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ECOLOGY AND CONSERVATION OF THE BAMBOO PIT VIPER: NATURAL HISTORY, DEMOGRAPHY AND EFFECTS OF TRANSLOCATION

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ECOLOGY AND CONSERVATION OF THE BAMBOO PIT VIPER: NATURAL HISTORY, DEMOGRAPHY AND EFFECTS OF TRANSLOCATION

BY

ELIZABETH ANNE DEVAN-SONG

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OF

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ABSTRACT

The bamboo pit viper (*Trimeresurus albolabris*, Gray 1842) is broadly distributed through South and Southeast Asia. This venomous snake occurs in high abundances in Hong Kong, and frequently comes into contact with humans. Thus it is viewed as a 'nuisance' species and is commonly translocated away from areas of human habitation. Despite being relatively abundant and a frequent focus of human-snake conflict in the region, very little is known about the ecology, demography, and the effects of long-distance translocation on this species. I captured 104 *T. albolabris* from throughout Hong Kong Special Administrative Region, China and collected morphometric and reproductive information. I conducted radio-telemetry on 41 individuals (21 translocated and 20 resident) and obtained information on survival, movements, reproduction and brumation. *Trimeresurus albolabris* exhibited an even sex ratio. Females attain sexual maturity at ~460 mm snout-vent length, and males at ~ 410 mm snout-vent length. Mating occurs between September and November and coincides with the onset of spermatogenesis. *Trimeresurus albolabris* displays post-nuptial vitellogenesis, and long-term sperm storage in females likely occurs over the winter. Females reproduce once every two or more years, except for very large females that may reproduce annually. Translocation decreased survival of *T. albolabris*, and translocated snakes were more likely to make unidirectional movements away from point of release. Translocated snakes also displayed aberrant movement patterns, with elevated frequency of movements and increased average daily movements. Translocation also negatively affected brumation behavior and reproduction. Long-distance translocation is not a viable conservation strategy for

addressing human-snake conflict in *T. albolabris*, and alternative strategies should be explored for management of this species. Knowledge of the natural history, demography, reproductive ecology, and responses to long-distance translocation of *T. albolabris* provide baseline ecological information for a species that contributes significantly to medically important snakebite injuries in the region and will be useful for prescribing improvements to current management strategies.

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DEDICATION

This thesis is dedicated to the memory of the wonderful Lily Glidden, my friend and field assistant. She contributed significantly to my data collection, and would have gone on to become a great field biologist.

PREFACE

Manuscript Format is in use for this thesis. Chapter 1 is formatted for submission to Herpetological Conservation and Biology. Chapter 2 is formatted for submission to Biological Conservation.

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CHAPTER 1

This chapter is in preparation for submission to Herpetological Conservation and Biology.

ECOLOGY OF THE BAMBOO PIT VIPER (*TRIMERESURUS ALBOLABRIS*, GRAY, 1842) IN SOUTH CHINA

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Abstract.—The bamboo pit viper (*Trimeresurus albolabris*) is broadly distributed through South and Southeast Asia. Despite being relatively common in a range of habitats, very little is known about the ecology of the species. In this study, we report on the ecology and demography of 104 vipers from mark-recapture surveys in Hong Kong, China, and reproductive states and growth rates of 20 radio-tagged individuals. *Trimeresurus albolabris* occurs in even sex ratios. This species displays sexual dimorphism, with females being larger, and all males, including neonates, displaying a white supralabial stripe on the head. Sexual dimorphism in relative tail length is apparent from birth, and also increases with age: males display a larger ontogenetic increase in tail lengths compared to females. Males attain sexual maturity ~ 410 mm snout-vent length or earlier, while females attain sexual maturity at ~ 460 mm snout-vent length, but only start reproducing at ~ 520 mm snout-vent length. Mating occurs between September and November, coinciding with the onset of spermatogenesis. *Trimeresurus albolabris* displays post-nuptial vitellogenesis, and long-term sperm storage in females likely occurs over the winter. Females gestate over the summer and parturition occurs in late July to August. Females reproduce once every two or more years, except for very large females that may reproduce annually. Females entered brumation within the first three weeks of December, using fossorial crevices or burrows for shelter and emerging to bask on sunny days. Understanding its demography and reproductive ecology can provide insights into the conservation and wildlife management of *T. albolabris* in the region and increase our understanding of sexual dimorphism, reproduction, and evolution of the cryptic *Trimeresurus* species complex.

Key Words.— Trimeresurus albolabris; reproduction; sexual dimorphism; sexual maturity; growth rates; Viperidae; brumation; parasites

INTRODUCTION

Fifty years after Wilfred Neill's observations on the 'egregiously complex' reproductive strategies of Asian snake species (Neill 1964), there is still a paucity of data on tropical snakes compared to their temperate counterparts (Böhm et al. 2013), and many patterns in the ecology of tropical snake groups have not been identified or recognized (Almeida-Santos and Salomao 2002; Scartozzoni et al. 2009). South and Southeast Asia, for example, harbor high diversity and endemicity of herpetofauna (Das and van Dijk 2013; Ganesh et al. 2013), yet many common and easily-captured snakes are not well studied, such as the widespread and abundant species in the genus *Trimeresurus* (Serpentes: Viperidae: Crotalinae). Members of the diverse *Trimeresurus* genus occupy a wide range of habitats and exhibit evidence of great variability in habits, ecology, and reproductive strategy (Malhotra and Thorpe 1997; McDiarmid et al. 1999; Orlov et al. 2002). *Trimeresurus* spp. contribute significantly to snakebite morbidity in the region (Hutton et al. 1990; Viravan et al. 1992; Blessmann et al. 2010), yet the ecology, population densities, and habitat use of these species are not well documented. One of the most widespread members of this genus is the bamboo pit viper (*Trimeresurus albolabris*), a small, sexually dimorphic arboreal pit viper that ranges from the Nicobar islands in India, to Bangladesh, Indochina, Southern China, Malaysia and Indonesia (Orlov et al. 2002). The medical significance of *T. albolabris* in snakebite injuries as well as its contentious phylogeny within the cryptic *Trimeresurus* genus has resulted in significant research into venom proteomics(Du et al. 2002; Rojnuckarin et al. 2006; Soogarun et al. 2008), toxicology and bite pathology (Chanhome et al. 2002; Chotenimitkhun and Rojnuckarin 2008; He et al. 2008), and phylogeny of this species (Malhotra and Thorpe 2000; Giannasi et al. 2001; David et al. 2011). However, very little has been published on its natural history, demography and ecology, even with much recent research that uses snakes as model organisms (Shine and Bonnet 2000).

Copulation by *T. albolabris* has been observed between late March to late May in northern Vietnam (Orlov et al. 2002) and a captive female was reported to store sperm for a year (Kamelin and Lukin 2003). Neonates in North Vietnam are born between late July and early August (Orlov et al. 2002) with clutch sizes of 4 to 14 (Orlov et al. 2002; Kamelin and Lukin 2003). However, given the lability in reproductive strategies in single species across a geographic range (Aldridge and Duvall 2002; Sasa et al. 2009; Siqueira et al. 2013) and that environmental factors correlate strongly with reproductive cycles (Tsai and Tu 2000,2001; Sasa et al. 2009), it cannot be assumed that other populations throughout its range display the same reproductive cycle seen in North Vietnam.

In Hong Kong, *T. albolabris* is the most commonly-encountered venomous snake (Karsen et al. 1998) and is by far the most prevalent cause of medically significant snakebites (Cockram et al. 1990; Hon et al. 2004; Shek et al. 2009), yet very little is known about its ecology in South China. In Hong Kong, the species is described as a habitat generalist, occurring in most terrestrial vegetation types at all elevations (Karsen et al. 1998).

The objective of this study is to shed light on demographic parameters, sexual dimorphism, and reproductive ecology of *T. albolabris* in Hong Kong. In addition, observations on parasites, diet and defensive behavior are reported.

MATERIALS AND METHODS

***Study Site.*—**This study was conducted in Hong Kong, China (2209’-2237’N, 11350’-11430’E), a special autonomous region of 1100 km^2. Hong Kong harbors a high-density urban area but also 23 national parks and expanses of rural land containing small traditional villages. Hong Kong occurs in the tropics and exhibits a seasonal monsoon climate of hot, humid summers with high precipitation from May to September and cool, dry and mild winters from November to February (Dudgeon and Corlett 1994). We sampled within active and abandoned agricultural land, secondary forest, shrubland, and grassland.

Animal sampling and sedation.— We conducted visual encounter surveys in 2012, however these efforts were not quantified and only vipers above 50 g were captured. From June to December 2013, we employed timed visual encounter surveys to capture pit vipers along a combined 32.1 km of hiking trails in 10 sites within Hong Kong (Table 1), including three on Lantau Island, two on Hong Kong Island, and five in the New Territories (Figure 1). Researchers walked slowly along hiking trails at night, scanning vegetation and the ground on and either side of the trail, and all vipers encountered were captured. Vipers encountered outside of timed surveys were also captured in 2013, although these vipers were not included in the calculation of capture rates. All captured vipers were sedated with Isoflurane, an inhalant anesthesia, for measurements described in sections below. A subset of vipers in both years were implanted with SB-2 or BD-2 radio transmitter (Holohil Systems Ltd, Carp, Ontario, Canada) weighing no more than 6% of viper body mass. Telemetered vipers were given two days to recover from surgery while non-telemetered snakes were allowed at least three hours for anesthesia recovery. All vipers were released within 5 m of capture site. We relocated vipers two to three times a week and recorded their locations with a global positioning system unit. Individuals that survived beyond 14 to 20 weeks had their transmitters replaced with new ones. At the end of each year, we captured all surviving telemetered vipers, removed their transmitters, and released them within 5 m of location of last capture.

***Morphometrics, sexual dimorphism and growth rate*.—**We measured the mass, snout-vent length (hereafter SVL) and tail length of sedated vipers. Injuries and truncated tails were noted. Hemipene probing was used to determine sex. In addition, presence of a white lateral stripe on the head and body was recorded. We implanted vipers subcutaneously with a unique passive integrated transponder (Biomark, Inc., Boise, Idaho, USA) using an 18-gauge needle. We did not measure SVL and tail length of vipers smaller than 30g that were captured between 4 June and 1 July 2013 due to logistical difficulties, and only determined sex and mass from these individuals.

Growth rates were measured using telemetered individuals that survived the tracking season. For males and nongravid females, we measured growth rate as the change in body condition (mass to SVL ratio) between time of capture (May to July) and hibernation (December), and for gravid females, growth rate was measured as the change in body condition between parturition (July/August) and hibernation (December). Body condition was chosen over SVL as a measure of growth as we were interested to document change in fat storage over the active season, and increases in SVL over the season failed to capture the emaciated conditions of some vipers.

Reproduction.—Male vipers' hemipenes were gently palped without everting them to determine if semen was present. We conducted ultrasound on the ovaries of female snakes to enumerate and measure follicles or embryos. For telemetered females that survived until December of either year, these measurements were obtained in June/July as well as December. We estimated parturition date of gravid telemetered individuals after weighing them *in situ* once we obtained visual indication of substantial weight loss. We also documented any intraspecific interaction of both telemetered and non-study vipers that were suggestive of mating behavior.

Brumation.— We recorded microhabitat (ground/ foliage/ canopy/ tree or rock wall crevice/ burrow) and height above ground with each relocation of telemetered snakes, and define 'first brumation event' as the range of dates between last locating a snake above ground, and first locating it in underground, beneath leaf litter or in an artificial rock wall crevice.

Parasites and diet.—We obtained fecal samples from 21 sedated vipers to identify fecal parasites occurring *T. albolabris* found in Hong Kong. Direct smears and fecal flotation were used to identify parasite ova under a light microscope. Coelomic, subcutaneous and intra-organ parasites were retrieved from any vipers during necropsies. In addition, we identified mammalian hair to family level if hairs were detected in the direct smears to document diet. Hair identification was aided with mammal hair samples from specimens at the Lee Kong Chian Natural History Museum, National University of Singapore.

Causes of mortality.—We performed necropsies on vipers that died during the radiotelemetry project as well as other carcasses encountered in the field to determine causes of death. We examined the carcasses for signs of external and internal infection and injury, determined condition of internal organs.

Statistical analyses.—We examined sex ratios for the 2013 survey results using a goodness-of-fit test. We used linear regression to quantify the relationship between SVL and clutch size. Male and female SVLs were compared using a Student’s t-test, and we used an analysis of covariance to detect differences in tail lengths between males and females, and interaction between sex and total length on tail length, using total length as the covariate. A Johnson-Neyman procedure was used to identify the nonsignificant regions of group mean tail length differences across total lengths. Individuals with injured or truncated tails were removed from relative tail length analyses. All other metrics are described in SVL to enable comparison across different studies and to utilize animals with truncated tails, however relative tail length was analyzed using total length instead of SVL.

RESULTS

During 204.5 person-hours of visual encounter surveys, we encountered and captured 90 vipers, resulting in a capture rate of one viper per every 2.3 person-hours of survey effort. If the surveys from the low-yielding Lantau Island transects were removed (6 vipers captured in 53 person-hours of survey), the capture rate was one viper every 1.8 person-hours. Number of recaptures was extremely low – only 5.5 % of the 90 vipers encountered over the seven-month study were recaptured individuals, and no vipers encountered incidentally were recaptured. We captured 85 unique vipers during visual encounter surveys in 2013, and an additional 19 unique individuals were incidentally encountered, for a total of 104 unique vipers captured and measured in 2013 (Table 1). Of these, SVL and tail length were not obtained for 18 individuals captured in June due to logistical difficulties. These 18 vipers were included in capture rate and sex ratios but not in any analyses involving SVL, tail length or total length.

Nine females were radio-tracked in 2012, three of which survived, and another seven in 2013, five of which survived. Four males were tracked in 2013, with two survivals.

Morphometrics, sexual dimorphism and growth rate.— Of 85 unique vipers encountered during the 2013 visual encounter surveys, 49.4% were male; of 19 incidental encounters, 42.1% were male. Sex ratios were even, regardless of method ($\chi^2 = 0.48$, df = 3, P = 0.922). Of the 16 neonates captured, 68.8% were male.

Hemipene probing to determine sex was 100% consistent with presence or absence of white stripe on the head, even for the smallest vipers. All males exhibited a faint to prominent lateral white stripe on the head and body, while no females displayed such markings on the head (Figure 3). However, it was not uncommon to find females with a white to yellow lateral stripe on the body. Ventral scale color varied from white to bright yellow to light green or white in both males and females. Females attained larger sizes than males, with the largest male measuring 512mm SVL and the largest female measuring 810mm (Figure 2). Mean SVL for male vipers was 347.8 mm (330.0 – 365.6 mm) and differed significantly ($t = 4.16$, $df = 84$, $P < 0.001$) from mean female SVL of 469.5 (446.8 – 492.2 mm). Relationships between body condition and SVL were similar between males and females until ~ 524 mm SVL (Figure 4), the length that corresponds to the smallest gravid female, and corresponds approximately to the largest male (512 mm SVL). Above an apparent 524 mm SVL threshold, body condition was extremely variable (Figure 4). We found a significant interaction between sex and the covariate of total length on the relative tail length of vipers ($F = 65.37$, $df = 1, 80$, $P < 0.001$). The limit of nonsignificant values fell between -1.72 and 195. 84 mm total length, which is smaller than the smallest neonate measured (Figure 5). Male tail length means were therefore higher than female tail length means at all total lengths of snakes.

Adult males decreased in body condition over the active season, as did two small (524 mm and 525 mm in SVL), gravid females (Figure 6). The other two gravid females we tracked, which were considerably more robust while gravid (580 mm and 710 mm SVL), increased slightly in body condition over the months after giving birth.

All but one non-gravid female increased in body condition over the active season, with two substantially increasing in body condition (Figure 6).

Reproduction.— The smallest gravid female encountered was 524 mm SVL, and the smallest sexually mature female found was 463 mm SVL. Two of the six (33.3%) adult female vipers encountered during the gestation period in 2013 were gravid, while 50% of the four adult female vipers encountered during that period in 2012 were gravid. It was not possible to tell if a female had been gravid that year if we encountered it after the gestation period. Clutch sizes of three gravid individuals captured in May and June 2012 and two gravid individuals captured in June 2013 ranged from 5 to 20 embryos (Figure 7). A clear positive relationship existed between SVL and clutch size ($R^2 = 0.98$, $P = 0.001$). The largest gravid viper gestated at least 20 embryos that overlapped within the body cavity, while smaller vipers had only five to six non-overlapping embryos.

Due to the low probability of seeing individuals when relocating vipers in dense vegetation, the exact date of parturition is unknown for all vipers. However we were able to estimate parturition within a few days based on dates where visual observations were obtained. All gravid vipers gave birth between 15 July and 9 August in both years (Figure 8). No post-parturition parental care was observed, and we did not observe any neonates in the vicinity of the female post-parturition. Our data suggest a relationship between large clutch size and earlier parturition dates (Figure 8) although sample size was too small for statistical analyses. Females were extremely emaciated following parturition, and lost ~3 g in mass per embryo. A necropsy of a telemetered female snake that was killed by a vehicle a few weeks after parturition revealed depleted fat reserves. Another female died of apparent starvation three months after parturition and had not been observed to eat for the entire period from parturition until death.

Follicle size at the end of the active season was reduced to inactive size (< 5 mm) in vipers that had been gravid in the summer of that season except for one individual that had enlarged follicles in December (Figure 9). This individual, tracked in 2012, was a very large female with substantial body mass even post-parturition and gained body mass over the active season after giving birth. Small adults retained primary follicles throughout the study period (Figure 9). Large adults that were not gravid in the summer and gained substantial mass over the active season (July-Nov), increased follicle size by the end of the year (7 – 15+ mm), corresponding to stage II- III vitellogenesis in the closely-related *Trimeresurus stejneger*i (Tsai and Tu 2001).

Over the course of two years, five instances of adult male vipers attending large females were observed between 17 August and 15 October. In all observations, males were perched on the same branch approximately 10 to 50 cm away from the large female viper with its head orientated towards the female. No two individuals of this solitary species were observed within such close proximity outside of the putative mating season, even on surveys where a high number of vipers were captured within a short stretch of forest trail. No copulation or other interaction was observed. On one of the five abovementioned occasions, two male adults were attending one large female. Five adult males ranging from 412 to 512 mm in SVL that were caught between 5 September and 15 October 2013 secreted semen when hemipenes were palped. One of these five adult males was captured while attending a large female, and the other four were solitary males captured during the visual encounter surveys.

