

Ecology and Reproductive Characteristics of the Skink *Sphenomorphus incognitus* on an East Asian Island, with Comments on Variations in Clutch Size with Reproductive Modes in *Sphenomorphus*

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Wen-San Huang (2010) Ecology and reproductive characteristics of the skink *Sphenomorphus incognitus* on an East Asian island, with comments on variations in clutch size with reproductive modes in *Sphenomorphus*. *Zoological Studies* 49(6): 779-788. I describe the diet, and male and female reproductive cycles of *Sphenomorphus incognitus*, an oviparous skink in Taiwan. Most individuals of *S. incognitus* were first observed in a leaf litter microhabitat or at the edge of a forest. The diet of *S. incognitus* consists mostly of orthopteran insects. Two prey categories, crickets and ants, numerically dominated the diet. The stomachs of 2 lizards contained spiders, 2 lizards had eaten insect larvae, and 2 had eaten the blind snake, *Ramphotyphlops braminus*. The mean snout-vent length (SVL) of adult males was 87.6 mm ($n = 45$), and that of females was 79.8 mm ($n = 43$). Males had a significantly larger SVL than females. Females exhibited spring and summer vitellogenesis, with parturition occurring from Mar. to July. The onset of vitellogenesis was not correlated with the female liver mass. Females produced 3-6 eggs per clutch, and clutch size was not correlated with the SVL. Male testis mass showed significant monthly variations, with an increase commencing in Dec. and a peak maintained from Jan. to Apr. Female and male liver masses did not coincide with the period of reproductive activity. Clutch size variations in other *Sphenomorphus* groups were compared to those in *S. incognitus*. Clutch sizes of oviparous skinks were not larger than those of viviparous ones, and clutch size relative to female SVL showed a positive correlation in oviparous skinks but not in viviparous ones. Similarities of the reproductive cycle found in this study and other congeneric *Sphenomorphus* inhabiting temperate and subtropical areas of Taiwan might be explained by phylogenetic constraints. <http://zoolstud.sinica.edu.tw/Journals/49.6/779.pdf>

Key words: Reproductive cycle, Clutch size, Lizard, Food habits.

Many ecological studies (i.e., examining spatial, temporal, feeding, and reproductive patterns) of lizards were carried out in the past 3 decades (Vitt and de Carvalho 1995, Vitt and Zani 1996a b). However, most studies on tropical lizards focused on the Amazon region (Vrcibradic and Rocha 1996, Vitt et al. 1997 2000) and Mexico (Ramirez-Bautista and Vitt 1998, Jimenez-Cruz et al. 2005, Ramirez-Sandoval et al. 2006, Ramirez-Bautista et al. 2006 2008), and little is known about other lowland rainforest lizards (but see Benabib 1994, Ramirez-Bautista et al. 2006), especially on tropical islands of East Asia.

The genus *Sphenomorphus* (Squamata: Scincidae) is an extremely heterogeneous and diverse group distributed in South and Southeast Asia, on islands of the West Pacific, and in Australia (Greer 1974, Ota 1991, Zhao and Adler 1993, Huang 1997a). In Australia, the surface-dwelling *Sphenomorphus* group is divided into 5 genera: *Eulamprus*, *Gnypetoscincus*, *Ctenotus*, *Notoscincus*, and *Eremiascincus* (Greer 1989). *Sphenomorphus incognitus* (Thompson 1912), a surface-dwelling skink, was long known under the name *S. boulengeri* by VanDenburgh (1912), but Thompson's description was apparently published

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1 mo earlier than VanDenburgh's. This species is a poorly known species ranging from southern China to Taiwan, including tropical Orchid I. (Zhao and Adler 1993), off the southeastern coast of Taiwan.

For most tropical oviparous lizards, both males and females seem to exhibit year-round gonadogenesis, with subsequent courtship, mating, and oviposition (Fitch 1970, Huang 2006a b), but some in the seasonal tropics are known to show seasonal cyclicity in reproduction (e.g., Auffenberg and Auffenberg 1989). Although Taiwan is generally categorized as a subtropical area, it does have tropical areas in the southern part of the main island, as well as on Orchid I. (Huang 2004). Climatic patterns on this island are similar to those of tropical regions. Previously, I demonstrated that annual reproductive patterns of 3 high-elevation Taiwanese lizards, *Takydromus hsuehshanensis*, *Eumeces elegans* (the genus has since been changed to *Plestiodon*), and *Sphenomorphus taiwanensis*, resemble those of temperate lizards (Huang 1996b 1997a b 1998); and patterns of 3 tropical lizards, *T. sauteri*, *Japalura swinhonis*, and *Mabuya longicaudata* also resemble those of temperate lizards (Huang 2006a b 2007). Although the reproductive biology of low-elevation subtropical lizards of Taiwan was examined (Cheng 1987), that of lizards of tropical areas such as those on Orchid I. has not been well studied (Huang 2006a b 2007).

