Different parasitism patterns of two hymenopterous parasitoids (Ichineumonidae and Ibaliidae) depending on the development of *Sirex nitobei* (Hym., Siricidae)

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Abstract: For the two parasitoid wasps, *Ibalia leucospoides* and *Megarhyssa praecellens* emerging together with their host woodwasp, *Sirex nitobei*, from trees of *Pinus densiflora*, the seasonal trends in number of emerging adults, their body size characteristics and fecundities were recorded to evaluate the life histories and parasitism patterns.

The mean female body mass of *M. praecellens* was about 1.8 times (fall population) or about 4.1 times (spring population) larger than that of *I. leucospoides*. The difference in body size was remarkable also between sexes in both species. The spring population of *M. praecellens* was about 3.7 times (male) or 2.3 times (female) larger in mean body weight than the fall population. The mean egg length of *M. praecellens* was about 10 times larger than that of *I. leucocpoides*, whereas *I. leucospoides* produced about 50 times greater numbers of eggs than *M. praecellens*. The percentage of parasitism on *S. nitobei* by both parasitoids was considerably large, accounting for more than 60%. Our results suggested that two parasitoid species could utilize larvae of *S. nitobei* in wood as their hosts at different development stages of woodwasp in different manners: egg and/or 1st instar larvae parasitized by *I. leucospoides* and maturated larvae by *M. praecellens*.

1 Introduction

Woodwasps (Siricidae) are primitive hymenopterans which have a specific feeding habit in which their larvae feed primarily on the sapwood of various coniferous and hardwood trees. Most woodwasp species are associated symbiotically with specific fungi, *Amylostereum* spp. Soon after a short dispersal flight, females drill several holes through the bark deep into the sapwood of new host trees and then deposit arthrospores of the fungus together with eggs in the holes (MORGAN, 1968; TALBOT, 1977).

In Australia, *Sirex noctilio* Fab., a European-originated woodwasp species induced accidentally into Australia, has caused serious damage to *Pinus radiata* D. Don trees. The availability of insect parasitoids, *Rhyssa persuasoria* Lin., *Megarhyssa nortoni nortoni* Cresson and *Ibalia leucospoides* Hochenw. introduced for the biological control of *S. noctilio* has thus been intensively studied in Australia (MADDEN, 1968, 1988; TAYLOR, 1976, 1978; TALBOT 1977; NUTTALL, 1980).

In Japan, *Sirex nitobei* Matsumura attacks various coniferous trees, mainly pine trees, which may be responsible for a larger part of the local mortality of pine trees than has ever been considered (KOBAYASHI et al., 1978). Both *Megarhyssa praecellens* Tosquinet and *Ibalia leucospoides* Hochenw. are known as major hymenopterous parasitoids of this woodwasp in Japan (KANAMITSU, 1978). However, their body size characteristics, fecundities, longevities, their seasonal trends in emergence and the proportion of parasitism have

scarcely been known. The primary objective of this study is thus to clarify the biological and ecological aspects of the parasitoids, which may provide fundamental information for the biological control of *S. nitobei*.

2 Materials and methods

2.1 Biologies of the insects

2.1.1 Woodwasp

S. nitobei is distributed all over Japan except Hokkaido Island. The life cycle of this species is usually completed on one year. It emerges from dead pine trees during August and November and usually oviposits weakened pine trees (KANAMITSU, 1978; FUKUDA et al., 1993). *S. nitobei* is associated symbiotically with the specific fungus, *Amylostereum areolatum* (TERASHITA, 1970).

2.1.2 Parasitoid wasps

In the present study, we recognized the two parasitoid species, *M. praecellens* and *I. leucospoides*, emerging from pine trees infested with their host woodwasp, *S. nitobei*.

M. praecellens: The biology of *M. praecellens* has scarcely been known, but other rhyssine species attacking woodwasps are considered to be attracted by smell to trees which had been infested with siricid fungi, *Amylostereum* spp. (SPRADBERY, 1970a; NUTTALL, 1980). The female drills randomly into the wood with her ovipositor until she reaches a siricid larva. The rhyssine larva makes no boring activity in the wood after host feeding, and usually passed about a year in the siricid tunnel

before pupation. Adults bite their way out of the wood and most emerge in spring. Some of the adults which emerge in summer can be progeny from the same season's oviposition (HOCKING, 1968; MADDEN, 1968; SPRADBERY, 1970a; NUTTALL, 1980).

