LITERATURE CITED

- BURNEY, D. A., H. F. JAMES, L. P. BURNEY, S. L. OLSON, W. KIKUCHI, W. L. WAG-NER, M. BURNEY, D. MCCLOSKEY, D. KIKUCHI, F. L. GRADY, R. GAGE, AND R. NISHEK. 2001. Fossil evidence for a diverse biota from Kaua'i and its transformation since human arrival. Ecol. Monogr. 71:615–641.
- CONANT, P., AND C. HIRAYAMA. 2000. *Wasmannia auropunctata* (Hymenoptera: Formicidae): established on the Island of Hawaii. Bishop Museum Occas. Pap. 64:21–22.
- FISHER, R., AND I. INEICH. 2012. Cryptic extinction of a common Pacific lizard *Emoia impar* (Squamata, Scincidae) from the Hawaiian Islands. Oryx 46:187–195.

JOURDAN, H., R. A. SADLIER, AND A. M. BAUER. 2001. Little fire ant invasion

(*Wasmannia auropunctata*) as a threat to New Caledonian lizards: evidences from a sclerophyll forest (Hymenoptera: Formicidae). Sociobiology 38:283–301.

McKEOWN, S. 1994. A Field Guide to Reptiles and Amphibians in the Hawaiian Islands. Diamond Head Publishing, Los Osos, California. 172 pp.

VANDERWOUDE, C., M. MONTGOMERY, H. FORESTER, E. HENSLEY, AND M. K. ADACHI. 2015. The history of the little fire ant *Wasmannia auropunctata* Roger in the Hawaiian Islands: Spread, control, and local eradication. Proc. Hawaiian Entomol. Soc. 48:39–50.

Wood, K. R., D. A. BURNEY, A. ALLISON, AND R. FISHER. 2013. *Emoia impar* (Squamata, Scincidae): not extinct in the Hawaiian Islands. Oryx 47:328.

Herpetological Review, 2021, 52(4), 719–724. © 2021 by Society for the Study of Amphibians and Reptiles

Effective Camera Trap Snake Surveys at a Rarely Accessible Longleaf Pine Savanna

Global reptile population declines and extirpations have received increasing recognition over the last twenty years (Gibbons et al. 2000; Todd et al. 2010; Doherty et al. 2020), but quantitative data supporting most assertions have been slow to accumulate. This lack of data has led to uncertainty in the global status and distribution of many reptile populations as well as the potential causes of declines (Todd et al. 2010). Obstacles to determining the status of reptile populations include detectability factors related to the organism (e.g., cryptic coloration and behavior), the survey approach (e.g., method, season, daily timing, environmental conditions), and the scale of the assessment (e.g., local, regional, ecosystemwide). Most reptile decline concerns stem from perceived range-wide contractions of species' distributions, and as such, status assessments of target reptile species frequently demand population data collected in methodologically or statistically comparable ways at regional to ecosystem scales. The time,

WADE A. RYBERG*

DANIELLE K. WALKUP TOBY J. HIBBITTS WAYNE PITTMAN VIVIAN H. PORTER BRANDON C. BOWERS COREY M. FIELDER PRICE BROWN ROEL R. LOPEZ

Natural Resources Institute, Texas A&M University, 578 John Kimbrough Boulevard, College Station, Texas 77843, USA JEREMY R. PRESTON

JUSTIN T. JOHNSON BRUCE W. HAGEDORN

Eglin Air Force Base Natural Resources Office, 107 Highway 85 North,

Niceville, Florida 32578, USA

*Corresponding author; e-mail: waryberg@tamu.edu

resources, and collaboration required to collect sufficient data at such large spatial scales are rarely obtainable due to a lack of funding, problem-solving, and continued engagement by adequately trained and dedicated biologists (e.g., Fritts et al. 2000). However, new survey and monitoring techniques can potentially reduce these resource demands for certain reptile species.

