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<th>Title</th>
<th>A Comparison of Butterfly Assemblages in and near Sapporo City, Northern Japan (With 8 Text-figures and 6 Tables)</th>
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<td>Author(s)</td>
<td>YAMAMOTO, Michiya</td>
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<td>Citation</td>
<td>北海道大学理学部紀要 = JOURNAL OF THE FACULTY OF SCIENCE HOKKAIDO UNIVERSITY Series VI. 20(4): 621-646</td>
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A Comparison of Butterfly Assemblages in and near Sapporo City, Northern Japan

By
Michiya Yamamoto
Zoological Institute, Hokkaido University
(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, Jūgoshima-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.

Before going further, I wish to express my sincere thanks to Prof. Mayumi Yamada, Dr. Shōichi 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, Jūgoshima-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:

621
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 Jugoshima-Takinosawa (A~B~C~D).
Comparison of Butterfly Assemblages

Jozankei route (JO, Fig. 2): About 320~480 m alt., along the road running from Hōsuibashi 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 I (Fig. 2).

Jūgoshima-Takinosawa route (JT, Fig. 3) or Jūgoshima-Misumai route (JM): Census belt is 6.8 km long from the Park Jūgoshima 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* (Méntries), *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: $O$ ($T_{AB}$≥$4T_{BC}$), Ow ($2T_{BC}$<$T_{AB}$<$4T_{BC}$)
- Forest species: $W$ ($4T_{AB}$≤$T_{BC}$), oW ($2T_{AB}$<$T_{BC}$<$4T_{AB}$)
- Eurytopic species: OW ($T_{AB}$=2 or $T_{BC}$=2)

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. 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 (3.0/3.0), Anthocaris scolymus* oW (0.5/0.5), Colias eurilochus OW (0.0/2.0), Minoia dryas* OW, Lethe diae OW (10.5/14.0), Harina callipteris W (1.0/15.0), Ninguta schrenckii Ow (3.0/1.0), Neoge goschkevitschii W (1.0/7.0).

**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 W (10.5/14.0), Harina callipteris W (1.0/15.0), Ninguta schrenckii Ow (3.0/1.0), Neoge goschkevitschii W (1.0/7.0).

**Nymphalidae:** Sasa okiwa W (0.0/0.5), Apatula ilia W (5.0/10.0), Neptis philage W (0.0/4.5), Ladoga camilla W (1.0/4.0), Neptis aceris* W, N. rutilaris OW (4.0/7.0), Araschnia burejana W (2.5/58.0), A. lecania OW (5.0/3.5), Polygonia c-album W (3.0/11.5), P. vanajia W (0.0/7.5), Vanessa indica O (0.5/0.0), V. cardui* O, Nymphalis xanthomelas W (0.0/2.5), N. antiope 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 adipe W (13.5/1.5), Argynone ilia W (3.0/0.5), Argynnis papilio OW (8.5/10.5), Speyeria aglais OW (7.0/16.5), Argynone rasbula W (22.0/7.5), Argynnis anathyomena* W, Benthis ino W (5.0/53.0).

**Lycaenidae:** Artopoetes praeter W (0.0/0.5), Araschnia burejana 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 (0.5/0.5), Usurana stygia* W, Waginio signata W (0.0/0.5), Nezophyronia testula W (0.0/2.0), Chrysopephyron smaragdinus* W, C. aurarius* W, Fac unwind orientalis* W (0.5/0.5), F. jezoensis* W, F. cognatus W (0.0/1.0), Strymonidia w-album W (0.0/1.0), Althbergia ferrea W (0.0/0.5), Lycaena philotes O (30.0/5.0), Scyllanthes orion W (0.0/7.0), Plebejus argus W (0.0/4.5), Celestina argiolus* OW (0.5/0.5), C. sugitanii W (0.0/4.5), Evers argiope OW (16.0/22.0).

**Hesperidae:** Bibasis aquilina W (0.5/9.0), Thymelicus glamourus OW (0.5/1.0), Ochloides venata Ow (19.5/7.5), Thoreosa variya W (3.5/31.0), Polytrems pellucida W (1.0/5.0), Erynnis montanus* W. The number of species belonging to various habitat types is as follows:

<table>
<thead>
<tr>
<th></th>
<th>O</th>
<th>Ow</th>
<th>W</th>
<th>oW</th>
<th>OW</th>
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</table>

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.
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):

