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Bayesian insights into Green Pit Viper *Trimeresurus* (*Cryptelytrops*) *macrops* sexual dimorphism with respect to influence of gravidity and habitat disturbance

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Sexual dimorphism is expressed in many taxa as a form of resource partitioning and as a response to unique challenges faced by male and female organisms. We investigated this phenomenon for an arboreal green pit viper species, *Trimeresurus macrops*, previously suggested to display obvious sexual dimorphism. We evaluated seven external characters and scaled mass index (SMI) of 73 vipers (N = 32 males, N = 41 females) obtained during night surveys and opportunistic searches in north-east Thailand from January 2015–January 2017. We utilised Bayesian inference to investigate the influence of sex, gravidity, and rural habitat disturbance on sexual dimorphism of *T. macrops*, and we provide 95 % highest density intervals (HDI) for the difference in means (posterior distribution). We also present ecologically relevant probabilities of observing dimorphism for each external character and SMI by sex, gravidity (gravid or not), and habitat type (rural or forest). Females were larger than males in both forested and rural habitat, females in rural habitat were larger than forest females, and all males displayed a conspicuous white eye-stripe. When gravid females were excluded from analyses, probability of observing dimorphism drastically decreased. Knowledge of niche partitioning and the specific challenges encountered by males and females, gravid and non-gravid females, and individuals persisting in rural habitats will prove valuable for conservation and snakebite mitigation of *T. macrops*.

Keywords: Difference of body size, south-east Asia, Bayesian inference, arboreal viper

ความแตกต่างระหว่างเพศ (sexual dimorphism) ถูกปรากฎในอนุกรมวิธานสัตว์ว่าเป็นรูปแบบหนึ่งของการแบ่งปันทรัพยากร (resource partitioning) และการท้าทายจำเพาะจากสิงมีชีวิตเพศผู้และเพศเมีย เราศึกษาปรากฏการณ์นี้ในกลุ่มงูเขียวหางไห้ที่มีถินอาศัยอยู่บนต้นไม้ ชนิดพันธุ์ งูเขียวหางไหม้ตาโต *Trimeresurus macrops* ซึงได้รับการเสนอในการศึกษาก่อนหน้าว่ามีการแสดงออกของความแตกต่างระหว่างเพศอย่างชัดเจน นักวิจัยทำการประเมินลักษณะภายนอกทั้ง 7 ลักษณะและScaled mass index (SMI) ของงูเขียวหางไหม้จำนวน 73 ตัว (ตัวผู้ 32 ตัว, ตัวเมีย 41 ตัว) จากการสำรวจตอนกลางคืนและการสำรวจตามโอกาสในพื้นทีภาคตะวันออกเฉียงเหนือของประเทศไทยตั้งแต่เดือนมกราคม พ.ศ. 2558 - มกราคม พ.ศ. 2560 เราใช้การอนุมานแบบเบย์เพื่อตรวจสอบอิทธิพลของเพศ การตั้งครรภ์ และการรบกวนถินอาศัยในพื้นทีเกษตรกรรมต่อความแตกต่างระหว่างเพศของงูเขียวหางไหม้ตาโต *T. macrops* และเราให้ช่วง HDI อยู่ที 95% สำหรับความแตกต่างของค่าเฉลีย (การแจกแจงหลัง) นอกจากนี้ เรานำเสนอความน่าจะเป็นทีเกียวข้องกับระบบนิเวศในการสังเกตความแตกต่างของลักษณะภายนอกและ SMI ตามเพศ การตั้งครรภ์ (มีหรือไม่มี) และประเภททีอยู่อาศัย (พื้นทีเกษตรกรรมหรือปา) การศึกษาพบว่า งูเขียวหางไหม้ตัวเมียมีขนาดใหญ่กว่าตัวผู้ทั้งทีอาศัยในปาและพื้นทีเกษตรกรรม โดยงูเขียวหางไหม้ตัวเมียในทีอยู่อาศัยพื้นทีเกษตรกรรมจะมีขนาดใหญ่กว่าทีพบในปา และตัวผู้ทุกตัวมีแถบตาสีขาวทีสังเกตเห็นชัดเจน ทั้งนี้เมืองูเขียวหางไหม้เพศเมียทีตั้งครรภ์ถูกแยกออกจากการวิเคราะห์ ค่าความน่าจะเป็นในการสังเกตความแตกต่างระหว่างเพศถูกลดทอนลงเป็นอย่างมาก โดยความรู้เกียวกับการแบ่งกลุ่มเฉพาะและความท้าทายจำเพาะทีพบโดยงูเขียวหางไหม้เพศผู้และเพศเมีย งูเพศเมียทีมีการตั้งครรภ์ และตัวอย่างอืน ๆ ทีอาศัยอยู่ในเกษตรกรรมจะพิสูจน์ได้ว่ามีคุณค่าสำหรับการอนุรักษ์และการลดปัญหาการถูกงูกัดของงูเขียวหางไหม้ตาโต *T. macrops* สืบไป

