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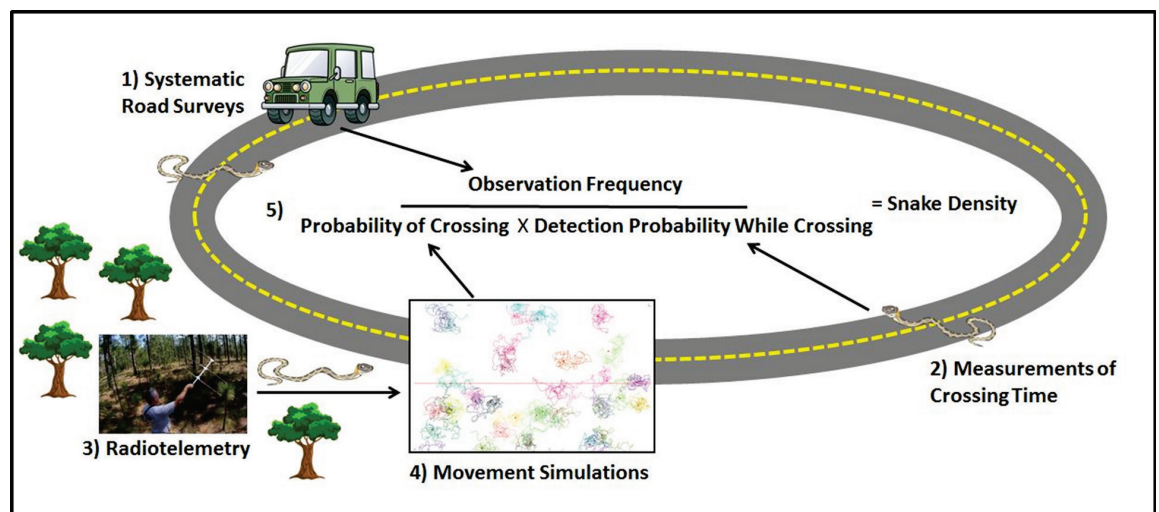


Environmental Security Technology Certification Program (ESTCP)

Estimating the Density of Secretive, At-risk Snake Species on DoD Installations Using an Innovative Approach: IDEASS

Patrick Wolff, Brett DeGregorio, John D. Willson,
Jennifer Mortensen, and Jinelle Sperry

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Estimating the Density of Secretive, At-risk Snake Species on DoD Installations Using an Innovative Approach: IDEASS

Patrick Wolff, Brett DeGregorio, John D. Willson, Jennifer Mortensen, and Jinelle Sperry

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Abstract

The Department of Defense (DoD) expends considerable resources managing and conserving threatened, endangered, or at-risk snake species. Management for these species is often hampered by a lack of basic knowledge regarding their population size and trajectory. The low detectability of most snakes makes it difficult to determine their presence, or to employ traditional methods to estimate abundance. This work demonstrated a novel, simulation-based method, Innovative Density Estimation Approach for Secretive Snakes (IDEASS), for estimating snake density based on systematic road surveys, behavioral observations of snake movement, and spatial movement (radio telemetry) data. This method was used to generate meaningful density estimates for two rare and cryptic snakes of conservation concern, the Southern Hognose and Eastern Diamondback Rattlesnake, at Fort Stewart, Georgia. IDEASS was also applied to an existing dataset to retroactively estimate density of a more common species of management concern, the Western Ratsnake, at Fort Hood, Texas. In all three cases, traditional density estimation via visual surveys and capture-mark-recapture (CMR) failed completely due to lack of captures and recaptures, despite extensive field effort. We conclude that IDEASS represents a powerful tool, and in some cases the only viable method, for estimating density of secretive snakes.

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Preface

Funding for this demonstration was provided by the Environmental Security Technology Certification Program (ESTCP) under Resource Conservation and Resiliency (RC) Project RC-201707, “Estimating the Density of Secretive, At-risk Snake Species on DoD Installations Using an Innovative Approach: IDEASS.” The ESTCP program manager was Dr. Kurt Preston.

This work was conducted by the Ecological Processes Branch (CNN), Installations Division (CN), Construction Engineering Research Laboratory (CERL), Engineer Research and Development Center (ERDC). Dr. Chris Rewerts was Chief, CEERD-CNN, and Dr. George Calfas was Chief, CEERD-CN. The associated Technical Director was Alan Anderson, CEERD-CZT. The Acting Deputy Director of ERDC-CERL was Ms. Michelle Hanson and the Acting Director was Dr. Kumar Topudurti.

COL Teresa A. Schlosser was Commander of ERDC, and Dr. David W. Pittman was the Director.

We thank the ESTCP for funding this project. We also thank the ESTCP staff, especially Dr. Kurt Preston, for support throughout this project. Roy King and Larry Carlisle of Fort Stewart were valued partners on multiple critical components of this demonstration/validation project. Shannon Pittman was instrumental in conceptual and computational design of IDEASS methodology and advised on numerous aspects of the project. Dirk Stevenson generously shared his deep knowledge of herpetofauna at Fort Stewart and contributed assistance in the field. Jeff Holmes and the Amphibian and Reptile Conservancy generously shared extensive radio telemetry data for Eastern Diamondback Rattlesnakes from Francis Marion National Forest. Terry Norton and Amanda Harris conducted transmitter implantation surgeries and advised on various aspects of the project. We would like to thank the many excellent graduate students, technicians, and volunteers who assisted with this project: Annamarie Saenger, Nick Schiltz, Alex Meinders, Sergi Picas, Jackie Guzy, Anant Deshwal, Pooja Panwar, Max Carnes-Mason, Matt Moore, and Meredith Swartwout.

Executive Summary

Introduction

The U.S. Department of Defense (DoD) spends considerable resources managing and conserving a number of threatened, endangered, or at-risk snake species. Management for these species is often hampered by a lack of basic knowledge regarding their population size and trajectory thus managers tasked with recovering these populations currently do not have an appropriate tool to provide them with the primary, yet basic, starting point to conservation: current abundance. The low detectability of most snake species makes it difficult to determine if they are even present at a particular site, let alone to quantify metrics related to their abundance or population density. Unfortunately, species with low individual detection probabilities are also often species that are of greatest conservation concern. Traditional methods such as capture-mark-recapture (hereafter, CMR) are the most frequently employed methods of quantifying snake population sizes. However, CMR cannot overcome the low detectability of most snake species and even when feasible, requires considerable investments of time and resources. Here, we demonstrate implementation of a novel, simulation-based method, Innovative Density Estimation Approach for Secretive Snakes (IDEASS) for estimating detection probabilities and densities of secretive terrestrial snakes using systematic road surveys, behavioral observations of snake movement, and spatial movement (radio telemetry) data.

Objectives of the demonstration

The objective of this project was to demonstrate how IDEASS can integrate spatial movement, road crossing behavior, and systematic road survey data to estimate densities of secretive snakes on DoD installations. Specifically, we studied two cryptic species of conservation concern, the Eastern Diamondback Rattlesnake and Southern Hognose, at Fort Stewart, Georgia (Figure ES-1) and aimed to directly compare the effectiveness of IDEASS to traditional CMR techniques based on VES. A second objective was to demonstrate how the IDEASS approach can make use of existing data sources to generate density estimates cost-effectively and retroactively, using the case study of WRS at Fort Hood, Texas.

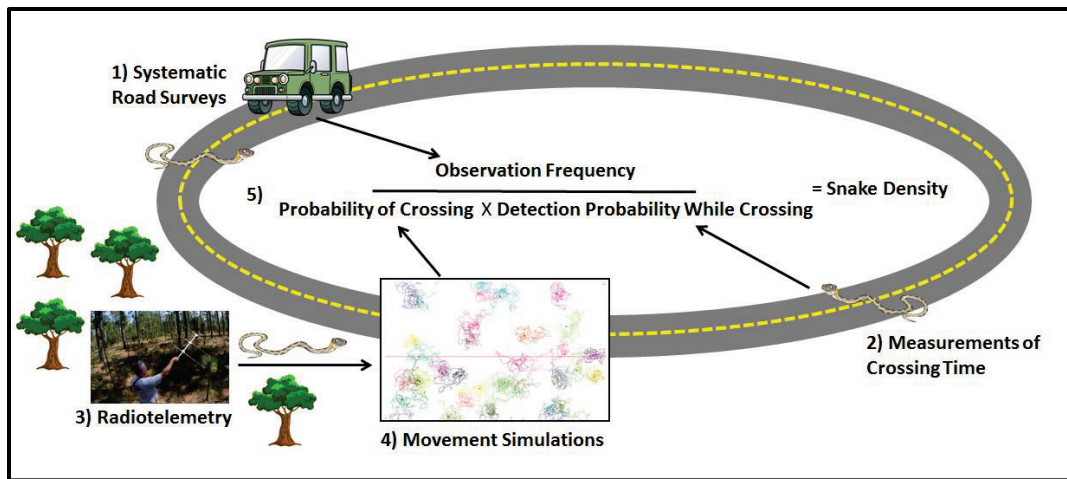
Figure ES-1. Three focal species and data sources used for demonstration of the IDEASS approach. FS = Fort Stewart; FH = Fort Hood; NC = North Carolina; SC = South Carolina.

			
	Eastern Diamondback Fort Stewart (FS) South Carolina (SC)	Southern Hognose Fort Stewart (FS) & North Carolina (NC)	Western Ratsnake Fort Hood (FH)
Road Surveys	New (FS)	New (FS)	Existing (FH)
Road Behavior	New (FS)	Existing (NC)	New (FH)
Radiotelemetry	New (FS) + Existing (SC)	Existing (NC)	Existing (FH)
Capture-mark-recapture (CMR)	New (FS)	New (FS)	Existing (FH)

Technology description

The IDEASS approach combines behavioral observations of road crossing behavior (crossing speed), effort-corrected road survey data, and simulation-based modeling of spatial movement to estimate population densities (Figure ES-2). Radiotelemetric data are collected to quantify movement metrics (frequency, distance, and direction of movement in relation to home range center and roads). These movement data are then used to parameterize individual-based movement models in a biased correlated random walk framework (Turchin 1998, Crone and Schultz 2008) to estimate the frequency with which individuals cross roads. Next, information on survey vehicle speed and snake crossing speed are used to determine the probability of detecting a snake, given that it crosses the road transect during a survey. Snake encounter frequencies during systematic road surveys are then interpreted in light of detection probabilities and simulation model results to estimate snake densities and to assess various factors likely to affect encounter rates. By combining all of these pieces in an IDEASS model, one can calculate individual detection probabilities and population density for even very secretive, rarely encountered species that are not tractable to CMR approaches. Because road collecting is the primary method of capture for many rare and secretive snake species (Willson 2016), the adaptability and applicability of IDEASS makes it a robust and adaptable approach for snake conservation and management.

Figure ES-2. Diagram illustrating the conceptual organization and data sources used to estimate density of secretive snakes from road surveys using the IDEASS method.



Performance assessment

Cryptic Upland Snakes of Conservation Concern at Fort Stewart, Georgia: We demonstrated the IDEASS methodology for two rare and cryptic upland snake species at Fort Stewart, Georgia. The first species is the Southern Hognose Snake (*Heterodon simus*; SHS), a relatively small highly fossorial species that is thought to be in decline due to apparent disappearances from large areas of its historical range (Tuberville et al. 2000), and that is currently petitioned for listing under the Endangered Species Act (USFWS 2020). Despite extensive apparently suitable habitat, SHS are apparently exceedingly rare at Fort Stewart; their presence has been documented in fewer than 10 historical records. Despite the fact that several researchers have conducted radio telemetry on the SHS (Willson et al. 2018),¹ the only information on their abundance is our previous implementation of IDEASS for this species based on data from North Carolina (Willson et al. 2018). The second focal species is the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*; EDR), the largest North American viper. EDR have declined across their range and are also petitioned for listing under the Endangered Species Act (USFWS 2020). Both species are diurnal and are most frequently encountered crossing roads in the late summer and fall. SHS are so secretive that virtually nothing is known about their abundance or population size. Under these circumstances, this species provides a case study for which IDEASS represents the only viable method for obtaining these important data. Although also secretive, EDR

¹ Also J. Beane, North Carolina State Museum of Natural Sciences, unpublished data; and T. Tuberville, Univ. Georgia, unpublished data.

are more detectable via VES and have been studied at the population level using traditional methods, such as CMR (Means 2017). Thus, EDR provide a potential opportunity to directly compare density estimates generated with IDEASS to those generated using CMR, and thus to validate the precision and cost of IDEASS relative to traditional approaches.

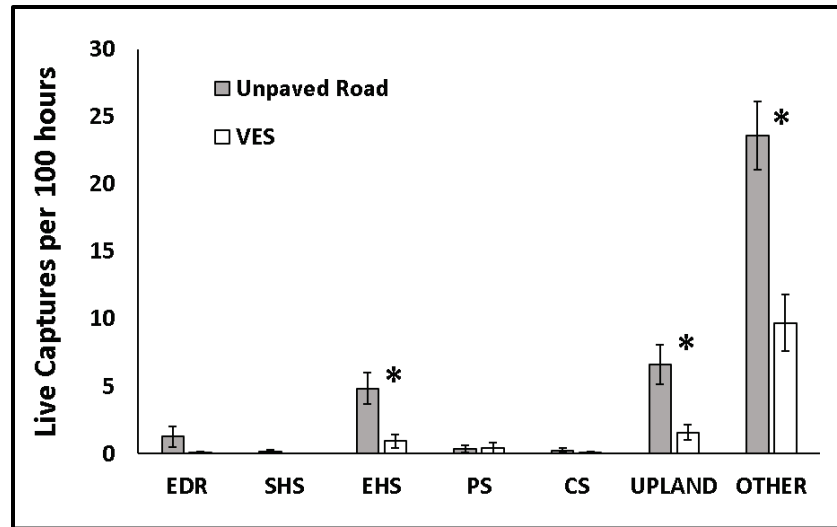
Our field data collection at Fort Stewart consisted of four components: (1) extensive systematic diurnal road surveys of paved and unpaved road transects bisecting habitat suitable for our target species, (2) radio telemetry of EDR, (3) behavioral observations of natural road crossing events to quantify snake crossing speeds, and (4) extensive systematic VES surveys to attempt validation of our density estimates through traditional CMR. We supplemented our field data with radio telemetry data for EDR from similar habitats in South Carolina and with radio telemetry and road crossing speed data for SHS from North and South Carolina (Figure ES-1).

Over three field seasons, we conducted 313 diurnal road surveys, totaling 270 hrs and 10,286 miles, on two paved road transects, and 564 surveys, totaling 570 hrs and 12,082 miles, on four unpaved road transects located in longleaf pine/sandhill habitats at Fort Stewart, Georgia. In total, road surveys yielded 211 live snake captures, only a minority of which were of rare upland species such as EDR, SHS, Eastern Hognose, Harlequin Coralsnake, and Florida Pinesnake. Surveys of paved road transects resulted in collection of more than 100 road-killed snakes, but very few live snake captures, and only one capture of a rare upland species, an Eastern Hognose. Surveys of unpaved road transects yielded much higher captures of snakes overall, including upland species. A total of six live EDR were captured on surveys of unpaved roads, as well as one live and one road-killed SHS. These SHS captures were the first records of this species at Fort Stewart in over a decade.

Concurrent with road surveys, we conducted 230 diurnal VES in the same habitats at Fort Stewart. These surveys were split between standardized, repeated, 2 person-hours VES of four, 25-ha CMR plots (18-28 surveys per plot), and 140 opportunistic VES, totaling 598 hrs, in habitat suitable for our target species across the base. VES of CMR plots were ineffective, yielding only 20 snake captures across 180 survey-hours and no captures of EDR or SHS. Opportunistic VES were somewhat more effective overall but resulted in mostly captures of non-target species. Only one EDR was captured on a VES and, critically, no marked snakes of any species were recaptured. Direct comparison of catch-per-unit-effort (CPUE) between

VES and road surveys of unpaved transects revealed substantially higher capture rates for road surveys (Figure ES-3).

Figure ES-3. Comparison of average catch-per-unit-effort (CPUE) of snakes between road surveys and visual encounter surveys (VES). Bars represent means across plot/transect-years $\pm$ 1 SE. Statistically significant differences (t-test, $p < 0.05$) are indicated with an asterisk (*). EDR = Eastern Diamondback Rattlesnake, SHS = Southern Hognose Snake, EHS = Eastern Hognose, PS = Pinesnake, CS = Harlequin Coralsnake, UPLAND = previous species combined, Other = all other snakes combined.



Capture rates per 100 survey-hours, averaged across plot/transect-years, were higher for all rare upland species, except for Pinesnakes, for which captures were similar between the methods. These differences were statistically significant for Eastern Hognose (t-test, $t = 2.06$, $df = 14.98$, $p = 0.008$), all upland species grouped together (t-test, $t = 3.22$, $df = 14.185$, $p = 0.006$), and all other snakes species (t-test, $t = 4.23$, $df = 20.70$, $p < 0.001$). Differences in capture rates of other rare upland species failed to achieve statistical significance due to small sample size (t-test, all $p > 0.05$). However, average CPUE of EDR was over eightfold higher for road surveys (0.78 captures per 100 survey-hours) than for VES (0.09 captures per 100 survey-hours).

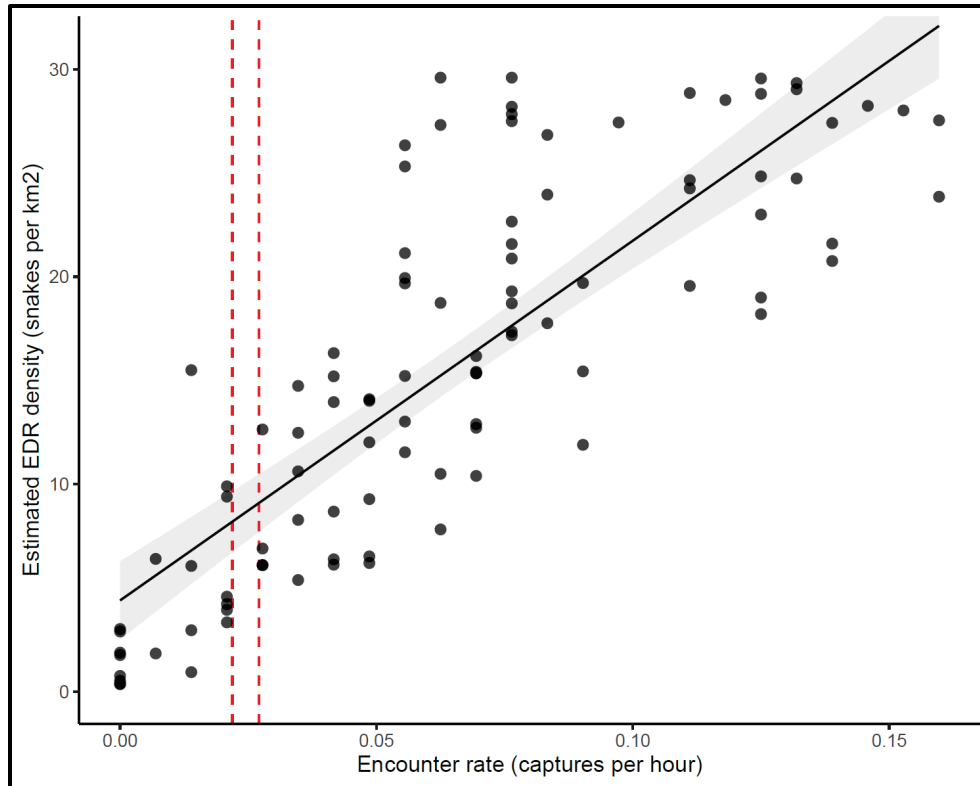
We tracked six individual EDR at Fort Stewart via radio telemetry and supplemented our data with 16 EDR tracked in similar habitats in South Carolina. The combined dataset represented 35 snake-years of data, with a mixed sex ratio (9M:13F) and an average of 33 (range This = 6-85) re-sightings per individual during our focal season of July to November. From these data, we calculated step size (distance between successive re-sightings), and path straightness (turning angle) and orientation

parameters and examined potential differences between the sexes in movement parameters. Examination of movement distances revealed the need to discretize movement data differently for males and females. Also, females exhibited smaller mean home range sizes, prompting us to alter female orientation parameters to best match home range size of simulated snakes to our empirical measurements of home range size. Our parameterization resulted in simulated males moving more frequently and randomly across the landscape than females, resulting in larger home ranges, an expected pattern of movement for this species. We also tested for road behavior (attraction to, or avoidance of roads) random walk paths based on each snake's movement data and comparing the number of observed road crossings to the frequency distribution of crossing events for simulated paths. We found some evidence of road avoidance in five of 21 EDR tested, but those patterns appeared to be related to avoidance of large, paved roads and extensive open habitats. Because we did not detect any avoidance of unpaved roads, we chose to have EDR respond neutrally to the simulated road transect.

We timed six natural crossing events of EDR along our unpaved survey transects at Fort Stewart and used a previously published dataset of nine timed natural road crossing events for SHS collected using the same methodology (Willson et al. 2018). Extrapolated to the mean width of our unpaved road transects, mean crossing time was 2.29 (0.41) minutes for EDR and 11.65 (5.45) minutes for SHS.

Simulation of our fully parameterized individual-based movement model for EDR yielded a predicted relationship between encounter rate during road surveys and density (Figure ES-4). By including a stochastic observation process within the simulation, this relationship also estimated a confidence interval (CI) reflecting variation in numerous model parameters, stochasticity, and uncertainty resulting from infrequent detections relative to survey effort. We plotted the average encounter frequencies of EDR from our two unpaved road transects where that species was detected, yielding estimated EDR densities of 9.10 (95% CI = 7.69-10.50) and 8.20 (95% CI = 6.71-9.69) EDR per km² along those transects.

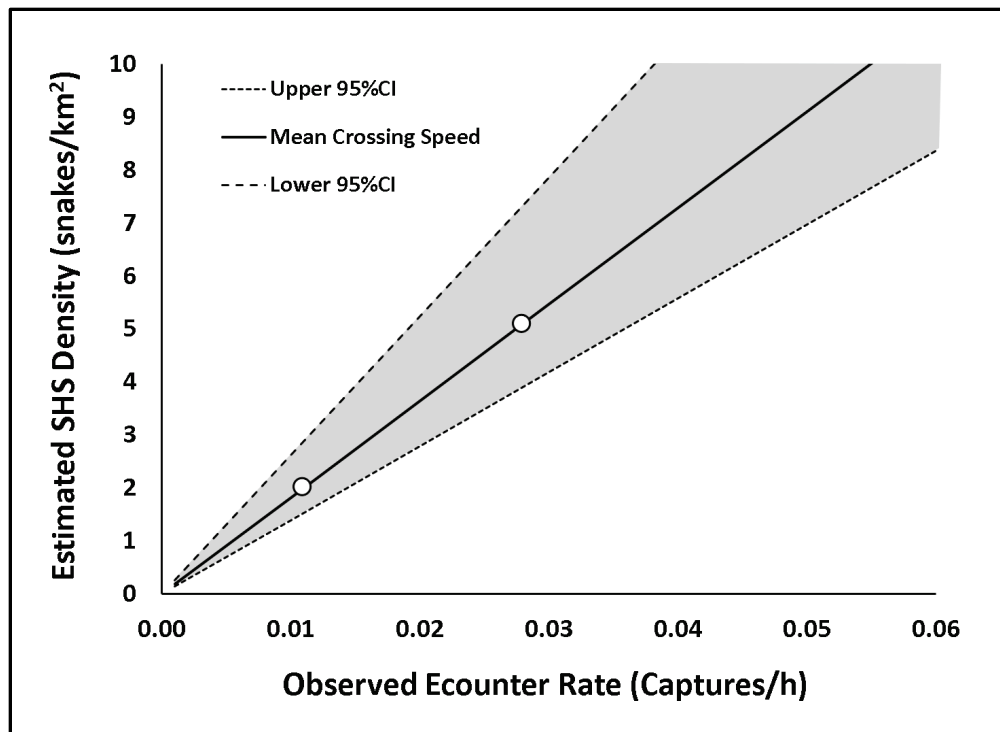
Figure ES-4. Relationship between encounter rate and estimated density of Eastern Diamondback Rattlesnakes (EDR), bounded by the 95% CI, based on 100 simulations of varying densities. Vertical red lines indicate mean observed encounter frequencies along our two unpaved road transects where EDR were captured (0.027 and 0.021 live EDR per survey-hour), which correspond to estimated densities of 9.10 and 8.20 EDR per km² along those transects, respectively.



