

PARASITOIDS FOR CLASSICAL BIOLOGICAL CONTROL OF *TINEOLA BISSELLIELLA* (LEPIDOPTERA: TINEIDAE)

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Abstract Two species of parasitoid wasps, *Apanteles carpatus* (Hymenoptera: Braconidae) and *Baryscapus tineivorus* (Hymenoptera: Eulophidae), are known to successfully parasitize larvae of tineid moths. We have evaluated each species potential impact on suppressing the pest *Tineola bisselliella* (Lepidoptera: Tineidae). Both parasitoids have shown high potential for biological control of webbing clothes moth larvae when tested on different host instars in the laboratory and field. Preferences for parasitizing older and larger host larval instars for egg largely overlap in both species. *Apanteles carpatus* is a solitary koinobiont and parthenogen, while *B. tineivorus* is a gregarious koinobiont, with a sex ratio of approximately 1:5 (male:female). Solitary reproduction in *A. carpatus* markedly suppressed the pest population early on but lagged large numbers of progeny in the F₁-generation. Gregarious reproduction resulted in a faster build-up of the F₁-generation but lagged the immediate control effect. Combining the release of both parasitoid species for pest control seemed to be the logical conclusion. We tested the reproductive success of both species when experimentally forced into intensive intraguild competition. For this, parasitoids had either to compete simultaneously or slightly time shifted on the same preferred host resource. Reproductive success of *A. carpatus* was not significantly influenced by the presence of *B. tineivorus*. *B. tineivorus* reproductive output was significantly reduced in the presence of *A. carpatus*. Overall suppression of host development was not significantly enhanced with both parasitoid species co-occurring when compared to their exclusive access to hosts. *B. tineivorus* does not significantly improve the control of webbing clothes moth hosts when occurring together with and having to compete against *A. carpatus*, at least in restricted laboratory conditions. Results show that *B. tineivorus* should be released with a temporal advantage of at least several days. For inundative release, reproduction strategies and even competition between parasitoids is negligible, and a deferred release strategy would not be required.

Key words *Apanteles carpatus*, *Baryscapus tineivorus*, biological control, inoculative release, intraguild predation.

INTRODUCTION

Biological control of pest insects is one cornerstone in modern concepts of IPM, not only in agricultural systems but also in museums, private households and the textile industry (Pinniger, 2001; Pinniger et al., 2016). *Tineola bisselliella* (Hummel) (Lepidoptera: Tineidae), webbing clothes moth, and *Tinea pellionella* (L.) (Lepidoptera Tineidae), case-making clothes moth, are important insect pests in these synanthropic environments (Cox and Pinniger, 2007), and parasitic wasps have been shown to be suitable for their biological control. One is *Apanteles carpatus* (Say) (Hymenoptera: Braconidae), a solitary koinobiont and parthenogen braconid wasp of approx. 4 mm in size (Fallis, 1942). This wasp is capable of parasitizing and completing development in all larval stages of *T. bisselliella* and *T. pellionella* (Plarre et al., 1999; Plarre and Balnuweit, 2003; Tibaut, 2005). The other is *Baryscapus tineivorus* (Ferrière) (Hymenoptera: Eulophidae), a gregarious koinobiont eulophid wasp of max. 2 mm and with a sex ratio

of approximately 1 male to 5 females (Jotzies, 2011). For successful development, *B. tineivorus* requires older host larvae. Younger hosts can be parasitized in principle but these lack the resources to allow completion of larval development or pupation (Matzke, 2016). Table 1 summarizes for both species the present state of scientific knowledge relevant for controlling clothes moths.

