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A Comparison of Butterfly Assemblages in and near Sapporo City, Northern Japan

By

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(*With 8 Text-figures and 6 Tables*)

The butterflies are one of the most well studied insect groups with numerous observations so far been carried out on their habits and distribution. But the majority of these contributions has been brought out by amateur naturalists, so that quantitative understanding of butterfly assemblages of a given area has not well explored until Morisita (1967). The present paper is an outcome of periodical butterfly censuses undertaken in three areas in and near Sapporo City, that is, Jozankei, Jûgoshima-Takinosawa, and the campus of Hokkaido University, to obtain the basic information on faunal makeup and phenology. The analysis was made at two levels, a local butterfly assemblage regarded as a whole, and its particular constituents with reference to their bionomic characters. A special emphasis was taken upon the influence of ever increasing urbanization upon the assemblage structure.

Befor going further, I wish to express my sincere thanks to Prof. Mayumi Yamada, Dr. Shôichi F. Sakagami and Dr. Hiromi Fukuda, Zoological Institute, Hokkaido University for their pertinent guidance to the present study.

Methods and the Areas Studied

The census was executed at three areas in 1973 in and near Sapporo City, Jozankei, Jûgoshima-Takinosawa between Jozankei and Sapporo City and the campus of Hokkaido University (Fig. 1). In all areas, any individuals of any species on the wing or at rest found within 10 m wide of both sides of the roads were registered without collecting. Certain species being difficult to identify at distance were captured and liberated soon after identification. Other methodological remarks are detailed in Yamamoto (1974 and 1975). The survey was continued from late April to late October in each census, made once or twice per ten days in each month. The topography and related conditions of each surveyed area are summarized as follows:

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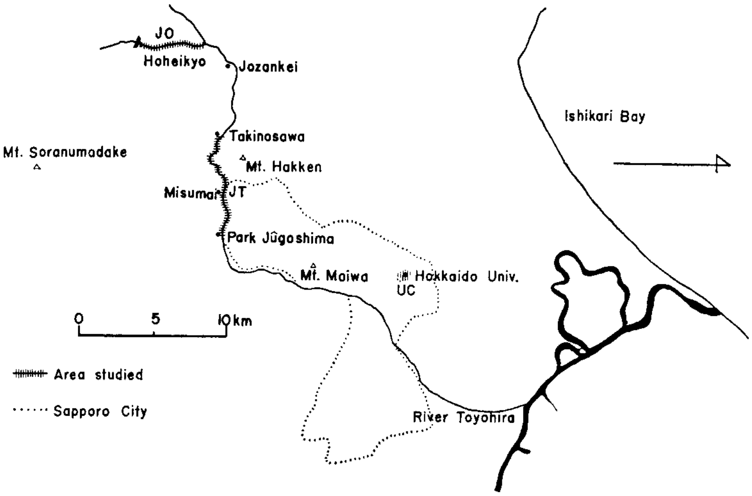

Fig. 1. Location and topography of the areas studied.

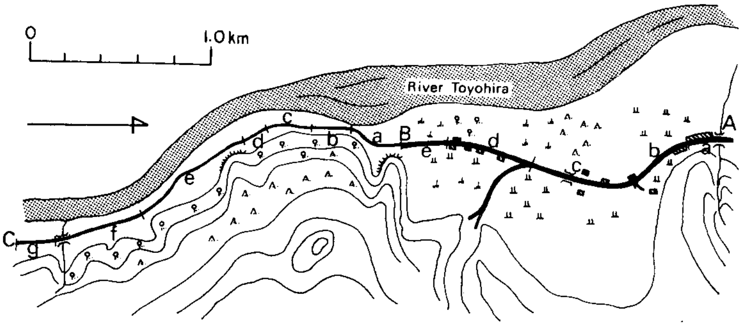

Fig. 2. Map of the census route at Jozankei (A～B～C).
AB (a, b, c, d, e) and BC (a, b, c, d, e, f, g) are subdivisions.

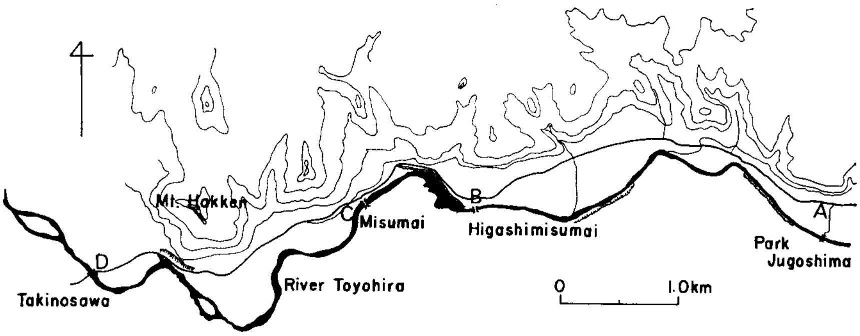

Fig. 3. Map of the census route at Jûgoshima-Takinosawa (A～B～C～D).

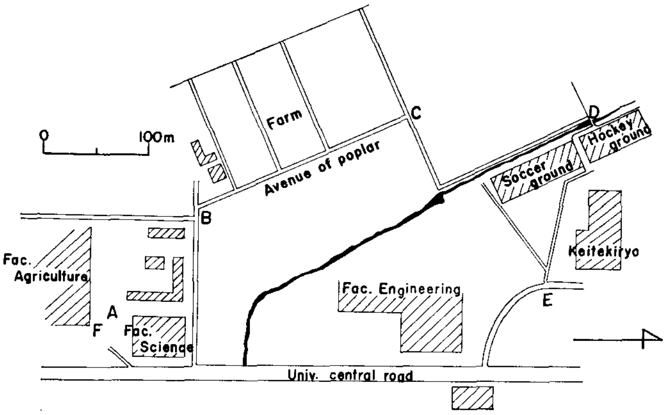

Fig. 4. Map of the census route at the campus of Hokkaido University (A～B～C～D～E～F).

Jozankei route (JO, Fig. 2): About 320～480 m alt., along the road running from Hôsuibashi to Hoheikyo. The census belt is divided into two sections. One, AB (Fig. 2, A～B), is 2.2 km long, penetrating a mosaic of paddy fields, cabbage and potato fields, human habitations and some fallows. The other, BC (Fig. 2, B～C), is 2.2 km long, running across secondary forests consisting of *Picea jezoensis, Abies sachalinensis,* larches, white birches and some other deciduous trees. AB and BC were subdivided respectively into five and seven parts as given in Section 1 (Fig. 2).

Jûgoshima-Takinosawa route (JT, Fig. 3) *or Jûgoshima-Misumai route* (JM): Census belt is 6.8 km long from the Park Jûgoshima through Higashi-misumai and Misumai (JM) to Takinosawa with the scenery similar to that of JO, and was subdivided into ten parts.

The campus of Hokkaido University (UC, Fig. 4): Census belt is about 4.6 km long, mostly consisting of crop fields with cabbage, potato, beet and corn but partly running along University buildings.

The details on the faunal makeup is consulted for Yamamoto (op. cit.). New additions to previous results are *Minois dryas bipunctatus* (Motschulsky), *Vanessa cardui* (Linnaeus) (Nymphalidae), *Zizeeria maha argia* (Ménétriès), *Antigius butleri* (Fenton) and *Chrysozephyrus smaragdinus* (Bremer) (Lycaenidae), *Parnara guttata* (Bremer et Grey) (Hesperiidae).

Results and Discussions

The results are divided into two parts, 1) habitat preferences and 2) relation between faunal makeup and urbanization. Some related discussions are given in each section.

1. Habitat preferences

As previously described, the census belt of Jozankei consists of two sections, AB represented by openland habitats and BC by forest. Consequently the habitat preference of each species is inferred from the relative prevalence at one of two sections. For this purpose, the corrected individual number in 1973 was sought for two sections T_{AB}, T_{BC} separately and the relative prevalence was expressed by the following arbitrary degrees.

Openland species: O ($T_{AB} \geqq 4T_{BC}$), Ow ($2T_{BC} < T_{AB} < 4T_{BC}$)
Forest species: W ($4T_{AB} \leqq T_{BC}$), oW ($2T_{AB} < T_{BC} < 4T_{AB}$)
Eurytopic species: OW ($T_{AB} \leqq 2T_{BC}$ or $T_{BC} \leqq 2T_{AB}$)

Obviously a clear cut segregation of openland and forest species is not expected on account of the environmental heterogeneity. Section AB contains some forest type environments. In forest section, BC, the census road itself represents a narrow belt of openland habitat[1]. The habitat preferences of all species, determined by this method are as follows. Asterisked species were rare (=corrected individual number less than 1.0) and their preferences were determined empirically:

Papilionidae: *Parnassius stubbendorfii* OW ($T_{AB}=12.0/T_{BC}=14.5$), *Papilio machaon* Ow (41.0/13.5), *P. macilentus** oW(0.5/1.0), *P. bianor* Ow (8.5/3.9), *P. maackii* OW (10.0/12.0).

