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Seasonal life cycles and resource use of flower- and fruit-feeding drosophilid flies (Diptera; Drosophilidae) in central Japan

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Running title: Seasonal life cycles of *Drosophila*

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Abstract

Seasonal life cycles and resource uses of flower- and fruit-feeding drosophilids (Diptera, Drosophilidae) were studied at low to high altitudes in central Japan to understand their adaptation to seasonal changes of environmental conditions. *Drosophila unipectinata* and *D. oshimai* specialized to flowers, *D. suzukii* and *D. subpulchrella* depended almost on fruits, while *D. lutescens*, *D. rufa*, *D. auraria*, *D. biauraria* and *D. sternopleuralis* used both of them. It was assumed that *D. unipectinata* moved from low to high altitudes in June while *D. oshimai*, *D. suzukii* and *D. subpulchrella* in July. Migration of *D. unipectinata* is considered as a means to avoid summer heat or exploit early-summer resources at high altitudes. On the other hand, *D. oshimai*, *D. suzukii* and *D. subpulchrella* have capacity to pass the summer at low altitudes, and therefore their migration is assumed as a means to escape from resource-poor conditions in summer at low altitudes or exploit resources at high altitudes. The generalist species, *D. lutescens*, *D. rufa*, *D. auraria*, *D. biauraria* and *D. sternopleuralis,* would not perform such extensive movements between low and high altitudes. They may pass the summer at low or mid altitudes depending on accidentally-fallen immature fruits and/or some other resources such as decayed leaves.

Key words: altitude, migration, resource availability.

INTRODUCTION

Migration is one of important means to cope with the seasonal changes of environmental conditions (Tauber *et al*. 1986; Wolda 1988). In *Drosophila*, some temperate species migrate from low to high altitudes in early summer and probably return to low altitudes in autumn (Kimura *et al*. 1978; Kimura & Beppu 1993; Beppu *et al*. 1996). We have assumed that migration of *D. curviceps* Okada et Kurokawa and *D. unipectinata* Duda to high altitudes is an adaptation to avoid summer heat at low altitudes, since they are heat intolerant (Kimura & Beppu 1993; Beppu *et al*. 1996). Furthermore, *D. curviceps* has not capacity to overwinter at high altitudes, and therefore its autumn migration to low altitudes is assumed as an adaptation to avoid winter low temperatures (Kimura & Beppu 1993). However, their migration could also have another function such as escape from resource-poor conditions. In fact, a number of insects including a herbage-breeding drosophilid *Lordiphosa magnipectinata* (Okada) have evolved aestival diapause to cope with the reduction of food quantity and/or quality in summer (Masaki 1980; Toda *et al*. 1984), suggesting that migration could also have such function. This possibility will be verified, if heat- and/or cold-tolerant species also move between low and high altitudes. On the other hand, if environmental conditions are not favourable in summer at low altitudes, it is questioned how non-migrant low-altitude species pass the summer.

Here, we studied seasonal life cycles and resource uses of several flower- and fruit-feeding drosophilids in central Japan to understand what kinds of species perform seasonal migration, what function their migration has, and how non-migrant species pass the summer at low altitudes. Among the study species, *D. unipectinata* is heat-intolerant as noted above, while the others are rather heat tolerant (Kimura 2004). In addition, it has been suggested in the study of their seasonal life cycles and diapause that they do not enter aestival diapause (Kimura 1988; Beppu 2000, 2006).

METHODS

The resource use was studied at low (the suburbs of Tokyo: <1000 m in altitude) and high altitudes (Shiga Heights: 1600-2000 m) in central Japan (Fig. 1A). In the suburbs of Tokyo, fallen flowers and fruits were collected in forests and groves at Nanakuni-yama, Oyamada, Naganuma, Tama Forest Park and Mt. Takao (Fig. 1B) from mid March to early November in 2005 to 2009. At Shiga Heights, samples were collected in forests and meadows around Institute of Nature Education in Shiga Heights, Shibu Pass and Yoshigataira (Fig. 1C) from mid June to mid August in 2005 to 2008. Samples collected were placed in vials with vermiculites and examined for the emergence of drosophilid flies.

To investigate the seasonality of drosophilid flies at different altitudes, periodical collections were carried out at various altitudes on Mt. Higashi-kagonoto in Nagano (Fig 1, A and D); A (2000 m), B (1540 m), C (1480 m), D (1460 m), E (1240 m), F (1040 m), G (860 m), H (760 m), I (680 m), J (630 m), K (530 m), L (500 m) and M (500 m). Sites A to F located in forests, sites G and H in river-side groves, and sites I to M in bushes or groves along rivers. A retainer trap baited with fermenting banana was set at each site from spring to autumn in 1990, and flies retained in the traps were sampled every 10 days (Kimura & Beppu 1993; Beppu *et al*. 1996). All of the females in the samples were dissected to check their ovaries, which were classified into three developmental stages, undeveloped, developing and mature (Watabe & Beppu 1977).

