BRILL

Amphibia-Reptilia 40 (2019): 163-178

brill.com/amre

# Space fit for a king: spatial ecology of king cobras (*Ophiophagus hannah*) in Sakaerat Biosphere Reserve, Northeastern Thailand

Benjamin Michael Marshall[1], Colin Thomas Strine[1,2,*], Max Dolton Jones[1,2], Taksin Artchawakom[3], Ines Silva[4], Pongthep Suwanwaree[2], Matt Goode[5]

**Abstract.** A species' spatial ecology has direct implications for that species' conservation. Far-ranging species may be more difficult to conserve because their movements increase their chances of encountering humans. The movements can take them out of protected areas, which is especially risky for species that are routinely persecuted. The king cobra (*Ophiophagus hannah*), a large venomous elapid, is subject to anthropogenic pressures, such as persecution and habitat loss. Here we present results from a study using radio telemetry to quantify movements and habitat use of nine king cobras in and around a protected area in Northeast Thailand. This study is the first investigation into the movements and habitat use of king cobras outside of the Western Ghats, India. On average, the tracked king cobra's use areas of 493.42 ± 335.60 ha (95% fixed kernel), moving 183.24 ± 82.63 m per day. King cobras did not remain in intact forested area. Five of the individuals frequently used the human-dominated agricultural areas surrounding the protected area, appearing to make regular use of irrigation canals. Two adult males showed increases in movements during the breeding season. One male's increased breeding season range caused him to venture beyond the protected area, shifting his habitat use from intact forests to scrub in human-dominated areas. King cobras' large home range and willingness to use anthropogenic landscapes merits special consideration from conservation planners.

*Keywords*: Elapidae, home range, movement, protected area, radio telemetry, snake, Southeast Asia.

## Introduction

Effective management of species must take into account spatial ecology (Berger-Tal et al., 2011). Animals move beyond the confines of protected areas for many reasons, including foraging, dispersal, and mating (Sanderson et al., 2002). Outside of protected areas, the animals are at risk from human conflict (Newmark et al., 1994; Forbes and Theberge, 1996) and direct exploitation (Bruner et al., 2001). Animals may also encounter manmade barriers, such as roads; attempting to cross barriers can lead to increased mortality risk (Forman and Alexander, 1998). Barriers and habitat degradation are contributing to the fragmentation of landscapes that harm animal populations via isolation and edge effects (Saunders, Hobbs and Margules, 1991). Thus, effective conservation efforts must take a landscape approach, if wide-ranging species are to be protected (Wikramanayake et al., 1998; Breininger et al., 2011). Wildlife managers require an understanding of habitat use and spatial ecology of species when designating protected areas and implementing management plans (Berger-Tal et al., 2011). Important factors may include spatial arrangement, connectivity, and availability of resources, such as refugia, potential mates, oviposition sites and basking sites (Macartney et al., 1988; Kenward, Walls and Hodder, 2001; Birchfield and Deters, 2005; Sperry and Weatherhead, 2009; Bauder et al., 2016b).

Across Southeast Asia, deforestation rates remain high, as human populations increase and land-use patterns exert pressure on natural habitats (Rosa et al., 2016; Hughes, 2017). Thailand

1 - Sakaerat Conservation and Snake Education Team, Nakhon Ratchasima Province, Thailand
2 - Suranaree University of Technology, Nakhon Ratchasima, Thailand
3 - Sakaerat Environmental Research Station, Nakhon Ratchasima, Nakhon Ratchasima Province, Thailand
4 - King Mongkutt's University of Technology, Thonburi, Bangkok, Thailand
5 - School of Natural Resources and Environment, University of Arizona, Tucson, Arizona 85721, USA
*Corresponding author; e-mail: colin_strine@sut.ac.th



DOI:10.1163/15685381-18000008

has experienced loss or degradation of 75% of its native forests, leading to a substantial loss of biodiversity (Akber and Shrestha, 2015). Protected areas are presented as an effective long-term solution for stemming illegal exploitation of wildlife and providing suitable habitats in human-dominated landscapes (Bruner et al., 2001; Gray et al., 2016; Phumee, Pagdee and Kawasaki, 2017). Although environmental policy in Thailand includes expansion of protected areas (OEPP, 1997), some apex predators are often overlooked. Large bodied, wide-ranging mammalian species are often focal species for conservation goals, as they typically have large spatial requirements, placing them at greater risk from fragmentation and inadequate protection than other, less vagile, species (Henle et al., 2004). Snakes are rarely included in management plans due to their secretive habits and a lack of credible ecological data (Steen, 2010), despite many species suffering from apparent population declines (Reading et al., 2010).

The king cobra *Ophiophagus hannah* (Cantor, 1836) is the longest venomous snake in the world, reaching lengths of up to 6 m (Cox et al., 2012). King cobras are present throughout Southeast Asia, ranging from southern China and Nepal to Indonesia and the Philippines, as well as in isolated pockets in southern India, such as the Western Ghats (Whitaker and Captain, 2004; Cox et al., 2012). Within their distribution, king cobras can be found from sea level to >2000 m elevation (Bashir et al., 2010), where they use a variety of habitats, including broadleaf forests, seasonal tropical dry forests, mangrove swamps and wet tropical rainforests (Bashir et al., 2010; Barve et al., 2013). King cobras are known to occur in areas associated with human habitation, including agricultural fields and rural villages (Whitaker and Captain, 2004; Barve et al., 2013). King cobras mostly prey on a variety of snake species (Krishna, 2002; Das and Ghodke, 2003; Hesed, 2006; Bhaisare et al., 2010; Barve et al., 2013), but in some populations, there may be individual heterogeneity in diet specificity (Bhaisare et al., 2010). There is evidence from the Philippines of yellow-headed monitor lizard predation (*Varanus cumingi*; Siler et al., 2011); at our study site in Thailand, adult male king cobras appear to prey primarily on clouded monitor lizards (*Varanus nebulosus*; Strine, unpublished data).

King cobra populations are thought to be declining throughout their entire distribution (Stuart et al., 2012). Thus, king cobras are listed as Vulnerable by the International Union for the Conservation of Nature (IUCN), due to increasing habitat fragmentation, and exploitation for various markets, such as Chinese medicine, local consumption, and as snake wine (Somaweera and Somaweera, 2010; Stuart et al., 2012; Aust et al., 2016). King cobras are considered dangerous and are frequently killed when encountered by humans (Shankar et al., 2013a). King cobras are long-lived and slow to reproduce (sexual maturity occurs at approximately 5-6 years in captivity; Stuart et al., 2012). In addition, females invest energy into nest building and can spend months guarding the nest (Whitaker and Captain, 2004; Whitaker, Shankar and Whitaker, 2013), although females in some areas appear to leave the nest within a few weeks of oviposition (Whitaker, Shankar and Whitaker, 2013). Investing time and energy into parental care likely restricts behavioural plasticity needed to deal with anthropogenic disturbance. Furthermore, the king cobras at our study site have a single breeding season per year (Feburary to April; Strine, unpublished data). The combination of wide-ranging movement patterns (Rao et al., 2013), specific nesting requirements, and slow maturation time suggests that king cobras may be at greater risk from habitat fragmentation than other snakes (Henle et al., 2004).

Despite serious conservation concerns, there has been relatively little research on king cobra spatial ecology and quantifying habitat selection. In this regard, the species has only been studied at a single site in the Western Ghats of India (Barve et al., 2013; Rao et al., 2013). The

Indian study provided a valuable initial glimpse into the lives of these elusive snakes; however, it was hampered by an extremely limited sample size of five individuals that were radio tracked over a four-year period (Bhaisare et al., 2010; Rao et al., 2013). There is a clear need to build upon previous work, expanding sample size and geographical coverage of this iconic species.

We aim to further elucidate the natural history of king cobras by: 1) determining their home range size and placement 2) quantifying habitat types used within home ranges, and 3) investigating seasonal shifts in home range use and placement at the Sakaerat Biosphere Reserve (SBR), Thailand.

## Materials and methods

*Study site*

We conducted our research at the Sakaerat Biosphere Reserve, Nakhon Ratchasima Province, Thailand (14.44-14.55° N, 101.88-101.95° E) from 01 March 2013 to 04 December 2014 (fig. 1). The total area of the reserve, including core, transitional and buffer zones, was 36 000 ha. The protected core area was only 8000 ha and is patrolled by Sakaerat Environmental Research Station staff members to deter poaching. The core area predominately consisted of primary growth dry evergreen forest (DEF 60%), dry dipterocarp forest (DDF 18%), and secondary reforestation (<18%; Bunyavejchewin, 1986). Directly to the south of the core area was a paved four-lane highway. Buffer zones were present to both the north and south of the core area. The buffer zone to the north was primarily unprotected forest but was exclusively agricultural plantations, to the south. The surrounding transitional zone expanded the biosphere reserve to 36 000 ha and consisted mostly of agricultural and settlement areas. The transitional zone of the SBR comprised nearly 82% of the total area and is characterised by small isolated forest fragments in a patchwork of agricultural fields (mostly cassava and rice), small plantation forests, and human settlements. There was no impermeable barrier between forested areas and unprotected areas; thus, SBR serves as an ideal location to assess king cobra movement patterns in protected and adjacent unprotected areas.