Pieridae: *Aporia crataegi* OW (5.0/5.5), *Anthocaris scolymus** oW (0.5/0.5), *Colias erate* O (145.5/15.5), *Pieris napi* OW (258.0/221.0), *P. melete* OW (3.5/5.5), *P. rapae* O (297.5/4.0).

Satyridae: *Ypthima argus* OW (3.0/3.0), *Erebia niphonica* W (0.5/3.5), *Coenonympha hero* W (0.0/2.0), *Minois dryas** OW, *Lethe diana* OW (10.5/14.0), *Harima callipteris* W (1.0/15.0), *Ninguta schrenckii* Ow (3.0/1.0), *Neope goschkevitschii* W (1.0/7.0).

Nymphalidae: *Sasakia charonda* W (0.0/0.5), *Apatura ilia* W (0.5/10.0), *Neptis philyra* W (0.0/4.5), *Ladoga camilla* W (1.0/4.0), *Neptis aceris** W, *N. rivularis* OW (4.0/7.0), *Araschnia burejana* W (2.5/58.0), *A. levana* OW (5.0/3.5), *Polygonia c-album* W (3.0/11.5), *P. vau-album* W (0.0/7.5), *Vanessa indica* O (0.5/0.0), *V. cardui** O, *Nymphalis xanthomelas* W (0.0/2.5), *N. antiopa* W (0.5/2.5), *Inachis io* oW (7.5/27.0), *Kaniska canace* W (0.0/0.5), *Aglais urticae* W (4.0/49.5), *Fabriciana adippe* O (13.5/1.5), *Argyronome laodice* O (3.0/0.5), *Argynnis paphia* OW (8.5/10.5), *Speyeria aglaia* oW (7.0/16.5), *Argyronome ruslana* Ow (22.0/7.5), *Argynnis anadyomene** W, *Brenthis ino* W (5.5/53.0).

Lycaenidae: *Artopoetes pryeri** oW, *Araragi enthea** W (0.5/0.5), *Antigius attilia* W (0.0/0.5), *A. butleri** W, *Japonica lutea* W (1.0/12.0), *Shirozua jonasi** oW (1.0/0.5), *Ussuriana stygiana** W, *Wagimo sigunata* W (0.0/0.5), *Neozephyrus** *taxila* W (0.0/2.0), *Chrysozephryus smaragdinus** W, *C. aurorius** W, *Favonius orientalis** W (0.5/0.5), *F. jezoensis** W, *F. cognatus* W (0.0/1.0), *Strymonidia w-album* W (0.0/1.0), *Ahlbergia ferrea* W (0.0/0.5), *Lycaena phlaeas* O (50.0/5.0), *Scolytantides orion* W (0.0/7.0), *Plebejus argus* W (0.0/4.5), *Celastrina argiolus** OW (0.5/0.5), *C. sugitanii* W (0.0/4.5), *Everes argiades* OW (16.0/22.0).

Hesperiidae: *Bibasis aquilina* W (0.5/9.0), *Thymelicus sylvaticus* OW (0.5/1.0), *Ochlodes venata* Ow (19.5/7.5), *Thoressa varia* W (3.5/31.0), *Polytremis pellucida* W (1.0/5.0), *Erynnis montanus** W. The number of species belonging to various habitat types is as follows:

	O	Ow	W	oW	OW
Papilionidae		2		1	2
Pieridae	2			1	3

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[1] It might be criticized that the adopted procedure cannot estimate strictly the relative abundance of some species, which are confined within forests, seldom visiting the roads penetrating forests. The experiences suggest the rarity of such extremely heliophobic species at least in Hokkaido. But this problem must be solved by another type of census method.

Nymphalidae	4	1	14	2	3
Satyridae		1	4		3
Lycaenidae	1		17	2	2
Hesperiidae		1	4		1

Indubitably various habitat types evolved independently, though the prevalence of some types is exhibited in some families.

However, two sections, AB and BC are both not homogeneous, involving several different subtypes of environments. The presence or not of preference for such microhabitats was further sought with thirteen predominant species (cf. Table 2, 1976). Twelve subdivisions of the survey route shown in Fig. 2 are characterized by the following environmental conditions (S=Subdivision, L=Length in km):

Environmental conditions of route sides
(Left and right given for the ascending direction)

S	L	Left side	Right side	Micro-habitat type (l/r)
Aa	0.2	Hill side with dense broad leaf trees	Low sparse secondary grassland	W/O
Ab	0.5	Paddy fields and human habitations	=left	O/O
Ac	0.6	Dense bush with *Polygonum sachalinense*	Mosaic of fallows, cultivated fields and human habitations	O/O
Ad	0.4	Human habitations and tall dense secondary grassland	Fallows and low dense secondary grassland and a few sparse broad leaf trees	O/O
Ae	0.5	Marsh interspersed with willows	Low sparse grassland and secondary openland developed after ruined human constructs	O/O
Ba	0.3	Tall sparse black alder forest with undergrowth of low sparse herbs	Hill side with poor plant cover	W/W
Bb	0.5	Tall dense mixed forest with undergrowth of bamboo grass	Openland with poor plant cover. Near Bc tall dense mixed forest	W/OW
Bc	0.3	Tall dense mixed forest with undergrowth of tall sparse herbs	*P. sachalinense* and tall sparse mixed forest with undergrowth of bamboo grass	W/W
Bd	0.2	Tall dense mixed forest with undergrowth of tall sparse herbs	Valley with thick grass cover	W/W
Be	0.4	*P. sachalinense* along rocky shelf	Low dense mixed forest with undergrowth of low dense herbs	W/W
Bf	0.4	Tall dense mixed forest with undergrowth of bamboo grass	Tall sparse mixed forest along valley with undergrowth of bamboo grass	W/W
Bg	0.1	Tall dense mixed forest with undergrowth of tall sparse herbs	Low sparse mixed forest with undergrowth of tall sparse herbs	W/W

The distribution of those thirteen species in these microhabitats is summarized below (N=Total individual number of species observed in 1973, L=Length in km, N_e=Total individual number expected; $N \times L/4.4$). Phenological detail is given only for the first species, *Pieris napi*.

Pieris napi (OW): Eurytopic species found in both AB and BC as follows:

Date	AB					BC							T_{ABC}
	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	
V 16	6		1					1		2	1		11
24		1		1			2	1	3	3			11
VI 5		1		1			1	8	1	2			14
7	1						2	5	3	9	1		21
13								4	1	1		1	7
17			1					2		1		1	5
21			3	2		1	6	4	1	6	5	4	32
28				1			1				1		3
VII 5			1					2			2		5
10	3	1	2	2						1			9
15	3	1	2	5		1		1				1	14
19	2		2	17		1	2	4		5		2	35
24	2	6	4	9		1	6	4	2	6	1	2	43
27	3	1	1			2	6	2		1	3		19
VIII 4	3	3	2	7	2	2	6	6	1	6	5	3	46
8			2	4	1	1	4	4	2	4	2		24
13	2	1	2	9		4	5	7	3	10	6	7	56
17	1	2	5	5		4	8	12	2	13	10	4	66
25	5	3	10	23	2	4	8	10	2	16	7	3	93
31	15	4	11	37	2	3	6	5	5	6	7		103
IX 5	3	3	19	46	5	1	2	4	2	11		1	100
14	6	4	11	18			1	2	4			1	49
17	6	3	10	19					1	1	2		43
20	3	5	8	12								2	30
26		1		5									6
X 4		1											1
10	1												1
N	65	41	97	223	12	25	74	88	33	104	55	30	847
L	0.2	0.5	0.6	0.4	0.5	0.3	0.5	0.3	0.2	0.4	0.4	0.1	4.4
N_e	39	96	115	77	96	58	96	58	39	77	77	19	847

A glance at the table, however, a heterogeneous distribution is obvious, being $N > N_e$ in Aa, Ad, Bc, Be and Bg, while $N < N_e$ in Ab, Ae, Ba, Bb and Bf. Although the heterogeneity could fully be explained only after the distribution of larval food plants would be elucidated, the preference for shaded areas is suggested by the abundance at Aa (running along forest), Ad-left (with dense and tall herbs) Bc, Be and Bg (with tall herbs). Preferred subdivisions are constant irrespective of different census dates, though preference for forest in spring is clearer.

Pieris rapae (O): Typical openland species.

	Aa	Ab	Ac	Ad	Ae	T_{AB}	Ba	Bb	Bc	Bd	Be	Bf	Bg
N	49	103	148	262	11	573	5	2	1				
N_e	52.1	130.2	156.3	104.2	130.2	573							

Remarkable deviations, $N>N_e$ at Ad and $N<N_e$ at Ae, are immediately noticed. This may be explained in part by the abundance of nectariferous plants at Ad-right, while their absence in Ae except the European dandelion. A slight invasion to BC suggests a good dispersal ability.