In particular, rare and secretive snake species with low occupancy and detection rates are expensive to monitor and study using traditional box traps with drift fences and other types of surveys (Kéry 2002; Burgdorf et al. 2005; Steen 2010; Adams et al. 2017). Active survey methods such as opportunistic surveys can be very effective, but have a high observer bias, while other survey methods, like road surveys, coverboards, or drift fence/traps or stand-alone funnel traps may be less biased, but situationally productive (Dorcas and Willson 2009). For rare snakes, all these methods are often labor intensive, with traps in particular requiring daily or every other day checking.

Recent research suggests that time-lapse-triggered camera traps combined with drift fencing can be more effective and efficient at detecting certain species of snakes than traditional monitoring approaches that use box traps with fencing (Neuharth et al. 2020). This effective survey technique has already decreased the cost of range-wide monitoring of the extremely rare, federally threatened Louisiana Pinesnake (*Pituophis ruthveni*) on public and private lands as well as military installations with limited access (Adams et al. 2017; Neuharth et al. 2020; unpubl. data). With limited conservation resources, more cost-effective camera trapping techniques can reduce competition between conservation objectives like searching for relictual populations (e.g., Anderson et al. 2020) or monitoring new populations from reintroduction programs (USFWS 2018), both of which require large survey efforts for a small number of individuals.

Additional benefits stemming from a more cost-effective design are that camera traps can be operational for longer periods than box traps are in most cases, including months outside of what might be considered the normal activity season of most snakes, or reptiles in general. Extending survey duration at negligible cost could be valuable in detecting shifting activity norms for reptiles under a changing climate (Henle et al. 2008; Le Galliard et al. 2012). While increasing survey duration, camera traps also allow more fine-scale monitoring of snake behaviors. Researchers can record exact dates, times, temperatures and other weather variables at the moment that snakes are detected using camera traps. Box traps allow only limited monitoring of snake activity at a resolution that depends on the frequency of box-trap checks, and frequent box-trap checks may be limited by constraints on trap access (e.g., military training, conflicting landowner activities, pandemic travel restrictions). By decreasing cost and increasing efficiency, time-lapse-triggered camera traps combined with drift fencing can help remove obstacles to snake status assessments by being operational daily over longer survey periods under variable environmental conditions, collecting data in methodologically and statistically comparable ways at regional to ecosystem scales (Neuharth et al. 2020).

Here, we describe the results of a time-lapse-triggered camera trap study designed to survey for snake species known to be residents of Longleaf Pine (Pinus palustris) forests and savannas. Prior to European settlement, Longleaf Pine forests were one of the most extensive ecosystems in North America, stretching from southeastern Virginia to east Texas, but recent estimates suggest that only about 2.2% of the original area remains, making it one of the most threatened ecosystems in North America (Jose et al. 2006). As a result, many of the snake species considered Longleaf Pine savanna specialists (i.e., all or most of the species' distribution is in Longleaf Pine savanna) are in decline, or perceived to be, and require extensive monitoring (Means 2006). For example, the Eastern Indigo Snake (Drymarchon couperi) is a federally threatened species whose recovery requires extensive monitoring to find and protect relictual populations or create new populations within the range of the species (USFWS 2018). The Eastern Pinesnake (Pituophis melanoleucus), Eastern Diamond-backed Rattlesnake (Crotalus adamanteus), and Southern Hog-nosed Snake (Heterodon simus), other residents of Longleaf Pine forests and savannas, are also thought to be in decline throughout their range, and have been petitioned for federal listing, although the H. simus listing was recently deemed not warranted (Tuberville et al. 2000; Means 2006; USFWS 2019). We conclude with a discussion of the benefits and limitations of using this time-lapse-triggered camera approach to survey and monitor for snake species within Longleaf Pine forests and savannas.

MATERIALS AND METHODS

We deployed 33 time-lapse-triggered camera traps (Reconyx PC800 Professional, default settings) at equal distances (ca. 170 m) along the silt-fence perimeter of three different Gopher Tortoise (*Gopherus polyphemus*) soft-release enclosures within long-leaf pine savanna habitat at Eglin Air Force Base (EAFB) in the Florida panhandle, USA (Fig. 1). The *D. couperi* Biological Opinion (USFWS 2018) and *G. polyphemus* translocation program at EAFB dictates that long-leaf pine savanna habitat be managed with prescribed fire to increase open canopy, reduce mid-story growth, and allow for increased herbaceous vegetation. We named the three enclosures surveyed A, B, and C, and each was 31, 41, and 20 ha, respectively. Enclosures A and B were 1.4 km apart, and each of them were 10.5 km and 11.6 km away from C, respectively. In addition, all enclosures were less than 0.5 km from permanent



