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Predation interactions among henhouse-dwelling arthropods, with a focus on the poultry red mite *Dermanyssus gallinae*
Running title: Predation interactions involving *Dermanyssus gallinae* in poultry farms

Ghais Zriki, Rumsais Blatrix, Lise Roy

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1 **Predation interactions among henhouse-dwelling**
2 **arthropods, with a focus on the poultry red mite**
3 ***Dermanyssus gallinae***

4 Running title:

5 Predation interactions involving *Dermanyssus gallinae*
6 in poultry farms

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15 ABSTRACT

16 BACKGROUND

17 Analysis of the poorly explored food webs of henhouse-dwelling arthropods
18 would improve biological control against the poultry red mite (PRM)

19 *Dermanyssus gallinae* (de Geer). This study aimed to identify trophic links

20 among indigenous predatory arthropods, PRM, and alternative preys. *In-*

21 *vitro* predation tests were carried out to assess (1) the ability of

22 indigenous predators to feed on PRM juvenile and adult stages in two
23 physiological statuses (unfed and freshly blood-fed) in the absence of any
24 physical barrier, (2) predator preferences between PRM and astigmatic
25 mites, and (3) predation interactions between PRM predators.

26 RESULTS

27 Ten arthropod taxa fed on PRM with predation rates ranging from 4 to 95%
28 in our experimental conditions. They belonged to 1) Acari: *Androlaelaps*
29 *casalis* (Berlese), *Cheyletus* spp., *Macrocheles muscaedomesticae*
30 (Scopoli), *M. penicilliger* (Berlese), *Parasitus fimetorum* (Berlese),
31 *Dendrolaelaps* spp. and *Uroobovella fimicola* (Berlese); 2) other Arachnida:
32 *Lamprochernes nodosus* (Schrank) and a linyphiid spider; and 3) Insecta:
33 *Lyctocoris campestris* (Fabricius). These predators varied in their
34 preference for PRM stages and physiological statuses (unfed or freshly
35 blood-fed). When given a choice, most predators preferred to feed on PRM
36 than astigmatic mites. Bidirectional predation occurred within two pairs of
37 PRM predators (*M. penicilliger*-*Lam. nodosus* and *A. casalis*-*Cheyletus*
38 spp.), and *M. penicilliger* had a 100 % predation rate on *A. casalis*.

39 CONCLUSION

40 Our study highlights the potential of various arthropod predators occurring
41 naturally in poultry houses for conservation and augmentative biological
42 control of PRM. Predation interactions between these predators should be
43 accounted for before developing biocontrol agents against PRM.

44 Keywords

45	<i>Dermanyssus gallinae</i> ; poultry red mite; food webs; biological control;	
46	henhouses.	
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84 **1 INTRODUCTION**

85 The poultry red mite (PRM) *Dermanyssus gallinae* (De Geer) is the most
86 important pest of laying hens worldwide.^{1,2} PRM is a nidicolous
87 ectoparasite attacking resting hens at night. After relatively rapid blood
88 meal, it retires to hide in different microhabitats like cracks, crevices, and
89 dry droppings in the farm building.^{3,4} PRM has significant effect on the
90 health and welfare of hens, it can cause anemia, decreased egg
91 production and increased hen mortality.^{5,6} The typical conventional control
92 of PRM by means of synthetic acaricides is often not sufficient. In addition,
93 the use of synthetic products has become increasingly reduced by stricter
94 legislation regarding active ingredients.^{7,8} Therefore, different alternative
95 methods of control have been developed such as plant-derived product,⁹
96 inert substances such as diatomaceous earth and silica,¹⁰ electronic
97 perches, biological control by means of natural enemies like
98 entomopathogenic fungi^{11,12} and predatory mites,^{13,14} and research on
99 vaccines is making progress.^{15,16}

100 The particular lifestyle of PRM as a nidicolous parasite living in a diversity
101 of habitats in poultry farms makes this mite less likely to be reached by
102 chemical treatment and more accessible for arthropod predators than
103 ectoparasites living on the host. This suggests that PRM is an ideal target
104 of biological control. Although biological control is well developed and has
105 been successfully adopted to control pest arthropods in crop farming, this
106 method has more recently begun to be developed against pests in
107 livestock production and is still in its infancy.^{1,7} To date, five predatory

108 mites were experimentally shown to have potential in PRM biological
109 control: *Cheyletus eruditus* (Schrank) and *C. malaccensis* (Oudemans),
110 *Androlaelaps casalis* (Berlese), *Hypoaspis aculeifer* (Canestrini), and
111 *Stratiolaelaps scimitus* (Womersley).^{13,14,17-19} The two predatory mites *A.*
112 *casalis* and *C. eruditus* are currently mass-reared and used as biocontrol
113 agents of PRM in laying poultry farms,^{7,20} but their efficiency in the field
114 should be improved by complementary research.^{18,20} Arthropods
115 associated to poultry production²¹⁻²⁵ include several predatory taxa some
116 of which are known to feed on various prey mite species.^{13,25} However, the
117 ability of the majority of these predators to feed on PRM has not been
118 investigated. Amongst the naturally-occurring arthropod predators in
119 poultry farms, various taxa are known to dwell in poultry manure.^{21,24-26}
120 Several are typically active hunters that have been recurrently observed
121 into microhabitats other than this substrate, including in PRM traps.¹³ This
122 makes them promising agents for PRM control in layer farm buildings.
123 The effect of predator communities on their prey's population may depend
124 on direct and indirect interactions between these predators like
125 competition and intraguild predation.^{27,28} Intraguild predation is very
126 common among generalist predators that exploit common food
127 resources^{27,29} which could significantly affect the dynamics of their shared
128 preys.^{28,30,31} The effect of intraguild predation on prey regulation can be
129 antagonistic, though many case reports do not confirm it, and it may even
130 be synergistic.³²⁻³⁴ When focal and alternative preys share the same
131 predatory species,³⁵ the availability of alternative prey can also influence
132 the behavior of the shared predator and can lead to either increased or

