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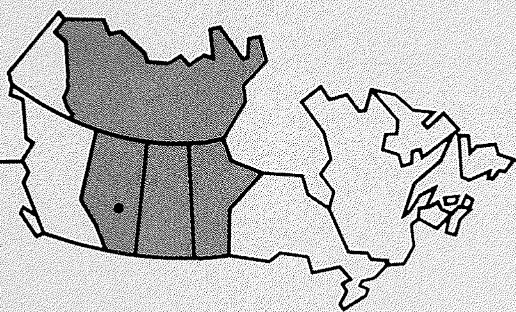

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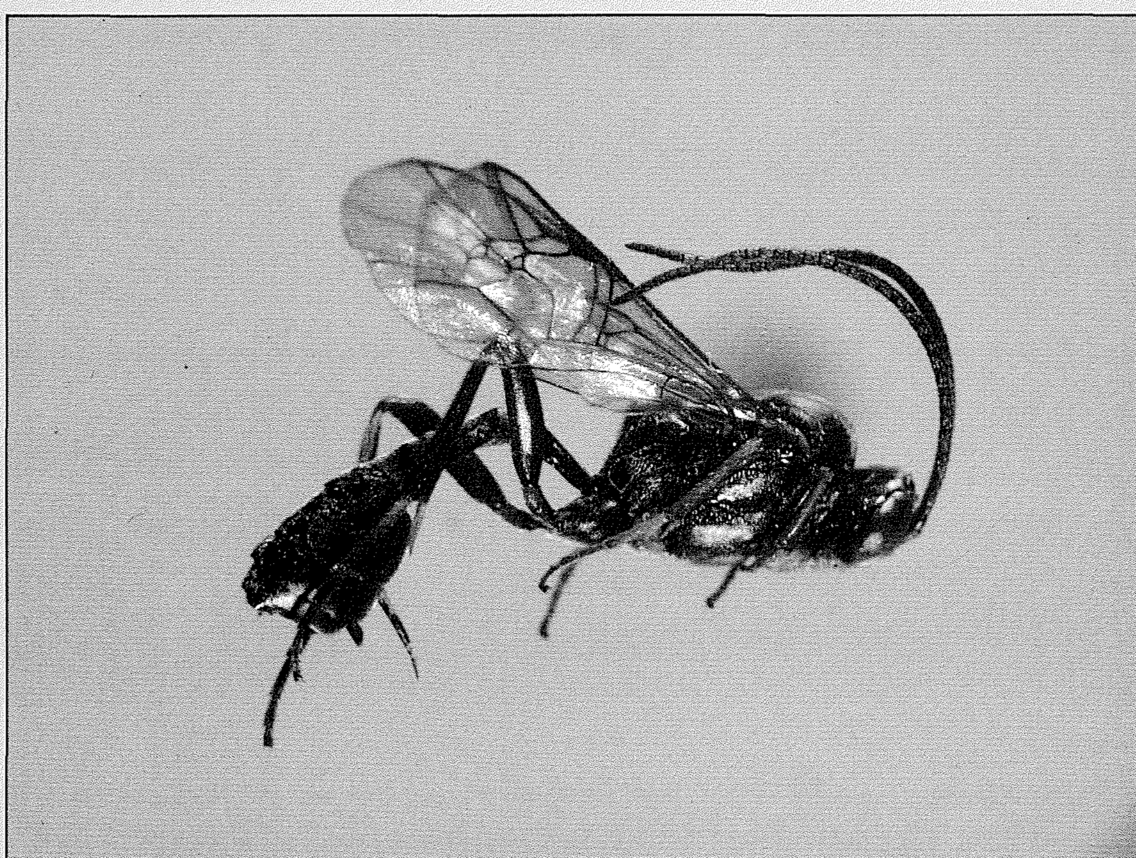

DISPERSAL OF *OLESICAMPE BENEFACTOR* AND *MESOCHORUS DIMIDIATUS* IN WESTERN CANADA

J.A. Muldrew and W.G.H. Ives

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ABSTRACT

Dispersal distance of *Olesicampe benefactor* Hinz, a parasite of the larch sawfly, *Pristiphora erichsonii* (Hartig), introduced in 1961 near Pine Falls, Manitoba, increased at a threefold annual rate from 220 m in 1964 to 370 km in 1971. Absolute numbers of *O. benefactor* in the occupied areas also increased about sevenfold per year, from the 214 released in 1961 to over 8 billion 8 years later. Rates of dispersal and increases in absolute numbers declined markedly after 1971, due to both the adverse effects of the hyperparasite *Mesochorus dimidiatus* Holmgren and the marked decrease in sawfly densities that occurred in southern Manitoba and northwestern Ontario. In some locations very low densities have persisted for 15 years. Since 1961, *O. benefactor* has been redistributed to 16 other locations in the prairie region. Parasite establishment followed by rapid buildup occurred wherever sufficient sawfly populations were present. Initial dispersal from most of these locations was more rapid than at Pine Falls.

RESUME

Le rayon de dispersion d'*Olesicampe benefactor* Hinz, parasite de la tenthrède du mélèze (*Pristiphora erichsonii* [Hartig]), introduit en 1961 près de Pine Falls, au Manitoba, a triplé chaque année, pour passer de 220 m en 1964 à 370 km en 1971. Ses effectifs se sont multipliés par 7 chaque année dans l'aire occupée, passant des 214 libérés en 1961 à plus de 8 milliards, 8 ans plus tard. Le rayon de dispersion et les effectifs ont augmenté beaucoup moins rapidement après 1971 à cause de l'hyperparasite *Mesochorus dimidiatus* Holmgren et de la densité moindre des tenthrèdes dans le sud du Manitoba et le nord-ouest de l'Ontario. Dans certaines localités, les densités sont restées très faibles durant 15 ans. Depuis 1961, *O. benefactor* a été libéré dans 16 autres localités des prairies. Il s'est implanté puis multiplié rapidement partout où les populations de tenthrèdes étaient suffisantes. Sa dispersion à partir de la plupart de ces localités a été plus rapide qu'à Pine Falls.

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INTRODUCTION

There have been many cases of successful biological control of forest pests; the importation method alone resulted in at least partial control for 157 species of pest insects and 29 species of pest weeds (Huffaker and Messenger 1976). Relatively few of these cases, however, have been documented by detailed population studies. Watt (1964) conducted an extensive search of the literature and concluded that "there is almost a total lack of detailed quantitative information on parasite population buildup after parasites have been released." He also noted that "quantitative studies on insect dispersion are almost totally lacking."

The following report presents information on the dispersal and population buildup of *Olesicampe benefactor* Hinz, an ichneumonid parasite (or more properly, parasitoid) that was successfully introduced into Canada from Europe to combat the larch sawfly, *Pristiphora erichsonii* (Hartig). Detailed information is presented for a release made in Manitoba, Saskatchewan, Alberta, and the Northwest Territories. The hyperparasite *Mesochorus dimidiatus* Holmgren and its relationship to *O. benefactor* were also studied. This hyperparasite was present in Canada prior to the first release of *O. benefactor* and now occurs in most release locations.

Insect Dispersal

Role of dispersal

Numerous examples of insect dispersal were provided by Johnson (1969). He generalized that dispersal is an evolved adaptation rather than a reaction to current adversity and is characteristic of species that have adapted part of their adult life, usually the prereproductive period, specifically for transit between breeding places.

Southwood (1962) concluded that the level of migratory movement was positively correlated with the degree of impermanence of the habitat. Migrants often began to leave a habitat long before a decline in the availability of food became apparent; the migratory process was triggered by token stimuli that had proven their worth as survival mechanisms. These stimuli were often related to the crowding of individuals, causing "mutual interference". Migration did not always result in a regular regression of numbers with distance from the source, because migrants often took off and flew long distances in swarms that usually moved with the wind. The evidence indicated that migrants were not blown passively but were kept airborne by active flight.

Berryman (1978) pointed out that in relation to insect population dynamics, insect dispersal had two basic effects: first, by expanding the perimeter of the population it brought additional units of habitat into occupancy; and second, by diluting the population in the occupied habitats it lowered population density there.

Dispersal behavior

Taylor and Taylor (1977) postulated that the spatial disposition of the individuals of a species resulted from the balance between two fundamentally different behavior reactions: attraction behavior that caused individuals to congregate wherever resources were most abundant, and repulsion behavior that resulted from selection pressure where the separation of individuals would maximize the use of the total resources available. They postulated that the balance between these conflicting tendencies as they operated on each individual determined its movements. They attempted to provide a functional mechanism for the distributive processes in a population that would lead to the diffusion rates and spatial dispositions observed in nature. Taylor et al. (1978) analyzed 156 sets of field data on the spatial distribution of many diverse species of organisms and found that in only two of these cases was spatial disposition essentially random at all population densities. Because spatial disposition is density-dependent, they deduced that spatial behavior is also density-dependent.

Dispersal of hymenopterous parasites

Studies on the dispersal of parasitic Hymenoptera include those on *Bathyplectes curculionis* (Thompson), which is a parasite of the alfalfa weevil, *Hyperica postica* (Gyll). Dysart and Puttler (1965) indicated that it may have dispersed 360 km in 2 years, but it seems more likely that it dispersed along with its host at a rate of about 100 km per year from the east coast to Illinois from 1951 to 1964 (Smilowitz et al. 1972). The mymarid egg parasite, *Anaphes flavipes* (Foerster), introduced against the cereal leaf beetle from 1966 to 1968, was found 320 km east of its release point in 1970 (Maltby et al. 1971). Tooke (1953) recorded dispersal of the egg parasite *Anaphoidea nitens* Gir. of 160 km in one year. DeBach (1974) cites the case of *Aphytus melinus* DeBach, released in Greece in 1962, that dispersed at about 100 km per year and traveled over water to islands 225 km from shore.

A well-documented case of the dispersal of an ichneumonid parasite is presented by Rose (1976). The parasite *Lophyroplectus luteator* Thunberg was liberated in southern Ontario in 1962 and 1964 against the European pine sawfly. During the first 7 years following release, it spread at a mean rate of 2.8 km per year; during the 13-year period 1962-1975 it spread at a mean rate of 23.5 km per year, but during the 3-year period 1973-1975, the mean rate was 75 km per year. The latter figure gives a more accurate estimate of the dispersal capabilities of the parasite than do the figures that include dispersal in the early years following liberation.

Olesicampe benefactor and *Mesochorus dimidiatus*

Olesicampe benefactor, a specific parasite of the larch sawfly, was obtained from Europe and first released in Canada in 1961 at a study plot located 16 km northeast of the town of Pine Falls, Manitoba. It became established readily and within 5 years was parasitizing approximately 90% of the hosts in the vicinity of the release point (Turnock and Muldrew 1971). Its biology was described by Muldrew (1967). Data on numbers released at Pine Falls and also at Riverton, Hodgson, and The Pas, Manitoba, and at Crutwell, Saskatchewan, with information on initial attack rates and dispersal to 1969, were reported by Turnock and Muldrew (1971). These and additional releases made in the prairie region since 1971 are summarized in Table 1. Ives (1976) summarized the data on buildup and impact of the parasite at the original release site.

The hyperparasite *Mesochorus dimidiatus* attacks *O. benefactor* but is not specific to this host. It was first recovered in the Pine Falls area in 1966, 5 years after the initial release. It was known to be a common parasite of *O. benefactor* in Europe and great care was taken not to release it in Canada when the early releases of *O. benefactor* were made. A search of museum collections showed that it had previously been collected in Canada in 1924 in Alberta and in 1961 in Nova Scotia from *Neodiprion abietis* (Harris) (Turnock and Muldrew 1971).

METHODS

Releases of *O. Benefactor*

Adult parasites were usually released, but in some of the releases of *O. benefactor* made in Alberta and the Northwest Territories small cocoons parasitized by *O. benefactor* were placed in screen cages (to prevent small mammal predation) and set out under a few inches of moss (Table 1). For the 1972 releases, cocoons were placed out in early spring, but for the 1981 releases they were placed out in the fall of 1980. The cages were picked up in late August and early September, and the cocoons they contained provided estimates of numbers of parasites that had emerged.

Annual estimates of total numbers of *O. benefactor*

Estimates were made of the total numbers of *O. benefactor* in successive years following its release in 1961 in the Pine Falls study plot. Estimates of the numbers of larch sawflies per hectare for the plot were used in conjunction with percentage parasitism figures for *O. benefactor* in locations at various distances from the release point and estimates of the total amount of tamarack present in various areas, using the amount present in the study plot as a standard. The parasite occupied increasingly larger areas each year, and each of these was subdivided into six to nine concentric circular areas or annular increments, with the radii increasing by a constant amount each year (Table 2).

The estimates of percentage parasitism at various distances from the release point were derived from the data presented in Figures 1 and 2. Parasitism values were read from the midpoints of the sections of radius delineating successive annular increments. Because not enough sampling points were taken in 1964 to fit a curve by eye, a normal curve constructed from area tables was used.

