

The predatory behavior of *Hydrotaea albuquerquei* (Lopes) larvae on the larvae of *Musca domestica* Linnaeus under laboratory conditions

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ABSTRACT

Larvae of *Hydrotaea* species are facultative predators of larvae of other fly species on poultry farms, chicken feces, pig, and decaying carcasses. The Neotropical species *H. albuquerquei* occurs together with *M. domestica* in these environments and might be useful in the biological control of the latter. To verify the predatory capacity of *H. albuquerquei* larvae on the larvae of *M. domestica*, we varied the size of the larvae and the densities of the predators and prey under controlled laboratory conditions. Adults were collected from a poultry farm for the experiment, and the larvae they produced were reared in the laboratory. The second and third instar larvae of *H. albuquerquei*, when at higher densities, suppressed populations of house fly larvae when the latter were smaller than the former. This means that the functional response increases gradually with an increase in prey population density and predator size. In these conditions, one *H. albuquerquei* larva consumes up to 29 *M. domestica* larvae at high prey densities and could reduce 100% of the house fly population under a 50% prey density. This study confirmed a pattern previously observed in other predatory larvae and our results have implications for the biological control and integrated pest management programs of *M. domestica* in poultry and swine farms.

Introduction

Musca domestica Linnaeus, 1758 (Diptera, Muscidae), the house fly, is a highly synanthropic species and the most common in urban environments and on livestock. Feces, carcasses and garbage accumulated in these areas attract flies (Greenberg, 1973), which can transmit almost a hundred pathogens (Khamesipour et al., 2018). More than 50 of those pathogens are bacteria (Geden et al., 2021). In the US, collective house fly control costs US\$ 1.87 billion in commercial establishments such as restaurants and facilities inspected by the Food and Drug Administration (FDA) (Hinkle and Hogsette, 2021). In poultry, swine and livestock farms combined, house fly control may cost from US\$ 500 million to US\$ 1 billion per year, due to the great numbers and degree of insecticide resistance of the flies (Freeman et al., 2019; Geden et al., 2021). Other alternatives besides chemical control have been explored, involving integrated methods such as biological control (Hinkle and Hogsette, 2021).

Predators are used in the biological control of house flies. Integrated Pest Management (IPM) incorporates biological control and must be

implemented when managing *M. domestica*. One notable biological control agent of the house fly on poultry and swine is *Hydrotaea* Robineau-Desvoidy, 1830 (Diptera, Muscidae) (Turner Junior and Carter, 1990; Tsankova and Luvchiev, 1993), in particular *Hydrotaea aenescens* (Wiedemann, 1818) in the USA and Europe (Nolan III and Kissam, 1985, 1987; Betke et al., 1991; Turner Junior et al., 1992).

Hydrotaea albuquerquei (Lopes, 1985), a Neotropical species distributed throughout tropical and temperate America (Carvalho et al., 2005; Patitucci et al., 2010), has similar nutritional needs to *H. aenescens* (Simon et al., 2011) and is common in rural areas (Costa et al., 2000). In addition, *H. albuquerquei* larvae and the larvae of other species of the genus have structures that characterize them as facultative predators (Skidmore, 1985; Krüger, 2002).

The methods employed in the use of predatory flies in the larval stage are mass rearing, and the inundative release of pupae to increase the density of the predator population (Farkas et al., 1998; Hogsette and Jacobs, 1999; Hogsette et al., 2002). After emergence, the adults of *Hydrotaea* are attracted to the substrates they oviposit and develop on, and their third-instar larvae will prey on *M. domestica* larvae (Schumann, 1982; Skidmore, 1985).

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Studies about the predatory interaction of *Hydrotaea* larvae on the larvae of *M. domestica* have established that two factors determine an increase in predatory capacity and, consequently, population control. The first is predator density with respect to prey density, and the second is the difference in the sizes of the larvae of the interacting species: larger *Hydrotaea* larvae will kill more larvae of *M. domestica* (Müller, 1982; Olckers and Hulley, 1984). This is consistent with the ecological theory of predation that postulates that larger predators have greater success impacting the prey population (Arim and Marquet, 2004; Holt and Huxel, 2007).

This study aims to investigate the effects of different instars and larval densities on the larval survival of *H. albuquerquei* and *M. domestica* under laboratory conditions. We tested (i) which density and larval instar of *H. albuquerquei* (predator) is more successful for impacting the survival of *M. domestica* (prey) and, consequently, (ii) if there is a difference in the functional response.

