Studies on Ecology and Behavior of Japanese Black Swallowtail Butterflies

I. Ecological Characteristics of Male Populations in *Papilio helenus nicconicolens* BUTLER and *P. protenor demetrius* CRAMER (Lepidoptera: Papilionidae)

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(Received June 25, 1984)

The mark-and-recapture method was adopted to study behavior and population dynamics of the black swallowtail butterflies (BSB), *Papilio helenus nicconicolens* and *P. protenor demetrius* in Kodakasa-yama, Kochi City, Shikoku, Japan. The data were analyzed by JOLLY's method.

Most of the butterflies captured at small gaps in the forest without nectar or host plants were males who frequently move in and out of these small gaps.

The following differences were observed between *P. helenus* and *P. protenor*. First, the highest incidence of *P. protenor* in a small gap appeared earlier than *P. helenus*. Secondly, *P. protenor* males were more resident at their habitat, and thirdly, higher population levels with a larger fluctuation were observed in *P. helenus* both seasonally and annually.

INTRODUCTION

Ten species of *Papilio* are present in Japan. *P. bianor dehaanii*, *helenus nicconicolens*, *maackii tutanus*, *machaon hippocrates*, *macilentus*, *memnon thumbergii*, *okinawensis*, *polytes polycles*, *protenor demetrius* and *xuthus* (KAWAZOE and WAKABAYASHI, 1976). Eight of these have black wings (black type) and wings of the other two, *P. machaon hippocrates* and *P. xuthus*, are yellow. These black type butterflies are referred to as BSB hereafter, instead of Japanese black swallowtail butterflies. Six species of *Papilio* are pests of such agricultural crops as citrus and umbelliferous vegetables (J.S.A.E.Z., 1980).

It is well known that most of the butterflies in this genus have the habit of tracking definite flight courses, so-called flyways, among the vegetation (EHARA et al., 1964; HIDAKA, 1974, 1975; WATANABE, 1979 a), and also show a "hilltopping" behavior, flying towards the summit of a hill (SHIELDS, 1967; SCOTT, 1968). These flight activities are believed to be closely related to their search for resources, e.g., host plants, nectar sources, mates, etc. Further, BSB were frequently observed flying about in shaded places within the forest (HIDAKA, 1974). *P. xuthus* is one of the typical yellow type butterflies of *Papilio* and its oviposition activity (YAMANAKA et al., 1978), host preference (SUZUKI et al., 1976; WATANABE, 1979 b) and fecundity (TSUBAKI, 1973; YAMANAKA et al., 1978) have been studied by many scientists. SUZUKI et al. (1974) also studied the recapture rate, dispersal and population size of adult *P. xuthus* by the mark-and-recapture method. Few ecological studies of BSB adults, however, have been conducted in Japan. This is partly due to their low incidence compared to *P. xuthus*, and partly due to the difficulty in applying the mark-and-recapture method to them because they are more difficult to catch. Since many BSB adults could be caught in forest gaps in Kodakasa-yama, Kochi City, however, the method using individual markings could be applied to study of the behavior and population size of this group.

STUDY AREA

The study was carried out at Kodakasa-yama, a small wooded hill in Kochi City in the southern part of Shikoku island. The hill is about 17.5 ha in area and the altitude of its peak is about 54 m. An urban residential area surrounds the hill and it is about 1 km far from the neighboring habitats of BSB (Fig. 1). The hillside of Kodakasa-yama is mostly covered with a typical laurel forest dominated by *Castanopsis* and *Quercus*. There were many small forest openings where there are cemeteries and three among these (designated A, B and C) were selected for study (Fig. 1).

Eggs and larvae of both *P. helenus* and *P. protenor* were observed only on trees of Rutaceae, *Zanthoxylum ailanthoides*. Tall trees of *Z. ailanthoides* grew randomly in the forest, while seedlings and young trees were more dense in the larger gaps. The main nectar sources utilized by BSB adults in Kodakasa-yama are listed in Table 1.

Meteorological data for this region is available for the past 30 years, and precipitation is concentrated in June, July and September. The mean monthly temperature has varied from 5 to 28°C. Weather conditions were not much different from the average during the years of study, except that there was rather little rain in the summers of 1977 and 1978.

