Many ways to stick the landing: novel righting strategies allow spotted lanternfly nymphs to land on diverse substrates

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Short title: Spotted lanternfly nymph righting

Keywords: spotted lanternfly, righting, landing, anti-predator, falling

Abstract

Unlike large animals, insects and other very small animals are so unsusceptible to impact-related injuries that they can use falling for dispersal and predator evasion. Reorienting to land upright can mitigate lost access to resources and predation risk. Such behaviors are critical for the spotted lanternfly (SLF) (*Lycorma delicatula*), an invasive, destructive insect pest spreading rapidly in the US. High-speed video of SLF nymphs released under different conditions showed that these insects self-right using both active midair righting motions previously reported for other insects, and novel post-impact mechanisms that take advantage of their ability to

27 experience near-total energy loss on impact. Unlike during terrestrial self-righting, in which an

28 animal initially at rest on its back uses appendage motions to flip over, SLF nymphs impacted

29 the surface at varying angles and then self-righted during the rebound using coordinated body

30 rotations, foot-substrate adhesion, and active leg motions. These previously-unreported strategies

31 were found to promote disproportionately upright, secure landings on both hard, flat surfaces and

32 tilted, compliant host plant leaves. Our results highlight the importance of examining

33 biomechanical phenomena in ecologically-relevant contexts, and show that, for small animals,

34 the post-impact bounce period can be critical for achieving an upright landing.

35

1. Introduction

37 Falling is a frequent and unavoidable fact of life for animals in a wide range of environments. In

38 response, many climbing arthropods and arboreal vertebrates have evolved a variety of strategies

39 to help them land safely, such as gliding (1), parachuting, and righting (i.e., reorienting so as to

40 land upright) (2). Although smaller organisms are not at direct risk from impact-related injury

41 (3), landing upright can still maximize survival by minimizing the metabolic cost of terrestrial

42 righting, facilitating predator evasion (4), and mitigating other risks (e.g., hunger, desiccation,

43 habitat and territory loss, etc.) (5). Because dropping is also a strategy used by animals for

44 dispersal (6) and predator avoidance (4), understanding these behaviors has a wide variety of

45 implications for ecology, as well as providing inspiration for robotics (7).

46

47 Among insects and other arthropods, righting behaviors have been categorized into two broad

48 groups: aerial righting and terrestrial righting (8). Aerial righting consists of body reorientation

49 during the fall, and typically includes an active push off of the surface with the limbs imparting

50 an initial rotation on the body. Some small arthropods use a stereotypical falling body posture to

51 take advantage of aerodynamic drag on the body and legs for aerial righting and even

52 maneuvering during gliding, as found for pea aphids, stick insect instars, canopy ants and spiders

53 (2,9–11). Repositioning of various body parts can also facilitate reorientation to an upright

54 posture and a controlled landing, ideally with feet in contact with the substrate. Just as some

55 larger, flexible vertebrates (e.g., cats, rabbits, squirrels, lizards) tend to use a combination of

56 body, limb, and tail inertia to right themselves while falling (2), similar strategies appear to be

57 used among falling stick insect nymphs, which have a relatively flexible and long body (12).

58

59 On the other hand, terrestrial righting consists of determining how an animal that is on its back

60 can get back onto its feet. Among insects, this usually involves a period of pushing off of the

61 substrate using a combination of legs, wings, and the body imparting a rocking motion on the

62 body until a leg can gain enough purchase to complete an upright flip, as observed in locusts and

63 cockroaches (7,13,14).

64

65 We elected to study falling and righting in the spotted lanternfly (*Lycorma delicatula*) (SLF), a

66 phloem-feeding planthopper native to China and south Asia that has become a major invasive

67 pest threatening agriculture and forestry in the US since its introduction in 2014 (15), making

68 research that can inform the development of more effective traps and other deterrents particularly

69 urgent (16). The spotted lanternfly undergoes a rapid lifecycle, quadrupling in length (15) and

70 progressing through four wingless nymphal stages (instars) in three to four months before

71 emerging as a winged adult (17). (Fig. 1A,B) Although nymphs and adults are able to cling

72 securely to leaflets, stems, branches and other surfaces using a combination of tarsal claws and

73 adhesive pads (arolia) (18,19), they frequently drop out of trees and climb back into the canopy

74 of the same or nearby trees in response to obstacles, wind, or predator attack (20). In light of

75 their rapid growth, the metabolic cost of frequent climbing and interruptions in time spent

76 feeding likely impose significant fitness costs. This raises the question of whether falling SLF

77 nymphs are able to land securely on lower leaves of their host plant. The SLF's preferred host,

78 the *Ailanthus altissima* tree, has dense layered foliage consisting of pinnately compound leaflets

79 (Fig. 1C, D) that likely offer numerous landing targets for falling insects. Our observations

80 indicate that SLFs that either drop or jump often land on underlying or neighboring plants.

81 Consistent with this, capture-mark-recapture studies have shown that SLFs frequently remain on

82 or nearby a healthy host *A. altissima* tree (21). We therefore hypothesized that this species

83 should exhibit righting during dropping onto leaves and the ground. As far as we are aware,

84 biomechanical studies of SLF nymphs have measured their walking, jumping and climbing

85 ranges and rates, not their behavior during dropping or their righting capabilities (6,22).

86

87 In this study, we addressed the following research questions via a series of laboratory

88 experiments on SLF fourth instar nymphs. First, we sought to quantify whether spotted

4

89 lanternfly nymphs indeed do self-right more often than expected by chance when dropped. Once

90 confirmed, we examined the strategies they used for righting and landing in general. Finally, we

91 asked whether these righting behaviors influence their ability to land on lower layers of foliage,

92 to avoid completely falling out of the tree.

93

94

95 Figure 1. A) Fourth instar spotted lanternfly nymphs on a trunk. B) Close-up of a fourth instar

96 spotted lanternfly nymph showing our definition of body length (gray arrow) (black line = 10

97 mm scale bar). Photographs of the spotted lanternfly's preferred native host tree, *A. altissima*,

98 showing (C) the release distance (white bar = 200 mm) used in most experiments in this study

99 and (D) a view from the ground looking upward into the canopy, showing how the densely

100 overlapping leaflets offer many landing opportunities for falling nymphs.

101

2. Methods

103 Live, fourth instar spotted lanternfly nymphs were collected and studied within a quarantine zone

104 in southeastern Pennsylvania, US (40.006525, -75.256714) in July-August 2020. All experiments

105 were performed indoors in still air at 24 ± 3 deg C. Nymphs were collected by hand or using an

106 insect net and scoop-shaped forceps from natural habitats, primarily *A. altissima* trees. Only

107 intact, healthy, and active insects were studied. Fourth instar nymphs were identified by their

108 distinctive red, black and white coloration. (Figs. 1A, 2A) Specimens not immediately used in

109 experiments were stored in a sealed container with freshly picked *A. altissima* foliage and wet

110 tissues. Insects maintained in this way retained their normal levels of activity for at least 48

111 hours. Because this species is the subject of an eradication program (23), all specimens were

112 euthanized by freezing after experimentation. For studies of dead specimens, we used frozen

113   insects that were thawed and either used within 30 min of thawing or stored in 49% relative

114   humidity chambers to avoid desiccation and to preserve their native biomechanical properties

115   (24). Specimen body length, L = 11.8 mm [10.3, 12.6] mm (mean, range) (Fig. 1B) was

116   measured to ± 0.05 mm either using digital calipers (model SV-03-150, E-base Measuring Tools,

117   Yunlin, Taiwan) or using the *measure* function in ImageJ (25) on digital photographs including a

118   mm-ruled scale. Body masses, m = 66 ± 18 mg, [40, 100] mg (N = 16, mean ± SD, range), were

119   measured to ± 0.4 mg with an analytical balance (Explorer, Ohaus, Parsippany, NJ US). (See S1

120   Table for morphometric data).

121

2.1 Video studies of dropping and landing experiments

123   We performed a variety of experiments on SLF nymphs filmed during dropping to determine

124   their midair body motions and center of mass trajectories while falling and their landing

125   behavior. Most high-speed videos of spotted lanternfly specimens were filmed using an SA-3

126   high-speed camera (Photron, Tokyo, Japan) (monochrome, 1024 × 1024 pixel resolution, 1000

127   frames/s; exposure 500 microsec) illuminated by a Nila Zaila LED light (Nila, Inc. Altadena,

128   CA). For filming SLFs releasing voluntarily from surfaces and falling on leaves, we used a color

129   Chronos 1.4 camera at a higher frame rate (800 × 600 pixels, 2837 fps; exposure 343 microsec,

130   Krontech, Burnaby, BC, Canada) and LED light source (SL-200W, Godox, Shenzhen, China). A

131   second perspective was provided by a mirror included in the field of view to allow visualization

132   of body pose and rotational behavior.