<table>
<thead>
<tr>
<th>S</th>
<th>L</th>
<th>Left side</th>
<th>Right side</th>
<th>Micro-habitat type (l/r)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Aa</td>
<td>0.2</td>
<td>Hill side with dense broad leaf trees</td>
<td>Low sparse secondary grassland</td>
<td>W/O</td>
</tr>
<tr>
<td>Ab</td>
<td>0.5</td>
<td>Paddy fields and human habitations</td>
<td>=left</td>
<td>O/O</td>
</tr>
<tr>
<td>Ac</td>
<td>0.6</td>
<td>Dense bush with Polygonum sachalinense</td>
<td>Mosaic of fallows, cultivated fields and human habitations</td>
<td>O/O</td>
</tr>
<tr>
<td>Ad</td>
<td>0.4</td>
<td>Human habitations and tall dense secondary grassland</td>
<td>Fallows and low dense secondary grassland and a few sparse broad leaf trees</td>
<td>O/O</td>
</tr>
<tr>
<td>Ae</td>
<td>0.5</td>
<td>Marsh interspersed with willows</td>
<td>Low sparse grassland and secondary openland developed after ruined human constructs</td>
<td>O/O</td>
</tr>
<tr>
<td>Ba</td>
<td>0.3</td>
<td>Tall sparse black alder forest with undergrowth of low sparse herbs</td>
<td>Hill side with poor plant cover</td>
<td>W/W</td>
</tr>
<tr>
<td>Bb</td>
<td>0.5</td>
<td>Tall dense mixed forest with undergrowth of bamboo grass</td>
<td>Openland with poor plant cover. Near Bc tall dense mixed forest</td>
<td>W/OW</td>
</tr>
<tr>
<td>Bc</td>
<td>0.3</td>
<td>Tall dense mixed forest with undergrowth of tall sparse herbs</td>
<td>P. sachalinense and tall sparse mixed forest with undergrowth of bamboo grass</td>
<td>W/W</td>
</tr>
<tr>
<td>Bd</td>
<td>0.2</td>
<td>Tall dense mixed forest with undergrowth of tall sparse herbs</td>
<td>Valley with thick grass cover</td>
<td>W/W</td>
</tr>
<tr>
<td>Be</td>
<td>0.4</td>
<td>P. sachalinense along rocky shelf</td>
<td>Low dense mixed forest with undergrowth of low dense herbs</td>
<td>W/W</td>
</tr>
<tr>
<td>Bf</td>
<td>0.4</td>
<td>Tall dense mixed forest with undergrowth of bamboo grass</td>
<td>Tall sparse mixed forest along valley with undergrowth of bamboo grass</td>
<td>W/W</td>
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<tr>
<td>Bg</td>
<td>0.1</td>
<td>Tall dense mixed forest with undergrowth of tall sparse herbs</td>
<td>Low sparse mixed forest with undergrowth of tall sparse herbs</td>
<td>W/W</td>
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</tbody>
</table>
The distribution of those thirteen species in these microhabitats is summarized below \((N=\text{Total individual number of species observed in 1973}, \quad L=\text{Length in km}, \quad N_e=\text{Total individual number expected}; \quad N \times L/4.4)\). Phenological detail is given only for the first species, *Pieris napi*.

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

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

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<td>115</td>
<td>77</td>
<td>96</td>
<td>58</td>
<td>96</td>
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</table>
Comparison of Butterfly Assemblages

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>T_{AB}</th>
<th>Ba</th>
<th>Bb</th>
<th>Bc</th>
<th>Bd</th>
<th>Be</th>
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<tr>
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<td>49</td>
<td>103</td>
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</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>T_{AB}</th>
<th>Ba</th>
<th>Bb</th>
<th>Bc</th>
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<td>2</td>
<td>5</td>
<td>1</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>Ba</th>
<th>Bb</th>
<th>Bc</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
<th>T_{BC}</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>7</td>
<td>46</td>
<td>15.7</td>
<td>26.1</td>
<td>25</td>
<td>13</td>
<td>10</td>
<td>10</td>
<td>4 115</td>
</tr>
<tr>
<td>N_e</td>
<td>15.7</td>
<td>26.1</td>
<td>15.7</td>
<td>10.5</td>
<td>20.9</td>
<td>20.9</td>
<td>5.2</td>
<td>115</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>Ba</th>
<th>Bb</th>
<th>Bc</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
<th>T_{BC}</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>4</td>
<td>2</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>21</td>
<td>21</td>
<td>10</td>
<td>17</td>
<td>23</td>
<td>11</td>
<td>106</td>
<td></td>
</tr>
<tr>
<td>N_e</td>
<td>14.6</td>
<td>24.1</td>
<td>14.4</td>
<td>9.6</td>
<td>19.3</td>
<td>19.3</td>
<td>4.9</td>
<td>106</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\( X^2_{(e)} = 22.58 > 22.457 \)  \( p < 0.001 \)
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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>( T_{AB} )</th>
<th>Ba</th>
<th>Bb</th>
<th>Be</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
</tr>
</thead>
<tbody>
<tr>
<td>( N )</td>
<td>5</td>
<td>5</td>
<td>16</td>
<td>59</td>
<td>1</td>
<td>86</td>
<td>3</td>
<td>4</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>( N_e )</td>
<td>7.8</td>
<td>19.6</td>
<td>23.5</td>
<td>15.6</td>
<td>19.5</td>
<td>86</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[ \chi^2_{4(1)} = 152.67 \quad p < 0.001 \]

