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SYMPOSIUM

Black Soldier Fly Larvae Rearrange under Compression

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Synopsis Thousands of black soldier larvae hatch simultaneously from eggs laid within rotting vegetation or animal carcasses. Over the next few weeks, they grow while compressed by both their surroundings and each other. When compressed, these larvae rearrange to reduce the forces upon them. How quickly can larvae rearrange, and what final state do they choose? In this experimental study, we use a universal testing machine to conduct creep tests on larvae, squeezing them to set volume fractions and measuring the time course of their reaction force. Live larvae come to equilibrium at a rate 10 times faster than dead larvae, indicating that their small movements can rearrange them faster than just settling. The relaxation of dead larvae is well described by stretched exponentials, which also characterize hierarchical self-avoiding materials such as polymers or balls of crumpled aluminum foil. The equilibrium pressures of live larvae are comparable to those of dead larvae, suggesting that such pressures are dictated by the physics of their bodies rather than their behavior. Live larvae perform fluctuations to actively maintain this equilibrium pressure. This ability to survive large pressures might have applications in the larvae-rearing industry, where both live and dead larvae are packed in containers for shipping.

Introduction

Black soldier fly larvae, *Hermetia illucens*, have several properties that make suitable for understanding how organisms deal with compression. The larvae are 10–20 mm long, large enough to visualize without microscopy but small enough to compress with a typical universal testing machine (UTM). It is inexpensive to obtain thousands of black soldier fly larvae, and they do not bite or transmit diseases to humans. Additionally, understanding the compression of black soldier fly larvae has potential applications to industry. These voracious larvae have promise as a consumer of human food waste and a sustainable protein source for chickens and fish. To make these visions a reality, startup companies worldwide are raising the larvae by the ton. Despite such efforts, little is known about optimal conditions to raise the larvae, such as the size of the container they should be grown in or the depth of larvae in the container. Investigating the behavior of these larvae under compression can yield insights to how tightly they can be packed during shipping in order to reduce shipping costs or increase their safety.

In this study, we consider the larvae as a granular viscoelastic material. They are granular because the interactions between larvae are associated with dissipation of energy through friction. They are viscoelastic because they act like both fluids and solids: if squeezed, they store energy like a spring, or flow to dissipate energy. In general, to determine the extent of the fluid and solid-like behavior of a material, a creep test is performed, in which the material is compressed under constant strain. In response, viscoelastic materials relax, or rearrange to dissipate energy and relieve stress, a phenomenon which is manifested as an exponentially decreasing stress with time (Christensen 1982). For many materials such as jello, the rate of this relaxation is characterized by a single parameter called the relaxation time, τ, where the stress scales as $e^{-\frac{t}{\tau}}$. However, there has been a rising interest in hierarchical materials, such

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as crumpled balls of paper or aluminum that consist of self-avoiding fractal structures due to the many length scales of crinkles (Gottesman et al. 2018). Hierarchical materials are also common in biology (Lakes 1993; Fratzl and Weinkamer 2007; Michel and Yunker 2019). The relaxation of these materials is best described by a stretched exponential in which the exponent is raised to a power so that stress scales as $e^{-(t/\tau)^{\beta}}$ (Sasaki et al. 1993; Phillips 1996; Albuquerque and Gomes 2002). The effect of the exponent is that the function is "stretched" and takes longer to come to a steady-state value than a normal exponential. In this study, we compress black soldier fly larvae to various volume fractions. Then we use a stretched exponential fit for pressure and extract properties such as the rate at which these larvae are able to rearrange and relax the pressure on their bodies.

Materials and methods

Larva care

For experiments compressing individual larvae, larvae were obtained from Grubbly Farms at an average mass of 0.1 g in August 2018. For all other experiments, batches of 10,000 larvae were obtained from EVO Conversion Systems (https://www.evoconsys.com/) at an average mass of 0.07–0.08 g during the period January to March 2019. To delay larvae from pupating, they were not fed between trials.

