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Differentiation in Life History Pattern and Oviposition Behavior, and Thelytoky in *Demotina* and *Hyperaxis* Beetles (Coleoptera, Chrysomelidae) in Western Japan

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Abstract The life history and oviposition behavior of five *Demotina* and a *Hyperaxis* species investigated in Gifu and Kobe, Japan, are reported. Two distinct types in life history and oviposition behavior are recognized within the congenial species. *Demotina tuberosa* (*Dt.*), *D. decorata* (*Dd*), *D. fasciculata* (*Df*) and *D. bipunctata* (*Db*) are spring breeders with hibernation stage at adult. *Hyperaxis fasciata* (*Hf*) shows the same life history pattern as the former species. *Demotina modesta* (*Dm*) is a summer breeder and probably hibernates as larvae or pupae. *Dm* lays eggs singly on leaf undersurfaces and covers them with excrements, whereas the other species lay eggs in soil as exposed masses. The absence of males in *Dt*, *Df*, *Dd*, *Dm*, *Db* and *Hf* from Kobe and Gifu collections suggests that thelytoky prevails in the two genera, at least in central and western Japan. The *Demotina* and *Hyperaxis* beetles feed on several species of the Theaceae and Fagaceae. *Dd* and *Df* abundantly occur on *Camellia japonica* and *Eurya japonica* (Theaceae), whereas *Dm*, *Db* and *Hf* are abundant on *Quercus serrata* and *Castanopsis cuspidata* (Fagaceae).

Introduction

I have investigated the community structure of tree-dwelling beetles in deciduous oak and evergreen forests in Gifu and Kobe, Japan. The following six species of *Demotina* and *Hyperaxis* have been recorded from Japan excluding the Ryukyu Islands: *D. tuberosa* CHEN (*Dt*), *D. fasciculata* BALY (*Df*), *D. decorata* BALY (*Dd*), *D. modesta* BALY (*Dm*), *D. bipunctata* JACOBY (*Db*) and *H. fasciata* (BALY) (*Hf*). Especially, *Db* is an important component of coleopterous community in pasania forests in both the localities. The ecology of these beetles has not been studied adequately, though the host plants in several species (CHÛJÔ & KIMOTO, 1961) and seasonal abundance of *Db* adult (ISONO *et al.*, 1986) have been reported.

In this paper I am going to show that 1) two types in life history pattern and oviposition behavior occur in the two genera and 2) a probable thelytoky occurs in these beetles. This paper also deals with the vertical distribution and the host plants of these beetles.

Study Sites and Methods

The study was made at six sites in a deciduous oak forest (Tsukuhara, Kobe, Japan; 135°6′E, 34°46′N) and four sites in an evergreen forest (Taisanji, Kobe, Japan; 135°4′E, 34°42′N). Konara oak (*Quercus serrata* THUNB.) dominates the deciduous oak forest, where *Dd*, *Df*, *Dm*, *Db* and *Hf* are commonly encountered. *Df*, *Db* and *Hf* occur in the evergreen forest where pasania (*Castanopsis cuspidata* (THUNB.)) dominates.

From July 1982 to June 1983, sampling was made at each site five times respectively. Beetles on various trees were randomly sampled by beating with an insect net. In order to investigate the seasonal appearance, vertical distribution and abundance on various trees, all the beetles were collected at every beating, and the season, stratum and the kind of tree species were recorded. The seasonal appearance pattern of *Dm*, *Db* and *Hf* on *Q. serrata* foliage was further investigated in 1984. The beetles collected in Kobe and Gifu (136°47′E, 35°26′N) were dissected to examine the ovarian development. Potential host plants were also judged by observing biting.

Results

1. *Seasonal abundance of beetles and the ovarian development*

The adults of *Db* and *Hf* were observed on foliage in the spring and autumn but not in the summer (Table 1 and Fig. 1). Although no sampling was made in the early spring, the beetles were already active in mid-April on young arakashi oak (*Q. glauca* THUNB.) leaves. In the autumn the beetles were abundant but they were reproductively immature. Females collected in the late spring through early summer possess mature eggs (Table 2). Under the room condition *Db* and *Hf* lay eggs from late April to late June, and the eggs hatch after a few weeks in both the species. In the field fully grown larvae and pupae of the two species were observed in late August, and the adults emerged in early September. Above observations suggest that young adults of *Db* and *Hf* appear in autumn and after hibernation as adults they lay eggs for two or three months.