I. leucospoides: This species is initially an endoparasitoid of siricids although its later larval instars feed externally. *I. leucospoides* oviposits into eggs and young larvae of the host. The female adult detects by smell a recent siricid oviposition hole, and inserts her hair-like ovipositor down to gain access to her hosts. Generally a single egg is laid in the hemocoel of the embryo or larva (CRYSTAL, 1930; MADDEN, 1968; SPRADBERY, 1970b; NUTTALL, 1980).

2.2 Experimental procedures

The present study was conducted from August 1992 to June 1994. Two sample trees were taken from the Tokyo University Forest in Aichi, situated about 20 km east of Nagoya City. One weakened tree of *Pinus densiflora* Sieb. et Zucc. infested with *S. nitobei* was felled and then to cut into 18 logs 1 m long, from which 10 logs with many oviposition holes of woodwasps were selected and transferred to an outdoor cage in the Nagoya University Campus in Nagoya City in August 1992 (Group 1), and another infested tree of *P. densiflora* was felled to cut into 17 logs 1 m long, from which 12 logs were selected in the same manner as Group 1 and also transferred to another outdoor cage in June 1993 (Group 2).

During the period from late August to early November in 1992 and late April to early November in 1993 for Group 1, and from late August to early November in 1993 and late April to late June in 1994 for Group 2, we counted the numbers of new adults of parasitoids, *M. praecellens* and *I. leucospoides*, as well as *S. nitobei*, emerging from the logs every day, and measured a few body size parameters for the emerging parasitoids, fresh body weights and ovipositor lengths. In this study, for *S. nitobei* and *M. praecellens*, the body weight of each female includes the weight of eggs because most eggs have already been maturated at the time of emergence.

S. nitobei and the two parasitoid wasps, *M. praecellens* and *I. leucospoides* were transferred individually soon after emergence in a glass jar (diameter: 15 cm × height: 20 cm) and reared with dilute sugared water under laboratory conditions (15–20°C) to detect longevities.

For female adults of *M. praecellens*, the number of mature eggs in the ovaries was counted under stereomicroscope soon after they died. In *I. leucospoides*, mature eggs in the ovaries of female adults could be found under stereomicroscope, but not all eggs were able to be taken out of the ovaries because the egg size is extremely small. In *S. nitobei*, on the other hand, there was a positive correlation between the fresh body weights of emerging females and in the number of eggs (FUKUDA et al., 1993).

Both *M. praecellens* and *I. leucospoides* have been considered as solitary parasitoids (CHRYSTAL, 1930; HOCKING, 1968; KANAMITSU, 1978), and hence one adult parasitoid is likely to derive from one host larva of *S. nitobei*. Thus, the percentage of parasitism in the selected logs could be estimated by the formula,

$$M/(S+M+I) \times 100 \ [\%] \text{ for } M. \ praecellens$$

or

$$I/(S+M+I) \times 100 \ [\%] \text{ for } I. \ leucospoides.$$

where *S*, *M* and *I* denote the number of emerging *S. nitobei* in the tree and the numbers of emerging parasitoids (*M. praecellens* and *I. leucospoides*) in the tree, respectively.

