

PREY-MEDIATED EFFECTS OF DROUGHT ON CONDITION AND SURVIVAL OF A TERRESTRIAL SNAKE

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Abstract. Drought can have severe ecological effects and global climate-change theory predicts that droughts are likely to increase in frequency and severity. Therefore, it is important that we broaden our understanding of how drought affects not only individual species, but also multitrophic interactions. Here we document vegetation and small-mammal abundance and associated patterns of Texas ratsnake (*Elaphe obsoleta*) body condition and survival before, during, and after a drought in central Texas, USA. Vegetation (grass and forbs) height and small-mammal capture rates were two times greater in wet years compared to the drought year. The decline of small mammals (the snakes' principal prey) during the drought was associated with a drop in ratsnake body condition, consistent with reduced food intake. During the drought, snake mortality also increased 24%. Although higher snake mortality was attributable to predation and road mortality rather than being a direct result of starvation, an increase in risk-prone behavior by foraging snakes probably increased their exposure to those other mortality factors. Drought conditions lasted only for 21 months, and vegetation, small-mammal abundance, and snake condition had returned to pre-drought levels within a year. Although estimates of snake population size were not available, it is likely that substantially more than a year was required for the population to return to its previous size.

Key words: *drought effects on species and their interactions; Elaphe obsoleta; multitrophic interactions; predator–prey system; small-mammal abundance; snake; survival.*

INTRODUCTION

Both short-term and prolonged droughts can have substantial ecological impacts. Drought has been shown to affect the survival and reproductive success of a wide variety of organisms, including mammals (e.g., Morton et al. 1995), birds (e.g., Smith 1970, George et al. 1992), and reptiles (e.g., Gibbons et al. 1983, Germano et al. 1994). Because studies of ecological effects of drought are necessarily largely opportunistic, however, our understanding of how different taxa are affected by drought remains limited. Global climate-change theory predicts that there will be an increase in the frequency and severity of droughts (Overpeck 1996, Gregory et al. 1997, Dai et al. 1998). Therefore, it is important that we broaden our understanding of how drought affects not only individual species, but also multitrophic interactions. Here we document how drought affected a predator–prey system of small mammals and the snakes that prey on them.

Drought can substantially reduce the growth and survival of vegetation (Sala et al. 1998, Hanson and Weltzin 2000). The bottom-up theory of community ecology would predict that decreased primary productivity would negatively affect herbivore populations, which in turn would negatively affect predator popula-

tions (Hunter and Price 1992). Small mammals, which eat both vegetation and arthropods, have been shown to decline in abundance following drought (Spevak 1983, Yahner 1992, Morton et al. 1995), most likely due to both starvation and decreased reproduction. A variety of studies (not all drought related) have shown a functional or numerical response by mammalian (White et al. 1996) or avian (Schmidt and Ostfeld 2003, Clotfelter et al. 2007) predators to short-term small-mammal population fluctuations. Because small mammals are also the primary prey of many snake species, declines in small-mammal abundance should negatively affect snake reproduction and survival.

Reptiles are declining globally and climate change is thought to be one of the causes (Gibbons et al. 2000). Not surprisingly, research on drought effects on snakes has focused on aquatic and semi-aquatic species. Drought was thought to be responsible for the decline of a frog-eating snake species in Australia due to drought-induced food shortages (Shine 1991). A severe drought in the southeastern United States produced long-term changes in aquatic-snake abundance and species composition, again most likely due to a dramatic reduction in suitable aquatic prey (Seigel et al. 1995). A series of studies in northern Australia have shown strong relationships between rainfall, prey abundance, and aquatic-snake survival and reproduction (Madsen and Shine 2000, Madsen et al. 2006, Brown and Shine 2007). Given that abundance of terrestrial prey can also be affected by drought, terrestrial snakes should also be

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vulnerable to drought. Here we document the effects of drought in oak–savannah habitat on vegetation growth and small-mammal abundance, and the corresponding effects on body condition and survival of Texas ratsnakes (*Elaphe obsoleta*; see Plate 1).

STUDY AREA AND METHODS

We conducted our study at Fort Hood, Texas, USA, an 88 500-ha military installation in central Texas (30°10' N, 97°45' W). Although we initiated this project in 2004, most data collection occurred from 2005 through 2007. The habitat of Fort Hood is predominantly oak–juniper (*Juniperus ashei* and *Quercus* spp.) woodlands and oak savannahs. Average annual rainfall in central Texas is 84.7 cm with peaks in May and October (NOAA, National Climatic Data Center; data available online),² although drought years occur fairly frequently (Stahle and Cleaveland 1988).