INTRODUCTION

Sexual dimorphism has independently evolved in many groups of animals (Williams & Carroll, 2009). Colouration, body size and body shape are some of the phenotypic differences which can be expressed by male and female organisms (Mori et al., 2017). Sexual dimorphism is thought to have evolved due to unique challenges faced by each of the two sexes and as a form of resource partitioning. In general, when the male is larger than the female, sexual size dimorphism (SSD) increases with body size, but decreases with body size in groups in which the male is smaller than the female ("Rensch's rule; Rensch, 1950; Fairbairn, 1997). Vipers (family

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Viperidae) express SSD in many forms, which provides an interesting study system for this phenomenon.

Many viper species display male-biased SSD (males express larger morphological characters), particularly New World representatives (such as the genera *Crotalus* and *Agkistrodon*). Male biased SSD is particularly prevalent for terrestrial species which engage in ritualised male-male combat behaviour, which selectively pressures for larger body mass and length (Shine, 1978; Bonnet et al., 1998). Females of some species of viper are larger than males, despite males of those species engaging in male-male combat (e.g. *Calloselasma rhodostoma* and *Vipera berus*; York, 1984; Madsen, 1988; Strine et al., 2015).

Phylogenetic study of Neotropical viperids suggest that SSD patterns are driven primarily through sexual selection on males rather than females, with the notable exception being arboreal species, which favour female biased SSD (Hendry et al., 2014). Arboreal Old World vipers may follow similar trends with most arboreal vipers displaying female biased SSD (as proposed for the genus *Tropidolaemus*, Kuch et al., 2007). Some arboreal species such as the insular *Gloydius shedaoensis* do not display obvious sexual dimorphism (Shine et al., 2002).

Male-biased SSD may enable individual males to outcompete other males and provide increased access to females (Shine, 1978). Alternatively, female-biased SSD may promote greater gravidity (King, 2000), larger clutch sizes (Seigel & Ford, 1987; Shine, 1993; Manjarrez et al., 2014) and larger offspring with better body condition at birth for larger females (Bronikowski, 2000; Kissner & Weatherhead, 2005; Manjarrez et al., 2014). Selection for large female body size due to increased reproductivity (Darwin, 1874; more recently termed "fecundity-advantage hypothesis", Trivers, 1972) may be associated with smaller and more mobile males (Trivers, 1972; Ghiselin, 1974; termed the "small male hypothesis" by Zamudio, 1998).

Snakes in human-disturbed habitats may also display SSD, similar to their natural habitat counterparts (Fearn et al., 2001). Significant direct mortality of snakes by humans can skew size distributions, however (Sasaki et al., 2008). Different expression of morphology may allow females and males to occupy separate ecological niches, particularly influencing food requirements and reducing intersexual resource competition (Shine, 1991; 1993; Houston & Shine, 1993; Pearson et al., 2002; Manjarrez et al., 2014). Reduction of intraspecific resource competition may be particularly crucial in tropical regions, where niche breadth is considerably narrower than temperate regions (Krasnov et al., 2008).

Green pit vipers (usually *Trimeresurus* spp.) are a tropical and sub-tropical group of pit vipers (sub-family Crotalinae), which have previously been suggested to exhibit significant sexual dimorphism and geographic variation of morphological characters. Female *T. vogeli* from Laos and Cambodia expressed significantly shorter tails, larger heads and reached larger overall body lengths than conspecific males (Malhotra et al., 2004). Female *T. albolabris* were also observed to be significantly heavier than males in captivity by Herrel et al. (2011), but no differences in head shape were found. Subsequent study of wild *T. albolabris* by Devan-Song et al. (2017) in Hong Kong further revealed significant dimorphism of size and colouration by sex. Interestingly, initial studies suggested *T. stejnegeri stejnegeri* to be sexually dimorphic in northern Taiwan (Tsai & Tu, 1998), although more recent studies of the species have not subsequently observed significant size differences between sexes (Tu et al., 2000; Creer et al., 2002).

