Geographic Variation of Flight Muscle Dimorphism in Adult Females of a Scarabaeid, *Heptophylla picea*

Shigeo TADA,¹ Kenpei HONMA,^{2,3} Masashi KAKIZAKI,⁴ Kenji FUJISAKI
and Fusao NAKASUJI

Entomology Research Group, Faculty of Agriculture, Okayama University, Tsushima-Naka, Okayama 700, Japan

² *National Research Institute of Vegetables, Ornamental Plants and Tea, Kanaya, Shizuoka 428, Japan*

⁴ *Hokkaido Central Agricultural Experiment Station, Naganuma, Hokkaido 069-13, Japan*

(Received 7 February 1994; Accepted 14 June 1995)

Adult males of the scarabaeid, *Heptophylla picea* MOTSCHULSKY, have flight muscles, whereas a portion of adult females loses their muscles. Geographic variation of the proportion of muscled females (PMF) in Japan was investigated with 54 population samples from diverse localities. Geographic trends in PMF variation were substantially different between the two areas; muscled females were prevalent in eastern-central Hokkaido (PMF = 100%), while in Oshima Peninsula, Honshu, and Shikoku, both types of females occurred and PMF varied irregularly from 0 to 100%. Based on the geographic trends, we hypothesize a possible process for the establishment of *H. picea* populations, including muscleless females, in the Japanese Archipelago, and discuss why the dimorphism is maintained in certain areas of its distribution.

Key words: *Heptophylla picea*, Scarabaeidae, geographic variation, flight muscle dimorphism

INTRODUCTION

Many insect species exhibit polymorphisms that affect flight ability, e.g., variations in wing length and flight muscle development (HARRISON, 1980). The mode of dispersal polymorphism in a habitat should indicate the ability of insects to respond to environmental factors that reflect local patch quality (HARRISON, op. cit.). Geographic variation of wing polymorphisms has been studied in several coleopteran species, such as coccinellid (POPE, 1977; HAMMOND, 1985) and carabid beetles (HONĚK, 1981; LANGOR and LARSON, 1983; LIEBHERR and HAJEK, 1986; SPENCE and SPENCE, 1988; AUKEMA, 1991). Geographic patterns in the variation of flight muscle polymorphism in beetles, however, still remain poorly understood.

In a scarabaeid, *Heptophylla picea* MOTSCHULSKY, all adult males have fully developed flight muscles, whereas adult females show a flight muscle dimorphism; muscled females and muscleless ones (TADA et al., 1991). NISHIGAKI and OHTAKI (1991) reported that only 4 of 137 adult females collected from Shizuoka had flight muscles and these were able to fly, the remaining 133 females did not have flight muscles. HONMA (1990) described the proportion of muscled females (PMF) in four localities in Japan, 1990: 100% in Hokkaido (Kurisawa), 5.2% in Tochigi (Nishi-Nasuno), 18.7% in Saitama (Iruma) and 1.2% in

¹ Present address: *National Institute of Sericultural and Entomological Science, Tsukuba, Ibaraki 305, Japan*

³ Present address: *823-29, Shimo-Kawashima, Shimodate, Ibaraki 308, Japan*

Table 1. Proportion of muscled females (PMF) of *Heptophylla picea* collected in Japan from 1990 to 1993