Colias erate (O): Openland species, though some individuals were observed in BC.

	Aa	Ab	Ac	Ad	Ae	T_{AB}	Ba	Bb	Bc	Bd	Be	Bf	Bg
N	15	36	78	104	25	258	7	11	3	1	2	5	1
N_e	23.5	58.6	70.4	46.9	58.6	258							

The concentration to Ad is explained by the reason given for *Pieris rapae* and a considerable invasion into BC indicates a high dispersal ability.

Araschnia burejana (W): Typical forest species.

	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	T_{BC}
N	1		2	1	1	7	46	25	13	10	10	4	115
N_e						15.7	26.1	15.7	10.5	20.9	20.9	5.2	115

The value of N is higher at Bb and Bc, while lower at Ba, Be and Bf than expected. The former subdivisions are all surrounded by tall and dense forests, the latter ones are relatively open, suggesting a preference for shaded habitats. This species seems rather sedentary in spite of its strong flight ability.

Brenthis ino (W): Typical forest species.

	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	T_{BC}
N	4		2	3	2	2	22	21	10	17	23	11	106
N_e						14.5	24.1	14.4	9.6	19.3	19.3	4.9	106

$\chi^2_{(6)} = 22.58 > 22.457$ $p<0.001$

The value N deviates significantly from N_e at Ba and Bg. The scarcity at Ba may relate to the poor nature of forest or the presence of bamboo grass. This species is sedentary in spite of a strong flight ability, having a habit of staying at bushes.

Lycaena phlaeas (O): Openland species, though sparsely found in BC, too.

	Aa	Ab	Ac	Ad	Ae	T_{AB}	Ba	Bb	Bc	Bd	Be	Bf	Bg
N	5	5	16	59	1	86	3	4	1			1	1
N_e	7.8	19.6	23.5	15.6	19.5	86							

$\chi^2_{(4)} = 152.67 \quad p<0.001$

An excessive concentration in Ad probably implies the abundance of larval food plants, *Rumex* spp., there.

Papilio machaon (OW): Prefering openland but invading BC as suggested by the higher values at Ba, Bb and Bc.

	Aa	Ab	Ac	Ad	Ae	T_{AB}	Ba	Bb	Bc	Bd	Be	Bf	Bg
N	5	27	15	14	20	81	7	8	5		2	2	2
N_e	7.4	18.4	22.1	14.7	18.4	81							

$\chi^2_{(4)} = 7.25<7.779 \quad p>0.10$

The concentration in particular subdivisions is not conspicuous, probably in part due to the strong flight capacity and wide roaming habit.

Aglais urticae (W): Forest species.

	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	T_{BC}
N	1	4		1	2	11	10	7	3	34	15	3	83
N_e						11.3	18.9	11.3	7.51	5.1	15.1	3.8	83

The most preferred subdivision, Be, is provided with low and dense herbs at the right side of the road. In spite of forest preference, the strong insolation seems the second important condition, and the presence of coltsfoot flowers at the right side of Be, frequently visited by this species in spring, the third condition.

Everes argiades (OW): Distributed homogeneously in AB and BC.

	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	T_{ABC}
N	6	5	9	10		2	3	3	8	14	13	1	74
N_e	3.4	8.4	10.1	6.7	8.4	5.0	8.4	5.1	3.4	6.7	6.7	1.7	74

Considering the weak flight ability, the scarcity at Ae suggests a mild isolation between two sections, probably conditioned by the poor plant cover there.

Inachis io (oW): Forest species.

	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	T_{BC}
N	1	1	4	3	2	4	5	3	4	17	3	2	38
N_e						5.2	8.6	5.2	3.5	6.9	6.9	1.7	38

The deviation of N from N_e at Be and Bf cannot be explained, for the food plants, insolation and plant cover did not markedly differ from other subdivisions. The concentration at Be was obvious in spring, but no marked concentration in particular subdivisions was found from summer to autumn. This species is sedentary, especially in spring, in spite of a strong flight ability.

Ochlodes venata (Ow): Openland species though found from many subdivisions of BC.

	Aa	Ab	Ac	Ad	Ae	T_{AB}	Ba	Bb	Bc	Bd	Be	Bf	Bg
N	8	1	8	16	6	39	1	7	1	3	3		1
N_e	3.5	8.9	10.6	7.1	8.9	39							

N deviates from N_e at Aa, Ab and Ad. At Ab, this is probably caused by the floristic poverty at paddy zone.

Thoressa varia (W): Forest species.

	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	T_{BC}
N	1	1	1	1	3	20	20	2	6	6	6	2	62
N_e						8.4	14.1	8.5	5.6	11.3	11.3	2.8	62

The deviation of N from N_e at Ba cannot be explained adequately, for the food plants, insolation and plant cover did not markedly differ from other subdivisions.

Argyronome ruslana (Ow): Openland species but found at BC, too.

	Aa	Ab	Ac	Ad	Ae	T_{AB}	Ba	Bb	Bc	Bd	Be	Bf	Bg
N	4	2	7	11	10	34	1	6	3	1		3	
N_e	3.1	7.7	9.3	6.2	7.7	34							

$\chi^2_{(3)} = 16.62 > 16.268$ $p < 0.001$

This species seems to prefer the shaded areas of openland habitat, Ad (tall and dense grassland) and Ae (willows).

Table 1. Habitat preference of thirteen predominant species at Jozankei, Pn=*Pieris napi*, Pr=*Pieris rapae*, Ce=*Colias erate*, Ab=*Araschnia burejana*, Bi=*Brenthis ino*, Lp=*Lycaena phlaeas*, Pm=*Papilio machaon*, Au=*Aglais urticae*, Ea=*Everes argiades*, Ii=*Inachis io*, Ov=*Ochlodes venata*, Ar=*Argyronome ruslana*, Tv=*Thoressa varia*.

Subdivision		Deviation of N from N_e		
		$N>N_e$	$N \doteqdot N_e$	$N<N_e$
AB	Aa	Pn, Ea, Ov.	Pr, Lp, Pm, Ar.	Ce.
	Ab	Pm.		Pn, Pr, Ce, Lp, Ov, Ar.
	Ac		Pn, Pr, Ce, Ea, Ov, Ar.	Lp, Pm.
	Ad	Pn, Pr, Ce, Lp, Ea, Ov, Ar.	Pm.	
	Ae		Pm, Ov, Ar.	Pn, Pr, Ce, Lp, Ea.
BC	Ba	Tv.	Au, Ii.	Pn, Ab, Bi, Ea.
	Bb	Ab, Tv.	Bi, Ov.	Pn, Au, Ea, Ii.
	Bc	Pn, Ab, Bi.		Au, Ea, Ii, Tv.
	Bd	Ea.	Pn, Ab, Bi, Ii, Tv.	Au.
	Be	Pn, Au, Ea, Ii.	Bi.	Ab, Tv.
	Bf	Ea.	Bi, Au.	Pn, Ab, Ii, Tv.
	Bg	Pn, Bi.	Ab, Au, Ea, Ii, Tv.	

Apparently the results given above (summarized in Table 1), are still incomplete. The lack of precise information on flight and dispersal abilities, as well as on the distribution of food plants, both of adults and larvae, make closer analyses difficult. The consideration given below are only tentative. A prelimiary synopsis of the distribution of food plants in the area and of dispersal abilities is presented in Table 2. A high degree of coexistence between *Pieris napi* and *Everes argiades* in AB is explained by their preference for tall grasslands involving shaded areas. The relation among other species is given by Fig. 5. In AB *Papilio machaon* stands remote from others on account of its high flight and dispersal abilities, while *Pieris rapae*, *Colias erate*, *Lycaena phlaeas*, *Argyronome ruslana* and *Ochlodes venata* show a similar habitat preference for grassland. In BC a strong similarity between *Araschnia burejana* and *Thoressa varia* is probably caused by the absence of insolation except for subdivision Ba, while that between *Aglais urticae* and *Inachis io* by the opposite cause. The similarity between *Pieris napi* and *Everes argiades* is higher at AB than at BC. A slight local change may give some subtle but effective difference of habitat conditions to each of these basically eurytopic species.

Table 2. Distribution pattern of larval food plants and nectariferous plants (⧺= abundant, +=present, −= absent), together with flight ability (Fl, ⧺= high, +=low) and sedentariness (Se, ⧺=high, +=present, −=absent) of predominant butterfly species.