Migration was assessed by seasonal changes of individual numbers in samples collected at low altitudes (<50 m in altitude), Oiso (Yamamoto 1992) and Tokyo (Beppu 2000, 2006), and at various altitudes on Mt. Higashi-kagonoto (this study). In addition, records of their breeding were used for reference in this study. If migration occurs from low to high altitudes in early summer, for example, individual numbers and records of breeding will decrease at low altitudes but increase at high altitudes in mid summer (Kimura & Beppu 1993). In addition, reproductive status of individuals at the start of fly season was used to assess whether they had overwintered at the collection site or not. If the season starts with individuals that have just overwintered, populations at the start (i.e., in early spring) will be mainly composed of reproductively immature individuals (Toda & Kimura 1978). If the season starts with migrants, populations at the start are often composed of reproductively mature (i.e., aged) individuals (Kimura *et al*. 1978; Kimura & Beppu 1993).

RESULTS

Resource use

Tables 1 and 2 show the number of major drosophilid flies that emerged from fallen flowers and fruits at low (<1000 m) and high altitudes (>1600 m), respectively. *Drosophila unipectinata* and *D. oshimai* almost exclusively emerged from fallen flowers. *Scaptomyza pallida* also emerged only from fallen flowers at high altitudes. On the other hand, *D. suzukii*, *D. subpulchrella*, *D. melanogaster*, *D. simulans*, *D.*

ficusphila and *D. biauraria* emerged almost only from fruits. The remaining species, *D. lutescens*, *D. rufa*, *D. auraria*, *D. biauraria*, *D. sternopleuralis*, *D. immigrans* and *Liodrosophila aerea* emerged from both fruits and flowers.

Drosophila unipectinata bred on *Camellia japonica* flowers in spring at low altitudes, but thereafter its breeding was not recorded at low altitudes (Table 1). At high altitudes, this species bred on male flowers of *Betula platyphylla* and *B. ermanii* in June (Table 2). On the other hand, *D. oshimai* bred on flowers of *Camellia japonica* and male flowers of *Carpinus tschonoskii* and *Alnus sieboldiana* in spring and some other flowers in early summer at low altitudes (Table 1). In mid summer, its breeding was not observed at low altitudes, but was observed on some kinds of flowers at high altitudes (Table 2).

Drosophila suzukii bred on *Aucuba japonica* fruits from mid April to late June and *Prunus* and *Morus* fruits from late May to late June at low altitudes (Table 1). In mid summer at low altitudes, its breeding was not observed (Table 1). On the other hand, this species bred on some kinds of fruits in July and August at high altitudes (Table 2). In autumn, this species bred on some kinds of fruits at low altitudes. *Drosophila subpulchrella* was similar in seasonal pattern of resource use to *D. suzukii*, although its breeding was observed less frequently.

The generalist species, *D. lutescens*, *D. rufa*, *D. auraria*, *D. biauraria*, *D. sternopleuralis*, *D. immigrans* and *L. aerea*, bred on various flowers and fruits in spring and early summer at low altitudes (Table 1). In mid summer, their breeding was sometimes observed on accidentally-fallen immature fruits, e.g. of *Sapium*, *Celastrus* and *Cornus*. These generalist species rarely emerged from fruits or flowers collected at high altitudes (Table 2).

Seasonal life cycles

At all collection sites on Mt. Higashi-kagonoto, *D. suzukii* and *D. subpulchrella* appeared in early July (Fig. 2). The July populations at higher altitudes (>1460 m) were mostly composed of reproductively mature individuals, while those at lower altitudes (<1240 m) were mainly composed of immature individuals. These two species disappeared in early September or October at site A (2000 m), but later at lower altitudes. Their populations in autumn were mostly composed of reproductively immature flies, suggesting that they entered reproductive diapause.

Drosophila lutescens and *D. auraria* scarcely occurred at high altitudes; only 20 individuals of *D. lutescens* were collected at an altitude of 2000 m, and only 7 individuals of *D. auraria* were collected at altitudes of >1000 m. In this area, these two species were collected from late April or early May to November (Fig. 3). Most *D. auraria* females in late April at 760-860 m and a part of *D. lutescens* females in mid May at 1040-1240 m were reproductively immature. In autumn, these species also entered reproductive diapause. Another fruit-feeding species such as *D. rufa*, *D. biauraria*, *D. sternopleuralis*, *D. simulans* or *D. melanogaster* were not or rarely collected in this area.

