Developmental niche construction in necrophagous larval societies: feeding facilitation can offset the costs of low ambient temperature

Running title: Niche construction in blow fly larvae

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Abstract

1. This study explored the trade-offs between thermal regulation and aggregation, two key factors impacting blow fly (Diptera: Calliphoridae) larvae development.

2. Recent works have demonstrated that necrophagous maggots engage in developmental niche construction, which provides adaptive benefits. First, each species has a preferential temperature, at which larvae grow fast and efficiently. Second, larvae are attracted by each other and aggregate in large maggot-masses. These groups modify the local environment and facilitate the exodigestion process (niche construction by perturbation). However, aggregation and relocation towards thermal preferendum are not always compatible under field conditions, forcing larvae to make choices.

3. To test the developmental consequences of such trade-offs, 40 or 80 *Lucilia sericata* larvae were placed on a thermal gradient (from 22°C to 48°C) with or without a captive aggregate of 40 larvae located at 22°C, and their development speed, size and survival were measured.

4. A previous study showed that in such situation, the free larvae alone relocated at 33°C, while in the presence of captive larvae they gathered with the captive group at 22°C. In the present developmental study, we observed that such 22°C aggregated larvae actually grew as fast as if they were at 33°C.

5. This result shows that niche construction, here resulting from larval gregarism and feeding facilitation, can compensate for the physiological costs of low ambient temperature. This finding confirms that aggregation of necrophagous Diptera larvae is an efficient adaptation to the carrion environmental constraints, and highlights the adaptive value of developmental niche construction.

Key words: larval societies, aggregation, thermal regulation, maggots, blow fly, forensic entomology

Introduction

Niche construction describes the process by which organisms, through their metabolism, activities and behavior, shape their own ecological niche (Odling-Smee *et al.*, 2013a). More specifically, developmental niche construction refers to the modifications of environmental conditions which affects the subsequent development of the organisms (Odling-Smee *et al.*, 2013b; Schwab *et al.*, 2017). Two main mechanisms can be used to reduce the selection pressures encountered by individuals: relocation and perturbation (Odling-Smee *et al.*, 2013a). Niche construction by relocation occurs when organisms move through space in search of alternative habitats. Conversely, niche construction by perturbation is closely associated with ecosystem engineering: living organisms actively shape one or more factors in their direct environment (Jones *et al.*, 1997). The altered condition may be abiotic (e.g., temperature), biotic (e.g., microbiota), or represent a feature created directly by the constructing organism (e.g., a nest). Aggregation usually sits in-between these two niche construction strategies: group formation most often involves both relocation (to join or follow a group) and perturbation of the local environment by the group (Costa *et al.*, 2006). For instance, social caterpillars, cockroaches as well as woodlice can actively create groups (relocation; Jeanson *et al.*, 2005; Devigne *et al.*, 2011; Liang *et al.*, 2019) that modify the selection pressures faced by the group

64 members (perturbation), e.g. by reducing water and/or heat loss (Klok & Chown,
65 1999; Yoder & Grojean, 1999; Broly *et al.*, 2014) .

66 Developmental niche construction is found in several holometabolous insects. Some
67 species modify the ontogenetic environment of larvae through nest building (e.g.
68 eusocial insects) or parental care (e.g. burying and dung beetles) (Duarte *et al.*,
69 2018; Schwab *et al.*, 2017). But many insect larvae build themselves their own
70 developmental niche, and aggregation can help in this task (Costa *et al.*, 2006). A
71 well-known example is tent-building caterpillars, who collectively build nests that
72 protect them against predators, rainfall and cold weather (Ruf & Fiedler, 2016). This
73 is also the case of necrophagous blow fly larvae (Diptera: Calliphoridae), which
74 develop on vertebrate carcasses.

75 Blow flies lay eggs in abundance (*circa* 200 per female) on carcasses and, once
76 emerged, larvae (i.e. maggots) quickly start to feed on fluids and decaying flesh.
77 They are however restricted to the limited carcass they have been laid on, and often
78 face rapid depletion of this resource (Benbow *et al.*, 2015). Carcasses also undergo
79 rapid biochemical and physical changes that lead to hostile biochemical conditions
80 (Junkins *et al.*, 2019). Further, the high value of carcasses generates both
81 exploitative competition among diverse insects and scavengers, and interference
82 competition by microbes and necrophagous insects (Janzen, 1977; Burkepile *et al.*,
83 2006; Benbow *et al.* 2015). Along with predation and parasitism pressures, rapid
84 consumption and the gradual decrease in food quality make carcasses a harsh and
85 ephemeral resource. Most necrophagous larvae are therefore specialized, have a
86 short development time and are gregarious (Norris, 1965). In this context,
87 developmental niche construction can explain how these organisms create and

maintain favorable micro-environmental conditions promoting their fast and efficient development.