The big-eyed pit viper (*T. macrops*) is a common and widespread species of arboreal green pit viper (found in central and northern Thailand, Cambodia and Laos; Stuart et al., 2012) which has previously been suggested to exhibit sexual size dimorphism (Strine et al., 2015). With total body length between 520–660 mm as adults (maximum 720 mm; Das, 2010; Cox et al., 2012) and mass between 36–108 g (Cox et al., 2012), *T. macrops* is a relatively small species. However, *T. macrops* accounts for a large percentage of venomous snake bites throughout Thailand (about 30 %; Viravan et al., 1992; Soogarun et al., 2006) and other south-east Asia countries.

Dimorphism can be an indicator of niche partitioning and intraspecific diet (Temeles et al., 2010) and inclusive understanding can be useful for snake conservation and ecological knowledge in natural and human disturbed habitats. We further describe sexual dimorphism of *T. macrops* at the Sakaerat Biosphere Reserve in northern Thailand, blending replication (refer to Fraser et al., 2020 and Marshall et al., 2021, for discussion and benefits of replication and reproducibility) with additional novel findings of influence of gravidity and habitat. We hypothesise 1) that gravidity will influence perception of SSD by investigators and 2) estimates and SSD will differ between forest and rural environments. We report (1) sexual size dimorphism (SSD) of *T. macrops* in rural and natural habitat, (2) assess the influence of female viper gravidity on dimorphism and (3) assess general morphological size differences of vipers in rural and natural habitats in northern Thailand. By approaching the SSD phenomenon from a Bayesian framework, we are able to incorporate previous knowledge and provide direct inferential conclusions (probabilities of observing males or females measurements being larger) which are ecologically meaningful and easy to interpret.

MATERIALS & METHODS

Study site

Our study was conducted in rural and forested areas of the Sakaerat Biosphere Reserve (SBR), Nakhon Ratchasima Province, Thailand (14.44–14.55° N, 101.88–101.95° E; Fig. 1). The reserve is comprised of a core (forest) area of approximately 80 km^2 and a further 360 km^2 comprising buffer and transitional (rural) areas. The protected (core, forest) area ranges in elevation from 280 to 762 m and consists of primary growth dry evergreen forest, dry dipterocarp forest and secondary reforestation (Trisurat, 2010). The buffer and transition (rural) areas of the SBR are comprised of human settlements and

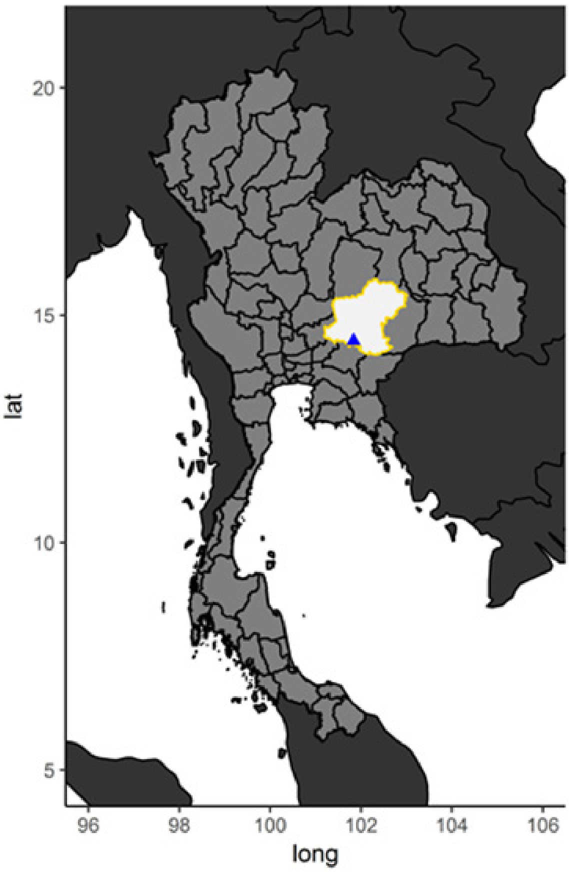

Figure 1. Map with Thailand highlighted in light grey, Nakhon Ratchasima province outlined in yellow, and study site (Sakaerat Biosphere Reserve) indicated by the blue triangle.

agriculture interspersed with small remnant patches of disturbed forest. Primary agriculture in the area includes rubber (*Hevea brasiliensis*), coconut, Eucalyptus tree (*Eucalyptus camaldulensis*), cassava and corn at various stages of cultivation.