FIG. 1. One of many time-lapse-triggered camera trap images with basking or moving Gopher Tortoises and snakes (in this case, *Heterodon platirhinos*) captured together within Gopher Tortoise soft-release enclosures at Eglin Air Force Base in the Florida panhandle, USA. In each instance, both species appeared to simply move around one another.

water (e.g., ponds, streams), although enclosure A was closest to permanent water (ca. 200 m from a 47-ha wetland).

Initially on 23 February 2018, we placed 18 and 15 cameras around A and B, respectively. After C was constructed, we removed four cameras each from A and B on 9 May 2018 and placed seven of those cameras along the perimeter of C, at 170 m spacing. We mounted cameras on u-posts facing down the fence line, ca. 1 m above the ground, and at an angle of 10 degrees from perpendicular. We programmed cameras to take a picture at a 1-min time interval from 0500-2100 h over the following dates: 23 February 2018 to 18 November 2018 at A and B, and 9 May 2018 to 18 November 2018 at C. We chose these dates to coincide with the release of Gopher Tortoises into the pens, and by starting in February, we surveyed a portion of the early activity period of D. couperi (Stevenson et al. 2003). We serviced the cameras (i.e., changing batteries and SD cards takes less than 2 min per camera) approximately every six weeks, although the time interval varied from 32-57 d (mean = 43.7 d) due to variation in base access.

From these camera trapping intervals, we manually scored images for *D. couperi* and other commensal snake species at an average rate of 10,000 images per hour. We identified snakes detected to species or genus when possible, or recorded it as an "unknown snake". We considered a series of strictly consecutive images for an individual snake as a single observation made at the date and time of the first picture in the series. Even a single picture gap in the snake presence in the picture (i.e., a single "empty" image) would start a new observation.

RESULTS

Over the 9 months the 33 cameras were running, we gathered a total of 6,788,710 images (total images with and without snakes). In time-lapse-triggered camera surveys around the enclosures, we collected a total of 808 snake observations which yielded 604 (74.8%) detections of 14 species that could be identified to the species level (Table 1). Of the 204 (25.2%) snake detections remaining, we identified 22 observations to genus (e.g., *Heterodon*, *Nerodia*), 1 to family (e.g., Viperidae), with 181 remaining

Scientific name	Common name	А	В	С
Agkistrodon piscivorus	Northern Cottonmouth	26	1	0
Cemophora coccinea	Scarletsnake	1	3	0
Coluber constrictor	North American Racer	203	28	0
Crotalus adamanteus*	Eastern Diamond-backed Rattlesnake	8	7	0
Heterodon platirhinos	Eastern Hog-nosed Snake	69	20	0
Heterodon simus*	Southern Hog-nosed Snake	10	15	0
Heterodon spp.	hog-nosed Snakes	16	5	0
Masticophis flagellum	Coachwhip	48	36	6
Micrurus fulvius	Harlequin Coralsnake	23	8	2
Nerodia fasciata	Southern Watersnake	15	0	0
Nerodia spp.	watersnakes	0	1	0
Pantherophis guttatus	Red Cornsnake	1	5	1
Pantherophis spiloides	Gray Ratsnake	1	0	0
Pituophis melanoleucus*	Eastern Pinesnake	4	4	1
Sistrurus miliarius	Pygmy Rattlesnake	34	11	0
Thamnophis sirtalis	Common Gartersnake	2	11	0
unknown snake	unknown snake	145	31	5





FIG. 2. Number of snake observations (A) per Julian Date and (B) per hour. Data were aggregated from all time-lapse-triggered camera traps across all enclosures.

unknown. Lack of snake identifications primarily resulted from the snake being too far from the camera, night-time images having washed out identifying characteristics, and/or cover from vegetation. We frequently detected the following species of conservation concern at the enclosures, using the camera traps: 15 *C. adamanteus* (petitioned for listing as federally threatened or endangered), 25 *H. simus* (vulnerable Florida Conservation Action Plan), and nine *P. melanoleucus* (petitioned for listing as federally threatened or endangered), which had at least one detection per enclosure. We detected no *D. couperi*, including among the unknown snakes, where we eliminated *D. couperi* as a possibility. Notably, we detected other small commensal species like the Gopher Frog (*Rana capito*; N = 12), which has been petitioned for federal listing (USFWS 2015).

