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Hits Close to Home: Repeated Persecution of King Cobras (*Ophiophagus hannah*) in Northeastern Thailand

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Abstract

Protected areas are often promoted as an important solution to preserving biodiversity. However, permeable edges can undermine the effectiveness of preserves because animals may move into adjacent human-dominated unprotected areas. We investigated attitudes toward, and sources of mortality of, a far-ranging apex predator, the king cobra (*Ophiophagus hannah*; Cantor 1836), in a biosphere reserve in northeastern Thailand. Our questionnaire revealed marked fear of snakes and hostility toward king cobras. Using radiotelemetry, we followed 23 king cobras over a 4-year period, during which time we documented the mortality of 14 individuals. We considered 10 of the deaths to be anthropogenic in origin, including road mortality, pollution, fish traps, and direct persecution; these deaths disproportionately occurred in unprotected areas. Our results highlight how dangerous human-dominated landscapes are for king cobras. Because king cobras move long distances and maintain large home ranges, it is likely that successful conservation of the species cannot be satisfactorily met by protected areas alone; a more holistic, education-focused conservation strategy is required. We stress the importance of a human dimensions approach that leads toward greater understanding of human attitudes toward king cobras, and snakes in general, combined with ecological research for more effective conservation.

Keywords

conservation, fear, mortality, elapid, snake, survival, human dimensions, attitudes, Thailand

Introduction

Many populations of snakes appear to be declining (Reading et al., 2010; Saha et al., 2018). To effectively counter declines and create appropriate conservation strategies, we must identify threats facing species (Peery, Beissinger, Newman, Burkett, & Williams, 2004; Steinmetz, Chutipong, & Seuaturien, 2006). Possible anthropogenic pressures include unsustainable harvest, invasive species, pollution, disease, habitat degradation, and mortality associated with roads and direct persecution (Gibbons et al., 2000; Trombulak & Frissell, 2000).

While there is evidence that protected areas can mitigate against anthropogenic pressures (Bruner, 2001; Gray et al., 2016; Newmark, Manyanza, Gamassa, & Sariko, 1994), problems remain concerning designation, maintenance, and boundary permeability (Baldi, Texeira, Martin, Grau, & Jobbágy, 2017; Forbes & Theberge, 1996; Rodrigues et al., 2004). When species travel outside of protected areas, they are more likely to come into conflict with humans, which can result in reduced survival (Smith, White, Stahler, Wydeven, & Hallac, 2016; Swanepoel et al., 2015). The likelihood

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of animals using anthropogenic areas will increase as protected areas become increasingly fragmented and isolated (Clark, Boakes, McGowan, Mace, & Fuller, 2013; DeFries, Hansen, Newton, & Hansen, 2005; Jones et al., 2018). Habitat loss in tropical regions is rapid (Bellard et al., 2014; Hughes, 2017; Roll et al., 2017; Sodhi et al., 2010), underscoring the need to better understand how animals can persist in unprotected anthropogenic landscapes (Hansen & DeFries, 2007).

Snakes are known to react to habitat loss by making use of novel anthropogenic landscapes (French, Webb, Hudson, & Virgin, 2018). However, this often leads to increased instances of human–snake conflict, which frequently result in removal or death of snakes (Anguiano & Diffendorfer, 2015; Miranda, Ribeiro, & Strüssmann, 2016; Pandey, Pandey, Devkota, & Goode, 2016; Saunders, Hobbs, & Margules, 1991; Shine & Koenig, 2001; Skole & Tucker, 1993). In addition, increased snake mortality (Akani, Eyo, Odegbune, Eniang, & Luiselli, 2002; Pandey et al., 2018; P. B. Whitaker & Shine, 2000) may compromise snakes' important role as mesopredators in ecosystems (O'Bryan et al., 2018; Willson & Winne, 2016).

Problems arising from snake–human conflict may be compounded by evolutionarily innate or culturally learned aversion to snakes or snake-like shapes (DeLoache & LoBue, 2009; LoBue & DeLoache, 2008; Öhman & Mineka, 2003; Pandey et al., 2016; Souchet & Aubret, 2016). Typically, people have limited knowledge of snakes, resulting in negative reactions, and subsequent attempts to kill snakes may lead to not only increased snake mortality but life-threatening bites from venomous snakes as well (Longkumer, Armstrong, Santra, & Finny, 2016; Miranda et al., 2016; Nonga & Haruna, 2015; Pandey et al., 2016; P. B. Whitaker & Shine, 2000). Human predisposition to kill snakes adds additional sources of mortality for snakes occupying human-dominated areas (Akani et al., 2002; Bailey, Campa, Harrison, & Bissell, 2011; Meek, 2012; Pandey et al., 2016; Shankar, Singh, Ganesh, & Whitaker, 2013; P. B. Whitaker & Shine, 2000; Wolfe, Bateman, & Fleming, 2017).

The tendency to kill snakes may be affected by characteristics of the species, such as size or aposematic markings (Miranda et al., 2016; Souchet & Aubret, 2016). The king cobra (*Ophiophagus hannah*; Cantor 1836) is a large snake with prominent aposematic signaling. Growing up to 5.85 m and possessing potent neurotoxic venom (Chanhome, Cox, Vasaruchapong, Chaiyabutr, & Sitprija, 2011; Das, 2010), king cobras inspire awe and fear in rural Indian communities (Shankar et al., 2013). King cobras are distributed throughout Southeast Asia, from India to southern China and eastward to the Philippines (Das, 2010). Although king cobras are typically associated with pristine natural areas (Stuart et al., 2012), they are known to use agricultural and degraded habitats (Rao et al., 2013; R. Whitaker & Captain, 2004).