Data collection

We followed similar methodology to Strine et al. (2015) for data collection. We captured vipers during surveys at night and opportunistic searches between January 2015–January 2017, and recorded morphometrics the following day using the acrylic tube method and isoflurane anesthesia as described by Wilkinson (2014). After complete body tone loss was achieved, we measured snout vent length (SVL) and tail length (TL) of vipers with a custom-made, semicircular measuring pipe. Snout vent length was defined as the distance from the tip of the snout to the posterior tip of the anal scale. Tail length was defined as the distance from the anterior tip of the first sub-caudal scale to the tip of the tail. Total body length (TBL) was then obtained by adding SVL and TL. Girth was measured at 25 %, 50 % and 75 % intervals of SVL, starting from the head, using digital callipers. Head length (HL) and head width (HW) were determined through the use of digital callipers also, from the widest part of the side of the head (HW) and from the notch behind the head which separates the head and neck (HL). We determined sex of each viper by inserting a probe into the cloaca and gently easing it into one of the cavities at the base of the tail, recording the distance the probe travelled in number of sub-caudal scales. For females it was possible to pass the probe only as far as the musk glands, which lie beneath the first one or two sub-caudal scales. The probe passed to at least the ninth sub-caudal scale for males. We further assessed body condition for *T. macrops* using a scaled mass index (SMI, Peig & Green, 2009) with previous *T. macrops* captured at the Sakaerat Biosphere Reserve as a comparison population (Strine et al., 2015). Finally, each *T. macrops* captured was uniquely marked with a Bovie® cauterising unit for future identification following Winne et al. (2006).

All measurements presented in our work are similar to Strine et al. (2015), except for girth which was not collected during that study period. We also determined female gravidity (gravid or not- indicated by presence or absence of ova) through light palpation while vipers were under anesthesia, which was not presented in Strine et al. (2015). We were unable to confidently determine gravidity for a small subsample of females (< 10 individuals). These vipers were still included in general analyses but not gravidity-specific analyses. After measurements were recorded, we photographed each individual viper's body, head, ventral and sub-caudal scales, tail, brand and other identifying characteristics such as scars. All vipers were returned to their location of capture within 72 hours of capture.

For recaptured snakes, we only used measurements obtained from the most recent capture. Juveniles and neonates were excluded from analyses. We considered individuals of both sexes greater than 450 mm TBL to be sexually mature, based on the smallest gravid female captured in SBR previously (Strine et al., 2015). Although males less than 450 mm TBL may be sexually mature, we selected our mature size conservatively (similar to Strine et al., 2015). No comprehensive investigation of reproductive ecology has yet been conducted for *T. macrops*, and the life history of the species remains understudied.

Statistical analyses

We used Bayesian methods in the R program package "wiqid" (version 0.1.5, Meredith, 2018) to estimate morphometric variables of male and female *T. macrops* in rural and forest habitats of SBR. Within the wiqid package, we used the function "Bnormal" which generates a Bayesian estimation of center (μ) and scale (σ) of a Gaussian ("normal") distribution based on 100,000 Metropolis-Hastings Markov chain Monte Carlo (MCMC) samples (with a 10,000 sample burn-in, thinning rate of 1 and 4 chains) to achieve > 10,000 effective samples obtained from a Gibbs sampler and our dataset. Well mixed traceplots and appropriate Gelman and Rubin statistics ($\hat{r} < 1.01$, Gelman & Rubin, 1992) suggested MCMC chains to have completely traversed all features of posterior distributions, resulting in achievement of stationary distributions. Flat (uniform distribution, reflecting lack of previous data) priors were initially applied for both rural and forest vipers collected during our study period. Our girth methodology has not been widely utilised (but could provide an additional tool for assessing body condition and dimorphism), so we only applied flat priors to these measurements.

For comparison to Strine et al. (2015) and to better understand the ecological implications of head size, we applied Bayesian linear regression models to these dependent (head width and head length) variables with SVL and SMI as predictor variables. We tested each variable for normality, homoscedasticity and independence. Linear regression models were run with the "brm" function in the "brms" package (version 2.9.0, Buerkner, 2017) of R, with flat priors and 100,000 Hamiltonian MCMC samples (with a 10,000 sample burn-in, thinning rate of 1 and 4 chains) to achieve > 10,000 effective samples obtained from a No-U-Turn Sampler (NUTS) and our dataset. Well mixed traceplots and appropriate Gelman and Rubin statistics ($\hat{r} < 1.01$) suggested regression MCMC chains to have completely traversed all features of posterior distributions, resulting in achievement of stationary distributions. We report model fit with widely applicable information criterion (WAIC; Gelman et al., 2014; McElreath, 2016) and leave-one-out cross-validation (LOO; Vehtari et al., 2016a; 2016b) metrics.

