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Life Cycles of *Aphodius* Dung Beetles (Scarabaeidae, Coleoptera) in Sapporo, Northern Japan

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Abstract

On the basis of the results obtained by the periodical field sampling, analyses of gonadal condition and rearing experiments made during 1982 to 1984, life cycles of twelve *Aphodius* species in Hokkaido Agricultural Experiment Station, Sapporo, northern Japan, were described with the following bionomic characters: flight period, pre-reproductive period, reproductive period, seasonal change in the frequency of inseminated females, hibernating stage and hibernaculum. All species were univoltine. Following the classification system by Kiuchi (1979), the life cycles were classified into the following four types: 1) Type A-a: Hibernating as adults that feed before hibernation: *A. uniformis, A. haemorrhoidalis, A. sublimbatus, A. rectus.* 2) Type A-b: Hibernating as adults that do not feed before hibernation: *A. haroldianus, A. pusillus, A. breviusculus, A. brachysomus, A. rugosostriatus.* 3) Type B: Hibernating as larvae: *A. sordidus, A. elegans.* 4) Type C: Hibernating as eggs: *A. pratensis.*

Key Words: Life cycle, *Aphodius* dung beetles, Sapporo

1. Introduction

Because of the common occurrence on dung of vertebrate animals, especially of large herbivores, three groups of scarabeid beetles are generally called "dung beetles". They are Aphodiinae, Scarabaeinae and Geotrupinae. Of these three groups, Aphodiinae is the most prevailing group in the north temperate zone (cf. Halffter & Edmonds, 1982). In these areas, a great number of individuals belonging to diverse species, in most cases of the largest genus *Aphodius*, are commonly found on dung, which is a kind of scattered and ephemeral food resources. Due to their overwhelming dominance in the numbers of both species and individuals, coupled with the characteristic ecological nature of their food resources, aphodiine beetles seem to be suitable for the analyses of interspecific relations among closely related coexisting taxa. A number of attempts have been made to clarify their various ecological aspects (e. g., Landin, 1961; Hanski & Koskela, 1977; Koskela & Hanski, 1977; Tych, 1981; Mohr, 1943; Paik, 1968; Merritt & Anderson, 1977; Holter, 1982; White, 1960). In Japan, too, the *Aphodius* fauna is relatively rich, including approximately fifty species (Ueno *et al.*, 1985), and much information has been accumulated on their life histories (Gotô, 1957; Masumoto, 1966, 1973; Hosogi *et al.*, 1979 a, b, 1980 a, b, c; Hosogi, 1985; Hayakawa *et al.*, 1976; Hayakawa,

1977, 1982; Hayakawa *et al.*, 1978; Hayakawa & Hasegawa, 1981; Yamashita *et al.*, 1978; Nakamura, 1975; Sakanoshita *et al.*, 1979; Tani, 1966; Kiuchi, 1979; Togashi, 1980; Yasuda, 1984).

However, our knowledge on the biology of these beetles is yet scarce and biased. In particular, their reproductive tactics has so far been paid little attention. Since 1982, we have been engaged in a comparative study on the biology of dung beetles in Sapporo, northern Japan. The main purpose of this study has been to clarify and compare the reproductive traits of several species of *Aphodius* beetles. As the first report of this study, the present paper describes and classifies life cycles of twelve *Aphodius* species in Sapporo on the basis of the results obtained during 1982 to 1984. Other parts of the study covering the reproductive traits of these beetles will be reported elsewhere.

2. Study Area and Methods

The periodical sampling and field observation were made at a pasture in Hokkaido Agricultural Experiment Station (43°0′N, 141°22′E; henceforth abbreviated as HAES) in Sapporo, northern Japan. The pasture was approximately 0.06 km² wide and was divided into seven areas by fences (Figure 1). Every year, the grazing was started in mid May when the snow almost disappeared, and continued until late November when the snow began to cover the ground. Approximately sixty individuals of cattle were grazed in the pasture and in the neighbouring

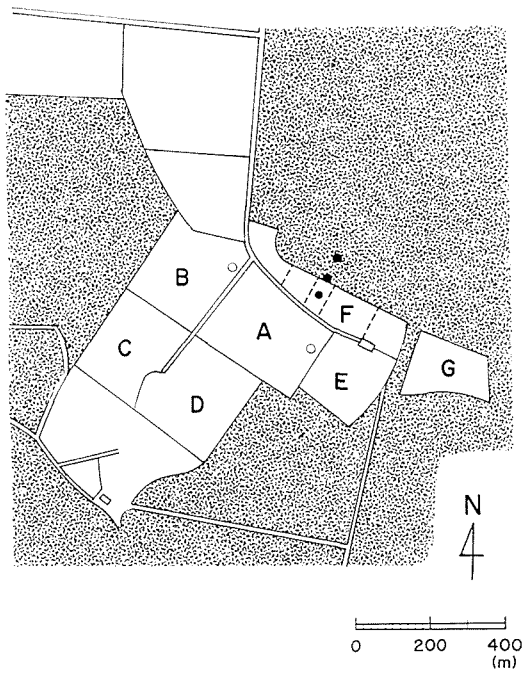


Figure 1. The study site in Hokkaido Agricultual Experiment Station (HAES) in Sapporo. A–G, codes of fenced areas. Black circles, trap sites. Open circles, waterplaces. Shaded, secondary forest.

broad-leaved deciduous forest through the years surveyed. Collection of beetles was mostly made at area A (Figure 1) where more than twenty cattle were always present during the grazing period. Principally once or twice in every week during the grazing periods in 1982 and 1983, dung beetles were collected from fresh and old cattle dung, the underlaying turf (ca. 3 cm thick) and from the soil beneath the dung (usually within 5 cm depth). The sampling was performed mostly during 11 : 00–15 : 00 on fine or cloudy days. The standard sampling unit was more than thirty individuals per species per sampling, though this condition was not always fulfilled. Quantitative sampling was not employed throughout the routine sampling.

In addition to the routine sampling, the collection by the light traps was attemped three times on fine or cloudy nights (July 1, 1982, August 6, 1982 and August 25, 1983) to know the nocturnal activity of adults. Three fluorescent black lamps (60 w) and a fluorescent lamp (40 w) were fixed 100–150 cm above the ground before the wall which was covered by white cotton cloth (90 × 160 cm). Lighting started before the sunset and ended after the sunrise. Beetles were collected at every quarter hour throughout the lighting.

In 1984, the data obtained by the previous years were supplemented by additional sampling, which included the following :

1) To know the activity of beetles before and at the start of grazing, beetles were collected by baited pitfall traps in 1984. The trapping method was similar to that described by Newton & Peck (1975). The trap was 2000 cc volume, 8.5 cm caliber and 24 cm depth with approximately 100 g of fresh cattle dung wrapped in cheese-cloth as bait and a 50 : 50 mixture of ethylene glycol and water in the bottom. Eight traps were set in each of the following three types of environment : pasture, margin of forest and forest (cf. Figure 1). Beetles were collected two days after the settlement of traps.

2) In the pasture there were small bare areas that were shaded by the foliage of trees growing sparsely around waterplaces (Figure 1). Species composition of *Aphodius* beetles in these areas and sunny turf-covered areas were studied four times in 1984. At each census, four dung droppings were chosen in each of the sunny turf-covered areas and the shaded bare areas, and the collected *Aphodius* beetles were identified and counted.

Meteorological data in the field were available from regular observatory records by HAES. Annual fluctuations of the air temperatures from 1982 to 1984 in the field are shown in Figure 2.

