



FIG.1. An adult male *Crotalus lepidus* scavenging a road-killed *Coelophosaurus texanus* at Indio Mountains Research Station, Hudspeth Co., Texas, USA.

observation suggests that *C. lepidus* use alternative modes of foraging in addition to an ambush approach.

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CROTALUS OREGANUS (Northern Pacific Rattlesnake). NON-RATTLING TAIL DISPLAY. Rattlesnakes exhibit three main tail displays: 1) rattling, an aposematic signal directed at predators (Klauber 1972. *Rattlesnakes: Their Habits, Life Histories, and Influence on Mankind*. University of California Press, Berkeley. 1580 pp.); 2) caudal luring, a form of aggressive mimicry used to attract insectivorous prey (e.g., Reiserer and Schuett 2008. *Biol. J. Linn. Soc.* 95:81–91); and 3) non-rattling defensive displays, exhibited by some species upon tactile stimulation (Rabatsky and Waterman 2005. *Herpetol. Rev.* 36:236–238). We recorded three instances of adult *Crotalus oreganus* exhibiting a non-rattling tail display. This display consists of snakes slowly flagging their raised tails from side to side (Fig. 1), and does not appear to function in prey capture or defense, making it different from previous reports of non-rattling displays in rattlesnakes. We recorded this behavior in one female and two males using fixed videography (Sony SNC-RZ25N cameras) at our field site, Blue Oak Ranch Reserve, Santa Clara Co., California (37.38208°N, 121.71209°W, WGS84; 800 m elev.). Our video cameras ran over a wireless internet connection and were controlled remotely by field assistants who watched their video feeds in real time at the field site. Their field of view was typically no more than 1.0–1.5 m. Our site's habitat is characterized by mixed oak woodland interspersed by grassland. Video of the tail displays can be viewed on our lab YouTube channel (https://youtu.be/_AXL4FYqIA).

The female (SVL = 79.5 cm) was recorded on 12 June 2011. We had implanted a radio-transmitter in her on 29 May 2011. At the time of the tail display, we considered her not recovered from surgery because she had not moved from the location where we released her and because she exhibited behaviors consistent with recovery (periodically moving in and out of one refuge and using a loosely coiled body position). She had emerged from her rocky burrow refuge at 1514 h that day and was approximately 30 cm from its entrance when the behavior occurred. In addition, she was fully exposed and no other animals were present on camera. At 1523 h, she lifted her tail above her body and proceeded to move it from side to side a

total of 9 times over the course of 124 sec. Eighty-six seconds after ceasing this tail display, she moved her head toward her burrow (thus becoming partially elongated) and rested in that position for 33 sec. She retreated to the burrow at 1528 h. She remained at the site, presumably recovering from surgery, until 25 June 2011.

We recorded a tail display in one male (SVL = 71.0 cm) on 9 June 2012. We implanted him with a radio-transmitter on 28 April 2012 and considered him recovered from surgery at the time of his display. This snake was within thick vegetation (mainly Bull Thistle, *Cirsium vulgare*) when the behavior occurred, and he also appeared alone as no other animals were present on camera. He arrived to the site at 1306 h and started the tail display at 1310 h by slowly moving his raised tail to one side (a behavior that lasted 6 sec). He moved his tail to the other side of his body 57 sec later (a movement that lasted 7 sec). He then exhibited two tail side sweeps 242 sec later (the first lasted 6 sec, the second lasted 11 sec). Forty-four seconds after ceasing the tail display, he probed the area for 74 sec by moving his head around and tongue-flicking. He abandoned the site at 1318 h, but only moved approximately 30 cm where he coiled in a new position. He remained at that site for 1–2 days thereafter.

