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ANNUAL REPRODUCTIVE AND LIPID STORAGE PATTERNS OF THE AGAMID LIZARD, *JAPALURA SWINHONIS MITSUKURII* IN SOUTHERN TAIWAN

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Jun Yi Lin and Hsien Yu Cheng (1986) Annual reproductive and lipid storage patterns of the Agamid Lizard, *Japalura swinhonis mitsukurii* in southern Taiwan. *Bull. Inst. Zool., Academia Sinica* **25**(1): 13-23.. *Japalura swinhonis mitsukurir* in southern Taiwan had a distinct breeding season from the emergence in March through August. Most females produced two clutches. The number of eggs per clutch for most clutches was 5 (with range from 3 to 8). The clutch size increased significantly during the breeding season.

Both sexes enlarged their fat bodies during the regression of sexual activity and the pre-hibernation period. The patterns of fat bodies utilization, however, were different in the two sexes. Males used the fat reserves mainly for maintenance of body metabolism and reproductive condition during winter-dormancy, whereas the fat reserves of females were mainly expended in the development of the first clutch during the March and early April.

Compared to *J. swinhonis formosensis*, *J. s. mitsukurii* were larger at the same age, and had smaller fat bodies, smaller ratio of reproductive elements to the body weight, and a longer breeding season.

A wealth of data has accumulated over the past decade on annual reproductive and lipid storage patterns in both temperate and tropical lirards (e. g., Derickson, 1976: Fitch, 1970, 1982; Ruibal, *et al.*, 1972; Vitt, 1983; Vitt and Goldberg, 1983; Vitt and Lacher, 1981). These data have also yielded hypotheses or the general patterns and the evolutionary strategies of lizard reproduction and energetics (Derickson, 1976; Pianka, 1976; Stearns, 1976; Tinkle, *et al.*, 1970). Nevertheless, the reproductive and energetics biology of most lizards remains poorly known, particularly for insular populations in the Pacific region (Schwaner, 1980). The annual reproductive and lipid storage pattern of *Japalura swinhonis mitsukurii* reported here was made as part of our comparative study on reproductive and energetic biology of lizards in Taiwan, a subtropical Pacific island.

J. s. mitsukurii is a diurnal and arboreal lizard, common in the woods, and known to occur from the plain to the elevation 1000 meters in southern and eastern Taiwan and its adjacent islands (Lan-yu Island and Green Island). It is one of the three geographical subspecies of *Japalura swinhonis*, the only agamid in Taiwan (Liang and Wang, 1975). The present study contains the data on the reproductive patterns, the fat body cycles and the liver cycles of both sizes of *J. s. mitsukurii.*

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These data are compared to those of *J. swinhonis formosensis* from central Taiwan (Cheng and Lin, 1977, 1978; Lin, 1979).

MATERIALS AND METHODS

Lizards were collected monthly from the woods, mainly *Acacia confusa*, at Hen-chun (22°0′0″ N; 120°30′ E; elevation of 60 meters), the most southern county of Taiwan, from March 1979 to April 1980.

Specimens were etherized within two days of capture, and weight and snout-vent length (SVL) were measured to nearest 0.01 g and 1 mm, respectively. Livers and fat bodies were removed and weighed to the nearest 1 mg. For males, the left testes with epididymis were dissected and weighed to nearest 1 mg, fixed in Bouin's solution, sectioned at eight microns and stained with Harris's hematoxylin and eosin. The diameters and thickness of seminiferous tubules and ductus epididymis were measured to nearest 0.1 micron. Six stages of annual spermatogenesis cycles, as shown in Cheng and Lin (1977), were used in classifying reproductive condition, which was judged by the histological appearance of the germinal epithelium and accessory sexual structures. The males in which testis abundant with all stages of spermatogenesis were considered as reproductive.

For females, follicles, oviducal eggs and corpora lutea were counted. Yolked follicles and oviducal eggs were then weighed to nearest 1 mg and measured to the nearest 0.1 mm. Females were classified as reproductive when either eggs or yolked ovarian follicles greater then 2 mm in diameter.

The meteorological data of the study area obtained from the meterological station at Heng-chun, about 1 km north of the study area.