Comparisons of clutch sizes in lizard species suggest that in addition to local adaptations (Ota 1994), plasticity in response to environmental variations (Huang 2004), physiological constraints, and phylogenetic constraints (James and Shine 1985, Vitt 1986) all play important roles in determining aspects of clutch size. Likewise, comparative studies of clutch size in animal species have often identified underlying causes responsible for observed reproductive patterns (Huang 2006b 2007). Most such studies suggest that clutch size variations are attributable to latitude, in that lower clutch sizes are found at lower latitudes (Lack 1947, Cody 1966, MacArthur 1972). However, the clutch size of the temperate *S. taiwanensis* ($X = 5.2$) is smaller than that of the subtropical *S. indicus* ($X = 7.3$) in Taiwan (Huang 1996a 1997a). Presently, no such attempts have been made for Taiwanese tropical lizards (i.e., *S. incognitus*), although a number of species have been studied (Okada et al. 1992, Huang 1998 2004).

I studied the ecology of the lizard *S. incognitus*,

including its morphology, clutch sizes, liver mass as an energy source, and reproductive cycles of males and females. I also compared its clutch size to those of other species of *Sphenomorphus* for which data are available.

MATERIALS AND METHODS

This study was conducted on tropical Orchid I. (*Lanyu* in Chinese) ($22^{\circ}02'N$, $121^{\circ}33'E$) situated 60 km off the coast of Taitung County, southeastern Taiwan, from Apr. 1997 to July 2001, at about 100 m in elevation. The mean maximum air temperature from June to Aug. ranged 25.75 - $26.11^{\circ}C$, and the minimum ranged 18.58 - $19.69^{\circ}C$ during Dec. to Feb. The mean maximum monthly precipitation for 11 yr of data in the study area was about 408 mm in Sept., most of which was brought by typhoons in that month (Fig. 1).

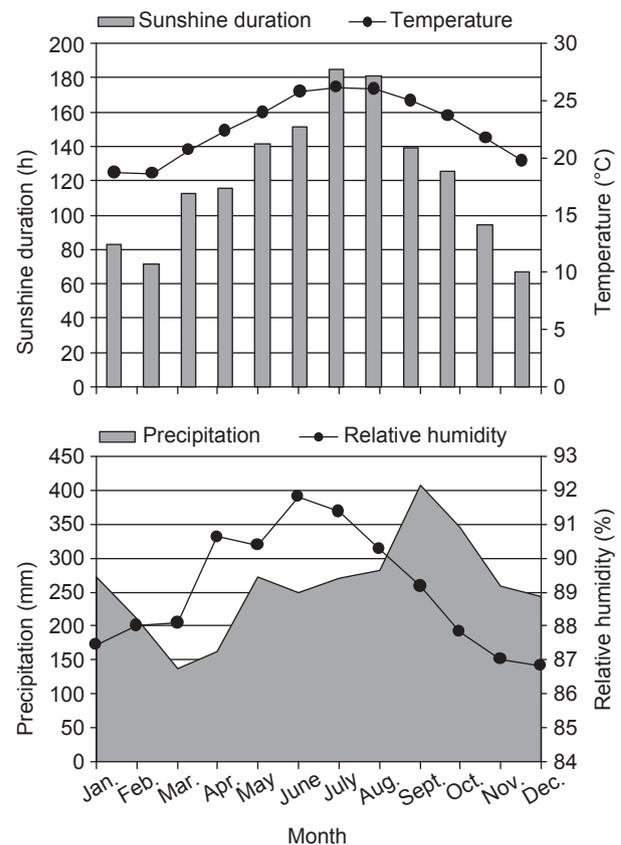


Fig. 1. Annual variation in sunshine duration, temperature, precipitation, and relative humidity during 1992-2002 (monthly average) on Orchid I., Taitung County, Taiwan ($22^{\circ}03'N$, $121^{\circ}33'E$) (Orchid I. Weather Station, Central Weather Bureau, Taipei, Taiwan).

