Too Cold, Too Wet, Too Bright, or Just Right? Environmental Predictors of Snake Movement and Activity

Evan A. Eskew[1,2] and Brian D. Todd[3]

Movement and activity patterns are fundamental to the basic ecology of any organism and can be influenced by a variety of environmental factors. For snakes, which are notable for being secretive and difficult to study, environmental influences on movement are often obscure. Here, we investigate environmental drivers of terrestrial activity for 23 snake species from a temperate community in the Atlantic Coastal Plain region of South Carolina, USA. Activity was strongly seasonal, with primarily fossorial species showing unimodal activity peaks in summer, whereas several aquatic species showed increased terrestrial movements to and from a wetland in both spring and fall. After controlling for seasonal activity, temperature and precipitation had consistent effects on snake movement, with activity of snakes increasing with temperature and decreasing with precipitation. The influence of moon illumination was more ambiguous but may have a weak, negative effect on snake activity. These environmental factors likely drive snake movements because of physiological constraints and trade-offs between foraging success and predation risk. Our results contribute to general knowledge of snake natural history and ecology and may help improve sampling of these elusive organisms that are increasingly in need of conservation attention.

AMONG the most fundamental aspects of an animal's ecology are its movement and activity patterns (Nathan et al., 2008), which can be shaped by many environmental cues that range from atmospheric (Mandel et al., 2008) to chemical (Nevitt et al., 2008). For example, temperature and other weather variables affect the timing of long-distance movements of vertebrates across terrestrial and aquatic systems (Block et al., 2011; Deppe et al., 2015). In addition, activity can be strongly influenced by large-scale ecosystem disturbances like fire (O'Donnell et al., 2016), while anthropogenic landscape changes, such as road construction, can alter movement patterns and space use (Leblond et al., 2013).

The influence of environmental factors on animal activity patterns is often readily apparent for ectotherms, whose body temperatures depend on the thermal environment, thereby making them especially sensitive to changes in temperature (Parmesan, 2007; Todd et al., 2011). Amphibian movements, in particular, show a high degree of correlation with environmental variables like temperature and rainfall (Todd and Winne, 2006). The movements of other terrestrial ectotherms like squamates (snakes and lizards) have been studied less often, perhaps in part due to challenges in obtaining sufficient captures for analysis (Steen, 2010; Willson et al., 2011; Durso and Seigel, 2015).

Studies of snake activity to date, although often limited in scope to a single species and/or a narrow subset of predictor variables, suggest various biotic and abiotic drivers of snake movement. First, differences in physiology and reproductive roles between sexes can generate sex-specific activity patterns (Gannon and Secoy, 1985; Sun et al., 2001). In addition, seasonal effects on snake activity are well established and appear to reflect seasonal variation in climate, resource availability, or reproductive behavior (Gibbons and Semlitsch, 1987; Bernardino and Dalrymple, 1992; Marques et al., 2001). For example, seasonally restricted mate searching behavior can lead male snakes to undergo more extensive movements than females (Maritz and Alexander, 2012). At shorter time scales, climactic factors have variable effects on snake movement. For some species, activity is heavily influenced by factors like temperature (Marques et al., 2001; Sun et al., 2001; Spence-Bailey et al., 2010). Increased moonlight may limit snake activity, especially in nocturnal species where lunar illumination can affect both foraging success and predation risk (Madsen and Osterkamp, 1982; Houston and Shine, 1994; Clarke et al., 1996). However, environmental factors can have apparently little effect on activity patterns of some snake species (Brown and Shine, 2002). If environmental variables have any general, predictable effects on snake activity, one might expect that such relationships are strongest in temperate systems where abiotic factors like temperature can vary greatly across the year.

The goal of the present study was to determine how environmental factors affect activity in a diverse, temperate snake community. Specifically, we evaluated activity patterns using data on 23 snake species representing over 900 individual captures. Our work adopts an explicit assemblage-level, rather than species-specific, perspective. Given conservation concern for various snake populations globally (Winne et al., 2007; Reading et al., 2010; Todd et al., 2010), greater understanding of general ecological influences in this secretive taxon is urgently needed.

MATERIALS AND METHODS

Data collection.—We analyzed data collected during two previous studies that used extensive drift fences with pitfall or funnel traps to census herpetofauna at the Savannah River Site near Aiken, SC, USA (UTM 17S E 430393 N 3676147) in the Atlantic Coastal Plain physiographic region. Habitat consisted of second-growth, managed pine forests composed mostly of loblolly pine (*Pinus taeda*) with an understory of holly (*Ilex opaca*) and wax myrtle (*Morella cerifera*). The first study—Land-use Effects on Amphibian Populations (LEAP)—used drift fences at four different upland locations all lying

[1] Graduate Group in Ecology, University of California, Davis, One Shields Avenue, Davis, California 95616.
[2] EcoHealth Alliance, 460 West 34th Street–17th Floor, New York, New York 10001; Email: eskew@ecohealthalliance.org. Send reprint requests to this address.
[3] Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, One Shields Avenue, Davis, California 95616; Email: btodd@ucdavis.edu.

approximately 5 km from one another. In total, it used 144 15 m and 16 45 m terrestrial drift fences made of aluminum flashing that was buried 6 cm into the ground. Every 5 m, a pair of 8 L plastic buckets was buried flush with the ground to capture animals moving along the fence. Pitfall traps were opened on 25 February 2004 and remained open through 23 July 2006 with the exception of each August, when traps were closed to prevent mortality of animals during the warmest parts of each year. Pitfall traps were checked between 0600–1100 hr each day. The second study used an approximately 2 km long aluminum drift fence that completely encircled a large Carolina bay wetland, Ellenton Bay. The aluminum drift fence, which was placed terrestrially, was buried 10 cm into the soil. A pair of traps was placed along the fence approximately every 30 m, and these included 41 pairs of 19 L plastic buckets, 21 pairs of 2.3 L metal coffee cans buried flush with the ground, and 20 pairs of wooden box funnel traps. Traps were opened from 1 February 2003–5 February 2004. Traps were checked each morning between 0700–0900 hr and often again from 1700–2000 hr. In both studies, all captured animals were identified to species and individually marked. However, recaptures comprised a very small portion (<5%) of total captures. Minimum temperature (°C) was recorded daily with a max/min thermometer, and rainfall in the previous 24 hr (mm) was recorded with a rain gauge. Additional details about the trapping design and locations of the first study can be found in Todd and Andrews (2008), while the same information for the second study can be found in Todd and Winne (2006) and Todd et al. (2007).

