Interspecific relations among three hymenopterous egg parasites of the pine moth, Dendrolimus spectabilis Butler (Lepidoptera : Lasiocampidae) in the Japanese black pine forest. II. : Spatial interspersion of the two egg parasites, Trichogramma dendrolimi and Telenomus dendrolimi in the pine crown

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Interspecific relations among three hymenopterous egg parasites of the pine moth, *Dendrolimus spectabilis* Butler (Lepidoptera: Lasiocampidae) in the Japanese black pine forest. II.

Spatial interspersion of the two egg parasites, *Trichogramma dendrolimi* and *Telenomus dendrolimi* in the pine crown[1]

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Abstract

A situation in interspecific relations between *Trichogramma dendrolimi* and *Telenomus dendrolimi* parasitic on the pine moth eggs, which allows avoidance of multiple parasitism, was observed in the Japanese black pine forest near Fukuoka. Census data obtained in 1963 indicated that there was a clear-cut difference in preferential ranges of the two egg parasites to the host population; *Trichogramma* tended to attack the host eggs in the higher crown of the pine tree, whereas *Telenomus* tended to prefer the host eggs in the lower crown of the tree. It was strongly suggested that such a difference in the attacking range between the two parasites was not due to the interaction between both species but to the differential responses of the adult females of both species to microclimatic conditions in a pine tree. Preferential attack by the two egg parasites on the host population in relation to the crown heights contributes to avoidance of multiple parasitism. It is, therefore, concluded that there is no appreciable interference between them and that both species can coexist as egg parasites of the pine moth.

Introduction

Pine moth eggs of the first generation in the Japanese black pine

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forest are heavily parasitized by *Trichogramma dendrolimi* and *Telenomus dendrolimi.* It is frequently observed that one host egg mass is simultaneously parasitized by both of these species. On the other hand, preliminary field observations made by the senior author during 1960-62 strongly suggested that attack by each parasite species on the host egg masses is dependent on the height of their positions in the pine crown. This preferential attack by the two egg parasites on the host population would more or less result in the avoidance of multiple parasitism. An attempt was made in 1963 to obtain accurate data concerning this problem. Methods used were described in the previous paper of this series (Hirose et *al.*, 1968) except for the following point. The height of the position of the host egg masses together with the height of the pine tree was measured to the nearest ten centimeters.

Results

1. Differential parasitization by *Trichogramma* and *Telenomus* with special reference to the height of host egg masses in the pine crown.

The host egg masses parasitized by either or both parasite species were examined in relation to the height of their positions above the ground (Table 1). The host egg masses can be divided into two types, viz. a small sized type and a large sized type (Hirose, 1967; Hirose et al., 1968). In general, the large-type egg mass tends to be deposited higher in the crown than the small-type one. For this reason, calculation for mean height of the position of host egg masses in Table 1 was made for each egg mass type. As shown in Table 1, the position of egg masses parasitized by *Trichogramma* alone was always higher than that parasitized by *Telenomus* alone regardless of the egg mass type. On the other hand, egg masses parasitized by both *Trichogramma* and *Telenomus* were found in the interzone between egg masses parasitized by each species alone, excluding the case of July 12 for egg masses of the large-type. Table 1 also shows that the position of egg masses parasitized by *Trichogramma* is much higher than the mean height of all egg masses including unparasitized ones, and that the position of those parasitized by *Telenomus* is lower than, or as low as that of all egg masses.

These facts follow that there is a considerable difference in the way of attack on the host population between *Trichogramma* and *Telenomus*, that is, regardless of the host egg mass type the former tends to attack the host egg masses in the upper crown, whereas the latter tends to prefer the host egg masses in the lower crown. The difference between the two egg parasites is also demonstrated clearly in Figs. 1 and 2, which are drawn from data obtained on Jnly 2.

Table 1. Heights above the ground of the position of the pine moth egg masses parasitized by *Trichogramma* and *Telenomus* in the first host generation. Figures in brackets denote the number of egg masses observed.