Compression tests with varying volume fraction

We measured larval activity by compressing aggregations of larvae with a Zwick Roell UTM. Figure 1a and Supplementary Video S1 demonstrate the experiment for the volume fraction $\phi = 0.80$. When the larvae were compressed by the UTM, they changed orientation, as shown by the schematics of their positions before and after compression (Fig. 1b, c). The loading cell is a compression plate with a diameter of $D_{\text{plate}} = 90$ mm and 1 kN maximum force. The container for larvae was composed of a clear acrylic tube with wall thickness 3.1 mm and inner diameter $D_{\text{chamber}} = 95$ mm, which forms a tight enough fit with the compression plate to prevent larvae from escaping. The tube was glued to a 5.2-mm thick acrylic plate.

Experiments were performed with 2000 randomly selected larvae, whose number, N, was estimated by the ratio of total weight (158 g) and mass of a single larva of $m_{\text{L}} = 0.08 \pm 0.02$ g. We estimated the volume of a larva, $V_{\text{L}} = m_{\text{L}}/\rho_{\text{L}}$ as its average mass, $m_{\text{L}} = 0.08$ g, divided by the density of water, $\rho_{\text{L}} = 1$ g/mL. Several days after the tests with live larvae were finished, the larvae were sacrificed in a household freezer for 24 h during which each larva reduced in mass to 0.06 g. Tests were then repeated using 158 g of thawed dead larvae. Since the dead larvae were lighter than live ones, we froze adequate numbers of larvae to offset their reduction in mass.

We report all data in terms of volume fraction ϕ, which is derived from the height H of the larvae measured by the UTM. Consider a cylinder of height H, bottom plate height H_{offset}, and diameter D_{chamber}. The volume fraction of larvae ϕ may be written as the ratio of the total volume of larvae, NV_{L}, to the inner volume of the cylinder $\frac{1}{4}\pi D_{\text{chamber}}^2(H - H_{\text{offset}})$:

$$\phi = \frac{4NV_{\text{L}}}{\pi D_{\text{chamber}}^2 (H - H_{\text{offset}})}. \quad (1)$$

Note that the height of the endcap, $H_{\text{offset}} = 5.2$ mm, was used in order to accurately measure larvae height using the UTM. Larvae in the tube are lightly shaken by hand before the test begins to randomize their arrangement and negate the effects of their own settling.

Once larvae are in the tube under the UTM, we performed creep tests to measure the time course of applied forces. A creep test applies forces to maintain the larvae at set volume fractions ϕ. We tested volume fractions between 0.56 and 0.80 by lowering the plate to heights H between 33 and 45 mm, with 1 mm increments between tests. The lowest volume fraction of 0.56 was set by the larvae's tendency to clump together. Giving them a larger volume than their preferred spacing resulted in incomplete contact between the larvae and the top plate. The test began with the plate being lowered onto the aggregation at 100 mm/min, and an initial force of 0.1 N, until it reached the specified separation between the plate and the floor of the UTM. The plate then stopped and the UTM recorded the force F for 1000 s. Each compression test was also recorded with a Sony Handycam (Model HDR-XR200V).

We calculated the pressure as the force divided by the area of the compression plate $\frac{1}{4}\pi D_{\text{plate}}^2$:

$$P = \frac{4F}{\pi D_{\text{plate}}^2}. \quad (2)$$

As a visualization of larvae settling, 2000 larvae with an average mass of 0.07 g/larva were placed in a 400 mL beaker and are allowed to settle for an hour, as shown in Fig. 1d, e and Supplementary Video S2.

