



## Article

# Feeding Behaviour of the Mite *Blattisocius mali* on Eggs of the Fruit Flies *Drosophila melanogaster* and *D. hydei*

Katarzyna Michalska <sup>1,\*</sup> , Agnieszka Mrowińska <sup>1</sup>, Marcin Studnicki <sup>2</sup>  and Manoj Kumar Jena <sup>1</sup>

<sup>1</sup> Section of Applied Entomology, Department of Plant Protection, Institute of Horticulture Sciences, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

<sup>2</sup> Department of Biometry, Institute of Agriculture, Warsaw University of Life Sciences, Nowoursynowska 159, 02-776 Warsaw, Poland

\* Correspondence: katarzyna\_michalska@sggw.edu.pl

**Abstract:** Many predatory mites use insects for dispersal; however, their possible negative effects on insect hosts during transportation and on insect offspring while preying in the hosts' habitats are still poorly understood. A recent study has revealed that the predatory mite *Blattisocius mali* can not only spread by means of drosophilid fruit flies but also feed on their bodies during dispersal. The aim of this study was to examine the capability of *B. mali* to prey upon the eggs of their fruit fly hosts and determine the effect of the egg's age on the voracity of this predator. *Drosophila melanogaster* oviposited on agar media for 1 h and *D. hydei* for 8 or 16 h. During 10-h experiments with fifteen fly eggs per cage, a single female predator totally consumed on average  $3.62 \pm 0.673$  "1-h" *D. melanogaster* eggs and  $3.00 \pm 0.612$  "8-h" eggs of *D. hydei*, while it partially consumed  $2.75 \pm 0.586$  and  $3.00 \pm 0.612$  eggs of each fly species. In the experiments involving *D. hydei*, the predator totally destroyed a similar number of "8-h" and "16-h" eggs, but it partially consumed significantly more younger eggs than older eggs. Ethological observations showed that mites returned to some partially fed eggs, usually from the side where the first puncture was made, and only then did they consume them whole.

**Keywords:** predatory mite; egg age; partial prey consumption; *Blattisocius*; *Drosophila*



**Citation:** Michalska, K.; Mrowińska, A.; Studnicki, M.; Jena, M.K. Feeding Behaviour of the Mite *Blattisocius mali* on Eggs of the Fruit Flies *Drosophila melanogaster* and *D. hydei*. *Diversity* **2023**, *15*, 652. <https://doi.org/10.3390/d15050652>

Academic Editors: Michael Wink, Monika Fajfer and Maciej Skoracki

Received: 21 March 2023

Revised: 22 April 2023

Accepted: 9 May 2023

Published: 11 May 2023



**Copyright:** © 2023 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (<https://creativecommons.org/licenses/by/4.0/>).

## 1. Introduction

Many mesostigmatic predatory mites use insects for dispersal to habitats that are potentially rich in food but discontinuous and ephemeral habitats [1,2]. These mite-insect associations can be phoretic, where a mite is entirely passive while being attached to its host [3–5]. Not infrequently, however, the mite feeds on insects during transportation, and, as an ectoparasite, it can exert a negative impact on their fitness [6–9]. Moreover, when foraging in the habitat of the insect host, mesostigmatic predators can also prey on its immature stages [1,10]. Thus, when investigating the possible negative effects of the mite on insect hosts, aspects related to the mite feeding on the juvenile offspring of the host should not be neglected.

Drosophilidae is a family of cosmopolitan flies that comprises two subfamilies, Drosophilinae and Steganinae, with approximately 4400 species [11]. The majority of these fruit flies are adapted to feed on bacteria, yeast, and other fungi and inhabit such substrates as rotting fruit, decaying herbs, or parts of logs. Others are phytophagous, or, as in the Steganinae subfamily, they are predatory as larvae and necrophilic or zoophilic (lachryphagous) as adults [12].

Both field and laboratory observations have shown that drosophilids can also be carriers for mesostigmatic predatory mites [8,9,13–17]. With reference to this, the relationships of *Macrocheles subbadius* (Berlese) and *M. muscadomesticae* (Scopoli) (Macrochelidae) as well as *Blattisocius* (*Paragarmania*) *mali* (Oudemans) (Blattisociidae) have been studied in detail. Both macrochelids turned out to be ectoparasitic in relation to the adult fruit fly hosts; they fed on them during transportation, deleteriously affecting their body condition and flight ability [6,8,18,19]. Moreover, the ectoparasitism of *M. subbadius* also adversely influenced

fruit fly reproduction and survival [6,20]. It has not been examined yet whether the mites also prey on drosophilid fruit flies in their immature stages. However, it is known that both those mites can be carried by the housefly and also readily prey on its eggs and 1st instar larvae [20,21].

*Blattisocius mali* is a polyphagous and cosmopolitan mite feeding on some acarid mites, nematodes, or eggs of moths [9,22–24]. It is the only representative of *Blattisocius* sp. recorded on drosophilid flies, although other species such as *B. keegani* Fox, *B. dendriticus* (Berlese), *B. patagorum* Treat, and *B. tarsalis* (Berlese) can also be spread by insects (pyralids and noctuid moths). *Blattisocius mali* has been found on Drosophilinae fruit flies *Drosophila littoralis* Meigen, *D. montana* Stone, *D. ezoana* Takada and Okada, *D. lummei* Hackman [15], and *D. hexastigma* Patterson and Mainland [16], as well as on a Steganinae fruit fly, *Phortica semivirgo* Máca [17].

A recent study by Michalska et al. [9] indicates the ectoparasitic association of *B. mali* with drosophilids. The hungry predatory females not only attached themselves to the bodies of the flightless forms of *D. melanogaster* Meigen and *D. hydei* Sturtevant but also fed on them during transportation, and their presence resulted in an increase in fly mortality.

Our preliminary observations also revealed that *B. mali* can consume drosophilid eggs, both those inserted into an agar medium as well as those laid on a substrate surface (Figure 1). Drosophilids tend to insert their eggs into the substrate, while the hatched larvae tend to burrow into it. However, some fruit fly eggs, even the majority, are also oviposited on a food surface, and some larvae may crawl on it [25–27], where they can be easily preyed upon by predatory mites.



**Figure 1.** (A). Eggs of *Drosophila hydei* (left) and *D. melanogaster* (right). (B). The egg of *D. melanogaster* is embedded in agar medium and consumed by a *Blattisocius mali* female.

Studies on the predation of *B. mali* on the eggs of the *Phthorimaea operculella* moth (Zeller) and *B. tarsalis* on the eggs of the moths *Ephesia kuehniella* Zeller and *Plodia interpunctella* (Hübner) have shown that some of the prey eggs were only partially fed on by these predators, and all punctures were lethal to the prey [23,28–30]. Moreover, the age of *E. kuehniella* eggs affected the extent to which the egg content was utilised by *B. tarsalis* [29]. We expect similar phenomena in *B. mali* in relation to drosophilid eggs. It should be noted that in addition to differences in the quantity and quality of nutrients, there are also morphological differences in insect eggs, including chorion thickness and the presence of chorion structures such as, e.g., dorsal appendages of drosophilid eggs [31,32] that may significantly affect the predator's handling time and also the number of eggs eaten. However, so far, no detailed observations on the feeding behaviour of *Blattisocius* mites on insect eggs have been carried out.

The aim of this study was to examine *B. mali* predation upon eggs laid on the substrate surface in two fruit fly species, *D. hydei* and *D. melanogaster*. Apart from the repertoire of

behaviours associated with *B. mali* feeding on fruit fly eggs, we also examined the predation rate on these eggs as well as the impact of the fly eggs' age on predator voracity.