Fig. 1. Map of the study area, Kodakasa-yama in Kochi City. A residential area separates it by at least 1 km from neighboring habitats (left). A, B and C are the study sites (right).

Table 1. Seasonal changes in main plant species utilized as nectar sources by the butterflies of *Papilio helenus nicconicolens* and *P. protenor demetrius* in Kodakasa-yama

Month	Species
May	<i>Ligustrum obtusifolium</i> , ^a <i>Deutzia crenata</i> , ^a <i>Styrax japonica</i> ^a <i>Lonicera japonica</i>
June	<i>Lonicera japonica</i>
July	<i>Albizia julibrissin</i> , ^a <i>Clerodendron trichotomum</i> ^a <i>Symplocos chinensis</i> , <i>Hemerocallis fulva</i>
August	<i>Clerodendron trichotomum</i> , ^a <i>Clematis terniflora</i> <i>Cayratia japonica</i> , <i>Zanthoxylum ailanthoides</i> ^a
September	<i>Clematis terniflora</i> , <i>Cayratia japonica</i>

^a Extremely abundant among the listed species.

METHODS

To collect information on the individual movements of the BSB and to estimate the size of its population, the mark-and-recapture method with individual markings was utilized in 1977, 1978 and 1979. Censuses were carried out twice a week from late June to mid-October in 1977, from mid-May to early October in 1978 and from early May to early September in 1979.

Butterflies were captured by net mainly at study site A (Fig. 1) and each individual was given a serial number on the upper surface of both fore wings with a black felt pen. Date and site of capture, sex and wing condition were recorded before release.

Release was made at the same place where the individual was caught. However, those individuals damaged on capture or which showed any difficulty in flying normally when released were not allowed to return to the original population. No behavioral differences were observed between marked and unmarked butterflies, except that some released individuals flew up and disappeared rapidly. It seems unlikely that marking affected mating behavior or the probability of predation, although this has not been demonstrated experimentally.

Table 2. Species, relative abundance and sex ratio of *Papilio* butterflies captured at study site A in Kodakasa-yama

	Year	No. of males captured	No. of males recaptured at least once (%)	No. of females captured	(♀/♀ + ♂)
<i>Papilio helenus nicconicolens</i>	1977	368	141 (38.3)	3	(0.008)
	1978	290	141 (48.6)	8	(0.025)
	1979	322	109 (33.9)	5	(0.015)
<i>P. protenor demetrius</i>	1977	274	115 (42.0)	2	(0.007)
	1978	213	93 (43.7)	9	(0.036)
	1979	267	114 (42.7)	2	(0.007)
<i>P. bianor dehaanii</i>	1977	14		1	
	1978	8		2	
	1979	17		0	
<i>P. memnon thunbergii</i>	1977	8		1	
	1978	8		2	
	1979	18		1	
<i>P. macilentus</i>	1977	1		0	
	1978	3		0	
	1979	1		0	

Table 3. Sex ratios of the two species of BSB as determined by the rearing of insects of immature stages collected from the study area

	Stages collected	Date of collection	No. of adults emerged			♀/♀ + ♂
			Female	Male	Total	
<i>Papilio helenus nicconicolens</i>	L5	24–30 Nov. 1978	2	3	5	0.40
	E	3–24 Jun. 1979	20	18	38	0.53
	E	7 Jul.–9 Aug. 1979	6	7	13	0.46
	E	18–22 Aug. 1979	6	8	14	0.43
<i>P. protenor demetrius</i>	E	28 Jul.–9 Aug. 1979	6	9	15	0.40
	E	18–22 Aug. 1979	9	7	16	0.56

Capture and recapture were made in the afternoon at study site A except on the 7th June 1978 when the daily rhythm of BSB was examined. Since the adults visiting the small gap were mostly males, the sex ratio of BSB was examined by rearing eggs and larvae collected in the study area.

Adult movement among the three gaps studied was traced for five consecutive days, 22–26, August 1979. The distances between sites A and B, and A and C were about 500 m and 550 m, respectively. Censuses at the three study sites were started and ended simultaneously by different observatory groups. A sufficient number of recaptures for two BSB species were obtained to permit data analysis for reliable estimates of male populations. The data were analyzed by JOLLY's (1965) method.