3 Results

3.1 Seasonal changes in the number of emerging adults of wasps

In Group 1, the adult emergence of *S. nitobei* continued for about 2 months, from early September to early November in 1992 (fig. 1). The emergence of two parasitoid species, *M. praecellens* and *I. leucospoides*, continued for about $1\frac{1}{2}$ months. The emergence duration was different between the two species; *M. praecellens* emerged from late August to early October in 1992, while *I. leucospoides* from mid-September to early November in 1992 (fig. 1). In spring 1993, only *M. praecellens* emerged from the logs from early May to mid-June, but no parasitoids emerged from the logs in fall 1993 (fig. 1). On the other hand, in Group 2 the adult emergence of *S. nitobei* continued for about $1\frac{1}{2}$ months, from mid-September to late October in 1993, while the adult of *I. leucospoides* emerged at almost the same period of emergence of *S. nitobei*, but none of *M. praecellens* emerged in this period. The percentages of parasitism on *S. nitobei* in the selected logs estimated by the above formula were considerably large, accounting for about 43% by *M. praecellens* and 26% by *I. leucospoides* in Group 1, and about 64% by *I. leucospoides* in Group 2.
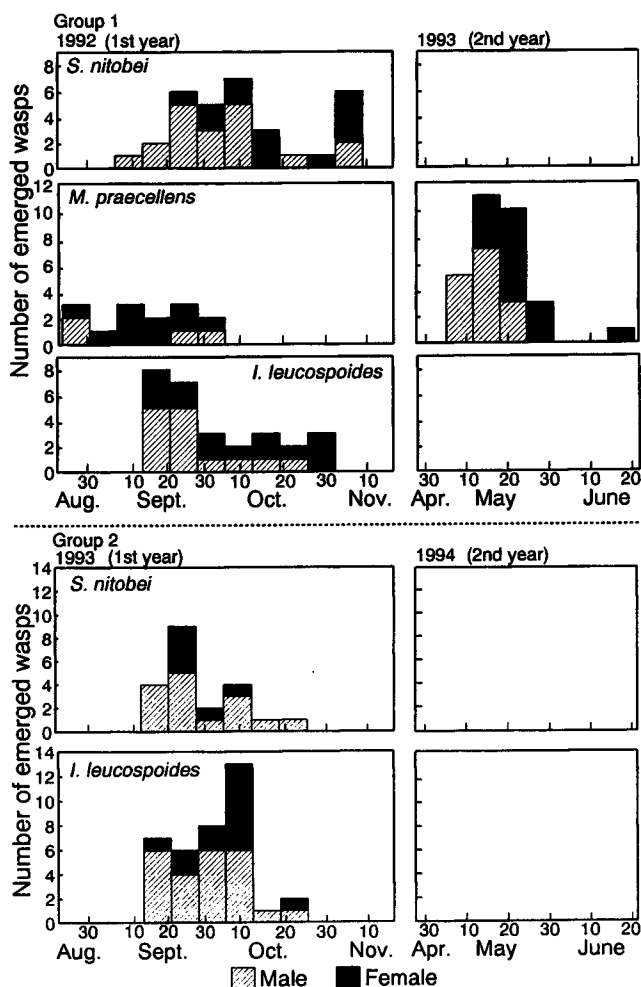

Fig. 1. Seasonal changes in the number of emerged adults of S. nitobei, M. praecellens and I. leucospoides

Table. *Size characteristics and longevities of emerged adults of the woodwasp (*S. nitobei*) and two parasitoid (*M. praecellens *and* I. leucospoides*) species (mean ± SE)*

| Group 1 | S. nitobei (1992) | | M. praecellens | | | | I. leucospoides (1992) | |
| | ♂ (n = 18) | ♀ (n = 14) | Fall population (1992) | | Spring populaiton (1993) | | ♂ (n = 13) | ♀ (n = 13) |
			♂ (n = 4)	♀ (n = 10)	♂ (n = 15)	♀ (n = 15)		
Fresh body weight (mg)	72.0±10.8	151.3±28.2	20.4±3.4**	73.6±11.0**	76.6±10.3	166.3±14.5	27.2±1.0	40.4±3.4
Ovipositor length (mm)	–	9.8±0.5	–	25.8±1.9**	–	36.8±1.5	–	9.4±0.5
Longevity (days)	5.8±0.5	5.1±0.3	3.8±0.9**	5.7±0.4**	6.5±0.6	9.3±1.2	13.5±1.3	17.9±2.0

| Group 2 | S. nitobei | | M. praecellens | | I. leucospoides | |
	♂ (n = 15)	♀ (n = 6)	♂ (n = 0)	♀ (n = 0)	♂ (n = 24)	♀ (n = 13)
Fresh body weight (mg)	50.5±5.1	74.1±13.5	–	–	22.4±2.1	38.1±3.3
Ovipositor length (mm)	–	8.2±0.4	–	–	–	8.9±0.5
Longevity (days)	7.8±0.6	4.0±0.3	–	–	12.8±1.3	15.6±2.2

Significantly different from the values for the spring population of *M. praecellens* (**P < 0.01; *t*-test).