For any applied pest control strategy, a mixed approach is considered advantageous, particularly if it results in a synergistic suppression of the pest. This also applies to biological means of control, where different species of pathogens, parasitoids or predators are released to reduce or eradicate pest populations (O'Neil and Obrycki, 2008). However, inter-specific competition between putative parasitoids or predators may be problematic (Brodeur and Rosenheim, 2000), especially when important biological niche parameters of the introduced beneficial species, like reproduction, are similar (De Moraes and Mescher, 2005). Although the reproductive strategies of *A. carpatus* and *B. tineivorus* differ, with each being solitary and gregarious respectively (Pennacchio and Strand, 2006), their host range and host larval instar preferences for egg laying largely overlap (Plarre et al., 1999; Matzke, 2016). Additionally, both species are koinobionts and endoparasitoids (Pennacchio and Strand, 2006). Indeed, *A. carpatus* and *B. tineivorus* can be regarded as members of the same guild (Hawkins and MacMahon, 1989), meaning that intraguild competition between these two beneficials is highly likely when the two species occur regionally and timely in sympatry (Ehler, 1992; Godfray, 1994; Pennacchio and Strand, 2006).

Intraguild competition could lower the reproductive success of a lesser competitor, hinder its sustainable build up of a residual population and reduce its efficacy in controlling the pest (Rosenheim et al., 1995; Brodeur and Rosenheim, 2000; Müller and Brodeur, 2002; Briggs and Borer, 2005). Competition in parasitoids during resource acquisition can be manifold (Godfray, 1994). For example, it may occur prior to oviposition during host searching and finding or by antagonistic behavior for individual hosts (Batchelor et al., 2005). Physical post-oviposition competition may result in intraguild predation by larvae of the superior species inside the host (Polis and Holt, 1992; Rosenheim et al., 1995; Hunter et al., 2002; Müller and Brodeur, 2002; Arim and Marquet, 2004). Host or territory-marking allomones, produced by primary parasitoids or predators which repel secondary ones are non-physical forms of competition, resulting in the marker becoming the superior parasitoid or predator (Polis et al., 1989; Gnanvossou et al., 2003). The superior species is likely to out-compete the inferior one, ending in competitive displacement (Amarasekare, 2002; Reitz and Trumble, 2002). In the extreme, this could lead to pest control failure, when the competitors are of equal strength and restrain each other's reproduction.

Here, we experimentally compete *A. carpatus* and *B. tineivorus* in a restricted environment. This is achieved by simultaneously release of both species onto a limited number of accessible hosts, by narrowing the developmental stage of the host to be optimal for both parasitoid species, and by constraining the available space. Competition avoidance strategies, as described by Polis et al. (1989) and Hatcher et al. (2008), is thus ruled out by the overall experimental design. This scenario may well be realistic, when parasitoids are released initially after the first detection of the pest, e. g. through monitoring pheromone traps (Trematerra and Fontana, 1996). At such an early stage, the pest population presumably still has an age-uniform structure. In this study, we evaluated the reproductive success of either parasitoid species in the F_1 -generation and their control effect on their common host *T. bisselliella*.

METHODS AND MATERIALS

***Tineola bisselliella*.** Larvae of webbing clothes moth were derived from stock cultures of the BAM (Federal Institute for Materials Research and Testing) Berlin, Germany. Stock insects have been reared for more than 10 years on goose feathers, soaked in 10% brewer's yeast/water solution, oven-tried at 60°C and cooled down to room temperature. Rearing conditions are 27°C±2°C and 70%±5%r h.

Under these conditions developmental time from egg to adult moth lasts approx. 7 to 8 weeks (Griswold, 1944; Plarre et al., 1999). Larvae for experiments were 5 weeks old, prepared out of their feeding tubes and transferred onto patches of 100% worsted wool which had been placed into glass-jars of 780 cm³ volume (ø10.5 cm x 9 cm height) and covered by a ventilated screw cap. During the next 24 hours, the larvae had spun new feeding tubes.

***Apanteles carpatus*.** Wasps were reared continuously for more than 5 years on cultures of *T. bisselliella* as described above. Newly over night emerged adult wasps were used in experiments. *Apanteles carpatus* is thelytokous, and therefore all wasps were female.

