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What goes up must come down: biomechanical impact analysis of falling locusts

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ABSTRACT

Many insects are able to precisely control their jumping movements. Once in the air, the properties of the actual landing site, however, are almost impossible to predict. Falling insects thus have to cope with the situation at impact. In particular, for insects jumping to escape predators, a controlled landing movement appears to be a major evolutionary advantage. A quick recovery into an upright and stable body posture minimizes the time to prepare for the next escape jump. In this study, we used high-speed recordings to investigate the falling and in particular the impact behavior of *Schistocerca gregaria* locusts, a common model organism for studies on the biomechanics of jumping. Detailed impact analyses of free-falling locusts show that most insects typically crashed onto the substrate. Although free-falling locusts tended to spread their legs, they mostly fell onto the head and thorax first. The presence of wings did not significantly reduce impact speed; however, it did affect the orientation of the body at impact and significantly reduced the time to recover. Our results also show that alive warm locusts fell significantly faster than inactive or dead locusts. This indicates a possible tradeoff between active control versus reduced speed. Interestingly, alive insects also tended to perform a characteristic bending movement of the body at impact. This biomechanical adaptation might reduce the rebound and shorten the time to recover. The adhesive pads also play an important role in reducing the time to recover by allowing the insect to anchor itself to the substrate.

KEY WORDS: Biomechanics, Jumping, Exoskeleton, Cuticle, Bending

INTRODUCTION

For many insects, both flight and jumping movements are means of efficient and fast locomotion. In general, these flight and jumping movements can be subdivided into three major phases: take-off, aerial phase and landing.

The biomechanics of the take-off before flight and jumping have been well studied across a variety of different insect species (Manzanera and Smith, 2015). Various sophisticated mechanisms and structural biomechanical adaptations allow efficient energy storage, highly synchronized leg movements and fast detachment from the surface (Sutton and Burrows, 2011; Rothschild et al., 1972;

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Christian, 1978). Locusts, for example, a typical model organism for jumping biomechanics, are able to control the initial trajectory of their jump in six degrees of freedom (Gvirsman et al., 2016; Sutton and Burrows, 2008; Eriksson, 1980). During the aerial phase, several other insect species show active and passive righting mechanisms, ensuring a controlled spatial orientation of the body (Chahl et al., 2016; Goodman, 1960).

However, whilst landing after flight is mostly a predictable movement that can be actively controlled by the insect (Manzanera and Smith, 2015; Borst, 1986), landing after a jumping movement has additional challenges.

Although the initial trajectory of the take-off and even the orientation of the body might be controlled by several jumping insect species (Burrows et al., 2019; Sutton and Burrows, 2008, 2011; Faisal and Matheson, 2001; Rothschild et al., 1972; Alexander, 1995; Heitler, 1974), external factors such as gusts of wind or unforeseen obstacles make it extremely difficult to reliably predict the mechanical properties of the landing site (Bennet-Clark and Alder, 1979). An insect landing after a jump thus must be able to cope with a large variety of possible surface properties. Surfaces could be elastic or inelastic, smooth or rough, plain or tilted, and each possible combination thereof. As reliable information about the physical properties of the impact side cannot necessarily be acquired and processed from visual cues during the limited time frame of the late aerial phase, falling insects will have to deal with the situation at impact.

For jumping insects such as *Cercopoidea* (froghoppers) or *Siphonaptera* (fleas) with a very small body mass, the impact on the substrate is probably not an important factor to take into account with respect to damage to the exoskeleton. However, for jumping insects with a body mass several orders of magnitude larger, such as locusts, it is probably more important to land in a controlled way to reduce the risk of damage to the exoskeleton. In addition, and probably more relevant, a successful and controlled landing movement resulting in a quick upright and stable body posture minimizes the time to prepare for the next jump. A minimum delay between landing and the next jump would increase the chances of a successful escape from a predator.

Minimizing the time between consecutive jumps can be achieved by controlling the body posture during flight and falling. Such air-righting mechanisms are relatively well understood (Weis-Fogh and Jensen, 1956; Zarnack, 1978; Robert and Rowell, 1992). For example, it has been shown that locusts are able to control tumbling during the aerial phase (Cofer et al., 2010). In addition, a previous study by Faisal and Matheson (2001) has shown that locusts use combinations of active and passive movements of their legs and wings to turn themselves mid-air, which significantly increases the chances of landing upright, even when dropped upside down (Faisal and Matheson, 2001).

However, despite increasing knowledge about the early and late aerial phase, the actual biomechanics of the impact itself are still mostly unclear. Even with a controlled body posture, do locusts just

crash into the substrate and rely on their stable exoskeleton to deal with the impact forces? Is some sort of landing control or energy-absorbing behavior present to ensure a quick recovery and stable position? Such active control of landing could involve similar actions to those described for air righting such as usage of legs or wings. If there are passive control effects involved, the exoskeleton of the locust might provide interesting features that favor landing in the upright position, such as aerodynamic structures or the performance of the adhesive pads.

To investigate active and passive control features of the late aerial and impact phase, a variety of landing parameters of free-falling locusts were observed under three different activity conditions. We further investigated the effect of body posture and activity state on the time required to reach a stable (i.e. ready for the next jump) body posture after impact.

MATERIALS AND METHODS
Insect specimen
Adult male and female *Schistocerca gregaria* Forsskål 1775 locusts were kept at room temperature (12 h day at 24°C, 12 h night at 19°C) and a relative air humidity of 50−60%. The insects were fed fresh food *ad libitum*. Locusts with missing legs or defective wings were excluded from the experiments. Each experiment was performed using 12 locusts (six male, six female; body mass 1.09±0.18 g).

The biomechanical experiments were in full agreement with the German and European animal protection law. The authors strictly followed ethical guidelines to replace and reduce the number of animal specimens and refine experimental methods wherever possible.