Data analysis.—Because the LEAP and Ellenton Bay datasets represent distinct sampling efforts that captured different subsets of the native snake community, we analyzed the two datasets separately. To determine the influence of environmental predictors on daily counts of snakes captured (our measure of snake movement and activity), we fit generalized linear mixed effects models with a negative binomial outcome. A negative binomial outcome was appropriate for our data given that counts were overdispersed in both datasets (i.e., variance was greater than the mean). We used the alternative parameterization of the negative binomial distribution that is described by a mean (μ) and dispersion (ϕ) parameter. Our overall modeling strategy was to define μ as a linear combination of environmental predictor variables and associated coefficients while also estimating ϕ.

Following Burnham and Anderson (2002), we developed and tested a specific set of well-considered, *a priori* candidate models. We first defined baseline models for each dataset that contained predictors we believed should be included in all models. For example, initial data visualization revealed strong, non-linear, seasonal trends in snake captures (Fig. 1). In addition, because there was some variation in daily trap deployment across both of the long-term sampling efforts, we anticipated that trap effort (total number of drift fence traps deployed on a given day) would have a positive association with captures. To account for these expected influences, all models in both datasets included three main effects: trap effort, day of year, and day of year squared (needed to generate non-linear responses to day of year). In addition, the Ellenton Bay dataset included a binary variable indicating whether or not wooden box funnel traps were deployed during the daytime only, which happened for several weeks to avoid entrapping amphibians. This predictor was included in the baseline Ellenton Bay model, and all
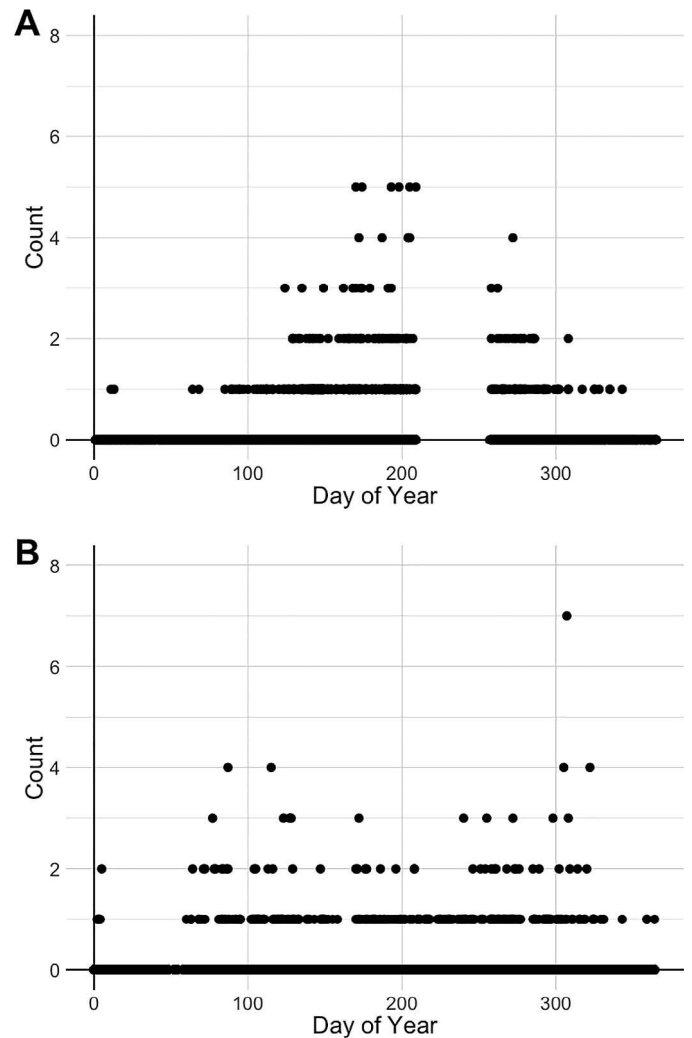
Fig. 1. Snake captures vs. day of year from two snake sampling efforts. Each point represents the observed snake count for a given species, and data from all sampling years are plotted. The Land-use Effects on Amphibian Populations (LEAP) dataset (A) represents captures of six primarily terrestrial, small-bodied snakes (2,069 unique sampling date/sampling location combinations). The Ellenton Bay dataset (B) comprises observations of a suite of 20 snake species that differ significantly in their body size, habitat use, and foraging ecology (363 unique sampling dates).

subsequent models, because it modifies realized trap effort. We also wanted to control for variability in counts that could be attributed to snake species identity and sampling location. Thus, all LEAP models included varying intercepts (i.e., random effects) by snake species and sampling location, whereas Ellenton Bay models only included varying intercepts by snake species since all these data came from a single location. Critically, the inclusion of varying effects by species helps to make our inferences generalizable across the entire snake assemblage rather than being species-specific since inherent differences in activity among species are being accounted for. Finally, LEAP data were collected across three years, and we therefore controlled for year effects in all LEAP models through the use of varying intercepts by years. In contrast, because Ellenton Bay data was dramatically imbalanced across years, with 327 unique sampling dates in 2003 and only 36 in 2004, we chose to pool data across years in all Ellenton Bay models.

