

REPRODUCTIVE BIOLOGY AND NATURAL HISTORY OF THE WHITE-LIPPED PIT VIPER (*TRIMERESURUS ALBOLABRIS* GRAY, 1842) IN HONG KONG

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Abstract.—The White-lipped Pit Viper (*Trimeresurus albolabris*) is broadly distributed through South and Southeast Asia, and very little is known about the natural history of the species. In this study, we report on the ecology, demography, reproductive states, and growth rates of *T. albolabris* in Hong Kong, China. The sex ratio is even in *Trimeresurus albolabris* populations. This species displays sexual dimorphism from birth. Females attain larger sizes, and all males, including neonates, displaying a white supralabial stripe on the head and have longer relative tail lengths. Males attain sexual maturity at about 410 mm snout-vent length (SVL). Females reach sexual maturity at about 460 mm SVL, but only begin reproducing at about 520 mm SVL. Mating occurs between August to October, 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. Brumation by females occurs within the first three weeks of December, but snakes will emerge to bask on sunny days. Understanding its demography and reproductive ecology can provide insights into the conservation and management of *T. albolabris* populations in the region and increase our understanding of sexual dimorphism, reproduction, and evolution of the cryptic *Trimeresurus* species complex.

Key Words.—brumation; demography; diet; growth rates; parasites; sexual dimorphism; sexual maturity; Viperidae

INTRODUCTION

The vast majority of our understanding of snake ecology originates from temperate species (Vitt 1983; Brown and Shine 2002), and there is still a paucity of ecological data on tropical snakes compared to their temperate counterparts (Böhm et al. 2013). This lack of data prevents many patterns in the ecology of tropical snake groups, such as comparative analyses of reproductive cycles, life-history attributes, or population dynamics from being identified or recognized (Almeida-Santos and Salomao 2002; Scartozzoni et al. 2009). South and Southeast Asia, for example, harbor a high diversity and endemism of herpetofauna (Böhm et al. 2013; Das and van Dijk 2013; Ganesh et al. 2013), yet even snakes that are relatively easily encountered are not well-studied, such as members of the diverse *Trimeresurus* complex (Serpentes: Viperidae: Crotalinae). Significant research has been conducted on *Trimeresurus* species on the subjects of 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 (Malhotra and Thorpe 2000; Giannasi et al. 2001; David et al. 2011); however, relatively little has been published on the natural history, demography, and reproductive biology of *Trimeresurus*.

Members of the genus *Trimeresurus* occupy a wide range of habitats and exhibit variability in habits, ecology, and reproductive strategy (Pope 1935; McDiarmid et al. 1999; Orlov et al. 2002). One of the widespread members of this genus is the White-lipped Pit Viper (*Trimeresurus* [*Cryptelytrops*] *albolabris*), also locally known in South China as the Bamboo Pit Viper. *Trimeresurus albolabris* is a small, sexually dimorphic, arboreal pit viper that ranges from India to Bangladesh, Indochina, southern China, Malaysia, and Indonesia (Orlov et al. 2002). In northern Vietnam, copulation by *T. albolabris* has been observed between late March to late May, a captive female was reported to