King cobras have multiple life history traits that increase vulnerability to extinction, including large body size, higher trophic position, restricted diet, and slower maturation (Böhm et al., 2016; Stuart et al., 2012; Todd, Nowakowski, Rose, & Price, 2017; Wolfe et al., 2017). Conservation strategies, such as snake relocation, are proving problematic and frequently unsuccessful, leading to aberrant behaviors and lower survival rates (Butler, Malone, & Clemann, 2005; Devan-Song et al., 2016; Dodd & Seigel, 1991; Fry, 2018; Germano et al., 2015; Plummer & Mills, 2000). Similar aberrant behavior has been recorded for king cobras in India but only for a single individual (Barve et al., 2013). Therefore, the need to study a larger sample of king cobras is clearly needed.

We aimed to examine prevailing attitudes toward snakes and to identify risks faced by king cobras, in the vicinity of a protected biosphere reserve using long-term radiotelemetric monitoring and questionnaires. Our overall goal was to provide valuable information pertaining to the conservation of king cobras in Thailand and throughout the species' range.

Methods

Study Site

We conducted our research in the Sakaerat Biosphere Reserve (SBR) based at the Sakaerat Environmental Research Station. The reserve is located in northeast Thailand in Nakhon Ratchasima Province (14°26′24″–14°33′0″ N, 101°52′48″–101°57′0″ E). It comprises three area types: a protected core area of 8,000 ha, and unprotected buffer and transitional zones that cover 36,000 ha. The core area is made up of dry evergreen forest (60%) and dry dipterocarp forest (18%), with the remaining areas (22%) classified as reforested, and very small areas of grassland or bamboo forest. Rangers patrol the core area daily on randomized routes according to Sakaerat Environmental Research Station to protect the forest and its fauna. The buffer zone consists mainly of unprotected forest, with large tracks of regrowth plantation among older dry evergreen forest. The transitional zone is largely agricultural and only contains highly fragmented forest patches. The agriculture is primarily cassava and rice, but there are areas of maize, sugar, and banana as well as small plantation forests. Human settlements are dotted across the area, housing over 72,000 people split across 159 villages (Thailand Institute of Scientific and Technological Research, 2018), most of which are adjacent to paved roads. Many of the paved roads connect to the major four-lane 304 highway that bisects the biosphere and runs adjacent to the southern boundary of the core area.

Village Questionnaire

We selected participants opportunistically in social settings of the biosphere reserve such as schools, shops, cafes, restaurants, local markets, and outside homes. We informed interviewees that all responses would be anonymous. We excluded interviews from individuals under the age of 18 years due to permit restrictions. Two native Thai speakers collected all questionnaire responses to limit interviewer biases. Participation was voluntary, and participants were allowed to stop the interview or decline to answer a question at any time. We divided the data set into two main categories, *spoken* and *written*, which were largely dependent on the literacy of participants. When we read the questionnaire to participants (due to literacy or unwillingness to read the document themselves), we labeled the resulting answers as *spoken* Thai team members presented the questionnaire, whether written or spoken, in Thai. We distributed and collected all questionnaires in June–July, 2015. We provide a full list of questions in Supplementary Materials (S1). Questions concerning the most dangerous snake and behaviors when faced with snakes were not limited to a single response.

King Cobra Capture and Processing

We employed several methods during the course of this study, including trapping, unstandardized road surveys, local snake rescue calls, and opportunistic captures. We completed some of the trapping effort from March 2012 to April 2013 as part of a separate study, when we opened traps 1 week per month. We deployed *Y*-shaped trap arrays using wire mesh drift fences and placed funnel traps at the ends of all three drift fences. We deployed a total of 24 trap arrays. In addition, we deployed 36 *T*-shaped trap arrays with larger 2-m-long funnel traps placed in locations deemed likely to capture king cobras, specifically.

On capture, we assigned each king cobra a unique ID identifying their age class (N—neonate, J—juvenile, or A—adult), sex (M—male and F—female), and sequential capture number (001–059). We used vaporized isoflurane to anesthetize captured king cobras so more consistent measurements could be collected (Setser, 2007). For each king cobra, we recorded snout-vent length (SVL), mass, and sex (sex was determined via cloacal probing; Schaefer, 1934). Using a cauterizing iron, we branded each individual with a unique marking (Winne, Willson, Andrews, & Reed, 2006). We selected king cobras of sufficient size, health, and captured within a practical distance from the research station for radiotransmitter implantation (AI-2T or SI-2T, Holohil Inc., Ontario, Canada). A local Thai veterinarian from Nakhon Ratchasima Zoo aided in the implantation of the transmitters into the coelomic cavity of each king cobra in accordance with Reinert and Cundall (1982). We released all king cobras as close as possible to their capture. During the first 2 weeks' post-release, we remained at least 50 m from radiotracked individuals to minimize disturbance.

We recaptured individuals every 6 to 8 months to examine their health. We replaced transmitters every 12 to 18 months due to battery life limitations. During these recaptures, we repeated all standard morphometric measurements and qualitatively assessed body condition by assigning snakes to one of the four categories: *excellent, good, fair and poor*.

Radioelemetry

We radiotracked snakes from March 2013 through March 2018. Prior to 2014, we undertook tracking following the methods described in Marshall et al. (2018). From March 22, 2014 until May 25, 2018, we tracked king cobras 4 times daily with approximately 4 h between each successful track. For each track, we determined an individual snake's location by triangulation and did not visually confirm the location unless the snake had remained stationary for over a week to avoid disturbing natural behaviors. Triangulation comprised of circling a snake's location until it was determined to be within a 5×5 m area, and then recording the location on a handheld Garmin GPS 62s or 64s unit using Universal Transverse Mercator (47N) WGS 84 projection. During triangulation, we always remained at least 10 m from the snake's location with no more than three personnel. After September 2016, we reduced the number of fixes to three per day due to staff limitations.