133

134   Dropping experiments were performed on live specimens and on dead SLF nymphs with their

135   legs contracted close to the body ("dead/tucked"). An additional set of dead nymphs

136   ("dead/spread") were pinned with their legs spread and fixed with a small drop of cyanoacrylate

137   glue applied using a fine needle to each leg joint (total added mass 1.0 ± 0.2 mg; 1-2% body

138   mass), so as to position the forelegs above the dorsal plane to approximate the posture we

139   observed for SLFs, which was similar to those reported for falling pea aphids (11). Glue was

140   applied so as to avoid coating the feet, which still adhered to substrates after being glued.

141   Following previous studies (5,11,26), we released specimens with the goal of achieving low

142   initial speed and spin while controlling initial falling orientation. Live and dead specimens were

143   released using featherweight entomology tweezers (DRENTF01, DR Instruments, Palos Hills, IL

144   US) (Fig. 2A) oriented side, head down or caudal end down, similar to methods used in (11,27).

145   To release specimens upright or upside-down, we grasped them initially with fingers on the sides

146   of the scutellum. If a nymph responded to handling by feigning death, it was breathed on until it

147   spread its legs and moved actively. All specimens were inspected after manipulation during

148   experiments and showed no effect of handling. Live specimens sometimes were measured in a

149   second session after being marked in one or two places with white paint (0.9 ± 0.2 mg; 1-2%

150   body mass); this added mass is unlikely to influence specimen motility given that heavier (6.5%

151   body mass) harmonic radar tags do not significantly affect SLF fourth instar nymph walking,

152   climbing, jumping or survivorship (22). While we tried to achieve a balanced study design, the

153   tendency of this species to fatigue rapidly limited our ability to conduct a uniform number of

154   trials on each specimen.

155

156   Specimens were dropped artificially (i.e., either from tweezers or manually) from a uniform

157   height of 200 mm, approximately 17 body lengths, measured using a nearby vertical ruler.

158   Preliminary tests established that this range was high enough for a large fraction of specimens to

159   land upright. This height allowed comparison with previous research on righting by pea aphids

160   that used a similar range of heights (11) and by stick insect nymphs (12), which self-righted

161   aerially over a similar height in terms of body lengths. We also note that this choice of falling

162   distance lies in the range of distances between neighboring leaflets in *A. altissima* trees. (Fig. 1C)

163

164   For video studies, specimens fell onto one of two landing substrates: 1) a hard, horizontal surface

165   covered with white, art-quality watercolor paper; 2) a freshly-harvested, freely-suspended *A.*

166   *altissima* leaf taped to a post such that the surfaces of its freely-suspended leaflets were inclined

167   by [0,30] deg relative to horizontal. SLF nymphs were observed to be able to achieve a secure

168   footing by using their tarsal claws and arolia on both hard and leaf substrates. Because it was

169   difficult to achieve a reproducible impact location on the leaflets, the leaf substrate experiments

170   provided insight only into impact and post-impact behaviors that resulted in a successful landing.

171

172   To study whether SLF nymphs able to launch voluntarily from surfaces exhibited different

173   behaviors during falling and landing, we also filmed SLF nymphs that were stimulated to release

174   from the wall of a clear acrylic box by moving a plastic insect toward them or gently breathing

175   on them—a trigger we observed to elicit dropping behavior in the field. Because of the known

176   tendency of these insects to climb (6), we were unable to control the drop distance in these trials

177   to agree with that used for the artificially released specimens.
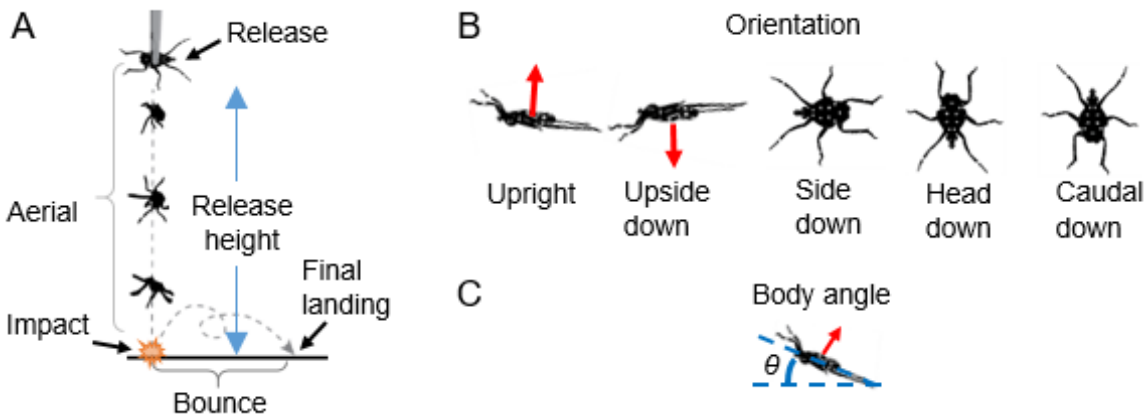
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179

180   Figure 2. A) Schematic of the dropping experiment, showing how the five different phases of

181   motion used to analyze the outcomes were defined. B) Illustration of the five orientations used to

182   describe releases, impacts and final landings. (Red arrows indicate dorsoventral axis.) C)

183   Geometry used to define the cranial-caudal body axis angle, θ, relative to horizontal.

184

185   We divided each falling trial into four periods for analysis: aerial, impact, post-impact, and final

186   landing. (Fig. 2A) Specimen orientation at initial impact and final landing (i.e., after coming to

187   rest post-impact) was scored by frame-by-frame video analysis into the best agreement with five

188   categories similar to definitions used in (11). (Fig. 2B) In the following, a body axis is referred

189   to as "horizontal" and "vertical" when it agrees with the respective direction within 45 deg; e.g.,

190   a horizontal cranial-caudal axis corresponds to $\theta \leq \pm 45$ deg. (Fig. 2C) With this convention,

191   specimens oriented "upright" or "upside-down" had their dorsal or ventral side uppermost,

192   respectively, and horizontal cranial-caudal and medio-lateral axes. The "side" orientation had a

193   horizontal cranial-caudal angle and vertical medio-lateral axis with the left side oriented

194   downward, while the "head" and "caudal" orientations had a vertical cranial-caudal axis and the

195   head or caudal side oriented downward, respectively. We also recorded whether the nymphs

196   bounced during landing, defined as vertical motion of the body center of mass after impact in

197   which at least two feet lost contact with the ground.

