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Habitat fragmentation effects on annual survival of the federally protected eastern indigo snake

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Keywords
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Abstract

The eastern indigo snake (*Drymarchon couperi*) is a federally listed species, most recently threatened by habitat loss and habitat degradation. In an effort to estimate snake survival, a total of 103 individuals (59 males, 44 females) were followed using radio-tracking from January 1998 to March 2004 in three landscape types that had increasing levels of habitat fragmentation: (1) conservation cores; (2) conservation areas along highways; (3) suburbs. Because of a large number of radio-tracking locations underground for which the state of snakes (i.e. alive or dead) could not be assessed, we employed a multistate approach to model snake apparent survival and encounter probability of live and dead snakes. We predicted that male snakes in suburbs would have the lowest annual survival. We found a transmitter implantation effect on snake encounter probability, as snakes implanted on a given occasion had a lower encounter probability on the next visit compared with snakes not implanted on the previous occasion. Our results indicated that adult eastern indigo snakes have relatively high survival in conservation core areas, but greatly reduced survival in conservation areas along highways and in suburbs. These findings indicate that habitat fragmentation is likely to be the critical factor for species' persistence.

Introduction

Population size estimates provide little information for management without quantification of the factors that influence population numbers (Van Horne, 1983; Pulliam, 1988). Populations are particularly sensitive to habitat factors that affect breeder survival, but such vital rates are rarely estimated, particularly in ways that account for the confounding effects of detection probabilities (Conroy, 1993; Mazerolle *et al*., 2007; Breininger *et al*., 2009). Habitat fragmentation threatens biological diversity worldwide, and many snake species are likely to be sensitive to habitat fragmentation because they occur in low densities, have limited dispersal abilities, and are subject to direct and indirect mortality caused by humans (Webb & Shine, 1998). Determining the severity, extent and cause of snake population declines is difficult because snake population parameters are difficult to quantify (Tuberville *et al*., 2000; Roe, Kingsbury & Herbert, 2004; Altwegg *et al*., 2005; Roe, Gibson & Kingsbury, 2006; Waldron *et al*., 2006; Winne *et al*., 2007; Hibbitts, Painter & Holycross, 2009). Snake survival can depend on many factors, such as body size, habitat, fire and drought. The eastern indigo snake (*Drymarchon couperi*) is a federally protected species whose survival is probably vulnerable to habitat fragmentation (US Fish & Wildlife Service, 1998; Dodd & Barichivich, 2007).

The population ecology of the eastern indigo snake is difficult to study using standard herpetological field techniques because it is a wide-ranging habitat generalist occurring in low densities, and it has inactive periods spent within den sites such as gopher tortoise (*Gopherus polyphemus*) burrows, debris piles or dense vegetation (Hyslop *et al*., 2009c; Stevenson *et al*., 2009). The diurnal species is seldom captured in traps, making typical capture–recapture techniques for studying population abundance, survival and recruitment difficult (Williams, Nichols & Conroy, 2002). Although eastern indigo snakes are rarely seen, they are docile and not difficult to capture by hand when observed on open ground, making it possible to study them using radio-tracking. Home range comparisons in landscapes varying in the degree of fragmentation indicate that indigo snakes often cross roads and enter areas where their survival is jeopardized, making survival estimation important (Breininger *et al*., 2011). Most radio-tracking studies rely on known-fate analytical methods (White & Garrott, 1990; Winterstein, Pollock & Bunck, 2001), but such methods are

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inappropriate for indigo snakes because it is often not possible to determine whether they are alive or dead when they are underground.

Our objective was to estimate indigo snake survival in landscape types with three increasing levels of habitat fragmentation. We hypothesized that survival decreases with increasing habitat fragmentation, particularly for males, which occupy large home ranges (Breininger *et al*., 2011). Because we often could not assess the state of snakes as alive or dead, we used multistate modelling to estimate apparent survival, as well as the encounter probability of live and dead snakes, and the effect of transmitter implantation on snake encounter probability.

