

Skewed Sex Ratio of the Chinese Green Tree Viper, *Trimeresurus stejnegeri stejnegeri*, at Tsaochiao, Taiwan

Shiuang Wang, Hua-Ching Lin and Ming-Chung Tu*

Department of Biology, National Taiwan Normal University, Taipei, Taiwan 116, R.O.C.

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Shiuang Wang, Hua-Ching Lin and Ming-Chung Tu (2003) Skewed sex ratio of the Chinese green tree viper, *Trimeresurus stejnegeri stejnegeri*, at Tsaochiao, Taiwan. *Zoological Studies* 42(2): 379-385. Preliminary collecting of adult Chinese green tree vipers, *Trimeresurus stejnegeri stejnegeri*, in Tsaochiao, northwestern Taiwan, yielded a male-biased sample. According to the sex ratio theory, a skewed sex ratio is unlikely at birth, and the above results may thus reflect sampling bias or differential mortality after birth. We collected litters of neonates of this viviparous snake from a broader area over a longer period to examine causes of such numerical dominance of males in the adult sample. We collected 23 gravid females from the Tsaochiao area in 3 consecutive reproductive seasons and obtained 50 male and 40 female neonates. The sex ratio at birth was not significantly biased. We marked and released a total of 169 male and 79 female *T. s. stejnegeri*. Marked snakes were recaptured 940 times. Regardless of season, time of day, transect, or sample area, we always encountered more males than females. Thus, sampling bias did not likely account for this skewed sex ratio. In the adult sample, the ratio of males was greatest in the largest size class, and this suggests that females are subjected to higher mortality. We thus hypothesize that the skewed sex ratio observed in overall adult samples of *T. s. stejnegeri* reflects such differential mortalities between sexes that are probably derived from a higher cost of reproduction in females. <http://www.sinica.edu.tw/zool/zoolstud/42.2/379.pdf>

Key words: Sex ratio, Mortality, Habitat, Activity, Snake.

Parents should invest an equal amount of reproductive effort into their male and female offspring (Fisher 1930). Assuming that the offspring of each gender costs the same, equal numbers of males and females should be produced over the reproductive lifetimes of the parents (Trivers and Willard 1973). Thus, in natural populations there should be equal numbers of males and females, a 1:1 sex ratio. In snakes, many populations actually show sex ratios that do not significantly deviate from this predicted value at birth (Shine and Bull 1977). However a few species, such as *Bitis arietans* (Pitman 1974), *Agkistrodon contortrix* (Fitch 1960 1961), *Notechis scutatus* (Shine and Bull 1977), and *Pituophis melanoleucus* (Gutzke et al. 1985), exhibit skewed offspring sex ratios.

A skewed sex ratio may result from a variety of causes. In species with temperature-dependent sex determination (TSD), such as most turtles

(Ewert et al. 1994), all crocodiles (Lang and Andrews 1994), and many lizards (Viets et al. 1994), the incubation temperature may skew the hatchling sex ratio. Indeed, skewed hatchling sex ratios are common among crocodylians and turtles (Bull and Charnov 1989). Differential mortalities in males and females (Julian 1951, Gutzke et al. 1985, Gibbons 1990) may also lead to skewed sex ratios (Comfort 1979). Causes of skewed sex ratios in samples include sexual differences in activity patterns (Semlitsch et al. 1981) and habitat utilization (Keenlyne 1972, Heatwole 1977, Reinert 1993), which may cause sampling bias for a particular sex.

We obtained a male-biased sample of the Chinese green tree viper, *Trimeresurus s. stejnegeri*, at Tsaochiao, northwestern Taiwan. In this snake, the gender is determined by the ZW sex chromosome system (Huang et al. 1991) like in

*To whom correspondence and reprint requests should be addressed. Tel: 886-2-29336234 ext. 321. Fax: 886-2-29312904. E-mail: biofv026@scc.ntnu.edu.tw

many other advanced snakes, (Gorman 1973, Vorontsov 1973). Although Burger and Zappalorti (1988) demonstrated that eggs of *P. melanoleucus* incubated at extreme temperatures experienced differential, gender-based mortality, similar research has not been conducted on viviparous snakes such as *T. s. stejnegeri*.

In snakes, a skewed sex ratio at birth (the primary sex ratio) rarely occurs. Nevertheless, the sex ratio observed for older age groups (the secondary sex ratio) frequently deviates from equality (Parker and Plummer 1987), indicating probable sampling bias as a result of ecological divergences between males and females (see above), or differential mortality between the sexes after birth. To examine the cause of the skewed sex ratio, we checked the gender for a number of newborn litters of *T. s. stejnegeri*. We also conducted additional sampling from a broader area over a longer period.