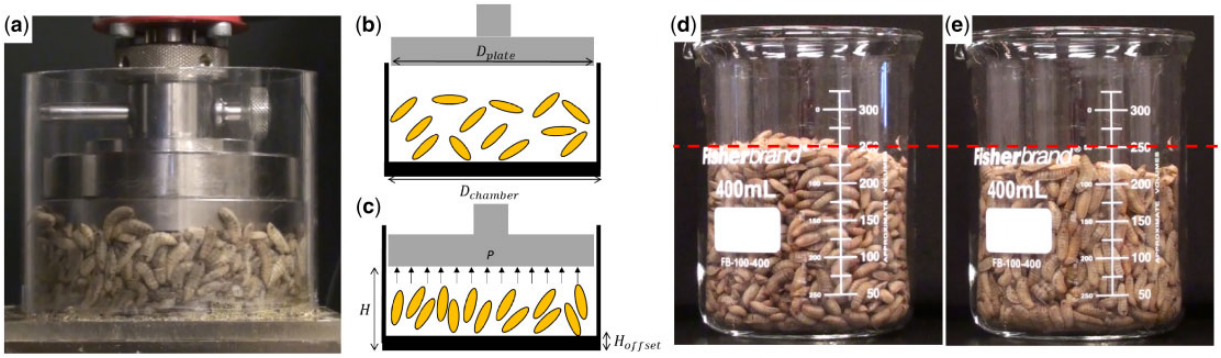

Fig. 1 a) Image of live larvae being compressed to $\phi = 0.80$. **b**) Schematic representation of larvae in the UTM before compression. **c**) When larvae are compressed by the UTM, they rearrange and exert a pressure P on the plate. **d**) 2000 larvae with an average mass of 0.07 g when they are initially placed in 400 mL beaker, at volume fraction $\phi = 0.55$. **e**) After 6 min in the beaker in (d), larvae self-compress to volume fraction $\phi = 0.61$. The dashed line in (d) and (e) across the 250 mL mark shows that larvae settle from 250 mL over time.

Experiments compressing individual larvae

To measure the maximum force that a single larva can tolerate, we compressed five larvae in five individual tests to a force of 40 N at a speed of 5 mm/min with an initial force of 0.2 N so that the top plate can contact the larva.

In experiments with a single larva, the pressure is estimated using the larva's initial top area. The top area is obtained by taking an image of a larva and measuring its area within ImageJ (Schneider et al. 2012). The pressure can then be written $P = \frac{F}{A}$. We take the peak in pressure as the stress at which the larva exploded. Pictures of the larvae from the top and side are taken with an Andonstar Digital Microscope. The strain ϵ for a single larva may be written $\epsilon = \frac{h_0 - h}{h_0}$, where h is the height of the compressed larva as measured by the UTM and h_0 is the initial height of the larva. Since the UTM compresses the larva to get a measurement of its height, we measure the side of the larva in ImageJ to obtain an initial height for these strain calculations.

Results

The jostling of live larvae in a jar causes them to settle, subjecting their bodies to greater compression. Figure 1d shows larvae when they are initially placed in a 400 mL beaker at a volume fraction of $\phi = 0.55$. Figure 1e shows them having settled after 6 min to a volume fraction of $\phi = 0.61$. Supplementary Video S2 shows larvae moving around and rearranging during this process. Their bodies, initially horizontal, align vertically as they crawl downward and become more closely packed. To quantify the response of the larvae to pressure, we conduct creep tests with a UTM. Larvae rearrange and settle in the UTM in a visually similar manner to their settling in the beaker, as shown in Supplementary Video S1 and in the schematics in Fig. 1b, c. Dead larvae also rearrange due to applied pressure but at a slower rate than their live counterparts.

Figure 2a shows the time course of the pressure exerted by dead larvae (dashed lines) and live larvae (solid lines) when compressed to four different volume fractions. There is an initial spike in pressure for both dead and live larvae, and then the pressure settles to an equilibrium over time. Figure 3a, b shows the time course of pressure for dead and live larvae at a volume fraction of 0.80. The dashed lines are a stretched exponential fit.

$$P = (P_0 - P_{SS})e^{-(t/\tau)^{\beta}} + P_{SS}, \tag{3}$$

where the boundary conditions are set by initial pressure P_0, measured from the experiments, and the added term is the steady-state pressure P_{SS}, calculated by the average of the last 100 s of the trial. We construct similar plots for volume fractions $\phi = 0.56$ to $\phi = 0.80$, but not for the lowest volume fraction $\phi = 0.56$ for the live larvae because the larvae are not fully touching the plate and a failed fit occurs due to an inconsistent pressure. The inset in Fig. 3b shows the time course of pressure of live larvae at volume fraction $\phi = 0.57$, in which the pressure initially dips below steady-state. The stretched exponential fits the live larvae poorly for low volume fractions such as the one shown in the inset. Nevertheless, it provides a useful quantitative comparison between relaxation of live and dead larvae. Specifically, we will compare the variables defined in Equation (3), including the initial pressure P_0, the relaxation time τ, and the exponent β found by least square best fit.

