

Interspecific combat observed among viperid snakes

Copperheads (*Agkistrodon contortrix*) and Cottonmouths (*A. piscivorus*) are relatively common viperid snakes occurring throughout the eastern and central United States. The two species are unlikely to encounter each other regularly, as Copperheads are associated with terrestrial habitats while Cottonmouths generally inhabit wetlands; thus, we know little about how the two species interact. On 6 September 2016 at approximately 18:45 h, the second author observed both snakes together outside Snowball, Searcy County, Arkansas and recorded their behavior for approximately 3 min and 40 s before leaving the area (Video S1). The landscape where the observation occurred can be considered generally overgrown farmland in a rural matrix of woods and infrequently mowed pasture; there are old cars, farm equipment and hay bales scattered throughout. The snakes were located next to a pile of corrugated tin alongside the edge of a sandy road bordered by tall overgrown vegetation. The pile of tin was located ~180 m from a creek and there are several stock

ponds within ~800 m. In general, one would expect the spot where the observation occurred to be representative of habitat suitable for Copperheads more so than for wetland-associated Cottonmouths, although the latter are well-known for terrestrial forays and migrations, especially in the fall (e.g., Glaudus et al. 2007).

The snakes' behavior in the video closely matches the stereotypical combat behavior demonstrated by males within the *Agkistrodon* genus and some other snake groups (Carpenter and Gillingham 1990, Fig. 1); we believe the video documents for the first time combat between two different snake species. It is generally accepted that combat between *Agkistrodon* snakes represents an attempt to establish dominance and secure reproductive rights to a nearby female (Schuett and Gillingham 1989); the larger individual typically wins the combat (Schuett 1997) as they are able to “offensive-hook” the other snake more often (Carpenter and Gillingham 1990). Only a handful of laboratory studies pertain to intraspecific snake combat and this behavior is rarely observed under natural conditions; as a result we have a limited ability to understand the fascinating interspecific interaction documented in our video.

That two different species of snakes would engage in combat immediately raises a host of ecological questions that warrant further study. Cottonmouths and Copperheads have hybridized and produced viable offspring in



FIG. 1. Artist's rendition of Copperhead (*Agkistrodon contortrix*) and Cottonmouth (*A. piscivorus*) engaged in combat as observed on 6 September 2016 in Snowball, Arkansas. Illustration by Gabriel Ugueto and corresponds generally to what was captured at 2:53 in associated video of the event (Video S1). [Color figure can be viewed at wileyonlinelibrary.com]

captivity (Mount and Cecil 1982); however, hybridization in the wild is likely rare, if it occurs at all. If these snakes were attempting to establish a dominance hierarchy and gain reproductive opportunities with a nearby female, what species was she and why did both consider her a potential mate? This observation, together with the potential for hybridization, reveals the need for studies on the mechanisms maintaining reproductive isolation between these closely related species, particularly because recent studies have come to different conclusions regarding the phylogeography and species delimitation of this group (Strickland et al. 2014, Burbrink and Guiher 2015).

Although we suggest that male–male combat is the most likely description for this interaction we cannot rule out alternative explanations. It is possible that we are witnessing a male and a female engaged in interspecific courtship, as courtship may appear similar to the initial stages of combat (Schuett and Duvall 1996). However, courtship does not typically include a prolonged vertical orientation or efforts to force each other to the ground like we see in the video (Carpenter and Gillingham 1990, Fig. 1). Similarly, although combat between a male and a female *Agkistrodon* has been documented (Graham and Sorrell 2010), the relatively large size of the Arkansas animals suggests they are both males.

Herpetologists have contemplated the possibility that snakes compete over resources; competition has even been suggested as a potential explanation for combat (Carpenter and Gillingham 1990) but there has long been little empirical support for the idea. However, indirect evidence has recently indicated that interspecific competition may result in character displacement (Steen et al. 2013) and competitive exclusion (Steen et al. 2014). Particularly fascinating (and relevant to the current observation) are recent observations of direct agonistic behavior between conspecifics defending refuges (Webb et al. 2015) or food (Huang et al. 2011, i.e., territoriality). This territorial behavior does not appear to be limited to interactions between individuals of the same species; Edgehouse et al. (2014) demonstrated that Common Garter Snakes (*Thamnophis sirtalis*) used physical aggression to force the closely related Aquatic Garter Snake (*T. atratus*) from the aquatic habitats that they both preferred. Notably, the pile of tin where our snakes were observed could represent refugia or a high-quality hunting site. In summary, it may be worthwhile to consider whether our Cottonmouth and Copperhead were fighting over a resource unrelated to reproduction.

Considering this interaction within the context of intraspecific social behavior may also lend important

insights. Reptiles have long been considered generally asocial; however a growing body of literature suggests that this perception is outdated and imprecise (Doody et al. 2012). The social lives of snakes in particular have recently come into increased focus thanks to the pairing of intensive behavioral observations with molecular methods (e.g., Clark et al. 2012). It is possible that females of both species were nearby and cues typically used to communicate with conspecific males further facilitated combat initiation. Additionally, Cottonmouths are well known for eating other snakes, including their own species, and it is interesting to consider why the Cottonmouth in the current observation perceived the Copperhead as a rival rather than a meal. Future research examining the signals and cues that initiate combat within and among species may help reveal answers.

We simply do not know whether the fight we observed between two different species of snakes was a consequence of their social behavior, reflective of an interspecific interaction, or was just a fluke event between two confused animals. It has been many years since snakes were designated as new model organisms in ecology (Shine and Bonnet 2000), but it is clear that we still have much to understand about this secretive and difficult to study group.

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