Analyses

We performed all analyses with R (R Core Team, 2017) in R Studio (R Studio Team, 2016) using the packages listed in the Supplementary Material (S2). We tested data for normality using Shapiro–Wilk tests and confirmed with an inspection of Q–Q plots. We completed Wilcoxon rank-sum tests and χ^2 tests to compare subsets of the questionnaire data. We explored snake attributes using Wilcoxon rank-sum tests and Spearman's rank test. We also calculated a Scaled Mass Index (SMI), based on measurements of SVL and mass at initial capture, as a quantitative proxy for body condition (Peig & Green, 2009, 2010). We selected SMI because of its performance compared with other indices (Peig & Green, 2010). We did not include dead on arrival king cobras in the SMI estimation because in many cases the body had degraded to a point where mass measurements would not be representative of the individual's mass on mortality. We compared weights and SMI at first and last capture using a Wilcoxon rank-sum test.

We used a staggered-entry KaplanMeier estimation to examine survival rates (Pollock, Winterstein, Bunck, & Curtis, 1989). We excluded JM002, AF004, and AM005 from the survival analysis because we tracked them using different protocols and there was a discontinuity between their tracked periods and the rest of the snakes. We standardized SVL for each sex to separate the effect of sex and SVL by taking a snake's SVL from the mean SVL of the snake's sex and dividing by the standard deviation (*SD*) of SVL for that sex (Rose & Todd, 2017). We investigated the effect of sex-standardized SVL, age, and sex on survival using a Cox proportional hazards regression model.

Results

Villager Opinions

A total of 59 individuals voluntarily participated in the questionnaire (35 female, 22 male, and 2 not given) with a mean age of 44 years (95% 40.05–47.28, $SD = 13.62$, range = 18–78). An unpaired Wilcoxon test showed that the *spoken* questionnaire subset was significantly older ($W = 594.5$, $p < .01$). Our χ^2 tests revealed no significant differences between sexes ($\chi^2 = 9.7246$, $p = .38$) or *spoken*/*written* subsets ($\chi^2 = 9.1164$, $p = .44$) and responses concerning fear of snakes, whether the respondents eat snakes, their importance to the environment, or the behavior when faced with a snake (Figure S3). This was also the case when we tested proportion of yes answers using Wilcoxon tests (sex, $W = 50.5$, $p = 1$; *spoken*/*written* $W = 51.5$, $p = .94$). Therefore, we pooled *spoken* and *written* data for subsequent analyses.

Villager surveys displayed a clear fear of snakes, with 50 of the 57 (87.7%) respondents indicating that they feared snakes (Figure 1(a)). Despite this fear, respondents commonly said that snakes are important to the environment (35/56, 62.5%; Figure 1(a)). Results indicated that half of the respondents eat snakes (27/54; Figure 1(a)). When asked which snake species participants considered the most dangerous, two results stand out—true cobras (*Naja* sp.) and king cobras (Figure 1(c)). These two species were by far the most feared species, with 29 and 27 responses, respectively. There were also three respondents who said all snakes were dangerous.

We also asked how respondents would react when faced with a snake (Figure 1(b)). The most frequently reported behavior was to attack the snake ($n = 15$). Other prominent behaviors included scare the snake away ($n = 12$), run away ($n = 11$), stand still ($n = 11$), and shout ($n = 8$). Least reported was call the police with one response. The two *other* responses involved doing nothing or calling someone other than the police to help.

King Cobra Details

From March 2013 to March 2018, we captured and processed a total of 41 individual king cobras. Data were skewed toward adult males and snakes captured via village notation (villager notation led to captures of 21 males and 4 females).

The 24 adult males all ranged between 1.92 and 8.44 kg ($\dot{x} = 4.55$ kg, 95% 3.80–5.29 kg, $SD = 1.75$ kg) and 2.08 to 3.71 m SVL ($\dot{x} = 2.72$ m, 95% 2.58–2.89 m, $SD = 0.35$ m). Our seven adult females weighed significantly less, between 1.43 kg and 3.60 kg ($\dot{x}$=2.18 kg, 95% 1.61–2.75 kg, $SD = 0.61$ kg; $W = 283$, $p < .01$), and were significantly shorter between 1.95 m and 2.54 m SVL ($\dot{x} = 2.15$ m, 95% 1.98–2.32 m, $SD = 0.19$ m; $W = 292.5$, $p < .01$). Of the 41 king cobras captured, 9 were juveniles that were significantly lighter ($\dot{x} = 1.03$ kg, 95% 0.57–1.65 kg, $SD = 0.63$ kg; $W = 280$, $p < .01$) and smaller than adults ($\dot{x} = 1.76$ m, 95% 1.47–2.08 m, $SD = 0.38$ m; $W = 278$, $p < .01$). Juveniles had a lower mass-to-SVL ratio than the pooled adult ratios (adults $\dot{x} = 1.48$, 95% 1.29–1.67, $SD = 0.51$; juveniles $\dot{x} = 0.55$, 95% 0.35–0.81, $SD = 0.27$; $W = 278$, $p < .01$). There was a significant correlation between SVL and mass in the overall sample (rho = .96, $S = 402.04$, $p < .01$).

We tracked 23 king cobras, of which 12 had confirmed mortalities during the 5-year study period. We released the snakes as close as possible to their capture site ($\dot{x} = 214$ m, 95% 130.33–298.54 m, $SD = 286$ m) and attempted to minimize the time the snakes were out of their natural habitat ($\dot{x} = 4.04$ days, 95% 2.84–5.25 days, $SD = 4.99$ days).