The estimates of the amount of tamarack available as food in these annular increments were made using Manitoba Forest Inventory maps and data[1]. This information was combined with life table and Forest

[1] In each annular increment the areas of the various stand types in which tamarack occurred were measured with a planimeter. Since the Pine Falls plot was in a stand type designated 100% tamarack, the sawfly densities measured in the plot could be applied against a "total adjusted area" of tamarack for each concentric ring. This total was obtained

Table 1. Release and recovery data for *O. benefactor* in the prairie provinces and Northwest Territories for 1961-81

Year	Province	Nearest named place	Location of release point: Latitude	Location of release point: Longitude	No. released: Males	No. released: Females	No. released: Total	Year of recovery
1961	Manitoba	Pine Falls	50°41′	96°05′	56	158	214	1962
1962	Manitoba	Riverton	51°16′	96°59′	65	152	217	1962
1963	Manitoba	Riverton	51°16′	96°59′	910	1 245	2 155	Present in 1962
1964	Saskatchewan	Crutwell	53°15′	100°06′	18	21	39	1966
1965	Saskatchewan	Crutwell	53°15′	100°06′	16	24	40	1966
1966	Saskatchewan	Crutwell	53°15′	100°06′	202	346	548	1966
1967	Manitoba	Hodgson	51°14′	97°18′	385	447	832	1967
1968	Manitoba	The Pas	53°51′	101°19′	694	737	1 431	1968
1969	Manitoba	Winnipeg	49°48′	97°08′	60	53	113	1974
1970	Manitoba	St. Labre	49°19′	96°00′	421	443	864	1970
1971	Manitoba	Seddon's Corner	50°03′	96°13′	245	262	507	Present in 1969
1972	Manitoba	St. Labre	49°19′	96°00′	75	74	149	Present in 1970
1972	Alberta	Primrose Lake	54°43′	110°04′	-	-	1 283[a]	Not recovered[b]
1972	Alberta	Jarvie	54°27′	113°58′	-	-	1 139[a]	1973
1972	Alberta	Grovedale	55°01′	119°06′	-	-	469[a]	1973
1972	NWT	Hay River	60°36′	116°06′	-	-	856[a]	No collections made
1973	Alberta	Ellscott	54°30′	112°57′	118	122	240	1974
1975	Alberta	Obed Lake	53°32′	117°04′	51	86	137	1975
1981	Alberta	Fitzgerald	59°55′	111°43′	-	-	36[c]	Not recovered
1981	NWT	Bell Rock	60°01′	112°07′	-	-	332	1981
1981	NWT	Fort Smith	60°01′	111°58′	-	-	30[c]	Not recovered

[a] Emerged in the field from small cocoons placed out in the spring. The cocoons were examined after the emergence of adults had ceased and those from which parasites had emerged were counted. The proportion of these that produced *O. benefactor* was based on the rearing of a sample of 600 cocoons for each location.
[b] Only one collection of six larvae made in 1975.
[c] Emerged in the field from small cocoons placed out in the fall of 1980.

Table 2. Data used to obtain estimates of total numbers of *O. benefactor* in the Pine Falls region, 1964-69

1964									
Annular increments (m)	0-40	40-80	80-120	120-160	160-200	200-240			
Adjusted area of tamarack (ha)	0.4	1.2	1.8	2.0	2.6	2.6			
Parasitism (%)	9.0	7.0	4.0	2.0	1.0	0.5			
1965									
Annular increments (km)	0.0-0.2	0.2-0.4	0.4-0.6	0.6-0.8	0.8-1.0	1.0-1.2			
Adjusted area of tamarack (ha)	7.10	12.78	16.27	17.50	31.02	39.15			
Parasitism (%)	37	18	9	4	1	0.5			
1966									
Annular increments (km)	0.0-0.4	0.4-0.8	0.8-1.2	1.2-1.6	1.6-2.0	2.0-2.4	2.4-2.8	2.8-3.2	
Adjusted area of tamarack (ha)	19.88	33.20	63.59	115.26	140.47	122.07	116.70	108.41	
Parasitism (%)	54	31	22	15	10	6	3	2	
1967									
Annular increments (km)	0.0-0.4	0.4-0.8	0.8-1.6	1.6-2.4	2.4-3.2	3.2-4.0	4.0-4.8	4.8-5.6	5.6-6.4
Adjusted area of tamarack (ha)	19.88	33.20	178.85	262.54	225.09	219.24	182.47	141.81	227.58
Parasitism (%)	96	87	51	33	23	13	6	3	1
1968									
Annular increments (km)	0.0-0.8	0.8-1.6	1.6-3.2	3.2-4.8	4.8-6.4	6.4-8.0	8.0-9.6	9.6-11.2	11.2-12.8
Adjusted area of tamarack (ha)	53.08	178.85	487.63	401.72	369.39	604.31	720.81	733.19	729.39
Parasitism (%)	98	97	93	76	46	28	15	5	1
1969									
Annular increments (km)	0-4	4-8	8-16	16-24	24-32	32-40	40-48	48-56	56-64
Adjusted area of tamarack (ha)	938.80	2 066.31	4 222.30	7 037.03	9 852.03	12 606.90	15 481.77	19 296.64	21 111.50
Parasitism (%)	95	91	78	25	11	6	4	2	1

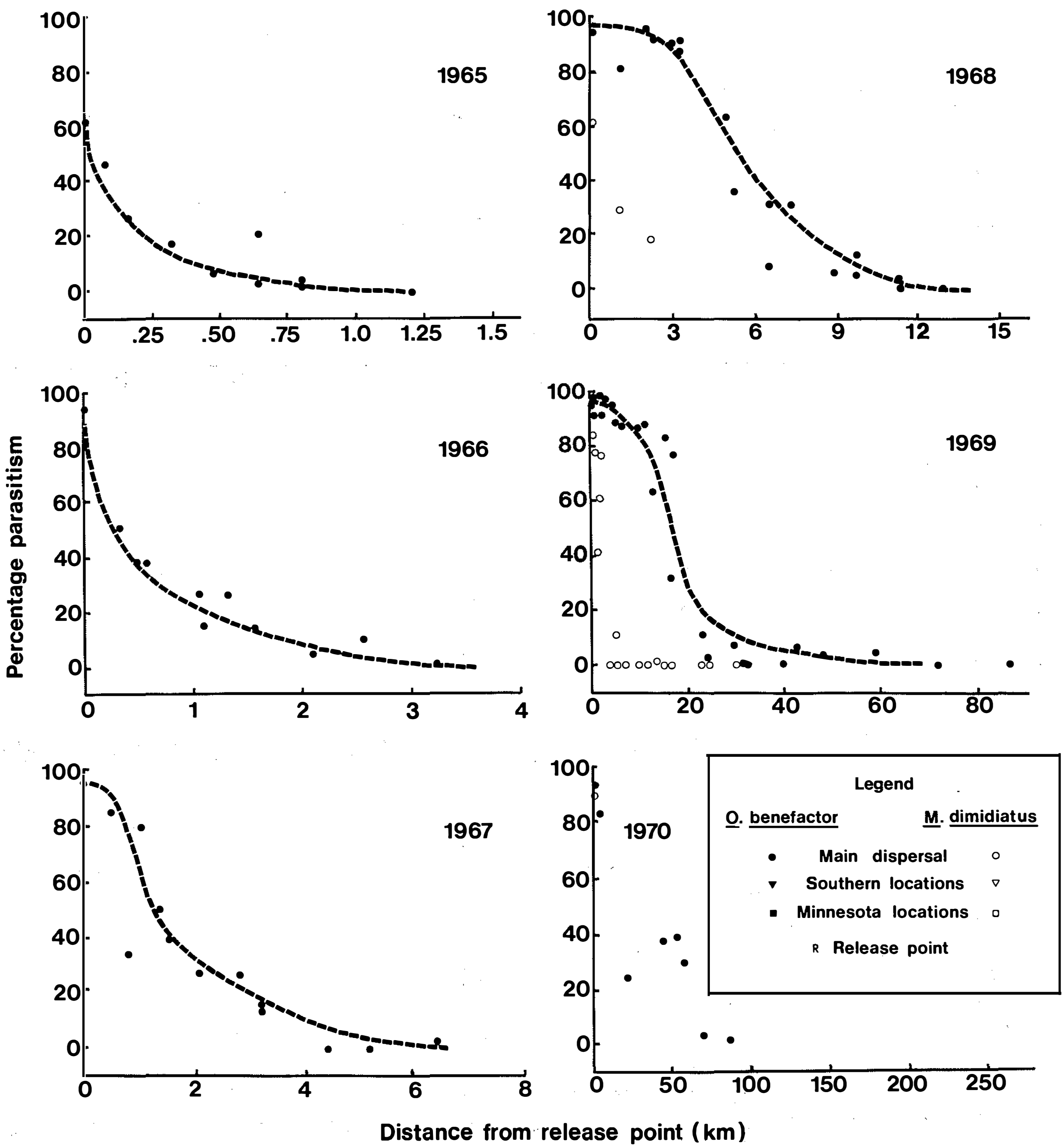

Figure 1. Parasitism by *O. benefactor* and *M. dimidiatus* in relation to distance from Pine Falls release point during 1965-70. The curves shown were fitted by eye and were used in estimating absolute numbers of *O. benefactor* for 1965-69.

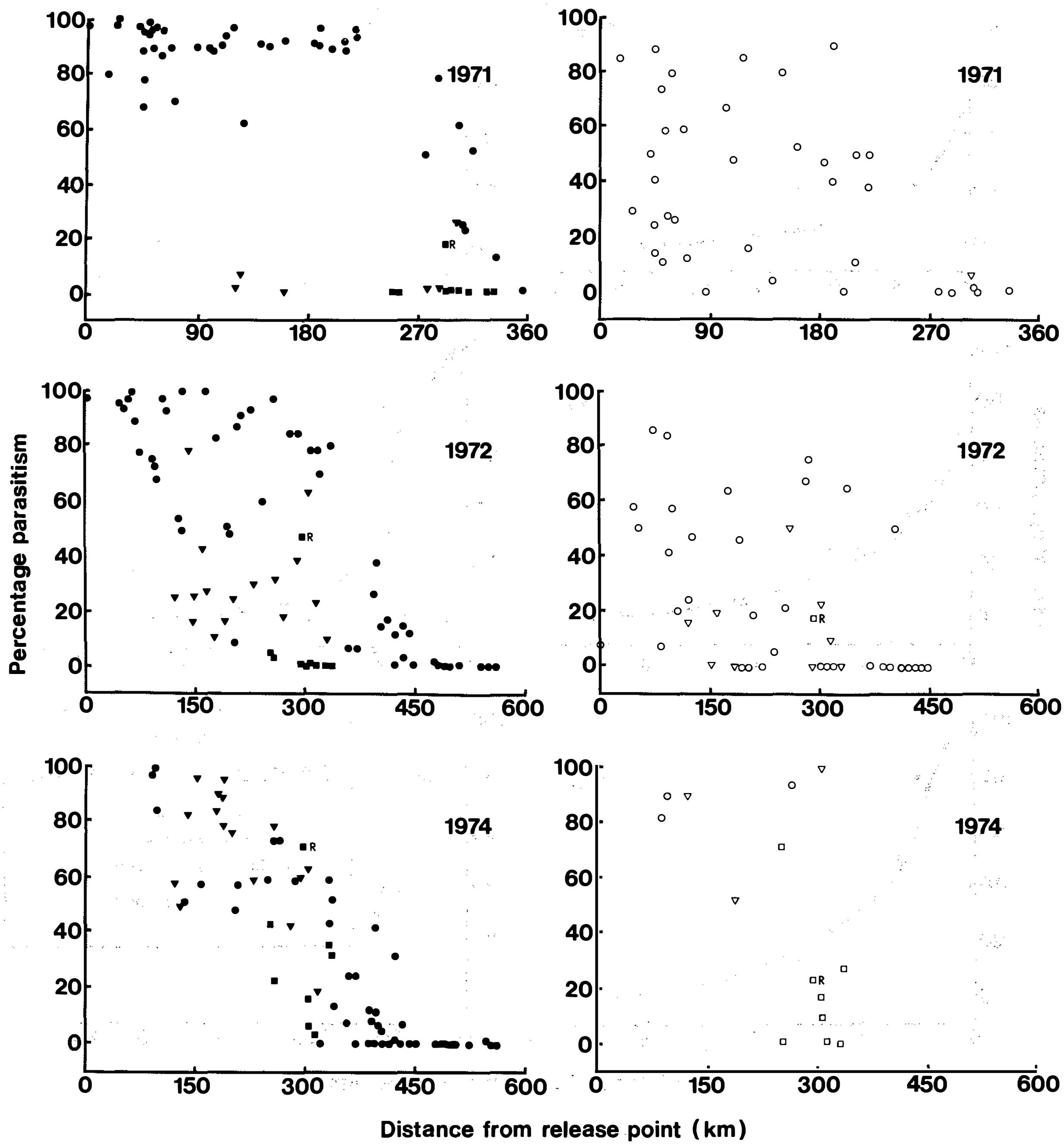

Figure 2. **Parasitism by *O. benefactor* and *M. dimidiatus* in relation to distance from the Pine Falls release point during 1971-74.** "R" designates a release location in Minnesota.

Insect and Disease Survey (FIDS) data to obtain crude estimates of sawfly densities.

The Pine Falls study plot measurements were used for larch sawfly densities for the 1964-66 data. For the 1967-69 data the influence of *O. benefactor* in reducing sawfly populations became appreciable (Fig. 3) and some allowance had to be made for this. Accordingly, the density measures in the plot in 1967, 1968, and 1969 were applied only to the inner circular area, out to 0.4, 0.8, and 4.0 km, respectively. As shown in Figure 4, the general larch sawfly density level for southeastern Manitoba as a whole area was moderate to severe and roughly the same in the 1967-69 period as it was in 1966. This was in contrast to the reduced population levels in the Pine Falls plot itself during the same period (Fig. 3). The density level for the plot for 1966 was therefore used as the best estimate available for all circular areas other than the innermost portion.

Estimation of percentage parasitism by *O. benefactor* and *M. dimidiatus*

Larch sawfly larvae parasitized by *O. benefactor* are smaller than nonparasitized females or females attacked by other parasites (Muldrew 1967), and size was therefore the criterion most commonly used to estimate parasitism by this species. Male larch sawflies usually comprise about 2% of the population and are typically about the same size as parasitized female sawflies. Thus, where parasitism by *O. benefactor* was low, it was necessary to dissect all small host larvae to differentiate the males from the parasitized females. For the latter, cocoon length was 19% smaller, head-capsule width 15% smaller, and larval weight 50% smaller than for the nonparasitized females.

From 1964 to 1968 most of the estimates of parasitism were based on length or weight measurements. For cocoon length Muldrew (1967) found that classifying those shorter than 9.25 mm as parasitized gave the least error due to overlap. This was based on collections from Pine Falls and Riverton, Manitoba. It was later found, however, that collections from other locations had different optimum division points and that this was especially true for collections that were partly starved or sickly because of poor rearing conditions. After 1968 a less time-consuming procedure was adopted in which collections of reared cocoons were simply sorted by eye to normal, small, and intermediate categories and sufficient numbers of the intermediates or smalls were dissected to give an accurate estimate of percentage parasitism. Living larvae removed from cocoons were examined for parasites by decapitating them, inverting their bodies on a blunt probe, and placing them in water over a black background for examination. The *O. benefactor* larvae usually float on the surface of the water because of their hydrophobic integuments. The *O. benefactor* larvae found were then dissected to determine if *M. dimidiatus* larvae were present in them. The parasitism estimates for the hyperparasite are expressed as a percentage of the number of *O. benefactor* larvae dissected rather than of the number of larch sawfly larvae dissected.

