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No drought about it: Effects of supplemental hydration on the ecology, behavior, and physiology of free-ranging rattlesnakes

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ABSTRACT

Hydration is a critical element for many physiological processes in vertebrates. While it seems intuitive that drought is stressful to animals, studies examining drought are typically observational and do not explicitly assess how the hydration state of study subjects influences their physiology and behavior. We examined how hydration affects several physiological and behavioral variables in free-ranging Northern Pacific rattlesnakes (*Crotalus oreganus oreganus*) by experimentally manipulating their hydration levels in the field. Our results suggest that supplemental water has a significant effect on reproduction, as all hydrated females gave birth during the experiment, while no control females did. We saw no effect of hydration on movement parameters; males moved a larger total distance and had larger home ranges than females, regardless of hydration status. Interestingly, body condition at the end of the study was significantly higher in hydrated snakes, suggesting that hydrated individuals might have been acquiring more food than control snakes. We saw no effect on baseline stress hormone concentrations or their increase in response to an acute stressor. Additional experimental studies are needed to better understand the pivotal roles of hydration in the physiology and behavior of reptiles.

1. Introduction

Hydration is a crucial component of the overall homeostatic balance an organism must maintain for survival. As such, the ability of an animal to acquire and use water efficiently is subject to strong selection in nature, especially in dry climates. Emphasizing the importance of an animal's water conservation strategies, scientists have documented a recent increase in drought severity in arid regions and predict this trend to continue (Trenberth et al., 2014). Prolonged drought may have serious impacts on animals in many different habitats, including arid areas where animals are often already highly water-stressed. Seasonal or annual variation in water availability can impact animals in diverse ways, including changes in behavior, feeding rates, and reproduction. Many studies on the relationship between hydration and these parameters have used reptiles as model organisms due to their myriad of adaptations to withstand long periods with little water (reviewed in Shoemaker and Nagy, 1977), as well as the ease with which individuals can be captured and studied in the wild. Prominent examples include reduction in activity during dry conditions in chuckwallas (Nagy, 1972), increased metabolic rate in desert tortoises in high rainfall years (Henen et al., 1998), reduced survival during drought years in water snakes (Winne et al., 2010), reliance of sea snakes on fresh water (Lillywhite et al., 2008), and strong effects of rainfall patterns on movement and reproduction in desert tortoises (Duda et al., 1999; Henen, 2002; Turner et al., 1986). Because studies that experimentally manipulate hydration typically take place in laboratory settings (e.g., Churchill and Storey, 1995; Moeller et al., 2013), the causative effects of hydration on ecological, behavioral, and physiological parameters of free-ranging animals are virtually unknown. In one of the only field studies manipulating hydration in individual animals, Gila monsters supplemented with water exhibited more surface activity and more fat stored in their tails than control lizards (Davis and DeNardo, 2009).

Most vertebrates expend a significant amount of energy during reproduction. In viperid snakes, females have been shown to invest over half of their body mass into vitellogenesis (yolk production) and embryo production during the fall and spring prior to summer

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birthing (Seigel and Fitch, 1984; Van Dyke and Beaupre, 2011). While numerous studies have focused on the importance of energy in reproduction in females (e.g., Taylor et al., 2005), fewer have considered the role of hydration. Water content of yolk is relatively high in reptiles, with estimates of >70% on the first day of incubation in bearded dragons (Packard et al., 1985). Due to the high water content of the yolk, drought may impact a female's ability to reproduce, or it might limit the number or size of offspring she is capable of producing. Additionally, placental lecithotrophic reptiles can compensate for deficits in water or ion content of the yolk via placental provisioning (Stewart et al., 1990). While water deprivation during pregnancy has no effect on litter size or mass in aspic vipers, pregnant females lost 89% greater mass than non-reproductive females when water-deprived (Dupoué et al., 2015). This suggests that female snakes may compromise their own water balance to benefit their offspring. However, in the event of extreme drought, it may be more beneficial to forego reproduction, or resorb developing follicles, in order to survive to reproduce another year. To date no studies have examined the effects of experimental manipulation of hydration on reproduction in free-ranging reptiles.

During a drought, animals may need to move more frequently and/or for longer distances in search of food. However, exposure to the elements may limit these movements. Spatial ecology may therefore change depending on water availability in the environment. Evaporative water loss increases with movement (Gans et al., 1968), and reptiles that decrease their movements may be doing so in an effort to minimize evaporative water loss. Instead of searching for water during drought, some species are more likely to remain stationary in an effort to conserve energy and water (Duda et al., 1999). Reduced movements as a result of drought may in turn cause reduced mating and foraging opportunities, which have negative fitness consequences.