***Baryscapus tineivorus*.** Wasps were reared continuously for more than 3 years on cultures of *T. bisselliella* as described above. Newly over night emerged adult wasps (males and females) were used in subsequent experiments.

Isochronic release of parasitoids. In each of six replicate experiments, 50 larvae of *T. bisselliella* were caged in glass-jars as described above, simulating realistic constricted host resource patches. After 24 hours, ten newly emerged *A. carpatus* females and 15 newly emerged *B. tineivorus* of mixed sex were simultaneously added to each replicate jar. Sexing live *B. tineivorus* is impossible without harming the insects. However, with a sex ratio of 1:5 (male/female) in *B. tineivorus*, it was assumed to have approximately even numbers of females from each parasitoid species. Both species had to compete with con-specifics and inter-specifics for host resources during the next 4 days, after which all parasitoids were removed. The patches with hosts were then incubated at rearing conditions to allow hatching of non-parasitized *T. bisselliella* larvae to adult moths, or in the case of parasitized individuals; development of each parasitoid species' F₁-generation.

For comparison and to evaluate the effect of interspecies competition, an equal number of set ups was prepared in the same way but with only one parasitoid species being released, respectively. For overall comparison an equal number of set ups was prepared in the same way without the release of any parasitoid species.

Metachronic release of parasitoids. In each of three replicate jars, 25 larvae of *T. bisselliella* were caged as described above. After 24 hours ten newly emerged *A. carpatus* females were added to each jar. Three days later, all *A. carpatus* were removed and 15 newly emerged *B. tineivorus* of mixed sex were added for the next 3 days. The same procedure was independently repeated but with introduction of parasitoids in reverse order. Direct pre-oviposition competition between the two parasitoid species was thus avoided. After removal of all parasitoids, the patches with hosts were incubated at rearing conditions to allow hatching of non-parasitized *T. bisselliella* larvae to adult moths or in the case of parasitized individuals; development of each parasitoid species' F₁-generation.

For comparison, equal numbers of replicates were prepared in the same way with either simultaneous release or no release of the parasitoid species.

Data Analysis

Data were analyzed statistically using two-sample t-Test for pairwise comparison of mean values. Differences at $p \leq 0.05$ were regarded as significant.

RESULTS

Isochronic Release Of Parasitoids

Development of clothes moth larvae to adults was reduced in all cases where parasitoids were introduced (Figure 1). This suppression, however, was statistically significant only when *A. carpatus* was present, either alone or in combination with *B. tineivorus* (Figure 1/II and 1/III). A significant reduction of the pest was not achieved when *B. tineivorus* acted alone under the above mentioned experimental condition (Figure 1/IV). Its contribution to moth mortality when both parasitoids species acted together was thus insignificant as well.

Reproductive success of *A. carpatus* in the F_1 -generation was not influenced by the simultaneous presence of *B. tineivorus* (Figure 2/I and 2/II). Approximately 20 F_1 *A. carpatus* individuals completed development in each experimental set up. With 10 females of *A. carpatus* depositing eggs over 4 days, this corresponds to a reproduction rate of 0.5 per parental female per day.

On the contrary, reproductive success of *B. tineivorus* in the F_1 -generation was significantly influenced by the simultaneous presence of *A. carpatus* (Fig. 2/III). Approximately 35 F_1 *B. tineivorus* completed development in the absence of *A. carpatus* (Figure 2/IV) but almost none when *A. carpatus* was present (Figure 2/III). Assuming a rate of 10 *B. tineivorus* females depositing eggs over 4 days, this corresponds to a reproduction rate of 0.9 and almost 0.0 per parental female per day, respectively.

Metachronic release of parasitoids

The development of clothes moth larvae to adults was significantly reduced in all cases where both parasitoids were present as compared to when parasitoids were absent (Figure 3). The order in which the parasitoids were released had no impact on pest population suppression (Figure 3/II, 3/III and 3/IV).

