Unlike Gray and Mackenzie (2016), the latter group predicted that amplexus can also be non-adaptive if it confers no reproductive advantages to the males.

Future research can study the implications of the length of amplexus on cane toads (Duellman and Trueb 1994). Since cane toads are such an effective model species (they readily amplex in the laboratory), they can also be used to further explore factors that influence the intensity of sexual conflict during this mating behaviour (Bowcock et al. 2008).

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