DISCUSSION

According to the present and previous (Nishiharu 1980) studies, major drosophilids exploiting flowers and fruits in central Japan are divided into three groups, 1) flower specialists (*D. unipectinata* and *D. oshimai*), 2) fruit specialists (*D. suzukii* and *D. subpulchrella*), and 3) generalists that exploit both of them (*D. lutescens*, *D. rufa*, *D. auraria*, *D. biauraria*, *D. sternopleuralis*, *D. immigrans* and *L. aerea*). In this study, *S. pallida* emerged only from fallen flowers, and *D. melanogaster*, *D. simulans* and *D. ficusphila* almost only from fruits. However, *S. pallida* mainly breeds on decayed leaves of herbaceous plants (Kimura 1976; Kimura *et al*. 1977), and the latter three species exploit various resources including fallen flowers (Kimura *et al*. 1977; Nishiharu 1980; Lachaise & Tsacas 1983; Mitsui & Kimura 2000a).

The four fruit- and flower-specialist species are assumed to perform seasonal migration between low and high altitudes. At low altitudes, *D. suzukii* bred on some kinds of fruits from April to June, but its breeding was not observed from July to late August. In addition, Yamamoto (1992) and Beppu (2000, 2006) reported that adults of this species occurred rather abundantly from late autumn to spring but decreased in summer at low altitudes in central Japan, although a few adult flies were collected even in mid summer. On the other hand, this species appeared in early July at altitudes of 500-2000 m on Mt. Higashi-kagonoto, and its high-altitude (>1500 m) populations were mostly composed of reproductively mature females. Its breeding was also observed in July and August at high altitudes. These results suggest that this species moves from low to high altitudes in early July, although some parts of its populations seem to stay at low altitudes.

The seasonal life cycle of *D. subpulchrella*, a closely related species of *D. suzukii*, was not clear because it was not abundant. However, it was similar in seasonal pattern of occurrence and resource use to *D. suzukii* (also see Nishiharu 1980; Beppu 2006), suggesting that they have similar seasonal life cycles.

The seasonal life cycle of *D. oshimai* was estimated on the basis of its resource use, since this species was scarcely collected by banana-baited traps. This species passed two generations in spring and early summer at low altitudes; the first generation bred from March to May and the second generation in June and July. In mid summer, its breeding was not observed at low altitudes, but observed at high altitudes (>1600 m). From these results, this species is considered to migrate to high altitudes in July.

The above three species occur in subtropical and temperate islands where high mountains are not found (Hirai *et al*. 2000; Kondo & Kimura 2008; Kimura unpublished data), and at least *D. suzukii* is rather heat tolerant (Kimura 2004). These facts suggest that migration of these species is not to avoid summer heat but to exploit resources at high altitude or to escape from resource-poor conditions at low altitudes. In fact, breeding of flower- and fruit-feeding drosophilids was rarely observed in summer at low altitudes, suggesting the scarceness of resources.

In comparison with the above three species, *D. unipectinata* seems to move to high altitudes earlier. At low altitudes, its breeding was observed on *Camellia japonica* flowers from March to May but was not thereafter. Beppu (2000) also reported that this species disappeared from low altitudes by mid May. On the other hand, this species appeared at an altitude of 2000 m on Mt. Higashi-kagonoto in June (Beppu *et al*. 1996) and bred on male flowers of *Betula platyphylla* and *B. ermanii*. These results suggest that this species migrates from low to high altitudes in late May or early June. In summer, this species rarely occurred below 2000 m on Mt. Higashi-kagonoto (Beppu *et al*. 1996), although *D. suzukii*, *D. subpulchrella* and *D. oshimai* frequently occurred. Thus, migration of this species may be a means to avoid summer heat as we have suggested (Beppu *et al*. 1996) and/or to exploit competitor-free resources of *Betula* male flowers at high altitudes.

These specialist species would perform return migration in late summer or autumn, but timing of this migration is not clear. In autumn, *D. suzukii*, *D. subpulchrella* and *D. oshimai* were observed to reproduce at low altitudes, but *D. unipectinata* was not. The last species may return later than the other three species since it is heat-intolerant.

