

Masses and Mass Conditions of Body, Clutch and Organs in the Viperid Snake, Habu (*Trimeresurus flavoviridis*) during Clutch Formation

Masahiko NISHIMURA

クラッチ形成に伴うハブの体, クラッチ, 器官の重量ならびに相対重量について

西村昌彦

Abstract : I weighed clutch, fat body, liver and carcass masses of 140 breeding females of habu, *Trimeresurus flavoviridis*. In order to remove the size effect I adopted the mass condition defined as mass/standard mass regressed on snout-vent length. Body mass conditions of the breeding snakes weighed in a month after capture were within the range of 0.8-1.2 in 86% cases. Body mass conditions of breeding and non-breeding females overlapped each other in more than 80% of adult females. The conditions of both clutch mass and fat body mass fluctuated greatly, while the conditions of liver mass and carcass mass fluctuated less greatly than body mass condition. Relative clutch mass, i.e. clutch mass/(total mass - clutch mass), was adjusted by the body mass condition. The adjusted relative clutch mass was negatively correlated to snout-vent length. Carcass mass of breeding females was less than that of non-breeding females. The mass and relative mass of each organ changed through the clutch formation. I simulated the growth in snout-vent length of females skipping breeding. In habu the body mass condition is a main determinant of mass allocation to the clutch and to each organ during clutch formation and determines to the post-reproductive condition of the female.

Key words : Relative clutch mass; Mass condition; Clutch; Fat body; Liver; Carcass; *Trimeresurus flavoviridis*; Okinawa

I Introduction

The degree of reproductive allocation is an important factor in population and life history studies^{1,2)}, especially in vertebrate species with multiple broods in its life. In spite of the several problems in the index^{3,4,5)} many works on snake reproduction have adopted the relative clutch mass (*RCM*) to evaluate the reproductive allocation^{6,7,8,9)}. Generally *RCM* is stable for a given species, and few studies have detected intraspecific changes of the index.

It is natural that masses of storage organs change greatly with body mass condition, which may be also true in the clutch mass. The analysis of relationships between the body mass condition and *RCM* is directly connected to the trade-off of energy allocation between maternal body and clutch, but only Barron¹⁰⁾ has mainly dealt with this theme. Barron used *RCM* adjusted by body mass condition for the water snake, *Nerodia*

sipedon. He indicated that compared to the non-adjusted *RCM* the adjusted *RCM* is more highly correlated to the residuals of clutch mass in the multiple regression on body mass and snout-vent length, and the adjusted *RCM* is a better index to explain the yearly variations in *RCM*. However, in Barron's method of adjustment *RCM* is only multiplied by an "adjustment factor" representing leanness of each female. In order to justify this method the relationships between *RCM* (or clutch mass) and body mass condition should be checked.

In a study of organ mass of habu (*Trimeresurus flavoviridis*) Nishimura¹¹⁾ proposed a new index for the organ mass condition as an organ mass divided by the standard organ mass regressed on snout-vent length. This standardized mass is a ratio but contains few statistical problems. The ratio does not have a measurement of each snake as its denominator, and is identical to the residual in the regression on snout-vent length. This index is free

from the size bias, and was suited to analyze the relationships between the body mass condition and the organ mass condition. This analysis contains a problem of organ mass being included in body mass. I did not use body mass subtracted by organ mass because it differs for each organ and can not be used as a common condition of body mass for each snake, and because body mass is one of the popular measurements. Nishimura¹¹⁾ compared organ masses of three snake groups (small snakes, large males and large non-breeding females) and described several patterns of changes in organ masses. For example, the condition of fat body mass changed greatly with the change of the body mass condition and the relative mass of fat body adjusted by the body mass condition was more highly correlated to snout-vent length than the non-adjusted relative mass.

For breeding females of habu, the body mass has been compared to that of non-breeding females^{12,13)}, but the organ masses have not yet compared. In the present work I calculated the standard masses of body, clutch, fat body, liver and carcass and the conditions of these masses in the breeding females of habu. Then I examined the effects of the body mass condition on the conditions of these organ masses and on *RCM*. I compared the present results of breeding females to the results of non-breeding females¹¹⁾ and estimated the patterns of organ mass changes during clutch formation. Finally I discussed on the body mass condition of adult females during the mating season.

II Materials and Methods

1. Materials

The habu, *T. flavoviridis*, inhabiting in the subtropical Ryukyu Archipelago, copulates between March and May¹⁴⁾, and about a half of the females larger than ca. 90 cm in snout-vent length (*SVL*) lay eggs in July^{12,15)}. Between 1981 and 1994, 140 breeding females were collected in the center and the south of Okinawa Island. Forty snakes of them were killed at the time of capture or in captivity and the other snakes died in captivity. The

definitions of the breeding conditions at the measurement and the abbreviations are shown in Table 1.

I measured *SVL* and weighed body mass (*BM*), fat body mass (*FM*), liver mass (*LM*), carcass mass (*CAM*, body mass without organs in the body cavity) and clutch mass (*CLM*). For the snakes collected between 1981-1984 *LM* and *CAM* were not measured. The mean error range at the measurement of *BM* is 6.0%¹⁶⁾. *BM* of most females kept in captivity for several months decreased. *BM* measured in a month after collection was regarded to represent the field condition.