Reproductive success of *A. carpatus* in the F_1 -generation was not influenced by the order of its release in relation to *B. tineivorus* (Figure 4/I, 4/II and 4/III). No difference in development was observed regardless of whether both parasitoids acted simultaneously or in succession. Approximately 12 new *A. carpatus* completed development in each experimental set up. With 10 females of *A. carpatus* depositing eggs over 3 days, this corresponds to a mean reproduction rate of 0.4 per parental female per day.

The reproductive success of *B. tineivorus* was strongly suppressed by the presence of *A. carpatus* (Figure 4/IV, 4V and 4/VI). However, with a 3-day time advantage *B. tineivorus* was able to slightly but significantly increase its reproduction rate (Figure 4/VI) when compared to 3-day time disadvantage or simultaneous release with *A. carpatus* (Figure 4/V and 4/IV).

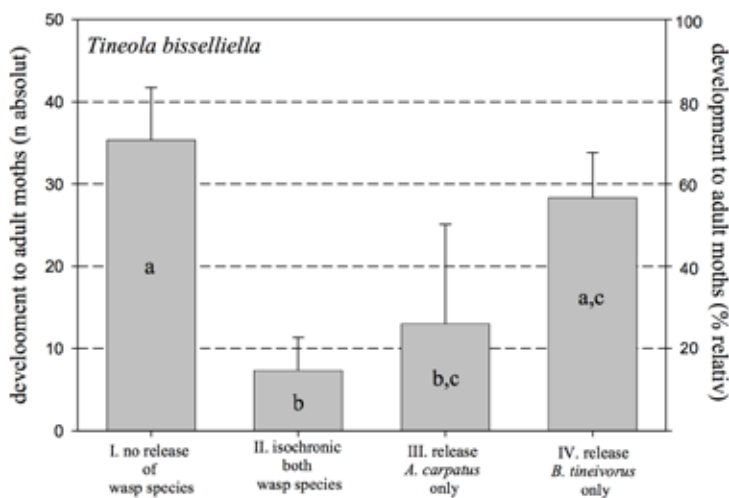


Figure 1. Mean absolute and mean percentile development of clothes moth larvae (*T. bisselliella*) to adult moths in respect to the presences of : I. no parasitoids, II. both parasitoids simultaneously, III. the koinobiont solitary larval parasitoid only, and IV. the koinobiont gregarious larval parasitoid only. Differences at the $p \leq 0.05$ level are indicated by different letters.

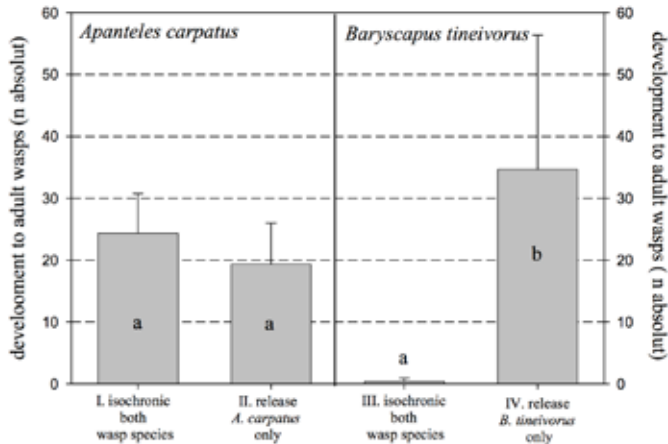


Figure 2. Mean absolute development of F_1 -generation of *A. carpatus* from its host *T. bisselliella* in respect to: I. simultaneous presence of parental *A. carpatus* with *B. tineivorus* and II. single presence of parental *A. carpatus* as well as mean absolute development of F_1 -generation of *B. tineivorus* from its host *T. bisselliella* in respect to: III. simultaneous presence of parental *B. tineivorus* with *A. carpatus* and IV: single presence of parental *B. tineivorus*. Differences at the $p \leq 0.05$ level are indicated by different letters.