## 2. Materials and Methods

### 2.1. Biological Materials and General Methodology

The primary population of *B. mali* was maintained on various stages of the mould mite *Tyrophagus putrescentiae* (Schrank) in wheat bran in the laboratory of the Department of Plant Protection at Warsaw University of Life Sciences (WULS) [9]. The rearing unit consisted of soaked foam platforms (22 cm × 15 cm × 2.5 cm), which were covered with foil and placed within broader vessels filled with a 1.5 cm layer of water, which provided humidity for mites and prevented them from escaping. The cultures of *B. mali* were maintained in a climatic room at 21–23 °C with a photoperiod of 16/8 h (L/D). The colonies of *T. putrescentiae* were kept in Erlenmeyer flasks with instant yeast pellets and closed with cotton plugs. They were maintained in a desiccator (Chemland, Stargard, Poland) in darkness at 26 °C and 75–80% RH. The desiccator was filled up in a lower deposit with saturated potassium chloride solution to provide constant and required humidity [1,33]. *Blattisocius mali* colonies were supplied with mould mites ad libitum on a weekly basis.

In this study, we used the eggs of two flightless drosophilid species, *D. melanogaster* Meigen and *D. hydei* Sturtevant, which are distributed commercially as live pet food [34]. The stock populations of these flies were obtained from the Amustela Zoological Centre, Warsaw, Poland, and reared on a standard fruit fly medium based on cornmeal, molasses, yeast, and propionic acid in an incubator (Panasonic, Osaka, Japan) at 25 °C and a 12/12 (L/D) photoperiod [9]. The species of these flightless fruit fly forms were identified in a previous study by Michalska et al. [9] using DNA barcoding and methods developed by Dabert et al. [35,36] and Mironov et al. [37].

All experiments were carried out using *B. mali* females that were randomly selected from a stock population and starved for 24 h before the experiments started.

As in the case of the mass rearing of *T. putrescentiae* (see above), we used desiccators to provide sufficient humidity for starving and then tested predators and fruit fly eggs.

For the starvation of predators and further experiments, we used glass cages, as described by Michalska et al. [9]. They possessed a drilled conical hole with an upper diameter of 0.8 cm and a lower diameter of 0.3 cm, and the bottom was made of white filter paper. Cages with individually starving predators were kept in a desiccator in a growth chamber at 23 °C with a 16/8 h (L/D) photoperiod.

In order to obtain the fruit fly eggs, 20–30 adults of *D. hydei* or *D. melanogaster* were collected from the stock cultures, which were under a light phase, and released into Petri dishes of 8.5 cm in diameter filled in half with medium based on grape juice, yeast, and 1% agar [38]. In the middle of each Petri dish, there was a single strip of fresh yeast paste (2 cm wide), which provided food for the flies and stimulated them to lay eggs. Since yeast “grows” at higher temperatures, the edges of the yeast strip were protected with two hard foil partitions measuring 8.5 cm × 1 cm. The partitions were placed in the medium before it solidified completely. As shown by Shaffer et al. [38], drosophilid fruit flies willingly lay eggs in the darkness, especially just after a transition from light conditions. Thus, the Petri dishes with flies (previously kept in a light phase) were transferred into a dark incubator at 25 °C and kept there, depending on the fly species, for 1 h (*D. melanogaster*), 8 h, or 14 h (*D. hydei*).

Since the fruit fly eggs were embedded within the agar medium, they were collected from Petri dishes using a needle. They were then “cleaned” off the medium residues in a drop of distilled water and carefully transferred into glass cages with the aid of a brush. We individually placed 15 eggs of *D. melanogaster* or *D. hydei* in each cage. To protect the eggs from drying out, the filter paper at the bottom of the cage was heavily moistened and additionally sealed with scotch tape to maintain humidity inside the cage. Immediately after transferring the eggs, the starved female of *B. mali* was released, and then the cage was closed with a coverslip sealed with paraffin at the edges. In the control cages, 15 fruit

fly eggs were maintained without predators. To estimate the *B. mali* predation rate on drosophilid eggs and larvae hatching, cages were kept in a desiccator at 23 °C, 70–80% RH, under light conditions.

## 2.2. Assay for Feeding Rates of *B. mali* on Fruit Fly Eggs

In this assay, we compared the feeding rate of 24-h starved *B. mali* females on “1-h” eggs of *D. melanogaster* and “8-h” eggs of *D. hydei*. The eggs of both species are similar in size, although *D. hydei* has four and *D. melanogaster* only two dorsal appendages [31,32] (Figure 1).

As eggs of both species develop quickly, and after 12–15 h at 25 °C, most *D. melanogaster* larvae had hatched, with *D. hydei* larvae hatching only several hours later, we conducted the tests for 10 h using relatively young eggs of both fly species. Our preliminary experiments showed that a 10-h period was sufficient to estimate the feeding rate of *B. mali* because, during that time, the predator usually consumed several fruit fly eggs. In the case of *D. melanogaster*, we were able to obtain a sufficient number of eggs already after 1 h of the fly females’ oviposition in agar-grape-juice medium. Although in the following days of life, *D. hydei* has a higher fecundity and a higher rate of oviposition than *D. melanogaster*, our preliminary tests have shown that *D. hydei* begins oviposition on the medium later than *D. melanogaster* does, usually after 4–5 h from the moment of the fruit flies’ release into Petri dishes. Therefore, to obtain a sufficient number of *D. hydei* eggs, we kept them on the media for a longer period than *D. melanogaster* females, i.e., for 8 h. As a consequence, some eggs of *D. hydei* were a few hours older than those of *D. melanogaster* and may have also differed to some extent from *D. melanogaster* eggs in their embryonic development. The eggs were then transferred into cages, and the predatory females were released into half of them. For both “1-h” eggs of *D. melanogaster* and “8-h” eggs of *D. hydei*, N = 16 replications, either with or without predators, were performed. After 10 h, the predators were removed from the cages, and the number of damaged eggs was counted. While we did not find any visibly damaged eggs in the control cages, in cages with a predator, apart from undamaged eggs, there were some totally flattened or slightly sunken eggs, which we categorised as totally consumed or partially consumed by the predator, respectively.

Since it was not known whether the slightly collapsed eggs were viable or not or what the influence of the presence of a predator in the cage could have been on other, apparently undamaged eggs, an additional test was performed to check the hatching of *D. melanogaster* larvae from the slightly collapsed or undamaged eggs in treatment cages and from undamaged eggs in control cages. To separate undamaged eggs from slightly collapsed eggs, the eggs of each type were either left in the cage or transferred to a new cage. This resulted in N = 7 cages with transferred eggs and N = 7 cages with remaining, slightly collapsed eggs, and similarly, N = 7 cages with transferred eggs and N = 7 cages with remaining, undamaged eggs. There were also N = 14 control cages, all with remaining, undamaged eggs. The cages with eggs from each category were kept in an incubator for 10 h, after which hatched larvae were counted.

To estimate the effect of the age of drosophilid eggs on the feeding rate of *B. mali*, we compared the feeding rate of 24-h starved *B. mali* females on “8-h” eggs (N = 16) and “14-h” eggs of *D. hydei* (N = 12). The eggs were obtained from Petri dishes with the media (see above) on which *D. hydei* females previously oviposited for 8 or 14 h. For each combination, we also prepared control cages with eggs from each age category but without predatory females. The experiment was conducted in an incubator for 10 h.

The effect of fly species and egg age on the mean numbers of eggs totally consumed, partially consumed, or undamaged by the predator was analysed using the one-factor generalised linear model (GLM) with a Poisson distribution. To compare the mean proportions of larvae hatching from undamaged eggs, which were either transferred to new cages or left in the experimental cages, as well as from the eggs kept in control cages, we applied the one-factor generalised linear model (GLM) with gamma distribution. GLM analysis was performed using R 4.2.1 software [39]. The data are given as mean ± SE.