Lizards were hand-collected each month. For each sampling, I attempted to collect 5 males and 5 females, but some monthly samples were smaller due to difficulty in finding lizards in rainy weather (total males, $n = 45$; total females, $n = 43$). After capture, 1) each specimen was weighed to the nearest 0.01 g; 2) its snout-vent length (SVL) was measured to the nearest 0.1 mm; and 3) it was dissected to remove the liver, gonads, and associated organs; all organs were weighed wet to the nearest 0.01 g. The stage of maturity for males was assessed by spermatogenic activity; the appearance of sperm bundles and/or free sperm in the seminiferous tubules in a given specimen was regarded as indicative of maturity.

The reproductive state of adult females was determined on the basis of the presence or absence of vitellogenic ovarian follicles of > 3 mm and oviductal eggs (Huang 2006a b 2007). Females with large vitellogenic follicles or eggs were defined as being reproductively active, and those with neither of these were defined as being inactive. Clutch size was estimated on the basis of the number of larger vitellogenic follicles or oviductal eggs (Huang 2006a b 2007). The time necessary to produce a clutch of eggs was estimated from the period between the dates when the 1st females with larger vitellogenic follicles and the 1st females with oviductal eggs were collected. Clutch frequency was calculated from the estimated laying dates of the 1st and last clutches, and the estimated time necessary to produce a clutch. Females with regressed ovaries which contained follicles of < 3 mm in diameter were considered to be post-parturient. Voucher specimens were deposited at the National Museum of Natural Science, Taichung, Taiwan (NMNS 3260, 3264, 3270, 3273, 3276, 3280, 3283, 3286, 3287, 3294, 3298, 3303, 3306, 3312, and 3366).

To analyze the diets, I removed the stomachs of the lizards, usually within 5 h following preservation, and spread out the prey items in a Petri dish, identified them to family level or the lowest taxonomic category possible, and enumerated them. I used the formula for a prolate spheroid to estimate individual prey volumes: $\text{volume} = 4/3 \pi (1/2 \text{ length} \times 1/2 \text{ width}^2)$ (Vitt and Zani 1996a).

The relationship between clutch size and female body size was examined using Pearson's correlation analysis. I used a t -test to examine sexual differences in SVL between adult males and females, and between viviparous and oviparous lizards. The other variables tested for sexual

differences were body mass (BM), waist diameter (WD, diameter of the waist between the hind limb and abdomen), head length (HL), head width (HW), head depth (HD), tail length (TL), forelimb length (FLL), hind limb length (HLL), 3rd toe length (TTL), and 4th toe length (FTL). Because the organ variables usually varied with SVL, I calculated a regression of all \log_{10} -transformed masses against \log_{10} SVL. Data on monthly differences in the \log_{10} -transformed liver mass (LM) in each sex, and testis mass (TM) in males were assessed by analysis of covariance (ANCOVA) using \log_{10} SVL as the covariate (SAS 8.2, SAS Institute, Cary, NC, USA). I also used ANCOVA (with SVL as the covariate) to determine differences between oviparous and viviparous species, and examined whether the slope of the SVL and clutch size regression differed between the 2 groups. I accepted the analyses if interactions between \log_{10} SVL and test variables were non-significant (homogeneity of slopes). The Mann-Whitney test was used to examine differences in clutch sizes in temperate, subtropical, and tropical lizards. I adopted a type I error level of 0.05 for all statistical tests.

RESULTS

Descriptions of lizard activities

Most *S. incognitus* individuals were first observed in a leaf litter microhabitat or at the edge of the forest. Nearly 79.5% ($n = 70$, including both males and females) of individuals were observed in leaf litter where they were foraging, as the temperature here is higher than in other habitats. The habitat and microhabitat distributions of *S. incognitus* suggest that it is a thermophilic species that mostly occurs in habitats and microhabitats with direct sun exposure.

Diet

Based on samples collected from individuals, 24 of 88 (27.3%) lizards had food items in their stomachs. The diet of *S. incognitus* on Orchid I. consisted mostly of orthopteran insects (35.29%). Two prey categories, crickets and ants, numerically dominated the diet. Two lizards' stomachs contained spiders, 2 lizards had eaten insect larvae (Table 1), and 2 had eaten the blind snake, *Ramphotyphlops braminus* (Table 1).