For king cobras recaptured during the study, qualitative assessments of recaptured snakes indicated a lack of discernible change in body condition during radiotracking; all individuals were deemed in *good* ($n = 15$) or *excellent* ($n = 7$) condition at the time of capture, except for AM024 who saw a deterioration from *good* to *poor* body condition and AM018 who went from *good* to *fair* condition on his first recapture (Figure 2; Figure S4). Visual inspection of the incision into which we implanted a radiotransmitter revealed no signs of infection or difficulties healing when examined for health status. All except three snakes showed consistency or improvements in SMI and mass during the study (Figure 2): AF010, AM024, and AM029. The individuals', AF010 and AM029, decrease in SMI is likely not explained by tracking pressure. We only tracked AM010 for 67 days of the 347 days between captures and AM029 for 7 of the 180 days between captures. We cannot discount the effects of transmitter implantation

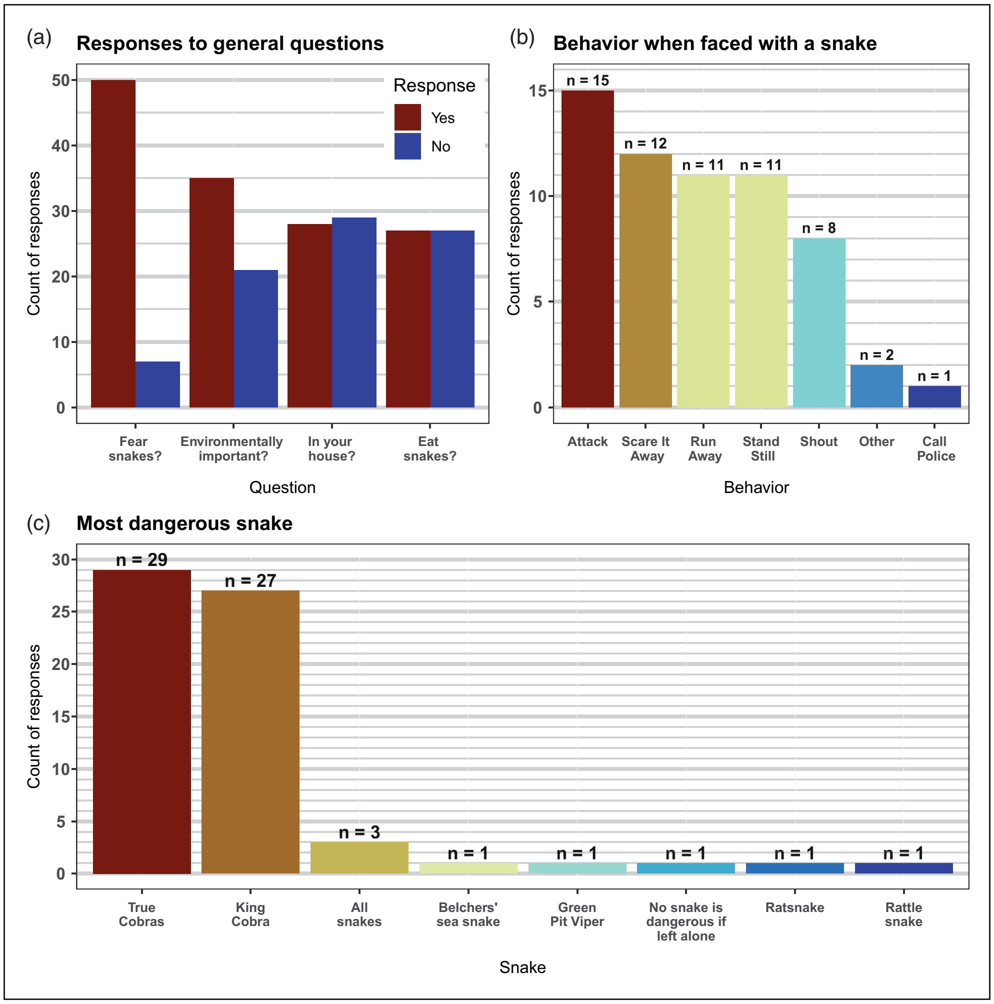

Figure 1. (a) The count of responses, yes and no, to the three questions aimed at assessing people's attitudes toward snakes. (b) The counts of reported behaviors when faced with a snake. (c) The count of snakes considered most dangerous. Respondents were able to give multiple answers.

even without tracking disturbance, but relative transmitter mass to body mass were minimal ($\dot{x} = 0.58\%$, 95% 0.36–0.80%, $SD = 0.50\%$).

Overall, there was no significant difference in snake mass ($V = 8$, $p = .18$), or SMI ($V = 16$, $p = .28$), from their initial capture mass compared with their final recapture mass. There remains no significant difference when partly untracked individuals are included (AM006, AF010, AM029, and JM019; mass, $V = 21$, $p = .31$; SMI, $V = 31$, $p = .57$).

Natural Deaths

We only recorded deaths by natural predators on two occasions—JM002 and AF004. Both deaths occurred within the core protected area of the SBR (Figure 3), and the bodies had marks that looked to be from predators.

Anthropogenic Sources of Mortality

Overall, we confirmed the deaths of 14 king cobras in the anthropogenic landscape of the SBR's transitional zone: nine mortalities were tracked king cobras and two we discovered opportunistically (Table 1; Figure 3).

The two mortalities we observed opportunistically were both road mortalities on the main highway (Figure 3). We discovered the first individual on April 30, 2015, which was a juvenile male (mass = 0.70 kg, SVL = 1.61 m). On August 20, 2017, we found the second individual that was a neonate of unknown sex (mass = 0.02 kg, SVL = 0.48 m).

Only one death that appeared anthropogenic in origin occurred in the protected forested area. We discovered an adult male, AM029, without a head in a forested area in what appears to be an act of persecution. We discovered this mortality near to a recently cleared roadway into the forest.

