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Distribution and Prolonged Diapause of the Rowan Seed Predators *Argyresthia conjugella* (Lepidoptera: Yponomeutidae) and *Megastigmus brevicaudis* (Hymenoptera: Torymidae) and their Parasitoids in Norway

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Abstract: The seed predator *Argyresthia conjugella* Zeller has rowan as its preferred host plant. In years of poor fruiting in rowan, it oviposits on apples. To improve the knowledge of this apple pest, rowanberries were collected from localities all over Norway from 1971 to 1985, and seed predators and their parasitoids were allowed to emerge for up to five years. Two species of seed predators, *A. conjugella* and *Megastigmus brevicaudis* Ratzeburg, and seven species of parasitic Hymenoptera were common. The distribution of these species is shown on EIS (European Invertebrate Survey) maps of Norway. The biology of the parasitoids is summarized based on the published literature and their behavior during emergence. The tendency for delayed emergence, which is an indication of prolonged diapause, was more pronounced in *M. brevicaudis* than in *A. conjugella*, the former appearing in all five years. Five of the parasitoids also delayed their emergence, and three of them to a high degree, up to five years. Prolonged diapause must be taken into account in studies of rowanberry insect guilds.



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1. Introduction

Rowan (mountain ash), *Sorbus aucuparia* L., is distributed in the forest belt of the northern temperate zone [1]. Rowan grows along the forest edges, in mixed stands of deciduous trees, or in open places in the forest [2]. The fruiting of rowan is intermittent, which is a phenomenon called masting [3]. The masting of rowan is synchronous over large areas and has probably evolved as a defense against seed predators [4]. In Scandinavia, two univoltine seed predators are common in rowan, the apple fruit moth, *Argyresthia conjugella* Zeller, and the mountain ash seed chalcid, *Megastigmus brevicaudis* Ratzeburg [4–6]. Both species are seed predators in their larval stage but differ in their overwintering habits. When fully grown in the autumn, *A. conjugella* larvae vacate the berries and hibernate as cocooned pupae in the litter layer [5,7], whereas *M. brevicaudis* larvae stay in the seeds through the winter and pupate there in the spring [8–10].

Prolonged diapause is a counter-adaptation to masting that allows seed predators to escape the poor crop years [11,12]. This trait is common in seed predators [11,13–15] and has also been found in *M. brevicaudis* [4,5] and *A. conjugella* [4,16,17]. Both masting and prolonged diapause will obviously affect parasitoids and other natural enemies of *A. conjugella* and *M. brevicaudis* [18–20], and prolonged diapause has been reported for some of the species at this trophic level as well [4,5].

Another way for the seed predators to escape poor crop years is to search for other host plants. In Fennoscandia, *A. conjugella* has long been known as a serious pest of apple in

the intermasting years of rowan [21]. However, *A. conjugella* is usually not able to complete its life cycle in apple ([17], N.T. and S.K. pers. obs.). Thus, the risk of *A. conjugella* attacking apple at a certain location depends on the relationship between the local population size of viable moth larvae emerging from rowan one year and that of the rowanberry crop next year [22,23]. Based on this principle, a warning system for Norwegian apple growers, now incorporated in the VIPS platform [24,25], was developed during the 1970s [23]. This warning system has also generated a valuable long-term data series on rowanberries [26,27], apple fruit moth larvae, and their parasitization rate [4,19].

The research made back in the 1970s and 80s to increase the knowledge on *A. conjugella* also produced some data that are still largely unpublished. In this paper, we summarize the data from two such studies, one on the geographical distribution of rowanberry seed predators and their parasitoids, and one on the occurrence of prolonged diapause in these insects. Only some of the data on the four most common species have been briefly presented elsewhere as support for a co-evolutionary relationship between rowan and associated insects [4]. Our objectives are to (1) increase the knowledge of seed predators and their parasitoids in Norwegian rowanberries and compare it to a Swedish rowanberry study conducted by O. Ahlberg 50 years earlier [5], and (2) explore the propensity for prolonged diapause in these species, thereby indicating which ones may be underestimated in (1).