Species	AB					BC								
	Aa	Ab	Ac	Ad	Ae	Ba	Bb	Bc	Bd	Be	Bf	Bg	Fl	Se
Pieris napi	+	−	+	⧺	−	+	+	⧺	+	+	−	−	+	−
P. rapae	−	+	+	⧺	−	−	−	−	−	−	−	−	⧺	−
Colias erate	+	+	+	+	+	+	+	+	+	−	+	−	⧺	−
Araschnia burejana	+	−	−	−	−	⧺	⧺	⧺	+	+	−	+	+	⧺
Brenthis ino	+	−	−	−	−	+	+	+	+	+	+	+	+	+
Lycaena phlaeas	+	+	+	+	−	+	+	−	−	−	−	−	⧺	−
Papilio machaon	+	+	+	+	⧺	+	⧺	−	+	−	−	−	⧺	⧺
Aglais urticae	+	−	−	−	−	⧺	⧺	⧺	+	+	−	+	⧺	⧺
Everes argiades	+	+	+	+	−	−	−	−	−	+	+	−	+	+
Inachis io	+	−	−	−	−	⧺	⧺	⧺	+	+	−	+	⧺	⧺
Ochlodes venata	+	+	+	+	+	−	+	+	−	+	+	+	⧺	+
Argyronome ruslana	+	−	−	−	−	+	+	+	+	+	+	+	+	−
Thoressa varia	+	−	−	−	−	+	−	+	+	⧺	+	+	⧺	⧺
Nectariferous plants (*=Exotic weeds)														
Angelica polyclada	+	−	+	−	−	+	+	⧺	+	+	−	+		
*Erigeron annus**	+	−	−	⧺	−	−	+	−	−	−	−	−		
Petasites japonicus	+	−	−	−	−	+	+	+	+	⧺	−	+		
*Rudbeckia laciriata**	+	+	+	−	⧺	?	?	?	?	?	?	?		
Solidago altissima	−	+	⧺	⧺	−	−	−	−	−	−	−	−		
Syringa vulgaris	+	+	+	+	−	−	−	−	−	−	−	−		
*Taraxacum officinale**	⧺	+	+	+	+	+	+	−	−	+	−	−		
*Trifolium pratense**	+	+	+	+	−	−	+	−	+	+	+	−		
Veronicastrum sibiricum	+	−	−	−	−	−	−	−	+	⧺	⧺	+		

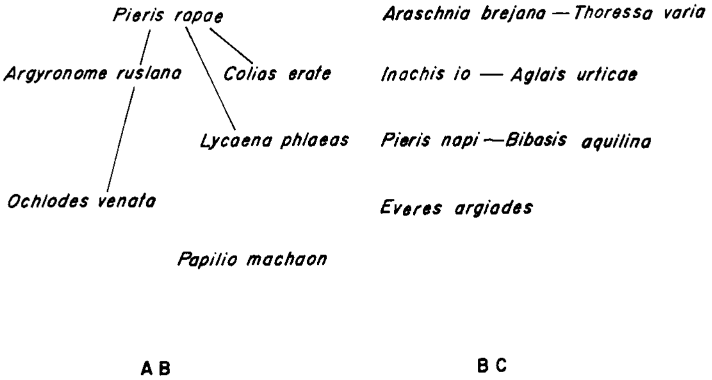

Fig. 5. Similarity of distribution pattern in two subsections (left=AB, right=BC).

2. Relation between faunal makeup and urbanization

Three surveyed areas show a gradient of increasing human impact, JO<JM <UC. Certainly, definite conclusions will be obtained only when several areas were studied for each stage of allogenic succession. The present study is regarded as a preliminary approach to such studies.

2.1. *Specific prosperity*: In this subsection, the specific prosperity at three surveyed areas is briefly compared. The predominant species in JO, JM and UC chosen by the value over the mean frequency (JO=28.6, JM=46.1, UC=91.0) are shown in Table 3, together with the index of specific prosperity ($Ps=N/I_\delta \times 100$, where N=total individual number, I_δ=Morisita's diversity index. Morisita 1967), and their phenology in Fig. 6. Three top predominants, *Pieris napi*, *P. rapae* and *Colias erate* are common to three areas in spite of rank difference. These three species probably predominate over the whole area of Hokkaido. Among them only *Pieris rapae* is predominant throughout Japan (Table 4). Some other remarks are itemized:

Table 3. Predominant species expressed by two indices at JO, JM and UC. H: Habitat type.

JO (28.6=mean frequency)			JM (46.1)			UC (91.0)		
Species	*Ps* (*N*)	H	Species	*Ps* (*N*)	H	Species	*Ps* (*N*)	H
Pieris napi	1,046 (479.0)	OW	*Colias erate*	1.762 (665.5)	O	*Pieris rapae*	3.132 (1,229.5)	O
P. rapae	0.674 (301.5)	O	*Pieris rapae*	1.621 (503.0)	O	*Colias erate*	2.180 (778.5)	O
Colias erate	0.375 (161.0)	O	*Pieris napi*	1.051 (384.0)	OW	*Pieris napi*	0.550 (231.5)	OW
Araschnia burejana	0.104 (60.5)	W	*Lycaena phlaeas*	0.255 (112.5)	O	*Lycaena phlaeas*	0.239 (132.5)	O
Brenthis ino	0.087 (58.5)	W	*Everes argiades*	0.202 (193.0)	OW	*Everes argiades*	0.142 (112.0)	OW
Lycaena phlaeas	0.079 (55.0)	O	*Ochlodes venata*	0.095 (89.0)	Ow	*Ochlodes venata*	0.066 (94.0)	Ow
Papilio machaon	0.070 (54.5)	Ow						
Aglais urticae	0.076 (53.5)	W						
Everes argiades	0.040 (38.0)	OW						
Inachis io	0.081 (34.5)	oW						
Thoressa varia	0.026 (34.5)	W						
Argyronome ruslana	0.050 (29.5)	Ow						
Ochlodes venata	0.035 (27.5)	Ow						
Total	1,387.5			1,947.0			2,578.0	
%	79.5			84.5			96.5	

Table 4. Rank order of five top species at three locations environmentally similar to JM (=openland and forest in mosaic) in Japan. Hirao: Southern Japan (Kawabata 1976), Kyoto: Western Honshu (Morisita op. cit.), Utsunomiya: Eastern Honshu (Gôda 1969)

	JM	Utsunomiya	Kyoto	Hirao	Gradient
Colias erate	**1**	**4**	15	11	N>S
Pieris rapae	**2**	**1**	**2**	**1**	N∼S
P. napi	**3**	46	—	—	N≫S
Lycaena phlaeas	**4**	7	12	21	N>S
Everes argiades	**5**	**5**	**4**	7	N∼S
Ypthima argus	8	**2**	**1**	**2**	N<S
Eurema hecabe	—	**3**	**3**	8	N<S
Neope goschkevitschii	17	28	**5**	9	?
Zizeeria maha	—	11	7	**3**	N<S
Papilio xuthus	—	19	21	**4**	?
Parnara guttata	—	12	6	**5**	N<S

1) Concentration of individual number upon a few predominants takes the following order, UC (6 sp. 96.5%)>JM (6 sp. 84.5%)>JO (13 sp. 79.5%) which goes in parallel with the intensity of urbanization.

2) In parallel with urbanization the forest species such as *Araschnia burejana*, *Brenthis ino*, *Aglais urticae*, *Inachis io* and *Thoressa varia* drop from the high ranks.

3) *Pieris rapae* and *Colias erate* give the highest *Ps* at UC, while *Pieris napi*, *Lycaena phlaeas*, *Everes argiades* and *Ochlodes venata*, at JM

The same procedure was applied to all constituents of the butterfly assemblages of three areas. Table 5 shows *Ps* of each species, accompanied with five principal bionomic characters as defined below:

A. Hibernation types (cf. Shirôzu and Hara 1962):
   1. Egg (A_e), 2. Larva (A_l), 3. Pupa (A_p), 4. Adult (A_a).
B. Larval food types (cf. Shirôzu and Hara 1962):
   1. Grasses and herbs (B_g), 2. Trees and shrubs (B_t), 3. Both B_g and B_t (B_{gt}).
C. Habitat types (cf. Hiura and Section 1): 1. Openland (C_o=O, Ow), 2. Forest (C_w=W, oW), 3. Both openland and forest (C_{ow}=OW).
D. Distribution types (cf. Fujioka 1973 and Hiura 1973):
   1. Northern Palaearctic element (D_n), 2. Japan-China-Himalayan element (D_c), 3. Typical oriental element and cosmopolitan or widespread species (D_s), 4. Endemic to Japan (D_h).
E. Life cycle types=Number of generations per year (cf. Shirôzu and Hara 1962): 1. One (E_1), 2. Two (E_2), 3. Three or more (E_3). Small letters given in Table 5, indicate the number of generations at southern Japan (p=more than three).