While feeding on carcasses, larvae form large aggregations called maggot masses. These larval societies can gather thousands of larvae representing multiple species, suggesting immediate benefits overcoming competition costs (Rivers *et al.*, 2011; Komo *et al.*, 2019, 2020; Fouche *et al.*, 2021; Hans & Vanlaerhoven, 2021). The larvae actually engage in physical modification of the food substrate through at least three distinct mechanisms: (1) release of metabolic heat (known as the "larval mass effect"), (2) secretion of digestive enzymes (i.e. exodigestion), and (3) secretion of antibiotic compounds (Rivers *et al.*, 2011; Charabidze *et al.*, 2021). First, larvae experiencing high temperatures grow faster than those facing colder environments (Grassberger & Reiter, 2001; Roe & Higley, 2015; Wang *et al.*, 2020). However, while large larval aggregates can generate their own heat, significant local temperature increase is only observed when larvae are present in very large numbers and at high density (Charabidze *et al.*, 2011). Furthermore, laboratory studies have since demonstrated that larval aggregation results in several other benefits than the sole local temperature increase (Johnson & Wallman, 2014; Scanvion *et al.*, 2018; Komo *et al.*, 2019). Second, as larvae are unable to ingest solid particles, they secrete proteolytic enzymes, lipases and amylases to liquefy their food before ingestion (Hobson, 1932, Sandeman *et al.*, 1990). Third, blow fly larvae release maternally inherited symbiotic microbiota into the feeding area, in combination with a variety of antimicrobial peptides and mechanical fragmentation (Thompson *et al.*, 2013; Poppel *et al.*, 2015; Tomberlin *et al.*, 2017; Maleki-Ravasan *et al.*, 2020). With these three processes, they establish a controlled environment that benefits their development (Green *et al.*, 2002; Rivers *et al.,* 2011; Junkins *et al.*, 2019). Maggots-masses thus

construct a developmental niche by perturbation: they deeply modify their immediate microenvironment which enhances resource exploitation. This process is amplified by number, a phenomenon known as Allee effect (Courchamp *et al.*, 2008), and results in life history changes, especially faster development compared to feeding by scattered larvae (Scanvion *et al.*, 2018). Furthermore, the presence of another species in the group can bring additional benefits through the mutualization of species-specific digestive enzymes or antimicrobial defenses (Komo *et al.*, 2019; Fouche *et al.*, 2021).

Blow fly larvae also build a developmental niche by relocation. This is due to their intense gregarious behavior: they tend to group with other individuals, whether conspecific or heterospecific (Boulay *et al.*, 2013; Fouche *et al.*, 2018). They also move when food is lacking or the local temperature changes, looking for a most favorable environment for their development (Podhorna *et al.*, 2017; Aubernon *et al.*, 2019). These two relocation strategies (attraction to congeners and thermal optimization) can sometimes force larvae to make choices, as recently evidenced in *Lucilia sericata* (Diptera: Calliphoridae) (Richards, 2007; Aubernon *et al.*, 2019). Aubernon *et al.* (2019) analyzed the behavior of *L. sericata* larvae facing constrained choices between thermal optimization and congeners: they observed a clear aggregation of larvae in the colder area containing congeners, at the expense of thermal optimization (Figure 1). The authors consequently questioned whether this choice was the most favorable for larval development, i.e. if larval aggregation strategy maximized their fitness. In such a case, the niche construction by perturbation resulting from aggregating should provide equal or greater benefits than those obtained by fewer larvae feeding at their thermal preferendum. This hypothesis was investigated here by comparing larval development between these two

138 situations: aggregation and thermal optimisation. For this purpose, the same setup
139 used by Aubernon *et al.* (2016) was used and the survival, development time until
140 pupariation and the size of puparia (i.e. fitness proxies) were analyzed.