133 decreased predation on focal prey.^{36,37} This depends on many factors
134 including the relative size of prey populations and predator preferences.
135 Astigmatic mites are microbivores/detritivores and they are the most
136 frequent and abundant taxa in poultry manure.^{25,38} They may serve as
137 main or alternative prey for many generalist predatory mites.^{39,40}
138 Evaluating the preferences of potential predators of PRM between
139 astigmatic mites (as possible alternative or competing prey) and PRM (as
140 focal prey) is essential to predict the effect of these predators on pest
141 regulation.⁴¹

142 The physiological status of PRM in terms of duration since the last blood
143 meal may have a substantial effect on predation. One can expect from the
144 fresh blood meal either a facilitating effect on predation owing to the
145 weakening of the highly extended cuticle (making it possibly easier to be
146 penetrated by the predator's chelicera) and the substantial slowing of
147 PRMs' movements (akinesis is observed quickly after feeding⁴²), or an
148 antagonistic effect owing to the oxidative stress produced by the ingestion
149 of fresh blood and/or the toxic products of its digestion (see adaptation
150 mechanisms in hematophagous arthropods to dealing with feeding on
151 fresh blood^{43,44}). The physiological status of prey in interaction with other
152 factors (species, sex, and size of the proposed preys) was shown to be an
153 important driver of prey selection by a spider predator that feeds on
154 mosquitoes.^{45,46} Lastly, adult individuals of certain prey species have a
155 greater ability to escape and better defense responses against predators
156 than juveniles.^{47,48} Prey consumption by several phytoseiid mite predators
157 was inversely related to prey size.⁴⁹⁻⁵¹ Hence, predators may be more or

158 less prone to feed on freshly fed PRM and/or on different stages of PRM in
159 farms.

160 This study aimed to characterize the potential trophic interactions
161 involving PRM, alternative preys like microbivorous mites and arthropod
162 predators that usually share the same microhabitats with PRM or those
163 prone to hunt this mite in such microhabitats. Our specific objectives were
164 to (1) identify potential predators of PRM based on their ability to consume
165 various forms of PRM (different stages and physiological statuses) when no
166 physical barriers hinder the access of these predators to their preys, (2)
167 evaluate the effect of the presence of alternative preys like astigmatic
168 mites on the predation on PRM, and (3) assess whether predation
169 interactions can occur between PRM predators.

170 **2 MATERIALS AND METHODS**

171 *2.1 Arthropod sources*

172 *2.1.1 Arthropod predators and microbivore mites*

173 To maximize the diversity of arthropod predators to be tested, we sampled
174 arthropods from several barn layer farms located in the Drôme
175 department (Rhône-Alpes-Auvergne region, France). These farms were
176 selected based on previous in farm surveys.²⁵ Barn layer farms have
177 slatted flooring under which manure is allowed to accumulate over long
178 periods (flock duration = ca. 1 year) which permits an important
179 development and establishment of manure-dwelling arthropods.⁵² We
180 focused on 13 taxa of arthropods including 12 manure-dwelling taxa and
181 one taxon of spiders. Certain mite taxa were multispecific and others were

182 monospecific (Table 1). These arthropods were not reared or maintained
183 on any transitional diet in the lab. Manure samples were kept into plastic
184 containers covered with nylon-filter lids (mesh size 80 μm) before the
185 extraction of arthropods.

186 Manure-dwelling arthropod individuals were extracted by dry sieving of
187 manure samples using a series of stacked sieves with decreasing mesh
188 size (from 1000 μm to 180 μm). In order to identify and differentiate mite
189 taxa, we used the definition of morphospecies in Roy *et al.* 2017.²⁵ After
190 performing predation tests on arthropods, the following taxa were
191 identified at the species level: Pseudoscorpionida, Heteroptera (Insecta),
192 *Macrocheles* spp. (Mesostigmata). For other morphospecies, the
193 taxonomic level was simply the level discernible under the
194 stereomicroscope according to Roy *et al.*²⁵ (species level for monospecific
195 morphospecies, higher levels for others; see Table 1).

196 2.1.2 PRM

197 PRM aggregates were collected from two farm buildings in sealable plastic
198 bags and kept fasting for one to three weeks in an incubator at 15 °C
199 before tests. To produce freshly fed PRMs, fasted individuals were
200 introduced into a PVC cylindrical container (60 L, 40 cm in diameter) with a
201 chick for 2 h at 25 ± 5 °C in complete darkness. The top of the container
202 was sealed with mite-proof nylon mesh (100 \times 100 μm , PE171.6, Diatex,
203 France). Pieces of folded paper were put in the container to provide
204 shelters for PRMs to aggregate after the blood meal and facilitate the
205 collection of fed individuals.

