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

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

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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 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.

KEYWORDS
aggregation, blow fly, forensic entomology, larval societies, maggots, thermal regulation

INTRODUCTION

Niche construction describes the process by which organisms, through their metabolism, activities and behaviour, shape their own ecological niche (Odling-Smee, Laland, & Feldman, 2013a). More specifically, developmental niche construction refers to the modifications of environmental conditions, which affect the subsequent development of the organisms (Odling-Smee, Erwin, et al., 2013b; Schwab et al., 2017). Two main mechanisms can be used to reduce the selection pressures encountered by individuals: relocation and perturbation. 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 members (perturbation), for example, by reducing water and/or heat loss (Broly et al., 2014; Klok & Chown, 1999; Yoder & Grojean, 1997).

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

Blow flies lay eggs in abundance (circa 200 per female) on carcasses and, once emerged, larvae (i.e., maggots) quickly start to feed on fluids and decaying flesh. They are however restricted to the limited carcass they have been laid on and often face rapid depletion of this resource (Benbow et al., 2015). Carcasses also undergo rapid biochemical and physical changes that lead to hostile biochemical conditions (Junkins et al., 2019). Further, the high value of carcasses generates both exploitative competition among diverse insects and scavengers, and interference competition by microbes and necrophagous insects (Benbow et al., 2015; Burkepile et al., 2006; Janzen, 1977). Along with predation and parasitism pressures, rapid consumption and the gradual decrease in food quality make carcasses a harsh and ephemeral resource. Most necrophagous larvae are therefore specialised, have a short development time and are gregarious (Norris, 1965). In this context, developmental niche construction can explain how these organisms create and maintain favourable 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 (Fouche et al., 2021; Hans & Vanlaerhoven, 2021; Komo et al., 2019, 2020; Rivers et al., 2011). 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 (Charabidze et al., 2021; Rivers et al., 2011). 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; Komo et al., 2019; Scanvion et al., 2018). 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 (Maleki-Ravasan et al., 2020; Pöppel et al., 2015; Thompson et al., 2013; Tomberlin et al., 2017). With these three processes, they establish a controlled environment that benefits their development (Green et al., 2002; Junkins et al., 2019; Rivers et al., 2011). Maggot 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 with 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 defences (Fouche et al., 2021; Komo et al., 2019).

Blow fly larvae also build a developmental niche by relocation. This is due to their intense gregarious behaviour: 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 favourable environment for their development (Aubernon et al., 2019; Podhorna et al., 2017). 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) (Aubernon et al., 2019; Richards, 2007). Aubernon et al. (2019) analysed the behaviour 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 favourable for larval development, that is, if larval aggregation strategy maximised 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 situations: aggregation and thermal optimisation. For this purpose, the same set-up used by Aubernon et al. (2016) was used and the survival, development time until pupariation and the size of puparia (i.e., fitness proxies) were analysed.

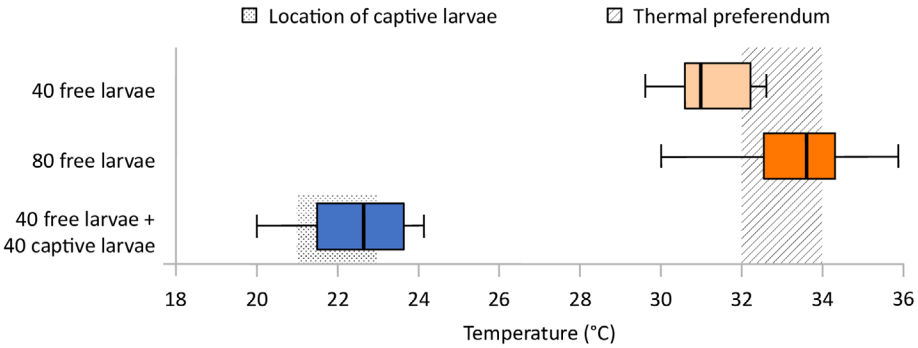

FIGURE 1 Mean selected temperatures (°C) by groups of free *Lucilia sericata* larvae on a thermal gradient according to Aubernon et al. (2016, 2019). While free larvae preferred high temperature, the presence of congeners located in a colder area changed their thermal behaviour. Light orange: 40 free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

MATERIAL AND METHODS

Biological material

L. 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, 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 8 to 18:30 (six and a half pm). Caster sugar and water were provided *ad libitum*. The colony was established in 6 months when experiments started (6–10 generations) and was supplied with new individuals every 3 months. Egg-laying was triggered by placing 20 ± 1 g of mixed beef liver inside the cage for 1 h. The eggs and young larvae were bred at 25 ± 1°C in the dark (ST4, POL-EKO Aparatura®, Wodzisław Śląski, Poland) on 20 ± 1 g of mixed beef liver until the beginning of the experiments.

