A novel approach for estimating densities of secretive species from road-survey and spatial-movement data

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Abstract

Context. Accurate estimates of population density are a critical component of effective wildlife conservation and management. However, many snake species are so secretive that their density cannot be determined using traditional methods such as capture–mark–recapture. Thus, the status of most terrestrial snake populations remains completely unknown.

Aim. We developed a novel simulation-based technique for estimating density of secretive snakes that combined behavioural observations of snake road-crossing behaviour (crossing speed), effort-corrected road-survey data, and simulations of spatial movement patterns derived from radio-telemetry, without relying on mark–recapture.

Methods. We used radio-telemetry data to parameterise individual-based movement models that estimate the frequency with which individual snakes cross roads and used information on survey vehicle speed and snake crossing speed 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 were then interpreted in light of detection probabilities and simulation model results to estimate snake densities and to assess various factors likely to affect abundance estimates. We demonstrated the broad applicability of this approach through a case study of the imperiled southern hognose snake (*Heterodon simus*) in the North Carolina (USA) Sandhills.

Key results. We estimated that *H. simus* occurs at average densities of 0.17 ha^{-1} in the North Carolina Sandhills and explored the sensitivity of this estimate to assumptions and variation in model parameters.

Conclusions. Our novel method allowed us to generate the first abundance estimates for *H. simus*. We found that *H. simus* exists at low densities relative to congeners and other mid-sized snake species, raising concern that this species may not only have declined in geographic range, but may also occur at low densities or be declining in their strongholds, such as the North Carolina Sandhills.

Implications. We present a framework for estimating density of species that have traditionally been considered too secretive to study at the population level. This method will greatly enhance our ability to study and manage a wide variety of snake species and could be applied to other secretive wildlife species that are most frequently encountered during road surveys.

Introduction

Knowledge of species distribution and abundance is a critical component of reasoned conservation and management decision-making. 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 whether 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 techniques (CMR; Rodda 2012) and spatially explicit mark–recapture methods (Royle and Young 2008). 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 among those 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 behaviour. Thus, the secretiveness (or low detectability) of most snake species makes it extremely difficult to determine even whether they are present at a particular site (either regionally or locally; Gibbons *et al*. 1997), let alone 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 behaviour and spatial ecology of secretive snake species (Kingsbury and Robinson 2016). Knowledge of movement patterns and behaviours gleaned from radio-telemetry studies can be used to parameterise 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 behaviours 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 behavioural states between which individuals shift probabilistically on the basis of 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.

In the present study, we develop a novel approach that integrates data from spatial ecology studies (i.e. radio-telemetric data) and encounter data of snakes during road surveys to estimate density of secretive species, without needing to recapture individuals. We demonstrate the method using one of the most poorly understood snakes in North America, the imperiled southern hognose snake (*Heterodon simus*). Although we focus on southern hognose snakes, our approach can be used on numerous other secretive snake species, many of which are frequently encountered on roads and have already been studied via radio-telemetry.

Materials and methods

Density-estimation approach

Our density-estimation approach combines behavioural observations of road-crossing behaviour (crossing speed), effort-corrected road survey data, and simulation-based modelling of spatial movement to estimate population densities. Radio-telemetric data are collected to quantify movement metrics, including frequency, distance, and direction of movement in relation to home range centre and roads. These movement data are then used to parameterise 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 speed of the survey vehicle and snake crossing speed are used to determine the probability of detecting a snake, given that it crosses the road transect during a survey. Encounter frequencies of snakes during systematic road surveys are then interpreted in the light of detection probabilities and simulation model results to estimate snake densities and to assess various factors that are likely to affect encounter rates.

Density-estimation model

The first component of our density-estimation approach uses information on vehicle speed and snake behaviour to estimate detection probability of snakes on roads, thereby allowing counts during systematic road surveys to be corrected for imperfect detection, yielding unbiased estimates of true road-crossing rate. So as to detect a snake that crosses the survey route during that survey, the surveyor's location and the snake's location must coincide in space. The distance the surveyor covers in the time it takes a snake to cross (detection distance, D_p (km)) is equal to the average snake crossing time (V_{snake} (min)) multiplied by the vehicle speed ($V_{vehicle}$ (km min^{-1})), as follows:

$$D_p = V_{snake} \times V_{vehicle} \qquad (1)$$

Thus, assuming that all snakes encountered by the survey vehicle are detected, the probability of detecting any individual snake that crosses during a survey ($\hat{p}$) is detection distance / total survey distance (D_{survey} (km)), as follows:

$$\hat{p} = \frac{D_p}{D_{survey}} \qquad (2)$$

Observed encounter rate (N_{obs} (snakes h^{-1})) can be translated to an estimated total crossing rate ($\hat{N}_{cross}$ (snakes km^{-1} h^{-1})) by dividing by $\hat{p}$ and the total survey distance, as follows:

$$\hat{N}_{cross} = \frac{N_{obs}}{\hat{p} \times D_{survey}} \qquad (3)$$

Finally, estimated total crossing rate can be translated to density ($\hat{N}$ (snakes km^{-2})) by dividing $\hat{N}_{cross}$ by the estimated hourly crossing rate of individual snakes obtained from movement simulation models (ρ (crossings snake^{-1} h^{-1})) and the width of the simulated landscape (A (km)), as follows:

$$\hat{N} = \frac{\hat{N}_{cross}}{\rho \times A} \qquad (4)$$

Because the extent of our simulated landscape was 500 m on each side of the road, the number of snakes predicted per kilometre of road is equivalent to the density per square kilometre, and can be converted to snakes per hectare by dividing by 100.