High-speed recordings
A high-speed camera (Fastcam APX RS MONO, Photron, Tokyo, Japan) with a 50 mm objective was used to record the landing performance of locusts at 1500 frames s^{-1} under bright ambient light conditions (about 20,000 lx). The camera was aligned to record the front and side view of the falling locust as well as the ground (smooth glass) using a surface mirror at 45 deg. To correct for lens distortion at different positions within the video frame, the setup was calibrated using a custom-written script utilizing the Python bindings for the calibration algorithms of OpenCV (http://www.drdobbs.com/open-source/the-opencv-library/184404319). The highest reprojection error recorded was 0.13.

A metal stand was used to ensure a constant dropping height of 0.6 m. This height corresponds to twice the height required for the previously reported air-righting behavior of locusts (Faisal and Matheson, 2001). To prevent any effect of pressure-induced thanatosis (Faisal and Matheson, 2001), the insects were carefully held by grabbing the folded wings with the thumb and index finger right behind their base. All insects were dropped without allowing the locust to push against any object and thereby adding unwanted torque to its fall.

The first set of locusts was dropped parallel to the ground, the second in a positive 45 deg pitch angle (head first) and the third in a negative 45 deg direction (abdomen first). The high-speed recordings of the locust landing were performed at 19°C with 50−60% relative air humidity. For each set, every locust was tested alive and warm (body temperature ∼24°C), alive but cooled (∼4°C) and finally dead. In insects, body temperature is obviously closely correlated with general activity and in particular flight (Mellanby, 1939; Taylor, 1963; Krogh and Weis-Fogh, 1951). The lower the body temperature of the locusts in our experiments, the less likely were any effects of active movements or control of the impact.

Insects that were dead but not dehydrated obviously had no control of the falling movement, whilst still having the same passive biomechanical properties of their exoskeleton (Aberle et al., 2017).

Usually, dead insects desiccate rapidly, which affects the biomechanical properties of the cuticle (Dirks and Taylor, 2012). Previous studies, however, have shown that freezing insect cuticle significantly affects neither its static nor its dynamic biomechanical properties (Aberle et al., 2017). Hence, locusts were killed by freezing them to −20°C, then thawing the dead insects to room temperature immediately before the experiments. The experiment was conducted on one locust at a time to minimize the cooling down and warming up, respectively, of the warm and cooled insects. None of the experiments took longer than 15 min for warm locusts and not longer than 3 min for cool locusts.

The end of the landing phase was defined as the moment when a locust reached a stable stance on the substrate, with the femora of the hind legs orientated at approximately 40 deg from the ground and the tibiae fully flexed (Faisal and Matheson, 2001), or when no further body movement was visible. The time frame between impact and reaching a final stable body posture was defined as the landing duration. For dead locusts, the end of the landing phase was the moment when it ceased bouncing and gliding on the ground surface.

To investigate the effect of the wings on impact speed and angles, paired experiments were performed on locusts with and without front and hind wings. Warm locusts were also dropped parallel to the ground undamaged and then after removal of the wings. The effect of adhesive pads was tested by removing all tarsal segments from the front, middle and hind legs.

Tracking and reconstruction
For automated motion tracking of the locusts, the center point between the eyes and mandibles on the frons and the central tip of the abdomen were chosen as markers. Calibrated high-speed recordings were automatically analyzed using pattern motion tracking scripts (Blender, version 2.78a, https://www.blender.org/). Markers were tracked in the front and side view as provided by the mirror. Manual interpolation or offset tracking of the marker position was required when the patterns were obscured by the wings, legs or rotation of the locust. The marker positions were manually checked and adjusted back and forth in time. Four main parameters of the fall were reconstructed from the video data: impact angle, impact speed, landing duration and body part of first contact.

A three-dimensional vector between the head and abdomen markers of the locust was reconstructed using the x- and z-coordinates from the front and the y-coordinates from the side view. This vector was used to calculate the locust angle relative to the horizontal ground surface assuming nearly orthogonal coordinate space from the image data. Angles generally were defined between the ground plane (x–y plane) and this longitudinal body vector. The impact angle was averaged over the last three frames before impact. Consequently, a positive impact angle means the locust hit the ground head first as opposed to abdomen first for a negative impact angle.

The same coordinates were used to reconstruct the speed of the locust. The impact speed was calculated from the movement of the head marker during the last three video frames prior to impact moment in all three dimensions. A third-order low-pass Butterworth filter (0.15 Hz) with initiation on the mean of the first 10 speed values was applied to reduce noise.

To correct our speed measurements for possible rotations of the body axis, we also calculated the rotation component of the fall based on the center of mass movement of the locust. The center of mass was determined by tracking the point at 40% of the head–

abdomen vector. This point lies approximately at the hind leg coxa of the locust, which is the center of mass for desert locusts (Taylor and Thomas, 2003). The center of mass movement was then calculated by subtracting the center of mass coordinates of two different time steps from each other (separated by 10 frames, equal to 6.66 ms). The same method was used to determine the head impact vector. The angle between the impact and center of mass vector was calculated with the scalar product, allowing a linear projection of the center of mass movement vector on the impact vector. Therefore, the impact can be described as translation (center of mass movement) and rotation (as the head rotates around the center of mass). These calculations were based on the assumption that the locust behaves nearly as a rigid body while free falling.

The part of the locust's body that first touched the ground was termed the 'first contact'. In this respect, both the antennae and head of the locust were considered a head contact, whilst 'full body' describes an impact with an indistinguishable part of the thorax or abdomen. Such first contacts only occurred when locusts were aligned horizontally before impact.

Additional qualitative observations of the falling behavior were also recorded. In many cases, characteristic bending movements of the abdomen were observed. The abdomen bent away from the longitudinal body axis after impact (see Figs 1 and 2). When this movement exceeded the threshold of 20 deg from the body's main axis, the abdomen was considered as 'bent'.

The source code of the Blender export algorithms can be downloaded at https://github.com/Amudtogal/blenderMotionExport. Detailed video and tracking data of this study are available from the corresponding author on request.