2. Materials and Methods

2.1. Sampling of Rowanberries

The first Norwegian large-scale sampling of rowanberries to map the apple fruit moth and other insects in the berries was carried out in August 1971, when the research entomologist T. Edland collected berries from more than a hundred sites in South Norway. The mapping continued in 1975 and lasted till 1984, aiming to cover the whole European Invertebrate Survey (EIS) grid of Norway. This grid consisted of 189 modified 50 × 50 km UTM squares [28]. Most samples contained 1–3 kg of berries, preferably from more than one tree per site, and were collected by agricultural advisors through the Norwegian warning system for apple fruit moth [23]. In the study period, this system encompassed 26–105 sites with rowan trees in regions with commercial apple production, and all of them were in South Norway. From each site, samples of 100 berry clusters were collected in early August and transported to NIBIO at Ås, which is 30 km south of Oslo. The surplus berries from these samples not spent in the warning system were used to rear adult insects for the mapping. In addition, hundreds of berry samples were collected from North Norway and parts of South Norway not covered by the warning system, mostly in the period 1975–1982.

2.2. Rearing of Insects for the Mapping

Before 1978, each berry sample was put in a clay pot with *Sphagnum* in the bottom and overwintered at 3 °C in the dark. From 1978, the overwintering took place under outdoor conditions in an insectarium, storing each sample in a 30 × 60 cm paper bag with a roll of corrugated cardboard (diameter 5–8 cm, length 5 cm). The *Sphagnum* and the cardboard served as preferred pupation sites for *A. conjugella* emerging from the berries, enabling easy sampling of this stage for the warning system. In early spring, about 1 kg of berries from each clay pot or paper bag was transferred to flowerpots (diameter 14 cm) with a transparent lid. The cardboard roll was also transferred. The inside of the flowerpots was lined with black cloth at the bottom and white filter paper on the walls for easier inspection. The flowerpots were kept in a greenhouse until the night frost had ceased, and then under outdoor conditions. They were checked for living imagines at least three times a week for as long as *A. conjugella* or any hymenopterans emerged.

2.3. Study of Prolonged Diapause

Some of the berry samples collected through the warning system in the years 1978–1984, i.e., from apple production areas in South Norway, were kept to study delayed emergence after they had been used for the mapping described above. They were pooled into plastic

buckets from the flowerpots and kept for 4 more years. There were three such buckets from each year in the period, with each bucket containing berries and cardboard rolls equivalent to about 5 kg of fresh material. The buckets were wrapped in black plastic and stored at 3 °C in the dark. In mid-May, the buckets were exposed to outdoor conditions for as long as *A. conjugella* or any hymenopterans emerged in a glass collector mounted at the top, usually for two to three months. Emerging insects were removed and counted.

2.4. Identification of Emerged Imagines

Usually, more than 50 mounted specimens of each Hymenoptera species were sent to K.-J. Hedqvist, Swedish Museum of Natural History, Stockholm, for identification. Some were also sent to K. Horstmann, Zoologisches Institut, Würzburg. Based on reference specimens and additional information given by Hedqvist, T. Edland and S. Kobro identified and counted the emerging Hymenoptera and *A. conjugella*. Voucher specimens were deposited at the entomological collections at NIBIO, the University of Oslo, and the University of Bergen.

3. Results

3.1. The Species Found and Their Geographical Distribution

In addition to the two seed predators, seven species of hymenopteran parasitoids emerged from the rowanberry samples in significant numbers (Figures 1 and 2). The fruit moth was more numerous than the seed chalcid, even if some fruit moths had been removed with the cardboard rolls. All nine species emerged from berries, and only *A. conjugella* and its specialist parasitoid, *Microgaster polita* Marshall [5], emerged from the corrugated cardboard.