Drought results in decreased primary productivity (Zhao and Running, 2010), which can impact rodent populations and therefore the reptile predators that eat them, causing their body condition to decline (Sperry and Weatherhead, 2008). Several aquatic snake species drastically declined in number and appeared to cease reproductive activities during severe drought (Seigel et al., 1995; Willson et al., 2006). These declines were partially attributed to lack of prey, which would cause a decline in body condition of snakes surviving the drought. These studies suggest that prey abundance may mediate the effect of drought on a predator species' body condition. Animals in low body condition or exposed to various other chronic stressors typically exhibit high circulating levels of adrenal glucocorticoids, which among other functions mobilize stored energy by stimulating protein and fat catabolism and gluconeogenesis. Elevated baseline glucocorticoids result in a shift away from unnecessary behaviors and redirect energy toward functions essential for survival, whereas dysfunction in stress reactivity prevents proper response to perturbations (Wingfield et al., 1998). These hormones are often used to quantify stress in vertebrates (Moore et al., 2000; Moore and Jessop, 2003; Bonier et al., 2009), but no studies have examined whether drought stress affects glucocorticoid levels.

Drought presents an unpredictable and severe environmental stressor. Rattlesnakes are excellent model organisms for physiological studies such as these because they are easy to study in the wild and are highly responsive to changes in the environment (Taylor et al., 2005; Lutterschmidt et al., 2009). Although it is difficult and potentially ethically problematic to experimentally dehydrate snakes in a field setting, it is possible to experimentally hydrate individuals. We conducted a manipulative field experiment to test the hypothesis that hydration positively impacts the spatial ecology, reproduction, and body condition of Northern Pacific rattlesnakes (*Crotalus oreganus oreganus*). Additionally, we examined whether hydration affects stress hormone levels and the reactivity of the hypothalamic-pituitary-adrenal axis in these snakes. We predicted that experimentally hydrated snakes would be more likely to reproduce, exhibit larger home ranges and movements, be in higher body condition, and have reduced glucocorticoid concentrations in comparison to control snakes.

2. Materials and methods

2.1. Study animals and site

Twenty-one adult *C. o. oreganus* (12 male, 9 female) were captured from Montaña de Oro State Park in Los Osos, San Luis Obispo County, California (35.27° N, −120.89° W, elevation: sea level) between 22 March 2014 and 7 July 2014. Snakes were captured by visual encounter surveys at two sites within the park (Bluff Trail and Sandspit). The sites consist of coastal dune habitat dominated by Black Sage (*Salvia mellifera*), California Sage (*Artemisia californica*), invasive Ice Plant (*Carpobrotus edulis*), Coyote Bush (*Baccharis pilularis*), and Poison Oak (*Toxicodendron diversilobum*). Typical annual rainfall in this area is about 43 cm; however, the two years preceding the study each averaged only about 10–15 cm, and less than 5 cm of precipitation was recorded during the course of the study (source: Morro Bay Fire Station weather station, http://www.ncdc.noaa.gov/). Effects of drought have been long-lasting at this site; many shrubs were dead during a 2016 survey despite a return to average rainfall levels this year (M. Ritter, pers. comm.). Collection and handling of rattlesnakes was carried out under California Department of Fish and Wildlife Scientific Collecting Permit #SC-12963 and a California State Parks Permit. Use and treatment of snakes was approved by California Polytechnic State University Institutional Animal Care and Use Committee (Protocol #1403).

Snakes were transported to California Polytechnic State University for radio transmitter implantation. Each snake was housed individually in a 71 by 61 by 30 cm vision cage (Model V221, LLL Reptile and Supply Company) with a heat pad and hide box (no food or water was provided). Snakes were anesthetized via isoflurane inhalation (Vet One, MWI, USA) and implanted intracoelomically with a 4–5 g SB-2 radio transmitter (Holohil Systems Ltd. Carp, Ontario, Canada) and a 3.25 g temperature data logger coated in Plastidip (model DS1921G, Maxim Integrated, San Jose, California). Snakes were allowed to recuperate for 1–2 days and then released at their site of capture. Both snout-vent-length (SVL) and mass were recorded at the time of surgery and approximately every three weeks thereafter for each snake.

2.2. Experimental manipulation of hydration

Snakes were randomly assigned to one of two experimental groups (hydrated and control) with assignments initially balanced between the sexes. Three snakes (two control females, one control male) died during the study; one apparently due to consumption of an excessively large meal, another due to predation, and a third to an infection. The male died mid-way during the study, so his data were still used for home range analysis. The first group (hydrated treatment, 6 males and 4 females) received an experimental hydration procedure twice per month (see below). The second group (control: 6 males and 3 females) received a sham procedure.

In early April 2014, prior to beginning treatments, blood samples were obtained from each snake via caudal venipuncture (1 cc syringe with 25 g needle) to acquire initial values for blood osmolality. Starting in mid-May, an intragastric tube procedure was used to introduce water into the stomach of each snake in the hydrated group (Davis and DeNardo, 2009). While secured in a