By design, we used a previously published IDEASS model for SHS (Willson et al. 2018) to estimate frequency of road crossing by SHS, in which we needed only to alter the detection process to reflect the road widths and average survey vehicle speeds for our transects at Fort Stewart. We then used this relationship to calculate an estimated density corresponding to observation rates of SHS along our survey transects. Our road surveys at Fort Stewart only yielded one live SHS capture, located on our eastern unpaved road transect in the southwestern portion of the base. Matching this encounter frequency to the encounter-density relationship generated with IDEASS yields an estimated average SHS density along our southeastern unpaved road transect of 2.0 per km² (0.020 ha⁻¹), with a range of 1.5–2.8 per km² across the 95% CI of snake crossing speed. Correcting our effort to the relatively small region along our transect where we detected SHS (three individuals; the only records for SHS on Fort Stewart in at least a decade), raises the density estimate within the small area occupied by SHS to 5.1 (95% CI: 3.9 – 7.3) per km². Given the extremely restricted range of

SHS on base and the low-density estimate we obtained, it is likely that the total adult population size of SHS on Fort Stewart is <100 individuals and may be as low as 30 adult individuals if the isolated cluster of observations we identified within a ca. 6 km² area is indeed the only extant population on base (Figure ES-5).

Figure ES-5. Relationship between encounter rate and estimated density of Southern Hognose Snakes (SHS), bounded by the 95% CI of observed road crossing speeds, based on IDEASS models modified from Willson et al. 2018. Open circles indicate estimated densities at the mean observed encounter frequency (0.011 live snakes per hour) along the one unpaved road transect at Fort Stewart where SHS were captured and within the constrained ~4 km section where all SHS records occurred. Thus, mean estimated density of SHS is 2.0 (95% CI: 1.5 – 2.8) per km² along the entire transect or 5.1 (95% CI: 3.9 – 7.3) snakes per km² within the apparently restricted area of occupied habitat.



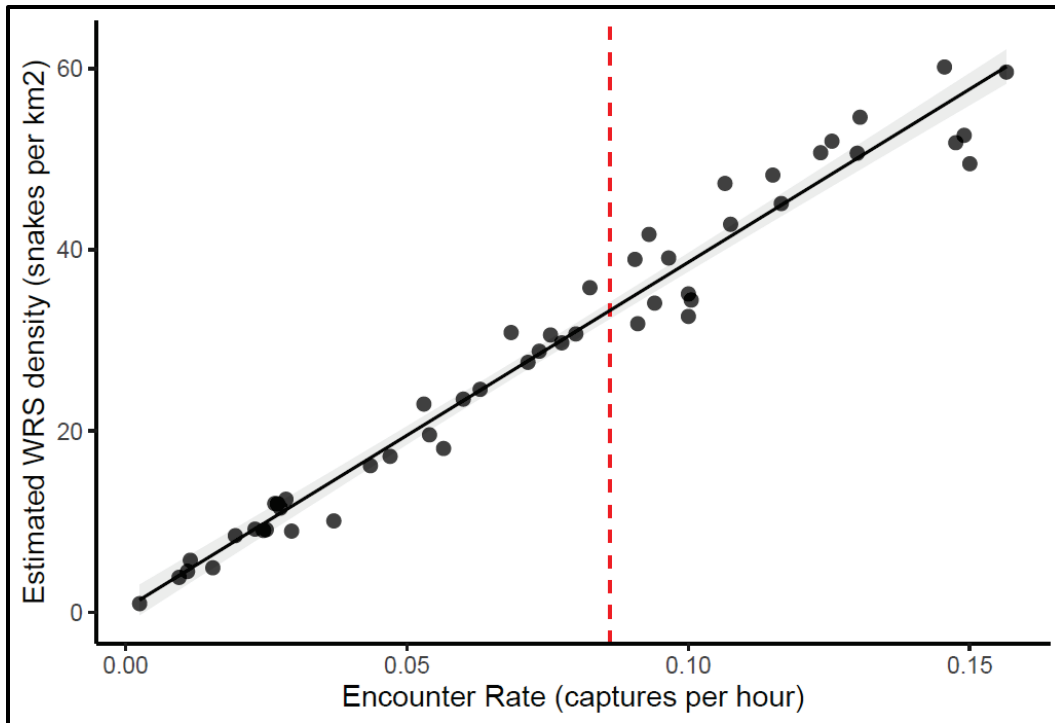
A total of 598 person-hours across 230 VES yielded only a single EDR capture and zero detections of SHS. With no recaptures, CMR density estimation was not possible. Although we could not directly validate our density estimates generated with IDEASS against those from CMR, our estimates are not far below the only two comparable (inland locality) density estimates that are available for this species: 11.2 per km² for Pinellas Co., Florida and 12 per km² from Tall Timbers Research Station, Florida (Means 2017).

Western Ratsnakes at Fort Hood, Texas: A further objective of our research was to demonstrate how IDEASS can be retroactively applied to existing datasets to generate more meaningful density estimates than those produced by traditional methods. To accomplish this objective, we took advantage of a robust dataset of WRS (*Pantherophis obsoletus*; WRS) collected on Fort Hood, Texas from 2004 to 2009 (Sperry et al. 2008, Sperry et al. 2009). WRS are not of conservation concern and are relatively common at Fort Hood but are of management interest because they are primary nest predators of two imperiled bird species. Our dataset for Fort Hood included 249 hrs of road surveys across 102 nights within a focal activity season of 14 April to 30 June, as well as data from 44 WRS radio-tracked over multiple years. We were able to generate a robust relationship between road encounter frequency and density for WRS using IDEASS (Figure ES-6), yielding a density estimate of 33.3 (95% CI = 32.4-34.2) WRS per km² at our mean observed encounter frequency of 0.086 WRS per survey-hour. Extensive, but opportunistic, surveys for WRS at Fort Hood using a wide array of field techniques yielded 119 WRS captures, but zero recaptures. Thus, CMR density estimation failed, even for this relatively common species.

Cost assessment

We assessed the cost of IDEASS and compared it to traditional VES/CMR based on data from our field work at Fort Stewart. We considered two scenarios: (1) EDR, a low-density and extremely cryptic species, and (2) Eastern Hognose, a much more common (higher density), yet still highly cryptic upland snake species. Based on our successful application of IDEASS to EDR with six captures, we assumed a minimum sample size of six snake captures needed for IDEASS to fully succeed. Generating a density estimate using CMR requires a number of snake encounters to capture and mark individuals and then a number of subsequent recaptures to evaluate the ratio of unmarked snakes to marked snakes. We conservatively set a target of 20 snake encounters as a minimum number needed to employ CMR. However, there is no guarantee that this sample size would yield the critical number of recaptures needed to permit a CMR density estimate, and most successful snake CMR studies have involved sample sizes greater than our threshold of 20 by an order of magnitude or more.

Figure ES-6. Relationship between encounter rate and estimated density Western Ratsnakes (WRS), bounded by the 95% CI, based on 100 simulations of varying densities. Vertical red lines indicate mean observed encounter frequencies along our survey transect at Fort Hood (0.08 live snakes per hour), which corresponds to a mean estimated density of 33.3 WRS per km².



We estimated a cost of approximately \$42,000 to successfully implement IDEASS for six snakes of a cryptic species like EDR and under \$30,000 for a more common species such as the Eastern Hognose. This included the cost associated with two field seasons of radio telemetry, which was fixed for the two species and the cost associated with capturing six individuals via road surveys, which was dramatically higher for EDR (\$2,689 per capture) than for Eastern Hognose (\$494 per capture). In comparison, cost of CMR was driven by labor associated with VES surveys, but a significant amount of fieldwork was needed to capture a conservative minimal sample size of EDR (20 individuals) for use of CMR, yielding a total estimated cost in excess of \$180,000. The estimated cost for Eastern Hognose was substantially lower (\$45,300) but was still approximately 50% higher than the cost of IDEASS, and there is no guarantee that 20 individuals would yield enough recaptures for CMR to be successful.

Overall, the need to recapture individuals makes CMR substantially more expensive than IDEASS and indeed CMR may not be viable for species with detectability or density as low as EDR.

Implementation issues

Our biggest challenge during this demonstration was site access. Despite the fact that we selected study sites that were away from high-use areas of the base, access restrictions and training activities often prevented us from accessing radio-tagged snakes and surveying VES plots and pre-established road transects on a systematic or randomized basis. This problem was exacerbated by the fact that our road routes often bordered or transected several base compartments and on any given day it was common for some of those compartments to be open and others to have accesses restricted. For such an approach to succeed, regular site access is absolutely critical. This is especially true for radio telemetry because fine-scale movement data are needed for IDEASS modeling.

We also chose to demonstrate this technique on a species that was far less common than anticipated. On southeastern maritime forests and barrier islands, EDR can occur at high densities and be relatively visible via VES (Means 2017). Because of the proximity of Fort Stewart to the coast and the high quality of its longleaf pine ecosystems, we expected that EDR would be relatively tractable to both road encounters and VES. We were wrong. EDR on Fort Stewart occur at low densities, frequently exploit difficult to search habitats, such as palmetto thickets, and spend considerable time in Gopher Tortoise and Armadillo burrows, where they cannot be seen. Thus, we generated far fewer encounters than we anticipated. We were still able to generate sufficient data to generate independent density estimates for two of our road transects with IDEASS, but we were unable to validate our estimates through direct comparison with those generated using CMR. Thus, a direct comparison of these approaches would still be highly beneficial but would need to focus on a situation where the focal species is more common or conspicuous (see Appendix B).

We also generated less radio telemetry data than we had anticipated. This was a direct consequence of our limited EDR encounters. Robust radio telemetry data are integral to accurately parameterizing and validating movement models. The combination of fewer study animals and limited access to track them caused problems. Fortunately, we were able to elicit data from colleagues studying the same species at nearby sites with similar habitats. These data were very important in our ability to demonstrate the IDEASS approach.

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1 Introduction

1.1 Background

The U.S. Department of Defense (DoD) spends considerable resources managing and conserving a number of threatened, endangered, or at-risk snake species. Management for these species is often hampered by a lack of basic knowledge regarding their population size and trajectory. Thus, managers tasked with recovering these populations currently do not have an appropriate tool to provide them with the primary, yet basic, starting point to conservation: current distribution and abundance. Both distribution and abundance estimation generally rely on a thorough understanding of detection probabilities. Without data on species' detection probabilities (i.e., the likelihood that any individual of a given species is detected in a given survey unit), the effort required to determine if a species occurs in a particular area is unknown and it is impossible to differentiate between true and false absences with statistical confidence. Likewise, knowledge of individual detection probabilities (i.e., the likelihood that a specific individual organism is detected in a given survey unit) is critical for estimation of species' abundances or densities. Several methods are traditionally used for estimating animal densities, including distance sampling, removal sampling, and most commonly, capture-mark-recapture (CMR) techniques (Rodda 2012). For species with extremely low detection probabilities or in situations where traditional techniques cannot be used, estimation of density is often impossible (Dorcas and Willson 2009). Unfortunately, species with low individual detection probabilities are often species that are of greatest conservation concern (Willson 2016).

Among reptiles, snakes are particularly secretive, and the density and trends of most snake populations remain unknown (Parker and Plummer 1987, Dorcas and Willson 2009, Steen 2010, Todd et al. 2010). Recently, snakes have gained recognition as important components of vertebrate biodiversity and for the critical roles they play as predators and prey in many ecosystems (DeGregorio et al. 2014, Steen et al. 2014, Willson and Winne 2016). Thus, the need for effective snake conservation has become more apparent (Gibbons et al. 2000, Todd et al. 2010). Numerous snakes are now listed or proposed for listing under state or federal law and thus many stakeholders are required to consider snakes in their management

plans. Although snakes can be abundant, many species are extraordinarily secretive and thus infrequently encountered (Dorcas and Willson 2009, Steen 2010). For example, recent experimental research has demonstrated that the detection rates for some snakes can be lower than 1%—that is, for every one snake found, investigators passed by more than 99 that remained undetected (Dorcas and Willson 2013). Without an understanding of individual detection probability, it is impossible to know whether low capture rates or failed surveys reflect true rarity, or simply secretive behavior. Thus, the secretiveness (or low detectability) of most snake species makes it extremely difficult to determine even if they are present at a particular site (Gibbons et al. 1997), let alone to determine the size or density of the population (Steen 2010). Lack of density information limits our ability to assess the status or trends of most snake populations (Dorcas and Willson 2009).

Estimating densities or detection probabilities typically requires intensive CMR studies, which are not feasible for many snake species (Dorcas and Willson 2009, Willson 2016). However, many secretive snake species can be effectively captured using road surveys (Enge and Wood 2002, Willson 2016) and many are frequently studied using radio telemetry (e.g., Steen and Smith 2009, Miller et al. 2012). Radio telemetry studies provide considerable insight into the behavior and spatial ecology of secretive snake species (Kingsbury and Robinson 2016). Knowledge of movement patterns and behaviors gleaned from radio telemetry studies can be used to parameterize individual-based models that simulate animal movement (Schwarzkopf and Alford 2002, Rupp and Rupp 2010). These types of individual-based movement models have been used to predict population responses to conservation actions, habitat loss, road effects, and to estimate the effects of landscape features on connectivity of populations (Piou et al. 2007, Wang and Grimm 2007, Coulon et al. 2015, Allen et al. 2016, Heinrichs et al. 2016). A basic random walk model defined by movement distance and turning angle distribution can be modified to incorporate behaviors such as home range maintenance or attraction to or avoidance of landscape features, including roads (Morales et al. 2004, McClintock et al. 2012). For example, Pauli et al. (2013) designed an individual-based model that modifies a basic random walk to incorporate multiple behavioral states between which individuals shift probabilistically based on factors such as life stage, past experiences, and the landscape through which they are moving. Random walk-based simulation models such as these

provide an opportunity to predict the likelihood of a snake crossing a road, and thus a method for relating observation rates during road surveys to snake abundance.

1.2 Objective of the demonstration

The objectives of this project were to demonstrate how the Innovative Density Estimation Approach for Secretive Snakes (IDEASS) can integrate spatial movement, road crossing behavior, and systematic road survey data to calculate individual detection probabilities and population densities of two at-risk snake species on DoD installations. Specifically, we aimed to directly compare the effectiveness of IDEASS to traditional CMR techniques based on visual encounter surveys (VES) and CMR. This direct comparison provided us the opportunity to conduct a cost comparison between the two technologies. A second objective was to demonstrate how IDEASS can make use of existing datasets to generate density estimates cost-effectively and retroactively.

1.3 Regulatory drivers

All federal land management agencies must comply with federal environmental laws and regulations. This demonstration specifically addresses the compliance challenges posed by the Endangered Species Act (ESA) of 1973. Protection of threatened or endangered reptiles under the ESA varies depending on whether the species is located on federal or private property. For listed species occurring on federal properties, section 7A of the ESA requires that land managers must consult with the U.S. Fish and Wildlife Service (USFWS) to ensure that proposed land-use actions result in “no-take” of the listed species. The result of these consultations is often a Biological Opinion in which the land managers and USFWS agree on actions to minimize impacts on methods of monitoring to ensure that impacts are avoided or minimized. Often, Biological Opinions rely on an understanding of the population size or density of target species, data that are often missing for secretive wildlife species such as snakes. Noteworthy examples of poorly understood snakes that are federally listed include the Puerto Rican Boa (*Epicrates inornatus*), Eastern Indigo Snake (*Drymarchon couperi*), Louisiana and Black Pine Snake (*Pituophis ruthveni* and *P. melanoleucus lodingi*), Eastern Massasauga (*Sistrurus catenatus*), and Mexican Gartersnake (*Thamnophis eques*) as well as dozens of additional species that are petitioned for listing or are protected at the state level. The proposed demonstration provides a

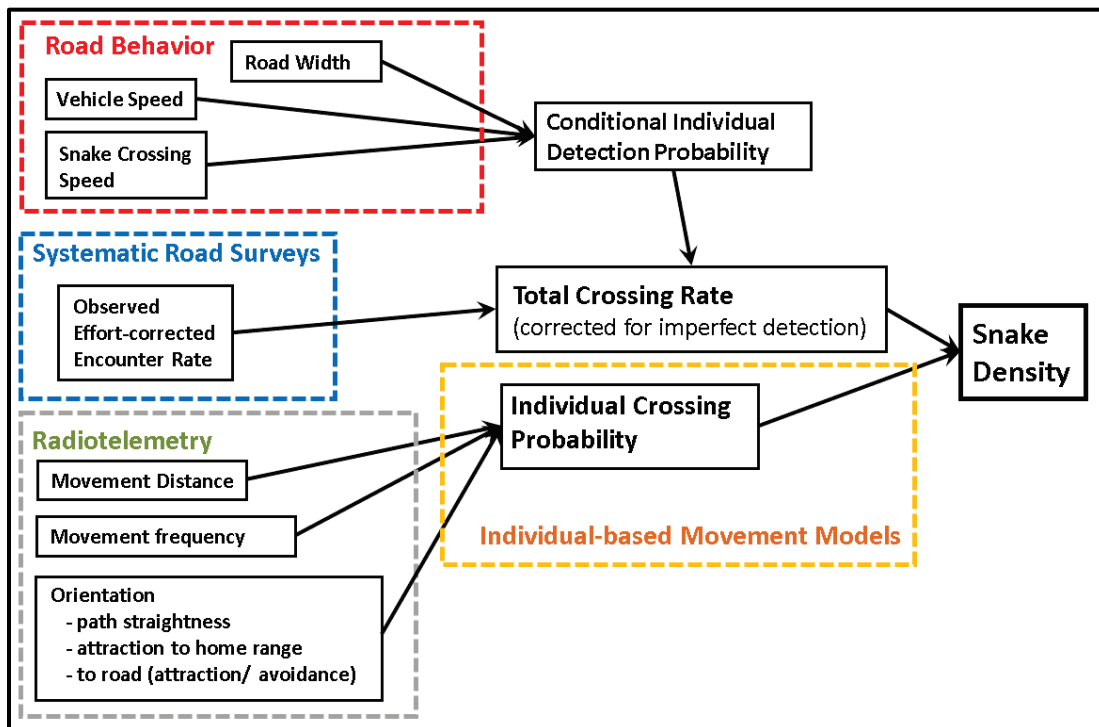
tool for addressing this data gap, focusing on two secretive species occurring on installations in the Southeast that have been petitioned for federal listing: the Eastern Diamondback Rattlesnake (*Crotalus adamanteus*) and Southern Hognose (*Heterodon simus*).

2 Technology/Methodology Description

2.1 Technology/methodology overview

IDEASS (Willson et al. 2018, see Figure 1) combines behavioral observations of road crossing behavior (crossing speed), effort-corrected road survey data, and simulation-based modeling of spatial movement to estimate population densities. Radiotelemetric data are collected to quantify movement metrics (frequency, distance, and direction of movement in relation to home range center and roads). These movement data are then used to parameterize individual-based movement models in a biased correlated random walk framework (Turchin 1998, Crone and Schultz 2008) to estimate the frequency with which individual snakes cross roads. Next, information on survey vehicle speed and snake crossing speed are used to determine the probability of detecting a snake, given that it crosses the road transect during a survey (conditional capture probability). Snake encounter frequencies during systematic road surveys are then interpreted in light of detection probabilities and simulation model results to estimate snake densities and to assess uncertainty in those estimates.

Figure 1. Conceptual diagram illustrating the IDEASS method for estimating density of secretive snakes from systematic road survey data.



The IDEASS model originated in 2013 from the critical need to develop a scientifically justifiable method to estimate the density of invasive Burmese Pythons in Everglades National Park, Florida. However, it became clear that the method was applicable to many species that are of conservation concern to state and federal agencies, including DoD. To date, IDEASS has been developed and demonstrated to quantify densities of Southern Hognose Snakes (SHS) in the Sandhills region of North Carolina (Willson et al. 2018) and Burmese Pythons in Everglades National Park, Florida. The IDEASS framework can be widely applicable to snakes (and other wildlife species) for which spatial ecology data, road encounter frequency, and road crossing behavior are known or can be collected.

To implement the IDEASS method (Figure 1), three types of raw data are needed: (1) systematic road survey data, which provide encounter frequencies that are eventually translated to a density estimate, (2) spatial movement data, generally collected via radio telemetry, that are needed to parameterize individual-based spatial movement models, and (3) data on the detectability of snakes on roads, including snake crossing speed, average vehicle speed, and widths of roads along the survey route. Having generated the three primary empirical data sources needed to implement IDEASS, the density estimation procedure consists of four steps: (1) GIS analysis and movement modeling to estimate road crossing frequency, (2) calculation of detection probability of snakes crossing roads, (3) density estimation, and (4) sensitivity and uncertainty analyses.

First, spatial movement data gathered using radio telemetry are analyzed (GIS and/or packages in Program R) to generate movement metrics to parameterize individual-based spatial movement models. This involves using the coordinates from each radio telemetry event to calculate Euclidean step sizes (distances between consecutive locations), movement frequency, path straightness and orientation to home range center (turning angle), and landscape elements including different habitat types, edges, and paved and dirt roads (Willson et al. 2018). Additionally, simulations are conducted to determine the optimal landscape size for simulations (A), such that snakes with home range centers at the edge of the landscape have a negligible ($<0.005\%$) chance of encountering the road (Willson et al. 2018). The resulting data are used to parameterize individual-based movement models (Program R) in a biased random walk framework and

conduct extensive simulations (Willson et al. 2018) to estimate the frequency with which individual snakes cross roads (ρ).

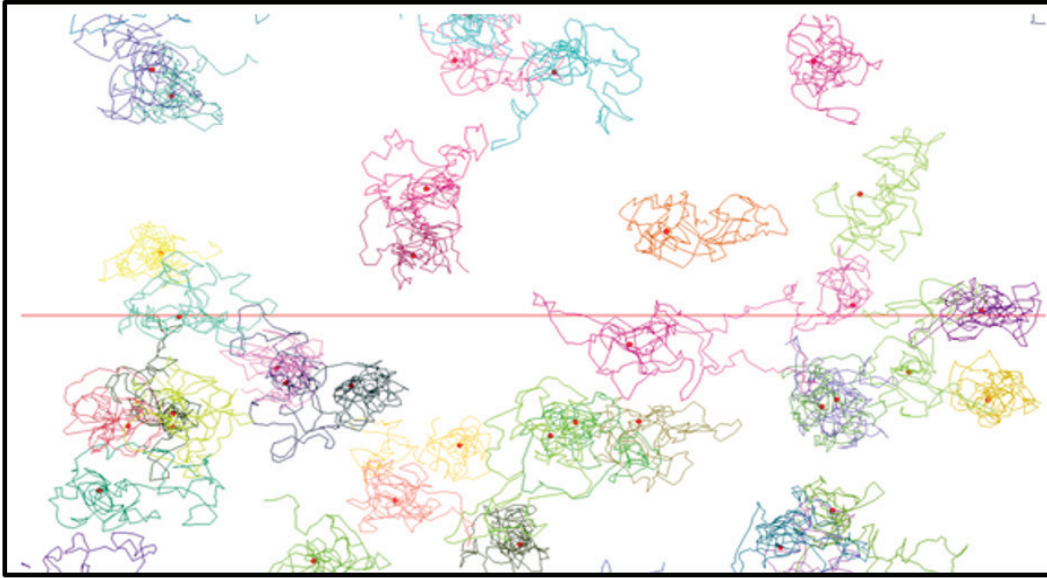
Once movement parameters are generated, IDEASS uses a simple individual-based model (Program R) to simulate snakes moving within a home range in order to estimate the daily probability that a snake will cross a road (Willson et al. 2018). Movement is modeled as a biased correlated random walk (BCRW) in continuous space with a wrapped Cauchy distribution of turning angles (Zollner and Lima 1999) and lognormal distribution of step sizes based on an analysis of the radio telemetry data. The bias parameter (β) represents the degree to which snakes choose a movement bearing according to the center of the home range and the bearing toward the road. The bearing that the animal chose at each time step is a weighted average of the bearing of the previous step (plus random error drawn from the wrapped Cauchy distribution) and the bearing toward the home range center (or road), following:

$$\varphi_t = (1 - \beta)(\varphi_{t-1} + \gamma_t) + \beta\delta_t \quad (1)$$

Where φ_t is the bearing at time t , β is the strength of bias toward home range center or road, γ_t is the turning angle drawn from the wrapped Cauchy distribution at time t , and δ_t is the bearing toward the home range center at time t (Crone and Schultz 2008, Barton et al. 2009). Snake movement distances are randomly generated from a lognormal distribution, and movement bearings are stochastic but also determined both by the location of the snakes' home range center and the location of the road. Each individual is assigned a random home range center within a buffer (landscape) of width (A) surrounding a linear road bisecting a uniform landscape and is given an initial movement bearing from a uniform distribution (1-360 degrees). The parameter (A) is defined on a species-by-species basis, such that the model has a high likelihood of simulating all snakes with a chance to cross the road. However, the estimated density is generally insensitive to simulated landscape size (Willson et al. 2018). Strength and direction (attraction, avoidance, or neutral) of road behavior is examined by comparing road crossing rates of simulated paths to observed crossings, and β adjusted to provide the best match to empirical data.