Beetles collected from in and under dung were carried alive to the laboratory with some dung fragments and soil. A part of these beetles were used for the rearing, of which procedure is explained later. Others were killed and dissected in an insect saline solution (0.75% NaCl) under a binocular dissecting microscope to determine their reproductive stages. Ovarian conditions were classified into the following four stages.

1) Undeveloped stage : Ovariole without differentiated oocytes, or with youngest transparent oocytes which were up to one fourteenth long as mature eggs.

2) Developing stage: Ovarioles with oocytes of various size, but without chorionated mature eggs.

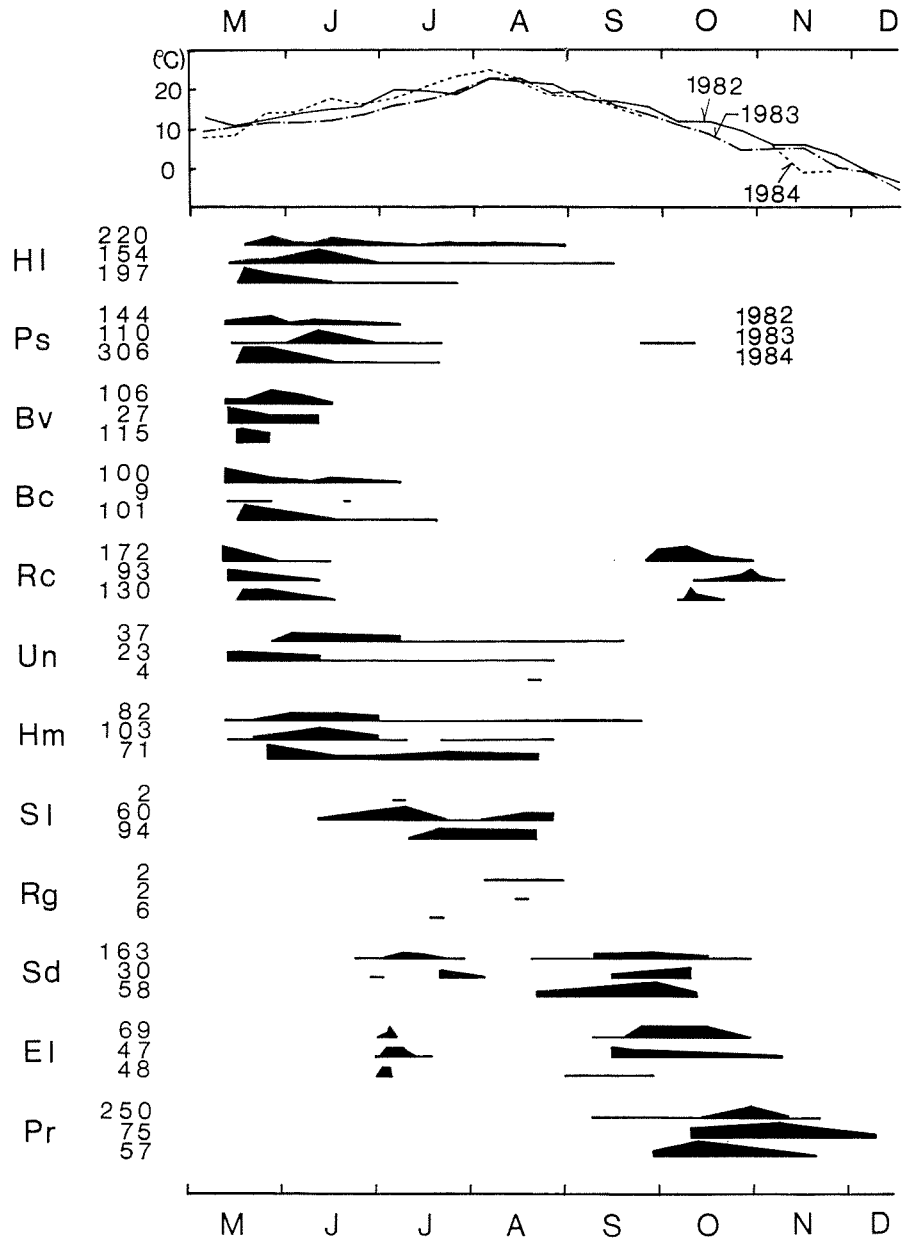


Figure 2. Seasonal distributions in adults of 12 *Aphodius* species in HAES. Abbreviations of species names in Table 1. Results of the three year survey are given for each species: Above, 1982; middle, 1983; below, 1984. Numerals at the right side of each abbreviated species name denote the total numbers of individuals collected in the year. Annual fluctuations of the mean air temperatures from 1982 to 1984 are given at the top. Further explanations in text.

3) Mature stage: Chorionated mature egg(s) present in ovarioles or oviduct.

4) Spent stage (post mature stage): Mature eggs absent; degenerating occytes sometimes present in ovarioles.

In addition to the ovarian condition, the contents of female spermathecae were examined in 1984 to know the seasonal changes in the frequency of inseminated females. Further, in 1982 to 1984, the generation overlap in the adult phenology of some species was studied by examining the degree of cuticular (tibial and prothoracic) wear that was classified into: Grade I, intact; grade II, slightly or moderately worn; grade III, heavily worn.

In order to supplement the information obtained by the above studies, beetles were reared by the following two methods in 1983 and 1984:

1) Outdoor culture using flower-pots: The flower-pot (15 cm diameter, 14 cm high) was filled with approximately a half volume of moist sand in the bottom and 100–150 g of fresh cattle dung on it. The number of individuals released was one or two pairs per flower-pot when the sexes of beetles could be determined externally, or ten to fifteen individuals per flower-pot when beetles could not be sexed. After releasing insects that had been collected in the reproductive peak of each species, the flower-pot was covered with cotton cloth to prevent the escape of the beetles. The flower-pot was then buried in the ground near the laboratory, leaving upper one fourth above the ground surface.

2) Laboratory culture using plastic cases: Flat plastic cases ($8 \times 15 \times 3$ cm) were used for small species. Each case contained soil (1 cm depth) and 60–80 g of fresh cattle dung. Five to twenty individuals were released in each rearing case and placed under the controlled room conditions (23°C, 16L8D).

The contents of these culture pots and cases were periodically inspected.

3. Species composition and general activity trend of *Aphodius* in HASE

A total of twelve species belonging to nine subgenera of *Aphodius* were re-

Table 1. List of *Aphodius* species collected during 1982–1984 in HAES. The abbreviations of the species names given here are consistently used in other tables and figures of the present paper

