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Period of adult activity and response to wood moisture content as major segregating factors in the coexistence of two conifer longhorn beetles, *Callidiellum rufipenne* and *Semanotus bifasciatus* (Coleoptera: Cerambycidae)

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Abstract. The cerambycid borers *Callidiellum rufipenne* (Motschulsky) and *Semanotus bifasciatus* (Motschulsky) infest coniferous logs in Japan, with the latter distributed in the north and at high altitudes, where both species occur sympatrically. *Semanotus bifasciatus* adults were active at low temperatures and very active after sunset, and less active but never inactive in the daytime, whereas *C. rufipenne* adults were usually active at high temperatures and almost only in the daytime. At an almost constant temperature, *C. rufipenne* adults were almost inactive at night, whereas *S. bifasciatus* adults showed only an obscure decline in activity in the morning. Of a horizontal log, the upper surface tended to be drier and lower surface wetter, and *C. rufipenne* larvae grew large if they were in the upper part of a log, whereas *S. bifasciatus* larvae grew large if in the lower part. Thus, the coexistence of these two species can be ascribed to two major segregation factors: adult segregation based on temperature and sunshine, and larval segregation associated with the moisture content of the wood.

INTRODUCTION

Resource partitioning, or niche segregation, is an important aspect of ecology, and for wood-boring insects, it is of paramount importance, especially in crowded conditions, because their larval habitat is usually restricted to the wood in which they occur (Beaver, 1984). Despite a large number of species in the Cerambycidae, there are very few studies on the niche segregation in sympatric species [e.g. Hellrigl (1971) on *Monochamus* spp.], compared to Scolytidae, for which there are many studies (e.g. Paine et al., 1981; Rankin & Borden, 1991).

Two cerambycid species (Cerambycinae: Callidiini), *Callidiellum rufipenne* (Motschulsky), which occurs in the Korean Peninsula, Sakhalin (Russia) and almost the whole of Japan (Niisato, 1992), and *Semanotus bifasciatus* (Motschulsky), in Japan (South Hokkaido, Honshu), the Korean Peninsula and China (Wu & Jiang, 1986; Niisato, 1992), are secondary borers of *Cryptomeria japonica* D. Don (Taxodiaceae), *Chamaecyparis obtusa* Sieb. & Zucc. (Cupressaceae) and *Thujopsis dolabrata* (L. fil.) Sieb. & Zucc. (Cupressaceae) in Japan (Kojima & Nakamura, 1986). Distribution of the latter species is limited to northern parts and high altitudes, where both species occur sympatrically. In Nagano Prefecture *Ch. obtusa* logs infested with *S. bifasciatus* are always also infested with *C. rufipenne* (Hori, 1970). The adult flight period of both species is early spring in Japan (Hori, 1970; Shibata, 1994), like in the other *Semanotus* species that occur in the temperate zones of the northern hemisphere (Wickman, 1968; Zhang et al., 1983; Kobayashi, 1984). These two species, thus, may provide a model for studying niche segregation in Cerambycidae.

After the first observation of the co-occurrence of both species at Yunokoya Lumberyard, Minakami, Gunma Prefecture, in *Ch. obtusa* and *T. dolabrata* logs in May 1989, observations were continued in this area until 1995 on the niche segregation of these two species.

MATERIAL AND METHODS

Field observations on the adult activity of *S. bifasciatus* were carried out in May 1990 at Takaragawa Field Research Station (FFPRI), Minakami, Gunma Prefecture, Japan (alt. 790 m) and at Yunokoya Lumberyard, Minakami (alt. 770 m). Further observations on the activities of adults of the two species were carried out in 1991–1992 at Yunokoya Lumberyard, Yamamoto Lumberyard (alt. 620 m) and Tsunako (alt. 550 m), Minakami, Gunma Prefecture. Air temperature, and numbers of individuals of both species active on, resting on, and emerging from logs were recorded.

Adult beetles of both species observed in the lumberyards in 1992 were captured, and brought into the laboratory, where the beetles were placed in two plastic containers (31 × 45 × 24 cm high), and their diel activity observed. In the evening of May 19 1992, ten males and five females of each of the two species were introduced into one of the plastic containers with 5 *Cr. japonica* logs. After about 20 h, their behaviour was observed for 10–15 min at hourly intervals over the following 24 h. Whether they were resting, walking, mounting, copulating or ovipositing was recorded. At each observation, the air temperature in the containers was recorded. During the period of observation the laboratory illumination was switched off from sunset to sunrise.