MATERIALS AND METHODS

Study sites

We conducted this study at Tsaochiao Village (24°37'N, 120°51'E), Miaoli County, northwestern Taiwan. The study area, approximately 0.5 km², includes rice paddies and a deciduous forest dominated by *Acacia confusa*, *Machilus zuihoensis*, and *Aleurites montana*. The forest is clustered on small hills ranging from 50 to 100 m above sea level (Fig. 1).

We began a monthly survey for vipers along our main transect (T1) in May 1996 which lasted until Apr. 1999. Transect T1 mostly runs along a ditch, which is about 3 m wide and 2.5 m deep, that winds along the edge of the forest. In July 1997, we established a 2nd transect (T2) and checked it monthly until Nov. 1998. T2 follows a small forest trail and largely parallels T1. We also checked 16 other sites in the study area on an irregular basis. These sites included 4 macrohabitats: grassland, bamboo forest, deciduous forest with a ditch like T1, and another deciduous forest trail, like T2.

Sampling and measurements

Trimeresurus s. stejnegeri exhibits pronounced sexual dimorphism (Mao 1962, Tsai and Tu 1998). Females have a relatively shorter and more slender tail than males. In addition, only

males usually have a red stripe running just beneath a ventrolateral white stripe on the body, although a small proportion of snakes does not exhibit such color dimorphism (Tsai and Tu 1998). It is easy to determine the sex of most individuals by these features, or when necessary, by checking the relative depth of the tail base, or by applying pressure there to see whether hemipenes evert. Neonates were sexed using a sex probe.

Throughout the study, the ground and branches at each sampling site were thoroughly examined for snakes during the night. In addition, T1 and T2 were surveyed monthly from Nov. 1997 until Oct. 1998 at dawn, noon, and dusk. When a snake was encountered, we used a power tape ruler to measure the snout-vent length (SVL) and tail length to the nearest 1 cm and used a Pesola pocket scale to measure the body weight to the

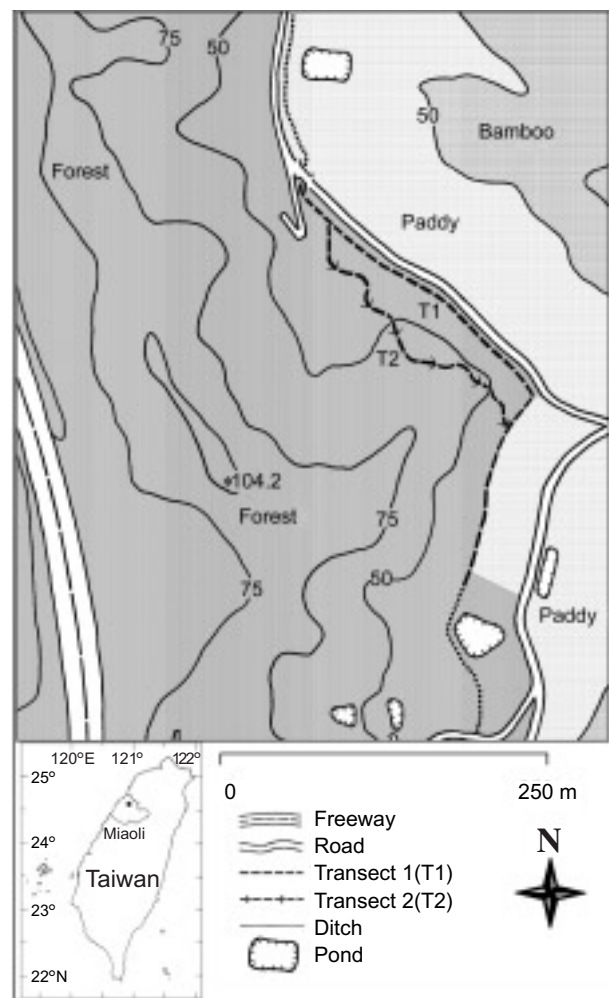


Fig. 1. Map showing roads, vegetation, and geomorphology at the study site in Tsaochiao.

