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COMPARATIVE REPRODUCTIVE BIOLOGY OF THE LIZARDS, *JAPALURA SWINHONIS FORMOSENSIS*, *TAKYDROMUS SEPTENTRIONALIS* AND *HEMIDACTYLUS FRENATUS* IN TAIWAN

II. FAT BODY AND LIVER CYCLES OF THE MALES[1]

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ABSTRACT

Hsien-Yu Cheng and Jun-I Lin (1978). *Comparative reproductive biology of the lizards,* Japalura swinhonis formosensis, Takydromus septentrionalis *and* Hemidactylus frenatus *in Taiwan. II. Fat body and liver cycles of the males.* Bull. Inst. Zool., Academia Sinica, 17(1): 67-74. During the winter months, *Japalura swinhonis formosensis* and *Takydromus septentrionalis* used almost all of the fat bodies deposited in the pre-winter time. The fat bodies were used mainly for maintaining their reproductive conditions (hypertrophied testes) and body metabolism during the winter time. Extremely large variances in monthly fat body changes were observed in *Hemidactylus frenatus* suggesting that the presence of the fat bodies was independent of reproduction.

The peak of the mean liver weight occurred in June in *J. swinhonis formosensis* and *T. septentrionalis* suggesting that June was the end of intense reproductive effort allowing the energy accumulation for lipid storage to begin. However, the fluctuation pattern of the liver weight in *H. frenatus* was not significant ($p>0.01$).

The contributions (C) of the seasoanl fluctuations of the liver and fat body weights to the fluctuations of the reproduction showed that the liver and fat body changes in *H. frenatus* ($C=62.8\%$) were mainly devoted to the energy demand for reproduction, while *J. swinhonis formosensis* expended a small portion of energy from the liver and fat body weights changes ($C=19.3\%$) to reproduction. *T. septentrionalis* stands in between ($C=35\%$).

An organism can be conveniently viewed as a simple input-output system, with its foraging tactics providing as input of materials and energy which are in turn 'mapped' into an output consisting of progeny[12]. An adaptive successful population should constrain the profit and the cost between reproductive and foraging tactics,

1. This is based partly on a M. S. thesis of the first author, guided by the second author, and approved by the Tunghai University.

and make the maximum profitable equilibrium. The lipid storage and utilization system could be used to understand the interaction between the foraging and reproductive tactics[12].

There are four types of lipid storage and utilization in lizards: 1) no lipid cycling, 2) cycling associated only with winter dormancy, 3) cycling associated only with reproduction, and 4) cycling associated with both winter dormancy and reproduction[4].

No studies on liver or fat body of the lizarads in Taiwan have been made. The purpose of the present investigation was to study the liver and fat body cycles and their relationship with reproduction.

MATERIALS AND METHODS

The three species of lizards and the study area have been described previously[2]. Samples were collected approximately biweekly for *Japalura swinhonis formosensis* and *Hemidactylus frenatus*, and monthly for *Takydromus septentrionalis* from November 1975 to May 1977. All specimens were etherized within two hours after capture, and their weight and snout-vent length (SV-length) were measured to the nearest 0.01 g and 0.1 mm respectively. The liver and paired abdominal fat bodies were dissected and weighed to the nearest 0.1 mg. For comparison with reproductive patterns, only the individuals used in the previous study[2] were analyzed in this study.

The contribution index (C) of the seasonal fluctuations of the liver and fat body weights to reproduction is estimated as follows:

$$C=\frac{d(\text{testis})+d(\text{kidney})}{d(\text{liver})+d(\text{fat body})}\times\frac{1}{E}\times 100\%$$

where

$d(X)$: the difference between the maximum and minimum monthly means of the X,

X: the four variables, i. e. testis, kidney, liver and fat body weights over body weights, and

E: the efficiency of the energy transformation of the liver and fat body. For comparative purpose, the efficiency (E) is assumed similar for all species and therefore can be omitted.

RESULTS

Japalura swinhonis formosensis—From November 1975 to May 1977, a total of 133 males larger than 70 mm in SV-length, were used in the analyses.

Monthly changes in the liver and fat body weights were shown in Fig. 1. The weight of the liver began to increase after emergence (March), and reached the peak in June, then decreased slightly and remained fairly constant from July to December. The mean liver weight of the newly emerged males in March 1976 and 1977 were 33% and 37.9% respectively less than that in the preceding November (Table 1).

Fat bodies were practically exhausted during the hibernation (Table 1), thus male emerged fat body-free in March and remained so until May (Fig. 1). Mean fat body weight increased sharply in June and steadily reached the peak in December. The absence of fat body accumulation in March, April and May was apparently related to the intense reproductive activities that occurred during this period.

Takydromus septentrionalis—From November 1975 to December 1976, a total of 112 males larger than 40 mm in SV-length, were used in the analyses.