Morphological parameters

Mean SVLs of adult males and females, at 87.6 ($n = 45$) and 79.8 mm ($n = 43$), respectively, significantly differed from each other ($t = 5.2$, $p < 0.001$), and the mean body mass of adult males (16.54 g, $n = 45$; range, 11.79-21.19 g) was greater than that of adult females (10.00 g,

$n = 43$; range, 6.61-15.18 g; $p < 0.002$) (Table 2). In addition to morphological differences between adult males and females based primarily on size, males had longer, deeper, and wider heads and longer legs than females when the effect of body size was removed (Table 2); whereas, adult males had TLs of 85.42-147.04 mm and adult females of 67.67-122.25 mm, which showed a significant

Table 1. Diet summary for *Sphenomorphus incognitus* from Orchid I. Frequency is the number of lizards containing each prey

Prey type	Volume (mm ³)	Volume (%)	Frequency	Frequency (%)
Orthoptera				
Gryllidae	2080	37.4	8	22.53
Acrididae	240	4.3	1	2.94
Tettigoniidae	660	11.9	3	8.82
Homoptera				
Aphrophoridae	450	8.1	2	5.88
Cicadellidae	550	9.9	2	5.88
Hemiptera				
Gymnocerata	100	1.8	2	5.88
Hymenoptera				
Formicidae	110	2	8	23.53
Lepidoptera	220	4	1	2.94
Blattaria				
Blaberidae	310	5.6	1	2.94
Spider	220	4	2	5.88
Insect larvae	350	6.3	2	5.88
Vertebrate				
Blind snake	270	4.9	2	5.88
Total	5560	100	34	100

Table 2. Morphology of 45 sexually mature male and 43 female *Sphenomorphus incognitus*. BM, body mass; FLL, forelimb length; FTL, 4th toe length; HD, head depth; HL, head length; HLL, hind-limb length; HW, head width; SVL, snout-vent length; TL, tail length; TTL, 3rd toe length; WL, waist length

	Males		Females		p value
	Mean ± S.E.	Range	Mean ± S.E.	Range	
SVL (mm)	87.56 ± 0.74	82.65 - 93.92	79.78 ± 0.70	70.07 - 91.78	< 0.001
BM ¹ (g)	16.54 ± 0.48	11.79 - 21.19	10.00 ± 0.87	6.61 - 15.18	< 0.002
WL (mm)	12.81 ± 0.20	10.40 - 16.64	10.54 ± 0.31	8.80 - 13.87	0.343
TL ¹ (mm)	120.73 ± 3.25	85.42 - 147.04	90.38 ± 2.61	67.67 - 122.25	0.006
FLL (mm)	23.60 ± 0.18	20.91 - 26.19	20.43 ± 0.18	17.81 - 22.66	< 0.001
HLL (mm)	39.09 ± 0.27	33.73 - 42.80	34.04 ± 0.23	31.55 - 37.14	< 0.001
TTL (mm)	5.95 ± 0.06	4.87 - 7.21	5.42 ± 0.07	4.50 - 6.26	0.027
FTL (mm)	5.47 ± 0.06	4.72 - 6.36	4.95 ± 0.06	4.15 - 5.69	0.007
HL (mm)	17.67 ± 0.09	16.27 - 18.81	15.22 ± 0.12	14.15 - 17.08	< 0.001
HW (mm)	11.39 ± 0.08	10.43 - 12.63	9.61 ± 0.10	8.06 - 10.92	< 0.001
HD (mm)	7.77 ± 0.08	6.53 - 8.82	6.55 ± 0.08	5.52 - 7.92	0.024

¹Some individuals lost their tails when captured; thus only 29 males and 30 females were analyzed for TL and BM.

sexual difference in size at maturity ($p = 0.006$; Table 2).

Reproductive cycle

The smallest reproductively active female of *S. incognitus* measured 72.54 mm SVL; therefore, only females with an SVL of ≥ 72.54 mm were considered to be adults. Fifty percent of adult females were reproductively active in Mar. and Apr., 33% in May, 60% in June, and 62.5% in July (Fig. 2). All adult females were determined to be in a non-reproductive state from Aug. to Jan. (Fig. 2).

The 1st vitellogenic females were found on 22 Mar., and the 1st females with oviductal eggs were found on 23 Apr. The interval between the dates when the 1st females with larger vitellogenic follicles and those with oviductal eggs were found was 32 d. I interpreted this as the approximate period required for a female to produce a clutch. There is evidence that some females produce 2 clutches per reproductive season: one of the 10 females collected in Apr. 1998 still had enlarged vitellogenic follicles after having laid eggs.