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>( T_{AB} )</th>
<th>Ba</th>
<th>Bb</th>
<th>Be</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
</tr>
</thead>
<tbody>
<tr>
<td>( N )</td>
<td>5</td>
<td>27</td>
<td>15</td>
<td>14</td>
<td>29</td>
<td>81</td>
<td>7</td>
<td>8</td>
<td>5</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>( N_e )</td>
<td>7.4</td>
<td>18.4</td>
<td>22.1</td>
<td>14.7</td>
<td>18.4</td>
<td>81</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

\[ \chi^2_{4(1)} = 7.25 < 7.779 \quad p > 0.10 \]

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>Ba</th>
<th>Bb</th>
<th>Be</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
<th>( T_{BC} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( N )</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>11</td>
<td>10</td>
<td>7</td>
<td>3</td>
<td>34</td>
<td>15</td>
<td>3</td>
<td>83</td>
<td></td>
</tr>
<tr>
<td>( N_e )</td>
<td>1</td>
<td>4</td>
<td>1</td>
<td>2</td>
<td>11</td>
<td>10</td>
<td>7</td>
<td>3</td>
<td>34</td>
<td>15</td>
<td>3</td>
<td>83</td>
<td></td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>Ba</th>
<th>Bb</th>
<th>Bc</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
<th>( T_{ABC} )</th>
</tr>
</thead>
<tbody>
<tr>
<td>( N )</td>
<td>6</td>
<td>5</td>
<td>9</td>
<td>10</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>8</td>
<td>14</td>
<td>13</td>
<td>1</td>
<td>74</td>
<td></td>
</tr>
<tr>
<td>( N_e )</td>
<td>3.4</td>
<td>8.4</td>
<td>10.1</td>
<td>6.7</td>
<td>8.4</td>
<td>5.0</td>
<td>8.4</td>
<td>5.1</td>
<td>3.4</td>
<td>6.7</td>
<td>6.7</td>
<td>1.7</td>
<td>74</td>
</tr>
</tbody>
</table>
Comparison of Butterfly Assemblages

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>Ba</th>
<th>Bb</th>
<th>Be</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
<th>TBC</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>1</td>
<td>1</td>
<td>4</td>
<td>3</td>
<td>2</td>
<td>4</td>
<td>5</td>
<td>3</td>
<td>4</td>
<td>17</td>
<td>3</td>
<td>2</td>
<td>38</td>
</tr>
<tr>
<td>Ne</td>
<td>1.7</td>
<td>5.2</td>
<td>2.8</td>
<td>3.2</td>
<td>5.2</td>
<td>6.9</td>
<td>6.9</td>
<td>1.7</td>
<td>38</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>T_AB</th>
<th>Ba</th>
<th>Bb</th>
<th>Be</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>8</td>
<td>1</td>
<td>8</td>
<td>16</td>
<td>6</td>
<td>39</td>
<td>1</td>
<td>7</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Ne</td>
<td>3.5</td>
<td>8.9</td>
<td>10.6</td>
<td>7.1</td>
<td>8.9</td>
<td>39</td>
<td>6.2</td>
<td>8.5</td>
<td>5.6</td>
<td>11.3</td>
<td>11.3</td>
<td>2.8</td>
<td>62</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>T_AB</th>
<th>Ba</th>
<th>Bb</th>
<th>Be</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>3</td>
<td>20</td>
<td>2</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Ne</td>
<td>20</td>
<td>21</td>
<td>34</td>
<td>1</td>
<td>1</td>
<td>20</td>
<td>2</td>
<td>6</td>
<td>6</td>
<td>6</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
</tbody>
</table>

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 ruscana* (Ow): Openland species but found at BC, too.

<table>
<thead>
<tr>
<th></th>
<th>Aa</th>
<th>Ab</th>
<th>Ac</th>
<th>Ad</th>
<th>Ae</th>
<th>T_AB</th>
<th>Ba</th>
<th>Bb</th>
<th>Be</th>
<th>Bd</th>
<th>Be</th>
<th>Bf</th>
<th>Bg</th>
</tr>
</thead>
<tbody>
<tr>
<td>N</td>
<td>4</td>
<td>2</td>
<td>7</td>
<td>11</td>
<td>10</td>
<td>34</td>
<td>1</td>
<td>6</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ne</td>
<td>3.1</td>
<td>7.7</td>
<td>9.3</td>
<td>6.2</td>
<td>7.7</td>
<td>34</td>
<td>1</td>
<td>6</td>
<td>3</td>
<td>1</td>
<td>3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$$\chi^2_{121} = 16.62 > 16.268 \quad p < 0.001$$
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.