Material and methods

Insect rearing

The colonies of *Hydrotaea albuquerquei* (predator) and *Musca domestica* (prey) were established from adults collected in a poultry farm belonging to Capão do Leão Campus of Federal University of Pelotas, situated in southern Brazil, State of Rio Grande do Sul (31°48'30 "S, 52°24'41"W). Flies were reared in laboratory conditions in plastic cages (30x30x30cm) under a controlled environment at 27°C and 80% R.H. with a photoperiod of 12 hours. Adults were supplied *ad libitum* with a mixture ration composed of one part of fish meal, two parts of powdered milk and two parts of refined sugar. Water was offered in 50 mL bottles. The conditions for rearing the immatures and adults followed Krüger et al. (2003, 2004).

Predation and survival

We estimated the predatory capacity of larvae of *H. albuquerquei* on larvae of *M. domestica* from the survival rate of both species compared to the control. The independent variables are the densities of predators to prey and the differences in predator and prey sizes.

We established five proportional densities between predator *H. albuquerquei* (represented by the capital letter H) and prey *M. domestica* (represented by the capital letter M) (Table 1), considering 200 larvae in each rearing container containing 400g of diet.

Each density (Table 1) was used to verify the effect of the different sizes of *H. albuquerquei* (H) and *M. domestica* (M) larvae. The larval sizes were consistent with the instars they were in. The subsequent H and M larval encounters were tested in agreement with Figure 1.

We set up each experiment in triplicate in each encounter versus density. Each sample was kept in a flask with a capacity of 500 ml, a diameter of 10 cm and 400g of a diet composed of 50% fish meal, 30% sawdust and 20% wheat flour, adding 250 mL of water to make the medium pasty. The flasks were kept in a Bio-Oxygen Demand (BOD) chamber at 27°C and 80% R.H. with a photoperiod of 12 hours.

Data analysis

We performed the survival calculation according to the formula below:

$$(a - b) / a ,$$

Table 1

Abundance (N) of *Hydrotaea albuquerquei* (H) and *Musca domestica* (M) larvae for each density.

Density	Proportional density (M)	N (H)	N (M)
1:1	50%	100	100
1:4	80%	40	160
1:9	90%	20	180
1:19	95%	10	190
1:39	97.5%	5	195
Control	100%	—	—

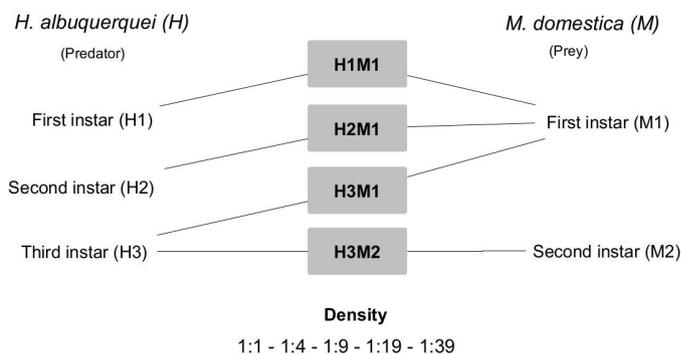


Figure 1. Diagram showing the sampling design of the interaction of larvae of different instars (1, 2 and 3) between the predator *Hydrotaea albuquerquei* (H) and the prey *Musca domestica* (M). The other encounters (HM) considered the differences in size between the larvae of the species. In each encounter (HM) of the different instars, 200 larvae of the species were placed together in different proportions considering the ratio of *M. domestica* larvae (M) to each *H. albuquerquei* larva (H), establishing proportional densities between predators (H) and preys (M) in agreement with Table 1. For each encounter and density, triplicates were performed.

where **a** is the number of larvae of *M. domestica* introduced on the medium and **b** is the number of larvae that did not emerge following Geden et al. (1988). The functional response of *H. albuquerquei* was obtained by s / c , where **s** is the surviving individuals of *M. domestica*, and **c** is the surviving individuals of *H. albuquerquei* at each density versus encounter following Geden et al. (1988), without considering the corrected mortality and the number of days that the house fly immatures were vulnerable to predation followed by these authors.

