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Ethological Studies on the Flower-visiting Behavior of *Luehdorfia* Butterflies (Lepidoptera; Papilionidae) I. Color Preference of Butterflies and Reflection Spectra of Flowers

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Abstract Color preferences in flower-visiting behavior of *Luehdorfia puziloi* and *L. japonica* were tested in caged conditions. When various colored papers were presented, both species visited dark and vivid blue papers more frequently than others. *L. puziloi* occasionally visited yellow (or bee-purple), while *L. japonica* did not. Neither species were attracted to red. In addition, the reflection spectra of the colored papers and spring flowers were measured and compared. Both the bluish papers and purplish flowers had a peak reflection around 450 nm. Because *Luehdorfia* butterflies usually visit purplish flowers in the field, I suggest that a peak reflection around 450 nm is a primary cue or releaser for flower-visiting behavior in both species.

Key words Flower-visiting behavior, Color preference, *Luehdorfia*, Papilionidae, Reflection spectrum

Introduction

Butterflies visit flowers for feeding. They seem to favor certain species or color(s) of flowers (e.g. Fukuda *et al.* 1972; Unno & Aoyama 1981).

Small tiger swallowtails, *Luehdorfia japonica* and *L. puziloi*, are found in Far East Asia including Japan (Fig. 1). They are univoltine, and adults are on the wing in early spring. Adult butterflies fly about above sunny ground in deciduous broadleaf forests, where many flowers such as *Erythronium japonicum*, *Heloniopsis orientalis* (both Liliaceae), *Viola vaginata* (Violaceae) are in bloom (e.g. Fukuda *et al.* 1982).

It is well known among Japanese lepidopterists that *Luehdorfia* butterflies usually visit purplish flowers like *E. japonicum* but scarcely visit yellowish ones (e.g. Fukuda *et al.* 1982; Hiura & Kanoh 1977; Tanaka 1982). Why do they prefer the purplish flowers? How do they discriminate these flowers from others? Which cue is important for them to find nectar sources, shape, size, color or odor? To answer these questions, I started a series of studies.

The following hypotheses might explain why *Luehdorfia* butterflies prefer several plant species as nectar sources:

(1) Butterflies indiscriminately visit any available flowers at random, therefore visiting common flowers in the habitat more frequently than others.

(2) *Luehdorfia* tend to fly along sunny places in forests (e.g. Fukuda *et al.* 1982). For this reason, they visit flowers that grow in sunny places more frequently.

(3) *Luehdorfia* butterflies visit flowers mostly in the morning and later afternoon (e.g. Fukuda *et al.* 1982), therefore visiting flowers which excrete nectars during those times more frequently.

(4) Butterflies discriminate those flowers from others by size, shape, color and/or odor. They prefer some flower traits to others.

Purplish flowers are more abundant than yellowish ones in most habitats in Honshu. When observed in their natural habitat, *Luehdorfia* visit flowers of a limited number of plant species. They seem to avoid not only yellowish flowers but also several purplish species. For example, in several habitats of Mt. Yasuteyama, Aomori, flowers of many species bloom in sunny patches of the forest. Adults of *L. puziloi* are observed to visit mostly *E. japonicum* and *V. vaginata* (both purple flower species). However, they scarcely visit other flower species such as *Viola brevistipulata* (yellow) and *Anemone pseudo-altaica* (purple). Several other butterfly species (e.g. lycaenids, *Celastrina argiolus* and *Callophyrus ferrea*) visit the flowers avoided by *Luehdorfia* (Fujii unpublished). Therefore, none of the first three hypotheses are likely to prove valid.

What about the last hypothesis? Because it is known in several butterfly species that flower color is a primary cue for flower-visiting behavior (e.g. Ilse 1928; Hidaka & Obara 1968; S. L. Swihart 1969, 1970, 1972; Swihart & Swihart 1970; C. A. Swihart 1971; Miyakawa 1976), I carried out color preference tests first. I also compared reflection spectra among the colored papers tested and the spring flowers found in or around their habitat.

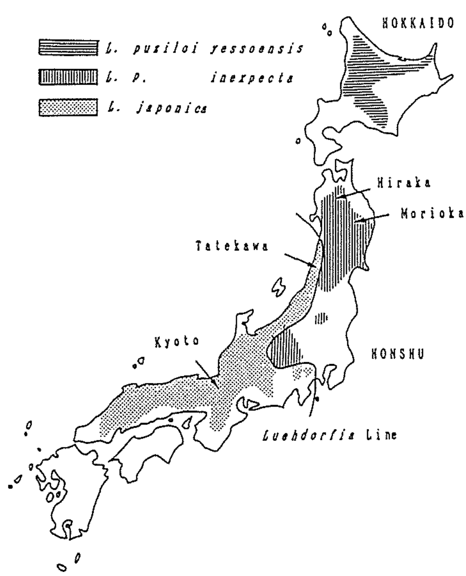


Fig. 1. Geographical distributions of *L. puziloi* and *L. japonica* in Japan. Localities of materials are shown here.

Materials and Methods

Experiment 1:

If color is a primary cue for flower-visiting behavior, *Luehdorfia* butterflies will be expected to visit purplish papers when tested.

Females of *Luehdorfia japonica* and *L. puziloi inexpecta* were collected at Tatekawa, Yamagata in May 1982 and at Hiraka, Aomori in April 1982, respectively (Fig. 1). Eggs were obtained from these females, and the hatched larvae were reared in the laboratory. Pupae were stored in a refrigerator till the beginning of April 1983. Adult butterflies that emerged from these pupae from 19-22 April 1983 were used in the experiment.

The experiment was carried out in an outdoor cage, in Hiraka, Aomori (Fig. 2) during the hours, 0700-1700 on 21 and 22 April 1983. The weather was fair and the ambient temperatures were 20-30°C throughout the experiment. Butterflies of 30-70 *L. puziloi* and 10-40 *L. japonica* were present in the cage. Several plant species (mostly *Viola selkirkii*) were flowering so that the butterflies involved could freely visit these flowers for feeding.

Twelve different colored papers (dark blue, vivid blue, light blue, pale blue, vivid green, vivid violet, light violet, vivid purple, light purple, pale purple, vivid red and white) were prepared for experiment. "Pale" here means being lighter than "light" in brightness. These colors except vivid green represent those of the flowers visited by *Luehdorfia* butterflies in their natural habitat. The papers were square and 5×5 cm^2 in size. Two sets of colored papers were fixed upon the leaves of *Asiasarum shieboldii* with cellophane tape.

I observed the behavior of the *L. puziloi* and *L. japonica* butterflies and counted the number of contacts with the colored papers.