A closer examination of Eqns 1–4 shows that several terms cancel out when these equations are combined, yielding a greatly simplified overall equation for estimating density, as follows:

$$\hat{N} = \frac{N_{obs}}{V_{snake} \times V_{vehicle} \times \rho \times A} \qquad (5)$$

The resulting simplified formula (Eqn 5) can be thought of as dividing the observed encounter rate by the length of road that could be monitored with a 100% chance of detecting any snakes that cross (detection distance), and then dividing the result by the estimated hourly crossing rate of individual snakes.

Modelling snake movement

We developed a simple model to simulate snakes moving within a home range (Fig. 1), so as to estimate the daily probability that a snake will cross a road. Movement was modelled as a biased correlated random walk (BCRW) in a continuous space, with a wrapped Cauchy distribution of turning angles (Zollner and Lima 1999) and log-normal distribution of step sizes, based on an analysis of the radio-telemetry data. The bias parameter was built into the model as the degree to which snakes choose a movement bearing according to the centre of the home range and the bearing towards the road. The bearing that the animal chose at each time step was a weighted average of the bearing of the previous step (plus random error drawn from the wrapped Cauchy distribution) and the bearing towards the home range centre (or road), as follows:

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

where φ_t is the bearing at Time t, β is the strength of bias towards home range centre or road, γ_t is the turning angle drawn from the wrapped Cauchy distribution at Time t, and δ_t is the bearing towards the home-range centre at Time t (Crone and Schultz 2008; Barton *et al.* 2009). Each individual was assigned a random home-range centre within a buffer (landscape) of width (A) surrounding a linear road bisecting a uniform landscape and was given an initial movement bearing from a uniform distribution (1–360 degrees). The Parameter A is defined on a species-by-species basis (see below), 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. Increasing landscape size will decrease the probability of detecting each individual snake, because snakes further from the road are less likely to cross. Thus, with a larger landscape, detection probability will be lower, resulting in a larger estimated population size; however, we would then divide by a larger landscape, yielding the same estimate of density. Each time step was considered to be 1 day, and each simulation was run for 31 days. We calculated the proportion of snakes that crossed the road on the 31st time step of the simulation to
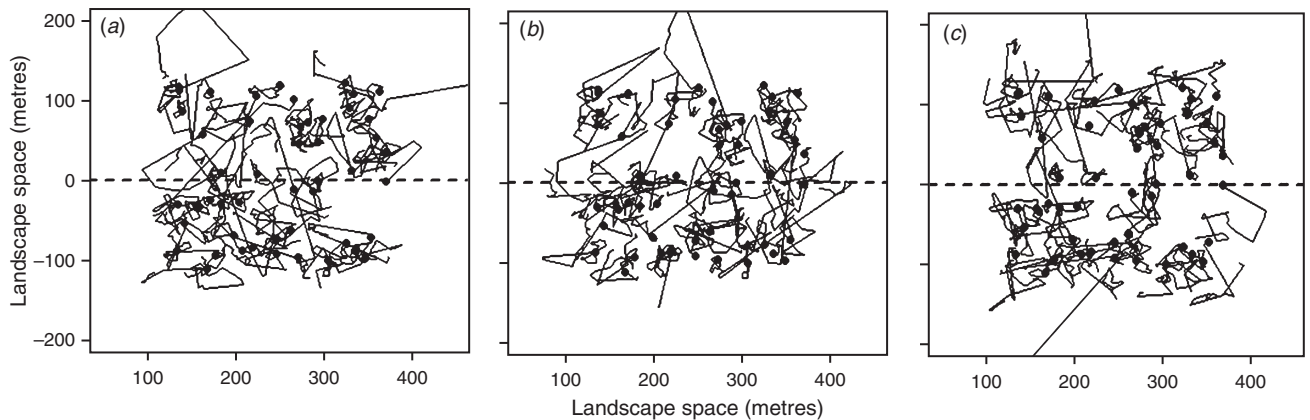

Fig. 1.   Examples of movement paths of simulated snakes, generated using individual-based spatial movement models parameterised using (*a*) no road bias (0, number of road crossings = 28), (*b*) strong road attraction (0.3, number of road crossings = 46), and (*c*) strong road avoidance (0.3, number of road crossings = 11). Paths crossing the horizontal dashed line represent road-crossing events.

estimate daily road-crossing probability, and then divided by the diel activity period (hours per day when snake activity occurs) to calculate hourly individual road-crossing probability (ρ). Because each snakes' initial location in the model was always 1 metre away from their home range centre, we ran the movement simulation for 30 time steps as a burn-in period to prevent initial location relative to home range centre from influencing the road-crossing probability. 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 centre and the location of a road. Behaviour when roads were encountered was incorporated into the model as an additional bias in movement bearing.

