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Studies on the Physiological and Ecological Adaptation of Temperate Insectivorous Bats

III. Annual Activity of the Japanese House-dwelling Bat, *Pipistrellus abramus*

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A study on annual activity cycle of ***P. abramus*** was carried out in Fukuoka City. The bats formed a colony and remained in one house all year, without seasonal migration. From May to September emergence time of the first bat averaged 12 minutes after sunset, though it was earlier in cloudy weather than in clear. As for nocturnal activity, there was both a major peak soon after sunset and a minor peak just before sunrise from May to August, but in October only the former occurred. When air temperatures dropped to 15°C and less, bats seldom emerged. The principal foraging period was within 2 or 3 hours after emergence in summer; and was synchronized with the emergence of most small Lepidoptera and Coleoptera, which constitute the major portion of the diet. In early spring and autumn Diptera became the main food. The size (body length) of available insects was 15mm and less. The increase ratios of body weight in late autumn to that in summer were 30.6 and 29.2 % in adult females and males, respectively. Hibernation lasted from early November until mid-March. During deep hibernation, arousal occurred once in 16 days, and the rate of weight loss (ca. 1 mg/g body weight/day) was about half of that during the shallow hibernation. Winter activities of genus *Pipistrellus* are various in different species. It may be attributed not only to variations in climate and food, but also to the degree of cold-resistance and of torpidity.

INTRODUCTION

In previous papers (Funakoshi and Uchida, 1975, 1978), we discussed about the phenomena of annual activities in some cave-dwelling bats from the viewpoint of adaptation to the temperate zone. In this paper we report the annual activities in *Pipistrellus abramus*. This species roosts exclusively in houses which are directly influenced by climatic changes, and uses the same house for roosting throughout the year with no seasonal migration. Therefore, it seems that this species is well adapted for seasonally hostile environment.

Seasonal and nocturnal activity patterns have been studied, in some insectivorous species (Venables, 1943; Dwyer, 1964; Nyholm, 1965; O'Farrell and Bradley, 1970; O'Shea and Vaughan, 1977). Little is known, however, of in-

terspecific variation in annual activity of bats (Dwyer, 1968, 1971; McNab, 1969, 1974). The purpose of this study is to analyse seasonal changes in activity of *P. abramus* related to weather, air temperatures and emergence of prey, and to discuss the special adaptability for the ecological phenomena in *P. abramus* compared with the other species of the genus *Pipistrellus*.

STUDY AREA AND METHODS

We examined twenty five colonies (as a rule, one colony per house), observing bat's emergence time, air temperature, relative humidity and light intensity in Fukuoka City, Fukuoka Prefecture (33°35′ N, 130°25′ E) from the spring of 1973 to the autumn of 1976 (Fig. 1). In order to know the nocturnal and seasonal activity patterns, we counted the number of bats going out and in through the wainscot of house. The foraging areas were confirmed by pursuing bats at the individual level. Bats were captured by a mist net covering the entrances of the roost at the emergence time. Their sex and age were noted, and then body weight and forearm length were measured, and every bat was marked with a wing-band before release at the capture point. Nocturnal changes in ratio of postfeeding body weight to prefeeding one at the individual level were evaluated to confirm foraging pattern in summer.

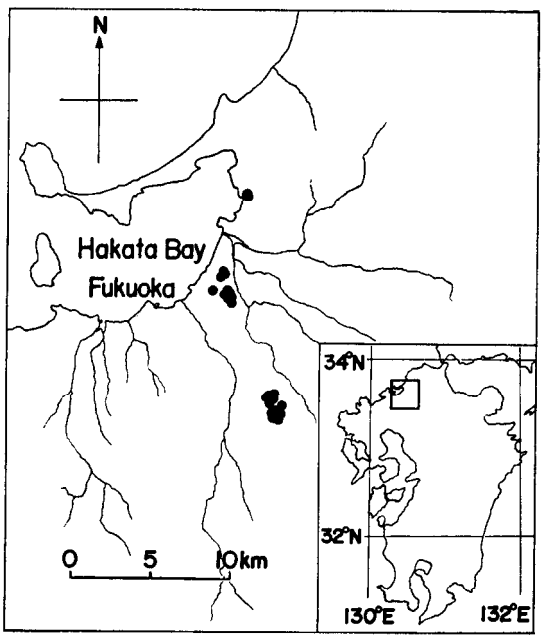

Fig. 1. Map showing locations of the study area in Fukuoka City. Fukuoka Prefecture. Solid circles indicate points of the roosts of P. *abramus*.

We analyzed bat's fifty feces every month to detect seasonal changes of the prey. Frequency of occurrence of each order of insects in fecal components is given as a ratio of the number of the feces including one or more fragments of a certain order of insects to the sum of the number of feces in which one or more fragments were found for each order. Identification of available insects for the bat was performed by means of comparing the fragments of insects in the feces with the corresponding parts of the insects (head, prothorax, abdomen, leg) collected by a light trap with 20-watt white and black lights at intervals of 30 minutes at the University Farm of Kyushu University where the bats were foraging.

In the laboratory, changes in weight loss of the bats were individually examined with water supply only in a constant dark room with room temperatures of 2.4–7.0°C from 1 November 1973 to 4 March 1974. Winter activity patterns of two bats under the same conditions were accurately checked by a Hitachi 24 channel operation recorder from 23 October 1976 to 27 February 1977. In addition, we performed experiments on the times required for the food containing particles of ion exchange resin (below 1 mm in diameter), to transit the digestive tract of *P. abramus* on 26-28 May 1978. Food was a mixture of banana, cheese and yolk of a boiled egg. After they had finished feeding, we noted the time when the bat began to defecate.