<table>
<thead>
<tr>
<th>Subdivision</th>
<th>Deviation of N from N_e</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>N&gt;N_e</td>
</tr>
<tr>
<td><strong>AB</strong></td>
<td></td>
</tr>
<tr>
<td>Aa</td>
<td>Pn, Ea, Ov</td>
</tr>
<tr>
<td>Ab</td>
<td>Pm</td>
</tr>
<tr>
<td>Ac</td>
<td>Pn, Pr, Ce, Lp, Ea, Ov, Ar</td>
</tr>
<tr>
<td>Ad</td>
<td>Pn, Pr, Ce, Lp, Ea, Ov, Ar</td>
</tr>
<tr>
<td>Ae</td>
<td>Pn, Pr, Ce, Lp, Ea, Ov, Ar</td>
</tr>
<tr>
<td><strong>BC</strong></td>
<td></td>
</tr>
<tr>
<td>Ba</td>
<td>Tv</td>
</tr>
<tr>
<td>Bb</td>
<td>Ab, Tv</td>
</tr>
<tr>
<td>Be</td>
<td>Pn, Ab, Bi</td>
</tr>
<tr>
<td>Bd</td>
<td>Ea</td>
</tr>
<tr>
<td>Bc</td>
<td>Pn, Au, Ea, Ii</td>
</tr>
<tr>
<td>Br</td>
<td>Ea</td>
</tr>
<tr>
<td>Bg</td>
<td>Pn, Bi</td>
</tr>
</tbody>
</table>

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 preliminary 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>AB</th>
<th>BC</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Aa Ab Ac Ad Ae</td>
<td>Ba Bb Be Bd Be Bg Fl Se</td>
</tr>
<tr>
<td><em>Pieris napi</em></td>
<td>+ - + + # -</td>
<td>+ + + + + - - - - + -</td>
</tr>
<tr>
<td><em>P. rapae</em></td>
<td>- + + + # -</td>
<td>- - - - - - - - - -</td>
</tr>
<tr>
<td><em>Colias erate</em></td>
<td>+ + + + + +</td>
<td>+ + + + + - + + + +</td>
</tr>
<tr>
<td><em>Araschnia brejana</em></td>
<td>+ - - - - -</td>
<td>+ + + + + - + + + +</td>
</tr>
<tr>
<td><em>Brenthis io</em></td>
<td>+ - - - - -</td>
<td>+ + + + + - + + + +</td>
</tr>
<tr>
<td><em>Lycaena phlaeas</em></td>
<td>+ + + + - +</td>
<td>+ - - - - - - - - -</td>
</tr>
<tr>
<td><em>Papilio machaon</em></td>
<td>+ + + + # +</td>
<td>+ # - - + - - + + + #</td>
</tr>
<tr>
<td><em>Aglais urticae</em></td>
<td>+ - - - - -</td>
<td>+ # # # # - - + + + +</td>
</tr>
<tr>
<td><em>Eveeres argiades</em></td>
<td>+ + + + - -</td>
<td>- - - + + + + + + + +</td>
</tr>
<tr>
<td><em>Inachis io</em></td>
<td>+ - - - - -</td>
<td>+ # # # + + + + + + +</td>
</tr>
<tr>
<td><em>Ochladodes venata</em></td>
<td>+ + + + + +</td>
<td>+ + + + + + + + + + +</td>
</tr>
<tr>
<td><em>Argyronome rustiana</em></td>
<td>+ - - - - -</td>
<td>+ - - + + + # + + + +</td>
</tr>
<tr>
<td><em>Thoressa varia</em></td>
<td>+ - - - - -</td>
<td>+ - - + + + # + + + +</td>
</tr>
</tbody>
</table>

Nectariferous plants (*=Exotic weeds)

<table>
<thead>
<tr>
<th>Species</th>
<th>AB</th>
<th>BC</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Angelica polyclada</em></td>
<td>+ - + + - -</td>
<td>+ + + # + + - - -</td>
</tr>
<tr>
<td><em>Erigeron annus</em></td>
<td>+ - - # - -</td>
<td>- + - - - - - - -</td>
</tr>
<tr>
<td><em>Petasites japonicus</em></td>
<td>+ + - - - -</td>
<td>+ + + + + # - + +</td>
</tr>
<tr>
<td><em>Solidago altissima</em></td>
<td>- + # + - -</td>
<td>- - - - - - - - -</td>
</tr>
<tr>
<td><em>Syringa vulgaris</em></td>
<td>+ + + + + -</td>
<td>- - - - - - - - -</td>
</tr>
<tr>
<td><em>Taraxacum officinale</em></td>
<td># + + + + +</td>
<td>+ + - - - - - - -</td>
</tr>
<tr>
<td><em>Trifolium pratense</em></td>
<td>+ + + + + -</td>
<td>- + - - + + + + +</td>
</tr>
<tr>
<td><em>Veronicastrum sibiricum</em></td>
<td>+ - - - - -</td>
<td>- - - + + + # # #</td>
</tr>
</tbody>
</table>

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 allogetic 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 \( Ps=N/I_s\times100 \), where \( N=\)total individual number, \( I_s=\)Morisita's diversity index. Morisita 1967, and their phenology in Fig. 6. Three top pre dominants, 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.