Statistics

Statistics were performed using R (version 3.3.2, http://www.R-project.org/). The index of the test statistics always represents the degrees of freedom (numerator, denominator if applicable). Shapiro–Wilk tests were used to test for normal distribution. As a two-sample test for homoscedasticity, the F-test was used. Either Student's t-test or Welch's t-test was chosen according to the prerequisite of variance. For non-normally distributed data, the Wilcoxon rank sum (Mann–Whitney) test was used.

Multiple samples were compared with different tests, depending on the prerequisites. For a one-way ANOVA, assumptions of both normality and homoscedasticity were met. For the Kruskal–Wallis (K–W) test, only homoscedasticity was required. For the Welch-corrected ANOVA (Welch's ANOVA) only the assumption of normality was met. Multi-sample comparison of variance was performed with Bartlett's test for normally distributed samples and Levene's test for non-normal data. When significance occurred, Dunn's test was used to distinguish the different subgroups for ANOVA and K–W tests. For Welch's ANOVA, a pairwise t-test with Holm–Bonferroni correction (Holm t-test) was used to distinguish the subgroups.

A significance level of $\alpha=5\%$ was used in all tests. If not stated otherwise, the provided values show the median with the median absolute deviation (median±m.a.d.). If mean values are given, the standard deviation is shown instead (mean±s.d.). Boxplots show the median and the last data point within 1.5 box lengths as whiskers.

RESULTS

A typical head speed progression of a living, warm locust over a whole video sequence is shown in Fig. 1. For detailed analysis, the
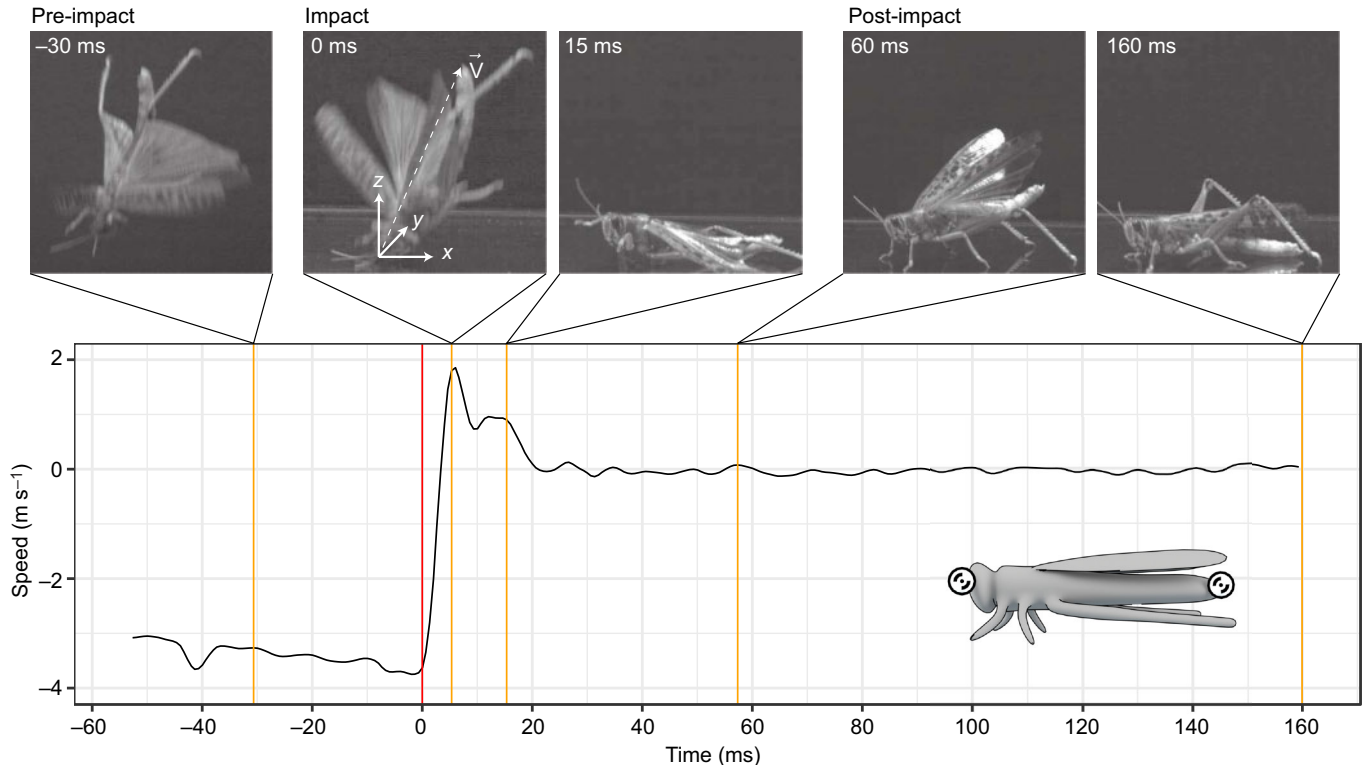

Fig. 1. Speed of the locust head over time for a typical recording of a living, warm locust falling from a height of 0.6 m onto a planar glass substrate. The frames show the locust at characteristic stages of the landing movement: pre-impact (ca. −30 ms), impact (0–30 ms) and post-impact (>30 ms). During the late pre-impact phase, often the front and hind wings were actively moving. Warm locusts tended to crash head first onto the substrate. This was followed by a characteristic bending movement of the abdomen (see Movie 1). A stable final stance was typically reached after about 139 ms. The schematic view of the locust (bottom right) shows the position of head and abdomen markers.

high-speed recordings were divided into three characteristic stages: pre-impact (ca. −30 ms), impact (0–30 ms) and post-impact (>30 ms). In the following sections, we present results on impact speed, impact angle and the effect of the wings during the pre-impact phase, followed by the observations of first contact, landing duration and energy dissipation during the post-impact phase.