RESULTS

1. Nocturnal and seasonal activities

Before taking up the main subject, we refer to the outline of seasonal changes in sex and age composition in colony of the bat. The colony size averaged 20 bats (range 4-36 bats) from spring to summer, before the young are born; but males were scarce. The number of adult males was only O-3 in colonies from March to mid-July (cf. Fig. 2). An unusual case was a solitary male that was captured on 11 June 1973. On the other hand, adult fe-

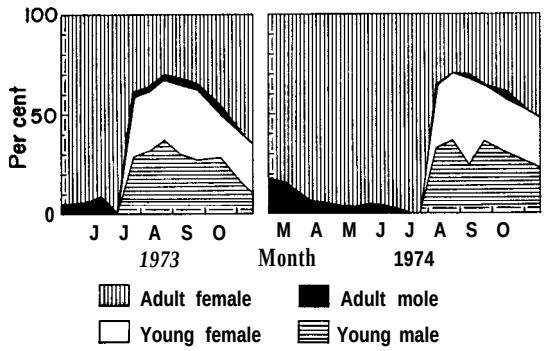

Fig. 2. Seasonal changes in ratio of the number of different age and sex groups to the total catch in optional roosts every half month in 1973 -1974.

males did not migrate, but used the same roost all year.

Parturition occurred from late June to early July. The mean litter size was 2.3, the sex ratio (♂/♀) being about 0.88. As shown in Fig. 2, the total catch of newly weaned young was remarkably more than that of adults in summer. But, on the basis of the data obtained by banding, the number of newly weaned young in each colony was nearly equal that of adults. This is the fact of the case, and indicates that the number of newborn young becomes reduced to about half in the course of nursing. The young weaned in summer reached sexual maturity in autumn of the year. There was almost no individual exchange among two or more colonies, even at the mating season in October. Bats born in summer were recaptured at the same roost in the spring of the following year. Almost all of them, however, were females, and their number was only one-fourth or one-third of newly weaned bats. Perhaps the other females emigrated. On the other hand, most of the adult males may become solitary or die within a year. Thus, sex and age composition in each colony changed remarkably every season.

Emergence time of the first bat, air temperature and light intensity at that time are shown in Fig. 3. The first emergence time (Fig. 3-A) was about 10–30 minutes after sunset, except in spring (April) and autumn (after mid-October). Especially from May to September, emergence began 12 minutes on an average after sunset, and continued for about 20 minutes with a peak about 3 minutes after its beginning. In addition, the first emergence time was earlier in cloudy weather than in clear. During the periods from March to April and from late October to November, the first emergence times were unstable and changed widely.

In May, when the first emergence time became stabilized, the light intensities were 40-150 lux (Fig. 3-B). The light intensity dropped to O-30 lux in June, the latter period of pregnancy, and again rose to 20-200 lux in July, and August when the newly weaned young were apt to be captured at the start of emergence. In September, the light intensity fell again to about 40 lux. In and after October, it further dropped to about 0 lux. The light intensity at the end of homing time before sunrise also changed seasonally in the same way as mentioned above.

The emergence patterns in the same colony after sunset are shown in Fig. 4. All or the great majority of bats flew out at air temperatures above 20°C (Fig. 4-B, C, D, I, N). When the air temperatures were 20°C and less, the emergence dragged sluggishly on (Fig. 4-A, E, G, H, K, M), and/or the total emergence number decreased (Fig. 4-A, E, F, J, K, L, M). At air temperature of about 16°C, the total emergence number was only 24 (Fig. 4-E). Further, when the air temperatures fell to 15°C and less the bats scarcely emerged, though it was not illustrated. The bats generally did not emerge in a heavy rain, but did occasionally in a light rain (Fig. 4-M).

The state of nocturnal activity after emergence is indirectly known from checking the number of emergence or homing bats. From May to June, there were two peaks of activity going out and in through the wainscot during the night. Namely, the first activity period was within 3 and more hours after

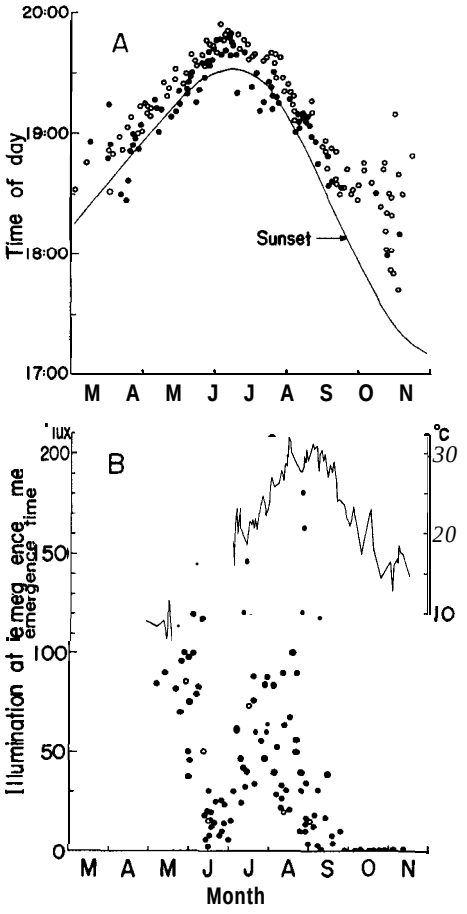

Fig. 3. Emergence time of the first bat (A). ○, a time in clear weather; ● , a time in cloudy weather. Air temperature and light intensity at emergence time (B). ●, illumination at the time when the first bat emerged ; ○, illumination at the time when the last bat returned before sunrise.

sunset, the second one being within 1 and more hours before sunrise (Fig. 5-A, B, C, D). Especially, in the latter half of pregnancy, the first activity period (Fig. 5-C D) gradually shortened in comparison with that in the first half (Fig. 5-A). In the lactating (Fig. 5-E) or weaning season, the flying activity became intermittent during the night. Afterwards, the two peaks of activity occurred again (Fig. 5-F) except that intermittent flights were observed sometimes (Fig. 5-G). In October, the flying activity outside roost was restricted within a few hours after sunset, and the activity before sunrise was scarcely observed (Fig. 5-H, I). Early in November when the air temperatures at sunset fell to 15°C and less, bats did not emerge and began to hibernate.

