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HABITAT MANIPULATION IN HUNTING RATTLESNAKES (*CROTALUS* SPECIES)

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Abstract—We used fixed videography to record the natural ambush foraging behavior of northern Pacific rattlesnakes (*Crotalus oreganus*) in central coastal California. We captured approximately 2,000 h of snake behavior over two field seasons. During this time we recorded two occurrences of an unusual behavior which has only been reported twice previously: after selecting sites at which to ambush prey, two different snakes used their anterior bodies to move vegetation away from their strike path. Both individuals used similar stereotyped behavior, forcibly jerking their head and neck upward in a rapid movement. The head jerks were either preceded or followed by head-scanning and lateral head movements. These observations suggest that hunting rattlesnakes may be able to anticipate future events and use past experiences to solve current problems. This report adds to the growing literature on reptile intelligence.

Resumen—Utilizamos videografía fija para grabar cascabeles del oeste (*Crotalus oreganus*) durante emboscadas naturales de caza en la costa central de California. Documentamos aproximadamente 2,000 horas de video del comportamiento de las víboras en dos temporadas. Durante este tiempo, observamos dos instancias de un comportamiento insólito que sólo se ha reportado en dos ocasiones anteriores: después de seleccionar los sitios de emboscada, dos serpientes utilizaron sus cuerpos anteriores para mover la vegetación fuera de la trayectoria de ataque. Ambas serpientes siguieron un comportamiento estereotípico, forzando la cabeza y el cuello hacia arriba en un movimiento rápido. Estos movimientos bruscos fueron precedidos o seguidos con movimientos de rastreo y movimientos laterales de la cabeza. Estas observaciones sugieren que las serpientes de cascabel a la caza pueden anticipar futuros sucesos y utilizar sus experiencias anteriores para resolver problemas actuales. Este informe se suma a la literatura creciente sobre la inteligencia en los reptiles.

Foraging demands are often linked to problem-solving skills and intelligence in several species, including humans (Huber and Gajdon, 2006; Griffin and Guez, 2014; Melin et al., 2014). Many organisms physically manipulate structures in their environment to enhance foraging (e.g., Seed and Byrne, 2010; Wiley et al., 2011). Snakes are not generally known to manipulate their habitat while foraging, but habitat manipulation is still apparent in this taxon: the nest building of king cobras (*Ophiophagus hannah*) (Chanhome et al., 2011) and pine snakes (*Pituophis melanoleucus melanoleucus*) (Burger and Zappalorti, 1991), the burrowing of fossorial species (Gans et al., 1978), and the cratering in loose sand of desert-dwelling vipers (Viperidae) (Secor and Nagy, 1994; Maritz, 2012). Here, we report on rattlesnakes in the genus *Crotalus* that use a form of habitat manipulation in the context of foraging.

Rattlesnakes are sit-and-wait predators that remain coiled at a hunting site, waiting to attack unsuspecting prey that wanders by (Secor and Nagy, 1994; Cundall and Greene, 2000; Clark et al., 2012). Rattlesnakes are top-level predators in many North American ecosystems and primarily prey on small mammals, although they are opportunistic and will also consume lizards, birds, amphibians, and arthropods (Klauber, 1972; Taylor, 2001; Clark, 2002; Dugan and Hayes, 2012). We spent 2 y (2011–2012) using fixed videography to monitor free-ranging northern Pacific rattlesnake (*Crotalus oreganus*) behavior. During this time, we recorded approximately 2,000 h of foraging behavior from 18 adult snakes (11 males, 7 females).

Our video recordings came from a population at the Blue Oak Ranch Reserve field site in Santa Clara Co., California (approximately 37.38208°N, −121.71209°W, datum: WGS84, elevation = 800 m). Snakes were implanted with temperature-sensitive radio transmitters (model G3; AVM Instrument Company Ltd., Colfax, California) and tracked at least once daily, but usually every one-half hour from May–July in 2011 and 2012. We used network security cameras (model SNC-RZ25N; Sony Electronics Inc., San Diego, California) attached to network radios (model NanoStation M2; Ubiquiti Networks Inc., San Jose, California) to record the behavior of radio-tagged snakes that were hunting (as evident by a stereotyped ambush body posture; Clark, 2004; Reinert et al., 2011). Snakes in this population primarily target California ground squirrels (*Otospermophilus beecheyi*) as their main prey item (Putman et al., in press). We used the snakes' head sizes to estimate the distances reported below.

Over the course of our fieldwork, we recorded two instances when coiled snakes used their head and neck to move overhanging vegetation away from their strike path. Rattlesnakes that manipulate habitat surrounding their ambush site prior to striking prey appear to exhibit the ability to problem-solve—to change the current state of their environment to a desired goal state (Barbey and Barsalou, 2009)—and to anticipate future events. To our knowledge, we have the first recorded video footage of this behavior, although researchers have reported it in other species of rattlesnake (Greene, 2003).