Judging from ovarian development, *Dt*, *Dd* and *Df* can also be regarded as spring breeders with adult hibernation stage (Table 2).

Dm beetles were found from early July to September (Table 1 and Fig. 1). They already possess mature eggs in July (Table 2). The oviposition was observed from late July to September and the egg period was a few weeks under the room condition.

Seasonal variation of body coloration was found in *Db*; the beetles collected in late August and early September were yellowish brown lacking elytral marking, but dark reddish brown in the other seasons with or without elytral marking.

2. *Oviposition behavior*

Usually *Df*, *Db* and *Hf* lay eggs in soil. Sometimes *Hf* deposits eggs in bud

Table 1. Seasonal abundance of *Demotina* and *Hyperaxis* beetles in deciduous oak (upper table) and evergreen forests (lower). Pooled number of beetles are shown.

Species	1982			1983		Total
	July 3–23	Aug. 10–24	Sept. 28–Oct. 10	May 18–27	June 14–30	
D. fasciculata	3	1	9	15	14	32
D. decorata	10	6	40	17	14	87
D. modesta	6	9	2	0	0	17
D. bipunctata	0	1	35	18	6	60
H. fasciata	0	0	28	10	0	38
No. of samples	825	885	870	1,189	1,170	4,939

Species	1982			1983		Total
	July 28–Aug. 6	Aug. 26–30	Oct. 12–21	May 4–9	June 3–7	
D. fasciculata	0	0	0	4	0	4
D. bipunctata	2	79	221	33	31	366
H. fasciata	0	20	7	7	4	38
No. of samples	555	600	600	848	877	3,480

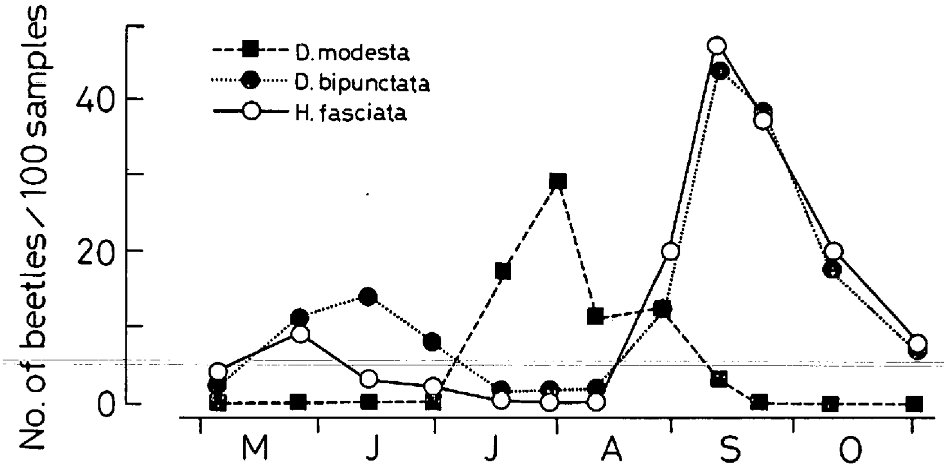

Fig. 1. Seasonal appearance pattern of *Demotina modesta*, *D. bipunctata* and *Hyperaxis fasciata* adults on *Quercus serrata* foliage in deciduous oak forest.

scales on twigs. *Dd* lays eggs in the torn leaf mine, though observed only one time. Their eggs are laid in mass and are glued with secretion.

Dm lays eggs singly on leaf undersurfaces. Egg masses consisting of two or three eggs are sometimes observed. The species lays eggs on the corner between the midrib and secondary vein or the side of the midrib. The eggs deposited on leaves are covered with excrements. Such eggs are observed also in the field. Hatched larvae break the cover and drop on the ground. The torn leaf mine is

Table 2. Seasonal change in ovarian development.
The number of beetles examined is shown.