### 2.3. Observations of *B. mali* Feeding Behaviour on Fruit Fly Eggs

In our assay on *B. mali* feeding rates, some drosophilid eggs were only slightly flattened, but no larvae hatched from such eggs. To confirm that such an egg injury was caused by a predator, detailed observations were conducted on the feeding behaviour of *B. mali* females. As in the tests on *B. mali* feeding rates, 15 “8-h” eggs of *D. hydei* and “1-h” eggs of *D. melanogaster* were inserted per cage ( $N = 10$ ), and a single 24-h starved *B. mali* female was released into each cage. Each predator was observed by one and the same person, at room temperature, continuously from the moment of predator release for 10 h, directly under a stereo dissecting microscope connected to a cool light source.

Apart from details on *B. mali* female behaviour, the moment of attack and the beginning and end of feeding for each egg, as well as the site where the egg was pierced, were recorded. As each attack of an egg was very quick (1–2 s) for both fly species, its time was not measured separately but estimated jointly with the time of egg consumption. A stopwatch was used for all-time measurements.

To compare *B. mali* predation on eggs of each fruit fly species, the mean time of pause before attack and consumption of the first egg, the mean time of attack and egg consumption, the mean time of the first and second attack and partial egg consumption, and the mean time of pause after attack and egg consumption were estimated. (1) The mean time of pause before attack and consumption of the first egg was the average length of time spent by the predator from the moment it was released into the cage until the attack of the first egg in the cage. (2) The mean time of attack and egg consumption concerned both eggs that were eaten by the predator once and consumed completely or only partially as well as eggs eaten twice. For the latter, the time was calculated as a sum of the time of the first and second attacks and partial egg consumption. (3) The mean time of first attack and partial egg consumption was calculated for eggs that were attacked once and consumed partially and for eggs that were attacked and consumed twice. (4) The mean time of the second attack and partial egg consumption refers only to eggs that were attacked and consumed twice. (5) The mean time of pause after attack and egg consumption refers to the time spent by the predator in pause after feeding on each egg until either the same or another egg was attacked, or until the end of a 10-h observation session. The mean time was estimated for all records of predator attack and egg consumption or pauses noted in each fruit fly species.

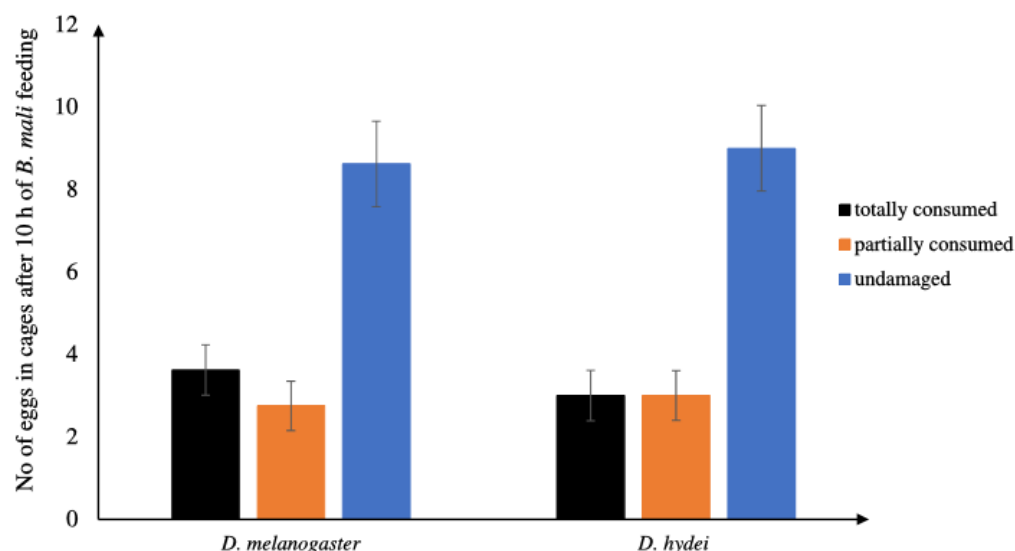
The statistical analyses were performed using R 4.2.1 software [39]. The proportions of eggs of *D. melanogaster* and *D. hydei* that were pierced either at the dorsal appendages, in the middle, or at the back in relation to all eggs pierced during 10-h observations were compared using the Z test of proportion. We also compared the differences between attack and consumption times and pauses before and after attack and consumption of *D. melanogaster* and *D. hydei* eggs using a t-test. Before the t-test was applied, the normality of the time distribution was tested using the Shapiro–Wilk test.

## 3. Results

### 3.1. Assay for Feeding Rates of *B. mali* on Fruit Fly Eggs

#### 3.1.1. Feeding Rates of *B. mali* Females on Eggs of *D. hydei* and *D. melanogaster*

Statistical analysis showed no significant effect of the species of fruit fly on the degree of damage to their eggs by the predator (GLM:  $\chi^2 = 0.8171$ ,  $df = 2$ ,  $p = 0.5642$ ). When we offered single *B. mali* females fifteen “1-h” eggs of *D. melanogaster* or “8-h” eggs of *D. hydei*, during the following 10 h, they totally consumed  $3.62 \pm 0.673$  ( $N = 16$ ) *D. melanogaster* eggs and  $3.00 \pm 0.612$  ( $N = 16$ ) eggs of *D. hydei* (GLM:  $\chi^2 = 0.4724$ ,  $df = 14$ ,  $p = 0.4919$ ) on average (Figure 2). In the cages with the predators, we also found partially collapsed eggs, i.e.,  $2.75 \pm 0.586$  ( $N = 16$ ) and  $3.00 \pm 0.612$  ( $N = 16$ ) eggs of each fly species (GLM:  $\chi^2 = 0.063835$ ,  $df = 14$ ,  $p = 0.8005$ ). In the control combinations, however, with either fifteen *D. melanogaster* ( $N = 16$ ) or *D. hydei* ( $N = 16$ ) eggs, no eggs became flattened or dried until the end of the test.



**Figure 2.** Feeding of 24-h starved females of *Blattisocius mali* on "1-h" *Drosophila melanogaster* eggs and "8-h" *D. hydei* eggs. Each cage (N = 16) contained a single predator and 15 fruit fly eggs.

### 3.1.2. Hatching of *D. melanogaster* Larvae from Partially Consumed or Undamaged Eggs

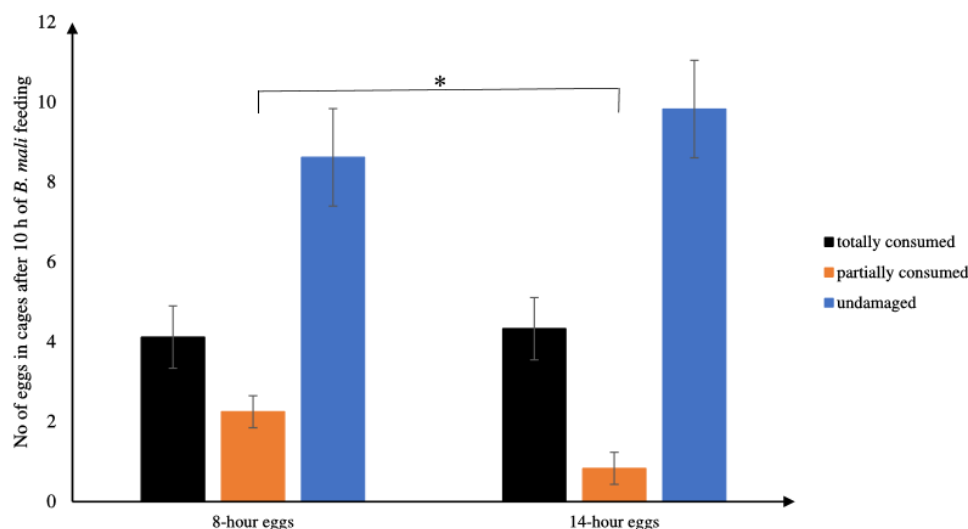
No larvae hatched from *D. melanogaster* eggs previously partially consumed by *B. mali* and then left for the next 10 h for hatching (Table 1). The presence of a predator in the cage did not have any destructive effect on the later emergence of *D. melanogaster* larvae from undamaged eggs. Similarly, transferring the undamaged eggs to new cages had no negative effect on the later hatching of larvae. As statistical analysis showed, there were no significant differences between the proportions of larvae hatching from undamaged eggs, which were either transferred to new cages or left in the experimental cages (after the removal of the predator), and from eggs kept in the control cages (GLM:  $\chi^2 = 0.2374$ ,  $df = 2$ ,  $p = 0.7904$ ).