Clutch size averaged 4.00 ± 1.00 (mean \pm S.D.; range, 3-6) and was not correlated with female SVL ($y = 0.1615x - 8.5834$; $r = 0.65$; $n = 10$; $p = 0.437$; Fig. 3). The clutch sizes of 29 other species of *Sphenomorphus* were correlated with female SVLs ($r = 0.45$, $p = 0.013$; some data are unavailable for a given species; Table 3). An analysis of the clutch sizes of 29 species of *Sphenomorphus* distributed in Taiwan, the Philippines, China, and Australia showed that those of oviparous skinks ($n = 22$, mean = 4.0 ± 1.5 eggs) were not larger than those of viviparous ones ($n = 7$, mean = 3.5 ± 1.2 eggs; $F_{1,27} = 0.35$, $p = 0.56$; ANCOVA, with SVL as the covariate), but SVLs of viviparous species were larger than those of oviparous ones ($t = -4.24$, $p = 0.001$). Clutch size relative to female SVL was positively correlated in oviparous skinks but not in viviparous ones ($n = 22$, $r = 0.52$, $p = 0.023$ in oviparous skinks; $n = 7$, $r = 0.25$, $p = 0.57$ in viviparous skinks; Pearson's analysis). Regression slopes of the 2 groups (oviparous and viviparous) showed no significant differences ($F_{1,27} = 0.013$, $p = 0.91$). Female liver masses showed significant monthly variations ($F_{9,32} = 4.05$; $p = 0.002$; ANCOVA, Fig. 4).

Male reproductive cycle

The left testis mass showed significant monthly variations ($F_{10,33} = 9.58$, $p < 0.0001$;

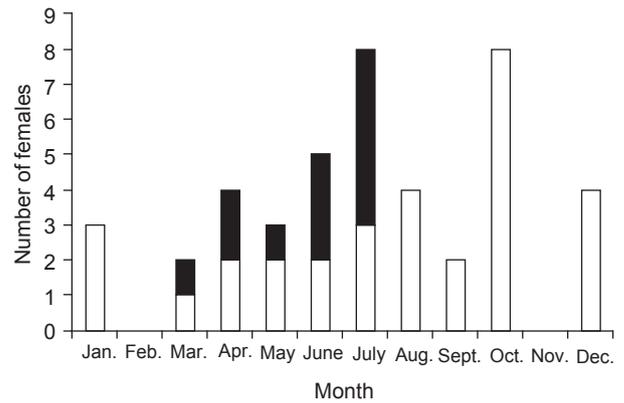


Fig. 2. Monthly sampling distribution of pregnant females of *Sphenomorphus incognitus* on Orchid I., Taiwan. Adult females were reproductively active from Mar. to July, and all adult females were in a non-reproductive state from Aug. to Feb. Black columns indicate the distribution of pregnant females.

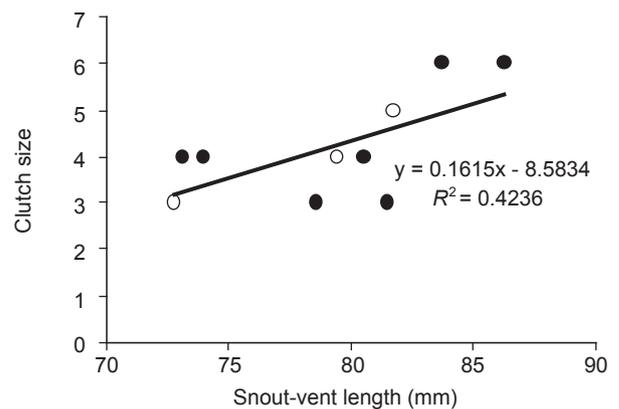


Fig. 3. Correlation between *Sphenomorphus incognitus* female body size (snout-vent length; SVL) and the number of large vitellogenic follicles (open circles) and oviductal eggs (solid circles) on Orchid I., Taiwan.

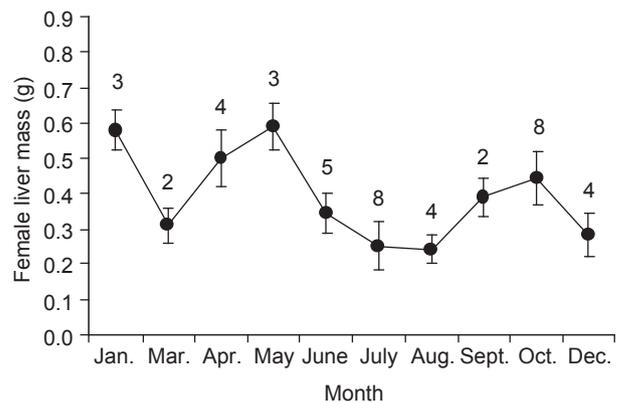


Fig. 4. Variation (mean \pm S.E.) in the mean liver mass during the annual reproductive cycle of females of *Sphenomorphus incognitus* on Orchid I., Taiwan. Numbers above the bars indicate sample sizes.