The frequency distributions of body mass condition (*BMC*) of breeding (n = 141) and non-breeding (n = 877) females in the field were obtained from the data used in Nishimura and Kamura¹³⁾. I set a breeding proportion in adult females to 0.5. In order to describe the relationships between *BMC* and the breeding proportion in an early breeding season, I selected the adult females collected between March and May (45 fertile and 43 non-breeding females).

SVL-BM regression equations were not significantly different between fertile and ovipositional females¹²⁾ (between May and July). *SVL-BM* regression equations of breeding and non-breeding females in the field were calculated based on the data used in Nishimura and Kamura¹³⁾ (Table 2).

2. Calculation of the Standard Masses and Mass Conditions

The standard masses and mass conditions of *CLM*, *FM*, *LM* and *CAM* were estimated by the methods presented in Nishimura¹¹⁾. The outline of the methods is as follows, i) select snakes with *BM* close (within $\pm 10\%$) to the standard *BM* (*SBM*: estimated by the equation in Table 2), ii) estimate the standard organ mass by *SVL*-organ mass regression equation calculated on these snakes, iii) calculate the organ mass condition through dividing an organ mass by the standard organ mass. These organ mass conditions were regressed to *BMC*.

I compared the patterns of organ mass change

Table 1. Definition of the breeding conditions of females of *Trimeresurus flavoviridis* and abbreviations of variables. Standard masses were estimated by the regression equations shown in Table 2.

Reproductive condition or abbreviation	Definition
<i>SVL</i>	Snout-vent length
Ovipositional female	Female having formed full-term clutch, including pre-ovipositional snakes that measured in the last half (post 15 July) of the ovipositional period
Fertile female	Female with oviductal eggs (pre 14 July) or enlarged follicles (> 12 mm long ¹⁵⁾)
Breeding female	Ovipositional or fertile snake
Non-breeding female	Adult female (<i>SVL</i> ≥ 90 cm) other than breeding one
<i>BM</i> *	Body mass including clutch or large follicles
<i>SBM</i>	Standard <i>BM</i>
<i>BMC</i>	Body mass condition (<i>BM</i> / <i>SBM</i>)
<i>BME</i> *	Body mass excluding clutch or large follicles
<i>BMCE</i>	<i>BME</i> condition (<i>BME</i> /standard <i>BM</i> of breeding females)
<i>BMCN</i>	Body mass condition (<i>BM</i> /standard <i>BM</i> of non-breeding females)
<i>BMCE</i> <i>N</i>	Body mass condition (<i>BME</i> /standard <i>BM</i> of non-breeding females)
<i>FM</i>	Fat body mass
<i>FMC</i>	<i>FM</i> condition (<i>FM</i> /standard <i>FM</i>)
<i>LM</i>	Liver mass
<i>LMC</i>	<i>LM</i> condition (<i>LM</i> /standard <i>LM</i>)
<i>CAM</i>	Carcass mass (body mass without organs in the body cavity)
<i>CAMC</i>	<i>CAM</i> condition (<i>CAM</i> /standard <i>CAM</i>)
<i>CLM</i>	Clutch mass
<i>CLMC</i>	<i>CLM</i> condition (<i>CLM</i> /standard <i>CLM</i>)
<i>RCM</i>	Relative clutch mass (<i>CLM</i> / <i>BME</i>)

* *BM* = *BME* for non-breeding females.

among fertile, ovipositional and non-breeding females, using the regressions of organ mass condition to body mass condition. The data of the

non-breeding females was based on the data utilized in Nishimura¹¹⁾. In these comparisons I adopted the standard masses of organs and body and the definition of *BM* as those of non-breeding females. For breeding females, *BM* without clutch and large follicles (*BME*) was divided by *SBM* of non-breeding females to get body mass condition (*BMCE**N*) comparable to *BMCN* of non-breeding females (*BMCE**N* = *BMCN* for non-breeding females).

3. Simulation of Changes in Organ Mass through Clutch Formation and Growth in Snout-vent Length instead of Forming Clutch

Based on the data used in Nishimura and Kamura¹³⁾ the *SVL*-*BM* regression line of breeding females between May and July (the oviposition season) was not different from that of the fertile females in earlier season (March and April, n = 7, both p > 0.05) when follicles are small^{15,17)} and negligible in mass. Therefore, I assumed that *BM* of a breeding female does not change throughout early spring and July. Without any information on the relative organ masses in a fertile female in early spring I assumed that these relative masses are same to those in a non-breeding female.

As for the *SVL* of most (137/140) breeding females was within the range of 90-150 cm, I adopted *SVL* of 120 cm for a medium size of the females. I simulated the changes in each organ mass through the clutch formation at *SVL* of 120 cm through *BMC* range and at *SBM* through *SVL* range, through subtracting the organ mass in post-ovipositional period from the organ mass in the early spring. The latter mass was estimated by the regression equations in non-breeding females¹¹⁾.

I simulated *SVL* growth between early spring and July in females skipping breeding, assuming the following initial parameters (in early spring) of *SVL*: 90, 120 and 150 cm; *BMC*: 0.7-1.3 and the final parameters (in July) of *BMC*: standard *BM* of non-breeding snakes and *SBM* of breeding snakes. I assumed that during the season of clutch formation a non-breeding female gets the same amount of energy as that of a breeding female of

the same initial *SVL* and *BM*. I calculated the expected *CLM* at each set of the initial parameters. Assuming that the energy value of *CLM* is 2.3 times of that of body⁸⁾, I calculated *BM* of non-breeding females in July as: initial *BM* + (2.3 - 1) × *CLM*. The expected *SVL* was then estimated using the *SVL-BM* regression equation of non-breeding females (Table 2).