**Table 1.** Mean proportion ( $\pm$ SE; N—number of replications) of *D. melanogaster* larvae that hatched after 10 h from eggs partially consumed or undamaged by *Blattisocius mali* or from eggs kept in control cages. Partially consumed or undamaged eggs were either transferred to new cages or left in the experimental cages. All the eggs in the control cages remained in the experimental cages.

Eggs Partially Consumed by a Predator		Eggs Undamaged by a Predator		Eggs from Control Cages
Transferred	Left	Transferred	Left	
0	0	$0.56 \pm 0.095$	$0.58 \pm 0.031$	$0.53 \pm 0.022$
(N = 7)	(N = 7)	(N = 7)	(N = 7)	(N = 14)

### 3.1.3. Effect of the Age of *D. hydei* Eggs on the Feeding Rate of *B. mali* Females

In our 10-h-long test, *B. mali* females damaged a similar number of "8-h" and "14-h" eggs of *D. hydei* (GLM:  $\chi^2 = 0.15$ ,  $df = 1$ ,  $p = 0.6982$ ). However, the age of *D. hydei* eggs had a significant impact on the degree of their damage (GLM:  $\chi^2 = 3.009$ ,  $df = 2$ ,  $p = 0.0445$ ). Although the mites totally consumed similar numbers of "8-h" and "14-h" eggs (GLM:  $\chi^2 = 0.03523$ ,  $df = 12$ ;  $p = 0.8511$ ), they partially consumed significantly more younger than older eggs (GLM:  $\chi^2 = 4.5342$ ,  $df = 12$ ,  $p = 0.0332$ ) (Figure 3).



**Figure 3.** Feeding of 24-h starved females of *Blattisocius mali* on “8-h” (N = 16) and “14-h” *D. hydei* eggs (N = 12) during 10 h. Each cage contained a single predator and 15 fruit fly eggs. \*  $p < 0.05$ .

### 3.2. Behavioural Observations on the Feeding of *B. mali* Females on Fruit Fly Eggs

#### 3.2.1. Repertoire of Feeding Behaviours

The sequence of *B. mali* behaviours accompanying feeding on the “1-h” eggs of *D. melanogaster* or the “8-h” *D. hydei* eggs was similar. After release into the cage, a 24-h-starved predatory female initially moved for some time all over the cage chamber, usually with the first pair of legs raised up. She did not use her legs while attacking an egg or consuming the egg’s contents. After approaching the egg, the female would stop by it, touch it once or several times with her pedipalps, and immediately cut the chorion with its chelicerae and insert them into the egg. The attack of the egg was very fast, taking one or two seconds. While feeding on the egg, the mite was motionless. Its pedipalps were slightly widened and laid over the egg, touching it. In some cases, after removing the chelicerae from the egg, the predator cleaned the chelicerae with the help of pedipalps. Sometimes, it also cleaned the pedipalps using the first pair of legs. However, grooming was not specifically associated with the predator feeding on the egg. It has also been observed in other situations, such as during mite exploration or resting.

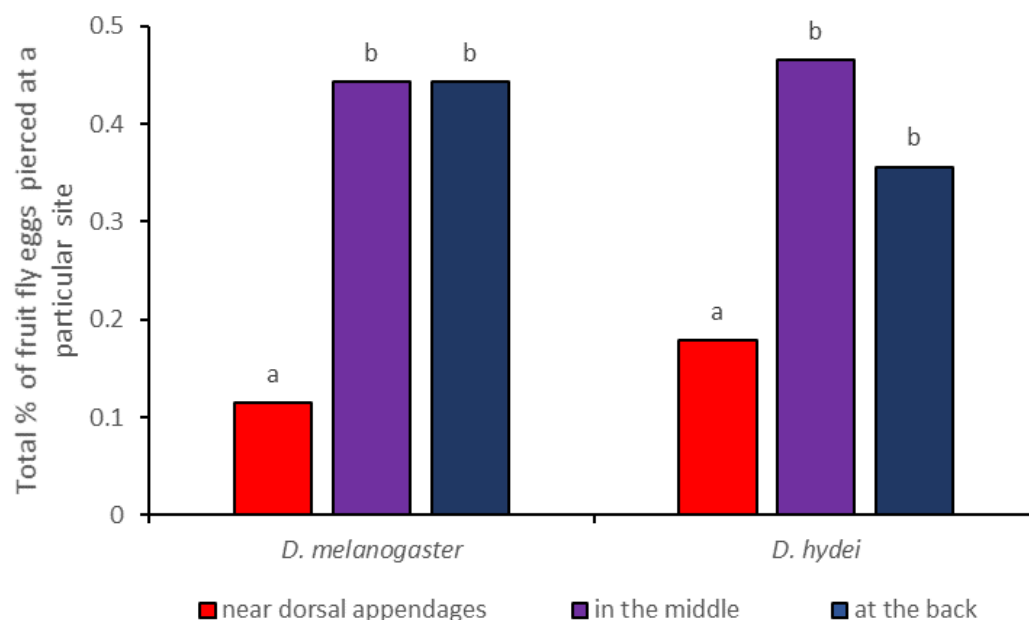
#### 3.2.2. The Site of the Insertion of Chelicerae into an Egg

The predator approached an egg either from the back, puncturing it terminally, or from the side, and then burrowed the chelicerae either in the middle part of the egg or closer to its dorsal appendages (Figure 4).



**Figure 4.** *Blattisocius mali* female feeding at the back of the egg of *Drosophila melanogaster*.

In the case of both *D. hydei* (Z test of proportion:  $\chi^2 = 13.849$ ,  $df = 2$ ,  $p < 0.0001$ ) and *D. melanogaster* eggs (Z test of proportion:  $\chi^2 = 22.671$ ,  $df = 2$ ,  $p < 0.0001$ ), the proportion of eggs pierced by *B. mali* near the dorsal appendages was significantly lower than those pierced at the back ( $p < 0.05$ ) or in the middle part ( $p < 0.05$ ) (Figure 5). Moreover, when a female touched the dorsal appendages by chance, she immediately left that egg without feeding. We observed three such situations in the trial with *D. melanogaster* eggs.



**Figure 5.** The proportion of eggs of *D. melanogaster* and *D. hydei* that were pierced either at the dorsal appendages, in the middle, or at the back by starved *Blattisocius mali* females in relation to all eggs pierced during the 10-h observational period. Bars with the repeated letters “a” or “b” mean no significant differences between means ( $p > 0.05$ ).