Type of egg masses	Collection date	Mean height (cm. above the ground) of the position of egg masses parasitized by					Mean height (cm. above the ground) of the position of all egg masses collected including unparasitized ones
		Trichogramma alone (1)	*Telenomus* alone(2)	Both *Trichogramma* and *Telenomus* (3)	*Trichogramma* (1)+(3)	*Telenomus* (2)+(3)	
Large	June 23	146.7 (3)	127.5 (8)	126.7 (3)	136.7 (6)	127.3 (11)	142.9 (24)
	July 2	201.2 (41)	106.2 (66)	150.5 (122)	163.3 (163)	134.9 (188)	145.1 (250)
	July 12	130.0 (3)	107.5 (8)	176.9 (23)	171.5 (26)	159.0 (31)	156.9 (35)
Small	June 23	140.0 (1)	97.9 (14)	—— (0)	140.0 (1)	97.9 (14)	106.5 (40)
	July 2	137.2 (29)	79.2 (426)	113.3 (24)	126.4 (53)	81.0 (450)	88.4 (627)
	July 12	122.5 (20)	83.4 (171)	115.4 (35)	118.0 (55)	88.8 (206)	91.0 (254)

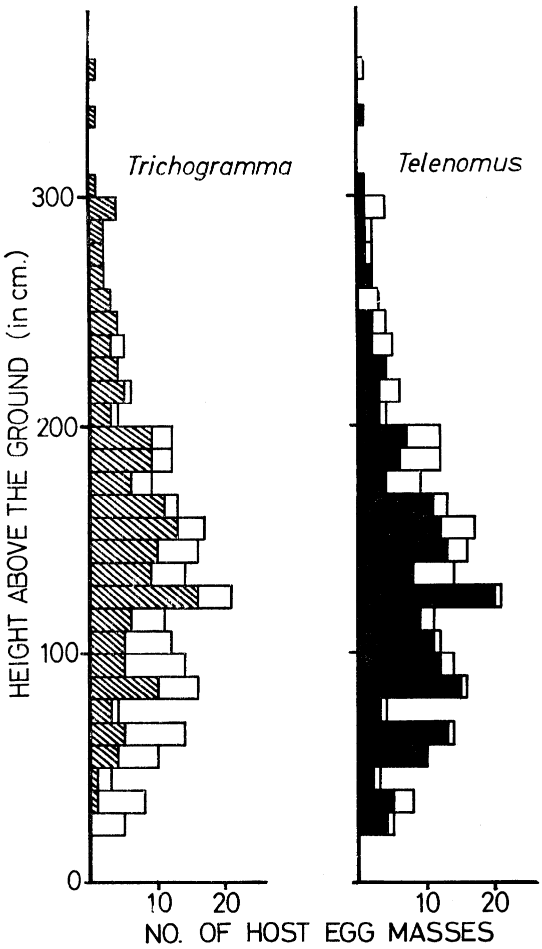

Fig. 1. Parasitization by *Trichogramma* and *Telenomus* of the large-type egg masses of the pine moth at different heights above the ground. The data are based on the collection of July 2. Area covered by oblique lines and solid area represent the number of host egg masses parasitized by *Trichogramma* and *Telenomus* respectively.

The data in Table 1 were based on materials collected from the pine trees which ranged from 0.7 m to 4.5 m or more in height, but most of the trees examined were quite uniform in height. To determine whether or not the above-mentioned phenomenon is maintained irrespective of the difference in height of individual trees, mean heights of egg