<table>
<thead>
<tr>
<th>Species</th>
<th>JO (28.6=mean frequency)</th>
<th>JM (46.1)</th>
<th>UC (91.0)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>( Ps ) (N) ( H )</td>
<td>( Ps ) (N) ( H )</td>
<td>( Ps ) (N) ( H )</td>
</tr>
<tr>
<td>Pieris napi</td>
<td>1.046 (479.0) OW</td>
<td>1.762 (665.5) O</td>
<td>3.132 (1,229.5) O</td>
</tr>
<tr>
<td>P. rapae</td>
<td>0.674 (301.5) O</td>
<td>1.621 (503.0) O</td>
<td>2.180 (778.5) O</td>
</tr>
<tr>
<td>Colias erate</td>
<td>0.375 (161.0) O</td>
<td>1.051 (384.0) OW</td>
<td>0.550 (231.5) OW</td>
</tr>
<tr>
<td>Araschnia</td>
<td>0.104 (60.5) W</td>
<td>0.255 (112.5) O</td>
<td>0.239 (132.5) O</td>
</tr>
<tr>
<td>burejana</td>
<td>0.087 (58.5) W</td>
<td>0.202 (193.0) OW</td>
<td>0.142 (112.0) OW</td>
</tr>
<tr>
<td>Brenthis ino</td>
<td>0.079 (55.0) O</td>
<td>0.095 (89.0) Ow</td>
<td>0.066 (94.0) Ow</td>
</tr>
<tr>
<td>Lycana phlaeas</td>
<td>0.070 (54.5) Ow</td>
<td>0.076 (53.5) W</td>
<td>0.040 (38.0) OW</td>
</tr>
<tr>
<td>Papilio machaon</td>
<td>0.070 (54.5) O</td>
<td>0.061 (34.5) O W</td>
<td>0.026 (34.5) W</td>
</tr>
<tr>
<td>Aglais urticae</td>
<td>0.076 (53.5) W</td>
<td>0.030 (29.5) Ow</td>
<td>0.050 (29.5) Ow</td>
</tr>
<tr>
<td>Eperes argiades</td>
<td>0.035 (27.5) Ow</td>
<td>1.947.0</td>
<td>2.578.0</td>
</tr>
</tbody>
</table>

Total \( 1,387.5 \) | 1,947.0 | 2,578.0 |

\( \% \) 78.5 | 84.5 | 96.5 |
Comparison of Butterfly Assemblages

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)

<table>
<thead>
<tr>
<th>Species</th>
<th>JM</th>
<th>Utsunomiya</th>
<th>Kyoto</th>
<th>Hirao</th>
<th>Gradient</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colias erate</td>
<td>1</td>
<td>4</td>
<td>15</td>
<td>11</td>
<td>N&gt;S</td>
</tr>
<tr>
<td>Pieris rapae</td>
<td>2</td>
<td>1</td>
<td>2</td>
<td>1</td>
<td>N~S</td>
</tr>
<tr>
<td>P. napi</td>
<td>3</td>
<td>4</td>
<td>21</td>
<td>11</td>
<td>N&gt;S</td>
</tr>
<tr>
<td>Lycaena phlaeas</td>
<td>4</td>
<td>7</td>
<td>4</td>
<td>7</td>
<td>N~S</td>
</tr>
<tr>
<td>Everes argiades</td>
<td>5</td>
<td>5</td>
<td>1</td>
<td>2</td>
<td>N&lt;S</td>
</tr>
<tr>
<td>Ypthima argus</td>
<td>8</td>
<td>3</td>
<td>8</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>Eurrema hecabe</td>
<td>17</td>
<td>28</td>
<td>9</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>Neope goschkevitschii</td>
<td>11</td>
<td>7</td>
<td>3</td>
<td>N&lt;S</td>
<td></td>
</tr>
<tr>
<td>Zizeeria maka</td>
<td>19</td>
<td>21</td>
<td>4</td>
<td>?</td>
<td></td>
</tr>
<tr>
<td>Parnara guttata</td>
<td>12</td>
<td>6</td>
<td>5</td>
<td>N&lt;S</td>
<td></td>
</tr>
</tbody>
</table>

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 Amschnia 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 Ochloides 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:

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).
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.
Comparison of Butterfly Assemblages