### 3.2.3. Time of Attack and Consumption of an Egg, Partial Egg Consumptions, and Pauses before and after Attack and Egg Consumptions

As in the assay for feeding rates, during our 10-h observations, *B. mali* females did not always consume the fruit fly eggs completely. Some eggs were attacked and only partially fed, which was manifested by a slight collapse of the chorion of the egg. In total, we registered nine out of 59 consumed eggs of *D. melanogaster* and 18 out of 66 consumed eggs of *D. hydei* that were only partially fed by the mites. During our observations, *B. mali* would partially consume the first encountered eggs as well as those encountered later, after consuming some other eggs. We also noted 12 *D. melanogaster* eggs and seven *D. hydei* eggs that were attacked and partially consumed twice. The predator would initially consume the egg, then leave it for some time, and after a pause from feeding or after feeding on another egg, it would return and complete its consumption. We “arbitrary” named these two behaviours as first attack and partial egg consumption and second attack and partial egg consumption, respectively (see Table 2). When the predator fed on the egg repeatedly, it usually returned to the egg and pierced it from a similar side as at the first partial feeding. We observed nine such situations out of 12 cases of repeated feedings on *D. melanogaster* eggs and six out of eight cases of repeated feedings on *D. hydei* eggs. Moreover, the mites would, though very rarely, insert the chelicerae into an egg using the same hole as before. Only two *B. mali* females that fed on *D. melanogaster* eggs once used a previously made hole.



**Table 2.** The mean time (s) (SE, min-max) of attack and egg consumption, first and second attack and egg consumption, and pauses before and after attack and egg consumption of “1-h” eggs of *D. melanogaster* and “8-h” eggs of *D. hydei* by 24-h starved *B. mali* females during the 10-h observation period. N—number of replications. As the time of attack was very short, it was measured and calculated jointly with the time of egg consumption. For a detailed description of all time parameters, see Section 2.3.

Mean Time	Fruit Fly Species		Statistics		
	<i>D. melanogaster</i>	<i>D. hydei</i>	<i>t</i> Test	Degree of Freedom	<i>p</i> -Value
Pause before attack and consumption of the first egg	302.80 ± 49.36 (93–556) N = 10	429.63 ± 57.31 (159–689) N = 8	−3.68	16	0.0115
Attack and egg consumption	89.41 ± 7.68 (6–286) N = 58	67.98 ± 6.34 (5–187) N = 65	2.15	121	0.0335
First attack and partial egg consumption	44.80 ± 8.45 (4–121) N = 22	21.36 ± 4.69 (5–120) N = 23	2.55	43	0.0143
Second attack and partial egg consumption	83.00 ± 20.91 (6–224) N = 11	57.88 ± 14.77 (15–137) N = 9	0.88	18	0.3394
Pause after attack and egg consumption	5218.43 ± 527.30 (88–16,445) N = 68	4447.59 ± 518.62 (21–18,883) N = 71	1.04	137	0.2991

As shown in Table 2, the average time spent by a starved *B. mali* female from the moment of release into the cage until the attack and consumption of the first egg was significantly longer for *D. hydei* than for *D. melanogaster* eggs during the 10-h observation period. By contrast, the average time of attack and egg consumption and the first attack and partial egg consumption were significantly shorter for *D. hydei* eggs than for *D. melanogaster* eggs. The statistical analysis also showed no significant differences in the meantime between the second attack and partial egg consumption and the pauses after the attack and egg consumption of *D. melanogaster* and *D. hydei* eggs.

#### 4. Discussion

Our study has shown that starved *B. mali* females can feed on both *D. melanogaster* and *D. hydei* eggs. However, not all the eggs destroyed by the mites were consumed completely. Some of the fruit fly eggs were only fed partially, and even if the chorion of those eggs was only slightly collapsed, no larvae hatched from them. Occasionally, predatory females returned to partially feed eggs, usually from the side where the first puncture was made, and then they consumed them completely. In the test with *D. hydei* eggs, the age of the eggs had no effect on the number of eggs destroyed by a predator. The mites damaged similar numbers of “8-h” and “14-h” eggs of this fruit fly. However, they exhibited different patterns of egg utilisation, partially consuming a greater number of younger than older *D. hydei* eggs.

These findings support our hypothesis that *B. mali* may partially consume fruit fly eggs and that predators’ partial feeding has a lethal effect on their hatchability. Moreover, as in the case of *B. tarsalis* feeding on *E. kuehniella* moth eggs [29], the age of the fruit fly egg may affect the degree to which its content is eaten by *B. mali*. Contrary to our expectation, however, partially consumed eggs of fruit flies can still be “attractive” for *B. mali*, and the remaining content of the eggs can also be fed on by this predator at a later time.

Our study is the first report of a predator of the genus *Blattisocius* feeding on the eggs of drosophilid fruit flies. A number of species of mesostigmatic mites, including species from Ascidae, Laelapidae, Melicharidae, Parasitidae, and Blattisocidae, have so far been reported to predate on eggs of drosophilid fruit flies, namely on *D. melanogaster* and

*D. suzukii* (Matsumura) [40–43]. Furthermore, *Lasioseius alli* Chant (Blattisocidae) developed and reproduced on *D. melanogaster* [44].

It should be emphasised that this study examined the predation of *B. mali* on fruit fly eggs for 10 h only. We also used random predatory females that had previously starved for 24 h and were thus generally highly motivated to feed. However, the rates of *B. mali* predation could have been substantially different if the predators were of similar age, e.g., young and gravid females, as practised in some studies, and fed by drosophilid eggs for 24 h or a longer time.

A characteristic feature of the eggs of drosophilids is the presence of so-called dorsal appendages, in varying numbers depending on the drosophilid species, which support the respiration of these eggs, especially when they are immersed in fluid. They are located near the micropyle and the so-called operculum, through which the larvae hatch from the egg [31,32].

In our study, the mites did not insert the chelicerae between the appendages but only from the side of an egg, close to these structures, and they did it less often than at the back or in the middle of the egg. It has to be stressed that the chorion within the operculum of a drosophilid egg has a different structure in some layers than that surrounding the main body of the egg [45]. That, plus the presence of the appendages, could have made egg piercing difficult for predatory mites. However, we did not observe any *B. mali* attempts to penetrate the eggs at this site. Strikingly, accidental touching of the appendages by the mites resulted in their escaping from the egg without feeding. This possible “discouraging” effect of the egg appendages could also explain the delay in *B. mali* feeding on the first egg of *D. hydei* (in comparison with *D. melanogaster* eggs), which has twice as many such structures compared to the *D. melanogaster* egg. This does not change the fact, however, that in general, the feeding rate on the eggs of both fruit fly species was similar during the “10-h” test. Moreover, starved *B. mali* females can eagerly feed on *D. melanogaster* eggs embedded in agar medium from which only those dorsal appendages protrude (Michalska K., unpublished).

Further research is needed to examine whether *B. mali*’s feeding on fruit fly eggs buried in the substrate or present on its surface would be similar. A study by Esteca [43] on predation on *D. suzukii* eggs appears especially interesting in this case. All five tested species of predatory mites (from Melicharidae and Lealepidae) fed on *D. suzukii* eggs present on the substrate, consuming them at different rates, from 2–10 eggs per day. However, when the fruit fly eggs were embedded in the fruit, only *Stratiolaelaps scimitus* (Womersley) fed on those eggs. According to Esteca [43], among the predators studied, *S. scimitus* had the longest chelicerae, which probably allowed it to pierce the fruit fly egg in the fruit and feed on it. The results presented in her work indicate, however, that this predatory mite fed on embedded eggs at a much lower rate than on unburied eggs. This may mean that it could have been more difficult for this mite to detect the eggs within the fruit, but also that the presence of protruding appendages could have made it difficult to feed on those eggs and/or that they acted aversively.