Adults of the two species were collected at Yunokoya Lumberyard early in May 1990, brought into the laboratory, and allowed to mate and copulate conspecifically in Petri dishes. Several pairs of both species were selected, released together into a container with a newly felled *T. dolabrata* log (about 8 cm in diameter and about 30 cm in length) and left to mate and oviposit on the log. Four months later, the bark of each log was

* Deceased in 1995.

TABLE 1. Numbers of *Callidiellum rufipenne* and *Semanotus bifasciatus* adult beetles observed at Minakami, Gunma Prefecture in 1991–1992.

Spot (alt.)	Date	Time period	Air temperature (°C)	*Callidiellum rufipenne*						*Semanotus bifasciatus*				Log species
				Active[a]		Resting[b]		Emerging[c]		Active[a]		Resting[b]		
				Male	Female	Male	Female	Male	Female	Male	Female	Male	Female	
Yunokoya Lumberyard (770 m)	May 1, 1991	13:00–14:00	not recorded	0	0	0	0	0	0	0	0	4	6	*T. dolabrata, Cr. japonica*
ditto	May 11, 1991	17:05–17:30	18	0	0	0	1	0	0	0	0	1	1	*T. dolabrata, Cr. japonica*
ditto	ditto	19:20–20:20	12	0	0	0	0	0	0	9	8	0	2	*T. dolabrata, Cr. japonica*
ditto	June 9, 1991	13:40–15:00	27	18	10	0	0	0	0	0	0	0	0	*T. dolabrata, Cr. japonica*
ditto	May 2, 1992	12:45–14:05	16	1	1	0	0	0	0	0	0	20	17	*T. dolabrata*
ditto	ditto	21:20–22:10	5	0	0	0	0	0	0	12	10	7	4	*T. dolabrata*
ditto	May 6, 1992	20:10–20:50	8	0	0	0	0	0	0	13	10	1	5	*T. dolabrata*
ditto	May 16, 1992	13:30–14:00	20	26	4	1	0	0	0	0	0	0	0	*T. dolabrata*
ditto	May 31, 1992	17:00–18:35	14	0	0	24	20	0	0	0	0	4	2	*T. dolabrata*
ditto	June 19, 1992	16:00–18:00	15	3	4	8	9	0	0	0	0	0	0	*T. dolabrata*
Yamamoto Lumberyard (620 m)	May 11, 1991	15:00–16:00	21	15	4	0	0	0	0	0	1	2	0	*Cr. japonica, Ch. obtusa*
ditto	ditto	21:10–21:35	13	0	0	0	0	0	0	3	2	2	0	*Cr. japonica, Ch. obtusa*
ditto	May 3, 1992	10:50–11:35	17	1	3	3	1	11	7	0	0	0	0	*Cr. japonica*
ditto	May 15, 1992	12:20	20	0	0	0	0	0	1	0	0	0	0	*Cr. japonica*
Tsunako (550 m)	May 03, 1992	12:20	15	0	0	0	0	0	0	0	1	0	0	*Cr. japonica*

[a] Those observed walking, flying or mating. [b] Those observed solitary without movement. [c] Those observed emerging out from the logs.

peeled off to expose the larval galleries. One log was selected as the best sample, and the area of all the galleries measured by applying paper to the xylem surface, tracing the galleries on the paper, photocopying the traces on high-quality paper, cutting out the traced gallery area, and measuring the area by weighing. We measured the sizes of the entrance holes, which were made by mature larvae of both species on the xylem surface in elliptic shape prior to forming pupal chambers. Then, after splitting the log, the adult beetles were removed from their pupal chambers, identified, and then the depths of the pupal chambers and the positions of the larval entrance holes of the two species on the log, namely whether on the upper, side or lower surface, were recorded.

To characterize the changes in and differences of the moisture contents of the upper, side and lower surfaces of horizontal logs of *Cr. japonica* and *Ch. obtusa* (45–118 cm long, 6.7–16.7 cm in diameter) they were subjected to the following experiment on 24 Sept. Five *Cr. japonica* logs and six *Ch. obtusa* logs were laid horizontally on the forest floor (University campus, Fujisawa, Japan; an airy, shady site under an evergreen-tree canopy with a thin leaf litter layer), and three *Cr. japonica* logs and four *Ch. obtusa* logs were laid horizontally in containers in the laboratory. From 3 Oct. to 27 Jan., a portion (1.5 × 1.0 × 0.5 cm thick) of wood was sampled from each of the three surfaces (upper, side and lower) of each log using a chisel and immediately weighed (w). The sample chip was then oven-dried (95–100ºC) to obtain the dry weight (w_0), and the moisture content calculated by using the following equation, which is widely used in wood science (Kollmann & Côté, 1968): $M = \{(w - w_0) / w_0\} \times 100\%$.