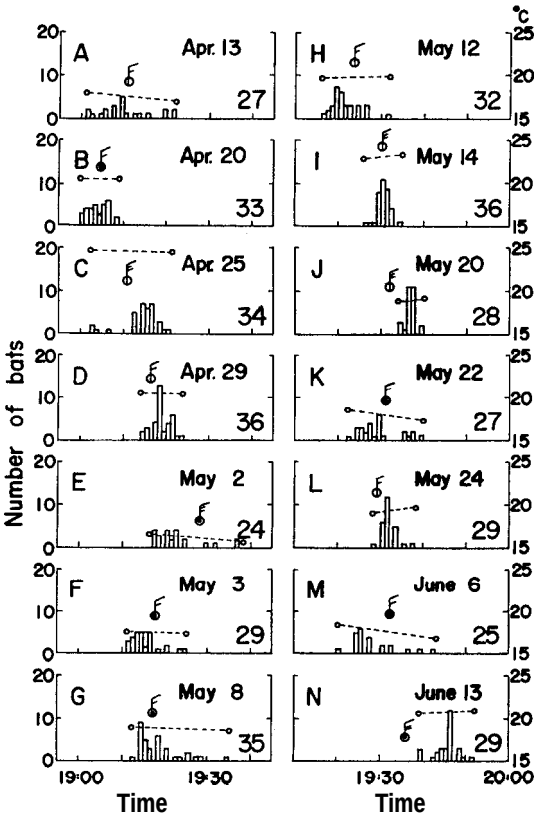

Fig. 4. Patterns of emergence in the same colony (34 females and 2 males) from 13 April to 13 June. Open histograms show the emergence number, and the lower right number of each diagram indicates the total number of emergence bats. Broken lines represent nocturnal changes of the air temperature.

The bat hibernated in crevices of the wall' mud or of the clod beneath roofing tiles. A few flying bats, however, were found on rare occasions on warm day as follows; 1 March 1973 (9. 8–18. 5°C), 4 February 1974 (12. 1°C), 15 February 1976 (15. 0°C).

Since it is difficult to confirm the fall and winter activity under natural conditions, it was examined under constant darkness in the laboratory (Fig. 6). Just before hibernation from 25 October to 4 November (Fig. 6-A), the period of circadian rhythm averaged 23.3 hours, and the duration of activity averaged 123 minutes at a room temperature of 15. 7°C on an average. As for the winter activity during the hibernation (Fig. 6-B), in the early hibernation from 10 to 14 November, the rhythm of another bat took the average of 24.0 hours, with the activity duration of average 41 minutes, at a room temperature of 13. 2°C on an average: from 14 November to 22 December, the activity occurred at intervals of 5 days at a room temperature of 10. 1°C as average;

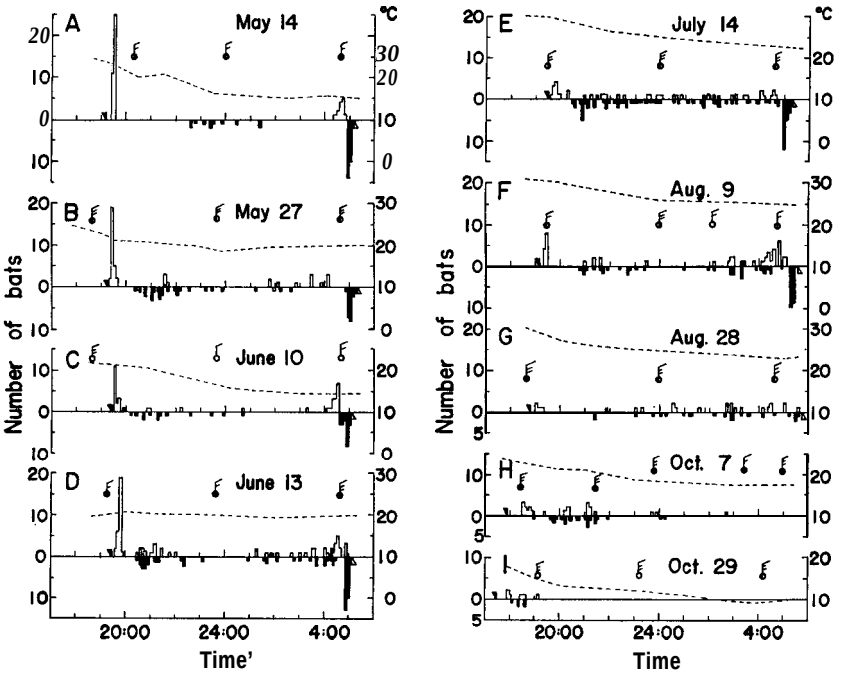

Fig. *5.* Seasonal and nocturnal changes of the flight counts in some colonies. Open histograms show the emergence number and the solid ones the return number. Broken lines represent nocturnal changes of the air temperature. ▼, sunset time; △, sunrise time.

in this case, the duration of activity shortened and averaged 20 minutes: further, in the deep hibernation from 22 December to 25 February, the bat had activity rhythm at intervals as long as 16 days, with the activity duration of only 16 minutes, at a room temperature of 6.1°C as average.

2. **Feeding activity and food habit**

Foraging flights were observed at various open areas, such as park, wasteland, field, paddy field, reservoir and river. Bats usually foraged through repeated circular flights. Some bats fed near the roost for a while, and then moved to farther areas. Some flew straightly towards definite areas at about 5 km distance from the roost as soon as they emerged. Most bats had some areas suitable for feeding and changed foraging area one after another during the night. Bats hung sometimes from the corner of such structures as emergency staircase and eaves at night. Thus, bats seem to have a resting time outside the roost at night. In experiments on the recovery of banded bats which were released at various distances from the home colony, some bats returned from a maximum distance of about 10 km.