When describing predatory behaviour, the time of handling is often estimated, and according to Holling’s definition, it includes the time a predator spends pursuing, subduing, and eating a prey item [46]. In our study, *B. mali* females devoted the greatest part of the handling time of either “1-h” eggs of *D. melanogaster* or “8-h” eggs of *D. hydei* to egg consumption. Their attack consisted of approaching the egg, touching it with pedipalps, and inserting the chelicerae, and lasted very briefly, 1–2 s only, similarly as described for *Glyptolaspis americana* (Berl.) (Macrochelidae) and *Parasitus coleoptratorum* (L.) (Parasitidae) feeding on the house fly eggs [47]. Interestingly, while rates of *B. mali* feeding on *D. hydei* and *D. melanogaster* eggs were similar, the mean time of attack and egg consumption and the mean time of first attack and partial consumption of *D. hydei* eggs were definitely shorter than those of *D. melanogaster* eggs. It suggests that *D. hydei* eggs may be more nutritionally valuable for *B. mali*, and a shorter feeding period (with a smaller amount of egg content) could be enough for predator satiation and/or gut filling. On the other hand,

however, predators may simply need more time to suck out a similar portion of food from *D. melanogaster* eggs than *D. hydei* eggs due to their biochemical properties. Therefore, to fully explain this phenomenon, more detailed tests are needed.

Partial prey consumption is common among vertebrates and invertebrates, including predatory mites [23,30,48–51]. This phenomenon is associated with increased prey availability and is internally regulated by the state of the predator's hunger and/or gut filling [52,53]. This is also in line with predictions of foraging optimization, according to which the predator should maximise net energy intake, handling time should be shorter, and partial consumption should be favoured when the prey is abundant [54].

Similarly to our study, partial egg consumption has also been reported for *B. mali* females feeding the eggs of the moth *Phthorimaea operculella* (Zeller) [23] as well as for *B. tarsalis* consuming the eggs of the moth *Ephestia kuehniella* Zeller [29,30]. In the study of Gallego et al. [23], the rate of *P. operculella* eggs partially consumed was low ( $3.59 \pm 12.03\%$ ), while in our test, *B. mali* females partially consumed nearly 50% of all destroyed eggs. It should be noted, however, that in addition to differences in prey species and the connected food quantity and quality per egg, different prey densities may have been at play. In a test by Gallego et al. [23], five moth eggs were offered to a single predatory female for 48 h, while our study involved 15 fruit fly eggs for 10 h. Interestingly, our behavioural observations showed that some completely consumed eggs were, in fact, fed twice. Not only did the predators approach and feed on the eggs from the same side as at the first partial feeding, but they could also, though rarely, continue to feed precisely at the same spot. Returns to partially consumed prey were also observed in some phytoseiid mites feeding on spider mites [49,55]. Sandness and McMurtry [49] observed up to seven returns of the predatory female *Amblyseius largoensis* (Muma) to partially fed female spider mites, *Oligonychus punicae* (Hirst). The relocation of the initially fed prey was presumably based on olfaction, considering that the removal of a dead spider mite caused the predator excitement after returning to the place where the prey had been [45]. The capability of locating and feeding on wounded, initially eaten, and dead prey seems to have significant selective value for mesostigmatic mites, as it may allow them to reduce the time and energy costs of handling related to chasing or subduing prey, but it may also enable them to survive through better utilisation of food resources and scavenging when potential prey is scarce. In *B. mali*, possible scavenging has been recently indicated by observations of the mite feeding on the dead bodies of the fruit flies *D. melanogaster* and *D. hydei* [9].

In many animals, eggs contain large amounts of nutritious yolk, lipid droplets, and glycogen, which are then absorbed in the process of embryogenesis [56]. In *D. melanogaster*, significant changes in the distribution of the yolk inside the egg and in the external appearance of the developing embryo can already be observed in the first hours after oviposition [57]. Our study showed that even a few hours' difference in the age of *D. hydei* eggs (eggs laid within an 8-h vs. 14-h period) had an impact on whether the predator consumed them partially or completely. Although the age of the eggs had no effect on the rate of feeding, the predators partially consumed a greater number of younger than older eggs. Interestingly, a similar phenomenon was observed by Nielsen [29], who fed *B. tarsalis* females with *E. kuehniella* eggs. Although there was no difference in the number of moth eggs consumed between the age categories from 0–1 days old to 3–4 days old, larger portions of older moth eggs were fed by the predator. Nielsen [29] believed that older eggs of *E. kuehniella* were presumably nutritionally inferior to young ones and that *B. tarsalis* mites compensated for this by eating a larger amount of each single egg.

It should be emphasized here that the older prey eggs may be eaten more willingly by some predatory mites. As shown by Akyazi et al. [58], the starved phytoseiid mites *Neoseiulus californicus* (McGregor) and *Amblyseius swirskii* Athias-Henriot consumed higher numbers of older eggs of *T. urticae* Koch than the younger eggs of this spider mite. Interestingly, in an experiment by Cavalcante et al. [59], *A. swirski* consumed more younger eggs (up to 24 h of age) than older eggs of *Bemisia tabaci* (Gennadius). Moreover, when feeding on the younger eggs of this hemipteran insect, it had a higher oviposition rate than

on its older eggs. However, when given a choice, the predator was clearly attracted to the older *B. tabaci* eggs despite the higher suitability of the younger eggs. Therefore, in order to confirm the hypothesis of the greater nutritional value of the younger *D. hydei* eggs and their possible attractiveness for *B. mali* further tests are necessary to examine the fecundity of the predator fed on these eggs and their choice by the predator.

Our research to date has shown that *B. mali* can not only be ectoparasitically associated with drosophilid fruit flies during dispersal [9], but, as it has been demonstrated in this study, they can also prey upon eggs laid by their fruit fly host. However, to assess how much egg predation by *B. mali*, negatively affects the fitness of their insect hosts, further investigations are needed, including studies on the food preferences of *B. mali* not only in relation to drosophilid fruit fly eggs, larvae (which can be hidden within the substrate), or pupae but also other potential prey of this predator co-occurring in colonies of these flies.

**Author Contributions:** Conceptualization, K.M.; methodology, K.M., A.M. and M.K.J.; software, M.S.; validation, K.M., M.S., A.M. and M.K.J.; formal analysis, M.S. and K.M.; Investigation, A.M., K.M. and M.K.J.; Resources, K.M. and M.S.; data curation, K.M. and M.S.; writing—Original Draft Preparation, K.M. and M.S.; writing—review and editing, K.M.; visualization, K.M., M.S., A.M. and M.K.J.; supervision, K.M.; project administration, K.M.; funding acquisition, K.M. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research received no external funding.

**Institutional Review Board Statement:** Not applicable.

**Data Availability Statement:** The data used in this study are available by email request to the corresponding author.

**Acknowledgments:** We thank D.J. Gwiazdowicz (Poznań University of Life Sciences) for identifying *Blattisocius mali*. We also thank M. Wit and E. Jabłońska (Warsaw University of Life Sciences) for their help in mite macrophotography.