*Capture*

During a separate study, we deployed 24 standardised plastic-mesh Y-shaped 20 × 20 × 20 m fencing arrays for a total of 360 funnel traps (50 cm in length) opened monthly for a week from March 2012 to April 2013. We placed the arrays randomly within the three SBR forest types. We also deployed 36 longer traps (2 m in length) along three separate T-shaped arrays in locations likely to capture king cobras. Additionally, we conducted unstandardised road cruising surveys for the duration of the study. We captured king cobras between 31 July 2012 and 11 October 2014 via hand capture, funnel traps, calls from local villages, and opportunistically. We assigned each king cobra a code that corresponded to their age-class (adult = A, juvenile = J, neonate = N), sex (male = M, female = F) and chronological order in which they were captured (e.g. the sixth snake captured, an adult male, was AM006).

After capture, we anesthetised king cobras using isoflurane at our field laboratory to ensure accurate morphometric measurements and to reduce stress (Setser, 2007). We measured mass (g, to nearest 1 g when mass was >1000 g or to nearest 0.1 g when mass was <1000 g), snout-to-vent length (SVL; mm, to nearest 1 mm), head dimensions (mm, to nearest 0.01 mm), and recorded sex (via cloacal probing; Schaefer, 1934). In addition, we collected scale clips and removed all obvious ectoparasites (primarily ticks). We marked individuals with a unique brand using a field cautery unit following the coding scheme of Winne et al. (2006). We implanted a VHF radio transmitter (Holohil model AI-2T or SI-2T, Holohil Inc, Ontario, Canada) into the coelomic cavity following a surgical procedure modified from Reinert and Cundall (1982). A veterinarian approved the surgery procedure and oversaw two of the surgeries. We made the decision to implant radio transmitters based on body size, qualitative assessment of body condition, and capture location. The ratio of transmitter mass to snake mass was 0.55 ± 0.47% (mean ± SD), well below the customary 5% threshold for radio telemetry research involving snakes.

We released snakes as close to their original capture site as possible, less than 24 hours after surgery. In a few cases, villagers refused to allow us to release snakes within the confines of the village. However, we did not release any snakes outside of their home ranges, as determined retrospectively based on home range data. We measured the distance from release site to the snake's first location and that indicated no release was greater than 426 m (mean ± SD = 133 ± 139 m). We reduced radio tracking intensity during the first two weeks after release to minimise disturbance while recovering from handling procedures.

*Radio telemetry*

After the initial two-week period of reduced radio tracking intensity, we radio tracked snakes on a near continuous basis, obtaining hourly fixes (verifiable locations) and checking for signal every fifteen minutes to ensure the animal was still stationary, similar to the Indian radio telemetry program (Bhaisare et al., 2010). After determining that king cobras tended not to move at night, we limited radio tracking intervals to between 06:00-22:00. After the death of AM005, as described by Strine et al. (2014), we altered radio tracking protocols to minimise disturbance to animals. Consequently, we located snakes four times/day, with approximately four hours between fixes. We verified locations using three-point-triangulation around the snakes' locations,

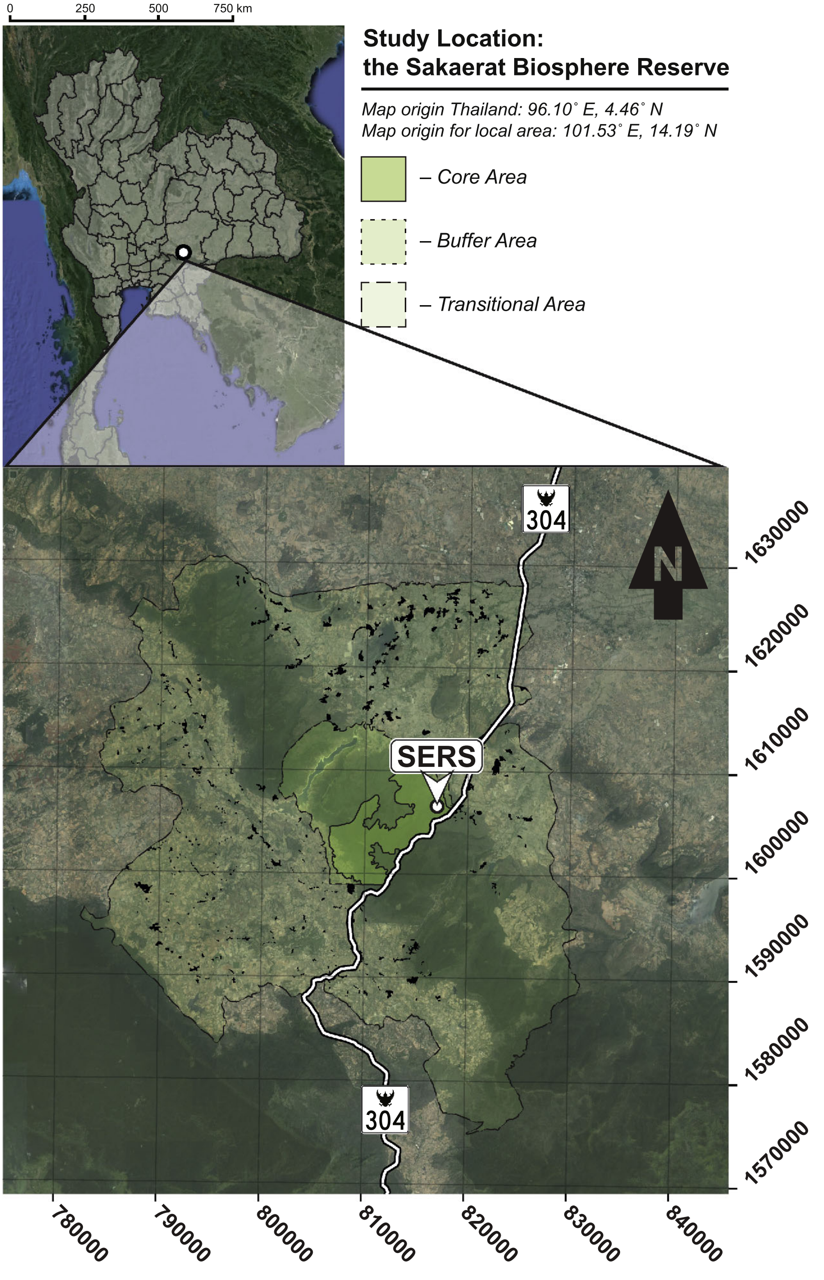


**Figure 1.** Location of the Sakaerat Biosphere Reserve (SBR) in Thailand. Alongside a map of the Core (smallest central green area), Buffer (intermediate lighter green area) and Transitional areas (largest and palest area) of the SBR. Scale is in m and corresponds to the 47N UTM region.

while maintaining a minimum distance of 10 m from the snakes. Upon determining the snakes' locations within a 5 × 5 m area, we recorded locations with hand-held Garmin GPS 62s or 64s units using Universal Transverse Mercator (UTM) WGS 84 projection. We obtained fixes with three or fewer personnel present, to minimise disturbance.

When we found snakes moving (detected via the fluctuations in radio-signal), we retreated to a minimum distance of 50 m while monitoring its movements. We continued to monitor snakes until they remained stationary for at least 15 minutes, after which time we moved in closer to confirm the final location.

*Analyses*

We estimated home ranges using two methods: 95% Minimum Convex Polygon (MCP), to allow for comparisons with other studies, and fixed density kernel (referred to here as "kernel"). Considering criticism of both kernel and MCP methods, we elected to report both (Blouin-Demers and Fox, 2006; Nilsen, Pedersen and Linnell, 2008). However, we based our interpretations and further analyses on the kernel method. We performed analyses using R (R Core Team, 2017) in R Studio (R Studio Team, 2017), using packages 'ctmm' (Fleming et al., 2017a), 'move' (Kranstauber, Smolla and Scharf, 2016), 'sp' (Pebesma and Bivand, 2005), 'ggplot2' (Wickham, 2009), 'adehabitatHR' (Calenge et al., 2015), 'rgdal' (Roger et al., 2017), and 'maptools' (Bivand et al., 2017).