Table 1. Captures from two snake sampling efforts. The Land-use Effects on Amphibian Populations (LEAP) dataset consists of data collected over 563 unique sampling dates between 25 February 2004 and 23 July 2006 from four discrete sampling locations. The Ellenton Bay dataset was gathered over 363 unique sampling dates between 1 February 2003 and 5 February 2004 at a single isolated wetland.

Snake species	Number of captures	
	LEAP	Ellenton Bay
Agkistrodon contortrix	—	1
Agkistrodon piscivorus	—	76
Cemophora coccinea	32	2
Coluber constrictor	—	129
Crotalus horridus	—	1
Diadophis punctatus	24	9
Farancia abacura	—	6
Farancia erytrogramma	—	7
Heterodon platirhinos	—	12
Masticophis flagellum	—	2
Nerodia erythrogaster	—	8
Nerodia fasciata	—	39
Nerodia floridana	—	5
Opheodrys aestivus	—	1
Pantherophis alleghaniensis	—	1
Pantherophis guttatus	—	2
Storeria dekayi	—	1
Storeria occipitomaculata	36	3
Tantilla coronata	447	—
Thamnophis sauritus	—	24
Thamnophis sirtalis	—	10
Virginia striatula	2	—
Virginia valeriae	67	—
Total captures	608	339

Building on the baseline models, we constructed models that accounted for other environmental influences. The three primary environmental predictors of interest were: 1) precipitation, the amount of rainfall (mm) in the previous 24 hr; 2) temperature, the minimum temperature (°C) recorded over the previous 24 hr; and 3) moon fraction, a measure of moon illumination that ranges from 0–1 (i.e., new moon = 0, full moon = 1). Moon fraction data were obtained from the US Naval Observatory (http://aa.usno.navy.mil). Note that due to the influence of local weather conditions (i.e., cloud cover), moon illumination is only a proxy for the amount of moonlight reaching Earth's surface. We fit models that added each of these predictors independently to the baseline model and one global model that included all three predictors, with additive effects. Thus, the final model set for each of the datasets contained five models: the baseline model, one incorporating a precipitation effect, one incorporating a temperature effect, one incorporating a moon fraction effect, and one global additive model incorporating precipitation, temperature, and moon fraction effects.

Because the Ellenton Bay data included many snake species with divergent natural histories, our modeling for this dataset required additional complexity. For example, Ellenton Bay snake species vary in their preference for aquatic habitat, and thus we expected these species might also vary in how precipitation affected their activity. To account for this potential source of variation, in all Ellenton Bay models that included a precipitation effect, we also allowed for varying precipitation coefficients by species. This strategy allowed us to estimate an "average" snake response to

precipitation while also controlling for and estimating any idiosyncratic, species-specific precipitation effects. In addition, the species observed at Ellenton Bay differ in their primary activity periods, which we recorded as a binary diurnal/nocturnal variable (in contrast, only nocturnal, small-bodied, litter-dwelling snakes were analyzed in the LEAP dataset [Todd and Andrews, 2008]). We expected that movement of diurnal and nocturnal species might be differently affected by moon fraction. Thus, for all Ellenton Bay models that included the effect of moon fraction, we also included our binary diurnal/nocturnal variable and an interactive effect between moon fraction and diurnality.

Seminatrix pygaea were captured at Ellenton Bay, but this species was excluded from all data visualization and analysis. *Seminatrix pygaea* is almost exclusively aquatic, and captures of this species in the terrestrial drift fences surrounding Ellenton Bay were tightly clustered around the timing of parturition when newborn animals disperse away from natal wetlands and are captured in pitfall traps along the fence that encircled the wetland (~day of year 220; Ernst and Ernst, 2003; Winne et al., 2005). Because captures of this species were so closely associated with this period of parturition, captures of *S. pygaea* do not represent the type of general daily snake movement and activity patterns we were interested in studying.

To specify and fit models, we used a Bayesian framework and employed the Stan programming language (Carpenter et al., 2017). We used the RStan package (Stan Development Team, 2016) to code and implement models within the R statistical computing environment (R Core Team, 2015). All continuous predictor variables were standardized prior to analysis. For each model, we sampled from the posterior distribution using three independent Markov chains, with each chain running for 1,000 warmup and 1,000 sampling iterations. As a result, our inferences are based on a total of 3,000 posterior samples from each model. Models were compared using the Watanabe-Akaike information criterion (WAIC), an estimate of pointwise predictive accuracy. We calculated WAIC for each model by storing pointwise log-likelihood values at each model iteration and passing these values to the function waic() from the R package loo (Vehtari et al., 2016). For general data manipulation in R, we used the packages dplyr (Wickham and Francois, 2016) and lubridate (Grolemund and Wickham, 2011). The rethinking package was used to aid in summarizing and visualizing model results (McElreath, 2015, 2016). We describe estimated model parameters using posterior means and 95% highest posterior density intervals (HPDI; McElreath, 2016).

RESULTS

Data summary.—The final LEAP dataset consisted of 608 snake captures from 563 unique sampling dates (Table 1; Fig. 1A). Six primarily fossorial species were captured in the LEAP sampling efforts. The final Ellenton Bay dataset represented 339 snake captures from 363 unique sampling dates (Table 1; Fig. 1B). The drift fence surrounding Ellenton Bay captured 20 snake species with a diversity of habitat preferences and body sizes.