In 2013, we observed large movements in males characteristic of mate-finding, with males moving an average of 12.6 m (10.9 –14.3 m) per day and females moving only 4.0 m (3.6 – 4.4 m) per day during the putative mating period (mid-August to late-October).

Brumation.—Brumation was observed in all female vipers that survived to the end of the project (either December 2012 or December 2013). Three types of brumation refugia were identified: small crevices in the ground covered by leaves, logs or other plant debris, crevices inside low human-made rock walls, and small mammal burrows either in soil, under loose stones, boulders or tree roots (Figure 10). A few vipers were found as far as 0.5m below the surface. The onset of brumation ranged between 9 to 12 December 2012, and 6 to 12 December 2013 (Figure 11). In December of both years, vipers emerged to bask on warm sunny days in low shrubs, on the ground or occasionally in trees. Vipers were not confined to one brumation site, and shifted between brumation sites within a few meters of each other. No communal brumation was observed. Neither of the two surviving males brumated over the winter and both were still active in low shrubs in December.

***Parasites and diet*.—**Multiple parasite ova were found in fecal matter of *Trimeresurus albolabris* comprised of the following groups: *Kalicephalus* sp., *Strongyloides* sp., *Capillaria* sp., *Oxyuris* sp., ascarids, and other hookworms. An unidentified coccidian parasite was also observed in several vipers.

Ascarid larvae were also found buried subcutaneously and within the coelomic cavities of several vipers. In one instance, a necropsy performed on a female revealed ascarid infection throughout the coelomic cavity, fat bodies, kidneys, liver, and loose subcutaneous parasites (Figure 12). This individual had been suffering from severe hepatitis with lesions around an inflamed, mottled and pale liver, with numerous hepatic nodular masses with parasites inside the cysts (Figure 12). The cause of death was due to asphyxiation during regurgitation and not infection, although it appeared that the viper would have eventually succumbed to the infection. The fish and bird tapeworm *Ligula intestinalis,* not previously recorded to infect *Trimeresurus albolabris*, was also found subcutaneously and retrieved from a sedated live viper.

We observed one individual eat a Chinese gecko (*Gekko chinensis*) during the study period, and no other predation events were observed. This same individual was noted to have eaten again seven days after consuming the gecko. Examination of fecal matter from vipers revealed Muridae hairs for several vipers and Soricidae hair for one viper.

***Causes of mortality*.—**In addition to the two females described above that died after parturition (one from a vehicle and one from apparent starvation), seven other mortalities were confirmed in telemetered snakes, six of which were eaten by other animals. One individual was eaten by a king cobra (*Ophiophagus hannah*), and several individuals were tracked to a transmitter that had been defecated by a snake predator.

These defecated transmitters were discovered at the base of very thick vegetation or in underground burrows, ruling out avian predators, and transmitters were covered in uric acid, ruling out mammalian predators. *Trimeresurus albolabris* is probably prey to a variety of ophiophagous snakes such as the commonly-encountered Chinese cobra (*Naja atra*) and many-banded krait (*Bungarus multicinctus*), and the less common king cobra (*Ophiophagus hannah*) and banded krait (*Bungarus fasciatus*). All six predation events on radiotagged snakes took place in the first two weeks of October in both years. The last mortality was caused by tissue and liver infections that were unrelated to the study. In 2012, we encountered a live non-study viper that had been attacked by a mammal. Deep lesions suggestive of small mammal claws or teeth were present on the dorsal and lateral sides of the body, and its spine was broken.

No mortalities were associated with either the mark-recapture or radiotelemetry projects. Pathology was confined to infections surrounding the surgery site in several vipers and infected tissue was encapsulated by healthy tissue.

Notes on defensive behavior.—We found *T. albolabris* in Hong Kong to strike readily upon disturbance, although most individuals attempted to rely on crypsis as a first line of defense. Larger individuals, and particularly very large females, were more likely to strike at researchers compared to smaller individuals. Tail-vibrating behavior was also observed in several disturbed individuals, in which they would strike their tails rapidly against the nearest surface to create a rattling sound, presumably as a warning. Tail vibration was always accompanied with striking behavior as we made movements towards the viper. We observed no defensive behavior in any of the neonates encountered.

DISCUSSION

Because of a low recapture rate of 5.5%, we could not estimate population sizes based on the mark-recapture data, and more exhaustive sampling efforts or different methods to sample vipers, or both, are necessary. Radio-tagged vipers were found to traverse the entire canopy, perching as high as 15 m, but only those < 4 m high were likely to be spotted by an averaged-height researcher during the visual encounter surveys, and such surveys are not an ideal method for surveying arboreal snakes. Low detection and recapture rates for snakes and difficulties measuring population parameters are not unusual (Parker and Plummer 1987; Steen 2010). Increased sampling effort (Steen 2010), and the use of other methods such as trapping or canopy searches across multiple seasons are necessary before population parameters can be estimated for this species.

Demography.—We documented even sex ratios of *Trimeresurus albolabris* encountered in Hong Kong. Too few neonates were captured in 2013 to detect a difference in sex ratio (5 F: 11 M). Sample size of sexually mature vipers during the gestation period was very low (four in 2012 and six in 2013). However, the ratios of gravid to nongravid females during this period (1.0 in 2012 and 0.5 in 2013) suggest that female vipers reproduce biennially or even less frequently. This is also consistent with body condition and vitellogenesis patterns observed in females. Females that were gravid in May-July exhibited primary follicles in November-December of that year and only one gained substantial mass. However, both large nongravid females showed follicle size increase from primary follicles in May-July to enlarged follicles by November-December and both increased substantially in body condition over this period (Figures 6 and 9).

Sexual dimorphism, sexual maturity and growth rate.—Sexual dimorphism is pronounced in this species, with females attaining much larger sizes. Sexual size dimorphism in this species is particularly interesting considering the relatively long distances that males move during the breeding season compared to females. Males, including neonates, displayed a white stripe above the supralabial scales; no females exhibited this characteristic. Sex could also be determined by hemipene probing at all ages.

Our relative tail length analysis is missing males between 333 to 450 mm in total length (or 271 to 355 mm SVL), possibly due to the fact that we did not sample between Jan-June of 2013. However, a clear pattern is detectible: sexual dimorphism in relative tail lengths increases with age, with males displaying a larger ontogenetic increase in tail lengths compared to females. The tendency for relative tail length dimorphism between the sexes to increase with age is well-documented (Klauber 1943), however, *T. albolabris* also displays distinct sexual dimorphism in relative tail length at the neonate stage. Sexual dimorphism in *T. albolabris* is present from birth, and it is possible to determine the sex of *T. albolabris* at all ages by the diagnostic white stripe on the head, the relative tail length to total length ratio, or by hemipene probing.

Sexual maturity in males probably occurs at or before ~ 410 mm SVL. The smallest male found retaining semen in our study was 412 mm, however, the closely-related *Trimeresurus stejnegeri* matures at ~370 mm SVL (Tsai and Tu 2000), and it is possible the *T. albolabris* males mature earlier than 412 mm SVL. Female *T. albolabris* mature sexually at ~460 mm SVL but probably do not start reproducing before ~520 mm SVL. This is supported by three lines of evidence: First, the smallest sexually mature female measured 463 mm in SVL, but the smallest gravid viper found was 524 mm. Second, growth trajectories are similar in males and females until females attain larger SVLs than males, which occurs at ~ 512 mm SVL. Finally, the great variation in body condition of telemetered female vipers appears to be related to reproductive state (Figure 6), with nonreproductive females increasing substantially in body condition over the active season, and gravid females increasing less in body condition, or even in decreasing body condition post-parturition. Sexual maturity in females probably occurs at ~ 460 mm, but reproduction is only initiated when body reserves exceed a threshold value, as in other snakes (Bonnet et al. 2002).

Reproduction.—Based on our observed data, we constructed a probable reproductive cycle for *T. albolabris* in Hong Kong (Figure 13). Our study provides evidence of gestation in May to July, parturition in July to August, mating in August to November coinciding with presence of semen in males, and onset of vitellogenesis before December. All of the above point to a post-nuptial vitellogenesis, or vitellogenesis following mating, and long-term sperm storage over winter, both characteristics of temperate snakes (Schuett 1992; Aldridge and Duvall 2002; Shine

2003). We hypothesize extension of vitellogenesis into the following year based on a post-nuptial vitellogenesis and long-term sperm storage, and estimated ovulation period based on gestation, vitellogenesis and parturition dates.

As we did not conduct surveys or track snakes from Jan-May 2013, we are unable to rule out the possibility of two mating seasons of *T. albolabris* in Hong Kong, as seen in some temperate pit vipers in the genera *Agkistrodon* and *Crotalus* (Aldridge and Duvall 2002) . However, based on 2012 surveys that began in February, we conclude that a spring mating season is unlikely. Although our 2012 survey efforts were not quantified, we observed very little viper activity and low capture rates from February to March 2012, and by the time substantial numbers of vipers had been captured (May 2012), gravid females with fully-formed embryos had already been found.

Ratios of nongravid to gravid vipers during gestation periods as well as follicle measurements suggest that females reproduce biennially or even less frequently. Biennial or less frequently reproducing snakes are unable to complete all events necessary for yearly reproduction within twelve months (Bull and Shine 1979) and is more common in temperate than in tropical species. For *T. albolabris* females, infrequent reproduction may be indicated by poor recovery of body condition after giving birth, that nongravid females begin vitellogenesis before winter, and that gravid females reduce follicle size to inactive sizes (<5 mm) after parturition. However, in one case, a gravid female appeared to undergo vitellogenesis in the same year after giving birth. Notably, this was the largest female tracked and second largest female captured in this study. Very large females may therefore have sufficient fat reserves and efficient postpartum body condition recovery to reproduce in consecutive years, as has been observed in captive *T. albolabris* (Kamelin and Lukin 2003). Reproductive output may therefore be determined by body reserves, similar to a typical 'capital breeder' *Vipera aspis* (Bonnet et al. 2002)

The temperate pit viper mating system, with temporally separated mating and fertilization events, evolved from the tropical pit viper reproductive pattern as a result of colder temperatures punctuating vitellogenesis (Aldridge and Duvall 2002). This temporal distinction may reflect the high cost of mating such as increased predation during the mating season (Aldridge and Duvall 2002). Interestingly, 100% of the predation events in 2012 and 2013 coincided with the mating season in our study. Mate-searching in males also appears to be costly to overall health, with low body condition and dehydration of males post-breeding season.

Our results highlight lability in reproductive traits of the same species across its geographic range. *Trimeresurus albolabris* in northern Vietnam appears to mate in spring (Orlov et al. 2002), despite being capable of long-term sperm storage (Kamelin and Lukin 2003). In contrast, *T. albolabris* in Hong Kong mates at the end of summer in the year preceding ovulation and fertilization. Other members of the *Trimeresurus* genus also display a variety of reproductive strategies. *Trimeresurus stejnegeri* in Taiwan display a postnuptial spermatogenesis and type II vitellogenesis, with vitellogenesis in females starting in the fall post-parturition, and copulation and the height of spermatogenesis occurring in the fall to winter (Tsai and Tu 2000,2001). *Trimeresurus flavoviridis* in the Ryukyu Islands of Japan copulate in spring, coinciding with vitellogenesis (Yokoyama and Yoshida 1994). Interestingly, the latitudes and climates of North Vietnam, Hong Kong, Taiwan and Ryukyu islands are not starkly different, and variation in reproductive strategies even within a species' geographic range is usually accompanied by distinctions in environmental factors (Aldridge and Duvall 2002; Sasa et al. 2009; Siqueira et al. 2013). *Trimeresurus albolabris* exhibits relatively high variability in reproductive traits within a small geographic zone with little climactic variation. The evolution of mating systems in the *Trimeresurus* genus, especially in relation to other crotalids and viperids is a topic that deserves further study.

Brumation.—Hibernation is an important life history event in ectotherms living in seasonal climates and can be critical for survival during the winter (Gregory 1982). The near-synchronized brumation of *T. albolabris* was observed in all female survivors within days of each other, suggesting an environmental cue such as temperature drops or reduced daylight hours.

Communal hibernation is common in many snake species (Hirth 1966; Rudolph et al. 2007; Gienger and Beck 2011), is characteristic of areas with more severe winters (Shine 1979), and may reflect scarcity of suitable refugia (Harvey and Weatherhead 2006). Conversely, solitary hibernation, such as seen in *Sistrurus catenatus catenatus* (Harvey and Weatherhead 2006), suggests refugia are not limiting. Based on our field research, we speculate that refugia are not limiting for *T. albolabris,* in which individuals brumate in multiple refugia over the season. The use of shallow refugia (0 to 0.5 m below surface) by *T. albolabris* also indicates overwintering areas are relatively warmer in Hong Kong compared with those available to temperate species (Shine 1979) and facilitates the basking behavior that we observed on warmer days.

Notably, neither male survivor occupied a brumation refugia in December. In Hong Kong, January is the coldest month of the year (Dudgeon and Corlett 1994), and mean minimum temperature is 16 ˚C (Hong Kong Observatory, Hong Kong). We speculate that males may brumate later in the winter when temperatures decline significantly, but our study did not extend beyond December in either year. These adult males could be exploiting food resources while conspecifics and ectothermic predators are hibernating, as the highly taxing large movements during the breeding season rendered both adult males dehydrated with poor body condition. We also cannot overlook the possibility that male mate-searching in this species carries on through December, as adult females still bask on sunny days and true dormancy over the winter probably does not occur. Our ability to make inferences about males' activities during the cold, dry season is limited by the low number that survived to this season.

Further research should be conducted to understand brumation site selection and use by *T. albolabris*. Questions of site fidelity, overwintering survival rates, and activity patterns, end dates of brumation, environmental brumation cues, and seasonal changes in body condition should be explored.

Parasites and diet.—The fecal parasite ova that we discovered in *T. albolabris* have been documented in the species previously. *Kalicephalus laticaudae*, *Capillaria* sp. and *Oxyurus* sp. was found in the feces of captive *T. albolabris* in Thailand (Chaiyabutr and Chanhome 2002). However, we were unable to identify the coccidian parasite present. We observed severe parasite-induced hepatitis in one individual infected with ascarid larvae; we suspect the individual probably would have succumbed to this infection eventually. Subcutaneous ascarid larvae also appear to be important parasites as they were found in fairly high numbers in several individuals.

Although diet was not a primary focus of this study, we found that *T. albolabris* prey on geckos, mice/rats and shrews. Brief notes in the literature suggest frogs (such as *Polypedates* spp.) form the bulk of the diet of *T. albolabris* (Orlov et al. 2002; Kamelin and Lukin 2003). However, small mammals may be important sources of prey especially for larger vipers, and high abundance of geckos encountered during visual encounter surveys suggests that geckos may be a food source. Asiatic toads *Duttaphrynus melanostictus* were common in the study area, but their skin is toxic and they are unlikely to be eaten by *T. albolabris*. Gunther's frogs (*Hylarana guentheri*) were more common in the sites we surveyed than brown tree frogs (*Polypedates megacephalus)*, and geckos, particularly *Gekko chinensis* and *Hemidactylus bowringii,* were more common than any frog species encountered. We made a few observations on the diet of the species, but the diet of *T. albolabris* and shifts in diet related to habitat or season remain largely unknown.

Notes on defensive behavior.—We observed striking and tail vibrating exhibited as defensive behaviors in *T. albolabris*. Tail vibrations, as a form of warning, have been widely reported in many snakes (Carpenter and Ferguson 1977; Greene 1988), but the significance of this behavior is poorly understood (Young 2003). We observed that *T. albolabris* striking may be correlated with tail vibrations, and this is consistent with observations of Chinese pit vipers (*Gloydius shedaoensis*) striking more frequently in individuals that tail-vibrated (Shine et al. 2002). However, these behaviors are not correlated in other vipers such as the North American species *Agkistrodon piscivorus* (Glaudas and Winne 2007), and the relationship between *T. albolabris* tail vibrations and striking should be examined further. Our observations on propensity for striking in larger individuals are anecdotal and contradict reports of juvenile pit vipers being more likely to strike and display anti-predator behavior (Sweet 1985; Greene 1988). Additionally, decline through ontogeny in anti-predator behavior is postulated in *Gloydius shedaoensis* (Shine et al. 2002). Questions addressing strike willingness in relation to body size and ontogenetic shifts in defensive behavior should be explored.

In this study, we have constructed the reproductive cycle of *T. albolabris* in south China, and demonstrated sexual differences in behavior and ontogeny, and substantial sexual dimorphism, even at the neonate stage. Knowledge of the natural history, reproductive ecology and demography of *T. albolabris* contributes to baseline ecological data of this poorly-studied species, and may be useful for conservation and management of this medically significant venomous snake. Geographic variation in response to environmental factors may have important implications understanding the evolution of this cryptic genus, as well as predictions of this species' response to changes in climate.

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LITERATURE CITED

Aldridge, R.D., and D. Duvall. 2002. Evolution of the mating season in the pitvipers of North America Herpetological Monographs 16:1–25.

Almeida-Santos, S.M., and D.A. Salomao. 2002. Reproduction in neotropical pitvipers, with emphasis on species of the genus *Bothrops*. Pp. 445–462 *In* Biology of the Vipers. Schuett, G.W., M. Hoggren, M.E. Douglas, and H.W. Greene (Eds.). Eagle Mountain Publishing, Eagle Mountain, Utah, USA.

Blessmann, J., C. Khonesavanh, P. Outhaithit, S. Manichanh, K. Somphanthabansouk, and P. Siboualipha. 2010. Venomous snake bites in Lao PDR: a retropsective study of 21 snakebite victims in a provincial hospital. Southeast Asian Journal of Tropical Medicine and Public Health 41:195–202.

Böhm, M. and B. Collen and J.E.M. Baillie and P. Bowles and J. Chanson and N. Cox and G. Hammerson and M. Hoffmann and S.R. Livingstone and M. Ram, et al. 2013. The conservation status of the world's reptiles. Biological Conservation 157:372–385.

Bonnet, X., O. Lourdais, R. Shine, and G. Naulleau. 2002. Reproduction in a typical capital breeder: costs, currencies, and complications in the Aspic Viper. Ecology 83:2124–2135.

Bull, J.J., and R. Shine. 1979. Iteroparous animals that skip opportunities for reproduction. American Naturalist 114:296–303.