Collecting sites ^a	Latitude (°N)/ altitude (m)	Vegetation types	No. of females examined	PMF (%)	Recessive gene frequency
1. Fukagawa	43.72/55	Japanese yew ¹	39	100.0	1.00
2. Takikawa	43.57/48	<i>Lonicera caerulea</i> ²	73	100.0	1.00
3. Bibai A	43.32/25	<i>L. caerulea</i>	310	100.0	1.00
Bibai B		<i>L. caerulea</i>	428	100.0	1.00
4. Kurisawa	43.12/20	<i>L. caerulea</i>	131	100.0	1.00
5. Sapporo	43.05/17	Copes	10	100.0	1.00
6. Naganuma A	43.00/13	<i>L. caerulea</i>	537	100.0	1.00
Naganuma B		Larch ³	479	100.0	1.00
7. Obihiro A	42.92/39	Japanese yew	87	100.0	1.00
Obihiro B		Larch	31	100.0	1.00
8. Nemuro A	42.90/80	Street trees	8	100.0	1.00
Nemuro B		Undergrowth	24	100.0	1.00
9. Tomakomai	42.62/6	Azaleas ⁴	34	100.0	1.00
10. Tohya A ^b	—/—	Larch	41	100.0	1.00
Tohya B ^b		<i>L. caerulea</i>	31	100.0	1.00
11. Toyoura ^b	—/—	Japanese yew	59	100.0	1.00
12. Date	42.48/84	<i>L. caerulea</i>	128	100.0	1.00
13. Iwamizawa	43.20/48	Japanese yew	115	98.3	0.99
14. Hiroshima ^b	—/—	Japanese yew	75	92.0	0.96
15. Yoichi	43.17/20	Japanese yew	35	28.6	0.53
16. Kuromatsunai	42.65/27	Japanese yew	157	7.0	0.26
17. Oshamanbe	42.52/10	Japanese yew	9	22.2	0.47
18. Ohno A	41.88/25	Japanese yew	469	11.3	0.37
Ohno B		Larch	143	12.6	0.35
19. Hakodate A	41.82/33	Azaleas	388	12.4	0.35
Hakodate B		Japanese yew	377	17.5	0.42
Hakodate C		Japanese yew	158	26.6	0.52
Hakodate D		Japanese yew	24	37.5	0.61
Hakodate E		Larch	11	0.0	0.00
Hakodate F		Larch	14	57.1	0.76
20. Hirosaki	40.62/55	Azaleas	581	13.9	0.37
21. Rokunohe	40.52/130	Blueberry ⁵	61	21.3	0.46
22. Morioka	39.70/155	Azaleas	325	10.8	0.33
23. Fukushima	37.75/67	Azaleas	275	3.3	0.18
24. Joetsu	37.10/13	Azaleas	138	62.3	0.79
25. Nakago	36.95/320	Azaleas	224	3.6	0.19
26. Nagano	36.67/418	Azaleas	121	0.0	0.00
27. Nishi-Nasuno	36.92/320	Azaleas	508	3.0	0.17
28. Iruma	35.80/148	Tea ⁶	371	15.1	0.39
29. Mizuho	35.77/137	Tea	101	36.6	0.60
30. Chiba	35.53/50	Azaleas	20	0.0	0.00
31. Fuji	35.18/65	Tea	70	0.0	0.00
32. Shimizu	35.05/3	Tea	144	0.0	0.00
33. Shizuoka	34.80/14	Azaleas	8	0.0	0.00
34. Kanaya	34.80/202	Tea	563	0.2	0.04

Table 1. (continued)

Collecting sites ^a	Latitude (°N)/ altitude (m)	Vegetation types	No. of females examined	PMF (%)	Recessive gene frequency
35. Makinohara	34.77/191	Tea	145	2.1	0.14
36. Toyohashi	34.72/23	Tea	170	0.0	0.00
37. Nagoya	35.85/51	Azalcas	10	0.0	0.00
38. Tsukigase	34.70/250	Tea	150	100.0	1.00
39. Yamazoe	34.67/350	Tea	36	100.0	1.00
40. Yonago	35.42/6	Azalcas	275	6.5	0.25
41. Kume	35.05/170	Bush clover ⁷	86	95.3	0.98
42. Okayama	34.65/3	Azalcas	103	3.9	0.20
43. Tokushima	34.07/2	Azaleas	135	74.8	0.86

^a A map is given in Fig. 1.

^b Data on latitude and altitude are unavailable.

¹ *Taxus cuspidata*; ² *Lonicera caerulea* L. var. *emphylllocaryx*; ³ *Larix leptolepis*; ⁴ *Rhododendron* spp.; ⁵ *Vaccinium corymbosum*; ⁶ *Camellia sinensis*; ⁷ *Lespedeza bicolor*.

Shizuoka (Kanaya), and pointed out the occurrence of a geographic morpho-ratio variation.

Since the flight muscle dimorphism of *H. picea* females follows a Mendelian trait with the muscleless form being dominant to the muscled one (TADA et al., 1994), it is predicted that PMF in newly established habitats will tend to show a large value relative to successive surrounding populations. Here, we describe geographic patterns in flight muscle dimorphism, and discuss the acquisition process of the dimorphism in *H. picea*.

MATERIALS AND METHODS

H. picea adults mating on the ground or in shrubs were collected from the various localities in Japan indicated in Fig. 1 and Table 1. Collections were carried out between 18:00 and 21:00 during mid June through early July, from 1990–1993. Latitude, altitude and vegetation of the collecting sites were recorded, and are summarized in Table 1. All specimens collected were preserved in 70% ethanol solution, and later, the metathorax of each female was dissected to observe the flight muscles.