206 2.2 *Experimental arenas for predation tests*

207 Predation tests were conducted following the protocol by El Adouzi *et al.*⁵³
208 In short, each predator was tested in an experimental arena constituted by
209 a well (flat-bottomed, 7 mm diameter) of a transparent polystyrene
210 microplate (Nunc™ 167008 F96 MicroWell 96-well × 400 µL, external
211 dimensions: 128 × 86 mm Cell Culture Microplate, Fyn, Denmark). We
212 added 2–4 µl of 1.5 % agarose gel into each well to prevent dehydration of
213 the arthropods, a technique validated by El Adouzi *et al.*⁵³ Microplates
214 were covered with stretched plastic paraffin film (Parafilm®, Bemis Co.,
215 USA).

216 2.3 *Predation test experiment*

217 A test consisted of confining one single predator and one or two preys
218 (depending on the modality, see below) into a well of a 96-well microplate,
219 wells of which were used as replicated experimental arenas. After a fixed
220 contact duration, prey mortality was recorded in each arena. Controls
221 consisted in the same single or paired prey(s) isolated into wells on the
222 same microplate without any predator (same number of wells for controls
223 as for tests with predators). Several different modalities of
224 predator/preys(s) combination were tested on the same microplate and at
225 the same time (= a series). To minimize the effect of random factors, (1)
226 each predator modality was tested on different microplates successively,
227 (2) two to four different modalities of predator/prey(s) combination were
228 tested together in each series, (3) the set of modalities to be tested
229 together was randomly rearranged for each series, so as to be free of
230 dependencies between modalities. Each modality was replicated dozens of

231 times on a microplate (one predatory individual per taxon and per well on
232 2 to 4 columns, ie 16 to 32 individual tests, and a similar number of
233 control wells), and this was repeated two to three time in different series.
234 Predators were fasted for 24 h before being tested. Microplates were
235 maintained in a climatic chamber at 25.0 ± 0.5 °C in complete darkness.
236 Prey condition in each experimental arena was examined under a
237 stereomicroscope after 24 hours of test duration. A prey was deemed to
238 be dead if no movement was triggered by contact with a thin paintbrush.
239 Arachnid predators do not swallow prey but only suck internal body
240 liquids,⁵⁴ making it difficult to differentiate predation events from prey
241 natural mortality. Thus, in each series, prey mortality in predation tests
242 was corrected by prey natural mortality recorded in the corresponding
243 controls to obtain the predation rate.

244 *2.4 Predation test types*

245 *2.4.1 Prey-choice tests*

246 Prey choice tests were used to evaluate (1) the predation rate of each
247 predator on each prey species and (2) the preference of predators
248 between these offered preys. The predation rate (1) was estimated as the
249 frequency of predation on a given kind of prey. Two prey individuals with
250 (test) or without (control) one predator individual were introduced per well.
251 The preference (2) was tested between two PRM developmental stages
252 (unfed juveniles and unfed adult females), or two physiological statuses of
253 PRM (freshly fed and unfed), or between unfed PRM and another prey
254 mite, with a focus on Astigmatic mites. The preference according to the

255 physiological status and between PRM and Astigmatic mites was tested
256 both with PRM juvenile and adult females. All in all, twelve putative
257 predatory taxa were tested in 31 modalities of prey-choice test (Table 2).

258 2.4.2 Predator-to-predator interactions

259 We evaluated whether six native predators engaged in predator-prey
260 interaction when no shared prey was offered, following five combinations:
261 (1) *A. casalis* vs *Cheyletus* spp., (2) *A. casalis* vs *M. penicilliger*, (3) *A.*
262 *casalis* vs *Lam. nodosus*, (4) *Lam. nodosus* vs *M. penicilliger*, and (5)
263 *Dendrolaelaps* spp. vs *Pro. parascolyti*. The choice of these combinations
264 was driven by the availability of predators in the successive sampling
265 campaigns. For each predator pair, one individual of each of the two
266 species (test) or a single individual (control) were introduced per well.
267 Note that since each of the two predators confronted in the test wells is
268 also a prey, two controls (one for each taxon) are associated with each
269 test. Combinations one to five were tested 39, 24, 24, 22 and 24 times
270 respectively.

271 2.4.3 Complementary tests

272 We performed a few complementary tests with the same protocol as prey-
273 choice tests (2.4.1) to document trophic relationships between tested
274 arthropods excluding PRM. Five predatory taxa and microbivore mites
275 were subjected to predation tests according to different combinations
276 described in Table 2. (Modalities 32 to 37).-

277 2.5 Data analysis

278 A predation test replicate was discarded from analyses if any of
279 predator(s) or prey(s) had escaped from the experimental arena, or if the
280 predator was dead at the moment of rating. In the case of predator-to-
281 predator interaction tests, the replicate was discarded when the two
282 predators were dead at the time of rating. In addition, a test
283 modality was considered invalid in a series where natural mortality of
284 prey(s) (or predators in the case of predator-to-predator interactions), i. e.
285 in controls, exceeded 15% or differed significantly between the two prey
286 species (or the two predators in predator-to-predator interactions; we used
287 the Chi-squared test to check for independence of natural mortality rates
288 between the two prey species).

289 To represent the potential trophic relationships between tested arthropod
290 taxa, we considered the frequency of predation per putative predator on
291 each prey species from all tests. The predation rate for each predator-prey
292 pair in each test series was estimated by correcting prey mortality with
293 natural mortality determined in the corresponding control (on the same
294 series) using the Abbott formula⁵⁵. The predation rate on each prey
295 species and for each predator was calculated as the average corrected
296 prey mortality over all test series. Predation rates on PRM were calculated
297 by considering all PRM stages and physiological statuses tested
298 indiscriminately.