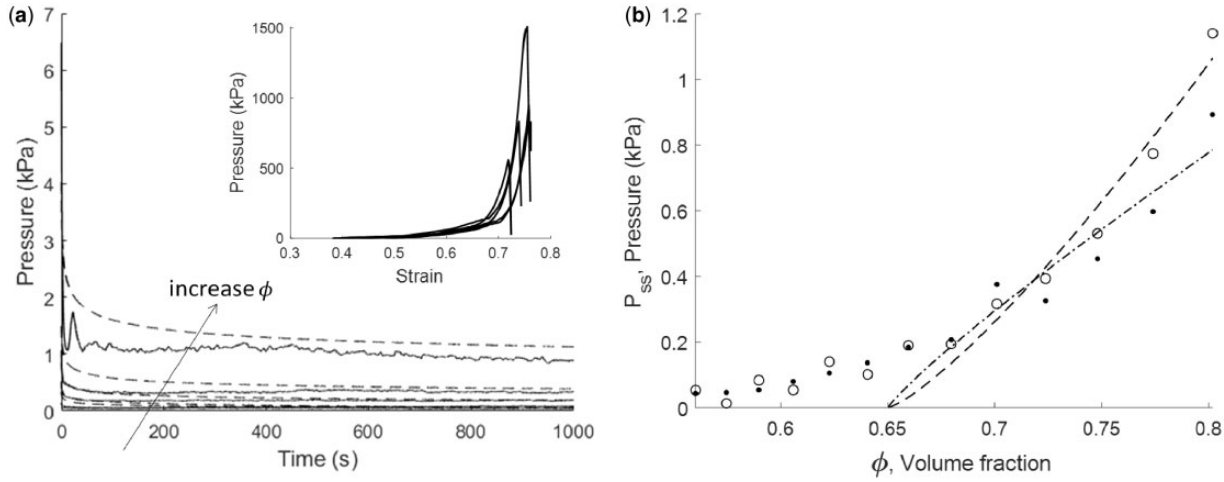

Fig. 2 a) Comparison of time series of pressure of dead larvae (dashed lines) with live larvae (solid lines) at increasing volume fractions. Inset: stress–strain curve of five single larvae individually compressed to 40 N until the larva bursts. **b**) Steady state pressure of dead larvae (circles) and the best fit for $\phi > 0.65$ (dashed line), live larvae (points), and the best fit for $\phi > 0.65$ (dash-dot line).