RESULTS

Adult *J. s. mitsukurii* were found active from early March to late November. They were rarely found in December and January, and absent in February.

Male patterns

The smallest and largest mature males were 63 mm and 91 mm SVL, respectively (Table 1). Only the males larger than 75 mm SVL were used for the analyses to minimized the influence of body size on the analyse (Atchley, Gaskins and Anderson, 1976). Minimum SVL was selected by the method as shown in Cheng and Lin (1977). The monthly mean SVL of the adult males were similar to all months (ANOVA, $p=.93$), and ranged from 78.0 mm to 82.6 mm. The yearly mean SVL was 80.4 mm (Table 1).

TABLE 1

Summary of snout-vent length of mature specimens used in the study and the previous studies (Cheng and Lin, 1977; Lin, 1979). Sexual maturity in males is the smallest male in which with all stages of spermatogenesis (Cheng and, Lin 1977); in females, with the presence of yolked follicles

Species	Sexual maturity	Minimum used	Maximum used	Monthly mean (range)
J. s. mitsukurii				
Male	63	75	91	80.4 (78.0-82.6)
Female	56	61	80	67.3 (65.0-72.4)
J. s. formosensis				
Male	54	70	85	76.4 (74.4-79.2)
Female	53	53	76	65.5 (53.3-76.5)

TABLE 2
Monthly mean diameters and thickness of seminiferous tubules and ductus epididymis (in microns; plus and minus one S. E. with each mean)

Month		N	Seminiferous tubules			Ductus epididymis	
			Diameter	Thickness	Cellular layer	Diameter	Thickness
1979	Mar.	13	191.2± 6.0	53.1± 3.7	13.6±0.8	142.7± 5.7	30.8±1.4
	Apr.	10	186.2± 7.8	46.0± 3.0	14.8±3.1	134.2± 6.9	29.5±1.6
	May	9	200.6± 6.5	50.9± 3.3	14.8±1.2	142.0±14.0	33.2±4.8
	June	10	151.5± 5.3	45.1± 1.8	15.5±1.0	123.7±11.8	38.6±2.6
	Aug.	14	141.4± 8.8	43.3± 2.2	13.4±0.8	126.4± 6.7	30.7±1.1
	Sept.	14	105.3± 8.3	29.0± 2.1	8.5±0.7	71.6± 4.2	23.5±1.4
	Oct.	7	51.3± 9.7	24.1± 2.6	4.0±0.4	44.7± 2.5	12.6±1.7
	Nov.	8	66.2± 3.5	35.6± 3.4	6.3±0.5	50.7± 4.5	12.9±1.4
	Dec.	8	104.6± 8.8	50.6± 4.1	14.0±3.5	50.4± 6.1	16.9±3.2
1980	Jan.	2	112.7±17.4	44.8±11.0	14.0±4.7	—	—

Testis.—Monthly mean change in the diameters of seminiferous tubules shows a distinct cycle (Table 2). At emergence in March, the seminiferous tubules are near maximum in diameter with a thick epithelium of about 13 to 15 cellular layers. Gonadal regression begins in June and is complete by October. During the month of October, the