Developmental experiments

Experiments were performed for 18 months, from September 2017 to January 2019. The chronological order of the conditions tested was randomised within this period. Developmental analyses were performed using a Thermograde, a set-up 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 set-up). For each replication, 40 22-h-old second instar *L. sericata* larva were deposited homogeneously within the Thermograde and the set-up was closed with an opaque plastic cap. Thirty-six hours after deposit, all larvae of a same replication were removed and placed into the same plastic box (108 × 83 × 64 mm, containing 100 ± 5 g of liver) at 25 ± 1°C (ST4, POL-EKO Aparatura®). 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 8 h (6:30 AM, 2:30 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 analysed.

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, that is, 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 four with 80 larvae. Third, 40 captive late second instar or early third instar larvae (46 h old at 25°C) were enclosed in a tulle bag (5 × 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 (five replications). The tulle bag alone did not affect the behaviour of the free larvae, as previously shown by Aubernon et al. (2019).

Data analysis

Developmental parameters (survival, size of puparia and development time) were analysed by mean comparisons between

conditions. The Student's t test was used when normality and homoscedasticity were respected, otherwise the Mann–Whitney's U-test was used. Comparisons were done between the condition testing 40 free larvae on thermal gradient and (1) control condition with 40 larvae at 33°C, (2) condition with 80 free larvae on thermal gradient, and (3) condition with 40 free larvae on thermal gradient with 40 captive larvae at 22°C. The differences in development time between 33 and 22°C were also compared with data from previous studies (see Supporting Information). The significance level was set at $\alpha = 0.05$ for all statistical tests, all performed with R software (version 4.0.4).

RESULTS

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

The puparia length did not differ between the condition with a homogeneous 33°C temperature and the condition with 40 larvae on the

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 ($n = 5$)

	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		
Conditions compared	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		

Note: 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 U-test) and the p-value.

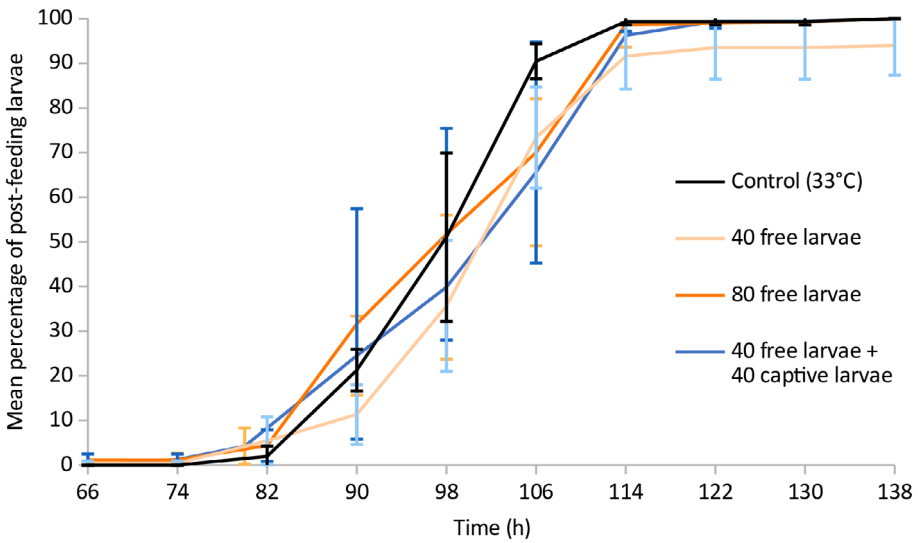

FIGURE 2 Larval development time until the post-feeding stage. Mean percentage (±SE) of post-feeding larvae as a function of time (h) for groups of 40 larvae reared at 33°C ($n = 4$; black), 40 free larvae on thermal gradient ($n = 6$; light orange), 80 free larvae on thermal gradient ($n = 4$; dark orange) and 40 free larvae on thermal gradient with 40 captive larvae at 22°C ($n = 5$; blue)