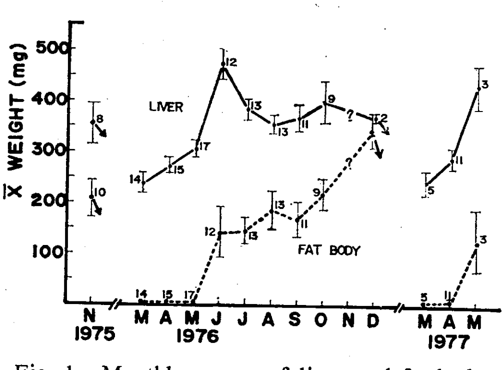

Fig. 1. Monthly means of liver and fat body weights from November 1975 to May 1977 in *Japalura swinhonis formosensis.*

TABLE 1
Comparison of liver and fat body weight changes before hibernation and after hibernation in *Japalura swinhonis formosensis*

	1975-'76	1976-'77
Liver		
Pre-hibernation wt. (mg)	187.3–547.9	242.8–664.4
$\overline{X}$	356.5± 39.0	386.4± 43.3
	N=8	N=11
Post-hibernation wt. (mg)	104.0–284.2	120.1–274.3
$\overline{X}$	238.9± 19.4	240.0± 20.1
	N=14	N=5
$\overline{X}$ wt. loss (mg)	117.6	146.4
% wt. loss	33.0	37.9
significance level	0.025	0.025
Fat body		
Pre-hibernation wt. (mg)	74.6–450.0	85.5–380.7
$\overline{X}$	207.2± 36.5	244.4± 29.0
	N=10	N=11
Post-hibernation wt. (mg)	0.0– 30.1	0.0– 18.1
$\overline{X}$	2.4± 2.1	8.4± 3.0
	N=14	N=5
$\overline{X}$ wt. loss (mg)	204.8	236.0
% wt. loss	98.8	96.5
significance level	0.005	0.005

Monthly changes in the liver and fat body weights were shown in Fig. 2. The mean liver weights began to increase in late May, and reached a maximum in June. Thereafter, the liver tended to decrease in weight, and declined to a minimum weight, then remained fairly constant in the rest of the months.

No considerable fat bodies occurred in the spring months. Only a slight accumulation in fat bodies occurred in the summer, and this slight increase corresponded with the peak of the liver weights. Then the marked increase in

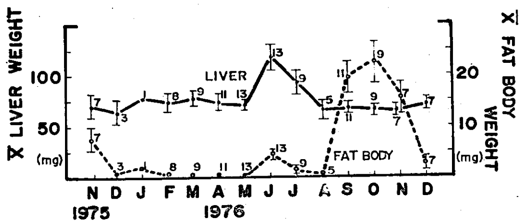

Fig. 2. Monthly means of liver and fat body weights from November 1975 to December 1976 in *Takydromus septentrionalis.*

fat bodies occurred in late August and reached the peak in September and October. The weights of fat bodies decreased markedly in November, and declined to a minimum in December.

Hemidactylus frenatus—From November 1975 to April 1977, a total of 155 males larger than 50 mm in SV-length, were used in the analyses.

The fluctuation pattern of the liver weight was not significant ($p>0.01$) (Fig. 3). However, the liver weight increased slightly during the summer and fall.

The monthly means of the fat body weight showed a cyclic pattern (Fig. 3). The peak appeared in the winter 1975 and 1976 respectively. However, the variances of the monthly means were extremely high ($\overline{CV}=48$, range 28%–100%). Thus, an alternative analysis was used (Table 2). Two stages in weight of the fat body were established, i. e. below 10 mg, and above 10.1 mg. The data indicated that the occurrence of greater size of fat bodies (Stage

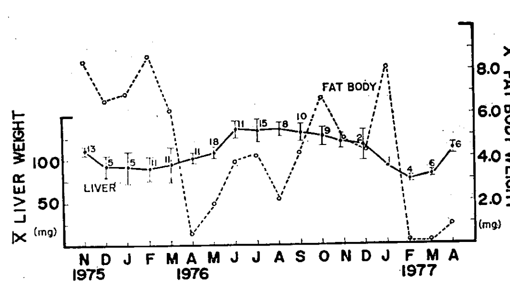

Fig. 3. Monthly means of liver and fat body weights from November 1975 to April 1977 in *Hemidactylus frenatus.*

TABLE 2
The percentage of distribution of fat body weights[1] in *Hemidactylus frenatus* during the study period

	1975			1976						
	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July
N	10	13	5	5	11	11	12	19	11	16
Stage 1-a	90	38	40	40	54	73	100	90	54	81
Stage 1-b	10	28	40	40	0	9	0	5	37	13
Stage 2-a	0	23	0	20	27	9	0	5	9	0
Stage 2-b	0	16	20	0	19	9	0	0	0	0

