

SHORT COMMUNICATION

Wind alters landing dynamics in bumblebees

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ABSTRACT

Landing is an important but understudied behavior that flying animals must perform constantly. In still air, insects decelerate smoothly prior to landing by employing the relatively simple strategy of maintaining a constant rate of image expansion during their approach. However, it is unclear whether insects employ this strategy when faced with challenging flight environments. Here, we tested the effects of wind on bumblebees (*Bombus impatiens*) landing on flowers. We find that bees' approach paths to flowers shift from multidirectional in still air to unidirectional in wind, regardless of flower orientation. In addition, bees landing in a 3.5 m s⁻¹ headwind do not decelerate smoothly, but rather maintain a high flight speed until contact, resulting in higher peak decelerations upon impact. These findings suggest that wind has a strong influence on insect landing behavior and performance, with important implications for the design of micro aerial vehicles and the ecomechanics of insect flight.

KEY WORDS: Insect flight, Animal flight, Pollinator, Bee, Physiological ecology, Optic flow, Collision avoidance

INTRODUCTION

Landing is a challenging behavior that flying animals must perform tens to hundreds of times each day while moving through natural environments, but it has received substantially less attention than other flight behaviors. Previous studies in honey bees (*Apis mellifera*) and fruit flies (*Drosophila melanogaster*) have demonstrated that the visual system plays an important role in controlling approach speed to landing surfaces (Evangelista et al., 2010; Srinivasan et al., 2000), as well as triggering key landing behaviors (van Breugel and Dickinson, 2012). In particular, recent work has shown that insects regulate flight speed during landing by the relatively simple strategy of maintaining a constant rate of image expansion (Baird et al., 2013), causing flight speed to decrease smoothly to zero as the landing target draws closer.

Although this landing strategy has the potential to work in nearly all situations, it is unknown whether flying insects can or do employ this strategy in the more challenging flight conditions characteristic of natural environments. One ubiquitous environmental challenge is wind: in natural environments, wind flows are highly variable and impact bees' flight stability (Combes and Dudley, 2009; Ravi et al., 2013).

Wind could also affect insects' landing patterns – or locomotory behaviors that precede landing – including the direction from

which insects approach a landing target, and changes in body attitude and velocity. Wind increases drag forces on the body and wings of flying insects, and this may make fine control of body attitude and flight speed more challenging. Wind could also restrict the range of angles from which an insect can approach a target, as flying cross-wind is likely to be more challenging than flying upwind.

In this study, we investigated the effects of wind on bumblebees (*Bombus impatiens*) landing on flowers, to test the hypotheses that (a) approach angles are restricted in the presence of wind, and (b) bees employ the same smooth deceleration strategy when landing on flowers, regardless of external wind conditions.

MATERIALS AND METHODS

Specimen preparation

Oxeye daisies (*Leucanthemum vulgare*) were collected at the Concord Field Station in Bedford, MA, USA, and trimmed to 31 cm, reflecting the average height in the field (31.3±5.60 cm; *N*=23). Bumblebees (*Bombus impatiens* Cresson 1863) were acquired from Biobest Laboratories and maintained between June and August 2015 with *ad libitum* access to pollen and nectar.

Prior to each experiment, similarly sized bees (intertegular span, 4.63±0.43 mm; mass, 0.165±0.038 g; *N*=28) were isolated, cold-anesthetized, and outfitted with a BEEtag (Crall et al., 2015) tracking marker (3×4 mm) attached to the dorsal side of the scutum with cyanoacrylate adhesive (Fig. 1A). Marked bees were starved for ~2 h before trials to increase feeding motivation.

Test conditions

Flight trials were conducted in a 6 m-long wind tunnel with a test section of 0.9×0.5×0.5 m. Grid patterns were fixed to the side panels of the working section to provide optic flow signals. For each trial, a fresh flower was placed in the upstream end of the test chamber with the stem elevated to form a ~50 deg angle with the floor of the working section.

A small drop of nectar (Biogluc) was placed on the flower before each trial. A single bee was released downstream from the flower, allowed to fly until it landed on the flower (Fig. 1A), and then recaptured after ~5 s of feeding and placed back at the initial release point.