Case study: southern hognose snake

The southern hognose snake (*Heterodon simus*) is a fossorial species found in areas with well drained sandy soils in the south-eastern Coastal Plain from North Carolina to southern Mississippi. Over the past few decades, *H. simus* has declined or been extirpated throughout much of its historic range, and it has not been found in Alabama or Mississippi since the 1970s (Tuberville *et al*. 2000). *Heterodon simus* has been proposed for listing under the USA *Endangered Species Act* and is listed as threatened, endangered, or of special concern in every state where it occurs (or historically occurred), except Florida. In states where it still occurs, its range has shrunk considerably (Tuberville *et al*. 2000; Gibbons and Dorcas 2005). Determining the current geographic range of *H. simus*, and the status of populations throughout its range, are critical for proper conservation and recovery management of the species. Unfortunately, because of the low detectability of these secretive snakes, estimates of their population densities are entirely lacking. *Heterodon simus* is almost exclusively diurnal and is most frequently found during daytime road surveys from mid-September to early November (Enge and Wood 2002; Gibbons and Dorcas 2005; Beane *et al*. 2014). Substantial data exist on both its spatial ecology collected using radio-telemetry and encounter rates on roads (Beane *et al*. 2014).

Data collection

Road-crossing speed

Determining the probability of detecting live snakes crossing roads during road surveys requires data on the time that snakes are detectable while crossing (see Discussion for comments on incorporating road-killed individuals). We gathered this information through direct behavioural observations and videography of *H. simus* encountered while naturally crossing roads. Specifically, in 2014, we conducted diurnal road surveys for *H. simus* on low-traffic paved roads located on the Savannah River Site (owned by the USA Department of Energy), Barnwell Co., South Carolina, with particular effort during September–November, when *H. simus* is most frequently encountered (Enge and Wood 2002; Beane *et al*. 2014). When a snake was encountered, we stopped the vehicle at least 10 m away from the snake, shut off the engine, and observed the snake as unobtrusively as possible for the duration of the crossing event. In most cases, the event was videotaped using a Canon 7D

digital camera or smartphone. Typically, the snake would freeze for a short period (usually <1 min) when the vehicle first approached, but would then resume crossing the road using rectilinear locomotion, which is typical for this 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. centre line, road edge, or obvious crack in pavement). Once the snake fully crossed, it was captured, measured (SVL, mass, sex) and released at its capture location. The distance traveled between landmarks was then measured (nearest centimetre), as well as the total width of the road. Any snake that turned around, froze for >5 min, or employed lateral undulation movement was considered disturbed and was not included in the dataset. In addition to our own observations, we queried other herpetologists in North Carolina and Florida who regularly encounter *H. simus*, recruited them to videotape snakes found naturally crossing roads, using the methods described above, and analysed the videos using the same methods. For each snake, crossing speed was calculated by dividing the distance traveled (cm) by the time elapsed (s) and extrapolated to total crossing time, by multiplying speed by a typical road width of 550 cm (average width of road measured during behavioural observations and typical width of a paved two-lane road).

Relative abundance: road surveys

We used an extensive existing and published database of systematic diurnal road surveys for *H. simus* conducted by J. C. Beane in the North Carolina Sandhills (predominantly in xeric uplands of Scotland and Moore counties) between 1996 and 2012. Most roads surveyed bisected high-quality sandhill habitats, dominated by longleaf pine (*Pinus palustris*), scrub oaks (*Quercus* spp.) and wiregrass (*Aristida stricta*), i.e. habitats historically preferred by *H. simus*, as well as sandy agricultural, residential or other disturbed areas also heavily utilised by the species (Beane *et al*. 2014). We restricted analyses to the *H. simus* peak activity period of 1 September to 15 November and included 9 years for which the survey effort was available (Table 1; Beane

Table 1. Systematic road-survey data for *Heterdon simus* for 9 years in the North Carolina Sandhills

Data have been adapted from Beane *et al.* (2014)

Year	Number of surveys between 1 September – 15 November	Number of survey hours	Live *H. simus* encountered	Encounters per hour
1996	17	80	14	0.18
1998	36	102	2	0.02
2000	25	83	7	0.08
2002	18	56	7	0.13
2005	28	60	1	0.02
2007	30	95	8	0.08
2009	34	76	9	0.12
2011	21	42	4	0.10
2012	27	62	2	0.03
Total	236	656	54	
			Mean	0.083
			s.d.	0.053

et al. 2014). The resulting dataset contained a total of 656 survey hours across 236 days (Table 1). Details of survey methodology are reported in Beane *et al*. (2014), but, importantly, an approximate driving speed of $48\,km\,h^{-1}$ (30 miles per hour; $V_{vehicle} = 0.8\,km\,min^{-1}$) was maintained and surveys were conducted on a haphazard, but 'essentially random' basis during the fall activity period (Beane *et al*. 2014). For this analysis, we included only snakes that were encountered alive (including living, but injured individuals; $n = 12$) during surveys, despite the fact that most individuals encountered were roadkilled.