The relative abundance of the species belonging to various bionomic types at three areas is given, together with the absolute number of species, in the following

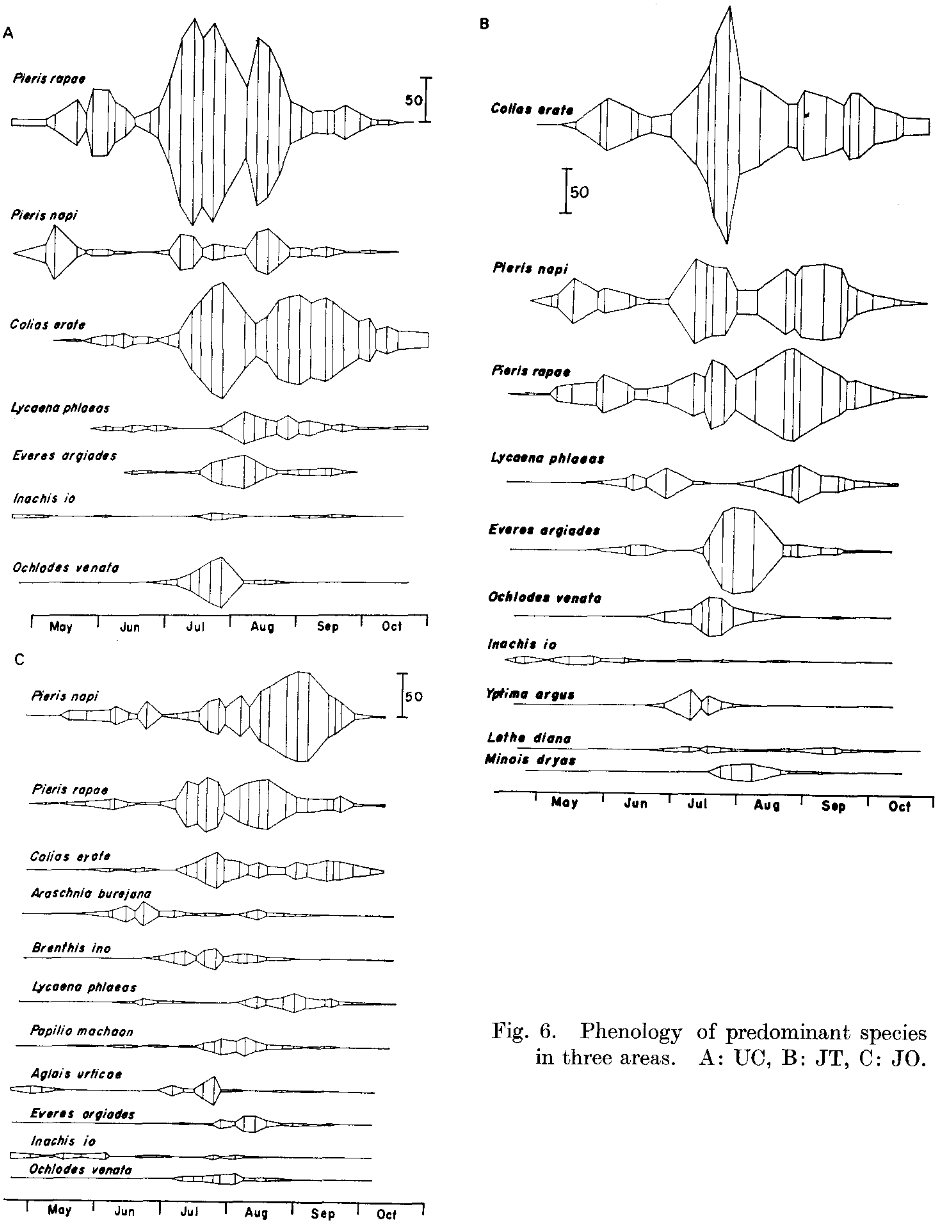

Fig. 6. Phenology of predominant species in three areas. A: UC, B: JT, C: JO.

Table 5. Species prosperity index (*Ps*) of all species in three areas, together with their bionomic characters (explained in text). + = rare species ($n_i = 0.5$)

Species	*Ps*				Characters				
	JO	JT	JM	UC	A	B	C	D	E
Erebia niphonica	0.35				l	g	w	c	1
Coenonympha hero	0.17				l	g	w	n	1
Neptis philyra	0.56	0.13			l	t	w	c	1
Kaniska canace	+				a	gt	w	s	1^{p}
Araragi enthea	+	+			e	t	w	c	1
Antigius attilia	+				e	t	w	c	1
Wagimo signata	+				e	t	w	c	1
Favonius orientalis	+				e	t	w	c	1
F. cognatus	+	0.18			e	t	w	c	1
Ahlbergia ferrea	+	+			p	gt	w	c	1
Scolytantides orion	0.57	1.28			p	g	w	n	1
Polytremis pellucida	0.50				l	gt	w	c	1^{2}
Erynnis montanus	+				l	t	w	c	1
Parnassius stubbendorfii	2.39	0.75	0.06		e	g	ow	c	1
Papilio macilentus	0.13	0.17	0.13		p	t	w	c	2
Anthocaris scolymus	+	1.29	0.51		p	g	w	c	1
Ypthima argus	0.28	5.10	2.99		l	g	ow	c	1^{p}
Harima callipteris	2.69	1.26	0.42		l	t	w	c	1
Ninguta schrenckii	0.44	0.03	0.03		l	g	o	c	1
Neope goschkevitschii	0.78	3.46	1.51		p	t	w	h	1
Sasakia charonda	+	0.56	+		l	t	w	c	1
Araschnia burejana	10.43	3.90	1.96		p	g	w	c	2^{p}
A. levana	1.53	5.21	4.10		p	g	ow	n	2^{p}
Nymphalis xanthomelas	0.12	1.93	0.56		a	t	w	c	1
N. antiopa	+	+	+		a	t	w	n	1
Aglais urticae	7.57	0.45	0.12		a	g	w	n	1
Brenthis ino	8.76	2.10	1.75		l	g	w	n	1
Japonica lutea	1.45	2.20	0.74		e	t	w	c	1
Shirozua jonasi	+	0.29	0.18		e	t	w	c	1
Neozephyrus taxila	0.33	+	+		e	t	w	c	1
Bibasis aquilina	1.14	0.12	0.03		l	t	w	c	1
Papilio machaon	7.01	2.73	1.44	3.67	p	gt	o	n	2^{p}
P. bianor	2.31	2.01	0.78	+	p	t	o	c	2
P. maackii	3.30	2.13	1.10	0.08	p	t	ow	c	2
Aporia crataegi	1.09	1.00	0.45	+	l	t	ow	n	1
Colias erate	37.48	310.77	176.21	217.98	l	g	o	c	3^{p}
Pieris napi	104.58	212.48	105.12	54.96	p	g	ow	n	3^{p}
P. melete	1.66	1.22	0.44	1.02	p	g	ow	c	2^{p}
P. rapae	67.38	217.98	162.09	313.15	p	g	o	n	3^{p}
Lethe diana	5.00	10.44	5.37	2.04	l	t	ow	c	1^{p}
Apatura ilia	0.51	1.56	0.99	0.69	l	t	w	n	1
Neptis rivularis	2.14	1.06	0.52	0.50	l	gt	ow	n	1
Polygonia c-album	6.81	2.25	2.08	+	a	gt	w	n	2
P. vau-album	0.48	3.91	1.50	+	a	t	w	n	1
Inachis io	8.09	9.46	2.08	2.15	a	g	w	n	2
Fabriciana adippe	2.07	0.49	0.40	+	e	g	o	n	1
Argyronome laodice	0.20	1.57	1.13	0.52	l	g	o	n	1

Table 5. (Continued)

species	*Ps*				Characters				
	JO	JT	JM	UC	A	B	C	D	E
Argynnis paphia	2.67	3.55	1.77	1.41	l	g	ow	n	1
Speyeria aglaia	4.80	1.04	0.12	0.17	e	g	w	n	1
Argyronome ruslana	5.01	1.60	1.40	0.91	e	g	ow	c	1
Lycaena phlaeas	7.90	37.37	25.45	23.86	l	g	o	n	2
Prebejus argus	0.50	+	+	+	e	g	w	n	1
Celastrina argiolus	+	1.53	0.39	+	p	gt	ow	n	2^p
Everes argiades	3.98	29.02	20.23	14.27	l	gt	ow	n	3^p
Thymelicus sylvaticus	0.13	1.00	0.93	+	l	g	ow	c	1
Ochlodes venata	3.50	12.67	9.32	6.64	l	gt	o	n	1
Thoressa varia	2.55	0.75	0.83	+	l	t	w	h	1^2

table, for each bionomic character separately (Ts=Total number of species, Sp=Number of species in each area).