RESULTS AND DISCUSSION

Adult activity in lumberyards and the laboratory

The behaviour of adult *S. bifasciatus* beetles observed in lumberyards in May 1990 (data not shown) indicated that they are active even at a low air temperature of 11.6°C.

The numbers of individuals of both species recorded in 1991–1992 are summarized in Table 1. It demonstrates that *S. bifasciatus* adults were active at temperature of 5–20°C and very active after sunset, and less active but not inactive in the daytime, whereas *C. rufipenne* adults were usually active at temperature above 15°C and almost only in the daytime.

The results of the hourly observations in the laboratory of the activity of adults of both species are presented in Fig. 1. Starzyk (1968) presented a comparison of the daily adult activity of *Gaurotes virginea* (L.) (Cerambycidae: Lepturinae: Rhagiini) in natural and laboratory conditions and suggested that there is little difference between the two. This may validate our results from the laboratory experiments. At an almost constant temperature, *C. rufipenne* adults exhibited almost no activity between 22:00 and 8:00 and were found hiding under or between the logs. This is consistent with Yogo's (1954) statement that it is a typical diurnal species. On the other hand, *S. bifasciatus* adults showed only an obscure decline in activity before midday. Hori (1970) stated that *S. bifasciatus* adult beetles are nocturnal and active when the temperature is above 5°C between sunset and sunrise. The weak daytime activity, exhibited by *S. bifasciatus*, was also recorded for the congeneric species, *S. japonicus* (Sugiyama et al., 1991, 1992). This difference in the activity pattern of the adults is the most important factor that segregates the adult niches of the two species. In both species, reproductive behaviour (mounting, copulating and ovipositing) generally occurred whenever the beetles were active.

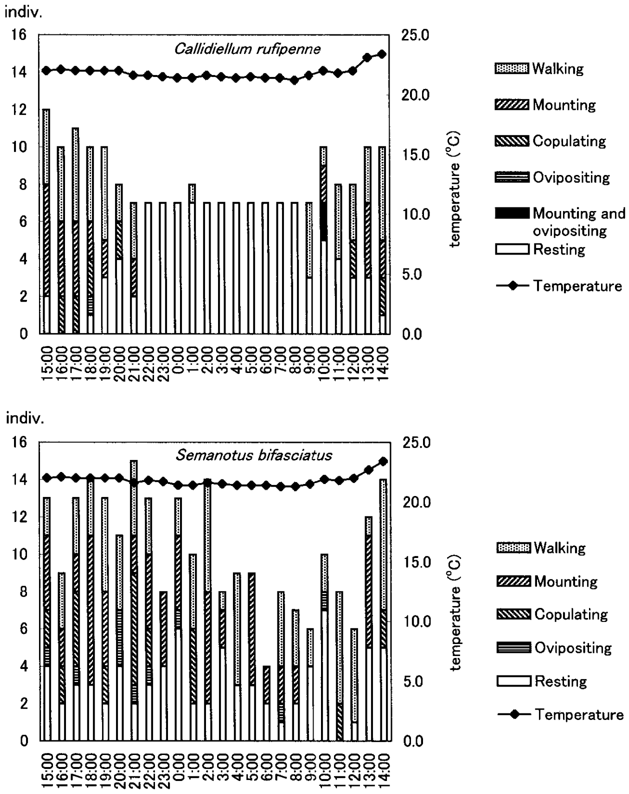

Fig. 1. Daily trends in the activities of adult *C. rufipenne* and *S. bifasciatus*. Observations were recorded every hour between 15:00, May 20 and 14:00, May 21.

Size and position of larval galleries and entrance holes

Distribution of larval entrance holes of the two species were concentrated in certain areas on the logs. The mean crowding values (Lloyd, 1967), in which the surfaces (lower, right side, top, left side) are treated as quadrats, are 11.6 for the two species collectively, 5.6 for *S. bifasciatus* and 2.4 for *C. rufipenne*, which indicate that *S. bifasciatus* shows a preference for a particular surface. Then, all the larval entrance holes were categorized as in either the top or lower surface to check whether the two species showed a preference for either surface. The result indicates that there was no significant preference (Fisher's exact probability test; $p = 0.49$).

Larval gallery area of *C. rufipenne* was 4.95 cm^2/beetle, whereas that of *S. bifasciatus* was 8.52 cm^2/beetle, indicating that the latter species eats about 1.7 times as much as the former species. This is consistent with the fact that adults of *S. bifasciatus* are larger than those of *C. rufipenne*.