In contrast to the above specialist species, the generalist species, *D. lutescens*, *D. rufa*, *D. auraria*, *D. biauraria* and *D. sternopleuralis*, were rarely collected and their breeding was seldom observed at high altitudes. At low altitudes, on the other hand, they occurred abundantly from spring to late summer, although *D. sternopleuralis* decreased in mid summer (Yamamoto 1992; Beppu 2000, 2006) Moreover, *D.*

lutescens and *D. auraria* were collected from early May at altitudes of 500-1500 m, and most *D. auraria* females in late April at altitudes of 760-860 m and a part of *D. lutescens* females in mid May at 1040-1240 m were reproductively immature. These results suggest that they have passed the winter there. It is therefore assumed that *D. lutescens, D. rufa, D. auraria, D. biauraria* and *D. sternopleuralis* do not perform so extensive movements as the specialist species, although some individuals of *D. lutescens* may move to relatively high altitudes (e.g., 1500 m). These generalist species may pass the summer at low altitudes depending on accidentally-fallen immature fruits or some other resources such as decayed leaves of herbaceous plants and stems of bamboo grasses (Kimura *et al*. 1977; Nishiharu 1980; Mitsui & Kimura 2000a).

Among domestic species, *D. immigrans* has already been reported to move between low and high altitudes (Kimura & Beppu 1993). Two other species *D. melanogaster* and *D. simulans* were rarely collected at altitudes above 1000 m in this study (data not shown), and their breeding was not observed at high altitudes. However, Beppu (1985, 1986) collected *D. melanogaster* around resort areas at high altitudes (about 1600 m). They would move to high altitudes in association with humans.

The specialist species were thus assumed to perform seasonal migration. Such long-distance movements would have profound effects on the coexistence of competing species. Previous studies have analysed the coexistence mechanisms of drosophilids at the resource patch or local levels and revealed the importance of resource partitioning and spatial aggregation (Dobzhansky & da Cunha 1955; Carson 1971; Kimura et al. 1977; Atkinson & Shorrocks 1977, 1981; Toda et al. 1999; Mitsui & Kimura 2000b; Takahashi et al. 2005). However, if drosophilid flies move so widely, their coexistence should be investigated not only at resource-patch or local scales but also at a landscape scale.

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Table 1 Number of drosophilid flies that emerged from various flowers and fruits at altitudes below 1000 m. Dates of collections, altitudes of collecting localities and number of samples are also given. Flowers or fruits collected at a location at a time were counted as one sample.

	Date of collection	Altitude (m)	No. of samples	Duni	Dosh	Dsuz	Dsub	Dmel	Dsim	Dfic	Dlut	Druf	Daur	Dbia	Dste	Dimm	Laer	others
Flowers																		
Camellia japonica L.	III/15-V/13	0-350	22	1577	774	-	-	-	-	-	4501	87	8	-	-	-	-	2
Alnus sieboldiana Matsumura	III/15	100	1	-	8	-	-	-	-	-	-	-	-	-	-	-	-	-
Carpinus tschonoskii Maxim.	III/24	300	1	-	545	-	-	-	-	-	-	-	-	-	-	-	-	-
Juglans mandshurica Maxim.	V/13	250	1	-	-	-	-	-	-	-	-	1	-	-	-	-	1	-
Styrax japonicus Sieb. et Zucc.	V/13-VI/17	100-800	12	-	611	13	-	-	-	-	10	-	8	-	931	2	16	16
Alangium platanifolium (Sieb. et Zucc.)	VI/17	350	1	-	-	-	-	-	-	-	4	-	-	-	22	-	39	-
Idesia polycarpa Maxim.	VI/17-24	350-450	3	-	32	-	-	-	-	-	16	-	-	1	27	63	2	3
Actinidia polygama (Sieb. et Zucc.)	VI/24-VII/15	350-800	3	-	29	-	-	-	-	-	2	-	-	-	13	1	-	-
Lespedeza bicolor Turcz.	IX/29	200	1	-	4	-	-	-	-	-	-	-	6	-	1	-	-	56
Camellia sasanqua Thunb.	X/14-28	200	2	-	12	-	-	-	-	-	-	-	-	-	-	-	-	-
Camellia sinensis (L.)	X/21-XI/5	100-250	3	-	311	-	-	-	-	-	-	-	-	-	1	-	-	-