299 To assess preferences of predators between prey species, Chi-squared
300 tests were applied to test for dependence between prey mortality and

301 prey species in the presence of each predator. In prey-choice tests, to
302 consider the three possible configurations (both prey dead, one prey dead,
303 no prey dead), 2 x 2 contingency tables were constructed as follows: prey
304 A dead or live x prey B dead or live. In tests of predator-to-predator
305 interactions, only tests where one and only one predator had died were
306 included in the analysis and 2 x 2 contingency tables were constructed as
307 follows: predator A or B x live or dead. All chi-squared tests were
308 conducted within the R environment,⁵⁶ *P* values were calculated by Monte
309 Carlo simulation with 2000 replicates

310 2.6 Ethical requirements

311 All the experiments involving hens were conducted in compliance with
312 regulations on animal experimentation (reference number of the Ethics
313 committee: 036; project number: APAFIS#2339-2015101122029640 v4).

314 **3 RESULTS**

315 By bringing together the results of all type of predation tests, we provide
316 an insight into the potential trophic interactions among selected
317 henhouse-dwelling arthropods, showing that PRM could potentially be part
318 of this partial food web. (Fig. 1).

319 3.1 Predation on PRM

320 In our experiments, ten indigenous arthropod taxa fed on PRM, with
321 predation rates (Abbott-corrected prey mortality percent) ranging from
322 100 to 4%: *M. penicilliger*, *Lam. nodosus*, *Cheyletus* spp., *M.*
323 *muscaedomesticae*, *Lyc. campestris*, linyphiid spider, *Par. fimetorum*, *A.*
324 *casalis*, *U. fimicola*, and *Dendrolaelaps* spp. (in order of decreasing

325 predation rates, Fig. 1). The last two did so only occasionally (8 and 4%
326 predation rates, respectively). In the presence of Uropodina spp. or of *Pro.*
327 *parascolyti*, PRM mortality did not exceed natural mortality in the
328 corresponding predator-free controls.

329 3.2 Preference of putative predators for PRM or astigmatic mites

330 Of the seven arthropods tested as predators, four fed significantly more on
331 PRM than on astigmatic mites in our conditions (*Cheyletus* spp.: $\chi^2 = 27$, P
332 $= 4.9 \times 10^{-4}$; *A. casalis*: $\chi^2 = 13$, $P = 9.9 \times 10^{-4}$; *M. muscaedomesticae*: $\chi^2 =$
333 21 , $P = 4.9 \times 10^{-4}$; *U. fimicola*: $\chi^2 = 8.5$, $P = 7.9 \times 10^{-3}$; Fig. 2). Neither
334 *Cheyletus* spp. nor *U. fimicola* fed on astigmatic mites in the presence of
335 PRM juveniles.

336 3.3 Effect of stage and physiological status of PRM preys on predation 337 preference

338 *Cheyletus* spp. and *A. casalis* fed significantly more on juveniles than on
339 adult females (*Cheyletus* spp.: $\chi^2 = 42$, $P = 4.9 \times 10^{-4}$; *A. casalis*: $\chi^2 = 12$, P
340 $= 4.9 \times 10^{-4}$; Fig. 3). Predation by *M. muscaedomesticae* and the linyphiid
341 spider did not differ significantly between the two stages.

342 The bug *Lyc. campestris* fed significantly more on freshly fed PRM
343 juveniles than on unfed ones ($\chi^2 = 8$, $P = 8.9 \times 10^{-3}$, Fig. 4A). *Cheyletus*
344 spp. fed significantly more on unfed adult PRM females than on freshly fed
345 ones ($\chi^2 = 17$, $P = 9.9 \times 10^{-4}$; Fig. 4B).

346 3.4 Predator-to-predator interactions

347 Predation occurred within all pairs of predators tested in our conditions
348 (Fig. 5). Predation was significantly asymmetric between the pairs *M.*

349 *penicilliger*-*A. casalis* ($\chi^2 = 48, P = 4.9 \times 10^{-4}$), and *Lam. nodosus*-*A. casalis*
350 ($\chi^2 = 13.1, P = 9.9 \times 10^{-4}$). *A. casalis* did not kill any of the two other
351 predators. It was more balanced and insignificant in the pair *A. casalis*-
352 *Cheyletus* spp., but mortality was twice as high in *Cheyletus* spp. as in *A.*
353 *casalis*. Predation interactions in the other pairs appear to be accidental.

354 **4 DISCUSSION**

355 *4.1 Potential food web involving PRM*

356 Although the predation interactions we observed occurred in the absence
357 of any physical barrier between predator and prey, our results suggest
358 that PRM in barn layer farms could be embedded in a food web containing
359 at least ten arthropod taxa able to feed on PRM. Eight of these taxa are
360 recorded to feed on PRM for the first time here: *Lyc. campestris*, *Lam.*
361 *nodosus*, a linyphiid spider, *M. penicilliger*, *M. muscaedomesticae*, *Par.*
362 *fimetorum*, *U. fimicola*, and *Dendrolaelaps* spp. The last two did so only
363 occasionally. We also confirmed predation on PRM by natural populations
364 of *Cheyletus* spp. and *A. casalis* which are actually commercially available
365 for release in layer buildings as biocontrol agent of PRM,²⁰ although in our
366 experimental design predation by *A. casalis* can be considered moderate
367 (19% predation rate).