Results of the measurement of larval entrance hole sizes and pupal chamber depths on the upper, side and lower surfaces of the log are shown in Table 2. The major axis of the ellipse of entrance hole opening of *S. bifasciatus* (av. 5.3 mm) is significantly larger than that of *C. rufipenne* (av. 3.3 mm) (Mann-Whitney *U* test, $|z| = 4.03$, $p < 0.001$). Also, the pupal chamber of *S. bifasciatus* (av. 28.9 mm) is significantly deeper than that of *C. rufipenne* (av. 14.7 mm) ($U = 10$, $p < 0.05$). These are again consistent with the difference in size of the two species.

If it is assumed that the size of larval entrance hole is correlated with beetle size, as in *Monochamus alternatus* Hope (Lamiinae) (Iwata et al., unpubl.), then the results indicate that *C. rufipenne* larvae grow larger when they develop in the upper surface, whereas *S. bifasciatus* larvae grow larger when in the lower surface. The difference in distribution is assumed to correspond to difference in moisture content in the log.

On the other hand, the depth of the pupal chamber appears not to be associated with beetle size; this parameter seems to be species-specific and probably associated with environmental conditions, including moisture.

As stated by Hori (1970), the positions of the entrance holes differed in the two species: in *C. rufipenne*, they are located at the end of the gallery, whereas in *S. bifasciatus*, they are located slightly off the end of the gallery, indicating a slight retrogression, as in *S. japonica* (Lacordaire) (Minagawa, 1938; Fujishita & Okada, 1968). These may be characteristic of the genera.

Hayakawa & Hori (1971) reported that the lower surface of *Ch. obtusa* logs, lying on the ground, is more favourable for the occurrence and development of *S. bifasciatus* than the top surface. They ascribed this to the lower loss of heat and moisture from the lower than the top surface of logs. The results of our laboratory rearing verified that *S. bifasciatus* occurs mainly in the lower surface and that this can only be ascribed to variation in moisture content since the experiment was carried out in the laboratory, where other environmental factors varied little.

Table 2. Sizes of larval entrance holes and depths of pupal chambers (av. ± S.D.) of *Semanotus bifasciatus* and *Callidiellum rufipenne* in different positions on a *Thujopsis dolabrata* log.

Species		Position on the log		
		upper	side	bottom
S. bifasciatus	*n*	4	4	8
	Major axis of elliptic entrance holes (mm)	4.50 ± 0.77	5.28 ± 1.19	5.62 ± 0.85
	Minor axis of elliptic entrance holes (mm)	2.85 ± 0.76	3.25 ± 0.82	3.55 ± 0.64
	Depth of pupal chambers (mm)	20.1 ± 5.1	26.0 ± 5.9	34.8 ± 7.1
C. rufipenne	*n*	2	3	5
	Major axis of elliptic entrance holes (mm)	3.50 ± 0.40	3.75 ± 0.40	3.02 ± 0.30
	Minor axis of elliptic entrance holes (mm)	2.30 ± 0.10	2.03 ± 0.53	1.92 ± 0.29
	Depth of pupal chambers (mm)	15.8 ± 4.5	15.9 ± 5.0	13.4 ± 2.3