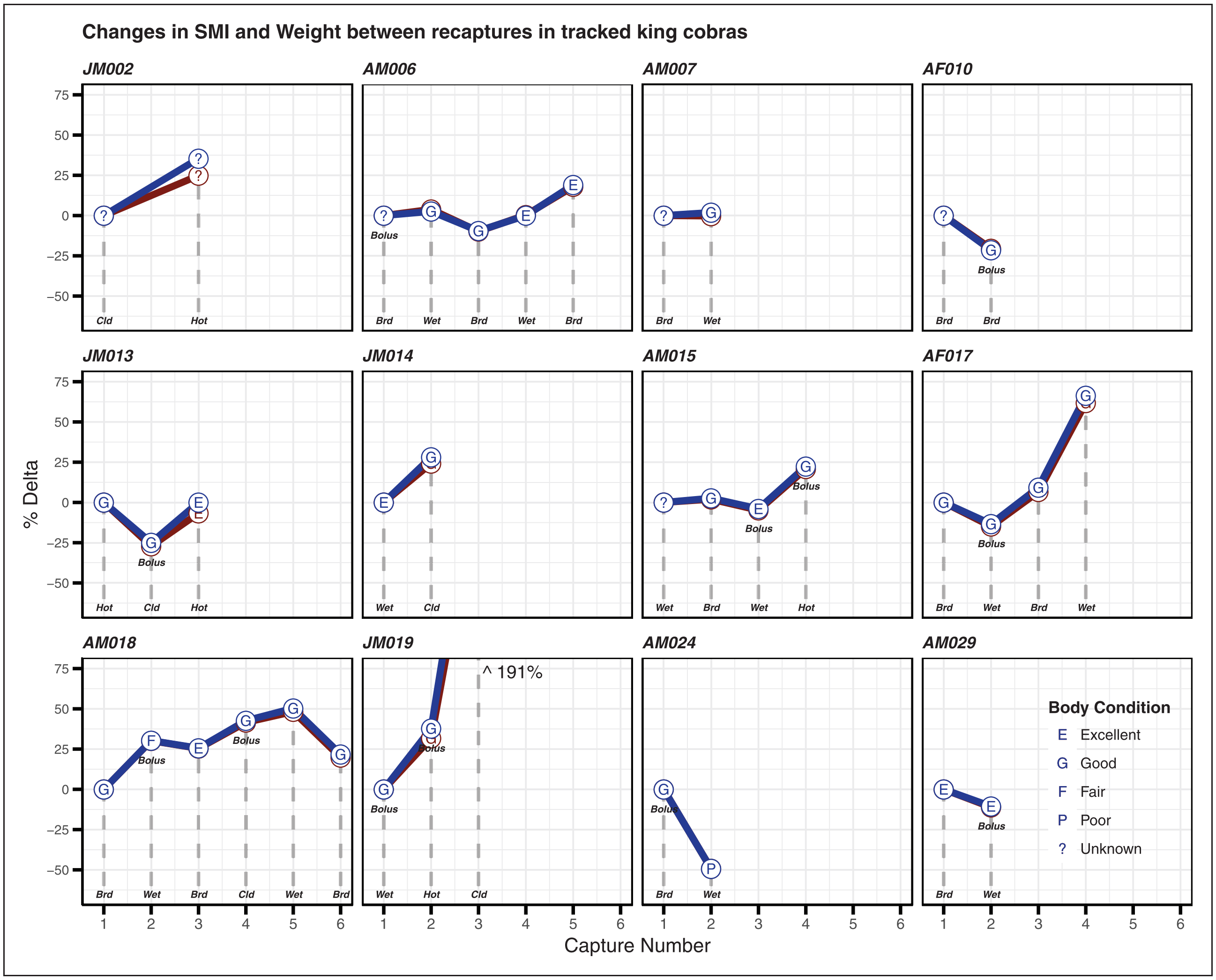

Figure 2. The percentage change in the tracked king cobra's SMI and weights between recaptures. Recaptures ranged from 6 to 8 months. Blue lines and letters show changes in SMI, and red indicates changes in weight. Abbreviations at the base of the graph correspond to the four seasons: Wet, Hot, Brd = breeding and Cld = cold.

We have also observed other evidence of trauma to king cobras in anthropogenic landscapes. We rescued a nontracked individual, AM016, after he was stabbed by a three-pronged spear. Another individual, AM018, had several soft body tumors perhaps resulting from contact with a roadside pollutant. Despite the tumors, he was active and behaving normally as of March 2018 (Strine, unpublished data).

Survival Analysis

Five transmitters failed prematurely that lead us to censor those five snakes in the survival analysis (Figure 4(a)). Our Kaplan–Meier analysis revealed a mean survival rate over the study period of 0.597 (95% 0.450–0.865: $n = 20$; Figure 4(b)). A Cox proportional hazards regression model showed similar results ($\dot{x}$ = 0.528, 95% 0.354–0.885) and failed to show any effect of sex (rho = .288, $\chi^2 = 0.562$, $p = .45$), age class (rho = −.073, $\chi^2 = 0.045$, $p = .83$), and sex-standardized SVL (rho = −.434, $\chi^2 = 1.473$, $p = .23$) on survival (likelihood ratio test = 2.06, $df = 3$, $p = .56$).

Discussion

Before any species can be successfully conserved, the pressures they face need to be identified (Peery et al., 2004; Steinmetz et al., 2006). We suspected that human activity and persecution was directly harming king cobras and managed to identify the direct sources of mortality as well as the local people's perception of snakes that may be responsible for the mortalities.

People inhabiting agricultural areas commonly have negative attitudes regarding snakes (Ceríaco, 2012,