Fruits																		
Aucuba japonica Thunb.	IV/11-VI/30	200-400	10	1	-	40	-	-	-	-	6	17	-	-	2	4	5	-
Prunus spp.	V/26-VI/24	100-600	15	-	-	350	-	55	-	-	340	173	12	35	137	104	22	3
Morus bombycis Koidz.	VI/15-24	200-600	4	-	-	73	3	-	-	-	67	1	-	9	53	17	1	-
Juglans mandshurica Maxim.	VII/15	800	1	-	-	-	-	-	-	-	1	-	-	11	20	14	2	-
Rubus crataegifolius Bunge.	VII/15	1000	1	-	-	4	20	-	-	-	54	-	-	1	7	18	-	-
Sapium japonicum Pax et Hoffm.	VII/19-IX/22	450	2	-	-	-	-	-	-	-	1	4	-	-	-	-	4	-
Celastrus orbiculatus Thunb.	VIII/12-26	350-550	3	-	-	-	-	-	-	-	-	23	-	-	9	-	131	-
Cornus controversa Hemsley	VIII/22-10/11	200-550	17	-	10	543	-	-	-	-	25	140	46	59	428	8	239	3
Diospyros lotus L.	VIII/27-X/7	400	4	-	-	-	-	-	-	-	-	1	-	-	2	-	7	1
Alangium platanifolium (Sieb. et Zucc.)	VIII/26	350	1	-	-	1	-	-	-	-	-	1	-	2	-	-	-	-
Idesia polycarpa Maxim.	VIII/26-IX/22	400-450	3	-	-	-	-	-	-	-	1	1	-	-	2	-	7	-
Camellia japonica L.	VIII/26-IX/22	350	2	-	-	-	-	-	-	-	-	29	-	-	8	-	13	1
Actinidia polygama (Sieb. et Zucc.)	VIII/26-IX/22	350-450	4	-	-	-	-	-	-	-	3	42	-	2	7	-	33	15
Diospiros kaki Thunb.	VIII/26-X/29	100-200	9	-	-	9	6	26	222	38	116	7	27	5	-	8	-	-
Cephalotaxus harringtonia (Knight)	IX/16-23	450	2	-	-	-	-	-	-	-	9	7	-	-	24	-	4	-
Cornus kousa Buerger	IX/15	450	1	-	-	3	-	-	-	-	-	-	-	-	-	-	-	-
Torreya nucifera Sieb. et Zucc.	IX/22-X/21	500	5	-	-	3	-	-	-	-	18	-	-	-	178	-	-	-

Parabenzoin praecox Blume	IX/22-X/7	300-450	4	-	-	-	-	-	-	-	-	-	-	-	33	-	1	-
Akebia quinata Decne	X/7	300	1	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-
Viburnum dilatatum Thunb.	X/22	100	1	-	-	6	-	-	-	-	-	-	-	-	-	-	-	-
Aphananthe aspera Planch.	X/22	100	1	-	-	-	-	-	-	2	1	2	-	-	1	-	-	-
Total				1578	2336	1034	29	81	222	40	5175	511	107	125	1914	239	527	99

Duni: *Drosophila unipectinata* Duda, Dosh: *D. oshimai* Choo et Nakamura, Dsuz: *D. suzukii* (Matsumura), Dsub: *D. subpulchrella* Takamori et Watabe,

Dmel: *D. melanogaster* Meigen, Dsim: *D. simulans* Sturtevant, Dfic: *D. ficusphila* Duda, Dlut: *D. lutescens* Okada, Druf: *D. rufa* Kikkawa et Peng,

Daur: *D. auraria* Peng, Dbia: *D. biauraria* Bock et Wheeler, Dste: *D. sternopleuralis* Okada, Dimm: *D. immigrans* Sturtevant, Laer: *Liodrosophila aerea* Okada.

Others include *D. triauraria* Bock et Wheeler, *D. bizonata* Kikkawa et Peng, *D. busckii* Coquilett, *D. lacertosa* Okada, *D. hydei* Sturtevant, *Lordiphosa collinella* Okada,

Scaptomyza pallida (Zetterstedt), *S. elmoi* Takada, *Hypselothyrea breviscutellata* Duda, *Microdrosophila nigripalpis* Okada, *M. purpurata* Okada

Table 2 Number of drosophilid flies that emerged from various flowers and fruits at altitudes above 1600 m. Dates of collections, altitudes of collecting localities and number of samples are also given. Flowers or fruits collected at a location at a time were counted as one sample.