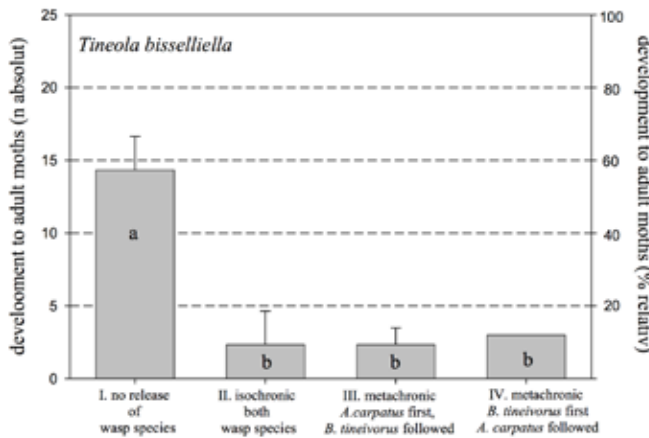


Figure 3. Mean absolute and mean percentile development of clothes moth larvae to adult moths in respect to: I. no parasitoids, II. simultaneous presence of parental *A. carpatus* and *B. tineivorus*, III. the metachronic presences of the larval parasitoid *A. carpatus* after 3 days by the larval parasitoid *B. tineivorus*, and IV. *B. tineivorus* followed after 3 days by *A. carpatus*. Differences at the $p \leq 0.05$ level are indicated by different letters.

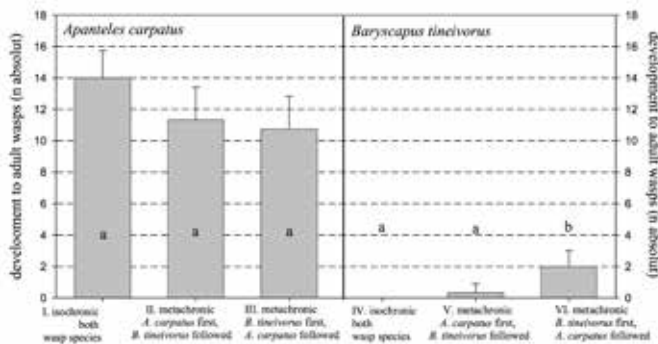


Figure 4. Mean absolute development of F_1 -generation of *A. carpatus* from its host *T. bisselliella* in respect to: I. simultaneous presence of both parasitoids, II. metachronic presences of the larval parasitoid *A. carpatus* followed after 3 days by the parasitoid *B. tineivorus*, and III. metachronic presences of *B. tineivorus* followed after 3 days by *A. carpatus*, and mean absolute development of F_1 -generation of *B. tineivorus* from its host *T. bisselliella* in respect to: IV. simultaneous presence of both parasitoids, V. metachronic presences of the parasitoid *A. carpatus* after 3 days by the larval parasitoid *Baryscapus tineivorus*, and VI. metachronic presences of *B. tineivorus* after 3 days by *A. carpatus*. Differences at the $p \leq 0.05$ level are indicated by different letters.

DISCUSSION

When parasitoids are released for biological control, two main objectives are pursued: a fast reduction of the pest below an economic threshold, and a rapid population build-up of the beneficial specie(s). *A. carpatus* and *B. tineivorus* differed considerably at our two main experimental restrictions on host use, which were limited time-window for parasitism and limited number of spatially confined hosts. In the absence of interspecific competitors, reproduction in the gregarious species, *B. tineivorus*, resulted in a higher number of F_1 -progeny per parental female per day (0.9) than in the solitary *A. carpatus* (0.5). This would have led to a faster population build up of *B. tineivorus* over subsequent generations. Initial suppression of pest development by F_1 -progeny was greater in *A. carpatus*. As a solitary parasitoid, a single egg is delivered to a different host individual, which resulted in 70% mortality of clothes moth larvae (Figure 1/III). Host mortality caused by *B. tineivorus* alone, by contrast, was only 40 % (Figure 1/IV), and did not significantly differ from the natural mortality of host larvae in our experiments (30 - 40%; Figure 1/I and 3/I) which is within the expected range for *T. bisselliella* (Griswold, 1944).