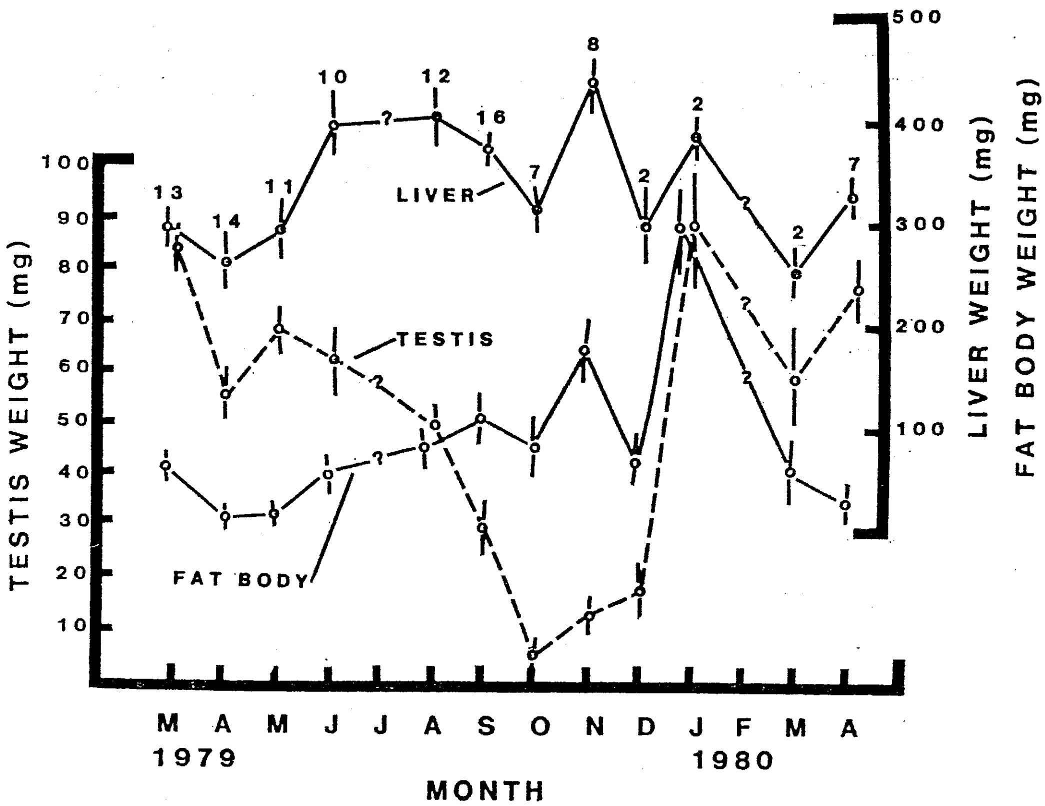

Fig. 1. Monthly mean weights of testis, liver and fat body of adult males (SV-length>75 mm). Vertical line indicates plus and minus one S. E.

seminiferous tubules are lined with a reduced geminal epithelium of less than 7 cellular layers. The testicular recrudescences begins rapidly with major growth in December. By January, the geminal epithelium consists of 14 cellular layers.

The cycle of testis weight essentially coincided with that of the seminiferous tubule diameters (Fig. 1), heavist from January to April, declinning from May to October.

Epididymis.—The ductus epididymis exhibited seasonal variation in duct diameter and height of their epithelial cells (Table 2). The ductus epididymis was large with a thick epithelial lining and contained variable amount of spermatozoa from March to August; it declined to its minimum size and contained no spermatozoa in October. The ductus remained small and had no spermatozoa in November and December. The diameters of the ductus epididymis without spermatozoa (mean=51.4±2.6 microns) were significantly ($p<0.001$) smaller than that those contained spermatozoa (mean=133.8±3.9 microns). Epithelial height of those were also significantly ($p<0.01$) different when they contained spermatozoa (mean=33.0±4.0 microns) as when they did not (mean=16.0±4.2 microns). An increase in diameter and epithelial height when spermatozoa were present indicates increased cellular activities and suggests that the epididymis may have been secreting the nourishment for spermatozoa.

Liver and Fat Body.—The mean liver weight increased after emergence (March), reached the peak in August, and then decreased to the lowest in October. Mean liver weights significantly increased and peaked in November, and then decreased slightly in the following January. The mean liver weight of the pre-hibernation males in November and January had 44% loss during the hibernation (Table 3).

Fat bodies were almost exhausted during hibernation (Table 3); thus, males emerged with very small fat bodies in March, and the fat bodies remained so until June (Fig. 1). Mean body weight increased steadily from June to October and increased sharply in November.