Our recording of the other male that exhibited a tail display is the most striking. This male (SVL = 101.0 cm) was implanted with a radio-transmitter on 29 May 2011 and was considered recovered from surgery. He appeared to exhibit the tail display in response to the presence of another adult male (SVL = 97.0 cm). Their interaction occurred on 2 July 2011, although they had been sharing the same burrow since 1700 h on 1 July 2011. The snake that exhibited the display (called Snake P) emerged from their shared burrow at 1303 h while the other snake (called Snake M), emerged at 1304 h. Snake P quickly assumed an S-shaped body posture approximately 60 cm from the burrow next to a fallen branch, while Snake M continued to slowly emerge from the burrow. The majority of Snake P's body was not within the camera frame when he began the tail display, but we were able to see his tail moving at 1307 h and 54 sec and a field assistant then used the pan/tilt/zoom function of the camera to center his body in the frame. At this time, Snake M remained elongated out of the burrow with his head on top of the body of Snake P. Snake P moved his raised tail from one side of his body to the other a total of 9 times over the course of 14 sec (Fig. 1), and Snake M moved his head over Snake P while tongue flicking. Snake P also tongue flicked during this interaction. Snake M retracted his head from off the body of Snake P, but remained close by. An adult California Ground Squirrel (*Otospermophilus beecheyi*) approached the snakes at 1311 h and immediately ran away (on camera < 4 sec). Snake P exhibited another bout of tail waving at 1313 h, moving his tail from side to side a total of 6 times over the course of 13 sec. At 1313 h and 34 sec, we observed Snake M moving his upper body back toward the burrow while tongue flicking. Snake M immediately began to retreat into the burrow, but then stopped abruptly at 1313 h and 50 sec. Snake M started movement again at 1314 h and 59 sec, but changed directions and moved to the left of the burrow and under the fallen oak branch. Snake P quickly fled the site at 1318 h. Snake P kept his tail raised above his body the entire time after first exhibiting the tail display and before leaving the site. We did not immediately track Snake P after this interaction so we lack data on the distance he moved after exhibiting the tail display. However, we found him with a large food bulge at 1630 h, and we deduced that he had consumed