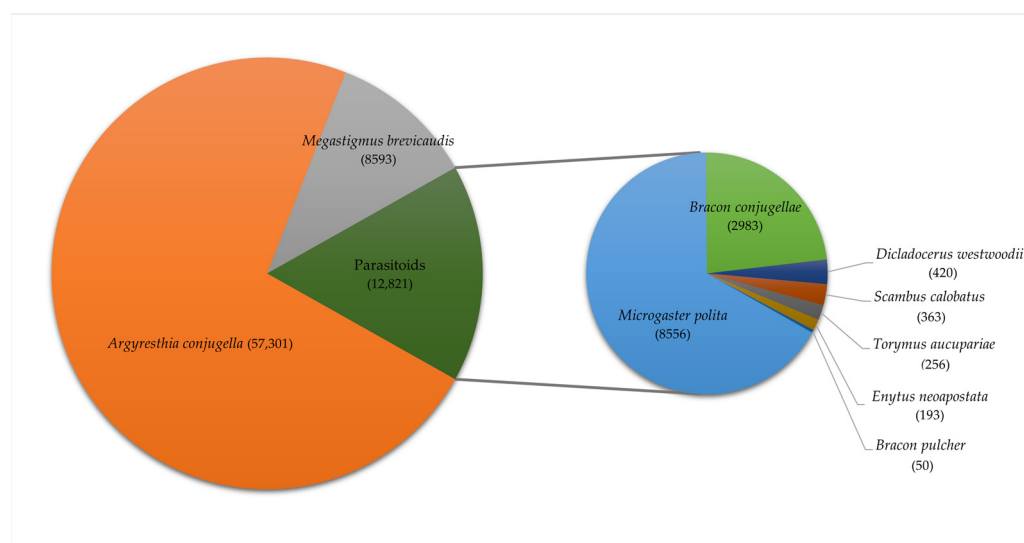


Figure 1. Numbers of the two seed predators and seven parasitoids emerging from rowanberry samples the year after berry collection. Pooled data for berry samples collected 1977–1981 and used for EIS-mapping. The two species of *Bracon* were not separated before 1980.

The distribution of the nine species found during this study is shown in Figure 3. Most EIS grid squares were sampled at least twice, but some were not sampled due to a lack of rowan or rowan with berries. *A. conjugella* was found north of 70° N in all three northernmost squares where it occurred. A few berry samples were collected in two squares north of this (no. 182 and 183), but no insects emerged. *M. brevicaudis* was found north of 69° N in two squares.

The parasitoid *M. polita* closely followed the distribution of its host *A. conjugella*, also in the far north. The host associations of the other parasitoids are probably looser and will be discussed later. Only two of them were confined to South Norway, but one of these

(*Bracon pulcher* Bengtsson) was also the least abundant species (Figure 1); moreover, it was not distinguished from *Bracon conjugellae* Bengtsson before 1980.