Female patterns

The smallest and largest mature females in the sample were 56 mm and 80 mm SVL. respectively (Table 1). However, sample (n=98) contained only three mature individuals with the 56 mm-60 mm SVL class. The three derived from the spring/early summer samples. Thus, 61 mm SVL was

TABLE 3
Comparison of liver and fat body weight changes between pre-hibernation and post-hibernation

Sex	Male	Female
Pre-hibernation (nov. 5, 1979)		
Mean liver weight (mg)	437.8±27.7	295.6±21.4
Mean fat body weight (mg)	169.6±31.6	33.6±12.7
	$n=8$	$n=8$
Post-hibernation (march 1, 1980)		
Mean liver weight (mg)	244.5±16.6	261.7±34.0
Mean fat body weight (mg)	48.5±34.3	62.7±23.7
	$n=2$	$n=7$
% of weight loss (−) or gain (+)		
Liver	(−) 44.4%*	(−) 11.5%[ns]
Fat body	(−) 71.4%*	(+) 86.6%*

*: Significant at 0.001 [ns]: Not significant

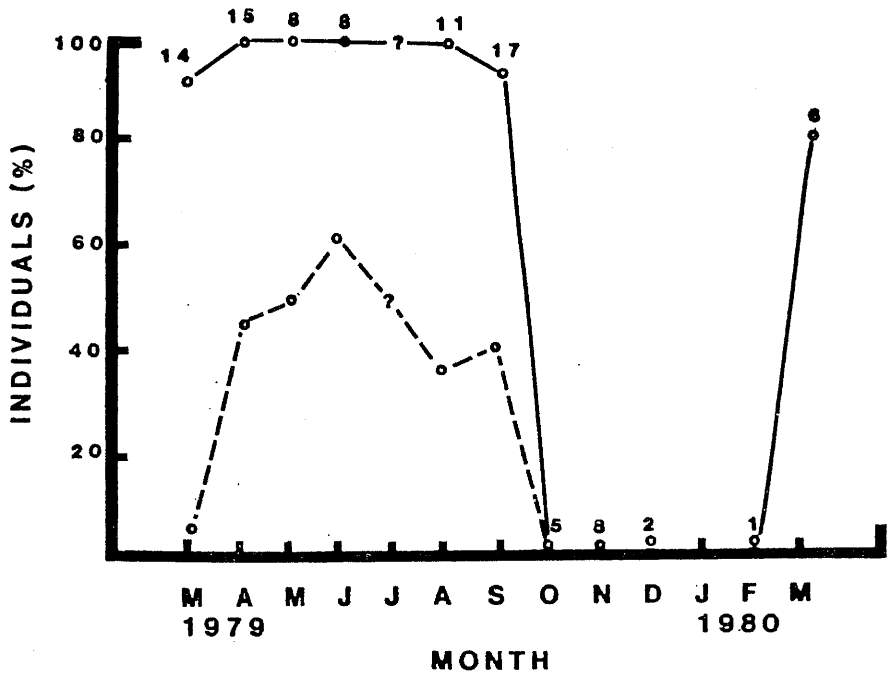

Fig. 2. Monthly changes in the reproductive state of adult females (SV-length > 60 mm). (o——o) shows the percentage of each sample that contained yolked follicles, oviducal egg or both; (o----o) shows the percentage of each sample that contained oviducal eggs.

chosen as the smallest female adult size used in the following analyses. The monthly SVL means were similar in all months (ANOVA, p=.91) and ranged from 65.0 mm to 72.4 mm. The overall yearly mean SVL was 67.3 mm SVL (Table 1).

Reproduction.—In 1979, all adult females captured from March through September were classified as reproductive (N=73, Fig. 2). The number of reproductive active females declined sharply in late September, and reached the lowest level (0%) in October. No yolked follicles (diameter=2.0 mm) were observed among the fifteen adult females sampled during October to December (Fig. 2).

During 1979, most females produced two clutches. By May and June, the majority (81%) of adult females contained both yolked follicles and oviducal eggs or both yolked folicles and corpora lutea. A few females may produce three clutches or merely one clutch. Because females containing oviducal eggs occurred in mid-March and would probably have oviposited in late March or early April, these females would have had nearly six months for reproduction, long enough to produce a second and perhaps a third clutch. The mean time necessary to produce a clutch was estimated to be two to three months. Commonly, females reached maturity from late June to early August. It seems unlikely that these younger adult could have produced more than one clutch during that year. To sum up, many females produced their first clutch in late April–June and a second clutch in July–September. A few females produced a first clutch in late March–early April, a second clutch in June, and a third clutch in August–September. A younger females produced one clutch in August–September.