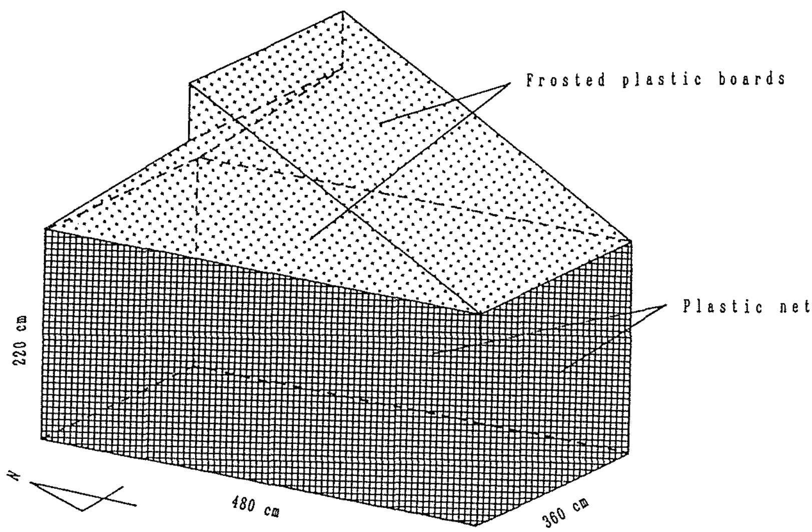
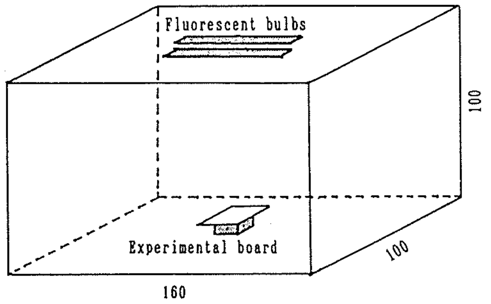


Fig. 2. Structure of the outdoor cage in Hiraka, Aomori. Experiment 1 was carried out in this cage.



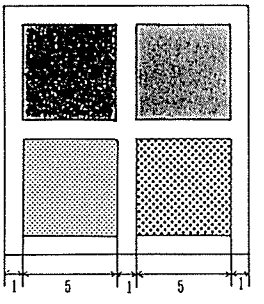


Fig. 3. Structure of the indoor cage in Nagaokakyo, Kyoto (left). Experiment 2 was carried out in this cage. The experimental board (right). Numbers indicate the lengths in cm.

Experiment 2:

In Experiment 1, the butterflies were expected to visit the purplish papers, but in fact they approached and alighted on the bluish papers most frequently (see Results). I then designed a series of experiments to determine color preference in detail.

An indoor cage was set by the window in a laboratory, in Nagaokakyo, Kyoto, in such a way that sunlight would illuminate the cage. To maintain brightness, fluorescent bulbs (30W×2) provided constant illumination during the experiments (Fig. 3, left). Temperature was maintained at a range of 20-25°C by means of an air-conditioner. Four papers of different colors were attached to a white experimental board (Fig. 3, right). The board was affixed to the center of the cage floor (Fig. 3, left). The colored papers used in each experimental series (a, b, c and d) are shown in Table 1.

L. japonica adults were collected in Kyoto and those of *L. puziloi* were collected in Morioka, Iwate during April-May 1984 (Fig. 1). Butterflies were fed with sugar solution every evening. The experiments were carried out during April-May 1984. In the experiments, I released 10-20 butterflies into the cage. Behavior was videotaped with a National MacLord throughout the experimental period (0800-1600 h), and was analysed afterward.

Spectroscopic analyses:

Spring flowers were collected in Kyoto and Aomori during April-May 1984. Some of the flowers collected are known to be species frequently visited by *Luehdorfia* butterflies in the field, and others are not (Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985; Kanda 1987; see Appendix). The petals and/or sepals of the flowers were prepared for spectroscopic analyses. Visible colors were very variable (Table 2). The colored papers used in the above experiments were also prepared for analyses.

Spectroscopic measurements were made with a Shimadzu UV-visible Recording Spectrophotometer UV-240 (Graphicord). Barium sulphate (KODAK White Reflectance Standard, LOT NO. M001-2) was used for control white.

Table 1. Colored paper used in Experiment 2. DB: dark blue, VB: vivid blue, LB: light blue, PB: pale blue, W: white, VV: vivid violet, LV: light violet, VP: vivid purple, LP: light purple, VY: vivid yellow, VR: vivid red, G: gray.

Series	Color											
	DB	VB	LB	PB	W	VV	LV	VP	LP	VY	VR	G
a		+								+	+	+
b		+	+	+	+							
c	+	+				+		+				
d						+	+	+	+			

Table 2. The flowers prepared for spectroscopic analyses.

Color (to us)	Flower	Family	Locality	Reflection spectrum
Red	*Camellia japonica*	Theaceae	Kyoto	Fig. 6-p
Yellow	*Kerria japonica*	Rosaceae	Kyoto	Fig. 6-l
	Forsytha suspensa	Oleaceae	Kyoto	Fig. 6-n
	Corydalis hetrocarpa var. *japonica*	Papaveraceae	Kyoto	Fig. 6-l
	Ixeris dentata	Compositae	Kyoto	Fig. 6-m
	Taraxacum japonicum	Compositae	Kyoto	Fig. 6-m
	Ranunculus japonicus	Ranunculaceae	Kyoto	Fig. 6-m
	Brassica napus	Cruciferae	Kyoto	Fig. 6-m
Pale yellow	*Stachyurus praecox*	Stachyuraceae	Aomori	Fig. 6-o
	Taraxacum albidum	Compositae	Kyoto	Fig. 6-a
	Petasites japonicus	Compositae	Aomori	Fig. 6-o
	Lamium album var. *barbatum*	Labiatae	Kyoto	Fig. 6-d
Pale green-yellow	*Lindera umbellata*	Lauraceae	Aomori	Fig. 6-o
Purple	*Rhododendron* sp.	Ericaceae	Kyoto	Fig. 6-e
	Lamiun amplexicaule	Labiatae	Kyoto	Fig. 6-f
	Phlox subulata	Gentianaceae	Kyoto	Fig. 6-e
	Epimedium grandiflorum	Berberidaceae	Kyoto	Fig. 6-j
	Astragalus sinicus	Leguminosae	Kyoto	Fig. 6-f
	Vicia sativa angustifolia var. *segetalis*	Leguminosae	Kyoto	Fig. 6-g
	Orychophragmus violaceus	Cruciferae	Kyoto	Fig. 6-h
	Erythronium japonicum	Liliaceae	Aomori	Fig. 6-g
Pink	*Weigela hortensis*	Caprifoliaceae	Kyoto	Fig. 6-j
	Prunus lannesiana var. *lannesiana*	Rosaceae	Kyoto	Fig. 6-e
Pale pink	*Prunus* × *yedoensis*	Rosaceae	Kyoto	Fig. 6-e
Violet	*Corydalis incisa*	Papaveraceae	Kyoto	Fig. 6-g
	Glechoma hederacea grandis	Labiatae	Kyoto	Fig. 6-f
Light violet	*Viola grypoceras*	Violaceae	Kyoto	Fig. 6-f
Blue-violet	*Hydrangea hirta*	Saxifragaceae	Kyoto	Fig. 6-k
	Viola vaginata	Violaceae	Aomori	Fig. 6-i
	Anemone pseudo-altaica	Ranunculaceae	Aomori	Fig. 6-g
Blue	*Veronica persica*	Scrophulariaceae	Kyoto	Fig. 6-g
White	*Abelia spathulata*	Caprifoliaceae	Kyoto	Fig. 6-b
	Spiraea thunbergii	Rosaceae	Kyoto	Fig. 6-c
	Rubus palmatus	Rosaceae	Kyoto	Fig. 6-c
	Corydalis ambigua	Papaveraceae	Aomori	Fig. 6-d
	Anemone pseudo-altaica	Ranunculaceae	Aomori	Fig. 6-c
	Anemone flaccida	Ranunculaceae	Aomori	Fig. 6-c
	Viola sieboldii	Violaceae	Kyoto	Fig. 6-f
	Trillium kamtschaticum	Liliaceae	Aomori	Fig. 6-c