Carpenter, C., and G. Ferguson. 1977. Variation and evolution of stereotyped behavior in reptiles. Pp. 335-554 *In* Biology of the Reptilia 7. Gans, C. and D.W. Tinkle (Eds.). Academic Press, New York, New York, USA.

Chaiyabutr, N., and L. Chanhome. 2002. Parasites in snakes of Thailand. Bulletin of the Maryland Herpetological Society 38:12.

Chanhome, L., O. Khow, T. Omori-Satoh, and V. Sitprija. 2002. Capacity of Thai Green Pit Viper antivenom to neutralize the venoms of Thai *Trimeresurus* snakes and comparison of biological activities of these venoms. Journal of natural toxins 11:251–259.

Chotenimitkhun, R., and P. Rojnuckarin. 2008. Systemic antivenom and skin necrosis after Green Pit Viper bites. Clinical Toxicology 46:122–125.

Cockram, C.S., J.C.N. Chan, and K.Y. Chow. 1990. Bites by the White-Lipped Pit Viper (*Trimeresurus albolabris*) and other species in Hong Kong - a survey of 4 years experience at the Prince of Wales Hospital. Journal of Tropical Medicine and Hygiene 93:79–86.

Das, I., and P.P. van Dijk. 2013. Species richness and endemicity of the herpetofauna of South and Southeast Asia. Raffles Bulletin of Zoology 29:269–277.

David, P., G. Vogel, and A. Dubois. 2011. On the need to follow rigorously the Rules of the Code for the subsequent designation of a nucleospecies (type species) for a nominal genus which lacked one: the case of the nominal genus *Trimeresurus* Lacepede, 1804 (Reptilia: Squamata: Viperidae). Zootaxa:1–51.

Du, X.Y., E. Magnenat, T.N.C. Wells, and K.J. Clemetson. 2002. Alboluxin, a snake C-type lectin from *Trimeresurus albolabris* venom is a potent platelet agonist acting via GPIb and GPVI. Thrombosis and Haemostasis 87:692–698.

Dudgeon, D., and R. Corlett. 1994. Hills and streams : an ecology of Hong Kong. Hong Kong University Press, Hong Kong.

Ganesh, S.R., S.R. Chadramouli, R. Sreekar, and P.G. Shankar. 2013. Reptiles of the central Western Ghats, India- a reappraisal and revised checklist, with emphasis on the Agumbe Plateau Russian Journal of Herpetology 20:181–189.

Giannasi, N., R.S. Thorpe, and A. Malhotra. 2001. The use of amplified fragment length polymorphism in determining species trees at fine taxonomic levels: analysis of a medically important snake, *Trimeresurus albolabris*. Molecular Ecology 10:419–426.

Gienger, C.M., and D.D. Beck. 2011. Northern Pacific Rattlesnakes (*Crotalus oreganus*) use thermal and structural cues to choose overwintering hibernacula. Canadian Journal of Zoology-Revue Canadienne De Zoologie 89:1084–1090.

Glaudas, X., and C.T. Winne. 2007. Do warning displays predict striking behavior in a viperid snake, the cottonmouth (*Agkistrodon piscivorus*)? Canadian Journal of Zoology-Revue Canadienne De Zoologie 85:574–578.

Greene, H.W. 1988. Antipredator mechanisms in reptiles. Pp. 1–152 *In* Biology of the Reptilia 16. Gans, C. and R.B. Huey (Eds.). Academic Press, New York, New York, USA.

Gregory, P.T. 1982. Reptilian hibernation. Pp. 53–154 *In* Biology of the Reptilia 13. Gans, C. and F.H. Pough (Eds.). Academic Press, New York, New York, USA.

Harvey, D.S., and P.J. Weatherhead. 2006. Hibernation site selection by Eastern Massasauga Rattlesnakes (*Sistrurus catenatus catenatus*) near their nothern range limit. Journal of Herpetology 40:66–73.

He, Q.Y., M. Deng, X.D. Yu, H. Li, Y.X. Lin, and X. Chen. 2008. Changes in hippocampal histamine receptors in rats after treatment with *Trimeresurus albolabris* venom. Neural Regeneration Research 3:728–732.

Hirth, H.F. 1966. Weight changes and mortality of three species of snakes during hibernation. Herpetologica 22:8–12.

Hon, K.L., L.W. Kwok, and T.F. Leung. 2004. Snakebites in children in the densely populated city of Hong Kong: a 10-year survey. Acta Paediatrica 93:270–272.

Hutton, R.A., S. Looareesuwan, M. Ho, K. Silamut, P. Chanthavanich, J. Karbwang, W. Supanaranond, S. Vejcho, C. Viravan, R.E. Phillips, et al. 1990. Arboreal green pit vipers (genus *Trimeresurus*) of South-east Asia: bites by *T. albolabris* and *T. macrops* in Thailand and a review of the literature. Transactions of the Royal Society of Tropical Medicine and Hygiene 84:866–874.

Kamelin, E.R., and Y.A. Lukin. 2003. Sperm storage in two species of snakes: Asian pit vipers *Trimeresurus albolabris* (Gray, 1842) and *Trimeresurus erythrurus* (Cantor, 1839), bred at the Leningrad Zoo terrarium. Pp 158–160. *In* Herpetologica Petropolitana. Proc. of the 12th Ord. Gen. Meeting Soc. Eur. Herpetol. Russian Journal of Herpetology, Saint Petersburg, Russia.

Karsen, S.J., M.W. Lau, and A. Bogadek. 1998. Hong Kong Amphibians and Reptiles. 2nd edition. Provisional Urban Council, Hong Kong.

Klauber, L.M. 1943. Tail-length difference in snakes with notes on sexual dimorphism and the coefficient of divergence. Bull. Zool. Soc. San Diego 18:5-60.

Malhotra, A., and R.S. Thorpe. 1997. New perspectives on the evolution of South-East Asian pit-vipers (genus *Trimeresurus*) from molecular studies. . Pp. 115–128 *In* Venomous Snakes: Ecology, Evolution and Snakebite 70. Thorpe, R.S., W. Wuster, and A. Malhotra (Eds.). Symp. Zool. Soc. Lond. .

Malhotra, A., and R.S. Thorpe. 2000. A phylogeny of the *Trimeresurus* group of pit vipers: New evidence from a mitochondrial gene tree. Molecular Phylogenetics and Evolution 16:199–211.

McDiarmid, R.W., J.A. Campbell, and T.A. Tuoure. 1999. Snake species of the world: a taxonomic and geographic reference. The Herpetologist's League, Washington DC

Neill, W.T. 1964. Viviparity in snakes: some ecological and zoogeographical considerations. The American Naturalist 98:35–55.

Orlov, H., N. Anajeva, and R. Khalikov. 2002. Natural history of pitvipers in Eastern and Southeastern Asia. Pp. 345–361 *In* Biology of the Vipers Schuett, G., M. Hoggren, M. Douglas, and H. Greene (Eds.). Eagle Mountain Pub., Eagle Mountain, Utah.

Parker, W.S., and M.V. Plummer. 1987. Population ecology. Pp. 253–301 *In* Snakes: ecology and evolutionary biology Seigel, R.A., J.T. Collins, and S.S. Novak (Eds.). The Blackburn Press Caldwell, New Jersey, USA.

Rojnuckarin, P., C. Muanpasitporn, L. Chanhome, J. Arpijuntarangkoon, and T. Intragumtornchai. 2006. Molecular cloning of novel serine proteases and phospholipases A(2) from Green Pit Viper (*Trimeresurus albolabris*) venom gland cDNA library. Toxicon 47:279–287.

Rudolph, D.C., R.R. Schaefer, S.J. Burgdorf, M. Duran, and R.N. Conner. 2007. Pine Snake (*Pituophis ruthveni* and *Pituophis melanoleucus lodingi*) hibernacula. Journal of Herpetology 41:560–565.

Sasa, M., D.K. Wasko, and W.W. Lamar. 2009. Natural history of the Terciopelo *Bothrops asper* (Serpentes: Viperidae) in Costa Rica. Toxicon 54:904–922.

Scartozzoni, R.R., M.G. Salomão, and S.M. Almeida-Santos. 2009. Natural history of the Vine Snake *Oxybelis fulgidus* (Serpentes, Colubridae) from Brazil. South American Journal of Herpetology 4:81–89.

Schuett, G. 1992. Is long-term sperm storage an important component of the reproductive biology of temperate pitvipers. Pp. 169–184 *In* Biology of the Pitvipers Campbell, J.A. and E.D. Brodie Jr (Eds.). Selva Press, Tyler, Texas.

Shek, K.C., K.L. Tsui, K.K. Lam, P. Crow, K.H. Ng, G. Ades, K.T. Yip, A. Grioni, K.S. Tan, D.C. Lung, et al. 2009. Oral bacterial flora of the Chinese Cobra (*Naja atra*) and Bamboo Pit Viper (*Trimeresurus albolabris*) in Hong Kong SAR, China. Hong Kong Med J 15:183–190.

Shine, R. 1979. Activity patterns in Australian elapid snakes (Squamata: Serpentes: Elapidae). Herpetologica 35:1-11.

Shine, R. 2003. Reproductive strategies in snakes. Proceedings of the Royal Society of London. Series B: Biological Sciences 270:995-1004.

Shine, R., and X. Bonnet. 2000. Snakes: a new 'model organism' in ecological research? Trends in Ecology & Evolution 15:221–222.

Shine, R., L.X. Sun, M. Fitzgerald, and M. Kearney. 2002. Antipredator responses of free-ranging pit vipers (*Gloydius shedaoensis*, Viperidae). Copeia 2002:843–850.

Siqueira, D.M., L.P. Nascimento, G.G. Montingelli, and M.C. dos Santos-Costa. 2013. Geographical variation in the reproduction and sexual dimorphism of the Boddaert's Tropical Racer, *Mastigodryas boddaerti* (Serpentes: Colubridae). Zoologia 30:475–481.

Soogarun, S., P. Sangvanich, M. Chowbumroongkait, S. Jiemsup, V. Wiwanikit, P. Pradniwat, A. Palasuwan, J. Pawinwongchai, S. Chanprasert, and T. Moungkote. 2008. Analysis of Green Pit Viper (*Trimeresurus alborabris*) venom protein by LC/MS-MS. Journal of Biochemical and Molecular Toxicology 22:225–229.

Steen, D.A. 2010. Snakes in the grass: Secretive natural histories defy both conventional and progressive statistics. Herpetological Conservation and Biology 5:183–188.

Sweet, S.S. 1985. Geographic variation, convergent crypsis and mimicry in Gopher Snakes (*Pituophis melanoleucus*) and Western Rattlesnakes (*Crotalus viridis*) Journal of Herpetology 19:55–67.

Tsai, T.S., and M.C. Tu. 2000. Reproductive cycle of male Chinese Green Tree Vipers, *Trimeresurus stejnegeri stejnegeri*, in northern Taiwan. Journal of Herpetology 34:424-430.

Tsai, T.S., and M.C. Tu. 2001. Reproductive cycle of female Chinese Green Tree Vipers, *Trimeresurus stejnegeri stejnegeri*, in northern Taiwan. Herpetologica 57:157–168.

Viravan, C., S. Looareesuwan, W. Kosakarn, V. Wuthiekanun, C.J. McCarthy, A.F. Stimson, D. Bunnag, T. Harinasuta, and D.A. Warrell. 1992. A national hospital-based survey of snakes responsible for bites in Thailand. Transactions of the Royal Society of Tropical Medicine and Hygiene 86:100–106.

Yokoyama, F., and H. Yoshida. 1994. The reproductive cycle of the female Habu, *Trimeresurus flavoviridis*. Journal of Herpetology 28:54–59.

Young, B.A. 2003. Snake bioacoustics: toward a richer understanding of the behavioral ecology of snakes. The Quarterly Review of Biology 78:303–325.

Table 1. Transect locations, distance, and search effort for surveys of *Trimeresurus albolabris* in Hong Kong.

District	**Location**	**Distance (km)**	**Search effort (# person hours)**
Lantau	Shek Pik	7.2	27.5
	Ngong Ping	4.4	18.5
	Mui Wo	2.4	7.0
Hong Kong Island	Pokfulam Reservoir	2.9	8.5
	Lady Clementi's Ride	3.4	21.0
New Territories	Shek Kong	4.3	4.0
	Ha Fa Shan	1.5	5.5
	Pakfalam	2.1	4.5
	Yan Yee Rd	3.2	76.0
	Pak Sha O	0.7	32.0
Total:		32.1	204.5

Table 2. *Trimeresurus albolabris* captured in Hong Kong in 2013.

Method	# Vipers	# Recaptures	# Used for telemetry in 2013
Timed VES (189 Person-Hours)	90	5	10
Incidental encounters	19	0	1
Total unique individuals	104	5	11
Measurement data obtained	86	—	—

Figure Legends

Figure 1. Location of transects surveyed for *Trimeresurus albolabris* in Hong Kong, China.

Figure 2. Frequency distribution of male and female snout-vent length for *Trimeresurus albolabris* in Hong Kong, China.

Figure 3. Sexual dimorphism in *Trimeresurus albolabris*. Males (left) have a lateral white stripe above the supralabial scales, a characteristic absent in females (right). Both individuals depicted are adults. Photos by A. Devan-Song.

Figure 4. Relationship between body condition and snout-vent length of male and female *Trimeresurus albolabris* in Hong Kong in 2013. Arrow indicates the snout-vent length of the smallest gravid female found (545 mm SVL)

Figure 5: Johnson-Neyman technique scatterplot of tail length against total length of *T. albolabris* in Hong Kong. Limits of nonsignificant regions are from y = -1.73 to y = 195.84. Two males with damaged tails were removed from this analysis.

Figure 6: Change in body condition over the active season for *T. albolabris* radio-tagged in 2012 and 2013in Hong Kong. Change in gravid females is measured from

parturition (August) until brumation, while all others are measured from capture date (Jun-July) until brumation.

Figure 7: Minimum clutch sizes of female *T. albolabris* in Hong Kong. Each data point represents lowest confirmed number of embryos within a gravid individual (n = 5).

Figure 8: Parturition date for 5 gravid *T. albolabris* in Hong Kong. Labels indicate SVL in mm and clutch size for each snake.

Figure 9: Change in follicle size over the active season for female *T. albolabris* in 2012 and 2013. Each bar represents one viper. Small adults stay in stage V vitellogenesis the whole season with primary follicles, while larger adults that were not gravid and gained mass over the active season had enlarged follicles characteristic of Stage II-II vitellogenesis. All but one of the gravid females returned to stage V vitellogenesis (with primary follicles) by the end of the year.

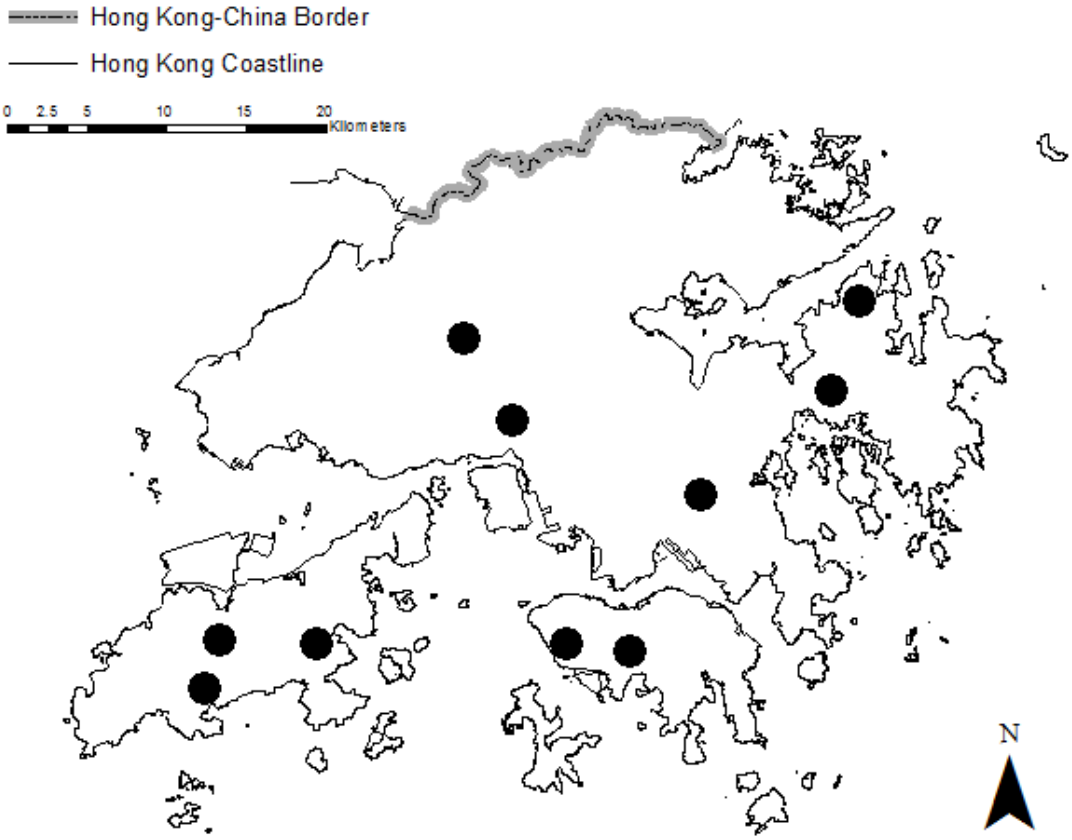
Figure 10: Brumation sites of the primarily arboreal *Trimeresurus albolabris*. A: under leaf litter and plant debris, B: inside man-made rock walls with white arrow pointing to body coil of snake, C: crevices under boulders, D: under a tree root and E: a snake basking on the ground outside entrance to its brumation site of small mammal burrow at the base of a plant.

Figure 11: First brumation event for surviving *T. albolabris* in Hong Kong.

Figure 12: Severe ascarid larve infection in *Trimeresurus albolabris*. A: Parasites within the coelomic cavity, B: loose subcutaneous parasites, C: severe hepatitis with lesions D: ascarid larvae within liver cyst.

Figure 13: Probable reproductive cycle of *T. albolabris* in Hong Kong.