Species	Abbreviations of species name
Aphodius (*Colobopterus*) *haroldianus* Balthasar	Hl
A. (*Otophorus*) *brachysomus* Solsky	Bc
A. (*O.*) *haemorrhoidalis* (Linné)	Hm
A. (*Pharaphodius*) *rugosostriatus* Waterhouse	Rg
A. (*Orodalus*) *pusillus* (Herbst)	Ps
A. (*Phaeaphodius*) *rectus* (Motschulsky)	Rc
A. (*Aphodius*) *elegans* Allibert	El
A. (*Agrilinus*) *breviusculus* (Motschulsky)	Bv
A. (*Ag.*) *uniformis* Waterhouse	Un
A. (*Ag.*) *pratensis* Nomura et Nakane	Pr
A. (*Bodilus*) *sordidus* (Fabricius)	Sd
A. (*Calamosternus*) *sublimbatus* (Motschulsky)	Sl

corded in HAES during 1982 to 1984 (Table 1). Of these species, *A. haroldianus*, *A. haemorrhoidalis*, *A. pusillus*, *A. rectus* and *A. pratensis* were abundant, *A. elegans*, *A. brachysomus*, *A. sordidus*, *A. breviusculus* and *A. sublimbatus* were relatively common, and *A. uniformis* and *A. rugosostriatus* were rare. The seasonal activity patterns of adults are schematically shown in Figure 2, in which the relative frequency of individuals caught on each census date to the yearly total individuals were plotted. Since quantitative sampling was not employed, the figure should not be regarded as representing the actual activity pattern of respective species. But, it is sufficient for estimating the general seasonal trends of activity patterns. There are two peaks in the seasonal activity of *Aphodius*, a conspicuous peak from spring to early summer and another less prominent one in autumn*. The activity was, as a whole, very low in mid summer. The following nine species appeared once a year: *A. haroldianus*, *A. pusillus*, *A. breviusculus*, *A. brachysomus*, *A. uniformis*, *A. haemorrhoidalis*, *A. sublimbatus*, *A. rugosostriatus* and *A. pratensis*. On the other hand, *A. rectus*, *A. sordidus* and *A. elegans* were observed twice a year.

4. Descriptions of life cycles and autecological notes

The life cycles of the twelve *Aphodius* species in HAES, which could be regarded as showing the general trends of life cycles in Sapporo and the vicinity, are described below for each species separately. The data concerning the life cycles of *Aphodius* beetles in HAES are summarized in Tables 2–5 and Figures 2–6. In addition, the results obtained by sampling and field observations made at and near a pasture in Agricultural Experiment Farm of Hokkaido University, which was some 10 km north of HAES, were also incorporated in the descriptions when necessary. The following bionomic characters, some of which are synoptically given in Table 2, are included in the descriptions.

Flight period: In the species appeared once a year, the flight period is the period from the first to the last discovery of adults, whereas in the species appeared twice, the flight period is divided into two active periods intervened by a distinct inactive period.

Pre-reproductive and reproductive period: The reproductive period was defined as the period from the first to the last date of discovery of the sexually matured females. In cases of species appeared once a year, the pre-reproductive period is the period from the first record of adults to that of the mature females. In twice occurring species, this is the period from the first appearance of adults in the flight period including the reproductive period to the discovery of mature females.

Frequency of inseminated females: Seasonal changes in the frequency of

* From mid to late May in every year, the spring occurring species often aggregated on or near the ground surface beneath dung when it was cold. The aggregation usually composed of a few different species and included eight to fifteen individuals (20 dung droppings). Aggregated species were *A. haroldianus*, *A. brachysomus*, *A. rectus*, *A. pusillus*, *A. breviusculus* and a scarabaeine species, *Caccobius jesoensis*. Sometimes, the aggregation was composed of only one species, *A. brachysomus*. Aggregated adults kept still and often buried anterior half to whole of their bodies into the ground.

inseminated females were studied in 1984 (Figure 3). From the increasing curve of mated females in the figure, the date when 50% of females had mated was estimated for each species.

Hibernating stage and hibernaculum: Hibernating stages and hibernacula of most species studied could be either ascertained under natural conditions or reasonably assumed from the rearing experiment and/or miscellaneous field observations.

The following abbreviations are used in the descriptions of life cycles given below.

Table 2. Some life cycle characters of 12 *Aphodius* species in HAES during 1982–1984. Fp: Length of flight period. Fp1, Fp2: Lengths of the first and the second flight period in twice occurring species. Pr: Length of pre-reproductive period. Re: Length of reproductive period. M 50: The day when approximately a half of females were assumed to have mated (cf. Figure 3). Abbreviations of species names, see Table 1

Species	Fp (Fp1+Fp2) (days)				Pr (days)				Re (days)				M 50
	82	83	84	mean	82	83	84	mean	82	83	84	mean	(date)
Hl	105	127	66	99.3	24	31	23	26.0	50	71	34	51.7	V. 28
Bc	58	15	66	46.3	ND	15	9	12.0	58	7	57	40.7	V. 19
Hm	137	88	89	104.7	23	31	24	26.0	111	29	68	69.3	mid Ⅷ
Rg	26	ND	ND	ND	—	—	—	—	—	ND	ND	ND	—
Ps	58	69	66	64.3	30	15	11	18.7	22	56	23	33.7	V. 16
Rc	47 +36	57 +31	33 +49	45.7 +38.7	ND	ND	ND	ND	36	43	33	37.3	X. 9
El	8 +37	21 +56	ND +30	14.5 +41.0	ND	ND	14	ND	45	57	14	38.7	—
Bv	37	31	9	25.7	16	31	3	16.7	14	10	9	11.0	before V. 15
Un	116	107	ND	111.5	23	—	—	ND	22	—	—	ND	ND
Pr	73	61	55	63.0	37	30	15	27.3	38	32	39	36.3	Ⅸ. 27
Sd	36 +73	20 +26	— +54	28.0 +51.0	ND	ND	ND	ND	66	27	54	49.0	Ⅷ. 20
Sl	ND	77	68	72.5	—	45	—	ND	ND	49	ND	ND	ND

—: no data. ND: not determined.

Table 3. Species and numbers of individuals trapped just before and after the beginning of grazing. Grazing started on May 17, 1984. Beetles were trapped twice: May 15–17 and 17–19, 1984. Only four species were trapped. Abbreviations of species names are given in Table 1

Species	Number of individuals collected				
	Before the start of grazing	After the start of grazing	Types of environment		
			pasture	forest margin	forest
Ps	185	415	522	76	2
Bv	415	579	497	406	91
Bc	17	47	59	5	0
Rc	92	176	219	45	4

Table 4. Species and number of individuals collected from dung in sunny turf-covered areas (T) and that in shady naked areas (N), in 1984. In each census, four dung droppings were examined for each type of environment. Abbreviations of species names in Table 1

Species	V, 24		VII, 9		VII, 19		VIII, 21		Total	
	T	N	T	N	T	N	T	N	T	N
Hl	23	1	14	9	2	2	0	0	39	12
Ps	25	1	0	5	18	6	0	0	43	12
Bv	4	0	0	2	0	0	0	0	4	2
Bc	7	0	1	0	2	0	0	0	10	0
Hm	51	0	13	0	11	0	6	3	81	3
Sl	0	0	0	34	0	6	0	7	0	47
Rc	19	17	0	0	0	0	0	0	19	17
El	0	0	1	0	1	0	0	0	2	0