LEAP modeling results.—Of the five LEAP models, the best-performing model was the global model, which included effects of precipitation, temperature, and moon fraction on snake captures (Table 2). Because of the overwhelming support for this model (100% of model weight), we derive

Table 2. LEAP data Bayesian model set. Detailed description of the five models is given in the main text. Watanabe-Akaike information criterion (WAIC) values were generated using pointwise log-likelihood values calculated at each model iteration. The $\hat{p}_{WAIC}$ value represents a model's estimated effective number of parameters, while ∆WAIC shows the difference in WAIC between a given model and the top model in the model set. Akaike model weights are given in the "wWAIC" column.

Model name	WAIC	$\hat{p}_{WAIC}$	∆WAIC	wWAIC
Global	3310.514	17.542	0.000	1.000
Precipitation	3326.741	15.857	16.228	0.000
Temperature	3340.727	15.331	30.213	0.000
Moon fraction	3349.798	15.398	39.285	0.000
Baseline	3350.700	14.590	40.186	0.000

Table 3. Ellenton Bay data Bayesian model set. Detailed description of the five models is given in the main text. Watanabe-Akaike information criterion (WAIC) values were generated using pointwise log-likelihood values calculated at each model iteration. The $\hat{p}_{WAIC}$ value represents a model's estimated effective number of parameters, while ∆WAIC shows the difference in WAIC between a given model and the top model in the model set. Akaike model weights are given in the "wWAIC" column.

Model name	WAIC	$\hat{p}_{WAIC}$	∆WAIC	wWAIC
Global	2078.016	32.764	0.000	0.951
Precipitation	2084.002	28.685	5.985	0.048
Moon fraction	2091.102	24.885	13.086	0.001
Temperature	2094.673	24.159	16.657	0.000
Baseline	2095.294	22.940	17.277	0.000

inferences from the LEAP dataset solely using parameter estimates from the global model (Fig. 2). The global model's intercept was negative (parameter estimate mean [95% HPDI] $=-3.88$ [–5.76, –1.88]), indicating few daily snake captures in general. Trap effort had a positive influence on snake captures (0.51 [0.35, 0.67]). The coefficient for the day of year squared variable was negative (–1.19 [–1.48, –0.90]), which dictates a unimodal, concave down relationship between day of year and snake counts (Fig. 1A). Precipitation was negatively related to snake captures (–0.32 [–0.45, –0.20]), whereas temperature had a positive effect (0.46 [0.23, 0.67]). Moon fraction had a weak, negative effect on snake captures (–0.08 [–0.16, 0.01]), and the 95% HPDI for the parameter included zero. Finally, the σ parameter describing the standard deviation of the species-level varying intercepts structure (1.82 [0.84, 3.07]) was larger in magnitude than the analogous σ parameter for either the year-level (0.70 [0.15, 1.80]) or location-level varying intercepts structure (0.49 [0.13, 1.05]).

Ellenton Bay modeling results.—As with the LEAP model set, the global model fit to the Ellenton Bay data was the best-performing model (Table 3). We derive our inferences from this best model (Fig. 3) because of its extremely high support (95.1% of model weight). The model intercept was strongly negative (–4.16 [–5.10, –3.11]), the trap effort coefficient was positive (0.36 [0.19, 0.55]), and the day of year squared coefficient was negative (–0.39 [–0.68, –0.10]). The binary variable indicating whether box funnel traps were deployed

only during the day had a negative coefficient (–0.47 [–0.92, –0.02]), indicating that reduced trapping time decreased snake captures. Precipitation (–0.49 [–0.87, –0.12]) and temperature (0.28 [0.01, 0.53]) had negative and positive influences on captures, respectively. However, moon fraction appeared to have no effect on snake captures in the Ellenton Bay data; the parameter estimate for the moon fraction coefficient was very close to zero, and the 95% HPDI substantially overlapped zero (0.03 [–0.14, 0.20]). The posterior distribution for the diurnal variable coefficient had a positive mean but encompassed an extremely wide range of potential values, both negative and positive (0.35 [–1.30, 1.88]). The coefficient for the interaction term between moon fraction and diurnality was negative (–0.30 [–0.56, –0.06]), suggesting that captures of diurnal species decreased with increasing moon fraction.