Type	Ts	JO	JM	UC
		Sp (%)	Sp (%)	Sp (%)
		61 (100%)	50 (100%)	29 (100%)
A. Hibernation types				
A_e	15	14(**23.0**)	10(**20.0**)	5(**17.2**)
A_l	26	24(39.3)	21(42.0)	12(41.4)
A_p	15	15(24.6)	12(24.0)	7(24.1)
A_a	9	8(**13.1**)	7(**14.0**)	5(**17.3**)
B. Larval food types				
B_t	30	27(**44.2**)	21(**42.0**)	7(**24.1**)
B_{gt}	9	9(14.8)	6(12.0)	6(20.7)
B_g	26	25(**41.0**)	23(**46.0**)	16(**55.2**)
C. Habitat types				
C_w	39	37(**60.7**)	25(**50.0**)	8(**26.6**)
C_{ow}	14	13(**21.3**)	14(**28.0**)	10(**34.5**)
C_o	12	11(**18.0**)	11(**22.0**)	11(**37.5**)
D. Distribution types				
D_c	32	30(**49.2**)	22(**44.0**)	7(**24.1**)
D_h	3	3(4.9)	3(6.0)	1(3.5)
D_n	27	26(**42.6**)	24(**48.0**)	19(**65.5**)
D_s	3	2(3.3)	1(2.0)	2(6.9)
E. Life cycle types				
E_1	48	45(**73.8**)	33(**66.0**)	17(**58.6**)
E_2	13	12(19.7)	13(26.0)	8(27.6)
E_3	4	4(**6.5**)	4(**8.0**)	4(**13.8**)

As shown in Gothic, the species belonging to types A_e, B_t, C_w, D_c and E_1 gradually disappear, while those to types A_a, B_g, C_{ow}, C_o, D_n and E_3 remain or even increase in parallel with urbanization.

Nextly the same aspect is analyzed with *Ps*, the values of which at three areas are shown in Table 5. Thirteen species observed only at JO are all belong to C_w or E_1. Most of 18 species observed both at JO and JM show higher *Ps* at JO than at JM, except *Anthocaris scolymus*, *Ypthima argus*, *Neope goschkevitschii*, *Araschnia levana*, *Nymphalis xanthomelas* and *Shirozua jonasi*. Ten out of 26 species observed at all three areas, containing three openland species, *Papilio bianor*, *Fabriciana adippe* and *Argyronome ruslana*, possess the order of *Ps*, JO>JM>UC. The order in the other species are:

JO>UC>JM: *Papilio machaon*, *Pieris melete*, *Inachis io* and *Speyeria aglaia*.
JM>JO>UC: *Pieris napi*, *Polygonia vau-album*, *Lethe diana* and *Thymelicus sylvaticus*.
JM>UC>JO: *Apatura ilia*, *Argyronome laodice*, *Lycaena phlaeas*, *Celastrina argiolus*, *Everes argiades* and *Ochlodes venata*. All are D_n species and only one species, *Apatura ilia* belongs to C_w.
UC>JM>JO: *Colias erate* and *Pieris rapae*. Both classified into B_g-C_o-E_3.

Consequently 41 species exhibit the highest *Ps* at JO, and 21 at JM, while 2 at UC. These results suggest two facts, general faunal impoverishment and replacement of some bionomic types by others given previously, in the order of JO>JM>UC.

In the following table, the relative prosperity of the species belonging to various bionomic types at three areas was shown by *Ps*. In each bionomic type for each area, the number of species, which possess the highest *Ps* at the area concerned was counted and converted to the % *Ps*. For instance, among 26 species belonging to A_l 14 species are the most prosperous at JO, 11 and JM, and only one at UC.

Type	JO	JM	UC	Total (100%)
	Sp (%)	Sp (%)	Sp (%)	
A. Hibernation types				
A_e	13(86.7)	2(13.3)		15
A_l	14(53.8)	11(42.3)	1(3.9)	26
A_p	9(60.0)	5(33.5)	1(6.5)	15
A_a	5(62.5)	3(37.5)		$8^{1)}$
B. Larval food types				
B_t	21(70.0)	9(30.0)		30
B_{gt}	6(66.7)	3(33.3)		9
B_g	14(56.0)	9(36.0)	2(8.0)	$25^{1)}$
C. Habitat types				
C_w	30(76.9)	9(23.1)		39
C_{ow}	6(42.9)	8(57.1)		14
C_o	5(45.5)	4(36.4)		

Type	JO	JM	UC	Total (100%)
	Sp (%)	Sp (%)	Sp (%)	
D. Distribution types				
D_c	22(68.8)	9(28.1)	1(3.1)	32
D_h	2(66.7)	1(33.3)		3
D_n	16(59.3)	10(37.0)	1(3.7)	27
D_s	1(50.0)	1(50.0)		2[1)]
E. Life cycle types				
E_1	32(68.1)	15(31.9)		47[1)]
E_2	9(69.2)	4(30.8)		13
E_3		2(50.0)	2(50.0)	4

1) *Vanessa indica* was excluded because *Ps* was JO=UC.

In most types, JO occupies the first rank, followed by JM, then UC, apparently due to the higher number of species censused. The ranks of % *Ps* within each area are:

Hibernation type: $A_e>A_a>A_p>A_l$ at JO, $A_l>A_a>A_p>A_e$ at JM and $A_p>A_l$ at UC.
Larval food type: $B_t>B_{gt}>B_g$ at JO, $B_g>B_{gt}>B_t$ at JM and only B_g at UC.
Habitat type: $C_w>C_o>C_{ow}$ at JO, $C_{ow}>C_o>C_w$ at JM and only C_o at UC.
Distribution type: $D_c>D_h>D_n>D_s$ at JO, $D_s>D_n>D_h>D_c$ at JM and $D_n>D_c$ at UC.
Life cycle type: $E_2>E_1$ at JO, $E_3>E_1>E_2$ at JM and only E_3 at UC.

Most of the species belonging to A_e, B_t, C_w, D_c, E_1 and E_2 prosper in JO, while about one half of the species belonging to A_l, B_g, C_{ow}, C_o, D_n and E_3 at JM and UC. Only two species, *Pieris rapae* and *Colias erate* show the highest % *Ps* at UC, both belonging to B_g, C_o and E_3 with extremely high values, apparently in part due to their dependence on cultivated plants as larval foods.

2.2. *Community prosperity*: Following the previous subsection, where each species was treated irrespective of relative abundance, the present subsection deals with the butterfly assemblage as a whole, considering both species and individual numbers, in order to apprehend the allogenic faunal succession.

Similarity of butterfly assemblages among three areas: The similarity of butterfly assemblages among three areas is sought by using the index of distance (*DI*) and harmonity index (*HI*) among them. Distance of resemblance (Distance index=*DI*) between the two different results, A and B, is calculated by the formula,

$$DI=\sqrt{\frac{\Sigma(f_{iA}-f_{iB})^2}{T}}$$

where f_{iA} and f_{iB} are the value of species i in results A and B, taking either 1 (=presence) or 0 (=absence) and T is total number of species. The numerator is therefore equal to the root of number of species registered only in one of both results.

The value of *DI* ranges from 0 (all species represented in both results) to 1 (the absence of any common species). The calculated *DI* is: JO～JM=0.545, JO～UC =0.758 and JM～UC=0.700. The relation is shown in Fig. 7 right top, where JM is intermediate between JO and UC.

The harmonity index is calculated with the equation,

$$HI=\frac{2\sum n_{1i}n_{2i}}{(\pi_1^2+\pi_2^2)N_1N_2}$$

where N=total corrected individual number, n_i=corrected individual number of species i, $\pi_1^2=\sum n_i^2/N_1^2$, $\pi_2^2=\sum n_i^2/N_2^2$, N_1, N_2 respectively total corrected individual number of assemblages I and II, and n_{1i} or n_{2i} individual number of species i found in the assemblage I or II. A value of *HI*, 1.0 shows the same makeup between two assemblages, while values, 0.0 the complete difference. The calculated *HI* are (left, JO treated as a whole; right, divided into AB and BC):

	JO	JT	UC
JO	/	0.810	0.618
JT	0.810	/	0.818
UC	0.618	0.818	/

	JT	UC	JO-BC
JO-AB	0.875	0.835	0.582
JO-BC	0.496	0.174	/

The results suggest a gradient JO-JT-UC, which corresponds to the order of increased urbanization in accordance with the results given in Subseciton **2. 1.**

Comparison among three areas: As a measure for community structure, Morisita invented index of community diversity,

$$\beta=\frac{T(T-1)}{\sum x(x-1)},\ \text{conveniently}\ \beta=\frac{T(T-0.5)}{\sum x(x-0.5)}$$

where T is $\sum x$, the corrected individual number of each species censused during definite interval (here ten days term). The value of index approaches 1.0 when the community is simple, i.e. most individuals belonging to a few species, while deviates from 1.0 in the opposite case. In the present study, the community prosperity index $T\beta$, or $T\beta/100$ was used to analyze the results. In annual total, the value $T\beta$ is the highest in JT (220.5), followed by JO (143.1) and UC (86.3). But the route of JT (6.8 km) is the longest among three. Using the data taken from the part running Jûgoshima and Misumai (4.3 km=JM) alone, the value of the index becomes 135.0, being intermediate between JO and UC, which gives the order of prosperity, JO>JM>UC.

Concerning the relation of butterfly fauna and of ruralization and urbanization, Hiura (1973) asserted the occurrence of some parallel trends as reproduced below.