Rainfall data were collected at a weather station located on Fort Hood for 2004 through 2006. Due to malfunction of the Fort Hood weather station, rainfall data for 2007 were from Robert Grey airfield (National Climatic Data Center), ~20 km from the study site.

We used height of ground vegetation (grasses and other herbaceous plants) as an indicator of primary productivity before, during, and after the drought. Height of ground vegetation was measured at snake-selected and paired random sites for a concurrent radiotelemetry study of snake habitat use. Here we used only vegetation height from random sites. We chose random sites by selecting a UTM coordinate at a random distance (10–200 m) and bearing from every second snake location.

We trapped small mammals over a 3-week period in early spring in 2005 through 2007. Trapping was restricted to early spring to avoid biases in abundance or mortality that can be caused by red fire ants (*Solenopsis invicta*; Masser and Grant 1986, Gettinger 1990). These ants are extremely abundant at Fort Hood and are inactive only during cooler weather. We created six trapping grids consisting of transects 15 m apart along which traps were placed every 15 m, resulting in a total of 504 traps. The trapping grids were positioned to maximize diversity of habitat types and included an approximately equal number of savannah and woodland sites. We used Sherman live traps (H. P. Sherman Company, Tallahassee, Florida, USA) baited with black oil sunflower seeds. Traps were baited at sunset and then checked at sunrise the following morning. Traps were open for three consecutive nights for a total of 1512 traps nights each year. All small mammals were identified to species and new captures were marked by clipping a small area of fur from the dorsal surface near the tail, which allowed us to differentiate new captures from any previously captured individuals.

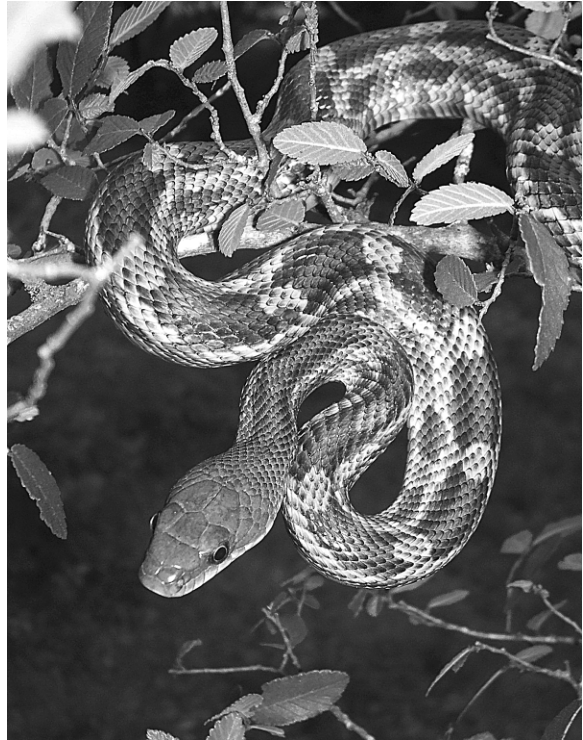


PLATE 1. Texas ratsnake (*Elaphe obsoleta*) at Fort Hood, Texas, USA. Photo credit: Christopher Taylor.

Although ratsnakes are perhaps best known as predators of nesting birds (e.g., Weatherhead and Blouin-Demers 2004), diet analyses across their range have shown that ratsnakes prey predominantly on small mammals (Fitch 1963, Weatherhead et al. 2003, Carfagno et al. 2006). The same is true of Texas ratsnakes (J. H. Sperry and P. J. Weatherhead 2009). We caught snakes opportunistically by hand throughout the field season. We measured snout-vent length (in centimeters) and mass (in grams) and for snakes for which transmitters would weigh <3% of body mass, we surgically implanted radio transmitters weighing either 9 g or 13 g, which had batteries lasting 12 and 24 months, respectively (Model SI-2T, Holohil Systems Limited, Woodlawn, Ontario, Canada). Transmitters were implanted using Blouin-Demers and Weatherhead's (2001) modification of the surgical technique described by Reinert and Cundall (1982). After recovery snakes were released at their capture location. We relocated snakes approximately every 48 h and recaptured them opportunistically (snakes were often not visible or accessible when relocated) throughout the season to determine length and mass, and to palpate females for presence of eggs. We visually examined carcasses from snakes with radio transmitters to determine cause of death.