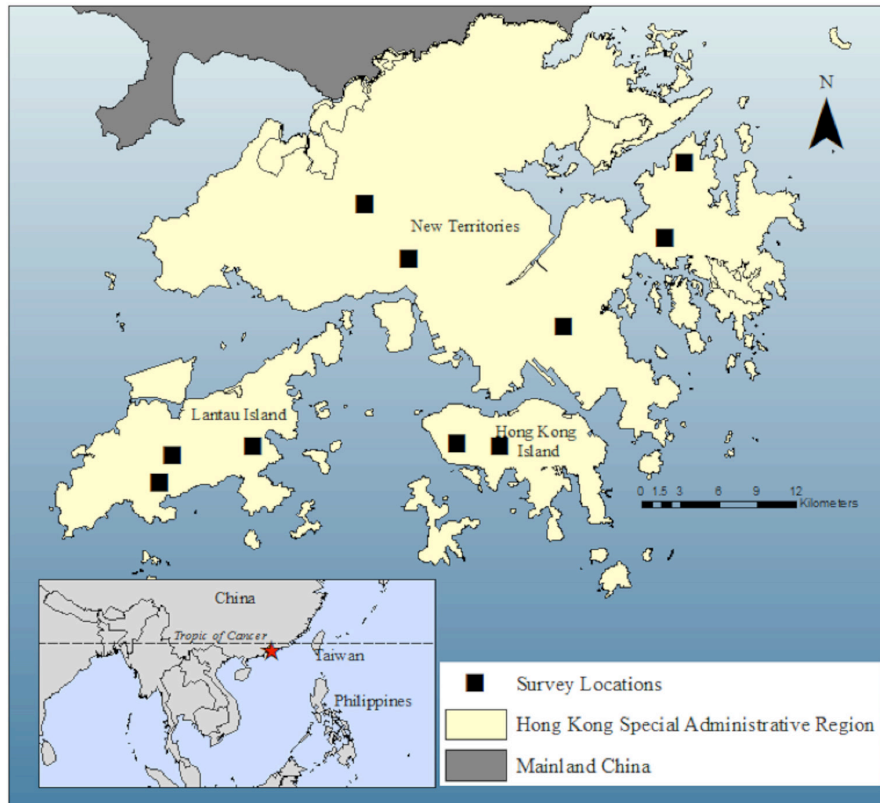


FIGURE 1. Locations of sites surveyed for White-lipped Pit Viper (*Trimeresurus albolabris*) in Hong Kong, China.

store sperm for a year, and neonates are born between late July and early August with litter sizes of four 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 one of the most commonly encountered snakes (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). *Trimeresurus albolabris* is described as a habitat generalist, occurring in most terrestrial vegetation types at all elevations in Hong Kong (Karsen et al. 1998), but no quantitative information is available on ecological aspects of this species in south China. The objective of this study was to shed light on demographic parameters, extent of sexual dimorphism, and reproductive ecology of *T. albolabris* in Hong Kong. In addition, we documented observations on brumation, parasites, and diet.

MATERIALS AND METHODS

Study site.—We conducted this study in Hong Kong (22°09' to 22°37'N, 113°50' to 114°30'E), a special autonomous region of China spanning 1,100 km² (Fig. 1). 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 within the tropics and exhibits a seasonal monsoon climate of hot, humid summer with high precipitation from May to September and cool, dry, and mild winter from November to February (Dudgeon and Corlett 1994). We sampled snakes within active and abandoned agricultural land, secondary forest, shrubland, and grassland.

Field methods.—We used visual encounter surveys to locate *T. albolabris* along 32.1 km of hiking trails at 10 sites within Hong Kong (Fig. 1). We conducted surveys from April to December 2012 and June to December 2013. In 2013, we surveyed each of the 10 sites three to nine times. However, we did not quantify survey efforts in 2012, and we captured only vipers > 50 g in body mass in that year. We captured all individuals encountered in the 2013 visual encounter surveys.

We also captured vipers encountered outside of timed surveys in 2013, but we did not include these individuals in the calculation of capture rates.

We anesthetized all vipers with Isoflurane, an inhalant anesthesia, for measurements described below, but we used only a subset of vipers for radio telemetry. We implanted snakes with SB-2 or BD-2 radio transmitters (Holohil Systems Ltd, Carp, Ontario, Canada) that weighed $\leq 6\%$ of the body mass of an individual. We waited 2 d for telemetered vipers to recover from surgery and at least 3 h for non-telemetered snakes to recover from anesthesia. We released all vipers within 5 m of capture site. We relocated telemetered snakes two to three times a week, with a mixture of day and night tracking, and we recorded their locations with a global positioning system. Individuals that survived 14–20 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.

We measured body mass, snout-vent length (SVL), and tail length of anesthetized vipers. Injuries and truncated tails were noted. We determined sex by probing the cloaca to detect hemipenes. In addition, we recorded the presence of a white lateral stripe on the head and body. We identified neonates by the presence of an ephemeral umbilical scar from shed yolk sacs. We implanted a passive integrated transponder (Biomark, Inc., Boise, Idaho, USA) subcutaneously in vipers anterior to the cloaca. We did not measure SVL and tail length of vipers < 30 g that were captured between 4 June and 1 July 2013, and only determined sex and mass from these individuals. We used the scaled mass index (Peig and Green 2009) as an estimate of body condition, and we calculated growth as change in body condition over the active season, with the active season defined as the period of time that the snake was not in brumation. For gravid females, we calculated change in body condition from the period post-parturition until brumation.

Reproduction.—We gently palpated anesthetized male snakes both posterior and anterior to the cloaca without evertting hemipenes to determine if semen was present. We conducted ultrasound scans on the ovaries of anesthetized, telemetered female snakes to enumerate and measure follicles or embryos. For telemetered females that survived until December of either year, we obtained these measurements in June and July, as well as December. We estimated the date range of parturition of gravid, telemetered individuals after obtaining visual indications of substantial weight loss. We measured mass loss through parturition by weighing postpartum snakes in situ. We also documented any intraspecific interaction between telemetered and non-study vipers that appeared to be mating.