368 *4.2 Predators' preference for different forms of PRM*

369 Among the four tested arthropod taxa that showed substantial predation
370 on PRM (predation rate > 10%), the largest-sized taxa (*M.*
371 *muscaedomesticae* and the linyphiid spider) did not feed differentially on
372 juveniles and adult PRM, whereas the smallest-sized (*Cheyletus* spp. and

373 *A. casalis*) preferred juveniles, consistent with previous findings that larger
374 predators use a wider range of prey sizes.^{57,58} Interestingly, PRM
375 consistently form multi-layered clusters with juveniles remaining in the
376 center and adult females staying at the top.⁴² This arrangement was
377 considered a protective behavior to preserve juveniles from predators.
378 Furthermore, predators with different prey-stage preferences do not affect
379 the population dynamics of prey and predator in the same manner.⁵⁹
380 Mathematical modelling of prey-predator population dynamics suggested
381 that only predators with no prey-stage preference allow Lotka-Volterra
382 periodic prey-predator oscillations to occur and be maintained.⁵⁹ Predators
383 that prefer juvenile stages induce a rapid increase in the prey-predator
384 oscillations' amplitude, which ultimately results in the extinction of both
385 predator and prey.⁵⁹ Selective predation focused on young preys is thus
386 more likely to lead to extinction than non-selective predation.^{59,60-}

387 The predatory bug *Lyc. campestris* was the only tested taxon that fed
388 more on freshly fed juveniles than on unfed ones. This is perhaps because
389 of the slower movement owing to blood ingestion, as preference for slow
390 moving preys over faster ones was reported in other predatory bugs.⁴¹ An
391 alternative explanation (though not exclusive) is that *Lyc. campestris*
392 could be prone to feed indirectly on vertebrate blood, as does an African
393 jumping spider.⁴⁵ The preference of *Cheyletus* spp. for unfed females over
394 freshly fed ones may be explained by the size and/or the motility of prey
395 instead of deleterious effects of the blood meal as these predators did not
396 show any preference for unfed/fed juveniles. In fact, individuals of
397 predator taxa for which no preference for unfed/fed PRM (juveniles or

398 adults) was detected frequently consumed both preys (fed and unfed
399 PRM), showing no aversion to taking a potentially deleterious meal of
400 vertebrate fresh blood. However, in these taxa, we may have missed
401 preferences between unfed and fed PRM by hungry predators that may
402 have recurrently chosen a particular status in the first act of predation.

403 4.3 Implications of interactions other than predator-PRM

404 The most abundant poultry mite taxon that can constitute an alternative
405 prey to PRM predators is Astigmata. A significant preference for PRM over
406 astigmatic mites was observed in *A. casalis*, *Cheyletus* spp., *Lam. nodosus*,
407 and *M. muscaedomesticae*. The former two are known to feed and
408 successfully develop on several species of astigmatic mites.^{38,39,61-63}
409 *Cheyletus* spp. is a sit-and-wait predator ("ambush" foraging mode) and it
410 rarely actively stalks its prey.⁶⁴ As astigmatic mites are very slowly
411 moving,³⁸ these mites are less likely to encounter the cheyletid predator
412 than the fast moving unfed PRM individual in the experimental arenas.
413 This could partially explain the complete absence of predation on
414 astigmatic mites by this predator in our experiments. As our results show
415 that intraguild predation is possible between several of the PRM predators,
416 the natural regulation of PRM populations might be affected by the
417 predator diversity in farms. Geden *et al.*²¹ reported the negative impact of
418 intraguild predation between two naturally-occurring predatory mites,
419 *Parasitus* sp. and *M. muscaedomesticae*, on the control of the house fly.

420 5 CONCLUSION AND PERSPECTIVES

421 Prior to the present study, information about native predators of PRM that

422 have been recorded from poultry farms to date was limited to three
423 species *A. casalis*, *C. eruditus* and *C. malaccensis*.^{13,14,19} Our study
424 revealed that six additional taxa native to poultry farms are substantial
425 predators of PRM, all with predation rates on PRM higher than that of *A.*
426 *casalis*. Among these, two (*Par. fimetorum* and *M. penicilliger*) are only
427 found occasionally in poultry farms, and thus, do not seem to establish
428 sustainably in this environment. The other four (the bug *Lyc. campestris*,
429 the pseudoscorpionid *Lam. nodosus*, the mite *M. muscaedomesticae*, and
430 the linyphiid spider) might be worth considering as additional candidates
431 for augmentative biological control. They could also provide an unknown
432 regulating ecosystem service that could be worth promoting via
433 conservation biological control practices. Intricate interactions of varying
434 degrees between arthropods in poultry ecosystems likely make actual
435 food-webs different from the present reconstruction, as inferred from
436 barrier-free tests. Ecosystem services provided by pest enemies are
437 strongly dependent on spatial heterogeneity and layout coupled with the
438 enemies' dispersal capabilities.^{65,66} Special attention should be paid to
439 spatial mapping of prey-predator meeting points in henhouses and
440 identification of their determining factors to anticipate impediments to
441 biological control owing to limited penetration by predatory mites into
442 pest-infested areas.⁶⁷ Further exploration of the potential of assemblages
443 of native predators in controlling PRM through semi-field or field
444 experiments would be most useful for future biocontrol applications in
445 poultry houses.