RESULTS

Species, relative abundance and sex ratio of Papilio butterflies

Species composition, relative abundance and sex ratio of the BSB species observed

Fig. 2. Daily rhythm of BSB flight activity (top) and changes in temperature and illumination (bottom) at study site A on 7 June 1978. Phn: *Papilio helenus nicconicolens*, Ppd: *P. protenor demetrius*.

during the three study years at site A are shown in Table 2.

Five species of BSB were captured during the three-year period: *P. helenus nicconicolens*, *P. protenor demetrius*, *P. bianor dehaanii*, *P. memnon thunbergii* and *P. macilentus*. All those previously recorded from Kodakasa-yama by naturalists were captured in this study. Although yellow types, *P. machaon hippocrates* and *P. xuthus*, were frequently observed flying above the bush in the study area, they were never captured in the small gaps.

Of the five BSB species, the two most abundant were *P. helenus* and *P. protenor*.

Males were predominant among all butterflies caught at the sites throughout the study. Sex ratio estimated for adults reared from field collected eggs and larvae, however, was about 1:1 (Table 3). Each year about 600 BSB individuals were marked. Percentage of the males recaptured at least once was about 34–49 in *P. helenus* and 42–44 in *P. protenor*. No significant differences in the ratio of recapture between the two species were detected in 1977 and 1978, but more *P. protenor* were recaptured ($p < 0.05$) in 1979 (Table 2).

Daily rhythm of flying numbers in a small gap

Only a few BSB adults were observable in the small gap A before noon and the number gradually increased towards late afternoon. The peak of *P. protenor* appeared about one hour earlier than *P. helenus* (Fig. 2). No correlation was observed between the number of BSB and temperature or illumination at the gap. Further details of flight activity will be reported elsewhere (SUZUKI et al., in press).

Fig. 3. Dispersal of BSB among the study sites (22–26, August, 1979). Arrows indicate inter- and intra-study site dispersal and the numerals beside the lines with sign? indicate butterflies marked but not recaptured.

Fig. 4. Seasonal changes in number of BSB males captured per hour at study site A. Filled columns show newly emerged individuals. ↓: start of census, ↑: end of census.

Dispersal among small gaps

To study the inter-gap movement of BSB, censuses were carried out simultaneously at the three study sites during 22–26, August, 1979. Movement between the small gaps is presented in Fig. 3 for *P. helenus* and *P. protenor*. Three points emerge from these figures. First, both species seem to utilize the entire area of Kodakasa-yama for their foraging. Secondly, a definite tendency of hilltopping was observed with the highest number of catches and recaptures at study site A which was the highest point in the study area (see Fig. 1). Thirdly, males of *P. protenor* were more resident than *P. helenus* judging from the recapture rates.

Seasonal occurrence of BSB

The earliest observations of BSB in the study area were in late April for *P. protenor*, and early May for *P. helenus*. The last appearance of newly emerged individuals of *P. helenus* was in early October and in *P. protenor* mid-October (Fig. 4); thus, the breeding season of *P. protenor* seems a little longer.

Seasonal changes in number of captured adults were similar in the two species; a few were observed in May and June, they increased in number through July showing peak incidences in August, then decreased in September in both species (Fig. 4). No

Fig. 5. Population trends of BSB males. Numbers were estimated by JOLLY's method. Solid and broken lines show average and standard error during the periods covered by the lines, respectively.

remarkable peaks in number of newly emerged adults were observed, but the number in July and August in both species was large.

Seasonal changes in population size of male BSB

Seasonal fluctuations in the number of male adults estimated by JOLLY's (1965) method are shown in Fig. 5 for *P. helenus* and *P. protenor*.

Although annual population trends vary with species and years, the peak density of males generally appeared in July and August in both species. There were no discrete peaks in density, probably due to the relatively long life span of male adults and the continuous emergence of adults during the breeding season.

In this work, we defined the summer generation of the two species as being from July to August when population density was high (solid lines in Fig. 5). The mean daily sizes of *P. helenus* in the summer generation were 126.4, 58.3 and 98.6 (7.22, 3.33 and 5.63 per hectare) in 1977, 1978 and 1979, respectively. The extent of annual change in size during the 3 years was 2.2 or 126.4/58.3 times and the ratios of standard error to mean population size were 0.44, 0.48 and 0.65 in 1977, 1978 and 1979, respectively.