The movement model is iterated with a 1-day timestep (Figure 2) to calculate daily road crossing probability. This value is then divided by the diel activity period of the snake species (hours per day when snake activity occurs) to calculate hourly individual road crossing probability (ρ).

Figure 2. Example image of movement paths of simulated snakes generated using an individual-based spatial movement model parameterized using snake radiotelemetric data. Paths crossing the red horizontal line represent road crossing events.



Finally, empirical data from snakes timed naturally crossing roads are used to calculate the average time it takes a snake to cross a paved or unpaved road (V_{snake} [min]) by multiplying the mean snake speed for each road type by the mean road width along the survey route.

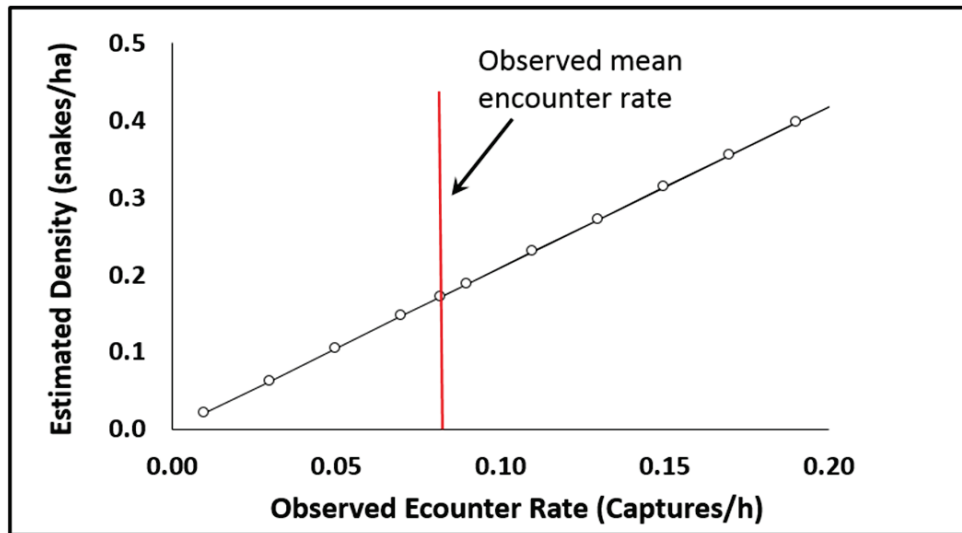
Having calculated parameters for snake crossing speed, individual crossing probability, and observed encounter rate, estimated snake density ($\hat{N}$ [snakes km^{-2}]) can then be calculated using the following formula (Willson et al. 2018):

$$\hat{N} = \frac{N_{obs}}{V_{snake} \times V_{vehicle} \times \rho \times A} \quad (2)$$

Where N_{obs} = average observed encounter rate [snakes/hr], V_{snake} = the time a snake is detectable while crossing a road, $V_{vehicle}$ = the average speed maintained by the vehicle during surveys, ρ = estimated crossing frequency per snake [crossings $\text{snake}^{-1} \text{ h}^{-1}$], and A is the simulated landscape size (km^2).

The IDEASS model can be simulated across a range of encounter frequencies to generate a relationship between encounter frequency and estimated density, as well as to pinpoint estimated density at the observed frequency of encounters (Figure 3).

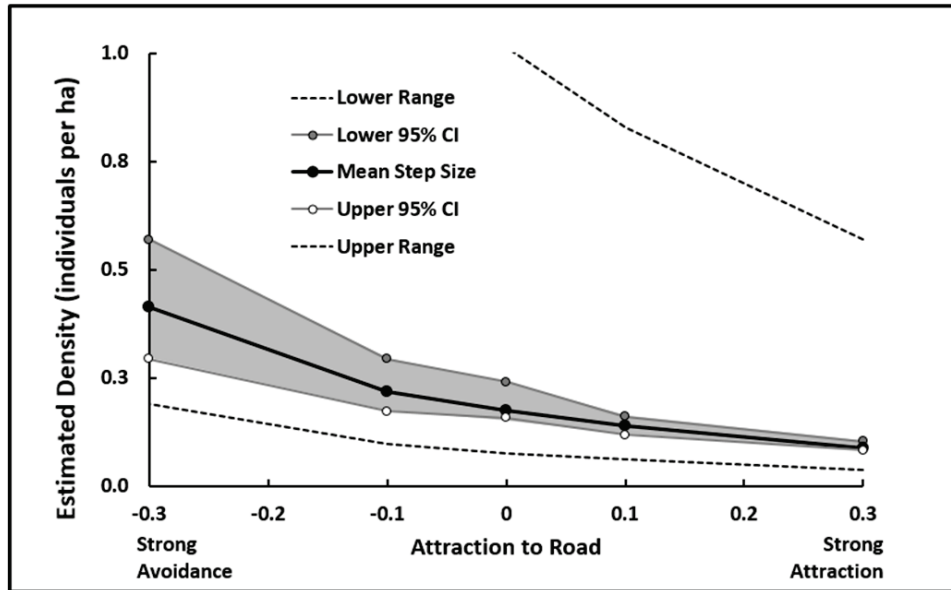
Figure 3. Relationship between encounter rate during systematic road surveys and population density for SHSs in the North Carolina Sandhills.



Adapted from Willson et al. (2018).

As initially developed (Willson et al. 2018), the IDEASS model can incorporate variation and stochasticity in some model parameters, but not others. Thus, previously we have conducted sensitivity across 95% confidence intervals for various model parameters to assess precision of density estimates and sensitivity to sources of uncertainty (Figure 4).

Figure 4. Sensitivity of IDEASS-generated density estimates for SHSs in North Carolina Sandhills to movement distance and road orientation parameters. Shaded region represents 95% CI relative to step size.



Adapted from Willson et al. 2018.

2.2 Technology/methodology development

As originally formulated (Willson et al. 2018), IDEASS uses movement simulations of a large number of simulated individual snakes to generate a mean road crossing frequency and then uses simple algebraic calculations to correct for imperfect detection and generate an average relationship relating encounter probability to estimated density (see section 2.1). Although this approach includes variation in movement parameters such as step size and orientation parameters, it does not fully account for variability in all model parameters, such as snake crossing speed, or fully account for the important role that stochastic variation (chance) may play when sample sizes (e.g., number of snake crossing events) are rare in simulations, or when sampling effort is low relative to the frequency of those events. As part of this demonstration, we modified the original IDEASS methodology to incorporate the detection process into movement simulations. This modification allowed us to incorporate variability in more model parameters and fully consider the importance of stochasticity by scaling the models to the volume of field data collected, thus, yielding a much more comprehensive assessment of uncertainty associated with density estimates generated using IDEASS.

To incorporate the detection process into movement simulations, each snake is assigned a road crossing time at the beginning of the simulation that is drawn from a truncated normal distribution defined by the mean, standard deviation (SD), and range of the empirical data on road crossing speed. Each time that snake encounters a road, its conditional detection probability ($\hat{p}$) is calculated based on its crossing speed, the average width of the road along the transect, and the length of the simulated road, relative to survey vehicle speed. Then a random (0-1) number is drawn and compared to that snake's conditional detection probability to determine if it is detected while crossing. Detection events are summed across the entire simulation and divided by the number of snake movement-hours represented by that simulation (model steps x diel activity window) to determine an hourly encounter rate for that simulation. Numerous simulations are conducted with densities of simulated snakes spanning the range of anticipated densities and a linear regression is fit to the relationship between density and hourly encounter rate to generate a mean relationship and associated 95% CI. As in the original model, observed encounter frequencies are then plotted along this regression to generate the associated density estimate and 95% CI.

Chance events in the movement and detection processes will tend to increase variation in model results (hourly encounter rates) when the number of snake crossing events in simulations is low, thereby widening the 95% CI associated with density estimate. To adequately scale this important source of uncertainty, factors influencing the number of crossing events in the model must be scaled to match those of empirical data that are being interpreted with the model. These factors influencing the number of detections per simulation include the number of steps in the model, the landscape size, and the densities of simulated snakes. To set an appropriate number of model steps, we considered the diel activity window (number of hours per day conducive to snake movement/road crossing) and the amount of road survey effort, such that the number of 'snake movement-hours' in simulations approximately matched the total number of survey-hours along the road transect. Specifically, for a model with a 1-day timestep, we calculated the appropriate number of timesteps by dividing the sum of survey-hours on the focal route by the diel activity window:

$$\# \text{ of timesteps} = \frac{\sum \text{survey-hours}}{\text{diel activity window (\# h suitable for snake movement per day)}} \quad (3)$$

Likewise, the length of the simulated road transect should approximate the length of the actual road transect to adequately scale detection probability of each simulated snake while crossing. Following the aforementioned procedure to set landscape size and number of steps in the simulation, the total number of snake crossing events in model simulations at snake densities predicted by the field observation rate should approximate the total number of snake crossings that occurred during actual road surveys, given the expended effort, thus scaling the role of stochastic variation in snake movement and detection to the appropriate sample size (number of crossing events).

2.3 Advantages and limitations of the technology/ methodology

IDEASS is appealing to land managers and installation biologists because it provides a method of estimating population size of snake species for which there is no suitable, acceptable alternative. The traditional method of CMR is either unsuitable for many species of snakes because of the inability to generate enough recaptures for model convergence or is extremely labor and time intensive to generate enough captures. For most species of snake, IDEASS represents the only viable approach for generating a density estimate because it bypasses the need for recaptures of individual snakes, the one piece of data absolutely necessary for CMR. Furthermore, IDEASS can often make use of existing databases that installations may have already collected. Researchers and managers working at numerous installations have conducted radio telemetry studies in the past or keep records of road encounter data. IDEASS can use these datasets and augment them with novel collected data, whereas CMR data need to be collected in a rigid, controlled framework that reduces the chances that previous datasets could be used. Despite the advantages of IDEASS, the method is not perfect.

IDEASS is inherently a data hungry modeling approach. It requires road encounter, road crossing behavior, and radio telemetry data. While some of these data are easily and inexpensively generated (e.g., road encounter data), radio telemetry can be costly and time intensive. Furthermore, some snakes are too small-bodied to carry transmitters. For these species, IDEASS would be infeasible. Finally, basic IDEASS models are coded in Program R and require familiarity with the R and GIS applications to implement. Application to particular species, study sites, or datasets, may entail proficiency in R and familiarity with spatial movement modeling to restructure models accordingly.

3 Performance Objectives

The overarching objective of the project was to demonstrate application of the IDEASS method to estimate densities of three snake species on DoD installations and to compare the success and cost of the IDEASS approach to traditional density estimation using VES and CMR. Specifically, we used five quantitative criteria and one qualitative criterion (Table 1) to assess the success of our demonstration.

Performance Objective 1 (PO1) (see Table 1) was a comparison of encounter rates generated by road surveys vs. VES. We compared the encounter rates generated from traditional plot/transect-based VES to those generated via effort-corrected road surveys as the first step in the IDEASS process. For each survey conducted, we calculated the total number of individuals of focal snake species, as well as the number captured per unit time. We averaged this catch-per-unit-effort (CPUE) across all surveys for each sampling unit (plot or transect) per year and compared encounter rates between the methods with a t-test, using $\alpha = 0.05$.

PO2 was a direct comparison between the density estimates generated by IDEASS and traditional CMR for EDR. Because rattlesnakes are relatively visible in comparison to many snake species, both approaches were expected to generate meaningful density estimates for this species. However, we expected that the 95% CI around the density estimate of IDEASS would be more precise than that generated by CMR, and that it would not encompass zero or fail to converge (common results in CMR analysis of data with few recaptures). Moreover, we expected IDEASS to yield meaningful independent EDR density estimates for more sampling units (transects) than CMR (VES plots). Additionally, we predicted that our density estimates generated via IDEASS would fall within the reported ranges of densities for this species in the literature (e.g., Means 2017), thus providing some degree of validation.

PO3 was very similar to PO2 but focused on the SHS. Because this species is extremely secretive and fossorial, we expected that each model would be populated based on data from relatively few encounters. Due to the reliance of CMR on high encounter frequencies and a minimum number of recaptures, we expected that CMR would be unable to generate meaningful

density estimates for SHS. We defined meaningful density estimate models as those that converge in 100% of iterations and have non-zero 95% CI that do not encompass zero. Additionally, we propose that a density estimate should be considered meaningful if the confidence intervals provide a relatively narrow range of uncertainty. Based on long-term snake CMR studies (5 to 17 yrs), we suggest that reliable estimates (95% CI) should range from 50 to 150% of the estimated population (e.g., King 1986, Lind et al. 2005). For example, if the estimated population size of a species is 100 individuals, a reliable estimate should have 95% CI spanning no more than 50 to 150 individuals. We predicted that IDEASS would be able to generate density estimates that meet these three criteria, while CMR would fail to do so.

PO4 addressed the ability of each method to generate meaningful density estimates for WRS at Fort Hood Texas using an existing dataset that contains more than 100 WRS captures and extensive radio telemetry data. Although WRS are relatively common at the site, we expected that their fossorial and arboreal habits would result in few recaptures. Due to the reliance of CMR on a minimum number of recaptures, we expected that CMR would be unable to generate meaningful density estimates for WRS or would generate an estimate with extremely high degree of uncertainty. We defined meaningful density estimate models as those that converge in 100% of iterations, had non-zero 95% CI that did not encompass zero, and that had a 95% CI narrower than 50 to 150 % of the estimated adult population (e.g., King 1986, Lind et al. 2005). We predicted that IDEASS would be able to generate density estimates that meet these three criteria, while CMR would fail to do so.

PO5 was our final quantitative metric and pertained to the quantity and value of data collected during application of IDEASS and CMR. DoD installations are often required to collect some amount of ecological data on at-risk snake species. These may be requirements dictated by USFWS as part of an installation's Biological Opinion or part of a species recovery plan. We compiled a list of the most common ecological metrics that installations have been required to collect to satisfy these requirements for various imperiled snake species. We tallied the number of these metrics that could be fully or partially satisfied by data collected during the application of either IDEASS for CMR and assessed whether our research on EDR yielded sufficient data to satisfy each metric. We then judged the

method that satisfied the most metrics to be of higher value to installations in terms of generating ancillary biological data.

PO6 was a qualitative metric that compared the cost of each survey technique. We predicted that generating a reliable density estimate via IDEASS would cost equal to or less than one produced by traditional CMR when labor, number of surveys, survey duration, mileage, equipment, and data processing and analysis costs were tabulated. To address this objective, we summed all labor and supplies necessary to generate estimates for EDR using the two methods and directly compared the unit (per snake capture) and total costs needed to successfully implement the two methods.

Table 1. Performance Objectives for Evaluation of an IDEASS on an Army Installation

Performance Objective	Metric	Data Requirements	Success Criteria	Results
<i>Quantitative performance objectives</i>				
1. PO1: Increase snake encounter rates and capture probability	Higher capture rates via road surveys than traditional visual surveys	• Encounters per unit effort from road and visual surveys • Encounters per unit effort via traditional CMR surveys	• Statistically more snakes encountered per unit effort during road surveys than visual surveys ($P < 0.05$; t-test)	• Significantly higher CPUE of both cryptic upland snakes (t-test, $i = 3.22$, $df = 14.185$, $p = 0.006$), and all other snake species (t-test, $i = 4.23$, $df = 20.70$, $p < 0.001$) for road surveys than for VES/CMR • 8X higher capture rates of EDR on road surveys • Zero SHS captures during standardized VES
2. PO2: Improve density estimation for Eastern Diamondback Rattlesnakes	Generate meaningful and reliable density estimate for focal species	• Density estimate and 95% CIs generated by IDEASS model • Density estimate and 95% CIs generated by CMR • Model convergence rate • Density estimate similar to those reported in the literature for the species	• IDEASS estimate has narrower 95% confidence intervals than CMR and does not overlap zero • IDEASS Models converge in 100% of iterations	• CMR models failed due to only 1 VES/CMR capture and zero recaptures • IDEASS density estimates of 9.10 (95% CI = 7.69-10.50) and 8.20 (95% CI = 6.71-9.69) EDR per km² along two unpaved road transects at Fort Stewart • Density estimates similar to the only published density estimates of EDR from non-coastal sites (11.2 and 12.0 per km²)

Performance Objective	Metric	Data Requirements	Success Criteria	Results
3. P03: Generate meaningful density estimate with IDEASS for Southern Hognose Snake	Generate meaningful and reliable density estimate for focal species	- Model convergence for IDEASS - Model convergence for CMR - Density estimate and 95% CIs generated by IDEASS model - Density estimate and 95% CIs generated by CMR	- CMR models fail to converge or encompass zero - IDEASS 95% CIs do not encompass zero 95% CIs do not range more than 50-150% of population estimate for IDEASS	- Zero SHS captures via VES/CMR - IDEASS density estimate of 5.1 SHS per km² (95% CI: 3.9–7.3) within the only small area where SHS were captured on road surveys
4. P04: Apply IDEASS to generate meaningful density estimate for Texas Ratsnake using existing data	Generate meaningful and reliable density estimate for focal species	- Model convergence for IDEASS - Model convergence for CMR - Density estimate and 95% CIs generated by IDEASS model - Density estimate and 95% CIs generated by CMR	- CMR models fail to converge or encompass zero - IDEASS 95% CIs do not encompass zero 95% CIs do not range more than 50-150% of population estimate for IDEASS	- Despite more than 100 WRS captures, CMR models failed due to zero recaptures - IDEASS - Density estimate of 33.3 WRS per km² (95% CI: = 32.4 - 34.2) at Fort Hood - Density estimate well within the range of published density estimates for ratsnakes (23-91 per km²)

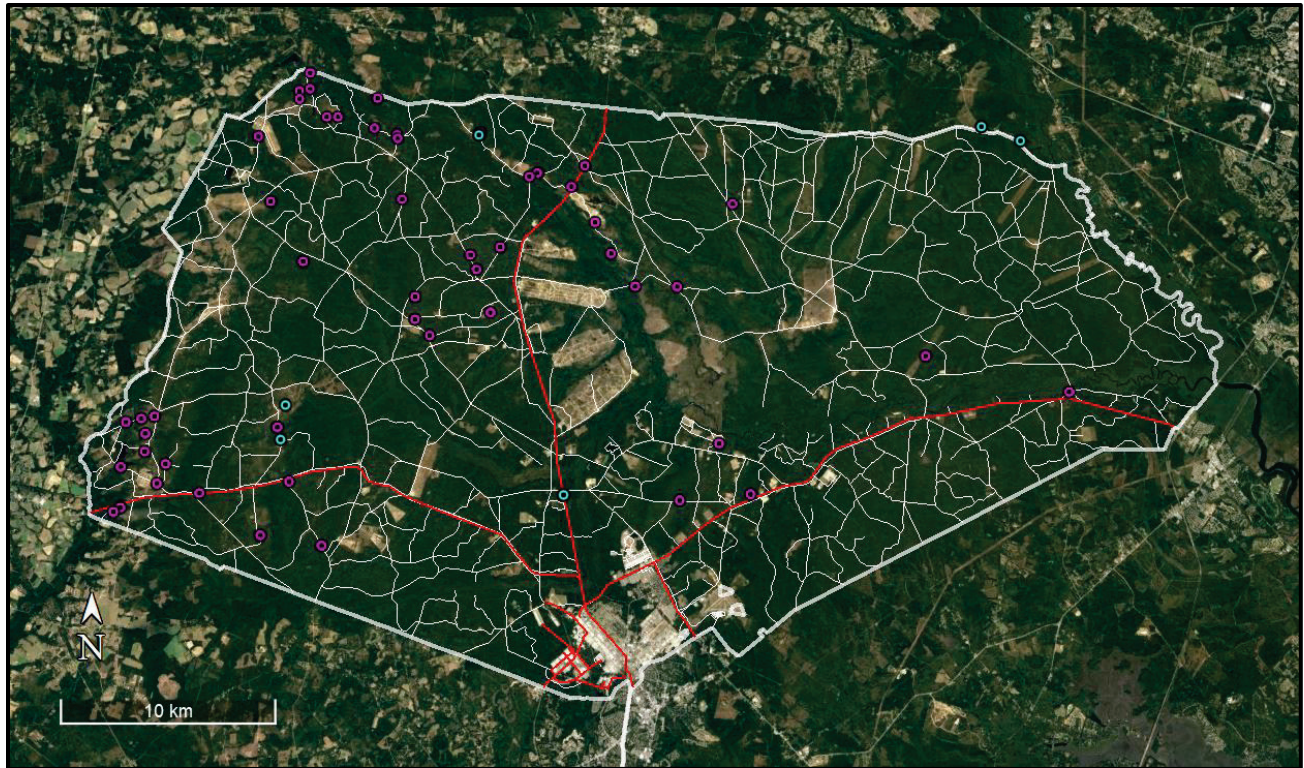
Performance Objective	Metric	Data Requirements	Success Criteria	Results
5. P05: Quantify relevant ecological data on Diamondback Rattlesnakes (i.e., more “bonus” data provided by IDEASS than CMR)	More behavioral and ecological metrics generated by IDEASS sampling than by CMR	• Distribution and encounter records • Annual mortality / survival rates • Road mortality rates and locations • Seasonal variation in distance moved per day and movement frequency (radio telemetry) • Habitat use vs. habitat availability (radio telemetry) • Demographic data (age structure, proportion gravid)	• More metrics (raw count data) able to contribute to Biological Opinions can be calculated from IDEASS than CMR sampling	• Count of relevant ecological metrics that could potentially be addressed with method: ○ IDEASS= 8 ○ CMR = 4 • Count of metrics for which we actually generated meaningful data in our research on EDR at Fort Stewart: ○ IDEASS = 7 ○ CMR = 0
<i>Qualitative performance objectives</i>				
6. P06: Cost efficiency of IDEASS model equal to or less than cost of traditional CMR	• Cost per survey • Number of surveys needed • Equipment costs	• Individual labor rates • Number of surveys needed for each method • Duration of surveys • Mileage costs • Radio telemetry equipment costs • Data processing and analysis costs	• Density estimate generated by IDEASS costs less than or equal to density estimate generated by traditional CMR	• Total cost of deployment for a minimal sample size of a rare species (EDR): ○ IDEASS = \$42,117.78 ○ CMR= \$180,450.00 • Total cost of deployment for a more common species (Eastern Hognose): ○ IDEASS = \$28,945.50 ○ CMR= \$45,300.00

4 Site Description

4.1 Fort Stewart Military Installation, Georgia

Fort Stewart Military Installation (Figure 5) encompasses approximately 113,064 ha of Coastal Plain habitat. The installation is home to extensive xeric sandhill communities including intact, mature longleaf pine – turkey oak – wiregrass habitat, young (5 to 15 years) to medium (16 to 40 years) slash or loblolly pine plantations, and recently restored longleaf pine habitats. The xeric pine habitats are interspersed with mesic pine flatwoods, mixed pine-oak forests, and bottomland hardwood habitats and depressional wetlands and blackwater creek swamps. Fort Stewart actively manages their land using prescribed burns, selective thinning, longleaf pine planting, wiregrass seeding, and control of xerophytic oaks via herbicide. The primary goals of this intensive management are to maintain a mosaic of different aged, open canopied longleaf pine habitats for conservation of Red-cockaded Woodpeckers, gopher tortoises, and other longleaf pine specialist species. Both EDR and SHS are known to occur on Fort Stewart, but essentially nothing is known about their population size or status. EDR are known from over 50 historical and recent records that are distributed nearly base-wide, with most records from upland sandhill and longleaf pine savannah habitats in the northwestern and southwestern sections of the base (Figure 5). SHS are exceedingly rare on Fort Stewart, with <10 historical records (Figure 5).