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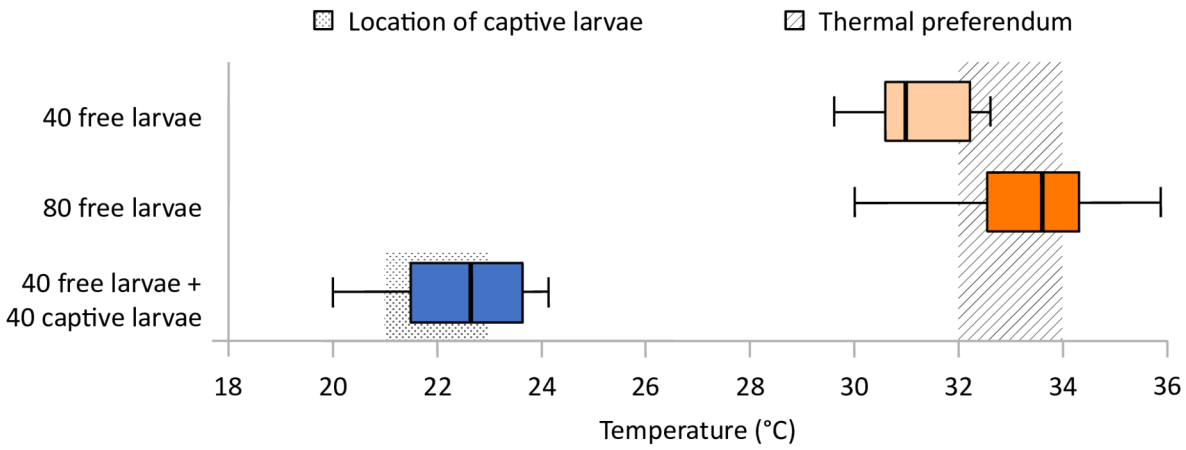

142 **Figure 1.** Mean selected temperatures (°C) by groups of free *L. sericata* larvae on a thermal gradient
143 according to Aubernon *et al.* (2016, 2019). While free larvae prefered high temperature, the presence
144 of congeners located in a colder area changed their thermal behavior. Light orange: 40 free larvae;
145 dark orange: 80 free larvae; blue: 40 free larvae with 40 captive *L. sericata* larvae confined in a bag
146 located at 22°C (dotted square). The striped square indicates the thermal preferendum of *L. sericata*
147 larvae according to Aubernon *et al.* (2016), i.e. 33.3 ± 1.5°C. The boxplots represent, in order, the
148 lowest value, the first quartile, the median, the third quartile and the highest value. Experiments with
149 40 free larvae alone, 80 free larvae alone and 40 free larvae with 40 captive larvae were replicated 6,
150 15 and 14 times, respectively (Aubernon *et al.*, 2016, 2019).

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Material and Methods

Biological material

Lucilia sericata (Meigen) is one of the most common blowfly species breeding on carcasses. These flies have a worldwide distribution and their development has been extensively studied, especially in the context of forensic entomology (Grassberger & Reiter, 2001; Wang *et al.*, 2020). Adult *L. sericata* were purchased at a commercial supplier in France (Verminiere de l'Ouest, La Lande, 35460 Tremblay, France) and kept in 50 × 50 × 50 cm tulle cages at 25 ± 2°C with both natural lightning (large window) and artificial neon light from 8h to 18h30. Caster sugar and water were provided *ad libitum*. The colony was established since 6 months when experiments started (6 to 10 generations), and was supplied with new individuals every three months. Egg-laying was triggered by placing 20 ± 1 g of mixed beef liver inside the cage during 1h. The eggs and young larvae were bred at 25 ± 1°C in the dark (ST4, POL-EKO Aparatura®, Poland) on 20 ± 1 g of mixed beef liver until the beginning of the experiments.

Developmental experiments

Experiments were performed during 18 months, from September 2017 to January 2019. The chronological order of the conditions tested was randomized within this period. Developmental analyses were performed using a Thermograde, a setup creating a controlled thermal gradient inside a steel bar (80 cm in length) containing a 2 cm layer of mixed beef liver (see Aubernon *et al.*, 2016 for detailed information on this setup). For each replication, forty 22h old second instar *L. sericata* larva were deposited homogeneously within the Thermograde and the setup was closed with an

opaque plastic cap. Thirty-six hours after deposit, all larvae of a same replication were removed and placed into a same plastic box (108 x 83 x 64 mm, containing 100 ± 5 g of liver) at 25 ± 1°C (ST4, POL-EKO Aparatura®, Poland). This feeding box was placed inside a larger one (143 × 105 × 59 mm) containing a 1 cm layer of dry sand. All boxes were kept in the dark until the end of pupariation. Wandering larvae (i.e. larvae located in the sand outside the feeding box) were then counted every 8h (06:30 am., 02:30 pm and 10:30 pm), removed and placed in separate plastic boxes until pupariation (one box was used for each counting time; 143 × 105 × 59 mm, 2 cm of sand, 25 ± 1°C). The survival until the post-feeding stage, the size of puparia (length) and the latency to observe 10%, 50% and 90% of post-feeding larvae were calculated. The following conditions were analyzed.