Smoothing factors are critical to home range estimates using kernels (Worton, 1989; Blouin-Demers and Fox, 2006). The $H_{ref}$ smoothing factor method can produce considerable overestimates of home range and areas of clumped points can lead to over smoothing (Worton, 1995). By contrast the $H_{LSCV}$ method, while favoured for reptile home ranges due to their relatively small sizes (Worton, 1989; Seaman and Powell, 1996), fails to create a biologically relevant estimate for a snake with such an extensive home range. The $H_{LSCV}$ method leaves areas in the centre of the home range empty and areas of use isolated and distant. Discontinuous ranges make little biological sense, as they imply zero use areas between two known locations. Therefore, we opted for an objectively selected smoothing factor, tailored to each snake, and for each season, when making seasonal comparisons. We chose the H smoothing factor that was the minimum whole number that generated a contiguous range, thereby guaranteeing that all locations were connected and areas between points displayed some degree of usage. This method avoids the overestimations of $H_{ref}$ and the discontinuous and isolated home range patches of $H_{LSCV}$. We also considered using $H_{plug\text{-}in}$, but it created discontinuous and heavily warped ranges. We considered methods that accounted for the autocorrelation in our data (Fleming and Calabrese, 2017b), but elected not to use them as home range size was negligibly affected (supplementary table S1) and the auto-correlated methods appeared to over-smooth range edges. To remain consistent with other studies of reptiles (Laver and Kelly, 2008), we chose the 95% contour as the maximum home range size, and the 50% contour to delineate the core area.

We determined if home ranges were asymptotic (i.e. stabilised), and therefore not increasing significantly with additional locations, using bootstrapping methods described in Bauder et al. (2016b). Unlike Bauder et al. (2016b), we tested home ranges using the kernel method, as suggested by Laver and Kelly (2008). We kept the smoothing value constant at the value that produced a contiguous home range for the full array of locations. However, to make the analysis more stringent, we decreased the threshold classifying a home range as asymptotic. Here, we classified a home range as being asymptotic when the average home range size derived from over 50% of randomly selected points was within 5% of the home range estimate using all locations. To construct final maps, we used QGIS (Quantum GIS Development Team, 2017), Google Maps (2017) for background satellite imagery, and the Database of Global Administrative Areas (GADM, 2015) for administrative boundaries.

We estimated movements by calculating the straight-line distance between points, and averaged distances across days to estimate mean daily displacement. The temporal resolution of our data ensured that this method of distance estimation represented the minimum possible distance travelled by the snakes (Secor, 1994).

We determined habitat use from previously collected land-use data for the SBR and surrounding area (Saurwatari, 2006; Trisurat, 2010). We defined scrub as agricultural land that remained covered by dense, mixed vegetation. We counted the number of locations within each land-use type and the percentage of each snake's home range area within land-use types. We then calculated Duncan's Index of Preference (Duncan, 1983) to compare seasonal shifts and individual habitat preference. Duncan's Index was selected because of the limited amount of data required to calculate it. We repeated the calculations for habitat preference and home range on a per season basis for individuals tracked over multiple seasons. This enabled us to compare seasonal shifts between breeding (February to April) and non-breeding seasons.

We calculated linear correlations between SVL, mass and home range characteristics. Our statistical hypotheses were tested by setting alpha at 0.05, and results are reported as mean $\pm$ SD, unless otherwise stated.

## Results

### *Captures and snakes*

We captured 15 king cobras: six adult males, four adult females, three juvenile males, one juvenile female and one hatchling female (table 1). Males were longer (2847 $\pm$ 433 mm) and heavier (4962 $\pm$ 1068 g) than females (SVL = 2110 $\pm$ 394 mm, mass = 2075 $\pm$ 182 g). Juveniles averaged 1493 $\pm$ 443 mm SVL in length and 775 $\pm$ 835 g mass. Ratio of length-to-mass was greater for juveniles (males = 0.57, females = 1.02, juveniles = 1.92). Spearman's rank tests reveal a significant relationship between SVL and mass for the radio tracked snakes ($S = 20$, $rho = 0.956$, $P < 0.0001$).

Overall, we radio tracked nine king cobras (four adult males, two adult females and three juvenile males). One juvenile, JM013, likely transitioned from juvenile to adult during the study.

**Table 1.** Characteristics of all caught king cobras. SVL = snout vent length. HL = Head length. HW = Head width. Snakes marked with * have their characteristics averaged over multiple captures.

| Snake ID | Age class | Sex | Mass (g) | SVL (mm) | HL (mm) | HW (mm) |
|---|---|---|---|---|---|---|
| NF001 | Neonate | Female | 21.9 | 440 | Unknown | Unknown |
| JM002* | Juvenile | Male | 494.4 | 1893 | 36.00 | 30.00 |
| AF003 | Adult | Female | 770.0 | 1622 | 38.00 | 31.00 |
| AF004 | Adult | Female | 1700 | 2110 | 52.00 | 38.00 |
| AM005 | Adult | Male | 6200 | 3714 | 88.40 | 60.00 |
| AM006* | Adult | Male | 4680 | 2742 | 72.12 | 49.99 |
| AM007* | Adult | Male | 5370 | 2747 | 85.15 | 57.09 |
| AF008 | Adult | Female | 2230 | 2120 | 57.52 | 35.15 |
| AM009 | Adult | Male | 5040 | 2618 | 72.86 | 48.55 |
| AF010 | Adult | Female | 3600 | 2586 | 61.90 | 36.61 |
| AM011 | Adult | Male | 5441 | 2734 | 80.20 | 52.63 |
| JF012 | Juvenile | Female | 118.4 | 906 | 29.46 | 17.02 |
| JM013 | Juvenile | Male | 2000 | 1770 | 53.31 | 27.65 |
| JM014 | Juvenile | Male | 489.1 | 1402 | 42.40 | 27.12 |
| AM015 | Adult | Male | 3040 | 2530 | 83.23 | 64.70 |

*Tracking durations*

We tracked king cobras for 1765 days (126 ± 76 days per individual), obtaining 4136 unique data points (459 ± 300 per individual), 1189 of which were new locations (132 ± 93 per individual; summarised in table 2). Radio tracking duration varied among individuals due to premature transmitter failure (AF010), being captured later in the study period (JM014, AM015) or mortality (JM002, AF004, AM005). The three moralities included a death caused by an unknown predator (JM002), a hog badger (*Arctonyx collaris*) predation as indicated by bite marks on the carcass and transmitter (AF004), and a death caused by plastic bag ingestion (AM005; Strine et al., 2014).

*Home ranges and movements*

Based on the 1189 unique locations, we generated home range estimations for each snake (fig. 2, supplementary table S1). Home range estimates using the 95% MCP method varied by more than an order of magnitude, from 19.48 ha (JM014) to 710.03 ha (AM006), averaging 337.47 ± 235.79 ha across all asymptotic home ranges; average kernel home ranges were larger (493.42 ± 335.60 ha), ranging from 52.65ha (JM014), to 1073.55 ha (AM006; table 2). Asymptotic home range estimates of the two females averaged 97.36 ha (MCP) and 229.13 ha (kernel); whereas the average male range was 520.82 ± 171.76 ha (MCP) and 799.42 ± 306.99 ha (kernel). Juvenile home ranges averaged 122.15 ± 90.30 ha (MCP) and 144.00 ± 79.92 ha (kernel). We did not detect any significant correlations between SVL and MCP area ($S = 26$, $rho = 0.690$, $P = 0.069$) or mass and MCP area ($S = 26$, $rho = 0.690$, $P = 0.069$). However, SVL and 95% kernel area were found to have a significant relationship ($S = 10$, $rho = 0.881$, $P = 0.007$), as well as mass and 95% kernel area ($S = 10$, $rho = 0.881$, $P = 0.007$).

One individual, JM013, made large unidirectional movements starting from where he was originally released. We interpret these movements as a juvenile to adult home range shift. Therefore, our home range estimates do not include the area used by this individual before it transitioned into an adult (fig. 2), which decreases the estimated kernel home range from 1332.94 ha to 200.98 ha.