Each bee was tested in four different experimental conditions: trials were conducted either with or without wind (3.5 m s⁻¹), and with the flower stem oriented either parallel or perpendicular to the long axis of the wind tunnel (i.e. the direction of flow when wind was present). Because the flexible stems allowed flowers to reorient in wind (Fig. S1), we ran two additional conditions with the flower stem immobilized while oriented either perpendicular or parallel to flow, to test for confounding effects of floral reorientation on bee approach angles (Fig. S2). Experimental conditions were presented in randomized order. Following the final trial, we immediately froze bees at -20°C, weighed them and measured their intertegular span.

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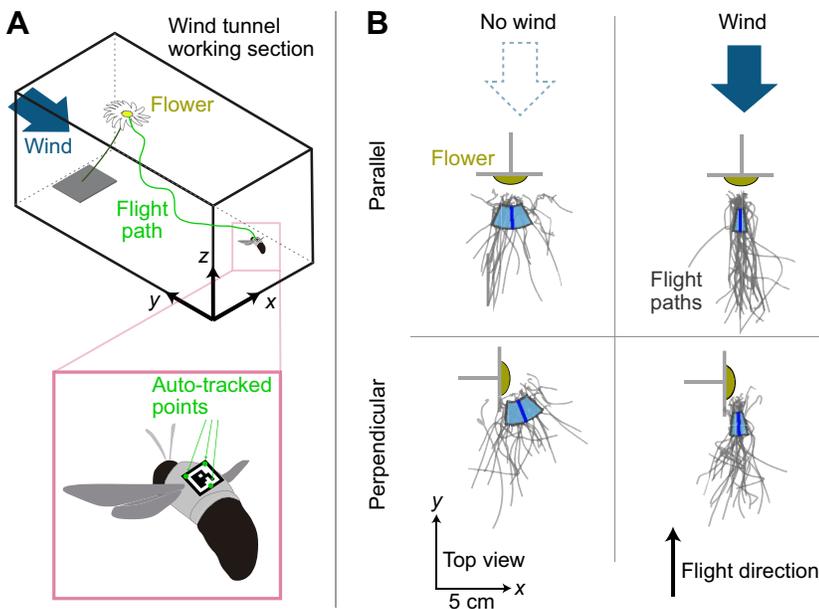


Fig. 1. Wind restricts approach angles of bumblebees landing on flowers. (A) Schematic illustration of the wind tunnel working section and BEtag markers used to digitize body trajectories and orientations. (B) Flight traces (gray lines) of bees approaching flowers in still air (left, $N=31$ parallel, $N=27$ perpendicular) or 3.5 m s^{-1} laminar flow (right, $N=29$ parallel, $N=25$ perpendicular), with flowers oriented either parallel (top, $N=31$ in still air, $N=27$ in wind) or perpendicular (bottom, $N=29$ in still air, $N=25$ in wind) to the long axis of the wind tunnel. Thick blue lines and light blue shaded regions show the mean and standard deviation, respectively, of landing angles across bees for each trial condition.

High-speed videography and analysis

Flight trials were filmed within a cubic interrogation volume with two Photron SA3 high-speed cameras recording at 1000 Hz. The volume was calibrated via DLT (Hedrick, 2008).

BEtag was used to track bees' body kinematics (Crall et al., 2015). The BEtag software was modified to extract the coordinates of three points on the tag (Fig. 1A), which were converted to three-dimensional coordinates using DLTdv5 (Hedrick, 2008). Digitization noise was removed from position data with a low-pass, 5th order Butterworth filter with a cutoff frequency of 100 Hz. Instantaneous velocities and accelerations were calculated through numerical differentiation, and instantaneous roll and pitch angles were calculated following Ravi et al. (2013).