Increase ratios of postfeeding to prefeeding body weight based on the recapture data in August are shown in Fig. 7. The ratios in adult females reached about 1.2 (an increase of ca. 1.5 g in body weight) at about 23: 00 hr,

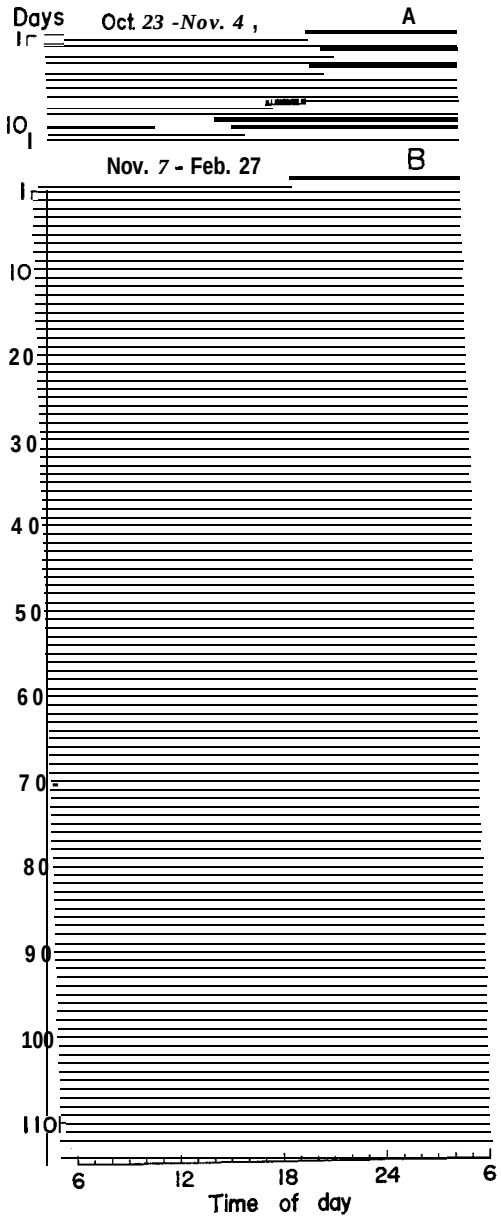

Fig. 6. Activity rhythm of ***P. abramus*** under constant darkness in 1976–1977. Records of 13 (A) and 113 (B) successive days for a single bat are shown, respectively. Solid blocks on each base line indicate duration of activity.

afterwards they were descending. The ratios in young were limited to less than 1.1 (an increase of ca. 0.5 g in body weight), one of them being less

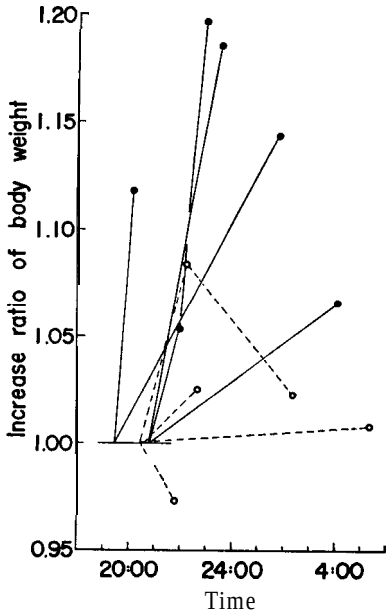

Fig. 7. Nocturnal changes in ratio of postfeeding to prefeeding body weight based on the recapture data on 2-3 August 1974. ., adult females; o, weaned young.

than 1.0, for newly weaned young had only several circular and short flights near the roost.

We could observe sometimes defecation in ***P. abramus*** recaptured within a

Table 1. Passage times of food through the digestive tracts of six adult females *(P. abramus)* at room temperatures of 25-26°C (1978).

Band no.	Postfeeding activity level					
	Inactive* (26 May)		Active** (27 May)		Inactive (28 May)	
	Food consumption (g)	Passage time after eating (min)	Food consumption (g)	Passage time after eating (min)	Food consumption (g)	Passage time after eating (min)
XK				49		79
XW	0.34 1.42	55	0.83 1.82	49	0. 1. 20 52	73
XS		72		43		77
XD	0. 0.48 28	81	0.39 0. 64	50	0. 0. 44 70	98
		60		47		78
XA	0.40	92	0.09	31	1.00	57
Mean		69		45		77

* Regarded as an "inactive" level, when the bats were in alert, mobile periods alternating with intervals of torpidity.

** Regarded as an "active" level, when the bats frequently moved about their cage, had their eyes fully open, and responded rapidly to noises.

few hours after emergence. Therefore, it seems likely that the passage time of food through the digestive tract is very short. In order to know the passage time, we made some experiments on it in the laboratory. As shown in Table 1, the food transit time in active *P. abramus* (six adult females) averaged only 45 minutes.

Nocturnal changes in dry weight of insects collected by the light trap are shown in Fig. 8. Main emergence time of insect prey was within a few hours after sunset. In summer (Fig. 8-A). Lepicloptera with body length of 15mm and less were much abundant from 20: 00 hr to 23: 00 hr, and Coleoptera with body length of 10 mm and less were abundant from 19: 00 hr to 21: 00 hr. Hemiptera and Diptera with body length of 10 mm and less also were found, but both were scanty. In autumn (Fig. 8-B), the emergence flight of insect prey diminished, and the volume of insects captured by light trap was as small as about one-tenth of that in summer (Fig. 8-A).

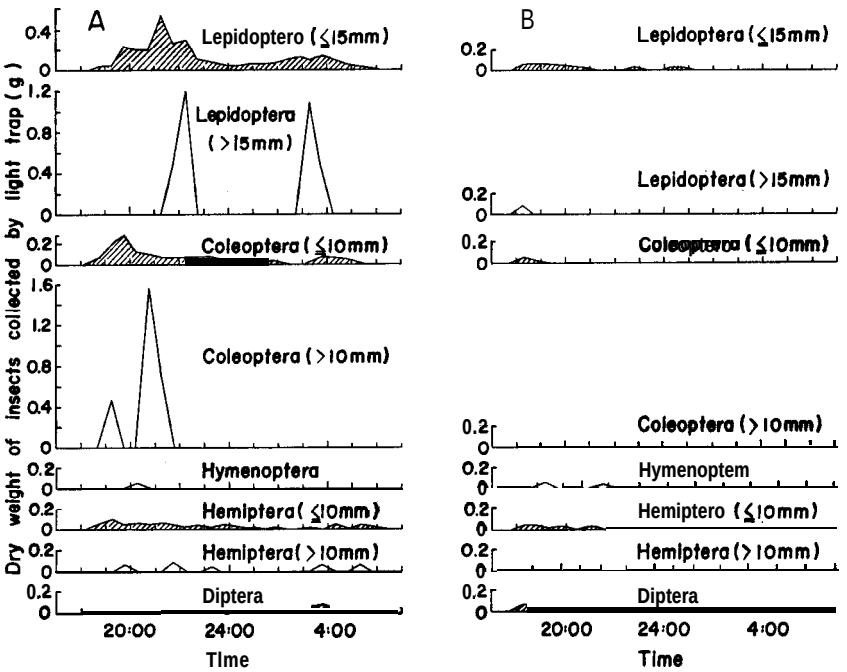

Fig. *8.* Nocturnal changes in dry weight of insects collected by light trap at the University Farm of Kyushu University on 20-21 August 1977 (A) and on 20-21 October 1977 (B). The obliquely hatched areas indicate that they **are used as available foods.**