Statistical analysis

Survival estimates for snakes captured in 2004 were included in analyses but all other results are from data

²(<http://www.ncdc.noaa.gov>)

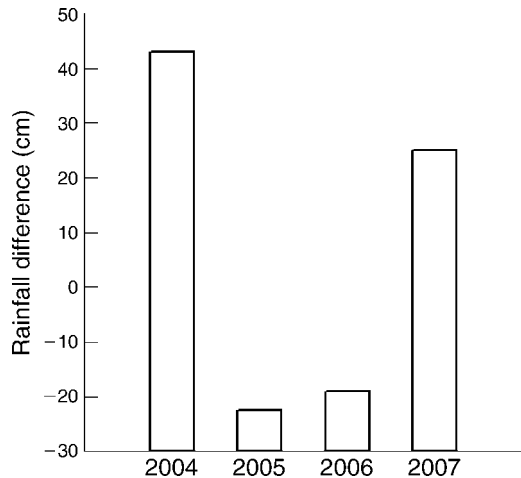


FIG. 1. Difference between long-term average rainfall (84.7 cm) and observed rainfall at Fort Hood, Texas, USA, between 2004 and 2007.

collected in subsequent years. All data were from the snake active season (1 April through 30 November). During winter months snakes had substantially reduced activity and we recorded no mortality. We used ANOVA to compare height of ground vegetation among months and years. Small-mammal abundance was estimated as the total number of unique individuals caught per 100 trap nights. We used repeated-measures ANOVA to test for yearly differences while controlling for trapping location. Snake body condition was estimated as the residuals from a regression of snout-vent length on body mass (Weatherhead and Brown 1996). Change in body condition over time was determined as the difference between residuals from measurements taken at the two captures. To control for time between captures, changes in condition were divided by the number of days between observations. To control for potential differences associated with reproductive status, we ran separate analyses for male and female snakes. We determined if change in condition was related to body size of snake (snout-vent length) using linear regression. Change in condition was compared among years using ANOVA. Individual yearly group means were compared using Tukey-Kramer tests ($P \leq 0.05$). All means are expressed ± 1 SE. All analyses were conducted using program NCSS (Hintze 2006).

We used the Kaplan-Meier product-limit analysis and SYSTAT (2004) to compare snake survival among all years as well as between wet and drought years. Survival analyses can be complex when the fate of an individual is unknown. Unknown fates occur when a radio signal is lost, when an individual is still alive at the completion of the study, or when a transmitter is removed by the researcher. In a Kaplan-Meier analysis, individuals in which the fate is unknown are still included in the analysis but are typically "censored," in that their fate

after a certain date is unknown but the time that they were alive and under observation is included in analysis. An assumption of the Kaplan-Meier analysis is that censoring is random and not related to the animal's fate (Pollock et al. 1989). However, predation of a marked animal that also destroys the transmitter violates this assumption because predation causes the signal to be lost. Although individuals for which signals were lost are typically considered censored data, this may not be appropriate for our study. We lost signals for only two snakes either before or after the drought but lost signals for six snakes during the drought. Radio signals can be lost due to snakes traveling out of range, radiotransmitter failure, or transmitter disablement by external factors (e.g., predation or crushed by a vehicle). Although we cannot rule out transmitter failure, we would expect rates of transmitter failure to remain constant over time and yet we saw a sharp increase in lost signals during the drought. To assure that the Kaplan-Meier assumption was not violated, we conducted two survival analyses. The first assumed that lost individuals were dead and the second assumed that lost individuals survived (Pollock et al. 1989). In both cases, we censored snakes that had their transmitters removed and snakes known to be alive at the end of the study. Only snakes that survived past a 7-d transmitter acclimation period were included in analysis. We used Tarone-Ware log-rank test to assess the effect of the drought on survival.

RESULTS

Rainfall was above the long-term average of 84.7 cm in 2004 (127.7 cm), below average in 2005 and 2006 (62.2 and 65.7 cm, respectively; Fig. 1) and, as of 30 November, above average for 2007 (102.7 cm). According to the United States Drought Monitor (National Drought and Mitigation Center; data *available online*),³ below-average rainfall began in March 2005 and drought conditions began in early July 2005 and continued until early April 2007. Although the drought began in the middle of 2005, the height of the snake active season, vegetation sampling and small mammal trapping were completed prior to the initiation of the drought. Therefore, we consider 2006 to be a drought year and 2005 and 2007 to be wet years.