We defined two spatial regions: a 'landing' region, spanning 1.5–3 cm from the flower (roughly 1–2 bumblebee body lengths, capturing the period of flight just prior to contact with the flower), and an 'approach' region, spanning 5–7 cm from the flower (the distance range when bees first entered the interrogation volume). The angle from which bees approached and landed on flowers (the 'landing angle') was calculated by averaging position data within the landing region, converted to spherical coordinates centered on the flower. We calculated average flight speed and roll and pitch angles within each of these spatial regions, and defined the maximum deceleration associated with collision/landing as the most negative instantaneous change in speed during the last 100 ms of each trial. Throughout this paper, 'flight speed' refers to ground speed (i.e. speed in the global coordinate system), rather than air speed (i.e. speed including the 3.5 m s^{-1} air flow in trials with wind).

Statistics

All statistical analyses were performed in R. For linear mixed effects (LME) models, initial models were run with wind, orientation and wind \times orientation as fixed effects and individual as a random effect using the 'lme' function in R. Non-significant effects were removed from the final model. For results on approach and landing speed, orientation and interaction (wind \times orientation) effects were not significant, and data were pooled for still air and wind trials.

RESULTS AND DISCUSSION

We tracked 112 flight paths of 28 different bees across the four primary experimental conditions: with a flexible flower positioned parallel to the long axis of the wind tunnel in still air ($N=31$) or in the presence of a 3.5 m s^{-1} wind ($N=27$), and with the flower positioned perpendicular to the tunnel axis in still air ($N=29$) or in a 3.5 m s^{-1} wind ($N=25$).

Effects of wind on floral approach angle

In still air, the landing angle changed significantly with flower orientation; bees approaching a perpendicularly oriented flower shifted their flight path to align more closely with the face of the flower (Fig. 1B; LME, d.f.=32, $t=-3.33$, $P=0.002$). In the presence of wind, landing angles did not differ significantly with flower orientation (Fig. 1B; LME, d.f.=27, $t=-1.00$, $P=0.33$); rather, bees flew directly upwind to land on the flower, regardless of its orientation. While this could theoretically be caused by floral reorientation in the presence of wind (Fig. S1), this does not appear to be the case here: we saw no difference in landing angle when flowers were immobilized with wire to prevent reorientation (Fig. S2). Landing angles were also more restricted (i.e. had lower variance) in wind compared with still air, regardless of how the flower was oriented (Fig. 1B; parallel: F -test, $F=0.109$, d.f.=26, $P\ll 0.01$; perpendicular: F -test, $F=0.236$, d.f.=28, $P\ll 0.01$). Yaw angles were also more restricted in all wind trials, with bees approaching the flowers with their bodies oriented more directly upstream than in still air, independent of flower orientation (data not shown).

The observation that landing angles are restricted in the presence of wind is consistent with the intuitive (but to our knowledge untested) hypothesis that cross-wind flight and landing is more challenging than flying with the body axis oriented directly upwind, as the former would require substantial side-slip and/or continuous readjustment of body yaw and roll. It is also possible that olfaction plays a role in restricting landing angles, as scents emitted from the flowers could be carried downstream, exposing bees to olfactory cues. However, given that bees are known to rely strongly on visual cues when in close proximity to a floral stimulus (Srinivasan et al.,

2000; Vladusich et al., 2005; Lunau, 1992), we believe that olfaction plays only a minor role (if any) in our results.

The restriction of bumblebee landing angles in wind observed here may have important consequences for the ecomechanics of pollination. Floral orientation is highly variable in nature, and past studies have shown that some orientations (e.g. horizontal or downward-facing flowers) promote unidirectional approach paths, allowing for more consistent contact with the flower's reproductive organs, as compared with other orientations (e.g. upward-facing flowers) that allow pollinators to approach from many directions (Fenster et al., 2009). Wind, already known to have important direct effects on flower reorientation (Etnier and Vogel, 2000), might add another dimension of complexity to the interaction between flowers and their pollinators.