As shown in Fig. 9, occurrence frequency of Diptera in feces was about 50% in March, and it gradually dropped from 39 % to 12 % from April to August, but afterwards it again increased rapidly and became 57% in October. The frequency of Lepicloptera fluctuated between 26 and 49% from April to September, though it was less than 20% in March and October. The fre-

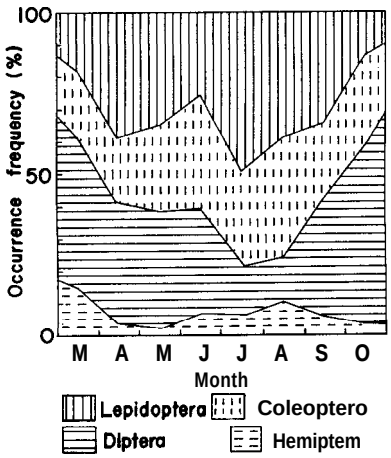

Fig. 9. Seasonal changes in occurrence frequency of food (order level of insects) in fecal matter in 1973. Occurrence frequencies in each order of insects in fecal components are given as the ratios of the number of the feces including one ***or*** more fragments of a certain order of insects in fifty feces to the sum of the number of the feces in which one or more fragments were found for each order.

quency of Coleoptera changed 18–37 %, including 30-37 % in summer, from March to October. In Hemiptera it was under 14% from March to October. Especially, the sum of occurrence frequency of both Lepidoptera and Coleoptera attained to about 80 % from July to August. The size of available prey was generally 15mm and less in body length.

3. **Seasonal change in** body weight

Prefeeding body weight of different age and sex groups was seasonally measured at the time of emergence from the roosts in 1974 (Fig. 10). The body weight of adults declined generally during hibernation. In adult females it decreased for some time after the awakening from hibernation, but began to increase late in April, and averaged 6.5 g in mid-May. After that, it increased noticeably with the growth and development of fetus, and averaged 11.2 g in late June just before parturition. Just after parturition, the weight dropped suddenly to a mean of 6.7 g, and then gradually increased. The body weight of adult males was by about 1 g less than that of adult females, excluding females in the pregnancy.

Towards the end of September, the body weight of adults in both sexes rapidly increased as a result of subcutaneous fat deposition, and the weight of adult females attained to 9.7 g on an average, and that of adult males did 9.1 g. Just before hibernation, the weight was 9.4 g in adult females and 8.4 g in adult males as average on 1 November 1973. In other words, the increase ratio of body weight in late autumn to that in summer was 30.6 % in adult females and 29.2 % in adult males. The body weight of adult females on 28 March 1974 just after hibernation averaged 6.4 g, that of adult males

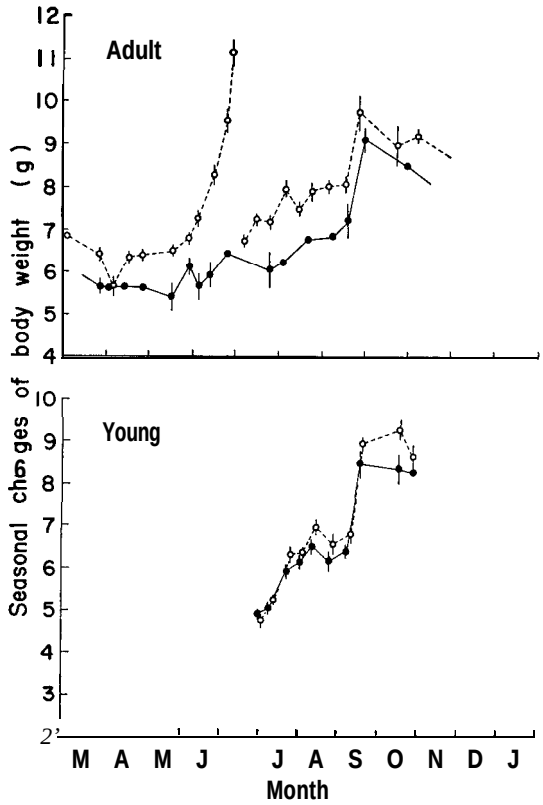

Fig. 10. Seasonal changes in body weight of the adults (upper) and young (lower). Solid circles show the mean weight for males and open ones for females. Standard errors are indicated by vertical lines.

being 5.7 g. The rates of weight loss in mg/g body weight/day, which were calculated from the changes in body weight between 1 November 1973 and 28 March 1974, were 2.2 mg in both sexes.

The body weight of newborn young ranged from 0.7 g to 1.6 g according to litter size, irrespective of sex. Newly weaned young, however, showed little difference in body weight among them (4.8 g in females, 4.9 g in males as average). Judging from the above, it is revealed that there is a rapid increase in body weight during the suckling period. After weaning, the body weight of young further increased, and took the average of 7. Og in females and 6.5 g in males at the end of August. At this time, the difference in body weight of young between the two sexes became clear, and the young body weight in both sexes approximated that of adult respectively. At the end of September the weight of young in both sexes increased rapidly from subcutaneous fat deposition, and attained to 9.3 g in females and 8.5 g in males on an average.

Analysis of weight changes by individuals during hibernation was made at

Table 2. Mean rate of weight loss (mg/g body weight/day) in winter from 1 November 1973 to 4 March 1974.