198

2.2 Image analysis

200 Videos were analyzed using custom image analysis code written in MATLAB v2020A with the

201 machine vision and curve fitting toolboxes (Mathworks, Natick MA) (Supplemental Materials);

202 all italicized functions referenced below are from MATLAB unless noted otherwise. The

203 MATLAB camera calibrator was used to calibrate and correct each camera for lens distortion

204 before analysis (mean reprojection error: ≤ 0.3 pixel). The spatial calibration was measured from

205 images of a ruler at the same distance as the specimen (range [1.7, 5.8] pixel/mm), and checked

206 using known body dimensions. The maximum bounce height (defined as the difference between

207 the body midpoint at the lowest and highest heights immediately after impact) was measured

208 manually using ImageJ (25). For automated tracking of specimens, all images were blurred using

209 a Gaussian filter using *imgaussfilt* with sigma of 0.6 mm to reduce noise. To isolate the

210 specimen's image from background, we then computed a background image by taking the

211 median intensity of the video using *median2*, and subtracted this background image from each

212 video frame using *imabsdiff* to compute the absolute difference between the two images. The

213 difference image was contrast-enhanced using *adapthisteq* to correct for nonuniform

214 illumination, and thresholded using *imbinarize* to create a binary image of a white specimen on a

215 black background. If necessary, the morphological command *imclose* was used to fill in holes on

216 the specimen due to white spots. For tracking and determining body orientation, the resulting

217 binary image was processed using the morphological operation *imopen* (a dilation followed by

218 an erosion over approximately 1.5 mm) to remove the legs, after which *regionprops* was used

219 compute the body centroid (x, y) and an ellipse that has the same normalized second central

220 moments as the body. The orientation angle, θ, of the body (i.e., the angle of the cranial-caudal

221 axis relative to horizontal) was tracked using a combination of the orientation of the body

222 ellipse's major axis and the angle at which the distance between the body's outline and its

223 centroid is at a maximum due to the protruding head.

224

2.3 Statistical methods and data analysis

226 The statistical analysis of data was performed with R v3.6.3 (28). Outcomes for experiments

227 were analyzed using Fisher's exact tests or χ^2 tests. Where Fisher's exact test sample size

228   exceeded computing capacity, simulated p-values were generated from 2000 simulations. All

229   results are reported as mean [95% C.I.] unless noted otherwise. ANOVA with Tukey's Honest

230   Significant Differences (HSD) was used to determine p-values between different conditions for

231   kinematics measures such as speeds and bounce heights. Data and code required to reproduce all

232   results are included in the Supplementary Materials.

233

234   The coordinate data from video tracking were analyzed without further processing using

235   nonlinear least squares fitting in MATLAB. The vertical falling trajectory (y vs time, t), was fit

236   to the equation of motion for the case of a drag force quadratic in speed:

237
$$y(t) = \frac{v_{ter}^2}{g}\ \ln\left(cosh\left(\frac{gt}{v_{ter}}\right)\right) \tag{1}$$

238   where v_{ter} is terminal speed and $g = 9.81$ m/s^2 is the acceleration of gravity. The horizontal data

239   (x vs t) were fit to a quartic polynomial (the lowest order polynomial found to result in mean fit

240   residuals < 0.8 mm). Goodness-of-fit was assessed using R^2 and residuals analysis. The speed

241   before impact, v_{imp}, and terminal speed, v_{ter} were determined from fit parameters, and then used

242   to compute Reynolds number, $Re = L\,v\,/\,\upsilon$, where L = body length and the kinematic viscosity of

243   air, $\upsilon = 15.34 \times 10^{-6}$ m^2/s (29), as well as the fractional collisional energy loss on impact, $e_{col} = 1-$

244   (gravitational potential energy)/(kinetic energy at impact) $= 1 - 2gh/\,v_{imp}{}^2$, where h = maximum

245   bounce height after impact.

246

247   We were also interested in measuring whether the rotation rate of the specimen about the normal

248   to the image plane varied during the fall. This quantity is relevant because conservation of

249   angular momentum dictates that the rotation rate about any given axis is constant for constant

250   specimen rotational inertia and zero net torque along that direction (30). Consequently, in order

251   for its rotation rate to vary throughout the fall, the specimen must either experience nonzero

252   torque due to aerodynamic drag or move its legs so as to vary rotational inertia. Using

253   MATLAB, we manually measured the specimen's average aerial rotation rate, $\Omega = \Delta\theta\,/\Delta t$, from

254   the change in the body angle on the image, $\Delta\theta$, between two frames recorded $\Delta t = 25$ ms apart.

255   The associated measurement uncertainty was determined from the error in determining the initial

256   and final orientations of the specimen's cranial-caudal axis on video. The initial rotation rate,

257   Ω_{rel}, was measured shortly (50 ms) after release, to ensure that the specimen was clear of the

258   tweezers or wall. To determine if Ω varied throughout the fall, the rotation rate also was

259   measured at the approximate midpoint of the fall (125 ms after release), Ω_{mid}, and immediately

260   before impact, Ω_{imp}.

261

262   3. Results

263   3.1 Effect of orientation at release on landing

264   We analyzed high-speed video of falling and landing on hard surfaces for five trials for each of

265   five release orientations from tweezers for five different live SLF nymphs (125 trials total). To

266   determine whether release orientation impacted the distribution of orientations on impact and

267   final landing, we considered three orientation outcomes for impact: upright, upside-down and

268   other (comprising side, caudal and head down) and two for landing: upright and upside-down.

269   (Fig. 3) We found that neither the orientation distribution on impact nor on final landing showed

270   significant differences based on release orientation (orientation at impact: Fisher's exact test, p =

271   0.22; orientation at final landing, χ^2 test, p = 0.80). This suggests that orientation upon impact

272   and landing are independent of release orientation. Similarly, for dead nymphs (30 specimens, 1

273   trial each per release orientation) dropped onto a hard substrate, the distributions of final landing

274   orientations did not depend significantly on release orientation for spread legs (χ^2 test, p = 0.86).

275   (S1 Dataset) We consequently analyzed these datasets summed over release orientations, and

276   only recorded data for a single release orientation (side down) when studying dead specimens
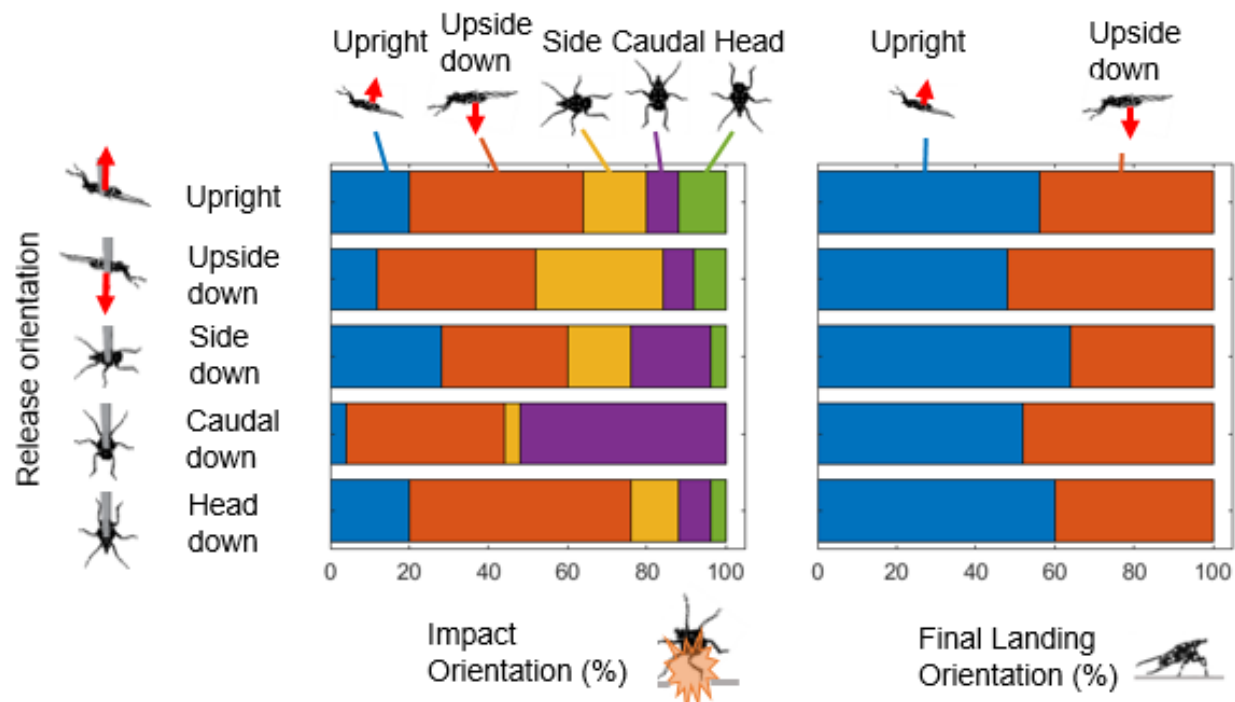
277   with legs spread and tucked.