RESULTS

The data obtained from each collecting site in different years were pooled for the calculations of PMF, since little yearly fluctuation was observed in the values; e.g., in Nishi-Nasuno, values were 5.2, 2.5, and 2.4% in 1990, 1991 and 1992, respectively. Table 1 shows PMF values for 54 sites at 43 localities in Japan, together with recessive gene frequencies calculated under the assumption of Hardy-Weinberg equilibrium.

Figure 1 depicts geographic trends in PMF variation. All females at most collecting sites of eastern-central Hokkaido had flight muscles (Spl. Nos. 1–12; PMF = 100%), except Yoichi (No. 15), Iwamizawa (No. 13) and Hiroshima (No. 14). In contrast, most samples from southwestern Hokkaido (the Oshima Peninsula; Nos. 16–19) contained only 10–20% muscled females. In Honshu and Shikoku (Nos. 20–43), PMF tended to be lower, as in southwestern Hokkaido, but varied irregularly from 0 to 100%. Almost all females were

Fig. 1. Collecting localities of *H. picea* adults examined. Numerals correspond to the localities given in Table 1. Samples are divided into four classes based on their recessive gene frequencies (Table 1).

muscleless in the coastal areas of the Pacific Ocean along southern Honshu (Nos. 30–37; PMF $\approx$ 0%).

The relationship between the latitude and the altitude of the collecting sites and the arcsine transformed PMF values were significantly positive ($r = 0.53$, $p < 0.001$), or insignificant ($r = -0.13$, $p > 0.05$), respectively. However, the former significance is expected to be no more than a reflection of the above mentioned geographic trends.

Table 2 summarizes the differences in recessive gene frequency among collecting sites based on vegetation type, dividing localities into eastern-central Hokkaido (hereafter referred to as northern area) and others (southern area). In the northern area, the recessive gene occurred in only a few populations on yew trees (*Taxus cuspidata*) which, at least in part, could be transplanted artificially. In the southern area, on the other hand, the gene fre-

Table 2. Frequencies of the recessive allele for muscled female in *Heptophylla picea* populations collected on different vegetation types. Given in mean $\pm$ SD, (range), and number of population samples.

Vegetation types	Gene frequency of populations in				
	Eastern-central Hokkaido			Other areas	
<i>L. caerulea</i> ¹ field	1.00	(1.00)	7	—	(—) 0
Hedge of yew ² trees	0.91 $\pm$ 0.17	(0.53–1.00)	6	0.44 $\pm$ 0.11	(0.26–0.61) 6
Larch ³ grove	1.00	(1.00)	3	0.37 $\pm$ 0.31	(0.00–0.76) 3
Shrubbery of azaleas ⁴	1.00	(1.00)	1	0.26 $\pm$ 0.26	(0.00–0.86) 14
Tea ⁵ field	—	(—)	0	0.35 $\pm$ 0.40	(0.00–1.00) 9
Others	1.00	(1.00)	3	0.72 $\pm$ 0.26	(0.46–0.98) 2
Total	0.97 $\pm$ 0.10	(0.53–1.00)	20	0.35 $\pm$ 0.31	(0.00–1.00) 34

¹ *Lonicera caerulea* L. var. *emphyllocalyx*; ² *Taxus cuspidata*; ³ *Larix leptolepis*; ⁴ *Rhododendron* spp.; ⁵ *Camellia sinensis*.

quency in populations on the most prevailing vegetation, azaleas (*Rhododendron* spp.) or tea plant (*Camellia sinensis*), tended to be lower than those on other types of vegetation. Even within the same vegetation, PMF values varied extremely among collecting sites in the southern area.

DISCUSSION

The present study demonstrated the geographic trend in flight muscle dimorphism in females of *H. picea*. The trends could be summarized as follows: 1) muscled females monopolized the northern area (eastern-central Hokkaido), while 2) dimorphism was observed in the southern area (Oshima Peninsula, Honshu, and Shikoku), where muscleless females prevail, but PMF varied from population to population. And, 3) populations in the coastal area of the Pacific Ocean in Honshu (hereafter referred to as the Coastal Area) were virtually monopolized by muscleless females. Based on these trends, the following scenario can be inferred.