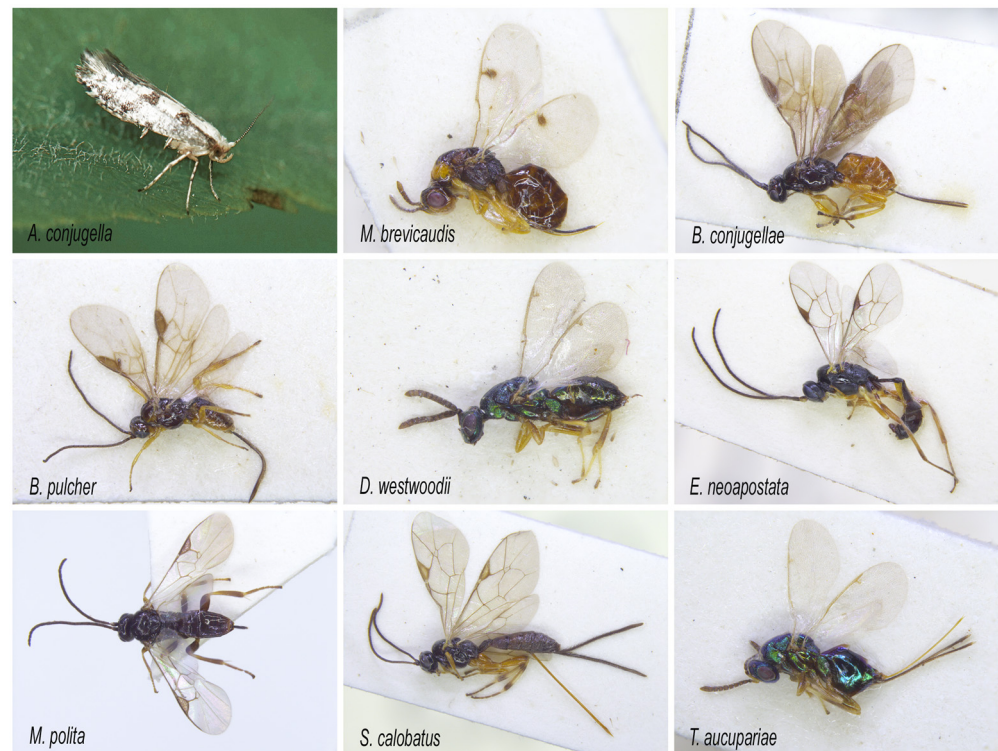


Figure 2. Photos of the nine species commonly reared from rowanberries (date of hatching): Two seed predators, *Argyresthia conjugella* (living specimen) and *Megastigmus brevicaudis* (25 April 1980), and seven parasitoids, *Bracon conjugellae* (10 May 1982), *Bracon pulcher* (August 1982), *Dicladocerus westwoodii* (3 August 1980), *Enytus neoapostata* (20 May 1985), *Microgaster polita* (10 May 1976), *Scambus calobatus* (30 March 1981), and *Torymus aucupariae* (24 April 1981). Photos by K. Westrum/NIBIO, except for *A. conjugella* by S. Kobro/NIBIO.

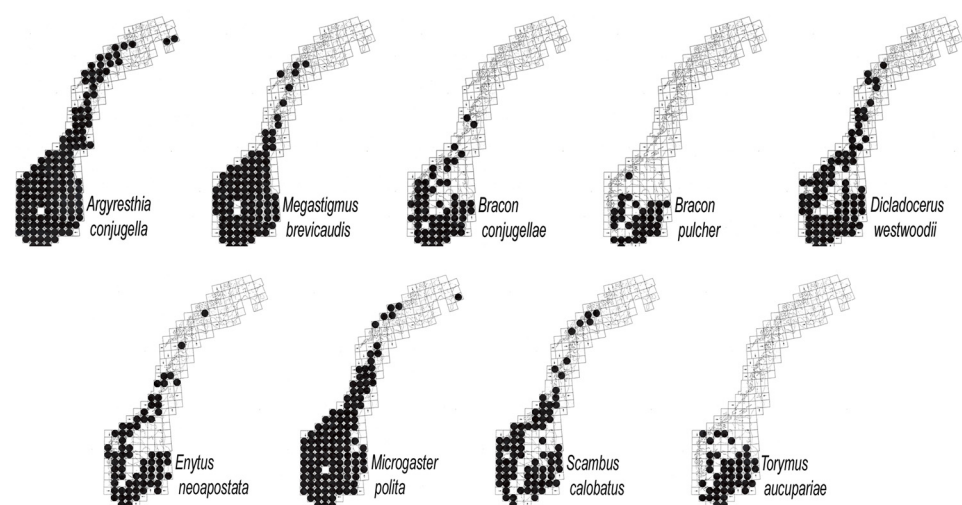


Figure 3. Geographical distribution of the insects commonly reared from rowanberries collected 1971–1984, plotted in The European Invertebrate Survey (EIS) grid of Norway [28]. *Argyresthia conjugella* and *Megastigmus brevicaudis* are seed predators; the others are parasitoids.

3.2. Prolonged Diapause

The ability of prolonged diapause, as indicated by the adult emergence two or more seasons after collecting the berries, was found in both species of the seed predators and in five of the seven parasitoids. A much bigger fraction of *M. brevicaudis* than *A. conjugella* delayed their emergence, and for a longer period (four vs. two years of maximum delay; Figure 4a). The fraction of delayers in the five parasitoid species was either small or large: two species delayed to a small degree (<20%) and three to a large (>80%; Figure 4b). One species, *Torymus aucupariae* Rodzianko, even peaked three years after sampling and also emerged in the fifth year. *Dicladocerus westwoodii* Westwood and *Scambus calobatus* Gravenhorst were not found to delay their emergence at all.