The mean daily population size of *P. protenor* was 52.6, 34.5 and 37.9 (3.00, 1.97 and 2.16 per hectare) in 1977, 1978 and 1979, respectively. The degree of annual changes during the 3 years was 1.5 (52.6/34.5) times indicating more stable population in *P. protenor* than *P. helenus*. The ratios of standard error to mean population size of *P. protenor* were 0.49, 0.34 and 0.34 which were almost equal to or a little smaller than those for *P. helenus*.

As regards the relative abundance of the two species, the ratio of *P. helenus* to *P. protenor* was 2.4, 1.7 and 2.6 in 1977, 1978 and 1979, respectively. For further analysis of population trends, the number of recruits was calculated by JOLLY's method.

The mean daily number of recruits in the summer generation for *P. helenus* was 37.3, 23.3 and 34.6 (2.13, 1.32 and 1.98 per hectare) in 1977, 1978 and 1979, respectively. In *P. protenor*, the mean number of recruits per day was 20.7, 12.9 and 14.3 (1.18, 0.78 and 0.82 per hectare). The extent of change in population members of *P. helenus* in the summer generation was greater than *P. protenor* throughout the study.

In conclusion, compared to *P. protenor*, *P. helenus* was more abundant and showed a greater annual fluctuation in summer density. Also, analyses suggested a greater degree of member change in the *P. helenus* population.

DISCUSSION

The mark-and-recapture method is useful not only for estimating the population size but also for tracking a butterfly's behavior. In order to have reliable data, however, the recapture rate should be high. In this study, recapture rates of two species were high enough for such analysis.

Throughout the study, most of the BSB adults were caught in the small gaps located in the forest without nectar or host plants, and the majority of them were males (Table 2). Sex related differences in behavior of some *Papilio* species have been studied. SUZUKI et al. (1974) reported that the recapture rate of *P. xuthus* males was higher than that of the females at its nocturnal roosting site. LEDERHOUSE (1982) also reported similar results in *P. polyxenes*, but found no difference between the sexes in *P. glaucus*. SUZUKI et al. (in press) reported that males of BSB fly almost continuously while females spend much of their time hidden in the vegetation and they fly only in the late afternoon for oviposition or to search for nectar sources.

Males of BSB moved among the small gaps (Fig. 3), a tracking behavior probably related to some adaptive strategy such as mating associated with hilltopping behavior (SHIELDS, 1967; SCOTT, 1968) and thermoregulation of body temperature (HIDAKA, 1974). Since our present knowledge on this matter is insufficient, the question remains to be resolved in the future.

Estimation of population parameters of *Papilio* by the mark-and-recapture method has been done by SUZUKI et al. (1974) and LEDERHOUSE (1983). In this study, the daily numbers of each BSB species were estimated by this method at the small forest gap. High densities of BSB males in July and August (Fig. 5), may have resulted from higher egg density and survival rate from egg to pupa in the summer generation than in other generations (WATANABE et al., 1984). Mean population density in this generation was 3.33–7.22 per hectare for *P. helenus* and 1.97–3.00 per hectare for *P. protenor* (Fig. 5). BSB seems more abundant than *P. polyxenes* (0.25–1 per hectare) whose males exhibit territorial behavior in hay fields in the U.S.A. (LEDERHOUSE, 1983).

Differences between *P. helenus* and *P. protenor* were suggested in several points from the mark-and-recapture study. First, the peak of daily activity in *P. protenor* males in the gap appeared earlier than that in *P. helenus* (Fig. 2). This may be explained by the higher body temperature of *P. protenor* than *P. helenus* results in its earlier peak activity during the daytime (SUZUKI et al., in press). Secondly, males of *P. protenor* were more resident in gaps judging from the recapture rates (Table 2, Fig. 3). SUZUKI et al. (in press) reported similar results. Thirdly, populations of *P. helenus* compared to those of *P. protenor* have higher densities and larger fluctuations both in seasonal

and annual changes (Fig. 5). These differences may derive from the fact that *P. helenus* forages and utilizes more effectively its habitat where nectar sources and host plants are available (SUZUKI et al., in press).