Our model structure for the Ellenton Bay dataset also allowed us to examine species-specific precipitation coefficient estimates. Deriving inference from the global Ellenton Bay model, the mean coefficient estimate for every species was negative (Fig. 4), which is congruent with the overall precipitation coefficient estimate from this model (–0.49 [–0.87, –0.12]; Fig. 3; also shown in Fig. 4 as a vertical dotted line). However, there was variation in the strength of the precipitation effect across species. Some species, like *Coluber constrictor* and *Heterodon platirhinos*, had coefficient estimates with 95% HPDI that were strictly negative, indicating strong support for a negative influence of precipitation on capture. In contrast, *Agkistrodon piscivorus* had a mean coefficient
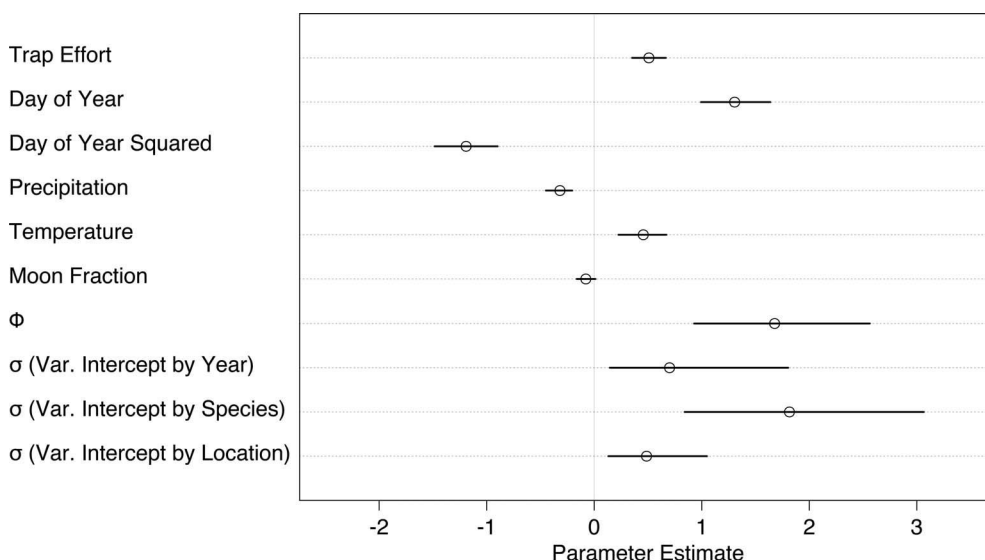
Fig. 2. Dotplot showing parameter estimates from the LEAP data global model. Parameter means (circles) and 95% highest posterior density intervals (solid black lines) are shown. The model intercept is excluded from this plot to ease visual interpretation of other parameters. Detailed description of the model structure, environmental predictor variables, and model fitting is given in the main text.
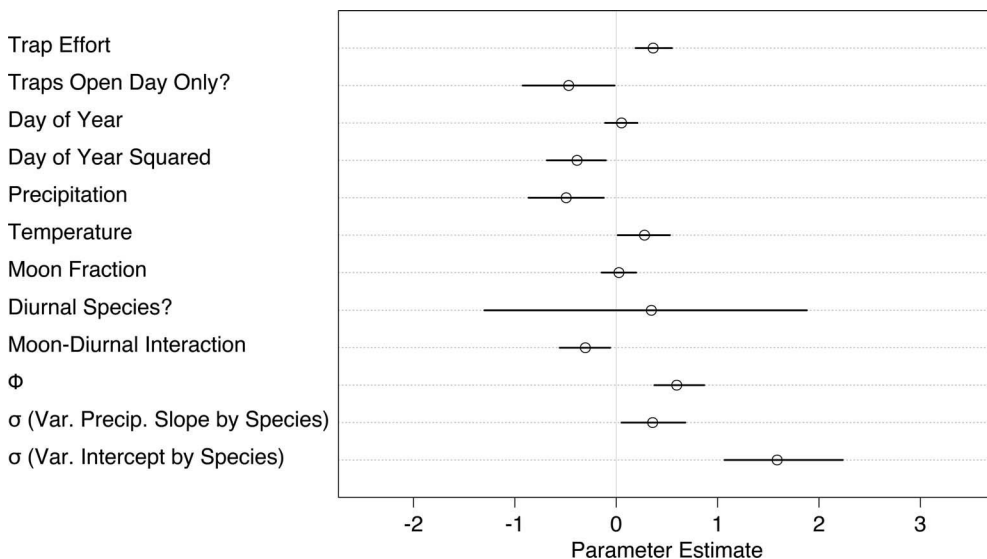
Fig. 3. Dotplot showing parameter estimates from the Ellenton Bay data global model. Parameter means (circles) and 95% highest posterior density intervals (solid black lines) are shown. The model intercept is excluded from this plot to ease visual interpretation of other parameters. Detailed description of the model structure, environmental predictor variables, and model fitting is given in the main text.

estimate close to zero, suggesting only a slight reduction in captures as a result of precipitation.

DISCUSSION

Our results indicate that snake movement and activity are correlated with key environmental factors. In both model sets, the global model, which included all three environmental predictor variables, garnered the vast majority of model support. Support for multiple predictors suggests that snake activity is best described with information that spans multiple environmental axes even though some predictors were estimated to have minor effects, in agreement with previous studies (Brown and Shine, 2002). Despite not being large in magnitude, environmental effects were consistently represented in our best models, affirming their role in driving snake activity. All environmental influences we describe should be interpreted solely in relation to terrestrial snake activity; although some primarily aquatic species were captured, drift fence data reflect terrestrial movement specifically.

Of the factors that affect snake movement and activity, seasonality is one of the most obvious and widely reported (Gannon and Secoy, 1985; Bernardino and Dalrymple, 1992;