We hypothesized that the combined release of both parasitoids with their different reproduction strategies could have resulted in an additive effect on host mortality and a fast build-up of a residual population of at least one beneficial species. The highest host mortality in our experiments was recorded when both parasitoids acted together (Figure 1/II). However, host mortality caused by both parasitoid species did not significantly differ from that caused by *A. carpatus* alone (Figure 1/III). The simultaneous presence of *A. carpatus* significantly reduced the reproductive success of *B. tineivorus* in the F_1 -generation to almost zero (Figure 2/III) and therefore prevented its population establishment. This demonstrates that *B. tineivorus* suffers significantly from intraguild competition with *A. carpatus* under restricted laboratory conditions, whereas *A. carpatus*' developmental success is not influenced by the presence of *B. tineivorus* (Figures 2 and 4).

Although pre-oviposition competition between the two parasitoids cannot completely be ruled out, the deferred and successive release strategies adopted by each parasitoid respectively, indicates that interspecific competition is strongest during post-oviposition, among larvae inside the host. The most likely mode of action is predation (Rosenheim et al., 1995; Brodeur and Boivin, 2004), with *A. carpatus* larvae not only feeding on host tissue but also on *B. tineivorus* larvae.

Larvae of solitary endoparasitoids do not tolerate other internal feeders. If they encounter competitors, their feeding habits are likely to require significant aggression towards that intra or inter specific competitor in order to survive (Brodeur and Boivin, 2004). Solitaries such as *A. carpatus* also do not have to constrain their tissue consumption habits to smaller portions inside the host, unlike in gregarious endoparasitoids, where a large degree of immobility inside the host would have been selected for to avoid the encountering of conspecific competitors (Boivin and van Baaren, 2000; Pexton and Mayhew, 2001). This may explain why *A. carpatus* larvae are superior competitors. Under our metachronic experimental conditions, their reproductive success did not differ, regardless of whether they had to compete simultaneously with *B. tineivorus*, or following delayed introduction (Figure 4).

Solitary parasitoids may only slow down aggressive feeding activities or enter developmental dormancy when the host provides insufficient resources, such as in small hosts for example (Lawrence, 1990). For gregarious larvae this kind of behavior would be fatal. The life histories of *A. carpatus* and *B. tineivorus* fulfill these assumptions: Susceptible host instars for *A. carpatus* range from old (large) to very young (small), with prolonged developmental times resulting from infestation of the latter (Plarre et al., 1999; Harvey et al., 2000). In *B. tineivorus*, only older hosts facilitate successful development. Matzke (2016) has previously shown that younger hosts do not provide sufficient resources for the brood to complete the life cycle. Collective dormancy in gregarious endoparasitoids is unlikely to have evolved because of the difficulty associated with synchronizing behavior or physiology amongst competing members of the same brood. Complete extraction of host tissue has been reported for *A. carpatus*

(Harvey et al., 2000), whereas in *B. tineivorus*, depending on the actual number of progeny, parasitoid larvae may not completely hollow out a given host (Jotzies, 2011).

As the inferior competitor over a restricted range of host conditions, *B. tineivorus* was only able to successfully compete with *A. carpatus* when given a temporal advantage. We have demonstrated here that a 3-day advantage leads to significantly increased reproduction rate of *B. tineivorus* (Figure 4/VI)). It remains unclear whether *B. tineivorus* larvae successfully avoided secondary parasitism through direct physical defense against *A. carpatus* eggs or egg-larvae, or via the release of a repellent allomone. Evidence for the latter comes from studies in hymenopteran parasitoids where unparasitized and parasitized hosts could be discriminated prior to oviposition (Tillman and Powell, 1992; Godfray, 1994), but whether *B. tineivorus* mark their hosts during or after egg-laying remains to be shown.