Materials and methods

Study area

Study sites included conservation lands and suburbs in central Florida with natural communities dominated by scrub, pine flatwoods, marshes, hammocks and swamps that were interspersed within the home ranges of individual indigo snakes (Breininger *et al*., 2011). Indigo snakes in the northern part of their range are restricted to sand hills and adjacent wetlands, largely because they need gopher tortoise burrows as den sites during winter (Speake, McGlincy & Colvin, 1981; Diemer & Speake, 1983). Indigo snakes are diurnal and actively forage for a variety of vertebrate prey, which often include other snakes (Stevenson *et al*., 2010).

We overlaid individual indigo snake home ranges on land-cover maps and classified them into one of three types using data and methods described in Breininger *et al*. (2011). Indigo snake home ranges in conservation areas that were not intersected by highways were termed 'conservation core'. Indigo snake home ranges within conservation areas (i.e. areas without buildings) that were intersected by highways (primary roads) were termed 'conservation highway'. Home ranges intersected by roads and containing housing/buildings were termed 'suburb.'

During this study, we captured 103 adult indigo snakes opportunistically by hand and by constant effort trapping from 1998 to 2002 (Breininger *et al*., 2011). A veterinarian anaesthetized and surgically implanted snakes with SB-2 radio transmitters (Holohil Systems, Ltd, Carp, ON, Canada). Transmitters ranged from 5.7 to 9.8 g and had 10–24-month lifespans. Surgical implantation procedures followed Reinert & Cundall (1982) by implanting transmitters two-thirds of the way from the head into the coelomic cavity and threading the antenna subcutaneously anterior to the transmitter. Ten snakes were given an antibiotic combined with ivermectin during surgery. The use of ivermectin was discontinued once it was discovered that it eventually resulted in the snake's death. All snakes given ivermectin were excluded from analyses from the time the antibiotic was administered. We held the snakes in captivity for 3 days post-surgery, and then returned them to their capture locations. We attempted to recapture snakes prior to expected battery failure in order to have their transmitters replaced.

Each week, we tried to observe the snake or at least determine snake movement to establish if it was alive, unless it was underground (Breininger *et al*., 2011). This allowed us to pinpoint the location of each snake on aerial photographs or by global positioning systems. Occasionally, we triangulated individuals when they were located in areas with limited accessibility, such as on private property. We recaptured 93% of the snakes prior to transmitter battery failure to replace their radio transmitters and extend their tracking period for longer than 1 year, and we recaptured 38% of the snakes twice to extend their tracking periods for longer than 2 years.

Following release, individuals were located every week until the transmitter failed, or the snake disappeared or died. Transmitters appeared to last for their expected lifespan except for one batch of 12 transmitters that began expiring after 10 months. Once this was recognized, we discontinued their use and attempted to recapture all snakes with those transmitters 10 months after their implantation. We attempted to determine the cause of death of each snake found dead. Snakes found along roadsides were assumed to have been killed by motor vehicles. On most occasions, snakes were precisely located, but their state (alive or dead) could not be assessed because they were in dens. Based on more than 100 snakes followed over 5 years, not many ventured outside the home ranges that were established during the first year of tracking, and we observed few movements >2 km. Some of the areas adjacent to our study site were not accessible, so there were many censored events (snakes not seen or precisely located, and therefore, not known to be alive or dead). This rendered inappropriate known-fate models (Kaplan–Meier product limit estimators) frequently used with radio-tracking data (Pollock *et al*., 1989; White & Garrott, 1990).