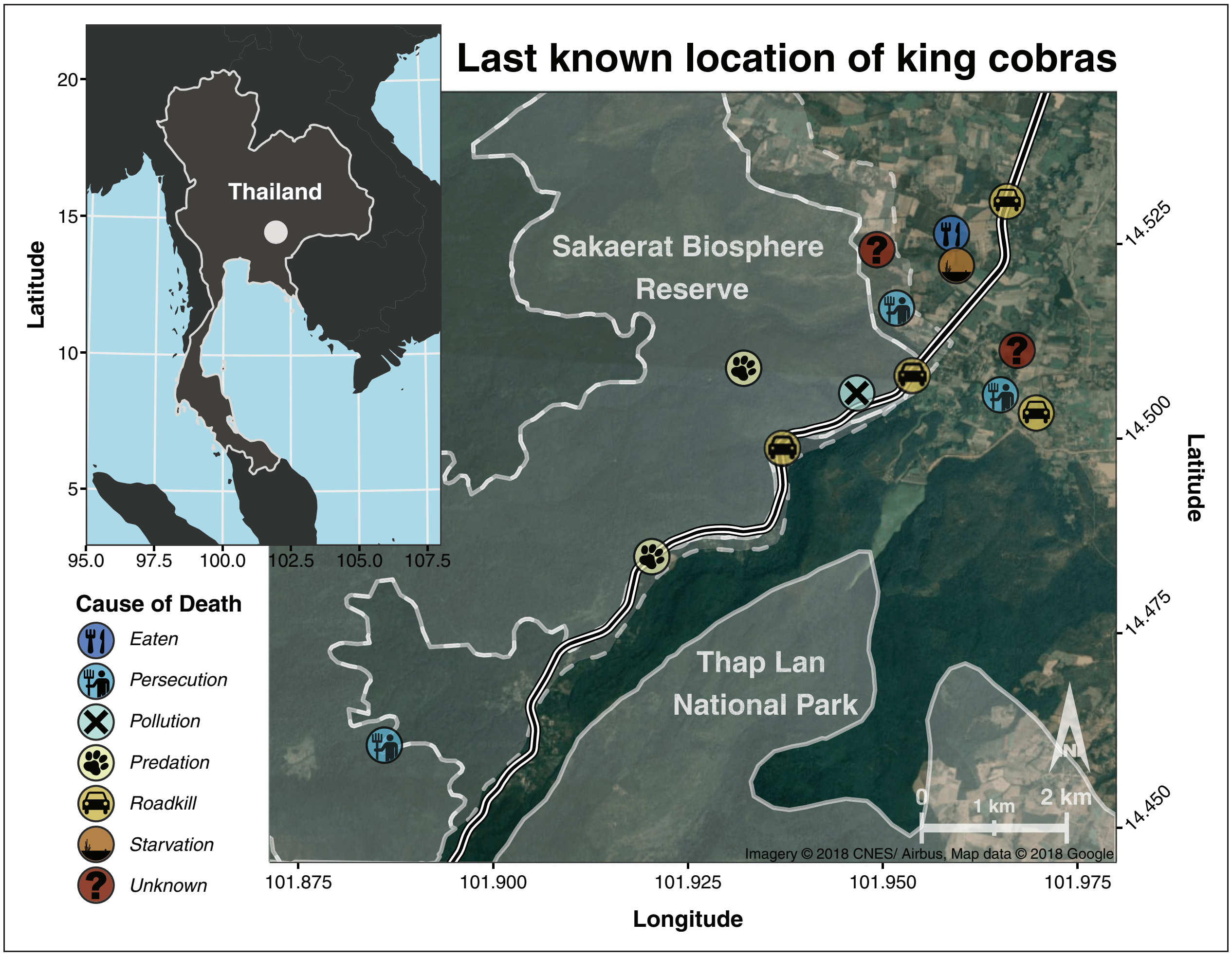

Figure 3. The study site location within Thailand, alongside the cause and location of king cobra deaths recorded during the study. Central line is the 304 highway. White areas with solid outlines are protected areas. The dashed line around the Sakaerat Biosphere Reserve is the buffer area (protected area mapping was acquired from UNEP-WCMC and IUCN [2018], imagery is from Google [2018]).

Table 1. Details of the Confirmed Deaths of Tracked King Cobras and Their SVL.

Snake ID	SVL (m)	Cause of death
JM002	1.89[a]	Natural—predated
AF004	2.11	Natural—predated
AM005	3.71	Anthropogenic—consumed plastic bag
AF010	2.54[a]	Anthropogenic—killed and eaten
AM015	2.56[a]	Anthropogenic—highway road mortality
AF017	2.08[a]	Anthropogenic—persecuted and left in plastic bag
JM019	2.12[a]	Anthropogenic—agricultural road mortality
AM021	2.48	Anthropogenic—caught in fish trap and stabbed
AM024	2.51[a]	Natural/anthropogenic—starved after leaving the protected area
AM025	1.91	Anthropogenic—death from apparent blunt trauma
JF027	1.87	Unknown/anthropogenic—transmitter found in irrigation canal
AM029	2.72[a]	Anthropogenic—found beheaded near logging access road

Note. SVL = snout-vent lengths.
[a]Indicate mean SVL calculated from multiple captures.