While uniform (flat) priors are the most frequently prior information utilised in ecological Bayesian models, they have recently been criticised for not actually being "non-informative," for simply providing the same results as frequentist methods, and perhaps most importantly potentially suffering the high Type I and Type M error rates as frequentist methods (summarised in Lemione, 2019). Weakly informative priors present one solution, incorporating basic biological sense-regularising data through constraining inferences (stabilising priors) to a feasible and reasonable range (Lemione, 2019). Weakly informative priors were compiled through review of previous literature (Malhotra et al., 2011; Cox et al., 2012; Strine et al., 2015) and this current work, specifically looking at minimum, maximum, standard deviation and mean values. We provide weakly informative priors with wide (but still biologically realistic) standard deviations as a reasonable constraint for all measurements (not distinguishing between sex, study area, or gravidity, Supplementary Table 1).

Mean and standard deviation measurements from Strine et al. (2015) were incorporated as informed priors for a subset of our data-forest snakes which included both gravid and non-gravid females as well as males (Supplementary Table 1). The Strine et al. (2015) study specifically investigated male and female *T. macrops* in dry evergreen and mixed deciduous forest of SBR, so we did not utilise them as a prior for rural vipers in our study. Additionally, we did not use Strine et al. (2015) results as a prior for non-gravid female and male comparative analyses because the previous study did not distinguish between female gravidity.

We provide 95 % highest density intervals (HDI) for the difference in means (posterior distribution) of viper sex in the forest and rural areas for each morphometric variable estimated, calculated with the "wiqid" R package. For each measurement, we also attempt to provide an ecologically relevant probability of observing a given difference between sexes (i.e. one sex being 15 g heavier) calculated through the posterior distribution.

RESULTS

We made 93 captures of 85 different vipers (8 recaptures) between January 2015–January 2017. After removing measurements from the first captures of recaptured snakes, juvenile and neonate snakes (N = 12), sample size for our analyses was 73 individuals. Similar to Strine et al. (2015), we also observed a postocular eye stripe present for all males analysed (N = 32), which was absent in females (N = 41). Final analyses included 41 individuals in forest habitat (N = 14 male and N = 27 females; N = 14 gravid, N = 7 non-gravid and N = 6 unknown gravidity females) and 32 individuals in rural habitat (N = 18 male and N = 14 females; N = 6 gravid, N = 6 non-gravid and N = 2 unknown gravidity females).

Initial analysis of male and female vipers (regardless of gravidity or capture location) followed a similar trend to Strine et al. (2015). All measurements showed obvious dimorphism between the sexes (Supplementary Table 2; 80–100 % probability of observing differences, Supplementary Table 3) with head length, head width and SMI exhibiting lowest dimorphism. Females were larger than males for all measurements, except for tail length (males longer than females, > 99 % probability).

We observed similar relationships between head size and SVL and SMI (Figs. 2 & 3, summarised in Supplementary Table 4) as Strine et al. (2015). Head size was positively correlated between SVL for both males and females (Fig. 2). Head size was positively correlated between SMI for females, but negatively for males (Fig. 3). There was a relatively weak relationship between head size and SMI for gravid and non-gravid females (Fig. 4).

Sexual dimorphism was strongly predicted for *T. macrops* in rural habitat (Supplementary Table 5; > 90 % probability of observing differences, Supplementary Table 6), with females estimated to be larger than males for all measurements other than TL, for which there was strong support (> 95 %) that males were longer than females. However, SMI was similar between the sexes (about 60 % probability of observing a difference) in rural habitat. Support for sexual dimorphism for forest vipers was strong (> 90 %) for SVL, TL, mass and girth measurements but not for total body length, head length and head width (about 54–80 %, Supplementary Table 6). Forest female viper SMI was clearly larger than male (Supplementary Table 5; > 95 % probability, Supplementary Table 6).