3.2 Adult body sizes and presumed longevity

The fresh body weight of the fall population of *M. praecellens* was smaller than the host insect, *S. nitobei* for both sexes (Male, P < 0.01; Female, P < 0.05, *t*-test), whereas the fresh body weight of the spring population of *M. praecellens* was as large as that of *S. nitobei* for both sexes in Group 1 (P < 0.05, *t*-test) (table). On the other hand, *I. leucospoides* had much smaller bodies than *S. nitobei* for both sexes in both groups. (P > 0.01, *t*-test) (table).

Differences in fresh body weight between sexes were larger in *M. praecellens* than in *I. leucospoides* in Group 1. The ovipositor lengths of *I. leucospoides* were as long as those of *S. nitobei* in both groups, whereas the ovipositor of *M. praecellens* was much longer than that of *S. nitobei* in Group 1 (table). The ovipositor of *M. praecellens* looked tough, but that of *I. leucospoides* was just hair-like. In Group 1, the body weight of *M. praecellens* was much larger in the spring population in 1993 than the fall population in 1992 (table). The longevity of *M. praecellens* were approximated within 1 week in Group 1, whereas that of *I. leucospoides* was about 2–3 weeks in both groups (table).

3.3 Fecundity and egg size

The observed number of eggs produced by a female of *M. praecellens* varied from 4 to 16, averaging about 11. The fresh body weight of a female adult of *M. praecellens* at the time of emergence was correlated positively with the observed number of eggs produced by a female of this species ($r = 0.87$, $P < 0.01$, $n = 26$) (fig. 2), as has been found in *S. nitobei* (Fukuda et al., 1993). The mean length of mature eggs of *M. praecellens* was about 2.3 mm. However, some eggs in the ovaries were scaled down. This suggests that part of egg contents could be reabsorbed in the body.

There were a large number of small-sized mature eggs in the ovaries of *I. leucospoides*: the mean length of egg was about 0.25 mm, but not all eggs in the ovaries were
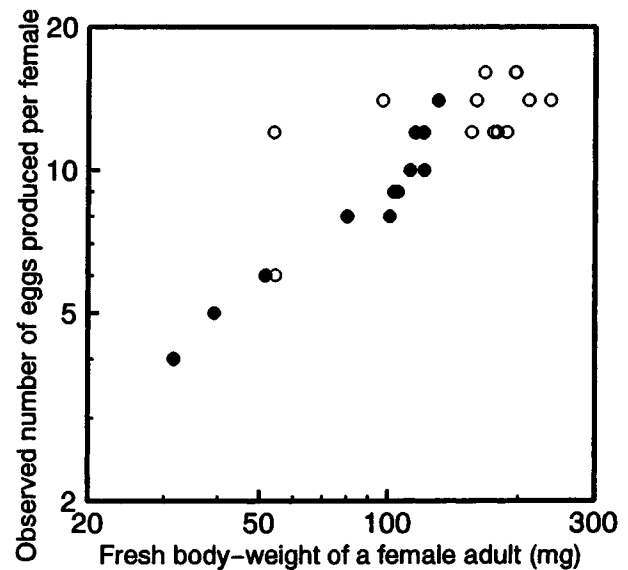

Fig. 2. *Relationship between fresh body weight of female adult and observed number of eggs produced per female of* M. praecellens *in Group 1, on log–log coordinates (*$r = 0.87$, $P < 0.01$, $n = 26$*).* ●: *fall population in 1992;* ○: *spring population in 1993*

able to be taken out. Therefore, we could not count the total number of eggs. Chrystal (1930) estimated that large female adults of this species produced more than 600 eggs.