Brumation.—We recorded microhabitat (ground/ foliage/ canopy/ tree or rock wall crevice/ burrow) and height above ground with each relocation of telemetered snakes. We defined onset of brumation as the range of dates between last locating a snake above ground and first locating it underground beneath leaf litter, or in a rock wall crevice, even if the snake was found to emerge from refugia to bask or shift brumation sites. If vipers were hiding in rocky crevices, we removed loose rocks to uncover vipers during brumation to determine depth of burrow or depth below ground.

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

Statistical analyses.—We compared sex ratios of *T. albolabris* using Chi-square. To assess normality of datasets, we used the Shapiro-Wilk test. Because male and female SVL were not normally distributed ($W = 0.875$, $P = 0.015$), we compared means using a Mann-Whitney U test. We then used Levene's test to determine if variance in scaled mass index of reproductive females was different from that of immature females, using the smallest gravid viper found (524 mm SVL) as an empirically determined threshold between the two groups, and removing eight female neonates from the analysis. We used a Johnson-Neyman procedure (D'Alonzo 2004) to identify the non-significant regions of male vs. female mean tail length differences across total lengths (i.e., at which SVL relative tail length in males and females overlapped). We chose this test as an alternative to Analysis of Covariance, as the latter is uninformative beyond unequal slopes, while the Johnson-Neyman procedure (D'Alonzo 2004) allows for comparison of differences along the entire length of both slopes. We removed individuals with injured or truncated tails from relative tail length analyses. We used linear regression to quantify the relationship between SVL and litter size. We tested significance at $\alpha = 0.05$. For snakes that we captured and measured multiple times, we used only measurements from initial capture for analyses, with the exception of growth rates and follicle measurements. We used only snakes from 2013 in statistical analyses, but we included snakes from 2012 in growth and reproductive data. We conducted all statistical analyses in R v. 3.1.2 (R Development Core

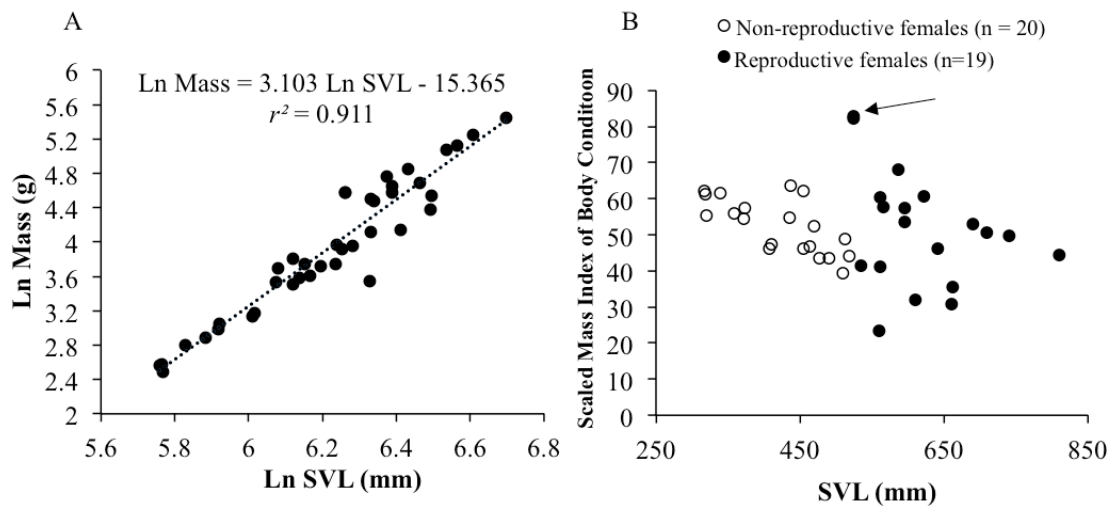


FIGURE 2. Relationship between (A) the natural log of snout-vent length mass of 39 female White-lipped Pit Vipers (*Trimeresurus albolabris*) in Hong Kong in 2013, excluding eight neonates, and (B) scaled mass index of non-reproductive and reproductive female *Trimeresurus albolabris*, with the arrow pointing to the smallest gravid female found.

Team, Vienna, Austria) except for the Johnson-Neyman procedure, which we calculated by hand.

RESULTS

During 204.5 person-hours of visual encounter surveys in 2013, we captured 90 vipers, resulting in a capture rate of 0.43 vipers per person-hour of survey effort. We recaptured only five of the 90 vipers. Of these 90 vipers, we did not obtain SVL and tail length for 18 individuals captured in June. We included these 18 vipers in capture rate and sex ratio analyses but not in any analyses involving SVL, tail length, or total length. We encountered an additional 19 vipers incidentally, and we took all measurements of these vipers and included them in analyses involving SVL, tail and total length, but not capture rates.