Analysis of snake movement

We used data from 18 *H. simus* (11 males and 7 females) individuals monitored using radio-telemetry in the Sandhills regions of North and South Carolina. In North Carolina, 16 individuals were tracked in the Sandhills Game Lands (SGL), and on some private lands, in Scotland County. The SGL represents a vast region (~25 400 ha, not all contiguous) of state-owned sandhill habitat, managed for both game and non-game species by the North Carolina Wildlife Resources Commission. Sandhills Game Lands is managed with frequent prescribed fire (most tracts on 2–3-year burn rotation), and represents an apparent stronghold for *H. simus* in North Carolina. Radio-telemetry occurred from 1998 to 2011, and each snake was radio-tracked for periods ranging from <2 months to >3 years, using mostly 5-g transmitters with 12-month battery life (SB-2 and SB-2T, Holohil Systems Ltd, Carp, Ontario, Canada), and a TRX-2000S receiver and three-element Yagi antenna (Wildlife Materials, Murphysboro, IL, USA). Snakes were relocated on varying schedules. However, so as to conform to the time step of the model, we restricted analyses to data for snakes that were tracked once per day on consecutive days (see below).

In South Carolina, two snakes (1 male and 1 female) were tracked on the Savannah River Site (SRS), Aiken and Barnwell Counties. The SRS is an 800-km^2 government reserve in the Upper Coastal Plain of South Carolina. Prior to the establishment of the SRS in the 1950s, most of the land was under intensive agriculture, with very little intact forest remaining except in the Savannah River floodplain. Although upland habitat on the SRS is currently managed for timber production, most areas are reforested and only 10% of the land has been developed for site operations. The animals included in the present study occurred in the north-eastern corner of the SRS in managed pine (primarily loblolly pine, *Pinus taeda*) plantations. Radio-telemetry occurred from 1998 to 2001, and each snake was radio-tracked for 1–2 years by using transmitters with a 12-month battery life (SB-2T, Holohil Systems), three-element Yagi antenna, and a Telonics receiver. Snake locations were recorded (within 1 m) using GPS technology (Trimble Pro-XR, Sunnydale, CA, USA).

To parameterise an individual-based movement model, we analysed the radio-telemetry data from snakes radio-tracked between 1 September and 15 November to match the survey effort and the peak activity period for hognose snakes (Beane *et al*. 2014). For each snake, we estimated the turning-angle distribution (path straightness), mean net distance moved per day (step size), and response to roads using ArcGIS 10.1

(ESRI, Redlands, CA, USA). We additionally tested for the effects of sex on movement parameters (Student's *t*-test). The time step of the simulation model consisted of 1 day; we, therefore, included only the movement-path data that were collected on a daily basis for calculating and parameterising mean step sizes and turning angle distributions. We calculated the mean daily movement distance (using only daily relocation data) for each snake and then we averaged the means across all snakes to generate the mean step size. Because the time scale of the simulation model and the time scale of the data were equivalent, we did not discretise the data for estimation of movement parameters. We investigated response to roads using a Monte Carlo approach by generating random walk paths for each snake using empirical distributions of step size and turning angles (Shepard *et al*. 2008). We generated 1000 paths per snake, and, for each simulated path, we calculated the number of times the snake crossed a road. We then generated an empirical distribution of the number of crossing events from the simulations. Using an α of 0.05, we rejected the null hypothesis of no response to road (neither attraction or avoidance) if the observed number of road crossings fell into the upper or lower 2.5% of the frequency distribution of the number of crossing events from the randomised paths.

Simulations

For *H. simus* movement simulations, each individual was assigned a random home range centre within 500 m ($A = 1\,km$) of a linear road bisecting a uniform landscape. This landscape size was selected to ensure that the model had a high likelihood of simulating all snakes with a chance to cross the road; using $A = 1\,km$, snakes had a less than 0.005% chance of crossing a road from that distance if the snake moved directly towards the road. Each time step was considered to be 1 day, and each simulation was run for 31 days. We calculated the proportion of snakes that crossed the road on the 31st time step of the simulation to estimate daily road-crossing probability, and then divided by 8 h (assuming that all activity occurs between 0900 hours and 1700 hours) to calculate hourly individual road-crossing probability (ρ).

We simulated the movement of snakes under different movement scenarios. For each replicate simulation, we specified the following movement parameters: mean vector length (parameter defining turning-angle distribution), strength of bias in response to road or home range centre, and mean step size. Mean step size was a measure of the net distance a snake moved per day on average; this was parameterised using only daily relocations from the radio-telemetry data. The radio-telemetric data in our case study included limited numbers of road crossings, and, thus, we were unable to precisely parameterise the road bias component of our model. We, therefore, simulated a range of possible values for road bias, including both road avoidance and road attraction, and explored the sensitivity of our model output to assumptions about road behaviour. The road-bias parameter, as defined in our model, ranged from –1 to 1. A road-bias value of 0 indicated that the snake biased its movement towards the home range centre and displayed no behavioural response to the road. We considered this scenario our 'null' road-bias scenario. A road-bias value of 0.1 indicated that the snake biased its movement 10% towards the

road and 90% towards the home range centre. Similarly, a road-bias value of –0.1 indicated that the snake biased its movement 10% away from the road and 90% towards the home range centre (examples of movement paths; Fig. 1). The mean vector length was a measure of the straightness of a snake's movement path; a mean vector length of 0 indicates a fully random walk and a mean vector length of 1 indicates a completely straight movement path (100% probability of turning 0 degrees).