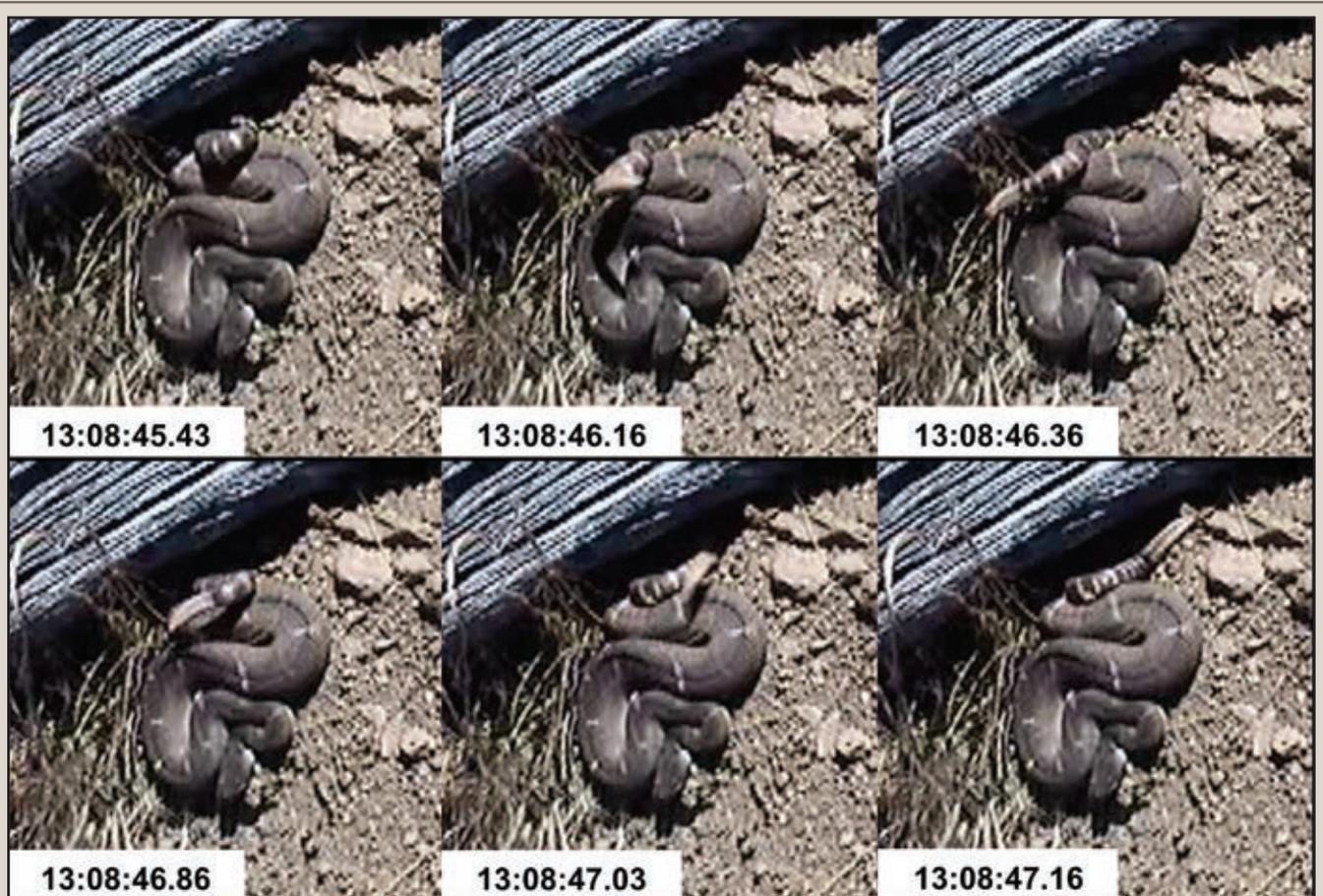


FIG. 1. Time-series of an adult male *Crotalus oreganus* exhibiting two flags from a non-rattling tail display bout. Time flows from left to right, top to bottom.

an adult squirrel because no other prey items at our site are comparable in body size.

Collecting precise descriptions of the contextual stimuli that elicit snake tail displays is necessary to better understand their function. The three instances we report above have a few commonalities. First, all snakes were in a loosely coiled body position. Second, the snakes exhibited the display intermittently over several minutes (approximately 2–6 min), then left their sites almost immediately after. Finally, the cloaca of the snakes appeared swollen when they were displaying, which could indicate that fluids were released from the cloaca and could function in communication. It is unlikely this tail display functions to attract prey because none of the rattlesnakes were in hunting body positions (ambush coil) when they exhibited the behavior. Many snake tail displays have an antipredator function (Greene 1973, *J. Herpetol.* 7:143–161), but no predatory threat was visible on camera (although predators could have been close by) when our rattlesnakes displayed. Furthermore, when threatened, rattlesnakes typically rely on crypsis before mounting behavioral defenses and many studies have shown that tactile stimulation or intense harassment are needed to induce behavioral defenses in exposed vipers (Glaudas et al. 2005, *Copeia* 2005:196–200; Maritz 2012, *Afr. Zool.* 47:270–274). Given that our snakes were not visually disturbed prior to waving their tails, it is unlikely that this display functions in defense against predators.

The tail displays we observed are likely functional considering the deliberate, prolonged movements and the attention

they could draw to otherwise cryptic snakes. Other pitvipers use tail displays during conspecific interactions. Tail writhing is displayed by defeated males after male-male combat in *Agkistrodon contortrix* (Schuett 1997, *Anim. Behav.* 54:213–224). Female *Crotalus molossus* that are disinterested in courting males have been observed exhibiting tail displays similar to what we recorded (E. Taylor, pers. comm.). Non-defensive tail displays in *C. oreganus* may thus be used to communicate with conspecifics, although this idea is speculative given our small sample size. We only captured one recording of two male rattlesnakes interacting when the tail display occurred, although conspecifics could have been close by but not visible in our other recordings due to our restricted field of view. The two males we recorded interacting did not behave aggressively toward each other. In addition, we did not film rattlesnakes during breeding seasons so we cannot associate these displays with mating behaviors. More observations are needed to formulate testable hypotheses concerning this behavior.

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