We radio-tracked 20 snakes, which included nine females in 2012 (three of which survived), seven females in 2013 (five of which survived), and four males in 2013 (two individuals survived). We lost two snakes mid-season, and causes of death were attributed mostly to predation and vehicle strikes. We observed no direct causes of mortality from anesthesia, transport, or surgery. Pathology was limited to localized sepsis at the incision site, while infected subcutaneous tissue and muscle became encapsulated and surrounded by healthy tissue.

Trimeresurus albolabris exhibited a sex ratio of 1.08 females to 1 male, which did not significantly deviate from an even ratio ($\chi^2 = 0.154$, $df = 1$, $P = 0.695$). All males exhibited a faint to prominent lateral white stripe on the head and body, whereas no females displayed

such markings on the head. 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. The mean SVL of females (469.5 ± 22.7 [SD] mm; range, 203.0–810.0 mm) was significantly greater than the mean SVL of males (347.8 ± 17.8 mm; range, 180.0–512.0 mm; $U = 471$, $P < 0.001$). Variance of scaled mass index for non-reproductive female body condition was significantly lower from that of reproductive females ($F_{1,37} = 5.64$, $P = 0.023$, Fig. 2). At all sizes, males had longer relative tail lengths (mean = 0.199 ± 0.002) than females (mean = 0.144 ± 0.002), including neonates (Fig. 3). The limit of non-significant values fell between -1.7 and 195.8 mm total length, which is smaller than the smallest neonate encountered (Fig. 3).

Adult males decreased in body condition over the active season, as did two females (Fig. 4). Three non-gravid females (455 mm, 580 mm and 642 mm in SVL) increased in body condition between parturition and brumation, and the larger two initiated vitellogenesis (Fig. 4). Only one female (710 mm SVL) that was gravid in the June/July period increased in body condition over the active season, and this same individual initiated vitellogenesis (Fig. 4).

Reproduction.—The smallest gravid female we encountered was 524 mm in SVL and 87 g in mass, and the largest gravid viper encountered was 710 mm in SVL and 245 g in mass. The smallest sexually mature female (determined by presence of ovarian follicles via ultrasonography) was 463 mm in SVL. Two of six

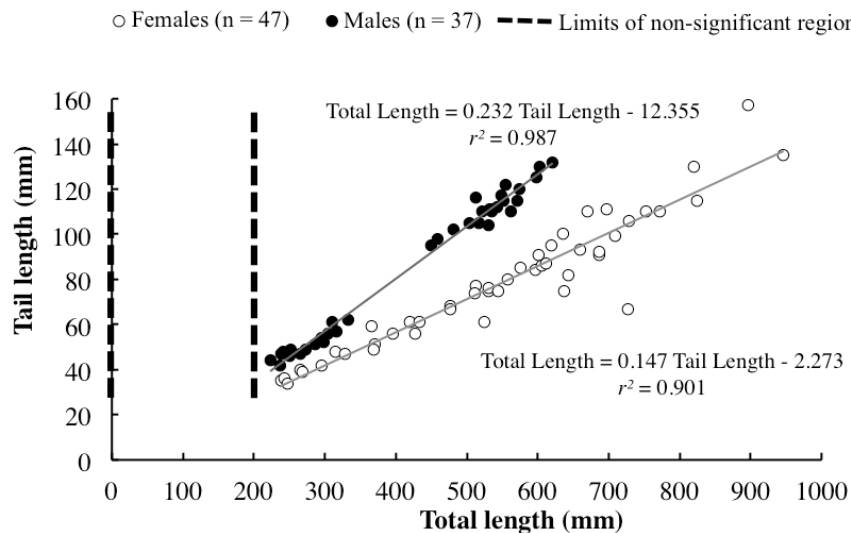


FIGURE 3. Johnson-Neyman technique scatterplot of tail length against total length of female and male White-lipped Pit Vipers (*Trimeresurus albolabris*) in Hong Kong in 2013. Limits of non-significant region fall to the left of the smallest neonate encountered, and male tail length is higher than female tail length at all sizes of snake. Data from two males with damaged tails were excluded from this analysis.

(33.3%) adult female vipers encountered during the gestation period (June–July) in 2013 were gravid, and two of four (50 %) adult female vipers encountered during that same period in 2012 were gravid. Litter size was strongly positively related to SVL ($r^2 = 0.98$, $F_{1,3} = 145.9$, $df = 4$, $P = 0.001$, Fig. 5). The largest gravid viper gestated at least 20 embryos that overlapped within the body cavity, whereas smaller vipers had only five to six non-overlapping embryos.