Effects of wind on landing speed and body orientation

Wind also had a significant effect on bee flight speed prior to landing. During the approach phase (5–7 cm from the flower), there was no difference in the mean speed of bees flying in wind versus still air (Fig. 2A–C; LME, d.f.=71, $t=0.075$, $P=0.94$). However, bees in still air reduced their ground speed significantly between approach and landing (Fig. 2A,D; mean change in speed, landing–approach = -0.171 m s⁻¹, paired t -test: $t=-14.26$, d.f.=54, $P\ll 0.001$), whereas bees flying in a 3.5 m s⁻¹ headwind showed no significant change in ground speed (Fig. 2B,D; mean change = -0.004 m s⁻¹, t -test: $t=-0.265$, d.f.=54, $P=0.79$). Peak deceleration upon landing was also significantly higher in wind than in still air (Fig. 2E,F; LME, d.f.=72, $t=-6.78$, $P\ll 0.01$).

Diverse taxa of flying insects use visual cues to decelerate smoothly (and thus reduce impact forces) when landing (Baird et al., 2013; Srinivasan et al., 2000; van Breugel and Dickinson, 2012), and the relatively simple control strategy of maintaining a constant rate of image expansion has been proposed as potentially universal, allowing smooth landing on a surface of any orientation (Baird et al., 2013). Our results confirm that bumblebees flying in still air follow a pattern of smooth deceleration consistent with that shown for honeybees [Fig. 2; albeit on a somewhat different spatial scale (Baird et al., 2013), consistent with recent work in bumblebees (Reber et al., 2016)].

Bumblebees landing on flowers in wind, however, do not follow this pattern; they do not reduce their speed smoothly – in fact, they do not reduce their speed at all prior to landing (Fig. 2D). As a result, they experience higher peak decelerations (and thus impact forces) upon landing (Fig. 2E).

Why do bumblebees landing in wind display such apparently anomalous behavior? There are at least two possible explanations. First, this pattern could result from an active shift in control strategy. Roll instability (quantified here as standard deviation of roll) was higher in wind (Fig. 3A; LME, d.f.=71, $t=7.55$, $P\ll 0.01$), and this increased instability could make it challenging for bees to maintain fine control over their speed. In other words, they may abandon a smooth deceleration strategy in favor of a reliable (but physically damaging) collision-based landing strategy.

Alternatively, the patterns we observed could be the result of reduced airflow in the immediate wake of the flower, which may cause bees' ground speed to rise suddenly, even if they are attempting to regulate speed using the same visual cues as in still air. Any object in flow creates a downstream region of reduced flow speed as a result of drag. An insect approaching an object such as a flower from downstream would experience this area of reduced flow as a sudden reduction in headwind, which (in the absence of any change in flight kinematics) would actually increase the ground speed of the insect. To effectively reduce ground speed when moving through this region of low flow, the insect would have to rapidly alter its wing and/or body kinematics to reduce its air speed far beyond what is normally required for smooth landing, to compensate for the sudden difference in environmental wind speed.

Our results lend tentative support to the latter hypothesis. Mean pitch angle was lower (i.e. more pitched forward) for bees flying in wind versus still air (Fig. 3B; LME, d.f.=71, $t=-20.62$, $P\ll 0.01$), consistent with the role of pitch in determining thrust angle and forward flight speed in bees (Dudley and Ellington, 1990). Bees flying in wind changed their pitch angle significantly between the approach and landing phases, pitching up by approximately 5 deg prior to landing (Fig. 3C; mean change, landing–approach = 4.89 deg, t -test: $t=6.41$, d.f.=54, $P\ll 0.001$). This was significantly greater than the change in pitch seen during flight in still air (Fig. 3C; LME, d.f.=70, $t=4.31$, $P<0.001$), which was not