**Conflicts of Interest:** The authors declare no conflict of interest.

## References

- Hunter, P.E.; Rosario, R.M.T. Associations of Mesostigmata with Other Arthropods. *Annu. Rev. Entomol.* **1988**, *33*, 393–417. [CrossRef]
- Szymkowiak, P.; Gorski, G.; Bajerlein, D. Passive dispersal in arachnids. *Biol. Lett.* **2007**, *44*, 75–101.
- Huck, K.; Schwarz, H.H.; Schmid-Hempel, P. Host choice in the phoretic mite *Parasitellus fucorum* (Mesostigmata: Parasitidae): Which bumblebee caste is the best? *Oecologia* **1998**, *115*, 385–390. [CrossRef]
- De Gasparini, O.; Kilner, R.M. Friend or foe: Inter-specific interactions and conflicts of interest within the family. *Ecol. Entomol.* **2015**, *40*, 787–795. [CrossRef] [PubMed]
- Kvifte, G.M.; Kaczmarek, S.; Marquardt, T.; Seniczak, A. Linked seasonality between a phoretic mite and its moth fly host (Parasitiformes: Mesostigmata and Diptera: Psychodidae). *Acarologia* **2022**, *62*, 956–964. [CrossRef]
- Polak, M.; Markow, T.A. Effect of Ectoparasitic Mites on Sexual Selection in a Sonoran Desert Fruit Fly. *Evolution* **1995**, *49*, 660–669. [CrossRef]
- Horn, C.J.; Luong, L.T. Proximity to parasites reduces host fitness independent of infection in a *Drosophila*—*Macrocheles* system. *Parasitology* **2018**, *145*, 1564–1569. [CrossRef]
- Durkin, E.S.; Proctor, H.; Luong, L.T. Life history of *Macrocheles muscaedomesticae* (Parasitiformes: Macrochelidae): New insights on life history and evidence of facultative parasitism on *Drosophila*. *Exp. Appl. Acarol.* **2019**, *79*, 309–321. [CrossRef]
- Michalska, K.; Mrowńska, A.; Studnicki, M. Ectoparasitism of the Flightless *Drosophila melanogaster* and *D. hydei* by the Mite *Blattisocius mali* (Acari: Blattisociidae). *Insects* **2023**, *14*, 146. [CrossRef]
- Flanders, S.E.; Badgley, M.E. Prey-predator interactions in self-balanced laboratory populations. *Hilgardia* **1963**, *35*, 145–183. [CrossRef]
- Toda, M.J. DrosWLD: Taxonomic Information Database for World Species of Drosophilidae. Available online: <https://bioinfo.museum.hokudai.ac.jp/db/index.php> (accessed on 20 March 2023).
- Máca, J.; Otranto, D. Drosophilidae feeding on animals and the inherent mystery of their parasitism. *Parasit. Vectors* **2014**, *7*, 516. [CrossRef] [PubMed]
- Ashburner, M. *Drosophila: A Laboratory Handbook and Manual*; Two Volumes; Cold Spring Harbor Laboratory: New York, NY, USA, 1989; ISBN 9780879693213.



14. Poinar, G.O.; Grimaldi, D.A. Fossil and Extant Macrochelid Mites (Acari: Macrochelidae) Phoretic on Drosophilid Flies (Diptera: Drosophilidae). *J. N. Y. Entomol. Soc.* **1990**, *98*, 88–92.
15. Lehtinen, P.T.; Aspi, J. A Phytoseiid mite *Paragarmania mali*, associated with drosophilid flies. In *Acari Physiological and Ecological Aspects of Acari-Host Relationships*; European Association of Acarologists: Krynica, Poland, 1992; pp. 537–544.
16. Perez-Leanos, A.; Loustalot-Laclette, M.R.; Nazario-Yepiz, N.; Markow, T.A. Ectoparasitic mites and their *Drosophila* hosts. *Fly* **2017**, *11*, 10–18. [[CrossRef](#)] [[PubMed](#)]
17. Kerezis, V.; Kiss, B.; Deucht, F.; Kontschán, J. First record of *Blattisocius mali* (Oudemans, 1929) in Hungary associated with the drosophilid fly *Phortica semivirgo* (Máca, 1977). *Redia* **2019**, *102*, 69–72. [[CrossRef](#)]
18. Polak, M. Effects of Ectoparasitism on Host Condition in the *Drosophila*–*Macrocheles* System. *Ecology* **1998**, *79*, 1807–1817. [[CrossRef](#)]
19. Luong, L.T.; Penoni, L.R.; Horn, C.J.; Polak, M. Physical and physiological costs of ectoparasitic mites on host flight endurance. *Ecol. Entomol.* **2015**, *40*, 518–524. [[CrossRef](#)]
20. Polak, M. Ectoparasitic Effects on Host Survival and Reproduction: The *Drosophila*–*Macrocheles* Association. *Ecology* **1996**, *77*, 1379–1389. [[CrossRef](#)]
21. Axtell, R.C. New Records of North American Macrochelidae (Acarina: Mesostigmata) and Their Predation Rates on the House Fly. *Ann. Entomol. Soc. Am.* **1961**, *54*, 748. [[CrossRef](#)]
22. de Moraes, G.J.; Venancio, R.; dos Santos, V.L.V.; Paschoal, A.D. Potential of Ascidae, Blattisociidae and Melicharidae (Acari: Mesostigmata) as Biological Control Agents of Pest Organisms. In *Prospects for Biological Control of Plant Feeding Mites and Other Harmful Organisms*; Springer International Publishing: Cham, Switzerland, 2015; pp. 33–75.
23. Gallego, J.R.; Gamez, M.; Cabello, T. Potential of the *Blattisocius mali* Mite (Acari: Blattisociidae) as a Biological Control Agent of Potato Tubermoth (Lepidoptera: Gelechiidae) in Stored Potatoes. *Potato Res.* **2020**, *63*, 241–251. [[CrossRef](#)]
24. Pirayeshfar, F.; Moayeri, H.R.S.; Da Silva, G.L.; Ueckermann, E.A. Comparison of biological characteristics of the predatory mite *Blattisocius mali* (Acari: Blattisociidae) reared on frozen eggs of *Tyrophagus putrescentiae* (Acari: Acaridae) alone and in combination with cattail and olive pollens. *Syst. Appl. Acarol.* **2022**, *27*, 399–409. [[CrossRef](#)]
25. Carton, Y.; David, J.R. Relation between the genetic variability of digging behavior of *Drosophila* larvae and their susceptibility to a parasitic wasp. *Behav. Genet.* **1985**, *15*, 143–154. [[CrossRef](#)] [[PubMed](#)]
26. Albornoz, J.; Dominguez, A. Genetic analysis of *Drosophila melanogaster* egg insertion behavior. *Behav. Genet.* **1987**, *17*, 257–262. [[CrossRef](#)] [[PubMed](#)]
27. Troncoso, B.; Godoy-Herrera, R.; Mora, W. The development of larval movement patterns in *Drosophila*. *Heredity* **1987**, *58*, 321–329. [[CrossRef](#)]
28. Darst, P.H.; King, E.W. Biology of *Melichares tarsalis* in association with *Plodia interpunctella*. *Ann. Entomol. Soc. Am.* **1969**, *62*, 747–749. [[CrossRef](#)]
29. Nielsen, S. The use of *Blattisocius tarsalis* (Acari: Ascidae) for biological control in flour mills. In *Proceedings of the 7th International Working Conference on Stored-Product Protection*, Beijing, China, 14–19 October 1998; Volume 2, pp. 1265–1268.
30. Nielsen, P.S. Predation by *Blattisocius tarsalis* (Berlese) (Acari: Ascidae) on eggs of *Ephesia kuehniella* Zeller (Lepidoptera: Pyralidae). *J. Stored Prod. Res.* **2003**, *39*, 395–400. [[CrossRef](#)]
31. Osterfield, M.; Berg, C.A.; Shvartsman, S.Y. Epithelial Patterning, Morphogenesis, and Evolution: *Drosophila* Eggshell as a Model. *Dev. Cell* **2017**, *41*, 337–348. [[CrossRef](#)] [[PubMed](#)]
32. Horne-Badovinac, S. The *Drosophila* micropyle as a system to study how epithelia build complex extracellular structures. *Philos. Trans. R. Soc. B Biol. Sci.* **2020**, *375*, 20190561. [[CrossRef](#)]
33. Kopecký, J.; Nesvorná, M.; Hubert, J. *Bartonella*-like bacteria carried by domestic mite species. *Exp. Appl. Acarol.* **2014**, *64*, 21–32. [[CrossRef](#)]
34. Lourenço, F.; Calado, R.; Medina, I.; Ameixa, O.M.C.C. The Potential Impacts by the Invasion of Insects Reared to Feed Livestock and Pet Animals in Europe and Other Regions: A Critical Review. *Sustainability* **2022**, *14*, 6361. [[CrossRef](#)]
35. Dabert, J.; Mironov, S.V.; Dabert, M. The explosive radiation, intense host-shifts and long-term failure to speciate in the evolutionary history of the feather mite genus *Analges* (Acariformes: Analgidae) from European passerines. *Zool. J. Linn. Soc.* **2022**, *195*, 673–694. [[CrossRef](#)]
36. Dabert, M.; Witalinski, W.; Kazmierski, A.; Olszanowski, Z.; Dabert, J. Molecular phylogeny of acariform mites (Acari, Arachnida): Strong conflict between phylogenetic signal and long-branch attraction artifacts. *Mol. Phylogenet. Evol.* **2010**, *56*, 222–241. [[CrossRef](#)] [[PubMed](#)]
37. Mironov, S.V.; Dabert, J.; Dabert, M. A new feather mite species of the genus *Proctophyllodes* Robin, 1877 (Astigmata: Proctophyllodidae) from the Long-tailed Tit *Aegithalos caudatus* (Passeriformes: Aegithalidae)—Morphological description with DNA barcode data. *Zootaxa* **2012**, *3253*, 54. [[CrossRef](#)]
38. Shaffer, C.D.; Wuller, J.M.; Elgin, S.C.R. Raising Large Quantities of *Drosophila* for Biochemical Experiments. *Methods Cell Biol.* **1994**, *44*, 99–108. [[PubMed](#)]
39. R Core Team. *Team, R.D.C. R: A Language and Environment for Statistical Computing*; R Core Team: Vienna, Austria, 2023.
40. Binns, E.S. Phoresy as Migration—Some Functional Aspects of Phoresy in Mites. *Biol. Rev.* **1982**, *57*, 571–620. [[CrossRef](#)]
41. Bowman, C.E. Studies on feeding in the soil predatory mite *Pergamasus longicornis* (Berlese) (Mesostigmata: Parasitidae) using dipteran and microarthropod prey. *Exp. Appl. Acarol.* **1987**, *3*, 201–206. [[CrossRef](#)]