Parturition occurred between 15 July and 9 August in both years. Due to the low probability of obtaining direct visual observations of individuals when tracking vipers in dense vegetation, the exact dates of parturition are unknown for all vipers. No post-parturition parental care was observed, and we did not observe any neonates in the vicinity of the female post-parturition. Females were emaciated following parturition and lost approximately 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.

Follicle size at the end of the active season was reduced to the size measured during the inactive season (< 5 mm) in vipers that had been gravid in the summer of that season, except for one individual that had enlarged follicles in December (Fig. 6). This individual, tracked June–December 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 (Fig. 6). Large adults that were not gravid in the summer and gained substantial mass over the

active season (July to November) exhibited increased follicle size of as much as 7–15 mm by the end of the year, which corresponds to stage II–III vitellogenesis in the closely related *Trimeresurus (Viridovipera) stejnegeri* (Tsai and Tu 2001).

Over the course of 2 y, we observed five instances of adult males attending large females between 17 August and 15 October. In all observations, males were perched on the same branch approximately 10–50 cm away from the female with its head orientated toward the female. We did not observe any two individuals of this solitary species within such close proximity outside of the putative mating season, even on surveys where we captured a high number of vipers within a short length of forest trail. We did not observe copulation or any other interactions. On one of the five above-mentioned occasions, two adult males were attending one large female. We captured five adult males 412–512 mm in SVL between 5 September and 15 October 2013 that secreted semen when palpated. We captured one of them while attending a large female, and the other four were solitary when captured.

Brumation.—We identified brumation refugia as: (1) small crevices in the ground covered by leaves, logs, or other plant debris, (2) crevices inside low human-made rock walls, and (3) small mammal burrows in soil, or under loose stones, boulders, or tree roots. We found a few vipers as deep as 0.5 m below the surface. The onset of brumation was 6–18 December in 2012 and 4–12 December in 2013. In December of both years, vipers emerged to bask on warm, sunny days in low shrubs, on the ground, or occasionally in trees. Each viper was

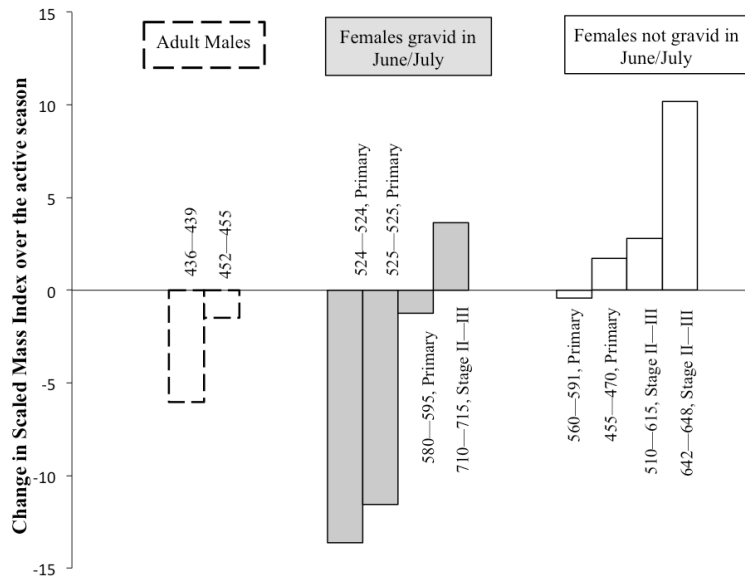


FIGURE 4. Change in scaled mass index over the active season for 10 White-lipped Pit Vipers (*Trimeresurus albolabris*) radio-tagged in 2012 and 2013 in Hong Kong. Change in gravid females is measured from parturition (August) until brumation, and loss in mass from parturition is not reflected here. All others are measured from capture date (June–July) until December. Data labels represent SVL (mm) in the beginning and end of the tracking period, and stage of follicle development in December.

not confined to one brumation site and shifted between brumation sites within a few meters from each other. We did find any communal brumation sites. Neither of the two surviving males brumated for the duration of this project and both were still active and above ground in low shrubs in December.

Parasites and diet.—We identified *Kalicephalus* sp., *Strongyloides* sp., *Capillaria* sp., *Oxyuris* sp., ascarids, and other hookworm ova in the feces of 21 vipers. We detected an unidentified coccidian parasite in fecal

matter of several vipers. We found ascarid larvae buried subcutaneously and within the coelomic cavities of several vipers. In one instance, a necropsy we performed on a female revealed ascarid infection throughout the coelomic cavity, fat bodies, kidneys, and liver (Fig. 7A). We also detected loose subcutaneous parasites (Fig. 7B). 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 (Fig. 7C and 7D). 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 reported to infect *T. albolabris*, was also found subcutaneously and retrieved from an anesthetized viper.