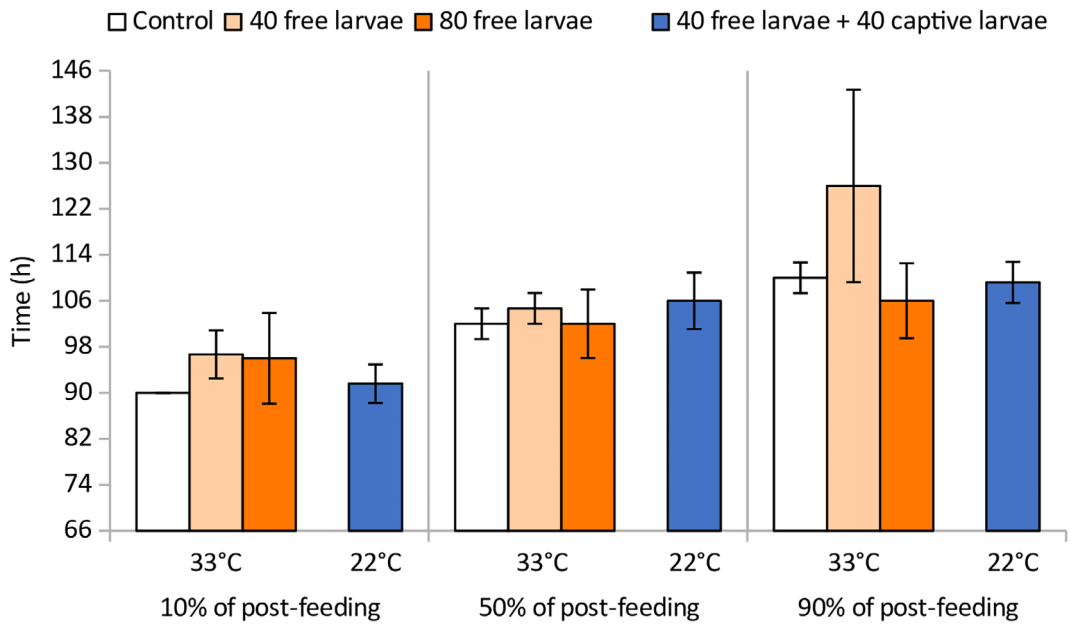

FIGURE 3 Development time of the first 10%, 50% and 90% of post-feeding larvae. No significant difference was observed when increasing the number of free larvae to 80 nor when adding 40 captive larvae (Student's *t* test and Mann–Whitney *U*-test). Mean time (±SE) in hours before 10%, 50% and 90% of 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

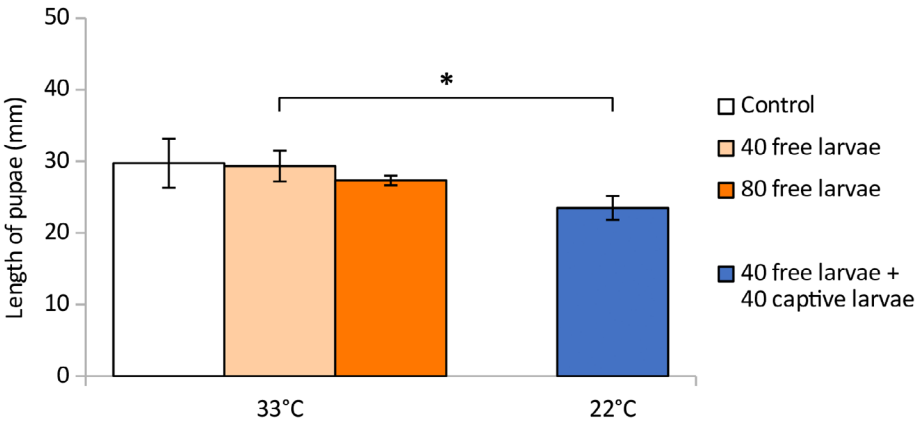

FIGURE 4 Size reached at pupariation. Puparia were significantly shorter when captive larvae were present (Mann–Whitney *U*-test, $W = 22$, $p = 0.038$). Mean length (±SE; mm) of puparia is displayed for groups of 40 larvae at 33°C ($n = 4$; white), 40 free larvae on thermal gradient ($n = 6$; light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

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 *U*-test, $W = 22$, $p = 0.038$; Figure 4).