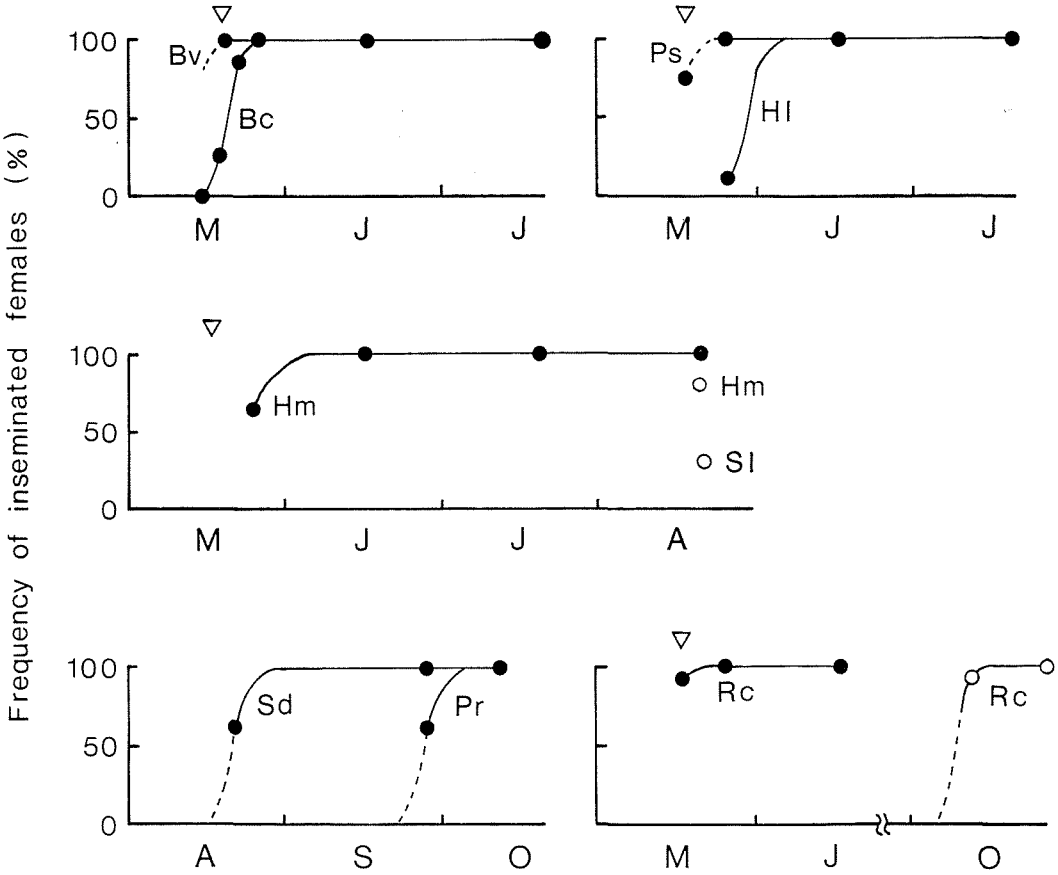


Figure 3. Seasonal changes in the frequency of inseminated females studied in 1984. Triangle, start of grazing. Open circles, prehibernating females in the species hibernating by the adult stage after foraging. Abbreviations of species names are in Table 1. The number of examined females per sample ranged from 10 to 40.

Fp (Fp 1, Fp 2): Length of flight period. In the twice occurring species, Fp 1 and Fp 2 are the lengths of the first and the second flight period, respectively.

Pr: Length of pre-reproductive period.

Re: Length of reproductive period.

M50: Date when approximately a half of females are assumed to have been inseminated. (Studied only in 1984.)

These values except for M 50 are represented by the mean values unless specifically mentioned.

1) ***Aphodius* (*Colobopterus*) *haroldianus* Balthasar:** *Probably hibernating by the adult stage at or near the pupated place in the soil; adults found from spring to late summer, reproducing mainly from June to July.*

Adults were observed from mid May to late August or mid September (Fp, 99.3 days), and abundant in May and June. Since this species was collected by neither baited pitfall traps (Table 3) nor routine sampling made before and soon after the start of grazing, it was probably not yet active at the beginning of grazing.

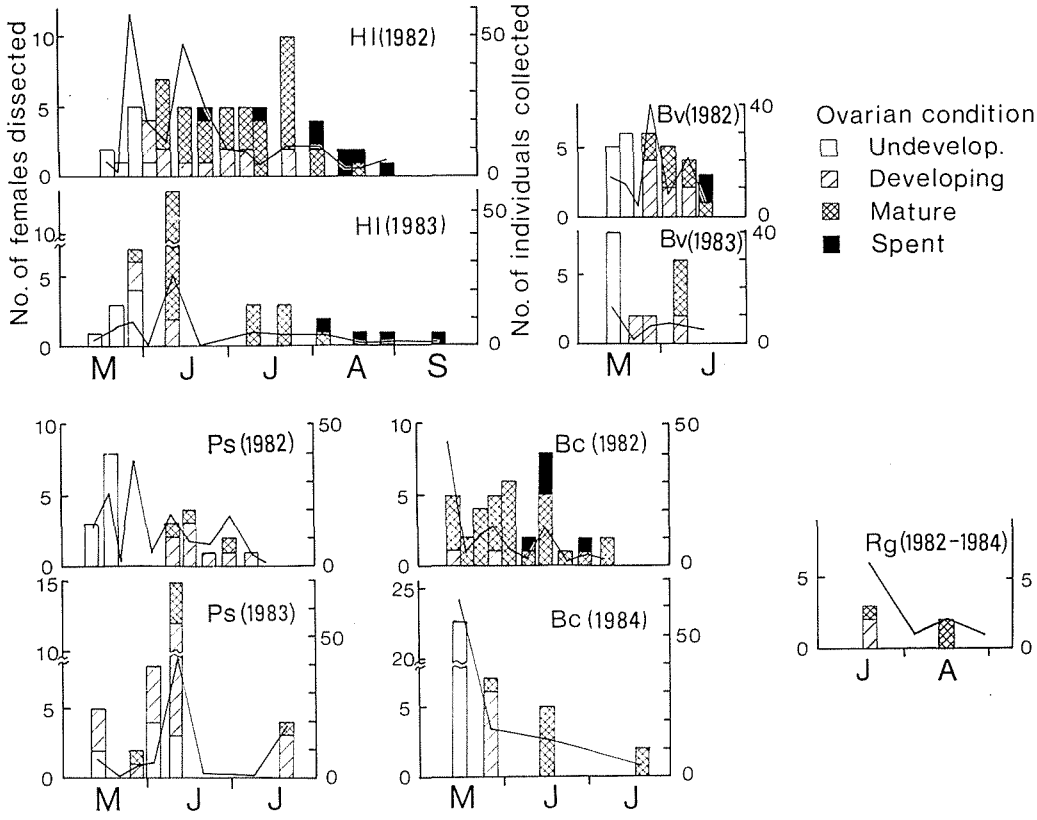


Figure 4. Seasonal fluctuations in the number of collected beetles (solid lines) and seasonal changes of ovarian stages (bars) in the five species hibernating as adults that do not forage before hibernation: *A. haroldianus* (Hl), *A. pussilus* (Ps), *A. breviusculus* (Bv), *A. brachysomus* (Bc), *A. rugosostriatus* (Rg).

Adults appeared on dung approximately one week (or more) after the beginning of grazing (Figure 4). Nearly all females were inseminated within ten days after the day when the first individuals of this species had been recorded (Figure 3, M 50, May 28). Mature females were observed from early June to late July or early August, and the activity of oviposition seemed to peak on mid June to early July. Pr, 26.0 days ; Re, long, 51.7 days. All adults collected at the field were considered as posthibernating ones. Flight of adults was frequently observed in the daytime. This species was not attracted to the light traps. Although not yet confirmed in the field, the following observation suggests that new adults of the present species emerge in late summer but do not depart from the pupated places or the vicinity until they pass winter.

Some adults caught on June 6, 1983 were released in flower-pots and plastic cases. New adults were discovered from the flower-pot culture on September 22, and from the plastic case culture on September 15, 1983. In the latter case, the new adults were found inactive nearby their pupated places in the soil.