In the calculations of masses and mass conditions for non-breeding females, I adopted the standard masses of non-breeding females¹¹⁾. Based on the definition, organ mass condition is one (standard) at *SBM*. In the simulations and at the adjustment of *CLM* (see the result), I adopted the regression equation of *BMC* to organ mass condition, passing the point of these two standards (Table 2, Appendix 2).

Regression lines were compared using ANCOVA.

Table 2. Regression equations of masses to *SVL* ($\log_{10}\text{-}\log_{10}$) and of mass conditions to *BMC* in adult females of *T. flavoviridis* (*b*: slope; *a*: intercept). Regressions of *BM* to *SVL* (the upper two) are those in the field condition based on the data used in Nishimura and Kamura¹³⁾. The other regressions are those of the ovipositional females, those to *SVL* are based on the snakes in *BMC* range of 0.9-1.1, and those to *BMC*, except for *RCM*, are calculated to pass the point of *BMC* = 1 and mass condition = 1. See Table 1 for the abbreviations.

	<i>b</i>	<i>a</i>	<i>n</i>	<i>r</i>
Regression to <i>SVL</i> ($\log_{10}\text{-}\log_{10}$)				
<i>BM</i> (breeding)	3.28	-4.04	141	.942
<i>BM</i> (non-breeding)	3.18	-3.93	877	.917
<i>BME</i>	3.44	-4.57	42	.980
<i>CLM</i>	2.96	-3.84	42	.904
<i>FM</i>	4.00	-6.95	42	.693
<i>LM</i>	3.71	-6.54	30	.892
<i>CAM</i>	3.58	-5.01	30	.985
Regression to <i>BMC</i>				
<i>BMCE</i>	0.766	0.234	93	.783
<i>CLMC</i>	1.354	-0.354	93	.814
<i>FMC</i>	1.881	-0.881	93	.542
<i>LMC</i>	0.636	0.364	63	.364
<i>CAMC</i>	0.505	0.495	65	.675
<i>RCM</i>	0.352	0.185	93	.393

III Results

1. Standard Masses and Mass Conditions in Ovipositional Females

The equations of the regressions between *SVL* and the masses and between *BMC* and the mass conditions in ovipositional females were obtained (Table 2). The slopes of the regressions between *BMC* and *BMCE* and between *BMC* and carcass mass condition (*CAMC*) were smaller than one (both $p < 0.01$). These results mean that *BMCE* and *CAMC* fluctuate less intensely than *BMC*. On the other hand the slopes of the regressions between *BMC* and *CLM* condition (*CLMC*) and between *BMC* and *FM* mass condition (*FMC*) were larger than one (both $p < 0.001$). *CLMC* and *FMC* fluctuate more intensely than *BMC*. Among the conditions of organ mass *CLMC* had the highest regression coefficient to *BMC* (Table 2). *RCM* was regressed positively on *BMC*.

2. Differences in the Relative Masses among Females

I compared *FMC*, *LMC* and *CAMC* among ovipositional, fertile and non-breeding females without accounting *CLM* and by setting the standard masses of body and organs to the masses of non-breeding females. The mass conditions of organs except for the clutch were regressed to *BMCEN* (Fig. 1). Among the regression lines of the three groups of females, the slope of *FMC* was largest in non-breeding snakes ($F_{2,280} = 3.432$, $p < 0.05$), the slope of *LMC* was smallest in ovipositional snakes ($F_{2,131} = 3.983$, $p < 0.05$) and position of *CAMC* was highest in non-breeding snakes ($F_{2,124} = 13.834$, $p < 0.001$).

The slope of *BMCEN-FMC* regression line was larger than one in each female group (all $p < 0.05$) (Fig. 1). Therefore, *FMC* fluctuates more greatly than *BMCEN*. *LMC* also fluctuates more greatly than *BMCEN* in fertile and non-breeding females (both $p < 0.01$), and *CAMC* fluctuates less greatly than *BMCEN* in each female group (all $p < 0.01$).

With the regression equation of *BMC-CLMC* (Table 2) I calculated an adjusted *CLM* of each snake under the condition of *SBM* by the following equation;

$$\text{Adjusted } CLM = CLM + 1.384 \times (1 - BMC) \times (\text{standard } CLM)$$

RCM adjusted by BMC is calculated as: adjusted CLM / (SBM - standard CLM). Adjusted RCM was negatively correlated to SVL significantly, while RCM with non-adjusted CLM (CLM/BME) was not significantly correlated to SVL (Fig. 2). This