The only predation event we saw was that of an individual *T. albolabris* eating a Chinese Gecko (*Gekko chinensis*). This individual was found with a food bolus much larger than the size of the gecko 7 d later, although this second prey item was not identified. Examination of fecal matter revealed Muridae hairs in several vipers and Soricidae hair in one viper.

DISCUSSION

Because of a low recapture rate of 5.5%, population parameters could not be measured based on the mark-recapture data, and more exhaustive sampling efforts or different methods to sample vipers are necessary, if studies aim to quantify populations. Low detection and

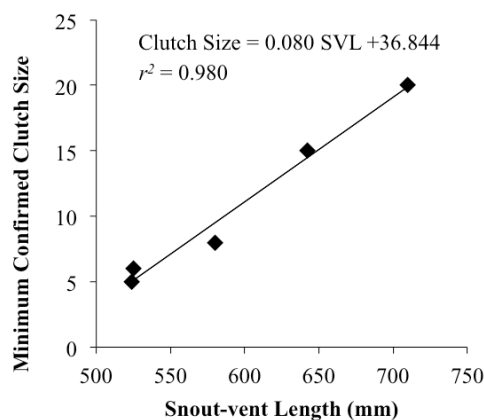


FIGURE 5. Litter size of gravid female White-lipped Pit Vipers (*Trimeresurus albolabris*) in Hong Kong captured in 2012 and 2013. Each data point represents lowest confirmed number of embryos within a gravid individual ($n = 5$). Embryos that were partially or fully covered from view by another embryo were not included in the litter size count.

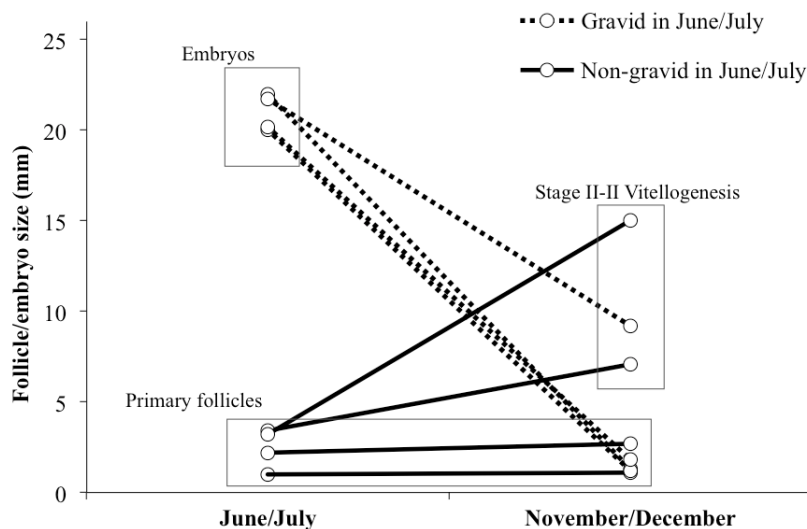


FIGURE 6. Change in follicle size over the active season for female White-lipped Pit Vipers (*Trimeresurus albolabris*) in 2012 and 2013. Each line represents one viper. Small adults remained in stage V vitellogenesis during the whole season with primary follicles, whereas larger adults that were not gravid in June/Jul and gained mass over the active season had enlarged follicles characteristic of stage II-II vitellogenesis in November/December. All but one (710 mm SVL) of the gravid females returned to stage V vitellogenesis (with primary follicles) by the end of the year.

recapture rates and difficulties measuring population parameters are not unusual in studies of snakes (Parker and Plummer 1987; Steen 2010). The ratio of male to female vipers showed that *T. albolabris* populations exhibit an even sex ratio in Hong Kong. We captured too few neonates in 2013 to detect a difference in the sex ratio (5 F:11 M) of juveniles.