Figures


Hong Kong-China Border
Hong Kong Coastline
0
2.5
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20
Kilometers
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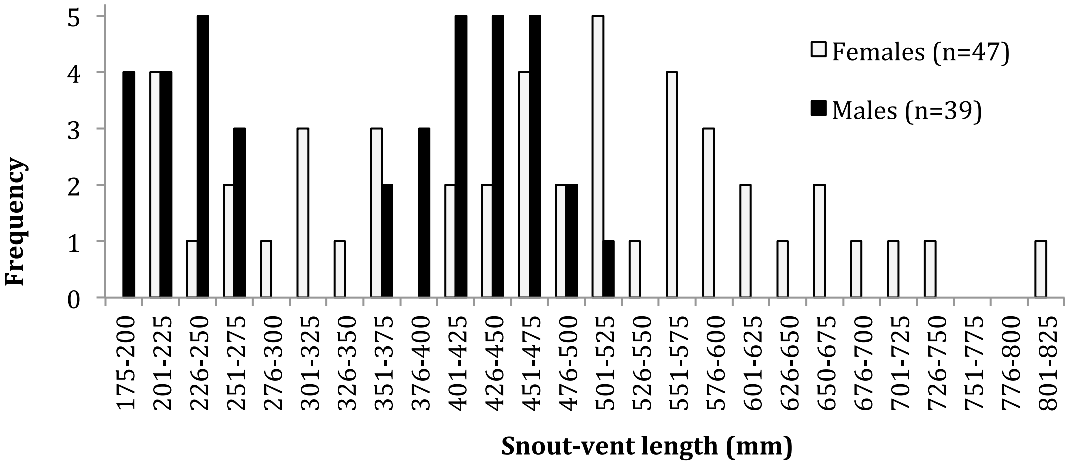
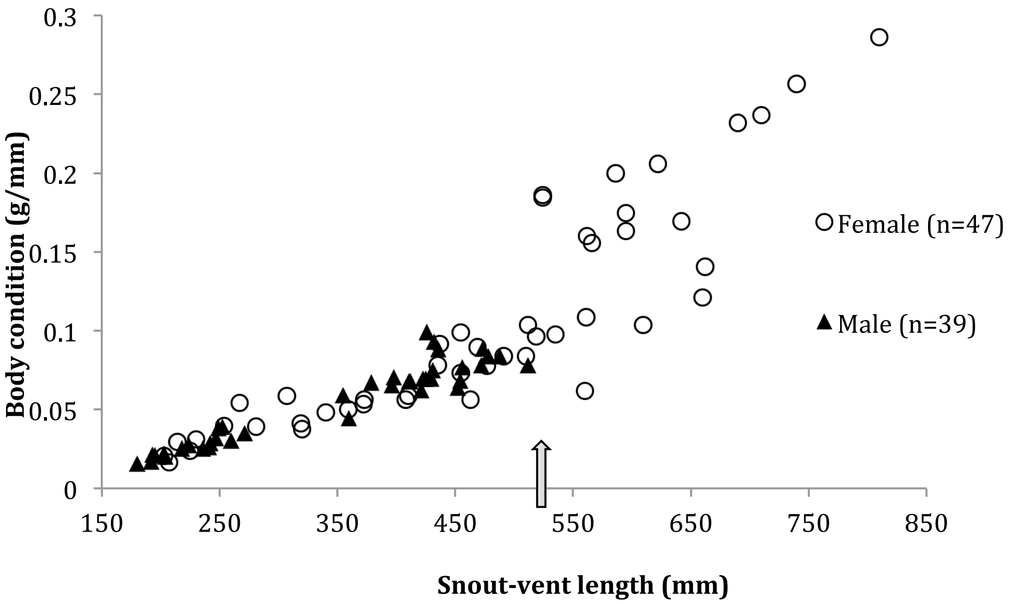
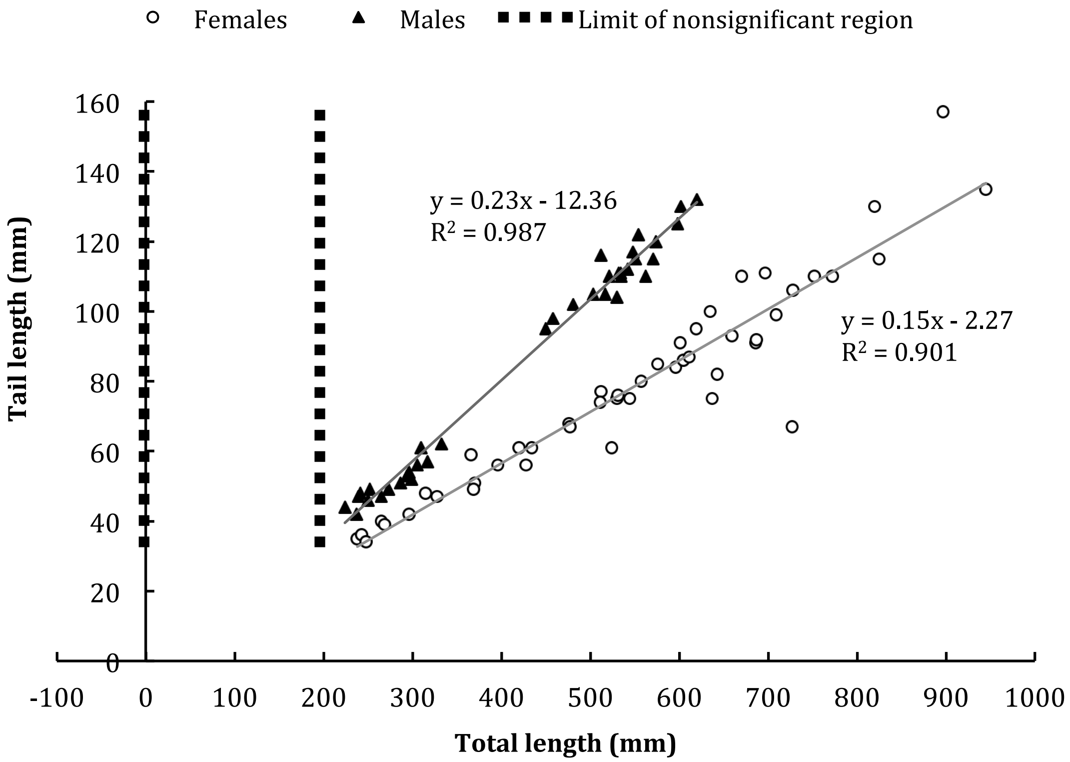
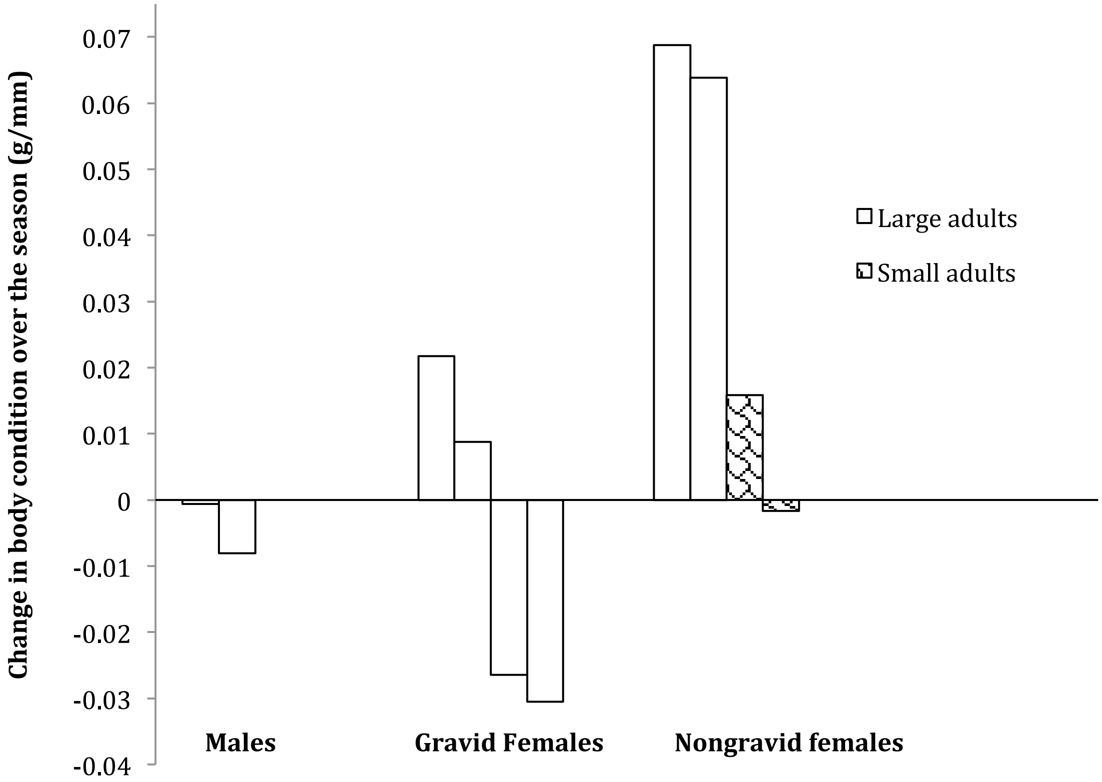
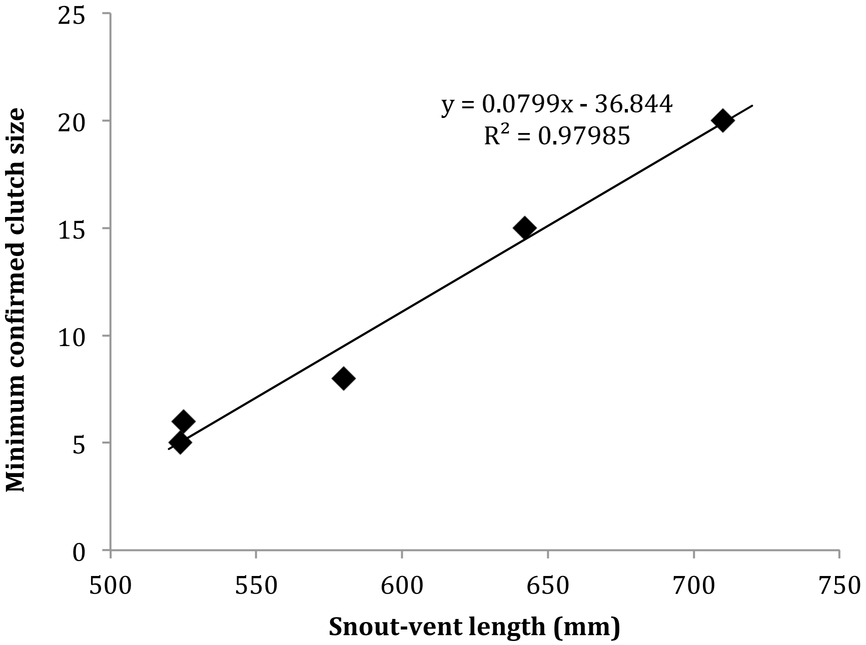

Frequency
0
1
2
3
4
5
Females (n=47)
Males (n=39)
175-200
201-225
226-250
251-275
276-300
301-325
326-350
351-375
376-400
401-425
426-450
451-475
476-500
501-525
526-550
551-575
576-600
601-625
626-650
650-675
676-700
701-725
726-750
751-775
776-800
801-825
Snout-vent length (mm)

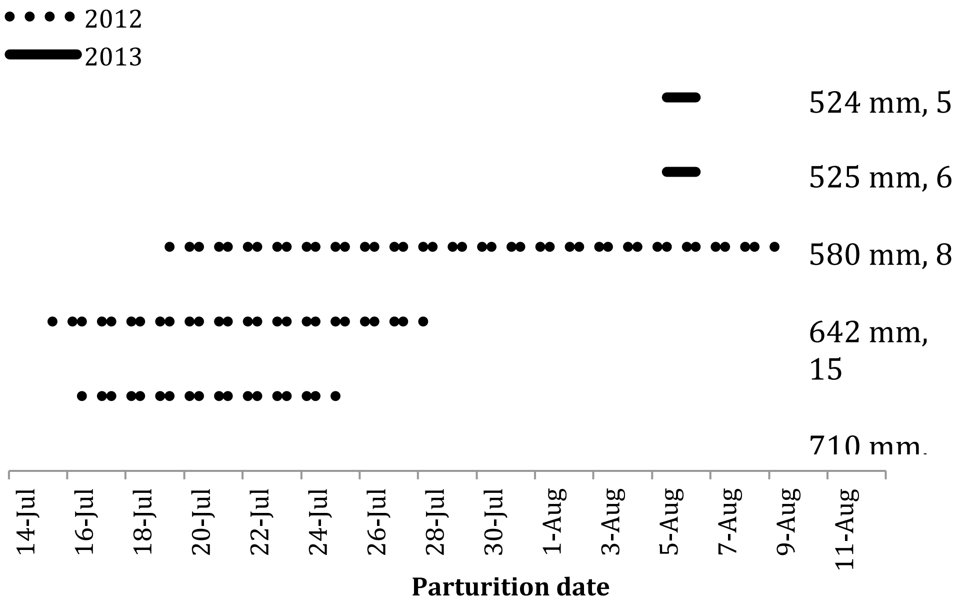

0.3
0.25
0.2
0.15
0.1
0.05
0
Body condition (g/mm)
150
250
350
450
550
650
750
850
Snout-vent length (mm)
○ Female (n=47)
▲ Male (n=39)

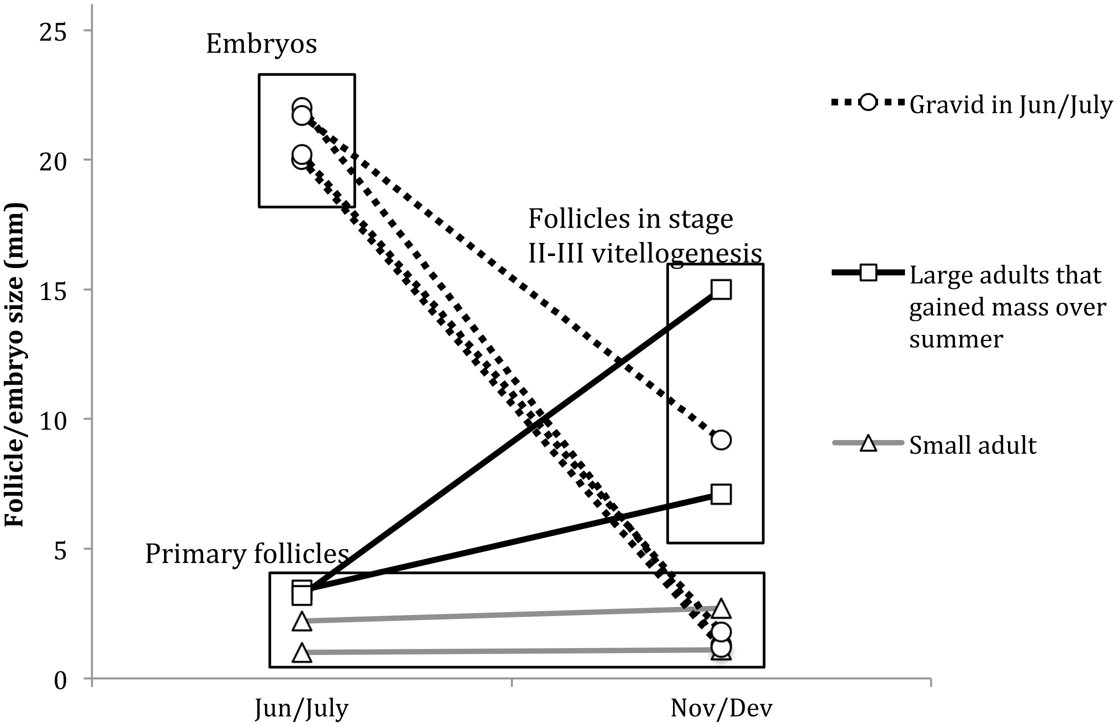

○ Females
▲ Males
■ ■ ■ ■ Limit of nonsignificant region
y = 0.23x - 12.36
R2 = 0.987
y = 0.15x - 2.27
R2 = 0.901
Tail length (mm)
160
140
120
100
80
60
40
20
0
-100
0
100
200
300
400
500
600
700
800
900
1000
Total length (mm)



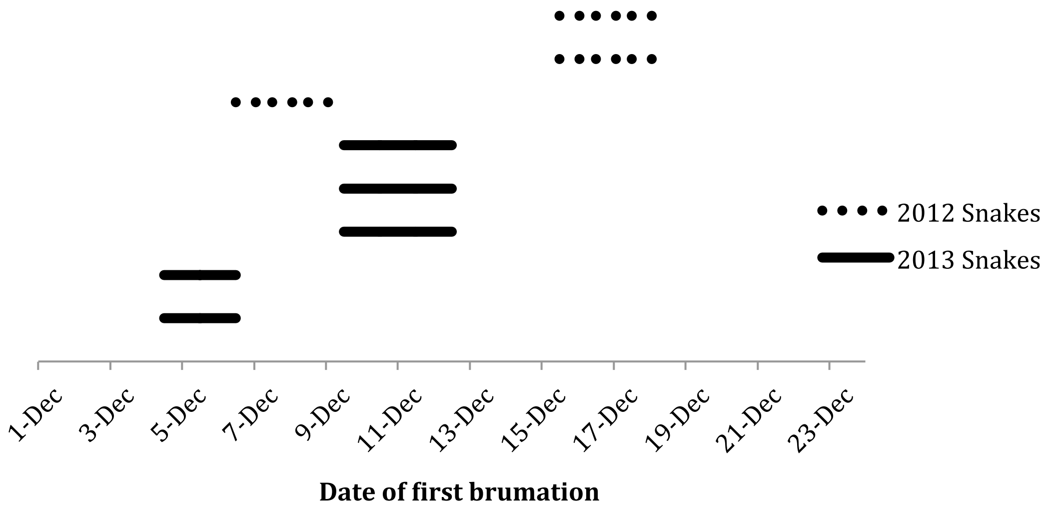
Change in body condition over the season (g/mm)
0.07
0.06
0.05
0.04
0.03
0.02
0.01
0
-0.01
-0.02
-0.03
-0.04
Males
Gravid Females
Nongravid females
Large adults
Small adults