We explored the sensitivity of the model to road bias, turning-angle distribution, and mean step size. We simulated a factorial set of plausible values for each of these parameters, including three levels of mean vector length (0.5, 0.7 and 0.9), five levels of road bias towards or away from a road (–0.3, –0.1, 0, 0.1, 0.3), and five levels of mean step size based on telemetry data (upper and lower ranges of step size, upper 95% confidence intervals (CI) and lower 95% CIs of step size, and mean step size). Therefore, we simulated a total of 75 combinations of snake-movement values. We simulated 35 000 snakes in each treatment combination and calculated the percentage of 35 000 snakes that crossed a road as a measure of daily road-crossing probability.

Results

Road-crossing speed

We successfully timed nine wild *H. simus* individuals encountered naturally crossing roads (Table 2) that did not exhibit behaviours indicating that they had been disturbed (prolonged freezing, turning, or movement via lateral undulation). These individuals represented a variety of snake sizes and included animals crossing both paved and unpaved (sand) roads. Crossing speed varied considerably among individuals (range = 0.6–2.9 cm s^{-1}; mean = 1.5 cm s^{-1}; Table 2), with no clear pattern relating to road type or snake size. Extrapolated to an average road width of 550 cm, we estimated that a snake would take an average of 7.69 min (95% CI = 5.42–9.96 min) to completely cross a typical road (V_{snake} = 7.69).

Encounter rate

A total of 656 h of systematic fall road surveys over 9 years in the North Carolina Sandhills yielded 54 captures of live *H. simus* (Table 1) and mean capture rate of 0.082 live snakes per hour of

survey (N_{obs} = 0.082). Capture rates varied considerably among years (Table 1), but calculating an annual grand average across years yields a nearly identical capture rate of 0.083 (s.d. = 0.053) live snakes per hour of survey.

Movement modelling

Parameterisation

Mean distance between daily relocations of 18 hognose snake individuals was 16.9 m (s.d. = 13.17; range: 3.61–36.3 m among individuals). We found no effect of sex on mean distance moved per day (t = 0.08, P = 0.94). Step sizes were best fit with a log-normal distribution. We did not find evidence of road attraction or avoidance in any snake within the study because of a small number of relocations per snake path. We, therefore, were unable to detect road avoidance or road attraction.

Movement model

We found that the daily probability of crossing a road was affected by movement parameters. Across all parameter combinations, daily road crossing probabilities of individuals ranged from 0.035% to 2.4%. Mean step size, mean vector length, and attraction to road were positively correlated with probability of crossing a road. The parameter combination most closely approximated by the radio-telemetry data yielded a daily road-crossing probability of 0.62%. For calculations of density (see below), we extrapolated this value to an hourly road-crossing probability of 0.077% (ρ = 0.00077), assuming random movement throughout an 8-h daily activity period (0900 hours to 1700 hours).

Density and model sensitivity

Inputting average values for snake crossing time, vehicle speed and individual road-crossing frequency into Eqn 5 yielded a positive relationship between the estimated density and encounter frequency during road surveys (Fig. 2). On the basis of this relationship and the average encounter rate during road surveys of 0.082 snakes per hour, the estimated density of *H. simus* in the North Carolina Sandhills is 17.14 snakes per km^2 or 0.17 snakes per hectare.

Table 2.   Data for timed natural road-crossing events of *Heterodon simus*
FL, Florida; NC, North Carolina; SC, South Carolina

Date	Location	Snake total length (cm)	Road type	Distance crawled (cm)	Time (s)	Speed (cm s^{-1})	Time taken to cross 550-cm road
29/5/2014	SC	48	Paved	270	180	1.5	6.64
18/10/2014	SC	49	Paved	300	229	1.3	7.62
18/10/2014	SC	20	Paved	269	93	2.9	3.28
19/10/2014	SC	19	Paved	95	105	0.9	10.48
19/10/2014	SC	43	Paved	70	52	1.3	7.34
24/10/2014	NC	18	Paved	162	90	1.8	5.26
12/10/2014	FL	47	Sand	145	91	1.6	6.24
24/10/2014	FL	19	Sand	24	39	0.6	15.41
22/10/2014	FL	18	Paved	45	33	1.4	6.94
					Mean	1.5	7.69
					s.d.	0.6	3.47

$$\hat{N} =$$

$$\frac{0.082 \; snakes \; h^{-1}}{7.69 \; min \times 0.8 \; km \; min^{-1} \times 0.00077 \; crossings \; snake^{-1} \; h^{-1} \times 1 \; km}$$