Closer inspection of sexual dimorphism with respect to gravidity of females yielded contrasting results to general differences observed between sexes in our study

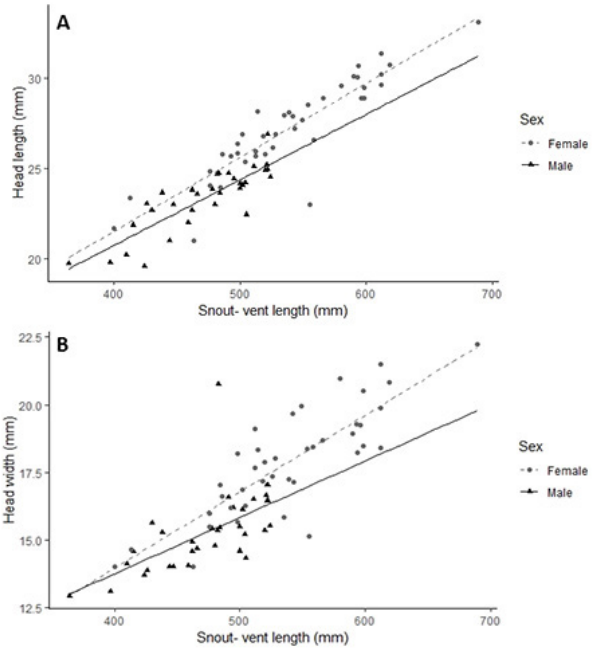

Figure 2. The relationship between **(A)** snout- vent length (SVL) and head length (HL) of male (N = 32) and female (N = 41), and between **(B)** SVL and HW of male (N = 32) and female (N = 41) *T. macrops*. Model summaries are presented in Supplementary Table 4.

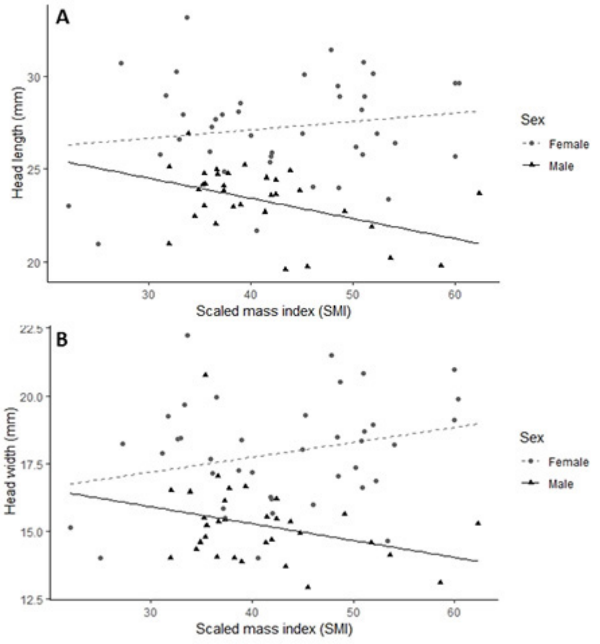

Figure 3. The relationship between **(A)** scaled mass index (SMI) and head length (HL) of male (N = 32) and female (N = 41), and between **(B)** SMI and HW of male (N = 32) and female (N = 41) *T. macrops*. Model summaries are presented in Supplementary Table 4.

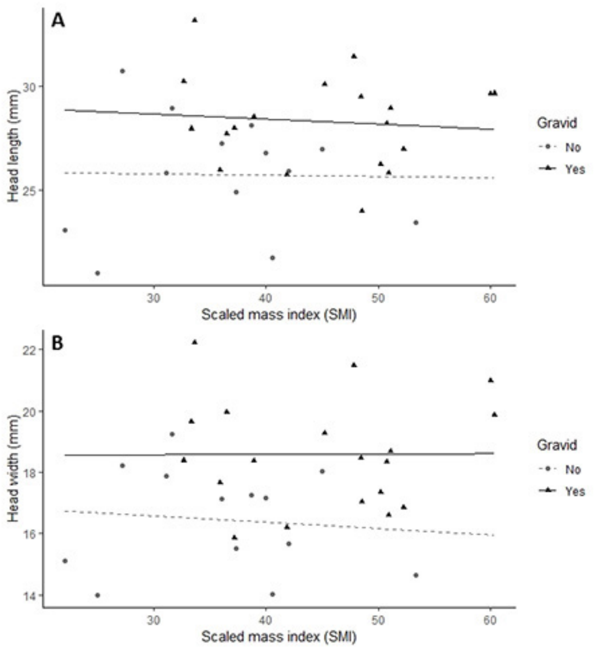

Figure 4. The relationship between **(A)** scaled mass index (SMI) and head length (HL) of gravid (N = 20) and non-gravid (N = 13), and between **(B)** SMI and HW of gravid gravid (N = 20) and non- gravid (N = 13) *T. macrops*. Model summaries are presented in Supplementary Table 4.

and previous study (Supplementary Table 7). Probability that females were 15 g heavier than males dropped from > 90 % in the forest area when gravid and non-gravid females were included in analyses down to just 8 % when only non-gravid females were gauged against males (Supplementary Table 8). Sexual dimorphism was even less pronounced for rural areas, when gravid females were excluded there was only about 2 % probability that non-gravid females were 15 g larger than males (compared to about 94 % with both gravid and non-gravid females analysed, Supplementary Table 8). Girth as a function of dimorphism also decreased with exclusion of gravid females, although markedly less so (Supplementary Table 8). Male body condition (SMI) was higher than non-gravid females in both study areas (Supplementary Tables 7 & 8).