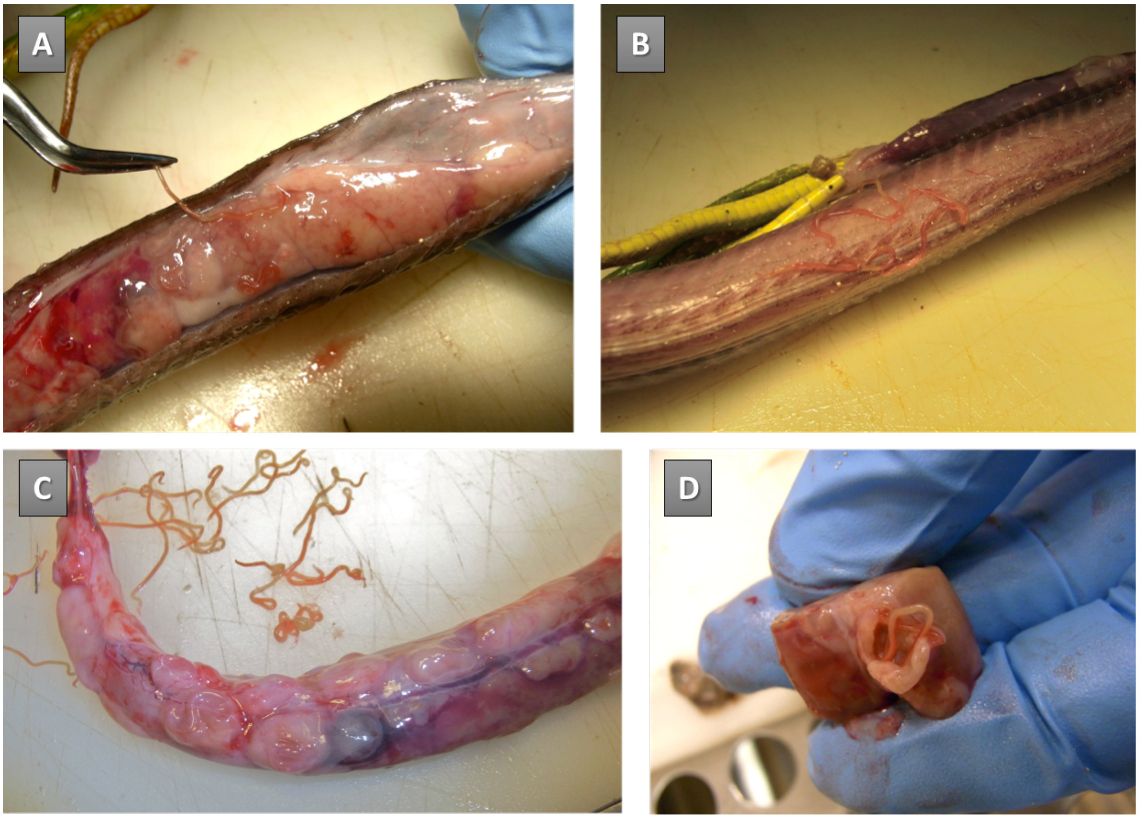

y = 0.0799x - 36.844
R² = 0.97985
Minimum confirmed clutch size
Snout-vent length (mm)
0
5
10
15
20
25
500
550
600
650
700
750

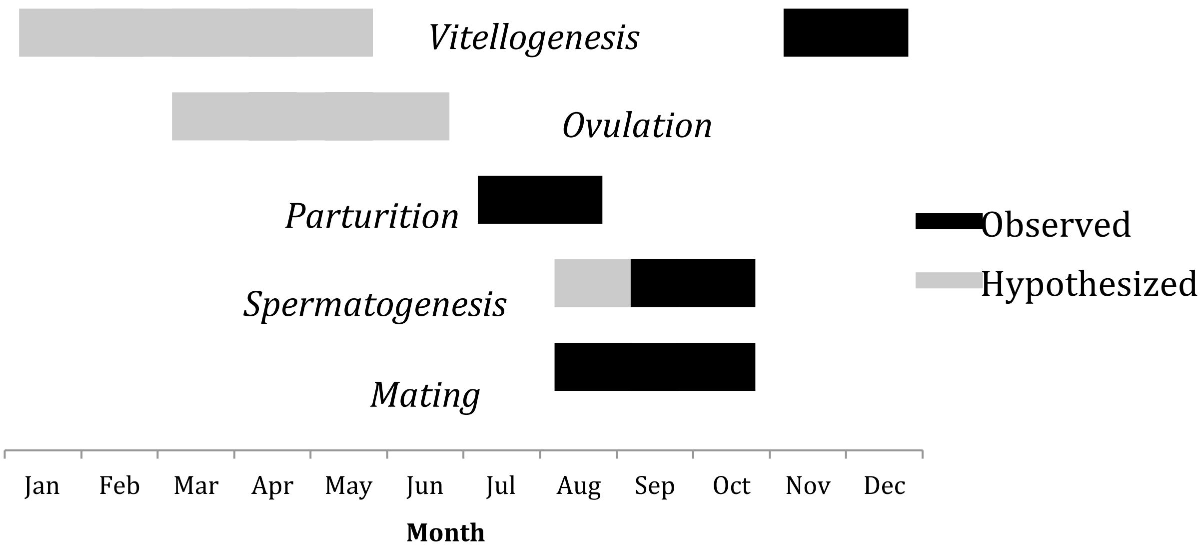

2012
2013
524 mm, 5
525 mm, 6
580 mm, 8
642 mm, 15
710 mm,
14-Jul
16-Jul
18-Jul
20-Jul
22-Jul
24-Jul
26-Jul
28-Jul
30-Jul
1-Aug
3-Aug
5-Aug
7-Aug
9-Aug
11-Aug
Parturition date


Follicle/embryo size (mm)
0
5
10
15
20
25
Jun/July
Nov/Dev
Embryos
Follicles in stage II-III vitellogenesis
Primary follicles
Gravid in Jun/July
Large adults that gained mass over summer
Small adult


A
B
C
D
E


2012 Snakes
2013 Snakes
1-Dec
3-Dec
5-Dec
7-Dec
9-Dec
11-Dec
13-Dec
15-Dec
17-Dec
19-Dec
21-Dec
23-Dec
Date of first brumation


A
B
C
D


Vitellogenesis
Ovulation
Parturition
Spermatogenesis
Mating
Observed
Hypothesized
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

CHAPTER 2

This chapter is in preparation for submission to Biological Conservation

Long-Distance Translocation is Not an Effective Conservation Option for Bamboo Pit Vipers (*Trimeresurus albolabris*) in South China

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ABSTRACT:

Translocation of 'nuisance' snakes is often employed on a large scale in densely populated areas in order to mitigate human-wildlife conflict. However, the methods used are often applied haphazardly and are rarely evaluated, especially in tropical Asia. The objective of this study was to assess the effects of long-distance translocation on the bamboo pit viper (*Trimeresurus albolabris*) in South China, where they are routinely removed from urban areas or homes and translocated into national parks. With the aid of radio telemetry, we compared the ecology and biology of 'resident' and 'translocated' snakes to determine if long-distance translocation is a viable conservation option. Translocation extended the period over which predation occurred and significantly decreased survival. Translocated snakes made unidirectional movements away from points of release, yet these movements were not oriented towards point of origin and there was no evidence for homing behavior. The effects of translocation also manifest very differently in males and females. Translocation significantly increased distances females moved from release sites and average daily movements, but no such differences were detected between resident and translocated males. However, translocated males exhibited a 100% mortality and

~71% of translocated females died. Overall, long-distance translocation increases mortality and has a negative effect on brumation, reproduction and movement of *T. albolabris*. Our results suggest that long-distance translocation is not a viable management or conservation option for this species. Findings of this study can be used to prescribe improvements for current strategies to deal with nuisance snakes in Hong Kong and around the region.

Keywords: Viperidae; Crotalinae: wildlife management; human-wildlife conflict; survival; movement patterns; reproduction; brumation; sexual dimorphism; Hong Kong.

1. Introduction

Human encroachment on natural habitats has led to a rise in human-wildlife interactions (Reinert and Rupert 1999), and these interactions are increasingly viewed as conflicting, especially in the urban environment (Craven et al. 1998) and at the interface of urban and rural areas. However, increases in human-wildlife conflict in recent decades has also come hand-in-hand with added pressure from the public to use alternative management methods rather than traditional lethal methods of shooting, culling, and poisoning (Massei et al. 2010), which are generally perceived to be inhumane. As a result, translocation of ‘nuisance’ wildlife – or the assisted movement of conflict animals from their origin to another – has become the preferred mitigation tool for many agencies (Brown et al. 2009; Butler et al. 2005b; Fischer and Lindenmayer 2000; Massei et al. 2010), and is generally focused on conservation of the species (Treves et al. 2009) rather than simply addressing management of an individual ‘nuisance’ animal. Translocation is a tool employed in many non-conflict situations including establishment or reintroduction of threatened or locally extirpated species (Griffiths and Pavajeau 2008; Moorhouse et al. 2009; Pedrono and Sarovy 2000; Tuberville et al. 2005), shielding threatened populations from direct anthropogenic impacts (Armstrong 2008), or introductions to increase genetic variation in existing populations (Madsen et al. 1999). Success therefore varies depending on source and number of translocated animals (Harvey et al. 2013; Roe et al. 2010), desired outcomes, and parameters examined (Harvey et al. 2013; Pinter-Wollman et al. 2009; Riedl et al. 2008). Translocation, when used to mitigate conflict that arises from the presence of ‘nuisance’ or unwanted animals, generally has lower success than other non-conflict motivated translocations (Germano and Bishop 2009).

The appeal of translocation as a human-wildlife mitigation tool arises from the widespread notion that it is a humane strategy (Craven et al. 1998; Dodd and Seigel 1991; Massei et al. 2010; Reinert 1991; Reinert and Rupert 1999) because translocation does not lead to the immediate death of the individual (Riedl et al. 2008), unlike euthanasia. The public perceives that the translocated animal will thrive in its new location (Mosillo et al. 1999), and that translocation programs are successful. ‘Success’ can be defined in various ways depending on the desired outcome and reasons for translocation (Fischer and Lindenmayer 2000), however in conflict-mitigating translocations, we define a program as ‘successful’ if no significant adverse effects on mortality, behavior and reproduction are detected in translocated individuals.

A closer inspection of the broad impacts of translocation on the subjects, however, reveals that this approach is often not always successful (Dodd and Seigel 1991; Germano and Bishop 2009; Massei et al. 2010; Plummer and Mills 2000). Despite this, translocation is often chosen over alternate methods, as management policies are often influenced by public pressure rather than being supported by scientific evidence or cost-benefit analysis (Sarrazin and Barbault 1996), even when alternatives may offer more effective long-term solutions (Craven et al. 1998). Many agencies involved in wildlife management are still plagued by a deficiency of supporting data in the published literature arising from poorly documented translocations and the reluctance to publish negative data (Dodd and Seigel 1991;

Fischer and Lindenmayer 2000; Germano and Bishop 2009). If progress is to be made towards more effective policies for addressing human-wildlife conflict, however, the impacts of translocation on wildlife require further investigation for informed management decisions to be made (Germano and Bishop 2009).

Reptiles represent a particularly threatened and data-deficient taxon (Böhm et al. 2013; Gibbons et al. 2000), and snakes are of particular interest in human-wildlife conflict mitigation. Human-wildlife interaction results in a greater likelihood of intentional mortality of snakes compared to other taxa, as they are viewed as potentially dangerous animals (Bonnet et al. 1999; Hardy et al. 2001; Nowak et al. 2002). Additionally, translocation of reptiles has a low success compared to other vertebrates (Dodd and Seigel 1991). Erratic movements in displaced snakes have been documented (Fitch and Hampton 1971; Landreth 1973), and controlled experiments on the effects of long-distance translocation on snakes to mitigate human-wildlife conflict have revealed adverse effects on individuals, with increased sizes of home ranges as snakes try to adjust to unknown habitats and increased mortality (Butler et al. 2005b; Nowak et al. 2002; Plummer and Mills 2000; Reinert and Rupert 1999). These findings are of concern for managing human-snake interactions, as long-distance translocation appears, on its surface, to be the better solution for achieving both human safety and protection of persecuted snakes. Lack of baseline biological and ecological data on snakes, compared to mammals and birds, also limits the inferences that can be made from studies of snake translocation and reduces the success of snake management programs (Plummer and Mills 2000).

Even with significant efforts to understand the effects of long-distance translocation on snakes, however, controlled experimental studies have been almost entirely restricted to snakes of North America and elapids in Australia (Butler et al. 2005a, b; Nowak et al. 2002; Plummer and Mills 2000; Reinert and Rupert 1999; Roe et al. 2010). Two studies have been published on Asian species- the effects of translocation on a single *Ophiophagus hannah* in India (Barve et al. 2013), and the spatial ecology of 11 translocated *Elaphe schrenkii* in South Korea (Lee and Park 2011). However, the effects of translocation on Asian snake taxa remain understudied, even though translocation is widely used in tropical Asia as a tool to alleviate human-wildlife conflict (Barve et al. 2013). Our limited understanding of the effects of translocation on these snakes is alarming considering the funds and labor required for snake management programs.

The overarching goal of this study was to determine if translocation is a viable management option for the bamboo pit viper (*Trimeresurus albolabris*), a common and widespread species that is translocated in large numbers in Hong Kong, China. Our objectives were to compare survival, movements, reproduction, and brumation between ‘resident’ and ‘translocated’ snakes. Besides being one of the most commonly translocated snakes in Hong Kong (Kadoorie Farm and Botanic Gardens, unpublished data), *T. albolabris*, a venomous species, is by far the most common cause of snakebite injury there (Hon et al. 2004) and an assessment of current and alternative management strategies is pertinent from both conservation and public health perspectives.

2. Methods

We conducted this experiment from May to December 2012 and June to December 2013 in the Hong Kong Special Administrative Region of China (2209’-2237’N, 11350’-11430’E). Hong Kong encompasses about 1,100 km^2, and is made up of over 250 islands and a section of mainland China. Although part of Hong Kong is high-density urban area, much of the land comprises rural and small villages and communities within or around 23 national parks and other reserves. This proximity of high human population densities and natural tropical forests creates the conditions that lead to human-wildlife conflict.

In Hong Kong, ‘nuisance’ snakes are generally those that find their way into or near houses or businesses and are captured by the Hong Kong Police. We obtained snakes from Kadoorie Farm and Botanic Garden that had been transported from districts all over Hong Kong. In a few cases, we received snakes directly from residents on private property. Resident snakes were captured during visual encounter surveys conducted along hiking trails in the Sai Kung and Ng Tung Chai districts of Hong Kong.

We transported snakes to the Veterinary Hospital of Ocean Park Corporation, and anesthetized them using vaporized Isoflurane, an inhalant anesthetic. Radio transmitters (Model SB-2 or BD-2, Holohil Systems Ltd., Carp, Ontario, Canada) weighing no more than 6% of the body mass of the snakes were surgically implanted into the coelomic cavity, posterior to the cloaca, and antennae were threaded subcutaneously, following the procedures described by Reinert (1992) and Hardy and Greene (1999). While the snakes were under anesthesia, we measured snout-vent length, tail length, and body mass. We measured the presence, number and measurements of ovarian follicles or embryos in female snakes using ultrasound (Hitachi-Aloka Medical Ltd. Prosound SSD 4000, Tokyo, Japan or Esaote Mylab™ 35, Indianapolis, Indiana, USA). We allowed the vipers two days for recovery, before releasing the resident snakes within five meters of capture site. Translocated snakes were released between 3 and 30 km from point of capture, and resident snakes were released within 5 m of capture site. Translocated snakes in 2012 were released in mixed shrubland/grassland/abandoned agricultural ponds habitat (hereafter referred to as shrubland), and those in 2013 were released in mixed broadleaf evergreen secondary forest/active or abandoned agricultural land (hereafter referred to as woodland). All residents were released in woodland in both years.

All vipers were relocated two to three times per week (with ‘relocation’ indicating every event a snake was located via radio tracking), except during periods of extreme weather, such as tropical cyclones, when vipers were relocated once a week. We recorded snake locations using a global positioning system. If the individual survived to the end of the transmitter battery life (14 to 20 weeks), the snake was recaptured and the transmitter was replaced using the procedures described above. All vipers that survived to the end of the year were recaptured, transmitters were removed under anesthesia, and snout-vent lengths, tail lengths and masses were obtained. We released these snakes at last point of capture after two days of recovery.

2.1 Data analysis

We used Kaplan-Meier survival estimates to obtain survival of resident and translocated snakes over the study period in both years, and we used a log-rank test to compare survival between translocated and resident snakes in 2013. We extrapolated survival over the study period to annual survival for both years for comparison with prior studies.

Three different metrics were used to quantify differences in movements between resident and translocated snakes: analysis of independence of linear parameters and orientation of trajectories, frequency of movements, and average daily movements. For the first analysis, trajectories were drawn for individual snakes using straight lines between consecutive GPS coordinates obtained during relocations. We used a test of independence (Wald and Wolfowitz 1944) to measure sequential autocorrelation linear parameters (change in X- and Y- coordinates; adehabitatLT 0.3.16 package for R; Calenge 2006). We used a goodness-of fit test to test for difference in proportion of snakes that made unidirectional movements between resident and translocated snakes. We also determined if homing patterns could be detected for translocated snakes using the following equation for orientation efficiency:

$$(D_i - D_f)/L,$$

where D_i = displacement distance, D_f = distance between last point of trajectory and original home, L = path length (Bodin et al. 2006; Pittman et al. 2014). Positive orientation efficiencies indicate homing behavior, and we used a one-tailed t-test to determine if the average orientation efficiency was positive and different than 0. For the second movement analysis, we calculated the frequency of movement for each snake by dividing the total number of times a snake moved > 5 m in between relocations by the total number of relocations for that individual. For females, we used a two-way analysis of variance to test for differences in movement frequencies, using experimental group (translocated/ resident) and year (2012/ 2013) as factors. We used a Student's t-test to test for differences between experimental and control frequencies of movement for males. For the last movement analysis, we calculated the average daily movements of each snake by dividing the total distance moved over the active season by the total number of days tracked over the active season. For females, we used a two-way analysis of variance to test for differences in average daily movements, using experimental group (translocated vs resident) and year (2012/ 2013) as factors. For males, we used a Student's t-test to test for differences between experimental and control average daily movements.

Data were log-transformed if they failed to meet assumptions of equal variance and normality of residuals for analysis of variance. All averages are reported with (SE). Spatial analyses for trajectories, average daily movements and statistical analyses were conducted in R 3.0.2 (R Development Core Team) and SAS 9.3. (SAS Institute, Cary, North Carolina, USA). ArcGIS 10.1 (ESRI, Redlands, California, USA) was used for visualization of spatial data.

Brumation and reproduction events were compared between surviving resident and translocated snakes. However no statistical analyses were conducted because of low survival and resulting low sample sizes.