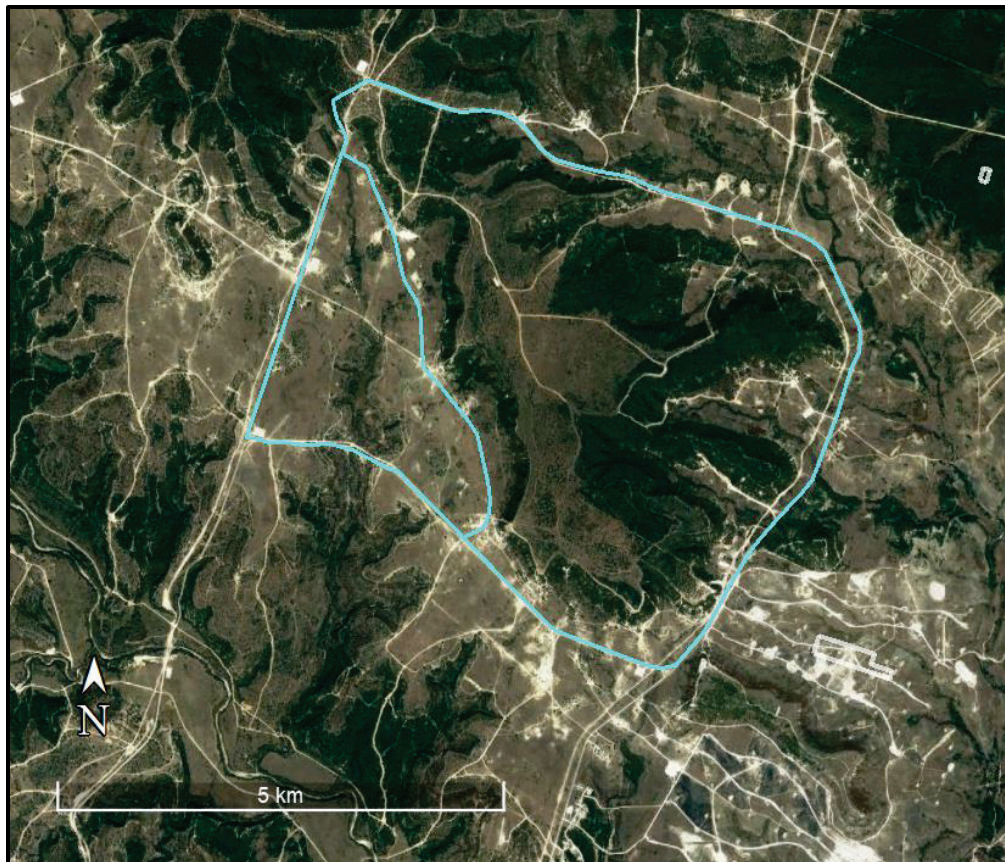
Figure 5. Map of historical records of EDRs (purple points) and SHSs (blue points), relative to the road network at Fort Stewart, Georgia. We selected two focal regions for surveys in the northwestern and northeastern sections of the base (see section 5.2).



4.2 Fort Hood, Texas

Fort Hood is an 87,890-ha military installation located in the Edwards Plateau region of central Texas (Figure 6). The topography of Fort Hood is characterized by flat-top mesas and oak savannah / oak-juniper woodland. Because of past disturbance regimes (grazing, military activity, fire), habitat on the mesa tops is comprised primarily of patchy, often early successional woody vegetation. Vegetation on steep mesa slopes, which prohibit military activity and grazing, consists primarily of dense, oak-juniper woods. The habitat off the mesas consists primarily of open oak savannah and grasslands. WRS; *Pantherophis obsoletus*) are not of conservation concern and are relatively common at Fort Hood but are of management interest because they are primary nest predators of two imperiled bird species, the Golden-cheeked Warbler and Black-capped Vireo (Sperry et al. 2009). Despite substantial previous research on WRS at Fort Hood, little is known about their population density or abundance.

Figure 6. Map of study site for demonstration of Western Ratsnake density estimation from existing data from Fort Hood, Texas. Highlighted roads are included in the 26 km road transect where snakes were sampled.



5 Test Design

5.1 Conceptual test design

Our general approach was to demonstrate the IDEASS methodology for two at-risk snake species that overlap in habitat use but differ in their life histories and detectability, and one common species of management interest (Figure 7). The first species is the SHS (*Heterodon simus*; SHS), a relatively small (to 61 cm), heavy-bodied species associated with sandy habitats (Gibbons and Dorcas 2015). Despite being a diurnal species, they are rarely encountered by researchers due to their highly fossorial habits (Gibbons and Dorcas 2015). The SHS is thought to be in decline, due to apparent disappearances from large areas of its historical range (Tuberville et al. 2000) and it is currently petitioned for listing under the ESA (USFWS 2020). Despite the fact that several researchers have conducted radio telemetry on the SHS (Willson et al. 2018),* the only information on their abundance is our previous implementation of IDEASS for this species based on data from North Carolina (Willson et al. 2018).

The second focal species is the EDR (*Crotalus adamanteus*), also petitioned for listing under the ESA (USFWS 2020). The EDR is the largest of the North American vipers (84 – 183 cm) and is also active primarily during daylight hours. This species can sometimes be located on the surface by observers as they remain coiled for long periods of time in ambush postures or make long-distance forays to search for mates during the breeding season (Gibbons and Dorcas 2015). These two species have life histories and behaviors that are representative of many of the threatened and endangered snake species for which DoD is currently managing or may be required to manage in the future. Additionally, each of these species occurs on a number of southeastern installations across multiple military branches (e.g., Camp Shelby, Fort Gordon, Fort Bragg, Marine Corps Base Camp Lejeune, Eglin Air Force Base).

We chose these two species in part to represent contrasting patterns of detectability. SHS are so secretive that virtually nothing is known about their abundance or population size. Under these circumstances, this species provides a case study for which IDEASS represents the only viable method for obtaining these important data. Additionally, we chose SHS because we

* Also J. Beane, North Carolina State Museum of Natural Sciences, unpublished data; and T. Tuberville, Univ. Georgia, unpublished data.

have access to existing radio telemetry data that can be applied to the IDEASS method, which reduces the costs and effort needed to produce a density estimate on Fort Stewart, where this species is thought to be exceedingly rare. Although also secretive, EDR are more detectable via VES and have been studied at the population level using traditional methods, such as CMR (e.g., Hoss et al. 2010, Means 2017). Thus, EDR provide a potential opportunity to directly compare density estimates generated with IDEASS and to those generated using CMR, and thus validate the precision and cost of IDEASS relative to traditional approaches.

A further objective was to demonstrate how IDEASS can be retroactively applied to existing datasets to generate more meaningful density estimates than those produced by traditional methods. To accomplish this objective, we took advantage of a robust dataset of Western Ratsnakes (*Pantherophis obsoletus*; WRS) collected on Fort Hood, Texas from 2004 to 2007 (Sperry et al. 2008, Sperry et al. 2009). This dataset consists of more than 6,000 radio telemetry re-sightings of over 60 individual snakes, most of which were captured via road surveys. We applied IDEASS to this dataset to estimate density of WRS and to compare to traditional CMR (Figure 7).

Figure 7. Three focal species and data sources used for demonstration of IDEASS. FS = Fort Stewart; FH = Fort Hood; NC = North Carolina; SC = South Carolina.

			
	Eastern Diamondback Fort Stewart (FS) South Carolina (SC)	Southern Hognose Fort Stewart (FS) & North Carolina (NC)	Western Ratsnake Fort Hood (FH)
Road Surveys	New (FS)	New (FS)	Existing (FH)
Road Behavior	New (FS)	Existing (NC)	New (FH)
Radiotelemetry	New (FS) + Existing (SC)	Existing (NC)	Existing (FH)
Capture-mark-recapture (CMR)	New (FS)	New (FS)	Existing (FH)

5.2 Baseline characterization and preparation

Operational scale demonstration of IDEASS took place on Fort Stewart, Georgia. We applied a hierarchical selection procedure to choose plots for VES/CMR and transects for road surveys. We developed a series of selection criteria for each site type (see below) and solidified our site selection through consultation with base biologists and on-the-ground site visits in July 2017.

First, we examined geographic distribution of historical records of EDR and SHS from Fort Stewart (Figure 5) and consulted with base biologists to identify two regions (northwest and southwest) of the base that contained records of both species, ample suitable xeric sandhill/longleaf pine savannah habitat, and were likely to be accessible on a regular basis. Within each of these regions, we then selected three road transects (two unpaved, one paved) according to five criteria:

1. The road segment was at least 7 km long and did not switch substrate across this extent (i.e., it was unpaved the entire way).
2. At least 75% of the transect traversed xeric sandhill habitat suitable for the two focal snake species.
3. Unpaved roads were large enough that they provided ample visibility of snakes crossing (i.e., they did not contain a vegetated median or consist of simple tire ruts), which allowed us to maintain a consistent speed of ~20 mph.
4. Transects received relatively little daily traffic from military personnel so that our survey activities did not interfere with local traffic and training schedules.
5. Transects occurred within areas of the base where we had the highest probability of regular access.

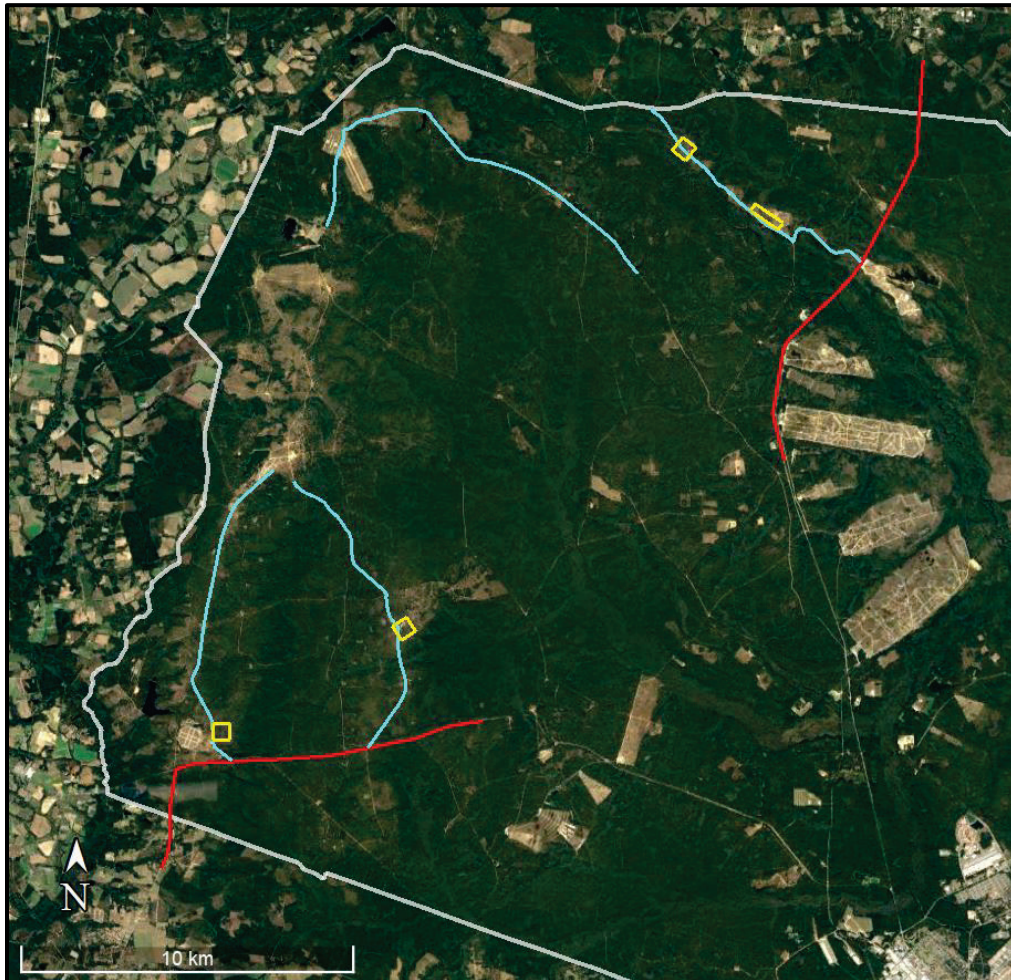
Our six selected road transects ranged from 8.7 to 13.8 km in length and included one paved and two unpaved transects located in xeric sandhill habitats in the northern and northwestern portions of the base, and one paved and two unpaved transects in longleaf pine savannah habitats in southwestern section of the base (Figure 8).

We delineated four, 25-ha plots for VES/CMR based on the following criteria:

1. Plots were located within our focal regions and contained 25 ha of xeric, open canopied sandhill habitats preferred by EDR and SHS.

2. Plots occurred in areas where the focal species had been documented by installation biologists or visiting researchers.
3. Plots were located adjacent to or bisected by our road transects.
4. Plots were located within areas of the base where we would have the highest probability of regular access. Locations of VES/CMR plots, relative to our road survey transects are illustrated in Figure 8.

Figure 8. Map of selected paved (red) and unpaved (blue) road survey transects and 25-ha VES/CMR plots (yellow) for EDRs and SHSs at Fort Stewart, Georgia.



5.3 Design and layout of technology and methodology components

As outlined in section 2.1, IDEASS requires three types of field data: (1) systematic road surveys, (2) road crossing speed measurements, and (3) spatial movement data (radio telemetry). We collected road survey and crossing speed data for EDR and SHS, and radio telemetry data for EDR at Fort Stewart, Georgia, in 2017-2019. We supplemented these data with existing radio telemetry data for Southern Hognose (North and South Carolina; Willson et al. 2018) and EDR (South Carolina; see section 5.5.4). For

comparison, we conducted standardized VES at Fort Stewart to generate abundance estimates via CMR.

We estimated density of WRS at Fort Hood using existing road survey and radio telemetry datasets collected at that site from 2004 to 2007 (Sperry et al. 2008, Sperry et al. 2009). Because these data were not collected with IDEASS in mind, snake crossing speed data were not collected. Thus, we used ratsnake crossing speed data that we collected opportunistically during field-work at Fort Stewart and elsewhere using methodology described for EDR and SHS below. For comparison, we conducted CMR analyses using ratsnake capture/recapture data from the surveys conducted at Fort Hood.

Section 5.4 (Table 2) details the timeline for demonstration of IDEASS and CMR for estimating EDR and Southern Hognose Snake densities at Fort Stewart, Georgia.

Section 5.5 describes the equipment and techniques for field data collection and data analysis for parameterization of models. Sections 2.1, 2.2, and 5.5 describe in detail the modeling procedures used to estimate densities of our three focal species using IDEASS.

5.4 Field testing

Table 2. Timeline for demonstration of IDEASS and CMR for estimating Eastern Diamondback Rattlesnake (EDR) and Southern Hognose Snake densities at Fort Stewart, Georgia.

Activity	Date Range	Description
Site selection	July 2017	Road survey transects and visual survey plots selected.
Systematic Road Surveys	July – November 2017, 2018, 2019	Systematic vehicle surveys of road transects on a rotating basis during suitable weather.
Visual Surveys of CMR plots	March – October 2018, 2019	At least 10, 2 person-hour visual surveys of each 25-ha VES plot per year during suitable weather. Opportunistic visual surveys throughout the base on a haphazard schedule.
Radio telemetry of Rattlesnakes	July – November 2018, 2019	Re-sighting of all tracked individuals three times per week, when not restricted by base activities.

5.5 Sampling protocol

5.5.1 Systematic road surveys

To maximize captures and precision of density estimates for EDR and SHS, we defined our focal season and survey timing for IDEASS to coincide with peak activity (Willson et al. 2018). Both EDR and SHS are

considered to be strictly diurnal and both exhibit a peak in road encounters during the latter part of the active season. Specifically, EDR have two peak periods: (1) August to September movements associated with mate searching (males) and parturition (females), and (2) late October to November associated with movement to overwintering sites (Means 2017). SHS are well known to exhibit one peak in road encounters during September-November (Enge and Wood 2002, Beane et al. 2014). Thus, to fully encompass the activity peaks of both species, we conducted systematic road surveys at Fort Stewart between 1 July and 14 November in 2017, 2018, and 2019. For SHS, we only used road survey data from 1 September to 14 November, to coincide with our telemetry data and movement analyses conducted previously for this species (Willson et al. 2018).

We conducted extensive systematic road surveys of our designated transects at Fort Stewart during our focal season and appropriate temperatures. Specifically, for at least 5 pre-determined days per week, we conducted surveys whenever ambient temperatures were between 70 °F and 90 °F. Below and above these temperatures, snakes seldom undertake extensive surface movements and paved road surfaces become too hot for snakes to cross when temperatures exceed this range. These temperature constraints generally resulted in surveys occurring in the morning and evening in the summer and in the mid-day in the late fall, which corresponds well with general perceptions of timing of activity for these species (Beane et al. 2014, Means 2017). We attempted to rotate among survey routes and included both a paved and an unpaved transect during each survey, but base operations often resulted in access restrictions that caused us to deviate from this schedule. Likewise, to accommodate access restrictions, we frequently substituted alternative road segments that were adjacent to our transects but passed through similar habitats that were appropriate for our target species. In 2019, base biologists generously arranged frequent escorts that allowed us to maintain a more systematic schedule in that year. For each survey, we recorded the following data at the start and end of the survey: time, mileage, observer(s), and environmental variables (air temperature, wind speed, and barometric pressure on a Kestrel 3500 Pocket Weather Meter; visual, categorical scores of cloud cover and precipitation). We also used a handheld GPS unit (Garmin eTrex 20) to continuously record the track of each survey. From these tracks, we calculated the mileage and time spent on each transect during each survey.

Road surveys consisted of slowly driving the selected transects and recording all snakes observed on the road. Due to safety concerns and the need to stop suddenly when a snake was spotted, we did not use cruise control, but attempted to maintain a constant speed of 32 kph (20 mph) on unpaved roads and 72 kph (45 mph) on paved roads. However, we were also able to calculate the actual vehicle speed directly from survey route data by dividing the distance of each road segment from the time elapsed on that segment directly from GPS track. Thus, we used these average speeds in our subsequent modeling.

When a snake was encountered, the time and air temperature of the observation was recorded, and the snake was timed for crossing speed if it was a target species (see below). All other snakes were immediately captured, identified to species, measured (snout-vent length, tail length, mass), and sexed by cloacal probing or visual inspection of tail morphology. Additionally, all EDR, SHS, and Pinesnakes captured were individually marked using a Passive Integrated Transponder (PIT) tag injected into the posterior body cavity (Gibbons et al. 2004), and all individuals were scanned with a PIT tag reader to identify recaptures. Following processing, all snakes were immediately released at their capture location unless they were a candidate for radio telemetry (see section 5.5.4).

We measured the width of roads along our survey transects in November 2017 and 2018 at 60 locations (N = 30 paved, 30 unpaved) systematically spaced and equally divided among our survey routes.

For estimation of WRS density at Fort Hood, Texas, we used an existing database of systematic road surveys conducted in 2005 and 2006 along a 26 km road transect that encircled a large (approximately 1,850-ha) mesa on the base (Figure 6). We restricted this dataset to surveys conducted between 20:00 and 23:00 h during the early summer WRS activity peak (15 April to 30 June). This survey route included both paved and unpaved roads, but survey effort was not recorded in sufficient detail to allow us to separate paved and unpaved roads in our analyses. Start and end times were generally recorded for these surveys, allowing us to calculate total time for each survey, but mileage was not. Thus, based on conversations with the researchers, we used a vehicle speed of 25 mph (40.2 km/hr), which is a typical driving speed when conducting nocturnal road surveys for snakes. The resulting database included 102 surveys totaling 249 survey-hours. All snakes encountered were immediately captured, identified

to species, measured (snout-vent length, tail length, mass), and sexed by cloacal probing or visual inspection of tail morphology. WDR were individually marked using a PIT tag implanted in the posterior body cavity (Gibbons et al. 2004), and all individuals were scanned with a PIT tag reader to identify recaptures.

5.5.2 Visual encounter surveys

We conducted systematic VES of CMR plots throughout the snake active season (March to October) in 2018 and 2019 at Fort Stewart. Our survey schedule was driven largely by accessibility and base operations, but we generally rotated among plots and attempted to survey each plot at least 10 times per field season, yielding a total of more than 80 standardized VES of CMR plots. Each of these standardized surveys consisted of 2 person-hours during the day when air temperature was <90 °F, generally in the morning during the summer and during mid-day in the spring and fall. The observer(s) slowly explored the entirety of the plot examining retreat and ambush sites preferred by snakes (e.g., Gopher Tortoise burrows, stump holes, palmetto thickets, hollow logs) and visually encountering snakes that were in visible ambush positions or moving on the surface. We supplemented these standardized surveys of CMR plots with opportunistic VES to achieve the highest probability of capturing our target species. Opportunistic surveys were conducted haphazardly with variable effort; we grouped these surveys within each year and included them as one unit alongside our four CMR plots for statistical comparison of capture rates.

All snakes encountered were captured, identified to species, measured (snout-vent length, tail length, mass), and sexed by cloacal probing or visual inspection of tail morphology. Additionally, all EDR, SHS, and Pinesnakes captured were individually marked using a PIT tag implanted in the posterior body cavity (Gibbons et al. 2004), and all individuals were scanned with a PIT tag reader to identify recaptures. Following processing, all snakes were returned to their capture location unless they were a candidate for radio telemetry (see section 5.5.4).

We compared capture rates between road surveys and VES by tabulating the captures per 100 survey-hours for each plot/transect-year for our focal species (EDR and SHS), as well as for other cryptic upland snake species (Eastern Hognose, Pinesnake, and Harlequin Coralsnake), as well as all of the aforementioned species combined as 'upland' species, and for all other

snakes combined. We then compared mean capture rates among methods using t-tests, with plot/transect-year as the statistical unit and $\alpha=0.05$.

WRS were captured at Fort Hood, Texas in 2004-2007 using a variety of methods, including road surveys, coverboards (N=50), opportunistic VES, and drift fences with funnel traps. These surveys were not standardized, but we combined captures within years and used year as our replicated sampling unit to attempt a site-wide CMR estimate of abundance (see section 5.5.7) for comparison with that generated via IDEASS.

5.5.3 Snake crossing speed

We gathered data on road crossing speed of our target snake species through direct behavioral observations and videography of snakes encountered naturally crossing roads during our surveys. Our timing procedure followed standard methods described in Willson et al. (2018). When a snake was encountered, we stopped the vehicle at least 5 m away from the snake, shut off the engine, and observed the snake as unobtrusively as possible for the duration of the crossing event. When possible, the event was videotaped using a smartphone or tablet PC. Typically, the snake would freeze for a short period (usually < 1 min) when the vehicle first approached but then resume crossing the road using rectilinear locomotion, which is typical for these species when undisturbed. Once the snake resumed movement, the observer or video reviewer noted the time at which the snake's nose or tail tip crossed two known landmarks (e.g., center line, road edge, or obvious crack in pavement). Once the snake fully crossed, it was captured and measured (snout-vent length, mass, sex). The distance traveled between landmarks was then measured (to the nearest cm), as was the total width of the road. Any snake that turned around, froze for more than 5 mins, or employed rapid lateral undulation movement was considered disturbed and was not included in the dataset. For each snake, crossing speed was calculated by dividing the distance traveled (cm) by the time elapsed (sec) and extrapolated to total crossing time, by multiplying speed by the average width of roads along our survey route (see below) plus the snakes total body length (since the snake is still visible on the road until it has crawled its own body length off the road and its tail is no longer visible).