Bootstrapping analysis revealed that AM015's home range failed to reach the 95% threshold set, indicating that we did not

**Table 2.** Movements and Home Range Size. "# Tracked" is the number of the days tracked for. "MDD" is the mean distance in metres covered per day. "MCP" is the area of the Minimum Convex Polygon based upon 95% of the locations in hectares. "95% K" is the 95% fixed density kernel in hectares. "50% K" is the 50% fixed density kernel in hectares. "H value" is the optimised h kernel smoothing factor used to estimate home range. "Most Used Land Use" is the habitat that contained the most unique locations. Land use abbreviations: DEF – Dry Evergreen Forest, DDF – Dry Dipterocarp Forest.

| Snake ID | # Tracked | MDD | MCP | 95% K | 50% K | H value | Most Used Land Use |
|---|---|---|---|---|---|---|---|
| JM002 | 223 | 113.53 | 189.25 | 178.38 | 24.95 | 80 | DEF |
| AF004 | 46 | 305.17 | 143.47 | 208.35 | 51.18 | 120 | DDF |
| AM005 | 173 | 232.55 | 374.74 | 467.72 | 133.07 | 161 | DDF |
| AM006 Breeding | 68 | 341.04 | 678.96 | 844.52 | 221.49 | 213 | DEF |
| AM006 Non-breeding | 171 | 206.36 | 397.83 | 392.17 | 105.45 | 115 | DEF |
| AM006 all | 242 | 242.78 | 710.03 | 1073.55 | 263.85 | 280 | DEF |
| AM007 Breeding | 56 | 479.11 | 568.31 | 825.80 | 237.31 | 237 | DEF |
| AM007 Non-breeding | 169 | 230.18 | 280.89 | 569.95 | 137.02 | 268 | DEF |
| AM007 all | 232 | 283.74 | 477.69 | 857.00 | 186.34 | 324 | DEF |
| AF010 | 66 | 104.29 | 51.24 | 249.91 | 64.10 | 176 | Agriculture |
| JM013 post-dispersal | 95 | 142.03 | 157.73 | 200.98 | 41.98 | 103 | Settlement |
| JM013 | 140 | 140.41 | 802.18 | 1332.94 | 216.25 | 387 | Settlement |
| JM014 | 56 | 91.22 | 19.48 | 52.65 | 11.81 | 86 | DDF |
| AM015 | 28 | 135.46 | 45.40 | 131.88 | 25.50 | 120 | Agriculture |

obtain enough locations to accurately estimate his home range (supplementary fig. S1; supplementary table S2). Additionally, the limited tracking window for AM015 was during a cooler and much lower activity season that would have reduced his movements. Therefore, we did not include AM015's results when calculating mean home range size because it likely represents an under estimation of his home range.

On average, mean daily displacement (MDD) of snakes was 183.24 $\pm$ 82.63 m, but this varied between individuals and over time. Adult males had the greatest MDD (253.03 $\pm$ 27.09 m), females averaged 204.73 $\pm$ 142.05 m per day, and juveniles were the lowest (115.59 $\pm$ 25.47 m; table 2). Our limited sample size limits statistically robust comparisons both within and between age classes and sexes. We did not find any significant correlations between SVL and MDD ($S = 38$, $rho = 0.548$, $P = 0.171$), mass and MDD ($S = 44$, $rho = 0.476$, $P = 0.243$), MCP area and MDD ($S = 34$, $rho = 0.595$, $P = 0.132$) or kernel area and MDD ($S = 32$, $rho = 0.619$, $P = 0.115$).

*Habitat use and preference*

Individual snakes varied in their habitat use and preference (fig. 3). Three individuals (JM002, AF004 and AM007) exclusively used protected forests within SBR. Whereas, AM005 and AF010 spent considerable time outside of protected forests, occasionally using human settlements. These two individuals showed a preference for scrub, and we frequently located AF010 in irrigation canals. Due to considerable disparity in radio tracking duration among individuals, we can only compare habitat preference for adult males. Adult male habitat preferences varied considerably among individuals, although all individuals tended to use forest in line with its availability.

Two individuals, AM006 and AM007, were radio tracked concurrently, allowing for directly comparisons. Both individuals largely used the SBR forested core, but used the two forest types to differing degrees. Occasionally, AM006 ventured beyond the protected area into agricultural land, while AM007 remained within DEF. Neither showed particular preference for any habitat type over the entire study period, but both used DEF as much as it was available. We observed these large male snakes sheltering

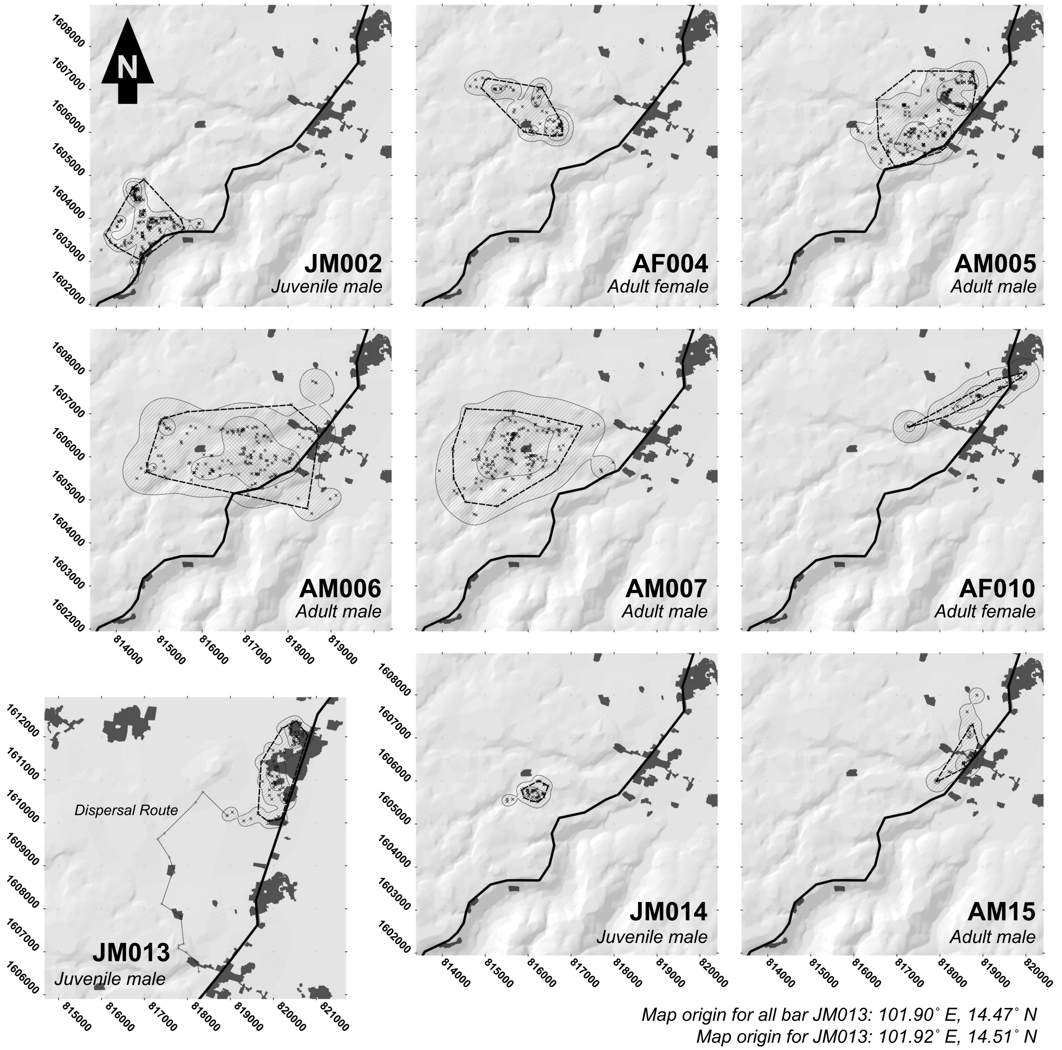


**Figure 2.** The home ranges of the tracked king cobras. Dark areas are settlements. Dark line is the 304 Highway. Scales is based in m and corresponds to the 47N UTM region. Dashed line shows the 95% MCP, single hashed areas correspond to the activity area, and the double hashed areas are the individual's core area. Crosses represent a confirmed snake location.

together on three separate occasions (03 June 2014, 16 August 2014, 18 August 2014) and in within 50 m of each other on one occasion (04 October 2014).

*Seasonal home range shifts*

We only assessed seasonal shifts in home range size and habitat use for AM006 and AM007, due to the small number of fixes obtained for other individuals. Breeding season for king cobras in Northeast Thailand occurs February-April, which coincided with our observation of AM006 and AF010 mating. Breeding season movements were greater and occurred in areas not used in other seasons. We compared 95% and 50% kernel estimates during the breeding season with all other locations outside of the breeding season (table 2, fig. 4). During the breeding season, AM006's range increased to 844.52 ha compared to 392.17 ha out-