Males in rural habitat were not markedly larger or smaller than male forest vipers for most measurements, except for mass and SMI (Supplementary Tables 9 & 10). Measurements of male SVL, TBL and girth (except at 50 % of the body) were particularly similar for both habitat types. Rural females were larger than forest females for all measurements, however, with the exception of TL (Supplementary Tables 9 & 10).

DISCUSSION

We observed similar trends of sexual dimorphism as previous study of *T. macrops* (Strine et al., 2015) and other green pit viper species such as *T. albolabris* (Devan-Song et al., 2017) and *T. vogeli* (Malhotra et al., 2004), with females attaining larger sizes than males (except for tail length). Similar to Strine et al. (2015), there was also pronounced colouration difference (eye stripe present for males, but not females) for *T. macrops* in our study. Sexual size dimorphism was clearly evident in both rural and natural forested habitat for *T. macrops* in our study, although to different degrees. Sexual dimorphism was greatly diminished when gravid females were excluded from analyses, however. Interestingly, we observed that males were similar in size in rural and forested habitats but females were larger (except for TL) in rural habitats.

Previous study of SSD for *T. macrops* by Strine et al. (2015) proposed morphological differences between males and females of this species to be due to several factors. Smaller size of males was suggested to increase mobility for finding and tracking females, decrease predation risk and the ability to utilise higher perches and more distal edges of vegetation. Explanation provided by Strine et al. (2015) for longer TL was that longer tails potentially contained longer hemipenes, thus leading to higher mating success of males. Increased perch availability was anecdotally supported by that study through several observations of predation of *T. macrops* by king cobras (*Ophiophagus hannah*). Support for increased mobility (compared to females) has somewhat been supported by subsequent Strine et al. (2018) and Barnes et al. (2017) radiotelemetric studies of *T. macrops* spatial ecology. This system might be female-biased due to reproduction costs of females for this viviparous species.

Recent publication of several observations of *T. macrops* mating at the Sakaerat Biosphere Reserve (Strine et al., 2018) provides mixed insight into sexual size selection of *T. macrops*. Females (larger in all observations) were observed pulling males, which suggests size may be important (except tail length, following the female reproductive output hypothesis, King, 1989) for this sex with regards to strength and subsequently being able to select microhabitat with reduced predation risk during copulation- which was observed to last as long as nearly 13 hours in duration. A second male was observed aggressively attempting to disrupt (wrestling and biting) a copulating male in one of the observations, although this larger intruder was unable to disrupt his competitor and ultimately failed to copulate with the female in the observation. The hemipenes of the copulating male were visibly stretched outside of the body while combat ensued, supporting selection for increased tail length of males (following the morphological constraint and male mating ability hypotheses, King, 1989; Shine et al., 1999). The failure of the larger male to disrupt the copulation may provide evidence for limited or lack of selection pressure for larger males from a reproductive context.

Our results suggest non-gravid females to be similar morphologically to males (particularly in rural areas), with much of the observed intraspecific dimorphism resulting from gravid individuals. Gravidity incurs unique challenges to viviparous snakes, particularly locomotion (movement and home range; Seigel & Ford, 1987; Johnson, 2000). Spatial ecology of *T. macrops* in rural areas of Sakaerat Biosphere Reserve by Barnes et al. (2017) previously suggested non-gravid females to exhibit increased median movement and larger median home ranges than gravid females, although these results were not statistically significant.