As described above, only the posthibernating adults appeared on the ground in HAES. Hayakawa (1977) reported that this species appeared once from spring

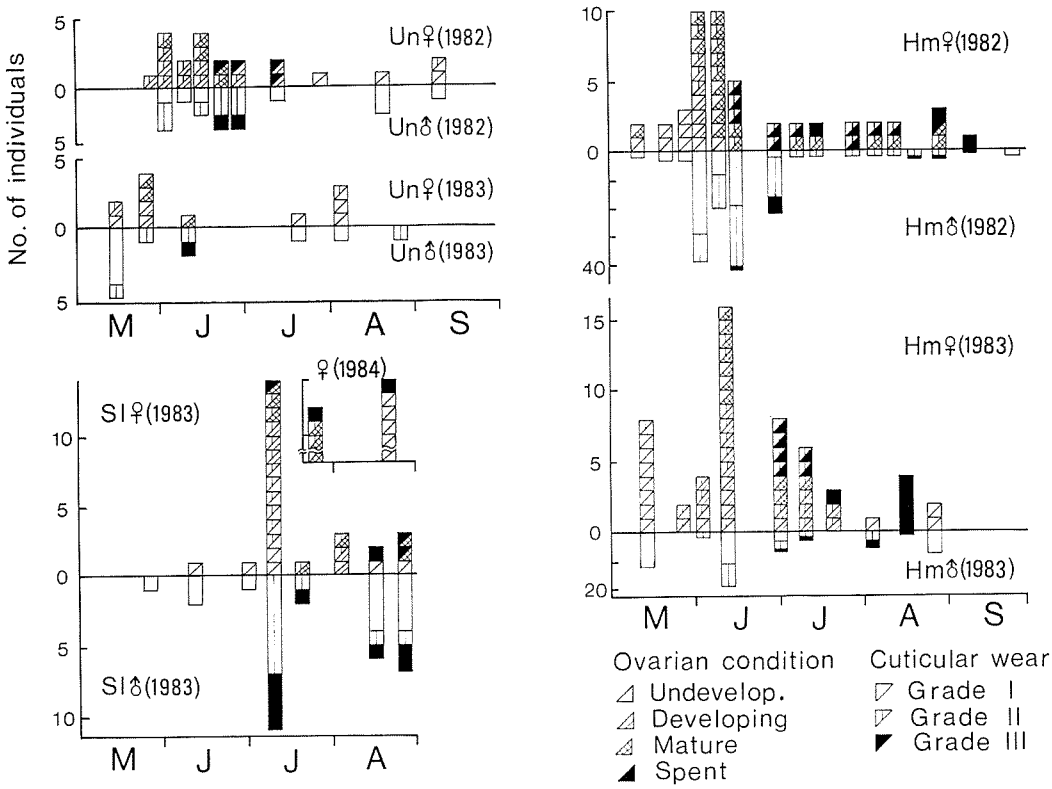


Figure 5. Seasonal changes of ovarian stages and grades of cuticular wear in species hibernating by the adult stage after foraging (part). Spring occurrence species, *A. uniformis* (Un) and *A. haemorrhoidalis* (Hm); summer occurrence species, *A. sublimbatus* (Sl).

to early summer in Iwate, Tohoku district, northern Japan, but he did not study whether the new adults appear before the hibernation or not. On the other hand, Hosogi (1985) reported (on the basis of the outdoor rearing) that in Kochi, southern Japan, the new adults of the present species appeared on the ground before hibernation and replaced the posthibernating adults.

2) ***A.* (*Otophorus*) *brachysomus* Solsky :** *Probably hibernating as adults in or near the pupal cells in the soil; adults found from spring to early summer, reproducing in May and June.*

Adults were observed from mid May and abundant in late May. But the flight period and the number of individuals collected considerably varied from year to year (Table 2, Fp, 46.3 days). Beetles were collected by baited pitfall traps before the start of grazing (Table 3). Mating took place as soon as grazing started (Figure 3, M 50, May 19). Females reproduced in May and June, and the peak of oviposition was, though largely variable according to years, in May to mid June. In 1982, this species was abundant and many females have mature ovaries in the early flight period. However in late May of the next year (1983), the number of individuals was small and only six females had mature ovaries. In 1984, beetles were abundant again as in 1982 but females were yet immature in mid May and became fully mature by mid June (Figures 2, 4). Pr, 12.0 days; Re, 40.7 days.

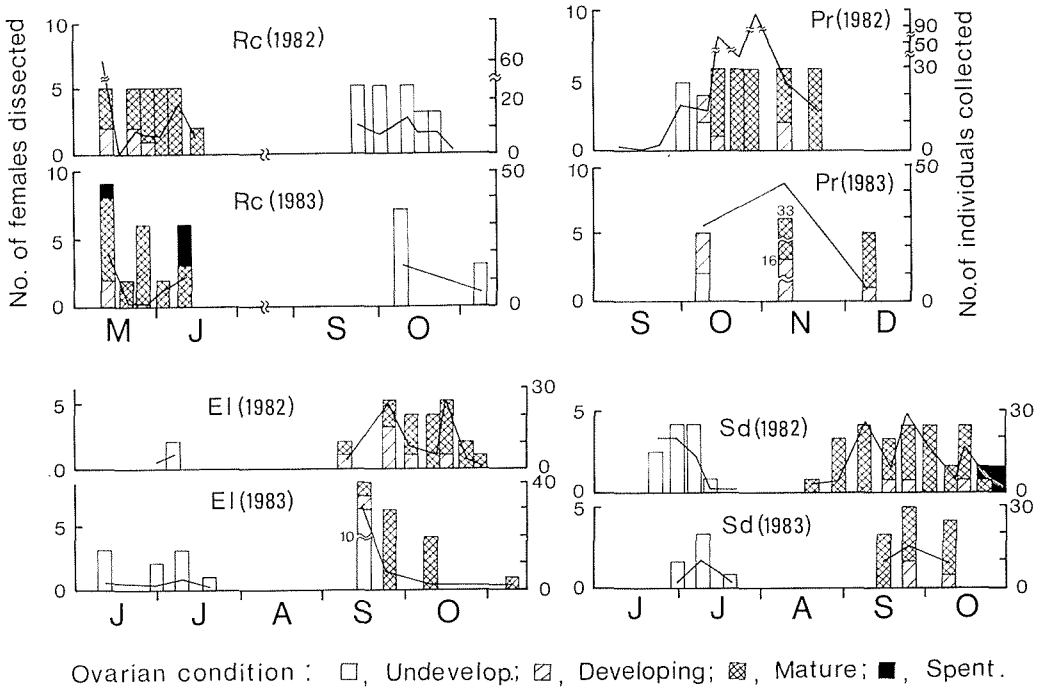


Figure 6. Ovarian conditions (bars) and the numbers of collected adults (solid lines) in species hibernating by the adult stage after foraging (spring-autumn occurrence species, *A. rectus*, Rc), by the larval stage (*A. elegans*, El and *A. sordidus*, Sd) and by the egg stage (*A. pratensis*, Pr).

The Pr and Re value were also largely variable. Adults seemed to prefer dung on sunny areas in the pasture (Tables 3, 4).

Under the rearing conditions, this species hibernated by the adult stage in or near the pupal cells constructed in the soil beneath dung. According to the plastic case culture made in 1983, the egg stage was ca. 8 days and the larval stage was ca. 50 days. Pupation took place within pupal cells* constructed in the soil. Inner space of the pupal cell was $15 \times 15 \times 10$ mm on the average. New adults were found inactive in the pupal cells on July 2, 9, 20 and 21, 1984. Since new adults were not collected in the field, they probably hibernate in the soil without feeding before hibernation.