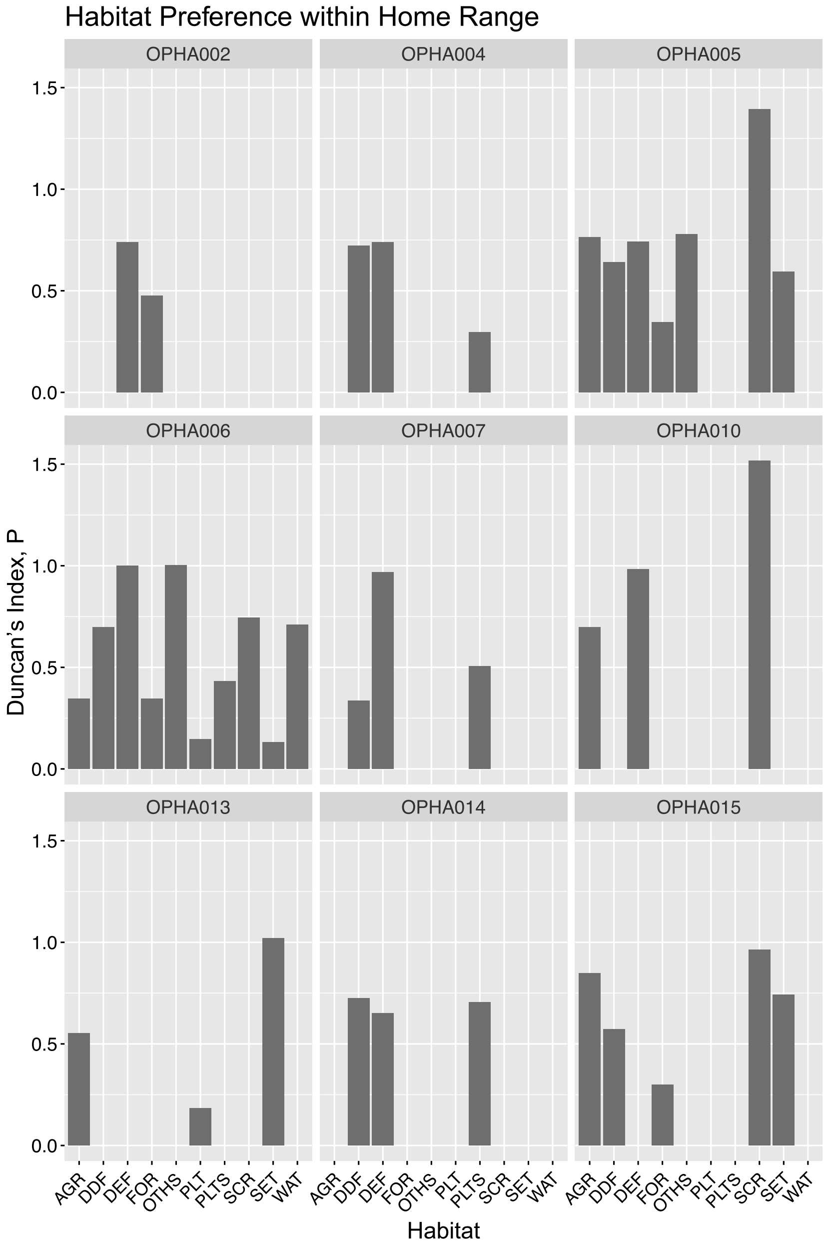


**Figure 3.** Habitat preferences for all the tracked king cobras calculated using Duncan's Index. All preferences are calculated using the 95% fixed kernel home range. Habitat codes: AGR – agriculture, DDF – dry dipterocarp forest, DEF – dry evergreen forest, FOR – forest fragments outside of core SERS area, OTH – other trace habitat types within core SERS area, PLTS – plantation forest within buffer SERS area, PLT – plantations outside of buffer SERS area, SCR – scrub, SET – settlement, WAT – waterbody.

side the breeding season, and AM007's breeding season range was 825.80 ha compared to 569.95 ha outside the breeding season. Habitat use also changed seasonally for AM006 and AM007 (supplementary fig. S2). Outside of breeding season, AM006 and AM007 showed no particular preference of any habitat type. During the breeding season AM007 continued to show no habitat preference, while remaining within the core and buffer areas of SBR and

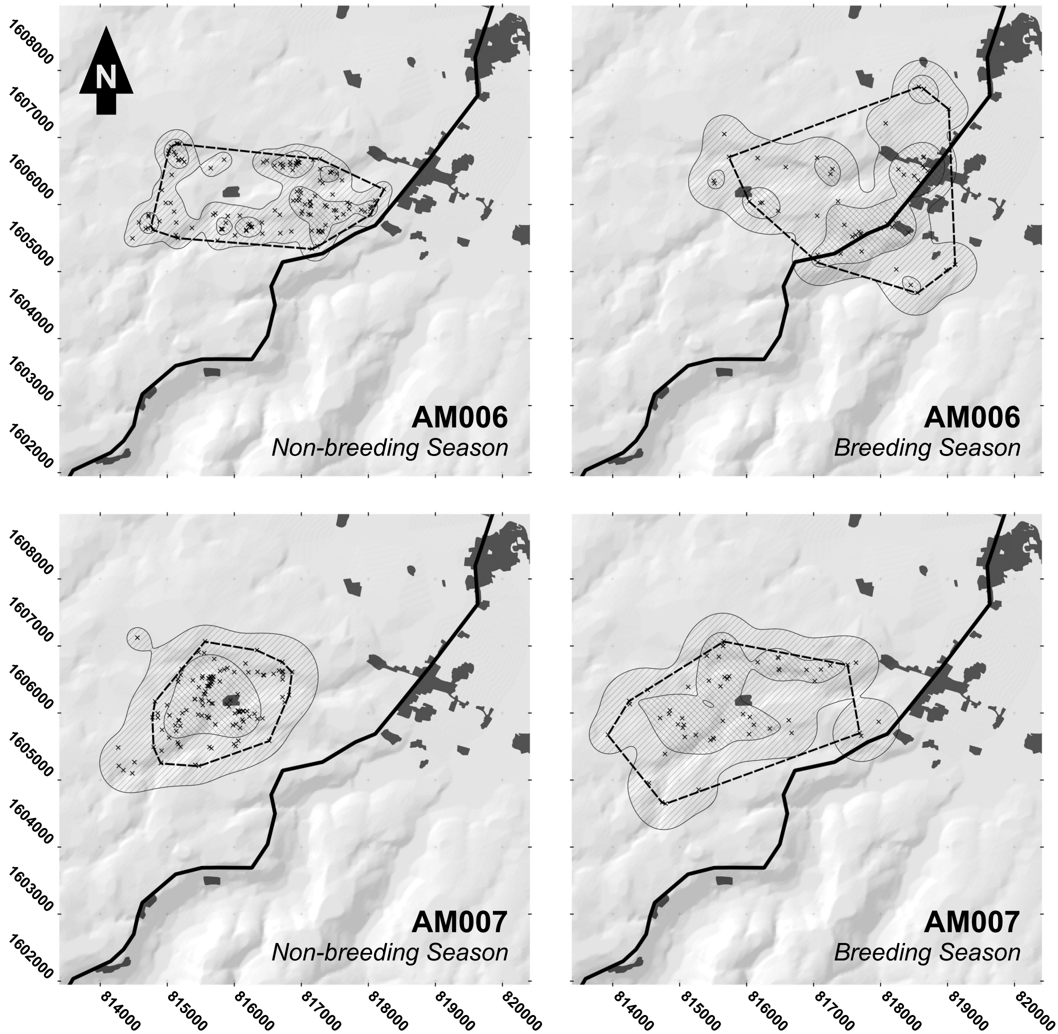


**Figure 4.** The home ranges of AM006 and AM007 during breeding (February, March, and April) and non-breeding seasons. Dashed line shows the 95% MCP, single hashed areas correspond to the activity area, and the double hashed areas are the individual's core area. Crosses represent a confirmed snake location. Scale is in m and corresponds to the 47N UTM region.

shifting his home range to include plantation regrowth forests. In contrast, AM006 travels outside of the SBR core, crosses the major highway adjacent to SBR and starts to show preference for several habitat types. Among the habitat types AM006 prefers during breeding season is scrub. His preference for scrub mirrors the preferences shown by two other snakes (AM005, AF010) who spent the majority of their time in unprotected agricultural land. The other habitats preferred by AM006 during breeding season are DEF and other habitat types within the SBR core, such as bamboo forest. Overall, AM006 used more varied vegetation and land-use types during the breeding season and was more frequently exposed to human-dominated areas.

## Discussion

### *Home range size*

King cobra home ranges at our study site are among the largest reported for native snakes (supplementary table S3). Indigo snakes (*Drymarchon couperi*) are the only species to rival the maximum male home ranges described here, with maximum 100% MCP areas of 1528 ha and mean area of 359 ha (Hyslop et al., 2014). Like king cobras, indigo snakes are relatively large, active foragers (Hyslop et al., 2014). Previous studies have suggested that large home ranges may result from higher energy demands of large bodied animals (McNab, 1963). Male king cobra prey (monitor lizards) in this area likely have considerable energy requirements (Christian et al., 1995), implying king cobras require a large energy budget to exploit them. Snake species that move more likely have higher energy requirements further supporting inferences of high king cobra energy demands (Lelièvre et al., 2012). Other than indigo snakes, Burmese pythons (*Python bivittatus*) have been shown to cover huge areas, some up to 8740 ha and an average of 2250 ha calculated via 100% MCP (Hart et al., 2015). However, the largest home ranges of Burmese pythons are reported from an introduced population in the Florida Everglades, USA, where snakes may be required to move large distances between resources (Hart et al., 2015).