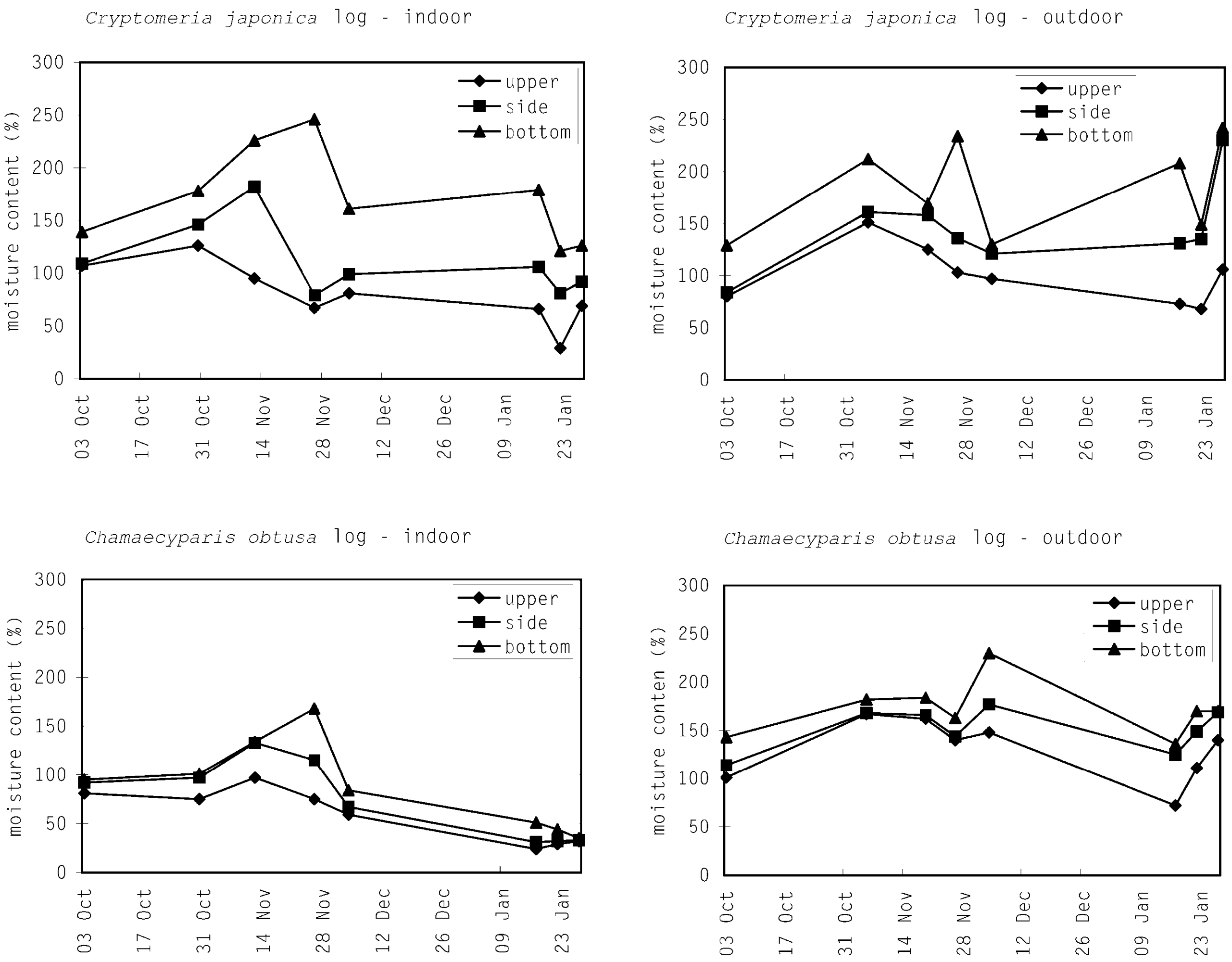

Fig. 2. Trend in the moisture contents of *Cr. japonica* and *Ch. obtusa* logs laid horizontally in the laboratory and the field.

Variations in the moisture content of the wood of horizontal logs

Since the larvae of *C. rufipenne* developed best in the upper surface and those of *S. bifasciatus* in the lower surface of logs, and this was ascribed to a difference in the moisture content of the wood, further experiments were conducted to evaluate the spatial/temporal variation in the moisture content of horizontal logs of *Cr. japonica* and *Ch. obtusa*. For both types of logs in both outdoor and indoor conditions, the moisture content of the lower surface was always the highest, followed by the sides and at the upper surface the lowest (Friedman's test, $p < 0.001$; Fig. 2). This distribution is ascribed to gravity causing the water to move downwards and variation in evaporation due to the different exposure to shade/sunny conditions, although Fisher et al. (1953) mentioned only the latter. The physical factors that mainly determined the distribution of subcortical insects in logs are moisture content and temperature (Graham, 1924, 1925; Hanks et al., 1999). Of these, fluctuation and variation in temperature were thought to be slight in the indoor laboratory condition, yet a variation in the moisture content of the top (dry) and lower (moist) parts of the log was clearly apparent (Fig. 2). The result of laboratory rearing, together with those of log moisture content experiments, indicate that the preference of *S. bifasciatus* and *C. rufipenne* for the lower and top surfaces of horizontal logs, respectively, are associated with the moisture content of the wood.

As well as the congeneric *Callidiellum villosum* (Fairmaire) from China, *C. rufipenne* is known to be a drywood borer in Japan, preferring dry logs, and because of its tolerance of dryness can be transported abroad in timber, as stated by Iwata et al. (2006). This is consistent with the results presented here. It is concluded that *S. bifasciatus* and *C. rufipenne* can coexist in coniferous logs, and their coexistence can be ascribed to two segregation factors: adult segregation based on temperature and sunshine preferences and larval segregation based on wood moisture content.

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