Figure 3. Distribution of orientation at impact and final landing for live spotted lanternfly fourth instar nymphs dropped on a hard surface from each of five release orientations. (Red arrow points towards the dorsal surface when viewed in lateral aspect.)

3.2 Aerial phase

Fig. 4A shows a typical sequence of motions by live SLF nymphs during the aerial phase of the dropping experiments. (S1 Movie) In the majority of trials (97.1% = 135/139) artificially released specimens assumed a stereotypical falling posture within 0.079 s [0.029, 0.129] s after release, in which they spread their legs fully and held them slightly above the dorsal plane until impact. (Fig. 4B) Results from kinematic data analysis are shown as summary statistics in Table 1. All measured trajectories of artificially released live and dead SLF nymphs were predominantly vertical (mean horizontal excursions ≤ 4.3 mm). We were successful at filming a total of 15 voluntary release trials for five specimens from 354 mm [342, 365] mm above the hard substrate (Fig. 5B). These trajectories displayed greater horizontal excursions (24 mm [13, 35] mm) than observed for the artificial releases. All falling trajectories for all conditions agreed well with a quadratic drag model ($R^2 \geq 0.9998$; fit-residuals 0.9 mm [0.7, 1.0] mm). (Fig. 4C) Terminal speed did not differ significantly between live specimens released voluntarily and

12

296   artificially (Tukey's HSD, p = 0.48) (Fig. 4D). Dead specimens with their legs tucked had a

297   mean terminal velocity that was greater and statistically different from all other conditions (i.e.,

298   live and dead with legs spread) (Tukey's HSD, p < 0.0001), whereas analysis of live and dead

299   with legs spread found no significant differences (Tukey's HSD, p > 0.74). (Fig. 4D). During

300   falling, all SLF nymphs studied here had speeds corresponding to Reynolds number Re in the

301   range, $[10^2, 10^4]$, consistent with values reported for gliding arthropods (29).
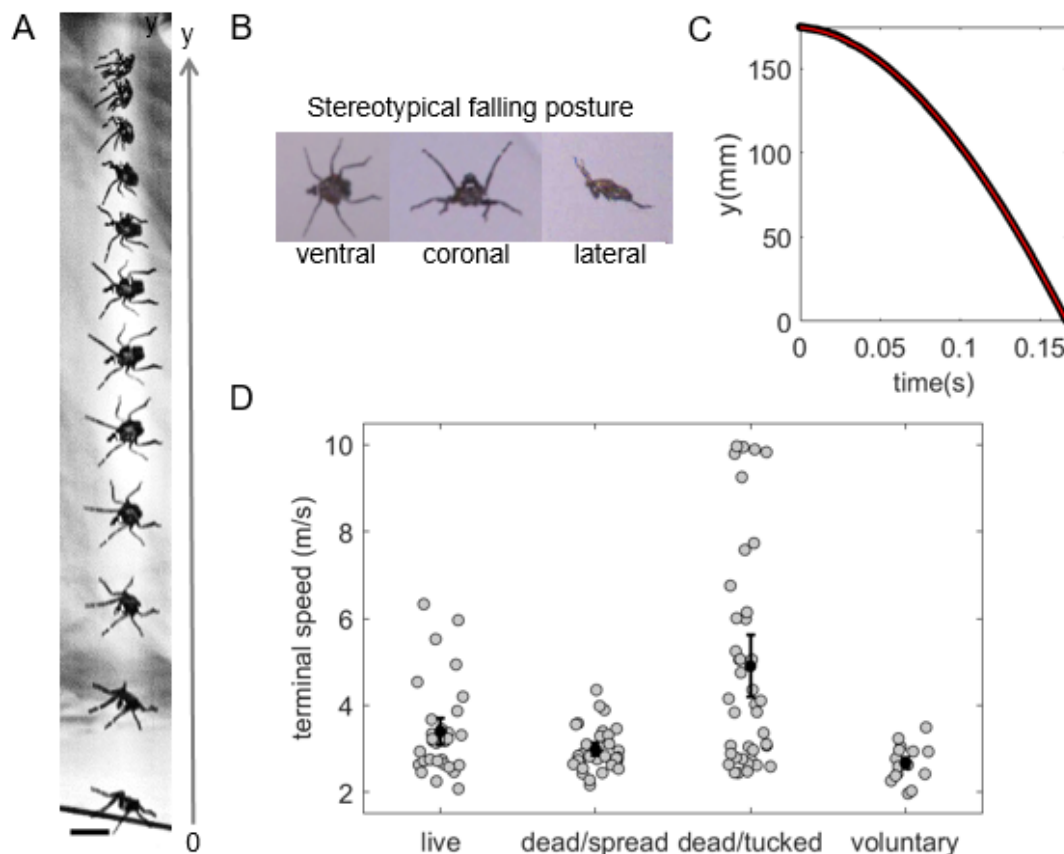
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303

304   Figure 4. A) Stereotypical falling posture assumed by spotted lanternfly nymphs after dropping.

305   B) Superimposed sequence of video frames recorded every 15 ms showing a spotted lanternfly

306   nymph falling 200 mm. (Scale bar: 10 mm). C) Measured (open circles) and fitted (red line)

307   vertical position, y, of the specimen shown in B) plotted vs time. D) Fitted terminal falling speed

308   distributions for live and dead specimens artificially dropped from 20 cm and live specimens

309   voluntarily releasing from 35 cm. (black circles: mean; error bars: 95% CI; gray circles: all

310   data, jittered for visibility.)

13

311

312   We next consider results for the aerial rotational kinematics, which differed significantly

313   between live and dead specimens. The rotation rate after release, Ω_{rel}, of live specimens was

314   significantly larger than for dead specimens (one-sided t-test p = 2.4 × 10^{-5} vs dead with legs

315   spread and p = 0.0013 vs dead with legs tucked). (Fig 5A) The value of Ω_{rel} was independent of

316   the release method for live specimens, and of pose for the dead specimens (two-sided t-test, p =

317   0.365 live by release method, p = 0.157 dead by pose). To illustrate how rotation rate changed

318   during falling, we computed the change in rotation rate magnitude, $\Delta|\Omega|$, at the midpoint and

319   impact relative to its value at release (Fig. 5B). These data showed that rotation rates tend to

320   decrease with fall time among live specimens, but increase or stay the same for the dead

321   specimens. In some cases, live nymphs changed the direction of their rotation or increased their

322   spin to a greater rotation rate mid-fall than at either release or impact. A variety of related

323   behaviors could be observed on some videos of live nymphs: 1) pushing off the wall (voluntary)

324   and tweezers (artificial) so as to impart an initial spin; 2) changing the orientation and extension