	Date of collection	Altitude (m)	No. of samples	Duni	Dosh	Dsuz	Dsub	Dlut	Dbia	Dste	Dimm	Dbiz	Spal
Flowers													
Betula spp.	VI/16-VII/1	1600-1900	2	19	1	-	-	-	-	-	-	-	8
Rhododendron japonicum (A.Gray)	VI/30	1600	1	-	-	-	-	-	-	-	-	-	5
Hosta albo-marginata (Hooker)	VIII/8	1600	1	-	6	-	-	-	-	-	-	1	158
Epilobium angutifolium L.	VIII/8	1600	1	-	28	-	-	-	-	-	-	-	1
Lilium leichtlinii Hooker	VIII/8	1600	1	-	3	-	-	-	-	-	-	-	2
Hydrangea paniculata Sieb. et Zucc.	VIII/8	1600	1	-	4	-	-	-	-	-	-	-	-
Fruits													
Prunus nipponica Matsumura	VII/26	1600	1	-	-	70	61	3	2	1	3	-	-
Vaccinium spp.	VIII/8-11	1600-2000	5	-	-	620	-	-	-	-	-	-	-

Gaultheria adenothrix (Miq.)	VIII/8	1600	1	-	-	33	-	-	-	-	-	-	-
Rubus microphyllus L.f.	VIII/8	1600	1	-	-	85	-	-	-	-	-	-	-
Total				19	42	808	61	3	2	1	3	1	174

Dbiz: *D. bizonata*, Spal: *S. pallida*. See Table 1 for abbreviations of the other species.

Legends to Figures

Figure 1 (A) Study locations in central Japan. (B) Collection sites on Mt Higashi-kagonoto (A-M). (C) Collection localities in the suburbs of Tokyo. Shaded areas indicate forests or groves. (D) Collection localities at Shiga Heights.

Figure 2 Seasonal changes in numbers and reproductive conditions of *D. suzukii* and *D. subpulchrella* females collected at sites A (2000 m in altitude) to M (500 m) on Mt. Higashi-kagonoto in Nagano. Data at sites B to D, E and F, G and H, and I to M were pooled.

Figure 3 Seasonal changes in numbers and reproductive conditions of *D. lutescens* and *D. auraria* females collected at sites A (2000 m in altitude) to M (500 m) on Mt. Higashi-kagonoto in Nagano. Data at sites B to D, E and F, G and H, and I to M were pooled.

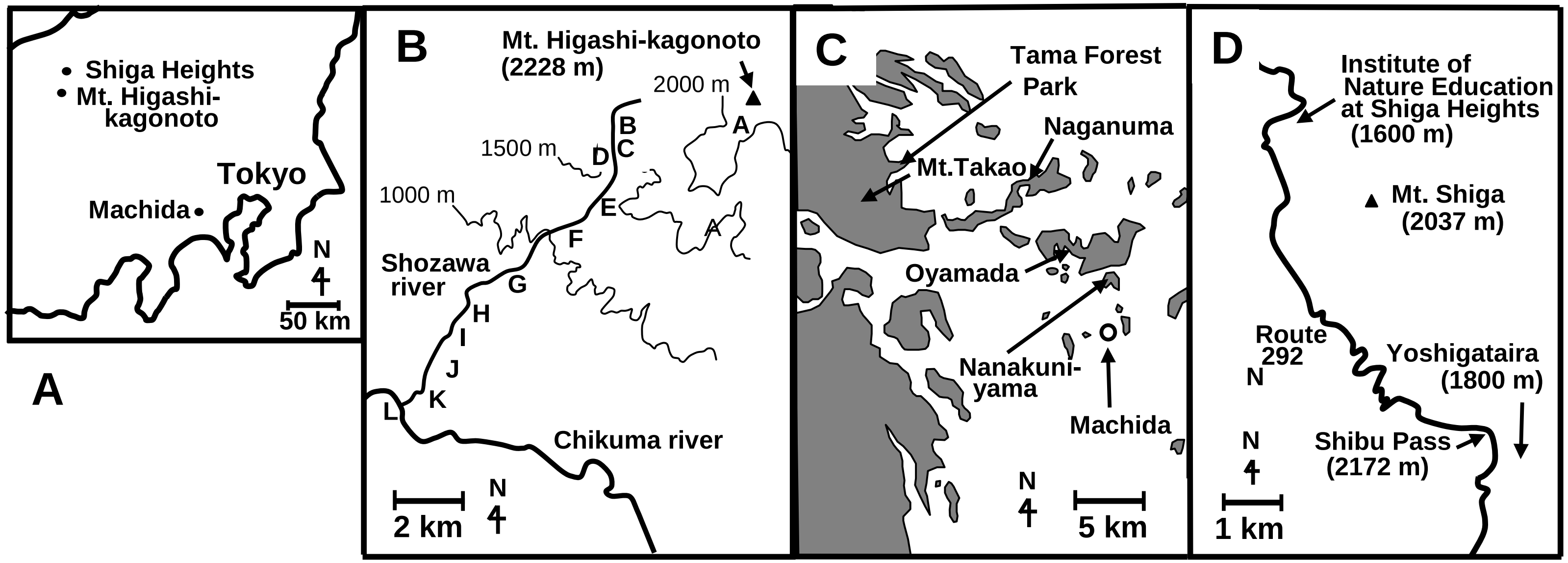
A
Shiga Heights
Mt. Higashi-kagonoto
Tokyo
Machida
N
50 km
B
Mt. Higashi-kagonoto (2228 m)
2000 m
1500 m
1000 m
A
B
C
D
E
F
G
H
I
J
K
L
Shozawa river
Chikuma river
2 km
N
C
Tama Forest Park
Mt.Takao
Naganuma
Oyamada
Nanakuni-yama
Machida
N
5 km
D
Institute of Nature Education at Shiga Heights (1600 m)
Mt. Shiga (2037 m)
Route 292
N
Yoshigataira (1800 m)
Shibu Pass (2172 m)
N
1 km