The mean number of eggs for all clutches was 4.6 as estimated either by the mean number of ovarian yolked follicles (N=63;

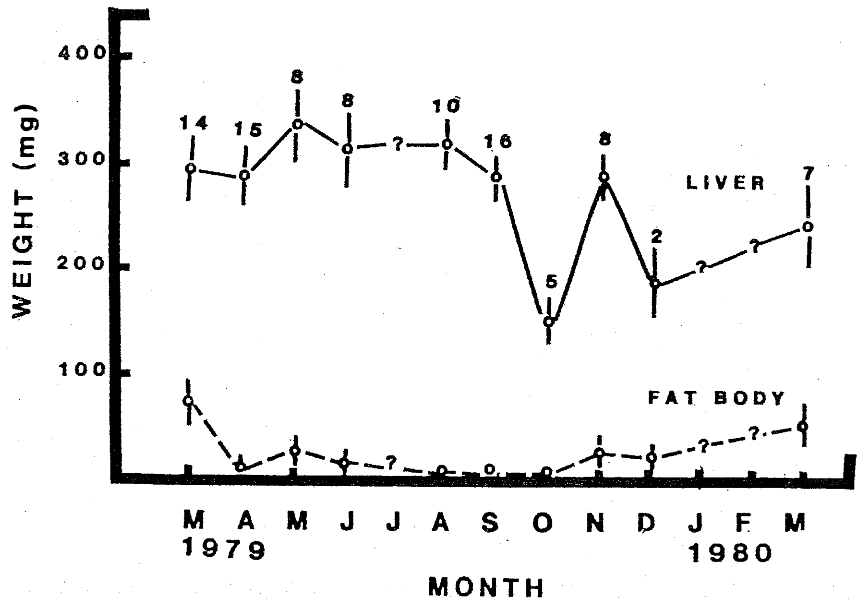

Fig. 3. Monthly mean weights of liver and fat body of adult females (SV-length > 60 mm). Vertical line indicates plus and minus one S. E.

range: 3–8) or by the mean number of oviducal eggs (N=28; range: 3–7). Clutch size had no significantly correlation with either SVL or total body weight. However, only females larger than 75 mm in SV-length had clutch size more than six eggs. All females smaller than 62 mm had clutches of five or fewer eggs. One atretic egg was found in the one 72 mm SVL female collected in April.

The number of eggs for the first clutch was 4.1 (N=12) as estimated by the mean number of oviducal eggs of females collected during March, April and May. This was lower than the mean number 4.7 (N=11) for the second clutch or the last clutch of the adults and the first clutch of the younger adults collected during August and September. In addition, the mean number of 4.5 eggs for the first clutch was also lower than that of 5.3 eggs for the second clutch as determinated by the six females with both oviducal eggs and yolked follicles, occurred during April, May and June. All differences were not more than one full egg, but all of them were very significant ($p<.01$).

Weight and maximum diameters of oviducal eggs varied from 174 to 488 mg (mean=291 mg, N=27) and from 9.4 to 14.9 mm (mean=12.1 mm, N=27). Those mature eggs which corpora lutea were smaller than 2.0 mm had mean maximum diameter of 13.0 mm (range: 11.9–14.9 mm, N=13) and mean weight of 363 mg (range: 300–488 mg, N=13). No females with oviducal eggs less than 12.0 mm in diameter had yolked follicles at the same time.

Inter-uterine migration of eggs was found to have occurred in 33% of the gravid females with no apparent bias toward the right or left oviduct. No obviously difference was found between the numbers of maturing follicles produced by the left ovaries and by right ovaries.

The mean incubation time of oviducal eggs ($n=12$) was 46.9 days. All eggs incubated at the room temperature (25–28°C). The mean hatching SVL was 22.4 mm.

Liver and Fat body.—The mean liver weight remained between 275 and 350 mg from emergence in March to November except for a sharp drop in October. No significantly difference of the mean liver weight occurred between the females in pre-hibernation and in post-hibernation (Table 3).