Pre-impact
Impact speed

From a dropping height of 60 cm, the still accelerating falling locusts reached their highest speed just before impact. After impact, the relative speed was 'positive' as most of the insects showed rebound movements from the ground. As the locusts reached their stable end positions the head speeds leveled out at zero.

Our results show a significant effect of activity state on impact speed (K–W H_2=12.581, $P<0.002$; see Fig. 2A). Pairwise comparison shows that at a horizontal drop angle, warm insects had a significantly higher impact speed (3.74 ± 0.13 m s^{-1}) than dead insects (3.33 ± 0.07 m s^{-1}, Dunn $P<0.005$). Warm insects also showed a higher (but not significantly higher, Dunn $P>0.09$) impact speed than cooled insects. The impact speed of cooled insects (3.44 ± 0.15 m s^{-1}) was again higher (but not significantly so, Dunn $P>0.06$) than the impact speed of dead insects. The rotation of the locust body axis during free falling was typically below 2.5% and showed no systematic effect on the overall measured impact speed (see Fig. S1). Changing the drop angle ±45 deg from the horizontal plane in general reduced the impact speed. Warm insects with a negative drop angle (abdomen first) had a significantly lower impact speed (3.28 ± 0.21 m s^{-1}) than those with positive or horizontal drops (K–W H_2=16.848, $P<0.001$, for both Dunn $P<0.001$; see Fig. 2B).

Impact angle

The effect of dropping angle on impact angle for all activity states is shown in Fig. 2B. At horizontal drop angles, the activity state significantly affected the impact angle (Welch's ANOVA $F_{2,19.85}$=25.409, $P<0.0001$ with all Holm t-test $P<0.05$). The steepest mean impact was found in warm locusts at 69.94 ± 14.84 deg. Cooled insects had a much lower mean impact angle of 2.32 ± 38.69 deg. Interestingly, the mean impact angle of dead locusts (27.32 ± 21.92 deg) was in between those of warm and cooled insects.

At a positive drop angle (head first), the activity state of cooled locusts (-2.27 ± 25.03 deg) showed significant differences to both warm and dead activity states (K–W H_2=10.020, $P<0.01$, for both Dunn $P<0.05$). The mean impact angle of warm locusts was not significantly different to the impact angle of dead locusts (59.37 ± 40.97 versus 30.10 ± 26.12 deg, Dunn $P=0.4048$).

For negative dropping angles (abdomen first), the locust activity state did not significantly affect impact angle (ANOVA F_2=3.3213, $P>0.15$).

Effect of wings

To investigate the effect of wings on impact speed and angle in detail, we used a pairwise comparison of warm locusts with and without front and hind wings. Our results show that the impact speed of a locust with front and hind wings was not significantly different to that of the same locust without wings (paired t-test t_{11}=0.4178, $P=0.68$; see Fig. 3A) when dropped parallel to ground. However, the impact angle did change significantly when the wings were removed (paired t-test t_{11}=−2.2647, $P<0.05$). Locusts without wings landed almost parallel at a mean angle of -3.44 ± 51.09 deg while winged locusts had a head-first impact of 39.28 ± 30.89 deg (see Fig. 3B). In addition, the mean landing duration of locusts without wings (0.25 ± 0.12 s) was significantly greater than when the locusts still had their wings (0.12 ± 0.03 s, paired t-test t_{11}=4.0476, $P<0.002$).

Post-impact factors
First contact

The relative distribution of the body parts that touched the ground first is shown in Fig. 4. Pooling the different activity states, at a plane drop angle, 58% of the locusts hit the ground head first. The front
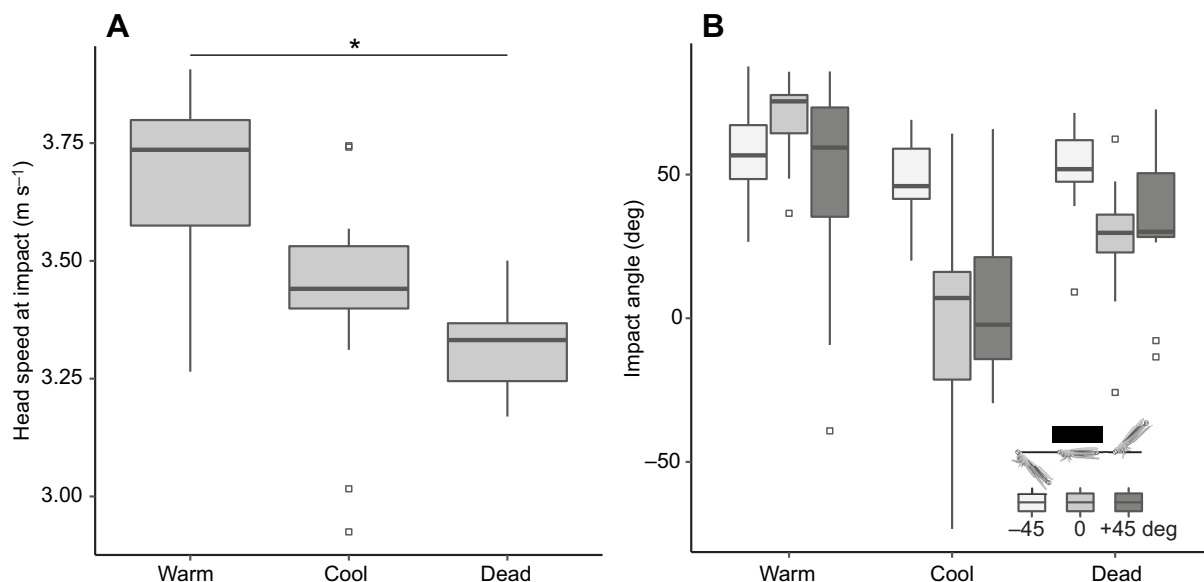

Fig. 2. Effect of activity state on impact speed and impact angle. (A) Warm locusts fell slightly yet significantly faster than dead locusts. Cooled locusts showed an impact speed in between that of warm and dead locusts. *$P<0.05$. (B) Warm locusts were able to correct for different dropping angles and rotate their bodies for a head-first impact. Cooled insects again showed a notably higher variance of impact angle in comparison to warm and dead insects. Horizontal (0 deg) and abdomen-first (−45 deg) drops resulted in a less-steep impact for cool and dead insects. Dead locusts showed a smaller variability of impact angle. Even at positive, abdomen-first dropping angles, the bodies of dead locusts rotated during the drop, resulting in a head-first landing. For details on statistics, see Results.