5.5.4 Radio telemetry

All EDR encountered during road or visual surveys were captured using snake tongs and placed inside a 5-gal bucket within a large Rubbermaid bin

with locking lid for transport. Each EDR weighing more than 600 g was implanted with either a 5 g or 9 g Holohil Systems Ltd. SI-2T temperature-sensitive transmitter that was <6% of the snake's body mass by an experienced reptile veterinarian (Terry Norton, DVM; Jekyll Island Sea Turtle Center, Georgia) using a modification of the methods used by Reinert and Cundall (1982). During transmitter surgery, we weighed (g), measured (snout-to-vent length, SVL; cm), and sexed via cloacal probing each snake. After surgery, EDR were held for a minimum of 2 days at >80 °F to monitor recovery, after which they were released at their capture location. We tracked EDR approximately two times per week during daylight hours between July and November in 2018 and 2019 using a handheld receiver (R-1000, Communications Specialists, Inc., Orange, CA) and three-element folding Yagi antenna (Advanced Telemetry Systems, Isanti, Minnesota). However, restricted access due to base operations frequently required us to deviate from this schedule. During the remainder of the year we tracked snakes periodically to monitor snake health and general location. Attempts were made to locate snakes in a different order each day to avoid temporal bias. The locations of the snakes were recorded at each sighting with a handheld global positioning system (GPS) unit (Garmin eTrex 20; approx. 3 m accuracy) in Universal Transverse Mercator (UTM) coordinates. We also recorded data on snake microhabitat associations and behavior at each resighting, but these data are not used in the IDEASS density estimation process.

Due to low number of EDR captured and tracked at Fort Stewart (see below), we supplemented our dataset with radio telemetry data collected on EDR by collaborators (Jeff Holmes; Amphibian and Reptile Conservancy) at Francis Marion National Forest (FMNF), Charleston County, South Carolina. This site is located approximately 200 km from Fort Stewart but is a similar distance from the coast and harbors a population of EDR that use similar habitats (longleaf pine savannah and sandhill ridges embedded within a matrix of deciduous lowlands). Radio telemetry methodology at FMNF was identical to ours and spanned 2015-2019. As with our data, we restricted our analyses to the July-November period for FMNF EDR.

Radio telemetry methods for SHS and WRS were similar to those described for EDR and have been described in detail elsewhere (SHS: Willson et al. 2018; WRS: Sperry et al. 2008, Sperry et al. 2009). However, in both these cases, snakes were generally tracked more frequently, allowing

us to focus on only daily (SHS) or 2-day (WRS) intervals and avoid having to discretize data (see section 5.5.6).

5.5.5 Analysis of snake movement

To parameterize individual-based movement models, we analyzed radio telemetry data for EDR, SHS, and WRS. For each species, we restricted analyses to data collected during the focal season for that species (Table 7) and excluded individuals with fewer than five re-sightings. For each snake, we estimated turning angle distribution (path straightness), mean net distance moved per day (step size), and mean bearing using Program R (packages `moveHMM` [Michelot et al. 2016] and `circular` [Agostinelli and Lund 2017]) or ArcGIS 10.1 (ESRI, Redlands, CA, USA,). For SHS and WRS, tracking was frequent enough that we were able to restrict analyses to daily (SHS) or daily and 2-day (WRS) re-sighting intervals. For EDR, however, less frequent tracking necessitated use of longer tracking intervals and thus, discretization of the data to conform to the 1-day time step of our movement models. For EDR, we excluded data with more than 7 days between re-sightings or zero movement and then plotted straight-line distance between re-sightings against elapsed time between re-sightings for males and females separately, averaged by snake-year. We interpreted instances where there was no correlation between distance moved and time elapsed (up to 7 days) as evidence that snakes made single long-distance movements at ≥ 7 day intervals, as is typical for many ambush-foraging snakes, and discretized the movement data by filling in zero distance movements for all but 1 day within each tracking interval. In cases where we found a positive correlation between distance moved and time between re-sightings, we discretized the data by equally dividing the distance among daily movements, representing daily shorter movements that sum to the total distance moved between points.

We additionally tested for the effects of sex on movement parameters (T-test). For each snake, we calculated the mean daily movement distance (using only daily re-sighting data) and then we averaged the means across all snakes to generate the mean step size. The parameter β , which describes attraction towards home range center, cannot be directly calculated from telemetry data. Thus, we parameterized β by matching home range size of simulated snakes to our empirical data from radio telemetry. Specifically, for each species, we calculated minimum convex polygon (MCP) home range size (package ‘`adehabitat`’ in R) for each snake-year in our dataset with complete data for our focal season. We then completed a series

of simulations wherein we held other parameters constant (at values derived as described above) and varied β from 0 – 1, by steps of 0.1. For each β value, we simulated 1000 snake paths with a number of steps equal to the number of days in our focal season and calculated the MCP home range of each path. We then selected the β value that best matched the mean home range of our real snakes.

We investigated potential response to roads (attraction to or avoidance of the road) using a Monte Carlo approach that consisted of generating random walk paths for each snake using the empirical size distributions and number of steps, a uniform distribution of turning angles, and the snake's starting location in UTM coordinates (Shepard et al. 2008, Willson et al. 2018). We generated 1000 paths per snake, plotted those paths against the road network at the snake's location, and calculated the number of times each simulated path crossed a road. We excluded unpaved roads that were so small that they had a vegetated median from this analysis because we did not include these roads in our surveys. We then generated an empirical distribution of number of crossing events from the simulations. Using an alpha of 0.05, we rejected the null hypothesis of no response to road (neither attraction or avoidance) if the observed number of road crossings for each snake fell into the upper or lower 2.5% of the frequency distribution of number of crossing events from the simulated paths.

5.5.6 Movement simulations and density estimation with IDEASS

Working within the original conceptual framework of IDEASS (see section 2.1), our modifications (see section 2.2) allow for a completely simulation-based estimation of density that accounts for variability in numerous model parameters and the role of stochastic variation that is balanced against sample size/volume of data. For these simulations it is important that landscape size (A) and number of steps in the simulation be proportional to the field data to capture the appropriate level of model uncertainty. Thus, we began our simulation process for EDR by setting these parameters (Table 7). Since we were estimating density separately for each unpaved road transect, we selected a landscape size of $A = 10 \text{ km} \times 10 \text{ km}$, which was similar in length to our transects and wide enough to ensure a high likelihood of simulating all snakes with a chance to cross the road (Willson et al. 2018). Considering that EDR are diurnal and are likely to cross roads whenever temperatures are ca. 70 °F – 90 °F, we assigned an 8 hr diel activity window for EDR, which captures a morning and evening activity window in the summer and activity throughout the day in the fall

when temperatures are cooler, but day length is shorter. Given, this diel activity window, we ran EDR simulations for 18 steps (for a total of 18 days x 8 hr/day = 144 sampling hrs) to align with our average sampling effort per unpaved road transect (Table 3).

We conducted 100 simulations of the model, each populated with a density of snakes drawn from a uniform distribution of densities between 0 and 30 per km² (i.e., 0 – 3,000 simulated snakes) and with 50% of the snakes in each simulation parameterized as males and 50% parameterized as females. Each individual was assigned a random home range center within a uniform landscape bisected by a linear road and was given an initial movement bearing from a uniform distribution (1-360 degrees). Thereafter, snake movement distances were randomly generated from a lognormal distribution and movement bearings were stochastic but also determined both by the location of the snakes' home range center. Whenever a snake encountered the road it was assigned a detection probability based on our calculated average vehicle speed of 22.7 mph on unpaved roads, length of the road transect (10 km) and a detection time drawn from a normal distribution with mean and variance defined by our empirical crossing speed measurements (Table 4). Then, detection probability was compared to a random draw (0-1) to determine whether or not the snake was detected while crossing. At the end of the 18-step simulation, the number of snake detections was tabulated and divided by the total movement time elapsed (18 days x 8 hr/day = 144 hrs) to determine an hourly detection rate. Following 100 simulations, we regressed hourly detection rate against density of each simulation and determined the 95% CI around the linear regression line. We then plotted our observed EDR encounter frequency (average captures per hour) for each transect where EDR were captured to determine the estimated density and associated 95% CI for each transect.

Previously, we used IDEASS to estimate frequency of road crossing by SHS, based on spatial movement data from radio telemetry studies conducted on this species in North and South Carolina (Willson et al. 2018). We used these same models to derive a relationship between SHS observation frequency and density for Fort Stewart, only modifying the models to alter the detection process to reflect the road widths and average survey vehicle speeds for our site. We then used this relationship to calculate an estimated density corresponding to observation rates of SHS along our survey transects.

We followed a procedure similar to that described for EDR above to estimate density of WRS at Fort Hood, Texas using existing road survey and radio telemetry datasets. However, we modified the model in two important ways to best conform to the existing data and the biology of the species. First, to best match the timescale of radio telemetry data, we constructed the model with a 2-day timestep and adjusted our calculations to account for crossing events and detections being spaced over a 2-day period. This allowed us to avoid needing to discretize movement data and because males and females did not differ significantly in movement distances (step size; t-test, $t = 0.90$, $p = 0.37$), we did not parameterize the sexes separately.

Second, previous research on WRS at Fort Hood (Sperry et al. 2008, Sperry et al. 2009) has revealed that WRS may be active nearly 24 hrs per day, but road surveys for that species were only conducted in the evening (20:00-23:00), violating the important assumption of basic IDEASS models that road surveys are unbiased relative to snake activity (Willson et al. 2018). Luckily fine-scale WRS activity data are available for WRS at Fort Hood, collected using automated telemetry (Sperry et al. 2008, Sperry et al. 2009). These data allowed us to correct conditional detection probability of simulated snakes for bias incurred by only sampling in the evening hours. Specifically, we examined raw data from Sperry et al. (2009) and calculated the average proportion of snake movement events in May and June that occurred between 20:00 and 23:00 (0.13; i.e., of all snake movements detected via automated telemetry in May and June, 13% occurred between the hours on 20:00 and 23:00). Thus, when calculating conditional capture probability of each simulated snake crossing, we factored in an additional multiplier of 0.13 to account for the 87% chance that that snake crossing occurred outside of the diel timeframe when road surveys were conducted. Otherwise, procedures for IDEASS modeling were the same as those described for EDR above, using a landscape size of 26 x 10 km and a 42 timesteps in the model to reflect our total of 249 hrs of road survey effort (249 hrs / 3 hr per day survey window x 2-day timestep = 41.5 steps).

5.5.7 CMR density estimation

We attempted to analyze yearly CMR data from systematic VES of 25 ha plots using closed population models in Program MARK (White and Burnham 1999). Specifically, for each plot-year, we constructed a matrix of individual snake IDs (rows) by survey dates (columns) and populated each

cell with a “1” indicating detection of an individual on a survey, or “0” indicating non-detection. We inputted these data into MARK, using the ‘Closed Captures/Full Likelihood p and c’ data type. For each dataset, we began with the simplest possible parameterization (fewest parameters), which included capture (p) and recapture (c) probabilities that were constant and equal across sampling intervals (i.e., time-varying, group (sex or size)-varying, or capture history-varying (behavioral responses) variation in capture probability). We judged a model as having failed to converge when the program produced an error and would not run or produced nonsensical parameter estimates (e.g., 95% CI of $p = <0.0001 - 1$). We applied the same CMR approach to existing Western Ratsnake capture data from Fort Hood using sampling year as our survey unit and combining all captures across the study area into one analysis.

5.6 Sampling results

5.6.1 Field sampling and snake captures

Over three field seasons, we conducted 313 diurnal road surveys, totaling 270 hrs and 10,286 miles, on two paved road transects, and 564 surveys, totaling 570 hrs and 12,082 miles, on four unpaved road transects located in longleaf pine/sandhill habitats at Fort Stewart, Georgia (Table 3). In total, road surveys yielded 211 live snake captures, only a minority of which were cryptic upland species such as EDR, SHS, Eastern Hognose, Harlequin Coralsnake, and Florida Pinesnake. Surveys of paved road transects resulted in collection of more than 100 road-killed snakes, but very few live snake captures, and only one capture of a cryptic upland species, an Eastern Hognose. Surveys of unpaved road transects yielded much higher captures of snakes overall, including upland species. A total of six live EDR were captured on surveys of unpaved roads, as well as one live and one road-killed SHS. These SHS captures were the first records of this species at Fort Stewart in over a decade. All six EDR captures occurred along our two unpaved transects in the northern portion of the base (Figure 6). Considering effort expended sampling the two transects where EDR were captured, our average encounter rates were 0.027 and 0.021 captures per survey-hour. Our average encounter rate for SHS on the one transect where one was detected was 0.011 captures per survey-hour. For purposes of cost analysis (See sections 7.1 and 7.2), we also tabulated capture rates of a more common upland species, the Eastern Hognose. Eastern Hognose were captured at an average rate of 0.054 per survey-hour along our unpaved road transects.

Concurrent with road surveys, we conducted 230 diurnal VES in the same habitats at Fort Stewart (Table 3). These surveys were split between standardized, repeated, 2 person-hour VES of four, 25-ha CMR plots (18-28 surveys per plot), and 140 opportunistic VES, totaling 418 hours, in habitat suitable for our target species across the base. VES of CMR plots were ineffective, yielding only 20 snake captures across 180 survey-hours and no captures of EDR or SHS. Opportunistic VES were somewhat more effective overall but resulted in mostly captures of non-target species. Only one EDR was captured on a VES and, critically, no marked snakes of any species were recaptured. For purposes of cost analysis (See sections 7.1 and 7.2), Eastern Hognose were captured at an average rate of 0.007 per survey-hour during VES.

Table 3. Survey effort and snake captures at Fort Stewart, GA, in 2017-2019. Road surveys were conducted during the day between July and November. VES were conducted throughout the snake active season and were split between systematic time-constrained searches of four, 25-ha CMR plots and opportunistic surveys of appropriate habitats. Numbers in parentheses represent road-killed individuals.

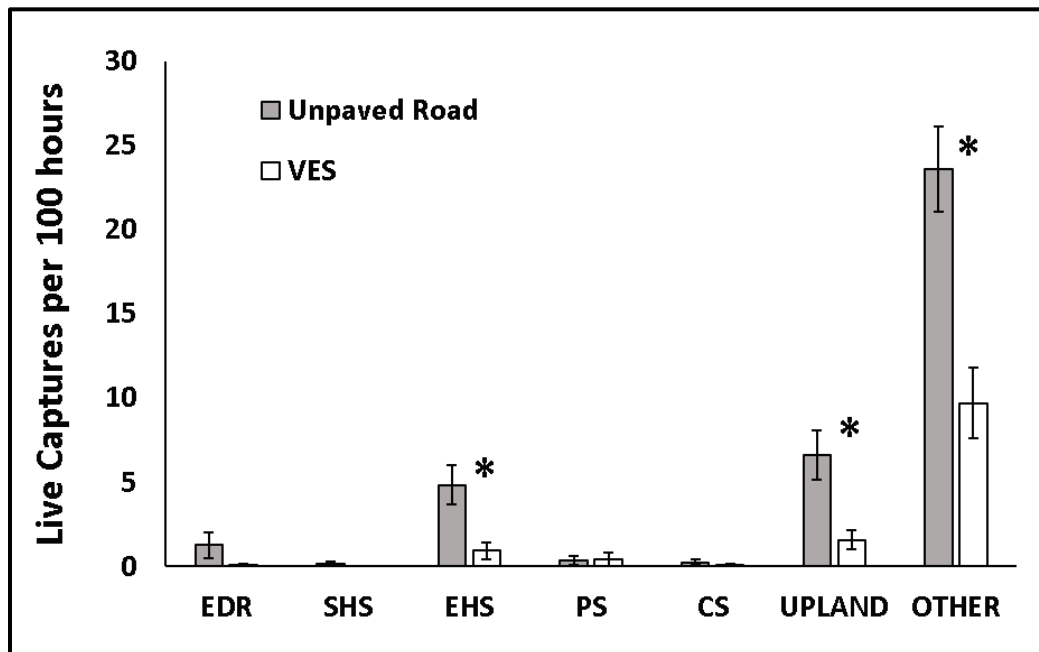
Type	Transect	# Surveys	Hours	Miles	EDR	SHS	EHS	CS	PS	Other
Road	Paved-N	104	85	3,354	0 (1)	—	—	—	—	6 (53)
Road	Paved-S	209	186	6,932	—	—	1	0 (2)	—	16 (78)
Road	Unpaved-NE	112	148	3,041	4	—	7	1	—	27 (1)
Road	Unpaved-NW	65	91	1,980	2	—	5	1	1	23 (1)
Road	Unpaved-SE	201	161	3,386	—	1 (1)	12 (1)	—	—	46 (10)
Road	Unpaved-SW	186	171	3,674	—	—	7 (1)	—	2 (1)	39 (4)
VES	NE Plot	28	56	NA	—	—	1	—	—	7
VES	NW Plot	23	46	NA	—	—	—	—	—	4
VES	SE Plot	21	42	NA	—	—	—	—	1	4
VES	SW Plot	18	36	NA	—	—	1	—	—	2
VES	Opportunistic	140	418	NA	1	—	2	1	1	54
Total Paved Road		313	270	10,286	0 (1)	0	1	0 (2)	0	14 (107)
Total Unpaved Road		564	570	12,082	6	1 (1)	31 (2)	2	3 (1)	74 (12)
Total VES		230	598	NA	1	0	4	1	2	46
Species codes: EDR = Eastern Diamondback Rattlesnake, SHS = Southern Hognose Snake, EHS = Eastern Hognose, CS = Harlequin Coralsnake, PS = Pinesnake, Other = all other snakes combined NA = Not Applicable										

Direct comparison of CPUE between VES and road surveys of unpaved transects revealed substantially higher capture rates for road surveys (Figure 9). Capture rates per 100 survey-hours, averaged across plot/transect-

years, was higher for all cryptic upland species, except for Pinesnakes, for which captures were similar between the methods. These differences were statistically significant for Eastern Hognose (t-test, $t = 2.06$, $df = 14.98$, $p = 0.008$), all upland species grouped together (t-test, $t = 3.22$, $df = 14.185$, $p = 0.006$), and all other snakes species (t-test, $t = 4.23$, $df = 20.70$, $p < 0.001$). Differences in capture rates of other cryptic upland species failed to achieve statistical significance due to small sample size (t-test, all $p > 0.05$). However, average CPUE of EDR was over 8-fold higher for road surveys (0.78 captures per 100 survey-hours) than for VES (0.09 captures per 100 survey-hours).

In total, 102 systematic evening road surveys were conducted between 15 April and 30 June in 2004 and 2005 along the 26 km road transect at Fort Hood, Texas, totaling 249 hrs of survey effort. Those surveys yielded a total of 21 live WRS captures, with a mean encounter rate of 0.086 per survey-hour.

Figure 9. Comparison of average CPUE of snakes between road surveys and visual encounter surveys (VES). Bars represent means across plot/transect-years ± 1 SE. Statistically significant differences (t-test, $p < 0.05$) are indicated with an asterisk (*). EDR = Eastern Diamondback Rattlesnake, SHS = Southern Hognose Snake, EHS = Eastern Hognose, PS = Pinesnake, CS = Harlequin Coralsnake, UPLAND = previous species combined, Other = all other snakes combined.



5.6.2 Snake crossing speed

We timed six natural crossing events of EDR along our unpaved survey transects at Fort Stewart (Table 4). Individuals were relatively consistent in crawling speed, with a mean (SD) speed of 7.30 (1.85) cm/sec. Width of unpaved roads along our transects averaged 8.41 m, based on 30 on-the-ground measurements spaced systematically spaced along our routes. Thus, extrapolated to an 8.41 m road, and considering that a snake is detectable while crawling the width of the road, plus its own body length as it leaves the road, the mean (SD) time that EDR were detectable while crossing was 2.29 (0.41) minutes.

Table 4. Data for timed natural road crossing events of EDRs at Fort Stewart, GA.

Location	Date	Road Type	Snake Total Length (cm)	Distance Crawled (cm)	Time (sec)	Snake Speed (cm/sec)	Time Detectable (min)*
Fort Stewart	11/1/2017	unpaved	135.5	1095	168	6.52	2.50
Fort Stewart	11/8/2017	unpaved	106.7	650	108	6.04	2.62
Fort Stewart	7/12/2019	unpaved	152	148	13	10.99	1.51
Fort Stewart	7/19/2019	unpaved	152	188	29	6.53	2.54
Fort Stewart	8/30/2019	unpaved	146.7	125	17	7.21	2.28
Fort Stewart	9/30/2019	unpaved	60	435	67	6.51	2.31
					Mean	7.30	2.29
					SD	1.85	0.41

* Time detectable on road was calculated as (841 cm + Snake Total Length / Crawling Speed).

For SHS, we used a previously published dataset of nine timed natural road crossing events collected using methodology identical to that used for EDR here (Willson et al. 2018). This dataset yielded a mean (SD) crossing speed of 1.5 (0.6) cm/sec. We extrapolated this speed to the mean width of unpaved roads along our transect to calculate that the mean (SD) time that SHS were detectable while crossing was 11.65 (5.45) minutes. This detection time was considerably longer than that of EDR and WRS (see below), which is not surprising given the small body size and slow rectilinear locative behavior of this species.

Although WRS were not timed crossing during previous research on this species at Fort Hood, we were able to opportunistically collect data on eight natural crossing WRS crossing events during the course of fieldwork at Fort Stewart and elsewhere (Table 5). Mean (SD) crossing speed of WRS was 8.65 (7.88) cm/sec, which was slightly slower and much more variable

than that of EDR. Extrapolated to a mean road width along the survey transect at Fort Hood (10.0 m, measured systematically along the route using aerial imagery in GIS), the mean (SD) time that WRS were detectable while crossing was 3.50 (2.11) minutes.

Table 5. Data for timed natural road crossing events of Western Rat Snakes.

Location	Date	Road Type	Snake Total Length (cm)	Distance Crawled (cm)	Time (sec)	Snake Speed (cm/sec)	Time Detectable (min)*
Florida	8/15/2016	paved	147	513	65	7.89	2.42
Fort Stewart	9/28/2018	unpaved	217	194	23.9	8.12	2.50
Fort Stewart	11/2/2018	unpaved	158	270	26.2	10.31	1.87
Fort Stewart	5/22/2019	unpaved	105	300	89	3.37	5.46
Fort Stewart	7/16/2019	unpaved	142	212	79	2.68	7.09
Fort Stewart	9/29/2019	unpaved	75	200	54	3.70	4.84
Fort Stewart	10/8/2019	unpaved	189	610	96	6.35	3.12
Arkansas	6/1/19	unpaved	150	694	26	26.80	0.72
					Mean	8.65	3.50
					SD	7.80	2.11

* Time detectable on road was calculated as (1000 cm + Snake Total Length / Crawling Speed).

5.6.3 Analysis of snake movement and derivation of movement parameters

We tracked six individual EDR at Fort Stewart via radio telemetry in 2018 and 2019 (Table 6) and supplemented our data with 16 EDR tracked in similar habitats in South Carolina in 2015-2019 (Table 7). The combined dataset represented 35 snake-years of data, with a mixed sex ratio (9M:13F) and an average of 33 (range = 6-85) re-sightings per individual during our focal season of July to November.

Table 6. Summary of radio telemetry data used to parameterize movement models for EDR, Southern Hognose Snakes (SHS), and Western Ratsnakes (WRS).