Multistate analyses

We used a multistate model with the φ (survival–transition probabilities) parameterization to model ϕ_i^{rs}, the probability that an animal alive in state r at period i survives to period $i+1$ and is found in state s at that time, p_i^s the probability that an animal in state s at period i is captured (Brownie *et al*., 1993; Williams *et al*., 2002). 'State' referred to whether the animal was observed as alive or dead each time it was located. In our application, the probability of survival was estimated by $\varphi_i^{alive-alive}$, the probability of being alive at time i and staying alive until time $i+1$. We fixed the probability of $\varphi_i^{dead-dead}$ to 1 (i.e. once dead, a snake remains dead). This model shares similar assumptions to that of the Cormack–Jolly–Seber model, namely that marks are not lost (i.e. transmitters remain active until the end of the study), individuals are correctly identified, and that snakes behave independently of one another (see Brownie *et al*., 1993; Williams *et al*., 2002).

In our multistate analysis, a '0' indicated a snake was either not located or located but its state was unknown, a '1' indicated that the snake was known alive, and '2' indicated the snake was known dead. Individuals were removed from

Table 1 Variables potentially influencing eastern indigo snake (*Drymarchon couperi*) apparent survival and encounter probabilities considered in the candidate multistate capture–recapture models

Parameter	Grouping variable	Biological interpretation
φ	Landscape	Survival varies across landscape type
	Sex	Survival varies between sexes
	Season	Survival varies across season
	Landscape*sex	Survival of males versus females differs across landscape type
	Season*sex	Survival of males versus females differs across season
p	TSI	Transmitter implantation influences encounter probability on next occasion
	Landscape	Encounter probability varies across landscape type
	Sex	Encounter probability varies between sexes
	State	Encounter probability varies across live and dead snakes
	Season	Encounter probability varies across season
	Landscape*TSI	Encounter probability of snakes implanted versus not implanted on previous occasion varies across landscape type
	Landscape*sex	Encounter probability of males versus females varies across landscape type
	Landscape*season	Encounter probability in a given landscape type varies across season
	Landscape*state	Encounter probability of live versus dead snakes varies across landscape type
	Sex*TSI	Encounter probability of snakes implanted versus not implanted on previous occasion varies between sexes
	Sex*season	Encounter probability of males versus females varies across season
	State*TSI	Encounter probability of live versus dead snakes depends on whether they were implanted on previous occasion

TSI, time since transmitter implantation.

the study at the end of the transmitter life or when they were found dead. The complement of survival $(1-\varphi_i^{alive-alive})$ included animals that became classified as known dead and animals that disappeared.

Our study period spanned 326 weeks, which would imply encounter histories consisting of a string of 326 characters. We opted for an alternative arrangement of the encounter histories to reduce the number of parameters in subsequent analyses. Because we did not suspect year-to-year differences in weekly survival of indigo snakes, but rather, seasonal effects, we started the encounter history of each snake in the first week of January of the year of its first release. The length of each encounter history was based on the snake having been followed for the longest period (in weeks) since the first week of January of the year of its first release. In our case, it spanned 189 weeks (3 years and 33 weeks). Thus, for each individual, we indicated whether it had been seen alive or dead, or had not been seen in each of the 189 weeks following its initial release. We treated snakes as if they had not been encountered if their status could not be assessed, for example, because they were underground. These locations were viewed as providing no information about the process being modelled (snake life–death).

We estimated the parameters of the multistate models by maximum likelihood with a modification of program SURVIV (White, 1983) by J. E. Hines. To facilitate convergence, we used relatively simple models to obtain initial parameter estimates for the more complex models. Given that the weekly survival of adult indigo snakes is typically high and not of direct interest, we converted the estimates to yearly survival by exponentiation (i.e. φ^{52}) and obtained variances for yearly survival with the delta method (Oehlert, 1992).

Candidate models

We built models to test the biological hypotheses that snake survival varies across landscape type, sex, season, the landscape type × sex interaction and the season × sex interaction (Table 1). Based on the literature, we predicted that apparent survival would be lowest for male snakes in the suburb (landscape × sex interaction) and lowest in summer (season × sex interaction, Dodd & Barichivich, 2007). We combined each of these potential effects on survival with different sources of variation for the encounter probabilities including time since transmitter implantation (TSI, i.e. week following implantation or not), landscape type, sex, state (alive or dead), season or combinations thereof (Table 1).

