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13. 3 (   ) 332. 4 g   24. 8 g   0. 18   0. 13
,   (24   27   30   33   )   21. 0 - 39. 0   (28. 3   )
,   5 d   ,
24   27   30   33   105. 4   78. 0   57. 8   51. 3
58. 6 d   ,   24   30
, 27   33   ,
,   33   SVL   ,
24   30
27   24   , 33
24   30   , 27   9
,   81. 2 %   SVL
(56. 9 %   ) ,
(24. 3 %   ) ,   , 24   30   33
27   [50   (4) : 541 - 550 , 2004]

Reproductive output and effects of incubation thermal environments on hatchling phenotypes of mucous rat snakes Ptyas mucosus *

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Abstract   We collected 15 gravid mucous rat snakes *Ptyas mucosus* in mid-June 2002 from a population in Lishui , Zhejiang , to study reproductive output and effects of incubation thermal environments on hatchling phenotypes. All females laid a single clutch of pliable-shelled eggs within three weeks of being captured. Snout-vent length (SVL) , tail length and body mass were taken for each post-oviposition female. Eggs were individually measured for length and width with a Mitutoyo digital caliper and weighed on a Mettler balance. A portion of viable eggs were incubated either at constant tem-

peratures (24 , 27 , 30 and 33) or at fluctuating temperatures (varying from 21. 0 to 39. 0) until hatching , and the remaining eggs were released to the site where the females were collected. We calculated variances in clutch size and egg size using the coefficient of variation (= standard deviation divided by the mean) and relative clutch mass (RCM) by dividing clutch mass by the female post-oviposition mass. Clutch size , clutch mass and egg size averaged 13. 3 (eggs) , 332. 4 g and 24. 8 g , respectively. Maternal size (SVL) is a major determinant of the reproductive output , with larger females producing more and larger eggs. The coefficient of variation was 0. 18 for clutch size and 0. 13 for egg size. Thus , clutch size is more variable than egg size in *P. mucosus*. Temporal variation in egg mass differed considerably among temperature treatments , primarily because incubation thermal environments affected water exchanges between incubating eggs and their surroundings. Hatching success and hatchling abnormality differed to some extent among temperature treatments , but the differences were not statistically significant. Temperature significantly affected duration of incubation and most hatchling traits examined. The incubation length at 24 , 27 , 30 , 33 and fluctuating temperatures averaged 105. 4 , 78. 0 , 57. 8 , 51. 3 and 58. 6 d , respectively. Eggs incubated at 24 and 30 produced more male hatchlings , whereas eggs at 27 , 33 and fluctuating temperatures more female hatchlings. However , we found no evidence supporting that *P. mucosus* has temperature-dependent sex determination. Energy expenditure for embryonic development was apparently higher in eggs incubated at 24 and 33 than those similarly incubated at moderate temperatures. Thus , a prolonged exposure of eggs of *P. mucosus* at low (< 24) or high (> 33) temperatures appears to have an adverse effect on embryonic development. Hatchlings derived from eggs incubated at 33 were smaller (SVL) than those from lower incubation temperatures (including fluctuating temperatures) and had larger residual yolk mass but smaller carcass mass and carcass ash relative to initial egg mass. A principal component analysis resolved two components (with eigenvalues 1) from nine size (initial egg mass) -free hatchling variables , accounting for 81. 2 % of variation in the original data. The first component (56. 9 % variance explained) had high positive loading for size-free values of SVL , wet mass , dry mass , lipid mass , energy contents , carcass dry mass and fatbody dry mass of hatchlings , and the second component (24. 3 % variance explained) had high positive loading for size-free value of residual yolk mass. Compared with hatchlings from 27 and fluctuating temperatures , hatchlings from 33 had significantly lower scores on the first axis of a principal component analysis but a significantly higher score on the second axis mainly representing egg size-free residual yolk mass [*Acta Zoologica Sinica* 50 (4) : 541 - 550 , 2004].