Fat bodies were almost exhausted during the production of the first clutch (March to June). Then, the fat bodies enlarged steadily from October. The females emerged in March had a little more fat bodies than the females in pre-hibernation period (November) had (Table 3).

DISCUSSION

J. s. mitsukurii in southern Taiwan has a distinct breeding season from the emergence in March through August (Fig. 4). Testicular atrophy began in late August, and both sexes ceased reproductive activity during pre-hibernation period, October–December. Spermatogenensis began in December but no spermiation occurred until the emergence (Fig. 4).

Most females produced two clutches but a few females may produce three clutches or merely one clutch during 1979 breeding season (op. cit.). The earliest clutches were laid in late March or early April, and the last clutches were laid in September. Since the incubation time is about 1.5 months, the hatchings are expected to occur from May to November and this is concordant with observations of recently hatched young (<25 mm in SVL) occurred from late May to early November.

These youngs would reach their maturity during the following reproductive season successively. It took about eight to ten months after hatching to reach the maturity (unpublished data). Some adults would

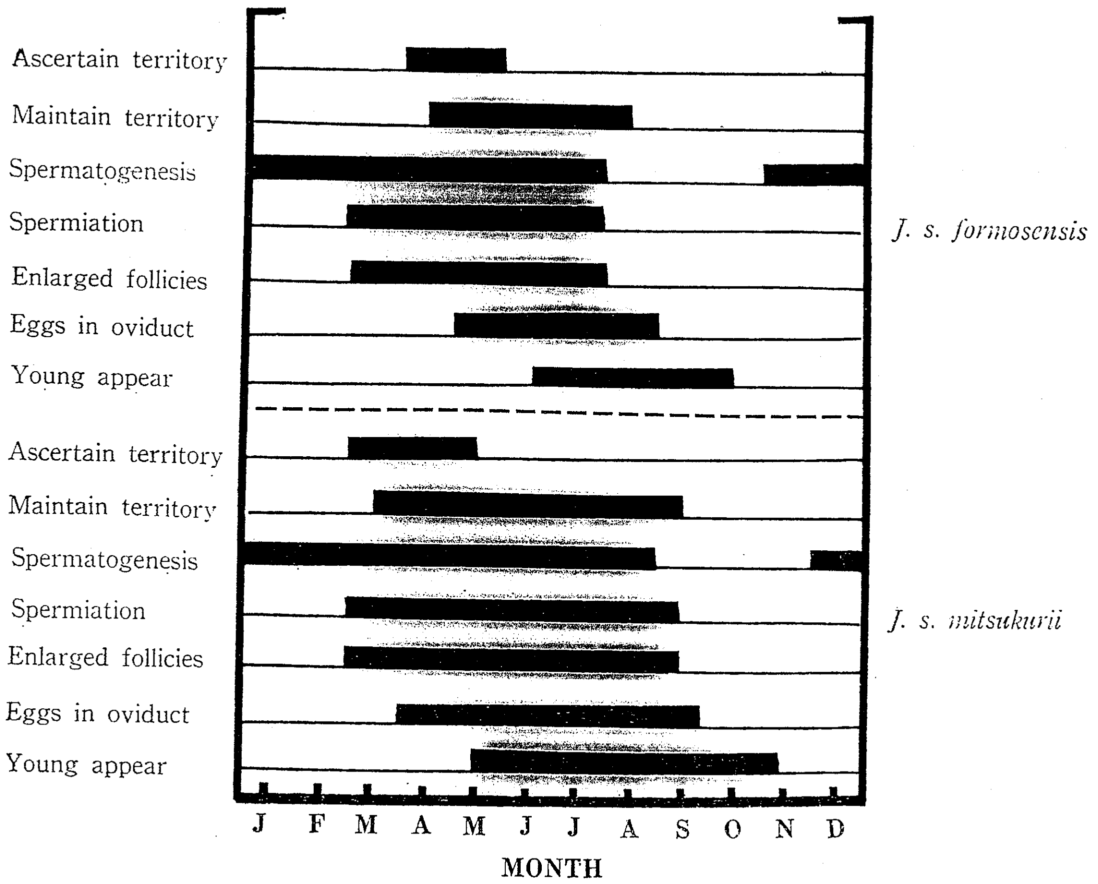

Fig. 4. Summary of seasonal reproductive and enegetic condition of *J. s. formosensis* and *J. s. mitsukurii.*

survive into the next following reproductive season and most of them produced only one clutch and disappeared during July and August that was evidant by the presence of some large females (SV-lengh; 70–80 mm, N=19) in our spring 1979 samples, and few large females (n=2) in our summer, autum and winter 1979 samples.