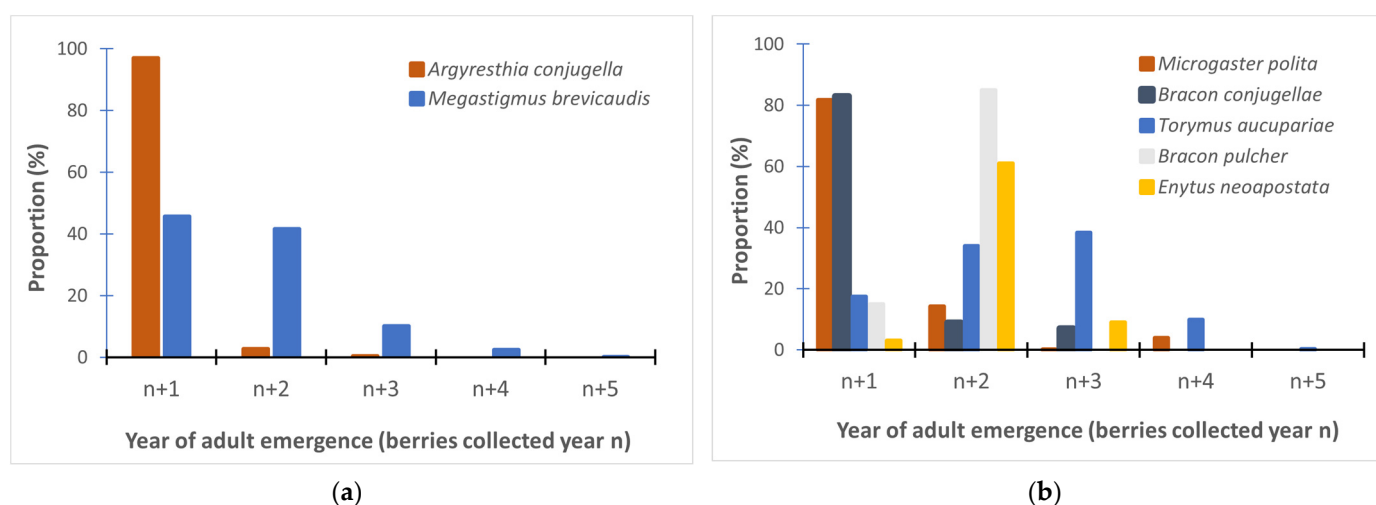


Figure 4. Relative annual emergence of adults for each of the insect species exhibiting delayed emergence from the rowanberry samples kept for five years. Pooled data for berries collected 1978–1984; species sorted by proportion emergence in year $n + 1$: (a) The two seed predators. (b) The five parasitoids.

4. Discussion

4.1. Geographical Distribution of the Seed Predators

The two seed predators of rowan, *A. conjugella* and *M. brevicaudis*, were found in most of Norway, with the fruit moth occurring somewhat further north than the seed chalcid (70 vs. 69° N). Such a close relationship between the geographical distribution of *A. conjugella* and its host plant, rowan, was hypothesized in 1906 [29] and was also found almost 100 years ago in the Swedish rowanberry study [5].

A third seed predator of rowan, the sawfly *Hoplocampa alpina* (Zetterstedt), is present in Scandinavia [30], but it did not emerge in the study presented here. This was also the case in the older Swedish study [5]; a possible reason for this being that its larvae exit the berries earlier than *A. conjugella* and thus were absent when samples were taken. A gall midge may also be part of the herbivore complex living in rowanberries ([31], S.K. pers. obs.). Rowanberries could thus be a good model system for studying competitive interactions in a confined space.