We detected a total of 604 snakes yielding 14 species at A, 186 detections yielding 12 species at B, and 15 detections yielding four species at C (Table 1). We commonly detected

Coachwhips (*Masticophis flagellum*), Eastern Hog-nosed Snakes (*H. platirhinos*), and North American Racers (*Coluber constrictor*) at A and B, but of those, only *M. flagellum* was detected at C. Two species were only detected at A: Southern Watersnakes (*N. fasciata*) and Gray Ratsnakes (*Pantherophis spiloides*).

We detected snakes during our entire camera trapping season from 23 February to 11 November 2018 (Fig. 2A). We detected snakes at all times of day while the cameras were operational, with a peak in detections between 0900–1200 h (Fig. 2B). Camera temperatures for snake detections varied from 16°C on 7 March 2018 for a basking *H. platirhinos* to 40°C on 1 September 2018 for a crawling *H. simus*. In addition to those snake behaviors, we also detected behaviors such as climbing, periscoping, and shuttling in and out of *G. polyphemus* burrows (Fig. 3). We captured basking or moving snakes and *G. polyphemus* together in numerous images (Fig. 1), and in each instance, both species appeared to simply move around one another.



FIG. 3. Examples of snakes observed with time-lapse-triggered camera traps on Eglin Air Force Base, Florida, USA: A) Southern Watersnake (*Nerodia fasciata*); B) Harlequin Coralsnake (*Micrurus* fulvius); C) Coachwhip (*Masticophis flagellum*); D) North American Racer (*Coluber constrictor*); E) Eastern Pinesnake (*Pituophis melanoleucus*); F) Eastern Diamond-backed Rattlesnake (*Crotalus adamanteus*).

DISCUSSION

The 14 snake species detected using this time-lapse-triggered camera trap approach represented approximately half of the snake species known from longleaf pine savannas at EAFB, although there were some notable species not detected (Means 2006). Still, a wide variety of activity types and feeding strategies were represented in this collection of snake species. Active, surface-foraging *M. flagellum* and *C. constrictor* were frequently detected, and more fossorial species, like *H. platirhinos* and *H. simus*, were not uncommon in the dataset. Even burrowing Scarletsnakes (*Cemophora coccinea*) and *P. melanoleucus* were

detected at multiple sites. Ambush foraging Pygmy Rattlesnakes (*Sistrurus miliarius*) and *C. adamanteus* as well as Northern Cottonmouths (*Agkistrodon piscivorus*) were also relatively common in the dataset.

Small, fossorial snake species (e.g., Storeria dekayi, S. occipitomaculata, Haldea striatula, Virginia valeriae) and kingsnakes (e.g., Lampropeltis calligaster, L. getula, L. triangulum) were not detected. The lack of small species detections is most likely explained by the horizon-facing position of the camera, which favors detection of larger snakes at the expense of smaller ones. Recent studies using time-lapse triggered cameras to survey snakes in similar habitat in east Texas, USA suggest that this sizebias in detection can be reduced by pointing cameras downward, so they directly face the ground (Anderson et al. 2020; Neuharth et al. 2020). The lack of kingsnake detections is more difficult to explain, as they are wide-ranging species found in other grassland habitats (Means 2006). Nearly a quarter of snake detections in the dataset, many of them made during low-light conditions, were not identified to species. Given that kingsnakes can shift activity to evening hours during summer months (Means 2006), it is possible that these species were captured by cameras but not identifiable in images due to lack of light. Time-lapse triggered cameras can be set with a flash to detect snakes active at night or in low-light conditions, but camera batteries will need to be changed more frequently to compensate for greater power loss from repeated flash use.