King cobras at our study site maintained smaller home ranges compared to a previous study in the Western Ghats of India (Barve et al., 2013). The two non-translocated king cobras in the Western Ghats maintained 95% MCP home ranges of 1480 ha and 3000 ha (Bhaisare et al., 2010; Barve et al., 2013). Perhaps these differences in home range size are linked to prey density, distance to resources, or configuration of land-use types (Roe, Kingsbury and Herbert, 2004; Baxley and Qualls, 2009; Corey and Doody, 2010).

Our data suggest that king cobras show a pattern seen in other snake species, where males move farther and maintain larger home ranges, potentially increasing their risk of mortality (Bonnet, Naulleau and Shine, 1999; Hyslop et al., 2009, 2014; Bauder et al., 2016b). However, our data must be interpreted cautiously given the lack of females studied, resulting in an inability to make robust statistical comparisons.

Long-distance dispersal observed in JM013 suggests that dispersal events present a period of elevated risk (Bonnet, Naulleau and Shine, 1999; Whitaker and Shine, 2000). This snake moved over 6.5 km to disperse, through various agricultural types and across six secondary roads. Snake mortality on roads is a widespread and significant problem (Forman and Alexander, 1998), especially considering the apparent animosity displayed by motorists towards snakes (Ashley et al., 2007).

We recommend that dispersal requirements of king cobras be strongly considered by conservation planners. Landscape connectivity has been shown to be critical to the ecology of other snake species (Dodd and Barichivich, 2007; Madsen and Ujvari, 2011). Ensuring that king cobras have a safe and reliable route across the landscape would likely mitigate the risks they face (Walston et al., 2010). We agree with previous research, which suggests that effective conservation of a large mobile snake species requires extensive areas of continuous and protected land (Dodd and Barichivich, 2007).

### *Heterogeneous habitat use*

Despite not showing active preference for forest, adult males tended to use protected forested areas, which may be due to a number of reasons, including access to mates (Duvall and Schuett, 1997; Jellen et al., 2007), increased prey abundance (Baxley and Qualls, 2009), greater opportunities for thermoregulation (Carfagno, Heske and Weatherhead, 2006), increased number of shelter sites (Whitaker and Shine, 2003), and protection from human persecution (Shankar et al., 2013b). The lack of preference expressed means that the use of forests can be somewhat accounted for by its availability. Both adult males AM005 and AM006, moved away from forested areas during the breeding season. Therefore, it seems less likely that male use of forested areas can be explained by greater access to mates.

Other studies have shown a link between home range size and prey resources (Madsen and Shine, 1996; Heard, Black and Robertson, 2004; Baxley and Qualls, 2009). Spatial ecology of prey, similar to clouded monitor lizards (Strine, unpublished data; Lei, Booth and Dwyer, 2017), could explain the large home ranges exhibited by our adult male king cobras. An active foraging snake could be required to undertake extended forays before suitable prey is located (Roe, Kingsbury and Herbert, 2004). Ultimately, it is likely that no one factor can adequately explain snake habitat use alone (Heard, Black and Robertson, 2004), and no satisfactory conclusions can be drawn concerning king cobras until there is more known about their energy requirements and prey densities.

Outside the protected reserve area, radio tracked king cobras frequently used agricultural scrub, which is primarily found along irrigation canals at our study site, and represents the only dense vegetation left in this human dominated landscape. The female (AF010) preferred irrigation canals, spending time below scrub vegetation. These isolated irrigation canals bisect the landscape and may harbour the highest density of prey. Green pit vipers (*Trimeresurus spp.*), a known prey item of king cobras at our study site (C. Strine, pers. obs.), are likely more abundant in these damp canals (Chanhome et al., 2011). Alternatively, canals may provide a route through an otherwise hostile and exposed landscape (Whitaker and Shine, 2000), and king cobras may be demonstrating behavioural plasticity in response to fragmentation (Mitrovich, Diffendorfer and Fisher, 2009).

### *Seasonal home ranges*

Snakes in tropical climates show seasonality despite being largely released from thermal constraints (Shine and Madsen, 1996; Brown, Shine and Madsen, 2002). Brown and Shine (2006) suggested that tropical snakes instead react to alternative biotic or abiotic factors affecting reproduction or neonate success.

During breeding season we found a considerable shift in home range size of the two large males that lead to a change in habitat use for one individual. Similar breeding season shifts in range have been documented in other snake species (Bauder et al., 2016a). Mate locations during the breeding season are thought to be critical for mating success (Duvall and Schuett, 1997). We suggest that the increase in space use and daily movements are a direct result of breeding activity. Other studies of elapids have also found seasonal patterns of mortality in anthropogenic areas (Akani et al., 2002). The high temperatures throughout breeding season are thought to be prompting the king cobras to shelter within cooler microhabitats, such as people's homes, which leads to increased contact with humans (pers. obs.; Shine and Madsen, 1996).

## Conclusion

Our data indicate that king cobras make use of large areas, have individual habitat preferences and do not remain confined to protected primary forest. Conservation efforts should treat king cobras as a large apex predator rather than a range-restricted species (Forbes and Theberge, 1996; Wikramanayake et al., 1998; Morrison and Boyce, 2009) and therefore, should incorporate landscape level assessments of connectivity (Sanderson et al., 2002; Dodd and Barichivich, 2007).

Our conclusions are limited due to difficulties in obtaining a representative sample size of king cobras. The failure of traditional trapping methods led to a reliance on opportunistic captures that resulted in a bias towards male snakes. Additional research is needed to better understand differences in spatial requirements among conspecifics, especially underrepresented females, as well as factors influencing breeding behaviour, nesting and offspring success. Research efforts need to be extended across the massive range of king cobras to capture variation in spatial ecology due to marked differences in available habitats.

**Acknowledgements.** We are grateful for crucial logistical and professional support provided by Sakaerat Environmental Research Station and Suranaree University of Technology. We thank all the dedicated Sakaerat Conservation and Snake Education Team members involved in the radio tracking, capture and documentation of king cobras. We thank Suranaree University of Technology's ethics and animal use committee for supervising this project. All activities were performed under the Institute of Animals for Scientific Purpose Development (IAD) license (U1-0537-2559). We could not have undertaken this research without the permissions of the National Research Council of Thailand (98/59). We thank Thailand Institute of Scientific and Technological Research, Nakhon Ratchasima Zoo, Dusit Zoo, Zoological Park Organisation, Thailand, Wanlaya Tipkantha, DVM and Pluemjit Boonpueng of Suranaree University of Technology for assisting with logistics. We thank the National Scientific and Technological Development Agency, Wildlife Reserves Singapore Conservation Fund and the Herpetofauna Foundation for supporting our project.

**Supplementary material.** Supplementary material is available online at:
https://brill.figshare.com/s/76ba83f60b4433e7930b

## References

Akani, G.C., Eyo, E., Odegbune, E., Eniang, E.A., Luiselli, L. (2002): Ecological patterns of anthropogenic mortality of suburban snakes in an African tropical region. Isr. J. Zool. **48**: 1-11.

Akber, M.A., Shrestha, R.P. (2015): Land use change and its effect on biodiversity in Chiang Rai province of Thailand. J. Land Use Sci. **10**: 108-128.

Ashley, E.P., Kosloski, A., Petrie, S.A. (2007): Incidence of intentional vehicle-reptile collisions. Hum. Dimens. Wildl. **12**: 137-143.

Aust, P.W., Van Tri, N., Natusch, D.J.D., Alexander, G.J. (2016): Asian snake farms: conservation curse or sustainable enterprise? Oryx **51**: 1-8.

Barve, S., Bhaisare, D., Giri, A., Shankar, P.G., Whitaker, R., Goode, M. (2013): A preliminary study on translocation of 'rescued' King Cobras (*Ophiophagus hannah*). Hamadryad **36**: 80-86.

Bashir, T., Poudyal, K., Bhattacharya, T., Sathyakumar, S., Subba, J.B., Subba, J.B. (2010): Sighting of King Cobra *Ophiophagus hannah* in Sikkim, India: a new altitude record for the northeast. J. Threat. Taxa **2**: 990-991.

Bauder, J.M., Breininger, D.R., Bolt, M.R., Legare, M.L., Jenkins, C.L., Rothermel, B.B., McGarigal, K. (2016a): Seasonal variation in Eastern Indigo Snake (*Drymarchon couperi*) movement patterns and space use in peninsular Florida at multiple temporal scales. Herpetologica **72**: 214-226.

Bauder, J.M., Breininger, D.R., Bolt, M.R., Legare, M.L., Jenkins, C.L., Rothermel, B.B., McGarigal, K. (2016b): The influence of sex and season on conspecific spatial overlap in a large, actively-foraging colubrid snake. PLoS One **11**: 1-19.