Key words Mucous rat snake , *Ptyas mucosus* , Reproductive output , Relative clutch mass , Egg , Incubation , Hatchling phenotype

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,

(Fecundity selection) (Survival selection) (Stearns , 1992 ; Sinervo , 1994 ; Bernardo , 1996)

(Sinervo , 1990 ; Clutton-Brock , 1991 ; Stearns , 1992)

, ; ,

(Forsman and Shine , 1995 ; Bernardo , 1996 ; Shine , 2003)

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(Smith and Fretwell , 1974 ; McGinley et al. , 1987 ; Forsman and Shine , 1995) ,

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, (Shine , 2003)

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(van Damme et al. , 1992 ; Braña and Ji , 2000 ;

, 2001 ; , 2002 ; , 2002 ; , 2002 ; Shine and Olsson , 2003)

, ;

, (*Podarcis muralis*) (Ji and Braña , 1999)

,

(Ji and Braña , 1999 ; Ji and Du , 2001a , 2001b ; , 1999 , 2001 , 2002 ; , 2001 ; Flatt et al. , 2001 ; Pan and Ji , 2001 ; , 2002 ; , 2002 ; Ji et al. , 2002a , 2003 ; , 2002 ; Aubret et al. , 2003 ; Du and Ji , 2003)

(*Ptyas mucosus*)

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(1) ( )

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1

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(× × = 0.6
m × 0.6 m × 0.5 m) ,

,

,

Mitutoyo
0.01 mm , Mettler
1 mg ;
(SVL , snout-vent length) , 1
mm 0.1 g ,
/ (Shine ,
1992) , (/)
(Shine and Seigel , 1996) (Seigel and
Ford , 1992) SVL
,
,
(Olsson and Shine , 1997)
SVL
(van Damme et al. , 1992)
,
( )
($n = 62$) (24 27
30 33) (Fluctuating temperature ,
F) , ($n = 88$)

(Ji et al. , 2003) , Tinytalk
(Gemini Pty , Australia) 1 h

(190 mm × 220 mm × 100 mm)
(- 12 kPa , = 1 2)
1/ 3 ,
,
,
5 d ,

1 h (
) ,
, ( ) ,
3
65
55

5.5 h ,
WGR-1 ( ) ,
700 12 h
, Kolmogorov-
Smirnov Bartlett
(Statistica) ,
Log_e
(ANOVA)
(ANCOVA) Tukey

G , ±
, = 0.05

表 1 (n = **15**)
Table 1 Descriptive statistics of reproductive characteristics of female Ptyas mucosus (n = **15**)

	Mean	Standard error	Range
Snout-vent length（mm）	1 386.5	15.3	1 290 - 1 510
Tail length（mm）	437.6	19.5	221 - 495
Post-oviposition body mass（g）	557.9	28.2	385.5 - 739.7
Clutch size	13.3	0.6	8 - 17
Clutch mass（g）	332.4	23.2	160.9 - 547.4
Egg mass（g）	24.8	0.8	20.1 - 32.2
Egg length（mm）	50.6	0.7	47.0 - 56.9
Egg width（mm）	28.1	0.6	23.8 - 32.8
Relative clutch mass	0.59	0.02	0.41 - 0.74

2

2.1

6 20 - 7 8 ,
1 (r^2
$= 0.54$, $F_{1,13} = 15.37$, $P < 0.002$) (r^2
$= 0.54$, $F_{1,13} = 15.57$, $P < 0.002$) ($r^2 =$
0.28 , $F_{1,13} = 5.04$, $P = 0.043$) SVL
(, 1)
0.18 0.13
($r^2 = 0.08$, $F_{1,13} =$
1.06 , $P = 0.322$) , SVL
($r =$
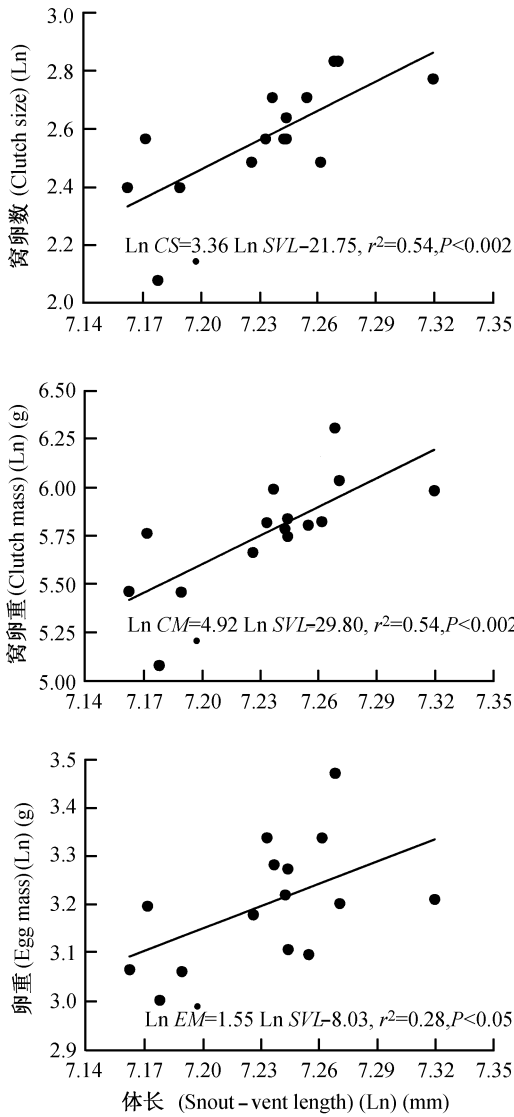0.32 , $t = 1.18$, $df = 12$, $P = 0.260$)
SVL ,
($r = 0.56$, $t =$