Fig. 1

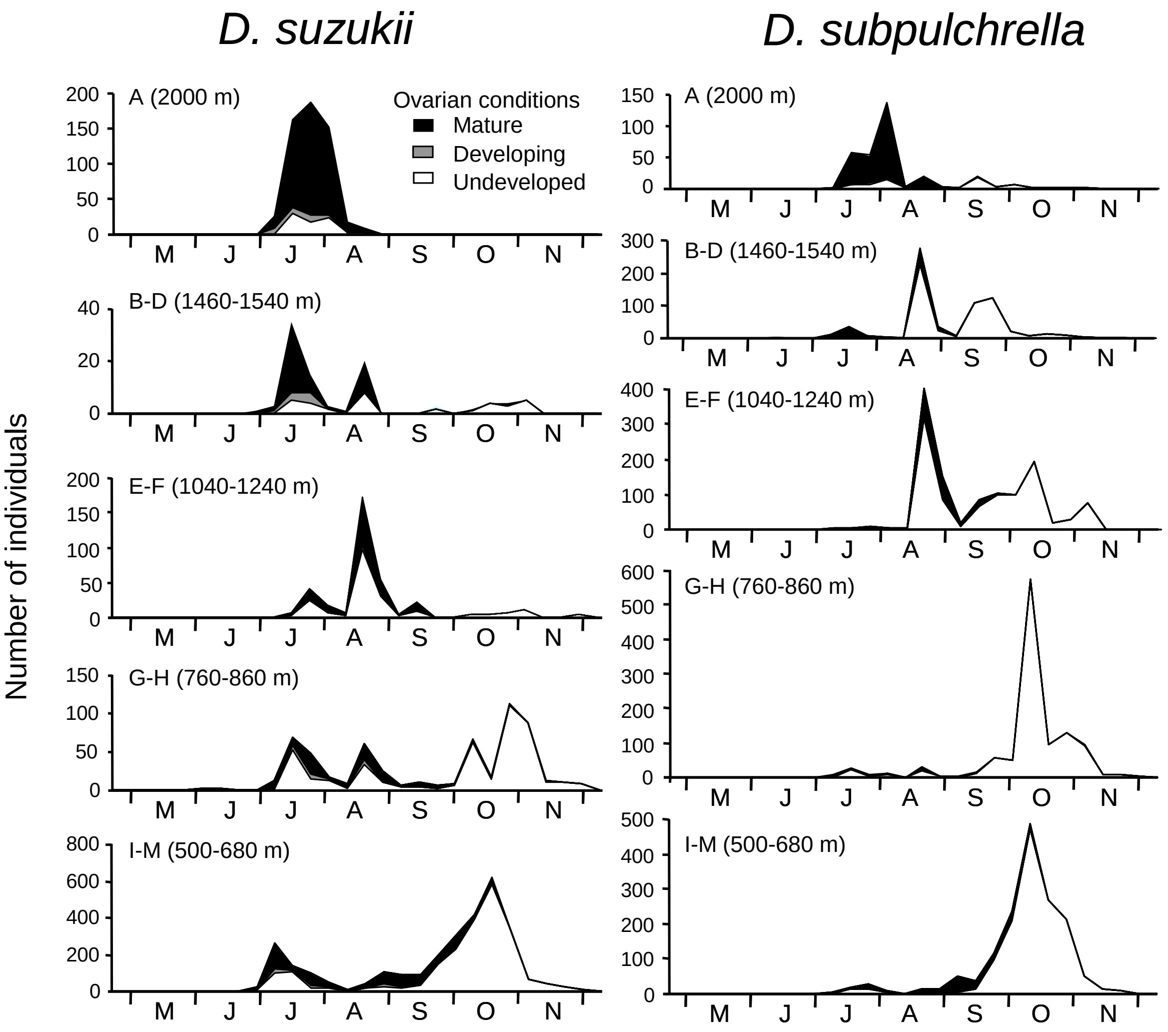
D. suzukii
D. subpulchrella
Number of individuals
Ovarian conditions
Mature
Developing
Undeveloped
A (2000 m)
B-D (1460-1540 m)
E-F (1040-1240 m)
G-H (760-860 m)
I-M (500-680 m)
M J J A S O N
0
50
100
150
200
20
40
300
400
500
600
800