Height of ground vegetation was measured at 194 random locations in 2005, 267 locations in 2006, and 101 locations in 2007. Height did not differ between months for any year (all $F \leq 1.36$, $P \geq 0.15$) so we combined all data into yearly averages. Height of ground vegetation differed substantially between years ($F_{2,559} = 43.41$, $P < 0.001$), with 2006 vegetation-height measurement 52% lower than 2005 and 62% lower than 2007 (Fig. 2). Tukey-Kramer test indicates that all years differ significantly.

³<http://www.drought.unl.edu/DM/monitor.html>

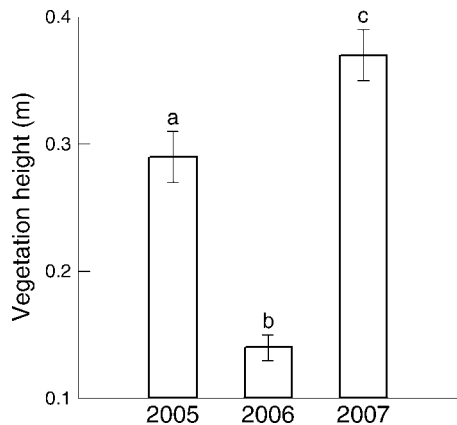


FIG. 2. Height of ground vegetation (grass and herbs) based on random samples at Fort Hood, Texas, between 2005 and 2007. Data are means \pm SE; letters above bars indicate significant differences between group means as determined by Tukey-Kramer tests.

We captured a total of 511 small mammals, most (88%) of which were *Peromyscus attwateri* and *P. pectoralis*. Mean capture rates in 2006 were 58% lower than in 2005 and 50% lower than 2007 (repeated-measures ANOVA: $F_{5,2} = 4.94$, $P = 0.03$; Fig. 3). Tukey-Kramer tests indicate that only 2005 and 2006 capture rates differed significantly.

Forty-three snakes with transmitters were measured at least twice, allowing us to determine change in body condition. Mean number of days between consecutive measurements was 172.17 ± 17.61 d (mean \pm SE) and was similar among years ($F_{2,60} = 0.13$, $P = 0.88$). Change in body condition was similar between males and females for all years (all $P > 0.32$), so data from both sexes were combined for further analysis. In addition, change in body condition was not related to snake body size ($R^2 = 0.16$). Snake body condition showed the greatest decrease in 2006 ($n = 16$ snakes, -0.49 ± 0.13)

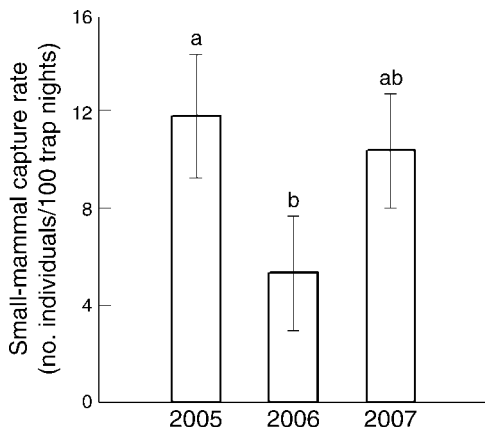


FIG. 3. Small-mammal capture rates per 100 trap nights at Fort Hood, Texas, between 2005 and 2007. Data are means \pm SE; letters above bars indicate significant differences between group means as determined by Tukey-Kramer tests.

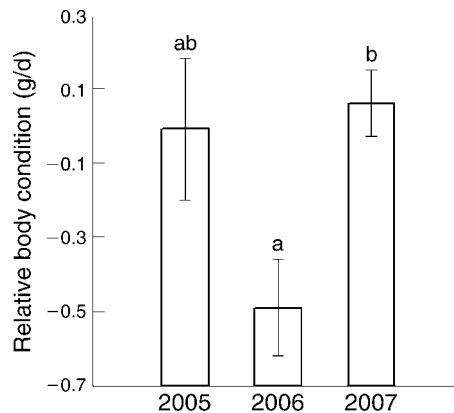


FIG. 4. Change in body condition of Texas ratsnakes (in grams per day) implanted with radio transmitters between measurement times at Fort Hood, Texas, 2004 through 2007. Body condition was determined using residuals from a regression of snout-vent length on mass. Data are means \pm SE; letters above bars indicate significant differences between group means as determined by Tukey-Kramer tests.