We kept the number of parameters in each model to a minimum, recognizing that the amount of data we had was limited for multistate models that estimate many parameters. We modelled seasonal effects by constraining survival and encounter parameters for each season (i.e. weekly estimates within a given season had the same value). Further, we only considered simple interactions. We formulated three complex models instead of a single global model, each consisting of φ (landscape*sex*season) with *p* (landscape*sex*state*TSI), *p* (season*landscape) or *p* (season*sex). These complex models were used to assess model fit.

We assessed goodness-of-fit with the pooled χ^2 of program SURVIV (White, 1983) and estimated c-hat as χ^2/degrees of freedom (d.f.). The model involving time since transmitter implantation on the probability of encounter, φ(landscape*sex*season) *p*(landscape*sex*state*TSI), fit the data well ($\chi^2 = 914.44$, d.f. = 892, $P = 0.2946$, c-hat = 1.02). The other two models defined by the alterna-

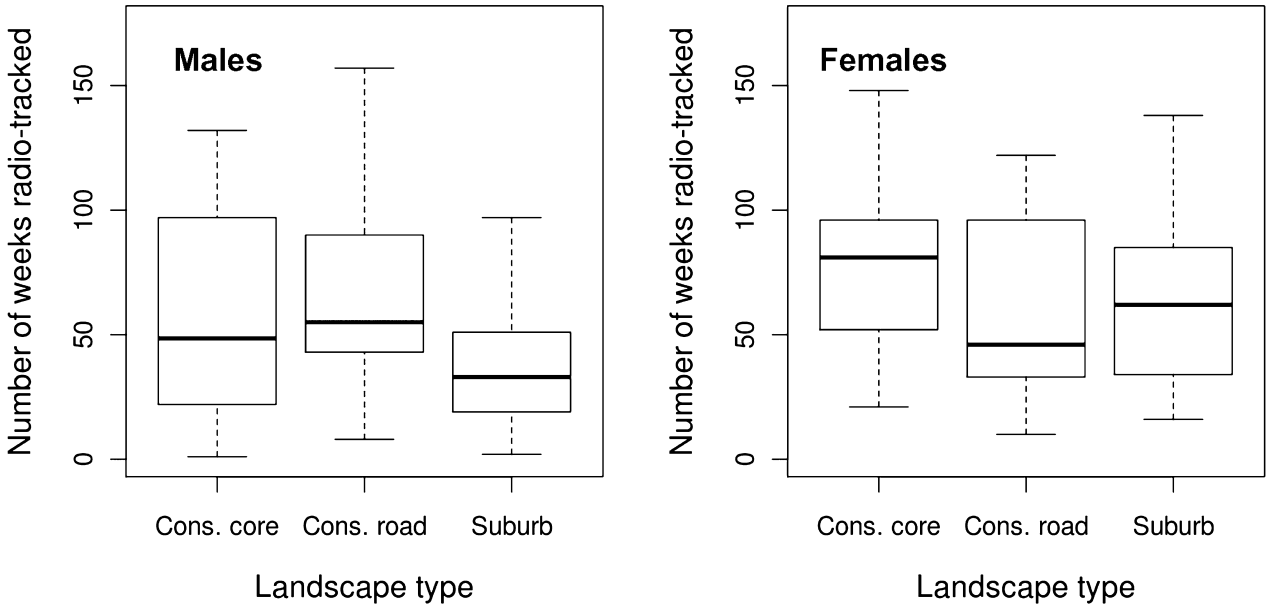

Figure 1 Number of weeks male and female eastern indigo snakes (*Drymarchon couperi*) were radio-tracked in habitats with different landscape types in Florida between 1998 and 2004. A total of 59 male snakes (26, 17 and 16 in conservation core, conservation road and suburb landscape types, respectively), and 44 female snakes (17, 13 and 14 in conservation core, conservation road and suburb landscape types, respectively) were implanted with transmitters and followed during the study. Note that upper and lower hinges of box plots indicate the first and third quartiles, and the median is the bold horizontal line within the box.

tive scenarios on encounter probability, p (season*sex) and p (season*landscape), did not fit the data. Model φ (landscape*sex*season) p (landscape*sex*state*TSI) yielded the smallest estimate of c-hat, and because it was very close to 1, we used the second-order Akaike information criterion to select the most parsimonious of our candidate models (Burnham & Anderson, 2002).