Baxley, D.L., Qualls, C.P. (2009): Black Pine Snake (*Pituophis melanoleucus lodingi*): spatial ecology and associations between habitat use and prey dynamics. J. Herpetol. **43**: 284-293.

Berger-Tal, O., Polak, T., Oron, A., Lubin, Y., Kotler, B.P., Saltz, D. (2011): Integrating animal behavior and conservation biology: a conceptual framework. Behav. Ecol. **22**: 236-239.

Bhaisare, D., Ramanuj, V., Shankar, P.G., Vittala, M., Goode, M.J., Whitaker, R. (2010): Observations on a Wild King Cobra (*Ophiophagus hannah*), with emphasis on foraging and diet. IRCF Reptilia-Amphibia **17**: 95-102.

Birchfield, G.L., Deters, J.E. (2005): Movement paths of displaced Northern Green Frogs (*Rana clamitans melanota*). Southeast. Nat. **4**: 63-76.

Bivand, R., Lewin-Koh, N. (2017): maptools: tools for reading and handling spatial objects. R package version 0.9-2. Available at https://CRAN.R-project.org/package=maptools.

Bivand, R., Keitt, T., Rowlingson, B. (2017): rgdal: bindings for the 'Geospatial' data abstraction library. R package version 1.2-16. Available at https://CRAN.R-project.org/package=rgdal.

Blouin-Demers, G., Fox, S.F. (2006): Kernels are not accurate estimators of home-range size for herpetofauna. Copeia **2006**: 797-802.

Bonnet, X., Naulleau, G., Shine, R. (1999): The dangers of leaving home: dispersal and mortality in snakes. Biol. Conserv. **89**: 39-50.

Breininger, D.R., Bolt, M.R., Legare, M.L., Drese, J.H., Stolen, E.D. (2011): Factors influencing home-range sizes of Eastern Indigo Snakes in central Florida. J. Herpetol. **45**: 484-490.

Brown, G.P., Shine, R. (2006): Why do most tropical animals reproduce seasonally? Testing hypotheses on an Australian snake. Ecology **87**: 133-143.

Brown, G.P., Shine, R., Madsen, T. (2002): Responses of three sympatric snake species to tropical seasonality in northern Australia. J. Trop. Ecol. **18**: 549-568.

Bruner, A.G., Gullison, R.E., Rice, R.E., da Fonseca, G.A.B. (2001): Effectiveness of parks in protecting tropical biodiversity. Science **291**: 125-128.

Bunyavejchewin, S. (1986): Ecological studies of tropical semi-evergreen rain forest at Sakaerat, Nnkhon [sic] Ratchasima, Northeast Thailand, II. Litterfall. Nat. Hist. Bull. Siam Soc. **34**: 35-58.

Calenge, C. (2006): The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. Ecological Modelling **197**: 516-519.

Carfagno, G.L.F., Heske, E.J., Weatherhead, P.J. (2006): Does mammalian prey abundance explain forest-edge use by snakes? Ecoscience **13**: 293-297.

Chanhome, L., Cox, M.J., Vasaruchapong, T., Chaiyabutr, N., Sitprija, V. (2011): Characterization of venomous snakes of Thailand. Asian Biomed. **5**: 311-328.

Christian, K.A., Corbett, L.K., Green, B., Weavers, B.W. (1995): Seasonal activity and energetics of two species of varanid lizards in tropical Australia. Oecologia **103**: 349-357.

Corey, B., Doody, J.S. (2010): Anthropogenic influences on the spatial ecology of a semi-arid python. J. Zool. **281**: 293-302.

Cox, M.J., Hoover, M.F., Chanhome, L., Thirakhupt, K. (2012): *Ophiophagus hannah* (Cantor, 1836). In: The Snakes of Thailand, p. 603-606. Chulalongkorn University Museum of Natural History, Bangkok.

Das, I., Ghodke, S. (2003): *Ophiophagus hannah* (King Cobra). Juvenile diet. Herpetol. Rev. **34**: 253.

Dodd, C.K., Barichivich, W. (2007): Movements of large snakes (*Drymarchon*, *masticophis*) in north-central Florida. Florida Sci. **70**: 83-94.

Duncan, P. (1983): Determinants of the use of habitat by horses in a Mediterranean wetland. J. Anim. Ecol. **52**: 93-109.

Duvall, D., Schuett, G.W. (1997): Straight-line movement and competitive mate searching in prairie rattlesnakes, *Crotalus viridis viridis*. Anim. Behav. **54**: 329-334.

Fleming, C.H., Calabrese, J.M. (2017a): ctmm: continuous-time movement modeling. R package version 0.4.1. Available at https://CRAN.R-project.org/package=ctmm.

Fleming, C.H., Calabrese, J.M. (2017b): A new kernel density estimator for accurate home-range and species-range area estimation. Methods Ecol. Evol. **8**: 571-579.

Forbes, G.J., Theberge, J.B. (1996): Cross-boundary management of Algonquin Park wolves. Conserv. Biol. **10**: 1091-1097.

Forman, R.T.T., Alexander, L.E. (1998): Roads and their major ecological effects. Annu. Rev. Ecol. Syst. **29**: 207-231.

GADM (2015): GADM database of global administrative areas. Version 2.8. Available at http://gadm.org.

Google Maps (2014): Satellite imagery. Retrieved via the OpenLayers QGIS plug-in https://www.google.co.uk/maps/@14.4997124,101.9376444,9589m/data=!3m1!1e3!4m2!17m1!1e1.

Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A., Scharlemann, J.P.W. (2016): Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nat. Commun. **7**: 1-7.

Hart, K.M., Cherkiss, M.S., Smith, B.J., Mazzotti, F.J., Fujisaki, I., Snow, R.W., Dorcas, M.E. (2015): Home range, habitat use, and movement patterns of non-native Burmese pythons in Everglades National Park, Florida, USA. Anim. Biotelemetry **3**: 1-13.

Heard, G.W., Black, D., Robertson, P. (2004): Habitat use by the inland carpet python (*Morelia spilota metcalfei*: Pythonidae): seasonal relationships with habitat structure and prey distribution in a rural landscape. Austral Ecol. **29**: 446-460.

Henle, K., Davies, K.F., Kleyer, M., Margules, C., Settele, J. (2004): Predictors of species sensitivity to fragmentation. Biodivers. Conserv. **13**: 207-251.

Hesed, K. (2006): *Ophiophagus hannah* (King Cobra). Diet. Herpetol. Rev. **37**: 480.

Hughes, A.C. (2017): Understanding the drivers of Southeast Asian biodiversity loss. Ecosphere **8**: e01624.

Hyslop, N.L., Meyers, J.M., Cooper, R.J., Norton, T.M. (2009): Survival of radio-implanted *Drymarchon couperi* (Eastern Indigo Snake) in relation to body size and sex. Herpetologica **65**: 199-206.

Hyslop, N.L., Meyers, J.M., Cooper, R.J., Stevenson, D.J. (2014): Effects of body size and sex of *Drymarchon couperi* (eastern indigo snake) on habitat use, movements, and home range size in Georgia. J. Wildl. Manage. **78**: 101-111.

Jellen, B.C., Shepard, D.B., Dreslik, M.J., Phillips, C.A. (2007): Male movement and body size affect mate acquisition in the Eastern Massasauga (*Sistrurus Catenatus*). J. Herpetol. **41**: 451-457.

Kenward, R.E., Walls, S.S., Hodder, K.H. (2001): Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. J. Anim. Ecol. **70**: 1-13.

Kranstauber, B., Smolla, M., Scharf, A.K. (2016): move: visualizing and analyzing animal track data. R package version 3.0.2. Available at https://CRAN.R-project.org/package=move.

Krishna, S. (2002): *Ophiophagus hannah* (King Cobra). Diet. Herpetol. Rev. **33**: 141.

Laver, P.N., Kelly, M.J. (2008): A critical review of home range studies. J. Wildl. Manage. **72**: 290-298.

Lei, J., Booth, D.T., Dwyer, R.G. (2017): Spatial ecology of yellow-spotted goannas adjacent to a sea turtle nesting beach. Aust. J. Zool. **65**: 77-86.

Lelièvre, H., Moreau, C., Blouin-Demers, G., Bonnet, X., Lourdais, O. (2012): Two syntopic colubrid snakes differ in their energetic requirements and in their use of space. Herpetologica **68**: 358-364.

Macartney, J.M., Gregory, P.T., Larsen, K.W., Herpetology, J., Mar, N. (1988): A tabular survey of data on movements and home ranges of snakes. J. Herpetol. **22**: 61-73.

Madsen, T., Shine, R. (1996): Seasonal migration of predators and prey – a study of pythons and rats in tropical Australia. Ecology **77**: 149-156.

Madsen, T., Ujvari, B. (2011): The potential demise of a population of adders (*Vipera berus*) in Smygehuk, Sweden. Herpetol. Conserv. Biol. **6**: 72-74.