Results

Experiment 1:

In this experiment, the butterflies were mainly presented with bluish and purplish colored papers. Total number of visits and the percentage of visits to respective colored papers are shown in Fig. 4. Butterflies were strongly attracted to dark blue and vivid blue in both species. Light blue also had an attractive effect. However, the purplish papers were less attractive. There was no difference in color preference between the two species ($P>0.05$, Chi-square test).

Experiment 2:

Series a

Vivid red, vivid blue, vivid yellow and gray papers were tested in this series. The butterflies visited the vivid blue paper most frequently in both species ($P<0.001$, Chi-square test and/or Fisher's exact test). *L. puziloi* adults were also attracted to the yellow one ($P<0.001$), while the *L. japonica* were not. The preferences were significantly different between the two species ($P<0.001$) (Fig. 5-a).

Series b

Among the three bluish papers (vivid blue, light blue and pale blue) and the white paper, vivid blue was significantly preferred to others in both species ($P<0.001$). The preferences were significantly different between the two species ($P<0.01$) (Fig. 5-b). This is probably because vivid blue paper attracted more *L. puziloi* than *L. japonica.*

Series c

When the butterflies were tested with the bluish and purplish papers, they preferred dark blue and vivid blue to vivid violet and vivid purple ($P<0.001$). There was no difference in color preference between the two species ($P>0.05$) (Fig. 5-c).

Series d

When purplish papers were presented, there was no specific preference for any color ($P>0.05$), and no preference difference between the two species ($P>0.05$) (Fig. 5-d).

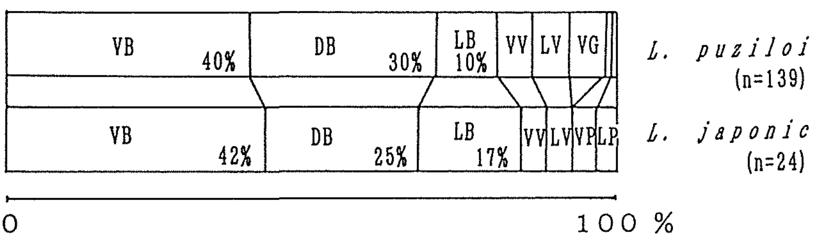


Fig. 4. Results of Experiment 1. VB: vivid blue, DB: dark blue, LB: light blue, VV: vivid violet, LV: light violet, VP: vivid purple, LP: light purple, and VG: vivid green.

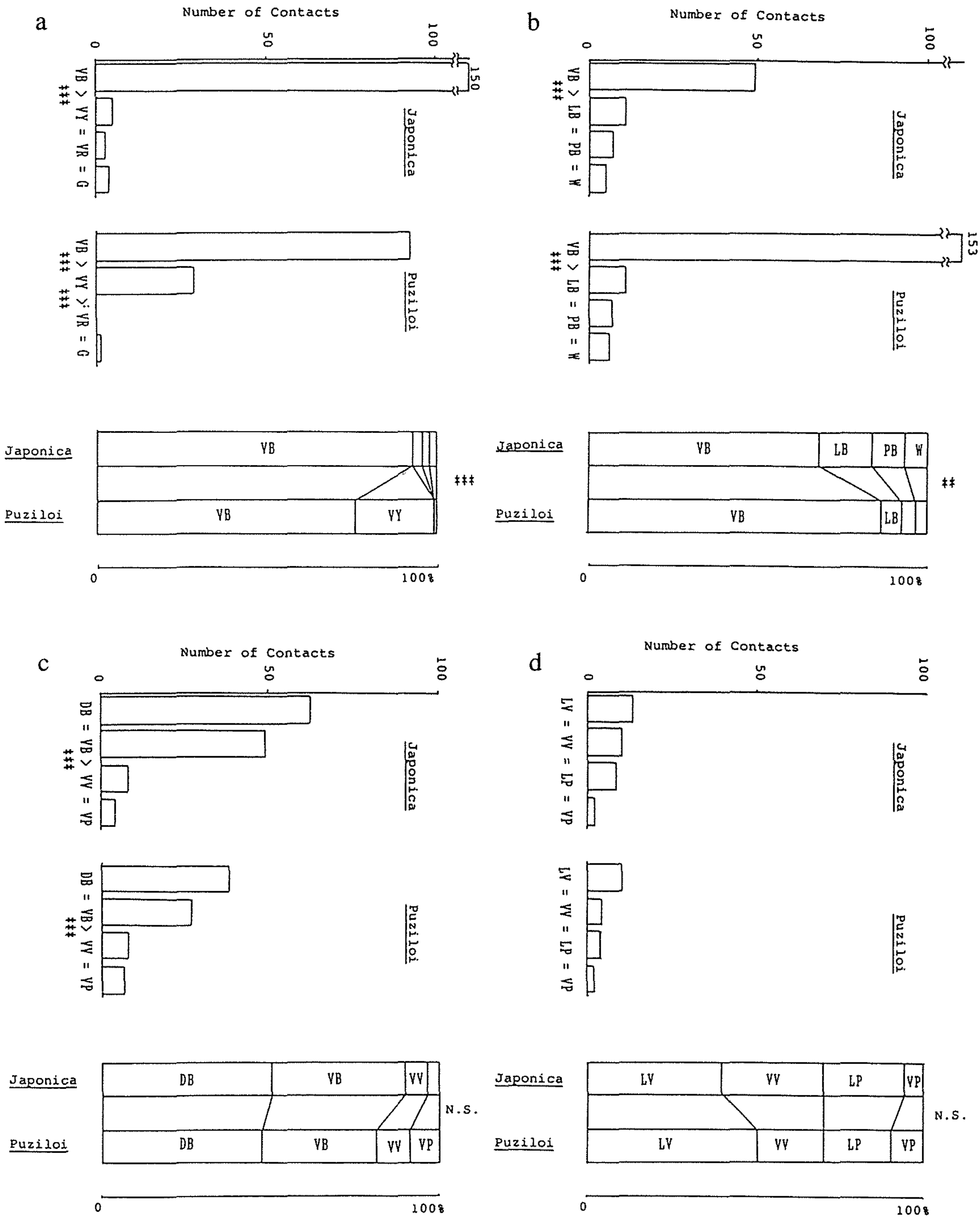


Fig. 5. Results of Experiment 2. a) Series a, b) Series b, c) Series c, and d) Series d. Numerals above the histogram indicate the number of contacts with the paper. ***: P<0.001, **: P<0.01, and N.S.: P>0.05 (Chi-square test and/or Fisher's exact possibility test).