In a control condition, the Thermograde was uniformly set at 33 °C and 40 larvae were spread inside (this control was replicated four times). The 33°C temperature has been formerly evidenced as the preferential temperature of third instar *L. sericata* larvae*,* i.e. the temperature selected by these larvae when placed on a thermal gradient (Aubernon *et al.*, 2016). Second, 40 or 80 larvae were spread inside the Thermograde set on a linear thermal gradient ranging from 22 ± 0.5°C to 47 ± 0.5°C (representing a linear increase of 1°C every 3 cm). Six replications were performed with 40 larvae and 4 with 80 larvae. Third, 40 captive late second instar or early third instar larvae (46h old at 25°C) were enclosed in a tulle bag (5 x 5 cm) and placed at 22°C to create a captive aggregate (Cičková *et al.*, 2013). Forty "free" larvae were then added in the device (5 replications). The tulle bag alone did not affect the behavior of the free larvae, as previously shown by Aubernon *et al.* (2019).

205 *Data analysis*

206 Developmental parameters (survival, size of puparia and development time) were
207 analyzed by mean comparisons between conditions. The Student's t test was used
208 when normality and homoscedasticity were respected, otherwise the Mann-Whitney's
209 test was used. Comparisons were done between the condition testing 40 free larvae
210 on thermal gradient and (1) control condition with 40 larvae at 33°C, (2) condition
211 with 80 free larvae on thermal gradient, and (3) condition with 40 free larvae on
212 thermal gradient with 40 captive larvae at 22°C. The differences in development time
213 between 33°C and 22°C were also compared with data from previous studies (see
214 Supporting Information). The significance level was set at $\alpha = 0.05$ for all statistical
215 tests, all performed with R software (version 4.0.4).

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217 **Results**

218 The time until 10% of larvae reached the post-feeding stage was not different
219 between 40 larvae at the homogeneous 33°C temperature and 40 larvae on thermal
220 gradient (Table 1). No significant difference was observed when increasing the
221 number of free larvae to 80 nor adding 40 captive larvae (Table 1, Figures 2 and 3).
222 The same results were observed when considering 50% and 90% of post-feeding
223 larvae (Table 1, Figures 2 and 3).

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Table 1. Comparisons of development time of the first 10%, 50% and 90% of post-feeding larvae between groups of 40 free larvae reared on thermal gradient (n = 6) and (1) groups of 40 free larvae reared at 33°C (n = 4), (2) groups of 80 free larvae on thermal gradient (n = 4), and (3) groups of 40 free larvae on thermal gradient with 40 captive larvae at 22°C (n = 5). For each comparison, mean times (± SE) in hours are reported first and followed by the value of the statistical test ("t": Student's t test; "W": Mann-Whitney's test) and the p-value.

Conditions compared	Time (h) before observing 10% of post-feeding larvae			Time (h) before observing 50% of post-feeding larvae			Time (h) before observing 90% of post-feeding larvae		
	mean ± SE	test's value	p-value	mean ± SE	test's value	p-value	mean ± SE	test's value	p-value
40 free larvae	96.7 ± 4.2	W = 18	0.21	104.7 ± 2.7	W = 15	0.56	126.0 ± 16.7	W = 15	0.56
Control (33°C)	96.0 ± 0.0			102.0 ± 2.7			110.0 ± 2.7		
40 free larvae	96.7 ± 4.2	t = 0.09	0.94	104.7 ± 2.7	t = 0.47	0.66	126.0 ± 16.7	W = 16	0.42
80 free larvae	96.0 ± 0.0			102.0 ± 6.0			106.0 ± 6.5		
40 free larvae	96.7 ± 4.2	t = 1.04	0.32	104.7 ± 2.7	t = -0.27	0.80	126.0 ± 16.7	W = 19	0.55
40 free + 40 captive larvae	91.6 ± 3.4			106.0 ± 4.9			109.2 ± 3.6		