McNab, B.K. (1963): Bioenergetics and the determination of home range size. Am. Nat. **97**: 133-140.

Mitrovich, M.J., Diffendorfer, J.E., Fisher, R.N. (2009): Behavioral response of the Coachwhip (*Masticophis flagellum*) to habitat fragment size and isolation in an urban landscape. J. Herpetol. **43**: 646-656.

Morrison, S.A., Boyce, W.M. (2009): Conserving connectivity: some lessons from Mountain Lions in Southern California. Conserv. Biol. **23**: 275-285.

Newmark, W.D., Manyanza, D.N., Gamassa, D.-G.M., Sariko, H.I. (1994): The conflict between wildlife and local people living adjacent to protected areas in Tanzania: human density as a predictor. Conserv. Biol. **8**: 249-255.

Nilsen, E.B., Pedersen, S., Linnell, J.D.C. (2008): Can minimum convex polygon home ranges be used to draw biologically meaningful conclusions? Ecol. Res. **23**: 635-639.

OEPP (1997): Thailand policy and perspective plan for enhancement and conservation of national environmental quality, 1997-2016. Bangkok, Office of Environment Policy and Planning, Ministry of Science, Technology and Environment.

Pebesma, E.J., Bivand, R.S. (2005): Classes and methods for spatial data in R. R News **5**. Available at https://cran.r-project.org/doc/Rnews/.

Phumee, P., Pagdee, A., Kawasaki, J. (2017): Energy crops, livelihoods, and legal deforestation: a case study at Phu Wiang National Park, Thailand. J. Sustain. For. **37**: 120-138.

Quantum GIS Development Team (2017): Quantum GIS geographic information system. Open source geospatial foundation project. Available at http://qgis.osgeo.org.

R Core Team (2017): R: a Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Available at https://www.r-project.org/.

R Studio Team (2016): RStudio: integrated development environment for R. Available at https://www.rstudio.com/.

Rao, C., Talukdar, G., Choudhury, B.C., Shankar, P.G., Whitaker, R., Goode, M. (2013): Habitat use of King Cobra (*Ophiophagus hannah*) in a heterogeneous landscape matrix in the tropical forests of the Western Ghats, India. Hamadryad **36**: 69-79.

Reading, C.J., Luiselli, L.M., Akani, G.C., Bonnet, X., Amori, G., Ballouard, J.M., Filippi, E., Naulleau, G., Pearson, D., Rugiero, L. (2010): Are snake populations in widespread decline? Biol. Lett. **6**: 777-780.

Reinert, H.K., Cundall, D. (1982): An improved surgical implantation method for radio-tracking snakes. Copeia **1982**: 702.

Roe, J.H., Kingsbury, B.A., Herbert, N.R. (2004): Comparative water snake ecology: conservation of mobile animals that use temporally dynamic resources. Biol. Conserv. **118**: 79-89.

Rosa, I.M.D., Smith, M.J., Wearn, O.R., Purves, D., Ewers, R.M. (2016): The environmental legacy of modern tropical deforestation. Curr. Biol. **26**: 2161-2166.

Sanderson, E.W., Redford, K.H., Vedder, A., Coppolillo, P.B., Ward, S.E. (2002): A conceptual model for conservation planning based on landscape species requirements. Landsc. Urban Plan. **58**: 41-56.

Saruwatari, T. (2006): Aerial photo interpretation of 50-year vegetation changes in Sakaerat Environmental Research Station (SERS), Northeast Thailand. Nakhorn Ratchasima, Laboratory of Tropical Forest Environment, Kyoto University.

Saunders, D.A., Hobbs, R.J., Margules, C.R. (1991): Biological consequences of ecosystem fragmentation: a review. Conserv. Biol. **5**: 18-32.

Schaefer, W.H. (1934): Diagnosis of sex in snakes. Copeia **1934**: 181.

Seaman, D.E., Powell, R.A. (1996): An evaluation of the accuracy of kernel density estimators for home range analysis. Ecology **77**: 2075-2085.

Secor, S.M. (1994): Ecological significance of movements and activity range for the Sidewinder, *Crotalus cerastes*. Copeia **1994**: 631-645.

Setser, K. (2007): Use of anesthesia increases precision of snake length measurements. Herpetol. Rev. **38**: 409-411.

Shankar, P.G., Ganesh, S.R., Whitaker, R., Prashanth, P. (2013a): King Cobra *Ophiophagus hannah* (Cantor, 1836) encounters in human-modified rainforests of the Western Ghats, India. Hamadryad **36**: 62-68.

Shankar, P.G., Singh, A., Ganesh, S.R., Whitaker, R. (2013b): Factors influencing human hostility to King Cobras (*Ophiophagus hannah*) in the Western Ghats of India. Hamadryad **36**: 91-100.

Shine, R., Madsen, T. (1996): Is thermoregulation unimportant for most reptiles? An example using Water Pythons (*Liasis fuscus*) in tropical Australia. Physiol. Zool. **69**: 252-269.

Siler, C.D., Welton, L.J., Brown, R.M., Infante, C., Diesmos, A.C. (2011): *Ophiophagus hannah* (King Cobra). Diet. Herpetol. Rev. **42**: 297.

Somaweera, R., Somaweera, N. (2010): Serpents in jars: the snake wine industry in Vietnam. J. Threat. Taxa **2**: 1251-1260.

Sperry, J.H., Weatherhead, P.J. (2009): Sex differences in behavior associated with sex-biased mortality in an oviparous snake species. Oikos **118**: 627-633.

Steen, D.A. (2010): Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. Herpetol. Conserv. Biol. **5**: 183-188.

Strine, C.T., Silva, I., Crane, M., Nadolski, B., Artchawakom, T., Goode, M., Suwanwaree, P. (2014): Mortality of a wild king cobra, *Ophiophagus hannah* Cantor, 1836 (Serpentes: Elapidae) from northeast Thailand after ingesting a plastic bag. Asian Herpetol. Res. **5**: 284-286.

Stuart, B., Wogan, G., Grismer, L., Auliya, M., Inger, R.F., Lilley, R., Chan-Ard, T., Thy, N., Nguyen, T.Q., Srinivasulu, C., Jelić, D. (2012): *Ophiophagus hannah*, King Cobra. The IUCN red list of threatened species. Available at www.iucnredlist.org. Downloaded on 20 October 2017.

Trisurat, Y. (2010): Land use and forested landscape changes at Sakaerat Environmental Research Station in Nakhon Ratchasima province, Thailand. Ekol. Bratislava **29**: 99-109.

Walston, J., Robinson, J.G., Bennett, E.L., Breitenmoser, U., Fonseca, G.A.B. da, Goodrich, J., Gumal, M., Hunter, L., Johnson, A., Ullas Karanth, K., Leader-Williams, N., MacKinnon, K., Miquelle, D., Pattanavibool, A., Poole, C., Rabinowitz, A., Smith, J.L.D., Stokes, E.J., Stuart, S.N., Vongkhamheng, C., Wibisono, H. (2010): Bringing the tiger back from the brink-the six percent solution. PLoS Biol. **8**: 6-9.

Whitaker, N., Shankar, P.G., Whitaker, R. (2013): Nesting ecology of the King Cobra (*Ophiophagus hannah*) in India. Hamadryad **36**: 101-107.

Whitaker, P.B., Shine, R. (2000): Sources of mortality of large elapid snakes in an agricultural landscape. J. Herpetol. **34**: 121-128.

Whitaker, P.B., Shine, R. (2003): A radiotelemetric study of movements and shelter-site selection by free-ranging Brownsnakes (*Pseudonaja textilis*, Elapidae). Herpetol. Monogr. **17**: 130-144.

Whitaker, R., Captain, A. (2004): King Cobra *Ophiophagous hannah*. In: Snakes of India – a Field Guide, p. 384-385. Draco Books, Chennai, India.

Wickham, H. (2009): ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag, New York.

Wikramanayake, E.D., Dinerstein, E., Robinson, J.G., Karanth, U., Rabinowitz, A., Olson, D., Mathew, T., Hedao, P., Conner, M., Hemley, G., Bolze, D. (1998): An ecology-based method for defining priorities for large mammal conservation: the tiger as case study. Conserv. Biol. **12**: 865-878.

Winne, C.T., Willson, J.D., Andrews, K.M., Reed, R.N. (2006): Efficacy of marking snakes with disposable medical cautery units. Herpetol. Rev. **37**: 52-54.

Worton, B.J. (1989): Kernel methods for estimating the utilization in home-range studies. Ecology **70**: 164-168.

Worton, B.J. (1995): Using Monte Carlo simulation to evaluate kernel-based home range estimators. J. Wildl. Manage. **59**: 794-800.

*Submitted: January 22, 2018. Final revision received: August 26, 2018. Accepted: August 31, 2018.*
*Associate Editor: José C. Brito.*