There was also habitat heterogeneity across the three sites and some variation in adjacent habitats, which can be seen in the varying *A. piscivorus* and watersnake detections across sites. The high number of detections for these species at A most likely reflected the proximity (ca. 200 m) of that enclosure to a 47-ha wetland. Relative variation in detection rates for other species across sites, some common (e.g., Harlequin Coralsnake [*Micrurus fulvius*], Common Gartersnake [*Thamnophis sirtalis*]) and some rare (e.g., Gray Ratsnake [*Pantherophis spiloides*], Red Cornsnake [*P. guttatus*]), are more difficult to explain, but might be due to habitat heterogeneity across sites or simply low sample sizes, respectively.

Although no D. couperi were detected, this time-lapsetriggered camera trapping technique proved to be effective at detecting other snake species considered rare or secretive (e.g., C. adamanteus, H. simus, and P. melanoleucus), which suggests that D. couperi could have been detected if present. With only 28 documented sightings of D. couperi since 1956, and no sightings since 1999 (J. R. Preston, pers. comm.), it is possible that the snake is extirpated at EAFB and unable to recolonize restored suitable habitats throughout EAFB without assistance. Alternatively, the species may persist in low numbers at EAFB, but remain undetected due to the low survey success of traditional methods of detection involving burrow scopes that are difficult to navigate around tight burrow corners or G. polyphemus occupants (USFWS 2018). To increase probability of D. couperi detection, additional search methods away from G. polyphemus burrows have been recommended, including searching for tracks in the sand, shed skins on the surface, and using dogs to locate individuals or their feces (USFWS 2018). We believe that the time-lapse-triggered cameras combined with drift fences described here (see also Neuharth et al. 2020; Anderson et al. 2020) provide a systematic survey technique that can be efficiently scaled up to sample installation-wide, regionally, or range-wide for D. couperi.

There are some limitations to the time-lapse camera trap methodology. Battery life varies based on the frequency of image capture timing (i.e., longer intervals mean longer battery life; this study, Adams et al. 2017) and time-lapse-triggered image capture reduces battery life faster than infrared-triggered image capture. Modifying the cameras for use with solar panels may be a relatively inexpensive and more environmentally friendly alternative to batteries but may also introduce logistical challenges if solar panels require more frequent maintenance (unpubl. data). There are also some alternative camera trapping approaches that may improve infrared methods, making them more applicable to future research. These include: the Adapted-Hunt Drift Fence Technique (AHDriFT), where there is a fixed focal length camera stationed in the top of an 18.9 L bucket, with the bucket having a narrow opening overlapping with the camera's infrared bands, increasing likelihood of triggering (Martin et al. 2017); the HALT trigger, a modification with an external near infrared (NIR) beam mounted above and parallel to an elevated threshold that reptiles can crawl over, triggering the camera (Hobbs and Brehme 2017); and The Camera Overhead Augmented Temperature (COAT) system, which includes a 30×30 cm cork board on the ground under the camera to present a more uniform background temperature as well as provide a higher temperature differential between the cork, the surrounding landscape, and the animals crossing it (Welbourne 2013). More recent research has shown that this last method is improved using time-lapse triggers in conjunction with infraredtriggers (Welbourne et al. 2019).

As this time-lapse-triggered camera trapping technique is used more frequently to monitor or search for rare and secretive snake species, it will be important to use the data gathered to develop detectability profiles for those species. Months and times of activity as reported here, along with field of view specifications (i.e., camera height and orientation) and time-lapse intervals necessary for detection based on species' size, rate of movement, and other behaviors will be critical information for detectability profiles. In addition to date and time stamps, moon phase, precipitation, and ambient temperature at the time of detection could also be collected for each image and incorporated into detectability profiles (e.g., Eskew and Todd 2017). While these detectability profiles will be most valuable in improving longterm monitoring of rare species that exhibit secretive behaviors such as D. couperi (USFWS 2018) and P. ruthveni (Anderson et al. 2020; Neuharth et al. 2020), the long-term records of fine-scale temporal activity generated will also help capture predicted shifts in snake activity over time with changing climates (Henle et al. 2008; Le Galliard et al. 2012).