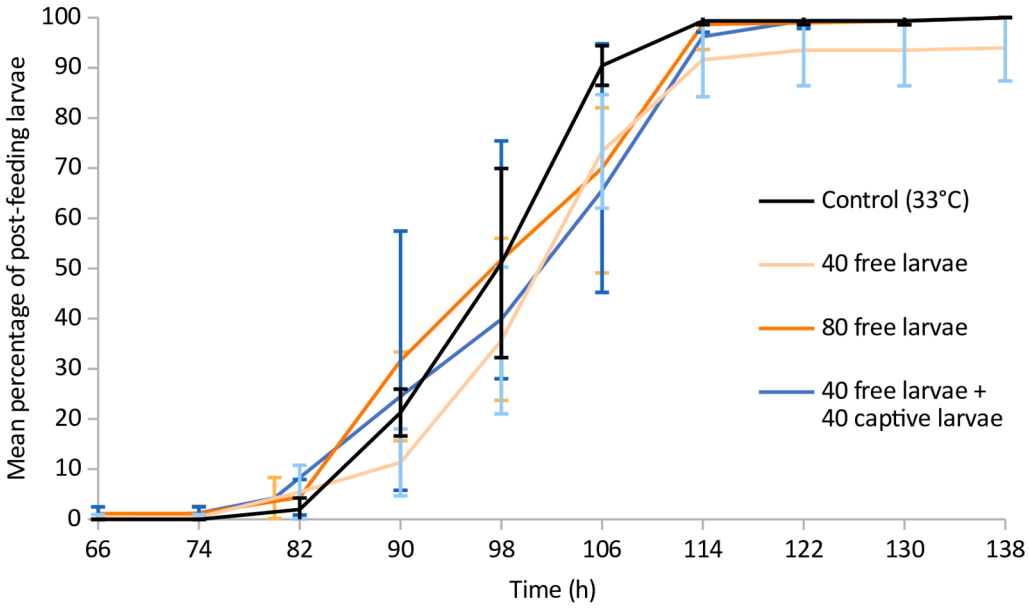


Figure 2. Larval development time until the post-feeding stage. Mean percentage (± SE) of post-feeding larvae as a function of time (h) for groups of 40 larvae reared at 33°C (n = 4; black), 40 free

larvae on thermal gradient (n = 6; light orange), 80 free larvae on thermal gradient (n = 4; dark orange), and 40 free larvae on thermal gradient with 40 captive larvae at 22°C (n = 5; blue).

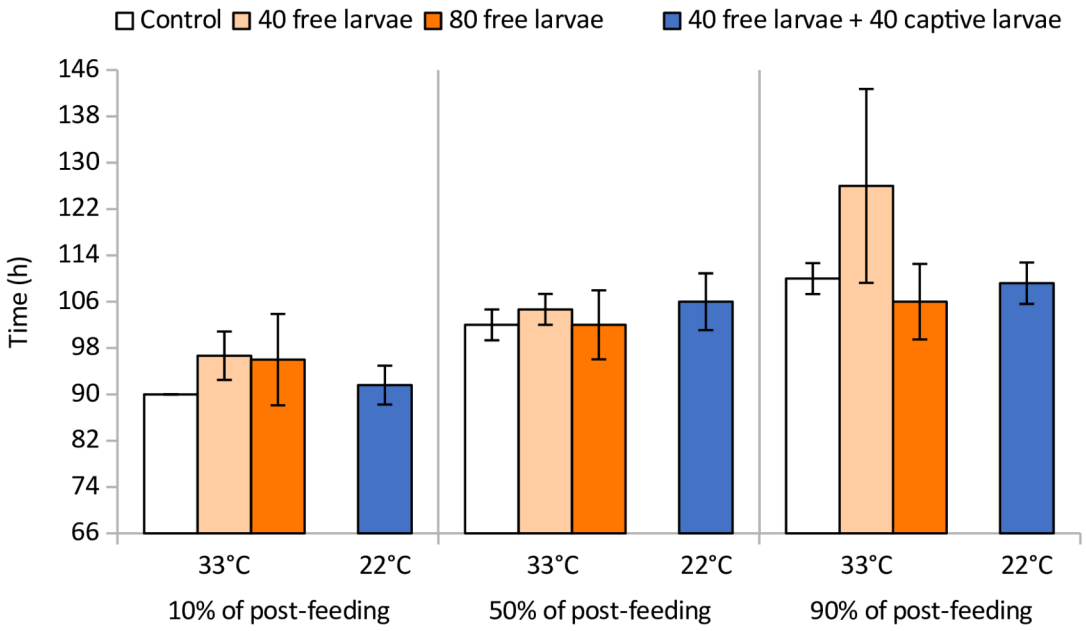


Figure 3. Development time of the first 10%, 50% and 90% of post-feeding larvae. No significant difference was observed when increasing number of free larvae to 80 nor adding 40 captive larvae (Student's t test and Mann-Whitney's test). Mean time (± SE) in hours before 10%, 50% and 90% of larvae were observed in the post-feeding stage is displayed for groups of 40 larvae reared at 33°C (n = 4; white), 40 free larvae on thermal gradient (n = 6; light orange), 80 free larvae on thermal gradient (n = 4; dark orange), and 40 free larvae on thermal gradient including 40 captive larvae at 22°C (n = 5; blue). The 33°C and 22°C temperatures indicate the temperature experienced by larvae.

The puparia length did not differ between the condition with a homogeneous 33°C temperature and the condition with 40 larvae on the thermal gradient (Student's t test, t = -0.11, d.f. = 5.59, *P* = 0.91; Figure 4). No difference was observed when increasing the number of larvae (40 vs 80 free larvae; Student's t test, t = 0.97, d.f. =

5.71, *P* = 0.37; Figure 4). However, puparia were significantly shorter when captive larvae were present (Mann-Whitney's test, W = 22, *P* = 0.038; Figure 4).