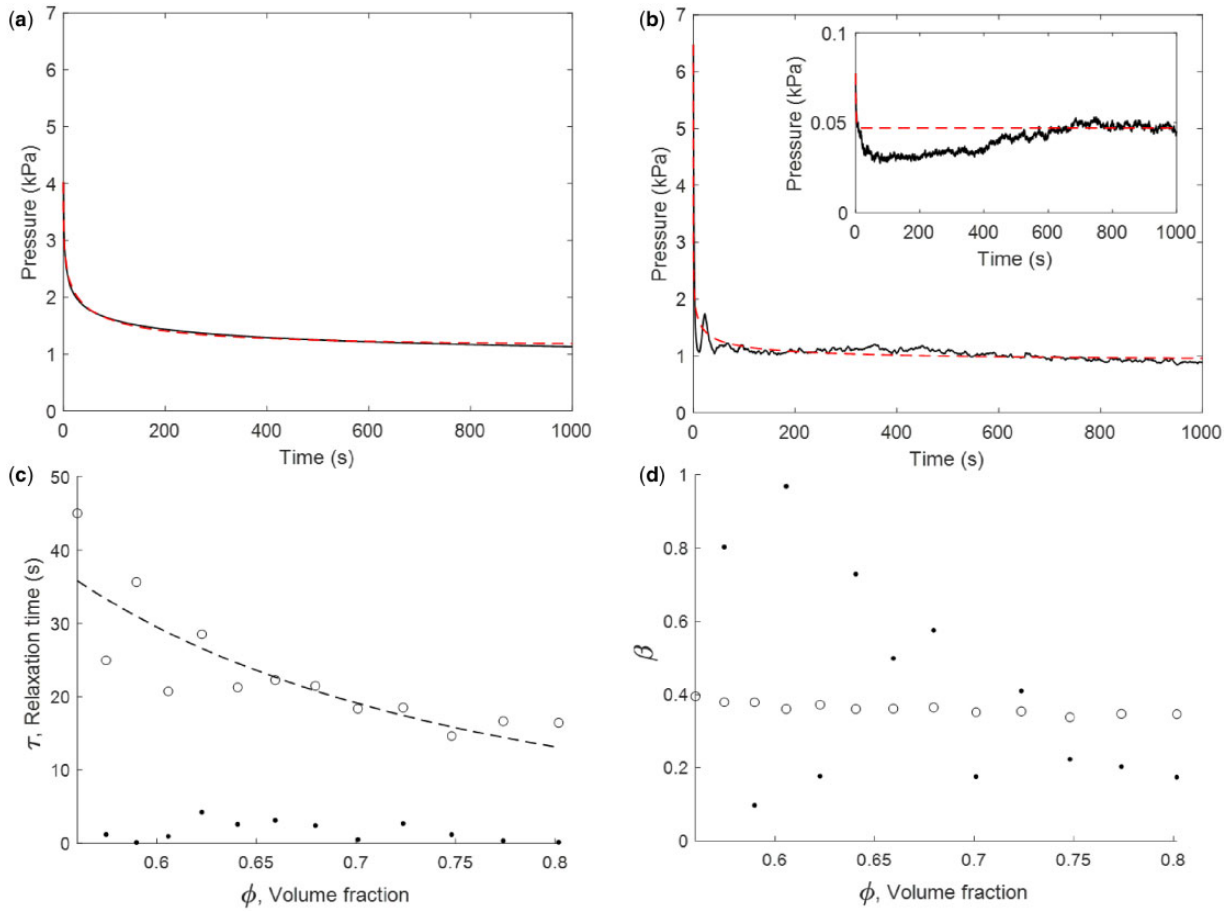

Fig. 3 a–**b**) Time course of pressures exerted by dead larvae (a) and live larvae (b) when compressed to $\phi = 0.80$. Inset of (b): time course of pressure of live larvae with stretched exponential fit when compressed to $\phi = 0.57$. Pressure data are a solid line and stretched exponential fit is dashed line. **c**) Relationship between relaxation time τ and volume fraction with a dashed line as the best fit to the dead larvae data. **d**) Relationship between exponent β and volume fraction. For c and d, dead larvae data are shown as circles and live larvae data are shown as points.

At the highest volume fraction of $\phi = 0.80$, live and dead larvae have comparable initial pressures ($P_0 = 6.5$ kPa for live larvae and $P_0 = 4.0$ kPa for dead larvae). These pressures are two orders of magnitude smaller than the pressures required to kill larvae, as shown in the inset of Fig. 2a. In our experiments, a larva can withstand a pressure of up to 935 ± 350 kPa and be compressed by a strain of $75 \pm 2\%$ of its initial height. This is more than 140 times greater than the maximum pressure experienced by the larvae in trials with 2000 larvae. Assuming a bulk density of compost of 500 kg per cubic meter (Schaub-Szabo and Leonard 1999), a 190 m tall pile of compost would need to be piled on a larva to kill it; the maximum pressure in our compression tests with multiple larvae is comparable to a 1.3 m pile of compost. Thus, the pressures experienced by larvae in the UTM are likely higher than pressures they would experience in their natural environment.