Spectroscopic analyses:

Color naming

Kevan (1978) proposed that colors should be named for insects analogously as for man according to the insect trichromatic diagram (Daumer 1956, 1958). However, electrophysiological studies have recently suggested that the color vision system of some insects are not trichromatic: tetrachromatic (in *Papilio aegeus*) and pentachromatic (in *Papilio xuthus*) color vision systems were reported in butterflies (Arikawa *et al.* 1987). The color vision system may differ from species to species. Thus, I used traditional color naming (Daumer 1956, 1958).

Flowers

The reflection spectra of the sample flowers are summarised in Fig. 6.

According to the reflection spectra, white flowers should be divided into the following two groups:

(1) Bee-white flowers, which reflect near-UV (ca. 350 nm in wavelength) through red (ca. 750 nm). Only *Taraxacum albidum* belonged to this group (Fig. 6-a).

(2) Bee-blue-green flowers, which reflect light longer than ca. 400 nm. Most visually-white flowers belonged to this group (Fig. 6-b-d). The reflection spectra of pale pink flowers were similar to this group.

Purplish (including pink), violet and bluish flowers have several different patterns of reflection in longer wavelength (> 600 nm), so human perception of their color is highly variable. In shorter wavelength, however, they usually have a peak reflection around 450 nm or blue-violet. If *Luehdorfia* butterflies have a bee-type color sense, these flowers might be bee-blue (Fig. 6-e-i).

However, the reflection spectra are slightly different from the above species in *Weigela hortensis*, *Epimedium grandiflorum* (Fig. 6-j) and *Hydrangea hirta* (Fig. 6-k). Although these flowers are visually purplish in color, the former two species reflect bee-violet (380-420 nm) while the last one reflects bee-blue-green (480-520 nm), in addition to bee-blue. These two groups might be divided from the bee-blue flowers.

Yellow flowers should be divided into three groups:

(1) Bee-purple flowers, which reflect near-UV as well as yellow (> 500 nm). Most of the yellow flowers belonged to this group (Fig. 6-l, m).

(2) Pure yellow flowers, which do not reflect near-UV but yellow (> 500 nm). Among the samples, only *Forsytha suspensa* belonged to this group (Fig. 6-n).

(3) Green-yellow flowers including *Petasites japonicus*, *Stachyurus praecox* and *Lindera umbellata*. These flowers might belong to the former group, but have slight reflection around 400-500 nm (Fig. 6-o). Since these flower species are occasionally visited by *Luehdorfia* (see Appendix), I separated this group from the pure yellow flowers.

I prepared only *Camellia japonica* fvor the red sample, because few red flowers were available in spring. This flower reflects not only red (> 650 nm) but also near-UV (ca. 350 nm). Thus, this is not a pure red flower but ultraviolet flower for most insects (Fig. 6-p).

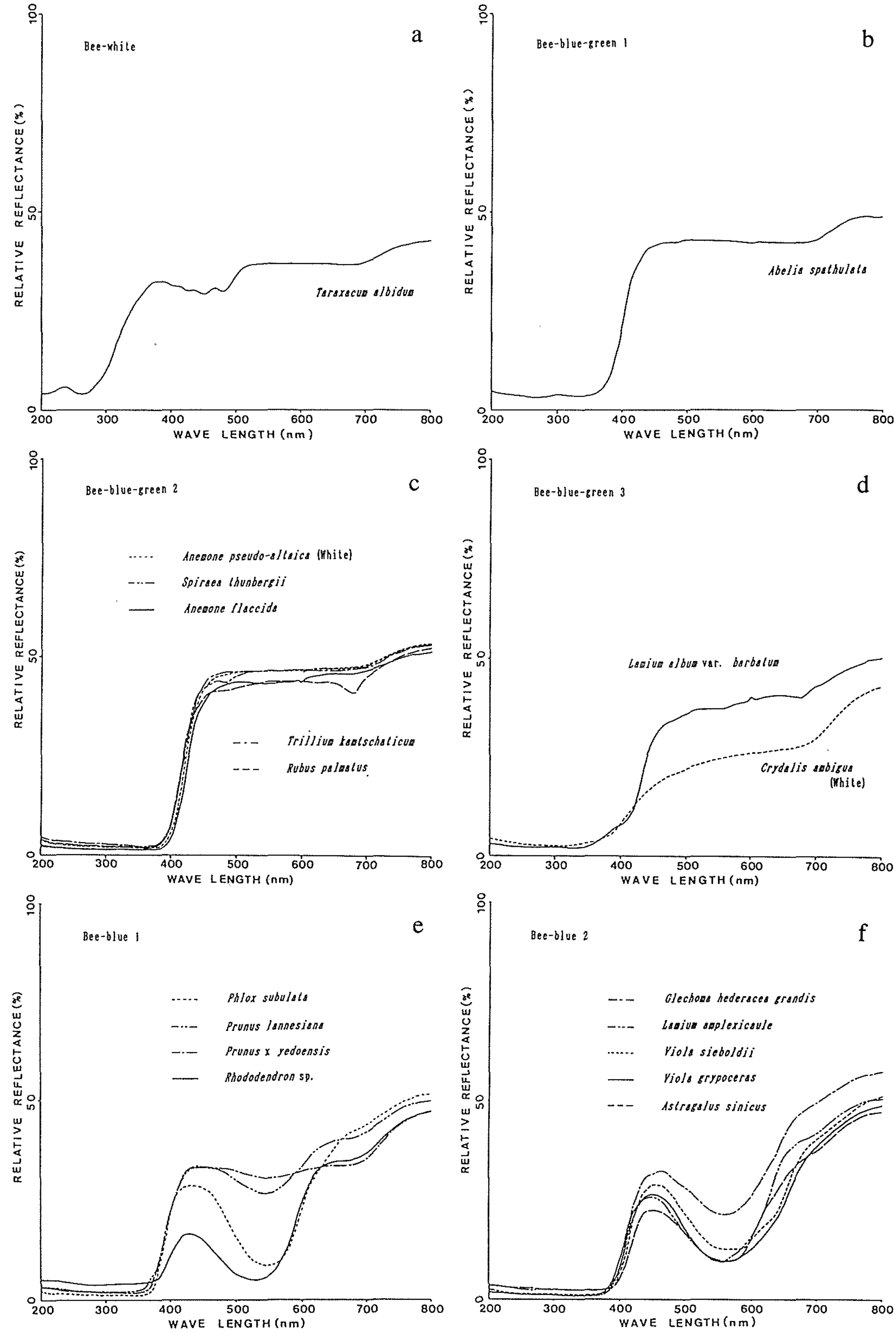


Fig. 6. Reflection spectra of spring flowers examined.