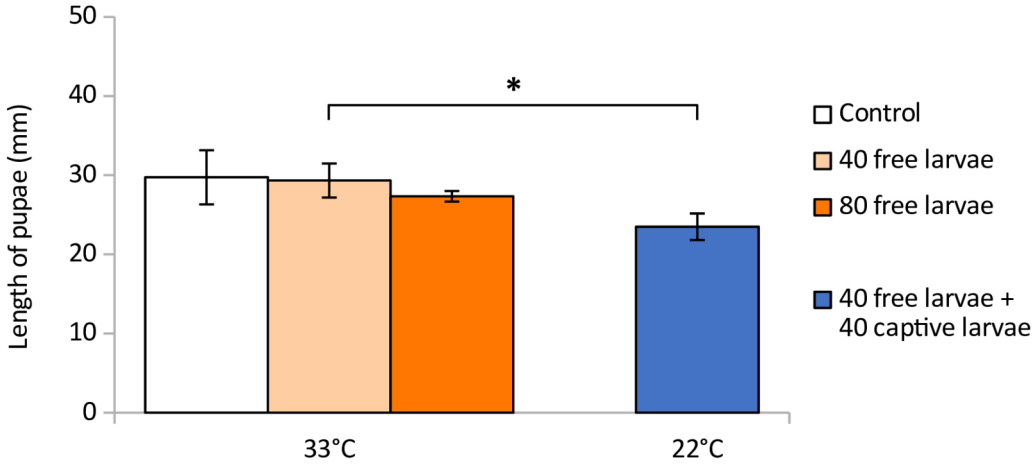
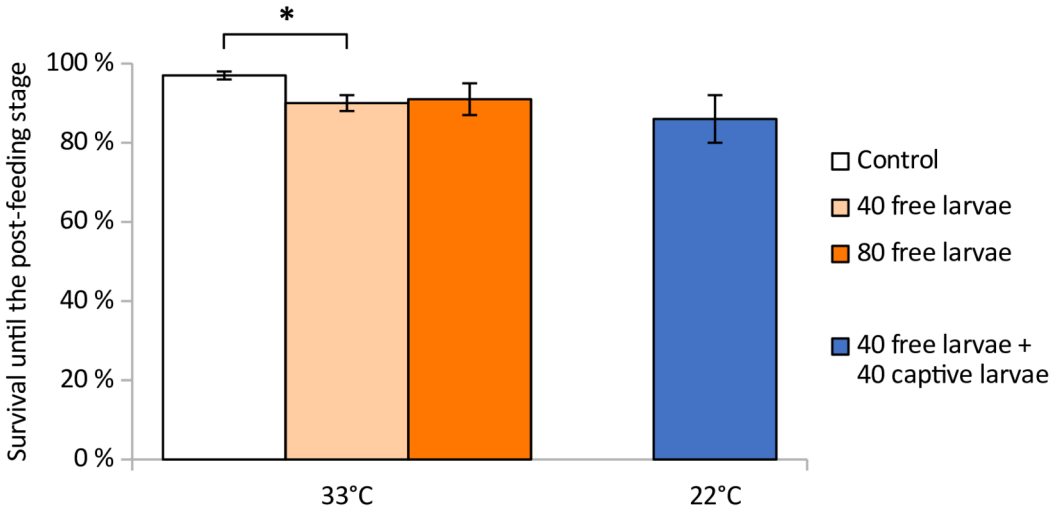


Figure 4. Size reached at pupariation. Puparia were significantly shorter when captive larvae were present (Mann-Whitney's test, W = 22, P = 0.038). Mean length (± SE; mm) of puparia is displayed for groups of 40 larvae at 33°C (n = 4; white), 40 free larvae on thermal gradient (n = 6; light orange), 80 free larvae on thermal gradient (n = 4; dark orange), and 40 free larvae on thermal gradient with 40 captive larvae at 22°C (n = 5; blue). The 33°C and 22°C temperatures indicate the temperature at the location of the larvae. The asterisk highlights a significant decrease in length (Mann-Whitney's test; * *P* < 0.05).

The survival rate until the post-feeding stage was significantly lower for the 40 larvae on the thermal gradient than the 40 larvae at 33°C (Student's t test, t = -2.99, d.f. = 7.95, *P* = 0.017; Figure 5). But survival did not differ neither when increasing larval density (40 vs 80 free larvae; Student's t test, t = -0.02, d.f. = 4.63, *P* = 0.98), nor when adding 40 captive larvae at 22°C (Mann-Whitney's test, W = 17.5, *P* = 0.71; Figure 5).