We analyzed the effect of density versus encounter on the survival and functional response of *M. domestica* larvae by generalized linear models (GLMs), validating the models by chi-square (Chi-square) tests. All statistical analyses were performed on software R.

Results

Survival

The density (Chi-square_{1;70} = 10.141, P < 0.001), encounter (Chi-square_{3;67} = 1.516, P = 0.001) and the interaction between density and encounter (Chi-square_{3;64} = 2.040, P < 0.001) influenced the survival rate of *M. domestica* larvae. The survival rate of *M. domestica* was lowest at 50% densities or 1:1 ratio and highest at 97.5% densities or even in the control. Therefore, the survival rate of *M. domestica* increases as prey density increases relative to predator density in the H2M1, H3M1 and H3M2 encounters, but not in the H1M1 encounter, where there was no significant variation (P = 0.071) (Figure 2).

An increase in prey density does not interfere with the survival rate of *H. albuquerquei* when compared to the control (Chi-square_{3;68} = 12.104, p = 0.714). The survival rate of *H. albuquerquei* was higher in the H3M2 encounter (77%) than in the others (62%) (Chi-square_{3;68} = 13.877, P = 0.011) (Figure 3).

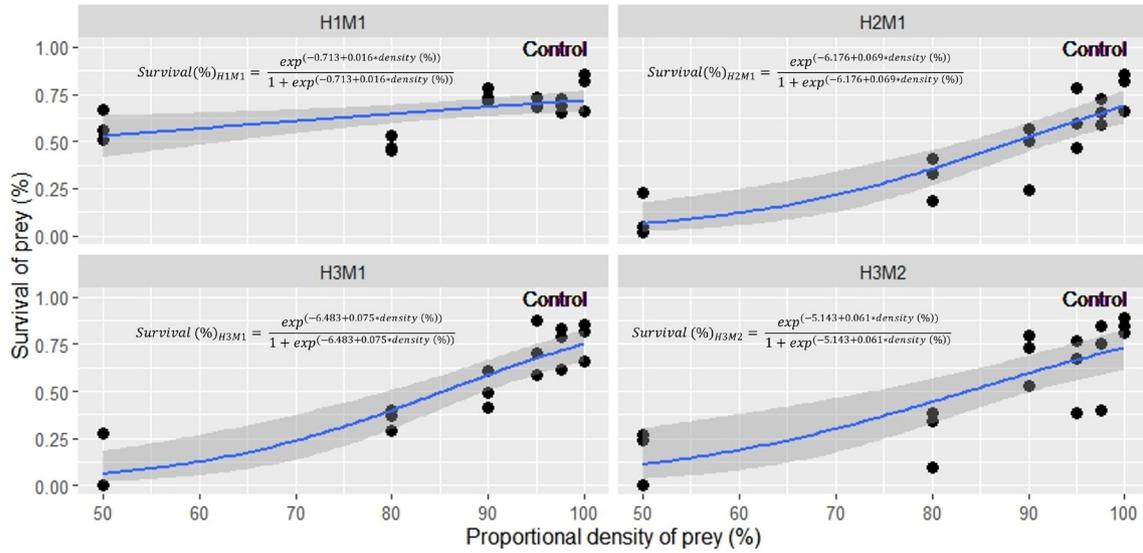


Figure 2. Survival of prey (%) of *Musca domestica* larvae (prey) at different proportional prey densities to the total number of larvae (200 individuals) of predators and prey in other encounters. The statistical model (Binomial distribution with correction of the distribution for Quasibinomial) of the prey survival is in the upper portion of each graph. H1M1, *H. albuquerquei* first-instar larvae versus *M. domestica* first-instar larvae. H2M1, *H. albuquerquei* second-instar larvae versus *M. domestica* first-instar larvae. H3M1, third-instar larvae of *H. albuquerquei* versus first-instar larvae of *M. domestica*. H3M2, third-instar larvae of *H. albuquerquei* versus second-instar larvae of *M. domestica*.

$$Survival_{H1M1,H2M1,H3M1} = \frac{\exp(0.908006 - 0.045445 \cdot \text{density} + 0.00048 \cdot \text{density}^2)}{1 + \exp(0.908006 - 0.045445 \cdot \text{density} + 0.00048 \cdot \text{density}^2)}$$