Marques et al., 2001). Ultimately, seasonal trends in snake activity likely reflect responses to abiotic variables that fluctuate seasonally (Gibbons and Semlitsch, 1987; Bernardino and Dalrymple, 1992). In contrast to some previous work on snake movement that investigated subtropical or tropical species (Marques et al., 2001; Brown and Shine, 2002; Spence-Bailey et al., 2010), our study focused on a temperate snake assemblage where greater variation in seasonal temperatures may drive stronger seasonal activity patterns. Indeed, both the LEAP and Ellenton Bay datasets were characterized by distinct seasonal peaks in snake captures. The LEAP data had a unimodal seasonality, with highest capture success around day of year 200, corresponding to mid-July. Greater summer activity agrees with previous research on several species in the study region, which also found activity peaks in summer (Gibbons and Semlitsch, 1987; Todd et al., 2008). In contrast, the Ellenton Bay data showed a longer period of snake activity (~day of year 100–300), with the suggestion of a bimodal distribution. This pattern is at least partially driven by annual wetland immigration and emigration movements of several highly aquatic species, including *A. piscivorus*, *Farancia abacura*, *F. erytrogramma*, *Nerodia erythrogaster*, and *N. fasciata* (Ernst and Ernst, 2003; Glaudas et al., 2007). Our data thus contribute to
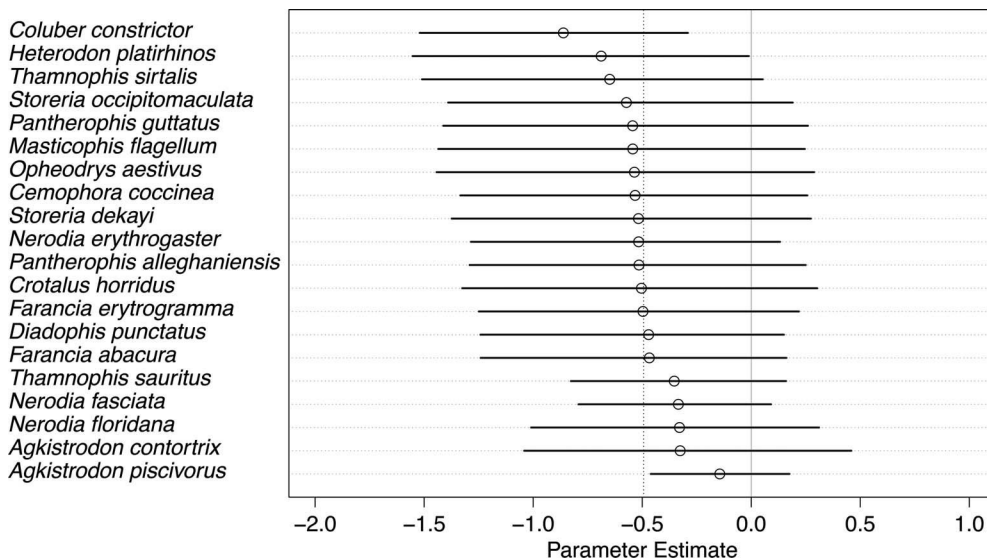
Fig. 4. Dotplot showing species-specific precipitation coefficient parameter estimates from the Ellenton Bay data global model. Posterior distributions for species-specific precipitation coefficient parameter estimates were generated by summing estimates for the overall precipitation coefficient and each species-specific varying coefficient at each model iteration. Parameter means (circles) and 95% highest posterior density intervals (solid black lines) are shown. Species are listed in ascending order of mean species-specific parameter estimate. The mean overall precipitation coefficient estimate (−0.49) is shown as a vertical dotted line.

a literature that suggests activity of any snake species should be examined with the awareness that seasonal effects are likely to be strong and ubiquitous.

Even after controlling for seasonal influences, we found that some environmental factors were correlated with snake activity in our models. Among the environmental variables we studied, temperature and precipitation had consistent effects across the LEAP and Ellenton Bay datasets. Our models indicated that the probability of snake capture increased with temperature and decreased with precipitation. As ectotherms, snake movement and activity should be influenced by thermal constraints, and many prior studies report a positive relationship between environmental temperature and snake activity (Marques et al., 2001; Sun et al., 2001; Sperry et al., 2013). This directional relationship is also consistent with trends between temperature and activity observed more broadly in squamates (Read and Moseby, 2001; Spence-Bailey et al., 2010). Although some studies have found that rainfall tends to increase snake activity, which contradicts our findings, those reports often come from arid, tropical systems where rainfall is highly seasonal (Spence-Bailey et al., 2010; McDonald, 2012). In such systems, where rain is sporadic, coordinating movement with precipitation may benefit snakes since some species favor humid conditions to avoid water loss and dehydration (Daltry et al., 1998) or because their prey depend on rainfall (Spence-Bailey et al., 2010). However, in our study region, precipitation is more evenly distributed throughout the year. Rainfall is unlikely to be highly limiting and may instead disrupt the sensory perception of snakes seeking prey or trying to avoid predators (see similar speculation for other taxa in Martin, 2011), thus being negatively correlated with their activity. Our species-specific estimates of precipitation effects seem to fit with this interpretation. For example, the species that was least negatively affected by precipitation, *A. piscivorus*, is highly aquatic and preys on amphibians, whose activity is strongly driven by rainfall (Todd and Winne, 2006). In contrast, the species for which precipitation most severely reduced activity, *C. constrictor*, is highly terrestrial (Ernst and Ernst, 2003), and the activity of its prey is not likely to be positively influenced by rain. In sum, the temperature and precipitation effects we observed are likely to be mediated by some combination of physiological, energetic, and foraging trade-offs.

While temperature and precipitation had clear, consistent influences across our two datasets, the fraction of the moon illuminated appeared to have a smaller, more idiosyncratic effect. Previous studies have found conflicting results regarding the influence of moonlight on snake activity. Some studies report reduced activity under brighter conditions (Madsen and Osterkamp, 1982; Houston and Shine, 1994; Clarke et al., 1996; Lardner et al., 2014), some suggest shifts in habitat use (Campbell et al., 2008), some find no association (Daltry et al., 1998; Sperry et al., 2013), and still others show increased activity (Spence-Bailey et al., 2010; Lillywhite and Brischoux, 2012). Additionally, effects of moonlight may be age-specific (Clarke et al., 1996), a factor we cannot account for in the present study, and one that could contribute to variation we observed in responses to moon fraction. We emphasize that our predictor variable, moon fraction, is an imperfect proxy for the amount of moonlight reaching Earth since cloudiness and other weather conditions can reduce illumination. Nevertheless, in the LEAP data, comprised exclusively of nocturnal, fossorial, litter-dwelling snakes, we found that captures

decreased as the fraction of the moon illuminated increased, albeit with a small effect size. However, there was considerable uncertainty about the moon fraction variable in the Ellenton Bay data, suggesting no effect. It should be noted that due to our model structure, this parameter estimate represents the moon fraction effect exclusively for nocturnal species. Prior work has especially emphasized the negative influence of moonlight on the activity levels of nocturnal snake species (Madsen and Osterkamp, 1982; Houston and Shine, 1994; Clarke et al., 1996; Lardner et al., 2014), but our analysis of the Ellenton Bay data suggests diurnal species may actually show a greater drop in activity closer to full moons. The negative estimate for the moon fraction*diurnality interaction term in our Ellenton Bay global model indicates that diurnal species would have reduced activity on brighter nights. Thus, we do find evidence from our LEAP data and for diurnal species at Ellenton Bay that supports previous findings that increasing moon fraction should decrease snake activity. However, the overall influence of moon fraction remains partly ambiguous as the direction of the effect is not uniform across all of our data subsets and its magnitude appears to be smaller than that of other more prominent environmental variables.