	1976					1977			
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.
N	9	10	10	2	6	1	4	6	6
Stage 1-a	78	60	50	50	83	0	100	100	100
Stage 1-b	22	30	10	0	0	100	0	0	0
Stage 2-a	0	10	30	50	0	0	0	0	0
Stage 2-b	0	0	10	0	17	0	0	0	0

1. Stage 1-a: below 5.0 mg
Stage 1-b: between 5.1 mg to 10.0 mg
Stage 2-a: between 10.1 mg to 15.0 mg
Stage 2-b: above 15.1 mg

2) was relatively more frequent during the winter time than during the spring and summer times.

DISCUSSION

A. The fat body:

During the winter months, *Japalura swinhonis formosensis* and *Takydromus septentrionalis* used almost all of the fat bodies that were deposited in the pre-winter time (Table 1, Fig. 2). The pattern appeared to belong to the Type 2, associated only with winter dormancy according to Derickson[(4)], i. e. fat bodies deposited in the fall were used exclusively for the body maintenance during the winter period. However, the pattern in *J. swinhonis formosensis* and *T. septentrionalis* was not similar in that the fat bodies were used both for maintenance of reprodutive purposes and body metabolism.

Both fat bodies and testicular activities in *J. swinhonis formosensis* and *T. septentrionalis* increased during the pre-winter time, and reached the peak in October and November[(2)]. The evidence suggested that the deposition of the fat bodies was not meant for the reproductive purpose during this period. By March, all fat bodies were exhausted while the testicular activities still remained unchanged. Undoubtedly the fat bodies were used for both the maintenance of reproductive condition and body metabolism during the winter time.

The fat body pattern in *J. swinhonis formosensis* and *T. septentrionalis* differed also from the Type 4 according to Derickson[(4)], i. e. the fat bodies were used partially for over-wintering, and the remaining part for reproductive activities in the next spring. Therefore, the fat bodies cycling in *J. swinhonis formonsis* and *T. septentrionalis* appeared to be unique in their utilization.

The absence of fat bodies during the spring and summer periods in *T. septentrionalis* and during the spring time in *J. swinhonis formosensis* was probably not the result of physiological inability to accumulate energy or of the shortage of food, but was due to the high expenditure of energy for intense breeding activities that occurred during these months. In addition, the breeding activities reduced the foraging time. Breeding activities and the reduced foraging time decreased the input of energy to such an extent that no fat bodies were accumulated.

J. swinhonis formosensis shows a strong territoriality and complex reproductive behavior similar to all other species in the family Agamidae. Only male adult emerged in early spring to settle a breeding site before female adults emerged. This behavioral pattern was not observed in *T. septentrionalis.* The different pattern in fat bodies in *J. swinhonis formosensis* and *T. septentrionalis* suggested that *J. swinhonis formosensis* concentrated their breeding activities in March, April and May, while *T. septentrionalis* spread out their breeding activity throughout the spring and summer time. The well-defined period of breeding activity and territorial behavior enabled *J. swinhonis formosensis* to accumulated energy more efficiently than *T. septentrionalis.* The total absence of fat bodies during the coldest months (December, January and February), and the greater variances of fat body observed in each month in *T. septentrionalis* indicated its inefficient system of lipid deposition and utilization. Mortality in *T. septentrionalis* in winter time was expected to be greater than in *J. swinhonis formosensis.* In short, *J. swinhonis formosensis* was obviously a more *K*-selected species and *T. septentrionalis* was a more *r*-seleced species.

Church[3] found no fat bodies throughout the year in his study on *Hemidactylus frenatus* in Java. However, fat bodies were observed in the present study. Unlike bilobed, yellowish fat tissues usually found on both sides of pelvic area in other lizard species, they were irregular in shape, whitish in color at the posterior end of the body cavity.

The fat bodies of *H. frenatus* were found every month in the samples with the peaks both in the winter times. However, the variances of the monthly means were extremely large, suggesting that the presence of the fat bodies was independent of reproduction. Non-cyclic pattern of fat bodies suggested that the fat body accumulation depended on the food availability. Marcellini[10,11] showed that the multiple chirp calls of *H. frenatus* was characteristic of territorial or dominant males. In addition, it has been observed the dominant males usually occupied a strategic feeding site and ensured themselves of sufficient food. If it is so, the fat body accumulation was simply an index to territorial hierarchy. Furthermore, *H. frenatus* is known to have a catholic feeding habit and its tail may serve as an energy supply during the winter[3]. Therefore, the less significant role of fat bodies in reproduction or metabolism and the observed fluctuation of fat body content was expected.