For research applications that require data collected from animals in-hand (e.g., morphology, mark/recapture, genetics), this time-lapse-triggered camera trap may be used to first establish presence or activity and determine a detectability profile for the target species in that area, and then be replaced by a traditional box trap for efficient species capture. While this additional start-up equipment (i.e., cameras plus box traps) increases costs at the beginning of research or monitoring projects (Kays and Slauson 2008; Long et al. 2008), that additional cost is offset by savings in travel and personnel costs from not having to check box traps on a daily schedule over several years (Adams et al. 2017). Monthly camera trap maintenance (e.g., change batteries and SD cards), as opposed to daily box trap checks, also minimizes interactions with private landowners and conflicts with mission activity at busy military installations like EAFB, as well as problems of trap shyness or mortality due to trap predation or sudden weather changes (Fogarty and Jones 2003). In summary, this time-lapse triggered camera trapping technique provided a less intrusive and more cost-effective alternative, or complement, to traditional box trapping methods for snakes, which allowed research and monitoring applications where access to study locations was not always available.

Acknowledgements.—This research was funded by the U.S. Air Force (Department of Defense), and conducted under Texas A&M University animal care permit number IACUC 2017-0347 and Florida Fish and Wildlife Conservation Commission permit number 18-00013.

LITERATURE CITED

- ADAMS, C. S., W. A. RYBERG, T. J. HIBBITTS, B. L. PIERCE, J. B. PIERCE, AND D. C. RUDOLPH. 2017. Evaluating effectiveness and cost of time-lapse triggered camera trapping techniques to detect terrestrial squamate diversity. Herpetol. Rev. 48:44–48.
- ANDERSON, A., W. A. RYBERG, K. L. SKOW, B. L. PIERCE, S. FRIZZELL, D. B. NEUHARTH, C. S. ADAMS, T. E. JOHNSON, J. B. PIERCE, D. C. RUDOLPH, R. R. LOPEZ, AND T. J. HIBBITTS. 2020. Modeling Louisiana pinesnake habitat to guide the search for population relicts. Southeast. Nat. 19:613–626.
- BURGDORF, S. J., D. C. RUDOLPH, R. N. CONNER, D. SAENZ, AND R. R. SCHAE-FER. 2005. A successful trap design for capturing large terrestrial snakes. Herpetol. Rev. 36:421–424.
- DOHERTY, T. S., S. BALOUCH, K. BELL, T. J. BURNS, A. FELDMAN, C. FIST, T. F. GARVEY, T. S. JESSOP, S. MEIRI, AND D. A. DRISCOLL. 2020. Reptile responses to anthropogenic habitat modification: A global meta analysis. Global Ecol. Biogeogr. 29:1265–1279.
- DORCAS, M. E., AND J. D. WILLSON. 2009. Innovative methods for studies of snake ecology and conservation. *In* S. J. Mullin and R. A. Seigel (eds.), Snakes: Ecology and Conservation, pp. 5–37. Cornell University Press, Ithaca, New York.
- Eskew, E. A., AND B. D. TODD. 2017. Too cold, too wet, too bright, or just right? Environmental predictors of snake movement and activity. Copeia 105:584–591.
- FOGARTY, J. H., AND J. C. JONES. 2003. Pitfall trap versus area searches for herpetofauna research. Proc. Ann. Conf. Southeast. Assoc. Fish Wild. Agen. 57:268–279.
- FRITTS, T. H., H. L. SNELL, L. CAYOT, C. MACFARLAND, S. EARSOM, C. MAR-QUEZ, W. LLERENA, AND F. LLERENA. 2000. Progress and priorities in research for the conservation of reptiles. Bull. de l'Institut Royal des Sciences Naturelles de Belgique 70:39–45.
- 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: reptile species are declining on a global scale. BioScience 50:653–666.
- HENLE, K., D. DICK, A. HARPLE, I. KÜHN, O. SCHWEIGER, AND J. SETTELE. 2008. Biodiversity and climate change: reports and guidance. Bern Convention Council of Europe Publishing, Strasbourg, France.
- HOBBS, M. T., AND C. S. BREHME. 2017. An improved camera trap for amphibians, reptiles, small mammals, and large invertebrates. PLoS ONE 12:e0185026.
- JOSE, S., E. J. JOKELA, AND D. L. MILLER. 2006. The Longleaf Pine

Ecosystem: Ecology, Silviculture, and Restoration. Springer, New York, New York. 438 pp.