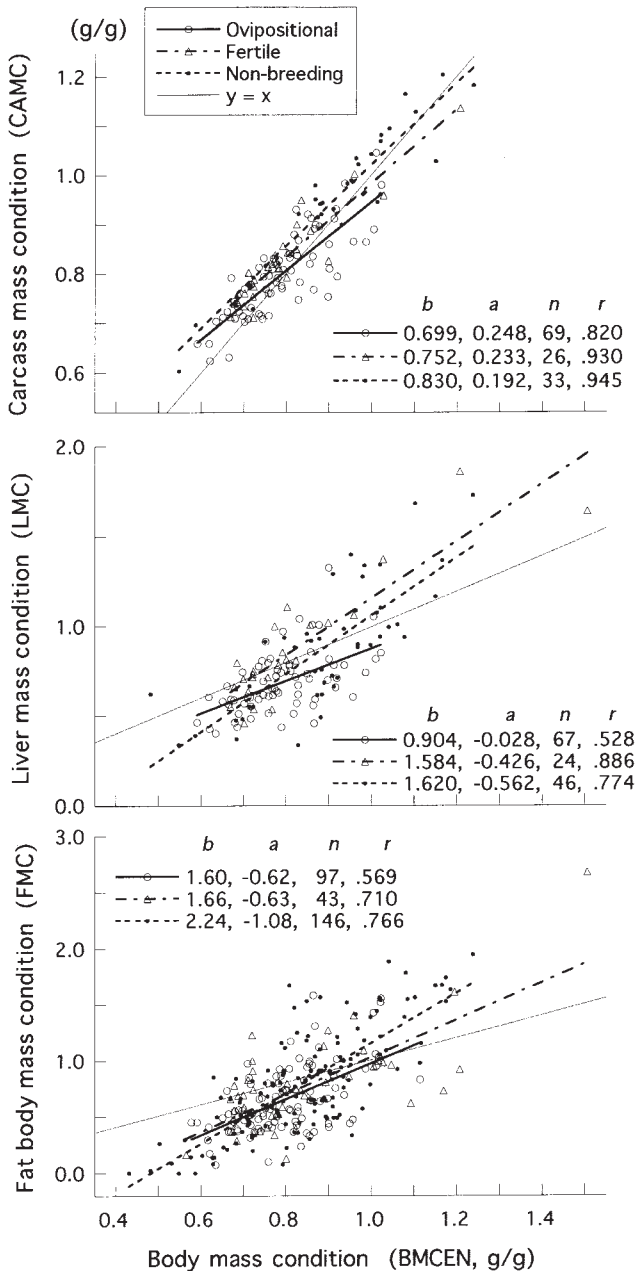


Fig.1. Body mass (BME) condition (BMCEN: BME /standard BME of non-breeding females) and the mass conditions of fat body, liver and carcass (body mass without organs in the body cavity) in the three groups of adult female *Trimeresurus flavoviridis*. See Table 1 for the breeding conditions and the abbreviations.

negative correlation between SVL and RCM may be explained by the change in the body shape of snakes at SBM. However, the simulated RCM also decreased with SVL increase under the condition of a fixed slenderness (mean slenderness at SVL of 120 cm, Fig. 2).

3. Body Mass Condition of Breeding Females and Organ Mass Changes through the Clutch Formation

SBM of breeding females was 125.6% of that of non-breeding females at SVL of 120 cm. BMC (field condition) of most (85.8%) breeding females were within 0.8-1.2 (Fig. 3). BMCN (field condition) overlapped at the range of 0.812-1.322 between fertile and non-breeding females collected between March and May (Fig. 3), and the proportion of females in this BMC range was 81.4% of all adult females. As for the minimum conditions for the females to breed, the minimum BMC and BMCN (divided by SBM of non-breeding female) were 0.638 and 0.800 and these two females had BMCEN of 0.577 and 0.590, respectively.

In breeding females at SVL of 120 cm, the simulated post-ovipositional mass condition of each organ and body increased in accordance with BMC increase in early spring, whereas the proportional

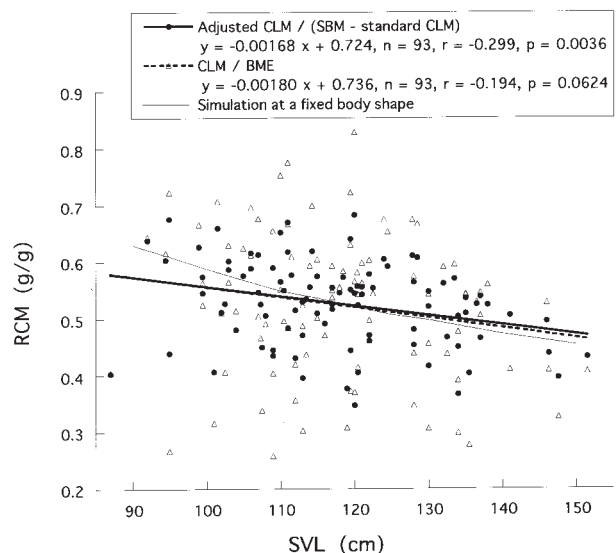


Fig.2. Regression of relative clutch mass (RCM) to SVL in *T. flavoviridis*. "Adjusted CLM" is $CLM + 1.354 \times (1 - BMC) \times (\text{standard } CLM)$. Thin line indicates a simulated relative mass of snakes at the mean slenderness ($BM/SVL^3 = 3.53 \times 10^{-4}$) of breeding female (SVL: 120 cm). See Table 1 for the abbreviations.