It is possible that Church[3] failed to find fat bodies in *H. frenatus* in Java as a result of his negligence. It is also possible that *H. frenatus* in Java did not have fat bodies as a result of favorable environmental conditions (abundance of food and uniform climate throughout the year) and/or continuous reproduction. However, the environmental conditions in Taiwan, particularly in the spring and summer times are as favorable as in Java. As noted before, *H. frenatus* is reproductively active during the spring and summer in Taiwan, and fat bodies were also observed during this period; thus the absence of fat bodies in *H. frenatus* in Java was not simply due to the reproductive energy demand and/or physiological acclimation. The occurrence of fat bodies in *H. frenatus* in Taiwan appeared to be an evolutionarily adaptive trait different from that in Java.

B. The liver:

Liver is probably an intermediary organ for both the storage and utilizations of lipids, especially for the reproductive purpose[7,13]. Hepatic nitrogen and glycogen may be essential for spermatogenesis and maintenance of spermatozoa[1,5]. Most of the investigations concentrated on the relationships of the liver to reprouction and to fat bodies[5,6,8,914].

The peak of the mean liver weight occurred in June in *J. swinhonis formosensis* and *T. septentrionalis*, suggesting that June was the end of intense reproductive effort allowing the energy accumulation for lipid storage to begin (Figs. 1, 2). As to the precise role of the liver functions, further experiments are needed.

C. Evolutionary consideration:

While seasonal fluctuations of the liver and fat body weights are thought to be related to reproduction[5,9,14], the extent to which they contribute is unknown.

As noted before, the testis and the kidney weights could be used as an accurate index to reproduction[2]. Then the maximum fluctuation of the reproduction can be estimated from the maximum fluctuation of the monthly means of the testis and the kidney weights throughout the year 1976. Substituting the data in Table 3 into the equation of contribution index (*C*), the value of *C* for *J. swinhonis formosensis* is 19.3%, for *T. septentrionalis* 35%, and for *H. frenatus* 62.8%.

The value *C* for *H. frenatus* (62.8%) indicates that the liver and fat body weight changes were mainly devoted to the energy demand for reproduction. While *J. swinhonis formosensis* expended a samll portion of energy from the liver and fat body weight changes to reproduction. *T. septentrionalis* stands in between the two species.

TABLE 3
Minimum and maximum monthly means of the proportionate testis, kidney, liver and fat body weights[1] and their differences in
Japalura swinhonis formosensis, *Takydromus septentrionalis* and *Hemidactylus frenatus*

	Item	Minimum observed	Minimum monthly mean	Maximum observed	Maximum monthly mean	Maximum difference throughout the year (Maxi. mean-mini. mean)
J. swinhonis formosensis	Testis	0.04	0.13	0.78	0.64	0.51
	Kidney	0.16	0.20	0.44	0.40	0.20
	Liver	1.28	1.87	3.91	3.12	1.25
	Fat body	0.0	0.02	2.48	2.45	2.43
T. septentrionalis	Testis	0.12	0.20	1.08	0.76	0.56
	Kidney	0.16	0.27	1.05	0.71	0.44
	Liver	1.48	2.93	6.26	4.75	1.82
	Fat body	0.0	0.0	2.49	1.04	1.04
H. frenatus	Testis	0.09	0.24	1.11	0.70	0.46
	Kidney	0.19	0.30	0.64	0.50	0.20
	Liver	1.66	2.27	4.60	3.11	0.84
	Fat body	0.0	0.02	0.80	0.23	0.21

i. proportionate weight $= \frac{\text{gross weight (mg)}}{\text{body weight (gm)}}$

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臺灣攀木蜥蜴 (*Japalura swinhonis formosensis*), 蛇舅母 (*Takydromus septentrionalis*) 與蝎虎 (*Hemidactylus frenatus*) 三種蜥蜴雄性生殖的比較

二、雄性蜥蜴的脂肪體和肝重週期的研究

鄭 先 祐　　林 俊 義

臺灣攀木蜥蜴 (*Japalura swinhonis formosensis*) 與蛇舅母 (*Takydromus septentrionalis*) 在過冬時，幾乎用盡所有在冬季之前的積存的脂肪體。這些脂肪體主要是在過冬時維持其精子發生所需之能量與其生理的正常代謝。蝎虎 (*Hemidactylus frenatus*) 每月的平均脂肪體重的分散度極大，表示脂肪體的存在與否和生殖週期的關連性很少。

分析整年的脂肪體和肝重季節性的變動，對於整年的生殖週期的貢獻 (*C*)，顯示出蝎虎的脂肪體的肝重季節性的變動對生殖變動上的需要，貢獻最大 ($C=62.8\%$)；而臺灣攀木蜥蜴，貢獻最小 ($C=19.3\%$)；而蛇舅母的貢獻值是介在兩者之間 ($C=35\%$)。