325   of their legs during falls so as to alter their rotational inertia (S1 Movie).
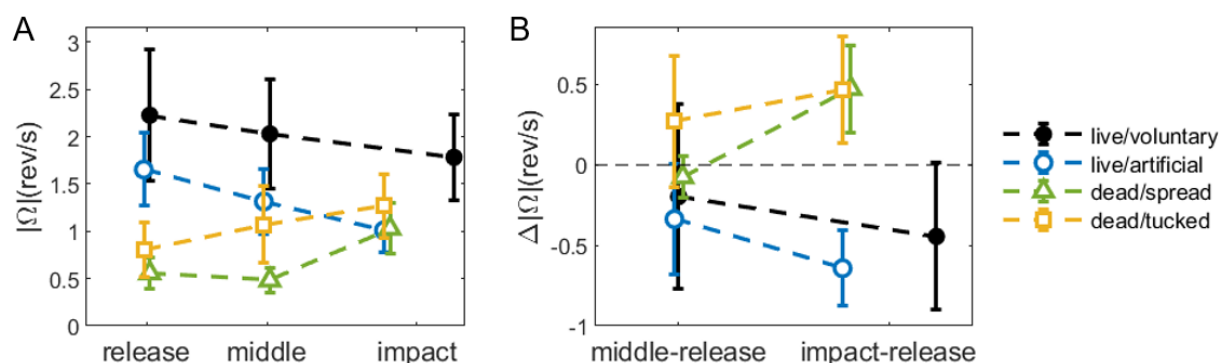
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327

328   Figure 5. Rate of spotted lanternfly nymph body rotation in the image plane upon release, at an

329   approximate midpoint during the fall, and immediately before impact. (A) Rotation rate

330   magnitudes show different trends during the fall period for live nymphs (circles) relate to dead

331   specimens with legs spread (triangles) or tucked (squares). (B) Plots of the change in rotation

332   rate magnitude between the midpoint and at impact relative to release (equivalent to scaling the

333   initial rotation rate at release to zero) for different release methods and specimen preparations.).

334   (Error bars show 95% CI, which were similar to instrumental measurement uncertainties.

335   Horizontal distances between data points are proportional to time; data also are jittered for

336   visibility.)

337

3.3 Impact orientation

339   Fig. 6 shows the orientation distributions for specimens at impact and final landing on the hard

340   substrate for live and dead SLF nymphs for artificial and voluntary releases. The impact

341   orientation was found to differ between live nymphs and dead with legs tucked (Fisher exact test,

342   p = 0.00005) but not between live and dead with legs spread (Fisher exact test, p = 0.95). For

343   voluntary releases, a greater fraction impacted upright (67%) than when artificially released, and

344   no specimens that released voluntarily impacted upside down (Fig 6B). The distributions of

345   orientations on impact differed significantly for live specimens between the two release

346   conditions (Fisher's exact test, $p < 8 \times 10^{-6}$ and p = 0.00039, impact and 200 mm respectively).

347   (Fig. 6) To make sure that release height did not influence this last finding, we also measured the

348   distribution of orientations after specimens that released voluntarily had fallen 200 mm, the

349   height used for artificial releases. This distribution also was similar to that found at impact

350   (Fisher's exact test, p = 0.71). (Fig. 6B)

351

352   We also compared these data with a probabilistic model that assumed the likelihood of a

353   specimen impacting the surface in a given orientation is proportional to the fraction of solid

354   angles corresponding to how we scored that orientation. Because we used a fixed angle, $\theta = 45$

355   deg, between the horizontal and the body's cranial-caudal axis to define orientation at impact,

356   this gives a probability of impacting either upright or upside down equal to the solid angle

357   subtended by a spherical cap with polar angle θ. This corresponds to a prediction that the fraction

358   impacting the surface upright should be 29.3% = $2\pi (1 - \cos \theta)/4\pi$ = (1 - cos 45 deg)/2, the same

359   fraction (29.3%) should impact upside down, and the remaining 41.4% impact at all other

360   possibilities combined. The predictions of this model were not consistent with data for nymphs

361   falling on the hard substrate for live or dead/tucked (χ^2 test, p < 0.0010 and $p < 9 \times 10^{-14}$,

362   respectively). For dead/spread, disagreement with the model could not be ruled out (p = 0.37).

363

364   While we were unable to release specimens above leaves reproducibly enough to study their

365   impact and landing distributions *per se*, we did film 49 trials in which 15 different nymphs

366 landed successfully on *A. altissima* leaves (1-6 landings/specimen). (Fig. 7A) Those specimens

367 that landed successfully impacted leaflets upright in 49% of cases and upside down 33% of the

368 time. The remaining 18% impacted on a combination of their caudal (6%), side (6%) or head

369 (2%), or clung on impact to the edge of a leaflet (4%). (Fig. 7B)

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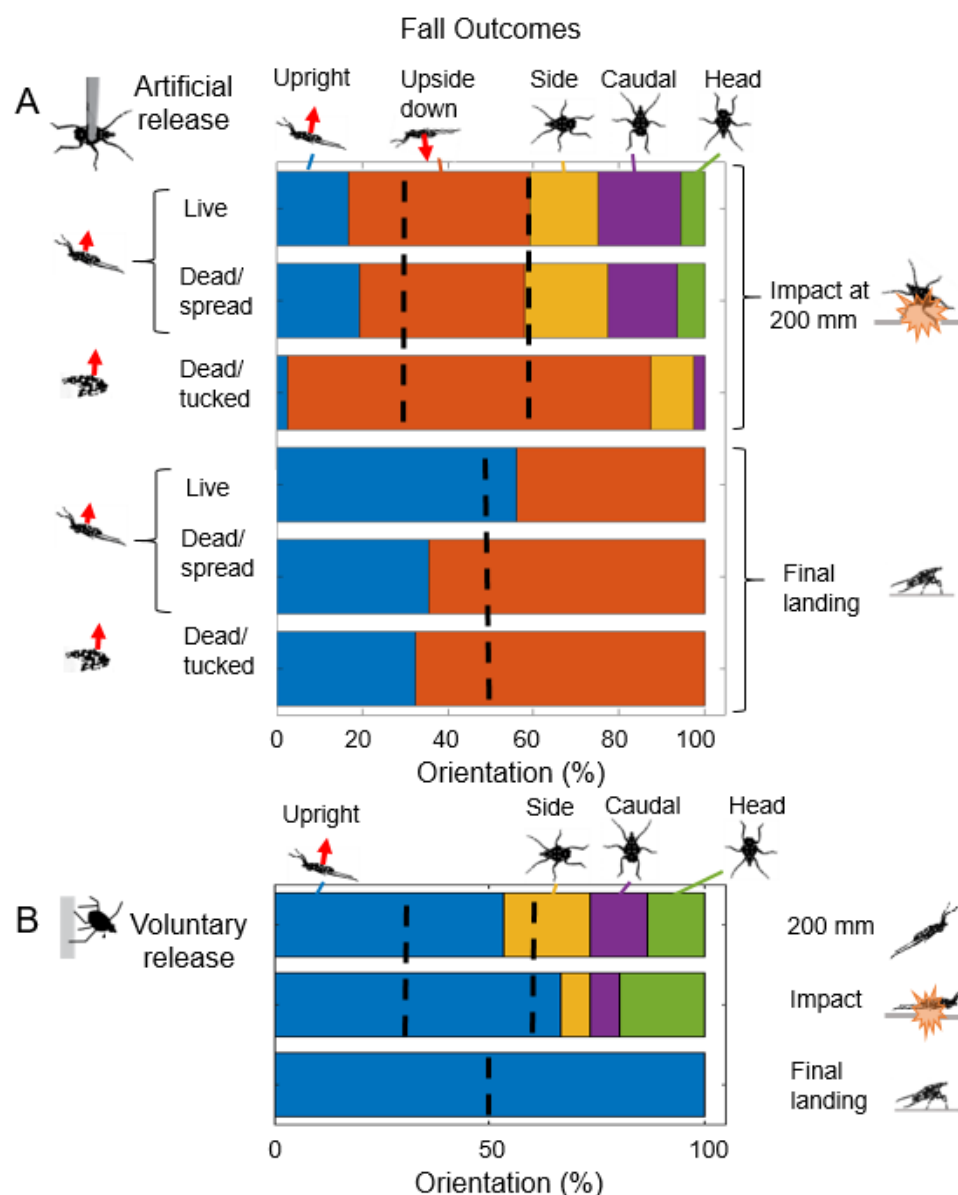
371