In conclusion, our results show that environmental factors like precipitation, temperature, and moon illumination can shape snake activity and suggest these influences are generalizable across many species. At an applied level, field research on snakes in the assemblage studied here should, in general, be more fruitful when sampling effort focuses on periods of relatively high temperatures and low precipitation. If available, information on seasonal activity peaks for particular study species should also be considered. Moon illumination appears to have the smallest impact on snake activity. Our findings contribute to the understanding of basic snake ecology, behavior, and natural history and may aid in improved monitoring of these elusive, enigmatic species (Steen, 2010; Durso et al., 2011; Durso and Seigel, 2015).

DATA ACCESSIBILITY

All of the raw data and R code necessary to replicate this analysis are available at https://github.com/eveskew/bayesian_snake_movement.

ACKNOWLEDGMENTS

LITERATURE CITED

Bernardino, F. S., Jr., and G. H. Dalrymple. 1992. Seasonal activity and road mortality of the snakes of the Pa-hay-okee wetlands of Everglades National Park, USA. Biological Conservation 62:71–75.

Block, B. A., I. D. Jonsen, S. J. Jorgensen, A. J. Winship, S. A. Shaffer, S. J. Bograd, E. L. Hazen, D. G. Foley, G. A. Breed, A.-L. Harrison, J. E. Ganong, A. Swithenbank, M. Castleton, H. Dewar, B. R. Mate, G. L. Shillinger, K. M. Schaefer, S. R. Benson, M. J. Weise, R. W. Henry, and D. P. Costa. 2011. Tracking apex marine predator movements in a dynamic ocean. Nature 475:86–90.

Brown, G. P., and R. Shine. 2002. Influence of weather conditions on activity of tropical snakes. Austral Ecology 57:596–605.

Burnham, K. P., and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-theoretic Approach. Springer-Verlag, New York.

Campbell, S. R., S. P. Mackessy, and J. A. Clarke. 2008. Microhabitat use by Brown Treesnakes (*Boiga irregularis*): effects of moonlight and prey. Journal of Herpetology 42:246–250.

Carpenter, B., A. Gelman, M. D. Hoffman, D. Lee, B. Goodrich, M. Betancourt, M. A. Brubaker, J. Guo, P. Li, and A. Riddell. 2017. Stan: a probabilistic programming language. Journal of Statistical Software 76:1–32.

Clarke, J. A., J. T. Chopko, and S. P. Mackessy. 1996. The effect of moonlight on activity patterns of adult and juvenile prairie rattlesnakes (*Crotalus viridis viridis*). Journal of Herpetology 30:192–197.

Daltry, J. C., T. Ross, R. S. Thorpe, and W. Wüster. 1998. Evidence that humidity influences snake activity patterns: a field study of the Malayan pit viper *Calloselasma rhodostoma*. Ecography 21:25–34.

Deppe, J. L., M. P. Ward, R. T. Bolus, R. H. Diehl, A. Celis-Murillo, T. J. Zenzal, Jr., F. R. Moore, T. J. Benson, J. A. Smolinsky, L. N. Schofield, D. A. Enstrom, E. H. Paxton, G. Bohrer, T. A. Beveroth, A. Raim, R. L. Obringer, D. Delaney, and W. W. Cochran. 2015. Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico. Proceedings of the National Academy of Sciences of the United States of America 112:E6331–E6338.

Durso, A. M., and R. A. Seigel. 2015. A snake in the hand is worth 10,000 in the bush. Journal of Herpetology 49:503–506.

Durso, A. M., J. D. Willson, and C. T. Winne. 2011. Needles in haystacks: estimating detection probability and occupancy of rare and cryptic snakes. Biological Conservation 144:1508–1515.

Ernst, C. H., and E. M. Ernst. 2003. Snakes of the United States and Canada. Smithsonian Institution Press, Washington, D.C.

Gannon, V. P. J., and D. M. Secoy. 1985. Seasonal and daily activity patterns in a Canadian population of the prairie rattlesnake, *Crotalus viridus viridis*. Canadian Journal of Zoology 63:86–91.

Gibbons, J. W., and R. D. Semlitsch. 1987. Activity patterns, p. 396–421. *In:* Snakes: Ecology and Evolutionary Biology. R. A. Seigel, J. T. Collins, and S. S. Novak (eds.). Macmillan Publishing Company, New York.

Glaudas, X., K. M. Andrews, J. D. Willson, and J. W. Gibbons. 2007. Migration patterns in a population of cottonmouths (*Agkistrodon piscivorus*) inhabiting an isolated wetland. Journal of Zoology 271:119–124.

Grolemund, G., and H. Wickham. 2011. Dates and times made easy with lubridate. Journal of Statistical Software 40:1–25.

Houston, D., and R. Shine. 1994. Movements and activity patterns of Arafura filesnakes (Serpentes: Acrochordidae) in tropical Australia. Herpetologica 50:349–357.

Lardner, B., J. A. Savidge, R. N. Reed, and G. H. Rodda. 2014. Movements and activity of juvenile Brown Treesnakes (*Boiga irregularis*). Copeia 2014:428–436.

Leblond, M., C. Dussault, and J.-P. Ouellet. 2013. Avoidance of roads by large herbivores and its relation to disturbance intensity. Journal of Zoology 289:32–40.

Lillywhite, H. B., and F. Brischoux. 2012. Is it better in the moonlight? Nocturnal activity of insular cottonmouth snakes increases with lunar light levels. Journal of Zoology 286:194–199.