Clutch size increased significantly during the 1979 reproductive season. The mean number of eggs for the second clutch was higher than those for the first clutch (op. cit.). This increase does not result from increasing body size of the adult females, because the monthly mean SVL were similar for all months (Table 1). Possibily, the increased clutch size resulted from greater food availability which was supposed to be positively correlated with rainfall and air temperature (Ballinger, 1977; Stamps and Tanaka, 1981).

The fat body cycle of *J. s. mitsukurii* is distinct for each sex, although both sexss show major enlargement of fat bodies during the regression of sexual activity and the pre-hibernation period (Fig. 1, 3). It is apparantly that the males used the fat reserves mainly for maintenance of body metabolism and reproductive condition during the winter-dormancy since the male had possessed enlarged testes with all stages of spermatogenesis during the pre-hibernation period (Fig. 1; Table 3). However, the female used the fat reserves mainly for the development of the first clutch during the March and early April (Fig. 2 and 3).

The liver weight in both sexes was positively correlated with reproductive activity combined the fat body size. As the mean fat body weight increased, the mean liver weight increased (Fig. 1, 3). As the regression of reproduction occurred during the late September and October, the mean liver weight decreased distinctly (Fig. 1, 2, 3). The evidence supposed that the liver is an intermediary organ for both the storage and utilizations of lipid, especially for the reproductive purpose as some studies pointed (Hahn, 1967; Reddy and Prasad, 1972; Cheng and Lin, 1978).

Comparison with *J. swinhonis formosensis*

The reproductive and energetic biology of *J. s. formosensis* have been published by Cheng and Lin (1977 and 1978), Lin (1979), Wei and Lin (1981), and Chen *et al.* (in press). The concordance of all the previous studies on annual reproductive cycles indicates that *J. s. formosensis* has consistant timing of the reproductive cycle (Chen *et al.*, in press). The studied area of *J. s. formosensis* is about 245 km north to the present studied area of *J. s. mitsukurii.*

J. s. mitsukurii has larger SV-length than *J. s. formosensis* at the same age. For hatching young, the difference is about 2.4 mm; for adult females, is about 2.5–3.5 mm; for adult males, is about 5.9–8.9 mm (Table 1). Longer photoperiods and potentially higher food availability in the study area of *J. s. mitsukurii* may play an important role in enhancing growth of *J. s. mitsukurii* (Fox and Dessauer, 1957; Stamps and Tanaka, 1981; Ballinger and Congdon, 1980).

Although the mean aldult weight of *J. s. mitsukurii* was larger than that of *J. s. formosensis*, *J. s. mitsukurii* had slightly lighter or similar mean weight of oviducal eggs in the females (mean=363 vs. 377.5 mg), and similar mean testis weight in the breeding males (mean=66.1 mg vs. 66.7 mg) than those of *J. s. formosensis*. The evidences indicated that the reproductive effort, estimated by the ratio of reproductive elements to the body weight, of both sexes of *J. s. mitsukurii* were slightly lower than that of *J. s. formosensis* (Table 1). However, *J. s. mitsukurii* had approximately six months of one reproductive season which about one month longer than that of *J. s. formosensis* (Fig. 4). *J. s. mitsukurii* may produce up to 3 clutches, and *J. s. formosensis* may produce only up to 2 clutches, although most females of both subspecies produce 2 clutches during one reproductive season. Thus, totally reproductive efforts during one year of both sexes of *J. s. mitsukurii* would be essentially similar to that of *J. s. formosensis* on a population level.