Fig. 3. Effect of wings for warm locusts falling from a horizontal dropping angle. (A) Effect of wings on impact speed. Warm locusts with wings showed a relatively large variation of impact speed. There was no significant difference in impact speed between locusts with or without wings. (B) Effect of wings on body angle. Locusts with wings had a significantly steeper impact angle in comparison to locusts without wings. (C) Landing duration with and without wings. Locusts with wings had a significantly shorter landing duration, and thus would most likely be able to perform a consecutive escape jump within a shorter period of time.

and middle legs were involved in almost equal proportions of 14% and 17%, respectively. The abdomen (6%), full body (3%) and hind leg (3%) were the least frequent first-contact points. At negative drop angles, the head and front leg represented most of the contact points, at 64% and 31%, respectively. At positive drop angles, the head proportion was slightly lower (42%) than for the horizontal drops, and front or middle leg occurrence was increased to 22%. The distinguishable body states can be seen in more detail in Fig. 4.

Combining the first contact data with impact speed, impact angle or landing duration did not provide enough data to be statistically solid. However, the results indicate that the contact point changes with the impact angle. As Fig. 4 illustrates, cool insects showed a notably higher variance of first-contact points than warm insects. The head was less involved, while the front and middle legs touched the substrate much more often. Interestingly, the dead insects again showed a more stereotypical pattern, similar to that of the warm locusts, as the head was the primary point of first contact at impact. The legs and abdomen were rarely involved.

Landing duration

The effect of activity state and dropping angle on landing duration of the locusts is shown in Fig. 5A. The dropping angle had no significant effect on the landing duration of locusts. The activity state, however, significantly affected the time to recover. At a horizontal drop angle, the warm locusts had a significantly shorter landing duration (0.139 ± 0.033 s) than the cool (0.240 ± 0.074 s) or dead (0.230 ± 0.069 s) insects (K–W $H_2=15.382$, $P<0.001$, for both Dunn $P<0.005$). A similar tendency was visible at positive and negative drop angles. There was no significant difference between landing durations of warm locusts at the three dropping angles (K–W $H_2=2.035$, $P=0.362$). The same applied to the cooled (K–W $H_2=0.713$, $P=0.7$) and dead locusts (K–W $H_2=0.334$, $P=0.846$).

In contrast to the warm and cooled locusts, which all sooner or later reached a stable upright resting position, dead locusts instead showed a variety of different final states after the mostly head-first impact. At a horizontal drop angle, 92% rested sideways and only 8% upright. When released with a positive drop angle, 84% rested
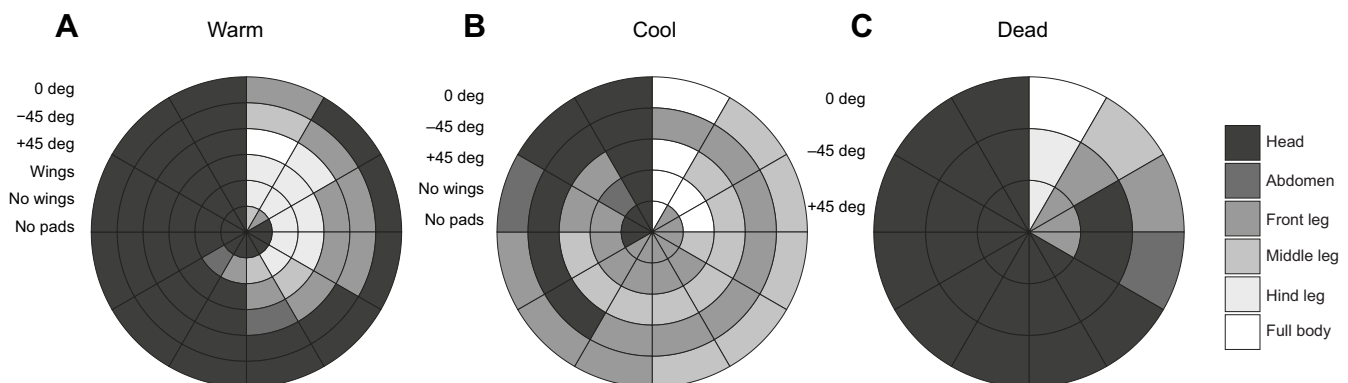