Phase	I	II		III	
Type of environment	Primary	Rural		Urban	
Location (with reference to human communities	Mountains and steep slopes	Mountainous villages	Plains villages	Suburbs	Centers of cities
Corresponding vegetation type	Forest	Savanna	Openland with grasses and herbs	Semi-desert	Desert
Historic age		Middle Jômon ~ Middle	Middle ~ Modern	Modern	Present
Sub-phase	I	II-A	II-B	III-A	III-B

In and near Sapporo City, JO–BC corresponds to I (Subphase), JO-AB and JT to II-A, UC to II-B ~ III-A, and the center of Sapporo City to III-B, where only a few species of butterflies can continue to survive. How then are butterflies affected by urbanization ? As suggested by Hiura (*op. cit.*), the most serious factor would be the change of vegetation. In parallel with the advance urbanization, many constituents drop from the primary vegetation (even at JO, most of nectariferous plants are exotic as shown in Table 2), resulting in the specific poverty and prosperity of limited number of plant species, those adapted to man-made environments. Many butterfly species must retreat from such environments by the lack of food plants, especially of the larvae. On the other hand, certain species feeding on cultivated plants and synanthropic weeds could prosper there. At UC some species were not observed in spite of the presence of larval food plants, for instance, *Parnassius stubbendorfii*, *Papilio macilentus*, *Anthocaris scolymus*, *Neptis philyra*, *Ussuriana stygiana*, *Neozephyrus taxila*, *Chrysozephrus smaragdinus*, *Ahlbergia ferrea*, *Celastrina sugitanii*, *Bibasis aquilina*, *Polytremis pellucida* and the species of Satyridae except for *Lethe diana* found in JO and JT. This indicates that the mere presence of food plants does not always make the occurrence of butterflies possible. The habitat is a complex of diverse conditions where food plants are an important but not exclusive factor. Each butterfly species has acquired its own mode of life through the lasting adaptation process to the habitat complex. The differentiation of openland and forest species repeatedly cited in previous sections is interpreted as an outcome of such adaptive radiation. To understand the relation of various bionomic characters to the urbanization series JO-JM-UC, the value $T\beta$ was calculated in three areas for species groups representing various bionomic types separately (Fig. 7 and 8).

A) Hibernation type (Fig. 7A): The order, $A_l > A_P > A_e > A_a$ is common to three areas. The index in A_l is highest at JM (JM>JO>UC), that in A_e, A_p and A_a decreases in the order JO>JM>UC, matching with the gradient of urbanization.

The same tendency was obtained in Subsection **2. 1.**, too, except for A_a. Hibernation with larvae is possibly suitable for grasses and herbs, because decaying of these annual plants obliges their feeders to disperse which is impossible by egg hibernation. As to pupal hibernation, the species belonging to this type generally pupate at places distant from their food plants, thus, avoiding decaying of the substrata. Thus, the order JM>JO in A_l may partly be a consequence of expansion of secondary openland. On the other hand, JM>UC in A_l must indicate a general faunal impoverishment, caused by oversimplification and fragmentation of vegetation in UC. Decline of A_e at UC is persuaded also by the fact that most A_e-type species are those ovipositing on trees. Decrease of A_a-type species from JO to JM is difficult to explain because they are much adapted to

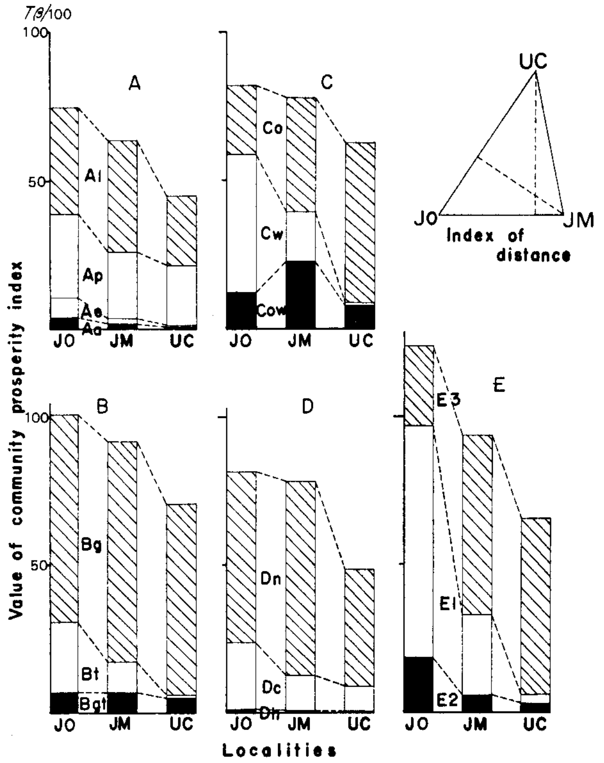

Fig. 7. Change of community propserity index among three areas calculated for each bionomic type separately.
A: Hibernation types, B: Food types, C: Habitat types, D: Distribution types, E: Life cycle types. Relation of similarity calculated by distance index among three areas given (right top). Further explanations in text.

openland habitat when their high dispersal ability is considered. Further studies on the condition of hibernating places may throw a light on the problem.

B) Larval food type (Fig. 7B): The prevalence of B_g-type species is common to three areas. Decline of B_t at JM and UC as obtained in Subsection **2. 1.**, too, is easily understood because the species feeding on grasses and herbs may prosper in openland. But an excessive urbanization probably expels even such species.

C) Habitat type (Fig. 7C): The order, $C_o>C_{ow}>C_w$ is common both to JM and UC, while $C_w>C_o>C_{ow}$ at JO. C_o increases, while C_w decreases in parallel with the gradient of urbanization. The result coincides with that obtained in Subsection **2. 1.** It is needless to explain the accordance of $T\beta$ and urbanization gradient because the comparison was begun based upon the disappearance of forest species in deforested areas.

D) Distribution type (Fig. 7D): The order $D_n>D_c>D_h$ is common to three areas. Fig. 7D resembles Figs. 7A and 7B with the order JO>JM>UC in D_c and JM>JO>UC in D_n. The former order is obtained in Subsection **2. 1.**, too. The difference of distribution types between openland and forest species could partly be explained by the assumption on the origin of secondary openland by Hiura (op. cit.). But further comparative studies on the habitat preference of various species related to the Japanese butterfly fauna are required.

E) Life cycle type (Fig. 7E): The order is $E_1>E_3>E_2$ at JO, and $E_3>E_1>E_2$ both at JM and UC. The order in E_3 is UC>JM>JO, while both in E_1 and E_2, JO>JM>UC. The same tendency was obtained in Subsection **2. 1.**, too, though E_2 gave the opposite gradient. The gradient of E_1 among three areas agrees with that of urbanization. But the species belonging to E_3 is less prosperous in JO than in JM and UC, which is not explained by a mere adaptation to openlands. As in item D, the historical background of openland or forest species must be sought through comparative studies. Fig. 8 gives percentage ratio of $T\beta$ for each bionomic character. The result indicates that some bionomic types are more likely to resist to urbanization, for instance, A_l, A_p, B_g, B_{gt}, C_o, D_n and E_3. Finally, $T\beta$ of each bionomic character is considered on the basis of habitat type. Table 6 shows number of species and individuals, β and $T\beta$-index after classified according to habitat type (C_w, C_{ow}, C_o). In C_w-type species all bionomic characters decline in the order of JO>JM>UC. In C_o-type species A_l, A_p, A_a, B_g, D_n, D_c, D_s and E_3 take higher value of $T\beta$-index in the order of UC>JM>JO, while A_e, B_t, B_{gt} and E_2, JO>JM>UC. In C_{ow}-type species the highest value of $T\beta$ at JM is shown by A_l, B_g, B_{gt}, D_n, E_1 and E_3. But it is possible that the value of $T\beta$ grows higher in the order of UC>JM>JO in spite of the poverty of C_o-type assemblage both at JM and UC. Because the high individual number of the particular species, *Pieris rapae* and *Colias erate* may affect the result. For this reason, the $T\beta$-index was calculated excluding *Pieris rapae* and/or *Colias erate.* In C_o-type, excluding *Pieris rapae*, the order of $T\beta$ is: UC (1,741.64)>JM (1,577.65) >JO (1,403.73) in agreement with Fig. 7C, while excluding the two species: JO

(1,024.46)>JM (629.37)>UC (621.51) with percentage ratio, UC (43.1%)>JO (14.9 %)>JM (13.9%). This is acceptable for a propserity gradient of C_o-type species, UC>JM>JO. In C_o-A_l type, excluding *Colias erate*, the order of $T\beta$ is UC (494.50)>JM (431.72)>JO (192.57) and C_o-B_g type excluding *Piers rapae* and *Colias erate*, JO (301.96=65.5%)>UC (206.27=64.5%)>JM (166.93=55.5%) and C_o-D_n type excluding *Pieris rapae*, UC (98.1%)>JM (91.6%)>JO (75.9%). On the other hand, C_o-A_p and C_o-D_c types are markedly affected by either of two species as