Reconstruction of the evolutionary history of H. picea in the Japanese Archipelago

H. picea is endemic to the Japanese Archipelago (MURAYAMA, 1950; KOBAYASHI, 1989). The three other congeneric species are also distributed in East Asia: *H. brevicollis* (FAIRMAIRE) in mountainous districts of central China (MEDVEDEV, 1951), *H. formosana* NIJIMA et KINOSHITA, in Puli, Taiwan Is. (NIJIMA and KINOSHITA, 1927), and *H. tosana* MIYATAKE on Shikoku Is., Japan (MIYATAKE, 1963). As the phyletic relationship among the four species has not yet been analyzed, it is difficult to speculate the ancestry of *H. picea* and the process of its invasion into the Japanese Archipelago. We can hypothesize, however, that ancestral populations invaded into the archipelago during one of the ice ages when the Korean and Tsushima Straits were closed, since the beetle cannot migrate over the sea.

During the final Würm ice age (ca. 22,000 yBP), they should have inhabited southern localities compared with the present distributional range, due to coldness at that time. But in the later post glacial age, they expanded northward, as in a coccinellid species, described by HOSHIKAWA (1983). In this process, earlier than the final opening of Tsugaru Strait (18,500 yBP), a mutation occurred producing a new dominant allele. Thus, muscleless

females appeared in a portion of the populations. That no other associated change was hitherto detected with the flight-muscleless mutation might indicate a relatively recent acquisition of this dominant allele.

At that time, populations at the front of the northward expansion consisted exclusively of recessive homozygote individuals, and the introgression of a new dominant gene followed after the front. The introgression had, however, been cut off by occurrence of a geographic barrier at the Kuromatsunai lowland, presumably in the Johmon Period (ca. 6,000 yBP). That brought two disjunct population groups of *H. picea*; one located northward of the barrier in which all females had flight muscles, and the other southward of the barrier in which females were dimorphic in flight muscle development.

The area where the mutation occurred is unknown, but the Coastal Area is a plausible candidate, since almost all females there (Nos. 30–37) are muscleless.

The barrier disappeared quite recently, and the two disjunct population groups made secondary contact. The occurrence of the dominant gene in a few populations in the northern area (Nos. 13–15) might be a result of this secondary contact, though a portion is probably due to artificial colonization. The above hypothesized process would result in the present state of geographic variation illustrated in Fig. 1.

Maintenance of the flight muscle dimorphism in H. picea populations in the southern area

It was confirmed that the flight muscle dimorphism of *H. picea* females follows a simple Mendelian trait with the muscleless form being dominant to the muscled one (TADA et al., 1994). Since muscleless females (dominant homozygotes or heterozygotes) are less mobile than muscled ones around their natal habitats, the dominant allele for musclelessness should increase in a stable habitat with constantly abundant resources. That is, in such a habitat, the emigration rate of the recessive allele should be higher. For this reason, the frequency of the dominant allele for musclelessness will increase in a stable habitat with advanced generations. The extremely small PMF in the Coastal Area (Spl. Nos. 30–37) might imply a high stability of the habitats there.

It is known that the quality of habitats affects the proportion of macropters in wing dimorphic Coleoptera (DEN BOER, 1970; HAMMOND, 1985). *H. picea* tends to prefer the vegetation of habitats in a certain successional phase, i.e., shrubs or sparse woods (Table 2). The dominant allele for musclelessness has a crucial disadvantage on this point. The progress of succession should deprive the flight-muscleless female of her advantage in exemption from mortality during dispersal, and finally should bring about the extinction of the whole population.

Although the details on how and to what degree the two morphs disperse in the field remain unknown at least in the case of *H. picea* inhabiting shrubs or sparse woods, the recessive allele for muscled females is indispensable to allow survival under changing environmental conditions.

ACKNOWLEDGEMENTS

We are grateful to C. KITAHARA and T. YUGUCHI for their help in this study and sincerely thank the following entomologists for cooperating in collection of insects: Y. ANDO, M. FURUYA, N. HABU, M. HASEGAWA, Y. HIRAI, K. HOSHIKAWA, R. IGARASHI, Y. IGARASHI, T. INOKO, I. ISHIKAWA, M. ISHITANI, S. KODOMARI, N. KUIOI, M. MATSUMURA, T. MIZUKOSHI, Y. MORO, Y. MUSA, Y. NAKANISHI, H. NAKAZAWA, T. OKADA, K. OKAMOTO, S. OKUYAMA, S. ÔYA, T. SANO, T. SATO, Y. SATO, M. SAWADA, H. TORIKURA, K. YAMAGISHI, A. YAMAMOTO, and M. YUKINARI. We also express our appreciation to T. NAKANE for providing us with valuable

references. We are extremely thankful to two anonymous referees for their many suggestive comments on earlier drafts of this paper.