$$= 17.14 \; snakes \; per \; km^2$$

Inputting upper and lower 95% confidence-interval values for snake-crossing speed (95% CI = 5.42–9.96 min) yielded density estimates ranging from 0.13 to 0.24 snakes per hectare, with faster crossing speeds increasing estimated density (Fig. 2). Likewise, our density estimate varied with snake movement rate (step size) and behavioural response (attraction to or avoidance of) to the road (Fig. 3).
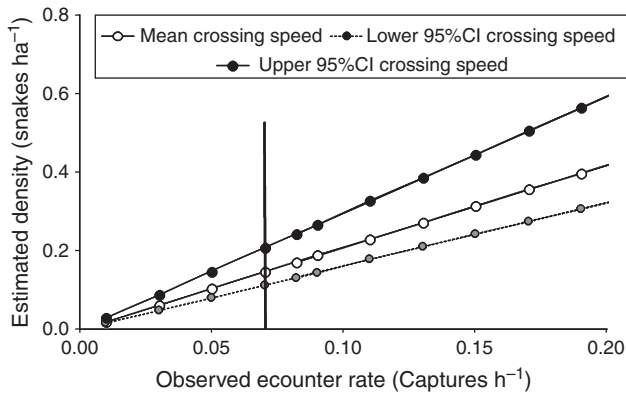
Fig. 2. Relationship between observed encounter rate (live captures per hour of road survey) and estimated density of *Heterodon simus*, bounded by the 95% confidence interval of road-crossing speeds observed in behavioural observations. Vertical bold line indicates mean observed encounter frequency (0.082 live snakes per hour) across 656 h of survey time over 9 years in the North Carolina Sandhills. Thus, mean estimated density is 0.17 snakes per hectare.

Specifically, parameter values that reduced road-crossing frequency (smaller step sizes or stronger avoidance of the road) increased estimated density. Smaller step sizes yielded lower road-crossing frequencies because snakes were less likely to move far enough away from their home-range centre to cross a road. Snakes were less likely to cross a road when road bias was smaller because negative road-bias values corresponded to road avoidance (Fig. 3). Mean vector length was not a strong determinant of road-crossing probability and, therefore, did not strongly affect expected density, likely because bias towards the home-range centre prevented high mean vector lengths from maximising net displacement of snakes (thus increasing road-crossing probability). Nevertheless, all movement-parameter combinations within the 95% CI of step size and corresponding to a lack of strong behavioural avoidance of the road (< -0.2) yielded density estimates less than 0.5 snakes per hectare (Fig. 3). The lower range for the mean step size and the strongest road avoidance yielded the greatest density estimate (3.03 snakes ha^{-1}). Therefore, across all movement-parameter combinations, estimated density ranged from 0.09 snakes ha^{-1} to 3.03 snakes ha^{-1}.

Discussion

In the present study, we have demonstrated an approach for estimating abundance on the basis of likelihood of detection during road surveys. Our method is independent of traditional CMR approaches and, thus, shows particular promise for estimating abundance of species that have inherently low individual detection probabilities, such as many snakes. Ultimately, our method should be validated through direct comparison with CMR in a species amenable to both methods. However, initially, we demonstrate the potential of our method using a case study of the southern hognose snake (*H. simus*).
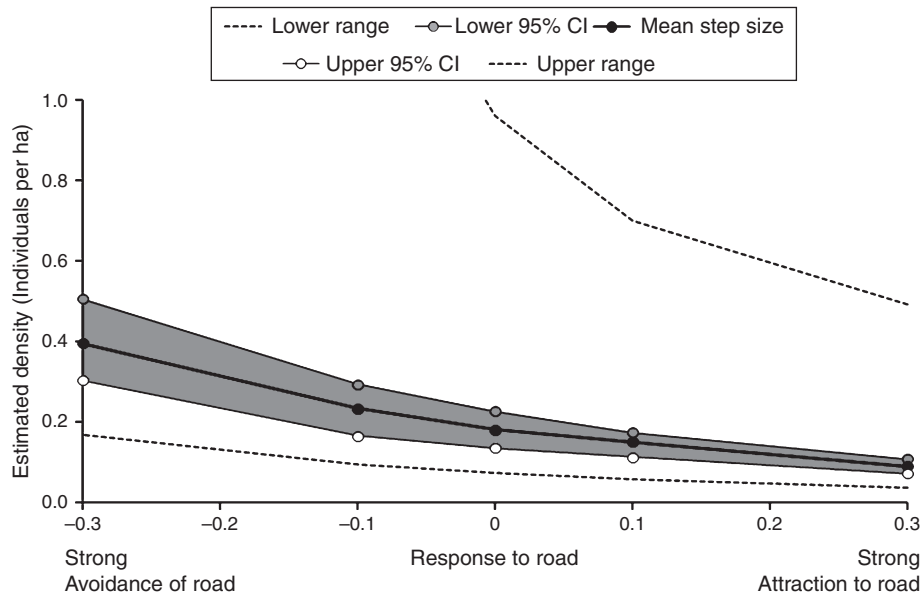

Fig. 3. Sensitivity of estimated snake density to assumptions about step size and road bias. Stronger road avoidance yielded greater density estimates than did road attraction. Step size also affected estimated density, with smaller step sizes yielding greater density estimates.

We chose *H. simus* because (1) it is an excellent example of a secretive snake most effectively sampled using road transects, (2) data already exist on *H. simus* movements and road-encounter frequencies and (3) it is a species of considerable conservation concern. Our approach provides the first density estimate for *H. simus* and provides an approach for generating baseline abundance data to inform effective conservation and management of secretive snakes for which density estimates were previously unobtainable.