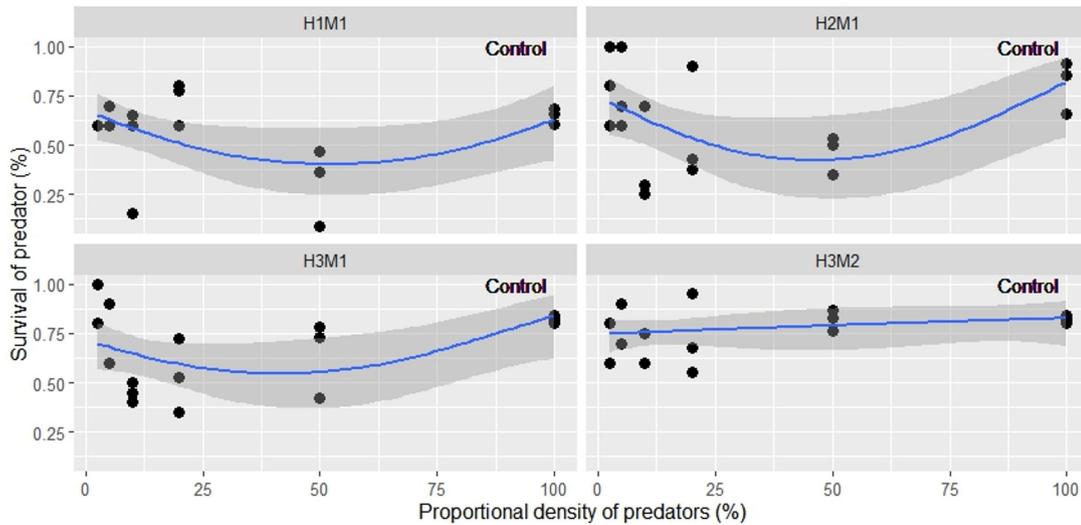


Figure 3. Survival of predator (%) of *Hydrotaea albuquerquei* larvae (predator) at different proportional densities of prey with the total number of larvae (200 individuals) of predators and prey in other encounters. The statistical model (Binomial distribution with correction of the distribution for Quasibinomial) of the predator's survival is in the upper portion of the graph to the H1M1, H2M1 and H3M1 encounters. H1M1, *H. albuquerquei* first-instar larvae versus *M. domestica* first-instar larvae. H2M1, *H. albuquerquei* second-instar larvae versus *M. domestica* first-instar larvae. H3M1, third-instar larvae of *H. albuquerquei* versus first-instar larvae of *M. domestica*. H3M2, third-instar larvae of *H. albuquerquei* versus second-instar larvae of *M. domestica*.

Functional response

The predatory capacity of *H. albuquerquei* larvae on *M. domestica* larvae ranged from 1 dead *M. domestica* larvae per *H. albuquerquei* larvae at 50% density (H3M2) to 29 dead *M. domestica* when *H. albuquerquei* larvae were at a density of 97.5% (H3M2) (Figure 4).

The increase in the density of prey to predators causes an increase in the individual predatory capacity of *H. albuquerquei* larvae (Chi-square_{1;58} = 145.27, *p* < 0.001) regardless of the encounter (Chi-square_{6;58} = 129.15, *p* = 0.418) (Figure 4).

Discussion

Survival

Our results demonstrate that third instar larvae of *H. albuquerquei* have a high predatory capacity over *M. domestica* larvae, maintaining high survival rates and suppressing house fly populations at 1:1 density.

Also, in our study, the differences in size, represented by different instars of the predator-prey encounter and the prey density with predators, determine the predation levels and prey survival, in agreement with