Fig. 4. Body parts making first contact with the substrate under different conditions. While warm locusts tended to land head first (A), cooled insects showed a notably greater variety of first contacts (B). Dead locusts, however, showed a tendency to land head first (C). Labels on the left of each panel correspond to outer to inner circles reading from top to bottom, respectively.
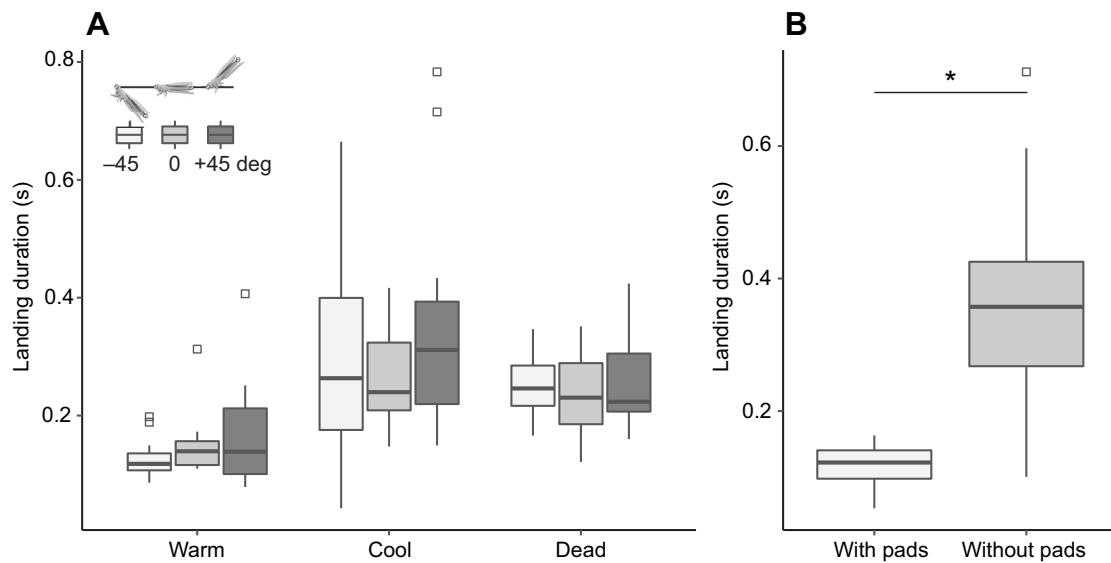
Fig. 5. Effect of activity state and adhesive pads on landing duration. (A) For all tested dropping angles, warm locusts needed significantly less time to reach a final resting position compared with cool or dead insects. Dead insects obviously showed no active self-righting behavior after impact. The time shown for dead insects is thus the time required for the body to stop moving after the impact, irrespective of the final orientation of the body. (B) Warm locusts without adhesive pads needed a significantly longer time to reach a final stable position after dropping from a horizontal orientation. *$P<0.05$.

sideways, and 8% each were backwards or upright. However, at a negative drop angle, only 59% rested sideways, while 33% rested upright (8% backwards).

Warm locusts that had had their tarsal segments removed, took significantly longer to reach a stable state after impact from a horizontal drop angle (Welch's t-test $t_{11.681}=4.959$, $P<0.001$). The mean landing duration of insects without adhesive pads was 0.366 ± 0.170 s compared with 0.118 ± 0.030 s for locusts with adhesive pads (see Fig. 5B).

Dissipation of kinetic energy
Detailed analysis of the high-speed recordings after impact revealed interesting characteristic biomechanical behavior of the abdomen. After impact, the abdomen either stayed almost completely in its initial 'straight' shape or bent upwards ('bending', see Fig. 6).

Our results show that the impact speed at the horizontal drop angle was not significantly different between locusts that bent or kept a straight abdomen (Student's t-test $t_{34}=-1.642$, $P>0.05$). However, as the bending behavior was not distributed equally between body states, these results have to be treated with care. Warm locusts at horizontal drop angles were much more likely to show bending behavior (83/17%) than cool (25/75%) or dead locusts (33/67%; see Fig. 7A). Taking into account all three locust states at a horizontal drop angle, insects showing no bending behavior after impact took significantly longer to recover (0.245 ± 0.087 versus 0.155 ± 0.050 s, Mann–Whitney test $W=74$, $P<0.01$). The landing duration is shown in Fig. 7B.

DISCUSSION
Controlled and predictable landing after flight has so far mostly been studied for various species of Calliphorinae. In these insects, the preparation for landing typically involves optical flow to estimate the distance to the ground, followed by preparatory movements of the legs, where the prothoracic legs are extended and slightly lifted to make first contact with the ground, whilst at the same time the mesothoracic and metathoracic legs are lowered (Borst, 1986; Goodman, 1960). These flying insects intentionally prepared for landing.

However, how do insects prepare for 'unpredictable' landing? After jumping, neither the duration of the aerial phase nor the quality of the landing can be reliably anticipated. In this study, we focused on the landing behavior, in particular the landing duration of a falling insect, and mechanisms that allow the insect to minimize this time frame. A short landing duration, i.e. the time between impact and readiness for the next jump, plays an important role for any escaping jumping insect. The faster an escaping locust is able to perform a consecutive escape jump, the more likely it is to escape a predator.

Minimizing landing duration can be achieved by combinations of two general strategies: an insect falling on its side or back after an escape jump could try to use an efficient and fast righting mechanism. This mechanism has been described for locusts in detail by Faisal and Matheson (2001) and mostly involves movements of the legs pressing against the ground, as well as rolling movements of the body. Typically, a locust turned upside down takes 600 ms to complete this
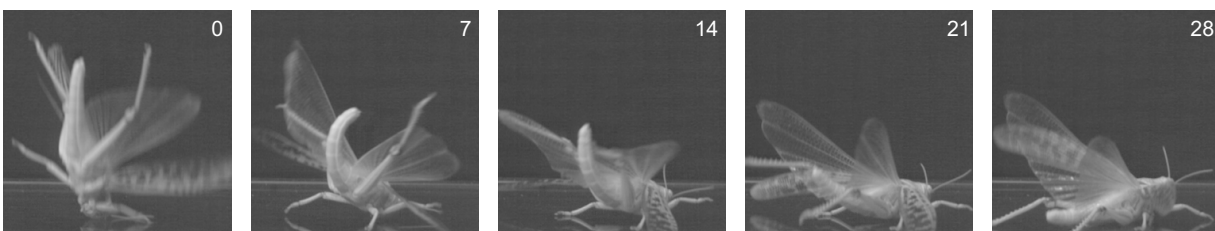