nearest 1 g. Snakes encountered along T1 and T2 were permanently marked with an implanted, subcutaneous mini transponder (Trovan, Cologne, Germany). The permanent marking allowed us to identify each individual and reveal a better sex ratio when 1 sex is much more active than the other sex. This treatment also allowed us to study their population ecology, the result of which will be published in the near future. Except for gravid females, whose conditions were determined by palpation, snakes were released at the collection site. We kept each gravid female in a separate, indoor cage containing a water dish, a shelter box, and perch twigs. Cages were set under natural light, and air temperature was maintained at 23-29°C. We fed each gravid female with a live frog (*Rana limnocharis* or *R. latouchii*) twice a month. Gravid females were kept until parturition and then were released at the site where they were collected. Within 24 h after birth, we sexed the neonates and used a power tape ruler to measure the SVL and tail length (to the nearest 1 cm), and used a digital scale to measure the body weight (to the nearest 0.1 g). Because the offspring sex ratio may vary

with maternal size, we transformed data for the female SVL and offspring sex ratio to determine the effect of the former on the latter variables following Dunlap and Lang (1990).

Sex ratios in different size classes

Excluding neonates, we classified marked snakes into 4 arbitrary size classes and compared the sex ratio among them. The size classes were: class 1, SVL < 33 cm; class 2, 33 < SVL < 43 cm; class 3, 43 < SVL < 53 cm; class 4, SVL > 53 cm. Females of *T. s. stejnegeri* become sexually mature at SVL > 43.2 cm (Tsai and Tu 1998).

RESULTS

Primary sex ratio

In 3 years, we collected 23 gravid female *Trimeresurus stejnegeri stejnegeri*. They gave birth to 50 male and 40 female neonates (Table 1). Although there were more male neonates than

Table 1. SVLs and masses before and after parturition of gravid female *Trimeresurus s. stejnegeri*, their offspring number of each sex, and average neonate mass of sexes

Gravid females			Neonates			
SVL (cm)	Mass (g)		Number		Mass (g) (average ± SD)	
	before	after	♂	♀	♂	♀
44.1	31.8	20.5	1	1	3.2	3.3
46.1	46.9	33.6	0	1	—	4.1
48.0	55.0	33.0	1	1	5.2	5.0
48.2	53.5	31.9	3	1	3.6 ± 0.2	2.6
48.5	54.8	30.7	4	0	2.8 ± 0.2	—
48.5	51.1	31.0	3	1	3.7 ± 0.0	3.7
48.8	73.0	33.4	2	3	4.4 ± 0.1	4.4 ± 0.0
49.0	39.9	30.4	1	0	3.4	—
50.5	64.2	27.9	3	2	3.6 ± 0.4	3.9 ± 0.1
50.5	58.4	38.5	2	1	3.5 ± 0.3	3.7
50.6	64.3	30.7	5	1	3.4 ± 0.1	3.2
52.0	71.0	41.4	2	2	2.9 ± 0.2	3.2 ± 0.1
52.5	73.4	35.2	3	1	4.1 ± 0.2	3.8
53.5	90.9	44.0	4	3	4.3 ± 0.1	3.6 ± 1.0
54.0	79.7	38.0	2	3	5.3 ± 1.1	5.5 ± 0.5
54.0	89.1	66.9	0	2	—	5.5 ± 0.0
55.0	86.1	52.2	3	3	3.5 ± 0.2	3.7 ± 0.2
55.0	85.1	48.0	1	3	5.3	4.9 ± 0.3
55.0	79.3	48.4	1	3	4.2	4.2 ± 0.3
55.5	76.8	47.0	2	2	4.0 ± 0.1	4.0 ± 0.2
57.5	83.1	62.8	1	3	4.8	4.6 ± 0.2
59.0	107.5	85.1	2	0	6.0 ± 0.1	—
59.0	91.2	49.2	4	3	3.4 ± 0.2	3.2 ± 0.1
			50	40	3.9 ± 0.8	4.1 ± 0.8

females, the primary sex ratio was not significantly biased toward males ($\chi^2 = 1.11$, $df = 1$, $p > 0.05$). The average body masses of male and female neonates of 3.9 g (SD = 0.82, range = 2.6-6.1), and 4.1 g (SD = 0.83, range = 2.5-5.9), respectively, did not significantly differ ($t = 1.39$, $p > 0.05$). The SVL of gravid females ranged 44.1-59.0 cm and averaged 52.0 cm (SD = 4.02). Litter size ranged from 1 to 7 and averaged 3.9 (SD = 1.70). There was no correlation between the neonate sex ratio (Arcsin % male) and maternal size (log SVL) ($r = 0.019$, $p > 0.05$).