Fig. 2

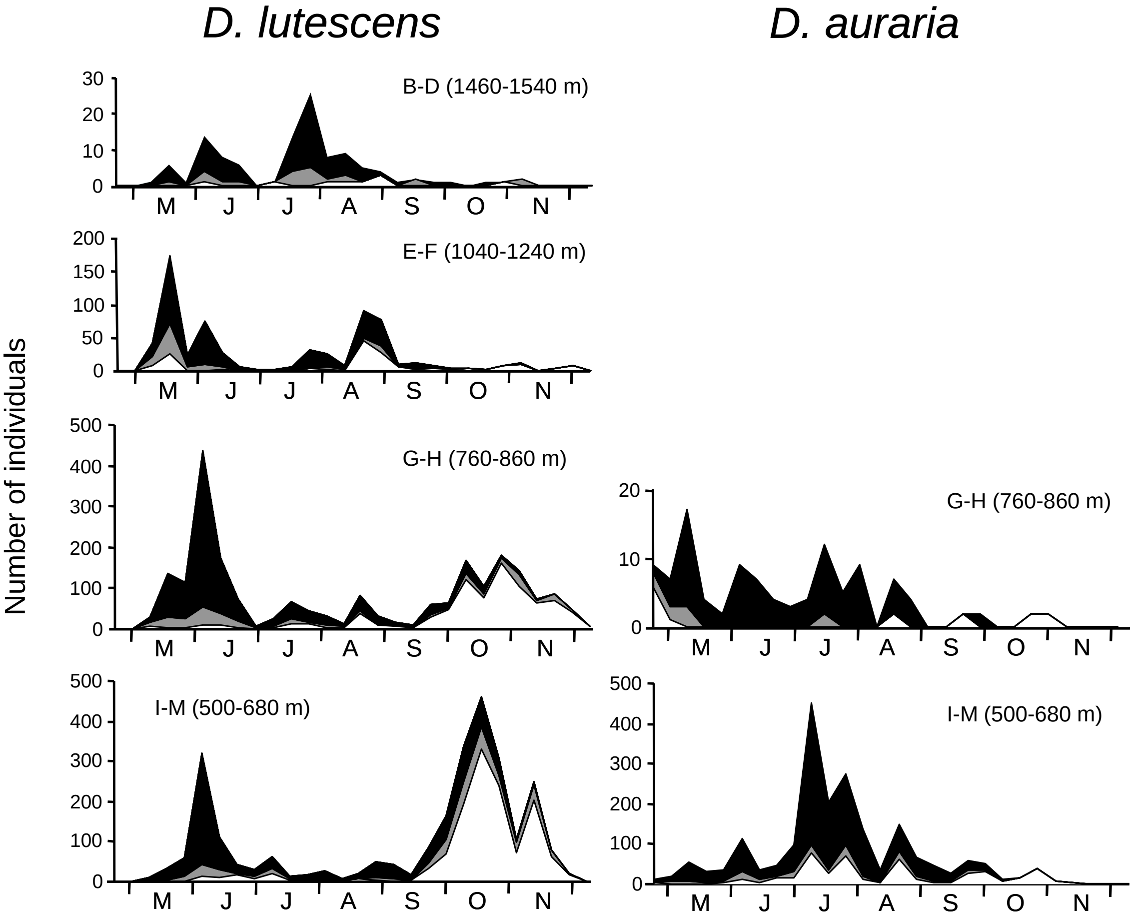
D. lutescens
D. auraria
Number of individuals
B-D (1460-1540 m)
30
20
10
0
E-F (1040-1240 m)
200
150
100
50
0
G-H (760-860 m)
500
400
300
200
100
0
G-H (760-860 m)
20
10
0
I-M (500-680 m)
500
400
300
200
100
0
I-M (500-680 m)
500
400
300
200
100
0
M
J
J
A
S
O
N

Fig. 3