According to Paik (1968), this species overwinters as larvae in Korea though it hibernated as adults in HAES. In addition, the oviposition behavior of this species in Korea (Paik, 1968) is distinctly different from that in HAES (unpublished data). Thus, Paik and we may have treated different species under *A. brachysomus*.

3) *A.* (*O.*) *haemorrhoidalis* (Linné): *Hibernating by the adult stage; adults found from spring to summer, ovipositing mainly in June; new adults emerging in summer, foraging for a while before hibernation.*

Flight period of this species was long, from mid May to September, but adults were abundant twice, from early to mid June and from late July to August. Fp, 104.7 days. The second smaller peak of occurrence was mainly composed of newly emerged adults. As shown in Figure 5, the degree of cuticular wear was grade I or II from May to June and grade III from June to August, whereas individuals of grade I increased from early to late August. Mating took place before and after the hibernation. More than a half of females were inseminated on the day when the first posthibernating adult was collected in May. Further, many new females collected in late August had already copulated (Figure 3). M 50, mid August. Mature females were observed from May to August in 1982, and the peak of oviposition seemed to be in June. Pr, 26.0 days; Re. 69.3 days but with a large variation (range, 29 to 111 days). In 1982, a small number of mature females were always observed from July to August, namely after the peak of oviposition. But only a few females oviposited after July in 1983 and 1984. Most individuals were collected in the sunny areas in the pasture especially in early summer (Table 4). Adults were not attracted to light traps. This species evidently hibernates by the adult stage but the hibernaculum is unknown.

Some adults were released in flower-pots and plastic cases on May 22, 1983. In the flower-pot culture, some larvae hatched between 5 and 9, June, and from the plastic case culture, four adults were obtained on August 3.

This species has been studied in North America (Mohr, 1943) and Europe (Landin, 1961; Holter, 1982). Landin (1961) already reported that this species prefer

* Pupated places were confirmed only in *A. brachysomus*, *A. elegans* and *A. haroldianus*. Of these, *A. brachysomus* and *A. elegrans* constructed hemioval pupal cells in the soil beneath the dung and pupated within them. On the other hand, *H. haroldianus* pupated in the soil but not constructed pupal cells. Although not confirmed, fragmentary observations suggested that most other species were of *A. haroldianus* type.

exposed habitats to shaded ones. According to Holter (1982), the seasonal occurrence of the present species in northern Europe were long compared to those of other European species and characterized by the unimodal seasonal distribution. He attributed the unimodality of this species to the overlap of two generations in a relatively short period. In the present study, too, the new generation replaced the old one with an overlapping period of 11.0 days (10.5% of Fp). As in Japan, this species hiberanates as adults and has been collected only in spring in North America (Mohr, 1943) but Landin (1961) reported that this species hibernates principally as third instar larvae in Finland.

4) ***A.* (*Pharaphodius*) *rugosostriatus* Waterhouse:** *Probably hibernating by the adult stage; adults found in summer, reproducing in summer.*

This species was rare, and a total of only 10 individuals were collected during three years. Four were obtained in August (1982 and 1983) and six on July 19, 1984. Among five females included in these individuals, three had mature eggs. They were caught on August 15, 1983 and July 19, 1984 (Figure 4). Only one adult was collected by the light trap on August 6, 1982. New adults were not taken. This species probably hibernates as adults though we have no direct evidence in support of this view.

5) ***A.* (*Orodalus*) *pusillus* (Herbst):** *Hibernating as adults in the soil; adults found from mid May to mid July, reproducing mainly in June; new adults not foraging before hibernation.*

Adults were found from mid May to mid July, abundant in May or June (Fp, 64.3 days). Since a large number of beetles were collected in spring by baited pitfall traps settled in the pasture, they were evidently ready to begin active when grazing started (Table 3). The guts of beetles trapped before the start of grazing (May 15 to 17) were empty but those trapped just after the beginning of grazing (May 17 to 19) were filled with food. Mating took place soon after the appearance in mid May. All females had been inseminated within 5 days after the collection of the first individuals (Figure 3; M 50, May 16). Eggs were laid from late May to June. But only a part of females had mature eggs even at the peak of oviposition in early June. Out of 57 females dissected in 1982 and 1983, only 8 had matured eggs (Figure 4). Pr, 18.7 days; Re, short, 33.7 days. Adults prefered sunny areas to shaded ones in the pasture but not so abundant in the forest (Tables 3, 4). All field collected adults seemed to be posthibernating ones judging from the field observations. Results of the rearing given below also support this view:

1) Larvae and pupae of this species were collected from old dung on August 4, 1983 and a total of fifteen individuals were released in plastic cases. New adults emerged from the culture between August 15–18, 1983.

2) Some posthibernating adults caught on June 3, 1983 were released in flower-pots and allowed to reproduce. From these flower-pots, eleven new adults were obtained on September 22, 1983 within 5–10 cm depth in the soil. All these new adults were released in the flower-pots again. They soon dug themselves in the soil and did not appear over the ground before hibernation. Nine individuals were still alive in the soil (within ca. 10 cm depth) on May 27, 1984. Fat bodies of

these posthibernating beetles were rich, guts were empty and ovaries of females were not developed.

According to Landin (1961), *A. pusillus* was bivoltine in southern Sweden, though this species was clearly univoltine in HAES.

6) *A.* (*Phaeaphodius*) *rectus* (Motschulsky): *Hibernating as adults; adults found in spring and autumn, reproducing from early May to mid June; new adults foraging in autumn.*

Adults occurred from May to late June and from September to October or November. The first flight period by posthibernating adults was ca. 10 days longer than the second one by new adults (Fp 1, 45.7 days; Fp 2, 38.7 days). The peak of activity by posthibernating adults was in mid May, and it was the earliest of all the species occurring in spring. Beetles were collected by baited pitfall traps prior to the start of grazing (Table 3). Reproduction began earliest of all the species studied. Every year, a few mature females were already observed on the day when grazing started. The reproduction mainly took place in mid and late May, and lasted until June. New adults were observed on fresh dung in the second flight period in autumn. They did not oviposit until the next spring judging from their ovarian conditions (Figure 6). Pr, not determined; Re, 37.3 days. Probably most females mate before entering hibernation. All females had already mated on May 17, 1984 and new adults mated soon after their emergence in autumn (Figure 3, M 50, October 9). Sperm of the previous year may be fertile in the next spring.

At the campus of Hokkaido University, the present species became active earlier than HAES and many adults flew in late April. At Agricultural Experiment Farm of the university, this species was found in spring within a large mass of compost which had heaped up in the last autumn. During April 26 to 28, 1984, when the snow had already melted away, a number of adults were observed at the boundary between the compost and the ground, each boring soil to a hemioval cell (9×5 mm). These beetles had small masses of liquid brown body in the mid guts and semi solid masses in the hind guts. Their fat bodies were scarce, and ovaries of most females were not developed. But some females terminated diapause and had slightly developed oocytes. Three dead beetles were found in the soil cells. Probably, they had died during hibernation.

7) *A.* (*Aphodius*) *elegans* Allibert: *Hibernating as larvae (or prepupae ?); adults found in late spring and from early September to October, reproducing in autumn.*

Adults were observed twice a year. In the first short flight period in early July, adults appeared synchronously and abundantly. The second flight period was from September to October (Fp 1, 14.5 days; Fp 2, 41.0 days). Ovaries developed rapidly soon after the second appearance and most females had mature eggs throughout the second flight period. The peak of reproduction was from late September to mid October (Figure 6). Pr, not determined; Re, 38.7 days. M 50, could not be confirmed.