4 Discussion

Figure 3 is a hypothetical diagram showing when parasitism of the two parasitoids on *S. nitobei* will occur in accordance with the life cycle of *S. nitobei*, based on the records of their emergence. *M. praecellens* has finished its emergence in early October, about 1 month before the last emergence of *S. nitobei*. This period corresponds to the period during which all larvae of *S. nitobei* have
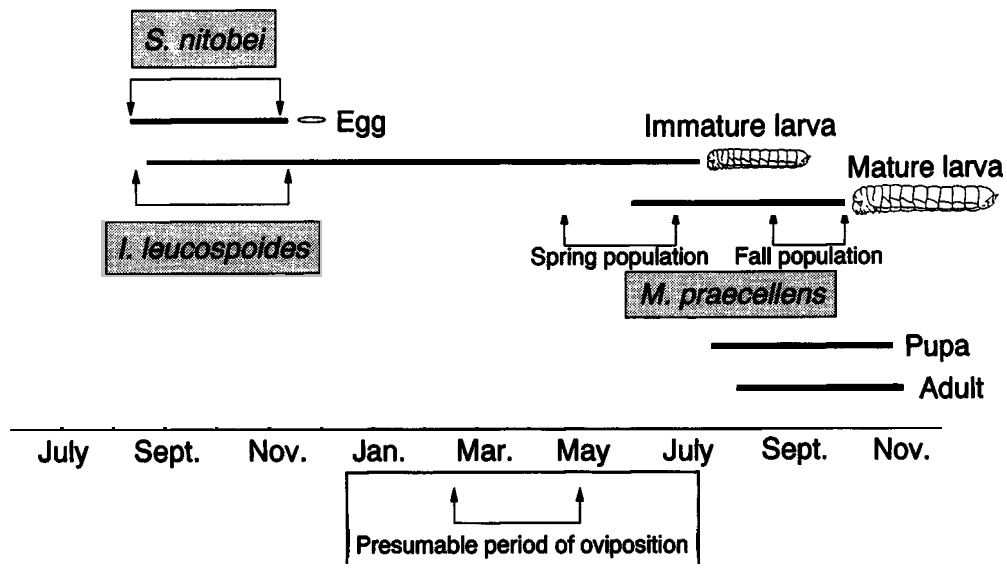
Fig. 3. *Presumable periods of oviposition in the two parasitoid wasps,* M. praecellens *and* I. leucospoides *in accordance with the developmental stages of* S. nitobei. *The life cycle of* S. nitobei *is based on our data and the description by* KATO *(1966)*

finished pupation. This fact suggests that *M. praecellens* will emerge in accordance with the developmental stages of the woodwasp as a host, and mostly can exploit its mature larvae.

The adult body sizes of *M. praecellens* were markedly larger in the spring population than in fall population (table). This difference strongly suggests that the body size of this parasitoid species could be dependent greatly on the initial host size at the time of parasitism. Figure 3 also illustrates that female adults of *M. praecellens* emerging between late April and late May can parasitize nothing but small immature larvae in logs, and therefore their offspring would grow up inevitably into small adults. Larger female adults of *M. praecellens* tend to produce larger number of eggs (fig. 2). The results of the emergence trait suggest that only individuals of *M. praecellens* emerging in early spring and thus parasitizing small host larvae during the period can re-emerge in fall and can reproduce next generation by utilizing large maturated host larvae at the time. This may be a possible reason why the spring population was larger in body size than the fall population.

I. leucospoides, on the other hand, emerged during almost the same period of emergence of *S. nitobei*. The oviposition of *S. nitobei* usually occurs soon after its emergence. It is thus likely that the emergence period of this parasitoid species could coincide with the egg or 1st instar larval stage of the host woodwasp.

The body mass of *M. praecellens* was much larger than that of *I. leucospoides*. Moreover, difference in body mass between sexes in *M. praecellens* was much larger than in *I. leucospoides* (table), and the observed number of eggs produced by a female of *M. praecellens* was much lower than that of *I. leucospoides*. These facts may be related to large efforts at host searching and oviposition activities of *M. praecellens*, inserting the ovipositor deep into the wood during its short life time (table).

Although the body mass of *I. leucospoides* is very

small, but the ovipositor length of *I. leucospoides* is as long as that of *S. nitobei*. This fact and its hair-like ovipositor may be associated closely with the egg laying behaviour of *I. leucospoides* that utilizes the oviposition holes of *S. nitobei*. Furthermore, the longevity of *I. leucospoides* is much greater than that of *M. praecellens*. Because the target for oviposition of *I. leucospoides* would be confined to egg or 1st instar larval stage of *S. nitobei* (fig. 2), *I. leucospoides* may have evolved to enhance the ovipositional success by increasing the life time. The two parasitoid wasps, *M. praecellens* and *I. leucospoides*, which were greatly different in morphological features and the periods of emergence and parasitize the larvae of *S. nitobei* at their different developmental stages, have coexisted in the present study site. Each parasitoid species has adapted its life history with the host's life cycle in a different manner, and thereby both species could exploit their hosts in wood most effectively.