Using spatial movement parameters derived from radio-telemetry, mean observed road-crossing speed, and encounter rate during road surveys, our analyses yielded a density estimate (including adults and juveniles) of 0.17 *H. simus* individuals per hectare in the North Carolina Sandhills. On the basis of our approach, it appears that *H. simus* occurs at lower densities than do many other terrestrial snakes (Parker and Plummer 1987). For example, densities based on CMR studies are between 1 and 10 per ha for both congeners, the eastern hognose snake (*H. platirhinos*) and the western hognose snake (*H. nasicus*; Platt 1969). Thus, low capture frequency of *H. simus*, even in suitable habitat, may be, in part, a result of low abundances. Low estimated density raises the concern that *H. simus* may not only have declined in geographic range (Tuberville *et al.* 2000), but may also be declining in its strongholds, such as the North Carolina Sandhills. Several reasons have been proposed for the decline of *H. simus*, including invasive fire ants and loss or fragmentation of the upland sandhill habitats it prefers (Tuberville *et al.* 2000). Our density estimate provides a baseline for abundance of *H. simus* across the North Carolina Sandhills region; however, care should be taken when extrapolating these densities to smaller land areas. In particular, our estimate should be viewed as representative of average density over the large area covered by road surveys. Densities of *H. simus* certainly vary across landscapes, over time and as a result of habitat quality (Enge and Wood 2002); thus, density estimates might vary considerably from our mean value (higher or lower, based on habitat quality) at smaller spatial scales. Future research should be conducted to determine how densities vary across the geographic range of *H. simus*, among various habitats, and temporally, so as to evaluate population trends.

Although our approach could be used to generate the first information on density of many secretive and rare snake species, it is not without assumptions and limitations and should ultimately be validated with a species that is also amenable to density estimation via CMR. The first important assumption of our approach is that animal movement does not change on the basis of animal density, or changes linearly. Whereas this is likely to be a fair assumption for secretive snakes, and we are unaware of any studies documenting density-dependent changes in snake movement, many other species dramatically alter movement behaviour on the basis of density (e.g. Guyer *et al.* 2012); in these cases, the relationship between density and movement behaviour would have to be incorporated into the model. Likewise, it is important that the model is constructed at the temporal scale at which animals are likely to make significant movements, and that the temporal scale of empirical movement data (i.e. telemetry data) matches that scale. If the model is constructed at coarser temporal scales, or if snakes move

extensively between relocations (i.e. movements are missed because tracking is too infrequent), the model may underestimate road-crossing probability and, therefore, overestimate density. Many snakes make long-distance movements relatively infrequently, making a 1-day time step appropriate for many species, including southern hognose snakes. However, finer-scale movement data, either through more frequent relocations or technologies that allow for automated relocation (e.g. satellite tracking or automated telemetry) or continuous tracking of movement paths (e.g. threadspooling or powder tracking; (Tozetti and Martins 2007; Furman *et al.* 2011) could provide insight into the appropriate temporal scale for the model (Ward *et al.* 2013). Ideally, the accuracy of movement models should be examined by testing estimated crossing frequencies and emergent spatial movement metrics (e.g. home-range size) against the empirical telemetry data.

Perhaps the strongest criticism of this method is that because it relies on abundance data collected using road surveys, extrapolation of density estimates generated using this method relies on assumptions about how representative roadside habitats are of the overall landscape. Without additional data comparing abundance or movement of snakes relative to roads, the implicit assumption is that roadside habitats harbour similar snake densities as do habitats that do not border roads. This assumption is unlikely to be completely valid under most situations, but the implications of making that assumption will vary on the basis of the biology of the species and characteristics of the landscape and roads. For example, for many species, roadside habitats are likely to harbour reduced snake densities because of road mortality, behavioural avoidance of roads or roadside habitats (e.g. Robson and Blouin-Demers 2013), or both. Alternatively, species that prefer edge habitats or high ground provided by road beds in low-lying areas may actually be concentrated in roadside habitats, leading to density estimates that are elevated relative to the overall landscape.

Despite these potential sources of bias, there are reasons to believe that assuming that roadside densities are representative of the overall landscape may not be totally unwarranted. In many regions of the world, road densities are so high that a large proportion of the total land area is close to a road. For example, a study in 2003 found that over 80% of the land area of the USA was within 1 km of a road (Riitters and Wickham 2003). Furthermore, although numerous authors have documented large numbers of road-killed snakes and expressed concern that road mortality negatively affects snake populations, little quantitative data exist demonstrating that snake population densities are depressed near roads. For example, Patrick and Gibbs (2009) deployed coverboard arrays systematically at different distances from roads across three sites, but found no relationship between snake abundances and distance to roads. Likewise, intensive road surveys of snakes along a transect in California in the 1970s and 1990s showed a dramatic increase in relative abundance of one species and little change in relative abundances of the remaining nine species over time, despite a substantial increase in traffic volume (Sullivan 2000). Thus, although future research will clearly be needed to evaluate the implications of road effects on density estimates of various snake species, there is currently little evidence that density estimates near roads would be strongly

biased, and our method represents an important baseline for species that were previously intractable to population-level research.