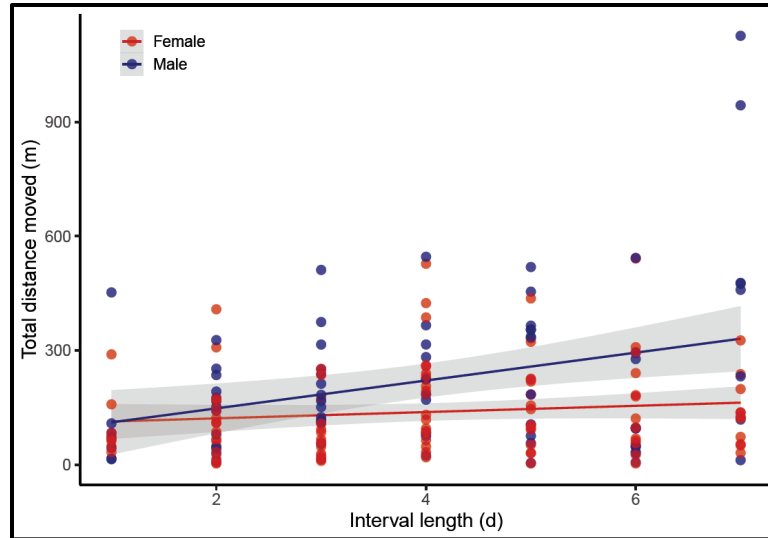
Species	Site	Time Period	N	Sex Ratio (M:F)	Mean # Locations (Range) during Focal Season	Source
EDR	Fort Stewart, Georgia	2018-2019	6	3:3	35 (9-51)	This Study
EDR	FMNF, South Carolina	2015-2019	16	6:10	29 (6-85)	Amphibian and Reptile Conservancy
SHS	North Carolina + South Carolina	1998-2011	18	11:7	21 (7-57)	Willson et al. 2018
WRS	Fort Hood, Texas	2004-2007	44	26:18	45 (18-107)	Sperry et al. 2008, 2009

Table 7. Summary of movement model parameters for EDR, SHS, and WRS.

	Focal Season	Landscape Size (A; km)	Discretization Method	Step Size (SD) (m)	Path Straightness (SD)	Bias towards Home Range (β)	Diel Activity Time (hrs)
EDR male	1 July – 14 Nov	10 x 10	Daily Mean	47.0 (61.9)	0.32	0	8
EDR female	1 July – 14 Nov	10 x 10	Zero-Inflated	36.6 (97.7)	0.32	0.7	8
SHS	14 Sept – 14 Nov	1 x 1	NA	16.9 (13.7)	0.7	0.5	8
WRS	14 Apr – 30 June	26 x 10	NA	76.7 (14.5)	0.7	0.3	24*
*See section 5.5.6 for correction based on survey time							

From these data, we calculated step size (distance between successive re-sightings), and path straightness (turning angle). Greater than daily tracking intervals required that we discretize the EDR step size data to conform to our models 1-day time step. We plotted distance between successive re-sightings against tracking interval for male and female EDR (Figure 10), yielding a positive correlation for males (linear regression; $p = 0.003$, $R^2 = 0.09$), but no correlation for females (linear regression; $p = 0.200$, $R^2 = 0.01$). We interpret the positive correlation as evidence that males make relatively frequent movements during our focal season and thus, we discretized the male step size data by equally dividing the total distance moved among daily movements. We interpret the lack of correlation between distance and tracking interval (up to 7 days) for females as evidence that females make relatively infrequent longer movements. Thus, we discretized the step size data for females by allocating the total distance moved to 1 day within each movement interval and filling in zero distance movements for other days within the interval.

Figure 10. Relationship between time between re-sightings (up to 7 days) and distance moved for EDRs at Fort Stewart, GA, and Francis Marion National Forest (FMNF). Lack of correlation for females indicates that females make infrequent long-distance movements, whereas males make more frequent, shorter movements.



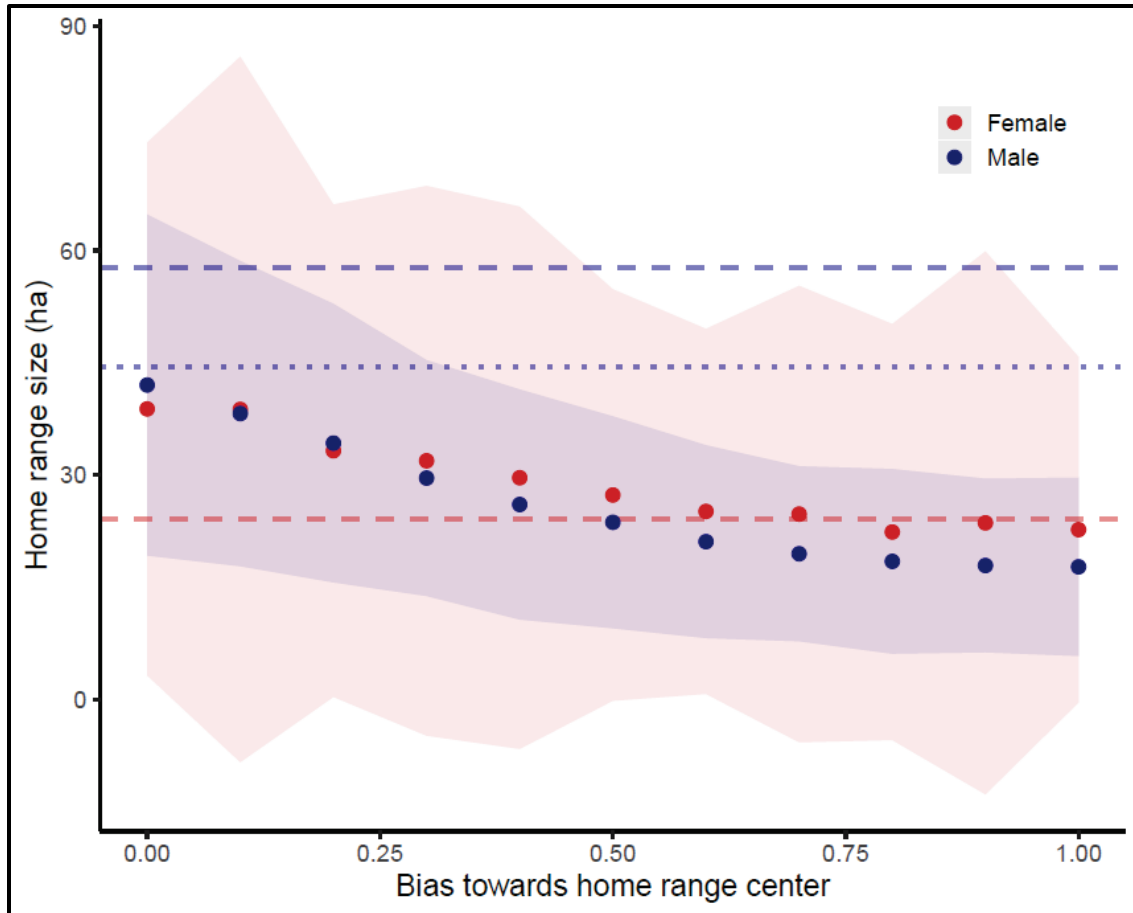
Having calculated all but the orientation towards home range center and/or road from the telemetry data, we conducted a series of simulations to determine the parameterization of β (attraction to home range center) that would produce simulated home ranges that best match our empirical data (Figure 11). For both simulated males and females, increasing β decreased 90-step MCP home range size from ~40-45 ha to 20-25 ha. A β value of 0.7 produced a mean home range size that best matched the observed mean female MCP home range size for August-October of 24.1 ha. For males, even $\beta=0$ underestimated the observed mean MCP home range size. However, excluding one male that had an extremely large home range resulted in a mean observed home range size (44.4 ha) that was a reasonable match for our simulated mean home range size for $\beta=0$ (42.0 ha). Thus, we used $\beta=0$ for males and $\beta=0.7$ for females. Taken together, our parameterization resulted in males moving more frequently and randomly across the landscape than females, resulting in larger MCP home range. This pattern of movement is appropriate, given that late summer is the mating season for EDR, when males are known to wander more widely in search of females (Means 2017).

We tested for attraction to or avoidance of roads for 21 EDR with more than 15 re-sightings, by simulating 1000 random walk paths for each snake and comparing the number of observed road crossings to the frequency distribution of crossing events for simulated paths. Although we found no evidence of attraction to roads, of the 21 snakes, two individuals from

FMNF crossed roads significantly less than expected by chance ($p < 0.025$), and three additional individuals (two from FMNF, one from Fort Stewart) also showed non-significant tendencies towards road avoidance. However, the four individuals from FMNF that tended to avoid roads were all individuals that frequently ranged within 500 m of paved roads, but never crossed (most other individuals at both sites were located well away from paved roads). Similarly, the individual at Fort Stewart that showed a pattern of road avoidance inhabited an area adjacent to a training area with roads that passed through extensive regions of open lawn and barren ground. Thus, for this individual, avoidance of roads was confounded with avoidance of open, human-modified habitats.

Based on the fact that (1) our density estimates focused on unpaved road transects, (2) most of our snakes freely crossed roads typical of our unpaved transects and showed no indication of response (negative or positive) to those roads, and (3) the few individuals that showed evidence of avoidance appeared to be responding primarily to paved roads or extensive modified habitats, we chose to have EDR in density simulations respond neutrally to the simulated road transect. However, our results (Table 8) demonstrate the need to more fully evaluate response to paved roads in future research and incorporate those responses when basing density estimates on surveys of paved road transects.

Figure 11. Simulation results for parameterization of β (orientation to home range center) for male and female EDR. Minimum Convex Polygon (MCP) home range size for Aug-October for simulated snakes (N=1000 per β value; dots =mean; shading = 1SD) at varying levels of β . Dashed horizontal lines represent mean observed MCP home range for (N=21 snake-years) EDR from Fort Stewart, GA, and FMNF. Dotted blue line represents mean male MCP home range excluding one individual with an extremely large home range. To best match observed home range size, we set $\beta=0$ for males and $\beta=0.7$ for females.



Our previous IDEASS research used a radio telemetry dataset of 18 SHS from North and South Carolina (Willson et al. 2018) to derive movement parameters needed to employ IDEASS (Table 9) and evaluate evidence for road behavior. We used those same models to interpret our road survey data for SHS at Fort Stewart.

Table 8. Results of simulations testing for road attraction or avoidance behavior of EDRs tracked via radio telemetry at Fort Stewart (FS), GA, and Francis Marion National Forest (FM), SC. Individuals exhibiting statistically significant avoidance or attraction, indicated by the number of observed road crossings falling into the upper or lower 2.5% of the frequency distribution of number of crossing events from 1000 simulated paths for each snake, are indicated in bold with (**). Those approaching significance are also bolded.

ID	Loc	Sex	No. of Locations	Observed Crossings	Median of Simulations	Range	Road Avoidance Prob ≤ Observed	Road Attraction Prob ≥ Observed
CA01	FS	F	54	11	5	0-20	0.976	0.083
CA02	FS	F	88	6	6	0-24	0.648	0.457
CA04	FS	M	37	0	5	0-20	0.041	1.000
CA05	FS	M	20	0	2	0-10	0.306	1.000
CA06	FS	M	17	2	3	0-10	0.493	0.819
FM01	FM	M	137	16	15	3-38	0.600	0.471
FM02	FM	F	18	2	3	1-11	0.391	0.654
FM03	FM	M	74	6	5	0-22	0.659	0.464
FM04	FM	F	70	16	12	0-31	0.838	0.206
FM05	FM	M	21	0	2	0-9	0.143	1.000
FM06	FM	M	25	1	3	0-12	0.261	0.904
FM07	FM	F	56	7	7	1-21	0.524	0.581
FM08	FM	F	20	1	2	0-9	0.410	0.892
FM11	FM	M	95	6	7	0-22	0.469	0.640
FM12	FM	M	38	0	4	0-17	0.036	1.000
FM13	FM	F	51	3	4	0-16	0.497	0.641
FM15	FM	F	40	0	5	0-16	0.013**	1.000
FM16	FM	F	100	0	6	0-15	0.039	1.000
FM17	FM	F	95	0	7	0-23	0.021**	1.000
FM18	FM	F	125	10	7	0-38	0.727	0.331
FM19	FM	M	25	4	3	0-11	0.784	0.367

For WRS at Fort Hood, Texas, we followed the procedure outlined for EDR above to generate movement parameters (Table 7), based on a previously-collected database of 49 individual WRS, with an average of 45 (range = 18-107) re-sightings per snake during our focal season of mid-April to June (Table 6). We tested for behavioral response to roads using the same procedure outlined above for EDR. However, many of the WRS were located far enough away from roads that neither the snakes nor random walk paths encountered roads frequently enough to make analyses meaningful. Of the 18 individuals that were located close enough to roads to be meaningful, none showed any evidence of avoiding roads (Table 9). Three individual WRS showed a pattern of crossing roads more frequently than expected by chance, but their degree of attraction to roads did not reach the level of statistical significance (Table 9). Given that ratsnakes are

known to select edge habitats (Blouin-Demers and Weatherhead 2001), it is not unexpected that they could be attracted to roadside habitats. Yet, we did not feel that our evidence for attraction was strong enough to warrant including this effect in our movement models.

Table 9. Results of simulations testing for road attraction or avoidance behavior of Western Ratsnakes (WRS) tracked via radio telemetry at Fort Hood, TX. Individuals exhibiting statistically significant avoidance or attraction, indicated by the number of observed road crossings falling into the upper or lower 2.5% of the frequency distribution of number of crossing events from 1000 simulated paths for each snake, are indicated in bold with (). Those approaching significance are also bolded.**

ID	Sex	No. of Locations	Observed Crossings	Median of Simulations	Range	Road Avoidance Prob ≤ Observed	Road Attraction Prob ≥ Observed
x181	M	184	2	2	0-15	0.550	0.574
x120168	M	278	8	4	0-21	0.768	0.290
x170	F	192	11	5	0-23	0.918	0.104
x541521	M	300	0	7	0-65	0.130	1.000
x240	F	147	5	4	0-29	0.632	0.430
x257	F	55	6	2	0-11	0.948	0.086
x339	M	74	5	2	0-17	0.816	0.238
x420	M	133	5	4	0-20	0.658	0.488
x582	F	109	12	4	0-17	0.958	0.064
x621	M	146	8	2	0-15	0.952	0.082
x703	F	144	13	6	0-20	0.966	0.054
x150	M	58	3	2	0-11	0.770	0.384
x930	M	28	8	2	0-11	0.980	0.032
x957	M	72	5	2	0-11	0.904	0.154
x337930	F	194	0	0	0-4	0.994	1.000
x019	M	64	4	3	0-28	0.696	0.408
x19	M	105	1	0	0-12	0.674	0.482
x462440	M	346	8	4	0-25	0.780	0.264

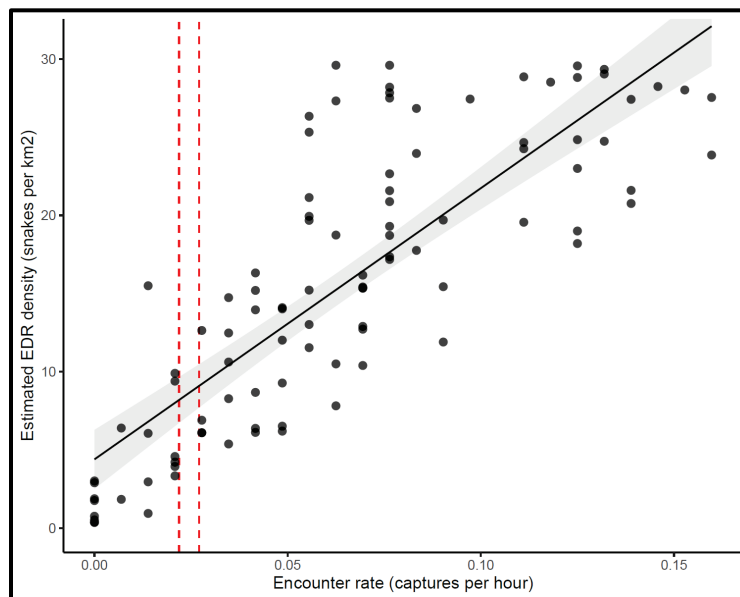
5.6.4 Density estimation using IDEASS

Simulation of our fully parameterized individual-based movement model for EDR yielded a predicted relationship between encounter rate during road surveys and density (Figure 12). By including a stochastic observation process within the simulation, this relationship also estimated a CI reflecting variation in numerous model parameters, stochasticity, and uncertainty resulting from infrequent detections relative to survey effort.

We plotted the average encounter frequencies of EDR from our two unpaved road transects where that species was detected, yielding estimated EDR densities of 9.10 (95% CI = 7.69-10.50) and 8.20 (95% CI = 6.71-

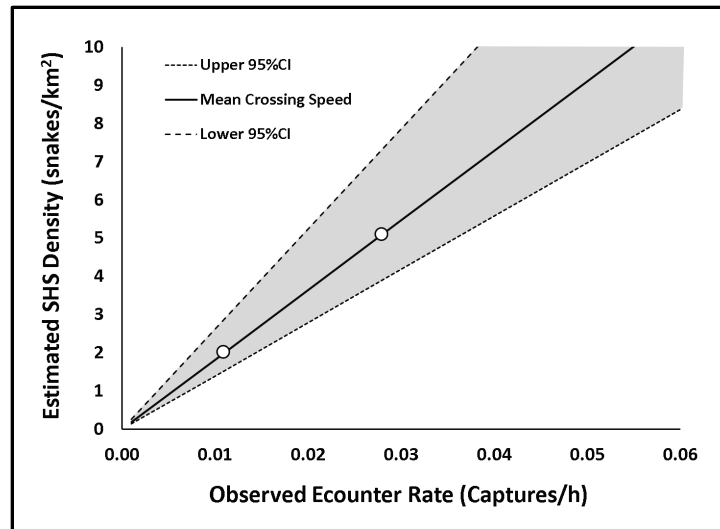
9.69), along those transects. Considering that the sandy uplands in the northern section of Fort Stewart (where all of our EDR detections occurred) encompass $<75 \text{ km}^2$, we estimate that the total adult population size of EDR in that region between 500 and 800 individuals. Our lack of EDR detections in the southwestern portion of the base precluded estimation of abundance there. However, given the large amount of survey effort we expended in the southwest (Table 3), we expect the EDR densities are much lower there than in northern portions of the base. Alternatively, EDR might move differently or avoid roads in southwestern portions of the base.

Figure 12. Relationship between encounter rate and estimated density of EDR, bounded by the 95% CI, based on 100 simulations of varying densities. Vertical red lines indicate mean observed encounter frequencies along our two unpaved road transects where EDR were captured (0.027 and 0.021 live EDR per survey-hour), which correspond to estimated densities of 9.10 and 8.20 EDR per km^2 along those transects, respectively.



Adjusting our previous IDEASS model for SHS (Willson et al. 2018) to represent our surveys at Fort Stewart yielded a predicted relationship between encounter rate during road surveys and density (Figure 13).

Figure 13. Relationship between encounter rate and estimated density of Southern Hognose Snakes (SHS), bounded by the 95% CI of observed road crossing speeds, based on IDEASS models modified from Willson et al. 2018. Open circles indicate estimated densities at the mean observed encounter frequency (0.011 live snakes per hour) along the one unpaved road transect at Fort Stewart where SHS were captured and within the constrained ~4 km section where all SHS records occurred. Thus, mean estimated density of SHS is 2.0 (95% CI: 1.5 – 2.8) per km² along the entire transect or 5.1 (95% CI: 3.9 – 7.3) snakes per km² within the apparently restricted area of occupied habitat.



Our road surveys at Fort Stewart only yielded one live SHS capture (Table 3), located on our eastern unpaved road transect in the southwestern portion of the base. This is the same area where our other two SHS detections (one roadkill, one on an opportunistic VES) occurred during the study, and all were found within 2.5 km of one another. Considering only road surveys conducted during our focal season for SHS (1 September to 14 November), we expended 88.59 hrs of survey effort along that transect, resulting in a mean encounter rate of 0.011 SHS per survey-hour. Matching this encounter frequency to our density relationship yields an estimated SHS density along our southeastern unpaved road transect of 2.0 per km² (0.020 ha⁻¹), with a range of 1.5–2.8 per km² across the 95% CI of snake crossing speed. Given the spatial clustering of records, however, it is likely that SHS only are present within a small area of that transect but occur at higher densities there. If we estimate that SHS are only found along ~4 km of that transect, approximately 40% of the survey effort on that transect likely occurred in areas where SHS are not present. Correcting our effort to account for this, raises our density estimate within the small area occupied by SHS to 5.1 (95% CI: 3.9 – 7.3) per km². Even this density within the small area of occupied habitat is substantially lower than the densities estimated by our previous work in the North Carolina Sandhills (17 per km²; Willson et al. 2018). Given the extremely restricted range of

SHS on base and the low-density estimate we obtained, it is likely that the total adult population size of SHS on Fort Stewart is <100 individuals and may be as low as 30 adult individuals if the isolated cluster of observations we identified within a ca. 6 km² area is indeed the only extant population on base.

An IDEASS model, parameterized using extensive existing radio telemetry dataset for WRS at Fort Hood, TX, allowed us to generate a robust predicted relationship between encounter frequency of WRS during road surveys and density (Figure 14). This relationship had a considerably shallower slope than the relationship for EDR (Figure 12), indicating that although WRS are much more common, their individual detection probability during road surveys is lower. For example, at a mean encounter frequency of 0.1 per survey-hour, estimated density of WRS (~45 per km²) would be approximately twice that of EDR (~20 per km²; Figure 12). At our mean observed encounter frequency of 0.086 per survey-hour at Fort Hood, the estimated density of WRS is 33.3 (95% CI = 32.4-34.2) per km².

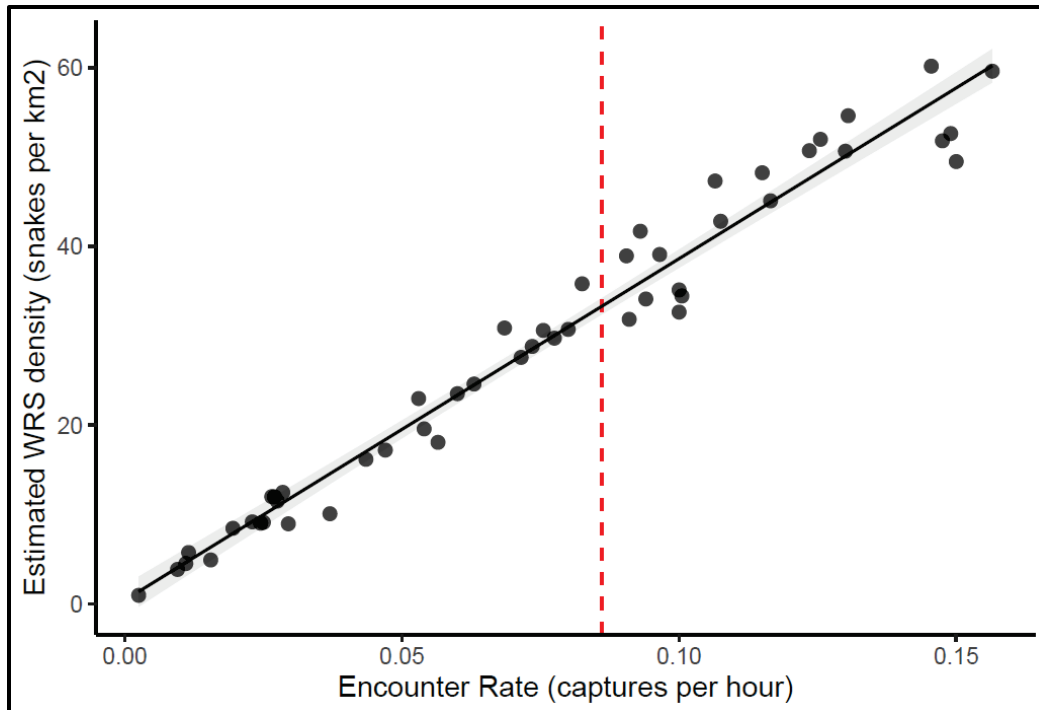
5.6.5 CMR density estimation

Across 82 systematic VES (164 person-hours) of four 25-ha plots at Fort Stewart, we failed to capture any EDR or SHS (Table 3). Including opportunistic VES resulted in one EDR capture but zero recaptures (Table 3). CMR density estimation fails completely with no captures at all. Even when we included all captures and simplified our CMR encounter matrix to one site-wide analysis and year as our survey unit (the simplest possible data formulation that conforms to CMR format), Program MARK yielded an error message, indicating that the model had failed to converge.