Species	Ovary stage	Season								
		A	M	J	J	A	S	O	N	D
*D. tuberosa*1)	immature	0	0	0	0	0	4	3	0	0
	mature	0	2	3	1	0	0	0	0	0
*D. fasciculata*2)	immature	0	0	0	0	9	1	0	14	0
	mature	6	13	4	0	0	0	0	0	0
*D. decorata*2)	immature	0	0	0	3	5	3	1	2	1
	mature	16	18	9	1	2	2	0	0	0
*D. modesta*2)	immature	0	0	0	14	2	0	0	0	0
	mature	0	0	0	34	17	4	0	0	0
*D. bipunctata*2)	immature	16	0	0	0	2	64	16	3	3
	mature	54	23	8	2	0	0	0	0	0
*H. fasciata*2)	immature	8	0	0	0	7	133	3	8	1
	mature	28	21	1	0	0	0	0	0	0

1) Population from Gifu. 2) Population from Kobe.

Table 3. Number of specimens examined in the study.

Species	Kobe		Gifu	
	Female	Male	Female	Male
D. tuberosa	—	—	13	0
D. fasciculata	56	0	15	0
D. decorata	66	0	—	—
D. modesta	164	0	—	—
D. bipunctata	203	0	120	0
H. fasciata	214	0	43	0

rarely used for the oviposition site. Furthermore, eggs covered entirely with excrements are found in a few case as in the other chrysomelid genera *Syneta* (Synetinae), *Lypethes* (Eumolpinae), *Chlamisus* (Chlamisinae), *Cryptocephalus* (Cryptocephalinae) and *Smaragdina* (Clytrinae) (Fujita, 1958; Nakane *et al.*, 1975).

3. *Occurrence of thelytoky*

Although many specimens were examined, no males were found in *Dt*, *Df*, *Dd*, *Dm*, *Db* and *Hf* collected in Gifu and Kobe (Table 3). This suggests that thelytoky prevails in these *Demotina* and *Hyperaxis* species at least in central and western Japan.

4. *Vertical distribution, host plants and habitat preference*

In the tree stratum, foliage more than 7 m above the ground, *Dm*, *Db* and *Hf* are abundant (Table 4). They occur selectively on *Q. serrata* foliage in the deci-

Table 4. Vertical distribution of *Demotina* and *Hyperaxis* beetles in deciduous oak and evergreen forests. Shrub stratum: <2 m above the ground; lower tree stratum: 2–7 m; tree stratum: >7 m.

Species	Deciduous oak forest				Evergreen forest			
	Stratum			Total	Stratum			Total
	Shrub	Lower tree	Tree		Shrub	Lower tree	Tree	
D. fasciculata	27	4	1	32	4	0	0	4
D. decorata	66	15	6	87	0	0	0	0
D. modesta	1	3	13	17	0	0	0	0
D. bipunctata	14	21	25	60	58	62	246	366
H. fasciata	0	12	26	38	9	6	23	38
No. of samples	1,670	1,910	1,359	4,939	1,074	1,458	948	3,480

Table 5. Abundance of *Demotina* and *Hyperaxis* beetles on various tree species in deciduous oak and evergreen forests. QS: *Quercus serrata*; QG: *Q. glauca*; CC: *Castanopsis cuspidata*; CJ: *Camellia japonica*; EJ: *Eurya japonica.*

Species	Tree species						Total
	QS	QG	CC	CJ	EJ	Others	
Deciduous oak forest:							
D. fasciculata	1	2	0	12	10	7	32
D. decorata	5	9	0	29	13	31	87
D. modesta	13	3	0	0	1	0	17
D. bipunctata	28	9	0	2	2	19	60
H. fasciata	22	4	0	0	0	0	38
No. of samples	1,205	576	0	348	316	2,494	4,939
Evergreen forest:							
D. fasciculata	0	1	0	1	1	1	4
D. bipunctata	0	13	286	3	3	61	366
H. fasciata	0	9	21	0	2	6	38
No. of samples	0	87	1,223	273	195	1,702	3,480

duous oak forest and on *C. cuspidata* foliage in the evergreen forest, respectively (Table 5). They feed on these trees and the other two Fagaceae, *Q. acutissima* CARRUTH. and *Castanea crenata* SIEB. et ZUCC. under the room condition. *Db* and *Hf* also feed young *Camellia japonica* L. leaves, though it is not favored.