Results

Ninety-five per cent of our study animals were captured opportunistically. Female snakes (mean = 1.6 m, range = 1.2–1.9 m) averaged shorter than male snakes (mean = 1.7 m, range = 1.3–2.1 m), and female snakes (mean 1.2 kg, range = 0.5–2.0 kg) averaged lighter than male snakes (1.5 kg, range = 0.4–3.0 kg). Fifty-one indigo snakes were alive at the end of the study when we terminated tracking, and 13 had disappeared without us being able to determine their fate (Fig. 1). We could not determine the cause of death for 11 snakes. We found 15 study animals dead along roads and five that were intentionally killed by humans. We observed one snake infested by intestinal, lung and external parasites that were the suspected cause of death. We believe that 10 snakes died from injections of ivermectin given during surgery. We observed one snake that may have died because of a leaking transmitter battery and no other problems caused by transmitters were observed by the veterinarian except those associated with ivermectin as described earlier.

There was strong evidence of variation of indigo snake apparent survival across landscape type. Model φ (landscape) p (landscape*TSI) ranked highest among the candidate models with most of the support ($w_i = 0.90$, Table 2). This model suggested that snake annual survival was highest in the conservation cores, and decreased with increasing habitat fragmentation (Fig. 2). Annual survival was higher in the conservation cores relative to conservation areas with roads [conservation core – conservation areas with roads = 0.26, 95% confidence interval (CI): 0.017, 0.499] and suburbs (conservation core – suburbs = 0.38, 95% CI: 0.129, 0.625). Survival of snakes between conservation areas with roads and suburbs was similar (conservation areas with roads – suburbs = 0.12, 95% CI: –0.192, 0.431). A second model had weak support for variations between male and female survival across landscape type, though this model had substantially lower weight ($w_i = 0.09$). There was no evidence supporting an effect of season on snake survival (Table 2).

Snake encounter probability varied across certain groups. Specifically, transmitter implantation had a negative effect on encounter probability, and this effect was relatively uniform within each landscape type (Fig. 3). The encounter probability of snakes in suburbs tended to be greater than in the other two landscape types (Fig. 3). However, there was no support in favour of encounter probabilities varying across snake state (live vs. dead), sex or season.

Discussion

Differences in survival between sexes can be substantial in some snake species (Bonnet, Guy & Shine, 1999), but we did not find differences in annual survival between male and female snakes, which concurred with Hyslop *et al.* (2009b).

Table 2 Top 10 multistate capture–recapture models for the radio-tracked eastern indigo snake (*Drymarchon couperi*) data following model selection based on the AICc

Model	Log-likelihood	*K*	ΔAICc	w_i
φ (landscape) *p* (landscape*TSI)	−2807.47	9	0	0.90
φ (landscape*sex) *p* (landscape*TSI)	−2806.70	12	4.55	0.09
φ (landscape) *p* (state*TSI)	−2816.79	6	12.58	0.00
φ (sex) *p* (landscape*TSI)	−2816.77	8	16.57	0.00
φ (landscape*sex*season) *p* (landscape*sex*state*TSI)	−2775.22	48	16.64	0.00
φ (landscape*sex) *p* (state*TSI)	−2815.79	10	18.66	0.00
φ (season) *p* (landscape*TSI)	−2816.00	10	19.08	0.00
φ (season*sex) *p* (landscape*TSI)	−2815.15	14	25.52	0.00
φ (landscape) *p* (TSI)	−2825.28	5	27.54	0.00
φ (landscape) *p* (sex*TSI)	−2824.32	7	29.66	0.00

AICc, the second-order Akaike information criterion; TSI, time since transmitter implantation.