compared to 2005 and 2007 ($n = 8$ snakes, -0.01 ± 0.19 , and $n = 39$ snakes, 0.06 ± 0.09 , respectively; $F_{2,60} = 6.08$, $P < 0.01$; Fig. 4). Tukey-Kramer tests show that change in body condition differed significant between 2006 and 2007 but not between 2005 and 2006. The small mean and large variance in 2005 probably reflects the fact that drought conditions began midway through 2005 and the drought was already affecting some 2005 data.

Although our evidence for the effects of drought on reproduction is anecdotal, that evidence is consistent with drought reducing snake reproduction. Compared to the nearly 38% (3 of 8) of females palpated during the 2005 breeding season that were gravid and the 25% (2 of 8) of females that were gravid in 2007, we did not detect any eggs in the six females we palpated in 2006. All of those females that were determined to be gravid in 2005 and 2007 successfully laid eggs. In addition, we saw evidence of mating behavior in two pairs of snakes (e.g., male and female relocated to same location during the mating season) before and after the drought, but we saw no evidence of mating behavior in 2006.

The 63 radio-tracked snakes available for the survival analysis included 7 individuals captured in 2004, 17 individuals in 2005, 18 individuals in 2006, and 21 individuals in 2007. Many snakes survived between years and so were included in the analysis for multiple years. Twenty-four snakes were confirmed dead, including 11 snakes in which the cause of death was not determined (e.g., transmitter found but no carcass). Two snakes were confirmed as road mortalities although we suspect road mortality was much higher because we recovered many transmitters near roads and road mortality was common for snakes not included in our study. The remaining 11 snake mortalities were likely due to predation, including seven mortalities from unknown predators (partially eaten carcasses or skeletons found) and four mortalities

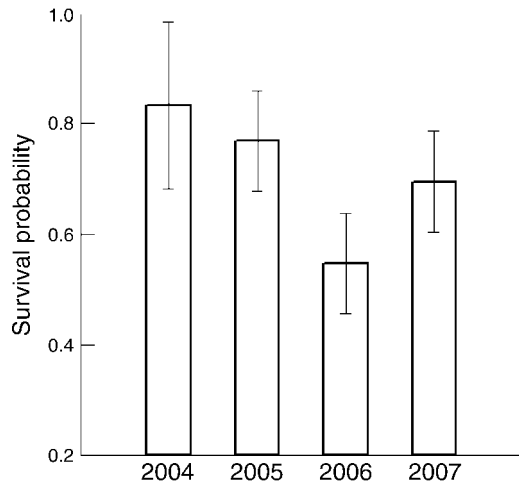


FIG. 5. Survival of Texas ratsnakes implanted with radio transmitters at Fort Hood, Texas, 2004 through 2007. Data are means \pm SE.

associated with avian predation (direct observation, talon or peck marks, and one instance where a transmitter was tracked to a raptor nest).

Snake survival was similar in 2004 and 2005 with a decrease in 2006 and a rebound in 2007 ($\chi^2 = 5.51$, $P = 0.14$, Fig. 5). Results were qualitatively similar when snakes with lost radio signals were not classified as having died (censored), although differences between years were not as substantial (survival 2004 = 0.83 ± 0.15 [mean \pm SE], 2005 = 0.82 ± 0.08 , 2006 = 0.65 ± 0.10 , 2007 = 0.718 ± 0.09 ; $\chi^2 = 1.73$, $P = 0.63$). A comparison between wet years (2004, 2006, 2007) and the drought year shows lower survival during the drought ($\chi^2 = 5.45$, $P = 0.02$, Fig. 6). Again, this pattern was evident but not as pronounced when lost individuals were censored (0.75 ± 0.07 and 0.65 ± 0.10 , respectively; $\chi^2 = 1.73$, $P = 0.19$).

DISCUSSION

During drought conditions in central Texas (USA) we recorded decreases in ground vegetation, small-mammal abundance, ratsnake body condition, and ratsnake survival compared to the years before and after the drought. As with most other studies of drought, our study was opportunistic and correlative (planned, experimental studies of drought pose obvious logistical challenges). This requires caution in attributing causality to the correlations we found. However, the similarity in response across all trophic levels strengthens support for a causal relationship. Specifically, the patterns are consistent with drought causing a reduction in vegetation, which caused small-mammal populations to crash, with that loss of prey causing snakes to lose body condition and suffer higher mortality.