1

**Fig. 1   The linear regressions of clutch size,
clutch mass and egg mass on female SVL in the
mucous rat snake** Ptyas mucosus

2. 37， $df = 12$， $P = 0.036$）

　　　　　　　　　，
　　　（ $r = 0.78$， $t = 4.33$， $df = 12$， $P < 0.001$），
　　　　　　　　　　　　（ $r = -0.34$， t
$= 1.26$， $df = 12$， $P = 0.232$）

2.2

　　　　　　　24.3 （ $SE = 0.2$，   ： 21.0 - 27.4）
33.7 （ $SE = 0.4$，   ： 23.5 - 39.0）   28.3
（ $SE = 0.3$，   ： 22.4 - 31.5）
　　　　　　　　　　（21.0 ）   24 ，

2
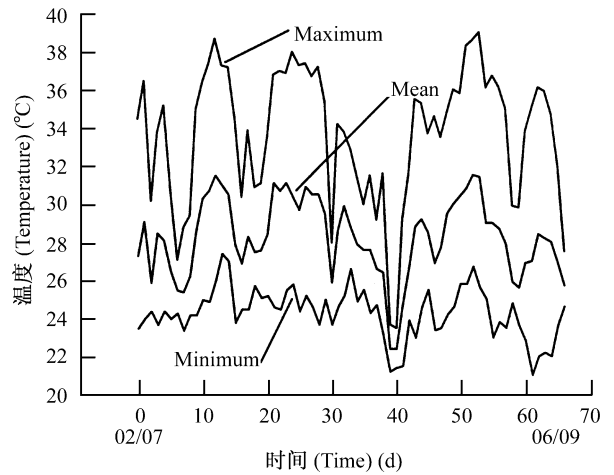
Fig. 2   The thermal environments in which Ptyas mucosus
eggs were incubated

Lines in the figure show daily maximum, average and minimum
temperatures.

3
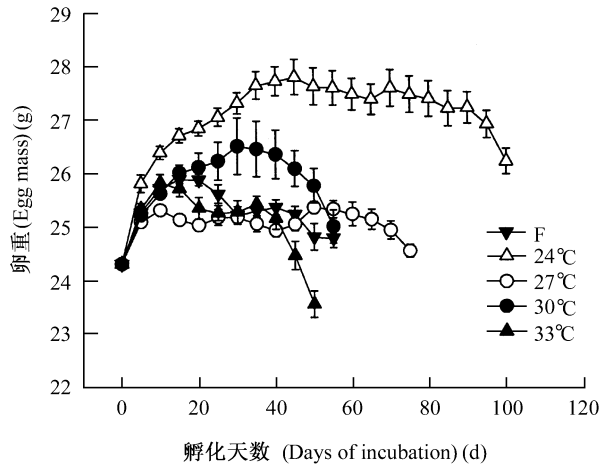
　　　　　　　　±　　　　　　　2

Fig. 3   Temporal changes in mass of *Ptyas mucosus* eggs
incubated in different thermal environments

Data are expressed as means ± SE. Sample sizes are indicated in
Table 2.