From 1971 to 1974, when numerous collections of sawflies were made in field surveys, the most common method of estimating parasitism by *O. benefactor* was by preserving larvae (usually fourth- or fifth-instar) in a 70% alcohol solution at the time of collection and measuring their head-capsule widths at a later date. A sufficient number of those having intermediate-sized head capsules were dissected to provide an accurate estimate of parasitism. Because the larvae had hardened in alcohol, they had to be cut open and their tissues teased apart with probes in order to determine if *O. benefactor* larvae were present. When such larvae were found, however, they could not be dissected for *M. dimidiatus* because of hardening of the tissues. For these years all *M. dimidiatus* estimates (Appendix 1) are based on portions of the collections that were reared rather than preserved as larvae when collected.

The estimates for *O. benefactor* represent potential parasitism because they express the total percentage of hosts actually attacked by it regardless of the eventual fate of the *O. benefactor* larva in the sawfly host. Where the host was first attacked by *O. benefactor* and subsequently by *Bessa harveyi* (Tnsd.), a tachinid, or *Mesoleius tenthredinis* Morley,

by applying the percentage of tamarack in each stand type against the total hectares for that type and summing the values obtained. These totals were further adjusted for cutting class and degree of crown closure as follows: areas of stands designated cutting class 2 to 5 were not reduced and areas of stands designated cutting class 1 (trees less than 3 m mean height) had their areas reduced by 50%; areas of stands designated crown closure class 4 (71-100% closure) were not reduced; areas of stands of class 3 (51-70% closure) were reduced by 30%; and areas of stands of class 2 (21-50% closure) were reduced by 50%. Species composition for class 0 (0-20% closure) was not given in the legend. The final totals for adjusted areas are given in Table 1.

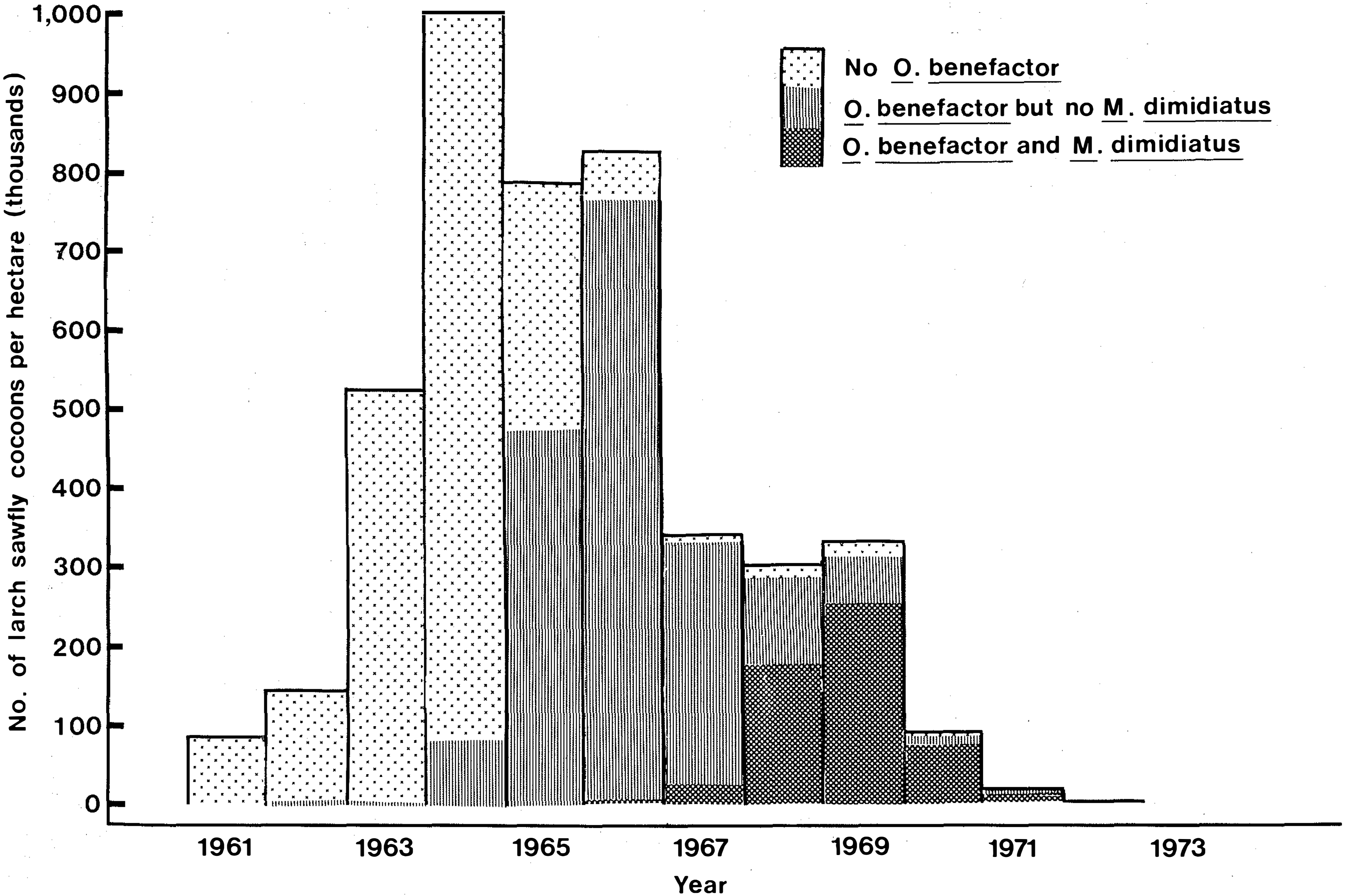

Figure 3. **Numbers of larch sawfly cocoons per hectare at the Pine Falls study plot, 1961 to 1973, showing numbers attacked by the primary parasite *O. benefactor* and the secondary parasite *M. dimidiatus*.**

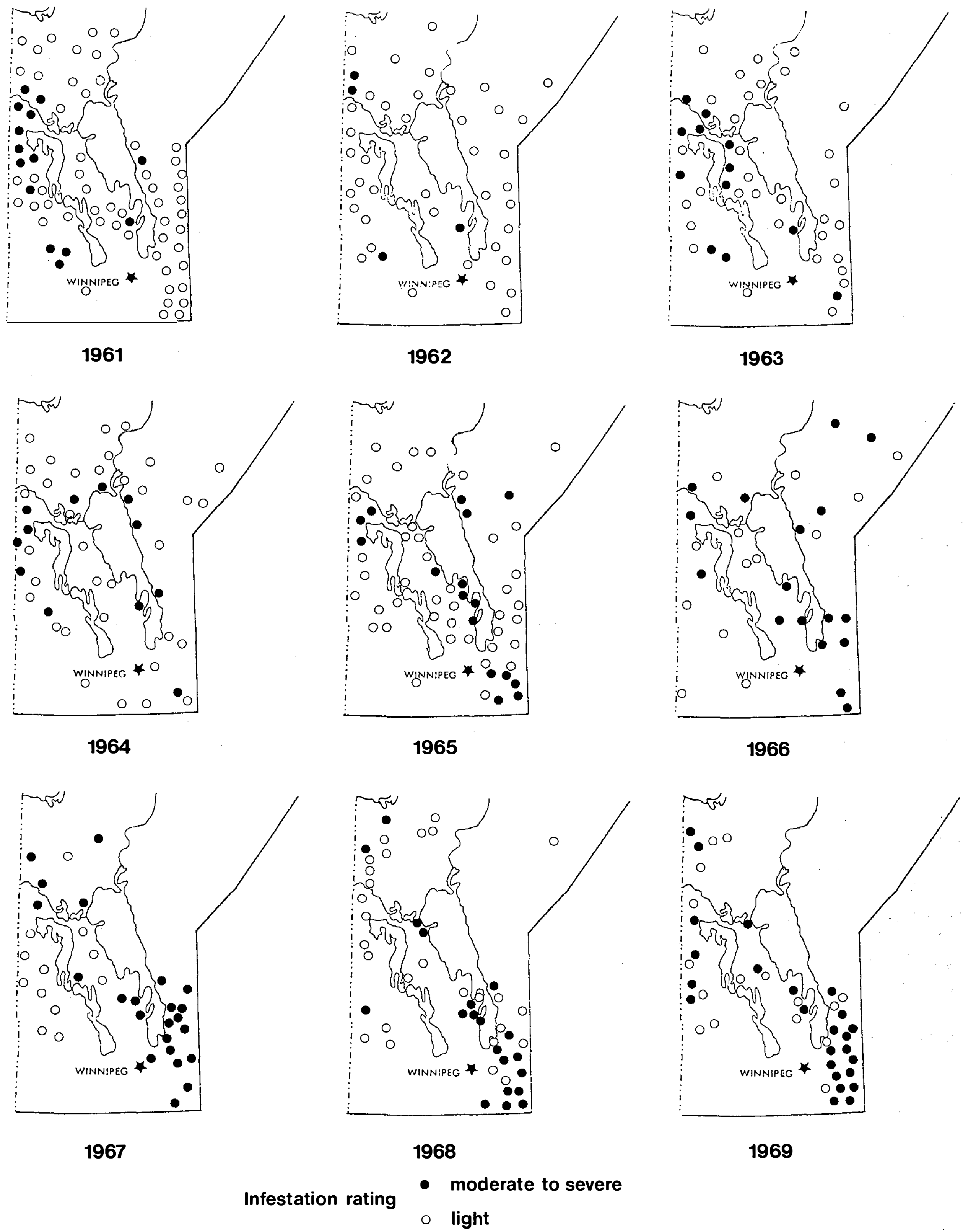

Figure 4. Larch sawfly infestations in southern Manitoba, 1961-69, based on collections made by the Forest Insect and Disease Survey.

an ichneumonid, the latter parasites were often the successful competitors. When these two competing parasites were found in dissections or had emerged as adults in rearings, prior attack by *O. benefactor* was presumed if the host was small.

The data are presented in detail in Appendix 1, including the latitude and longitude of the locations at various distances from the release point and sample sizes used to obtain the estimates of parasitism by *O. benefactor* and *M. dimidiatus*. Similar data published by Minnesota workers on sampling to detect dispersal of *O. benefactor* (Thompson et al. 1977) are also included.

DISPERSAL OF *O. BENEFACTOR* AND *M. DIMIDIATUS* FROM PINE FALLS

Results

Host density fluctuations

Collections of larch sawfly made by the FIDS rangers throughout southeastern Manitoba showed that sawfly populations outside of the plot generally remained high from 1965 to 1969 (Fig. 4). Similar population trends occurred in the life table plots (Fig. 5) south of Pine Falls (Ives 1967): at Rennie the sawfly increased from 1961 to 1967 and remained relatively high until 1970, at Seddon's Corner the sawfly increased from 1963 to 1964 and remained relatively high until 1971, and at Darwin the populations increased from 1964 to 1967 and stayed relatively high until at least 1969.

The relationships between numbers of cocoons per hectare, numbers of cocooned prepupae containing *O. benefactor* larvae, and numbers of *O. benefactor* attacked by the hyperparasite *M. dimidiatus* in the study plot near Pine Falls during 1961 to 1973 are shown in Figure 3. The gradually increasing numbers of larch sawflies during 1961 to 1964 and the relatively high densities attained during 1965 and 1966 allowed *O. benefactor* to build up to relatively high numbers[2]. After 1966, the high sawfly mortality in this plot caused by *O. benefactor* was partly responsible for the decline in sawfly numbers in the plot.

Dispersal data

The degree of dispersal of *O. benefactor* during 1965-74 is shown in Figures 1 and 2, expressed as percentage parasitism for various collections in relation to distance from the Pine Falls release point. Note that the scale for the distance from the release point increases for each year up to 1972. In the spring of 1965, before adult sawfly emergence began, several small collections of cocoons were made at various distances along a line extending north from the release point. Parasitism near the release point was 9%. Collections were made out to 550 m, but the parasite was not found beyond 220 m, where parasitism was 0.5%. Collections made by FIDS during 1964 and 1965 at 8-16 km from the release point did not reveal the presence of *O. benefactor*.

The maximum dispersal was 0.8 km in 1965 and 3.2 km in 1966. In 1966 the hyperparasite *Mesochorus dimidiatus* was recovered in the plot for the first time at a rate of attack on *O. benefactor* of 0.4%. In 1967, when only a few collections were made, maximum dispersal was 6.4 km. In a special collection of 15 000 larvae made at a mean distance of 1.4 km from the release point, parasitism by *O. benefactor* was about 50%.

In a more extensive survey in 1968, maximum dispersal was 11.3 km. In 1969 intensive sampling at the Rennie and Seddon's Corner plots, at distances of 86.9 and 70.8 km from the Pine Falls release point, revealed 0.9% and 0.4% parasitism by *O. benefactor*, respectively. *M. dimidiatus*, which had increased its attack rate on *O. benefactor* at the Pine Falls plot from 8% in 1967 to 61% in 1968 and 84% in 1969, had now dispersed to a distance of 12.9 km. The hyperparasite appeared to be dispersing from a concentration near the release point in much the same manner that *O. benefactor* had dispersed 3 years previously. As stated above, it was already present in the areas into which it was dispersing, but on hosts other than

[2] Ives, W.G.H.; Smith, R.M. 1975. Larch sawfly population dynamics. Environ. Can., Can. For. Serv., North. For. Res. Cent. Edmonton, Alberta. Unpublished File Rep. 098.