269 **Figure 5.** Survival rate until the post-feeding stage. Mean survival (± SE) is displayed in percentage
270 for groups of 40 larvae at 33°C (n = 4; white), 40 free larvae on thermal gradient (n = 6; light orange),
271 80 free larvae on thermal gradient (n = 4; dark orange), and 40 free larvae on thermal gradient with 40
272 captive larvae at 22°C (n = 5; blue). The 33°C and 22°C temperatures indicate the temperature
273 experienced by larvae. The asterisk highlights a significant decrease in survival on thermal gradient
274 compared to the 33°C constant temperature (Student's t test; * $P < 0.05$).

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276

277 ## Discussion

278 By focusing on the benefits of the microenvironment modification induced by larval
279 aggregation, this study aimed to determine to what extent developmental niche
280 construction is a key strategy in the adaptation of necrophagous larvae to the carrion
281 environment. For this purpose, we considered the preference of larvae for
282 aggregating at low temperatures over moving at hotter spots (Aubernon *et al.*, 2019).
283 We analyzed if this choice to renounce thermal optimum to aggregate at a lower
284 temperature produced developmental benefits and thus may have an adaptive value.

285 Our results showed both a benefit (fast development) and a cost (reduced size) of
286 this choice.

287 The development of blow fly larvae depends on several biotic and abiotic factors
288 (Erzinçlioglu, 1996). Environmental factors, such as temperature and photoperiod
289 can play important roles in insect development. While temperature is clearly the key
290 determinant of development rate, laboratory experiments have also highlighted that
291 development time also changes according to light-dark cycle (Nabity *et al.*, 2007;
292 Mello *et al.*, 2012; Fisher *et al.*, 2015). In the present study, larvae were kept in the
293 dark during all their development to prevent any light influence and focus on the
294 effect of temperature and larval populations. Furthermore, the present work only
295 focused on the survival, size and development time of larvae (i.e. the fitness
296 consequences of behavioral choices). While detailed behavioral observations were
297 published in former studies by Aubernon *et al.* (2016, 2019), it was not possible here
298 to determine the exact location of numerous larvae at different times without
299 changing ambient conditions, disrupting aggregates and *in fine* affecting larval
300 development. However, we visually observed the same trends as Aubernon *et al.*
301 (2016, 2019): when captive larvae were absent, the free larvae were found
302 aggregated at their preferential temperature. When captive larvae were added, the
303 free larvae were observed closely aggregated with their captive congeners in the
304 colder area of the setup (Figure 1).

305 On a medium range of value, there is a linear correlation between the local
306 temperature perceived by larvae and their development rate: the more heat larvae
307 are exposed to, the faster they grow (Grassberger & Reiter, 2001; Roe & Higley,
308 2015; Wang *et al.*, 2020). Larval metabolism indeed accelerates with temperature,

309 increasing food intake, digestion, and other growth-related physiological processes.
310 In this context, several studies have evidenced the strong thermal regulation
311 behavior of maggots (Richards *et al.*, 2009; Slone & Gruner, 2007; Johnson *et al.*,
312 2014; Podhorna *et al.*, 2017; Heaton *et al.*, 2018; Aubernon *et al.*, 2019). Placed on a
313 thermal gradient, *L. sericata* larvae were formerly observed to move to 33°C area, a
314 temperature thus described as their thermal preferendum (Aubernon *et al.*, 2016).
315 This 33°C preferendum was supposed to result from a trade-off between a fast and
316 an efficient development, finally maximizing the fitness of larvae (Grassberger &
317 Reiter, 2001; Aubernon *et al.*, 2016).

318 In the present study, we first compared the development of larvae bred on a thermal
319 gradient or in the same setup but under a 33°C homogeneous temperature. We
320 observed no difference in development speed and puparia length between the 33°C
321 control and the larvae placed on the thermal gradient. This control experiment
322 demonstrates that 33°C is not only the temperature selected by larvae but the
323 temperature at which they actually developed. Only a slight decrease in survival (of
324 7%) was observed in the thermal gradient compared to homogeneous temperature,
325 which may be a side effect of the higher temperatures present in this condition.
326 Indeed, larvae were randomly spread at the beginning of the experiments, with some
327 individuals experiencing for a short time the hottest setup temperature (up to 47°C).

328 Secondly, we used the same thermal gradient setup but added a captive aggregate
329 consisting of 40 larvae captive at 22°C. Under such circumstances, free larvae were
330 formerly observed to join that captive aggregate and stay at 22°C instead of
331 gathering at 33°C (Aubernon *et al.*, 2019). This choice demonstrates that the
332 gregarious behavior of larvae can be stronger than thermal regulation behaviors. It is
333 also an indication that gregarious behavior may entail benefits superior or at least