Madsen, T., and M. Osterkamp. 1982. Notes on the biology of the fish-eating snake *Lycodonomorphus bicolor* in Lake Tanganyika. Journal of Herpetology 16:185–188.

Mandel, J. T., K. L. Bildstein, G. Bohrer, and D. W. Winkler. 2008. Movement ecology of migration in turkey vultures. Proceedings of the National Academy of Sciences of the United States of America 105:19102–19107.

Maritz, B., and G. J. Alexander. 2012. Dwarfs on the move: spatial ecology of the world's smallest viper, *Bitis schneideri*. Copeia 2012:115–120.

Marques, O. A. V., A. Eterovic, and W. Endo. 2001. Seasonal activity of snakes in the Atlantic forest in southeastern Brazil. Amphibia–Reptilia 22:103–111.

Martin, G. R. 2011. Understanding bird collisions with man-made objects: a sensory ecology approach. Ibis 153:239–254.

McDonald, P. J. 2012. Snakes on roads: an arid Australian perspective. Journal of Arid Environments 79:116–119.

McElreath, R. 2015. rethinking: Statistical Rethinking book package. R package version 1.57.

McElreath, R. 2016. Statistical Rethinking: A Bayesian Course with Examples in R and Stan. CRC Press, Boca Raton, Florida.

Nathan, R., W. M. Getz, E. Revilla, M. Holyoak, R. Kadmon, D. Saltz, and P. E. Smouse. 2008. A movement ecology paradigm for unifying organismal movement research. Proceedings of the National Academy of Sciences of the United States of America 105:19052–19059.

Nevitt, G. A., M. Losekoot, and H. Weimerskirch. 2008. Evidence for olfactory search in wandering albatross, *Diomedea exulans*. Proceedings of the National Academy of Sciences of the United States of America 105:4576–4581.

O'Donnell, K. M., F. R. Thompson, and R. D. Semlitsch. 2016. Prescribed fire alters surface activity and movement behavior of a terrestrial salamander. Journal of Zoology 298:303–309.

Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. Global Change Biology 13:1860–1872.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/

Read, J. L., and K. E. Moseby. 2001. Factors affecting pitfall capture rates of small ground vertebrates in arid South Australia. I. The influence of weather and moon phase on capture rates of reptiles. Wildlife Research 28:53–60.

Reading, C. J., L. M. Luiselli, G. C. Akani, X. Bonnet, G. Amori, J. M. Ballouard, E. Filippi, G. Naulleau, D. Pearson, and L. Rugiero. 2010. Are snake populations in widespread decline? Biology Letters 6:777–780.

Spence-Bailey, L. M., D. G. Nimmo, L. T. Kelly, A. F. Bennett, and M. F. Clarke. 2010. Maximising trapping efficiency in reptile surveys: the role of seasonality, weather conditions and moon phase on capture success. Wildlife Research 37:104–115.

Sperry, J. H., M. P. Ward, and P. J. Weatherhead. 2013. Effects of temperature, moon phase, and prey on nocturnal activity in Ratsnakes: an automated telemetry study. Journal of Herpetology 47:105–111.

Stan Development Team. 2016. RStan: the R interface to Stan, version 2.9.0.

Steen, D. A. 2010. Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. Herpetological Conservation and Biology 5:183–188.

Sun, L.-X., R. Shine, Z. Debi, and T. Zhengren. 2001. Biotic and abiotic influences on activity patterns of insular pit-vipers (*Gloydius shedaoensis*, Viperidae) from north-eastern China. Biological Conservation 97:387–398.

Todd, B. D., and K. M. Andrews. 2008. Response of a reptile guild to forest harvesting. Conservation Biology 22:753–761.

Todd, B. D., D. E. Scott, J. H. K. Pechmann, and J. W. Gibbons. 2011. Climate change correlates with rapid delays and advancements in reproductive timing in an amphibian community. Proceedings of the Royal Society B 278:2191–2197.

Todd, B. D., J. D. Willson, and J. W. Gibbons. 2010. The global status of reptiles and causes of their decline, p. 47–67. *In:* Ecotoxicology of Amphibians and Reptiles. D. W. Sparling, G. Linder, C. A. Bishop, and S. K. Krest (eds.). CRC Press, Boca Raton, Florida.

Todd, B. D., J. D. Willson, C. T. Winne, R. D. Semlitsch, and J. W. Gibbons. 2008. Ecology of the Southeastern Crowned Snake, *Tantilla coronata*. Copeia 2008:388–394.

Todd, B. D., and C. T. Winne. 2006. Ontogenetic and interspecific variation in timing of movement and responses to climatic factors during migrations by pond-breeding amphibians. Canadian Journal of Zoology 84:715–722.

Todd, B. D., C. T. Winne, J. D. Willson, and J. W. Gibbons. 2007. Getting the drift: examining the effects of timing, trap type and taxon on herpetofaunal drift fence surveys. American Midland Naturalist 158:292–305.

Vehtari, A., A. Gelman, and J. Gabry. 2016. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. arXiv:1507.04544v5.

Wickham, H., and R. Francois. 2016. dplyr: a grammar of data manipulation. R package version 0.5.0.

Willson, J. D., C. T. Winne, and B. D. Todd. 2011. Ecological and methodological factors affecting detectability and population estimation in elusive species. Journal of Wildlife Management 75:36–45.

Winne, C. T., M. E. Dorcas, and S. M. Poppy. 2005. Population structure, body size, and seasonal activity of Black Swamp Snakes (*Seminatrix pygaea*). Southeastern Naturalist 4:1–14.

Winne, C. T., J. D. Willson, B. D. Todd, K. M. Andrews, and J. W. Gibbons. 2007. Enigmatic decline of a protected population of Eastern Kingsnakes, *Lampropeltis getula*, in South Carolina. Copeia 2007:507–519.