Age and sex group	1 Nov. to 28 Dec. Rate N	M±S. E.	28 Dec. to 5 Feb. Rate N	M±S. E.	5 Feb. to 4 Mar. Rate N	M±S. E.
l-year females	6	1. 93±0. 19	6	1.21 ±0. 10	6	1. 89±0. 25
l-year males	5	2. 27±0. 10	5	1. 11±0. 15	3	1.97 i0.27
2-year-plus ***females***	9	1. 79±0. ***09***	9	***0.71*** ±0. ***09***	9	2. 26±0. ***28***
2-year-plus male	1	(2.50)	1	(1.35)	1	(1.73)

The weight loss of bats was individually examined with only water supply in a constant dark room with ambient temperatures of 2. 4–7. 0°C.

room temperatures of 2. 4–7. 0°C with a mean of 4. 1°C under constant darkness. Table 2 shows the average rates of weight loss in mg/g body weight/day at each period of hibernation. The average rate was about 2 mg during both the first period from 1 November to 28 December and the last period from 5 February to 4 March (shallow hibernation), while only about 1 mg during the middle period from 28 December to 5 February (deep hibernation), though there was a little difference between ages or sexes.

DISCUSSION

1. Daily cycle of activity

The first emergence time in ***P. abramus*** was nearly synchronized with the sunset time, i. e., 12 minutes on an average after sunset from May to September (Fig. 3), being earlier by about eight minutes than that in *Pipistrellus pipistrellus* occurring in England (Church, 1957; Stebbings, 1968). The correlation of emergence with sunset has been reported on some insectivorous bats (Eisentraut, 1952 ; Gaisler, 1963 ; Dwyer, 1964 ; Herreid and Davis, 1966; Maeda, 1974; Funakoshi and Uchida, 1975; O'Farrell and Studier, 1975). Awakening before sunset and light sampling behavior also have been recognized in some insectivorous bats (Twente, 1955; Phillips, 1966; Funakoshi and Uchida, 1975). In the case of ***P. abramus***, shivering or rustling sounds and vocalizations were heard at roosts about 30 minutes before sunset. Prior to emergence time, the bat crawled forward a narrow slit in a wainscot.

It is suggested, as mentioned by DeCoursey and DeCoursey (1964), that awakening is caused by endogenous rhythm, and that start of emergence is a manifestation of photoperiodic response by light sampling behavior related directly to the time of sunset. The earliest emergence time in ***Tadarida*** *femorosacca* is more closely related to solar radiation on the day of emergence, and is 45 minutes on an average after the zero point of solar radiation for the summer (Gould, 1961). Further, he indicated that temperature and total amount of solar radiation during the day did not appear to affect ***emergence*** time. The emergence time in ***P. abramus*** was rather early on cloudy days compared with that on fine days.

At rainy ***or very*** windy night ***P. abramus*** seldom emerged. ***In*** contrast with

this, bad weathers such as wind, rain and frost do not restrain the emergence of *P. pipistrellus* in Czechoslovakia and England (Hůrka, 1966; Stebbings, 1968). Thus, it is revealed that *P. abramus* is more sensitive to the weather, and has a tendency to avoid rain and strong wind.

Wide ranges in light intensity selected by *P. abramus* at the first emergence time are due to both late emergence of pregnant females in the latter period of gestation and early emergence of newly weaned young. In this connection, Stebbings (1968) stated that the juveniles of *P. pipistrellus* should predominate among the early emergers, and Venables (1943) also reported that in August the bat commenced to emerge around sunset earlier than in the other months.

Such an unstable emergence around sunset in spring as that which is seen in *P. abramus* has been shown also in *Miniopteus schreibersi fuliginosus* (Funakoshi and Uchida, 1975). Further, *Myotis mystacinus* in Finland emerges in the daytime in May, and its activity duration is short at that time, though it generally emerges after sunset in summer and its activity is limited between dusk and dawn (Nyholm, 1965). Moreover, he noted that the air temperature only in the daytime was higher than the threshold temperature (ca. 7°C) for emergence of the bat or insect prey in May. Taking the unstable food supply in spring into consideration, it is assumed that craving for food overcomes an antipathy to sunlight.

In and after October, the selected light intensity at the first emergence time in *P. abramus* was about 0 lux, and the emergence was more concentrated after sunset that in the other seasons (Fig. 3), in contrast with the early emergence of *M. vnystacinus* before sunset (Nyholm, 1965) and *M. s. fuliginosus* at about sunset (Funakoshi and Uchida, 1975) in the same season. When air temperatures were 15°C and less, *P. abramus* scarcely emerged in Fukuoka City (33°35′ N, 130°25′ E). Its threshold temperature for emergence is higher than that (12°C and less) in the same species occurring in Tsuruoka City (39" N, 140" E), Yamagata Prefecture of the northeastern part of Japan (Kanda, personal communication), or that (40°F≒4. 4°C) in *P. pipistrellus* distributing in England with about 52°N of latitude (Venables, 1943). *Pipistrellus hesperus* inhabiting southwestern New Mexico and adjacent southeastern Arizona is active at high temperatures from 14°C to 29°C (Jones, 1965), while in Sabino Canyon, Arizona the bat scarcely flies when air temperature is below 19. 0°C (Cross, 1965). In this connection, O'Farrell and Bradley (1970) reported that *P. hesperus* was active at air temperatures between -8" and 31°C in the low desert of southern Nevada. We assume, however, that the flying activity under severe cold conditions as low as -8°C means rather a physiological response to the abrupt lowering of the temperature than an usual activity under normal conditions.

As for the nocturnal activity outside the roost, *P. abramus* tended to become most active soon after sunset and secondly active before sunrise from May to August (Fig. 5-A, B, C, D, F), except for irregular activity during the lactating (Fig. 5-E) and weaning periods (Fig. 5-G), but it was active only shortly after sunset in October (Fig. 5-H, I). The similar tendency with the

principal activity shortly after sunset during the warmer months has been shown also in ***P. hesperus*** (Jones, 1965; O'Farrell and Bradley, 1970). Further, the presence of two activity periods during the night has been reported also in *Antrozous pallidus* (O'Shea and Vaughan, 1977) and *M. mystacinus* (Nyholm, 1965). In any case, such a nocturnal activity pattern and its seasonal change appear to be closely correlated with the emergence of insect prey.