Reduced plant growth in response to drought is straightforward. The link between vegetation and small mammals also seems reasonable. The mammal species

we caught were predominantly omnivores, with diets consisting of a wide variety of plants and arthropods (Stancampiano and Caire 1995, Schmidly 2004). Although we did not record species of vegetation or measure arthropods directly, overall vegetation was greatly reduced during the drought, which also likely reduced arthropod abundance (Bell 1985, Frampton et al. 2000). Therefore, during the drought, small mammals had less vegetation and probably fewer arthropods to eat. In turn, reduced food availability is likely to have reduced small-mammal reproduction and increased starvation (Spevak 1983, Yahner 1992, Morton et al. 1995).

Ratsnakes prey primarily on small mammals and on birds' eggs and nestlings (Fitch 1963), although even during the avian breeding season small mammals remain the most common prey (Weatherhead et al. 2003, Carfagno et al. 2006, Sperry and Weatherhead 2009). The coincident decline of the snakes' principal prey and the snakes' body condition indicates that snakes were feeding less during the drought. Although mortality was also higher during the drought, most snake mortality was not attributable directly to starvation but instead appeared to result from an increase in predation by raptors and more road casualties. Snakes in poorer condition may be more likely to engage in risk-prone behavior to acquire prey. In addition, the decrease in cover due to decreased ground vegetation may exacerbate predation risk because snakes that are searching for food may be more vulnerable because of both increased activity and lack of concealment. Reptiles have been shown to have widely varying responses to drought, with some species increasing activity (Plummer and Congdon 1994) and others decreasing activity or entering aestivation (Duda et al. 1999, Winne et al. 2006). Drought

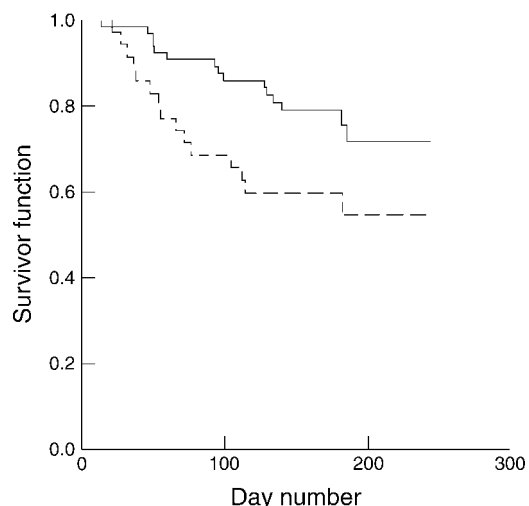


FIG. 6. Kaplan-Meier survival curves for Texas ratsnakes implanted with radio transmitters at Fort Hood, Texas, in wet years (2004, 2005, and 2007) and a drought year (2006). Wet years are indicated by a solid line, and drought year is dashed.

response most likely depends on a species life history and on prey availability.

During the drought the size of the ratsnake population is likely to have declined as a result of the combination of higher adult mortality and lack of reproduction. Decreases in prey availability that result in lowered body condition have been shown to reduce reproduction for several snake species (Shine and Madsen 1997, Madsen and Shine 2000, Reading 2004, Madsen et al. 2006). Although our reproduction data were anecdotal, we found evidence for suppressed reproduction during the drought. In contrast to the years before the drought, we did not witness any mating behavior or document evidence of gravid females or egg laying during the drought. In concert with body condition recovering quickly, however, we observed evidence of reproduction in the year immediately following the drought. Similar patterns have been documented in other snake species (Madsen et al. 2006, Winne et al. 2006).

We were able to associate drought with the predator-prey dynamic between small mammals and snakes, although there was probably a cascading effect across other taxa. In addition to direct effects on their predators, previous work has demonstrated a multi-trophic response to fluctuations in small-mammal numbers. For example, songbird nest predation rates can vary with small-mammal abundance, either from direct predation by the mammals or because of prey-switching by top predators such as hawks (Schmidt and Ostfeld 2003, Clotfelter et al. 2007). Several species of raptors are present on Fort Hood and they are known predators of songbirds, small mammals, and snakes. The decrease in small mammals due to the drought may have increased predation on snakes by hawks, and increased predation on secondary prey such as songbirds by both hawks and snakes.