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449 the pseudoscorpions. In addition, we thank Tristan Gambin, Jordan Dijoux,
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669 **8 TABLES**

670 **8.1 Table1**

Table 1. List of arthropods species/morphospecies collected from poultry farms and used in predation tests.				
Order	Suborder	Family	Species	Guild
Mesostigmata	Gamasina	Dermanyssidae	<i>Dermanyssus gallinae</i>	hematophagous
	Gamasina	Laelapidae	<i>Androlaelaps casalis</i>	predator
	Gamasina	Digamasellidae	<i>Dendrolaelaps presepum</i> (dominant species), <i>Dendrolaelaps</i> spp. and unidentified Digamasellidae	predator
	Gamasina	Melicharidae	<i>Proctolaelaps parascolyti</i>	fungivorous/omnivorous
	Gamasina	Parasitidae	<i>Parasitus fimetorum</i>	predator
	Gamasina	Macrochelidae	<i>Macrocheles muscaedomesticae</i>	predator
	Gamasina	Macrochelidae	<i>M. penicilliger</i>	predator
	Uropodina	Urodinychidae	<i>Uroobovella fimicola</i>	predator and detritivorous
	Uropodina	other families	Uropodina spp.	predator and detritivorous
	Trombidiformes	Eleutherengonides	Cheyletidae	<i>Cheyletus</i> spp.
Sarcoptiformes	Astigmata	various families	-	microbivore and detritivorous
Pseudoscorpionida	Locheirata	Chernetidae	<i>Lamprochernes nodosus</i>	predator
Aranea	Araneomorpha	Linyphiidae	Linyphiidae sp.	predator
Hemiptera	Heteroptera	Anthocoridae	<i>Lyctocoris campestris</i>	predator

671 **8.2** Table 2:

672

Table 2. Modalities of predation tests performed between putative predators and preys. Each line corresponds to a predator taxon and each column to a prey combinations it was confronted with. M1-M37: Modality ID, n= number of test replicates for each modality; (n) represent only the number of retained replicates of validated test in all test series. (A replicate= one predator individual with two prey individuals into one well of a microplate), N1: protonymph of PRM, AF: Adult female of PRM.

Predator speceis/ morphospecies	Prey combination (one individual of each type)					
	Prey-choice tests				Complementary tests	
	Unfed N1 & Astigmat a	Unfed N1 & unfed AF	Unfed N1 & fed N1	Unfed AF & fed AF	Unfed PRM & other prey	One or two prey species other than PRM
<i>A. casalis</i>	M1 (n=37)	M8 (n= 76)	M15 (n=42)	M22 (n=27)	M28: unfed N1 & <i>Dendrolaelaps</i> spp. (n= 24) M29: unfed AF & <i>Uropodina</i> spp. (n= 29)	M32: Uropodina spp (15)† M33: Astigmatic mites (23)† M34: <i>Dendrolaelaps</i> spp & Astigmatic mites (37)
<i>Dendrolaelaps</i> spp.	M2 (n=43)	-	M16 (n=21)	-	-	
<i>Pro. parascolyti</i>	M3 (n=22)	M9 (n=29)	-	-	-	
<i>P. fimetorum</i>	-	-	M17 (n=23)	-	-	M35: Astigmatic mites (15)†
<i>M. muscaedomestica</i> e	M4 (n=35)	M10 (n=28)	M18 (n=22)	M23 (N=46)	M30: unfed N1 & <i>Dendrolaelaps</i> spp. (n= 15)	M36: <i>Dendrolaelaps</i> spp & Astigmatic mites (15)
<i>M. penicilliger</i>	-	-	-	M24 (N=23)	-	
<i>U. fimicola</i>	M5 (n=75)	M11 (n=31)	-	-	M31: unfed N1 & <i>Dendrolaelaps</i> spp. (n= 22)	
Uropodina spp.	-	M12 (n=15)	-	-	-	
<i>Cheyletus</i> spp.	M6 (n=37)	M13 (n=67)	M19 (n=56)	M25 (N=56)	-	

	M7		M20	M26		M37: Astigmatic mites (22)†
<i>Lam. nodosus</i>	(n=15)	-	(n=23)	(N=44)	-	
		M14				
Linyphiidae sp.	-	(n=41)	-	-	-	
			M21	M27		
<i>L. campestris</i>	-	-	(n=15)	(N=30)	-	

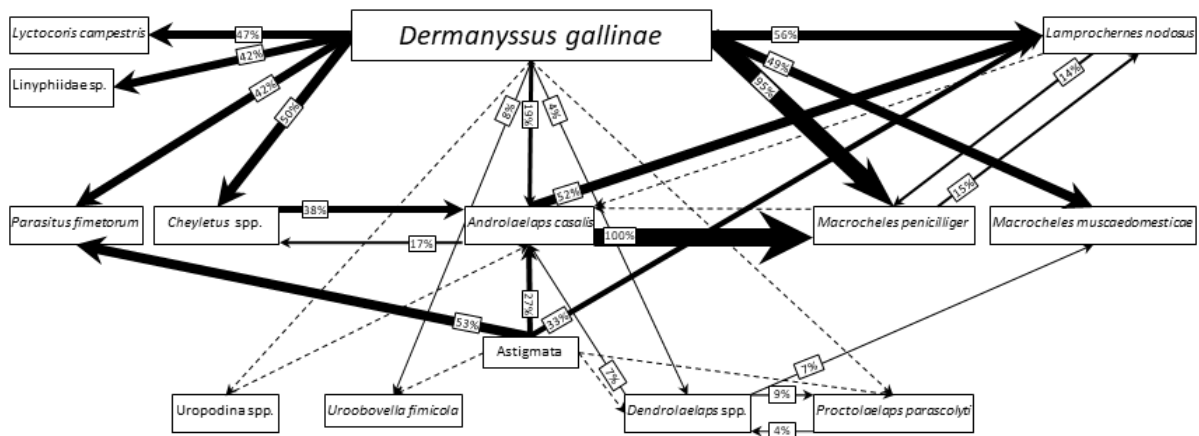
(†): two individuals of the same prey species were offered.