2. Feeding activity

Food transit time in active *Myotis* ***lucifugus*** with light body weight (ca. 8 g) is within an hour after eating (Buchler, 1975). Transit time of food marked with barium sulfate through the digestive tract in ***Eptesicus fuscus*** being about twice the weight of ***M. lucifugus*** averages 122 minutes (Luckens ***et al.,*** 1971). *M.* s. ***fuliginosus*** weighing about 13 g begins to defecate within about an hour after eating food of about 1.5 g marked with barium, and all of the feces are evacuated within 6 hours (Funakoshi and Uchida, 1975). In ***P. abramus*** (ca. 7.3 g) an average of passage time was only 45 minutes for the active bats in captivity (Table 1). In this way, food transit time in insectivorous bats is very short in general, and consequently their body weight will change continuously during the night. Accordingly, nocturnal feeding pattern can be indirectly revealed through pursuing the changes in body weight, though a net intake of food can not be directly obtained.

Body weight of adult females increased rapidly within 2 or 3 hours after emergence in summer (Fig. 7). Its period corresponded with the time of most emergence of such available insects as small Lepidoptera and Coleoptera (Fig. 7, Fig. 8-A). Six or seven hours after emergence, the increase ratio of body weight had a tendency to decrease, though there was a secondary active period before sunrise. Similar active feeding shortly after emergence has been observed also in ***Pipistrellus*** *subflavus* collected at Mashpee, Massachsetts in August, i. e., the two bats weighing 5.3 g and 6.7 g accumulated 1.4 g and 1.7 g of stomach contents in 30 minutes of feeding time, respectively (Gould, 1955).

Nocturnal feeding patterns, together with the time of its peak, varies with the species, season, sex and age (Ross, 1964; Kunz, 1973, 1974; Funakoshi and Uchida, 1975; Anthony and Kunz, 1977; Fenton ***et al.,*** 1977). ***Pipistrellus*** *nanus* in Rhodesia (18°10′ S, 23°13′ E) has three feeding periods between dusk and dawn, and uses additional night roosts as resting places near the feeding grounds (Fenton ***et al.,*** 1977). Lovett (1961) stated that ***P.*** *pipistrellus* in captivity would eat up to 1/3 or more of its body weight. Thus, food intake to the body weight in ***P. pipistrellus*** seems to be more than that in ***P. abramus***. The body weight of adult female ***P. pipistrellus*** averages 5.19 g in summer (Stebbings, 1968), being less than that (ca. 7.2 g) of ***P. abramus***. Judging from this, it is probable that the smaller the species, the more the food consumption, owing to the higher metabolic rates.

Increase in weight of newly weaned young during the night was only within about 0.5 g (Fig. 7). Food intake to their body weight was less than 1/3 of that in adult females. Such a less food intake has been shown also in young ***M. lucifugus,*** and their food intake was about half of that in adult females

(Anthony and Kunz, 1977). It may be considered, therefore, that young improve foraging efficiency as they grow.

Adult females of *P. pipistrellus* leave their nursery roost immediately after weaning (Stebbings, 1968). He suggested that this might be to prevent competing for food with young. In *P. abramus*, however, all adult females and the majority of young did not leave the nursery roost but used it as a constant roost throughout the year. The usual number in nursing colonies of *P. pipistrellus* is up to 300, and 1,000 individuals may not be uncommon (Stebbings, 1977). On the other hand, that in *P. abramus* was usually less than 50, and the case of more than 100 individuals was rare. Judging from the fact abovementioned, it is considered that such a relatively small, scattered colony acts to restrain intraspecific competition for food. Consequently, in *P. abramus* the colony mixed with adult female and young groups appears to be maintained consecutively.

Insect prey in autumn became scanty rapidly in comparison with that in summer (Fig. 8). Seasonal changes in number of insects collected by light trap at night have been minutely investigated by Williams (1935, 1939). According to these reports, quantitative catches of all insects per night began to increase in April and were at the highest from June to August, after that they began to decrease in September and were at the lowest from February to March. Seasonal changes in occurrence frequency of insect prey on the level of order in fecal matter of *P. abramus* corresponded with qualitative changes of insect prey collected by light trap (Figs. 8 and 9). In this case, the principal food in summer was Lepidoptera and Coleoptera, and that in early spring and autumn was Diptera which was not so important as in summer. *P. pipistrellus* feeds chiefly on Diptera and Lepidoptera (Poulton, 1929).

Most of the emergence times of Diptera were concentrated within l-2 hours after sunset in autumn, though its quantitative catch was little, and besides it became reduced somewhat compared with that in summer (Fig. 8). The activity period of *P. abramus* outside roost in autumn, also, was restricted to only l-2 hours after sunset. Thus, it is assumed that food intake of *P. abramus* in autumn is remarkably less than that in summer as well as that of *M.* s. *fuliginosus* (Funakoshi and Uchida, 1975). The decline of flight activity in *P. abramus* had a negative correlation with the remarkable increase of body weight caused by subcutaneous fat deposition from late September to early October (cf. Figs. 5 and 10). It has a metabolic significance that start of fat deposition in *P. abramus* is earlier by about a month than that in *M. s. fuliginosus* (Funakoshi and Uchida, 1975).

As for food babits of bats, for example, *Myotis velifer* (Ross, 1967; Kunz, 1974) and *M. lucifugus* (Belwood and Fenton, 1976; Buchler, 1976; Anthony and Kunz, 1977), the preference for the order level of insects varies with different region even in the same species. Some insectivorous species flexibly changes their diet in correlation with nocturnal or seasonal changes in emergence of prey (Kunz, 1974; Funakoshi and Uchida, 1975; this study). In any case, prey size seems to be limited in accordance with bat species. For example, the size of available food for *M. s. fuliginosus* (ca. 13 g) is less than 25mm in body

length (Funakoshi and Uchida, 1975), for *M. velifer* weighing 10–13 g is less than 20 mm (Kunz, 1974), for *M. lucifugus* weighing some 8 g is 3 to 10 mm (Anthony and Kunz, 1977), for *P. hesperus* is 2 to 10 mm (Ross, 1967), and for *P. abramus* was 15 mm and less. Namely, bat size confines the maximum size of prey in general.

Most of the insectivorous species show not only selective feeding but also opportunistic feeding (Kunz, 1974; Funakoshi and Uchida, 1975; Fenton and Morris, 1976; Anthony and Kunz, 1977). Such a dietary flexibility is supported by the fact that Diptera becomes a common principal food also for several cave-dwelling species in the Kyushu districts under a shortage of food supply.