CONCLUSION

Under restricted experimental conditions, *A. carpatus* clearly outcompetes *B. tineivorus*. Simultaneous release of both species for biological pest control is therefore not recommended in situations where both parasitoid species are under severe competition for a restricted range of host conditions. Although such conditions are quite realistic in specific environments (e. g. new pest infestations), they do not represent the full range of host conditions found in nature. Nonetheless, in such conditions, we have shown that it may be effective to combine the benefits of a solitary reproductive strategy (*A. carpatus*) which has the advantage of higher initial host suppression, with a gregarious reproductive strategy (*B. tineivorus*) which has the advantage of a faster eventual build up of a residual population of beneficials. Deferred release of the two species, by which the inferior competitor is given a time advantage, represents a potential means of implementing such a mixed strategy (De Moraes and Mescher, 2005; Everard et al., 2009; Cusumano et al., 2011). Because *B. tineivorus* is gregarious, the consequent initial numeric superiority of this species' reproductive success in the F₁ generation is a significant factor that also should be considered when trying to give long term predictions (Table 1). *B. tineivorus* requires only 18 days to complete development in 5-week old, well fed *T. bisselliella* larvae (Matzke, 2012). This is in contrast to *A. carpatus*, which requires 34 days to complete development (Plarre et al., 1999).

Table 1. Reproduction life history of *Apanteles carpatus* and *Baryscapus tineivorus*.

Life History Data		<i>Apanteles carpatus</i>	<i>Baryscapus tineivorus</i>
Reproduction strategy		endoparasitoid, koinobiont	
Solitary parthenogenic (thelytoky)		Gregarious males and females (1:5)	
Range of host species		<i>Tineola bisselliella</i> , <i>Tinea pellionella</i>	
Range of host developmental stage		All larval stages	Larval stages 5 - 7 weeks old
Mean development time (days)		35, rang of 60 - 25 depending on host stage	18
Parasitism rate (hosts/♀ wasp)		Maximum 60	Mean 5
Mean Re- production capacity	F ₁ /host	1	4, maximum 20
	F ₁ /♀ wasp	30, maximum 65	38, maximum 75

Mean ♀ Longevity (days)	With food*	27, maximum 40	9, maximum 27
	With host**	Not determined	4, maximum 13
	With food*	Not determined	11, maximum 16
	With host**		
	Without food*	Not determined	3, maximum 11
	Without host**		

* Honey water; ** Larvae of *T. bisselliella*

Therefore, given a few days time advantage, in combination with a faster life cycle, *B. tineivorus* could in principle stably coexist alongside *A. carpatus*, and establish respectable population size (Amarasekare, 2002; Price and Morin, 2004; Briggs and Borer, 2005; Hatcher et al., 2008).

We emphasize, however, that our conclusion applies mainly to inoculative release strategies where the principal goal is to establish a sustainable population of the beneficial species in a uniform host environment. In many cases, a more heterogeneous and widespread pest (host) population in more diverse environments would create opportunities for coexistence through competition avoidance strategies (Godfray, 1994; Křivan, 2000; Borer, 2002; Revilla, 2002; Nakazawa and Yamamura, 2006; Amarasekare, 2007; Bampfylde and Lewis, 2007; Holdt and Huxel, 2007; Janssen et al., 2007; Cusumano et al., 2011).

For inundative release, in which a pest-infested environment is flooded with beneficials for immediate pest control, reproductive strategies and even competition itself between parasitoids, will have a negligible impact on the host (Rosenheim et al., 1995; Bográn et al., 2002), unless both species negatively influence each other in their host-finding abilities. But for *A. carpatus* and *B. tineivorus* this is not the case. Here, a deferred release strategy would not be required.

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