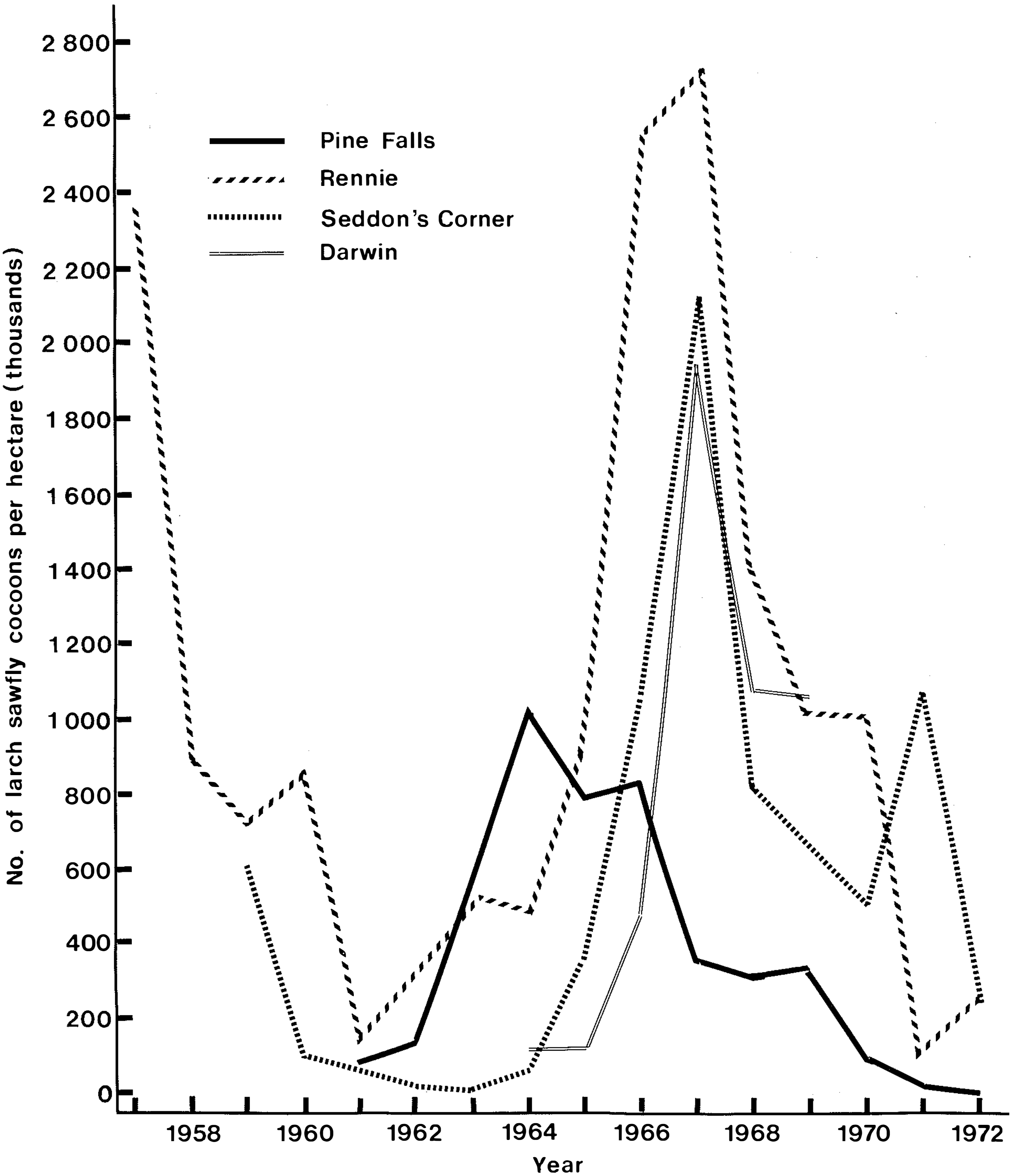

Figure 5. **Trends in larch sawfly cocoon densities per hectare in the four study plots at Pine Falls, Rennie, Seddon's Corner, and Darwin, during 1957 to 1972.**

O. *benefactor* and at a very low density. After building up to very high densities on *O. benefactor*, its dispersal was similar to that of a newly-introduced species.

In 1970 a marked drop in sawfly numbers occurred in the vicinity of the study plot; however, large numbers of *O. benefactor* were being produced at distances of 20-25 km from the plot as sawfly density in these locations remained high. No systematic survey was carried out in 1970, and the limited dispersal data shown in Figure 1 were derived from the life table study plots plus a few other locations. Minnesota workers, however, unexpectedly detected an instance of long-distance dispersal when they found two *O. benefactor* (5.4%) in a sample of 37 adults that emerged from 198 reared cocoons obtained in their prerelease sampling about 290 km south of the Pine Falls release point (Thomson et al. 1977). Their first releases were not made until 1971. Sampling in Manitoba in 1970 did not extend beyond 87 km from the release point. The evidence from Figure 1 indicates, however, that if sampling had been done beyond this distance at the relatively low level of intensity typical of other years, the parasite probably would not have been found beyond 200 km.

In an extensive survey in 1971, *O. benefactor* was found at Ignace, Ontario, 357 km from the release point. High rates of attack averaging 90% were found at distances of about 225 km east and 80 km south of the release point. At locations further south than these, a lesser degree of parasitism occurred (Fig. 2). Dispersal to the south and southeast was not as rapid as to the east, possibly because the prevailing winds are from the west, but also partly because both tamarack and the sawflies feeding on it were relatively abundant on an area basis in southeastern Manitoba. The dispersing parasites would therefore require more time to build up to high levels of abundance where interference and competition among adults would stimulate them to disperse more rapidly. In the plot where Minnesota workers found *O. benefactor* in 1970, parasitism was 18% in 1971 (Thompson and Kulman 1976). This was a plot where 58 females were released in 1971. In seven other Minnesota plots in which similar numbers of *O. benefactor* females were released in 1971, the average parasitism in that year was only 0.13%. Although host density was lower in the plot having 18% parasitism, a considerable portion of the parasitism that occurred here was probably due to parasites already present in 1970. This plot is designated by an "R" in Figure 2 because the other eight Minnesota plots shown are check plots only.

Large increases in parasitism were recorded at some of the collection points between 1970 and 1971. At Rennie for example, parasitism by *O. benefactor* increased from 4 to 85% and, at Seddon's Corner, from 4 to 69%. The larch sawfly was still quite abundant in some locations in Manitoba. In a collection of over 50 000 larvae made near Lac du Bonnet, approximately 90% were parasitized by *O. benefactor*.

M. dimidiatus was recorded at distances of up to 316 km in 1971, with attack rates on *O. benefactor* as high as 90% at distances up to 190 km. Its rate of attack on *O. benefactor* was highly variable out to about 200 km (Fig. 2). In contrast, the rates of attack by *O. benefactor* on the larch sawfly were relatively constant out to about 225 km. The great extension in detected range for *M. dimidiatus* as a parasite of *O. benefactor* from 13 km in 1969 to 316 km in 1971, and the marked variability in rates of attack, may indicate that the hyperparasite had transferred to *O. benefactor* in many locations other than at Pine Falls. At the release plot in 1969 and 1970 and at many nearby locations, however, many more *M. dimidiatus* adults emerged from sawfly cocoons than did *O. benefactor* adults (Fig. 3). These numerous hyperparasite adults available for dispersal contributed significantly to the widespread increase of *M. dimidiatus* attacks in 1971. The high rates of attack by the hyperparasite would markedly reduce the supply of adult *O. benefactor* available for dispersal because each *M. dimidiatus* adult replaces a potential *O. benefactor* adult.

In 1972 the larch sawfly population in the Pine Falls plot dropped to only 2200 cocoons per hectare. Only four cocoons were obtained from 100 larval-drop trays that covered an area of 0.18m^2 per tray (Ives et al. 1968), and two of these hosts had been attacked by *O. benefactor*. A sample of 45 larvae collected within 0.2 km of the release point was dissected and showed 98% parasitism by *O. benefactor*, of which only 7% had been attacked by *M. dimidiatus*, a marked decrease from previous rates in this location.

A general decrease in larch sawfly populations occurred throughout southeastern Manitoba and northwestern Ontario in 1972. Parasitism by *O. benefactor* prior to 1972 had not been high enough in all of these locations to account for this decrease. At Lac du Bonnet, where mass collections of the larch sawfly were made in 1971, populations were now light and only 3752 cocoons were obtained. Parasitism of these by *O. benefactor* was 55%. Parasitism by *M. dimidiatus*

Table 3. Percentage parasitism by *O. benefactor* and *M. dimidiatus* at Pine Falls and Seddon's Corner locations, 1977-83

	Pine Falls area							
	Near release plot		8 km south of plot		8 km north of plot		Seddon's Corner plot	
Year	*O. benefactor*	*M. dimidiatus*	*O. benefactor*	*M. dimidiatus*	*O. benefactor*	*M. dimidiatus*	*O. benefactor*	*M. dimidiatus*
1977	0 (72)[a]							
1978	2 (1730)	86 (14)	19 (424)		0 (237)		5 (75)	
1980			15 (535)	75 (32)			0 (152)	
1981	10 (31)	100 (2)	17 (166)	93 (27)			8 (24)	0 (2)
1982	60 (15)	0 (8)	9 (44)	33 (3)	17 (6)	0 (1)	0 (54)	
1983	no sawfly larvae found						0 (25)	

[a] Numbers in parentheses indicate sample size.

again showed great variability, with an unusual record of 50% parasitism in a sample of 12 *O. benefactor* collected 404 km from the release point. Maximum dispersal of *O. benefactor* in 1972 was 476 km (Fig. 2).

In the Pine Falls plot in 1973, no larch sawfly eggs were found on 220 branches sampled nor were any cocoons obtained in 100 larval-drop trays[3]. An extensive dispersal survey was not conducted in 1973.

In 1974, sampling in the Pine Falls study plot again did not reveal the presence of the larch sawfly. In a 2-hour search on trees within 0.1 km of the plot on July 22, evidence of feeding by four colonies of larch sawflies was observed but larvae were not present on the branches. Larch sawfly populations were light in most locations in southeastern Manitoba and northwestern Ontario and it was difficult to find sufficient larvae for samples, particularly at locations within 100 km of the release point. Only three locations were found in southeastern Manitoba where there were sufficient larch sawflies to make mass collections. Dispersal of *O. benefactor* and rates of attack by the parasite were similar to what occurred in 1972 (Fig. 2). The parasite was found, however, just east of Kakabeka Falls, Ontario, a distance of 540 km from the release point. The southeastern locations (toward Fort Frances, Ontario) now showed greater increases in rates of attack by *O. benefactor* than the increases toward Thunder Bay.

Large-scale dispersal studies and intensive sampling near the release points were terminated in 1974. In 1977 a collection of 37 fifth-instar larvae and 35 fourth-instar larvae all had head-capsule widths typical of larvae not parasitized by *O. benefactor*. Dissection of seven of the fifths and seven of the fourths that had somewhat smaller head capsules than the other larvae revealed no parasitism. Further collections were made at locations near the Pine Falls and Seddon's Corner release plots during 1978-83 (Table 3). In some cases all sawfly larvae were dissected, but for the larger samples estimates of percentage parasitism by *O. benefactor* were based on an initial sorting of the sawflies by cocoon size or head-capsule width size and the dissection of all doubtfuls and portions of the typically small or normal size of sawflies.

Near the release plot at Pine Falls, parasitism by *O. benefactor* increased from 0 in 1977 to 60% in 1982, while parasitism by *M. dimidiatus* was high except in 1982. At the location 8 km south of the plot, *O. benefactor* parasitism was relatively constant from 1978 to 1981 and *M. dimidiatus* parasitism was relatively high. There was an apparent decline in the rate of parasitism by both species in 1982. At Seddon's Corner *O. benefactor* parasitism was quite low during the period (mean of 2%) compared to the value of 93% obtained in this area in 1973. Because of the low values of *O. benefactor* parasitism here, attack by *M. dimidiatus* could not be estimated. In 1981 an additional collection in Manitoba was made near Hadashville (48 km south of Seddon's Corner) and no *O. benefactor* were found in 29 larvae dissected. Parasitism had been 95% in this area in 1974.

[3] Ives, W.G.H.; Smith. R.M. 1975. Larch sawfly population dynamics. Environ. Can., Can. For. Serv., North. For. Res. Cent. Edmonton, Alberta. Unpublished File Rep. 098.

Parasitism by *Mesoleius tenthredinis*, however, was quite high in this location in 1981, being 86% total and 54% effective (in 63% of the parasitized hosts, egg hatch was successful in spite of the resistance reaction involving encapsulation by blood cells). Comparatively high rates of attack by this parasite were also found in the Seddon's Corner collections for 1980 and 1982, at 37 and 52% with successful hatch being 67 and 86%, respectively. Values as high as these were rarely encountered in Manitoba prior to the release of the Bavarian strain of *M. tenthredinis* at the Rennie plot in 1964 (Turnock and Muldrew 1971). These high rates may therefore be due to the influence of the Bavarian strain, indicating a dispersal from the Rennie plot of at least 50 km.

The trees near the Rennie plot were examined for evidence of larch sawfly feeding during the period 1977-83, but none was observed. Even in the locations where collections were made near Pine Falls and Seddon's Corner during this period, the sawfly density was so low that several hours of intensive searching were required to collect the larvae. In 1983 no larvae were found in the Pine Falls area in spite of some intensive searching.

Much of the data for the Pine Falls, Seddon's Corner, and Rennie plots are presented in Figure 6. In addition, larch sawfly population levels since 1947 as indicated by defoliation estimates are plotted.

In 1974, 3% of the *O. benefactor* larvae found in 162 sawflies collected near McMunn, Manitoba, were dead and enclosed in capsules of blood cells similar to those found around eggs of *Mesoleius tenthredinis* in larch sawfly hosts (Muldrew 1953). The count increased to 60% in 1975, then dropped to 12, 17, and 20% in 1976, 1977, and 1978, respectively. Attacks on *O. benefactor* by *Mesochorus dimidiatus* were very high during this period and there was some evidence that excessive probing by adult female hyperparasites searching for suitable hosts killed the *O. benefactor* larvae, resulting in their encapsulation. Parasitism by *O. benefactor* averaged about 20% for 1976-78 and possibly because of this, sawfly larvae were comparatively easy to collect at this location during these years.