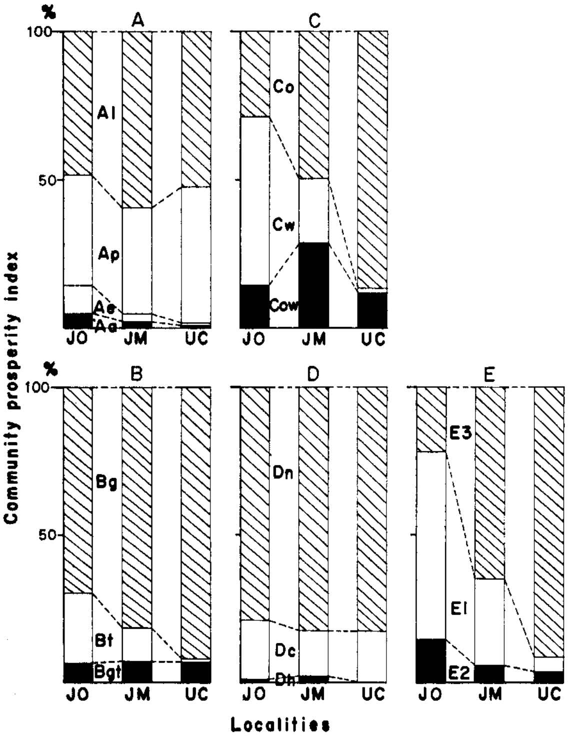

Fig. 8. Change of community propserity index given by percentage ratio.

follows: JO (92.95=25.3%)>JM (33.16=6.8%)>UC (7.7=1.5%) in C_o-A_p type and JO (90.47=12.6%)>JM (29.51=5.1%) UC (10.62=1.9%).

The results described above indicate that A_l, B_g, D_n and E_3 types of openland species can prevail with urbanization and that *Pieris rapae* and *Colias erate* seem to deviate from the category of openland species, probably by their dependence on cultivated plants, regarded as the species most resistance to urbanization.

Table 6. Relation between habitat type and the other four bionomic types.
Sp: Number of species, In: Number of individuals.
Further explanations in text.

		C_w-type			C_{ow}-type			C_o-type		
		JO	JM	UC	JO	JM	UC	JO	JM	UC
A_e	Sp	11	7	3	1	1	0	2	2	2
	In	49.5	19.0	6.5	26.0	2.0	0	44.5	9.5	9.5
	β	3.3	3.6	2.3	1.0	1.0		1.8	2.1	1.1
	Tβ	165.0	69.2	14.9	26.0	2.0		81.2	19.6	10.6
A_l	Sp	12	8	2	7	8	6	5	4	4
	In	151.5	31.0	4.0	109.5	334.0	128.0	251.0	872.5	1,014.0
	β	4.5	4.0	2.2	4.5	2.7	1.3	2.1	1.6	1.6
	Tβ	680.2	123.2	8.6	496.4	906.0	166.4	533.1	1,433.5	1,648.8
A_p	Sp	7	4	0	5	5	4	3	3	3
	In	83.5	30.0	0.0	519.5	415.5	239.0	367.5	521.0	1,235.5
	β	1.9	3.4		1.2	1.2	1.1	1.4	1.1	1.0
	Tβ	154.1	100.4		609.4	485.3	254.7	528.3	558.3	1,247.9
A_a	Sp	7	6	3	0	0	0	1	1	2
	In	116.0	28.0	18.0	0.0	0.0	0.0	0.5	1.0	3.0
	β	3.1	4.4	1.1					1.0	1.5
	Tβ	363.4	121.8	20.2					1.0	4.5
B_g	Sp	10	7	4	7	8	4	8	8	8
	In	249.0	46.0	20.0	548.0	517.5	242.5	570.0	1,297.0	2,161.5
	β	5.3	4.7	1.4	1.3	1.8	1.1	2.7	2.4	2.2
	Tβ	1.322.2	214.4	27.5	713.5	916.5	265.9	1,532.7	3,080.4	4,712.1
B_t	Sp	23	17	3	3	3	3	1	1	1
	In	129.5	57.0	8.0	57.0	31.0	7.0	11.5	6.0	0.5
	β	8.5	10.9	2.9	2.8	2.1	2.2	1.0	1.0	1.0
	Tβ	1,100.7	602.9	23.4	157.4	63.6	15.5	11.5	6.0	0.5
B_{gt}	Sp	4	1	1	3	3	3	2	2	2
	In	22.0	5.0	0.5	50.0	203.0	117.5	82.0	101.0	100.0
	β	2.0	1.0	1.0	1.6	1.1	1.1	1.8	1.3	1.1
	Tβ	440.1	5.0	0.5	80.3	224.3	129.2	148.7	127.9	112.8
D_n	Sp	13	10	7	7	8	6	6	6	6
	In	225.0	48.5	27.0	567.0	659.5	356.0	457.0	725.0	1,471.0
	β	6.0	6.0	2.4	1.4	2.3	1.9	2.1	1.9	1.4
	Tβ	1,353.1	292.5	63.9	787.0	1,537.3	682.4	976.2	1,392.7	2,059.4
D_c	Sp	20	12	0	6	6	4	4	4	3
	In	128.0	47.0	0.0	88.0	92.0	11.0	206.0	678.0	788.0
	β	3.9	7.5		4.2	3.7	4.0	1.6	1.0	1.0
	Tβ	496.8	351.8		371.4	341.8	43.8	324.9	703.1	796.7

Table 6. (Continued)

		C_W-type			C_{OW}-type			C_O-type		
		JO	JM	UC	JO	JM	UC	JO	JM	UC
D_h	Sp	3	3	1	0	0	0	0	0	0
	In	47.0	12.5	1.5	0.0	0.0	0.0	0.0	0.0	0.0
	β	1.7	1.5	1.0						
	$T\beta$	80.3	19.1	1.5						
D_s	Sp	1	0	0	0	0	0	1	1	2
	In	0.5	0.0	0.0	0.0	0.0	0.0	0.5	1.0	3.0
	β	1.0						1.0	1.0	1.5
	$T\beta$	0.5						0.5	1.0	4.5
E_1	Sp	32	19	6	7	8	5	6	6	6
	In	284.5	76.0	11.0	97.5	143.0	16.0	80.0	105.5	115.5
	β	9.2	11.1	4.9	5.1	5.2	3.7	3.5	1.4	1.5
	$T\beta$	2,604.8	844.4	54.7	499.2	745.0	58.4	276.5	145.2	171.5
E_2	Sp	5	6	2	4	4	3	3	3	3
	In	116.0	32.0	17.5	40.5	31.5	7.5	121.0	130.5	139.0
	β	2.7	3.9	1.1	2.6	2.9	2.8	2.4	1.3	1.1
	$T\beta$	308.9	125.8	18.7	106.2	92.2	21.3	290.8	173.5	152.8
E_3	Sp	0	0	0	2	2	2	2	2	2
	In	0.0	0.0	0.0	517.0	577.0	343.5	462.5	1,168.5	2.007.5
	β				1.2	1.8	1.8	1.8	2.0	1.9
	$T\beta$				598.0	1.040.3	613.5	847.3	2,292.6	3,814.3

Summary

The butterfly fauna of three areas, Jozankei (JO), Jûgoshima-Takinosawa (JT) and the campus of Hokkaido University (UC) in and near Sapporo City were surveyed by censusing once or twice per ten days from mid or late April to late October in 1973. Main results are:

1) In total, 61 species and 3,276 individuals were counted at JO, while 50 species, 5,593 individuals at JT and 29 species, 5,004 individuals at UC. Among predominant species, *Pieris napi*, *Pieris rapae* and *Colias erate*, determined by the index of species prosperity are common to three areas. Other predominant species vary from area to area, for instance, *Araschnia burejana*, *Burenthis ino* and *Papilio machaon* in JO, and *Lycaena phlaeas*, *Everes argiades* and *Ochlodes venata* in JT and UC.

2) Based upon the data obtained at JO, habitat preference was determined for all species. Among several predominant species, *Pieris napi* and *Everes argiades* prefer for both openland and forest, while *Papilio machaon*, *Pieris rapae*, *Colias erate*, *Lycaena phlaeas* and *Ochlodes venata* are classified into openland species and *Araschnia burejana*, *Inachis io* and *Thoressa varia* into forest species.

3) The degree of community propserity is the highest in JO, followed by JM (=corrected value of JT) and UC, showing a decreased prosperity in parallel with increased urbanization.

4) To understand the relation between prosperity and mode of life, the species censused were classified in several groups by several bionomic characters (hibernation, food, habitat, distribution and number of generations per year) and the community prosperity index was calculated for each group separately. The result shows the replacement of forest species by openland species and a general impoverishment of the fauna in parallel with mild urbanization.

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