42. Houck, M.A.; Clark, J.B.; Peterson, K.R.; Kidwell, M.G. Possible Horizontal Transfer of *Drosophila* Genes by the Mite *Proctolaelaps regalis*. *Science* **1991**, *253*, 1125–1128. [[CrossRef](#)] [[PubMed](#)]
43. Esteca, F.; de Cassia Neves, F. Environmental Management Strategies for Pest Control in Strawberry Crop. Ph.D. Thesis, Universidade de São Paulo, Piracicaba, Brazil, 2021.
44. Nawar, M.S.; Rakha, M.A.; Ali, F.S. Laboratory studies on the predaceous mite, *Lasioseius bispinosus* Evans (Acari: Mesostigmata: Ascidae) on various kinds of food substances. *Bull. Soc. Entomol.* **1990**, *69*, 247–255.
45. Margaritis, L.H.; Kafatos, F.C.; Petri, W.H. The eggshell of *Drosophila melanogaster*. I. Fine structure of the layers and regions of the wild-type eggshell. *J. Cell Sci.* **1980**, *43*, 1–35. [[CrossRef](#)]
46. Papanikolaou, N.E.; Kypraios, T.; Moffat, H.; Fantinou, A.; Perdakis, D.P.; Drovandi, C. Predators' Functional Response: Statistical Inference, Experimental Design, and Biological Interpretation of the Handling Time. *Front. Ecol. Evol.* **2021**, *9*, 749. [[CrossRef](#)]
47. Wernz, J.G.; Krantz, G.W. Studies on the function of the tritosternum in selected Gamasida (Acari). *Can. J. Zool.* **1976**, *54*, 202–213. [[CrossRef](#)]
48. Hoyt, S.C. Effect of Short Feeding Periods by *Metaseiulus occidentalis* on Fecundity and Mortality of *Tetranychus mcdanieli*. *Ann. Entomol. Soc. Am.* **1970**, *63*, 1382–1384. [[CrossRef](#)]
49. Sandness, J.N.; McMurtry, J.A. Prey consumption behavior of *Amblyseius largoensis* in relation to hunger. *Can. Entomol.* **1972**, *104*, 461–470. [[CrossRef](#)]
50. Flechtman, C.H.W.; McMurtry, J.A. Studies on how Phytoseiid mites feed on spider mites and pollen. *Int. J. Acarol.* **1992**, *18*, 157–162. [[CrossRef](#)]
51. Fantinou, A.A.; Perdakis, D.C.; Maselou, D.A.; Lambropoulos, P.D. Prey killing without consumption: Does *Macrolophus pygmaeus* show adaptive foraging behaviour? *Biol. Control* **2008**, *47*, 187–193. [[CrossRef](#)]
52. Holling, C.S. The functional response of predators to prey density and its role in mimicry and population regulation. *Mem. Entomol. Soc. Can.* **1965**, *45*, 5–60. [[CrossRef](#)]
53. Johnson, D.M.; Akre, B.G.; Crowley, P.H. Modeling arthropod predation: Wasteful killing by damselfly naiads. *Ecology* **1975**, *56*, 1081–1093. [[CrossRef](#)]
54. Samu, F. Wolf spider feeding strategies: Optimality of prey consumption in *Pardosa hortensis*. *Oecologia* **1993**, *94*, 139–145. [[CrossRef](#)]
55. Ballard, R.C. The Biology of the Predacious Mite *Typhlodromus Fallacis* (Garman) (Phytoseiidae) at 78 degrees F. *Ohio J. Sci.* **1954**, *54*, 175–179.
56. Jeong, Y.E.; Chung, H.M.; Ahn, T.I. Utilization of a storage protein in the embryonic development of *Drosophila* and *Xenopus*. *Korean J. Biol. Sci.* **2001**, *5*, 85–90. [[CrossRef](#)]
57. Bownes, M. A photographic study of development in the living embryo of *Drosophila melanogaster*. *J. Embryol. Exp. Morphol.* **1975**, *33*, 789–801. [[CrossRef](#)]
58. Akyazi, R.; Altunc, Y.E.; Soysal, M. *Amblyseius swirskii* ve *Neoseiulus californicus* (Mesostigmata: Phytoseiidae)'un Tüketim Kapasitesine Ayrı Yumurta Yaşının Etkisi. *Türk Tarım Doğa Bilim. Derg.* **2018**, *5*, 628–633. [[CrossRef](#)]
59. Cavalcante, A.C.C.; Borges, L.R.; Lourenção, A.L.; de Moraes, G.J. Potential of two populations of *Amblyseius swirskii* (Acari: Phytoseiidae) for the control of *Bemisia tabaci* biotype B (Hemiptera: Aleyrodidae) in Brazil. *Exp. Appl. Acarol.* **2015**, *67*, 523–533. [[CrossRef](#)] [[PubMed](#)]

**Disclaimer/Publisher's Note:** The statements, opinions and data contained in all publications are solely those of the individual author(s) and contributor(s) and not of MDPI and/or the editor(s). MDPI and/or the editor(s) disclaim responsibility for any injury to people or property resulting from any ideas, methods, instructions or products referred to in the content.