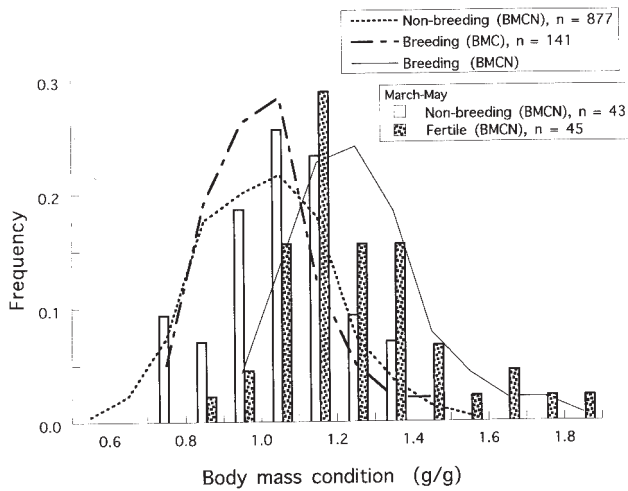


Fig.3. Frequency of the field body mass condition in adult females of *T. flavoviridis* (based on the data in Nishimura and Kamura¹³⁾). Bars are those of snakes collected in the copulating season. Lines are those of the whole sample. The body mass condition is *BMCN*, except for the thick chained line of breeding females (*BMC*). See Table 1 for the abbreviations.

LM and *CAM* (post-ovipositional mass / *BME*) were nearly constant (Fig. 4a). The relative losses of *LM*, *CAM* and relative *CLM* (represented as mass loss of body in Fig. 4b) through the clutch formation increased with *BMC* at *SVL* of 120 cm, but that of *FM* did not increase (Fig. 4b). Because *FM* changes more greatly with *BMC* than *LM* and *CAM* (Fig. 1), the mass loss of *FM* increased with *BMC* at a rate similar to the mass losses of *LM* and *CAM* (Fig. 4b). The mass condition of each organ in post-ovipositional females varied greatly with *BMC*, especially in *FM*. These simulations on *BMC* indicate that females with higher *BMC* lose greater proportion of organ mass (especially in *FM*) during clutch formation, but still keep higher conditions of organ mass after oviposition.

At *SBM* the relative loss in each organ mass decreased or was similar in accordance with *SVL* increase (Fig. 4d). Except for *FM*, the post-ovipositional mass conditions of each organ and

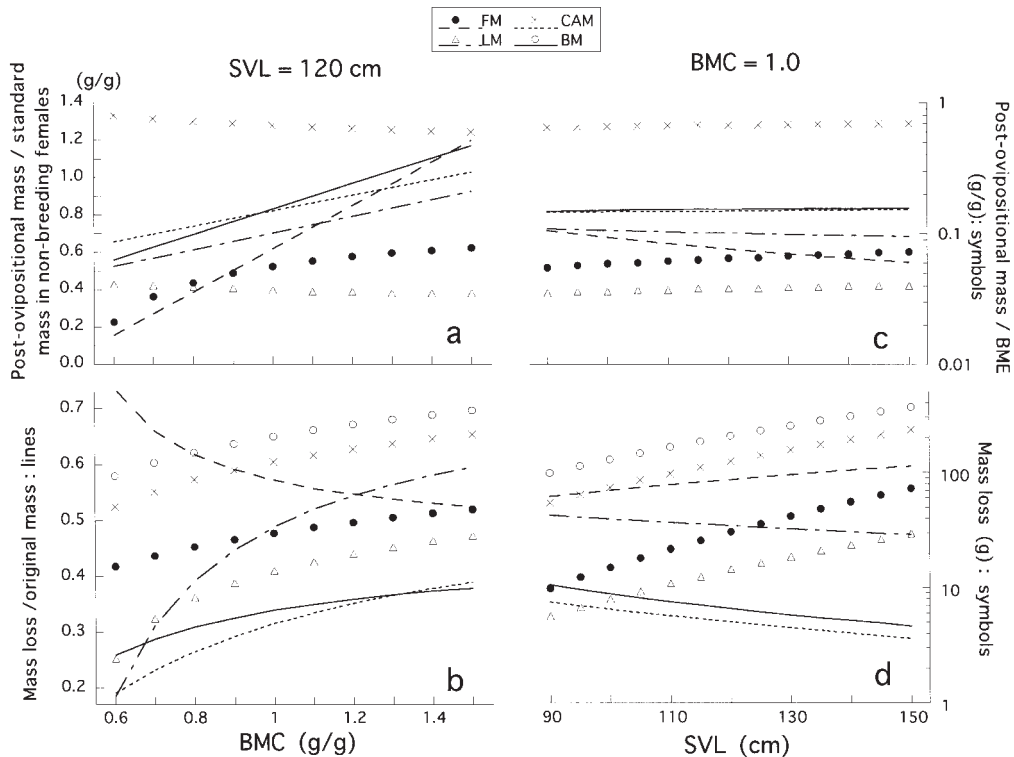


Fig.4. Post-ovipositional mass condition (a, c) and changes in the mass between early spring and post-ovipositional period (b, d) in the breeding females of *T. flavoviridis*. a, b: simulated on each *BMC* in early spring at the center of *SVL* range (120 cm); c, d: simulated on each *SVL* at *SBM* of breeding females. See Table 1 for the abbreviations.

body and the proportional mass of each organ (post-ovipositional mass / *BME*) were nearly constant at *SBM* throughout the *SVL* range of the adult females (Fig. 4c). *FMC* decreased and proportional *FM* increased with *SVL* increase. These simulations on *SVL* indicate that larger females lose smaller proportions of *LM*, *CAM* and *BM* and greater proportions of *FM* during clutch formation, and have lower *FMC* but greater proportion of *FM* after oviposition.