ESTIMATES OF TOTAL NUMBERS OF *O. BENEFACTOR* ORIGINATING FROM THE PINE FALLS RELEASE FOR 1964-69

The estimated densities of sawfly cocoons per hectare in the study plot for 1964-69 (1 008 300, 783 000, 822 900, 340 000, 301 400, and 326 100, respectively) were used with the estimates of parasitism to derive the estimated total numbers of *O. benefactor* originating from the 1961 release. The estimated numbers of parasites for 1964-69 were 273 200, 5 953 700, 65 294 900, 272 343 500, 1 187 004 000, and 8 250 978 000, respectively (Fig. 7).

Using an exponential equation of the form $Y = ae^{bX}$, where Y is the estimated number of *O. benefactor* present and X is the number of years after the release of *O. benefactor* in 1961, the equation $Y = 1578e^{1.973X}$ ($r = 0.989$) was derived by least squares fit. The mean increase in numbers of *O. benefactor* per year was 7.2-fold. The number of *O. benefactor* present in 1961 ($X = 0$) extrapolated from the equation is 1578 in terms of parasites present in cocooned hosts. In 1961 the estimated number of first-instar sawfly larvae in the study plot was 680 079 per hectare and the number of sawfly cocoons formed was 87 600 per hectare. From the survival rate of 12.88%, it can be calculated that from a population of 12 252 first-instar hosts containing *O. benefactor*, 1578 *O. benefactor* larvae would be present in the sawfly hosts present in the cocoons in the fall. The 158 mated adult female *O. benefactor* released would thus have had to parasitize successfully an average of approximately 78 hosts each to arrive at this figure. Ives (1976) stated in reference to *O. benefactor* that "the limited data available suggested that 200 eggs per female was a reasonable estimate of their fecundity." When this figure was used as an imposed upper limit in one of his models, a good fit was obtained between observed and calculated number of attacks per female *O. benefactor* during the period 1964-71 for the Pine Falls plot data (Fig. 15 in Ives 1976). The figure of 200, however, applies to parasites that emerge naturally in the field. The parasites released in 1961 had a mean age of approximately 7 days at the time of release. Half of these parasites had been reared in Belleville, shipped to Winnipeg, placed in mating cages for 2 or 3 days, and then transported to the Pine Falls plot for release. The other half of the adults released were obtained from cocoons that had been forwarded to Winnipeg from Belleville prior to their rearing. Mortality of adults between the time of emergence and the time of release was 28%; thus, an appreciable percentage of those released were probably in a weakened condition when released. Additionally, 29 of

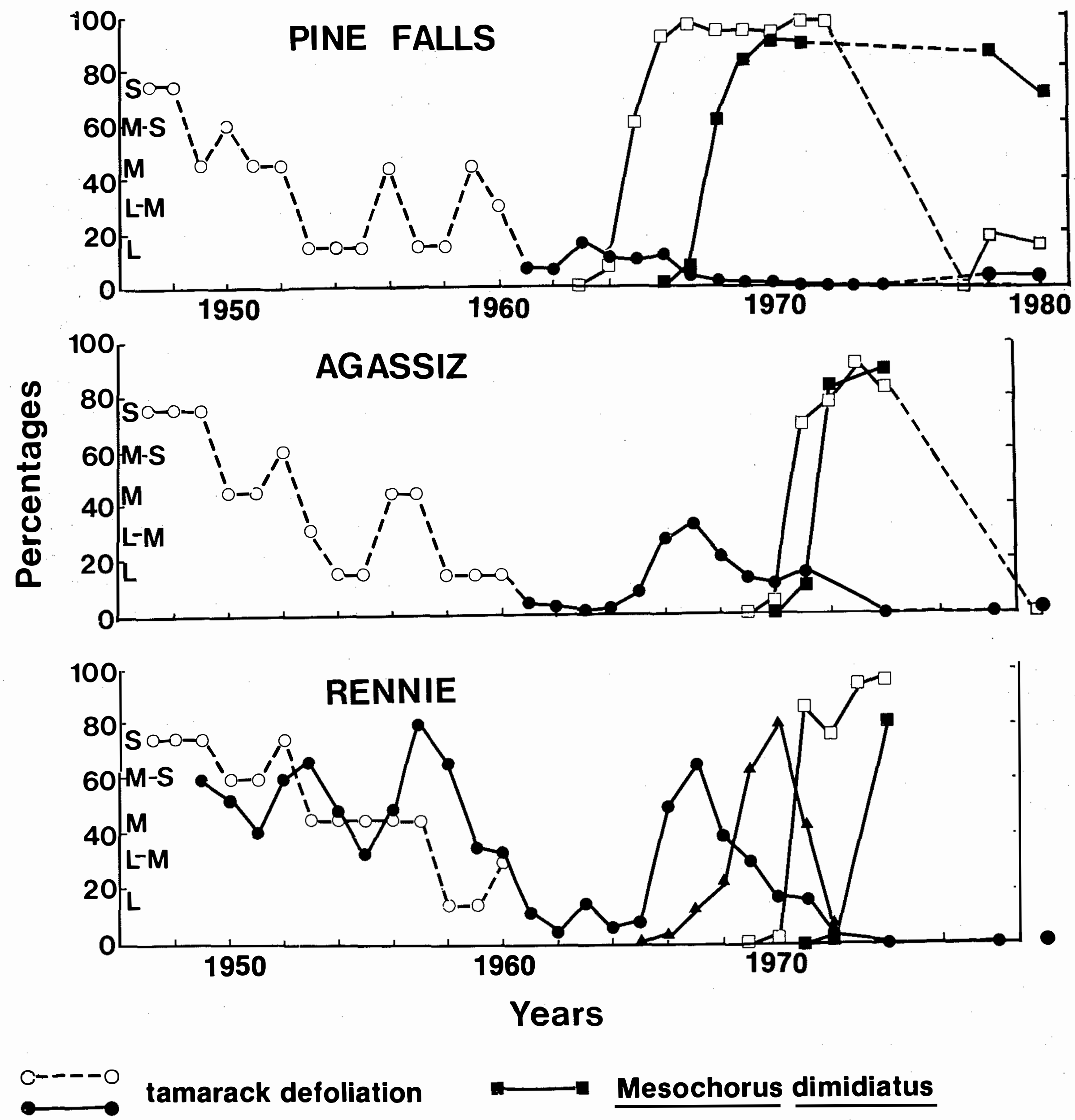

Figure 6. Defoliation of tamarack and parasitism of the larch sawfly in three plots in Manitoba.

Open circles - defoliation estimates by Forest Insect and Disease Survey personnel: S = severe, M = moderate, L = light.
Solid circles - defoliation estimates based on detailed analysis of 50 trees per plot and visual estimates after 1971.
Open squares - percentage parasitism by *O. benefactor*.
Solid squares - percentage attack on *O. benefactor* by *M. dimidiatus*.
Solid triangles - percentage parasitism by *M. tenthredinis*

the adults had been used in parasitization cages for 5 days prior to release and had deposited some of their eggs in larch sawfly larvae that had been placed in the cages with them. The figure of 78 first-instar hosts attacked per female parasite released in 1961 would therefore seem to be a reasonable estimate.

RATE OF DISPERSAL OF *O. BENEFACTOR* FROM THE PINE FALLS RELEASE POINT

A high rate of attack (over 80%) by *O. benefactor* extended out to 3.5 km in 1968, 10 km in 1969, 150 km in 1971, and 300 km in 1972 (Fig. 2). Because high densities of hosts occurred in much of these areas during these years, high populations of *O. benefactor* were produced. As noted above, the total numbers of *O. benefactor* present, expressed as parasites in overwintering hosts, were roughly estimated as 1 billion in 1968 and 8.2 billion in 1969. Extrapolation from the equation in Figure 7 provides an estimate of over 80 billion in 1970, but the decline in the rate of dispersal beginning about 1970 suggests that this figure might be too high. The greater the numbers of the parasites dispersing from the central area each year, the greater the chance of recovering the parasite at long distances from the release point. Figure 7 shows the values obtained for maximum dispersal distance from the release point plotted against the number of years from the release year in 1961. The best fit by the least squares method is described by the equation $Y = 0.116e^{1.05X}$ ($r = 0.991$), which gives a straight-line relationship when plotted on semilogarithmic paper. Maximum dispersal distance tended to level off after 1969, suggesting that maximum dispersal capability was reached by about 1970. Mean annual rates of dispersal calculated on the basis of the original release date (1961) provide values considerably lower than when the earlier years are omitted and dispersal is calculated for periods starting from 1965 or 1968, as shown in Table 4. The data indicate that dispersal capabilities for this and other introduced species are underestimated if mean dispersal distances are calculated over a series of years starting from the year of release. For *O. benefactor*, dispersal during 1968-72 averaged approximately 110 km per year.

When intensive sampling of the larch sawfly was carried out, as in the life table plots (Ives et al. 1968) and by the Minnesota workers (Thompson et al. 1977), *O. benefactor* was discovered considerably beyond the maximum dispersal distance expected on the basis of less-intensive sampling. The maximum detected distances for 1962-68 are therefore underestimated because sampling was not intensive. The maximum distance for 1964 of 220 m and the extrapolated distances for 1961, 1962, and 1963 (11, 33, and 95 m, respectively) should probably be much larger, but how much larger is difficult to judge.

Table 4. Mean annual rates of dispersal (km) of *O. benefactor* from the Pine Falls release point, based on the original release date of 1961 and calculated for periods starting in 1961, 1965, and 1968

	Starting date used in calculating average		
Year	1961	1965	1968
1964	0.073		
1965	0.200		
1966	0.644	2.42	
1967	1.07	2.82	
1968	1.61	3.49	
1969	10.86	21.53	75.63
1970	32.56	58.44	140.87
1971	35.7	59.37	115.24
1972	43.3	67.89	116.18
1974	42.2	60.91	89.62

DISPERSAL OF *O. BENEFACTOR* FROM OTHER RELEASE POINTS

Riverton, Manitoba

Parasite releases of *O. benefactor* made in 1962 and 1963 at Riverton are shown in Table 1. Parasitism by *O. benefactor* was 3% in 1963, 36% in 1964, and 84% in 1965. Severe flooding occurred in the plot in 1966, causing sawfly populations to decrease markedly. Coincident with this, parasitism by *O. benefactor*

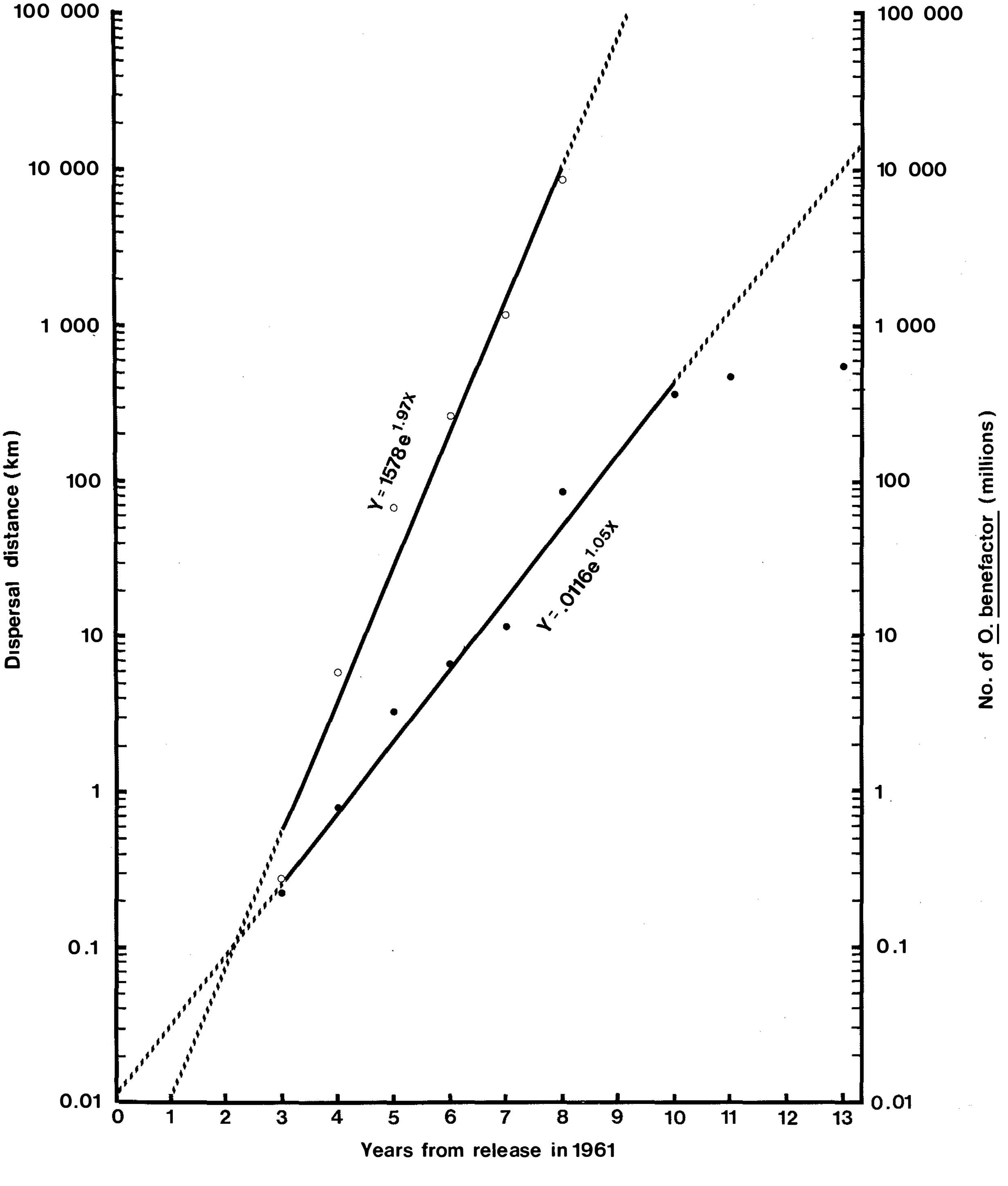

Figure 7. **Annual increase in *O. benefactor* dispersal distance for 1964-74 (solid circles) and an estimate of the total number of overwintering *O. benefactor* in the Pine Falls region for 1964-69 (open** circles). The equation for dispersal distance was derived from the points shown excluding the last two, 1972 and 1974, when it leveled off, and 1970, when insufficient sampling was carried out.

dropped to 77% in 1966 and 66% in 1967. After host density increased in 1968, parasitism recovered to 98% and in 1969 it was 96%. Larch sawfly populations had become very scarce by 1970, so sampling was discontinued. Initial dispersal was more rapid than at Pine Falls, being 274 m by 1964 and 1.6 km by 1965, 2 and 3 years after release, respectively (Muldrew 1967). This was probably partly due to the larger number of mated female parasites released at Riverton (1397) and to the lower host densities at Riverton after 1962.