In the shrub stratum, foliage less then 2 m above the ground, *Dd* and *Df* are abundant (Table 4). They favor the two Theacea shrubs, *C. japonica* and *Eurya japonica* THUNB., for their dwelling site (Table 5). *Df* feeds on not only the two Theacea but also several Fagaceae, *Q. serrata*, *Q. actissima*, *Q. glauca*, *C. cuspidata* under the room condition. The *Demotina* and *Hyperaxis* beetles feed leaf tissue, midribs, leafstalks and even young twigs that grew in the spring.

Dd and *Dm* inhabit only the deciduous oak forest, though some potential host plants grow also in the evergreen forest (Table 5). *Df*, *Db* and *Hf* occur in both the forests, but *Db* is much abundant in the evergreen forest (Table 5). The dominance of *Db* in evergreen forest is also found in Gifu, Japan (ISONO *et al.*, 1986).

Discussion

Morphologically *Db* closely resembles *Dm*. KIMOTO (1964, 1969, 1980) treated six species and one variety including *Db* as being synonymous with *Dm*, but KIMOTO (1964) also stated that *Dm* might be a complex of several species. *Db* and *Dm* are different in life history, oviposition behavior and habitat preference. They can be distinguished according to the differences in body size, body coloration and hair shape on dorsal surface (NAKANE, 1963). Therefore, these two should be treated as good species.

Hibernating stage is an important factor to determine the life history pattern. It is often fixed even at genus or family level in insects, but not in *Demotina* beetles; i.e., *Dt*, *Db*, *Dd* and *Df* are spring breeders with adult hibernation, whereas *Dm* is a summer breeder and probably hibernates as larvae or pupae. However, some questions still remain with generation time and hibernating stage in *Demotina* and *Hyperaxis* species. In the Eumolpinae to which *Demotina* and *Hyperaxis* species belong, *Basilepta pallidula* (BALY) is the only Japanese species whose life history is known. The species has two year life cycle with two larval hibernation periods in soil (NAKAHARA *et al.*, 1965). Larvae in soil generally take a few years to complete a generation. *Demotina* and *Hyperaxis* species, whose larvae are also root feeders, probably have a generation time longer than a year and may undergo second hibernation at larval or pupal stage.

That parthenogenetic forms occur with different geographic range from that of their close bisexual relatives is termed as geographic parthenogenesis, which has been reported in many animals (CUELLAR, 1977; GLESENER & TILMAN, 1978). *Demotina* and *Hyperaxis* species have been recorded from India, Ceylon, Burma, Indochina, China, Taiwan, Korea and Japan (JACOBY, 1908; CHÛJÔ, 1956; GRESSITT & KIMOTO, 1961; KIMOTO, 1964; TAKIZAWA, 1978; KIMOTO & GRESSITT, 1982). All species in central and western Japan may be thelytokous, but males are recorded in *Dt* from south China (GRESSITT & KIMOTO, 1961), which suggests that the geographic parthenogenesis occurs in the species. Males are also known in *D. elegans* CHÛJÔ et SHIRÔZU from Yakushima (CHÛJÔ & SHIRÔZU, 1955), *D. aurosquama* CHÛJÔ from Amami-Oshima (CHÛJÔ, 1961), *D. sasakawai* NAKANE et KIMOTO from Amami-Oshima and Okinawa (NAKANE & KIMOTO, 1959), and all the Taiwanese species, *D. taiwana* CHÛJÔ, *D. decoratella* CHÛJÔ, *D. alni* CHÛJÔ, *D. montana* CHÛJÔ, *D. major incostata* TAKIZAWA and *D. punctata* TAKIZAWA (CHÛJÔ, 1956; TAKIZAWA, 1978). These facts show that bisexual reproduction occurs in the Ryukyu Islands, Taiwan and South China. Unfortunately, there is no further information about the geographic range of the parthenogenetic forms of these beetles. However, that thelytoky of these beetles occurs in northeastern part of the generic distributional range should be noted. The parthenogenetic forms might have arisen from bisexual ancestors with the expansion of their geographic ranges. The establishment of the parthenogenetic forms would be closely associated with the two unique features, i.e., the double-folded fecundity and an ability of every individual to found a new colony, which allow them to invade and occupy open habitats faster than bisexual forms (CUELLAR, 1977). The isolation by the sea of the parthenogenetic forms from their bisexual ancestors would also play an important role in this process. However, why *Demotina* and *Hyperaxis* species reproduce asexually only in central and western Japan awaits further study.

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