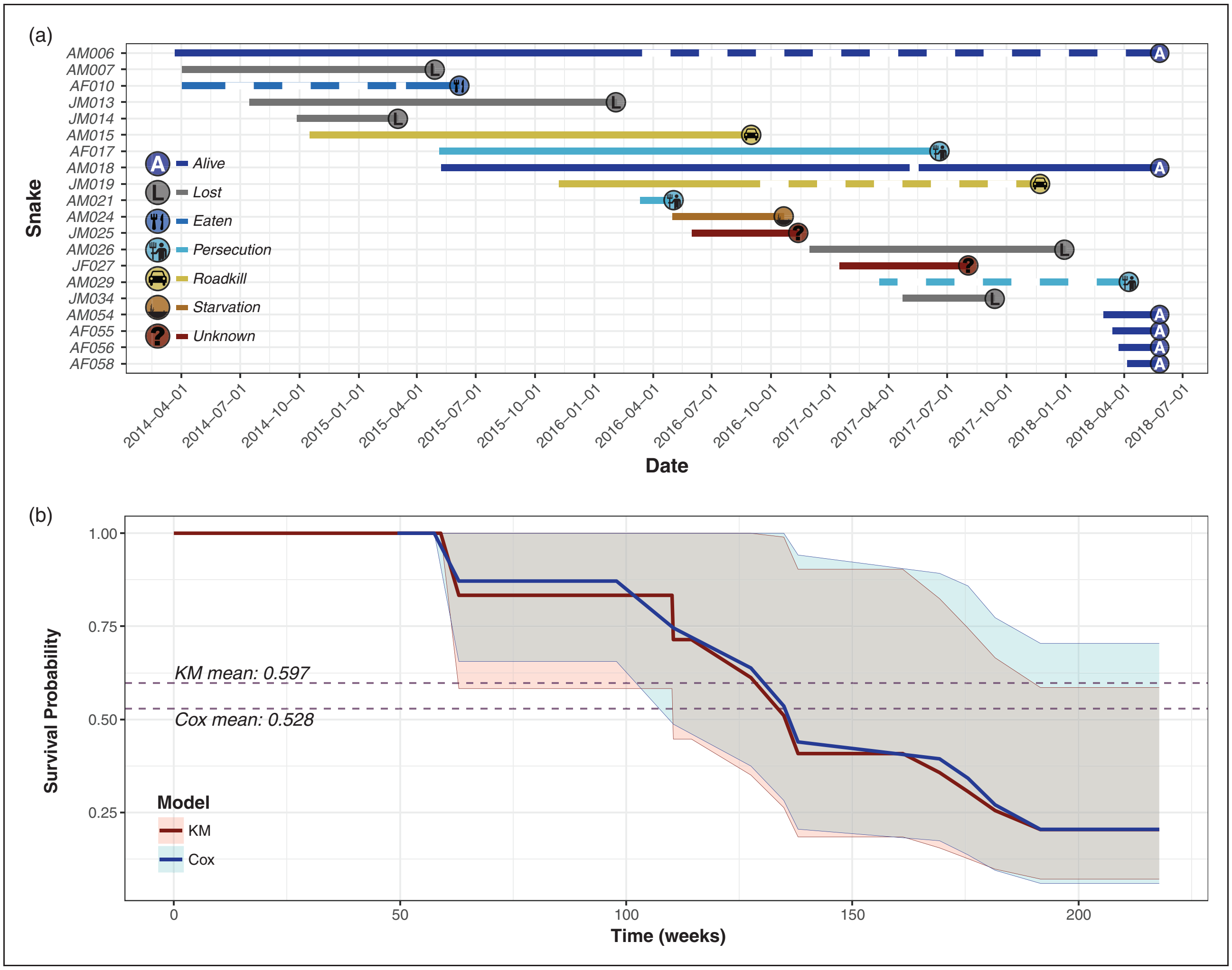

Figure 4. (a) Tracking duration and fate of the king cobras. The dashed regions indicate periods of no active tracking. Symbol corresponds to the ultimate fate of the king cobra. (b) The results of the Kaplan-Meier (KM) and Cox proportional hazards models with overall mean survival rates.

Kaltenborn, Bjerke, & Nyahongo, 2006; Pandey et al., 2016). Similar to other locations (Alves et al., 2014; Pandey et al., 2016), the villagers in the SBR, 84% of which work in agriculture (Thailand Institute of Scientific and Technological Research, 2018), show a clear fear of snakes. Other studies of king cobras suggested that they are likely to be killed on sight (Shankar et al., 2013), a behavior likely to be common in the Sakaerat area. The perception that king cobras are the most dangerous snake species contradicts what hospital records suggest; the records show king cobra bites are extremely uncommon (Pochanugool et al., 1998; Viravan et al., 1992). The disconnect between the perceived danger king cobras pose and the reality may be explained by their size and predisposition for defensive displays (Miranda et al., 2016; Souchet & Aubret, 2016). There may also be a bias toward saying king cobras are the most dangerous snake species because they are readily identifiable. Furthermore, the king cobra's distinctive appearance could amplify persecution justified via the idea that killing a snake now will prevent future conflict. People could be inclined to kill a snake because the possibility of lethal envenomation, regardless of the actual likelihood (Miranda et al., 2016; Moleón et al., 2011). The prevailing attitudes in local village areas pose a significant conservation concern, especially because of the proximity to the protected SBR core area.

We were unable to use any of the recommended sensitive questioning methods that are designed to reduce biases originating from social pressures or self-incrimination (Nuno & St. John, 2014). King cobras are a protected species in Thailand; therefore, respondents may have been reluctant to admit to harming one. Although, we doubt that the king cobra's protected status is widely known in the rural Sakaerat area. Reluctance to admit anti-snake sentiments may have been exacerbated by the well-publicized purpose of our work in the area and snake conservation advocacy (St. John, Keane, Jones, & Milner-Gulland, 2014). Our conservation purpose may have also elevated positive views on the snake's environmental importance. Future work in the area should endeavor to account for some of these biases.

Our results show repeated instances of king cobra mortality attributable to humans. The survival rate calculated here is comparable to studies looking at other highly mobile snakes (0.61; 0.40–0.82, Hyslop, Meyers, Cooper, & Norton, 2009), while studies with considerably higher survival rates can be explained by the ideal habitat and protection (Bailey et al., 2011). However, prominent in our data are the anthropogenic sources of mortality and the pattern of deaths outside of protected forested areas. The multiple mortalities outside of the reserve may be partially explained by our sample of king cobras, which comprised of many adult males that were captured from people's homes. Far-ranging large males may be more susceptible to anthropogenic mortality sources than other less mobile demographics (Bonnet, Naulleau, & Shine, 1999). The lack of effect of snake characteristics on survival we discovered may be an artifact of the small and adult male bias data set or heavily staggered entry times.

We do not believe that the tracking of these snakes significantly increased their mortality. Our tracking of the king cobras prevented several potential persecution events, where we used careful diplomacy to convince locals that we could remove the snake safely and there was no need to kill the individual. In addition, king cobras that had been tracked for the longest durations did not show any demonstrable loss of body condition.

Natural Deaths

Natural deaths were uncommon. Other studies report that natural predations are rare when the populations are subject to anthropogenic pressures (Baker, Dreslik, Wylie, & Phillips, 2016; Kapfer, Coggins, & Hay, 2008; Meek, 2012; P. B. Whitaker & Shine, 2000). We identified two natural mortalities (JM002 and AF004); both were predator attacks within the protected area. However, our initial intensive tracking regime may have led the individuals to take greater risks foraging as tracking disturbance may have reduced prey availability. The transmitter of AF004 had bite marks that were characteristic of a hog badger. Due to our skewed sample, we are unable to make any inferences concerning the rate of natural predation on king cobras. However, we only recorded predation on juvenile or female king cobras, the smaller of our captured king cobras. There may be a connection between the smaller size and their vulnerability to predation (Meek, 2014; Mushinsky & Miller, 1993).