In addition to potential road effects on snake abundance, removal of snakes that were crossing roads could also lead us to underestimate snake density. For example, because it was not possible to determine if a road-killed individual would have been detected crossing naturally had it not been hit, we excluded all dead *H. simus* individuals from our road-survey dataset. It is also possible that some snakes that would have otherwise been detected were removed by predators or snake collectors while crossing roads. Neither of these sources of negative bias in road-encounter data have been quantified and they are not currently accounted for in our models. An alternative extension of our approach that would allow researchers to take advantage of roadkill data would be to use data on traffic volumes and crossing speed to calculate the probably that a snake would be hit while crossing (e.g. Andrews and Gibbons 2005) and, thus, be detectable as roadkill. We do not have the data to attempt this with our *H. simus* dataset, but doing so would greatly increase the number of road detections in the dataset. For example, most (643 of 764) of *H. simus* individuals detected by Beane *et al*. (2014) were dead. Additionally, our model currently assumes that all snakes encountered by a survey vehicle are detected. This assumption is probably reasonable for our study because surveys were conducted during the day at low speed. However, under more challenging viewing conditions (e.g. night, higher speed, smaller species, or unpaved road), detection probability might need to be adjusted to account for imperfect detection. Finally, our density estimate for *H. simus* might be an underestimate because we radio-tracked only adult snakes, whereas our road dataset included both juveniles and adults. In many snake species, juveniles move less extensively than adults (e.g. Jellen and Kowalski 2007). If true for *H. simus*, this could lead to a lower probability of juveniles crossing roads. If this is the case, shorter movement distances (smaller step sizes) of a component of the population would cause us to underestimate density (Fig. 3).

Our movement modelling approach provides a framework for incorporating behavioural complexity of snakes into the abundance estimation process, and exploring the relationship between assumptions about behaviour and density estimates should be a focus of future efforts. For example, our approach makes the assumption that habitat surrounding roads is homogenous and that snakes are randomly distributed throughout the landscape. Longer-term and finer temporal scale radio-telemetry studies could provide the information needed to create spatially explicit models in which habitat type and species movement behaviour vary throughout the landscape or in response to conspecifics (clumped or uniform distribution of home ranges, for example). Likewise, although we did not detect sex differences in movement parameters of *H. simus* during our short temporal study window, future extensions could incorporate differential movement among sexes, which is common in many snake species. Finally, our model was particularly sensitive to assumptions about road bias. A clear understanding of how roads affect the movement decisions (e.g. Andrews and Gibbons 2005) of animals is critical to the implementation of this modelling approach,

especially in situations where animals display strong road avoidance. Few studies have rigorously addressed how roads influence snake behaviour or snake spatial movement (but see Andrews and Gibbons 2005; Robson and Blouin-Demers 2013; Siers *et al*. 2014). Robson and Blouin-Demers (2013) found evidence that *H. platirhinos* behaviourally avoided paved roads but did not avoid unpaved roads. Therefore, snake reactions to roads may be context-dependent, necessitating further research into the mechanisms or cues underlying snakes' interactions with roads.

Our case study demonstrated the applicability of the method for a variety of secretive snake species for which traditional CMR studies are infeasible. Many of the most poorly known and imperiled snakes in North America are fossorial, spending the majority of their lives underground, where they are not available for capture. Examples include other upland species such as pinesnakes (*Pituophis* spp.), coralsnakes (*Micrurus fulvius*) and short-tailed kingsnakes (*Lampropeltis extenuatum*), as well as many desert species, and even some fossorial lizards such as the beaded (*Heloderma* spp.) and legless lizards (*Ophisaurus* spp.). An extreme example is the Louisiana pinesnake (*Pituophis ruthveni*), a species for which extensive trapping and field sampling have yielded a total of only a few dozen captures over the past decade (Rudolph *et al*. 2006). For invasive snakes such as the Burmese python (*Python molurus bivittatus*), issues with very low detection probability (Dorcas and Willson 2011) are further complicated by the fact that release of captured individuals is potentially harmful to the environment. For many of these species, road surveys are the most effective standardised survey method (Willson 2016) and some have been studied previously using radio-telemetry, providing data on spatial movement patterns. Our approach shows strong promise for understanding the status, conservation, and management of these species, and, in some cases, could be implemented using existing data sources.

Finally, several factors should be considered when implementing our method to estimate the density of secretive snakes. First, because our model currently assumes that road crossings are randomly distributed in space and time, relative to survey effort, a large volume of road survey data should be collected (to average out variation owing to environmental conditions and other factors) and, ideally, surveys should be randomly or systematically timed (i.e. not concentrated on particular or 'best' conditions). Also, for this reason, it may be best to constrain data collection and analyses to seasons when road-crossing movements are expected to peak, as we have done for *H. simus*. Obviously, 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 (daily for most species, but perhaps more frequently for species that move extensively). Finally, unless models are extended in a more complex, spatially explicit fashion, our approach is probably best suited to relatively uniform landscapes where dramatic shifts in density or movement are not expected. Keeping these guidelines in mind, our method will undoubtedly improve our ability to study and manage rare and secretive snake species that have previously been considered intractable to population-level research.

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