The steady-state pressures P_{SS} of dead larvae (circles) and live larvae (points) at four volume fractions are shown in Fig. 2b. At volume fractions above the critical volume fraction of $\phi_c = 0.65$, steady-state pressure increases rapidly, likely due to jamming and friction (O'Hern et al. 2003; Majmudar et al. 2007). We thus fit a power law to the data for $\phi > \phi_c$ of the form

$$P_{SS} = a(\phi - \phi_c)^b. \quad (4)$$

The dashed and dashed-dotted lines are fits for dead and live larvae, respectively, and the corresponding equations are $P_{SS} = 11.4(\phi - 0.65)^{1.26}$ and $P_{SS} = 4.1(\phi - 0.65)^{0.88}$. As shown by the positive exponents, the steady-state pressure increases with volume fraction. This makes sense because the higher the volume fraction, the more the larvae are filling the container and the more elastic energy is stored during the test. The increase in pressure at higher volume fractions (and, thus, higher strains) for both live and dead larvae is as expected for a material under compression, but does not follow Hooke's law with a constant modulus E, $P = E\epsilon$, because of the spaces between the larvae. They also do not fit an ideal gas law, which would yield a fit of $P_{SS} \sim \phi$. Nevertheless, we can say that dead larvae are "stiffer" than live larvae because at a given volume fraction, dead larvae exert a 20% higher pressure than live larvae, due to their not being able to move to dissipate their internal stress.

The relaxation time τ for live and dead larvae is shown in Fig. 3c by the points and circles, respectively. The relaxation time gives the time scale at which stresses are relieved by rearrangement. In particular, live larvae relax quickly, in $\tau = 1.7 \pm 1.4$ s. This time scale is less than the time scale of their motion, $\tau_b = 7$ s, given by the ratio of their length $L = 14$ mm and crawling speed $U = 2$ mm/s. This makes sense because larvae likely need to move only a small amount in order to break the force chains stretching from the top to the bottom of the container. Dead larvae, on the other hand, take between 15 and 45 s to relax, 10 times slower than live larvae. Their relaxation time decreases as a power law with the volume fraction, $\tau \sim \phi^{-2.8}$, as shown by the dashed line. The stretched exponential form, consistent with the behavior of other relaxing systems (e.g., binary mixtures), indicates an underlying mechanism that is characterized by a broad distribution of relaxation times rather than a single time (Piazza et al. 1988). The power-law decay with volume fraction therefore represents the evolution of this distribution with volume fraction. While we do not have a specific interpretation of the power-law behavior (as opposed to other functional forms), we note that power-law scaling of the time scale is seen in other relaxing systems (Piazza et al. 1988). Dead larvae at higher volume fractions can relax more quickly due to the greater elastic potential energy at these levels of compression.

The stretched exponential fit does not consistently describe the behavior of live larvae. In Fig. 3b at the highest volume fraction of $\phi = 0.80$, live larvae overshoot the equilibrium pressure by 0.8 kPa by insufficiently rearranging. This behavior might be due to some kind of flight or fight reaction due to the applied force. On the other hand, when larvae are compressed to one of the lower volume fractions, $\phi = 0.57$, the pressure decreases below the equilibrium before ramping back up as shown in the inset of Fig. 3b. This may be caused by larvae not contacting the entire pressure plate at all times. Such oscillations might be accounted for by spring-like and damper-like terms in the sensory system of the larvae, and possibly their memory span.

We verify the relaxation times of live and dead larvae by calculating the time it takes live and dead larvae to reach 50% of steady-state pressure, shown in Supplementary Figure S1. This "half-time" of live larvae is 1.2 ± 0.4 s; it decreases with a power law, $\phi^{-2.6}$, for dead larvae. These results are comparable to those calculated with stretched exponential fits.

In Fig. 3d, we compare the exponent, β, defined in Equation (3), for live and dead larvae. Most physical systems have $\beta < 1$, which acts to slow the decay of the exponential by stretching it across longer times. Studies of crumpled balls of aluminum foil are

associated with a β of 0.24–0.40 (Albuquerque and Gomes 2002). As shown by the open points in Fig. 3d, dead larvae have a $\beta = 0.36 \pm 0.02$, whose small standard deviation shows that the fit works well across volume fractions. The similarity in exponents for crumpled paper and the collection of larvae suggest that piles of dead larvae may have some hierarchy involved, such as the force chains resulting from their bodies pressing into one another. When live larvae are fitted to a scaled exponential function, they have a more variable $\beta = 0.42 \pm 0.29$. The large range of β for live larvae is likely due to their motion or initial configuration, which can vary between trials.