A 1973 sample of 65 larvae collected at Mafeking, Manitoba, 322 km northwest of the Riverton release point, showed 6% parasitism by *O. benefactor*. Dispersal at Pine Falls after the same number of years (11) was 467 km. The parasite could have dispersed from The Pas, Manitoba, 166 km to the north, where the parasite was released in 1968, but The Pas dispersal data indicated that dispersal from there could not have been this rapid.

The hyperparasite *M. dimidiatus* was first discovered at the Riverton release plot in 1968, 6 years after initial release of *O. benefactor* at that plot. Its rate of attack on *O. benefactor* increased from 13% in 1968 to 67% in 1969.

Crutwell, Saskatchewan

Two small releases in 1964 and 1965 and a larger one in 1966 were made at Crutwell (Table 1). *O. benefactor* from Europe was released in 1964, but it could no longer be readily collected there by 1965, so parasites from the Pine Falls release location were liberated in 1965 and 1966. Parasitism at the Crutwell site was 2% in 1966, 14% in both 1967 and 1968, and 44% in 1969. By 1970 the sawfly had become too scarce to make collections. Maximum dispersal distance detected was 0.4 km in 1967, 1.6 km in 1969, and 27.0 km in 1970.

Hodgson, Manitoba

A relatively large release was made at Hodgson in 1967 (Table 1) at this site, and in the same year 18% parasitism occurred in a nearby study plot. Part of this parasitism, however, was likely due to dispersal from the Riverton release area 22.5 km to the east, where *O. benefactor* had been released 4 years earlier.

Sampling was carried out in an area surrounding the plot and seven samples collected within 40-75 m showed a mean parasitism of 5%. A 7% parasitism rate at the most distant sample indicated that a base level of about 5% parasitism here was due to dispersal from the Riverton release point. One year after release, parasitism reached 61% and was 95% in 1969. In 1970 sawfly density was low and only 15 cocoons were recovered from 100 sampling traps in the plot, all of which were parasitized by *O. benefactor*. The rates of dispersal from this plot and the Riverton plot could not be separated.

M. dimidiatus was first recorded in the Hodgson plot in 1968, attacking 4% of the *O. benefactor*. This rate increased to 39% in 1969 and 67% in 1970.

The Pas, Manitoba

A large release of parasites obtained near Pine Falls was made near The Pas in 1968 (Table 1). In the same year parasitism was 6.5% at the release point, increasing to 52% in 1969 and 65% in 1970. Both the rate of buildup and rate of dispersal were more rapid than those that occurred at Pine Falls, undoubtedly partly due to the relatively lower sawfly density near The Pas in 1968 compared to the Pine Falls site in 1961.

Dispersal was detected only at less than 0.8 km north and south of the release point in 1969, but increased to 1.6 km by 1970, 18 km by 1973, and to 57 km by 1975. The 57-km location, south of The Pas, was at the north end of The Bog, an area where an outbreak of the larch sawfly had been present for several years and one of the few locations in the prairie provinces where larch sawfly larvae could be easily collected after 1975. In 1977 approximately 14 000 cocoons reared from larvae collected in The Bog had 12% parasitism by *O. benefactor*, 73% of which were parasitized by *M. dimidiatus*. In recent years the larch sawfly has been very scarce in The Bog; however, a collection of 68 sawflies from the north end of The Bog in 1983 was 15% parasitized by *O. benefactor*. Parasitism of these sawflies by *M. dimidiatus* was 100%.

St. Labre, Manitoba

A release of 443 mated females reared from cocoons collected at Pine Falls was made in 1970 at St. Labre (Table 1). Trays designed to catch falling larvae and allow them to spin cocoons were set out at 14 locations in 1970 and 1971. Percentage parasitism by *O. benefactor* is shown in Table 5.

Table 5. Rates of parasitism for larch sawfly larvae trapped at various distances from a parasite release made in 1970

Year	0-5 m (4 traps)	10-15 m (5 traps)	15-20 m (2 traps)	20-25 m (2 traps)	30 m (1 trap)
1970	17%	6%	10%	2%	6%
1971	16%	16%	18%	4%	8%

An additional 16 larval drop traps were set out in pairs along a line at intervals of approximately 100 m out to 800 m. In the cocoons obtained from these traps, *O. benefactor* was not found in 1970 but was discovered in 1971 at 100 m (8% of 210) and at 300 m (5% of 160).

By 1972 dispersal of *O. benefactor* from the Pine Falls release reached this location, negating further studies on dispersal at St. Labre. Parasitism here was 43% in 1972 and 82% in 1973.

Seddon's Corner, Manitoba

In 1971, 507 *O. benefactor* adults (262 females) and 371 *M. dimidiatus* adults (253 females) were released in Seddon's Corner to determine whether the hyperparasite would be noticeably detrimental to *O. benefactor* when an approximately equal number of each species was present. Parasitism by *O. benefactor* prior to the release had been 0.4% in 1969 and 3.7% in 1970. In the year of release it jumped to 69%, undoubtedly due to mass invasion from the Pine Falls release area, thus invalidating the original study. Table 3 shows parasitism by *O. benefactor* and *M. dimidiatus* since 1977. Sawflies have become progressively more difficult to collect at this site since 1980.

Ellscott, Alberta

A total of 240 *O. benefactor* adults (122 females) were released near Ellscott in 1973. In 1974 a sample of sawfly larvae collected near the release point showed 14% parasitism by *O. benefactor* and a sample of 288 collected in 1975 showed 61% parasitism.

Obed Lake, Alberta

A release of 137 *O. benefactor* was made at Obed Lake in 1975, 86 of which were mated females. That fall eight cocoons were collected from soil at the site and six of these were typically small, parasitized ones, confirming establishment. In 1978 approximately 8000 cocoons were collected mainly 1 km west of the release point, where some complete defoliation of tamarack had occurred. Because of high populations, some of the larvae had starved and it was difficult to sort the cocoons into parasitized and nonparasitized groups on the basis of size. Most of the cocoons were sent to the Pacific Forest Research Centre (PFRC), Victoria, British Columbia, for incubation. In these and in a sample of 1000 cocoons incubated at the Northern Forest Research Centre (NoFRC), Edmonton, parasitism by *O. benefactor* was about 1%. Mortality of sawflies in the cocoons sent to PFRC was 82% and in the cocoons reared at NoFRC was 50%. Because of the high mortality rates, the estimates of *O. benefactor* parasitism may have been low: parasitism had increased to 88% by 1979 at the same location, 1 km west of the release point, based on a sample of 1299 cocoons. Similarly in 1979, at 2 km to the west the parasitism was 80% in a sample of 131 eonymphs and at 1 km to the east it was 89% in a sample of 269. Over 1400 small, presumably parasitized cocoons from the Obed area were shipped to PFRC for release purposes. A sample of 39 living *O. benefactor* larvae from this collection was dissected and no *M. dimidiatus* larvae were found. Parasitism by *O. benefactor* and *M. dimidiatus* in subsequent years is detailed in Table 6.

M. dimidiatus first appeared in collections made near the release point 5 years after the release and has built up rapidly since then. It reached the location 13 km to the east in 1983, although it had disappeared from the release location in the same year. The density of the larch sawfly declined markedly in the Obed area in 1982 and 1983, and sawflies were much more difficult to find compared to previous years.

Table 6. Percentage parasitism by *O. benefactor* and *M. dimidiatus* at two locations near the Obed Lake, Alberta, release point, 1980-83

Year	1 km west of release point		13 km east of release point	
	O. benefactor	*M. dimidiatus*	*O. benefactor*	*M. dimidiatus*
1980	93 (6158)[a]	0.02 (1 reared adult)	17 (507)	0 (23)
1981	96 (5329)	12 (76)	84 (631)	0 (52)
1982	97 (595)	56 (63)	99 (166)	0 (31)
1983	93 (534)	0 (53)	16 (79)	43 (7)

[a] Numbers in parentheses indicate sample size.

Other Alberta and Northwest Territories locations

In 1971 approximately 20 000 sawfly larvae were collected in southeastern Manitoba and reared to the cocoon stage. Parasitism by *O. benefactor* was approximately 60% based on size of cocoons. Parasitism by *M. dimidiatus* was 5.3%. The sawfly cocoons were utilized to make releases in the spring of 1972 at Primrose Lake, Jarvie, and Grovedale in Alberta and at Hay River in the Northwest Territories. Estimated numbers of emerged parasites and hyperparasites were 1283 *O. benefactor* and 72 *M. dimidiatus* at Primrose Lake; 1139 *O. benefactor* and 64 *M. dimidiatus* at Jarvie; 469 *O. benefactor* and 26 *M. dimidiatus* at Grovedale; and 856 *O. benefactor* and 48 *M. dimidiatus* at Hay River.

The sawfly became scarce at Hay River in 1973 and thereafter, and no collections could be made for a number of years. The 1972 release point near Hay River was 32 km southwest of Hay River and 7 km northeast of Enterprise. Collections of 16 sawflies made at Hay River and 17 made at Enterprise in 1983 showed no parasitism by *O. benefactor*. At Primrose Lake in 1975 only six larvae were found after much searching and none of these was parasitized by *O. benefactor*. The population at Grovedale in 1973 was light, and of 11 hosts reared to the cocoon stage, 82% were attacked. In 1975, 65% of 88 cocooned eonymphs were parasitized by *O. benefactor*. At Jarvie a collection of 38 eonymphs had 34% parasitism by *O. benefactor* in 1973 and 41% in 1975 in a sample of 175.

In the fall of 1980 cocoons reared from larvae collected near the Obed Lake release site were placed in three screen cages, 1000 to a cage, and placed out under approximately 5 cm of moss and soil at one location in Alberta and two in the NWT where moderate infestations of the larch sawfly were present (Table 1). The cocoons received insufficient warmth and only the cage placed out near Bell Rock had a fairly good emergence (332 *O. benefactor* adults). It was at this location only that the parasite was recovered from larval collections made during the summer of 1981. The cocoons placed out near Fitzgerald produced only 36 *O. benefactor*, and the cocoons placed out near Fort Smith produced only 30. In 1982 a sample of 100 sawflies was collected 1.6 km west of the Bell Rock release point, but no *O. benefactor* were found in 31 of the smallest larvae that were dissected. Larvae were not found near the release point, where there was little defoliation. Trees 1.6 km west of this location were stripped. A collection of 45 larvae made at the Fort Smith townsite in 1983 showed no parasitism by *O. benefactor*. The three release points were 13 and 5 km west and 13 km southeast of the townsite.

DISCUSSION AND CONCLUSIONS

Role of mutual interference

Nicholson and Bailey (1935) proposed an area of discovery (a) for searching parasites where

$$a = \frac{1}{\text{parasite density}} \times \log_e \frac{\text{no. of hosts exposed to attack}}{\text{no. of hosts attacked}}$$

Hassell and Varley (1969) plotted the relationships between $\log_{10}a$ and $\log_{10}$ *parasite density* for five parasites and found they could be represented fairly well by the straight line formula, $\log a = \log Q - m \log P$ or $a = QP^{-m}$, and they termed Q the *quest* constant and m the *mutual interference* constant. Because of m, searching efficiency a declines as parasite density P increases. Hassell and May (1973) showed that this relationship could produce a stable equilibrium in the Nicholson-Bailey model rather than increasing oscillations of both host and parasite density.

Some workers believe that interference would not be important at the level of parasite densities expected in nature (Griffiths and Holling 1969) or at equilibrium densities of host and parasite (Free et al. 1977). Free et al. (1977) also showed that where the host distribution was patchy, the aggregation of parasites where hosts were most dense produced a decrease in parasite-searching efficiency, which they termed pseudo-interference. Hassell et al. (1976) suggested that with aggregation of parasites there would be increased interference between them and increased dispersal. Griffiths and Holling (1969) concluded that the time wasted by parasites after encountering other parasites would be greater in nature than in cage studies.

Hassell (1978) suggested that if the rate of dispersal accelerated as parasites became increasingly abundant, the cause was likely an increasing degree of interference between the adult parasites. This is what occurred in the present study. Ives (1976) calculated a mutual interference constant of 0.91 for *O. benefactor*, although, as Hassell (1978) pointed out, this high value has to be treated with some reservation because the estimate is based on estimates of populations in the field, which are subject to sampling error.

Beddington et al. (1978) searched the literature and found six cases of successful biological control in which there were sufficient data from which to calculate a ratio, which they termed the q value, where

$$q = \frac{\text{host equilibrium density after parasite was introduced}}{\text{host equilibrium density before parasite was introduced}}$$

These six values were less than 0.025 and were much lower than q values obtained from laboratory or cage studies. They were unable to explain these low q values using models that incorporated variable searching efficiencies of parasites or variation in the mutual interference factor. Their models indicated that incorporating spatial heterogeneity, i.e., the patch distribution of the host and the differential exploitation of the patches by the parasite, was probably the key to explaining the low q values. One of their cases was that of the larch sawfly and the parasite *O. benefactor*. The larch sawfly feeds gregariously on tamarack, which in turn has a scattered distribution, and levels of infestation vary greatly between stands (Turnock 1960). The host of *O. benefactor* thus has a very patchy distribution, which may partly account for the very low q value obtained.