ANCOVA, Fig. 5A), with an increase commencing in Dec. and a peak maintained from Jan. to Apr. Male liver mass showed no monthly variations ($F_{10,33} = 1.17$, $p = 0.35$; ANCOVA, Fig. 5B).

DISCUSSION

Diet

The predominant prey items of *S. incognitus* were orthopterans (35.29%) and hymenopterans (23.53%). Two prey categories, crickets and ants, dominated the diet. Two lizard's stomachs

Table 3. Clutch sizes (CSs) of 36 species of surface dwelling *Sphenomorphus* groups in Taiwan, the Philippines, China, and Australia. SVL, snout-vent length; RM, reproductive mode; O, oviparous; V, viviparous

Species	<i>n</i>	Locality	Mean SVL (mm)	Mean CS	Range	RM	Source
Taiwan							
<i>Sphenomorphus incognitus</i>	10	Tr Taiwan	79.8	4	3-6	O	This study
<i>S. indicus</i>	24	ST Taiwan	81.8	7.3	4-11	V	Huang 1996a
<i>S. taiwanensis</i>	9	TE Taiwan	57.8	5.2	4-8	O	Huang 1997b
The Philippines							
<i>S. jagori</i>	-	Tr Philippine	75	1.9	1-4	O	Auffenberg and Auffenberg 1989
China							
<i>S. maculatus</i>	1	China	128	5	5	O	Zhao et al. 1999
Australia							
<i>Ctenotus ariadnae</i>	1	Australia	64	4	4	O	Greer 1989
<i>C. arnhemicus</i>	1	Australia	53	4	4	O	Greer 1989
<i>C. atlas</i>	2	Australia	64	1.5	1-2	O	Greer 1989
<i>C. calurus</i>	6	Australia	42	2.7	2-4	O	Greer 1989
<i>C. colletti</i>	1	Australia	45	2	2	O	Greer 1989
<i>C. essingtoni</i>	48	Australia	59	2.9	-	O	Greer 1989
<i>C. fallens</i>	-	Australia	-	4	4	O	Greer 1989
<i>C. gemmula</i>	1	Australia	56	2	2	O	Greer 1989
<i>C. helenae</i>	19	Australia	80	3.5	1-6	O	Greer 1989
<i>C. impar</i>	1	Australia	63	2	2	O	Greer 1989
<i>C. labillardieri</i>	-	Australia	-	-	2-4	O	Greer 1989
<i>C. leae</i>	3	Australia	59	3.7	3-4	O	Greer 1989
<i>C. leonhardii</i>	7	Australia	62	4.7	2-7	O	Greer 1989
<i>C. mimetes</i>	1	Australia	80	6	6	O	Greer 1989
<i>C. pantherinus</i>	11	Australia	76	6.1	3-9	O	Greer 1989
<i>C. schomburgkii</i>	6	Australia	46	3	2-4	O	Greer 1989
<i>C. storii</i>	1	Australia	39	2	2	O	Greer 1989
<i>C. taeniolatus</i>	-	Australia	-	3.7	1-7	O	Greer 1989
<i>Eremiascincus richardsonii</i>	5	Australia	94.6	4.6	3-7	O	Greer 1989
<i>Notoscincus wotjulum</i>	9	Australia	34	2.8	2-4	O	Greer 1989
<i>Notoscincus</i> sp. nov.	2	Australia	37.5	4	4	O	Greer 1989
<i>Eulamprus amplus</i>	1	Australia	-	5	-	V	Greer 1989
<i>E. heatwolei</i>	73	Australia	87.5	3.1	2-5	V	Greer 1989
<i>E. kosciuskoi</i>	19	Australia	69.1	3.1	1-6	V	Greer 1989
<i>E. leuraensis</i>	1	Australia	-	2	2	V	Greer 1989
<i>E. luteiateralis</i>	2	Australia	85	3.5	3-4	V	Greer 1989
<i>E. murrayi</i>	5	Australia	87.8	3.6	2-5	V	Greer 1989
<i>E. quoyii</i>	21	Australia	101	4.8	2-7	V	Greer 1989
<i>E. tenuis</i>	1	Australia	-	7	7	V	Greer 1989
<i>E. tympanum</i>	67	Australia	-	3.7	1-8	V	Greer 1989
<i>Gnypetoscincus queenslandiae</i>	28	Australia	70.1	3.2	2-6	V	Greer 1989