ACKNOWLEDGEMENTS

We thank Mr. A. NIIZUMA of the Department of Zoology, Faculty of Science, Kyoto University and Ms. K. YAMASHITA of the Laboratory of Entomology, Faculty of Agriculture, Kyoto Prefectural University for their assistance in the field.

REFERENCES

- EHARA, S., H. TAKAHASHI, T. HOMMA, Y. YAMASHITA and S. F. SAKAGAMI (1964) Spring activities of a Japanese black swallowtail, *Papilio maackii tutanus* FENTON at a fly-way. *Jap. J. Ecol.* **14**: 175–181.
- HIDAKA, T. (1974) Life style and behavior of butterflies and their environments. In *Behavior and Adaptation in Insects* (C. OSHIMA, ed.), Baifukan, Tokyo, pp. 1–15 (in Japanese).
- HIDAKA, T. (1975) *Why Does the Butterfly Fly?* Iwanami, Tokyo, 178 pp. (in Japanese).
- JOLLY, G. M. (1965) Explicit estimates from capture-recapture data with both death and immigration — stochastic model. *Biometrika* **52**: 225–247.
- J.S.A.E.Z. (1980) *Major Insect and Other Pests of Economic Plants in Japan*. (Japanese Society of Applied Entomology and Zoology, ed.), Japan Plant Protection Association, Tokyo, 307 pp. (in Japanese).
- KAWAZOE, A. and M. WAKABAYASHI (1976) *Coloured Illustrations of the Butterflies of Japan*. Hoikusha, Osaka, 422 pp. (in Japanese).
- LEDERHOUSE, R. C. (1982) Factors affecting equal catchability in two swallowtail butterflies, *Papilio polyxenes* and *P. glaucus*. *Ecol. Entomol.* **7**: 379–383.
- LEDERHOUSE, R. C. (1983) Population structure residency and weather related mortality in the black swallowtail butterfly, *Papilio polyxenes*. *Oecologia* **59**: 307–311.
- SCOTT, J. A. (1968) Hilltopping as a mating mechanism to aid the survival of low density species. *J. Res. Lepid.* **7**: 191–204.
- SHIELDS, O. (1967) Hilltopping. *J. Res. Lepid.* **6**: 69–178.
- SUZUKI, Y., M. TAKAGI and M. YAMANAKA (1974) Studies on the dispersal of *Papilio xuthus* L. (Lepidoptera: Papilionidae) by mark-and-recapture method at their nocturnal roosting sites. *Kontyû* **42**: 79–86 (in Japanese with an English summary).
- SUZUKI, Y., K. YAMAGUCHI, M. IGA, Y. HIROSE and H. KIMOTO (1976) Spatial distribution of the eggs of *Papilio xuthus* LINNÉ (Lepidoptera: Papilionidae) in a citrus grove. *Jap. J. appl. Ent. Zool.* **20**: 177–183 (in Japanese with an English summary).
- TSUBAKI, Y. (1973) Natural mortality and its factors on the immature stages in the population of the swallowtail butterfly, *Papilio xuthus* LINNÉ. *Jap. J. Ecol.* **23**: 210–217 (in Japanese with an English summary).
- WATANABE, M. (1979 a) Natural mortalities of the swallowtail butterfly, *Papilio xuthus* L., at patchy habitats along the flyways in a hilly region. *Jap. J. Ecol.* **29**: 85–93.
- WATANABE, M. (1979 b) Oviposition of the swallowtail butterfly, *Papilio xuthus* L. (Lepidoptera: Papilionidae) in a deforested area. *Appl. Ent. Zool.* **14**: 484–487.
- WATANABE, M., K. NOZATO, K. KIRITANI and S. MIYAI (1984) Seasonal fluctuations of egg density and survival rate in Japanese black swallowtail butterflies. *Jap. J. Ecol.* **34**: 271–279.
- YAMANAKA, M. Y., SUZUKI and M. TAKAGI (1978) Estimation of egg number oviposited per day by a female of *Papilio xuthus* LINNÉ (Lepidoptera: Papilionidae). *Kontyû* **46**: 329–334 (in Japanese with an English summary).