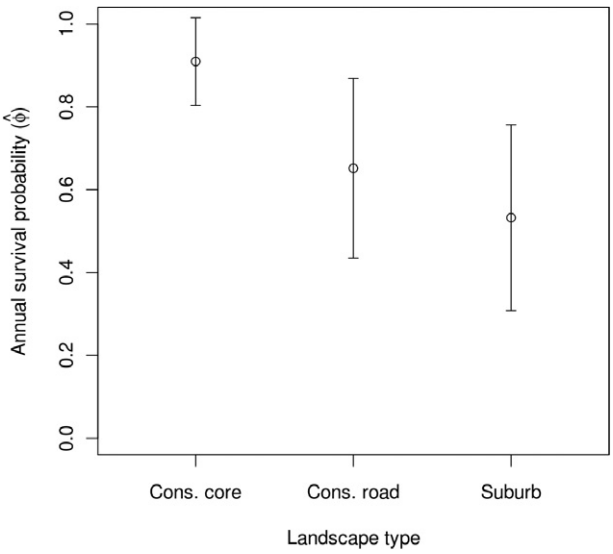

Figure 2 Annual apparent survival (±95% confidence interval) of radio-tracked eastern indigo snakes (*Drymarchon couperi*) in Florida across the three landscape types. Estimates shown from the top-ranked multistate model, φ (landscape) *p* (landscape*time since transmitter implantation).

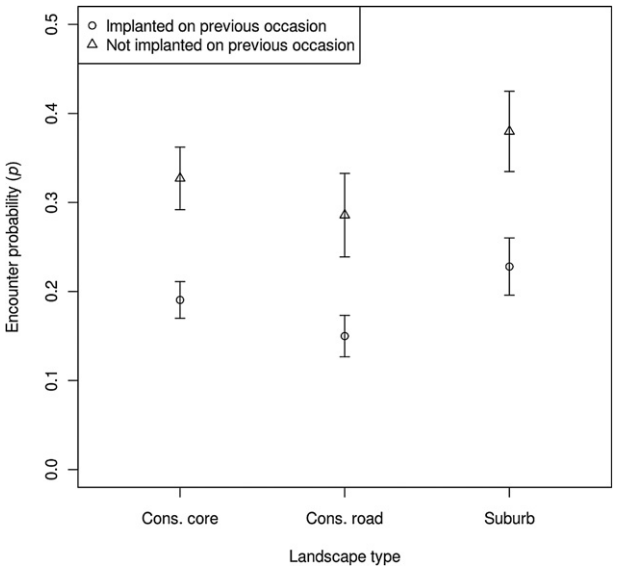

Figure 3 Encounter probability (±95% confidence interval) of radio-tracked eastern indigo snakes (*Drymarchon couperi*) in Florida across the three landscape types. Note that encounter probabilities for snakes implanted with a transmitter on the previous occasion were lower than for snakes not implanted on the previous occasion.

We found that at least 55% of known snake mortalities not associated with implantation procedure problems were caused by humans directly or indirectly along roads. We found little evidence for natural predation, probably because the snakes are relatively large predators themselves, and were often concealed in dense vegetation or underground. We found landscape-specific differences in survival, which are rarely investigated in vertebrates once potential differences in detection probabilities among landscape types are considered (Conroy *et al*., 1996; Breininger *et al*., 2009). The estimation of survival rates, while accounting for detection probabilities and other problems in data collection, is one of the most glaring deficiencies in snake population studies (Parker & Plummer, 1987; Brown, Kery & Hines, 2007; Hyslop *et al*. 2012).