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. $= 4.63$,

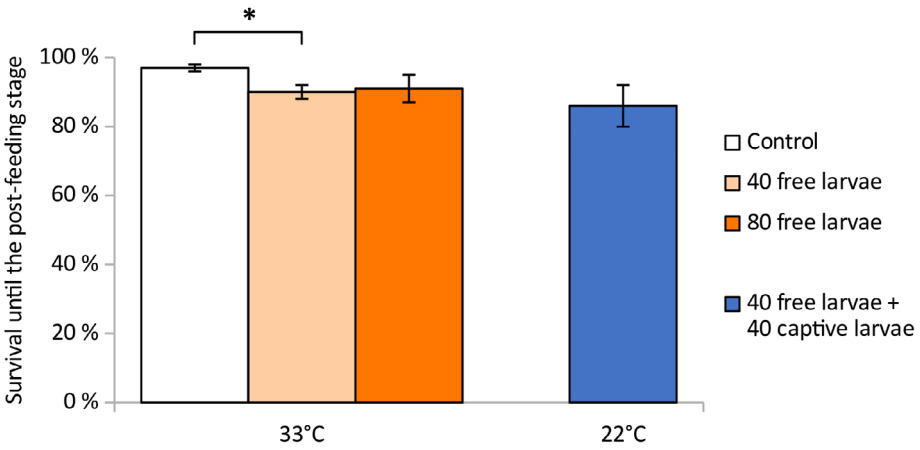

FIGURE 5 Survival rate until the post-feeding stage. Mean survival (±SE) is displayed in percentage for groups of 40 larvae at 33°C ($n = 4$; white), 40 free larvae on thermal gradient ($n = 6$; light orange), 80 free larvae on thermal gradient ($n = 4$; dark orange) and 40 free larvae on thermal gradient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

$p = 0.98$) nor when adding 40 captive larvae at 22°C (Mann–Whitney *U*-test, $W = 17.5$, $p = 0.71$; Figure 5).

DISCUSSION

By focusing on the benefits of the microenvironment modification induced by larval aggregation, this study aimed to determine to what extent developmental niche construction is a key strategy in the adaptation of necrophagous larvae to the carrion environment. For this purpose, we considered the preference of larvae for aggregating at low temperatures over moving at hotter spots (Aubernon et al., 2019). We analysed if this choice to renounce thermal optimum to aggregate at a lower temperature produced developmental benefits and thus may have an adaptive value. Our results showed both a benefit (fast development) and a cost (reduced size) of this choice.

The development of blow fly larvae depends on several biotic and abiotic factors (Erzinçlioglu, 1996). Environmental factors such as temperature and photoperiod can play important roles in insect development. While temperature is clearly the key determinant of development rate, laboratory experiments have also highlighted that development time also changes according to light–dark cycle (Fisher et al., 2015; Mello et al., 2012; Nabity et al., 2007). In the present study, larvae were kept in the dark during all their development to prevent any light influence and focus on the effect of temperature and larval populations. Furthermore, the present work only focused on the survival, size and development time of larvae (i.e., the fitness consequences of behavioural choices). While detailed behavioural observations were published in former studies by Aubernon et al. (2016, 2019), it was not possible here to determine the exact location of numerous larvae at different times without changing ambient conditions, disrupting aggregates and *in fine* affecting larval development. However, we visually observed the same trends as Aubernon et al. (2016, 2019): when captive larvae were absent, the free larvae were found aggregated at 33°C. When captive larvae were added, the free larvae were observed closely aggregated with their captive congeners in the colder area of the set-up (Figure 1).

On a medium range of value, there is a linear correlation between the local temperature perceived by larvae and their development rate: the more heat larvae are exposed to, the faster they grow (Grassberger & Reiter, 2001; Roe & Higley, 2015; Wang et al., 2020). Larval metabolism indeed accelerates with temperature, increasing food intake, digestion and other growth-related physiological processes. In this context, several studies have evidenced the strong thermal regulation behaviour of maggots (Aubernon et al., 2019; Heaton et al., 2018; Johnson et al., 2014; Podhorna et al., 2017; Richards et al., 2009; Slone & Gruner, 2007). Placed on a thermal gradient, *L. sericata* larvae were formerly observed to move to a 33°C area, a temperature thus described as their thermal preferendum (Aubernon et al., 2016). This 33°C preferendum was supposed to result from a trade-off between a fast and efficient development, finally maximising the fitness of larvae (Aubernon et al., 2016; Grassberger & Reiter, 2001).