The rapid response to drought conditions demonstrates how even a relatively short-term drought can impact an ecosystem. An equally rapid subsequent recovery of vegetation, small-mammal abundance, and snake body condition and survival to pre-drought conditions within one year post-drought indicated a general resiliency to drought effects. All of the species studied are probably adapted to short-term drought conditions because drought is relatively common in the region (Stahle and Cleaveland 1988). We were not able to measure snake population size, however, which due to higher mortality and lowered reproductive output, likely requires much longer than a year to recover. Global climate-change models predict that droughts will increase both in frequency and severity (Overpeck 1996, Gregory et al. 1997, Dai et al. 1998). An increase in drought severity or length would make it more difficult for populations to recover between drought episodes, which could have pronounced implications for ecosystem health.

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LITERATURE CITED

- Bell, H. L. 1985. Seasonal variation and the effects of drought on the abundance of arthropods in savanna woodland on the Northern Tablelands of New South Wales. *Austral Ecology* 10:207-221.
- Blouin-Demers, G., and P. J. Weatherhead. 2001. Habitat use by black rat snakes (*Elaphe obsoleta obsoleta*) in fragmented forests. *Ecology* 82:2882-2896.
- Brown, G. P., and R. Shine. 2007. Rain, prey and predators: climatically driven shifts in frog abundance modify reproductive allometry in a tropical snake. *Oecologia* 154:361-368.
- Carfagno, G. L. F., and P. J. Weatherhead. 2006. Intraspecific and interspecific variation in use of forest-edge habitat by snakes. *Canadian Journal of Zoology* 84:1440-1452.
- Clotfelter, E. D., A. B. Pedersen, J. A. Cranford, N. Ram, E. A. Snajdr, V. Nolan Jr., and E. D. Ketterson. 2007. Acorn mast drives long-term dynamics of rodent and songbird populations. *Oecologia* 154:493-503.
- Dai, A., K. E. Trenberth, and T. R. Karl. 1998. Global variations in droughts and wet spells: 1900-1995. *Geophysical Research Letters* 25:3367-3370.
- Duda, J. J., A. J. Krzysik, and J. E. Freilich. 1999. Effects of drought on desert tortoise movement and activity. *Journal of Wildlife Management* 63:1181-1192.
- Fitch, H. S. 1963. Natural history of the black rat snake (*Elaphe o. obsoleta*) in Kansas. *Copeia* 1963:649-658.
- Frampton, G. K., P. J. Van Den Brink, and P. J. L. Gould. 2000. Effects of spring drought and irrigation on farmland arthropods in southern Britain 37:865-883.
- George, T. L., A. C. Fowler, R. L. Knight, and L. C. McEwen. 1992. Impacts of a severe drought on grassland birds in western North Dakota. *Ecological Applications* 2:275-284.
- Germano, D. J., D. F. Williams, and W. Tordoff III. 1994. Effect of drought on blunt-nosed leopard lizards (*Gambelia sila*). *Northwestern Naturalist* 75:11-19.
- Gettinger, R. D. 1990. Effects of chemical insect repellents on small mammal trapping yield. *American Midland Naturalist* 124:181-184.
- Gibbons, J. W., J. L. Greene, and J. D. Congdon. 1983. Drought-related responses of aquatic turtle populations. *Journal of Herpetology* 17:242-246.
- Gibbons, J. W., D. E. Scott, T. J. Ryan, K. A. Buhlmann, T. D. Tuberville, B. S. Metts, J. L. Greene, T. Mills, Y. Leiden, S. Poppy, and C. T. Winne. 2000. The global decline of reptiles, déjà vu amphibians. *BioScience* 50:653-666.
- Gregory, J. M., J. F. B. Mitchell, and A. J. Brady. 1997. Summer drought in northern mid-latitudes in a time-dependent CO₂ climate experiment. *Journal of Climate* 10: 662-686.
- Hanson, P. J., and J. F. Weltzin. 2000. Drought disturbance from climate change: reponse of United States forests. *Science of the Total Environment* 262:205-220.
- Hintze, J. 2006. NCSS, PASS and GESS. NCSS [Number Cruncher Statistical Systems]. Kaysville, Utah, USA.
- Hunter, M. D., and P. W. Price. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724-732.