Sexual dimorphism, sexual maturity, and growth.—

Based on our data, we determined that it is possible to determine the sex of *T. albolabris* at all ages by any one of the following: males have a diagnostic white stripe on the head and females do not; male relative tail length is higher than mean female tail length at all total lengths of snakes; and presence of hemipenes is evident in all sizes of male snakes. Sexual dimorphism in relative tail length of juvenile and adult snakes is well documented (Klauber 1943; Shine et al. 1999), and in *T. albolabris*, this is evident at the neonate stage, not just juvenile and adult stage. Based on our measurement and reproductive data, we estimated the sizes at sexual maturity for both males and females. Sexual maturity in males probably occurs at or before about 410 mm SVL, as the smallest male found retaining semen in our study was 412 mm. Female *T. albolabris* are sexually mature at about 460 mm SVL, but probably do not start reproducing before about 520 mm SVL. This is supported by three lines of evidence: (1) the smallest sexually mature female measured 463 mm in SVL, but the smallest gravid viper found was 524 mm, (2) large variation in body condition in relation to SVL only appears in females after they

have attained about 525 mm in SVL, and (3) high variation in body condition of telemetered female vipers appears to be related to reproductive state. Reproduction in sexually mature females is therefore probably only initiated when body reserves exceed a threshold value, as in other snakes (Bonnet et al. 2002).

Reproduction.—Based on our data, we constructed a probable reproductive cycle for *T. albolabris* in Hong Kong (Fig. 8). Our study provides evidence of gestation in June (or earlier) to July, parturition in July to August, suggests that mating takes place in August to October coinciding with the presence of semen in males, and shows that onset of vitellogenesis in females occurs before December. These observations suggest a post-nuptial vitellogenesis (vitellogenesis following mating) and subsequent long-term sperm storage over winter, both of which are characteristics of temperate snakes (Schuett 1992; Aldridge and Duvall 2002; Shine 2003). We hypothesize that vitellogenesis extends into the following year based on post-nuptial vitellogenesis and long-term sperm storage, and we estimated that the ovulation period occurs between March to June based on gestation, vitellogenesis, and parturition dates (Fig. 8). However, as we did not conduct surveys or track snakes from January to 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 *Agkistrodon* and *Crotalus* (Aldridge and Duvall 2002).

Along with ratios of non-gravid to gravid adult female vipers during gestation periods, follicle measurements