673

674 **9 FIGURE LEGENDS**

675 **9.1 Figure 1.**

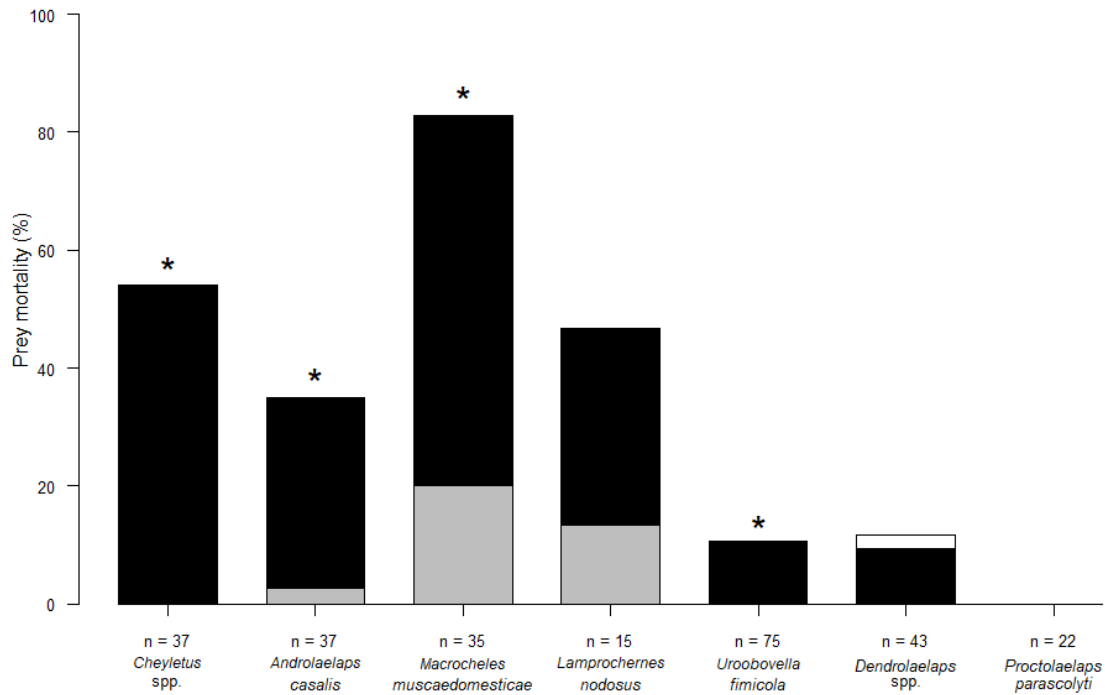
676 Primary reconstruction of potential food-webs between arthropods in layer
 677 farms centered on *D. gallinae* (PRM) as a prey according to our in-vitro
 678 tests. Arrows are orientated from prey to predator. Values at the start of
 679 arrow indicate percentage of predation (with Abbott correction), thickness
 680 of arrows proportional to this percentage, dashed line = absence of
 681 interaction, no line = untested interaction.



683 **9.2 Figure 2.**

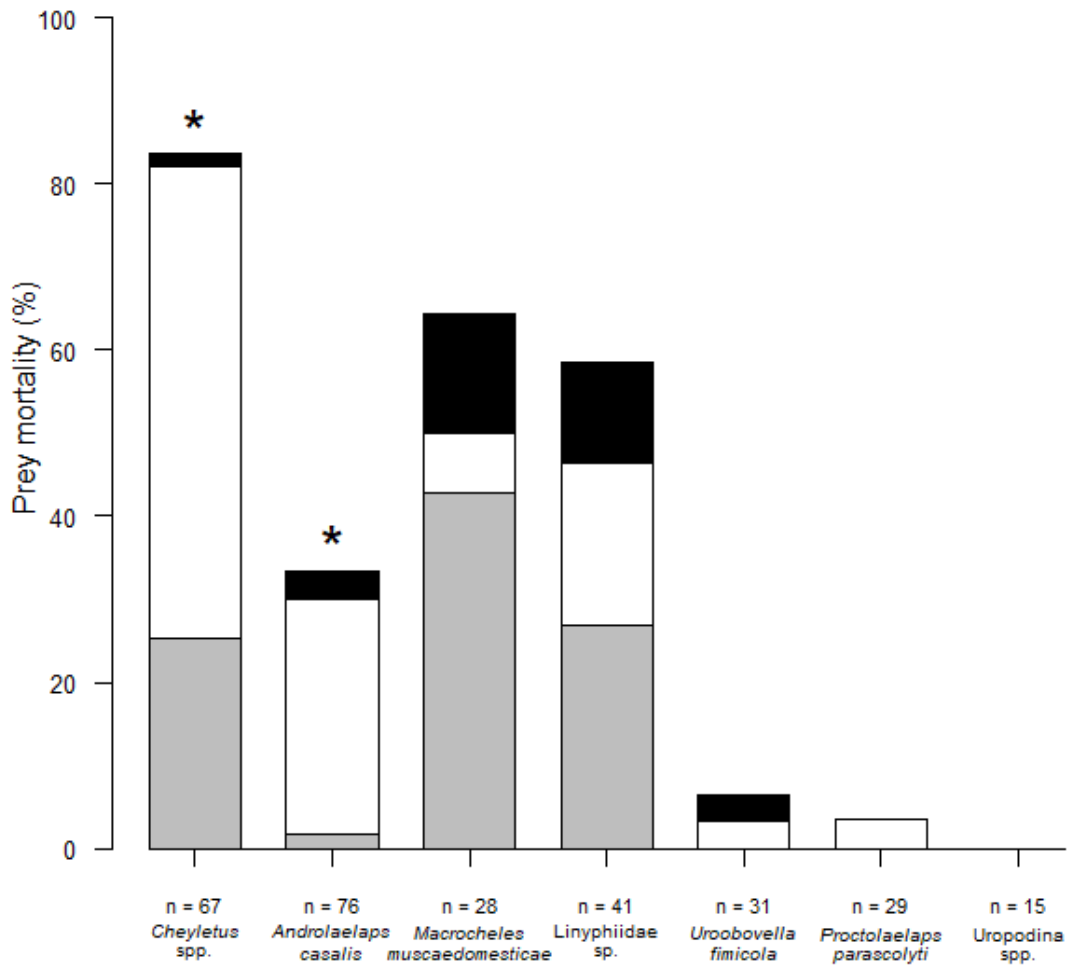
684 Mortality (%) in *D. gallinae* and astigmatic mites in the presence of single
 685 predatory individuals. n = number of tested replicates. Black: mortality of
 686 *D. gallinae*, white: mortality of astigmatic mite, grey: mortality of both
 687 preys. Bars are labeled with * when mortality rates differ significantly
 688 between preys within the corresponding modality. Significant difference
 689 means predator preference for the prey with the highest mortality rate