- Madsen, T., and R. Shine. 2000. Rain, fish and snakes: climatically driven population dynamics of Arafura file-snakes in tropical Australia. *Oecologia* 124:208–215.
- Madsen, T., B. Ujvari, R. Shine, and M. Olsson. 2006. Rain, rats and pythons: climate-driven population dynamics of predators and prey in tropical Australia. *Austral Ecology* 31: 30–37.
- Masser, M. P., and W. E. Grant. 1986. Fire ant-induced trap mortality of small mammals in east-central Texas. *Southwestern Naturalist* 31:540–542.
- Morton, M. L., M. L. Morrison, L. S. Hall, and M. E. Pereyra. 1995. Life history parameters in mice exposed to a prolonged drought. *Southwestern Naturalist* 40:18–28.
- Overpeck, J. T. 1996. Warm climate surprises. *Science* 271: 1820–1821.
- Plummer, M. V., and J. D. Congdon. 1994. Radiotelemetric study of activity and movements of racers (*Coluber constrictor*) associated with a Carolina bay in South Carolina. *Copeia* 1994:20–26.
- Pollock, K. H., S. R. Winterstein, C. M. Bunck, and P. D. Curtis. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53: 7–15.
- Reading, C. J. 2004. The influence of body condition and prey availability on female breeding success in the smooth snake (*Coronella austriaca* Laurenti). *Journal of Zoology* 264:61–67.
- Reinert, H. K., and D. Cundall. 1982. An improved surgical implantation method for radio-tracking snakes. *Copeia* 1982: 702–705.
- Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.
- Schmidly, D. J. 2004. *The mammals of Texas*. University of Texas Press, Austin, Texas, USA.
- Schmidt, K. A., and R. A. Ostfeld. 2003. Songbird populations in fluctuating environments: predator responses to pulsed resources. *Ecology* 84:406–415.
- Seigel, R. A., J. W. Gibbons, and T. K. Lynch. 1995. Temporal changes in reptile populations: effects of a severe drought on aquatic snakes. *Herpetologica* 51:424–434.
- Shine, R. 1991. *Australian snakes: a natural history*. Cornell University Press, Ithaca, New York, USA.
- Shine, R., and T. Madsen. 1997. Prey abundance and predator reproduction: rats and pythons on a tropical Australian floodplain. *Ecology* 78:1078–1086.
- Smith, R. I. 1970. Response of pintail breeding populations to drought. *Journal of Wildlife Management* 34:943–946.
- Sperry, J. H., and P. J. Weatherhead. 2009. Does prey availability determine seasonal patterns of habitat selection in Texas rattlesnakes? *Journal of Herpetology*, in press.
- Spevak, T. A. 1983. Population changes in a Mediterranean scrub rodent assembly during drought. *Southwestern Naturalist* 28:47–52.
- Stahle, D. W., and M. K. Cleaveland. 1988. Texas drought history reconstructed and analyzed from 1698 to 1980. *Journal of Climate* 1:59–74.
- Stancampiano, A. J., and W. Claire. 1995. Food habits of *Peromyscus* and *Reithrodontomys* in the Wichita Mountains Wildlife Refuge, Oklahoma. *Proceedings of the Oklahoma Academy of Science* 75:45–49.
- SYSTAT. 2004. SYSTAT, version 11. SYSTAT Software, San Jose, California, USA.
- Weatherhead, P. J., and G. Blouin-Demers. 2004. Understanding avian nest predation: why ornithologists should study snakes. *Journal of Avian Biology* 35:185–190.
- Weatherhead, P. J., G. Blouin-Demers, and K. M. Cavey. 2003. Seasonal and prey-size dietary patterns of black ratsnakes (*Elaphe obsoleta obsoleta*). *American Midland Naturalist* 150: 275–281.
- Weatherhead, P. J., and G. P. Brown. 1996. Measurement versus estimation of condition responses of kit foxes to a short-term decline in mammalian prey. *Journal of Mammalogy* 77:370–376.
- White, P. J., C. A. Vanderbilt White, and K. Ralls. 1996. Functional and numerical in snakes. *Canadian Journal of Zoology* 74:1617–1621.
- Winne, C. T., J. D. Willson, and J. W. Gibbons. 2006. Income breeding allows an aquatic snake *Seminatrix pygaea* to reproduce normally following prolonged drought-induced aestivation. *Journal of Animal Ecology* 75:1352–1360.
- Yahner, R. H. 1992. Dynamics of a small mammal community in a fragmented forest. *American Midland Naturalist* 127: 381–391.