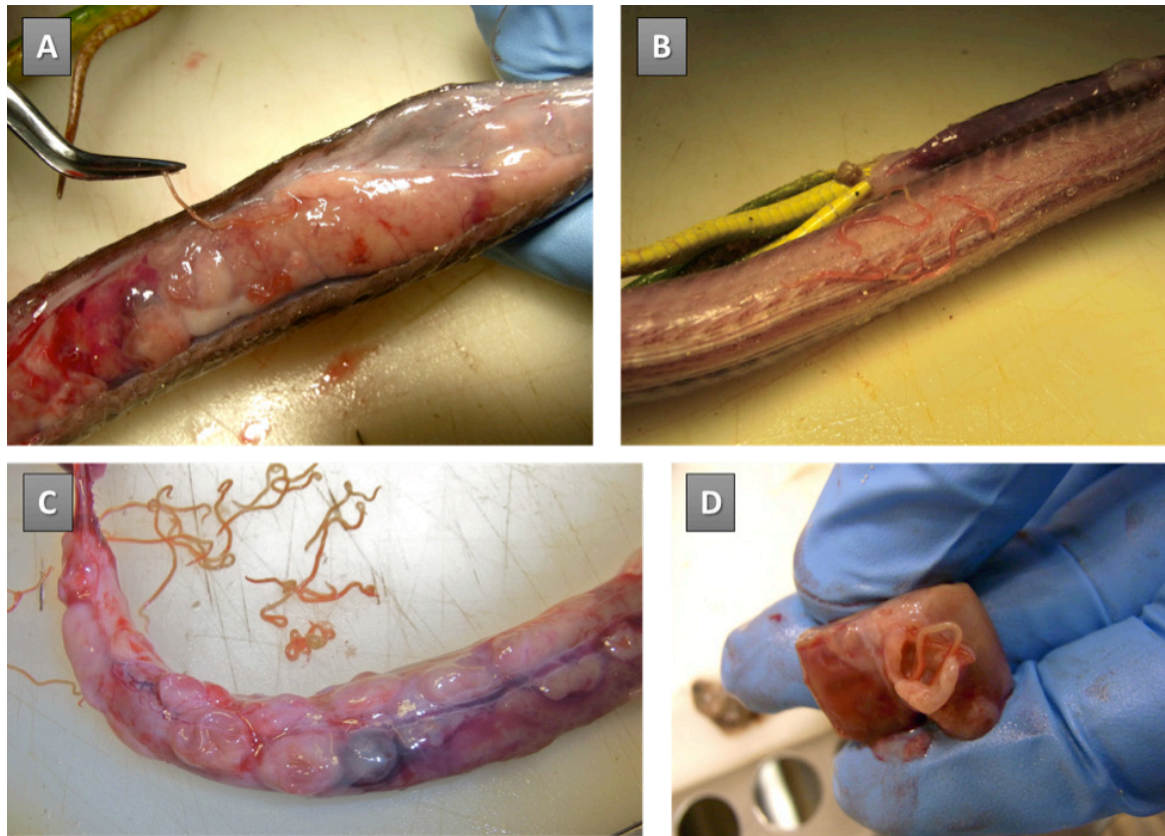


FIGURE 7. Severe ascarid larvae infection in White-lipped Pit Vipers (*Trimeresurus albolabris*). (A) Parasites within the coelomic cavity, (B) loose subcutaneous parasites, (C) severe hepatitis with lesions, and (D) ascarid larvae within liver cyst. (Photographed by Anne Devan-Song).

and growth rates 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 12 mo (Bull and Shine 1979) and are more common in temperate than in tropical species. Females that were gravid in June and July reverted to primary follicles in December of that year, while large non-gravid females commenced vitellogenesis by December. However, in one case, a gravid female appeared to undergo vitellogenesis in the same year after parturition. Notably, this was the largest female tracked and was the 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 in *T. albolabris* may therefore be determined by body reserves, similar to a typical Capital Breeder, such as *Vipera aspis* (Bonnet et al. 2002).

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 probably mates at the end of summer in the year preceding ovulation and fertilization. Interestingly, the latitudes and climates of North Vietnam and Hong Kong are not starkly different, and variation in reproductive strategies even within the geographic range of a species 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 climatic variation.

Natural history.—Brumation is an important life-history event in ectotherms living in seasonal climates and can be critical for survival during the winter (Gregory 1982). Communal brumation is common in many snake species (Hirth 1966; Rudolph et al. 2007; Gienger and Beck 2011). It is characteristic of species that inhabit areas with more severe winters (Shine 1979) and may also reflect scarcity of suitable refugia (Harvey and Weatherhead 2006). Conversely, solitary brumation, such as is seen in *Sistrurus c. catenatus* (Harvey and Weatherhead 2006), suggests refugia are

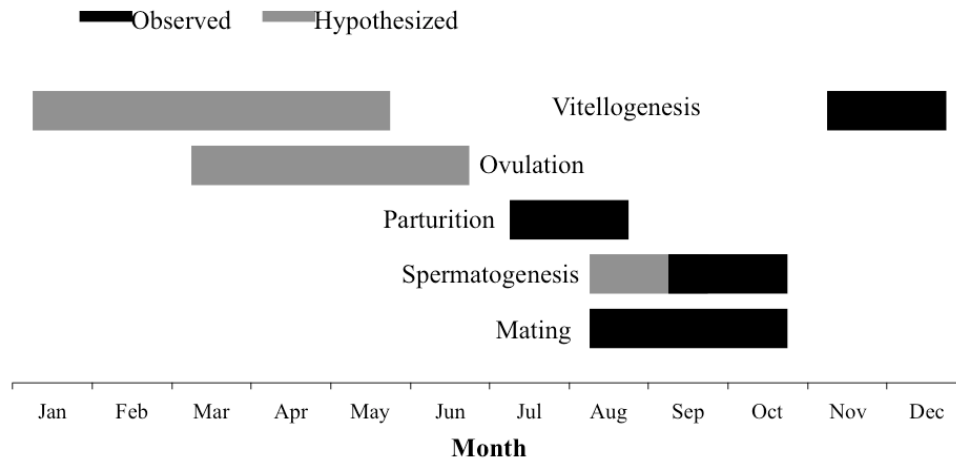


FIGURE 6. Presumed reproductive cycle of White-lipped Pit Vipers (*Trimeresurus albolabris*) in Hong Kong, China.

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 (0–0.5 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.

All fecal parasite genera that we discovered in *T. albolabris* have been previously documented in the species. *Kalicephalus laticaudae*, *Capillaria* sp. and *Oxyurus* sp. were found in the feces of captive *T. albolabris* in Thailand (Chaiyabutr and Chanhom 2002). However, we were unable to identify the coccidian parasite present. Subcutaneous ascarid larvae also appear to be important parasites as they were found in fairly high numbers in several individuals. 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). Pope (1935) documented *Calotes versicolor* (Agamidae) and rats as commonly found prey items, and small mammals may be important sources of prey especially for larger vipers. High abundance of geckos encountered during visual encounter surveys suggests that geckos may be a food source.

In this study, we have constructed the reproductive cycle of *T. albolabris* in south China. We also have demonstrated sexual differences in behavior 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, which is the major cause of snake bites in Hong Kong. This knowledge will be useful for the conservation and management of this venomous snake.

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