$$\text{Predatory capacity} = \exp(-2.464 + 0.052 * \text{density}(\%))$$

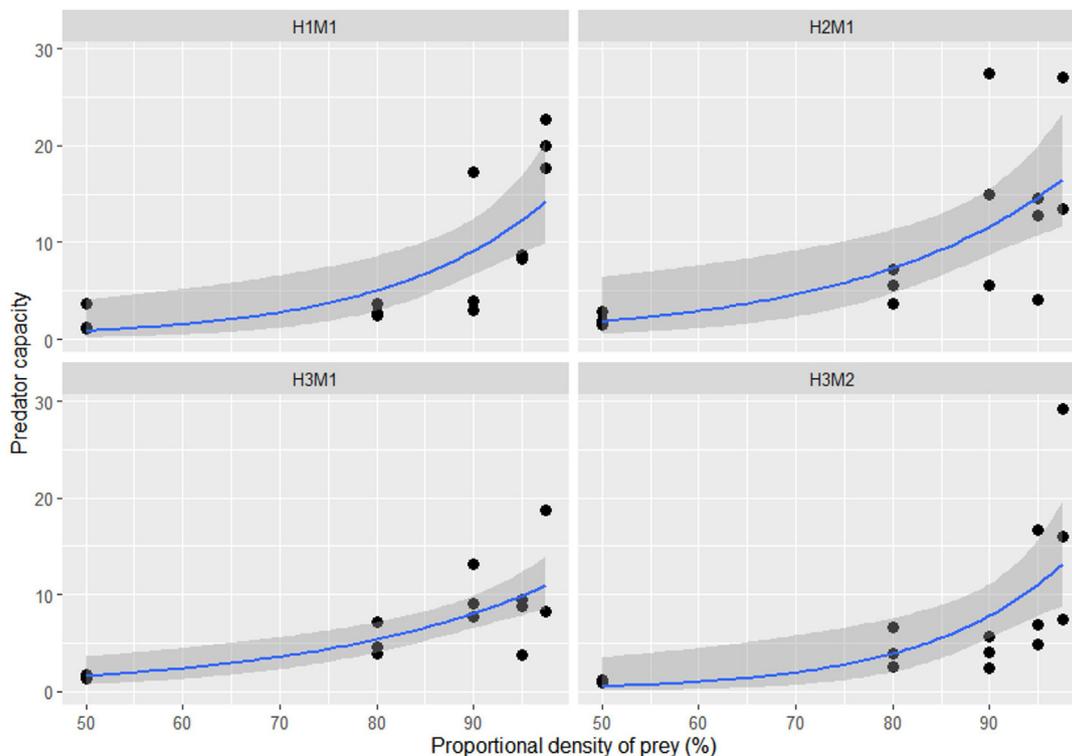


Figure 4. Functional Response. The predatory capacity of *H. albuquerquei* larvae (predator) on *Musca domestica* larvae (prey) at different proportional prey densities to the total number of larvae (200 individuals) of predators and prey in other encounters. The statistical model (Poisson distribution with correction of the distribution for Quasipoisson) of the predatory capacity is in the upper portion of the graph. H1M1, *H. albuquerquei* first-instar larvae versus *M. domestica* first-instar larvae. H2M1, *H. albuquerquei* second-instar larvae versus *M. domestica* first-instar larvae. H3M1, third-instar larvae of *H. albuquerquei* versus first-instar larvae of *M. domestica*. H3M2, third-instar larvae of *H. albuquerquei* versus second-instar larvae of *M. domestica*.

the first hypothesis. Consequently, as predator density increased, the survival of *M. domestica* larvae decreased. Along with the importance of predator-prey density in the system, we demonstrate that the reduction in prey population survival is more effective when there are size differences between species. Also predators must be more significant than prey, explaining the results in the H2M1, H3M1 and H3M2 when compared to the H1M1.

Our results corroborate other studies with other species of *Hydrotaea*, e.g., *H. aenescens*, *H. leucostoma* (Wiedemann, 1817), *H. ignava* (Harris, 1780) [= *H. capensis*] over *M. domestica* (Anderson and Poorbaugh, 1964; Müller, 1982; Olckers and Hulley, 1984; Turner Junior and Carter, 1990; Tsankova and Luvchiev, 1993), demonstrating an effective predation behavior, reducing prey populations.

The mean larval survival in the present study on 1:4 or 80% prey density is like the experiments conducted by Farkas and Jantnyik (1990) with 100 g of pig manure and approximate larval proportions. Their results showed that *H. aenescens* could reduce the *M. domestica* population to 86 to 100% of its original size, indicating high levels of predation. Vibe-Petersen (1998) also showed that *H. aenescens* could suppress the 1st instar larvae of *Scatella fusca* Maquart (Diptera: Ephydriidae) at the 3rd instar with a 1:1 proportion.

The observed results agree with the ecological theory of predation, which postulates that predators will prefer prey that are smaller than them (Faria et al., 2004), even when they hunt collectively (Polis et al., 1989). This is confirmed by experimental work on sarcosaprophagous flies larvae (Müller, 1982; Farkas and Papp, 1990; Duarte et al. 2013).