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

Secondly, we used the same thermal gradient set-up but added a captive aggregate consisting of 40 larvae captive at 22°C. Under such circumstances, free larvae were formerly observed to join that captive aggregate and stay at 22°C instead of gathering at 33°C (Aubernon

et al., 2019). This choice demonstrates that the gregarious behaviour of larvae can be stronger than thermal regulation behaviours. It is also an indication that gregarious behaviour may entail benefits superior or at least equal to thermal optimization (Johnson & Wallman, 2014; Rivers et al., 2011). Compliant with this last hypothesis, we observed no difference in development duration nor survival rate between the larvae reared at 33°C and those that developed at 22°C with a captive aggregate of 40 congeners. In other words, larvae facing a choice between aggregation with congeners and thermal optimization aggregated with congeners at 22°C but developed as fast as if they were at 33°C. This result demonstrates a beneficial effect of larval aggregation: if the presence of captive larvae was neutral, the development of the free larvae should have been up to 25 h longer (see Supporting Information). Interestingly, when the number of free larvae was doubled, the 80 free larvae aggregated at 33°C (Aubernon et al., 2019; Figure 1), but did not develop faster than the 40 free larvae alone (also aggregated at 33°C) nor the 40 free larvae aggregated at 22°C with 40 captive larvae. This suggests that (1) maximal larval development speed was already reached with 40 larvae at 33°C, with no Allee effect with 80 larvae, and (2) the Allee effect due to the presence of 40 captive larvae was sufficient to reach this maximum speed at 22°C.

Consistent with the protective role of niche construction described in other harsh environments (Cornwallis et al., 2017; Mesterton-Gibbons & Dugatkin, 1992; Trappes, 2021), our results confirm the existence of an Allee effect in *L. sericata* larvae resulting from a developmental niche construction by perturbation. The presence of a greater number of conspecifics and the local modification they induced benefited all larvae by cancelling the low development rate usually associated with low local temperature (Davies & Ratcliffe, 1994; Grassberger & Reiter, 2001). These developmental benefits were likely reached through collective exodigestion processes and the control of microbial populations (Barnes et al., 2010; Benbow et al., 2015; Komo et al., 2019; Scanvion et al., 2018). However, we observed that larvae that aggregated at 22°C also resulted in slightly smaller puparia compared with the 33°C control (20% decrease in length), which could be explained by a decrease in the efficiency of digestive and/or antibacterial enzymes at low temperature, only partially counterbalanced by the easier feeding due to higher number of congeners (exodigestion). Trade-offs between development speed and size or weight have already been observed in blow fly species, especially when changing larval density (Goodbrod & Goff, 1990; Ireland & Turner, 2006; Komo et al., 2019, 2021; Rivers et al., 2010). Such a reduction in size may lead to reduced fecundity in adulthood (Honek, 1993; Vogt et al., 1985), and consequently reduce the fitness of these individuals. Smaller puparia may also result in higher pre-adult mortality, a fitness trait that was not considered in this study. But compared with the benefits of a faster development, noticeably the reduced risk of predation, parasitism and food depletion that are especially intense in the harsh carrion environment (pre-adult mortality in *L. sericata* can reach 97% per generation; Wall et al., 2001; Benbow et al., 2015), it is likely that the costs of the small size reduction we observed have a low impact on the overall fitness. Further, these costs could actually be compensated in the field. Indeed, if larvae eventually choose to gather on colder areas of a carcass, their collective attraction towards warm spots should most of the time allow the group as a whole to leave cold areas for hotter ones (Aubernon et al., 2019; Boulay et al., 2016; Fouche et al., 2021). To further analyse the final output of trade-offs between development speed and size on lifetime fitness, future studies may focus on comparing the reproductive success of larvae developing at different speed, on cadavers where predation or parasitism pressures vary in intensity. 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 behavioural 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 behaviour in larvae growing on such ecosystems with rich but ephemeral resources would allow a better understanding of the conditions that favour it (Charabidze et al., 2021).

CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Cindy Aubernon and Damien Charabidze designed the project. Cindy Aubernon collected the data. Cindy Aubernon, Quentin Fouche and Damien Charabidze analysed the data. Quentin Fouche and Damien Charabidze wrote the manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in figshare at http://doi.org/10.6084/m9.figshare.16782862.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

Figure S1. Difference in larval development time from 33°C. The mean difference (±SE) in hours was calculated by subtracting the development time of either (1) 40 free larvae on thermal gradient ($n = 6$; light orange), (2) 80 free larvae on thermal gradient ($n = 4$; dark orange), or (3) 40 free larvae on thermal gradient with 40 captive larvae at 22°C ($n = 5$; blue), from the development time of 40 larvae reared at 33°C ($n = 4$; see Table 1 for the exact values). The development time was measured before 10%, 50% or 90% of larvae were observed in the post-feeding stage. The 33 and 22°C temperatures indicate the temperature experienced by larvae. The grey bar represents the mean development time difference (28 h) between larvae reared at 33 ± 1°C and larvae reared at 22 ± 1°C, calculated with data from three previous studies*. Visually comparing the blue and grey bars shows that multiplying larval density by twice at 22°C induced a shortening of up to 25 h of development time.

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