- KAYS, R. W., AND K. M. SLAUSON. 2008. Remote cameras. *In* R. A. Long, P. MacKay, W. J. Zielinski, and J. C. Ray (eds.), Noninvasive Survey Methods for Carnivores, Second edition, pp. 110–140. Island Press, Washington, D.C.
- KERY, M. 2002. Inferring the absence of a species: a case study of snakes. J. Wildl. Manag. 66:330–338.
- Le GALLIARD, J. F., M. MASSOT, J. P. BARON, AND J. CLOBERT. 2012. Ecological effects of climate change on European reptiles. *In* E. Post, D. Doak, and J. Brodie (eds.), Wildlife Conservation in a Changing Climate, pp. 179–203. University of Chicago Press, Chicago, Illinois.
- Long, R. A., P. MacKay, W. J. ZIELINSKI, AND J. C. RAY. 2008. Noninvasive Survey Methods for Carnivores. Second edition. Island Press, Washington, D.C. 400 pp.
- MARTIN, S. A., R. M. RAUTSAW, F. ROBB, M. R. BOLT, C. L. PARKINSON, AND R. A. SEIGEL. 2017. Set AHDriFT: Applying game cameras to drift fences for surveying herpetofauna and small mammals. Wildl. Soc. Bull. 41:804–809.
- MEANS, D. B. 2006. Vertebrate faunal diversity of longleaf pine ecosystems. In S. Jose, E. J. Jokela, and D. L. Miller (eds.), Longleaf Pine Ecosystems: Ecology, Silviculture, and Restoration, pp. 157–213. Springer, New York, New York.
- NEUHARTH, D. B., W. A. RYBERG, C. S. ADAMS, T. J. HIBBITTS, D. K. WALKUP, S. L. FRIZZELL, T. E. JOHNSON, B. L. PIERCE, J. B. PIERCE, AND D. C. RUDOLPH. 2020. Searching for rare and secretive snakes: are camera-trap and box-trap methods interchangeable? Wildl. Res. 47:476–484.
- STEEN, D. A. 2010. Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. Herpetol. Conserv. Biol. 5:183–188.
- STEVENSON, D. J., K. J. DYER, AND B. A. WILLIS-STEVENSON. 2003. Survey and monitoring of the eastern indigo snake in Georgia. Southeast. Nat. 2:393–408.
- TODD, B. D., J. D. WILLSON, AND J. W. GIBBONS. 2010. The global status of reptiles and causes of their decline. *In* D. W. Sparling, C. A. Bishop, and S. Krest (eds.), Ecotoxicology of Amphibians and Reptiles, Second edition, pp. 47–67. CRC Press, Pensacola, Florida.
- TUBERVILLE, T. D., J. R. BODIE, J. B. JENSEN, L. LACLAIRE, AND J. W. GIBBONS. 2000. Apparent decline of the southern hog-nosed snake, *Heter-odon simus*. J. Elisha Mitchell Sci. Soc. 116:19–40.
- (USFWS) U.S. FISH AND WILDLIFE SERVICE. 2015. Endangered and threatened wildlife and plants; 90-day findings on 31 petitions. Federal Register 80:37568–37579.
- ——. 2018. Species status assessment report for the eastern indigo snake (*Drymarchon couperi*). Version 1.0 November, 2018. Atlanta, GA.
- 2019. Endangered and threatened wildlife and plants; twelve species not warranted for listing as Endangered or Threatened Species. Federal Register 84:53336–53343.
- Welbourne, D. 2013. A method for surveying diurnal terrestrial reptiles with passive infrared automatically triggered cameras. Herpetol. Rev. 44:247–250.
- WELBOURNE, D. J., A. W. CLARIDGE, D. J. PAULL, AND F. FORD. 2019. Improving terrestrial squamate surveys with camera-trap programming and hardware modifications. Animals 9:388.