Extensive, but opportunistic, surveys for WRS at Fort Hood in 2004-2009 using a wide array of field techniques yielded 119 WRS captures, but zero recaptures. Similar to EDR, when inputted into Program MARK, the program yielded an error message, indicating that the model had failed to converge.

Thus, VES/CMR failed to yield any meaningful information on population density for any of our target species.

Figure 14. Relationship between encounter rate and estimated density Western Ratsnakes (WRS), bounded by the 95% CI, based on 50 simulations of varying densities. Vertical red lines indicate mean observed encounter frequencies along our survey transect at Fort Hood (0.086 live snakes per hour), which corresponds to a mean estimated density of 33.3 WRS per km².



6 Performance Assessment

PO1: Compare encounter rates generated from traditional plot/transect-based visual encounter surveys (VES) to those generated via effort-corrected road surveys. We predicted that road surveys would be more effective for capturing snakes, especially cryptic upland species, than traditional VES/CMR surveys. Surveys of our four unpaved road transects yielded relatively high capture rates of snakes overall (Total = 178 live captures), including 43 captures of cryptic upland species such as EDR, SHS, Eastern Hognose, Pinesnake, and Harlequin Coralsnake. A total of six live EDR were captured on surveys of unpaved roads, as well as one live and one road-killed SHS. These SHS captures were the first records of this species at Fort Stewart in over a decade. Systematic VES of CMR plots were ineffective yielding only 20 total snake captures across 140 surveys (280 survey-hours) and no captures of EDR or SHS. Opportunistic VES were somewhat more effective, but only yielded on EDR capture and zero SHS captures. Direct comparison of CPUE between VES and road surveys of unpaved transects revealed substantially higher CPUE for road surveys. Capture rate per 100 survey-hours, averaged across plot/transect-years, was higher for all cryptic upland species, except for Pinesnakes, for which captures were similar between the methods. These differences were statistically significant for Eastern Hognose (t-test, $t = 2.06$, $df = 14.98$, $p = 0.008$), all cryptic upland species grouped together (t-test, $t = 3.22$, $df = 14.185$, $p = 0.006$), and all other snakes species (t-test, $t = 4.23$, $df = 20.70$, $p < 0.001$). Differences in capture rates of other cryptic upland species failed to achieve statistical significance due to small sample size (t-test, all $p > 0.05$). However, average CPUE of EDR was over 8-fold higher for road surveys (0.78 captures per 100 survey-hours) than for VES (0.09 captures per 100 survey-hours). Thus, we consider this objective met for IDEASS.

PO2: Use IDEASS to generate meaningful estimates of density for Eastern Diamondback Rattlesnakes (EDR) at Fort Stewart, GA, and compare to traditional CMR. Based on previous research on EDR and our own experiences at other field sites, we expected EDR to be common enough at Fort Stewart, and detectable enough during VES, to allow for a side-by-side comparison of IDEASS and CMR approaches for estimating density. Unfortunately, this turned out not to be the case. We only captured a total of 11 live EDR in the course of our fieldwork at Fort Stewart. Of those, four were incidentally captured while conducting radio

telemetry or based on a reliable report from base biologists. Of the remaining captures, six were on systematic road surveys and only one was on a VES. With only one VES capture and no recaptures, CMR density estimation failed completely for this species. However, based on our six road captures we were able to generate density estimates for EDR along our two northern unpaved road transects using IDEASS: 9.10 (95% CI = 7.69-10.50) and 8.20 (95% CI = 6.71-9.69) EDR per km², for our northeast and northwest routes, respectively. Based on long-term snake CMR studies (5 to 17 yrs), we suggest that meaningful estimates (95% CI) for snakes should range from 50 to 150% of the estimated population (e.g., King 1986, Lind et al. 2005). The 95% CIs around our density estimates were narrower than this criterion. Moreover, although we could not directly validate our density estimates against those from CMR, our estimates are not far below the only two comparable (inland locality) density estimates that are available for this species: 11.2 per km² for Pinellas Co., Florida and 12 per km² from Tall Timbers Research Station, Florida (Means 2017). Given that these were very rough estimates of density (Means 2017), and given the apparent scarcity of this species, we consider our estimates to be very reasonable. Thus, we conclude that this objective was partially met, given that IDEASS was able to produce two independent meaningful and plausible estimates of EDR density at Fort Stewart, but direct comparison between IDEASS and CMR was not possible, due to the inability of CMR to produce an estimate.

PO3: Generate meaningful estimates of density for Southern Hognose Snakes (SHS) at Fort Stewart. SHS are one of the rarest snakes in the United States and have declined dramatically in recent decades (Tuberville et al. 2000, Beane et al. 2014). However, due to their extremely secretive and fossorial behavior, essentially nothing is known about their population densities (Willson et al. 2018). SHS are extremely rare at Fort Stewart, being known from less than 10 historical records prior to our study. Our surveys yielded three SHS captures (one live and one dead individual on systematic road surveys and one during an opportunistic VES). These were the first individuals that have been found on Fort Stewart in at least a decade and all were found within 4 km of one another. With zero captures during extensive systematic VES surveys of delineated plots and no recaptures, CMR models failed to converge, yielding no information on abundance/density of this species. Conversely, inputting our road survey data into previously constructed IDEASS models for this species (Willson et al. 2018) allowed us to construct a relationship

between road encounter frequency and estimated SHS density for Fort Stewart and estimate that average SHS density along our southeastern unpaved road transect was 2.0 per km², with a range of 1.5–2.8 per km² across the 95% CI of snake crossing speed. Further constraining our analysis to the approximately 4 km section of that transect that is apparently occupied by SHS raised our density estimate within that small area to 5.1 (95% CI: 3.9 – 7.3) per km². These density estimates meet our pre-defined definition of ‘meaningful’ (95% CI narrower than 50–150% of the mean). Thus, we consider this objective met for IDEASS, but not for CMR.

PO3: Generate meaningful estimates of density for Western Ratsnakes (WRS) at Fort Hood Texas using an existing data. We predicted that we would be able to apply IDEASS to retroactively estimate density of WRS at Fort Hood based on an existing dataset of road captures and radio telemetry, but that CMR would fail to perform adequately for this application. We were able to generate a robust relationship between road encounter frequency and density for WRS using IDEASS, yielding a density estimate of 33.3 (95% CI = 32.4–34.2) WRS per km² at our mean observed encounter frequency of 0.086 per survey-hour. This estimate meets our criteria of being a meaningful snake density estimate. Moreover, it is well within published density ratsnake density estimates, which include 28 per km² in Maryland (Stickle et al. 1980) and 91 per km² in Kansas (Fitch 1963). As predicted, however, CMR density estimation failed completely for this species, based on lack of recaptures. Thus, we consider this objective to be met for IDEASS, but not for CMR.

PO5: Quantify relevant ecological data on Diamondback Rattlesnakes. Practitioners of both IDEASS and VES/CMR incidentally collect data beyond just those observations used in abundance estimation. For instance, application of IDEASS entails extensive road surveys and frequent radio telemetry. The IDEASS model requires data inputs regarding road encounter frequency and certain movement metrics – but the collected data can inform investigation of distribution, demography, habitat selection, and other relevant ecological questions. Similarly, CMR studies entail repeated surveys and can generate multiple encounters with the target species as well as non-target species. These data are used for abundance estimation but also provide information on demographic parameters and microhabitat selection.

Here, we list several ecological metrics often associated with studies of imperiled snakes on installations and determine whether, during the course of IDEASS or VES/CMR application, we generated the data needed to analyze each metric. For each metric, we consider two questions: (1) does the method have the potential to generate data for that metric, and (2) were we able to generate sufficient data to conduct an analysis using that metric in the course of our demonstration at Fort Stewart, GA. For example, radio telemetry associated with IDEASS generated approximately 250 re-sightings of EDR, providing the foundation for a use vs. availability macrohabitat selection study. Our VES/CMR surveys yielded only one EDR encounter, which is not a robust enough sample size for a macrohabitat selection study. Even if it were enough, the placement of study plots within particular habitats would bias such an analysis.

We selected eight ecological metrics associated with snake studies (Table 10). We judged whether IDEASS, CMR, or both, had the potential to generate data related to each of these metrics and then scored the metrics that were actually addressed through our research on EDR and SHS at Fort Stewart. IDEASS could theoretically provide the data needed for all eight of the metrics, whereas CMR had the potential to generate data for half (four of eight) metrics. During the course of our study, IDEASS generated enough meaningful data for seven of the ecological attributes, whereas CMR failed to generate enough data to address any of the metrics. Thus, we consider this performance metric met for IDEASS.

Table 10. Comparison of relevant ecological data generated with IDEASS versus VES/CMR.

	IDEASS: possible	IDEASS: accomplished	CMR: possible	CMR: accomplished
Distribution and occupancy data	Yes: road surveys generate especially explicit encounters	Yes: spatially explicit encounters for 14 EDR plus telemetry data	Yes: repeated visual surveys can generate spatially explicit encounters	No: Only one spatially explicit EDR encounter on surveys
Annual Mortality / Survival Rates	Yes: repeated telemetry of individuals provides data for known fates analysis	Yes: 247 telemetry locations acquired	Yes: can estimate survival rates with sufficient recaptures, but these estimates may be confounded by movement out of survey plots	No: no recaptures documented during study
Road Mortality Rates and Locations	Yes: simply need to document location and times of road mortality	Yes: six EDR road mortalities observed with dates and locations	No: surveys do not take place on roads and would be very rare to encounter dead EDR during survey	No

	IDEASS: possible	IDEASS: accomplished	CMR: possible	CMR: accomplished
Seasonal variation in movement patterns	Yes: telemetry provides distance moved per day, movement frequency, and home ranges for all tracked snakes	Yes: telemetry provides distance moved per day, movement frequency, and home ranges for all tracked snakes	No: Some movement parameters can be deduced from repeated encounters but violates many assumptions of spatial ecology	No
Habitat Selection: Macrohabitat	Yes: telemetry provides use of each habitat related to its availability on landscape	Yes: telemetry provides use of each habitat related to its availability on landscape	No: Encounters are biased due to plots only occurring in certain types of macrohabitat	No
Habitat Selection: Microhabitat	Yes: radio telemetry data provides these data with each tracking event	Yes: radio telemetry generated 248 snake locations and associated habitat	Yes: if enough encounters are recorded	No: while CMR could provide these data, our encounters were insufficient
Demographic Data: Age and size class distribution, sex ratio, proportion gravid	Yes: if enough encounters are recorded	No: limited evidence provided by road encounters, but sample size was minimal (14)	Yes: if enough encounters are recorded	No: Although possible, would rely upon large number of encounters and we only generated 1
Specimens for museum vouchers, dissection for diet contents, parasite loads, etc.	Yes: Road-killed specimens can be used, without needing to sacrifice animals	Yes: one road-killed specimen each of EDR and SHS, and numerous specimens of other species collected	No: Collection of specimens would require sacrifice of healthy study animals	No

PO6: Compare costs associated with application of IDEASS and CMR. See chapter 7.

7 Cost Assessment

7.1 Cost model

To estimate the cost of using IDEASS and CMR to estimate density of cryptic snake species, we quantified the cost of field data collection at Fort Stewart. We considered two scenarios based on our data: (1) EDR, a low-density and extremely cryptic species, and (2) Eastern Hognose, a much more common (higher density), yet still highly cryptic upland snake species. Based on our successful application of IDEASS to EDR with six captures, we assume a minimum sample size of six snake captures needed for IDEASS to fully succeed. Generating a density estimate using CMR requires a number of snake encounters to capture and mark individuals and then a number of subsequent recaptures to evaluate the ratio of unmarked snakes to marked snakes. It is impossible to know how many captures are needed to generate the required number of recaptures for a given species because recapture probabilities depend on factors such as behavior, movement patterns, and survival. Thus, we conservatively set a target of 20 snake encounters as a minimum number needed to employ CMR. However, there is no guarantee that this sample size would yield the critical number of recaptures needed to permit a CMR density estimate, and most successful snake CMR studies have involved sample sizes greater than our threshold of 20 by an order of magnitude or more.

7.1.1 IDEASS and CMR

7.1.1.1 *Costs associated with data analysis*

Both techniques require data analysis after field data collection. However, we assume that the labor associated with analyses for each method are equivalent and offset one another; thus, we do not quantify those costs here. While IDEASS likely requires more analytical methods, this does not directly translate to a higher cost for future practitioners, who will be able to modify the code provided by this demonstration to streamline analyses. CMR analyses require user familiarity with either Program MARK or Program R, and IDEASS modeling requires familiarity with Program R.

7.1.1.2 *Costs associated with each encounter for each method for EDR*

Because both IDEASS and CMR are based on encounters with focal species, we begin our cost analysis by calculating the costs associated with

each encounter for each method for EDR (Table 11). Encounter data were data gathered during the course of this demonstration. We also calculate the cost of radio telemetry equipment and the labor cost of tracking a sample of snakes.

Table 11. Cost model for estimation of EDR density using IDEASS.

Cost Element	Data Tracked	Formula	IDEASS	Total Cost
Mileage per encounter	Miles driven in POV per encounter with snake	# miles X \$0.575	2,095 X \$0.575	\$ 1,204.63
Observer labor per encounter	Labor, time	Labor Rate X Hours	\$15.00/hr X 99 hrs	\$1,485.00
Total cost per snake	Mileage, effort (hrs)	Mileage + Labor	\$1,204.63 + \$1,485.00	\$2,689.63
Materials	Radio-transmitters	Cost of transmitter X no. of snakes	\$300 X 6	\$1,800
	Radio receiver	Cost of one unit	\$895 X 1	\$895
	Transmitter implantation surgery	Cost of surgery from veterinarian office	\$250 X 6	\$1,500
	Antenna, cables, and batteries	Cost of antenna, three cables, and rechargeable batteries	\$185	\$185
Total cost of materials	All materials	Sum of all materials	\$1,800 + \$895 + \$1,500 + \$185	\$4,380
Labor for tracking snakes	Hours per tracking event, snakes tracked, labor cost	Hours X Labor X Snakes X No. of tracking events	2 X \$15.00 X 6 X 120	\$21,600
Total Cost for six Snakes	Total cost per snake encounter, Materials, Labor for tracking 6 snakes	Total cost per snake encounter X 6 + Materials + Labor for tracking 6 snakes	\$2,689.63 X 6 + \$4,230 + \$21,600	\$42,117.78

7.1.2 IDEASS

7.1.2.1 Driving and labor costs

Generating encounters via IDEASS requires driving surveys, which entails a cost per mile as well as labor. During our demonstration, we drove 12,573 mi of surveys on unpaved roads and generated six encounters with EDR at a cost of \$0.575/mi. This required 594 hrs of technician labor time at a cost of \$15/hr. This resulted in an average of 99 hrs of labor and 2,095 miles driven per encounter with this low-density species. Fortunately, six encounters were sufficient to populate the IDEASS model and generate independent density estimates for this species at two locations on Fort Stewart. Although each encounter with an EDR required approximately \$2,700 in mileage and labor, the objective was clearly met. Additional encounters would improve our model but were not necessary.

7.1.2.2 Costs of radio telemetry materials

IDEASS relies upon radio telemetry, which can be a costly endeavor. Each snake that is tracked requires a radio-transmitter to be implanted within its body cavity. The transmitters we used (Holohil Systems Ltd, SI-2 transmitters) were priced at \$300 per unit. Implanting radio-transmitters requires a surgery performed by an accredited veterinarian. The cost of our surgeries was \$250 per snake. Telemetry then requires a radio receiver (Communications Specialists R1000), antenna, and associated coaxial cables and batteries for an additional \$895, \$150, and \$35, respectively. The total cost of materials to track six EDRs was \$4,830.

7.1.2.3 Costs associated with labor for radio telemetry

We assumed a mean time of 2 hrs per tracking event, per snake. This included locating the snake, recording data, and exiting the area. Based on the amount of radio telemetry conducted during the course of our demonstration, we consider an ideal target to be 120 tracking events per snake, representing one location every other day during the 4-month focal season for 2 years. At an hourly technician rate of \$15.00/hr and six individual snakes, this is a total of 720 radio-tracking events, costing approximately \$21,600 (Table 12).

Table 12. Cost model for estimation of Eastern Hognose density using IDEASS.

Cost Element	Data Tracked	Formula	IDEASS	Total Cost
Mileage per encounter	Miles driven in POV per encounter with snake	# miles X \$0.575	390 X \$0.575	\$224.25
Observer labor per encounter	Labor, time	Labor X Hours	\$15.00/hr X 18 hrs	\$270.00
Total cost per snake	Mileage, effort (hrs)	Mileage + Labor	\$1204.63 + 1485	\$494.25
Materials	Radio-transmitters	Cost of transmitter X no. of snakes	\$300.00 X 6	\$1,800
	Radio receiver	Cost of one unit	\$895 X 1	\$895
	Transmitter implantation surgery	Cost of surgery from veterinarian office	\$250 X 6	\$1,500
	Antenna, cables, and batteries	Cost of antenna, three cables, and rechargeable batteries	\$185	\$185
Total cost of materials	All materials	Sum of all materials	\$1,800 + \$895 + \$1,500 + \$185	\$4,380
Labor for tracking snakes	Hours per tracking event, snakes tracked, labor cost	Hours X Labor X Snakes X No. of tracking events	2 X \$15.00 X 120 X 6	\$21,600
Total Cost for six Snakes	Total cost per snake encounter, Materials, Labor for tracking 6 snakes	Total cost per snake encounter X 6 + Materials + Labor for tracking 6 snakes	\$494.25 X 6 + \$4,230 + \$21,600	\$28,945.50

7.1.2.4 Cost per capture of eastern hognose

Eastern Hognose were encountered much more frequently than EDR, requiring on 390 miles and 18 hrs of labor per capture. Thus, total cost per capture of Eastern Hognose was only \$494.25.

7.1.2.5 Materials and labor for radio telemetry of eastern hognose

Costs associated with radio telemetry of six Eastern Hognose are identical to those described for EDR, above (Table 13).

Table 13. Cost model for estimation of EDR density using VES/CMR.

Cost Element	Data Tracked	Formula	Capture-Mark-Recapture	Total Cost
Observer labor per encounter	Labor, time	Labor X Hours	\$15.00 X 600	\$9,000.00
Materials	Miscellaneous equipment	Costs of tongs, 20 PIT tags, GPS unit	Sum of all equipment costs	\$450
Total Cost for 20 snakes	Cost per snake, no of snakes needed, materials cost	Cost per Snake X No. Encounters + Materials cost	\$9,000 X 20 + \$450	\$180,450

7.1.3 CMR

7.1.3.1 Snake encounters and recaptures

During our demonstration it took approximately 600 hours of VES to encounter only one single EDR. If we assume 20 encounters would be minimally necessary to successfully employ CMR, the total expenditure would be 12,000 hours, for a cost of \$180,000. It should also be noted that this cost accounts only for time spent actually searching for snakes in the field and does not include associated time and vehicle costs of traveling to and from sites.

7.1.3.2 Materials

CMR requires minimal equipment. Observers likely need a handheld GPS unit (~\$100) to ensure they stay within designated plots. Observers likely use snake hooks or snake tongs (~\$150) to help move debris and cover objects and to capture snakes upon encounter. Likewise, snakes must be marked in some way. This can be done with PIT tags (~\$10 each) or cauterization of ventral scales or tail painting (minimal cost).

Table 14. Cost model for estimation of Eastern Hognose density using VES/CMR.

Cost Element	Data Tracked	Formula	Capture-Mark-Recapture	Total Cost
Observer labor per encounter	Labor, time	Labor X Hours	\$15.00 X 149.5	\$2,242.50
Materials	Miscellaneous equipment	Costs of tongs, 20 PIT tags, GPS unit	Sum of all equipment costs	\$450
Total Cost for 20 snakes	Cost per snake, no of snakes needed, materials cost	Cost per Snake X No. Encounters + Materials cost	\$2,242.20 X 20 + \$450	\$45,300

7.1.3.3 Snake encounters and materials

Our 600 hrs of VES at Fort Stewart yielded four captures of Eastern Hognose, yielding an average of 149.5 hrs of labor needed per capture (Table 14). If we assume 20 encounters would be minimally necessary to successfully employ CMR, the total expenditure would be 2,990 hrs, for a cost of \$44,850. The materials cost is the same as for EDR, above.

7.2 Cost drivers

The cost and utility of IDEASS and CMR is ultimately dictated by the rarity (or density) of the focal snake species. Snakes that are particularly rare, occur in low densities, or are very difficult to find in the field will require enormous inputs of time and associated labor costs. It should be noted that most (maybe all) efforts to estimate the density of snakes on DoD installations are aimed at imperiled snake species that are by definition, rare (e.g., Indigo Snakes, Mexican Garter Snakes, Louisiana Pine Snakes). Studies aimed at exceedingly rare species will need to rely on extremely high levels of effort to generate the encounters necessary for density estimation techniques. The majority of the cost of a CMR study is for the labor associated with generating encounters of snakes. IDEASS, on the other hand, is split relatively evenly between costs associated with generating snake encounters (labor and mileage) and radio telemetry. The cost of radio telemetry is constant regardless of the rarity of the snake species, but the costs associated with generating encounters can decrease significantly for both methods when the species is more common. This was especially apparent when IDEASS was applied to the Eastern Hognose Snake, a species that occurs in more moderate densities, but still remains cryptic.

7.3 Cost analysis and comparison

We compared the costs associated with IDEASS vs. CMR under two scenarios: a very low-density snake (EDR) and a moderately low-density

snake (Eastern Hognose). IDEASS will always have a hard floor in cost associated with the need to conduct a radio telemetry data. The rest of the cost will fluctuate dramatically depending on how much effort is needed to generate snake encounters. This effort will always be less than CMR and the cost will scale based upon the rarity of the focal snake species. In both scenarios, IDEASS generates density estimates with fewer snake encounters and at a lower cost relative to CMR. Additionally, there is no guarantee that CMR will ever be able to generate enough recaptures to make a density estimate feasible for particularly low-density snakes regardless of the effort applied to the endeavor.

7.3.1 IDEASS

The goal of conducting both a CMR and an IDEASS study was to generate density estimates for a species at a location. Both approaches rely upon building encounters with snakes: CMR uses VES and IDEASS uses road surveys. Our demonstration of these two approaches using the EDR on Fort Stewart, GA showed that collecting all of the raw data needed to generate an IDEASS estimate from scratch costs approximately \$42,000 plus labor associated with analyses. This includes thousands of miles of road surveys, hundreds of hours of technician labor, and led to conduct a radio telemetry study for an entire active season. The cost will increase if the snake is rarer or occurs in lower density and the cost will be reduced if the snake species of interest is more easily encountered. In this regard, cost analysis for Eastern Hognose is informative. Though still cryptic, Eastern Hognose were much more frequently encountered during our surveys and the costs associated with capture were greatly reduced compared to EDR. For Eastern Hognose, the primary cost driver is labor associated with radio telemetry and the overall cost associated substantially reduced to under \$30,000 for six snakes.

The costs to conduct an IDEASS study can be broken into two categories: cost per snake encounter and radio telemetry.

Cost per snake encounter is a function of the density of snakes, the rate at which they are encountered, and effort (mileage and hours). By increasing survey effort, more encounters can be generated. The more encounters that are generated, the more robust the density estimate. Fortunately, a robust IDEASS density estimate can be generated with fewer than 10 snake encounters and this does not require a single recapture. The cost associated with radio telemetry is driven by the number of individuals tracked.

Each additional individual included in the radio telemetry study has an equipment cost, surgery implantation cost, and the cost of labor associated with tracking the animal. Studies can rely upon existing data for species of interest if it occurs in a similar geographic region and if movement parameters are not expected to vary much. IDEASS generally needs intense radio telemetry data for a small number of individuals (5-10) during the same season that road surveys occur. Long-term radio telemetry studies are not needed.

Our demonstration suggests that an IDEASS approach for a relatively secretive, low-density snake can be conducted at a new site for approximately \$56,000. Using existing datasets can reduce this cost substantially if such data are available.