372 Figure 6. Distribution of impact and final landing orientations for spotted lanternfly nymphs (A)

373 dropped artificially from tweezers and (B) releasing voluntarily onto a hard paper surface. The

374 distributions from B) recorded at 200 mm below the release point corresponded to the same

375 falling distance as those recorded for impact in A). From left to right, top to bottom in each plot:

376 the dotted lines represent model predictions for upright landings (29.3%) and upside down

377 landings (29.3%) at impact, and the expectation for upright vs upside down final landing

378 orientation (50%), if landing orientation were random. (red arrows = dorsoventral axis)
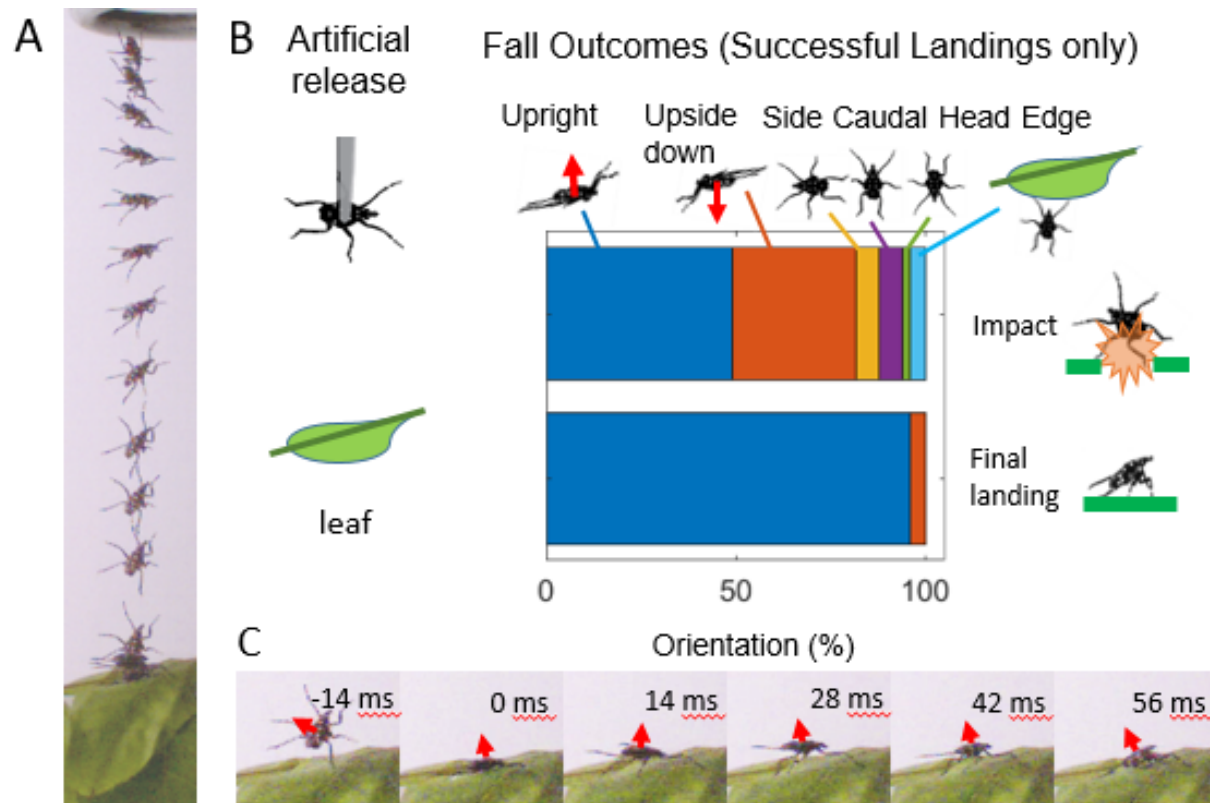
379

380

381 Figure 7. A) Typical image sequence for spotted lanternfly nymphs falling onto *A. altissima*

382 leaflets. B) Orientation distributions at first impact and landing for specimens that successfully

383 landed on leaflets. Because we only characterized successful landings on leaves, these results

384 cannot be compared to the data and models shown in Fig. 6. C) Image sequence showing

385 bouncing from a leaflet. (impact = 0 ms; red arrows = dorsoventral axis)

386

3.4 Bouncing post-impact

387

388 Table 2 gives summary statistics for the results of analyzing the post-impact bouncing behaviors.

389 After impact, the vast majority of SLF nymphs bounced at least once, with rebound heights at

390 most a few mm. (Fig. 7C, Fig. 8A) (S1 Movie) As expected from their greater release height,

391 specimens released voluntarily impacted the surface at a significantly higher speed than those

392 released artificially (Tukey's HSD, p = 0.001); impacts speeds did not differ significantly

393   between any of the other conditions (Fig. 8B). For bounce height, dead/tucked was significantly

394   different from all live conditions (Tukey's HSD, p < 0.001). The only other significant

395   difference was between voluntarily released live specimens and dead/spread (Tukey's HSD, p =