　　（39.0 ）   33 （   2）

（   3）
　　　　　，
　　　（ANCOVA， $F_{5,50} = 10.25$， $P < 0.0001$）
Tukey's　　　　　　： 24　　　　　　， 33
　　， 24
　　　　（ $P < 0.002$）

2. 3 （ 2） （ $G =$

ANOVA （ $F_{1,46} = 0.58$, $P =$ 0. 55 , $df = 4$, $P > 0.95$） （ $G =$

0. 451） （ $F_{4,46} = 1.03$, P 4. 17 , $df = 4$, $P > 0.25$） ,

= 0. 400） , ;

（ $F_{4,46} = 4\ 009.04$, $P < 0.0001$） （ $G = 6.86$, $df = 4$, $P > 0.10$） , 24

: 24 - 30 , 27 33

33 3 , （ 2）

27. 4 20. 2 6. 5 d ; 58. 6 d

2

Table 2　Effects of incubation thermal environments on duration of incubation , hatching success , and sex ratio and abnormality of hatchlings

（ ）Temperature	Incubated eggs	（d）Duration of incubation	（ %）Hatching success	（ / ）Sex ratio	（ %）Abnormality
24	10	$105.4^{a} \pm 0.3$ （103. 8 - 106. 3）	90 （9/ 10）	2/ 8	40 （4/ 10）
27	15	$78.0^{b} \pm 0.2$ （75. 7 - 79. 2）	100 （15/ 15）	12/ 3	6. 7 （1/ 15）
30	11	$57.8^{c} \pm 0.3$ （55. 8 - 59. 2）	100 （11/ 11）	4/ 7	18. 2 （2/ 11）
33	14	$51.3^{d} \pm 0.4$ （50. 5 - 51. 8）	78. 6 （11/ 14）	11/ 3	14. 3 （2/ 14）
F	12	$58.6^{c} \pm 0.3$ （57. 3 - 60. 0）	83. 3 （10/ 12）	9/ 3	8. 3 （1/ 12）

± （ ） , （ Tukey's test , = 0. 05） ;

Data on duration of incubation are expressed as mean ± S E （range）. Means with different superscripts differ significantly （ Tukey's test , = 0. 05） .
Dead embryos are taken into account when calculating the sex ratio and the percentage of abnormality.

3

Table 3　Effects of incubation thermal environments on size and composition of hatchlings

	Temperature （ ）					ANCOVA F Tukey's
	24 （ $n = 9$）	27 （ $n = 15$）	30 （ $n = 11$）	33 （ $n = 11$）	F （ $n = 10$）	F values of ANCOVA , significance levels and results of Tukey's multiple comparisons
Snout‑vent length （mm）	332.4 ± 4.3	337.3 ± 3.6	328.7 ± 2.9	309.0 ± 4.0	33.46 ± 2.0	10.50^{***} , 24^{a} , 27^{a} , 30^{a} , 33b , F^{a}
Tail length （mm）	97.7 ± 2.0	103.6 ± 1.1	95.9 ± 3.5	99.5 ± 2.1	106.4 ± 1.7	3.15^{*} , 24^{ab} , 27^{ab} , 30^{b} , 33^{ab} , F^{a}
Hatchling wet mass （g）	15.0 ± 0.5	16.5 ± 0.2	15.5 ± 0.4	14.7 ± 0.5	16.6 ± 0.2	4.59^{**} , 24^{ab} , 27^{a} , 30^{ab} , 33^{b} , F^{a}
Hatchling dry mass （g）	3.65 ± 0.09	4.34 ± 0.06	3.94 ± 0.09	4.30 ± 0.10	4.31 ± 0.05	8.24^{***} , 24^{b} , 27^{a} , 30^{b} , 33^{a} , F^{a}
Hatchling energy （KJ）	80.1 ± 2.1	97.2 ± 1.8	84.5 ± 1.8	93.5 ± 1.9	94.8 ± 1.3	9.63^{***} , 24^{b} , 27^{a} , 30^{b} , 33^{a} , F^{a}
Hatchling lipids （g）	0.87 ± 0.03	1.10 ± 0.02	0.94 ± 0.06	1.09 ± 0.03	1.09 ± 0.02	4.96^{**} , 24^{b} , 27^{a} , 30^{b} , 33^{a} , F^{a}
Hatchling ash （g）	0.42 ± 0.01	0.47 ± 0.01	0.44 ± 0.01	0.43 ± 0.02	0.46 ± 0.01	2.19^{ns}
Carcass dry mass （g）	2.67 ± 0.05	2.93 ± 0.06	2.70 ± 0.07	2.51 ± 0.04	2.89 ± 0.05	8.53^{***} , 24^{bc} , 27^{a} , 30^{bc} , 33^{c} , F^{ab}
Fat body dry mass （g）	0.59 ± 0.03	0.77 ± 0.02	0.57 ± 0.03	0.66 ± 0.02	0.74 ± 0.02	8.27^{***} , 24^{c} , 27^{a} , 30^{c} , 33^{bc} , F^{ab}
Residual yolk dry mass （g）	0.37 ± 0.06	0.66 ± 0.05	0.65 ± 0.05	1.21 ± 0.06	0.69 ± 0.04	27.06^{***} , 24^{c} , 27^{b} , 30^{b} , 33^{a} , F^{b}
Carcass ash （g）	0.40 ± 0.01	0.42 ± 0.01	0.39 ± 0.01	0.35 ± 0.02	0.42 ± 0.01	5.52^{***} , 24^{ab} , 27^{a} , 30^{ab} , 33^{b} , F^{a}
Residual yolk ash （mg）	25.9 ± 4.1	47.5 ± 3.9	43.3 ± 4.2	85.2 ± 4.8	44.4 ± 3.1	21.06^{***} , 24^{c} , 27^{b} , 30^{bc} , 33^{a} , F^{bc}
Hatched eggshell dry mass （g）	0.92 ± 0.01	0.94 ± 0.01	1.04 ± 0.01	1.00 ± 0.01	1.06 ± 0.01	26.53^{***} , 24^{c} , 27^{c} , 30^{ab} , 33^{b} , F^{a}
Hatched eggshell ash （g）	0.21 ± 0.01	0.24 ± 0.01	0.28 ± 0.01	0.26 ± 0.01	0.29 ± 0.01	6.99^{***} , 24^{c} , 27^{bc} , 30^{ab} , 33^{ab} , F^{a}