7.3.2 Capture-mark-recapture

The primary cost driver of CMR studies is the labor associated with generating encounters. We use this method for secretive, low-density snakes, so many hours are often expended to generate encounters during effort-control VES. We found that 600 hrs of effort were needed to generate a single encounter with an EDR on Fort Stewart. Unfortunately, CMR requires not just encounters but encounters with previously marked individuals. This necessarily requires a much larger number of encounters than to allow for some ratio of those individuals to be previously marked. While we can only guess what it would take, we assume that 20 EDR encounters would generate a sufficient ratio of recaptures to generate a density estimate. By our demonstration, this would require 12,000 hrs of visual encounter survey effort, leading to a cost of approximately \$180,000. For snakes that occur in high densities or that do not have secretive natures, this cost could substantially be reduced. CMR is likely a cost-effective method for documenting the density of certain species of snake, but for secretive snakes that are typically of conservation concern, CMR is unlikely to generate meaningful estimates even if extremely large amounts of effort are expended.

8 Implementation Issues

Our demonstration illustrates the applicability of IDEASS for estimating density of secretive and/or rare snake species and confirms that traditional VES/CMR studies are infeasible for these species. Due to the complete failure of VES/CMR for our species, there is still a great need to validate the IDEASS method with a species that is tractable via both methods. Yet, the density estimates we obtained for EDR and WRS were plausible, within the range of published density estimates for those species, and in line with our perceptions of relative abundance of those species at our study sites, relative to other locations where we have worked with these species. Thus, IDEASS shows strong promise for understanding the status, conservation, and management of a variety of species; in some cases, IDEASS could be used to generate approximations of density using existing data sources. Resulting data could be used to assist with regulatory consultations, such as Chapter 7 consultations under the ESA (16 U.S.C. 1531-1544, 87 Stat. 884) and estimating “Take” of training and testing missions that may affect listed species. With the aforementioned assumptions in mind, we have several specific recommendations for implementing this method on DoD lands. Specifically, we discuss species and landscapes that are most amenable to IDEASS and considerations for data collection and analysis.

8.1 Focal species

Although IDEASS provides an opportunity to understand populations of a variety of secretive or rare snakes, some species conform more readily to the assumptions of the approach (Willson et al. 2018) than others, and characteristics of the species must be considered carefully before implementing our method. Appendix B includes a list of snake species documented on DoD lands (based on the DoD PARC Herpetofauna Database), biological characteristics that affect the species’ suitability for IDEASS, and that rank them in terms of suitability. Perhaps most obviously, IDEASS is only suitable for species that are effectively sampled using road surveys and those that are large enough to study via radio telemetry or other methods of monitoring spatial movement. Additionally, because temporal scale of spatial movement data must be sufficiently fine to capture road crossing movements, our method is most suitable for relatively sedentary species. For species that make frequent and/or extensive non-linear movements (e.g., racers, coachwhips, and other active species) it is likely that road

crossing frequency would be substantially underestimated by models based on daily re-sightings. Indeed, for such species, it may be nearly impossible to monitor fine-scale movements or to time natural road crossing velocity without influencing the snake's behavior. Currently, our method is therefore likely to be most appropriate for species that make linear long-distance movements relatively infrequently, such as those that use ambush foraging or those that are primarily fossorial. However, it is likely that future technological advances, especially GPS/satellite and automated telemetry, will greatly increase the pool of species amenable to our movement modeling approach, thereby allowing quantitative assessment of the optimal temporal scale for movement models. Additionally, as radio-transmitter technology continues to miniaturize, more snake species will be suitable candidates for telemetry studies. Currently, transmitters that are safe to surgically implant in snakes and have up to 8-week battery life are approximately 1.4 g in weight (BD-2 transmitters from Holohil Systems Ltd) and thus require snakes with a body mass of at least 28 g (assuming that transmitters should not exceed 5% of an individual's body mass). Beyond weight, body shape also comes into play. It is more difficult to implant transmitters into narrow-bodied snakes compared to wide-bodied snakes, like rattlesnakes. Variation in movement and road encounter frequency data (and thus imprecision of abundance estimates) can be minimized by focusing on species with distinct seasonal and diel activity patterns, as was the case for our species. Finally, our demonstration illustrates the ability of IDEASS to take advantages of existing datasets to estimate density with minimal collection of original empirical data. Thus, managers might particularly consider species that have already been studied via radio telemetry and/or road surveys. However, in this case, particular attention should be paid to potential bias incurred by the temporal distribution of road surveys and telemetry re-sightings. For example, our existing dataset of road surveys for WRS at Fort Hood included only surveys conducted between 20:00 and 23:00 h, thus violating the assumption that our survey times were unbiased relative to snake movements (Willson et al. 2018). This potential source of bias required that we correct our encounter probabilities to account for the fact that snake movement was temporally non-random with respect to our surveys (see section 5.5.7).

A diverse array of North American snake species, some of which are of conservation concern, conform well to the criteria listed above and are excellent candidates for our density estimation approach (Appendix B). Perhaps most obvious are vipers (i.e., rattlesnakes, copperhead,

cottonmouth), which are generally ambush foragers that make infrequent long-distance movements, especially during the breeding season. Additionally, ambush foragers tend to have thick bodies and large average body sizes and can handle transmitter implantation well. Other good candidates include many of the larger terrestrial and/or fossorial species such as gopher and Pinesnakes (*Pituophis* spp.), kingsnakes and their relatives (*Lampropeltis* spp.), hognose snakes (*Heterodon* spp.), and ratsnakes (*Pantherophis* spp.). Even some fossorial lizards such as the beaded (*Hemiderma* spp.) and legless lizards (*Ophisaurus* spp.) and terrestrial turtles (e.g., box turtles, *Terrapene* spp.) may be candidates for our approach. For many of the aforementioned species, road surveys are the most effective standardized survey method (Willson 2016) and some have been studied previously on DoD lands.

8.2 Focal landscapes

Our method is based on a random walk and currently the only sources of movement bias are the past movement (i.e., orientation towards a home range center) and potentially the road (i.e., attraction to, or avoidance of the road). Although our movement models can be expanded to incorporate additional spatial complexity, IDEASS is currently most applicable to relatively uniform landscapes that contain long road transects that pass through natural habitats. It is also particularly important that roadside habitats be as representative of the overall landscape as possible since density estimates are specific to areas adjacent to the road (Willson et al. 2018). Thus, researchers should avoid situations where land use near roads is different from that of the surrounding landscape (e.g., agricultural or residential development along roads). Finally, ideal study sites will have well-maintained roads with low traffic to minimize loss of detections to collection and roadkill and maximize safety of surveyors. Fortunately, many military installations meet all of these criteria and thus provide ideal landscapes for implementation of this technique. As with any work on active installations, researchers should be sure that field activities do not disrupt base operations and that appropriate safety precautions are taken when in the field.

8.3 Broad surveys

IDEASS assumes that road surveys are unbiased relative to snake movements. The ideal way to meet this assumption is to pre-define conditions (season, time of day, weather conditions) that are suitable for snake

movement and then conduct road surveys on a randomized or systematic basis throughout those pre-defined activity windows. A critical point is that surveys not be concentrated on particular or 'best' conditions unless enough data on activity exist so that capture probabilities could be adjusted to account for this source of bias. Also, for this reason, it may be best to constrain data collection and analyses to relatively short seasons when road crossing movements are expected to peak, as we have done in our demonstration. Finally, although our modifications to the IDEASS method (See section 2.2) incorporate uncertainty due to small sample size (low effort), a large volume of road survey data should be collected to average out chance variation in road captures due to environmental conditions and other factors.

IDEASS also assumes perfect detection of live snakes on roads (i.e., crossing snakes are not overlooked). Although the model could easily be modified to relax this assumption, researchers should take steps to maximize detectability, such as selecting roads that offer good visibility and have low traffic, using only trained observers, maintaining a speed that allows for careful monitoring of the road, and having a second observer in the vehicle. In cases where imperfect detection seems likely (small species, challenging viewing conditions, etc.), researchers could conduct experiments to quantify detection rates and incorporate empirical estimates of detection probability into calculations.

8.4 Telemetry and movement modeling

Because IDEASS is critically dependent on the ability of movement models to accurately predict road crossing frequency, we suggest collecting movement (i.e., radio telemetry) data at the same location where road surveys are occurring, and including all representative demographic groups (i.e., both sexes, different ages). Telemetry data should coincide with the seasonality of road collection data, and the temporal scale of telemetry data collection should be appropriate to the expected movements of the species (ideally daily for most species, but perhaps more frequently for species that move extensively). Likewise, given that our results are sensitive to responses of snakes to roads (avoidance or attraction), researchers should attempt to track animals near roads, allowing for quantitative evaluation of road response behaviors, as we have demonstrated here. These studies should also consider potential differences between paved and unpaved roads, as snakes have been shown to respond differently to different road surfaces in previous research (Robson & Blouin-Demers 2013). Results of our demonstration revealed some evidence of avoidance of paved roads by

EDR, but most paved roads were rare in our landscapes, making it difficult to draw definitive conclusions from those data. Future studies in landscapes where snakes encounter paved roads more frequently would be extremely informative.

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Appendix B: Suitability of Snake Species Found on DoD Lands for Road-Based Density Estimation

Table B-1 lists all snake species documented to occur on DoD lands in the continental United States (based on the DoD PARC Herpetofauna Database), attributes that affect their suitability for IDEASS, and suitability ranking for each species (1-4 score, with 4 being most suitable). Species attributes based on literature review (Ernst and Ernst 2003) and author's expert opinion. Species most suitable for road-based density estimation are highlighted. Table reprinted from Willson and Pittman (2017).

Table B-1. Snake species documented to occur on DoD lands in the continental United States.

Latin Name	Common Name	Habitat†	Telemetry†	Road Survey†	Active†	Ranking†
<i>Agkistrodon contortrix</i>	Copperhead	T	Y	Y	N	4
<i>Agkistrodon piscivorus</i>	Cottonmouth	A/T	Y	Y	N	4
<i>Arizona elegans</i>	Glossy Snake	T/F	Y	Y	?	4
<i>Boa constrictor</i>	Boa Constrictor	T/Ar	Y	?	N	4
<i>Bogertophis subocularis</i>	Trans-Pecos Ratsnake	F	Y	Y	N	4
<i>Carphophis amoenus</i>	Common Wormsnake	F	N	N	N	1
<i>Carphophis vermis</i>	Western Wormsnake	F	N	N	N	1
<i>Cemophora coccinea</i>	Scarletsnake	F	N	Y	?	2
<i>Charina bottae</i>	Northern Rubber Boa	T/F	Y	?	N	4
<i>Chilomeniscus stramineus</i>	Variable Sandsnake	F	N	Y	N	2
<i>Chionactis occipitalis</i>	Western Shovel-nosed Snake	F	N	Y	N	2
<i>Clonophis kirtlandii</i>	Kirtland's Snake	A/T	?	N	?	0
<i>Coluber bilineatus</i>	Sonoran Whipsnake	T	Y	N	Y	0
<i>Coluber constrictor</i>	North American Racer	T	Y	Y	Y	3
<i>Coluber flagellum</i>	Coachwhip	T	Y	Y	Y	3
<i>Coluber lateralis</i>	Striped Racer	T	Y	Y	Y	3
<i>Coluber schotti</i>	Schott's Whipsnake	T	Y	Y	Y	3
<i>Coluber taeniatus</i>	Striped Whipsnake	T	Y	Y	Y	3
<i>Contia tenuis</i>	Common Sharp-tailed Snake	F	N	N	N	1
<i>Crotalus adamanteus</i>	Eastern Diamond-backed Rattlesnake	T	Y	Y	N	4
<i>Crotalus atrox</i>	Western Diamond-backed Rattlesnake	T	Y	Y	N	4
<i>Crotalus cerastes</i>	Sidewinder	T	Y	Y	N	4
<i>Crotalus cerberus</i>	Arizona Black Rattlesnake	T	Y	Y	N	4
<i>Crotalus horridus</i>	Timber Rattlesnake	T	Y	Y	N	4

Latin Name	Common Name	Habitat†	Telemetry†	Road Survey†	Active†	Ranking†
<i>Crotalus lepidus</i>	Rock Rattlesnake	T/F	Y	Y	N	4
<i>Crotalus mitchellii</i>	Speckled Rattlesnake	T	Y	Y	N	4
<i>Crotalus molossus</i>	Black-tailed Rattlesnake	T	Y	Y	N	4
<i>Crotalus oreganus</i>	Western Rattlesnake	T	Y	Y	N	4
<i>Crotalus ornatus</i>	Eastern Black-tailed Rattlesnake	T	Y	Y	N	4
<i>Crotalus pricei</i>	Twin-spotted Rattlesnake	T/F	?	N	N	1
<i>Crotalus ruber</i>	Red Diamond Rattlesnake	T	Y	Y	N	4
<i>Crotalus scutulatus</i>	Mohave Rattlesnake	T	Y	Y	N	4
<i>Crotalus stephensi</i>	Panamint Rattlesnake	T	Y	Y	N	4
<i>Crotalus tigris</i>	Tiger Rattlesnake	T	Y	Y	N	4
<i>Crotalus viridis</i>	Prairie Rattlesnake	T	Y	Y	N	4
<i>Crotalus willardi</i>	Ridge-nosed Rattlesnake	T	?	N	N	1
<i>Diadophis punctatus</i>	Ring-necked Snake	T/F	N	?	N	2
<i>Drymarchon couperi</i>	Eastern Indigo Snake	T	Y	?	Y	3
<i>Drymarchon melanurus</i>	Central American Indigo Snake	T	Y	?	Y	3
<i>Farancia abacura</i>	Red-bellied Mudsake	A	Y	Y	?	3
<i>Farancia erythrogramma</i>	Rainbow Snake	A	Y	?	?	0
<i>Gyalopion canum</i>	Chihuahuan Hook-nosed Snake	F	N	Y	N	2
<i>Haldea striatula</i>	Rough Earthsnake	F	N	N	N	1
<i>Heterodon nasicus</i>	Plains Hog-nosed Snake	T/F	Y	Y	N	4
<i>Heterodon platirhinos</i>	Eastern Hog-nosed Snake	T/F	Y	Y	N	4
<i>Heterodon simus</i>	Southern Hog-nosed Snake	T/F	Y	Y	N	4
<i>Hypsiglena chlorophaea</i>	Desert Nightsnake	T/F	N	Y	N	2
<i>Hypsiglena jani</i>	Chihuahuan Nightsnake	T/F	N	Y	N	2
<i>Hypsiglena ochrorhyncha</i>	Coast Nightsnake	T/F	N	Y	N	2
<i>Lampropeltis californiae</i>	California Kingsnake	T/F	Y	Y	N	4
<i>Lampropeltis calligaster</i>	Yellow-bellied Kingsnake	T/F	Y	Y	N	4
<i>Lampropeltis elapsoides</i>	Scarlet Kingsnake	T/F	?	N	N	1
<i>Lampropeltis extenuata</i>	Short-tailed Kingsnake	F	N	Y	N	2
<i>Lampropeltis gentilis</i>	Western Milksnake	T/F	?	?	N	2
<i>Lampropeltis getula</i>	Eastern Kingsnake	T	Y	?	N	4
<i>Lampropeltis holbrooki</i>	Speckled Kingsnake	T	Y	?	N	4
<i>Lampropeltis nigra</i>	Eastern Black Kingsnake	T	Y	?	N	4
<i>Lampropeltis splendida</i>	Desert Kingsnake	T/F	Y	Y	N	4
<i>Lampropeltis triangulum</i>	Milksnake	T/F	Y	?	N	4
<i>Lampropeltis zonata</i>	California Mountain Kingsnake	T/F	Y	N	N	3
<i>Lichanura orcutti</i>	Northern Three-lined Boa	F	Y	Y	N	4
<i>Lichanura trivirgata</i>	Rosy Boa	F	Y	Y	N	4
<i>Liodytes alleni</i>	Black Swampsnake	A	N	N	N	0
<i>Liodytes rigida</i>	Glossy Swampsnake	A	?	N	N	0
<i>Micruroides euryxanthus</i>	Sonoran Coralsnake	F	N	Y	?	2
<i>Micrurus fulvius</i>	Harlequin Coralsnake	T/F	?	Y	?	2
<i>Micrurus tener</i>	Texas Coralsnake	T/F	?	Y	?	2

Latin Name	Common Name	Habitat†	Telemetry†	Road Survey†	Active†	Ranking†
<i>Nerodia clarkii</i>	Saltmarsh Watersnake	A	Y	?	?	0
<i>Nerodia cyclopion</i>	Mississippi Green Watersnake	A	Y	?	?	0
<i>Nerodia erythrogaster</i>	Plain-bellied Watersnake	A/T	Y	Y	?	3
<i>Nerodia fasciata</i>	Southern Watersnake	A	Y	Y	?	3
<i>Nerodia floridana</i>	Florida Green Watersnake	A	Y	?	?	0
<i>Nerodia rhombifer</i>	Diamond-backed Watersnake	A	Y	?	?	0
<i>Nerodia sipedon</i>	Common Watersnake	A	Y	?	?	0
<i>Nerodia taxispilota</i>	Brown Watersnake	A	Y	?	?	0
<i>Opheodrys aestivus</i>	Rough Greensnake	T/Ar	N	Y	?	1
<i>Opheodrys vernalis</i>	Smooth Greensnake	T	N	?	?	1
<i>Pantherophis alleghaniensis</i>	Eastern Ratsnake	T/Ar	Y	Y	N	4
<i>Pantherophis emoryi</i>	Great Plains Ratsnake	T/F	Y	Y	N	4
<i>Pantherophis guttatus</i>	Red Cornsnake	T	Y	Y	N	4
<i>Pantherophis obsoletus</i>	Western Ratsnake	T/Ar	Y	Y	N	4
<i>Pantherophis ramspotti</i>	Western Foxsnake	T	Y	Y	N	4
<i>Pantherophis slowinskii</i>	Slowinski's Cornsnake	T	Y	Y	N	4
<i>Pantherophis spiloides</i>	Gray Ratsnake	T/Ar	Y	Y	N	4
<i>Pantherophis vulpinus</i>	Eastern Foxsnake	T	Y	Y	N	4
<i>Phyllorhynchus browni</i>	Saddled Leaf-nosed Snake	F	?	Y	N	2
<i>Phyllorhynchus decurtatus</i>	Spotted Leaf-nosed Snake	F	N	Y	N	2
<i>Pituophis catenifer</i>	Gophersnake	T/F	Y	Y	N	4
<i>Pituophis melanoleucus</i>	Pinesnake	T/F	Y	Y	N	4
<i>Pituophis ruthveni</i>	Louisiana Pinesnake	T/F	Y	Y	N	4
<i>Python molurus bivittatus</i>	Burmese Python	T	Y	Y	N	4
<i>Ramphotyphlops braminus</i>	Brahminy Blindsnake	F	N	N	N	0
<i>Regina grahamii</i>	Graham's Crayfish Snake	A	?	?	N	1
<i>Regina septemvittata</i>	Queensnake	A	?	N	N	0
<i>Rena dissecus</i>	New Mexico Threadsnake	F	N	?	N	0
<i>Rena dulcis</i>	Texas Threadsnake	F	N	?	N	0
<i>Rena humilis</i>	Western Threadsnake	F	N	?	N	0
<i>Rhadinaea flavilata</i>	Pine Woods Littersnake	F	N	N	N	1
<i>Rhinocheilus lecontei</i>	Long-nosed Snake	F	Y	Y	?	4
<i>Salvadora grahamiae</i>	Eastern Patch-nosed Snake	T	Y	Y	Y	3
<i>Salvadora hexalepis</i>	Western Patch-nosed Snake	T	Y	Y	Y	3
<i>Sistrurus catenatus</i>	Massasauga	T	Y	?	N	4
<i>Sistrurus miliarius</i>	Pygmy Rattlesnake	T	?	Y	N	2
<i>Sonora semiannulata</i>	Western Groundsnake	F	N	?	N	2
<i>Storeria dekayi</i>	Dekay's Brownsnake	T	N	Y	N	2
<i>Storeria occipitomaculata</i>	Red-bellied Snake	T/F	N	N	N	1
<i>Storeria victa</i>	Florida Brownsnake	T	N	Y	N	2
<i>Tantilla coronata</i>	Southeastern Crowned Snake	F	N	N	N	1
<i>Tantilla gracilis</i>	Flat-headed Snake	F	N	N	N	1

Latin Name	Common Name	Habitat†	Telemetry†	Road Survey†	Active†	Ranking†
<i>Tantilla hobartsmithi</i>	Smith's Black-headed Snake	F	N	Y	N	2
<i>Tantilla nigriceps</i>	Plains Black-headed Snake	F	N	Y	N	2
<i>Tantilla planiceps</i>	Western Black-headed Snake	F	N	Y	N	2
<i>Tantilla relicta</i>	Florida Crowned Snake	F	N	N	N	1
<i>Thamnophis atratus</i>	Aquatic Gartersnake	A/T	?	?	?	1
<i>Thamnophis butleri</i>	Butler's Gartersnake	T	?	?	?	1
<i>Thamnophis cyrtopsis</i>	Black-necked Gartersnake	A/T	?	?	?	1
<i>Thamnophis elegans</i>	Terrestrial Gartersnake	T	Y	Y	?	4
<i>Thamnophis eques megalops</i>	Mexican Gartersnake	A/T	?	?	?	1
<i>Thamnophis hammondi</i>	Two-striped Gartersnake	A/T	?	?	?	1
<i>Thamnophis marcianus</i>	Checkered Gartersnake	T	Y	Y	?	4
<i>Thamnophis ordinoides</i>	Northwestern Gartersnake	T	?	?	?	1
<i>Thamnophis proximus</i>	Western Ribbonsnake	T	?	?	?	1
<i>Thamnophis radix</i>	Plains Gartersnake	T	?	?	?	1
<i>Thamnophis sauritus</i>	Eastern Ribbonsnake	T	?	?	?	1
<i>Thamnophis sirtalis</i>	Common Gartersnake	T	Y	Y	?	4
<i>Trimorphodon lambda</i>	Sonoran Lyresnake	T/F	?	Y	N	2
<i>Trimorphodon lyrophanes</i>	California Lyresnake	T/F	?	Y	N	2
<i>Trimorphodon wilkinsonii</i>	Texas Lyresnake	T/F	?	Y	N	2
<i>Tropidoclonion lineatum</i>	Lined Snake	T/F	N	?	?	1
<i>Virginia valeriae</i>	Smooth Earthsnake	F	N	N	N	1

†Definitions:

Habitat: T = terrestrial; F = Fossorial; A = aquatic; Ar = Arboreal. Terrestrial and Fossorial species are most ideal for road-based density estimation.

Telemetry (Y/N/?): Is the species large enough for current implantable radio-transmitters.? = only some individuals suitable for transmitters with short battery life.

Road Survey (Y/N/?): Are road surveys a viable method for sampling the species. Y = frequently captured using road surveys at most locations where species occurs;? = captured frequently during road surveys at some locations; N = generally not captured using road surveys

Active (Y/N/?): Does the species make frequent or extensive movements on a daily basis.? = spatial movement patterns are not well known.

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14. ABSTRACT The Department of Defense (DoD) expends considerable resources managing and conserving threatened, endangered, or at-risk snake species. Management for these species is often hampered by a lack of basic knowledge regarding their population size and trajectory. The low detectability of most snakes makes it difficult to determine their presence, or to employ traditional methods to estimate abundance. This work demonstrated a novel, simulation-based method, Innovative Density Estimation Approach for Secretive Snakes (IDEASS), for estimating snake density based on systematic road surveys, behavioral observations of snake movement, and spatial movement (radio telemetry) data. This method was used to generate meaningful density estimates for two rare and cryptic snakes of conservation concern, the Southern Hognose and Eastern Diamondback Rattlesnake, at Fort Stewart, Georgia. IDEASS was also applied to an existing dataset to retroactively estimate density of a more common species of management concern, the Western Ratsnake, at Fort Hood, Texas. In all three cases, traditional density estimation via visual surveys and capture-mark-recapture (CMR) failed completely due to lack of captures and recaptures, despite extensive field effort. We conclude that IDEASS represents a powerful tool, and in some cases the only viable method, for estimating density of secretive snakes.					
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