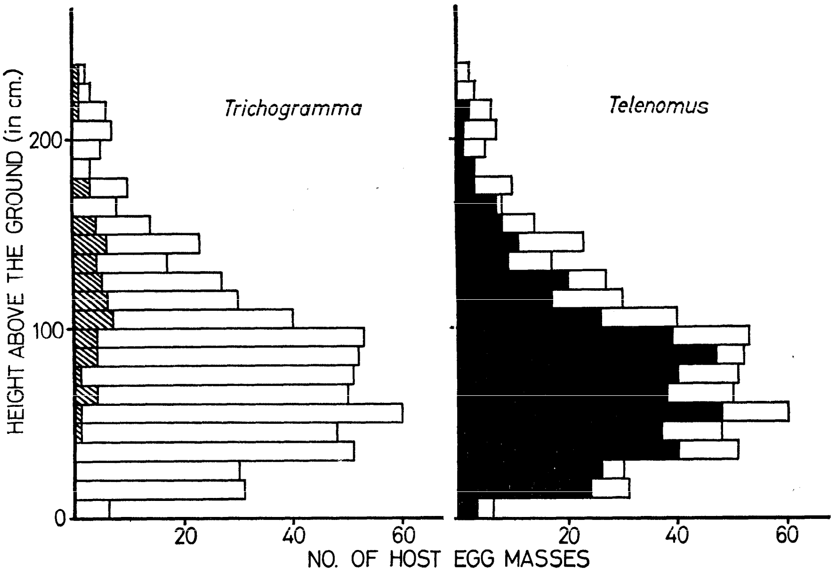

Fig. 2. Parasitization by *Trichogramma* and *Telenomus* of the small-type egg masses of the pine moth at different heights above the ground. The data are based on the collection of July 2. Area covered by oblique lines and solid area represent the number of host egg masses parasitized by *Trichogramma* and *Telenomus* respectively.

masses parasitized by the two parasite species was calculated for each height group of trees (Table 2). Table 2 clearly indicates that the position of egg masses parasitized by *Trichogramma* is higher than that parasitized by *Telenomus* in every tree except for extremely short trees. Moreover, from Table 2 it can be seen that regardless of height of individual trees *Trichogramma* tends to attack the host egg masses in the upper crown and *Telenomus* in the lower crown as compared with the mean height of all egg masses collected.

The above-mentioned difference in the parasitic habit of *Trichogramma* and *Telenomus* has been analyzed without involving the number of eggs parasitized by the two species. In that case, an egg mass in which only one egg was parasitized was treated as a parasitized egg mass. As the number of egg masses parasitized does not always represent the degree of parasitization, such a treatment often might lead into errors especially in large egg masses. To get more accurate information on this point, the percentage parasitism of *Trichogramma* and *Telenomus* at different heights above the ground was calculated for large-type egg masses collected on July 2 (Fig. 3). Fig. 3 shows that *Trichogramma* attacks the host population in the upper crown, while

Table 2. Relations between heights above the ground of the position of the pine moth egg masses parasitized by *Trichogramma* and *Telenomus* and heights of tree with their egg masses. The data are based on the collection of July 2. Figures in brackets denote the number of egg masses observed.

Type of egg masses	Height of tree with host egg masses(in cm.)	Mean height (cm. above the ground) of the position of egg masses parasitized by		Mean height (cm. above the ground) of the position of all egg masses collected including unparasitized ones
		Tichogramma	*Telenomus*	
Large	100>	72.5 (4)	72.5 (4)	72.5 (4)
	110~150	94.0 (5)	84.2 (12)	84.4 (18)
	160~200	125.9 (51)	107.3 (66)	113.5 (79)
	210~250	159.8 (52)	142.8 (64)	146.0 (80)
	260~300	185.4 (26)	157.0 (23)	173.1 (35)
	310~350	250.0 (15)	217.0 (10)	225.0 (20)
	360<	255.0 (10)	230.0 (9)	232.1 (14)
Small	100>	— (0)	42.3 (13)	41.8 (17)
	100~150	93.3 (3)	68.5 (88)	69.8 (121)
	160~200	105.6 (25)	77.2 (172)	79.7 (226)
	210~250	142.2 (18)	85.2 (115)	93.5 (160)
	260~300	194.0 (5)	107.4 (43)	121.0 (63)
	310~350	— (0)	112.9 (14)	145.5 (33)
	360<	125.0 (2)	122.0 (5)	128.6 (7)

Telenomus works in the lower crown. The result supports the conclusion drawn from Tables 1 and 2 and Figs. 1 and 2.

2. An analysis of simultaneous presence of *Trichogramma* and *Telenomus* on the same host egg mass.

As mentioned in the previous section, it has been found that there is a striking difference in preferential ranges of *Trichogramma* and *Telenomus* to the host population in relation to the crown heights. There-