REFERENCES

- AUKEMA, B. (1991) Fecundity in relation to wing-morph of three closely related species of the *melanocephalus* group of the genus *Calathus* (Coleoptera: Carabidae). *Oecologia* **87**: 118–126.
- DEN BOER, P.J. (1970) On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). *Oecologia* **4**: 1–28.
- HAMMOND, P.M. (1985) Dimorphism of wings, wing-folding and wing-toiletry devices in the ladybird, *Rhyzobius litura* (F.) (Coleoptera: Coccinellidae), with a discussion of inter-population variation in this and other wing-dimorphic beetle species. *Biol. J. Linn. Soc.* **24**: 15–33.
- HARRISON, R.G. (1980) Dispersal polymorphisms in insects. *Annu. Rev. Biol. Syst.* **11**: 95–118.
- HONĚK, A. (1981) Wing polymorphism in *Notiophilus biguttatus* in Bohemia (Coleoptera, Carabidae). *Věst. Čs. Společ. Zool.* **45**: 81–86.
- HONMA, K. (1990) Geographic variation of the proportion of female adults with flight muscles in *Heptophylla picea* MOTSCHULSKY (Coleoptera: Scarabaeidae). *Tea Res. J.* **72** (suppl.): 82–83 (in Japanese).
- HOSHIKAWA, K. (1983) Host-race formation and speciation in the *Henosepilachna vigintioctomaculata* complex (Coleoptera, Coccinellidae) II. Geographic variation of food preference in *Henosepilachna vigintioctomaculata*. *Kontyû* **51**: 339–350.
- KOBAYASHI, H. (1989) *A Check List of Japanese Insects. I* (Entomol. Lab., Fac. Agric., Kyushu Univ. and Japan Wildlife Res. Center, eds.). Entomol. Lab., Fac. Agric., Kyushu Univ., Fukuoka, Japan, 540 pp. (in Japanese).
- LANGOR, D.W. and D.J. LARSON (1983) Alary polymorphism and life history of a colonizing ground beetle, *Bembidion lampros* HERBST (Coleoptera: Carabidae). *Coleopt. Bull.* **37**: 365–377.
- LIEBHERR, J.K. and A.E. HAJEK (1986) Geographic variation in flight wing development and body size of the tule beetle, *Tanystoma masculicolle* (Coleoptera: Carabidae). *Pan-Pacific Entomol.* **62**: 13–22.
- MEDVEDEV, S.I. (1951) Scarabaeidae, Melolonthinae. *Fauna SSSR* **10** (1): 1–512 (in Russian).
- MIYATAKE, M. (1963) A new species of the genus *Heptophylla* from Shikoku, Japan (Coleoptera: Melolonthidae). *Trans. Shikoku Entomol. Soc.* **8**: 23–25.
- MURAYAMA, J. (1950) *Iconographia Insectorum Japonicum*, 2nd ed. Hokuryukan, Tokyo, 1738 pp. (in Japanese).
- NIJIMA, Y. and E. KINOSHITA (1927) Die untersuchungen über Japanische Melolonthiden III. Erster Nachtrag der Melolonthiden Japans und ihre Verbreitung. *Res. Bull., Coll. Exp. Forest Coll. Agric., Hokkaido Imp. Univ.* **4**: 1–97 (in Japanese with German summary).
- NISHIGAKI, J. and K. OHTAKI (1991) Flight dimorphism of the yellowish elongate chafer, *Heptophylla picea* MOTSCHULSKY (Coleoptera: Scarabaeidae). *Appl. Entomol. Zool.* **26**: 255–261.
- POPE, R.D. (1977) Brachyptery and wing-polymorphism among the Coccinellidae (Coleoptera). *Syst. Entomol.* **2**: 59–66.
- SPENCE, J.R. and D.H. SPENCE (1988) Of ground-beetles and men: introduced species and the synanthropic fauna of western Canada. *Mem. Entomol. Soc. Can.* **144**: 151–168.
- TADA, S., A. YAMAMOTO and J. NISHIGAKI (1991) Flight muscle dimorphism of female adults in the yellowish elongate chafer, *Heptophylla picea* MOTSCHULSKY (Coleoptera: Scarabaeidae). *Appl. Entomol. Zool.* **26**: 515–521.
- TADA, S., K. HONMA, M. KAKIZAKI, K. FUJISAKI and F. NAKASUJI (1994) Genetic mode of flight muscle dimorphism in a scarabacid, *Heptophylla picea* MOTSCHULSKY. *Appl. Entomol. Zool.* **29**: 303–305.