The estimates of Beddington et al. (1978) for equilibrium host densities with parasites present were very rough. In the larch sawfly-*O. benefactor* case, the host has become almost locally extinct in some locations, and an equilibrium level has apparently not yet been reached. This would make the q value even lower than the 0.025 given. This example is complicated by the role of *M. dimidiatus*, which markedly affects the efficiency of *O. benefactor*.

Free et al. (1977) did not deny the importance of interference when parasite densities were well above equilibrium values, such as had commonly occurred following the successful introduction of a parasite, where the parasites increased rapidly to exceptional densities before they caused a decline in host numbers and subsequently their own. Hassell (1978), in discussing the case of *O. benefactor* released against the larch sawfly in North America, pointed out that its rate of spread accelerated as it became progressively more abundant and that the relationship between distance and time was an exponential one. He thought it was likely that interference was serving to increase the rate of dispersal. If dispersal were random, he suggested, then the relationship between distance and time would have been a linear one. The data documenting the exponential increase in *O. benefactor* dispersal are summarized in Figure 7.

It seems that as the density of the larch sawfly decreased progressively in the Pine Falls area from 1964 to 1970, largely due to the influence of *O. benefactor*, an increasing degree of competition between the adults of this parasite would have occurred, probably involving both females and males, which would have led to increased mutual interference and dispersal. In addition to encounters between adults, the females would have had increasing difficulty in finding hosts unattacked by *O. benefactor*. Since this species has a strong tendency to avoid egg wastage due to superparasitism (Muldrew 1967), this would also have led to increased dispersal. It would be difficult to determine the relative importance of mutual interference between adult parasites and a shortage of unparasitized hosts in causing an increased rate of dispersal.

Role of *M. dimidiatus*

It had been standard practice in biological control to avoid introducing secondary parasites. Van den Bosch (1971) pointed out that this policy has not been developed out of careful study of hyperparasitism, but "stems from an instinctive feeling that anything which destroys a primary parasite must be bad". With obligate hyperparasites, which cannot develop on the nonparasite host, May and Hassell (1981) concluded on the basis of mathematical analysis that stability is most likely if the attack distributions of parasite and hyperparasite are clumped and the area of discovery of the hyperparasite is larger than that of the parasite. They found that in theory the addition of an obligate hyperparasite to a two-species system increases the equilibrium level of host density.

In the present study, where the hyperparasite *M. dimidiatus* is an obligate acting on the primary *O. benefactor*, it was postulated (Muldrew 1973) that the hyperparasite "may actually be performing a useful role by decreasing the rate of parasitism by *O. benefactor* at low sawfly densities, thus preventing the local extermination of both its host and, as a consequence, itself. The danger of such local extinction is that re-invasion of an area by the host only may occur, and outbreaks develop before *O. benefactor* can re-invade".

Messenger (1975) discussed a similar case, that of the biological control of the walnut aphid in California brought about by the primary parasite, *Trioxys pallidus*. After the introduction of an Iranian ecotype in 1968, widespread control was achieved within 2 years in spite of the primary being attacked by a number of species of nonspecific hyperparasites. Messenger (1975) stated that careful observations suggested that these "collectively may serve as a dampening agent, preventing the very efficient *T. pallidus* from overexploiting its host population". Even with nearly 100% of the primary parasites being parasitized themselves by secondaries late in the season, attack rates by primaries in the spring could be as high as 98% These data suggest that if it were not for the high rate of attack by secondaries the primary parasite "might annihilate its host resource, at least in a local sense, resulting in the demise of the primary parasitoid itself, and a subsequent rapid, unchecked resurgence of the aphid" (Messenger 1975). In a later publication on this project, however, van den Bosch et al. (1979) avoided suggesting that the role of the hyperparasites might actually be beneficial. These authors simply concluded that the hyperparasites, even though they were very abundant, did not impair the efficiency of *T. pallidus*.

A conclusion that a hyperparasite can play a beneficial role in controlling a pest implies that the deliberate introduction of hyperparasites might be recommended in certain biological control programs. Because of the obvious risks involved, such a conclusion would have to be based on very strong evidence, and the danger of the hyperparasite transferring to other parasite species would have to be taken into account. In the larch sawfly situation, the evidence supporting the view that *M. dimidiatus* is beneficial is not very strong. Situations in which *O. benefactor* has acted against the larch sawfly over extended periods of time in the absence of *M. dimidiatus* have not yet occurred in Canada, although the recent release of *O. benefactor* in British Columbia may provide such evidence. In the absence of *M. dimidiatus* in this region, the highly efficient primary parasite may cause the extinction of both its host and itself in certain areas, ultimately allowing larch sawfly buildup in these areas. Additionally, although the sawfly still remains in low numbers in Manitoba despite *M. dimidiatus* having affected *O. benefactor* for up to 14 years, there still exists the danger that the hyperparasite will have a sufficiently detrimental effect on *O. benefactor* in the future to allow the larch sawfly to increase to outbreak numbers.

Future prospects for control by *O. benefactor*

The larch sawfly has remained at very low densities for 15 years at the Pine Falls plot and for about 10 years in most other locations in southeastern Manitoba (Fig. 6). Ives (1976) showed that these low density levels are due to the presence of *O. benefactor* in the control complex. The high levels of attack by *O. benefactor* that prevailed in most locations up to about 1974, however, have now dropped to much lower levels over much of southeastern Manitoba and now range from 0 to 20%.

Larch sawfly control by *O. benefactor* can be compared with the control of the prickly pear cactus (*Opuntia* spp.) by the introduced moth, *Cactoblastis cactorum*, reported in Australia and other countries. Prior to 1900 a number of species of *Opuntia had been* introduced to Australia and had spread widely. By 1925 about 26 million ha were infested and in half of this area the cactus was impenetrable by man and animals. Following the introduction of *C. cactorum* from Argentina in 1925, a great reduction in cactus density occurred down to a level of four or fewer per hectare.

Two explanations of the moth-cactus interaction have been advanced. Myers et al. (1981) and others who have studied the relationship have found that the cactus and the moth now exist at relatively constant equilibrium levels (at least in open woodland sites), with the main controlling mechanism apparently being the nonrandom distribution of moth eggs, resulting in overcrowding on many plants and no attack on others. Birch (1971) suggested that if egg-laying were random, the rate at which the moth could destroy the cactus would be increased.

This scenario is quite different from the hide-and-seek mechanism proposed by Nicholson (1974) and others, which postulates large fluctuations in density of host and parasite, with local extinction being common. A certain proportion of the cactus plants are missed by the searching moth females, and the prickly pear is able to increase in density and disperse its fruits. Eventually these larger patches are found by the moth and wiped out, but the dispersed fruits initiate new patches, ensuring the survival of the cactus. Myers et al. (1981) believe that this explanation applies only to a few pasture populations, with the woodland populations serving as refuges.

With the larch sawfly-*O. benefactor* case, it is probably too early to tell whether either of these possibilities is applicable. At the location 8 km south of the Pine Falls release area, there is an indication that the host, the parasite, and the hyperparasite have reached fairly stable equilibrium values. At Seddon's Corner and perhaps Hadashville there is some evidence that cases of temporary local extinction of *O. benefactor* occur. There also seem to be locations where the larch sawfly is not present over a considerable area.

Perhaps an important difference between the two cases lies in the fact that up to 50% of the larch sawflies may have a prolonged diapause and not emerge until the second summer after cocoon formation. Only a small percentage of its parasites show this extended survival. Parasites may thus die out in a particular location and the sawfly might appear later to initiate a buildup. The parthenogenetic nature of the sawfly increases the chance of this happening. The cactus apparently cannot survive in the same locality in a similar fashion.

At very low levels of parasitism, which usually coincide with low host density levels, the question of whether *O. benefactor* can survive on alternate sawfly hosts arises. There are no records of *O. benefactor* being reared from other sawflies in Canada or in Europe, where Pschorn-Walcher and Zinnert (1971) failed to rear it from 25 other sawfly species. On the other hand, these authors state that the hyperparasite *M. dimidiatus* is polyphagous, having been reared from *Olesicampe* species associated with the sawflies *Pristiphora geniculata* Htg., *P. moesta* Zadd., *Croesus septentrionalis L.*, and *Hemichroa crocea* Geoff. *M. dimidiatus* should thus have a better chance of surviving in a particular location in spite of extremely low densities of *O. benefactor* than would *O. benefactor* in regions where the larch sawfly was scarce.

With the current low levels of *O. benefactor* attack, observations and small-scale sampling should reveal whether the larch sawfly will build up in density given a favorable period of weather or reduced pressure by other natural enemies. The evidence to date indicates that *M. dimidiatus* continues to play a significant role in keeping the numbers of *O. benefactor* low in relation to larch sawfly numbers. Further studies are required to determine if the fact that *M. dimidiatus* can persist in a region on alternate hosts, in contrast to *O. benefactor*, will give it an advantage over *O. benefactor* to the extent that it will prevent *O. benefactor* from responding efficiently to an increase in larch sawfly density. If this should occur, a relatively small rerelease of *O. benefactor* should duplicate the results of this study, because the numbers of *M. dimidiatus* persisting on alternate hosts are almost certain to be very low.

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APPENDIX I

Locations of sampling points with distance from the Pine Falls release points, percentage parasitism by *O. benefactor* and *M. dimidiatus*, and sample sizes for these estimates

Year and location no.	Percentage parasitism *O. benefactor* %	Sample size	*M. dimidiatus* %	Sample size	Distance from release point (km)	Latitude °	′	Longitude °	′
1965									
1	61	1814	0	363	-	50	41	96	05
2	47	211			0.08	50	41	96	05
3	26	110			0.16	50	41	96	05
4	18	130			0.32	50	41	96	06
5	7	88			0.48	50	41	96	06
6	3	313			0.64W	50	41	96	07
7	22	207			0.64N	50	41	96	06
8	4	23			0.80N	50	42	96	06
9	2	55			0.80S	50	40	96	05
10	0	10			1.21	50	40	96	05
11	0	80			2.01	50	42	96	06
1966									
1	93	1529	0.4	454	-	50	41	96	05
4	51	401			0.32	50	41	96	06
5	38	421			0.48	50	41	96	06
12	37	158			0.56	50	41	96	06
13	26	31			1.05	50	41	96	05
14	15	92			1.09	50	40	96	05
15	26	317			1.32	50	40	96	06
16	14	224			1.54	50	40	96	06
17	5	219			2.09	50	40	96	05
18	10	270			2.82	50	42	96	06
19	1	233			3.22	50	40	96	03
1967									
1	97	631	8	98	-	50	41	96	05
5	85	223			0.48	50	41	96	06
9	33	33			0.80	50	40	96	05
20	50	16 000 (approx.)			1.40 (mean)	50	40	96	04
16	39	41	19	16	1.54	50	40	96	06
17	27	22			2.09S	50	40	96	05
18	27	22			2.82S	50	42	96	06
19	14	14			3.22S	50	39	96	06
21	16	31			3.22N	50	43	96	07
22	0	45			4.43S	50	39	96	06
23	0	23			5.15S	50	38	96	07
24	3	33			6.44N	50	44	96	08

Over 100 adult sawflies were reared from collections made at various distances between 6.6 and 11.0 km, but no *O. benefactor* were recovered.

Year and location no.	Percentage parasitism O. benefactor %	Sample size	M. dimidiatus %	Sample size	Distance from release point (km)	Latitude °	′	Longitude °	′	
1968										
1	95	561	61	154	-	50	41	96	05	
13	81	36	31	29	1.05E	50	41	96	05	
11	96	26			2.01N	50	42	96	06	
17	94	17	19	16	2.09S	50	40	96	06	
18	90	21			2.82S	50	42	96	06	
19	87	40			3.22S	50	39	96	06	
21	91	32			3.22N	50	43	96	07	
22	63	68			4.43S	50	39	96	06	
23	36	14			5.15S	50	38	96	07	
24	32	98			6.44N	50	44	96	08	
25	8	48			6.44S	50	38	96	07	
26	31	143			7.24N	50	45	96	09	
27	6	102			8.85S	50	37	96	08	
28	13	114			9.66W	50	46	96	10	
29	5	119			9.66S	50	36	96	08	
30	3	60			11.27S	50	35	96	09	
31	1	94			11.27N	50	46	96	11	
32	0	16			12.87N	50	47	96	12	
33	0	23			15.30S	50	34	96	11	
1969										
1	94	606	84	203	-	50	41	96	05	
8	98	112	78	37	0.8N	50	42	96	06	
9	91	290	41	152	0.8S	50	40	96	05	
11	91	32	61	13	2.01N	50	42	96	06	
17	98	192	77	101	2.09S	50	40	96	05	
21	97	213	0	169	3.22N	50	43	96	07	
22	95	136	11	81	4.43S	50	39	96	06	
23	89	184	0	112	5.15S	50	38	96	07	
24	87	131	0	62	6.44N	50	44	96	08	
28	87	348	0	213	9.66W	50	46	96	10	
31	88	355	0	267	11.27N	50	46	96	11	
32	64	348	0.6	168	12.87N	50	47	96	12	
33	84	362	0	259	15.3S	50	34	96	11	
34	33	320	0	86	16.1N	50	47	96	12	
35	77	284	0	188	16.1SE	50	32	96	06	
36	11	265	0	29	22.5SW	50	37	96	23	
37	3	363	0	6	23.5N	50	51	96	14	
38	7	58	0	4	29.0N	50	53	96	15	
39	0.5	220	0	1	29.9N	50	54	96	15	
40	0	102	-	3	30.6N	50	54	96	1	
41	0.5	568	0	3	38.8N	50	58	96	17	
42	7.5	107	0	8	41.8	50	26	96	32	
43	4	26	0	1	46.7	50	28	95	31	
44	5.5	127	0	7	57.9	50	19	95	35	
45	0.4	506	0	2	70.8	50	04	96	14	Agassiz plot
46	0.9	344	33	3	86.9	50	00	95	31	Rennie plot