Under the initial parameter of *BMC* > 0.9 and under the final parameter of *SBM* of breeding or non-breeding females most of the simulated *SVL* growths in non-breeding females, in the season of clutch formation were greater (Fig. 5) than the yearly growth in adult females of 90, 120 and 150 cm in *SVL*, 10, 7 and 4 cm, respectively¹⁸⁾.

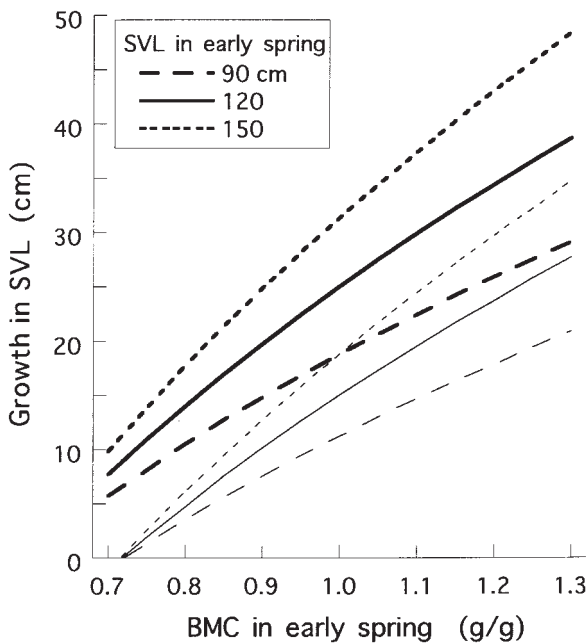


Fig.5. Simulation of *SVL* growth between early spring and July in female *T. flavoviridis* skipping breeding. I calculated the expected *CLM* for snakes under the parameters of three *SVL* (90, 120 and 150 cm) and of *BMC* range of 0.7-1.3 in early spring. I assumed that *BM* of a breeding female is constant during the period and that the energy value of clutch is 2.3 times of that of body. Then I estimated the *BM* increase for non-breeding female in July. Finally I calculated *SVL* in July under the two *BMCEN*: 1.0 (thick line) and 1.256 (the mean condition of breeding females, thin line). See Table 1 for the abbreviations.

IV Discussion

A peak in liver mass during vitellogenesis has been described in *Chamaeleo jacksoni*¹⁹⁾ and *Hemidactylus turcicus*²⁰⁾. Therefore, great proportion of liver mass in the fertile females of habu may be the result of move of lipid from fat body to liver during clutch formation.

Most studies on reproduction in snakes and lizards have failed to detect correlations between *RCM* (or *CM/BM*) and body size (but see Cueller²¹⁾); relative clutch mass correlated neither to *SVL* (in many species, see Seigel et al.²²⁾; ; Dunham et al.²³⁾), to *BM* (in *V. aspis*²⁴⁾), nor to yearly mean of *BMC* (in *V. berus*²⁵⁾). Barron¹⁰⁾ used *RCM* adjusted by body mass condition for the water snake, *N. sipedon* studied by him and in re-calculation of other results on *RCM* in several snake species. Comparing to the results with non-adjusted *RCM*, Barron indicated that adjusted *RCM* represents the reproductive biology more accurately in these snake species. Barron did not describe the basis of his adjustment (relationships between *RCM* and *BMCE*). By his method *RCM* of a female with *BMCE* of 0.9 is simply adjusted to elevate 10%. However, in the present results in habu *RCM* is only 7.4% lower than the average in a female of this condition (based on the *BMC-CLMC* regression equation in Table 2). Therefore, at the adjustment of *RCM* by *BMC* or by *BMCE* the relationships between the two variables should be studied. The present study described that *RCM* correlates positively with *BMC* and negatively with *SVL*. A result similar to the former was described as the greater lipid allocation to clutch in *A. piscivorus* at a higher relative lipid (lipid mass/*BM*)²⁶⁾. In a sense *CLM* is a extra part of *BM*. It is natural that an extra mass fluctuates greatly with *BMC* with high correlation coefficient. With the adjustment by *BMC*, *RCM* may be correlated with *SVL* in many snake species.

The minimum *BMCEN* of the ovipositional females was 0.577. In habu other than breeding females few snakes had *BMCN* lower than 0.7 in the field¹¹⁾. Therefore, *BMCN* of about 1.0 (0.8 for *BMC* in

breeding female) may be the minimum condition for a female to breed (Fig. 4a). Ovipositional females with high *BMC* made large clutch and kept high *BMCE*N (Fig. 4a). The high *BMCE*N may lead to a higher chance of survival and a greater growth after oviposition in these females.

During clutch formation breeding females exhausted a considerable energy contained in carcass (Fig. 4b). This result indicates that an ovipositional female has a large abdominal cavity for its size, which ensures to produce a large clutch. On the other hand, it may take time for females to recover the carcass mass and this may be the primary reason of the lower *CAMC* observed in the non-breeding females than that in the large males¹⁹⁾.