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

<table>
<thead>
<tr>
<th>Species</th>
<th>$Ps$</th>
<th>Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td>Erebia niphonica</td>
<td>0.35</td>
<td>l g w c 1</td>
</tr>
<tr>
<td>Coenonympha hero</td>
<td>0.17</td>
<td>l g w n 1</td>
</tr>
<tr>
<td>Neptis philyra</td>
<td>0.56</td>
<td>l t w c 1</td>
</tr>
<tr>
<td>Canisca canace</td>
<td>+</td>
<td>a g t w s 1P</td>
</tr>
<tr>
<td>Araragi enthea</td>
<td>+</td>
<td>e t w c 1</td>
</tr>
<tr>
<td>Angustius attilia</td>
<td>+</td>
<td>e t w c 1</td>
</tr>
<tr>
<td>Wagimo signata</td>
<td>+</td>
<td>e t w c 1</td>
</tr>
<tr>
<td>Favonius orientalis</td>
<td>+</td>
<td>e t w c 1</td>
</tr>
<tr>
<td>F. cognatus</td>
<td>+</td>
<td>p g t w c 1</td>
</tr>
<tr>
<td>Ahlbergia ferrea</td>
<td>+</td>
<td>p g t w c 1</td>
</tr>
<tr>
<td>Scolytantides orion</td>
<td>0.57</td>
<td>p g w n 1</td>
</tr>
<tr>
<td>Polytimeium pellucida</td>
<td>0.50</td>
<td>l g t w c 1</td>
</tr>
<tr>
<td>Erupnia montanus</td>
<td>+</td>
<td>l t w c 1</td>
</tr>
<tr>
<td>Papusiesius stubbendorfii</td>
<td>2.39</td>
<td>e g w c 1</td>
</tr>
<tr>
<td>Pappilo macilentus</td>
<td>0.13</td>
<td>p t w c 2</td>
</tr>
<tr>
<td>Anthocoris scolymus</td>
<td>+</td>
<td>p g w c 1</td>
</tr>
<tr>
<td>Harima collisteris</td>
<td>2.69</td>
<td>l t w c 1</td>
</tr>
<tr>
<td>Ninguta schreneckii</td>
<td>0.44</td>
<td>l g o c 1</td>
</tr>
<tr>
<td>Neopto goscheutschi</td>
<td>0.78</td>
<td>p t w h 1</td>
</tr>
<tr>
<td>Sasakia charonda</td>
<td>+</td>
<td>l t w c 1</td>
</tr>
<tr>
<td>Araschnia burejana</td>
<td>10.43</td>
<td>p g w e 2P</td>
</tr>
<tr>
<td>A. lesva</td>
<td>1.53</td>
<td>p g w c 1</td>
</tr>
<tr>
<td>Nymphalia xanthohelas</td>
<td>0.13</td>
<td>a t w c 1</td>
</tr>
<tr>
<td>N. antiopa</td>
<td>+</td>
<td>a t w n 1</td>
</tr>
<tr>
<td>Aglais urticae</td>
<td>7.57</td>
<td>a g w n 1</td>
</tr>
<tr>
<td>Benthis isio</td>
<td>8.76</td>
<td>l g w n 1</td>
</tr>
<tr>
<td>Japonica lutea</td>
<td>1.45</td>
<td>e t w c 1</td>
</tr>
<tr>
<td>Shiroza jonas</td>
<td>+</td>
<td>e t w e 1</td>
</tr>
<tr>
<td>Neozephyrus taxila</td>
<td>0.33</td>
<td>e t w c 1</td>
</tr>
<tr>
<td>Bibanis aquilina</td>
<td>1.14</td>
<td>l t w c 1</td>
</tr>
<tr>
<td>Pappilo mchaon</td>
<td>7.01</td>
<td>p g t o n 2P</td>
</tr>
<tr>
<td>P. bianor</td>
<td>2.31</td>
<td>p t o e 2</td>
</tr>
<tr>
<td>P. maackii</td>
<td>3.30</td>
<td>p t o w c 2</td>
</tr>
<tr>
<td>Aporia crotaugi</td>
<td>1.09</td>
<td>l t o w n 1</td>
</tr>
<tr>
<td>Colias erate</td>
<td>37.48</td>
<td>l g o c 3P</td>
</tr>
<tr>
<td>Pieris napi</td>
<td>104.58</td>
<td>p g o w n 3P</td>
</tr>
<tr>
<td>P. melette</td>
<td>1.66</td>
<td>p g o w c 2P</td>
</tr>
<tr>
<td>P. rapae</td>
<td>67.38</td>
<td>p g o n 3P</td>
</tr>
<tr>
<td>Lethe diana</td>
<td>5.00</td>
<td>l t w c 1</td>
</tr>
<tr>
<td>Apatura ilia</td>
<td>0.51</td>
<td>l t w n 1</td>
</tr>
<tr>
<td>Neptis rivularis</td>
<td>2.14</td>
<td>l g t w o n 1</td>
</tr>
<tr>
<td>Polygonya c-album</td>
<td>6.81</td>
<td>a g t w n 2</td>
</tr>
<tr>
<td>P. eau-album</td>
<td>0.48</td>
<td>a t w n 1</td>
</tr>
<tr>
<td>Inachis io</td>
<td>8.09</td>
<td>a g w n 2</td>
</tr>
<tr>
<td>Fabriciana adigge</td>
<td>2.07</td>
<td>a g o n 1</td>
</tr>
<tr>
<td>Argyronome ladice</td>
<td>0.20</td>
<td>l g o n 1</td>
</tr>
</tbody>
</table>
Table 5. (Continued)