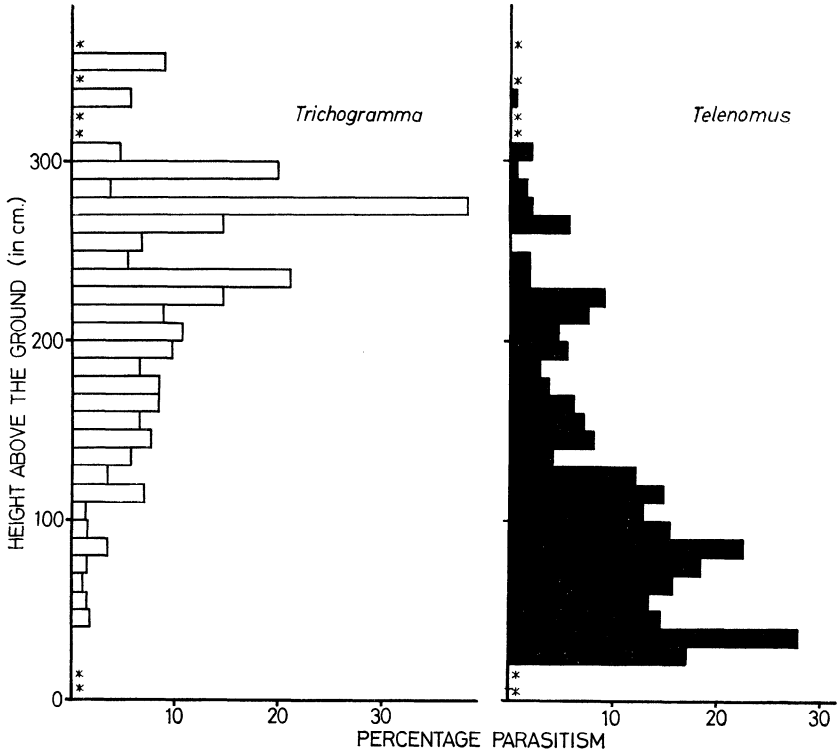

Fig. 3. Change in percentage parasitism of *Trichogramma* and *Telenomus* in the large-type egg masses on the pine moth at different heights above the ground. The data are based on the collection of July 2. Asterisks indicate the classes of height where host egg masses were absent.

fore, we may expect that such a difference contributes to diminution in chance of simultaneous presence of the two parasite species in the same host egg mass. It might be expected that the observed frequency of egg masses parasitized by both species is lower than the calculated frequency based on the assumption that each species attacks the host egg masses at random. As shown in Table 3, in large-type egg masses D_1 was nearly equal to D_2 in all cases. The result indicates that each species attacks the host egg masses at random, and this fails to meet our expectations. On the other hand, in small-type egg masses D_1 was much smaller than D_2, so that the coefficients of interspecific association calculated for July 2 and July 12 were negative to a considerable extent and very significant. Needless to say, the result meets our expectations.

Table 3. Simultaneous presence of *Trichogramma* and *Telenomus* on the same egg mass of the pine moth in the first host generation.

Type of egg masses	Collection date	Total no. of egg masses collected (A)	No. of egg masses parasitized by		No. of egg masses parasitized by both species		Coefficient of inter-specific association[b] $C \pm \sigma$
			Trichogramma (B)	*Telenomus* (C)	Observed (D_1)	Expected[a] (D_2)	
Large	June 23	25	6	11	3	2.6	
	July 2	250	163	188	122	122.6	-0.027 ± 0.151
	July 12	36	27	32	24	24.0	0 ± 0.034
Small	June 23	43	1	15	0	0.3	
	July 2	635	55	455	26	39.4	-0.340 ± 0.081*
	July 12	258	55	208	35	44.3	-0.237 ± 0.066*

* Significant at the 1 % level.

a $D_2 = BC/A$

b This is Cole's index which indicates the degree of association between two species. It takes values between +1 (the complete positive association) and −1 (the complete negative association). The value zero indicates that there is no association between the two species. Significance of this index, C can be evaluated by using the chi-square test (d. f. =1), if the standard error of C, σ, is given (Cole, 1949 for a fuller account).

It is yet uncertain why the result obtained in large-type egg masses fails to meet our expectations. As already shown, preferential attack by the two egg parasites on the host population in relation to crown heights was maintained regardless of the host egg mass type. Nevertheless, large-type egg masses may have slight tendency to be more frequently attacked by either parasite species than small-type ones. It is possible that such a tendency may follow the unexpected result obtained in the large-type egg mass. In addition, special attention should be given to the fact that in the analysis attempted in this section the degree of parasitization within an egg mass has not been taken into consideration at all.