Some females, died just before oviposition, had oviductal eggs full of abdominal cavity between gallbladder and vent with expanded skin (Nishimura, unpublished data). In these snakes the mass allocation towards clutch seems to be limited by the size of abdominal cavity⁷⁾. However, *CLMC* was low in females with low *BMC*, and at least in these females the constraint according to the abdominal cavity may not occur.

In snake species with biennial or less breeding frequency, females are not supposed to breed before acquiring enough *BMC* or *FM* (see Seigel and Ford²⁷⁾). In these snakes *BMC* may be one of the key factors to decide whether a female becomes fertile or not. In Japanese mamushi, *Agkistrodon blomhoffii blomhoffii*, most females with larger follicles and performing mating behaviors had higher *BMC* than the other females²⁸⁾. In contrast, we can judge the breeding condition of only about 20% of female habu from their *BMC* in the mating season. In red-sided garter snakes, *Thamnophis sirtalis parietalis*, yearly mean of *BM* in the breeding season did not correlated to the proportion of the vitellogenic females²⁹⁾. Therefore, high *BMC* is not always indispensable to female reproduction in several snake species.

The simulated *SVL* growth estimated for female habu which skipped breeding was too great. The reasons of this over-estimation may be as follows;

non-breeding females get energy less than fertile ones: energy cost of growth in length is more than that of clutch formation: energy value per *BM* of fertile females is more than that of non-breeding ones. Even if a non-breeding female with the initial *BMC* of 0.95 (1.2 in *BMC*N) gained extra *SVL* growth of 20 cm (Fig. 5), the snake could produce extra 3 eggs at most in the following season (Nishimura, unpublished data). Therefore, by skipping breeding a female with low *BMC* may avoid a critical low *BMCE* rather than expect the increase in the number of its offsprings in the following season.

Acknowledgments: Thanks are due to many persons for collecting snakes; Takao Kamura for keeping snakes; Hitoshi Shiroma for measuring some snakes; Akira Mori for comments on the paper and help with literature; Tsutomu Hikida for providing statistical programs.

V References

- 1) *Williams, G.C. (1966) Adaptation and natural selection. Princeton Univ. Press, Princeton, New Jersey.
- 2) Pianka, E.R. and W.S. Parker (1975) Age-specific reproductive tactics. *Am. Natur.*, 109: 453-464.
- 3) Atchley, W.R., C.T. Gaskins and D. Anderson (1976) Statistical problems of ratios. I. empirical results. *Syst. Zool.*, 25: 137-148.
- 4) Shine, R. (1980) "Costs" of reproduction in reptiles. *Oecologia*, 46: 92-100.
- 5) Dunham, A.E., D.B., P.J. Morin and H.M. Wilbur (1988) Methods for the study of reptile populations. In C. Gans and R.B. Huey (eds.) *Biology of the Reptilia 16, ecology B, defence and life history*. Alan R. Liss, Inc., New York, pp.331-386.
- 6) Seigel, R.A. and H.S. Fitch (1984) Ecological patterns of relative clutch mass in snakes. *Oecologia*, 61: 293-301.
- 7) Shine, R. (1992) Relative clutch mass and body shape in lizards and snakes: Is reproductive investment constrained or optimized?. *Evolution*, 46: 828-833.