3. **Hibernation and winter activity**

P. abramus and *P. pipistrellus* hibernate in any crevice that can afford contact with dorsal and ventral body surfaces, where is susceptible to the fluctuations of outside air temperature and relative humidity (Hůrka, 1966; Racey, 1974; this study). In Czechoslovakia ambient temperatures beside hibernating *P. pipistrellus* in a building change from -2" to 9°C with an average of 3.5°C from November to January (Hurka, 1966). In England ambient temperatures close to the same hibernating species vary from -5" to 12°C with a median of 3.4°C from November to March (Racey, 1974). In this connection, the average air temperature in London from November to March is 5.5°C (Tokyo Astronomical Observatory, 1978). The average air temperature in Fukuoka City was calculated at 8.1°C from November to March. Accordingly, it is assumed that *P. abramus* hibernates at relatively high ambient temperatures in comparison with *P. pipistrellus*. Body temperature of hibernating *P. abramus* averaged 7.4°C at an ambient temperature of 7.0°C.

At the beginning of November, *P. abramus* began to hibernate and slept deeply until late February and afterwards its hibernation became shallow, though few flights were rarely observed on warm days. During the deep hibernation period, activity occurred only at intervals of 16 days on an average under constant darkness (Fig. 6-B), and the rate of weight loss reduced to about one half of those during the shallow hibernation periods in the laboratory (Table 2). These results indicate that winter activity of *P. abramus* is remarkably low, being much different from those of some cave-dwelling bats (Funakoshi and Uchida, 1978). *P. abramus* could survive 120 days or more under fasting through depending almost upon the consumption of deposited fat. Occasional arousals during the hibernation may be mainly caused by endogenous rhythm or physiological requirements (cf. Funakoshi and Uchida, 1978).

Hibernating roosts of *P. abramus* are unfavorable for water intake in contrast to those of cave-dwelling bats. The relative humidities in Fukuoka City ranged 34 to 97% with a mean of 71% from November to March, being lower than those (70–100%) in caves where *M. s. fuliginosus* hibernates (Funakoshi and Uchida, 1978). Thus, more body water of *P. abramus* may be evaporated during the hibernation than in *M. s. fuliginosus*. It is therefore probable, as stated in the previous paper (Funakoshi and Uchida, 1978), that the water produced in the process of gradual resolution of the deposited fat supplies a demand for body water.

P. pipistrellus does not arrive at its hibernacula until late November or during December (Hůrka, 1966 ; Racey, 1973). This fact indicates that this bat is in a high activity level even at relatively low air temperatures just before hibernation. Flight activity during the winter in this species also is observed at a rather low air temperature (Venables, 1943). ***P. hesperus*** in southern Nevada is active throughout the year with peaks of seasonal activity during the warmer months, but in winter months it is active only for a while after dusk and the activity ceases when air temperatures drop (O'Farrell and Bradley, 1970). ***P. subflavus*** hibernates for an extended period in subtropical Florida with a relatively high upper temperature limit for torpor (ca. 18°C), and its fat deposition reaches maximally about 1/3 of the total body weight (McNab, 1974).

Judging from the above, it is revealed that activities of genus ***Pipistrellus*** vary with the species. Such variations may be caused not only by climatic changes and food conditions, but also by degree of tolerance for cold and acquisition of torpidity or long-term hibernating ability. In order to understand this question thoroughly, we must consider the transition of geographical distribution of each species, too.

Distribution of ***P. pipistrellus*** is widespread throughout the western Palaearctic east to Kashmir and north to about latitude 68" in Scandinavia (Stebbings, 1977). This species would have obtained a tolerance for cold, and probably can go with occasional feeding through the winter. A similar property is applicable also to ***P. hesperus***. On the other hand, ***P. abramus*** had a tendency to become torpid, even when the air temperature was relatively high, and slept deeply through depending largely upon the consumption of a large quantity of deposited fat. ***P. subflavus*** also may possess the same property as has ***P. abramus***. Such differences of winter activity have been shown also among some cave-dwelling species in the Kyushu districts (Funakoshi and Uchida, 1978).

4. Distribution of genus *Pipistrellus* in Japan

The genus ***Pipistrellus*** in Japan involves three species of ***P. abramus***, ***P. endoi*** and ***P. savii,*** which are allopatric each other as follows; ***P. abramus*** is common in lowlands of Kyushu, Shikoku and Honshu, ***P. endoi*** occurs in mountainous districts of central and northern Honshu, ***P. savii velox*** and ***P. savii coreensis*** are very rare in Hokkaido and Tsushima, respectively (Imaizumi, 1970).

Taking notice of specialization in baculum (Imaizumi, 1970) and karyotypic alteration (Uchida ***et al.,*** 1971; Andô ***et al.,*** 1977; Park and Won, 1978), ***P. abramus*** is regarded as the most specialized species among the three. ***P. abramus*** would have originated on southern regions and extended its distribution to Japan. This species exclusively inhabits human habitations with cultivated lands such as paddy field and so on, where the other species do not occur. As mentioned above, this species became torpid in early spring and late autumn, and slept deeply in winter when the available food decreased rapidly. In this connection, it is worthy of note that acquisition of such properties in ***P. abramus*** seems to be related with the disappearance of insects harming rice

plants (cf. Kuno, 1968).

In caves of the Akiyoshi-dai Plateau, Yamaguchi Prefecture in the western part of Honshu, deposits of *P. endoi*, regarded as from Wiirm to the Post-glacial age, have been gathered by Kuramoto (unpublished). At present, however, *P. endoi* does not occur in this region, inhabiting forests only in northeastern Japan. Judging from the above, it seems likely that when the last glacial age began to recede, and subsequently the weather became warm during the Post-gracial age, *P. endoi* having a long-term hibernating ability would have removed to farther north and colder regions, whereas some species would have found refuge in caves for the time being. As for *P. savii*, on the basis of its geographical distribution (Ellerman and Morrison-Scott, 1951), it is assumed that this species would have penetrated into Japan from northern regions.

In the future, we will further make the origin of *P. abramus* clear by discussing about systematic aspects.

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