3. An examination for the occurrence of interspecific interaction between *Trichogramma* and *Telenomus*.

The pine moth eggs of the second generation are rarely parasitized by *Trichogramma* as noted in the previous paper (Hirose et *al.*, 1968). If a difference in the parasitization by *Trichogramma* and *Telenomus* in relation to crown heights is caused by interactions between these two parasite species, such as by fighting between the adults (Hokyo and Kiritani, 1963, 1966), the height of the position of egg masses parasitized by *Telenomus* in the second host generation should be higher than that in the first host generation. Thus, the mean heights above the ground of the position of egg masses parasitized by *Telenomus* between the first and the second host generations were compared (Table 4). The seventh column in Table 4 shows that in large-type egg masses there is no significant difference in the figures between the two generations, but that in small-type egg masses the position in the second host generation is higher than that in the first host generation and the difference is very significant. The difference in the small-type egg masses, however, may be due solely to the difference in the height of total egg masses collected including those not parasitized, because there was a significant difference between the two host generations in the figures of total egg masses collected as shown in the last column in Table 4. In other words, there was only an apparent increase in the height of the position of the small-type egg masses parasitized by *Telenomus* in the second generation. Probably the increase in the height of the position of host egg masses in the second generation was seasonable, partly caused by the tree growth since summer and partly by the host oviposition behavior influenced by such changes in the pine trees. Therefore, it may be concluded that the preferential attack by *Trichogramma* and *Telenomus* on the host population is primarily caused by the oviposition habit inherent to the respective parasite species.

Table 4. Heights above the ground of the position of the pine moth egg masses parasitized by *Trichogramma* and *Telenomus* in the two different host generations. Figures in brackets denote the number of egg masses observed. For ready comparison, figures in the second host generation are calculated on the basis of the material collected in the same area as in the first host generation.

Type of egg masses	Host generation	Mean height (cm. above the ground) of the position of egg masses parasitized by: *Trichogramma* alone (1)	*Telenomus* alone(2)	Both *Trichogramma* and *Telenomus* (3)	*Trichogramma* (1)+(3)	*Telenomus* (2)+(3)		Mean height (cm. above the ground) of the position of all egg masses collected including unparasitized ones	
Large	First	193.2 (47)	105.2 (82)	154.1 (148)	163.5 (195)	136.7 (230)		146.2 (309)	
	Second	— (0)	134.7 (43)	220.0 (1)	220.0 (1)	136.6 (44)		138.8 (50)	
Small	First	131.4 (50)	80.8 (611)	114.6 (59)	122.3 (109)	83.8 (670)	*	89.9 (921)	*
	Second	— (0)	105.8 (114)	— (0)	— (0)	105.8 (114)		106.2 (126)	

* Significant at the 1% level.

Discussion and conclusion

In the case of the synchronous competition by two or more parasite species for one stage of a host population, preferential attack by the parasite species in such a small host-inhabited area as a tree crown has been reported by several authors (Flanders, 1947 ; Jaynes, 1954 ; Kot, 1962). However, factors affecting such a phenomenon have not been extensively analyzed. Such information was given in detail in the case of parasitization by *Apanteles fumiferanae* and *Glypta fumiferanae*, the two larval parasites of the spruce budworm, *Choristoneura fumiferanae*. Jaynes (loc. cit.) and Miller (1958) found that the percentage parasitism of *Apanteles* on balsam fir trees varied at different crown levels, being greater at the higher level, while *Glypta* was randomly distributed in budworm larvae at all crown heights. Dodge (1961) confirmed the same fact for *Apanteles* on Douglas fir trees, and stated that contrary to the fact in *Apanteles*, parasitism by *Glypta* was significantly higher in the lower and middle crowns than in the upper crown. Judging from the results obtained by Lewis (1960) and Dodge (loc. cit.), the difference between the two parasite species, both in balsam fir and in Douglas fir, seems to be mainly due to the differential oviposition behavior of the two parasite species to the host larvae in the foliage and to those in the bark ; *Apanteles* with its shorter ovipositor most successfully parasitize mobile budworm larvae in the foliage of the upper and middle crowns before the hibernacula was formed, whereas *Glypta* is more successful in attacking immobile larvae within the hibernacula in the coarse bark crevises of the lower and middle part of the crown. Thus, the above-mentioned difference in the vertical distribution of the two parasite species is due to the difference in the condition of host larvae themselves.