Fig. 6. Bending sequence of a locust falling from a positive drop angle recorded at 1500 frames s^{-1}. Immediately after impact, the abdomen showed an upwards bending movement. Within the following 21 ms, the abdomen performed a downwards rolling movement. Numbers indicate time in ms after impact.
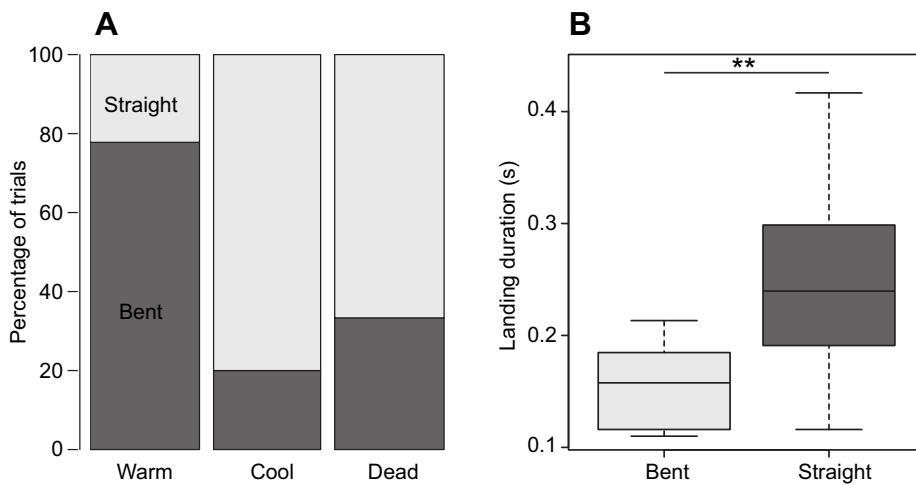
Fig. 7. Bending behavior of abdomen in warm, cool and dead locusts. (A) Percentage of locusts showing bending movements of the abdomen at the three different activity states (horizontal drop angle). Warm locusts showed a notably higher degree of bending than cooled or even dead locusts. Interestingly, dead locusts also showed bending of the abdomen to some degree, indicating a possible passive contribution of the exoskeleton towards this behavior. (B) Landing duration of locusts with and without abdomen bending (horizontal drop). Locusts with bending showed a significantly shorter landing duration than locusts with no bending movement of the abdomen. **$P<0.01$.

righting movement and be ready for a consecutive jump. A time frame of 600 ms, however, can be a relatively long period of time when jumping for your life. A second additional strategy would therefore be to initially land in a correct (or at least close to correct) position, which requires only small correction of the body posture.

Active and passive factors for pre-impact control

Our experiments with free-falling locusts at different activity states show that irrespective of the initial dropping angle, free-falling active locusts, with the highest degree of control, had a characteristic impact angle of approximately 60 deg. Active locusts mostly fell head first onto the substrate (see Fig. 2). These observations are very consistent with results previously published by Faisal and Matheson (2001). Irrespective of the dropping angle, free-falling dead locusts also showed a characteristic head-first impact position, very similar to the impact angle of active locusts. These results confirm the passive aerodynamic air-righting effect of the locust exoskeleton, suggested earlier by Faisal and Matheson (2001).

Surprisingly, the results of this study show that inactive alive locusts fell with a less-steep impact angle in comparison to active locusts. They also showed a notably higher degree of variation in comparison to both the active and the dead locusts. Hence, regarding impact angles, having no control of your body movement (dead) seems to be better than having limited control of your body (cold).

This observation seems surprising, but might be explained by uncoordinated corrective active movements of the cold locusts. Our video recordings show that falling warm locusts often extend their hind tibiae and spread their wings (see Movie 2). These movements might help to improve the chances of a head-first landing. In inactive (cold) insects, with limited control of their body movements, these compensatory movements are far less frequent and might also have resulted in less effective correction of the impact angle. Detailed comparison of wing and body movements of cold and warm locusts based on high-speed recordings might help to clarify this point. Our experimental setup unfortunately did not allow for this kind of analysis.

As the wings presumably play an important role in the air-righting behavior during take-off (Burrows et al., 2019) and landing of insects (Faisal and Matheson, 2001), one explanation could well be that falling active locusts actively use their wings to steer (gain control). Indeed, locusts with wings were able to control their impact angle during free fall, whilst wingless locusts landed at almost the same impact angle they had been dropped with (see Fig. 3B).

In addition, active or passive movements of the wings could add thrust or air resistance to the falling locust. This might explain the large variation of impact speed (see Figs 2A and 3A) as well as measured impact speeds higher than the speed of a free-falling body in a vacuum observed during some experiments. Again, detailed high-speed recordings of the wing movements during the entire aerial phase might help to clarify this point.

Interestingly, a direct comparison of locusts with and without wings shows that the presence or absence of wings does not completely explain variations in impact speed (see Fig. 3A). Body posture itself might also have an effect on the impact speed. In particular, the orientation (and thus air resistance) of the legs could be an additional factor determining falling speed. This effect has previously been indicated by studies on falling insects (Faisal and Matheson (2001) and take-off of jumping insects (Burrows et al., 2019). Our video recordings show that both active and inactive locusts often had their hind legs stretched out (see Movie 2), which might increase air resistance. Further high-speed recordings of the free-fall phase might help to answer this open question.

In summary, our results show that locusts use both active (wings) and passive (exoskeleton) mechanisms to control their descent during a free fall. Given the outstanding biomechanical properties of the exoskeleton cuticle (for example, a very high work of fracture; Dirks and Taylor, 2012), impact speed seems not to be a critical factor to protect the exoskeleton. During free fall, locusts will not reach a speed at which the exoskeleton would be at risk of damage. Instead, the above-mentioned results indicate that the impact angle seems to be a more important parameter to control. Whilst the presence of the wings does not clearly affect the impact speed, wings do significantly affect the control of the impact angle. At higher dropping heights, or when landing after flight, the wings might play a different role in deceleration and even enable the locusts to change their fall into a gliding movement.

Post-impact biomechanics

To minimize the time to recover to a stable body position and prepare for the next jump, locusts need to cope with the kinetic energy of the impact. One possibility to minimize the kinetic energy after a jump or fall is controlled active deceleration using the wings (parachute before the impact) or legs (damping after the impact). Such behavioral responses can be found in a great variety in many different animals (Alexander, 1995).