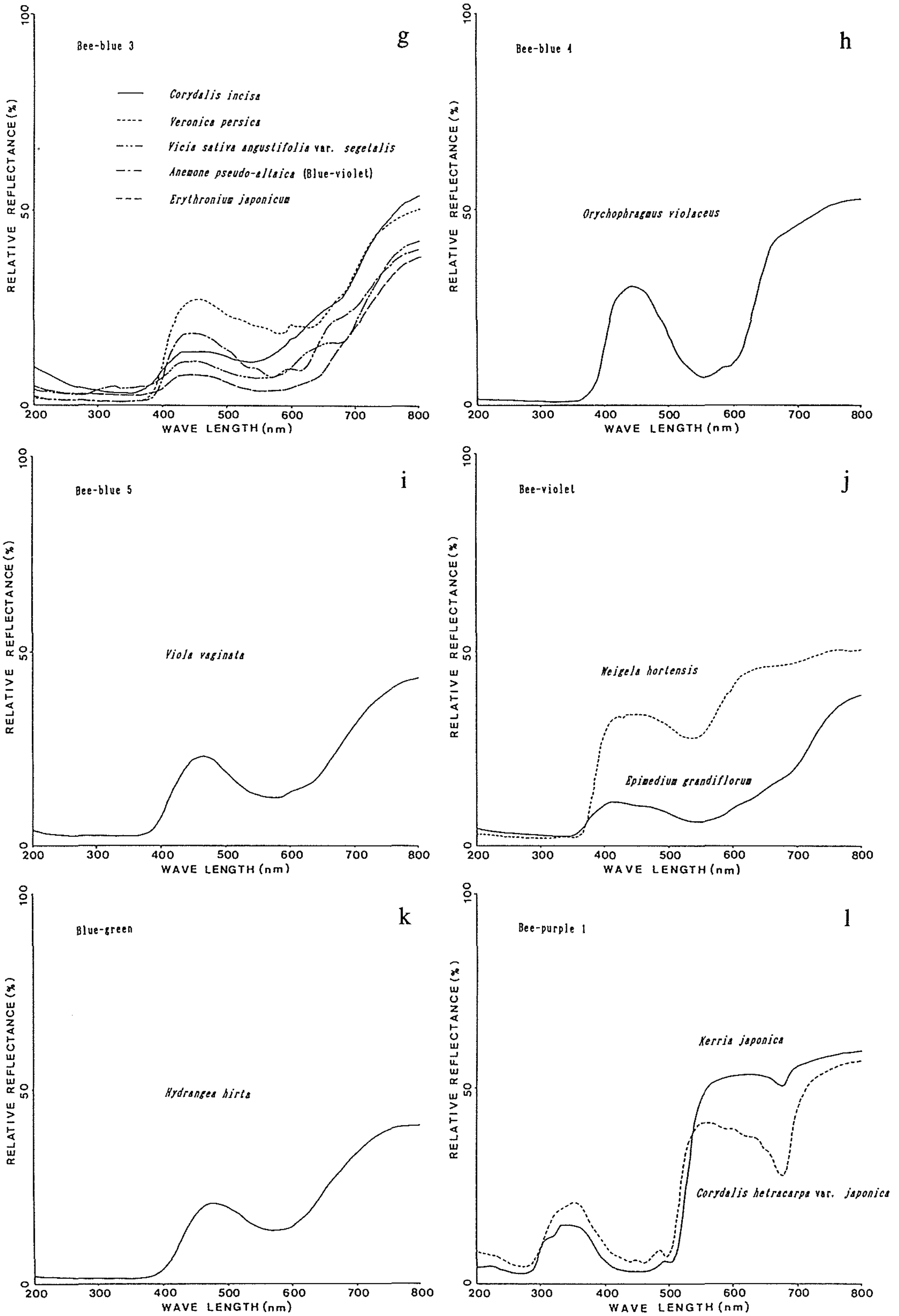


Fig. 6. *(Continued)*

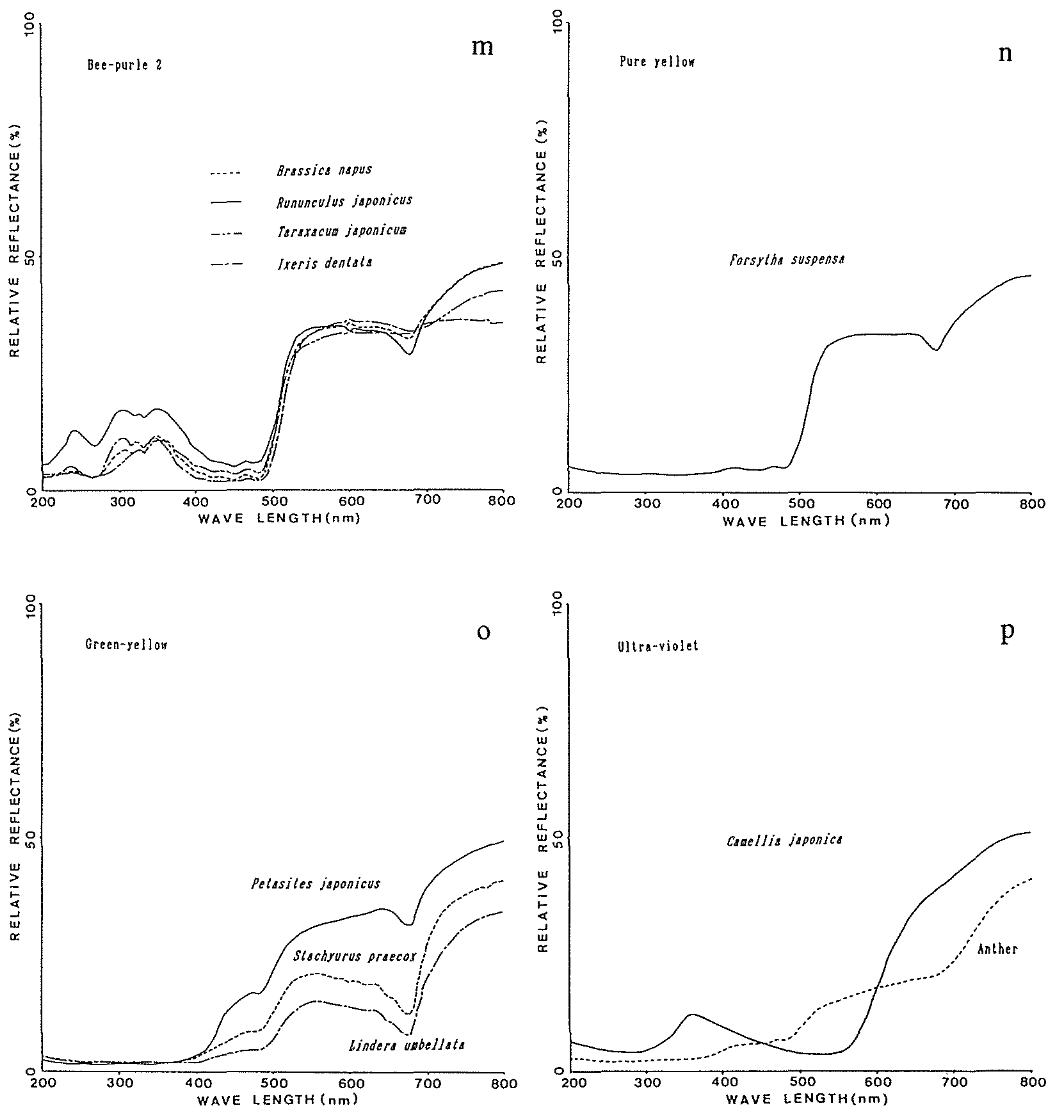


Fig. 6. (*Continued*)

Colored papers

The results of the spectroscopic analyses on the colored papers are shown in Fig. 7. Most of the papers did not have a peak reflection of near-UV (300-380 nm). White and yellow papers had, however, a peak reflection of near-UV. Therefore, these papers might be referred to as bee-white and bee-purple rather than white and yellow, respectively. The yellow (bee-puple) paper had similar reflection spectra to most wild yellow (bee-purple) flowers, while white (bee-white) paper had different reflection from most native white (bee-yellow) flowers.

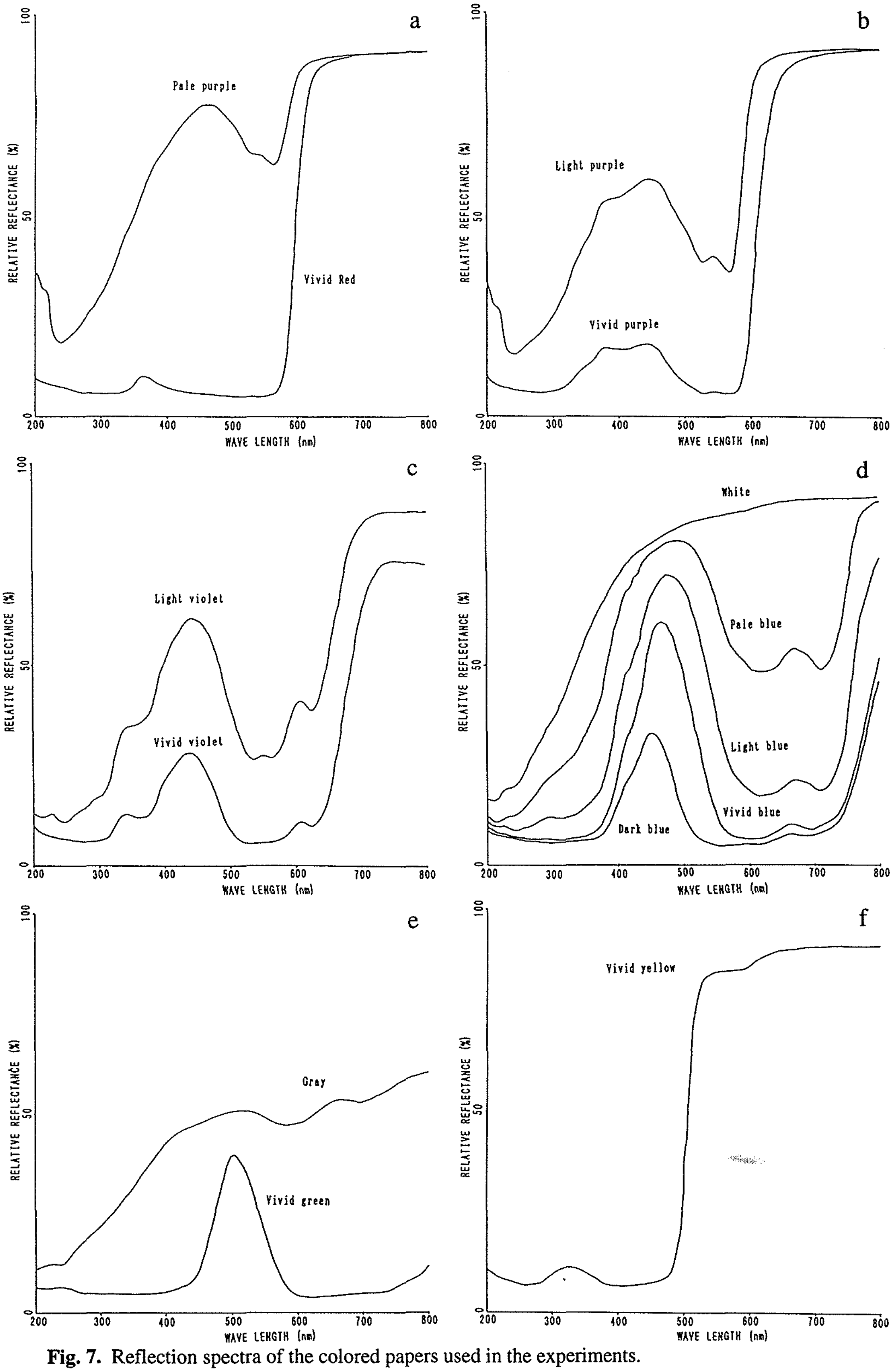


Fig. 7. Reflection spectra of the colored papers used in the experiments.

Discussion

The results of experiments suggest that *Luehdorfia* butterflies recognize nectar sources in response to the colors of flowers. Blue-violet is the most attractive color for flower-visiting behavior in both *L. puziloi* and *japonica*, but hues are also of some importance. Yellow, or bee-purple, has minor attractive qualities in *L. puziloi* only. Red is not attractive to both species at all.

When reflection spectra of bee-blue flowers were compared with those of the dark and vivid blue papers, all had a peak reflection around 450 nm in wavelength, or blue-violet reflection, in addition to strong reflection over 700 nm. Purplish papers similarly had two peaks of reflection, but a peak in shorter wavelength (around 420 nm) was slightly shorter than that of the bee-blue flowers and the bluish papers. The red paper did not have a peak reflection in shorter wavelength, whereas it reflected light over 700 nm.