contained spiders, 2 lizards had eaten insect larvae, and 2 had eaten the blind snake, *R. braminus* (Table 1); thus, this species utilizes a mid-sized diet range among lizards studied on Orchid I. (Huang 2004). Lizard diets are typically closely related to their foraging microhabitats, activity periods, and foraging strategies (Greene and Jaksic 1983, Vrcibradic and Rocha 1996, Vitt and Pianka 2004), and that is also true on Orchid I. For example, diurnal species (*Mabuya longicaudata*, and *Japalura swinhonis*) predominately eat arthropods (grasshoppers, bees, or ants) which are active in the daytime, whereas the main food item of a nocturnal species (e.g., *Gekko hokouensis*) is crickets, suggesting that some of the observed differences in diet among these species result from their different activity periods (Huang 2004). However, *S. incognitus* predominately eating ants and crickets seemingly does not mesh with it being active in the daytime, but might be correlated to its foraging areas. For example, some crickets were found in leaf litter during the daytime, and this might be the reason that *S. incognitus* ate this prey item. Likewise, the blind snake, *R. braminus*, an ant predator that is active in leaf litter, is also a palatable food item of *S. incognitus*.

Reproductive cycles

Species in seasonal environments (i.e., temperate regions) experience cyclic reproduction and thereby avoid harsh climatic extremes, whereas species in aseasonal environments (i.e., tropical regions) may be able to continually reproduce (Benabib 1994, Ramirez-Bautista and Vitt 1998, Pianka and Vitt 2003). Temperate-zone lizards have a consistent seasonal pattern of reproduction, with oviposition in late spring or summer months (James and Shine 1985), and this generalization holds true for all scincid, pygopodid, gekkonid, agamid, and varanid lizard taxa studied to date (Shine 1985), except for some viviparous lizards which ovulate in autumn (Fitch 1970, Guillette 1983, Guillette and Mendez-de Cruz 1993). The present results indicate that in females of *S. incognitus*, the reproductive period commences in spring (Mar.) and lasts until early summer (July). This seems to fit the reproductive pattern of many oviparous temperate-zone lizards. These findings greatly differ from the generally accepted reproductive pattern of some tropical lizards being capable of breeding throughout the year, in contrast to temperate lizards which are spring breeders (Fitch 1985). The reproductive timing of a temperate oviparous scincid lizard, *S. taiwanensis*, in which large vitellogenic follicles and oviductal eggs appear in late spring and early summer (May and June) (Huang 1997a), fits the temperate-zone pattern. Similar patterns were also reported for a viviparous scincid, *S. indicus* (Huang 1996a), and an oviparous agamid, *J. brevipes* (Huang 1997b), both of which occur in high-elevation areas (temperate regions) of Taiwan.

Various studies revealed that phylogenetic constraints have a strong influence on the seasonal timing of quiescence and recrudescence of gonadal activity in a few species (Huang 2006a b 2007). However, the reproductive patterns of *Sphenomorphus* in Taiwan mentioned above can simply be explained on phylogenetic grounds, and are more likely to reflect primary physiological responses to environmental stimuli as in some temperate-zone lizards.

Comparisons of the clutch sizes of 29 species of various *Sphenomorphus* groups (Table 3) suggest that species of viviparous and oviparous skinks seemingly have invariable clutch sizes. This finding is in contrast with a study of clutch size variations in the viviparous *S. indicus* (7.3 offspring) and the oviparous *S. taiwanensis* (5.2 eggs), which

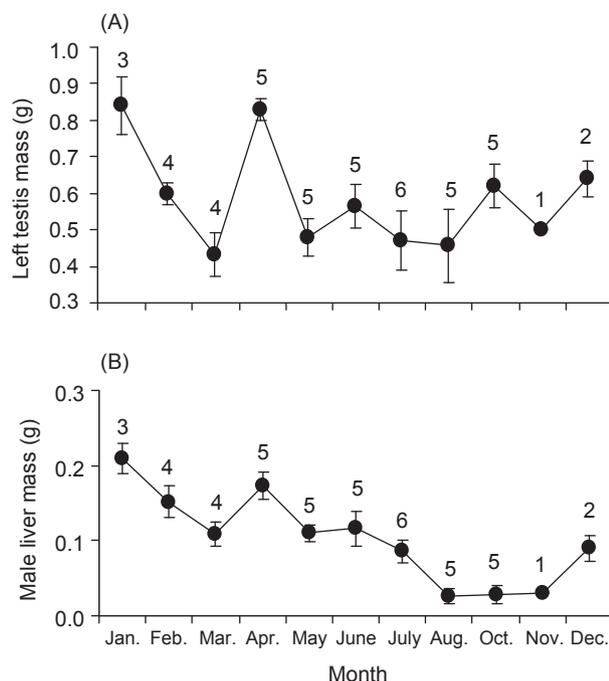


Fig. 5. Variation (mean \pm S.E.) in the mean testis mass (A) and mean liver mass (B) during the annual reproductive cycle of males of *Sphenomorphus incognitus* on Orchid I., Taiwan. Numbers above the bars indicate sample sizes.