Judging from the following information obtained by the present study and previous studies made in other localities, this species probably hibernates as mature

larvae, but the hibernation as prepupae is also not excluded from consideration.

On November 9, 1983, three individuals of first instar, twenty-three of second instar, and fifty-four of third instar larvae were found in the field in dung and nearby soil. Some third instar larvae collected in the autumn in 1982 were reared under the room condition. They pupated in the next June and emerged in late June, 1983. Pupae were found in the pupal cells constructed in the soil.

The life cycle of this species in Kochi, southern Japan, has been studied by Hosogi and his co-workers (Hosogi, 1985; Hosogi *et al.*, 1979, b; Yamashita *et al.*, 1978). Their results suggest that this species hibernates as third instar larvae there.

8) ***A.* (*Agrilinus*) *breviusculus* (Motschulsky):** *Hibernating in the soil as adults, which do not forage before entering hibernation; adults found only in spring, reproducing from late May to early June*

Flight period of this species is the shortest of all the species studied. Adults were observed on fresh dung from mid May to mid June (Fp, 25.7 days). This species probably began to active immediately after the snow melting. M 50 could not be estimated but nearly all females had mated at the start of grazing in 1984 (Figure 3). On May 15, 1984, when grazing did not start yet, a small number of adults were found in old dung that had dropped in the last autumn. The guts of these beetles were filled with food, fat bodies were slender, and ovaries of females were in the process of development. Evidently, at least a part of this species started feeding before the beginning of grazing. Between May 15 and 19, numerous adults were also caught at the pasture, the forest and its margin by the baited pitfall traps (Table 3). Oviposition took place from late May to early June (Figure 4). Pr, 16.7 days; Re, shortest, only 11.0 days. The Fp and the Pr value given above (Table 2) are apparently underestimated because the present species began feeding before the start of our field census.

Thirteen adults collected on May 20 and 26, 1983 were released in the flower-pot culture cases. In the soil of these flower-pots, a total of twenty-two adults were obtained on September 22, 1983. Ten individuals of them were released in flower-pots again on the same day, and recollected on April 28, 1984. Ten of them were alive in the soil.

In Kochi, newly emerged beetles appeared in autumn and active through winter (Hosogi *et al.*, 1979 a; Yamashita *et al.*, 1978). This species, however, apparently flies only in spring in HAES.

9) *A.* (*Ag.*) *uniformis* Waterhouse: *Hibernating by the adult stage; adults found from spring to late summer, reproducing in June; new adults appearing in late summer.*

This species was relatively rare in HAES. Flight period was from mid May to mid September. A small number of beetles were collected every week from late May to mid September in 1982, but were not collected from mid June to mid July in both 1983 and 1984 (Fp, longest, 111.5 days). On August 6, 1982, ten individuals were collected by light traps during 19 : 30–22 : 30. Analyses of pro-thoracic and tibial wear indicate that two generations overlapped in 1982 (Figure 5). Posthibernating adults appeared from May to early July and new adults were

found from July to September. M 50 could not be determined. Mature eggs were observed from late May to June and the peak of reproduction seemed to be early June. Examination of ovaries revealed that new adults of this species emerged in late summer and fed fresh dung but did not oviposit before entering hibernation (Figure 5). Pr, 23 days; Re, 22 days in 1982. This species evidently hibernates by the adult stage but the hibernaculum is unknown.

In Iwate, adults appeared twice in a year (Hayakawa, 1977).

10) *A.* (*Ag.*) *pratensis* Nomura et Nakane: *Hibernating as eggs in dung; adults found only in autumn, ovipositing from mid October to December.*

Flight period was the latest of all the species. Adults were observed from September to just before the beginning of snowing in December, abundant in October and November (Fp, 63.0 days). About a half of females had mated at the start of flight period (Figure 3, M 50, September 27). Oviposition took place from mid October to early December. The peak of reproduction was in late October in 1982, and mid November in 1983 and 1984 (Figure 6). Pr, 27.3 days; Re, 36.3 days. Only this species hibernates as eggs. Larvae hatch out in early spring and feed on the old dung which was dropped in the last autumn (Table 5).

Table 5. Immature stages of *A. pratensis* confirmed in spring of 1984 in the old dung dropped in the last autumn. This species hibernates by the egg stage

Date	Number of individuals counted				Wet weight of dung examined (g)
	egg	1st. instar larva	2nd. instar larva	3rd. instar larva	
IV. 14	28	0	0	0	35.7
IV. 21	4	8	2	0	40.0
IV. 29	0	21	1	10	25.0
V. 4	1	1	16	35	34.0

11) *A.* (*Bodilus*) *sordidus* (Fabricius): *Probably hibernating as larvae; adults found in late spring and from late August to October, reproducing from late August to mid October.*

Adults were observed twice a year, namely, from late June to July and from late August to October. Beetles appeared synchronously on the fresh dung in the first flight period, but during summer, adults paused their activity. The second flight period was longer than the first one, ranging from August to October with the peak of flight in late September (Fp 1, 28.0 days; Fp 2, 51.0 days). Beetles did not mate until mid summer (M 50, August 20) and females having mature eggs were not observed during the first flight period. The oviposition took place soon after the beginning of the second flight period and continued from late August to mid October. Pr, not determined; Re, 49.0 days. All field caught adults were of the same generation according to the ovarian conditions of females (Figure 6).

Only one individual was collected by light traps on July 7, 1982. Judging from the adult phenology above and the result of rearing below, this species probably hibernates by the larval stage(s).

Twenty adults were collected on September 28, 1984 and reared in plastic cases under the controlled room conditions. From this culture, thirteen larvae were obtained on November 17, when the released adults were already dead. These larvae were unfortunately died by mid December due to the error in the rearing.

Paik (1968) reported that this species overwintered as eggs, young larvae and adults in Korea. But, this species hibernates as larvae in Kochi, southern Japan (Yamashita *et al.*, 1978) and in Finland (Landin, 1961).

12) *A.* (*Calamosternus*) *sublimbatus* (Motschulsky): *Hibernating as adults; adults found in summer, reproducing in July and early August; new adults appearing in summer.*

Flight period was from mid June to late August, but adults were abundant only in mid and late summer (Fp, 72.5 days). There were two peaks of adult activity. The first peak by posthibernating adults was in July and the second peak by new adults in mid August (Figure 5). M 50 could not be determined but approximately 30% of females of the new generation were mated before entering hibernation (Figure 3). Females reproduced from July to August in 1983. The peak of oviposition was in mid July. Newly emerged females were easily discernible by their immature ovaries (Figure 5). Pr, 45 days; Re, 49.0 days in 1983. Eleven beetles were captured by light traps during 19 : 00–23 : 30 on August 6 and 25, 1982.

Unlike other species that were mainly collected from dung on the sunny-turf covered areas, *A. sublimbatus* seems to prefer the dung dropped on the shaded bare areas in HAES (Table 4). Due to this definite habitat preference and rather restricted flight period, this species was not sufficiently collected in 1982. In 1983 and 1984, many individuals were collected at two very small bare areas shaded by sparse trees around waterplaces (cf. Figure 1).

Kiuchi (1979) mentioned that this species occurred twice in middle Japan while only once in Sapporo. He attributed this local difference in adult activity to the lack of flight activity by new adults in Sapporo. As described above, however, new adults foraged in HAES in Sapporo, too, though two successive generations overlapped in late summer there. The seasonal flight activity of this species in Korea (Paik, 1968) seems to be similar to that in Sapporo.