334 equal to thermal optimization (Rivers *et al.*, 2011; Johnson & Wallman, 2014).
335 Compliant with this last hypothesis, we observed no difference in development
336 duration nor survival rate between the larvae reared at 33°C and those that
337 developed at 22°C with a captive aggregate of 40 congeners. In other words, larvae
338 facing a choice between aggregation with congeners and thermal optimization
339 aggregated with congeners at 22°C but developed as fast as if they were at 33°C.
340 This result demonstrates a beneficial effect of larval aggregation: if the presence of
341 captive larvae was neutral, the development of the free larvae should have been up
342 to 25h longer (see Supporting Information). Interestingly, when the number of free
343 larvae was doubled, the 80 free larvae aggregated at 33°C (Aubernon *et al.*, 2019)
344 (Figure 1), but did not develop faster than the 40 free larvae alone (also aggregated
345 at 33°C) nor the 40 free larvae aggregated at 22°C with 40 captive larvae. This
346 suggests that (1) maximal larval development speed was already reached with 40
347 larvae at 33°C, with no Allee effect with 80 larvae, and (2) that the Allee effect due to
348 the presence of 40 captive larvae was sufficient to reach this maximum speed at
349 22°C.

350 Consistent with the protective role of niche construction described in other harsh
351 environments (Mesterton-Gibbons & Dugatkin, 1992; Cornwallis *et al.*, 2017;
352 Trappes, 2021), our results confirm the existence of an Allee effect in *L. sericata*
353 larvae resulting from a developmental niche construction by perturbation. The
354 presence of a greater number of conspecifics and the local modification they induced
355 benefited all larvae by cancelling the low development rate usually associated with
356 low local temperature (Davies & Ratcliffe, 1994; Grassberger & Reiter, 2001). These
357 developmental benefits were likely reached through collective exodigestion
358 processes and the control of microbial populations (Barnes *et al.*, 2010; Benbow *et*

359 *al.*, 2015; Scanvion *et al.*, 2018; Komo *et al.*, 2019). However, we observed that
360 larvae that aggregated at 22°C also resulted in slightly smaller puparia compared to
361 the 33°C control (20% decrease in length). That could be explained by a decrease in
362 the efficiency of digestive and/or antibacterial enzymes at low temperature, only
363 partially counterbalanced by the easier feeding due to higher number of congeners
364 (exodigestion). Trade-offs between development speed and size or weight have
365 already been observed in blow fly species, especially when changing larval density
366 (e.g., Goodbrod & Goff, 1990; Ireland & Turner, 2006; Rivers *et al.*, 2010; Komo *et*
367 *al.*, 2019, 2021). The reduction in size may lead to reduced fecundity in adulthood
368 (Vogt *et al.*, 1985; Honek, 1993), and consequently reduce the fitness of these
369 individuals. Finally, smaller puparia may also result in a higher pre-adult mortality, a
370 fitness trait that was not considered in this study. But compared to the benefits of a
371 faster development, noticeably the reduced risk of predation, parasitism and food
372 depletion that are especially intense in the harsh carrion environment (for instance,
373 pre-adult mortality in *L. sericata* can reach 97% per generation; Wall *et al.*, 2001;
374 Benbow *et al.*, 2015), it is likely that the costs of the small size reduction we observed
375 have a low impact on the overall fitness. Further, these costs could actually be
376 compensated in the field. Indeed, if larvae eventually choose to gather on colder
377 areas of a carcass, their collective attraction toward warm spots should most of the
378 time allow the group as a whole to leave cold areas for hotter ones (Boulay *et al.*,
379 2016; Aubernon *et al.*, 2019; Fouche *et al.*, 2021). To further analyze the final output
380 of trade-offs between development speed and size on lifetime fitness, future studies
381 may focus on comparing the reproductive success of larvae developing at different
382 speed, on cadavers where predation or parasitism pressures vary in intensity.
383 Implications to forensic entomology, especially in estimating the development

duration (i.e. the age) of larvae sampled within a maggot-mass, should also be considered.

From a more general perspective, our results highlight the interest of studying the trade-offs between different behavioral strategies to more accurately assess their respective benefits. Our study focused on only one species, but recent experiments involving mixed-species groups showed that such trade-offs can be strongly modified depending on which species composes the group and their relative abundance (Aubernon & Charabidze, unpublished data). Developmental niche construction is common in larvae, and could be a key to the ecological success of several species (Laland & Sterelny, 2006). This strategy is noticeably found in many species living decomposing matter, including dung beetles (Schwab *et al.*, 2017) and burying beetles (Duarte *et al.*, 2018; Gruszka & Matuszewski, 2021). Studying the social part of developmental niche construction behavior in larvae growing on such ecosystems with rich but ephemeral resources would allow a better understanding of the conditions that favor it (Charabidze *et al.*, 2021).

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Author contributions

CA and DC designed the project. CA collected the data. CA, QF and DC analyzed the data. QF and DC wrote the manuscript.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Figure S1. Difference in larval development time from 33°C.

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