First contact

The detailed analysis of the post-impact phase shows that instead of using body appendages such as the legs to absorb impact energy, the majority of active locusts crashed literally head first (see Fig. 4A).

Neither the presence nor the absence of wings or adhesive pads notably affected the first point of contact (see Fig. 4A). The head-first crash was also found in dead locusts (see Fig. 4C), which further supports the role of the exoskeleton aerodynamics as a passive factor controlling locust landing.

The inactive locusts with different impact angles show a large variety of first contact points (see Fig. 4B), with the legs and abdomen involved. These contact points are obviously correlated to the variation of impact angle.

One additional very interesting observation (which requires further investigation) in our video recordings was a characteristic small movement of the locust head in relation to the pronotum at impact. Detailed analysis of the video recordings indicates that after impact, the head slightly moved backwards into the pronotum. This movement occurred shortly before any other reaction (such as bending of the abdomen, see below) was observed. Looking at the complex morphology of the head–thorax connection in locusts (Shepheard, 1974; Leubner et al., 2017), it seems likely that the anterior margin of the pronotum in combination with the posterior part of the head (occiput) might function as a neck support collar. This structure would act as a temporary head-arresting mechanism, reducing the risk of impact damage to the relatively small neck joint. Future studies involving high-resolution scans of the neck morphology will help to clarify this point.

Dissipation of energy

To gain control of their landing movements and quickly reach a stable body posture, falling insects need to dissipate the kinetic energy of their free fall through their exoskeleton. Otherwise, they would bounce off the substrate.

Comparing the landing time of inactive and dead insects allows closer investigation for the presence of active damping mechanisms of the exoskeleton. The time it took for inactive insects to reach a stable, 'jump-ready' position was not significantly different from the time it took the exoskeleton of a dead locust to come to rest on the substrate. Hence, there seems to be no active damping mechanism involved in reducing the kinetic energy of the falling locust after impact. The detailed analysis of the landing behavior in our video recordings indeed confirms that locusts did not use any noticeable protrusive movements of their legs to dampen their impact.

How can kinetic energy be dissipated? A simple and easy way to prevent any 'rebound' is to use an anchoring mechanism to the substrate. The adhesive pads of insects are an obvious structure to provide such a mechanism (Dirks and Federle, 2011). Typically, secure and firm attachment to smooth or rough substrates does not require any active controlled movements of the insect foot (Endlein and Federle, 2008), hence adhesive pads could passively operate in 'real time' immediately after impact. Indeed, our results show that the landing duration increased when the adhesive pads were removed. The adhesive pads, and their ability to attach to a substrate, thus play an important passive role in improving the landing of jumping locusts.

However, the observed differences in landing duration between active and inactive locusts with adhesive pads further indicate the presence of an additional, body temperature-dependent dissipation mechanism. Indeed, many video recordings show that just after impact, alive insects tend to perform a distinct bending movement of the body, where the abdomen is bent upwards just after impact (see Fig. 6). The presence of such bending movements to dissipate energy will significantly reduce the landing duration and thus could be regarded as a key feature for a fast and secure landing.

Our recordings also show that bending movements of the abdomen sometimes occurred in inactive and dead locusts. This indicates that at least to a certain extent the upwards bending movements could be a passive result of the exoskeleton morphology. The reduced occurrence of bending in dead and cool insects could be explained by either different biomechanical properties of the exoskeleton (such as reduced hemolymph pressure, different damping properties of muscles and joints, etc.) or missing or reduced active bending movements of the exoskeleton. Regardless, this biomechanical adaptation apparently helps to reduce rebound and shortens the time to recover. Similar principles can be found in several martial arts, where falling athletes use rolling movements of their body extremities to dissipate energy away from the impact site and reduce impact forces (Groen et al., 2007).

Landing duration

The focus of this study was to investigate the landing duration of free-falling locusts, as this time frame determines the maximum jumping frequency when escaping from a predator.

Our results show that landing duration was independent of the dropping angle (see Fig. 5A), which is to be expected as the dropping angle did not significantly affect the impact angle. Hence, all active insects had almost the same 'starting position' at the beginning of the post-impact phase. This preferred initial head-first position results in an almost immediate recovery into a jump-ready body posture, with all legs in contact with the substrate. The ability to orientate its body during free falling thus allows the locust to quickly perform a consecutive jump, without the need to re-align its body.

For a locust lying upside down (arguably a worst-case scenario after landing), it takes on average 585 ms to recover into a body position that allows a consecutive jump (Faisal and Matheson, 2001). Our experiments show that the typical landing duration of a free-falling active locust was only 139 ms. Hence, landing in or close to an optimal body position can reduce the time to the next escape movement by a factor of almost 4, which is likely to be a major evolutionary advantage for any escaping locust.

Non-surprisingly, the landing duration for inactive insects was significantly longer (230 ms) than the time taken by active locusts. For inactive insects, the landing duration also showed a notably larger degree of variability, which could be a result of less coordinated body movements, as already observed for the air-righting mechanism.

Conclusion

In conclusion, our results show that falling locusts crash into the substrate and thus rely on the biomechanical properties of their cuticle exoskeleton to deal with the impact forces. Using their wings and probably other aerodynamic properties of their exoskeleton, locusts are, however, able to actively control the impact angle. By crashing head first onto the substrate, locusts ensure a predetermined body posture, which allows the time between consecutive jumps to be minimized. The adhesive pads and a bending movement of the abdomen could help to dissipate energy and ensure a quick recovery after the impact.

Visualization: S.V.R.; Supervision: S.L., J.-H.D.; Project administration: J.-H.D.; Funding acquisition: J.-H.D.; Software: S.V.R.

Data availability
The source code of the Blender export algorithms can be downloaded at https://github.com/Amudtogal/blenderMotionExport. Detailed video and tracking data of this study are available from the corresponding author on request.

Supplementary information
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