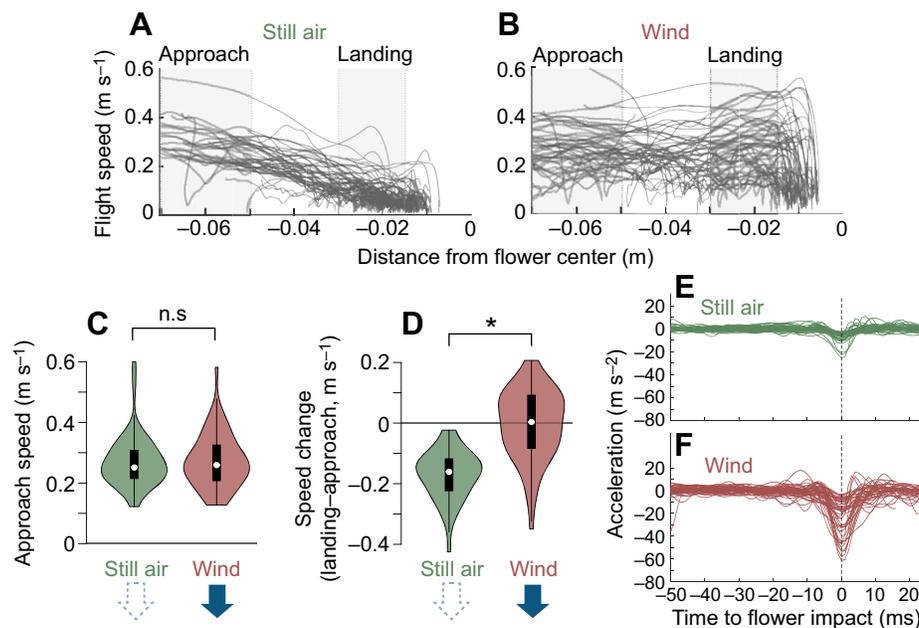


Fig. 2. Wind affects landing speed and impact decelerations. (A,B) Flight speed versus impact distance from the flower center in (A) still air and (B) 3.5 m s⁻¹ wind. Each gray line represents data from a single trial, with trials pooled from parallel and perpendicular flower orientations. (C) Mean speed during the approach phase (5–7 cm from the flower) in still air versus wind. (D) Speed change between approach and landing phases (1.5–3 cm from flower) in still air versus wind. (E,F) Acceleration versus time to flower impact in (E) still air and (F) wind. Asterisk indicates significant difference at the $\alpha=0.05$ level. Distributions in C and D are shown as violin plots, which depict the estimated kernel density plot (curved line), in addition to median (white-filled marker), interquartile range (thick black line) and 95th percentile range (thin black line). $N=60$ for still air trials, $N=52$ for wind trials.

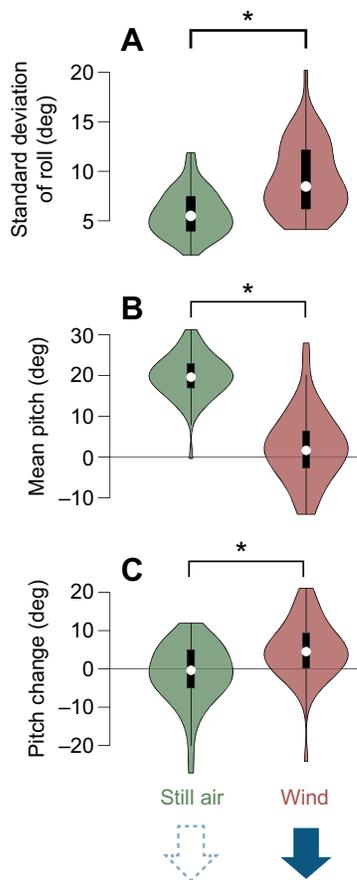


Fig. 3. Wind affects body orientations during approach and landing.

(A) Standard deviation of roll angle in still air versus 3.5 m s^{-1} wind over the entire flight sequence. (B) Mean pitch angle in still air versus 3.5 m s^{-1} wind over the entire flight sequence. (C) Change in pitch angle between approach and landing phases in still air versus 3.5 m s^{-1} wind. Distributions are shown as violin plots, which depict the estimated kernel density plot (curved line), in addition to median (white-filled marker), interquartile range (thick black line) and 95th percentile range (thin black line). Asterisks indicate a significant difference between groups at the $\alpha=0.05$ level. $N=60$ for still air trials, $N=52$ for wind trials.

significantly different from zero (Fig. 3C; mean change = -1.32 deg , t -test: $t=-1.14$, d.f.=44, $P=0.26$). This result suggests that bees may actually be attempting to reduce their flight speed in preparation for landing, but because of the sudden reduction in wind behind the flower, their ground speed remains constant.