4.2. Biology and Distribution of the Parasitoids

The seven parasitoid species regularly emerging from the collected berries were from four families of Hymenoptera (Table 1). As the rowanberries were picked from the trees before *A. conjugella* larvae exited the berries and *M. brevicaudis* does not pupate until spring, all seven species must be larval parasitoids that are able to locate the larvae inside the berries. *M. polita* is a koinobiont as it allowed its host *A. conjugella* to enter the corrugated cardboard before killing it. The preferred host in rowanberries for the other six parasitoids is less clear. In the Swedish study [5], where at least five of these occurred, Ahlberg did

make an effort to find the host of each (Table 1). However, most of the parasitoids are idiobionts and, therefore, are likely to be able to exploit more than one of the host taxa present in rowanberries [32,33].

Table 1. Overview of the seven larval parasitoids (Hymenoptera) regularly emerging from rowanberries collected in Norway 1971–1984 and what is known about their biology.

Species	Family	Type of Parasitoid (Host Groups Known)	Host in Rowanberries (Ahlberg 1927) [5]	References
<i>Bracon (Glabrobracon) conjugellae</i> (Bengtsson, 1924)	Braconidae	Idiobiont ectoparasitoid of concealed hosts (<i>Megastigmus brevicaudis</i> , <i>Argyresthia conjugella</i> , and <i>Pontiana</i>)	<i>M. brevicaudis</i>	[5,34–36]
<i>Bracon (Glabrobracon) pulcher</i> (Bengtsson, 1924)	Braconidae	Ectoparasitoid of concealed hosts (<i>M. brevicaudis</i> , <i>A. conjugella</i> , and <i>Metzenera lapella</i>)	<i>M. brevicaudis</i>	[5,34–36]
<i>Dicladocerus westwoodii</i> Westwood, 1832	Eulophidae	Idiobiont ectoparasitoid (various Lepidoptera and Diptera)	<i>A. conjugella</i> ¹	[37,38]
<i>Enytus neoapostata</i> ² (Horstmann, 1969)	Ichneumonidae	Koinobiont endoparasitoid (<i>Depressaria assimilella</i>)	This parasitoid not found by Ahlberg? ³	[39,40]
<i>Microgaster polita</i> ⁴ Marshall, 1885	Braconidae	Koinobiont endoparasitoid (<i>A. conjugella</i>)	<i>A. conjugella</i>	[5,41,42]
<i>Scambus calobatus</i> Gravenhorst, 1829	Ichneumonidae	Idiobiont ectoparasitoid (various Lepidoptera, Coleoptera, and Hymenoptera)	<i>A. conjugella</i> ⁵	[5,29,40,43]
<i>Torymus aucupariae</i> Rodzianko, 1908	Torymidae	Not known? (<i>Megastigmus</i>)	<i>M. brevicaudis</i> ⁶	[5,37]

¹ In Ahlberg (1927), the name of *D. westwoodii* was *Diglyphus rugifrons* Thomson 1878 [37]. ² At the time of the study, this species was in the genus *Diadegma*. ³ Ahlberg found *Angitia exareolata* (Ratz.). Horstmann 1969 [39] synonymized this with *Diadegma apostata* (now *Enytus apostata*, [44]), and noted some confusion on the identity of *apostata* specimens collected by Thomson. ⁴ At the time of study, the name of this species was *M. politus*. ⁵ In Ahlberg (1927), *S. calobatus* was in the genus *Epiurus*. ⁶ In Ahlberg (1927), *T. aucupariae* was in the genus *Syntomaspis* [37].

Moreover, most of the parasitoids are also known from other habitats than rowan trees (Table 1), and some of them are found on exophytic hosts. In particular, *S. calobatus* is reported to have a wide range of hosts and host habitats [34,43], including other parasitoids. *D. westwoodii* is also a habitat generalist and is reported as a parasitoid of various Lepidoptera that feed on conifer needles [38,45]. However, there is still a lot we do not know about these wasps. For example, *B. conjugellae* was recently reared from *Pontania* galls on *Salix* [35], after more than a hundred years with only rowanberry associations in the literature. Nevertheless, the conclusion from the Swedish study [5] also holds for the Norwegian one: *M. polita* is the most important parasitoid of the apple fruit moth, both because of its abundance and because it seems to be the only *A. conjugella* specialist. For *M. brevicaudis*, the little studied *T. aucupariae* may be the most important parasitoid.