3. Results

We radio-tracked 18 females (nine resident, nine translocated) in 2012 and 15 females (seven resident, eight translocated) and eight males (four resident, four translocated) in 2013. Different females were tracked between years (Table 1). Tracking took place over 31 weeks in 2012 (Figure 1) and over 26 weeks in 2013 (Figure 2). We obtained a total of 1245 relocations of 41 snakes over 2012 and 2013. No mortalities of study snakes were associated with capture, handling, sedation, surgery, transport or recovery.

3.1. Survival

Survival for 2012 resident snakes over 31 weeks (0.342) was similar to that of translocated snakes over 18 weeks (0.333). Extrapolation of survival of translocated snakes to 31 weeks (0.181) revealed lower survival than resident snakes over 31 weeks (Table 2). In 2013, resident snakes had a higher probability ($\chi^2 = 5.27$, d.f. = 1) of survival (0.71) over the 26-week study period than did translocated snakes (0.25).

We extrapolated survival over a year to obtain annual survivorship, and translocated snakes exhibited very low annual survival (0.042 in 2012 and 0.063 in 2013) compared with those of resident snakes (0.136 in 2012 and 0.499 in 2013).

3.2. Mortality

Predation was by far the most common cause of death among both resident and translocated snakes, however a higher percentage of translocated snakes were predated (Figure 3). Additionally, nearly 20% (4 of 21) of translocated snakes died under unusual circumstances with no clear explanation for their cause of death. Two translocated individuals were found as intact healthy carcasses, and necropsies by a veterinarian revealed no underlying infection, disease, predation, injury, or any other explanation for the cause of death. One individual was found desiccated but intact. One translocated snake was found being consumed alive by ants and another translocated snake was found intact but dead, with no signs of injury or illness except wasps eating the inside of its mouth. We could not determine the cause of death for any of these five translocated individuals.

We noticed temporal differences in dates of predation between resident and translocated snakes. All five predation events of resident snakes (three in 2012 and two in 2013) occurred in the first two weeks of October, but predation events occurred in translocated snakes over more than three months from 10 July to 19 November (Figure 4).

3.3. Movements

Trajectories of all individual snakes were projected in the same geographic scale for visual comparison. Resident females appeared to have more nucleated movement patterns with evidence of backtracking, but translocated females made larger, apparently unidirectional movements (Figure 5). Interestingly, we saw an opposite pattern in male snakes, wherein residents made large movements characteristic of mate-finding, and translocated snakes either did not attempt to find mates, or died before doing so (Figure 6). None of the 16 resident trajectories displayed non-independent sequential linear parameters, but six of the 17 trajectories for translocated snakes exhibited non-independent linear parameters, indicating uni-directionality patterns of movement in these snakes. One of these six non-independent trajectories belonged to a male, and the other five were female trajectories. Of these five females, two were translocated in woodland and three in shrubland. Translocated snakes were more likely to make unidirectional movements than resident snakes ($\chi^2 = 4.73$, df = 1, P = 0.030).

Translocated snakes had an average orientation efficiency of 0.010 ± 0.126, and we detected no clear homing patterns (t = 0.12, df = 18, P = 0.452). We found no evidence of homing in translocated snakes and their trajectories were not orientated towards points of origin. We documented no discernable relationship between positive orientation efficiencies and autocorrelated linear trajectories; of the six individuals that displayed non-independent linear parameters, four had positive orientation efficiencies.

We found that regardless of year tracked, translocated snakes moved more frequency than resident snakes (F = 8.440, df = 1, 24, P = 0.008, Figure 7), and females moved more frequently in 2012 than 2013 (F = 4.95, df = 1, 24, P = 0.036). There was no interaction between experimental group and year for the frequency of movement analysis for females (F = 0.19, df = 1, 23, P = 0.670). We found no differences between translocated and resident male frequency of relocations (F = 0.885, df = 1, 6, P = 0.383, Figure 8).

We found that regardless of year tracked, translocated females moved more per unit time than resident females (F = 17.32, df = 1, 23, P < 0.001, Figure 9), and there was no difference between years (F = 2.66, df = 1, 23, P = 0.117). We found no interaction between experimental group and year for the average daily movements for females (F = 3.10, df = 1, 22, P = 0.092). There were no differences found between translocated and resident male average daily movements (F = 0.29, df = 1, 6, P = 0.610, Figure 10).

3.4 Reproduction

We only compared reproduction between translocated and resident snakes in 2013, as their reproductive status during the gestation period (June– July) was known. Several snakes tracked in 2012 were captured after the gestation period, and their reproductive status during the gestation period were unknown.

Of the five surviving resident females in 2013, two were large females that gained substantial mass over the active season (101% and 57% increase in body condition, measured by mass/snout-vent length). Neither female was gravid in June or July 2013, and both were undergoing stage II-II vitellogenesis in December 2013, suggesting preparation for ovulation the following spring (Table 4). In contrast, two of the three surviving translocated females in 2013 were large females that increased substantially in body condition (72% and 52%) over the active season, were not gravid in June - July 2013, yet still displayed primary follicles in December 2013 (Table 4). These two translocated females were unlikely to be preparing to reproduce the following spring.

Translocated males did not appear to successfully make large mate-searching movements, and all of them died well before the end of the active season. Resident males, on the other hand, made large movements characteristic of mate-searching, some moving large distances (Figure 6). Two of the resident males survived the active season, although both exhibited decreased body condition (Table 4).

3.5. Brumation

Differences in brumation patterns between resident and translocated snakes were observed in 2012 and 2013. In 2012, all three surviving females found brumation refugia on the ground within days of each other, yet only one surviving translocated female of three displayed brumating behavior (Figure 11). The other two translocated females were still active in the vegetation above ground until the end of the 2012 study period. In 2013, all translocated and resident females moved to brumation refugia, however the timing of brumation for resident and translocated females differed. In 2013, the date of the first brumation event for translocated snakes ranged from mid-November until the end of December. In contrast, all resident snakes commenced brumation within a few days of each other in mid-December (Figure 12). None of the resident males brumated, however comparisons cannot be made as no translocated males survived to winter.

4. Discussion

There is a growing body of research detailing the negative impacts of long-distance translocation on snakes, and our results are congruent with previous studies in which survival or movements or both are negatively impacted by long-distance translocation (Barve et al. 2013; Butler et al. 2005a; Lee and Park 2011; Nowak et al. 2002; Plummer and Mills 2000; Reinert and Rupert 1999). Key results of other translocation studies suggest that *T. albolabris* should be a good candidate for translocation. Although no related information is available for snakes, at least in mammals and birds, threatened or sensitive species generally have lower translocation success than common and widespread species (Griffith et al. 1989). Second, sedentary snakes that operate as sit-and-wait predators are hypothesized to be less affected by translocation than active foragers or wide-ranging snakes if released in optimal habitat (Plummer and Mills 2000; Shine and Fitzgerald 1996). *Trimeresurus albolabris* is widespread and common in Hong Kong and is a sedentary, sit-and-wait predator (Karsen et al. 1998), and, thus, theoretically a good candidate for translocation. We suggest the relative severity of translocation effects on *T. albolabris* compared to that of other snake taxa results from either or both of the following reasons: low background survival in resident populations compared to other crotalid snakes, and considerable sexual size dimorphism in this species and a corresponding inverse relationship between body size and magnitude of movements between the sexes.

Differences in survival between resident and translocated snakes in 2013 are indisputable; translocation clearly impacted survival. In 2012, however, relationships are less clear, with a difference in survival observed only when survival of translocated snakes is extrapolated to match the tracking period of the 2012 resident snakes. Differences in survival in 2012 could not be statistically compared because of unequal tracking periods. However a 0.34 probability of survival for residents compared with an extrapolated 0.18 probability of survival in translocated snakes suggests that a difference may exist. Extrapolated over a year, survival in resident snakes is starkly different from that of translocated snakes, and this difference may be underestimated because of temporal differences in causes of death. 'Unexplained' causes of death attributed by 20% of translocated snakes represents a significant source of mortality that appears aseasonal and may persist throughout the year for the translocated snakes. Survival among resident and translocated snakes may not exhibit similar trajectories across the year for, with overall survival prospects for translocated snakes appearing bleaker than for resident snakes.

The eightfold decrease in annual survivorship in translocated snakes observed in 2013 is more severe than that of translocated *Crotalus* spp., which display a two to threefold decrease (Hare and McNally 1997; Nowak et al. 2002; Reinert and Rupert 1999) or in *Notechis scutatus* which had no discernable difference over six-month study period (Butler et al. 2005a). The only published study reporting decreases in survival of the magnitude we observed in 2013, was on the colubrid *Heterodon platirhinos* (Plummer and Mills 2000). This suggests that snake species exhibiting naturally-low survival probabilities may be more adversely impacted by translocation. Notably, the aquatic colubrid *Nerodia sipedon* has resident survival probabilities similar to those of *T. albolabris* and *H. platirhinos,* yet this species' survival is not as severely affected by translocation as the latter two (Roe et al. 2010). However, there is evidence that reptiles constrained by habitat preference (such as highly aquatic species) are less likely to stray from translocated release sites, and are therefore better candidates for translocation (Attum et al. 2013). The results of my study suggest that snakes with little habitat specificity and low background survival levels may respond poorly to translocation compared to other snake taxa, and translocation programs should take into account natural survival and natural history traits of species targeted for translocation.

Translocation results in a higher likelihood of unidirectional movements in *T. albolabris*. Interestingly, these unidirectional movements were not oriented to the snakes' points of origin, as we found no evidence for homing in translocated snakes. Non-native Burmese pythons (*Python molorus*) in Everglades National Park in the U.S. orient towards point of origin after being displaced, with an average orientation efficiency of 0.55 ± 0.18 (Pittman et al. 2014), and several long- and short- distance snake translocation studies report that individuals made straight-line or parallel movements, eventually returning home (Brown et al. 2009; Hare and McNally 1997; Nowak et al. 2002; Reinert and Rupert 1999). However, we found no relationship between directional movements of translocated snakes and place of origin. Unidirectional movements made by translocated vipers may instead be driven by fleeing from the point of release or exploration to find a new home range, without navigational cues influencing direction of travel. Alternatively, these translocated snakes may have been experiencing distorted navigational cognition, where an individual may have attempted to home, but lacked the spatial cognition to orientate itself accurately.

Translocation appeared to severely affect movements of female snakes, but not those of male snakes. Translocated females displayed different movement patterns than those of resident females for all movement metrics assessed, with a clear trend of unidirectional and large movements away from point of release and larger distances moved per unit time. Differences in sex ratios and unequal sampling periods resulting from the premature death of all translocated males, rendered combined sex models incapable of teasing out any relationships between season, experimental group, and sex. The aberrant and highly variable movements observed in translocated *T. albolabris* were consistent with movements following long-distance translocations in other snake taxa (Barve et al. 2013; Butler et al. 2005b; Lee and Park 2011; Plummer and Mills 2000; Reinert and Rupert 1999; Roe et al. 2010). Increases in the frequency of movements and distances moved by snakes are strongly correlated with increased risk of predation (Bonnet et al. 1999; Madsen and Shine 1993; Shine and Fitzgerald 1996), and results from the study on *T. albolabris* suggest a causal relationship between increased movements and increased predation. This relationship is also strongly implied in other long-distance translocation studies of crotalids (Nowak et al. 2002; Reinert and Rupert 1999).

While translocation has a negative impact on the movement and brumation patterns of females, the habitat in which snakes are translocated to appears to exacerbate negative effects on *T. albolabris*. In both shrubland and woodland, translocated snakes are more likely to make unidirectional movements away from point of release than resident snakes, and move larger distances per unit time. However in shrubland, two of the three surviving translocated snakes failed to brumate in December, while all surviving translocated snakes in woodland found refugia for the winter.

Translocation had multiple negative impacts on *Trimeresurus albolabris*, however, these negative effects manifested differently in males and females. Male movements appeared to be unaffected by translocation, but survival was not, as all four translocated males died in the middle of the 2013 study period. Survival was less impacted in translocated females, but translocated females displayed altered movement patterns. We hypothesize that natural movements of resident males put them at greater risk of mortality because of predators and other sources, as small-bodied males make very large mate-searching movements, compared to more sedentary, heavy-bodied female counterparts. Movement in snakes is energetically costly (Gregory et al. 1987), and this appears to be particularly true in male *T. albolabris*. A translocated male, however, will therefore have to cope with the increased energy demands associated with translocation. On the other hand, adult females have more substantial fat reserves than males and therefore may have higher capacity for coping with translocation-induced changes in movement than males. We documented an inverse relationship between sex-related body size and movements in *T. albolabris*: adult males are half to one-eighth the size of adult females yet make substantially larger movements than females. This relationship has not been documented in other snake species subjected to long-distance translocation, and may partly explain why *T. albolabris* was so strongly impacted by translocation.

As no translocated males survived the breeding season, we were unable to predict the reproductive and brumation fate of male snakes that survive translocation. Some translocated females survived to brumation, however fecundity was negatively affected. Female *T. albolabris* breed once every two or more years, except for very large females which may reproduce in consecutive years (A. Devan-Song, unpublished data). In 2013, large translocated females, despite not gestating and having gained substantial mass over that year, did not undergo vitellogenesis, when their resident equivalents were doing so. The earliest ovulation and gestation season that these translocated females would participate in is summer 2015, two years after the end of the project, as an individual preparing to ovulate in summer 2014 would have already commence vitellogenesis in winter 2013. The chances of translocated snakes surviving one, let alone two years, is very slim, and overall prospects for reproduction by translocated females are bleak.

As with reproduction, our comparison of brumation in translocated and resident snakes is only possible for female snakes as no males survived. Brumation is an important life history event that snakes employ to survive the harsher conditions of winter in seasonal climates (Gregory 1982). For example, in a study examining repatriated and translocated massasauga snakes (*Sistrurus catenatus*), 100% of snakes that did not hibernate died over winter (Harvey et al. 2013), and dormancy appears to be critical for thermoregulation and survival especially in colder climates. In our study, brumation in female translocated snakes was unsynchronized, and two translocated snakes did not appear to brumate. It is possible that the two active translocated survivors in 2012 eventually found brumation sites in January after we removed transmitters from these snakes, however, they still would have missed the environmental cues that appeared to be synchronized among resident snakes in both years. Unsynchronized brumation patterns documented in translocated snakes in both years suggest reduced ability to respond to environmental cues, and provides insight as to how translocation may affect cognition in snakes. Translocation has been shown to increase the medial cortex volume in rattlesnakes in response to increased navigational demands (Holding et al. 2012), and other cognitive processes may be affected by neurological changes. *Trimeresurus albolabris* is also a solitary species with no communal hibernation or apparent cues from conspecific as to locations of refugia, unlike several *Crotalus* species in translocation experiments, which trailed conspecifics to locate hibernacula in their new sites (Nowak et al. 2002; Reinert and Rupert 1999). Reduced brumation initiation as well as unsynchronized brumation in translocated snakes may reflect this solitary brumation aspect of *T. albolabris*, where translocated snakes are unable to find hibernacula by trailing resident conspecifics. It should also be noted that translocated snakes that successfully initiate brumation are still not immune to overwintering mortality (Reinert and Rupert 1999), however we did not track beyond December to determine overwintering survival in our study.

Two factors need to be considered with regard to our results. We tracked each snake for a relatively short time. Reinert and Rupert (1999) and Nowak (2002) highlight the importance of evaluating long-term effects on translocated snakes, as atypical behavior may still be present in seasons following the first winter. However, except in the case of very large female *T. albolabris*, this species is small and would require two to three transmitter replacements a year because of the relatively short battery life in smaller transmitters. Nevertheless, results from our first year were unambiguous and the negative impacts of translocation on *T. albolabris* were clear. The second limiting factor is the absence of data on change in body condition, which results from *Trimeresurus albolabris* being a highly arboreal species with apparent preference for very dense vegetation (A. Devan-Song, unpublished data). It would have been impossible to capture and measure snakes at comparable intervals without significant destruction of surrounding vegetation and/or severe disturbance to snakes, which may have caused artificial movements. However, translocation is not strongly correlated with change in body condition (Nowak et al. 2002; Reinert 1991), and growth rates for translocated snakes may not have revealed underlying stress or pathology in my study.

Despite some limitations, this study indicates that long-distance translocation has a negative impact on the survival, movements, reproduction and brumation of *T. albolabris*. Long-distance translocation lowers the probability of survival and increases the duration of predation period. Movement patterns of translocated snakes suggest impaired spatial cognition and increased energy expended on movements. Translocation reduces fecundity and renders *T. albolabris* less effective at finding brumation refugia and responding to environmental cues that trigger brumation. Finally, translocation to shrubland over woodland exacerbates the already negative effects on movements and brumation of *T. albolabris*.

5. Implications for Management

All results indicate that translocation is an ineffective tool for resolving human-wildlife conflict involving *T. albolabris*, especially if individuals are translocated to shrubland instead of woodland. Not only is there substantial evidence that long-distance translocation is not an effective measure for the welfare of these snakes, such approaches must also consider the potential for negative effects on recipient resident populations in translocation sites. Genetic outbreeding is one possible negative effect of sustained long-distance translocation (Weeks et al. 2011; Whiting 1997), as is the risk of introducing pathogens from translocated individuals to resident populations (Cunningham 1996; Dodd and Seigel 1991; Kock et al. 2010; Viggers et al. 1993). Overall, there is little indication of any benefits of long-distance translocation for *T. albolabris*, and alternative methods to deal with 'nuisance' snakes should be explored.

Alternatives to long-distance translocation include 'soft' releases where individuals are kept in an enclosure *in situ* to encourage side fidelity, and increase the probability of a successful translocation (Bradley et al. 2005; Tuberville et al. 2005). However, this is labor- and time-intensive. There is also mounting evidence for the effectiveness of short-distance translocation of snakes as an alternative, in which an individual is moved within or close to its original home range. Short-distance translocation has been studied in some species of rattlesnakes, with higher success than long-distance translocation on the survival of displaced snakes (Brown et al. 2009; Hare and McNally 1997; Sealy 1997). Short-distance translocation and frequent handling also do not appear to adversely affect stress response and behavior (Holding et al. 2014a) or thermoregulation (Holding et al. 2014b) in northern pacific rattlesnakes (*Crotalus oreganus oreganus*). Although the issue of translocated individuals returning to their site of capture may be a complication of short-distance translocation (Brown et al. 2009), it can be argued that long-distance translocation does not alleviate human-snake conflict, and systematic removal of snakes from private property over the years has not substantially lowered the numbers of nuisance snake encounters (KFBG, unpublished data). A logical approach would therefore be to design conflict-mitigating programs that are informed by knowledge on the life history traits and demographic characteristics of the targeted species.