Dead larvae are merely a granular material and can only relax the pressure on them through their material properties. Live larvae, however, are able to relax the forces on them by moving around and actively adjusting their bodies. The fluctuations above and below the equilibrium pressure show that they have mechanisms for restoring a base state despite a pressure being too high or too low. If the pressure on the larvae is too high, they move into open spaces to relieve pressure. Conversely, if the pressure is too low, larvae can push up against the plate and each other to increase the pressure. The scale of the fluctuations is 0.007 kPa, which is 38% of the pressure exerted by one larva body weight. In comparison, the dead larvae in Fig. 3a show a smooth decay without fluctuations, indicating they can only dissipate the pressure but not increase it.

Discussion

Larvae are just one example of many living systems that undergo compression on a regular basis, from people to farm animals to other insects. A Tokyo subway system can pack passengers so tightly that a dedicated pusher has to squeeze them in to close the doors. When given a choice, most vertebrate animals avoid such high densities because their bodies can be injured. Nevertheless, to reduce shipping costs we often pack animals in high densities. When transported, pigs, chickens, and other farm animals are often packed tightly and keeping them alive in these conditions is a challenge faced by farmers all over the world (Lambooy et al. 1985; Mitchell and Kettlewell 1998).

Invertebrate animals are not governed by animal welfare laws, and they often experience large forces on a regular basis. Genetically modified mosquitoes for use in reducing malaria are packed densely in syringes to protect them from being thrown around during shipping (Chung et al. 2018). An ant can survive up to hundreds of times body weight before injury (Mlot et al. 2011). If forces are applied, ant aggregations can flow to dissipate those forces, exhibiting behaviors of both fluids and solids (Phonekeo et al. 2016; Tennenbaum et al. 2016). Earthworms have soft bodies and are compressed as they dig, exerting forces up to 500 times their body weight. The mechanical properties of their bodies limit how well they can dig into soil (Quillin 2000; Ruiz and Or 2018). This study provides a method for measuring the rearrangement of animals that might be applied to other types of invertebrates.

Black soldier fly larvae can experience forces due to the weight of mulch or fellow larvae on top of them. Our study shows that larvae can mitigate these forces by rearranging, even when the forces are orders of magnitude higher than would occur naturally. Moreover, the force that a single larva can survive exceeds body weight by a factor of 53,000. Unlike inactive materials, their behavior under compression over time can have interesting characteristics. They exert both small oscillations, individually pushing against the pressure plate to exert low forces, and large oscillations in which they collectively increase or decrease their force before returning to equilibrium. This is reminiscent of a control system with a feedback loop, which can actively respond to external forces to reach the desired state, as opposed to a simple mass-spring-damper, which can take longer to converge.

Our study shows that larvae are very robust to packing. It should be possible to tightly pack larvae for shipping without damaging them. Currently, larvae are loosely packed with soil or other substrate in HDPE plastic containers with tight lids. Shipping costs may be lowered by omitting the substrate and packing the larvae more tightly. However, since the pressure at higher volume fraction is close to 1 kPa, it may be difficult to design a container with a lid that can be closed tightly enough to hold compressed larvae.

Conclusion

In this study, we performed compression testing to measure the rate that black soldier fly larvae rearrange to relieve applied pressure. The pressures applied are orders of magnitude greater than they would feel naturally, yet larvae still had the ability to rearrange to reduce this pressure. Live larvae rearranged at time scales of 2 s, which is 9–27 times faster than dead larvae, which settled more slowly due to applied pressure. The equilibrium pressures

of both live and dead larvae are the same, indicating that live larvae do not seek pressures different from those that arise from their material properties and geometry. For dead larvae, the reduction of applied forces due to rearrangement is well described by stretched exponential functions. Live larvae are not consistently described by such functions, but instead seemed to be characterized by oscillation in pressure, indicating the presence of a feedback system.

Author contributions

O.S. contributed to the data collection and analysis, participated in the design of the study, and drafted the manuscript. J.T. contributed to the data collection. P.Y. and S.F. contributed to the data analysis. D.L.H. conceived, designed, and coordinated the study, and helped draft the manuscript. All authors gave final approval for publication.

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Supplementary data

Supplementary data are available at *ICB* online.

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