found a significant correlation of clutch size with reproductive mode (Huang 2004). Clutch sizes of *Sphenomorphus* species are unlikely to be affected by the reproductive mode. However, primary differences among geographically separated species of *Sphenomorphus* appear to be associated with clutch frequency per season and perhaps the time interval between clutches. For example, the clutch size of *S. incognitus* (4 eggs) is smaller than that of *S. indicus* (7.3 offspring), but the clutch frequency per season is higher in the former (2) than the latter (1).

Shine and Greer (1991) attributed an invariant clutch size to habitats with low variability. For example, spatial fluctuations in resource availability may be particularly low in tropical areas. Presumably, such limited resource supplies may negatively impact the production of larger clutches. This pattern is consistent with tropical lizards, the invariant clutch sizes of which are proportionately more common, such as among Australian scincids, than among their temperate-zone relatives (James and Shine 1985). This tendency is also the same for tropical iguanids (Shine and Greer 1991). The current study indicates that 33 species in the *Sphenomorphus* group seemingly fit this pattern.

In *Sphenomorphus*, clutch size relative to female SVL has a positive correlation in oviparous skinks ($X = 3.6$ eggs) but not in viviparous ones ($X = 4.2$ offspring). This result is in conflict with the hypothesis that lizard clutch sizes usually increase with female body size unless clutch sizes are small (e.g., 3 or 4 eggs/clutch) (Pianka and Vitt 2003). Factors affecting clutch sizes in different reproductive modes of closely related species of *Sphenomorphus* may also be complex. For example, clutch sizes of the viviparous *S. indicus* and oviparous *S. taiwanensis* were positively correlated with female body size ($r = 0.58$, $p < 0.005$ in *S. indicus*; Huang 1996a; $r = 0.93$, $p < 0.001$ in *S. taiwanensis*; Huang 1997b), but this was not found in the current study of *S. incognitus* ($r = 0.65$, $p = 0.437$). Clutch size of *S. incognitus* being unrelated to female body size may have been caused by the unique reptile community on Orchid I., because of the large population of a reptile-egg-eating snake, *Oligodon formosanus* (Huang 2006a). For example, the lizard *J. swinhonis* achieves a clutch size of 4.6 eggs on Taiwan, which is larger than the 3.1 eggs on Orchid I. Furthermore, females of *J. swinhonis* produce more eggs in the 2nd clutch than the 1st clutch in Taiwanese populations (Cheng and Lin 1977), but this was not found in the Orchid I. population

because large clutch sizes are easily located by the reptile-egg-eating snake, jeopardizing egg survival (Huang 2006c 2008 2009). The small clutch size of *S. incognitus* could likewise help avoid detection by this egg-eating snake. These differences might be used to suggest that the reptile-egg-eating snake, *O. formosanus*, affects lizard fecundity on Orchid I., in that females may adjust their investment to minimize predation by this snake.

Sexual dimorphism is common in many lizard species (Huang 1996a), and is usually attributed to sexual selection or trophic divergence (Huang 1996a, Ramirez-Bautista et al. 2008). Males have larger body sizes than females in *S. incognitus* (Table 2), which contrasts with the viviparous *S. indicus*, where females have larger SVLs than males. Fitch (1981) stated that females of viviparous species tend to have a relatively large body in order to support the growth of embryos in oviducts for a much-longer period than those of oviparous species. The current study is consistent with this hypothesis, that viviparous species have larger SVLs than those of oviparous ones. Shine (1989) demonstrated that the widespread distribution of sexual dimorphism in trophic morphology among animals could be consistent with either sexual selection or trophic divergence. For example, head size may be relative to prey size in several reptilian taxa (Huang 2004). In the current study, males have larger head sizes than females, suggesting a divergence in food habits or allometric growth between males and females, because I found no male-male competition (sexual selection) in the wild.

Stored lipids may be used for winter dormancy and/or reproduction (Derickson 1976). In *S. incognitus* and in other *Sphenomorphus* groups (Greer 1989), there are no fat bodies. This suggests that energy accumulated by members of this genus for use in active months may be stored in other organs, such as the liver or tail. However, liver fluctuations observed in males and females did not concur with reproductive activities on Orchid I.

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