± , ANCOVA （ 24. 3 g） F : $*P < 0.05$, $**P < 0.01$, $***P < 0.001$ （ Tukey's test , = 0. 05 , a > b > c）

Date are expressed as adjusted mean ± S E. Initial egg mass is the covariate （set at 24. 3 g） in all ANCOVA models. Symbols immediately after F values represent significant levels： ns $P > 0.05$; $*P < 0.05$, $**P < 0.01$, $***P < 0.001$ means corresponding to temperatures with different superscripts differ significantly （ Tukey's test , = 0. 05 , a > b > c） .

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3) 33　　　　　SVL　　　，
　　　　　　　　　　　　　24
30　　　　　　　　　　，27
　　　　24　　30
　　　　　　　　　　　　　27
　　　　　　24
，33

9　　　　　　　　（Eigenvalue 1)　　，　　　　　　　81. 2 %
（　4)　　　SVL

（　56. 9 %　），
（　24. 3 %
）（　4)　　　　　　（ANOVA，$F_{4,50} = 5.83$，$P < 0.001$；24^{abc} 27^a 30^{bc} 33^c F^{ab}，Tukey's test，a > b > c)
（ANOVA，$F_{4,50} = 10.84$，$P < 0.0001$；24^b 27^b 30^b 33^a F^b，Tukey's test，a > b)，　　　24　30　33
27　　　　　　　　　　（　4)

4　9

Table 4　Loading of the first two axes of a principal component analysis on nine variables of hatchling traits

	Factor loading	
	PC 1	PC 2
Snout-vent length	**0. 712**	- 0. 616
Tail length	0. 538	- 0. 303
Wet body mass	**0. 803**	- 0. 218
Dry body mass	**0. 805**	0. 514
Hatchling lipids	**0. 773**	0. 546
Hatchling energy	**0. 909**	0. 367
Carcass dry mass	**0. 886**	- 0. 367
Fat body dry mass	**0. 883**	0. 143
Residual yolk dry mass	- 0. 213	**0. 905**
Variance explained	56. 9 %	24. 3 %