It is thus suggested that *Luehdorfia* butterflies frequently visit bee-blue flowers mainly in response to a peak reflection around 450 nm in wavelength or blue-violet reflection from flowers. Though electrophysiological studies are necessary, *Luehdorfia* butterflies might be red-blind so that they sense slightly shorter wavelength light than human beings (e.g. 300-650 nm like honey bees: Daumer 1956, 1958). Or they might be also able to sense longer wavelength light as reported in several butterfly species (e.g. Arikawa *et al.* 1987), but strong reflection over 600 nm might have reduced the attractive effect of a peak reflection around 450 nm. In any case, the color preference for blue-violet should be adaptive in nature, because purplish flowers are the most available nectar sources in the habitat: natural selection favors those that initiates flower-visiting behavior innately in response to blue-violet reflection from flowers.

As for bee-purple (or yellow) flowers, *L. puziloi* exhibited a minor preference, but *L. japonica* did not. This difference in color preference is possibly a species-specific attribute. It may also be a result of learning because the materials were collected from the natural habitats. *L. puziloi* butterflies could have learned that bee-purple (or yellow) objects indicate nectar sources. Further studies are needed to determine this.

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References

Arikawa, K., K. Inokuma & E. Eguchi 1987 Pentachromatic visual system in a butterfly. *Naturwissenshaften* 74: 297-298.

Daumer, K. 1956 Reizmetrische Untersuchung des Farbensehens der Bienen. *Z. vergl. Physiol.* 38: 413-478.

Daumer, K. 1958 Blumenfarben, wie sie die Bienen sehen. *Z. vergl. Physiol.* 41:49-110.

Fujisawa, S. 1983 Gifu-cho to kan'aoi. [*Luehdorfia* and its host plants.] 403pp., 40pls., Gifucho Kenkyu-kai, Iiyama, Nagano (in Japanese).

Fukuda, H., K. Kubo, T. Kuzuya, A. Takahashi, B. Tanaka & M. Wakabayashi 1972 Insect's life in Japan. Vol.3. Butterflies. 278pp., 56pls., Hoikusha, Osaka (in Japanese).

Fukuda, H., E. Hama, T. Kuzuya, A. Takahashi, M. Takahashi, B. Tanaka, H. Tanaka, M. Wakabayashi & Y. Watanabe 1982 The life histories of butterflies in Japan Vol.I. 277pp., Hoikusha, Osaka (in Japanese with English summary).

Hidaka, T. & Y. Obara 1968 Small cabbage white —Butterfly behavior—. A scientific film by Iwanami Productions, Inc.

Hiura, I. & Y. Kanoh 1977 Gifu-cho no otozureru hana (I). [Flowers visited by *Luehdorfia japonica*. (I).] *Nature Study* 23: 38-40 (in Japanese).

Ilse, D. 1928 Über den Farbensinn der Tagfalter. *Z. vergl. Physiol.* 8: 658-692.

Kanda, S. 1987 "Chodan-fuhatsu (2)": Dohoku no hime-gifu-cho wa kiiro ga daisuki. [Notes on butterflies (2): *Luehdorfia puziloi yessoensis* strongly prefer the colour yellow in northern Hokkaido.] *Usubaki* (74): 1-2 (in Japanese).

Kevan, P. G. 1978 Floral coloration, its colorimetric analysis and significance in anthecology. In A. J. Richards (ed.) *The pollination of flowers by insects*. pp.51-78, 5pls., Academic: Press, London.

Miyakawa, M. 1976 Flower-visiting behaviour of small white butterfly, *Pieris rapae crucivora*. *Annot. Zool. Jap.* 49: 261-273.

Swihart, C. A. 1971 Colour discrimination by the butterfly, *Heliconius charitonius* Linn. *Anim. Behav.* 19: 156-164.

Swihart, C. A. & S. L. Swihart 1970 Colour selection and learned feeding preferences in the butterfly, *Heliconius charitonius* Linn. *Anim. Behav.* 18: 60-64.

Swihart, S. L. 1969 Colour vision and the physiology of the superposition eye of a butterfly (Hesperiidae). *J. Insect Physiol.* 15: 1347-1365.

Swihart, S. L. 1970 The neural basis of colour vision in the butterfly, *Papilio troilus*. *J. Insect Physiol.* 16: 1623-1636.

Swihart, S. L. 1972 The neural basis of colour vision in the butterfly, *Heliconius erato*. *J. Insect Physiol.* 18: 1015-1025.

Tanaka, T. 1982 Cho no houka. [Butterfly flower-visiting.] *Amica* 27: 207-255 (in Japanese).

Unno, K. & J. Aoyama 1981 Butterflies of Japan. 192pp., Shogakkan, Tokyo (in Japanese).

Watanabe, S. 1985 Nihon no konchu 1. Gifu-cho. [Insects of Japan. 1. *Luehdorfia japonica*.] 148pp., 8pls., Bun'ichi-sogo-shuppan, Tokyo (in Japanese).

Appendix. The list of flowers recorded to have been visited by *Luehdorfia* butterflies.

Flower			Butterfly (Reference)		
Family	Species	Color	*L. japonica*	*L. Puziloi inexpecta*	*L. puziloi yesscensis*
Liliaceae	*Heloniopsis orientalis*	Violet, Purple, Pink	Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985	Tanaka 1982; Fujisawa 1983	
	Gagea lutea	Yellow			Tanaka 1982; Fujisawa 1983; Watanabe 1985
	Erythronium japonicum	Purple	Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985	Tanaka 1982; Fujisawa 1983	Tanaka 1982; Fujisawa 1983; Kanda 1987
	Amana edulis	White	Tanaka 1982; Watanabe 1985		
	Amana latifolia	White	Tanaka 1982; Watanabe 1985		
	Fritillaria amabilis	Pale yellow	Tanaka 1982; Watanabe 1985		
	Hyacinthus orientalis	Purple, Violet	Tanaka 1982; Fujisawa 1983		
Caryophyllaceae	*Cerastium holosteoides* var. *hallaisanense*	White	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa 1983; Watanabe 1985		
Ranunculaceae	*Anemone nikoensis*	White			Tanaka 1982; Fujisawa 1983
	Anemone flaccida	White	Tanaka 1982; Fujisawa 1983; Watanabe 1985		
	Anemone pseudo-altaica	Blue-violet, White	Tanaka 1982; Fujisawa 1983; Watanabe 1985	Tanaka 1982; Fujisawa 1983	
	Caltha palustris barthei	Yellow			Tanaka 1982; Fujisawa 1983; Watanabe 1985; Kanda 1987
	Adonis amurensis	Yellow			Watanabe 1985; Kanda 1987