Although this experiment focused on *T. albolabris*, the negative effects we observed may also extend to species with similar life history traits such as other small, sexually dimorphic pit vipers, including other members of the genus *Trimeresurus*, many of which are also widespread and common (Malhotra and Thorpe 1997; Orlov et al. 2002) and are likely to be conflict snakes within their ranges. Our results are also applicable to non-conflict situations such as reintroduction/repopulation and possibly repatriation, if the differences between sources of snakes are taken into account. Although non-conflict translocation is motivated by different reasons and results are often assessed at the population and not individual level, our results along with those of previous studies suggest lower survival and reduced fecundity for adult snakes, which can render conservation-motivated reintroduction a wasted effort if too few individuals survive. Translocation for both conflict mitigation and non-conflict purposes should also take into account the possibility of impaired spatial cognition and response to environmental cues in snakes (depending on distance displaced), over and above elevated mortality and pathological movements.

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References

Armstrong, A.J., 2008. Translocation of black-headed dwarf chameleons *Bradypodion melanocephalum* in Durban, KwaZulu-Natal, South Africa. African Journal of Herpetology 57, 29-41.

Attum, O., Cutshall, C.D., Eberly, K., Day, H., Tietjen, B., 2013. Is there really no place like home? Movement, site fidelity, and survival probability of translocated and resident turtles. Biodiversity and Conservation 22, 3185-3195.

Barve, S., Bhaisare, D., Giri, A., 2013. A preliminary study on translocation of “rescued” king cobras (*Ophiophagus hannah*).

Bodin, C., Benhamou, S., Poulle, M.-L., 2006. What do European badgers (*Meles meles*) know about the spatial organisation of neighbouring groups? Behavioural processes 72, 84-90.

Böhm, M., Collen, B., Baillie, J.E., Bowles, P., Chanson, J., Cox, N., Hammerson, G., Hoffmann, M., Livingstone, S.R., Ram, M., 2013. The conservation status of the world’s reptiles. Biological Conservation 157, 372-385.

Bonnet, X., Guy, N., Shine, R., 1999. The dangers of leaving home: dispersal and mortality in snakes. Biological Conservation 89, 39-50.

Bradley, E.H., Pletscher, D.H., Bangs, E.E., Kunkel, K.E., Smith, D.W., Mack, C.M., Meier, T.J., Fontaine, J.A., Niemeyer, C.C., Jimenez, M.D., 2005. Evaluating wolf translocation as a nonlethal method to reduce livestock conflicts in the northwestern United States. Conservation Biology 19, 1498-1508.

Brown, J.R., Bishop, C.A., Brooks, R.J., 2009. Effectiveness of short-distance translocation and its effects on western rattlesnakes. Journal of Wildlife Management 73, 419-425.

Butler, H., Malone, B., Clemann, N., 2005a. Activity patterns and habitat preferences of translocated and resident tiger snakes (*Notechis scutatus*) in a suburban landscape. Wildlife Research 32, 157-163.

Butler, H., Malone, B., Clemann, N., 2005b. The effects of translocation on the spatial ecology of tiger snakes (*Notechis scutatus*) in a suburban landscape. Wildlife Research 32, 165-171.

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.

Craven, S., Barnes, T., Kania, G., 1998. Toward a professional position on the translocation of problem wildlife. Wildlife Society Bulletin 26, 171-177.

Cunningham, A.A., 1996. Disease risks of wildlife translocations. Conservation Biology 10, 349-353.

Dodd, C.K., Seigel, R.A., 1991. Relocation, repatriation, and translocation of amphibians and reptiles - are they conservation strategies that work? Herpetologica 47, 336-350.

Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. Biological Conservation 96, 1-11.

Fitch, H.S., Hampton, W.S., 1971. A radiotelemetric study of spatial relationships in some common snakes. Copeia 1971, 118-128.

Germano, J.M., Bishop, P.J., 2009. Suitability of amphibians and reptiles for translocation. Conservation Biology 23, 7-15.

Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, deja vu amphibians. Bioscience 50, 653-666.

Gregory, P.T., 1982. Reptilian hibernation, In Biology of the Reptilia. eds C. Gans, F.H. Pough, pp. 53–154. Academic Press, New York, New York, USA.

Gregory, P.T., Macartney, J.M., Larsen, K.W., 1987. Spatial patterns and movements, In Snakes: ecology and evolutionary biology. eds R. Seigel, J. Collins, S. Novak, pp. 366-395.

Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool: status and strategy. Science(Washington) 245, 477-480.

Griffiths, R.A., Pavajeau, L., 2008. Captive breeding, reintroduction, and the conservation of amphibians. Conservation Biology 22, 852-861.

Hardy, D., Greene, H., Tomberlin, B., Webster, M., 2001. Relocation of nuisance rattlesnakes: problems using short-distance translocation in a small rural community. Sonoran Herpetologist 14, 1-3.

Hare, T., McNally, J., 1997. Evaluation of a rattlesnake relocation program in the Tucson, Arizona, area. Sonoran Herpetologist 10, 26-31.

Harvey, D.S., Lentini, A.M., Cedar, K., Weatherhead, P.J., 2013. Moving massasaugas: insights into rattlesnake relocation using *Sistrurus c. catenatus* Herpetological Conservation and Biology 9, 67-75.

Holding, M.L., Frazier, J.A., Dorr, S.W., Henningsen, S.N., Moore, I.T., Taylor, E.N., 2014a. Physiological and behavioral effects of repeated handling and short-distance trans locations on free-ranging Northern Pacific Rattlesnakes (*Crotalus oreganus oreganus*). Journal of Herpetology 48, 233-239.

Holding, M.L., Frazier, J.A., Taylor, E.N., Strand, C.R., 2012. Experimentally altered navigational demands induce changes in the cortical forebrain of free-ranging Northern Pacific Rattlesnakes (*Crotalus o. oreganus*). Brain Behavior and Evolution 79, 144-154.

Holding, M.L., Owen, D.A.S., Taylor, E.N., 2014b. Evaluating the thermal effects of translocation in a large-bodied pitviper. Journal of Experimental Zoology Part A: Ecological Genetics and Physiology 321, 442-449.

Hon, K.L., Kwok, L.W., Leung, T.F., 2004. Snakebites in children in the densely populated city of Hong Kong: a 10-year survey. Acta Paediatrica 93, 270–272.

Karsen, S.J., Lau, M.W., Bogadek, A., 1998. Hong Kong Amphibians and Reptiles, 2nd edn. Provisional Urban Council, Hong Kong.

Kock, R., Woodford, M., Rossiter, P., 2010. Disease risks associated with the translocation of wildlife. Revue scientifique et technique (International Office of Epizootics) 29, 329-350.

Landreth, H.F., 1973. Orientation and behavior of the rattlesnake, *Crotalus atrox*. Copeia, 26-31.

Lee, J.H., Park, D., 2011. Spatial ecology of translocated and resident Amur ratsnakes (*Elaphe schrenckii*) in two mountain valleys of South Korea. Asian Herpetological Research 2, 223-229.

Madsen, T., Shine, R., 1993. Costs of reproduction in a population of European adders. Oecologia 94, 488-495.

Madsen, T., Shine, R., Olsson, M., Wittzell, H., 1999. Conservation biology: restoration of an inbred adder population. Nature 402, 34-35.

Malhotra, A., Thorpe, R.S., 1997. New perspectives on the evolution of South-East Asian pit-vipers (genus *Trimeresurus*) from molecular studies. , In Venomous Snakes: Ecology, Evolution and Snakebite. eds R.S. Thorpe, W. Wuster, A. Malhotra, pp. 115–128. Symp. Zool. Soc. Lond. .

Massei, G., Quy, R.J., Gurney, J., Cowan, D.P., 2010. Can translocations be used to mitigate human-wildlife conflicts? Wildlife Research 37, 428-439.

Moorhouse, T., Gelling, M., Macdonald, D., 2009. Effects of habitat quality upon reintroduction success in water voles: evidence from a replicated experiment. Biological Conservation 142, 53-60.

Mosillo, M., Heske, E.J., Thompson, J.D., 1999. Survival and movements of translocated raccoons in northcentral Illinois. The Journal of Wildlife Management 63, 278-286.

Nowak, E.M., Hare, T., McNally, J., 2002. Management of 'nuisance'vipers: effects of translocation on western diamond-backed rattlesnakes (*Crotalus atrox*), In Biology of the Vipers. eds G. Schuett, M. Hoggren, M. Douglas, H. Greene, pp. 533-560. Eagle Mountain Pub., Eagle Mountain, Utah.

Orlov, H., Anajeva, N., Khalikov, R., 2002. Natural history of pitvipers in Eastern and Southeastern Asia, In Biology of the Vipers. eds G. Schuett, M. Hoggren, M. Douglas, H. Greene, pp. 345–361. Eagle Mountain Pub., Eagle Mountain, Utah.

Pedrono, M., Sarovy, A., 2000. Trial release of the world's rarest tortoise *Geochelone yniphora* in Madagascar. Biological Conservation 95, 333-342.

Pinter-Wollman, N., Isbell, L.A., Hart, L.A., 2009. Assessing translocation outcome: comparing behavioral and physiological aspects of translocated and resident African elephants (*Loxodonta africana*). Biological Conservation 142, 1116-1124.

Pittman, S.E., Hart, K.M., Cherkiss, M.S., Snow, R.W., Fujisaki, I., Smith, B.J., Mazzotti, F.J., Dorcas, M.E., 2014. Homing of invasive Burmese pythons in South Florida: evidence for map and compass senses in snakes. Biology Letters 10.

Plummer, M.V., Mills, N.E., 2000. Spatial ecology and survivorship of resident and translocated hognose snakes (*Heterodon platirhinos*). Journal of Herpetology 34, 565-575.

Reinert, H.K., 1991. Translocation as a conservation strategy for amphibians and reptiles - some comments, concerns, and observations. Herpetologica 47, 357-363.

Reinert, H.K., Rupert, R.R., 1999. Impacts of translocation on behavior and survival of timber rattlesnakes, *Crotalus horridus*. Journal of Herpetology 33, 45-61.

Riedl, S.C., Mushinsky, H.R., Mccoy, E.D., 2008. Translocation of the gopher tortoise: difficulties associated with assessing success. Applied Herpetology 5, 145-160.

Roe, J.H., Frank, M.R., Gibson, S.E., Attum, O., Kingsbury, B.A., 2010. No place like home: an experimental comparison of reintroduction strategies using snakes. Journal of Applied Ecology 47, 1253-1261.

Sarrazin, F., Barbault, R., 1996. Reintroduction: challenges and lessons for basic ecology. Trends in Ecology & Evolution 11, 474-478.

Sealy, J., 1997. Short-distance translocations of timber rattlesnakes in a North Carolina state park. a successful conservation and management program. Sonoran Herpetologist 10, 94-99.

Shine, R., Fitzgerald, M., 1996. Large snakes in a mosaic rural landscape: The ecology of carpet pythons *Morelia spilota* (serpentes: Pythonidae) in coastal eastern Australia. Biological Conservation 76, 113-122.

Treves, A., Wallace, R.B., White, S., 2009. Participatory planning of interventions to mitigate human-wildlife conflicts. Conservation Biology 23, 1577-1587.

Tuberville, T.D., Clark, E.E., Buhlmann, K.A., Gibbons, J.W., 2005. Translocation as a conservation tool: site fidelity and movement of repatriated gopher tortoises (*Gopherus polyphemus*). Animal Conservation 8, 349-358.

Viggers, K.L., Lindenmayer, D.B., Spratt, D.M., 1993. The Importance of disease in reintroduction programmes. Wildlife Research 20, 687-698.

Wald, A., Wolfowitz, J., 1944. Statistical tests based on permutations of the observations. The Annals of Mathematical Statistics 15, 358-372.

Weeks, A.R., Sgro, C.M., Young, A.G., Frankham, R., Mitchell, N.J., Miller, K.A., Byrne, M., Coates, D.J., Eldridge, M.D., Sunnucks, P., 2011. Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4, 709-725.

Whiting, M.J., 1997. Translocation of non-threatened species for 'humanitarian' reasons: what are the conservation risks? . South African journal of science 93, 217-218.

Tables

Table 1: Sex and sample sizes of translocated and resident *Trimeresurus albolabris* in Hong Kong. All snakes, except for females translocated in 2012, were released in mixed cultivated/woodland habitat.

	May-December 2012	June-December 2013
Resident	9 Female	7 Female 4 Male
Translocated	9 Female	8 Female 4 Male
Total	18	23

Table 2: Kaplan-Meier estimates of *T. albolabris* survival in 2012.

2012	Resident n=9	Translocated n=8
Survival over study period	(31 Weeks) 0.342	(19 Weeks) 0.333
Extrapolated survival over equal study period (30 weeks)	0.342	0.181
Extrapolated annual survival	**0.137**	**0.042**

Table 3: Kaplan-Meier estimates of *T. albolabris* survival in 2013.

2013	Resident n=11	Translocated n=12
Survival over study period	(26 Weeks) 0.707	(26 Weeks) 0.25
Extrapolated annual survival	**0.499**	**0.063**

Table 4: Mass gain and reproductive activity in surviving *T. albolabris* in 2013. Resident female 4 and 5 have follicle sizes corresponding to Stage II-II vitellogenesis, while all other snakes only have primary follicles (Stage V). Loss in mass of Female 2 does not take into account mass lost from parturition.

	Survivor	Description	% change in body condition over 2013	Follicles in December	Largest size (mm)
RES	Male 1	Adult	-1	NA	NA
	Male 2	Adult	-9	NA	NA
	Female 1	Juvenile	20	Small	1.3
	Female 2	Gravid in 2013	-22	Small	1.5
	Female 3	Small adult	-2	Small	3.0
	Female 4	Very large female	66	Enlarged	7.8
	Female 5	Very large female	36	Enlarged	15.0
TRANS	Female 1	Small adult	23	Small	2.4
	Female 2	Very large female	63	Small	1.4
	Female 3	Very large female	52	Small	2.5

Figure Captions

Figure 1: Study period and sample size for radio-tracked *T. albolabris* in Hong Kong, May –December 2012. Eight translocated snakes were tracked for 18 weeks, and one individual was tracked for eight weeks. Residents were tracked for 30 weeks.

Figure 2: Study period and sample size for radio-tracked *T. albolabris* in Hong Kong, June –December 2013.

Figure 3: Causes of deaths for *T. albolabris* in 2012 and 2013 combined.

Figure 4: Dates on which predation of *T. albolabris* was discovered in 2012 and 2013. Predation of resident snakes was discovered within the first two weeks of October; predation of translocated snakes was discovered from 15 August - 19 November in both years.

Figure 5: Trajectories for female resident (n = 12) and female translocated (n = 13) *T. albolabris* in Hong Kong. Each line represents one individual, and all trajectories are displayed in the same geographical scale. Asterisks (*) indicate the start of trajectories that were autocorrelated for sequential linear parameters.

Figure 6: Trajectories for male resident (n = 4) and male translocated (n = 4) *T. albolabris* in Hong Kong. Each line represents one individual, and all trajectories are

displayed in the same geographical scale. Asterisks (*) indicate the start of trajectories that were autocorrelated for sequential linear parameters.

Figure 7: Boxplot of log-transformed frequency of relocations for female resident and translocated *T. albolabris* in 2012 and 2013.

Figure 8: Boxplot of frequency of relocations for male resident and translocated *T. albolabris* in 2013.

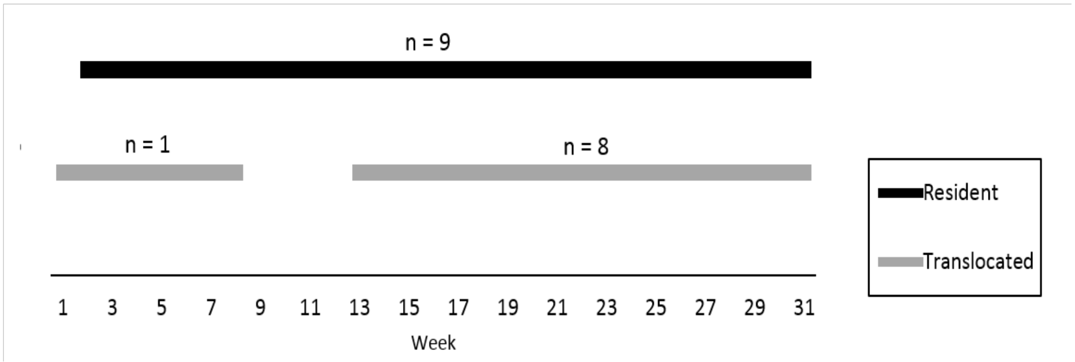
Figure 9: Boxplot of log-transformed average daily movements for female resident and translocated *T. albolabris* in 2012 and 2013.

Figure 10: Boxplot of average daily movements for male resident and translocated *T. albolabris* in 2013.

Figure 11: Dates of first brumation event for *T. albolabris* surviving in 2012. All three resident survivors found brumation refugia (black lines), but only one of the three translocated survivors found refugia (gray line).

Figure 12: Dates of first brumation event for surviving female *T. albolabris* in 2013. All resident and translocated female survivors displayed brumation behavior. The five female survivors found brumating refugia within a few days of each other, but translocated snakes brumated either much earlier or much later than resident snakes.