396   0.014). (Fig. 8B, C)
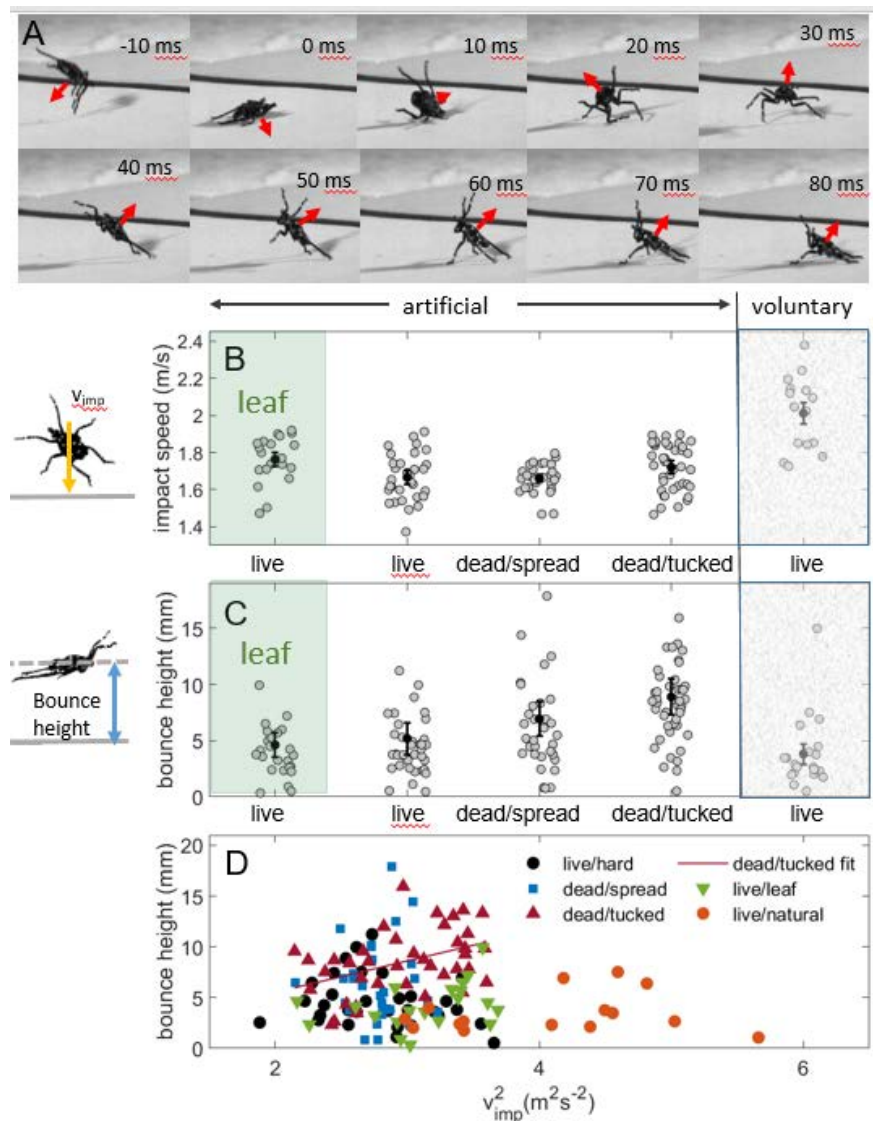
397

398

399   Figure 8. A) Image sequence from a video of fourth instar spotted lanternfly nymph landing on

400   its back on the hard substrate, bouncing, and finally landing upright. (impact = 0 ms; red arrows

401   = dorsoventral axis) Distributions for B) bounce height and C) impact speed, v_{imp}, for live and

402   dead specimens artificially dropped from 20 cm onto the hard substrate and leaves and live

403   specimens voluntarily releasing from 35 cm. (black circles: mean; error bars: 95% CI; g circles:

404   all data, jittered for visibility.) D) Bounce height vs v_{imp}^2 ($\propto$ kinetic energy before impact).

405

406   For the 20 trials for which the bounce trajectory could be measured for landing on leaflets, the

407   impact speed and maximum bounce height were consistent with that for live nymphs impacting

408   the hard substrate. (Fig. 8B, C) One notable difference was that the compliant leaflets always

409   recoiled and vibrated after impact. (S1 Movie) For both substrates and all specimen preparations,

410   these bounce heights corresponded to a near-total loss of initial kinetic energy upon colliding

411   with the substrate. Bounce height was weakly correlated with kinetic energy ($\propto v_{imp}^2$) among live

412   specimens, and only dead/tucked specimens had bounce heights that varied linearly with kinetic

413   energy (Fig. 8D). We suspect that the difference in bounce height between live and dead

414   specimens (Fig. 8C) was due in part to the tendency of live, but not dead, nymphs to adhere to

415   the substrate on or immediately after impact with one or more feet. We also observed some high

416   bounces among dead/spread specimens when their legs remained extended on impact, appearing

417   to act as springs rather than collapsing as observed for live specimens.

418

419   3.5 Final landing behavior

420   First we consider results for the orientation at final landing (e.g., when the specimen came to rest

421   on the substrate.) A comparison of final landing distributions found that artificially released SLF

422   nymphs were significantly more likely to land upright on the hard substrate when live (56%)

423   than dead with legs spread (35%) or tucked (33%) (Fisher exact test, p = 0.046 and 0.011

424   respectively). (Fig. 6A) While the number of upright final landing distribution for live

425   specimens released artificially (χ^2 test, p = 0.180) were consistent with random chance, this was

426   not true for those releasing voluntarily, 100% of which finally landed upright (p = 0.00011). In

427   addition, compared to artificially released specimens, significantly more SLF nymphs releasing

428   voluntarily were oriented upright on final landing (p = 0.00043). (Fig 6B) The fraction of dead

429   specimens that landed upright was lower than predicted by random chance for legs tucked (χ^2

430   test, p = 0.0027); for legs spread, the smaller number of observations led to an insignificant test

431   (p = 0.106).

432

433

434   Next, we consider how the orientation at final landing relates to that at first impact. For live

435   nymphs released artificially, the distributions of orientations at impact were significantly

436   different from those upon final landing on the hard substrate (Fisher's exact test, $p < 1.3 \times 10^{-10}$),

437   with a higher percentage achieving an upright orientation at final landing (56%) than on impact

438   (17%). The impact and final landing orientation distributions for voluntary releases also differed

439   significantly (Fisher's exact test, $p = 0.042$). The reason why the impact and final landing

440   distributions differed was due in part to the fact that most specimens bounced at least once upon

441   impact and frequently changed orientations as a consequence. Those nymphs that did not land

442   fully upright immediately after bouncing often were able to pull themselves upright as part of a

443   continuous sequence of motion. (S1 Movie) The minority of nymphs that did not bounce on

444   impact either adhered immediately to the substrate upon impact, rolled, or slid to a stop. We

445   observed during preliminary trials that many nymphs that did not come to rest upright upon

446   landing eventually were able to self-right terrestrially without assistance, although we did not

447   study this behavior further.

448

449   For landing on leaves, the distribution of orientations also differed significantly between impact

450   and final landing for successful landings (Fisher's exact test, $p < 1 \times 10^{-7}$). The vast majority

451   (96%) of successful final landings were upright, with the remainder oriented upside down.

452   Because we only characterized successful landings on leaves, we did not compare these results to

453   data for all fall outcomes for the other conditions, or to the model, which requires an analysis of

454   all outcomes. SLF nymphs relied on behaviors similar to those found for the hard substrate to

455   cling to leaves after impact. Due to a combination of bouncing, sliding or leaflet vibration, in

456   33% of the successful landings, the nymphs landed on a surface different from the one on which

457   they made initial impact (i.e., a different leaflet or nearby stem.) In several cases, we observed

458   nymphs grasping a leaflet by its edge by one or more feet and pulling itself successfully onto the

459   surface after a struggle. (S1 Movie)

460

461 ## 4. Discussion

462   In summary, our study supports the following conclusions: first, spotted lanternfly nymphs

463   falling through ecologically relevant distances used a combination of all righting mechanisms

464   available to them (8), including aerial re-orientation, re-orientation during bouncing, and

465   terrestrial righting, the last of which we do not discuss here. This diverse, flexible arsenal of

466   landing tactics provides SLF nymphs with a variety of ways to respond to surfaces with

467   unpredictable positions, orientations, compliances, textures and other mechanical properties.

468   Second, our measurements also provide support for SLF nymphs employing both passive and

469   active righting. In virtually all trials, live SLF nymphs assumed a stereotypical falling posture

470   similar to those reported previously for falling pea aphids (11), stick insect instars (2), and

471   geckos (31), as well as gliding ants (9) and spiders (10). On average, they assume this posture

472   within 0.079 s [0.029, 0.129] s after release. Supporting the hypothesis that this posture

473   increases drag, we found that the terminal speed for live and dead specimens with legs spread

474   was significantly lower than for dead ones with legs tucked compactly against the body. Dead

475   specimens with legs tucked also were significantly less likely to impact upright than either live

476   or dead specimens in the falling posture. This supports the argument that the stereotypical falling

477   posture contributes to aerial righting (9,11). When live specimens were able to release

478   voluntarily from surfaces, they were predominantly oriented upright after falling 200 mm to a

479   greater extent than live specimens released artificially. This suggests that when allowed to

480   release voluntarily, SLFs may be modulating initial release conditions to achieve greater upright

481   landing success. The rotational kinematic data during falling indicated that compared to dead

482   specimens, live nymphs rotated more quickly upon release and decreased their rotation rates

483   during falls, likely due to their observed ability to push off the surface of last contact and actively

484   move their legs midair, whereas dead specimens tended to increased their mean rotation rates

485   during falling. Because a nonzero change in rotation rate during the aerial phase requires either a

486   net aerodynamic torque or a change in rotational inertia, these findings suggest likely roles for a

487   combination of aerodynamic torque and active control in determining fall outcomes. Taken

488   together, our kinematic results point to a role for active control to achieve righting during the

489   aerial phase.