S. nitobei in the present study and *S. noctilio* are similar to each other in the points of not only being congener but being associated with the same fungal symbiont, *Amylostereum areolatum* (TERASHITA, 1970). The same type of decline in pine trees as caused by *S. noctilio* also occur sporadically due to the attack of *S. nitobei* (KOBAYASHI et al., 1978). However, no serious decline of pine trees caused by *S. nitobei* has hitherto occurred in Japan, unlike as in the case of *S. noctilio* in Australia where there were no native natural enemies for *S. noctilio*. Our results demonstrated that the two parasitoid wasps of *S. nitobei* recorded in the present study, *I. leucospoides* and *M. praecellens* could utilize the larvae of *S. nitobei* in wood as their hosts at different developmental stages of the woodwasp: eggs and/or 1st instar larvae are available for *I. leucospoides*, whereas maturated larvae exclusively for *M. praecellens*. Considerably high proportion of parasitism on *S. nitobei* in this study area may be interpreted in terms of such a multiple parasitism pattern by the two different types

of parasitoids. The parasitism pattern also may explain in part consistently low population densities of *S. nitobei* in Japanese pine trees. Moreover, this suggests that if *S. nitobei* happen to be introduced in other countries where there are no natural enemies specific to this wood-wasp, it may give rise to serious damage to the native trees, as was the case of *S. noctilio* in Australia.

Acknowledgements

References

CHRYSTAL, R. N., 1930: Studies on *Sirex* parasites. Oxford Forestry Memories 11.

FUKUDA, H.; KAJIMURA, H.; HIJII, N., 1993: Fecundity of the woodwasp, *Sirex nitobei* Matsumura, in relation to its body size. J. Jpn. For. Soc. 75, 405–408.

HOCKING, H., 1968: Studies on the biology of *Rhyssa persuasoria* L. (Hymenoptera: Ichneumonidae) incorporating an X-ray technique. J. Aust. Ent. Soc. 7, 1–5.

KANAMITSU, K., 1978: Woodwasps and their hymenopterous parasitoids in Japanese conifers. Kontyû, Tokyo., 46, 498–508. (in Japanese with English Summary).

KATO, Y., 1966: The developmental processes of pine bark beetles and the patterns of tree decline. Shinrin-Boeki (Forest Pests) 15, 178–185. (in Japanese).

KOBAYASHI, T.; SASAKI, K; ENDA, N., 1978: Correlation between *Sirex nitobei* and *Amylostereum*, associated with the death of Japanese pine trees during winter season. J. Jpn. For. Soc. 60, 405–411. (in Japanese with English Summary).

MADDEN, J. L., 1968: Behavioral responses of parasites to symbiotic fungus associated with *Sirex noctilio* F. Nature 218, 189–190.

—, 1988: *Sirex* in Australasia. In: Dynamics of forest insect populations—Patterns, causes, implications. Ed. by BERRYMAN A.A. Plenum Press, New York & London, 407–429.

MORGAN, F. D., 1968: Bionomics of Siricidae. Ann. Rev. Ent. 13, 239–256.

NUTTALL, M. J., 1980: Insect parasites of *Sirex* (Hymenoptera: Ichneumonidae, Ibaliidae, and Orussidae). N. Z. For. Serv., For. Res. Inst., Forest and Timber Insects in New Zealand 47.

SPRADBERY, J. P., 1970a: Host finding by *Rhyssa persuasoria* (L.), an ichneumonid parasite of siricid woodwasps. Ann. Behav. 18, 103–114.

—, 1970b: The biology of *Ibalia drewseni* Borries (Hymenoptera: Ibaliidae) Proc. the Royal Ent. Soc., London (A) 45, 104–113.

TALBOT, P. H. B., 1977: The *Sirex-Amylostereum-Pinus* association. Ann. Rev. Phytopathol. 15, 41–54.

TAYLOR, K. L., 1976: The introduction and establishment of insect parasitoids to control *Sirex noctilio* in Australia. Entomophaga 21, 429–440.

—, 1978: Evaluation of insect parasitoids of *Sirex noctilio* (Hymenoptera: Siricidae) in Tasmania. Oecologia 32, 1–10.

TERASHITA, T., 1970: A Basidiomycete symbiotic to a siricid in Japan. J. Jpn. For. Soc. 52, 313–316. (in Japanese).

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