- 8) Shine, R. and L. Schwarzkopf (1992) The evolution of reproductive effort in lizards and snakes. *Evolution*, 46: 62-75.
- 9) Niewiarowski, P.H. and A.E. Dunham (1994) The evolution of reproductive effort in squamate reptiles: costs, trade-offs, and assumptions reconsidered. *Evolution*, 48: 137-145.
- 10) Barron, J.N. (1997) Condition-adjusted estimator of reproductive output in snakes. *Copeia*, 1997: 306-318.
- 11) Nishimura, M. (1998) Relative organ masses with applications of a new index in the viperid snake, *Trimeresurus flavoviridis*, especially in relation to the body mass condition. *Biol. Mag. Okinawa*, 36: 59-68.
- 12) Nishimura, M. and T. Kamura (1994) Body mass changes in *Trimeresurus flavoviridis* (Viperidae) on Okinawa Island, Japan. *Res. Popul. Ecol.*, 36: 173-179.
- 13) Nishimura, M. and T. Kamura (1994) Body mass condition in *Trimeresurus flavoviridis* (Viperidae) from the Okinawa Islands — regional differences with the examination of the sampling methods. *Ann. Rep. Okinawa Pref. Inst. Heal. Env.*, 28: 95-101.
- 14) Nishimura, M. and Kamura, T. (1992) Creamy white material ejected by male habu, *Trimeresurus flavoviridis* (Viperidae). *Jpn. J. Herpetol.*, 14: 163-165. (in Japanese with English abstract)
- 15) Nishimura, M. and T. Kamura (1995) Proportion of reproductive females in habu, *Trimeresurus flavoviridis*, on Okinawa Island. *Biol. Mag. Okinawa*, 33: 1-9.
- 16) Nishimura, M. and T. Kamura (1992) Frequency of water intake and defecation and body weight change in wildy captured habu, *Trimeresurus flavoviridis* — an attempt to estimate frequencies of water intake and feeding in field. *Nippon Herpetol. J.*, 40: 1-13. (in Japanese)
- 17) Shiroma, H. (1993) Follicular growth and fat body cycle of female habus, *Trimeresurus flavoviridis*, in the Okinawa Islands. *Jpn. J. Herpetol.*, 15: 53-58.
- 18) Nishimura, M. (1993) Estimation of age and growth of habu, *Trimeresurus flavoviridis* (Serpentes: Viperidae), in the Okinawa Islands. *Jpn. J. Ecol.*, 43: 83-90. (in Japanese with English synopsis)
- 19) Lin, E.J.I. (1979) Fatbody and liver cycles in two tropical lizards *Chamaeleo hohneli* and *Chamaeleo jacksoni* (Reptilia, Lacertilia, Chamaeleonidae). *J. Herpetol.*, 13: 113-117.
- 20) Selcer, K.W. (1987) Seasonal variation in fatbody and liver mass of the introduced Mediterranean gecko, *Hemidactylus turcicus*, in Texas. *J. Herpetol.*, 21: 74-78.
- 21) Cuellar, O. (1984) Reproduction in a parthenogenetic lizard: with a discussion of optimal clutch size and a critique of the clutch weight/body weight ratio. *Am. Midl. Nat.*, 111: 242-258.
- 22) Seigel R.A., H.S. Fitch and N.B. Ford (1986) Variation in relative clutch mass in snakes among and within species. *Herpetologica*, 42: 179-185.
- 23) Dunham, A.E., D.B. Miles and D.N. Reznick (1988) Life history patterns in squamate reptiles. In C. Gans and R.B. Huey (eds.) *Biology of the Reptilia 16, ecology B, defence and life history*. Alan R. Liss, Inc., New York, pp.441-511+appendix.
- 24) Nealleau, G. and H. Saint Girons (1981) Poids des nouveau-nes et reproduction de *Vipera aspis* (Reptilia: Viperidae), dans des condition naturelles et artificielles. *Amphibia-Reptilia*, 2: 51-62.
- 25) Andren, C. and G. Nilson (1983) Reproductive tactics in an island population of adders, *Vipera berus* (L.), with a fluctuating food resource. *Amphibia-Reptilia*, 4: 63-79.
- 26) Scott, D.E., R.U. Fischer, J.D. Congdon and S.A. Busa (1995) Whole body lipid dynamics and reproduction in the eastern cottonmouth, *Aghistrodon piscivorous*. *Herpetologica*, 51: 472-487.
- 27) Seigel, R.A. and N.B. Ford (1987) Reproductive ecology. In R.A. Seigel, J.T. Collins and S.S. Novak (eds.) *Snakes, ecology and evolutionary biology*. Macmillan, New York, pp. 210-252.
- 28) Isogawa, K. and M. Kato (1995) Mating season of

the Japanese mamushi, *Agkistrodon blomhoffii blomhoffii* (Viperidae: Crotalinae), in southern Kyushu, Japan: relation with female ovarian development. Jpn. J. Herpetol., 16: 42-48.

- 29) Whittier, J.M. and D. Crews (1990) Body mass and reproduction in female red-sided garter snakes (*Thamnophis sirtalis parietalis*). Herpetologica, 46: 219-226.

* Not referred directly.

VI 要約

ハブの繁殖雌140個体について、クラッチ・脂肪体・肝臓・内蔵なしの体の重量を計測した。野外における体重を保つ個体に限った場合、繁殖雌の86%の肥満度(体重/標準体重)が 1.0 ± 0.2 の範囲内であり、繁殖雌と非繁殖雌の80%以上で肥満度の重なりがあった。肥満度の変動にたいして、クラッチと脂肪体の状態(重量/標準重量)はより激しく、また、肝臓と内蔵なしの体の状態はよりゆるやかに変動した。相対クラッチ重、すなわちクラッチ重/(体重 - クラッチ重)を肥満度で補正した結果、それは頭胴長にたいし負の相関を示した。繁殖雌の内蔵なしの体の重量は、非繁殖雌のものより小さかった。クラッチ形成に伴う各器官の重量と相対重量の変化、ならびに繁殖しない雌の頭胴長の成長を試算した。ハブの雌にとって肥満度は、繁殖の有無との関連は低いが、

繁殖への投資量と繁殖後の雌の状態を決める主要な要因である。

Appendix 1

The *SVL-BM* regression equation of non-gravid females in Fig. 5 in Nishimura and Kamura¹²⁾ was wrong. The correct one is;

$$\log Y = 3.183 \log X - 3.932 \quad (n = 862, r = .918)$$

Appendix 2

Regression equations of mass conditions to *BMC* in *T. flavoviridis* (*b*: slope; *a*: intercept) based on the data used in Nishimura¹¹⁾. Regressions are calculated to pass the point of *BMC* = 1 and mass condition = 1. See Table 1 for the abbreviations.

	<i>b</i>	<i>a</i>	<i>n</i>	<i>r</i>
Small ($45 \leq \text{SVL} < 90$ cm) snakes				
<i>FMC</i>	2.510	-1.510	150	.729
<i>LMC</i>	1.264	-0.264	82	.817
<i>CAMC</i>	0.727	0.273	71	.951
Non-breeding females				
<i>FMC</i>	1.720	-0.720	146	.780
<i>LMC</i>	1.451	-0.451	46	.792
<i>CAMC</i>	0.773	0.227	33	.942
Large ($90 \leq \text{SVL}$) males				
<i>FMC</i>	2.061	-1.061	201	.806
<i>LMC</i>	1.098	-0.098	48	.602
<i>CAMC</i>	0.925	0.075	26	.975