Regardless of the specific mechanism, our results indicate that insects either do not choose to or are unable to perform controlled, low-impact landings in the presence of strong wind. Thus, high-impact landings are likely to occur regularly for insects flying in challenging, natural environments. This suggests the need for robust morphological designs capable of absorbing repeated impact forces while avoiding catastrophic damage, such as the buckling joints present in some insect wings (Mountcastle and Combes, 2014). Future work investigating the design of the landing apparatus in insects will be informative for understanding the evolutionary

ecology of insect flight, as well as providing potential design principles for biomimetic, robotic applications.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Specimen preparation and data collection were performed by J.J.C.; J.D.C. performed statistical analysis. All authors contributed equally to the conception and design of the experiments, and interpretation of results being published. J.J.C. and J.D.C. contributed equally to the writing of the paper.

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Data availability

Kinematic data and example tracking scripts are available at zenodo.org (<http://www.zenodo.org/record/60234#.V7Mv4pMrKt8>).

Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.137976.supplemental>

References

- Baird, E., Boeddeker, N., Ibbotson, M. R. and Srinivasan, M. V. (2013). A universal strategy for visually guided landing. *Proc. Natl. Acad. Sci. USA* **110**, 18686–18691.
- Combes, S. A. and Dudley, R. (2009). Turbulence-driven instabilities limit insect flight performance. *Proc. Natl. Acad. Sci. USA* **106**, 9105–9108.
- Crall, J. D., Gravish, N., Mountcastle, A. M. and Combes, S. A. (2015). BEEtag: a low-cost, image-based tracking system for the study of animal behavior and locomotion. *PLoS ONE* **10**, e0136487.
- Dudley, R. and Ellington, C. P. (1990). Mechanics of forward flight in bumblebees: I. Kinematics and morphology. *J. Exp. Biol.* **148**, 19–52.
- Etnier, S. A. and Vogel, S. (2000). Reorientation of daffodil (*Narcissus: Amaryllidaceae*) flowers in wind: drag reduction and torsional flexibility. *Am. J. Bot.* **87**, 29.
- Evangelista, C., Kraft, P., Dacke, M., Reinhard, J. and Srinivasan, M. V. (2010). The moment before touchdown: landing manoeuvres of the honeybee *Apis mellifera*. *J. Exp. Biol.* **213**, 262–270.
- Fenster, C. B., Armbruster, W. S. and Dudash, M. R. (2009). Specialization of flowers: is floral orientation an overlooked first step? *New Phytol.* **183**, 502–506.
- Hedrick, T. L. (2008). Software techniques for two- and three-dimensional kinematic measurements of biological and biomimetic systems. *Bioinspir. Biomim.* **3**, 034001.
- Lunau, K. (1992). Innate recognition of flowers by bumble bees: orientation of antennae to visual stamen signals. *Can. J. Zool.* **70**, 2139–2144.
- Mountcastle, A. M. and Combes, S. A. (2014). Biomechanical strategies for mitigating collision damage in insect wings: structural design versus embedded elastic materials. *J. Exp. Biol.* **217**, 1108–1115.
- Ravi, S., Crall, J. D., Fisher, A. and Combes, S. A. (2013). Rolling with the flow: bumblebees flying in unsteady wakes. *J. Exp. Biol.* **216**, 4299–4309.
- Reber, T., Baird, E. and Dacke, M. (2016). The final moments of landing in bumblebees, *Bombus terrestris*. *J. Comp. Physiol. A* **202**, 277–285.
- Srinivasan, M. V., Zhang, S. W., Chahl, J. S., Barth, E. and Venkatesh, S. (2000). How honeybees make grazing landings on flat surfaces. *Biol. Cybern.* **83**, 171–183.
- van Breugel, F. and Dickinson, M. H. (2012). The visual control of landing and obstacle avoidance in the fruit fly *Drosophila melanogaster*. *J. Exp. Biol.* **215**, 1783–1798.
- Vladusich, T., Hemmi, J. M., Srinivasan, M. V. and Zeil, J. (2005). Interactions of visual odometry and landmark guidance during food search in honeybees. *J. Exp. Biol.* **208**, 4123–4135.