，

Size effects are removed in all cases by using residuals from the regressions on egg mass. Variables with the main contribution to each factor in bold face
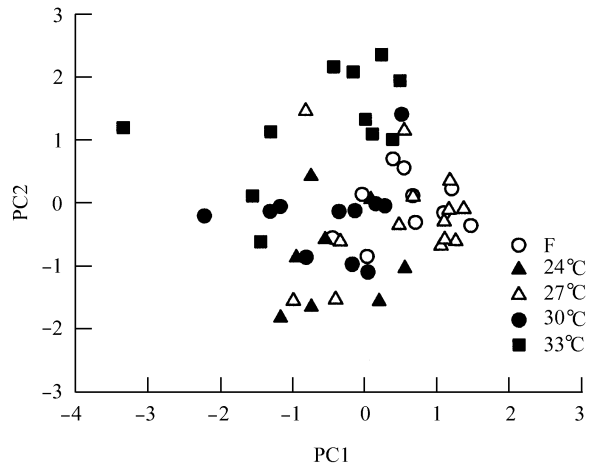

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Fig. 4　Positions of hatchlings from different incubation thermal environments (symbols on the top right corner) in the space defined by the first two axes of a principal component analysis based on nine egg size-adjusted hatchling variables
Effects of egg size were removed using residuals from the regressions of corresponding variables on initial egg mass.

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3. 1

　　　　　　　6 - 7　　　　　　　　　　，
（　　　）　　　　　　　SVL　　　　　，

（ *Dinodon rufozonatum* ）（　　，1999；　　　　　，2002)
（ *Elaphe carinata* ）(Ji et al. , 1997a；Ji and Du , 2001b)　　　　　　（ *E. taeniura* ）(Ji et al. , 1999)　　　　　（ *Ptyas korros*)(Ji and Sun , 2000；　，2002)　　　　　　（ *Zaocys dhumnades*)（　　，2000)　　　　　　　（ *Naja atra*)(Ji and Du , 2001a)
，　　　　　SVL
SVL　　　　　，
（　　，2000)
，　　　　　　；
，
（　　，2000)
，
，

(Ji and Braña , 2000 ;   , 2000) ，

(0. 24 - 0. 34)

(0. 15 - 0. 20) （   ,

2000) ， (0. 18)

(0. 13) ，

，

，

(Stewart , 1979 ; Ford and Killebrew , 1983 ; Ford
and Seigel , 1989 ; Sinervo , 1994 ; Olsson and
Shine , 1997) , (*Elaphe rufodorsa-
ta*) (Ji et al. , 1997b) (*Sinonatrix
annularis*) (Ji et al. , 2001)

，

，

(Iverson and Ewert , 1991)

，

(Shine , 2003) ，

，

SVL

，   (*Eumeces
chinensis*) (, 2000)
(*Eumeces elegans*) (, 2001)
(*Calotes versicolor*) (Ji et al. , 2002b)
(, 2000) ，

蝘
(*Sphenomorphus indicus*)

，
(Ji and Braña , 2000 ;   , 2000 ;
, 2000)   ，

，   (Avery et al. ,
1982 ; Garland et al. , 1990 ; Sinervo , 1990 ;
Braña and Ji , 2000)

，

(Ferguson and Fox ,
1984 ; Sinervo et al. , 1992)

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3. 2

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(, 1998 ; Ji and
Braña , 1999 ; Flatt et al. , 2001 ; Ji and Du ,
2001a , 2001b ;   , 2002)

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(28.3) (27)   ，

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30   , 27 33

(2)   ，

，

(24)   ，

，

，   (
3)

，

(Ji et al. , 1997b , 1999 , 2002a ;
Ji and Braña , 1999 ; Ji and Sun , 2000 ; Ji and Du ,
2001a , 2001b)

，
(Ji and Braña , 1999 ; Ji and Du , 2001a , 2001b ; Ji
et al. , 2002a) 24   (SVL)
(27 30   )   ，
， 24

27   (3) ,
24

24   ，

10   ，

24   (   )

，   ，

(33)   ,
,   (3)   33
(3) ,

,

,   (,
2001;   , 2002)   (Ji and Braña,
1999)   (, 2001)
(Ji et al. , 2002a)   (*Rhabdophis*
tigrinus lateralis) (, 2002)
(*Xenochrophis piscato*) (, 2001)
(Ji and Du , 2001a)   (Ji and Du ,
2001b)   ,

,
(Gutzke and Packard , 1987; Gutzke et al. , 1987;
van Damme et al. , 1992;   , 1999 , 2001,
2002; Flatt et al. , 2001; Ji and Du , 2001a,
2001b;   , 2001;   ,
2002;   , 2002; Ji et al. , 2002b,
2003; Aubret et al. , 2003; Du and Ji , 2003)

30   24   33
,   27
,   27
(3)   , 30   27   20 d
(2)
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30

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27

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