Year and location no.	Percentage parasitism: *O. benefactor* %	*O. benefactor* Sample size	*M. dimidiatus* %	*M. dimidiatus* Sample size	Distance from release point (km)	Latitude °	Latitude ′	Longitude °	Longitude ′	
1970										
1	94	847	91	162	-	50	41	96	05	
21	83	313			3.2	50	39	96	06	
47	25	1109			22.5	50	37	96	24	
48	38	13			46.7	50	23	96	34	
49	39	23			54.7	50	12	96	05	
44	30	243			57.9	50	19	95	35	
45	4	948	0	34	70.8	50	04	96	14	
46	2	1854	0	43	86.9	50	00	95	31	
1971										
1	98	492			-	50	41	96	05	
34	80	40	85	27	15.3	50	34	96	11	
47	97	371			22.5	50	37	96	24	
38	100	79	29	49	25.9	50	53	96	15	
42	96	347	50	8	41.8	50	26	96	32	
50	78	49	14	14	45.1N	51	01	96	15	
51	88	66	41	22	45.1S	50	26	95	35	
52	95	260	88	50	45.1	50	18	95	50	
53	67	108	25	53	45.1	51	05	96	01	
54	94	85	11	44	49.9	51	07	96	16	
55	98	56	74	35	49.9	50	32	95	27	
56	95	158	59	76	51.5	50	35	95	25	
57	96	750			53.1	50	28	95	31	
58	88	111	28	83	54.7	50	53	95	24	
44	97	243	80	102	57.9	50	19	95	35	
59	95	65	26	43	61.2	51	00	95	25	
60	86	580			61.2	50	09	95	48	
61	89	149	59	116	67.6	50	56	95	19	
45	69	1991	12	469	70.8	50	04	96	14	
46	90	248	0	17	86.9	50	00	96	31	
62	89	266			90.1	50	02	96	55	
63	88	8	67	3	98.2	50	14	94	57	
64	90	182	48	27	103.0	50	09	94	51	
65	93	108	85	20	109.4	50	02	94	51	
66	97	252	16	37	115.9	49	54	94	56	
67	2	215			120.7	49	38	95	40	S[a]
68	6	86			127.1	49	36	95	37	S
69	61	126	4	24	128.7	49	44	95	07	
70	91	272	80	20	140.0	49	55	94	56	
71	90	73	52	21	148.1	49	48	94	37	
72	0	68			160.9	49	18	95	42	S
73	92	104	47	30	160.9	49	46	94	27	
74	91	64	40	15	183.5	49	42	94	10	
75	96	53	90	29	189.9	49	30	93	48	
76	88	172	0	36	199.6	49	34	94	02	

Year and location no.	Percentage parasitism O. benefactor %	O. benefactor Sample size	M. dimidiatus %	M. dimidiatus Sample size	Distance from release point (km)	Latitude °	Latitude ′	Longitude °	Longitude ′	
77	89	183	50	16	209.2	49	52	93	34	
78	92	38	11	9	209.2	50	35	93	10	
79	96	114	38	45	217.3	50	30	93	07	
80	93	149	49	85	218.9	49	57	93	20	
81	0.1	1182	-		251.1	48	36	94	45	*b
82	0	397	-		254.3	48	31	94	57	*
83	50	143	0	21	276.8	49	46	92	34	
84	1	171	-		276.8	48	43	93	53	S
85	78	199	0	64	286.5	49	54	92	17	
86	1	375	-		288.1	48	40	93	46	S
87	18	79	-		292.9	48	15	94	33	*
88	0	108	-		294.5	48	17	94	23	*
89	62	183	0	46	302.6	49	37	92	19	
90	26	144	6	16	304.2	48	40	93	27	S
91	0.4	243	-		304.2	48	23	93	47	*
92	0.3	692	-		304.2	48	16	94	06	*
93	25	450	2	45	305.8	50	08	91	57	
94	24	59	0	4	309.0	50	10	91	55	
95	0	79	-		312.2	48	14	93	58	*
96	52	309	1	76	315.4	49	34	92	07	
97	0	314	-		329.9	47	56	94	20	*
98	0	178	-		331.5	48	00	94	05	*
99	12	646	0	18	334.7	49	29	91	49	
100	1	177	-		357.3	49	28	91	35	
1972										
1	98	45	7	14	-	50	41	96	05	
101	95	191	58	45	45.1	50	12	96	06	
54	94	36	-		49.1	51	07	96	16	
58	97	33	50	4	54.7	50	53	95	24	
59	100	57	-		61.2	51	00	95	25	
61	89	28	-		67.6	50	56	95	19	
45	78	68	86	7	70.8	50	04	96	14	
46	75	548	7	192	86.9	50	00	96	31	
102	73	142	84	50	93.3	49	53	96	23	
103	68	1740	41	626	93.3	49	52	96	00	
104	97	280	58	26	99.8	49	52	95	32	
105	93	145	20	15	107.8	49	51	95	25	
67	25	1183	16	122	120.7	49	38	95	40	S
106	54	245	23	53	125.5	49	40	95	24	
68	49	1027	47	146	127.1	49	36	95	37	
69	100	33	-		128.7	49	44	95	07	
107	78	197	-		140.8	49	27	96	21	S
108	17	178	-		142.4	49	27	95	28	S
109	26	97	-		144.8	49	27	95	26	S
110	43	509	1	75	156.1	49	20	95	54	S
73	100	40	-		160.9	49	26	94	27	

Year and location no.	Percentage parasitism O. benefactor %	Sample size	M. dimidiatus %	Sample size	Distance from release point (km)	Latitude °	′	Longitude °	′	
111	28	173	20	5	162.5	49	19	95	20	S
112	11	334	-		175.4	49	09	95	48	S
113	83	36	64	11	177.0	50	55	93	36	
114	16	178	0	15	189.9	49	03	95	43	S
115	50	74	46	26	191.5	51	18	93	37	
116	49	127	0	34	191.5	51	33	93	47	
117	24	315	0	5	197.9	49	00	95	23	S
118	9	105	0	4	199.6	49	33	94	02	
119	87	98	-		202.8	49	30	94	00	
78	92	47	19	16	209.2	50	35	93	10	
120	94	17	0	13	222.1	50	57	92	58	
121	30	98	-		228.5	48	48	95	07	S
122	60	30	6	17	238.2	51	02	92	46	
81	5	476	-		251.1	48	36	94	45	*
82	3	156	-		254.3	48	31	94	57	*
123	96	273	22	9	255.9	49	52	92	52	
124	32	269	50	14	259.1	48	43	93	55	S
84	18	401	-		276.8	48	43	93	53	S
125	85	58	67	3	280.0	50	06	92	17	
126	85	67	75	4	285.7	50	06	92	12	
86	38	344	0	21	288.1	48	40	93	46	S
87	48	23	18	11	292.9	48	15	94	33	*
88	1	90	-		294.5	48	17	94	23	*
90	63	202	23	66	304.2	48	40	93	27	S
91	0	14	-		304.2	48	23	93	47	*
92	1	87	-		304.2	48	16	94	06	*
93	79	29	0	8	305.8	50	08	91	57	
94	79	37	0	4	309	50	10	91	55	
95	0	156	-		312.2	48	14	93	58	*
127	23	298	10	10	313.8	48	45	93	04	S
128	70	159	0	23	315.4	50	11	91	52	
97	0	170	-		329.9	47	56	94	20	
129	10	124	0	4	329.9	48	47	92	30	S
98	0	64	-		331.5	48	00	94	05	*
99	81	167	66	47	334.7	49	29	91	49	
100	6	66	-		357.3	49	28	91	35	
130	6	159	0	5	370.1	48	44	92	07	
131	26	115	0	3	391.1	50	14	90	41	
132	37	193	0	10	392.7	50	41	90	32	
133	14	128	50	12	403.9	49	15	90	58	
134	17	78	0	8	408.8	48	47	91	23	
135	12	110	0	5	420.0	51	07	90	12	
136	0	31	-		421.6	51	16	90	14	
137	3	228	0	3	428.1	51	28	90	10	
138	14	79	0	9	429.7	49	07	90	41	
139	12	100	0	5	441.0	48	43	90	57	
140	0	192	-		449.0	49	03	90	27	

Year and location no.	Percentage parasitism O. benefactor %	O. benefactor Sample size	M. dimidiatus %	M. dimidiatus Sample size	Distance from release point (km)	Latitude °	Latitude ′	Longitude °	Longitude ′	
141	1.4	139	-		476.4	48	43	90	14	
142	0	107	-		479.6	51	48	89	34	
143	0	89	-		482.8	48	40	90	02	
144	0	50	-		489.2	48	53	89	56	
145	0	57	-		511.8	48	37	89	48	
146	0	59	-		540.7	48	25	89	33	
147	0	403	-		548.8	48	23	89	23	
148	0	239	-		558.4	48	23	89	20	
1973										
57	76	33	-		53.1	50	28	95	31	
44	86	42	-		57.9	50	19	95	35	
45	93	45	-		70.8	50	04	96	14	
46	95	403	-		86.9	50	00	96	31	
62	78	9	-		90.1	50	02	96	55	
103	83	100	-		93.3	49	52	96	00	
67	76	101	-		120.7	49	38	95	40	S
68	79	90	-		127.1	49	36	95	37	S
107	86	99	-		140.8	49	27	96	21	S
110	82	100	-		156.1	49	20	95	54	S
81	30.1	336	11	9	251.1	48	36	94	45	*
82	4.8	416	5	20	254.3	48	31	94	57	*
87	39.5	81	32	32	292.9	48	15	94	33	*
88	11.4	70	0	8	294.5	48	17	94	23	*
91	5.3	95	0	5	304.2	48	23	93	47	*
92	2.8	214	0	6	304.2	48	16	94	06	*
95	0.2	1682	0	3	312.2	48	14	93	58	*
97	0	194	-		329.9	47	56	94	20	*
98	2	193	0	4	331.5	48	00	94	05	*
1974										
46	96	26	86	11	86.9	50	00	95	31	
103	99	117			93.3	49	52	96	00	dissected sample
103	84	4850	90	100	93.3	49	52	96	00	reared mass collection
67	58	5601	89	107	119.1	49	38	95	40	S reared mass collection
68	50	226			127.1	49	36	95	37	S
69	51	240			132.0	49	44	95	07	
149	83	151			138.4	49	30	95	33	S
110	96	127			151.3	49	20	95	54	S
150	57	99			154.5	49	44	94	57	
151	84	346			180.2	49	05	96	05	S
152	90	315			183.5	49	11	95	14	S
153	89	451			183.5	49	05	95	38	S

Year and location no.	Percentage parasitism *O. benefactor* %	Sample size	*M. dimidiatus* %	Sample size	Distance from release point (km)	Latitude °	′	Longitude °	′	
154	95	338			188.3	49	03	95	46	S dissected sample
154	78	4182	52	73	188.3	49	03	95	46	S reared mass collection
117	76	333			197.9	49	00	95	23	S
155	48	276			201.2	49	33	94	02	
156	57	62			206.0	49	51	93	34	
121	59	152			228.5	48	48	95	07	S
157	59	142			247.8	49	53	92	55	
81	43	73	71	31	251.1	48	36	94	45	*
82	22	641	2	138	254.3	48	31	94	57	*
123	74	162			255.9	49	52	92	52	
124	79	218			259.1	48	43	93	55	S
158	74	564	94	54	262.3	48	43	94	13	
159	43	152			276.8	48	43	93	54	S
60	59	249			286.5	49	37	92	22	
86	60	360			288.1	48	40	93	46	S
87	72	29	24	21	292.9	48	15	94	23	*
89	63	164	100	11	304.2	48	38	93	27	S
91	16	637	17	6	304.2	48	23	93	47	*
92	6	336	10	20	304.2	48	16	94	06	*
95	3	5534	0.6	160	312.2	48	14	93	58	*
127	19	134			313.8	48	45	93	04	S
161	0	175			317.0	49	33	92	03	
162	59	354			329.9	48	46	92	47	
163	43	445			329.9	48	46	92	36	
97	36	11	0	4	329.9	47	56	94	20	*
98	32	57	28	18	331.5	48	00	94	05	*
99	52	279			334.7	49	29	91	49	
164	14	328			338.0	48	45	92	28	
100	8	272			357.3	49	28	91	35	
130	25	488			360.5	48	44	92	07	
165	25	456			363.7	49	35	91	28	
166	0	143			366.9	49	52	91	10	
167	13	267			386.2	48	46	91	22	
168	0	384			387.9	50	12	90	44	
131	8	400			391.1	50	14	90	42	
132	42	31			392.7	50	41	90	32	
169	0	100			392.7	48	46	91	44	
170	12	127			395.9	50	45	90	31	
171	7	169			395.9	48	46	91	38	
172	5	234			399.1	48	46	91	32	
133	0	543			403.9	49	15	90	58	
173	0	112			413.6	52	21	90	49	
174	0	85			418.4	59	19	90	44	

Year and location no.	Percentage parasitism O. benefactor %	O. benefactor Sample size	M. dimidiatus %	M. dimidiatus Sample size	Distance from release point (km)	Latitude °	Latitude ′	Longitude °	Longitude ′
175	1	256			419.3	48	45	91	15
135	32	264			420.0	51	07	90	12
136	0	440			421.6	51	16	90	14
176	0	240			423.3	52	17	90	38
137	0	319			428.1	51	28	90	10
138	7	328			429.7	49	07	90	41
177	0	40			431.3	52	14	90	30
139	0	281			444.2	48	42	90	53
140	0	615			449.0	49	03	90	27
178	0	432			453.8	51	40	89	52
142	0	369			479.6	51	49	89	33
143	0	225			479.6	48	40	90	19
179	0	180			486.0	48	41	90	10
144	0	444			489.2	48	53	89	56
180	0	193			495.7	48	40	90	03
181	0	58			502.1	48	38	89	58
182	0	212			524.6	48	37	89	43
146	0	49			540.7	48	25	89	33
147	1.2	196			548.8	48	23	89	23
183	0	262			555.2	48	23	89	20
148	0	227			558.4	48	23	89	19

[a] S = Sample from southern part of region.

[b] * = Minnesota sample (from Thompson et al. 1977).