<table>
<thead>
<tr>
<th>Characters</th>
<th>JO</th>
<th>JT</th>
<th>JM</th>
<th>UC</th>
<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
<th>E</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Species</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Argyronome ruslana</td>
<td>5.01</td>
<td>1.60</td>
<td>1.40</td>
<td>0.91</td>
<td>e</td>
<td>g</td>
<td>w</td>
<td>n</td>
<td>1</td>
</tr>
<tr>
<td>Lycaena phlaeas</td>
<td>7.90</td>
<td>37.37</td>
<td>25.45</td>
<td>23.86</td>
<td>l</td>
<td>g</td>
<td>o</td>
<td>n</td>
<td>2</td>
</tr>
<tr>
<td>Prebjesus aragus</td>
<td>0.50</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>e</td>
<td>g</td>
<td>w</td>
<td>n</td>
<td>1</td>
</tr>
<tr>
<td>Celastrina argiolus</td>
<td>+</td>
<td>1.53</td>
<td>0.59</td>
<td>+</td>
<td>p</td>
<td>g</td>
<td>t</td>
<td>o</td>
<td>w</td>
</tr>
<tr>
<td>Erynes argioles</td>
<td>3.98</td>
<td>29.02</td>
<td>20.23</td>
<td>14.27</td>
<td>l</td>
<td>g</td>
<td>t</td>
<td>o</td>
<td>w</td>
</tr>
<tr>
<td>Thymelicus sylvaticus</td>
<td>0.13</td>
<td>1.00</td>
<td>0.65</td>
<td>+</td>
<td>l</td>
<td>g</td>
<td>o</td>
<td>w</td>
<td>c</td>
</tr>
<tr>
<td>Ochlodes Leontina</td>
<td>5.50</td>
<td>12.67</td>
<td>9.32</td>
<td>6.64</td>
<td>l</td>
<td>g</td>
<td>t</td>
<td>o</td>
<td>n</td>
</tr>
<tr>
<td>Thoressa varia</td>
<td>2.55</td>
<td>0.75</td>
<td>0.83</td>
<td>+</td>
<td>l</td>
<td>t</td>
<td>w</td>
<td>h</td>
<td>12</td>
</tr>
</tbody>
</table>

As shown in Gothic, the species belonging to types A<sub>e</sub>, B<sub>i</sub>, C<sub>l</sub>, D<sub>c</sub> and E<sub>i</sub> gradually disappear, while those to types A<sub>o</sub>, B<sub>g</sub>, C<sub>ow</sub>, C<sub>o</sub>, D<sub>n</sub> and E<sub>3</sub> remain or
Comparison of Butterfly Assemblages

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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 scolyms*, *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 napi*, *Inachis io* and *Speyeria aglaia*.

$JM > JO > UC$: *Pieris napi*, *Polygonia van-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 $A_1$, 14 species are the most prosperous at JO, 11 and JM, and only one at UC.

<table>
<thead>
<tr>
<th>Type</th>
<th>JO</th>
<th>JM</th>
<th>UC</th>
<th>Total (100%)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Sp (%)</td>
<td>Sp (%)</td>
<td>Sp (%)</td>
<td></td>
</tr>
<tr>
<td>A. Hibernation types</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$A_e$</td>
<td>13(66.7)</td>
<td>2(13.3)</td>
<td></td>
<td>15</td>
</tr>
<tr>
<td>$A_l$</td>
<td>14(53.8)</td>
<td>11(42.3)</td>
<td>1(3.3)</td>
<td>26</td>
</tr>
<tr>
<td>$A_p$</td>
<td>9(60.0)</td>
<td>5(36.5)</td>
<td>1(6.5)</td>
<td>15</td>
</tr>
<tr>
<td>$A_x$</td>
<td>5(62.5)</td>
<td>3(37.5)</td>
<td></td>
<td>8</td>
</tr>
<tr>
<td>B. Larval food types</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$B_1$</td>
<td>21(70.0)</td>
<td>9(30.0)</td>
<td></td>
<td>30</td>
</tr>
<tr>
<td>$B_{cl}$</td>
<td>6(66.7)</td>
<td>3(33.3)</td>
<td></td>
<td>9</td>
</tr>
<tr>
<td>$B_g$</td>
<td>14(56.0)</td>
<td>9(36.0)</td>
<td>2(8.0)</td>
<td>25</td>
</tr>
<tr>
<td>C. Habitat types</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$C_w$</td>
<td>30(76.9)</td>
<td>9(23.1)</td>
<td></td>
<td>39</td>
</tr>
<tr>
<td>$C_{ow}$</td>
<td>6(42.9)</td>
<td>8(57.1)</td>
<td></td>
<td>14</td>
</tr>
<tr>
<td>$C_o$</td>
<td>5(45.5)</td>
<td>4(36.4)</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
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 $P_s$ within each area are:

**Hibernation type:** $A_e > A_a > A_p > A_1$ at JO, $A_1 > A_a > A_p > A_e$ at JM and $A_p > A_1$ 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:** $C_w > C_a > C_{ow}$ at JO, $C_{ow} > C_a > C_w$ at JM and only $C_a$ at UC.