Anthropogenic Sources of Mortality

Outside the SBR, there were numerous instances of human-caused mortality. The effects on mortality are poorly known in areas of growing human populations, especially among snakes (Crane et al., 2016; Thompson, Nowakowski, & Donnelly, 2016).

The anthropogenic mortalities were the result of vehicle collisions, plastic pollution (Strine et al., 2014), deliberate killing or persecution, and being killed for consumption. It has been documented that snakes that frequently move large distances are at greater risk from road mortality (Akani et al., 2002; Bonnet et al., 1999). The two tracked individuals killed on the roads were large sexually mature males who occupied large home ranges (>700 ha; Marshall et al., 2018). However, the two dead on arrival king cobras were considerably smaller indicating that roads may not be exclusively impacting far-ranging adult males, but a larger sample would be required to discern any pattern. We cannot confirm whether the road mortalities are indicative of persecution. There is evidence indicating that road users will disproportionately target snake species (Ashley, Kosloski, & Petrie, 2007; Langley, Lipps, & Theis, 1989). Within the reserve's transitional area, we have witnessed vehicles swerve to run over already deceased snakes on the side of the major highway (B. M. Marshall 2015-09-09, personal observation), and there is considerable evidence that the highway is exerting a significant mortality burden on snake species (I. Silva 2017, personal communication). However, we have yet to detect significant targeting of snakes (B. M. Marshall 2018, unpublished data). Moves to create and maintain ecopassages below large highways may prove valuable to the conservation of highly mobile snake species (Baxter-Gilbert, Riley, Lesbarrères, & Litzgus, 2015; Colley, Lougheed, Otterbein, & Litzgus, 2017).

The death of AM029 is especially worrying because it occurred within the protected area. The newly cleared road in close proximity, that we believe was cleared to aid sustainable timber harvest, may have facilitated AM029's death. The existence of roads in forested areas is known to lead to greater penetration by poachers and illegal harvesters (Clements et al., 2014), and the unmapped nature of these roads means they are not being incorporated into conservation planning and their impacts underestimated (Hughes, 2018).

Anthropogenic snake mortality can also occur without intent, via passive means, such as AM005's death via plastic pollution (Strine et al., 2014). There is growing evidence that fish traps left in the irrigation canals may be posing a problem for snake species, trapping them, and making them vulnerable to persecution. Both king cobras and Malayan kraits (*Bungarus candidus*) have been recorded trapped in fish traps that are placed within the irrigation canals in this area (Crane et al., 2016). We suspect that fish traps are having a considerable impact on various snake species that use the canals as movement corridors (C. T. Strine 2018, personal communication). The traps may be catching them incidentally because of their placement in choke points in water channels or snakes may be encouraged into the traps by trapped prey, such as snakes in the case of king cobras.

At least three deaths, and one further instance of significant harm, cannot be attributed to accidental or incidental actions. Two of these instances occurred to reproductive age females. Although we have insufficient data to investigate any pattern of seasonality in the deaths, both deaths occurred as the females returned to their usual home ranges after nesting. Gestation and nesting may elevate female risk during this time (Hyslop et al., 2009). Both females made uncharacteristically large moves to and from nesting sites during this time (C. T. Strine 2018, unpublished data), potentially exposing themselves to anthropogenic threats (Bonnet et al., 1999). The loss of these females likely has a greater impact on the local king cobra population than losing conspecific males (Gruber, Brown, Whiting, & Shine, 2017; Robertson, Elliott, Eason, Clout, & Gemmell, 2006). Mitigating deaths linked to nesting movements may be critical to maintaining populations in agricultural areas. Currently, we have no evidence of female king cobras nesting outside of the protected areas.

The repeated occurrences of deaths caused by humans likely represent a significant source of mortality for king cobras in human-dominated landscapes. Future work should aim to investigate king cobra mortality patterns over a greater area and assess whether the anthropogenic mortality sources are impacting the viability of king cobra populations.

Implications for Conservation

Among the dire reports of king cobra deaths there are positives; many villagers (63.3%) recognize the importance of snakes within ecosystems. Our findings are unsurprising, as many people use snakes for medicine, goods, and food, the effects of which on local snake populations are still relatively unknown (Pandey et al., 2016). Consumption of snakes appears commonplace in our study area. Yet, the recognition of snakes' services and valuable position in the ecosystem could pose an opportunity to mitigate persecution. The roles snakes play controlling agricultural pests (Civantos, Thuiller, Maiorano, Guisan, & Araújo, 2012; Singleton, 2003; Singleton & Petch, 1994) could form the basis of an effective snake education initiative. King cobra's propensity to predate on venomous snakes, often those often linked to higher bite rates such as pit vipers (Bhaisare et al., 2010; Pochanugool et al., 1998), could be used to champion the species and their integral role in the local ecosystem. However, there may also be potentially potent sociocultural motivations to protect species, outside of purely utilitarian justifications (Bekessy, Runge, Kusmanoff, Keith, & Wintle, 2018). Examining existing attitudes via more nuanced questionnaire efforts may elucidate behaviors or views that can be targeted to reduce snake persecution.

In situ education and conservation are preferable to the alternative, that is, the long-distance translocation of "problem" snakes. The current consensus remains skeptical that translocation can be a long-term solution that is not harming snakes (Barve et al., 2013; Devan-Song et al., 2016; Fry, 2018; Sullivan, Nowak, & Kwiatkowski, 2015; Wolfe, Fleming, & Bateman, 2018). As king cobras, with their large home ranges, cannot be contained in protected areas, conservation efforts must target in situ education and landscape level dynamics.

The results presented here illustrate a diverse array of mortality sources for a large venomous elapid—the king cobra. Identifying the sources of mortality in an ever-growing anthropogenic landscape is critical to mitigating those threats and conserving king cobras. The sources of mortality described likely represent an underdocumented pressure on Thailand's king cobras. Greater efforts to explore people's views on snakes' utility may prove fruitful in combating the entrenched stigma that is resulting in king cobra's repeated persecution.

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Supplemental Material

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