690 (black + grey for *D. gallinae*, white + grey for astigmatic mite). ($P < 0.05$,
 691 Chi-squared tests).



693 **9.3** Figure 3.

694 Mortality (%) of *D. gallinae* females and juveniles in the presence of single
 695 predatory individuals over a 24-h contact period. n = number of tested
 696 predators. Black: mortality of unfed females, white: mortality of unfed
 697 juveniles, grey: mortality of both preys. Bars are labeled with * when
 698 mortality rates differ significantly between preys within the corresponding
 699 modality. Significant difference means predator preference for the prey
 700 with the highest mortality rate (black + grey for females, white + grey for
 701 juveniles). ($P < 0.05$, Chi-squared tests).



703 **9.4** Figure 4.

704 Mortality (%) in *D. gallinae* with two physiological statuses. A: unfed and

705 freshly fed juveniles; B: unfed and freshly fed females. 24-h contact

706 period. n = number of tested predators. Black: predation on freshly fed

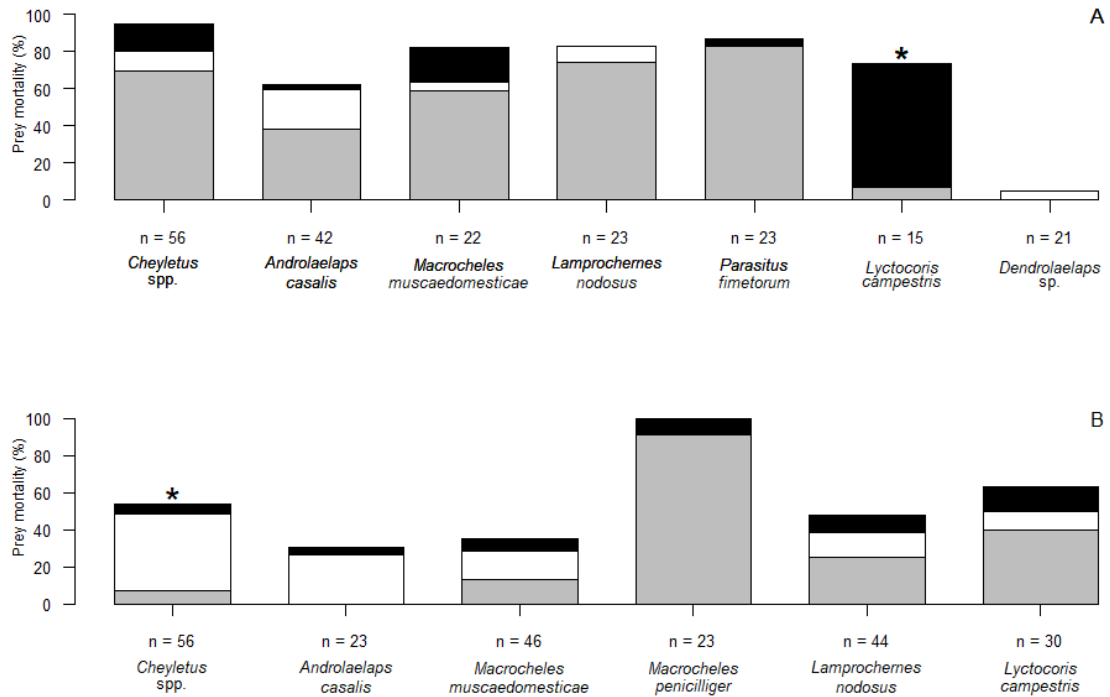
707 prey, white: predation on unfed prey, grey: predation on both preys. Bars

708 are labeled with * when mortality rates differ significantly between preys

709 within the corresponding modality. Significant difference means predator

710 preference for the prey with the highest mortality rate (black + grey for

706 freshly fed preys, white + grey for unfed preys). ($P < 0.05$, Chi-squared
 707 tests).



709 9.5 Figure 5.

710 Proportion of killed individuals in different combination of native
 711 henhouse-dwelling arthropod predators. No extraguild prey was offered,
 712 No: number of test replicates for each combination. (Chi-squared tests).