For long-lived snakes, reduced survival may increase the extinction probability of populations (Webb, Brook & Shine, 2002). Using population viability analyses, eastern indigo snake populations were predicted to be vulnerable to extinction in conservation areas bordered by roads and suburbs, based on survival rates similar to those reported in our study (Breininger, Legare & Smith, 2004). Road mortality has particularly negative effects on herpetofauna and other animals that have large movement ranges, low reproductive rates and low natural densities (Fahrig & Rytwinski, 2009). Direct killing by humans and road mortality have long been established as factors that make many large vertebrate species vulnerable to extinction in conservation areas with high edge to surface ratios (Woodroffe & Ginsberg, 1998; Kerley *et al*., 2002; Schwartz, Haroldson & White, 2010). Many studies show that edge to surface ratios are relevant to many herpetofauna and smaller vertebrate populations (Mumme *et al*., 2000; Driscoll, 2004; Balme, Slotow &

Hunter, 2010; McCall *et al*., 2010). Although roads often account for only a small portion of landscapes, their influence can extend across large areas because they restrict dispersal and gene flow (Trombulak & Frissell, 2000; Forman *et al*., 2003; Shine *et al*., 2004; Steen & Gibbs, 2004; Row, Blouin-Demers & Weatherhead, 2007; Clark *et al*., 2010).

We suspect that indigo snakes could have higher survival in roadless conservation areas than observed in our study sites. All snakes occurred in areas that had at least some off-road vehicle traffic, and we recorded two snake deaths along roads only passable by off-road vehicles. It would be useful to repeat this study across a broad range of traffic volumes and road densities (e.g. Schwartz *et al*., 2010). Performing such a study is limited by the ability to capture enough study animals. We had success capturing study animals using traps designed by Rudolph *et al*. (1999). However, capture rates were low and traps had to be checked once or twice a day because of weather and the risk of capturing other protected species (Dyer, 2004).

Snake studies using telemetry usually rely on known-fate analyses, which was not appropriate in our study because we often could not determine if snakes underground were alive or dead. Combining radio-tracking methods with multistate capture–recapture analyses allowed us to reliably estimate survival for an animal that is rarely captured in traps, or whose fate often cannot be reliably determined even when an animal with a transmitter is located. We found one snake survival study that used multistate models, but such models were used in the conventional manner where the states referred to different habitats and not snake condition (live or dead; Lyet *et al*., 2009). A potential alternative to our approach would be to use multistate models with state uncertainty to exploit the information on underground locations (Nichols *et al*., 2004; Kendall, 2009). Although our study measured apparent survival and did not account for habitat-specific emigration, we never observed permanent emigration from home ranges between years or seasons (Breininger *et al*., 2011).

We agree with colleagues (Hyslop, 2007) that indigo snakes need large tracts of habitat for sustainable populations because individuals have large home ranges and are vulnerable to mortality caused by humans. Indigo snake populations, like many other species residing in fire-maintained habitat, may themselves be influenced by fire history. Indeed, gopher tortoises require regular fires and these species provide necessary den sites for indigo snakes, at least in some portions of their range (Speake, McGlincy & Colvin, 1978; Waldron, Welch & Bennett, 2008; Hyslop, Cooper & Meyers, 2009a).

Conservation implications

In this study, we showed that annual survival of indigo snakes decreased as levels of fragmentation increased to the extent that the viability of populations might be impacted. This reinforces our earlier argument that species conservation planning is needed to keep critical conservation areas from having too many edges that result in high indigo snake mortality (Breininger *et al*., 2004). Many existing conservation lands may be too small, especially if they become bordered by highways and suburbs. Conservation lands are often linked together to form larger systems, which is an excellent strategy when focusing on birds and vagile mammals. However, indigo snakes residing within corridors may be particularly vulnerable to extinction if they are too fragmented or too narrow. Corridors suitable for indigo snakes may need to be wider, unfragmented by roads and shorter than those needed for more vagile animals. In addition, all of our study animals were adults, there is a need for research to quantify how population vital rates are impacted by fragmentation of other life history stages (e.g. Hyslop *et al*. 2012) as younger animals may react differently to habitat perturbations.

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