Activity patterns

From May 1996 to Apr. 1999, we marked and released a total of 248 *Trimeresurus stejnegeri* (169 males and 79 females) and found a significant male-biased sex ratio (2.1; $\chi^2 = 32.66$, $df = 1$, $p < 0.001$). From these marked individuals, we obtained 940 recaptures (688 male and 252 female), which also exhibited a significant male-biased sex ratio (2.7; $\chi^2 = 202.23$, $df = 1$, $p <$

0.001). The number of recaptured individuals fluctuated seasonally, but we always found more males (Fig. 2). Even among the snakes that were recaptured at dawn, noon, and dusk, we still found more males than females (Table 2). For marked individuals, the sex ratios were significantly skewed toward males at dawn ($\chi^2 = 4.17$, $df = 1$, $p < 0.05$) and dusk ($\chi^2 = 5.59$, $df = 1$, $p < 0.05$).

Habitat utilization

Habitat utilization did not likely account for the male-biased sex ratio. Along T1, we marked and recaptured 878 *T. s. stejnegeri* (644 males and 234 females), that consisted of 232 marked individuals (159 males and 73 females). The marked snakes had a significantly male-biased sex ratio (2.2; $\chi^2 = 31.88$, $df = 1$, $p < 0.001$). Similarly, we found significantly more males than females along T2 (Table 2). We checked 16 other sites in the study area. No *T. s. stejnegeri* were found at 8 sites. At the other 8 sites, we captured a total of 298 *T. s. stejnegeri* (225 males, 63 females). Again, males were significantly greater in number than females ($\chi^2 = 91.13$, $df = 1$, $p < 0.001$).

Sex ratios in different size classes

We marked more males than females in all 4 size classes. Only in class 1 were males not significantly greater in number than females. Significant male-biased sex ratios were found in the other 3 size classes. The sex ratio index, defined as the number of marked males divided by the number of marked males and females, increased from class 1 (0.63) to class 4 (0.83). The largest size class had the highest male-biased sex ratio index (Table 3).

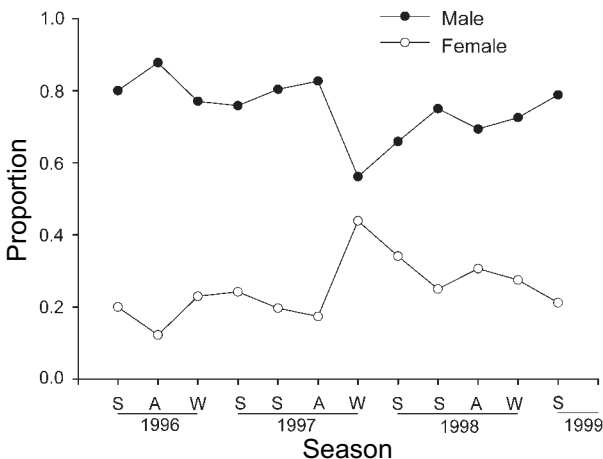


Fig. 2. Proportions of males and females of *Trimeresurus s. stejnegeri* captured along transects T1 and T2 at the study site.

DISCUSSION

Table 2. Numbers of *Trimeresurus s. stejnegeri* captured at different times of the day (dawn, noon, dusk), and along different transects (T1 and T2)

		Marked and recaptured individuals		Marked individuals			
		♂	♀	♂	♀	χ^2	significance
Time	dawn	25	10	20	9	4.17	$p < 0.05$
	noon	19	15	17	12	0.86	NS
	dusk	50	25	38	20	5.59	$p < 0.05$
Transect	T1	644	234	159	73	31.88	$p < 0.001$
	T2	44	18	35	14	9.00	$p < 0.01$

According to Fisher's theory, if male and female offspring cost the same to produce, organisms should produce them in equal numbers. But, if 1 sex is less expensive to produce, the sex ratio will be biased toward it. Because there was not a significant difference in the neonate mass between males and females (Table 1), the skewed sex ratio observed in adult *Trimeresurus stejnegeri stejnegeri* does not seem to have resulted from differences in the cost of male and female offspring. Other factors may influence offspring sex ratios. Large female garter snakes tend to reproduce more males than do small females (Dunlap and Lang 1990). Because no correlation existed between offspring sex ratio and maternal size in *T. s. stejnegeri*, the maternal size effect does not explain the observed sex ratio bias. A similar result was obtained in *T. flavoviridis* from Okinawa, Japan (Nishimura and Kamura 1993).