In the case of *M. domestica*, in which the larvae have a faster development rate (Wang et al., 2018) than those of *H. albuquerquei*

(Duarte et al., 2015), the coexistence in a temporary habitat of an intraguild predation system is possible because the prey could escape predation, as observed by Müller (1982) in experiments between *H. aenescens* and *M. domestica*. At high densities of *H. aenescens*, *M. domestica* larvae developed faster to escape predation. The predatory capacity of *H. albuquerquei* on *M. domestica* will be reduced in encounters among the first instar larvae of both species (H1M1), because when the larvae of *H. albuquerquei* are ready for predatory activity (third instar), the house fly larvae are ready to abandon the substrate. Shiao and Yeh (2008) described a similar scenario for some calyptrate species with similar biology. When the prey numbers and size of predators and prey are similar (in natural conditions, that would be when they first arrive at the shared resource), the foraging capacity gives the predators an advantage. Farkas and Jantnyik (1990) also reported that if eggs or first instar larvae of *H. aenescens* and *M. domestica* are observed simultaneously on pig manure, predators would not be able to predate facultatively. Therefore, insufficient knowledge about the synchrony between the biological cycles of both species and the best developmental stage of the predator for inundative release in the system may hinder biological control methods.

Functional response

The increase in the proportional density of *M. domestica* larvae caused a rise in the individual predatory capacity of the surviving *H. aenescens* larvae, corroborating our second hypothesis.

The results of the present study are similar to those of Farkas and Jantnyik (1990) on the predatory capacity of *H. aenescens*, where one

predator could consume five prey items in a 10% density proportion (180 larvae). According to Olckers and Hulley (1984) and Tsankova and Luvchiev (1993), one *H. ignava* (= *H. capensis*) larva can kill 4 to 17 prey larvae. *H. leucostoma* can eat up to 20 *M. domestica* larva (Anderson and Poorbaugh, 1964).

Like those species, when more larvae are available to prey on, *H. albuquerquei* will choose to obtain energy through predation activity rather than through shared food. This behavior is presumably more energetically costly, as Müller (1982) noted for the interaction between *H. aenescens* and *M. domestica*. On the other hand, animal tissues can have a high nitrogen content, being energetically worthwhile and providing more nutrient conversion (Ireland and Turner, 2006). These considerations also suggest that, although the shared food is inanimate and might have similar nutrient apportion for the prey, pre-adaptation to predation may influence the predatory feeding, as already reported by Müller (1982) for *H. aenescens*, Olckers and Hulley (1984) for *H. ignava*, Duarte et al. (2013) for *Muscina stabulans*, Shiao and Yeh (2008) for *Chrysomya rufifacies*, and Rosa et al. (2006) for other blowflies, where the predator population was not affected by the high number of competitors, even with few individuals.

The similar predation capacity of other *Hydrotaea* species suggests that the use of *H. albuquerquei* as a biological control agent is a possibility. This may apply to other species of this genus (Tsankova and Luvchiev, 1993; Hogsette and Washington, 1995; Vibe-Petersen, 1998; Geden et al., 2021). Control measures must consider the larval stage, time and density to release the biological agents to the environment for the effectiveness of augmentative control methods using predators such as *Hydrotaea*.

Final considerations

Under field conditions, the larvae of *H. albuquerquei* must be established in the substrate for at least two days before the houseflies' oviposition. The third instar of *H. albuquerquei* must meet the first instar larva of *M. domestica* to achieve the most significant reductions in the house fly population. Thus, it is crucial to determine the periods of pupae development and the pre-oviposition period of females under natural conditions. In Pelotas, Brazil, the development of *H. albuquerquei* pupae ranges from almost nine days in the summer to about 40 days in the mid-winter (Krüger et al., 2011). The pre-oviposition period for *H. albuquerquei* females lasts about 4 to 5 days (Krüger et al., 2004). Considering these periods, inundative releases should take roughly 13 to 14 days before the substrate becomes available to *M. domestica* females to ensure synchronization. This species can be effectively used as a biological control agent for *M. domestica* in IPM programs on poultry and swine farms.

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Conflicts of interest

The authors declare no conflicts of interest

Author contribution statement

RFK and WDT conducted the experiments and registered the data. WDT, GDR and AMG analyzed the data, conducted statistical analyses

and wrote the first version of the manuscript. WDT, RFK, DFM and GDR created the figures, reviewed and wrote the final version.

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