Berberidaceae	*Epimedium grandiflorum*	Purple	Watanabe 1985		
Papaveraceae	*Corydalis lineariloba*	Purple	Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		
	Corydalis lineariloba var. *papilligera*	Purple	Watanabe 1985	Tanaka 1982	
	Corydalis ambigua	Bluish violet, White			Tanaka 1982; Fujisawa 1983; Kanda 1987
	Corydalis incisa	Purple	Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		
	Corydalis heterocarpa var. *japonica*	Yellow		Fujisawa 1983	
Cruciferae	*Cardamine* spp.	White	Fukuda *et al.* 1982		
	Cardamine flexuosa	White	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa 1983; Watanabe 1985		
	Brassica campestris napus var. *nippo-oleifera*	Yellow	Tanaka 1982; Fujisawa 1983; Watanabe 1985		
Leguminosae	*Astragalus sinicus*	Purple	Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		
Oxalidaceae	*Oxalis griffithii*	White	Tanaka 1982; Fujisawa 1983; Watanabe 1985		
Buxaceae	*Pachysandra terminalis*	White, Pale green			Fukuda *et al.* 1982
Violaceae	*Viola* spp.	Violet, Purple, White	Tanaka 1982; Fukuda *et al.* 1982	Tanaka 1982	
	Viola yedoensis	Violet	Fujisawa 1983; Watanabe 1985		
	Viola keiskei	White & violet	Tanaka 1982; Fujisawa 1983 Watanabe 1985		
	Viola tokubuchiana var. *takedana*	Light purple		Fujisawa 1983	

	Viola sieboldii	White & purple	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa 1983; Watanabe 1985	
	Viola vaginata	Light violet	Tanaka 1982; Fujisawa 1983; Watanabe 1985	Tanaka 1982; Fujisawa 1983
	Viola bissetii	Light violet	Fujisawa 1983	
	Viola kusanoana	Light violet		Tanaka 1982; Fujisawa 1983
	Viola rostrata var. *japonica*	Light violet	Tanaka 1982	Tanaka 1982; Fujisawa 1983
	Viola grypoceras	Light violet	Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985	Tanaka 1982; Fujisawa 1983
	Viola ovato-oblonga	Light violet	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa 1983; Watanabe 1985	
	Viola obtusa	Violet	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa 1983; Watanabe 1985	
	Viola verecunda	White & violet	Hiura & Kanoh 1977; Fujisawa 1983; Watanabe 1985	
	Viola brevistipulata	Yellow & violet		Tanaka 1982; Fujisawa 1983
Umbelliferae	*Cryptotaenia japonica*	White	Tanaka 1982	
Diapensiaceae	*Schizocodon soldanelloides* var. *magnus*	Pink	Tanaka 1982; Fujisawa 1983; Watanabe 1985	
Gentianaceae	*Gentiana thunbergii*	Blue, Blue-violet	Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985	
Labiatae	*Glechoma hederacea grandis*	Purple	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa 1983; Watanabe 1985	Fujisawa 1983

Polemoniaceae	*Phlox subulata*	Purple, Red	Tanaka 1982; Fujisawa 1983; Watanabe 1985		
Scrophulariaceae	*Veronica persica*	Blue	Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983: Watanabe 1985		
	Mazus miquelii	Purple	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa1983; Watanabe 1985		
Compositae	*Taraxacum* spp.	Yellow, White		Tanaka 1982	
	Taraxacum officinale	Yellow			Watanabe 1985; Kanda 1987
	Taraxacum hondoense	Yellow			Tanaka 1982; Fujisawa 1983
	Petasites japonicus	Pale yellow	Watanabe 1985	Tanaka 1982; Fujisawa 1983	Tanaka 1982; Fujisawa 1983; Kanda 1987
	Bellis perennis	Purple, Violet		Tanaka 1982	
Salicaceae	*Salix sachalinensis*	Pale yellow		Fujisawa 1983	
	Salix sp.	Pale yellow	Fujisawa 1983; Watanabe 1985		Tanaka 1982
Theaceae	*Camellia japonica*	Red, Purple	Tanaka. 1982; Fujisawa 1983; Watanabe 1985		
Rosaceae	*Potentilla fragarioides* var. *major*	Yellow		Tanaka 1982; Fujisawa 1983	
	Potentilla freyniana	Yellow	Watanabe 1985	Tanaka 1982	
	Prunus spp.	Pink, White	Fukuda *et al.* 1982	Tanaka 1982	
	Prunus mume	White, Red	Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		
	Prunus japonica	White, Pink	Tanaka 1982; Fujisawa 1983		
	Prunus persica	Pink	Fujisawa 1983; Watanabe 1985		
	Prunus apetala var. *pilosa*	Pink	Tanaka 1982; Fujisawa 1983; Watanabe 1985	Fujisawa 1983	

	Prunus subhirtella	Pink	Fujisawa 1983; Watanabe 1985	Fujisawa 1983	
	Prunus yedoensis	Pink	Hiura & Kanoh 1977; Fujisawa 1983; Watanabe1985	Tanaka 1982; Fujisawa 1983	
	Prunus nipponica var. *kurilensis*	Pink			Fujisawa 1983
	Prunus sargentii	Pink	Fujisawa 1983; Watanabe 1985	Tanaka 1982; Fujisawa 1983	Tanaka 1982; Fujisawa 1983
	Prunus jamasakura	Pink	Hiura & Kanoh 1977; Fujisawa 1983; Watanabe 1985		
	Kerria japonica	Yellow	Tanaka 1982; Fujisawa 1983; Watanabe 1985	Tanaka 1982; Fujisawa 1983	
	Rubus palmatus	White	Tanaka 1982; Fujisawa 1983	Tanaka 1982; Fujisawa 1983	
	Rubus palmatus var. *palmatus*	White	Watanabe 1985		
	Rubus palmatus var. *coptophyllus*	White	Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		
	Rubus microphyllus	White	Hiura & Kanoh 1977; Tanaka 1982; Fujisawa 1983; Watanabe 1985		
	Amelanchier asiatica	White	Tanaka 1982; Fujisawa 1983; Watanabe 1985		
	Chaenomeles japonica	Red, Orange	Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		
	Chaenomeles speciosa	Red, Purple, White	Tanaka 1982; Watanabe 1985		
Thymelaeaceae	*Daphne pseudo-mezereum jezoensis*	Yellow			Tanaka 1982; Fujisawa 1983; Watanabe 1985; Kanda 1987
	Edgeworthia chrysantha	Yellow	Tanaka 1982; Watanabe 1985		

Elaeagnaceae	*Elaeagnus umbellata*	Pale yellow	Fukuda *et al.* 1982; Fujisawa 1983		
Stachyuraceae	*Stachyurus praecox*	Light yellow	Tanaka 1982; Watanabe 1985	Tanaka 1982: Fujisawa 1983	
Ericaceae	*Epigaea asiatica*	Pink	Tanaka 1982; Watanabe 1985		
	Pieris japonica	White	Hiura & Kanoh 1977; Tanaka 1982; Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		
	Rhododendron spp.	Purple, White, Orange	Tanaka 1982; Fukuda *et al.* 1982		Tanaka 1982
	Rhododendron dauricum	Purple			Tanaka 1982; Fujisawa 1983
	Rhododendron obtusum var. *kaempferi*	Orange	Fujisawa 1983; Watanabe 1985		
	Rhododendron reticulatum	Purple	Hiura & Kanoh 1977; Watanabe 1985		
	Rhododendron dilatatum	Purple	Fukuda *et al.* 1982; Fujisawa 1983; Watanabe 1985		