Our first observation occurred at 1324h on 3 July 2011 and came from an adult male snake (snout–vent length = 95.0 cm). The behavior occurred almost immediately after the snake had selected a new ambush site (it had just moved approximately 50–70 cm from one ambush site to another and remained in our camera field of view). Although it was difficult to see this snake when it arrived at its new site, vegetation began moving in directions away from its body, suggesting that the snake was using its coils to create a suitable ambush spot (similar to the cratering behavior observed in desert vipers). About 30 s after

FIG. 1—Screenshot from a recording of a rattlesnake (*Crotalus oreganus*) pushing vegetation upward at the Blue Oak Ranch Reserve, San Jose, California on 26 June 2012. The dashed white line outlines the snake's body. The white arrow points to the ventral side of the head and neck and indicates the direction that the head moved during the behavior.

arriving at the site, the snake raised his head vertically, slightly above his body (1–3 cm) as if scanning the area. Seven seconds later, the snake forcibly jerked his head upward (approximately 10–15 cm) using the dorsal side of the neck and dorsal–posterior part of the head to push overhanging vegetation away from his body (Fig. 1). This jerking movement was rapid and lasted less than 1 s. This snake also made two lateral head movements approximately 15–25 cm forward and away from the center of its coil. These lateral movements occurred 3 s and 42 s after the vertical head jerk and might have indicated the intended strike path of the snake, which was now cleared. This snake abandoned its site at 1506h when he retreated into a nearby squirrel burrow.

Our second observation occurred at 1340h on 26 June 2012 and came from a different adult male snake (snout–vent length = 89.5 cm). This snake had moved to its ambush site sometime between 1045 and 1245h. Its behavior was similar to our previous observation. He first slightly raised his head above his body (1–3 cm), scanned the area, and then lowered it back down. Next, he moved his head laterally 20–25 cm away from the center of his coil (while tongue-flicking) and then retracted it back. He exhibited four other head-scanning movements 20, 60, 96, and 139 s later and, immediately following this last head movement, he forcibly jerked his head and neck upward but only by 8–9 cm. Similar to our previous observation, this snake also used the dorsal part of the head and neck to move the vegetation. The snake lowered his head back down but continued to keep it raised above his body. He then exhibited a second vertical head jerk 8 s later during which he pushed the vegetation upward twice, moving it away from the area he had scanned previously (presumably the intended strike path). He jerked his head and neck 17 cm above his body (Fig. 1). This head jerking movement was slower (approximately 2 s in duration) than the head jerk we observed by the other snake in 2011. This snake ceased manipulating the surrounding vegetation after this time. We stopped recording this snake's behavior at 1650h and it was still in ambush in the same spot by the end of our recording. It consumed a juvenile squirrel at an unknown time later on this date. A video of this example is viewable at our laboratory YouTube channel (http://youtu.be/hx_9OT3frpA; 3 March 2015).

Similar behaviors in other rattlesnake species have been previously observed. In the summer of 1995, an adult *Crotalus viridis* (sex unknown) was observed to manipulate the vegetation near a deer mouse (*Peromyscus* species) nest burrow (J. Wright, pers. comm.). The researcher was using radio telemetry to track the snake and found the snake inspecting the deer mouse burrow while tongue-flicking. The snake then set up ambush next to the burrow in some tangled grass and weeds. After some time, it stretched out its head and neck from its coil and pushed some vegetation aside and also pressed down other vegetation, apparently making a clear strike-path. Greene (2003) also describes an experience observing a hunting adult male *Crotalus molossus* using his head and neck to press down a dried fern a few inches in front of him. The snake had previously spent 13 min tongue-flicking a rodent runway before selecting an ambush site nearby. The snake manipulated the surrounding vegetation 2 min after setting up ambush.

The behavior we recorded in two individual rattlesnakes was moving the vegetation away from the snake's strike path. Although rattlesnakes prefer to set up ambush in microhabitats that enhance their crypsis, these same microhabitats could also contain obstructions that limit their ability to successfully detect and attack prey. Manipulation of the ambush site might increase snakes' foraging success at sites that seem profitable (based on prey presence) but that are also difficult to maneuver through. It is possible that this behavior is an innate, fixed action pattern, but it also has the potential to stem from trial-and-error learning, the ability to problem solve through repeated varied attempts (e.g., Fiorito et al., 1990). These snakes could have learned from previous strike attempts that had failed due to vegetation blocking the strike path. Alternatively, this behavior could stem from inferential reasoning, the ability to solve a novel problem by generalizing from a previous, unrelated experience (Zeithamova et al., 2012). Male rattlesnakes use a similar behavior when fighting rival males in competition over females (Hersek et al., 1992). The snakes of known sex observed using this behavior were all male. They could have co-opted their combat behavior to solve a novel problem in a different context. We believe these compelling field observations could form the basis of several intriguing hypotheses that deserve further experimental testing.

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