490   Third, our findings indicate SLF nymphs make use of novel active righting behaviors

491   immediately after impact. These motions are distinct from terrestrial righting as previously

492   studied because the nymphs in question enact them before coming to rest on their backs. This

493   interpretation is supported by our finding that, in spite of impacting the surface with similar

494 speeds and orientations, live SLF nymphs finally landed upright significantly more often than

495 dead specimens, even those with legs spread. To understand this phenomenon, we first note that

496 almost all live and dead specimens bounced after impact so as to dissipate most of their pre-

497 impact energy (> 97% for live and >94% for dead specimens), similar to values reported for

498 crash-landing locusts (76%) (24) and cockroaches running into walls (95%) (32). This is

499 important because nymphs benefit from dissipating most of their kinetic energy quickly in order

500 to land securely, while retaining enough kinetic energy to surmount potential energy barriers that

501 can prevent the reorientations required for righting. (7) Consistent with this picture, live SLF

502 nymphs were observed to reorient while rebounding from the substrate, often using grasping or

503 adhesion to the substrate and complex leg motions to lever into a final upright posture.

504

505 Collisional energy losses, bounce heights, and subsequent reorientation motions during rebounds

506 were similar for SLF nymphs landing on compliant leaves and hard surfaces. However, several

507 new landing behaviors also were observed, including clinging to the very edge of leaflets,

508 grasping stems and bouncing onto and landing on lower-lying leaflets after initial impact. This

509 was true in spite of the fact that specimens impacted leaves oriented at a variety of angles to the

510 horizontal, and that the leaves recoiled and oscillated on impact. The SLF nymphs' effectiveness

511 at clinging with a single foot or claw on leaves and their ability to use their arolia for adhesion

512 enhance their ability to settle into a final upright orientation successfully following impact at a

513 variety of angles. This is important because leaflets and other potential perches are encountered

514 at a wide variety of angles in natural habitats.

515

516 Taken as a whole, these findings indicate that SLF nymphs falling into underlying foliage could

517 slow down gradually via successive collisions, each of which affords the SLF an opportunity for

518 landing securely. This interpretation is consistent with an earlier study in which pea aphids were

519 induced to drop when on different host plants. The authors found that the probability of dropping

520 pea aphids landing within a host plant instead of on the ground increases approximately linearly

521 with increasing release height (5)--as would be expected if landing success depends on multiple

522 attempts--as opposed to reaching a plateau--as would be expected if the limiting factor was the

523 time required to self-right aerially. Thus, the ability of SLF nymphs to cling securely to the

524 complex foliage of their preferred host suggest that landing upright in itself might not be a

525   necessary or preferred strategy. This possibility deserves to be considered in studying of aerial

526   righting and related phenomena.

527

528   Finally, we found that the outcomes of landings after SLF nymphs launched voluntarily from

529   walls were very different from when they were released artificially with minimal speed and

530   rotation rate. Similarly, falling pea aphids were reported to self-right only when released with

531   nonzero initial spin (11). This finding suggests that there is some aspect to preparation or

532   voluntary release that can potentially alter the initial conditions of the fall, setting them up for

533   more upright outcomes. It remains to be explored how the more detailed aerial motions of this

534   species relate to postural control with the goal of ensuring an upright landing. For example, ants

535   (9), spiders (10) and stick insect instars (12) have been shown to use coordinated motions of their

536   legs and appendages during falling to initiate, reorient and stabilize their body orientation.

537

538   Taken together, these results point to the importance of studying both aerial and post-impact

539   righting behavior. While most studies on righting behavior during falling have focused on aerial

540   righting, for spotted lanternfly nymphs, post-impact reorientation plays a central role in

541   achieving a final, upright posture in an exceedingly short period of time. Reorientations after

542   impact due to bouncing in particular are so rapid that they cannot be detected without high-speed

543   imaging. The significantly different outcomes observed when specimens were allowed to launch

544   voluntarily from surfaces, combined with some of the unique behaviors observed during falling

545   on leaves, points towards the need to conduct tests in naturalistic environments whenever

546   possible, to better understand ecologically significant behaviors.

547

548   Acknowledgements

554

Competing Interests

The authors have no conflicting interests to declare.

Data Availability

All data and software required to reproduce the figures and results are included in the Supporting Information.

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652

Tables

654

Specimen / substrate	# specimens/trials	Terminal speed, v_{ter} (m/s)	Re at v_{ter}	$|\Omega_{rel}|$(rev/s)	$|\Omega|_{mid}$(rev/s)	$|\Omega_{imp}|$(rev/s)
Live, voluntary release/ paper	15 (5 specimens; 2-5 trials/specimen)	2.7 [2.5, 2.9]	2071 [1896, 2246]	2.17 [1.59, 2.75]	2.03 [1.49, 2.57]	1.78 [1.36, 2.21]
Live/paper	31 (5 specimens, 6-7 trials/specimen)	3.4 [3.0, 3.8]	2431 [2144, 2718]	1.62 [1.27, 1.96]	1.32 [0.99, 1.64]	1.01 [0.79, 1.23]
Dead/spread, paper	31 (5 specimens, 5-10 trials /specimen)	3.0 [2.8, 3.2]	2157 [2018, 2295]	0.55 [0.40, 0.70]	0.48 [0.36, 0.61]	1.03 [0.78, 1.28]
Dead/tucked, paper	40 (5 specimens, 5-10 trials /specimen)	4.9 [4.1, 5.7]	3620 [3020, 4220]	0.79 [0.53, 1.05]	1.07 [0.69, 1.45]	1.27 [0.96, 1.58]

Table 1. Summary statistics for spotted lanternfly fourth instar (N4) nymph aerial kinematics.

Specimen/substrate	N	n_{total} (n per specimen)	Fraction bouncing (%)	N_{bounce}	v_{imp} (m/s)	bounce height (mm)	e_{col} (%)	Pearson correlation coefficient; linear regression D.F., F statistic, p value
Live, voluntary release/ paper	5	15 (2-5)	100	1.07 [0.93, 1.21]	2.01 [1.91, 2.11]	3.6 [2.5, 4.6]	98.3% [97.9, 98.8]	0.17; 13, 0.38. 0.55
Live/paper	5	31 (6-7)	93	1.02 [0.88, 1.18]	1.67 [1.62, 1.71]	4.7 [3.7, 5.6]	99.0% [98.8, 99.2]	-0.22; 29, 1.5, 0.23
Dead/spread, paper	5	28 (3-7)	90	1.06 [0.85, 1.27]	1.66 [1.63, 1.69]	6.6 [5.0, 8.1]	95.5% [94.5, 96.5]	0.023; 26, 0.014, 0.91
Dead/tucked, paper	5	39 (5-9)	93	0.78 [0.64, 0.91]	1.72 [1.68, 1.76]	8.5 [7.5, 9.5]	94.4% [93.8, 95.1]	0.42; 37, 8.1, 0.007
Live/ leaflet*	8	20* (1-5)	71	1.05 [0.89, 1.21]	1.76 [1.71, 1.82]	4.2 [3.2, 5.2]	97.3% [96.8, 97.9]	0.36; 18, 2.6, 0.12

Table 2. Summary statistics for spotted lanternfly fourth instar (N4) nymphs impact and post-impact (bouncing) kinematics. (N = number of specimens; n_{total} = total number of trials; N_{bounce} = number of bounces during landing; v_{imp} = speed immediately before impact; e_c = collisional energy loss). * Only trials in which the nymph landed successfully were analyzed for landing on leaves.