Berry sampling has been the approach in all the studies on parasitoids of endophytic insects in rowanberries that we are aware of [5,16], including this one. Thus, nothing is known of any parasitoids specializing on *A. conjugella* larvae or pupae on the ground, or on the endophytic *M. brevicaudis* pupae in the spring. Predation of *A. conjugella* pupae on the ground has been briefly studied [46]. Egg parasitoids were looked for in the Swedish study without success [5], but on apples, *Trichogramma* has been reared from *A. conjugella* eggs in Latvia [47].

4.3. Prolonged Diapause

The rowanberry crop is rarely very low (with close to zero berries) for several years in a row. In a 22-year time series from the Norwegian apple fruit moth warning system,

a very poor crop year occurred 5–6 times, but not for more than two years in a row [4]. Based on this, delayed emergence for 1–2 years should be relatively common in seed predators dependent on rowanberries, and longer delays rare. This was certainly the case for *M. brevicaudis*; in this species, one year of delay was almost as common as no delay. In a later study, a specimen of *M. brevicaudis* emerged 7 years after the berry crop [S.K. pers. obs.]. In contrast, only three percent of *A. conjugella* appeared delayed, and only for one or two years. Hanski [11] suggested that interspecific competition may lead to such quantitative differences in the distribution of diapause lengths, thereby easing coexistence.

The response of the two seed predators may also have been affected by the 9–10 months in a cold and dark storage room each year, but the same type of difference between a moth and a seed chalcid has been found in other studies, for example, between *Megastigmus strobilobius* Ratzeburg and the seed moth *Cydia strobilella* (L.) in spruce cones [11,14]. In the comprehensive Swedish study of rowanberry insects [5], prolonged diapause was noted in *M. brevicaudis*, but not in *A. conjugella*. In general, prolonged diapause is rather common in species of *Megastigmus* [15], while we have not found reports of it in other species of *Argyresthia* than *A. conjugella*.

Additionally, the seven parasitoid species differed in their pattern of delayed emergence: either they did not display it at all (two species), or to a small extent (two species), or as their most common strategy (three species). Explaining such patterns at the third trophic level in a food chain with masting at the first level is not easy [19]. An added complication is the possibility of parasitoids receiving physiological cues about prolonged diapause from their host, especially for koinobionts, while the host is still alive [20]. The delay pattern of the koinobiont *M. polita* was similar to that of its host, *A. conjugella*. The same was true for the pair of *T. aucupariae* and *M. brevicaudis*.

Prolonged diapause is costly, and in herbivores feeding on plant structures with intermittent occurrence, it only occurs in specialists that are not able to feed on anything else [48,49]. The same is probably true for parasitoids, meaning that species capable of exploiting hosts in other niches than rowanberries will be less inclined to prolong their diapause. In accordance with this, both parasitoid species were not found to delay emergence, *S. calobatus* and *D. westwoodi*, have a broad host spectrum (Table 1). As they were more abundant in the mapping samples than two of the species found in the delay study (Figure 1), their absence from the delay study probably was not due to a small sample size.

It should be noted that the two rarest species in the mapping samples, *B. pulcher* and *Enytis neopostata* Horstmann, were among the three parasitoids with the most pronounced delay pattern (the third was *T. aucupariae*). More studies are needed on their biology and host preferences to understand their propensity for delayed emergence, taking into account the fact that standard rearing for one season will not give a complete picture. For example, if all the mapping samples in our study had been kept for five years, the relative abundance of these three parasitoids would have increased, possibly along with their geographical distribution. This is also true for the seed chalcid.

Improved knowledge on prolonged diapause in parasitoids and their hosts is important to understand the potential effects of climate change in temperate ecosystems [50]. This includes how the attacks of the apple fruit moth on apples will develop in the future.

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Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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