Gender-based differences in activity patterns or habitat utilization (Gibbons and Semlitsch 1987, Shine 1993) may lead to a sampling bias for a particular sex. A false bias in the sex ratio may thus be obtained if a survey is conducted during a limited period of time or in an area representing only limited types of habitats. In snakes, males are generally more active than conspecific females during the mating season (Gibbons and Semlitsch 1987) and gravid females tend to become inactive, particularly in viviparous species (Fitch and Twining 1946, Krohmer and Aldridge 1985, Gibbons and Semlitsch 1987). Post-ovipositional female habu (*T. flavoviridis*) tend to stay with their eggs which can result in a change in the sex ratio in the ovipositional season (Nishimura and Kamura 1994). We found that parturient females were hardest to locate in the summer. The mating season of *T. s. stejnegeri* begins during late summer and lasts until winter, with the peak during autumn (Tsai and Tu 2000). This may probably explain why we observed a fluctuant sex ratio through dif-

ferent seasons (Fig. 3). Although the proportion of females in samples increased sometimes, females never outnumbered males.

Many species of snakes exhibit sexual dimorphism. A size difference may enable males and females to exploit different habitats, reducing competition between the sexes (Shine 1986 1989). Habitat divergences between males and gravid females and between gravid and nongravid females are common (Reinert 1993). Habitat divergence between male and nongravid female snakes is less pronounced, but has been reported in a few species (Fitch and Shirer 1971, Shine 1986). Nevertheless, no divergence of microhabitat (Tu et al. 2000) or macrohabitat utilization was found between male and female *T. s. stejnegeri*, which are both arboreal. Thus, the skewed sex ratio of *T. s. stejnegeri* is not likely due to habitat divergence.

Clearly, differential mortality after birth is the most likely cause of the male-biased sex ratio of *T. s. stejnegeri*. In field studies of *Crotalus viridis* in which the sex ratio is male-biased, the bias was interpreted as a result of a higher female mortality rate (Diller and Wallace 1984). Similarly, Nishimura and Kamura (1994) attributed the male-biased ratio of habu to the higher rate of survival and/or activity in males than in females. Some studies have suggested that a lower survival rate among gravid squamate reptiles may, in part, result from decreased locomotor ability during gestation. The increasing body mass of gravid garter snakes (*Thamnophis marcianus*) during pregnancy reduces their speed and endurance (Seigel et al. 1987). Reduced locomotor ability may make gravid females especially vulnerable to predation during their prolonged gestation and decrease their foraging ability. Female snakes were found to be emaciated after oviposition (Luiselli et al. 1996) or parturition (Luiselli et al. 1997, Bonnet et al. 2001), due to their high expenditures of energy dur-

Table 3. Sex ratio index, defined as the number of marked males divided by the number of all marked individuals in each of the 4 size classes of *Trimeresurus s. stejnegeri* at the present study site

Class	Snout-vent length	Number of marked individuals		Sex ratio index $\delta / (\delta + \text{♀})$	χ^2	Significance
		♂	♀			
Class 1	SVL < 33 cm	23	15	0.63	1.68	NS
Class 2	43 > SVL \geq 33	33	17	0.66	5.12	$p < 0.05$
Class 3	53 > SVL \geq 43	81	41	0.66	13.12	$p < 0.001$
Class 4	SVL \geq 53 cm	30	6	0.83	16.00	$p < 0.001$

ing gestation. These effects could be exacerbated if foraging by reproductive females is reduced by gestation (Shine 1988, Brodie 1989, Madsen and Shine 1992). Thus, females may have a high mortality rate after reproducing due to high reproductive output (Madsen and Shine 1993, Bonnet et al. 1999).

In the laboratory, on the morning of July 18, 1999, a gravid female *T. s. stejnegeri* was having difficulty during labor. After a couple minutes of observation, we decided to remove the neonate from the cloaca of its mother and found that it was dead. The parturient female seemed exhausted but eventually recovered. In the field, the female may have had difficulty expelling the dead neonate, and could have died. Like *T. flavoviridis* (Nishimura and Kamura 1994), larger female Chinese green tree vipers reproduce more frequently than do smaller females (Tsai and Tu 2001). This combined with a high mortality risk in reproduction may probably result in the highest male-biased sex ratio index in the largest size class. A similar result and reasoning were found in the freshwater turtle, *Chinemys reevesii* (Takenaka and Hasegawa 2001). Whether female reptiles especially viviparous species frequently have a high mortality risk in reproduction and thus induce an age-dependent skewed sex ratio merit further studies.

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