5. Patterns of life cycles

As described above, all the twelve species of *Aphodius* dung beetles studied by us were univoltine, though a few bivoltine species were reported in Europe (Landin, 1961). Life cycles of Japanese species of *Aphodius* beetles have been classified by Tani (1966), Miyake (after Masumoto, 1973) and Kiuchi (1979). Of these, Kiuchi's system, which classified the life cycles of ten species of Japanese *Aphodius* into five types on the basis of the methods of hibernation, seems to be

most reasonable and useful. Basically following his system, the life cycles of the twelve species described in the present paper are classified below with brief remarks (Figure 7).

Type A-a: *Hibernating by the adult stage*; *new adults feeding on dung before entering hibernation.* The following four species are included: *A. uniformis, A. haemorrhoidalis, A. sublimbatus* and *A. rectus. A. rectus* was found hibernating within the compost in the campus of Hokkaido University. Hibernacula of the other species are not exactly known but probably beneath the old dung or amid the litter layer. The following three subtypes are recognized in the phenology of adult beetles: 1) Spring occurrence subtype: *A. uniformis* and *A. haemorrhoidalis*; 2) Summer occurrence subtype: *A. sublimbatus*; 3) Spring-autumn occurrence subtype: *A. rectus.* In the former two subtypes, the seasonal distribution of adults is unimodal. Adults in the earlier longer part of the flight period were posthibernating ones whereas those in the later shorter part consisted

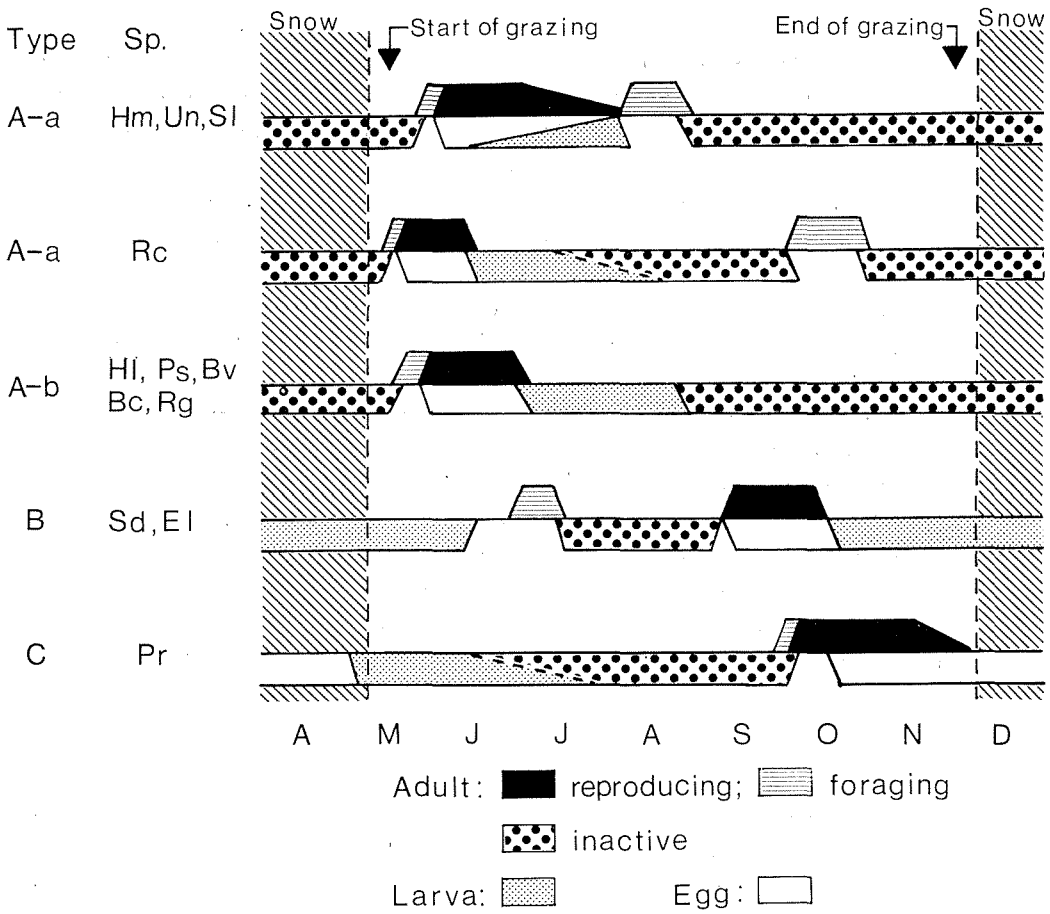


Figure 7. Life cycle patterns of twelve *Aphodius* species observed in HAES. Abbreviations of the species names, see Table 1. Further explanations in text.

of new adults (Figure 5). A part of females of these two subtypes are inseminated before the hibernation (Figure 3). In the last subtype, posthibernating adults reproduce in spring and autumn adults are newly emerged ones (Figure 6). Females are inseminated before entering hibernation though they do not oviposit until the next spring (Figure 3).

Type A-b: *Hibernating by the adult stage at the pupated places or the nearby soil; new adults do not appear on the ground surface until the next spring.* The following five species are included: *A. haroldianus, A. pusillus, A. breviusculus, A. brachysomus* and *A. rugosostriatus.* The former four species reproduce from spring to early summer, while the latter one in summer (Figure 4). Females are inseminated soon after the appearance in the next year (Figure 3).

Type B: *Hibernating by the larval stage(s) in the old dung or the nearby soil.* Two species, *A. sordidus* and *A. elegans*, seem to belong to this type. Adults emerge from spring to early summer and feed on fresh dung for a while. After that they disappear in summer. They reappear in late summer and reproduce till autumn (Figure 6). On May 1, 1983, larvae of unidentified *Aphodius* species were collected in HAES from the old dung and the soil beneath the dung (up to ca. 5 cm depth). These larvae consisted of two size classes, the large and the small ones, and may have been those of *A. elegans* and *A. sordidus*, respectively. Although we designated the hibernating stages of these species as larvae, the hibernating stages may be prepupae.

Type C: *Hiberbating by the egg stage in the old dung.* One species: *A. pratensis.* Adults are active only from late autumn to early winter (Figure 6). Larvae hatch in spring and feed on the old dung dropped in the previous year.

The differences between Kiuchi's (Kiuchi, 1979) and our systems are 1) Kikuchi did not classify type A-a into subtypes, and 2) the type A-c by Kiuchi, the winter occurrence type, was not found in the present study. Remarkably, life cycles were different between species belonging to the same subgenus. The life cycle of *A.* (*Otophorus*) *haemorrhoidalis* was type A-a, whereas that of *A.* (*O.*) *brachysomus* was A-b. Further, *A.* (*Agrilinus*) *uniformis* was type A-a, *A.* (*Ag.*) *breviusculus* was type A-b and *A.* (*Ag.*) *pratensis* was type C. On the basis of his personal unpublished observations, Kiuchi (1979) classified the life cycles of the following seven *Aphodius* species in Sapporo: *A. haroldianus, A. pusillus, A. rectus, A. elegans, A. pratensis, A. sordidus* and *A. sublimbatus.* His classification was consistent with ours except for the status of *A. sublimbatus.* This species was regarded by him as appearing only once in a year after the hibernation in Sapporo (Type A-b), but as shown in Figure 5, the new adults of this species appeared in a short period in summer in Sapporo (Type A-a).

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