**Distribution type:** $D_c > D_h > D_n > D_e$ at JO, $D_e > D_n > D_h > D_c$ at JM and $D_n > D_c$ at UC.

**Life cycle type:** $E_2 > E_1$ at JO, $E_2 > E_1 > E_3$ at JM and only $E_3$ at UC.

Most of the species belonging to $A_e$, $B_t$, $C_w$, $E_2$, $E_1$ and $E_2$ prosper in JO, while about one half of the species belonging to $A_1$, $B_g$, $C_{ow}$, $C_a$, $D_n$ and $E_3$ at JM and UC. Only two species, *Pieris rapae* and *Colias erate*, show the highest $P_s$ at UC, both belonging to $B_g$, $C_a$ 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 allogetic 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,

$$DI = \sqrt{\frac{\sum (f_{ia} - f_{ib})^2}{T}}$$

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.

<table>
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<tr>
<th>Type</th>
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<th>JM</th>
<th>UC</th>
<th>Total (100%)</th>
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<td></td>
<td>Sp (%)</td>
<td>Sp (%)</td>
<td>Sp (%)</td>
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<tr>
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<td>27</td>
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<td>2</td>
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<td>E. Life cycle types</td>
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<td>2(50.0)</td>
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</table>

1) *Vanessa indica* was excluded because $P_s$ was JO = UC.
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,

$$HI = \frac{2\sum n_1n_2}{(\pi_1^2 + \pi_2^2)N_1N_2}$$

where $N=$ total corrected individual number, $n_1=$ corrected individual number of species $i$, $\pi_1^2=\sum n_1^2/N_1^2$, $\pi_2^2=\sum n_2^2/N_2^2$, $N_1$, $N_2$ 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 $BC$):

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<th>$JT$</th>
<th>$UC$</th>
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<td>0.618</td>
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<td>$JT$</td>
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<td>/</td>
<td>0.818</td>
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<tr>
<td>$UC$</td>
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The results suggest a gradient $JO$-$JT$-$UC$, which corresponds to the order of increased urbanization in accordance with the results given in Subsection 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 Jūgoshima 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.
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 scolytus, Neptis philype, Ussuriana stygiana, Neozephyrus taxila, Chrysozephrus smaragdinus, Ablbergia ferrea, Celastrina sugitanii, Bibasis aquilina, Poly tremis 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 $T_β$ was calculated in three areas for species groups representing various bionomic types separately (Fig. 7 and 8).

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A) Hibernation type (Fig. 7A): The order, $A_1 > A_p > A_e > A_a$ is common to three areas. The index in $A_1$ 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 Aa. 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 A1 may partly be a consequence of expansion of secondary openland. On the other hand, JM > UC in A1 must indicate a general faunal impoverishment, caused by oversimplification and fragmentation of vegetation in UC. Decline of Aa at UC is persuaded also by the fact that most Aa-type species are those ovipositing on trees. Decrease of Aa-type species from JO to JM is difficult to explain because they are much adapted to

Fig. 7. Change of community prosperity 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 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, $C_o>C_w>C_w$ is common both to JM and UC, while $C_w>C_o>C_w$ 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 $E_l>E_a>E_2$ at JO, and $E_q>E_1>E_2$ both at JM and UC. The order in $E_q$ 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 $E_q$ gave the opposite gradient. The gradient of $E_l$ among three areas agrees with that of urbanization. But the species belonging to $E_q$ 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, $A_i$, $A_p$, $B_g$, $B_{gt}$, $C_o$, $D_n$ and $E_q$. Finally, $T\beta$ of each bionomic character is considered on the basis of habitat type. Table 6 shows number of species and individuals, $\beta$ and $T\beta$-index after classified according to habitat type ($C_w$, $C_o$, $C_o$). In $C_w$-type species all bionomic characters decline in the order of JO>JM>UC. In $C_o$-type species $A_l$, $A_p$, $A_s$, $B_g$, $D_n$, $D_c$, $D_q$ and $E_q$ take higher value of $T\beta$-index in the order of UC>JM>JO, while $A_c$, $B_t$, $B_{gt}$ and $E_q$, JO>JM>UC. In $C_o$-type species the highest value of $T\beta$ at JM is shown by $A_i$, $B_g$, $B_{gt}$, $D_n$, $E_1$ and $E_q$. 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
Comparison of Butterfly Assemblages

(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 prosperity gradient of C_o-type species, UC > JM > JO. In C_o-A type, excluding Colias erate, the order of Tβ is UC (494.50) > JM (431.72) > JO (192.57) and C_o-B 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 type excluding Piers rapae, UC (98.1%) > JM (91.6%) > JO (75.9%). On the other hand, C_o-Ap and C_o-De types are markedly affected by either of two species as

![](image)

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

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

The results described above indicate that A_t, B_b, D_n and E_s types of openland species can prevail with urbanization and that Piers 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.

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Summary

The butterfly fauna of three areas, Jozankei (JO), Jūgoshima-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 prosperity 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.

References


——— 1976. Further observations on butterfly phenology at Jozankei (Sapporo): Comparisons of the results in two successive years. Ibid. 20: 343-358.