In addition to sexual size dimorphism, Malhotra et al. (2011) also suggested geographic variation between populations of *T. macrops*. Our results suggest habitat and human disturbance may influence external morphology expression. Rural female *T. macrops* in our study were larger morphologically than forest individuals (mean 553.1 cm, 534.2 cm SVL, respectively). Mean home range sizes (minimum convex polygon estimation method) of female vipers from rural areas of SBR from Barnes et al. (2017) were somewhat smaller than female vipers from more protected forested areas in the Strine et al. (2018) study (0.099 ha and 0.175 ha, respectively). Reduced habitat complexity and availability of suitable habitat (reflected by smaller home range size compared to forest females, which are smaller morphologically), thus increasing intrasexual selection, may provide a possible explanation for this observation. Additionally, rural environments pose unique challenges to venomous snakes, and we have observed both mortality (snake) and human-snake conflict for other species at our study site in northeast Thailand (Knierim et al., 2017; Marshall et al., 2018). However, gravid rural females in our study appeared to skew sexual dimorphism results more significantly than forest snakes (potentially influencing inclusive comparison of females in the two habitat types), which requires further investigation. Male *T. macrops*, however, were similar in size morphologically between forest and rural habitat. How males utilise habitat and space is more difficult to adequately address due to limitations of technology (current radio transmitter size and corresponding battery life restrictions) and significantly smaller body size of this sex.

Future study to better understand the role of SSD for *T. macrops* and other green pit viper species requires an increase in ecological and natural history study. Radiotelemetry has traditionally been the go-to method for addressing such questions for snakes, however, green pit viper size (particularly males) makes this a costly and potentially unethical endeavour due to multiple transmitter replacements and size of transmitters compared to mass and girth. Harmonic tracking may provide a suitable alternative for spatial, movement and habitat selection investigation of green pit vipers due to smaller tag size and nature of the technology (tags reflect, rather than transmit signals; methodology presented specifically for small snakes by Engelstoft et al., 1999). Furthermore, fixed camera technology has shown remarkable promise for prey selection, activity period, conspecific interactions and general behaviour investigation of green pit viper species at SBR (Barnes et al., 2018; Barnes & Knierim, 2019; Barnes et al., 2020).

Long-term investigations are required for better understanding of green pit viper basic biology and ecology. Interestingly, our longest individual (689 mm SVL, 829 mm TBL and 88.9 g), a gravid female, was captured in the forested study area and was longer than sizes previously reported by Cox et al. (1998; 720 mm TBL), Das (2010, 720 mm TBL), Malhotra et al. (2011; 629 mm SVL), Cox et al. (2012; 660 mm TBL), Chanhome et al. (2011, 600 mm TBL) and Strine et al. (2015; 663 mm

SVL, 791 mm TBL). This individual was initially captured as an adult on 1 June 2014 (thus, was part of both our and Strine et al. 2015 study; 663 cm SVL, 791 cm TBL) and then again on 2 May 2015 (674 cm SVL, 806 cm TBL) before the last/final capture (17 September 2016) which was used for our analyses. Furthermore, this individual supported previous small home range hypotheses for the species nicely (< 0.5 ha minimum convex polygon method; Barnes et al., 2017; Strine et al., 2018, Barnes et al., 2019)- all captures were < 150 m of each other (or an area of 0.3 ha when the points are connected). Thus, multi-year morphological investigations such as ours (or longer) can provide valuable insight into survival and growth, as well as dimorphism and other ecological variables of interest. For green pit viper species (or other snake taxa) which are threatened with imminent extinction (such as the Kanburi pit viper, *Trimeresurus kanburiensis*), photographic image processing programs (such as ImageJ) can provide less invasive alternatives (refer to Astley et al., 2017 for comparison; and Herrel et al., 2011 for use with another green pit viper) to traditional measuring methods utilised for morphological investigations.

Despite being one of the more commonly encountered snake species at SBR, *T. macrops* can be relatively difficult to locate during quantified searches at this site (9.1 surveyor hours to find one at all study locations, total 228.7 surveyor hours surveyed during our study period). Although logistically challenging and requiring much thought into study design, comprehensive natural history and ecology work would prove invaluable to understanding green pit viper sexual size dimorphism and general biology. Conservation and snakebite management may also benefit from further SSD study, such as diet and habitat differences between males and females (niche partitioning), particularly through application of Bayesian frameworks which have the potential to incorporate previous knowledge and the benefit of providing intuitive and useful probabilities (crucial for lay-people and managers with limited statistical background) rather than arbitrary p–values (refer to Ellison, 2004 for benefits, caveats, comparison to frequentist methodology and application of Bayesian inference to date in the field of ecology).

DATA & CODE AVAILABILITY

Supplementary Table 1 contains previous knowledge incorporated into priors utilised for this study; Supplementary Tables 2–10 contain summary inferential information including summaries of mean differences, probabilities of observing differences and posterior summaries and convergence statistics; Supplementary Table 11 contains basic data (month of capture, whether a capture was in the forest or rural site, viper sex and if a viper was gravid or not) of vipers included in analyses; and example R code to run “wiqid” models are available at https://osf.io/rgf4y and “brms” model code is available at https://osf.io/gbzw5.

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