Apart from the budworm parasites, in host-searching the parasitic hymenopterous females seek first the environment frequented by the host. Therefore, Flanders (loc. cit.) pointed out that for parasite females the power to occupy host-inhabited areas is an attribute which constitutes the elements of the power of host discovery and that it depends on the responses of the female parasite to such factors as plant surfaces, odors, air movement, light, temperature and humidity. As an example involving the power to occupy host-inhabited areas, Flanders (loc. cit.) quoted parasitization by *Anagrus optabilis* (= *Paranagrus optabilis*), an egg parasite of the sugar cane leafhopper. In this case, the degree of parasitization of host eggs by this species differs according to the degree of sunshine which depends on the height of the leaves above the ground.

In the authors' view, preferential attack by *Tr. dendrolimi* and *Tel. den-*

drolimi on the pine moth egg population is likely due to the differential responses of the parasites rather to microclimatic conditions in a pine tree as exemplified by Flanders (loc. cit.) than to hosts themselves as shown in the relations between the budworm larva and its parasites. A field experiment carried out by Aino and Nobuchi (1960) is very suggestive in regard to this subject. They tried to place artificially the cultured pine moth eggs in different parts of a pine tree, which resulted in much higher parasitization by *Tr. dendrolimi* at the apical portion of the leader than on the lower shoots or on the trunk. The present study reveals a considerable degree of correspondence with the result obtained by Aino and Nobuchi (loc. cit.), as far as *Tr. dendrolimi* is concerned. Aino and Nobuchi (loc. cit.) concluded that such a difference in parasitization by *Tr. dendrolimi* within a pine tree is due to the positive phototaxis exhibited by this parasite. This follows that light may play an important role in the above-mentioned phenomenon in regard to *Tr. dendrolimi* and *Tel. dendrolimi*. However, *Tel. dendrolimi* is also strongly photopositive, as far as we are aware under laboratory conditions. In addition to light, air movement may be an important factor influencing the parasitization by both species. Stein (1962) studied the distribution of *Trichogramma embryophagum cacoeciae* in apple trees and concluded that the mechanical influence of the wind on the parasitization was greater than the physiological one of the sun. At any rate, further study in regard to the host searching behavior of the two egg parasites both in the laboratory and in the field is necessary for this subject.

A member of the genus *Trichogramma* often competes with that of the genus *Telenomus* for lepidopterous eggs. In such cases, so far as known, the former usually eliminates the latter from the host. Parsons and Ullyett (1936) stated that a difference in seasonal activity of *Tr. luteum* and *Tel. ullyetti* parasitic on the eggs of the cotton bollworm, *Heliothis armigera* may be attributed not only to the seasonal difference in temperature but also to elimination of *Tel. ullyetti* by *Tr. luteum*. Their view was supported by Jones (1937), who showed clearly that *Tr. luteum* practically eliminates *Tel. ullyetti* in the field. A similar relationship between *Trichogramma* and *Telenomus* was revealed by Ōtake (1956) in the event of *Tr. japonicum* and *Tel. dignus* (= *Phanurus beneficiens*), egg parasites of the rice stem borer, *Chilo suppressalis*, though in another paper he (1957) expressed some doubt as to his own view.

It is unknown whether or not the above-mentioned relationship between both genera is maintained in the case of *Tr. dendrolimi* and *Tel. dendrolimi* which share the same niche in the Japanese black pine forest. It seems likely, however, that there is little interference, if any, between these two egg parasites because of the preferential attack by them on the host population in the pine crown. The present study shows that such a preferential attack by the two egg parasites on the host population is primarily caused by the oviposition habit inherent to the respective parasite species, and that this contributes to avoidance of simultaneous presence of the two egg parasites on the same host egg mass. Therefore, it is considered that there is no elimination of *Tel. dendrolimi* by *Tr. dendrolimi* even if the latter is successful in cases of multiple parasitism by the two species,[1] and that both species can coexist as egg parasites of the pine moth.

Finally it should be pointed out that a difference in the vertical distribution of *Tr. dendrolimi* and *Tel. dendrolimi* in a pine tree presents a difficult problem in sampling to obtain valid estimates of the degree of parasitization. Neither eggs from upper crowns nor eggs from lower crowns might be expected to give a true picture of parasitization because of the preferential attack in relation to the crown heights. It may be stated here that taking an entire tree as a sampling unit would be appropriate in estimating the percentage parasitism of the two egg parasites.

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[1] At present there is no sufficient evidence to warrant conclusion that *Tr. dendrolimi* is intrinsically superior to *Tel. dendrolimi* in multiparasitic competition between the two species. This problem will be published elsewhere.

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(*Read in abstract only)