The patterns of fat bodies deposition and utilization of both sexes of *J. s. mitsukurii* appeared to be essentially similar to those of *J. s. formosensis*. The liver weights in both sexes of *J. s. mitsukurii* and *J. s. formosensis* appeared to be positively correlated with reproductive activity combined the fat body size (Fig. 1, 2, 3; Cheng and Lin, 1978; Lin, 1979). However, *J. s. formosensis* was evident to accumulate more fat bodies than *J. s. mitsukurii*. The higher level of mean fat body weight occurred in the last month of reproductive season was 99 mg for the male and 0 mg for the female of *J. s. mitsukurii*, and was 188 mg for the male and 14 mg for the female of *J. s. formosensis*. The peak of mean fat body weight cycle occurred in post-hibernation was 291 mg for the male and 34 mg for the female of *J. s. mitsukurii* (Fig. 1, 3), and was 349 mg for the male and 115 mg for the female of *J. s. formosensis* (Cheng and Lin, 1978, Lin, 1979). The lesser fat in *J. s. mitsukurii* might be partially due to one or two more days of starvation of *J. s. mitsukurii* than those of *J. s. formosensis* (only less than three hours) from the time of capture to sacrifice. Otherwise, the higher growth rate and possible higher social interactions occurred in *J. s. mitsukurii* would cause them hard to deposit more fat during the reproductive or non-reproductive season.

The meteological and phenological data for *J. s. mitsukurii* show some dependent on both photoperiod and temperature for the regulation of their seasonal reproductive activity as *J. s. formosensis* did. The testiscular atrophied started during August for both subspecies, *J. s. formosensis* and *J. s. mitsukurii*, as the daylight decreased in July. However, *J. s. mitsukurii* atrophied their testis more slowly and reached completely atrophied level during October, about one month later than that of *J. s. formosensis* (Fig. 4, Table 2, Table 4). It would due to the higher temperature (monthly mean=27.0°C) in the habitat of *J. s. mitsukurii* than that (monthly mean=25.3°C) in the habitat of *J. s. formosensis* during August and September. The time for hypertrophied testis started in *J. s. mitsukurii* occurred was also about one month later than that of *J. s. formosensis* (Fig. 4, Table 2, Table 4). The most possible cause was that the relatively low temperature (monthy mean=24°C) was obtained during October for *J. s. formosensis*, but was not obtained until November for *J. s. mitsukurii*. These evidences indicated that the regulation patterns of the annual testis cycles of both *J. s. formosensis* and *J. s. mitsukurii* were similar to that of *Anolis carolinensis* which was studied experimently to demonstrate the pattern by Licht (1971).

Like as in *J. s. formosensis*, the vitellogenesis of *J. s. mitsukurii* started as the daylight, temperature and the occurrances of male courtship behavior during the spring, about two months before the monsoon rains began (Fig. 4; Lin, 1979). The females would cease their reproductive activities just after regression on testes in male occurres during September (it was August for *J. s. formosensis*), as the daylight was relatively short and the temperature was relatively low. It is seemed that all photoperiod, temperature and male behavior are important in determinging the onset and termination of reproductive activities of the females in both subspecies, *J. s. mitsukurii* and *J. s. formosensis* (Cheng and Lin, 1977; Lin, 1979; Crews, 1978; Licht, 1973).

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南臺灣攀木蜥蜴 (*Japalura swinhonis mitsukurii*) 的生殖和脂肪積存之年周期

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南臺灣攀木蜥蜴 (*Japalura swinhonis mitsukurii*) 雌雄的生殖期均自每年 3 月（多眠後）開始至 8 月止。大部份雌個體每年產兩窩。大多數每窩有 5 個蛋（範圍由 3 個到 8 個）。在生殖期後半段的平均每窩蛋數顯著的比在前半段的多。

雌雄個體均在生殖活動停止至進入多眠前，積存其體內脂肪體。雄個體體內積存的脂肪主要使用於過多時維持其精子發生所需之能量與其生理的正常代謝。雌個體則使用其體內積存的脂肪於過多後（3 月和 4 月間）其產生第一窩蛋所需之能量。

和臺灣攀木蜥蜴 (*J. swinhonis formosensis*) 比較，南臺灣攀木蜥蜴有較大的體長，較小的脂肪體，較小的生殖組織與身體的重量比，和較長的生殖季節。