Figures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Translocated
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7
9
11
13
15
17
19
21
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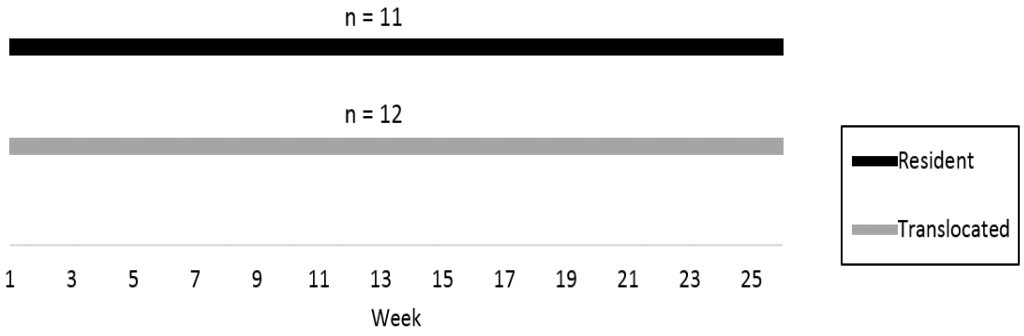
25
27
29
31
Week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Translocated
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19
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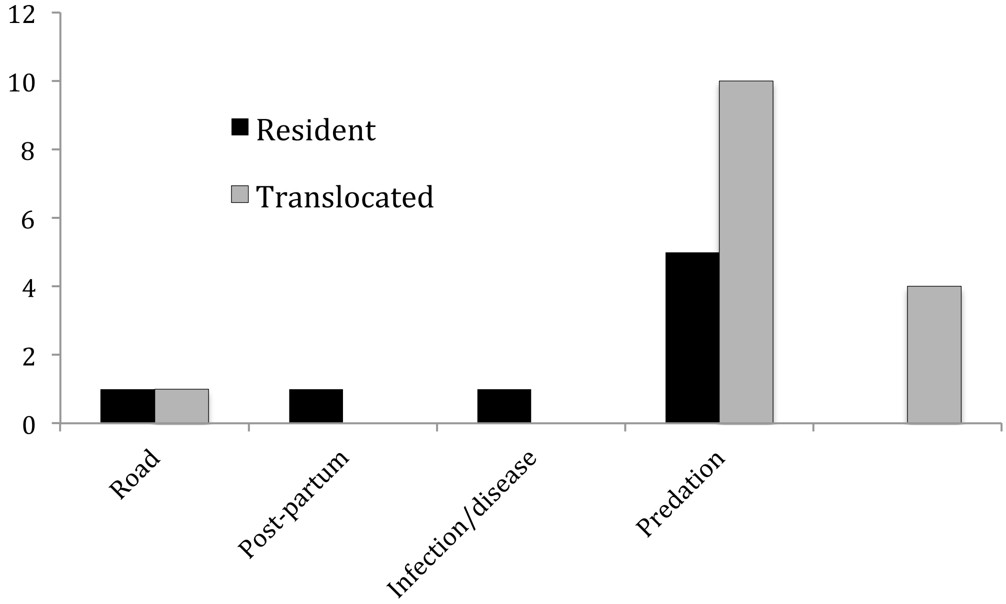
23
25
Week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2
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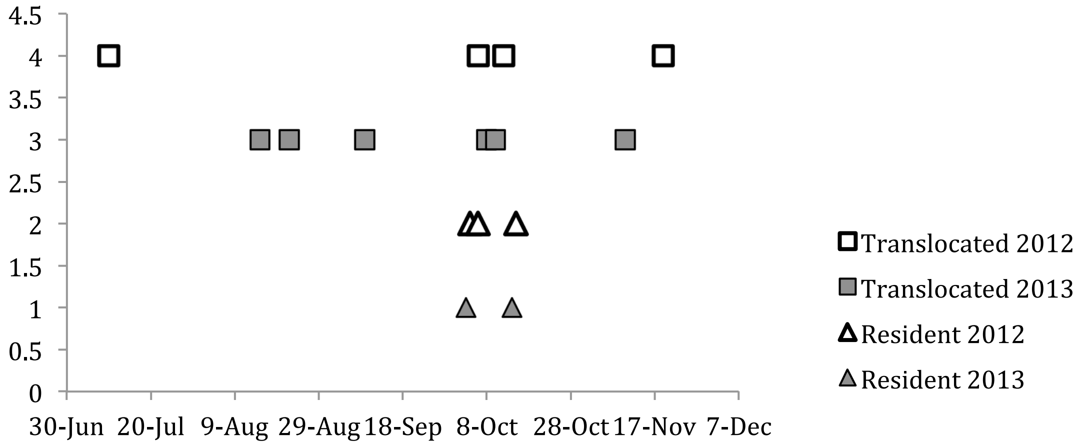
Resident
Translocated
Road
Post-partum
Infection/disease
Predation


4.5
4
3.5
3
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2
1.5
1
0.5
0
30-Jun
20-Jul
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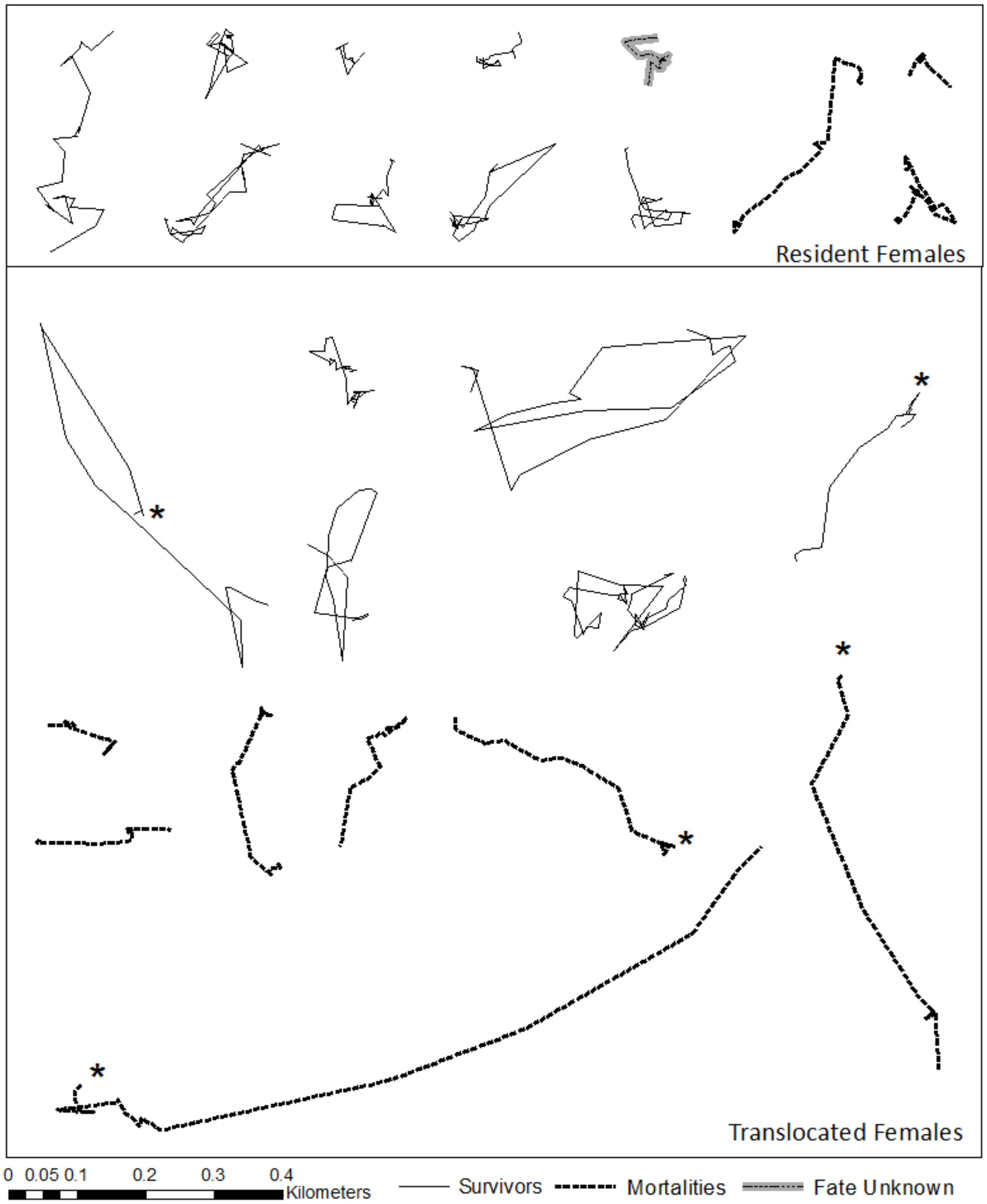
18-Sep
8-Oct
28-Oct
17-Nov
7-Dec
Translocated 2012
Translocated 2013
Resident 2012
Resident 2013


Resident Females
Translocated Females
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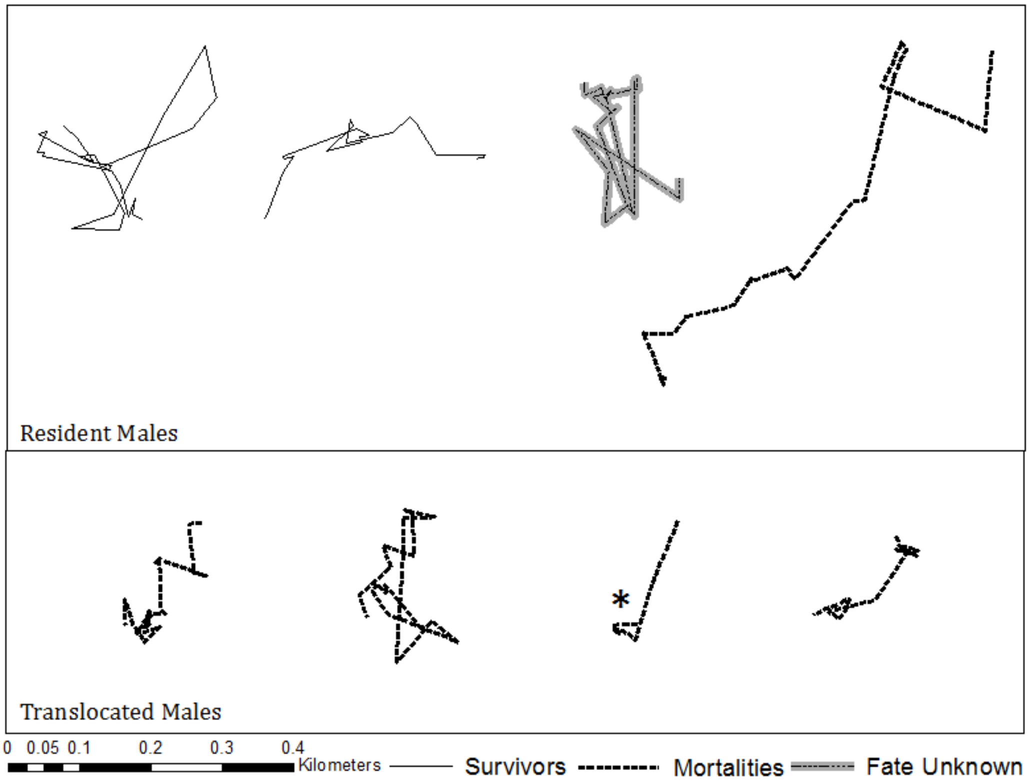
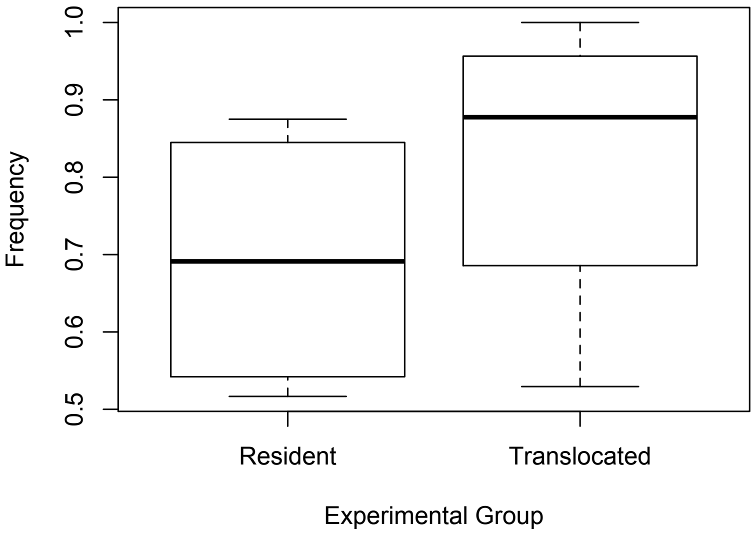
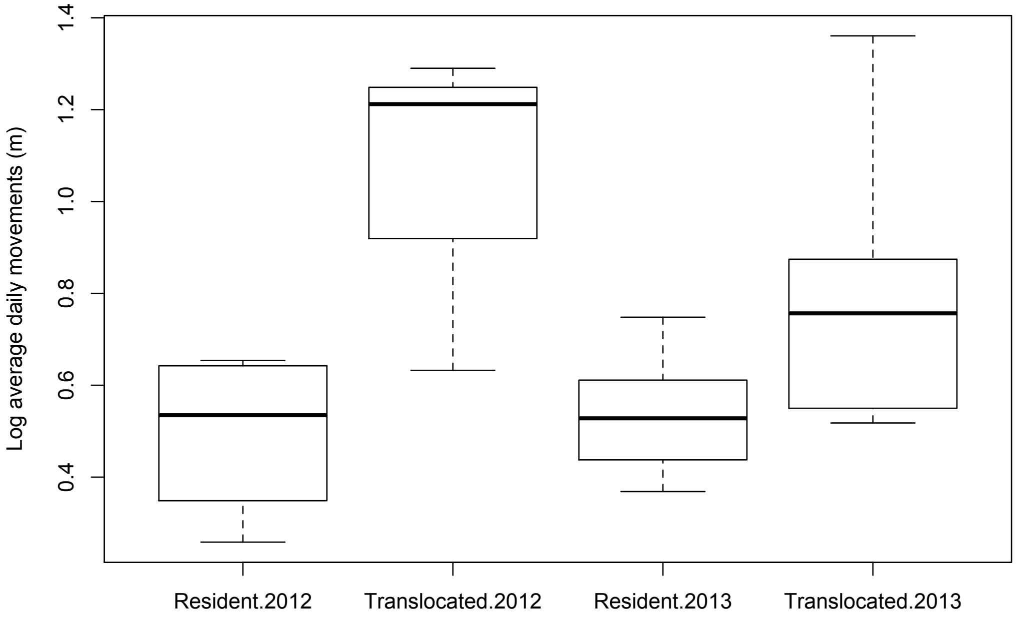
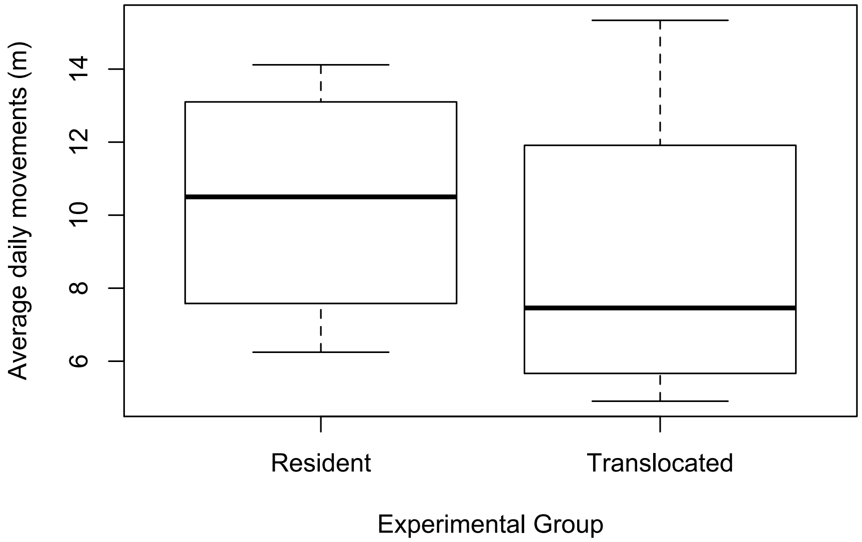
0.05
0.1
0.2
0.3
0.4
Kilometers
Survivors
Mortalities
Fate Unknown

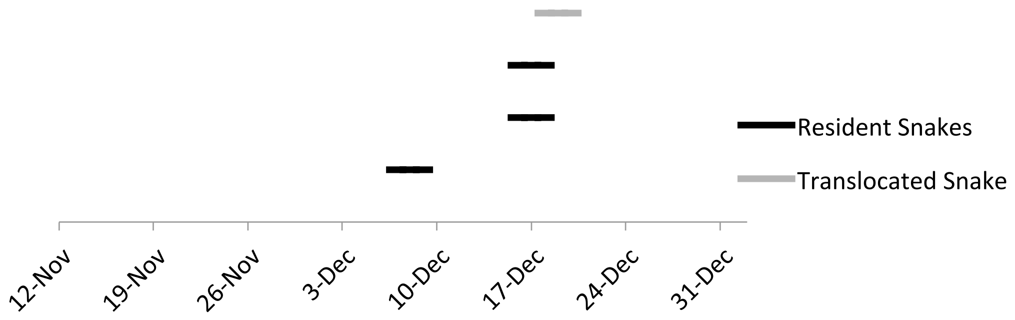

Resident Males
Translocated Males
*
0 0.05 0.1 0.2 0.3 0.4
Kilometers
Survivors
Mortalities
Fate Unknown

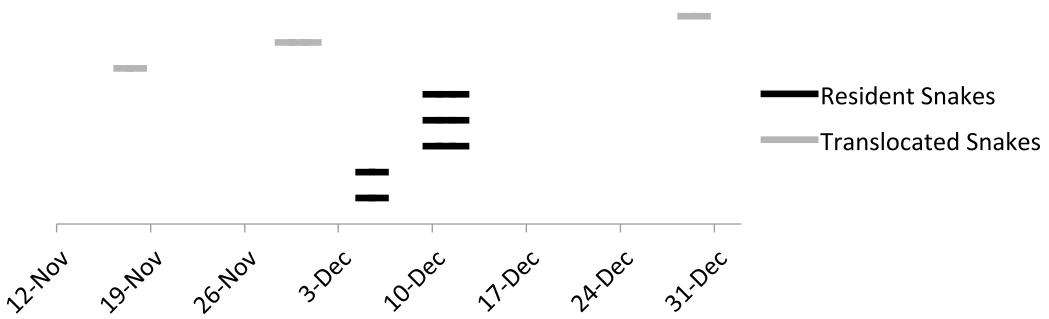

Log frequency
0.0
-0.1
-0.2
-0.3
-0.4
Resident .2012
Translocated.2012
Resident .2013
Translocated.2013


Frequency
1.0
0.9
0.8
0.7
0.6
0.5
Resident
Translocated
Experimental Group


Log average daily movements (m)
0.4
0.6
0.8
1.0
1.2
1.4
Resident.2012
Translocated.2012
Resident.2013
Translocated.2013


Average daily movements (m)
6
8
10
12
14
Resident
Translocated
Experimental Group


Resident Snakes
Translocated Snake
12-Nov
19-Nov
26-Nov
3-Dec
10-Dec
17-Dec
24-Dec
31-Dec



Resident Snakes
Translocated Snakes
12-Nov
19-Nov
26-Nov
3-Dec
10-Dec
17-Dec
24-Dec
31-Dec